DISSERTATION

BEHAVIORAL RESPONSE OF MULE DEER TO NATURAL GAS DEVELOPMENT IN

THE PICEANCE BASIN

Submitted by

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ABSTRACT

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THE PICEANCE BASIN

One of the primary threats to the conservation of biodiversity is the loss and modification of

habitat due to land-use change (Sala et al. 2000). Over the last decade, large expanses of North

America have experienced major land-use change due to rapid increases in energy development

(United States Energy Information Administration [U.S. EIA] 2012). This development is

projected to continue to increase, with over 200,000 km^2 of new land estimated to be impacted

by 2030 (McDonald et al. 2009, U.S. EIA 2014). Energy development causes numerous

environmental impacts, including air (Armendariz 2009, Howarth et al. 2011), water (Jackson et

al. 2011), and noise pollution (Francis et al. 2009), conversion and fragmentation of habitat

(Sawyer et al. 2006), increases in wildlife mortality (Kunz et al. 2007) and invasions of non-

native species (Bergquist et al. 2007). In addition, development requires a large infrastructure

(i.e., roads, pipelines, and transmission lines) which can exacerbate these impacts (Forman and

Alexander 1998).

Although the recent increase in energy development has occurred across numerous

sectors, exploration and production of energy from hydrocarbon (oil and natural gas) resources

has seen a particularly rapid increase (U.S. EIA 2012). One of the main reasons for this increase

has been technological advancements (i.e., directional drilling and hydraulic fracturing) that have

allowed for development of resources that previously were economically unviable. The resulting

land-use change has raised concerns over the impacts to wildlife, with a number of recent studies

documenting impacts to an array of species (Naugle 2011). For some species these impacts are

direct, with the development itself causing mortality (Timoney and Ronconi 2010), or being

linked to alteration of important parameters related to population growth (Aldridge and Boyce

2007, Sorensen et al. 2008, Doherty et al. 2010, Holloran et al. 2010, Wasser et al. 2011). For

other species, the impacts are more nuanced and depend on species life history strategies and the

nature of development (Dale et al. 2008, Moseley et al. 2009, Francis et al. 2011a, Francis et al.

2011b, Hamilton et al. 2011). For the majority of studied species, these effects are behavioral,

including altered habitat selection, (Doherty et al. 2008, Sawyer et al. 2009b, Carpenter et al.

2010, Harju et al. 2010, Harju et al. 2011), and movement or home range patterns (Dyer et al.

2002, Sawyer et al. 2009b, Webb et al. 2011c). Such behavioral responses can lead to increased

nutritional stress (Wasser et al. 2011), lower abundance (Ingelfinger and Anderson 2004, Walker

et al. 2007a, Dale et al. 2008), decreased survival, and altered reproductive behavior and success

(Dzialak et al. 2011c, Jarnevich and Laubhan 2011, Webb et al. 2011a), ultimately leading to

population declines (Walker et al. 2007b, Sorensen et al. 2008). Despite the fact that behavioral

responses are among the most commonly documented impacts of hydrocarbon development,

understanding the specific nature of these responses is complex. Developments are constructed

in stages that differ in their intensity, and human activity at these developments and along related

infrastructure varies spatially and temporally, as well as among different development types

(e.g., well pads in different stages of construction; Sawyer et al. 2009a). In addition, behavioral

responses and subsequent population-level impacts of development are highly species-specific

and might not be manifested for time periods of up to a decade (Webb et al. 2011a). In light of

the substantial complexities in the relationship between energy development and wildlife,

obtaining a more complete understanding of these responses is a critical step in informing wildlife management, and development and mitigation plans.

Mule deer and hydrocarbon development

In western North America, much of the recent hydrocarbon development has overlapped with the range of mule deer (*Odocoileus hemionus*). Mule deer is a recreationally and economically important species, with over 80,000 animals harvested each year in the state of Colorado alone. However, deer populations across Western North America have declined over the last 20 years from historical highs (Unsworth et al. 1999), and recent research has highlighted hydrocarbon development as a potential driver of large scale displacement of deer from preferred areas on their winter range (Sawyer et al. 2006). On winter range, deer face a net negative energy balance due to limited access to forage (Parker et al. 1984, Torbit et al. 1985), often leading to high over-winter mortality (Bartmann and Bowden 1984). During summer, resources are abundant, but deer face high energetic demands as they birth and rear between 1 and 3 fawns (Wallmo et al. 1977, Wallmo 1981). Increased disturbance from energy development could displace deer from preferred areas during either season, leading to higher energy expenditure, decreased foraging time, or increased predatory exposure. Thus, obtaining a more complete understanding of the potential impacts of development is critical for the conservation and management of the species.

My dissertation focuses on the behavioral response of adult female mule deer to ongoing natural gas development in the Piceance Basin of Northwestern Colorado. The Piceance Basin is a top energy reserve in the United States, containing natural gas and oil shale. In addition, this area holds one of the largest migratory mule deer herds in North America. As discussed above, the response of wildlife to development is complicated by the dynamic and variable nature of

development, along with climatic conditions and deer condition, age, and reproductive status. I focus on behavioral responses of individual deer in an attempt to address some of this complexity. Throughout my dissertation (aside from Chapter 1, which is a review) I utilize global positioning system (GPS) radio collar data and contemporary statistical techniques developed in the field of animal movement ecology to assess the complex behavior of mule deer. Over the last decade, the field of animal movement ecology has progressed rapidly (Nathan et al. 2008), with a major focus on the development of methods that account for the complex spatial and temporal structure in movement data (e.g., Morales et al. 2004, Johnson et al. 2008b, Hooten et al. 2010, McClintock et al. 2012a). This progression has provided a plethora of new tools for ecologists to use in understanding animal behavior. However, these methods are difficult to implement for practitioners and thus the development of new methods has far outpaced their use in applied conservation and management contexts. I use these methods to gain insight into mule deer behavior, and to assess the impacts of natural gas development on these behaviors.

This dissertation is organized as follows. In chapter one, I review the global knowledge on the impacts of five energy sectors on terrestrial wildlife to set my work in the context of the current state of knowledge. In chapter two, I assess the effects of helicopter capture on mule deer behavior. The purpose of this chapter was to understand how our capture methods influenced subsequent inference related to mule deer behavior. In chapter three, I assessed an assumption of one of the primary methodologies used to examine the habitat selection process in animals, and one which I make use of in a later chapter, resource selection functions (RSFs). In chapter four, I apply what was learned in chapter three to mule deer data, fitting RSFs to winter range data from 2008 – 2010. In chapter five, I assess landscape factors influencing seasonal range size and philopatry of mule deer to understand the influence of development on mule deer space use. In

chapter six, I examine the factors influencing foraging behavior of mule deer to understand how

development impacts this behavior. Finally, in chapter seven, I assess the relationship between

mule deer genetics, migratory behavior, and condition.

ACKNOWLEDGEMENTS

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CHAPTER ONE

CHARACTERIZING THE IMPACTS OF EMERGING ENERGY DEVELOPMENT ON

WILDLIFE, WITH AN EYE TOWARDS MITIGATION

INTRODUCTION- RAMIFICATIONS OF THE NEW ENERGY FUTURE

Global demand for energy is projected to increase by 40% in the next 20 years (International

Energy Agency (IEA) 2009). With the potential peak in world conventional oil production (Kerr

2011), rising oil prices (Erturk 2011), and concerns over greenhouse gas emissions and

subsequent climate change (IPCC 2007), energy demand increasingly will be met with

alternative and unconventional (e.g., gas shale, oil sands) energy sources. The numerous

economic and societal benefits of alternative and unconventional domestic energy production

(e.g., job creation, national security), technological advancements such as hydraulic fracturing

(United States Energy Information Administration (U.S. EIA) 2010; Kerr 2010) and directives

and legislative mandates for renewable energy (U.S. EIA 2008, European Commission 2009)

have spurred a rapid increase in global alternative and unconventional energy production over

the last decade (IEA 2009, U.S. EIA 2010). This production, and related development, is poised

to continue its upward trajectory (IEA 2009), with over 200,000 km^2 of new land projected to be

developed in the U.S. alone by 2035 (McDonald et al. 2009). From an ecological perspective,

development can cause large-scale and novel alterations to ecosystems, resulting in habitat loss

and fragmentation (Leu et al. 2008, McDonald et al. 2009) that strongly impact terrestrial

wildlife populations and their ecosystems. In light of the new energy future, understanding and

mitigating the impacts of energy development will be one of the major global challenges for ecologists in the coming decade.

The potential environmental effects of energy development (e.g., water contamination, deforestation, climate change) garner much public interest and engender important debates. It is critical that the impacts of development to wildlife are part of this conversation, and that the best knowledge on this issue is available to decision makers. As such, there is an explicit need to summarize and synthesize the current literature on the impacts to wildlife in order to (1) characterize the type of development-caused environmental risks to wildlife, (2) understand general patterns of wildlife responses, (3) summarize results that offer guidance for mitigating impacts through on-site mitigation and best management practices (BMPs; i.e., measures employed by industry that reduce environmental impacts), and (4) highlight the need for such information where it is lacking. To this end, we reviewed the literature on recent energy development and development mitigation throughout the world. For the U.S. and Canada, where the majority of such research was focused, we quantified and summarized impacted species, the geographic location and ecoregions where research on impacts took place, and the robustness of study designs in terms of informing mitigation measures.

IMPACTS OF EMERGING ENERGY SECTORS TO WILDLIFE

Five energy sectors have driven the global increase in energy development: unconventional oil and gas, wind, bioenergy (including biofuels and biomass electricity production), solar, and geothermal energy (IEA 2009, U.S. EIA 2010). These sectors differ in their geographic locations, spatial extent, and impacts to wildlife, and thus have received various levels of

attention in the literature. We conducted a systematic review of the global literature on the

impacts of the above energy sectors to terrestrial wildlife (see Appendix 1 for a detailed

description of the review protocol and resulting literature). We focused on empirical studies or

meta-analyses that examined wildlife impacts relative to these sectors, while excluding model-

based simulation studies. We did not review impacts from conventional oil development, as this

type of development has been ongoing for several decades and is on the decline (U.S. EIA 2010).

Finally, we used detailed information from studies specific to the U.S. and Canada for direct

quantification of impacts to species as well as the geographic locations and ecoregions impacted

(the latter for the U.S. alone). These focal countries dominated the published literature (>70% of

reviewed studies; Appendix 1), hold major reserves of unconventional oil and natural gas and

substantial potential for renewable energy (Lu et al. 2009; World Energy Council (WEC) 2010,

2012, Dinçer 2011), are two of the largest global producers (Table 1.1), and have publicly

available information on energy production and potential. The U.S. and Canada also are on the

forefront of developing cutting-edge production methods (e.g., hydraulic fracturing) that are

likely to expand into other regions. Thus, the energy development and subsequent

environmental impacts in these countries reflect the current, and likely future, global trends in

development (IEA 2009).

Wind

Although the debate on environmental impacts of many energy sectors has focused on carbon

emissions or pollutants, the primary impact of wind energy has been to wildlife. The most

common impact of this sector was the direct mortality of bats and birds from collisions with

wind turbines (Table 1.2; Kunz *et al.* 2007; Kuvlesky *et al.* 2007; Rydell *et al.* 2010). The spatial

distribution of studies in the reviewed literature was limited, focusing on the U.S., Canada, or Western Europe despite substantial global potential and interest (Lu et al. 2009; Table 1.1). In the U.S. and Canada, the population repercussions of this mortality source were of greatest concern for bats due to the magnitude of such mortality, and the lack of information on demography and population sizes (Kuvlesky et al. 2007). Most mortalities in this region were of migratory, tree-dwelling bats (Kunz et al. 2007; Appendix 1). The patterns of mortality in Europe stood in contrast to the U.S. and Canada, as migratory and non-migratory bats were killed in similar proportions, and the species for which mortalities were most common were generally thought to have stable populations (Rydell et al. 2010). Despite these differences, the underlying mechanisms for these mortalities appeared to be similar between the two continents, and included bats engaging in behaviors that make them more susceptible to collisions, or being attracted to turbines for roosting or foraging. In general, these proximate causes for collisions remained untested, but the ultimate driver appeared to be that wind farms were located in high-use areas (Kunz et al. 2007, Rydell et al. 2010).

As with bats, siting of wind farms in areas actively used by birds (e.g., flyways) was a major driver of mortalities (Kuvlesky et al. 2007). In North America, fewer birds (relative to bats) were killed due to collisions with turbines, and population-level consequences have not been documented (Kuvlesky et al. 2007), while in Europe wind turbine collisions likely have contributed to the decline of some species (e.g., the Egyptian vulture (*Neophron percnopterus*); Carrete *et al.* 2009), and impacted breeding success and fecundity of others (e.g., the griffon vulture (*Gyps fulvus*) and the white-tailed eagle (*Haliaeetus albicilla*); Dahl *et al.* 2012; Martinez-Abrain *et al.* 2012). On both continents wind farms negatively impacted bird abundance and elicited behavioral responses (e.g., avoidance), though this impact was species

and site dependent (de Lucas et al. 2004, Stewart et al. 2007, Pearce-Higgins et al. 2009, Garvin et al. 2011; Appendix 1).

Aside from bats and birds, we found only 6 studies that examined impacts of wind energy on terrestrial wildlife (two on ungulates, three on desert tortoises (*Gopherus agassizii*) and one on ground squirrels (*Spermophilus beecheyi*); see Appendix 1 for citations). Ungulates in these studies showed no behavioral responses to wind energy. Likewise tortoises showed no population-level response, but mortality related to culverts in wind energy facilities was hypothesized to be a potentially significant source of mortality. Ground squirrels showed behavioral alteration likely due to acoustic masking from wind turbines.

Bioenergy

The debate over the environmental impacts of bioenergy has centered on carbon emissions and deforestation, but the cultivation of crops used in this sector can elicit large-scale land-use change with implications for wildlife (Fargione et al. 2010). Importantly, bioenergy production occurs on all continents, but the literature on the impacts to wildlife is limited to only a few countries (e.g., the U.S., United Kingdom, and Indonesia; Table 1.1). This literature can be categorized by the nature of land conversion required for bioenergy cultivation. In temperate regions, where we only found studies from the U.S., Canada, and the United Kingdom, herbaceous crops (e.g., corn or miscanthus (*Miscanthus giganteus*)) and short-rotation woody crops (e.g., poplar (*Populus spp.*) or willow (*Salix spp.*)) were typically cultivated on lands that already have been converted for agricultural purposes (though in the U.S. some of these lands have been reclaimed; i.e., through the Conservation Reserve Program). In tropical regions, crops such as oil palm (*Elaeis guineensis*) and sugarcane (*Saccharum spp.*) were harvested as biodiesel

feedstocks and often required land conversion from primary or secondary native forests. Although cultivation of these crops occurred in a number of countries, we only found studies from Borneo, Malaysia, and Guatemala (Appendix 1).

The environmental impacts of oil palm cultivation has become a global conservation issue in the last decade (Fitzherbert et al. 2008). Oil palm cultivation and its associated deforestation represents one of the greatest threats to biodiversity in some tropical countries (Koh et al. 2011). Literature on the direct impacts to wildlife largely focused on bird diversity, with oil palm plantations having substantially lower diversity and disproportionately lower numbers of sensitive and rare species than non-palm forests (Fitzherbert et al. 2008, Danielsen et al. 2009, Edwards et al. 2010). The degree of biodiversity loss depended on the proximity of plantations to intact native forest or forest fragments (Koh 2008) and likely was related to lower vegetative diversity and limited food resources in plantations. Most research on the impacts of bioenergy production from oil palm to wildlife was from southeast Asia, but oil palm could be grown throughout the tropics, with similar conservation implications (Butler and Laurance 2009). Similar to oil palm, the production of biodiesel from sugarcane or soy (*Glycine sp.*) contributed, along with other factors, to land clearing in the Amazon (Nepstad et al. 2008). Although empirical research on the direct impacts to wildlife in this area was lacking, large-scale deforestation will impact a host of species across numerous taxonomic groups. Critically, deforestation of the Amazon was not only a result of local demand for bioenergy, but influenced by global markets. Increased production of bioenergy from corn in the U.S. was linked to raising prices for soy, and thus further Amazonian land clearing for production of this crop (Laurance 2007).

In temperate regions, the most commonly documented impacts of herbaceous bioenergy crops was lower songbird and small mammal species richness, diversity, and abundance relative to reference areas (e.g., field margins or undisturbed grasslands; Semere & Slater 2007; Sage *et al.* 2010; Riffell *et al.* 2011; Robertson *et al.* 2011a; Robertson *et al.* 2011b). These patterns, however, depended on the surrounding land use (Bellamy et al. 2009). Furthermore, if bioenergy crops composed only a small proportion of the landscape, an increase in species richness could result (Meehan et al. 2010) through increased habitat heterogeneity (Roth et al. 2005, Robertson et al. 2011a). In some areas, bioenergy crops such as corn provided high quality forage for large herbivores, thus cultivation was hypothesized to alter space-use of these animals (Walter et al. 2009b).

Short-rotation woody crops, planted in temperate regions, increased nesting habitat for birds in some areas, and enhanced species diversity and abundance for birds, mammals and some reptiles relative to undisturbed forest, but potentially decreased amphibian diversity and abundance (Berg 2002, Sage et al. 2006, Dhondt et al. 2007; see Appendix 1). For birds, the understory vegetation in woody bioenergy crops provided an important food source (Fry and Slater 2011). Again, these impacts depended on the surrounding habitat and the type of land that was converted for energy development. The largest body of research on impacts of woody bioenergy crops to wildlife was from the United Kingdom, where historically much of the land was converted to farmland. Thus, these impacts may not apply for areas where cultivation occurs at the expense of natural habitat.

As with other energy sectors, the impacts of bioenergy crops differed by species and, therefore, their cultivation led to altered species composition (Roth et al. 2005, Riffell et al. 2011). Specific responses varied by crop, land type, (Berg 2002, Tilman et al. 2006, Semere and

Slater 2007, Meehan et al. 2010, Robertson et al. 2011a), and harvest practices (Roth et al. 2005), and depended on the remaining habitat within crops or plantations (Koh 2008). These impacts were of greatest conservation concern when crops or plantations replaced native forests, crop margins, or lands in conservation holdings (Riffell et al. 2011). Such conversion is likely to become more common with greater economic incentives for bioenergy crop cultivation. Another major concern with herbaceous and woody bioenergy production was the potential for crops to become invasive species. Many prospective bioenergy crops have similar characteristics to successful invasive species (e.g., rapid growth with little chemical or nutrient input) and were more likely to become invasive than reference plants (Buddenhagen et al. 2009). For wildlife, such invasions are likely to act synergistically with other bioenergy impacts.

Unconventional Oil and Gas

Unconventional oil or natural gas reserves exist on every continent, and their development is set to become a major energy sector worldwide (WEC 2010, 2012). Information on global production of unconventional natural gas and assessments of reserves, however, are noticeably lacking at this time, while unconventional oil extraction currently occurs in few countries (Table 1.1). The U.S. and Canada produce the greatest amount of unconventional oil and natural gas energy globally (U.S. EIA, 2010, WEC 2012) and, reflectively, the related literature was predominantly concentrated on these countries (Appendix 1). With development likely to increase globally in coming years, the impacts documented in this region are salient globally. Development of unconventional oil and natural gas broadly impacted wildlife by (a) fragmentation through the creation of complex road and pipeline networks, (b) direct habitat conversion from the development footprint, (c) eliciting behavioral responses, particularly

avoidance, due to development related activity (construction, increased human activities and anthropogenic noise), and (d) inviting further fragmentation, resource extraction and direct mortality of wildlife through increased human access to wild lands. Globally, studies mainly focused on impacts to large mammals. Importantly, we note that global studies did not distinguish between conventional and unconventional development and, therefore, we limited our review to a select group of key studies outside the U.S. and Canada (see Appendix 1 for detailed discussion of evaluation protocols). In the U.S. and Canada, most studies documented negative impacts of unconventional oil and natural gas development to wildlife (Fig. 1.1). Studies of these impacts focused mainly on ungulates, greater sage grouse (*Centrocercus urophasianus*), and a variety of song bird species.

The impacts of unconventional oil and gas development on ungulates and other large mammals were well characterized due to the economic and conservation importance of these species. For large mammals, behavioral impacts were most commonly documented and included large-scale displacement from developed areas and around development infrastructure (Sawyer et al. 2006), altered movement or home range patterns (Dyer et al. 2002), and more fine-scale behavioral modifications likely in response to variable human activity, traffic, or disturbance from seismic exploration (Dyer et al. 2002, Sawyer et al. 2009a, Wrege et al. 2010, Wasser et al. 2011). These responses varied by spatial scale and across species, and not all large mammals are impacted by development infrastructure (Kolowski and Alonso 2010, Rabanal et al. 2010).

Few studies documented population-level impacts for specific species of large mammal from development, though oil and natural gas extraction likely has influenced population declines of caribou (*Rangifer spp.*; Sorenson *et al.* 2008; Wasser *et al.* 2011), led to decreased survival of elk (*Cervus elaphus*; Dzialak *et al.* 2011b), and contributed to heightened grizzly bear

(*Ursus arctos*) mortality (Nielsen et al. 2006). One study documented increased nutritional and

psychological stress of caribou, likely in response to human activity related to oil and natural gas

development (Wasser et al. 2011). Although direct population-level impacts from this sector

were infrequently documented, in Africa development contributed to unsustainable levels of

bushmeat extraction due to increased human presence (Thibault and Blaney 2003) and any

increases in development that may accompany unconventional oil and gas development are

likely to exacerbate this situation. Impacts of oil and gas development on the migrations of large

mammals have not been rigorously examined, but it is likely that migrations of some individuals

will be disrupted by development (Sawyer et al. 2009b). Lastly, altered behavioral patterns could

lead to increased vulnerability to predators for certain species.

For bird species the most common impact of oil and gas development was reduced

abundance around development infrastructure (Pitman et al. 2005, Jarnevich and Laubhan 2011).

Such impacts often were species-specific, leading to alterations in species composition in

developed areas (Bayne et al. 2008, Gilbert and Chalfoun 2011). Anthropogenic noise produced

from oil and gas extraction also altered species composition (Bayne et al. 2008, Francis et al.

2011a; Appendix 1), which indirectly influenced plant pollination and seed dispersal (Francis et

al. 2012). Such noise affected reproductive parameters such as mate pairing success, age

distribution, and nesting frequency and abundance (Francis et al. 2011a; Appendix 1). Noise

also caused birds to alter their song characteristics, which can exacerbate negative impacts and

potentially increased predatory exposure (Francis et al. 2011a; Appendix 1). Other, less

commonly reported impacts from unconventional oil and natural gas development included

changes in songbird territory size and shape due to habitat alteration from seismic exploration

(Machtans 2006; Appendix 1), and direct mortality or contamination from landing on wastewater

ponds produced from oil and gas drilling and oil sands extraction, or ingesting toxicants therein (Gurney et al. 2005, Ramirez 2010). Seismic exploration and wastewater ponds accompany almost any development project in this sector, so such impacts likely were more widespread than suggested by the literature. Although there was little research on the impacts of oil and gas development to bird species outside of the U.S. and Canada, the creation of development related roads and other linear features in the tropics will likely hasten human-caused deforestation and colonization of forested areas (Laurance et al. 2009).

Although specific only to the U.S. and Canada, impacts of energy development on sage grouse were possibly the best characterized due to their conservation status (listed as warranted but precluded under the Endangered Species Act in the U.S. and endangered under Canada's Species at Risk Act) and overlap with significant unconventional natural gas reserves. Research on the response of sage grouse to energy development primarily was focused on understanding the reasons for population declines. Numerous studies documented impacts that directly affect sage grouse reproductive output in developed areas, including lower frequency of nest initiation (Lyon and Anderson 2003), greater probability of brood loss (Aldridge and Boyce 2007), and lower recruitment of juveniles to leks (Holloran et al. 2010). In addition, sage grouse had decreased lek attendance (a metric used to monitor populations; Doherty *et al.* 2010) and lower survival probability (Holloran et al. 2010) in developed areas. Sage grouse also avoided areas around developments (Doherty et al. 2008). These impacts likely were exacerbated by the fact that development decreased available grouse habitat, while increasing habitat for predators (Bui et al. 2010) and mosquitoes carrying West Nile virus (Zou et al. 2006), to which grouse are susceptible. Regulations were in place to provide protection for sage grouse in areas being

actively developed for natural gas, though these regulations likely were insufficient (Doherty et al. 2008).

Studies on the impacts of unconventional oil and gas development on species other than birds and large mammals was limited (Fig. 1.1). We found only one study examining the influence of oil and gas development on amphibians or reptiles with no documented response (see Appendix 1).

Solar and Geothermal

We found no empirical peer-reviewed research on the impacts of either solar or geothermal energy development on wildlife. These sectors also are the least developed globally (Table 1.1). Lovich and Ennen (2011) reviewed the available literature (mostly from unpublished reports) and hypothesized that habitat loss and fragmentation, and microclimate alteration around solar arrays were the most likely impacts to wildlife (Table 1.2). The desert southwest of the U.S. holds some of the greatest potential for solar energy in the U.S. and Canada, thus wildlife in this area face the greatest threat (Table 1.3; Lovich & Ennen 2011). Similar to other sectors, the location of solar arrays relative to wildlife migration routes and critical habitat figures to be important in dictating the conservation implications (Lovich and Ennen 2011). Geothermal energy development can involve the emission of pollutants (Pimental 2008), and will involve habitat alteration and related impacts, at least at a small scale (Table 1.2). Literature on empirical studies regarding impacts from this sector was lacking globally. The majority of geothermal energy potential in the U.S. and Canada lays in the west and southwest of the U.S. (Table 1.3; Appendix 2).

Summary, General Patterns, and Research Needs

The impacts of energy development to wildlife varied among species and sectors (Table 1.2). In our quantification of studies from the U.S. and Canada, most studies documented negative impacts (Fig. 1.1). Behavioral alterations in response to development were the most common impact reported and likely precede demographic or population-level consequences. Behavioral responses included large-scale displacement, as well as more nuanced changes to habitat selection and movement patterns related to habitat fragmentation. Fragmentation is an unavoidable byproduct of development, potentially resulting in both the loss of migratory routes and decreased connectivity within and between populations, as well as further impacts related to human access to wild lands. The preponderance of behavioral alterations may have resulted from the large body of research on unconventional oil and gas development in the U.S. and Canada, for which behavioral responses were typical, or due to a disproportionate number of studies in this sector focused on behavioral impacts over other factors. Broadly, across studies in different regions, results demonstrated wide variation in the response of species to the same or similar disturbance, thus altered species composition and interactions appear to be a likely outcome of any development project. Although less common, the impacts with the most direct conservation implications included those that caused decreased survival, altered reproduction, and population declines. These impacts were documented for some species in response to unconventional oil and natural gas development and wind energy but were undocumented in other sectors, probably reflecting limited research.

Although the literature on impacts of unconventional and alternative energy development to wildlife has initiated important discussion and further research, a number of major shortcomings exist and must be addressed. Importantly, the literature was severely limited

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geographically, both globally (Table 1.1) and in the U.S. and Canada (Fig. 1.2). In many cases, research on impacts in the U.S. and Canada did not overlap the ecoregions with the greatest potential for development (Olson *et al.* 2001; Table 1.3; see also Appendix 2), and similar patterns likely exist worldwide. Such ecoregions and the component species are potentially at the greatest risk but severely understudied (see Appendix 2). In addition, the literature was focused on few species (Fig. 1.1), and the majority of studies were retrospective (less than 20% of the reviewed studies from the U.S. and Canada had any before-after component). These factors strictly limit the inferences that can be drawn from such studies. A broadening of the current knowledge base in terms of both species and geography, as well as more robust study design are needed to assess the impacts to wildlife.

BEST MANAGEMENT PRACTICES AND ON-SITE MITIGATION

Identifying the wide variety of energy development driven impacts to wildlife is the first step in understanding how each sector is altering environments. Subsequently, providing tangible recommendations on mitigating these impacts is important to successful conservation actions aimed at ensuring more sustainable development. Here we summarize the BMPs and on-site mitigation measures suggested in the published literature and highlight the need for such research where it is lacking (see also Appendix 1).

Wind

Direct mortality, the primary impact to wildlife from wind energy development, is more easily quantified than the often indirect impacts related to other sectors. Thus, in many cases mitigation

can produce more tangible results (i.e., mortality reduction), and a number of studies directly

assessed mitigation in a before-after context (Fig. 1.3). For bats, increasing the wind speed at

which turbines begin spinning (cut-in speed) was shown to effectively reduce mortalities

(Baerwald et al. 2009, Arnett et al. 2010). For birds, seasonal stoppages, upgrading turbines to

newer and taller models, moving food sources to reduce collision potential, and stopping turbines

during certain wind conditions reduced mortalities (Smallwood and Karas 2009, Smallwood et

al. 2009b, Martinez-Abrain et al. 2012). In addition, in areas of intensive monitoring, stopping

specific turbines when birds were seen flying nearby reduced mortalities (de Lucas et al. 2012).

The above studies provided the best guidance on mitigation measures. Despite the fact

that many studies were not designed to directly test mitigation (Fig. 1.3), documentation of

disproportionate mortality at certain turbines or wind farms was used to suggest BMPs and on-

site mitigation measures. Chief among these measures was locating wind farms to avoid areas of

generally high density of birds and bats, feeding and foraging sites for soaring birds, migratory

routes, nesting areas, and bat colonies (Kuvlesky et al. 2007, Smallwood et al. 2007, Carrete et

al. 2009, Baerwald and Barclay 2011, Dahl et al. 2012). Risks associated with development

siting can be readily assessed in the predevelopment environmental impact assessment stage,

however in some cases such assessments were misleading (e.g., Ferrer et al. 2012) and would be

more accurate if conducted at the individual turbine level taking species-specific factors into

account (e.g., for soaring birds avoid placement in areas that produce certain winds; de Lucas *et

al.* 2008; de Lucas *et al.* 2012; Ferrer *et al.* 2012). For bats, echolocation detectors were

suggested to be effective for such assessments (Weller and Baldwin 2012). In addition, building

wind farms on developed lands (e.g., agricultural lands) could benefit wildlife by reducing land

use change (Kiesecker et al. 2011). Aside from adequately assessing the locations of wind farms,

stopping wind turbines during times when bats and birds are particularly active or vulnerable (for birds during times when food was limited; Martinez-Abrain *et al.* 2012; for bats when insects were most active, during clearer weather, falling barometric pressure, just after sunset and particularly at taller turbines; Barclay *et al.* 2007; Horn *et al.* 2008; Baerwald & Barclay 2011) was projected to provide the greatest reduction in mortalities. In addition, assessing the effectiveness of seasonal shutdowns is recommended (Johnson et al. 2004b), as is removal of specific turbines at which there are a disproportionate number of collisions (Carrete et al. 2009). Habitat offsets, particularly for areas with traits described above, have been suggested as a means of decreasing population level impacts to birds (Smallwood and Thelander 2008). Other mitigation measures, such as altering the physical characteristics of turbines, may be effective but vary geographically, and among species in the same area (see Appendix 1). Many of these recommendations likely are species and site specific and not widely applicable.

Although most of the research on wind energy impacts to wildlife focused on mortalities among avian and bat species, research on non-volant species was limited and produced equivocal results (see Appendix 1). Impacts are likely species and site specific, and will require further research to elucidate general patterns useful for mitigation.

Bioenergy

Suggested measures for the mitigation of bioenergy impacts to wildlife varied widely depending on the crop and region. In tropical regions, where crops often replaced native forests, extensive pre-development assessments of economic benefits and environmental costs were suggested to fully understand impacts (Danielsen et al. 2009). In addition, if crops replace areas of high conservation value, habitat offsets may be required to ensure sufficient habitat is left unaltered

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(Edwards et al. 2010). In some cases improvements within plantations (e.g., promoting understory or epiphytic growth) and maintenance of forest fragments nearby plantations were suggested to enhance biodiversity (Koh 2008). Ultimately, ensuring large tracts of native forest are left intact will provide the greatest conservation benefit.

In temperate regions the cultivation of bioenergy crops may require no new development (i.e., use of previously cultivated lands). In these areas, degraded land brought back into production with high diversity polycultures of plants could in fact increase habitat for some wildlife species (Tilman et al. 2006). Thus, the discussion of BMPs and mitigation in temperate regions centered not on the development itself but on the conservation value of the cultivated land and what crops were planted. A greater proportion of studies directly assessed mitigation for this sector than any other (Fig. 1.3), and a number of suggestions for BMPs and mitigation were provided. For birds that may nest in bioenergy crops, harvesting post-fledging was offered as an important BMP (Roth et al. 2005). In addition, maintaining habitat structure through planting mosaics of harvested and unharvested crops, or crops and undisturbed land was suggested to provide a greater amount of habitat for a range of species (Murray and Best 2003, Roth et al. 2005, Sage et al. 2010). With short-rotation woody crops, the specific vegetative characteristics of cultivated species influenced nesting propensity for certain species of birds and, therefore, site and species specific guidelines will need to be developed in new areas (Verschuyl et al. 2011). As with herbaceous crops, in short-rotation woody crops, maintaining habitat diversity by planting a variety of cultivars positively impacted a diverse array of species (Dhondt et al. 2007). For small mammals, habitat appeared to be enhanced by maintaining residual coarse-woody debris and constructing piles or windrows (Sullivan et al. 2011; Appendix 1). We caution that the literature on bioenergy was limited in geographic extent and with expansion of these crops into

other countries, mitigation measures will depend greatly on current land use and management goals (e.g., if endangered species are present in an area, then general species diversity likely will be of lesser concern).

A number of other studies assessed wildlife response to bioenergy crops and made mitigation suggestions based on their findings. High diversity polycultures (Tilman et al. 2006), or crops that mimic native vegetation were recommended for planting on degraded lands (Semere and Slater 2007, Meehan et al. 2010, Robertson et al. 2011a, Robertson et al. 2011b). Again, any measures that increase habitat diversity or maintain within-crop structural variability, such as rotational harvest or planting crops at the intersection of two habitat types is likely to increase habitat for a range of species (Berg 2002, Sage et al. 2006, Robertson et al. 2011a). Lastly, maintaining weed species within crops through soil disturbance during harvest, or maintaining crops in different stages of maturity was offered as a means to provide food sources and habitat for wildlife species (Bellamy et al. 2009, Fry and Slater 2011). In contrast, cultivation of crop margins, lands in conservation holdings and the conversion of native habitats negatively impacted wildlife (Riffell et al. 2011).

Unconventional Oil and Gas

Unconventional oil and natural gas differs from other sectors in that, typically, the energy resource, and thus the extraction period, is finite (though we note that new technologies can extend the life span of infrastructure, with development potentially lasting several decades). Therefore, on-site mitigation and BMPs are critical for bringing wildlife through the development period, after which habitat can be restored. Several BMPs and on-site mitigation measures were outlined to address the impacts of this sector (Table 1.2). However, few studies

were designed to directly test mitigation in a before-after comparison, or even correlatively (Fig. 1.3), and thus few measures were supported in the literature. Those studies that were designed in this manner provided the most definitive evidence for the efficacy of specific BMPs or on-site mitigation and we first discuss these measures.

Although unconventional oil and natural gas development typically only removes a small proportion of physical habitat (oil sands mining being a notable exception), the location and interface of these surface disturbances with wildlife space use can amplify or reduce its impacts. Several methods were suggested to manage this interface. Anthropogenic noise that elicits a multitude of behavioral responses by wildlife, our understanding of which is in its infancy, can be managed with a number of methods. Such methods included selective placement in relation to natural noise barriers, installing fewer, centralized compressors, constructing noise retaining walls, or installing noise suppression devices on compressors (Bayne et al. 2008, Francis et al. 2011a; Appendix 1). Similarly, installation of remote liquid gathering systems reduced human activity at well pads and thus decreased behavioral impacts (Sawyer et al. 2009a). Clustering developments, maintaining buffers between development and critical habitat (e.g., nesting habitat), and designing projects to maintain sufficient cover or "refuge" habitat were recommended to provide haven from the perceived risk associated with development (Sawyer et al. 2009a; Appendix 1). Particularly if developments are clustered in future projects, maintenance of sufficient undeveloped habitat will be important to avoid numerous large development clusters with little habitat in between. Reducing the fragmentation caused by linear features (i.e., pipelines and seismic lines) so as to limit impediment to wildlife movement or territory formation was suggested by revegetation or simply constructing more narrow features, particularly in areas of extensive seismic exploration (e.g., boreal Canada; Machtans 2006).

Lastly, issues associated with birds landing on wastewater ponds were reduced by using innovative deterrent methods or by placing netting over ponds (Ronconi and Cassady St. Clair 2006, Ramirez 2010).

Although the above studies provided the best guidance for mitigation, a number of other studies made useful suggestions based on documentation of wildlife response to development. Such suggestions, though less supported than those above, provide useful starting points for more directed studies of mitigation measures. Specifically, employing methods to decrease infrastructure and human activity were commonly suggested mitigation measures from studies documenting behavioral responses to development. Limiting public access to industrial roads also was recommended to decrease mortalities of some mammal species (Nielsen et al. 2006, Dzialak et al. 2011c). Helicopter-assisted or remote seismic exploration could decrease behavioral impacts and subsequent displacement of and stress to some wildlife species in the long term, though care must be taken as the use of helicopters negatively impacts other species (Dyer et al. 2002, Doherty et al. 2010, Kolowski and Alonso 2010, Wasser et al. 2011). Helicopter-assisted exploration may be particularly important in tropical areas, where fragmentation leads to progressively greater threats to biodiversity (Laurance et al. 2009). The above measures will provide disproportionate benefits for certain species (e.g., African elephants (*Loxodonta africana*); Rabanal *et al.* 2010), or if employed during sensitive time periods (e.g., lekking for sage grouse) or in sensitive habitat (e.g., nesting habitat; Lyon & Anderson 2003). In instances where the buffering of critical habitat, or maintenance of refuge habitat are not possible, enhancing existing habitat through treatments or planting of native vegetation may be effective alternatives (Aldridge and Boyce 2007). Habitat improvements also could be used to offset nutritional stress that may occur with development disturbance. Lastly, in areas where

bushmeat hunting is of particular concern resource extraction companies may need to prohibit human access and hunting (Thibault and Blaney 2003).

On-site mitigation and BMPs have the potential to effectively reduce impacts of unconventional oil and natural gas development on certain species. Other species, however, simply do not coexist well with energy development. Numerous studies documented negative impacts to both caribou and greater sage grouse from development in the U.S. and Canada, and although BMPs and though on-site mitigation measures were suggested by some studies, these typically involved maintaining large tracts of undeveloped land or employing large buffer distances between development and critical habitat (see Appendix 1). Such measures may only be viable in limited circumstances and, in the best case, will be difficult to implement; identifying critical habitat (buffered adequately from development) and determining how much is required is a daunting task and likely to be inexact. Thus, for these species, prioritizing habitat or populations to keep undeveloped, while promoting development in other areas (i.e., habitat offsets), may be the most effective mitigation measures (Doherty et al. 2010, Schneider et al. 2010). For better or worse, such measures can only be undertaken after sufficient evidence has been accrued to indicate the lack of effective BMPs or on-site mitigation measures.

Solar and Geothermal

We found no research on mitigating the impacts of solar or geothermal development on wildlife, thus no recommendations were supported by the literature. Energy is produced from these sectors in most regions of the world (Table 1.1) and the most likely impacts from both sectors are displacement from areas around development, leading to altered species composition and behavior (Table 1.2). Best management practices and mitigation measures from other sectors are

likely to be applicable; in particular, proper siting of these developments through pre-development assessments will undoubtedly be of importance in reducing impacts to wildlife.

MITIGATION FOR A SUSTAINABLE ENERGY FUTURE

Recent and emerging energy development impacts wildlife species through the reduction and fragmentation of habitat, displacement, and direct mortality, all of which can contribute to population declines. At the same time, energy development provides numerous societal benefits and is a strategically important domestic objective for many countries. Thus, reduction of impacts through creative mitigation measures and BMPs will be important for resolving these contradictory issues and securing a sustainable energy future.

Although the development of mitigation measures and BMPs is in its infancy in many areas and sectors, the literature offered a number of promising measures. Common to all reviewed energy sectors was the importance of rigorous pre-development assessments. Determining environmental characteristics of areas slated for development and dynamics in wildlife occupancy is essential for predicting likely impacts. In many cases, such assessments will lead to the identification of sites where mitigation may be economically unfeasible (e.g., migratory flyways requiring shutting down of wind farms for large portions of the year). In these cases, areas of higher conservation priority may be unsuitable for the proposed energy development and could be protected as an offset for development of less important areas (Doherty et al. 2010, Schneider et al. 2010).

In regions where development is deemed to be feasible, assessments can provide further guidance on which BMPs or mitigation measures will be most effective. In general, the literature

suggested that impacts of all of the reviewed sectors can be reduced by spatially and temporally

consolidating development activity and infrastructure, thereby localizing impacts. Any methods

that reduce human activity and presence on the land (e.g., liquid gathering systems at natural gas

well pads) or decrease the propagation of anthropogenic noise (e.g., concentrated compressor

stations with sound retaining barriers) appear to be broadly applicable as well. Unfortunately, the

mitigation approaches suggested in the literature tended to be less targeted and our understanding

of their effectiveness is limited. In particular, with oil and natural gas development there are

multiple interacting, and potentially synergistic impacts (e.g., sound disturbance, fragmentation,

human activity), and few studies pinpointed the mechanisms eliciting wildlife responses. In

contrast, due to the nature of development and of impacts, assessments of mitigation for wind

and bioenergy tended to be more straightforward, and the literature provided suggestions for

mitigation in greater detail. Despite the broad generalities discussed here, measures reported may

be valid only at the development densities and for the particular disturbances studied. It is likely

that development thresholds exist, and exceeding these thresholds will lead to population-level

consequences. Few studies addressed such prospects, but it is important that potential thresholds

are investigated. In addition, due to the lack of research in many ecoregions and countries that

are or will become developed (Fig. 1.2; Table 1.1 & 1.3), the applicability of the BMPs and

mitigation measures outlined above to other areas is uncertain.

Although predevelopment assessments are clearly desirable for any development project,

we note that energy infrastructure currently exists for which assessments can no longer be made.

In such cases, several of the above mitigation measures may not be possible (e.g., selecting

infrastructure location), and measures that can be implemented retroactively should be

attempted, while other measures not dependent upon predevelopment assessments (e.g.,

increasing wind turbine cut-in speed) should be explored.

Despite the mitigation measures offered above, a preponderance of the reviewed studies

were not designed to explicitly test mitigation (Fig. 1.3). Indeed, in the literature from the U.S.

and Canada 36% of oil and gas studies, 30% of wind studies, and 23% of bioenergy studies made

no mention of measures to mitigate documented impacts. Only 19% of oil and gas studies, 15%

of wind studies and 38% of bioenergy studies were designed to examine the effectiveness of

mitigation in a before-after context or even correlatively (Group 1 and 2 in Fig. 1.3; Appendix

2). Furthermore, we note that for many studies it was often difficult to determine the extent to

which the effectiveness of mitigation measures was assessed. Thus, the majority of suggested

BMPs and mitigation measures discussed above should be considered provisional, until they are

examined by future studies, in different ecological contexts, and with robust study designs aimed

at directly assessing mitigation. In addition, a handful of studies were designed to allow for

assessments of mitigation, but did not report on this aspect. We urge researchers to put BMPs

and mitigation at the forefront of their findings, as this will aid future researchers, managers,

regulators, and industry.

The above shortcomings have led to a situation where the current literature is not broad

enough to provide mitigation strategies for the breadth of species and ecosystems being affected

by expansion of unconventional and renewable energy development. Furthermore, the paucity of

research on the impacts to ecoregions, sectors, species, and entire countries is a concern as we

move forward with best practices and mitigation recommendations. Importantly, we found

limited research on the impacts of development to amphibians and reptiles. In the U.S. and

Canada, little work was published from the eastern U.S., where large-scale natural gas

development has been ongoing in the Marcellus shale, and where entire ecoregions lie squarely within some of the richest reserves on the continent (Table 1.3; Appendix 2). Globally, the lack of research from entire countries and regions is even more apparent (Table 1.1).

Addressing the shortcomings in the energy development literature will require a shift from solely identifying impacts to directly addressing BMPs and on-site mitigation measures that can be part of sustainable solutions to development impacts. Such a direction will require studies that either seek to obtain a mechanistic understanding of development impacts (i.e., what is actually causing documented patterns) or directly test BMPs and mitigation measures in an experimental framework. Such efforts will require collaboration with both industry and government regulatory agencies and will hold numerous benefits for all involved. Knowledge of development plans can be used to implement before-after-control-impact designs, dialogue with industry and regulatory agencies can allow for studies that directly assess the efficacy of economically and biologically feasible mitigation measures and BMPs (see Arnett *et al.* 2010 for an example) and, lastly, collaborations increase the likelihood of actual implementation of research findings. These collaborations will require researchers willing to engage industry, but also it is essential that industry is open and transparent with development data and plans, as such information is a necessity for robust study designs. Further, it is crucial that industry abides by development plans where such plans formed the basis for research design, as alteration of development activities can be fatal to research projects and, therefore, our ability to derive meaningful inference about the system and question. Ideally, collaborative planning needs to be implemented in the pre-development process to ensure the greatest return from such endeavors. We note that such a shift will take time to implement, and as noted above energy development already has occurred in vast areas throughout the world. Thus mitigation measures that show the

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most promise should be implemented immediately, but their provisional nature must be understood by all involved. These measures can be assessed for their efficacy regularly and an adaptive framework can be used to alter mitigation when necessary.

Due to the known environmental impacts of energy development, funds will continue to be available for mitigation and BMPs. Applied wildlife ecology research must play a role in reconciling the intertwined costs and benefits of development and provide realistic recommendations for the most effective use of such funds. We call for researchers to unambiguously outline the BMPs and on-site mitigation measures suggested by their results, and to be more explicit in the recommendation of potentially subjective measures, such as habitat offsets and maintenance of critical habitat (i.e., how much, what type, and what entails critical habitat). Such efforts will ensure a greater probability of implementation of BMPs and on-site mitigation measures, and a more efficient and effective use of funds. Large-scale domestic energy development represents a new reality for terrestrial ecosystems, and conservation consequences are inevitable. Designing and implementing creative and effective BMPs and on-site mitigation measures will be one of the major conservation challenges of the next 20 years. Current research must rise to meet this reality with innovative studies designed to address these challenges.

TABLES

Table 1.1. Energy produced by region from five unconventional or alternative energy sectors (bioenergy-biofuels and biomass electricity, wind, solar, geothermal, and unconventional oil) number of countries in each region, number of countries producing energy for each sector, and number of countries with studies on the impacts of bioenergy and wind energy development on wildlife[*].

Region (no. of countries)	Wind[†] (no. countries producing)	No. countries with studies; wind	Biofuels[‡]; biomass electricity[†] (no. countries producing)	No. countries with studies; bioenergy	Solar[†] (no. countries producing)	Geothermal[†] (no. countries producing)	Shale oil[§]; other unconventional oil[¶] (no. countries producing)
Africa (56)	1.96 (8)	0	0.99; 1.47 (13)	0	0.04 (8)	1.52 (1)	0; 0 (0)
Asia and Oceania (46)	78.75 (20)	0	99.21; 37.94 (19)	2	4.42 (19)	26.59 (7)	375; 24 (2)
Central and South America (44)	3.29 (20)	0	588.25; 36.79 (22)	1	0.001 (6)	3.16 (5)	200; 14778 (5)
Eurasia (16)	0.62 (8)	0	4.36; 3.56 (5)	0	< 0.001 (1)	0.44 (1)	355; 773 (3)
Europe (40)	142.44 (27)	8	248.31; 137.32 (29)	4	21.98 (31)	10.22 (7)	0; 1191 (3)
Middle East (14)	0.26 (4)	0	0.1; 0.05 (2)	0	0.43 (2)	0 (0)	0; 0 (0)
North America (6)	100.52 (3)	2	914.42; 77.04 (3)	2	1.44 (3)	21.95 (3)	0; 6645 (3)

[*]No studies were found examining the impacts of solar and geothermal energy development to wildlife. Unconventional oil studies were not quantified because the source (i.e., conventional versus unconventional) was not determinable from global studies (see Appendix 1). Information on unconventional natural gas production was not available globally.
[†]Billion kilowatt hours produced. Data obtained from the United States Energy Information Administration (http://www.eia.gov/cfapps/ipdbproject/IEDIndex3.cfm)

[‡]Thousand barrels per day produced. Data obtained from the United States Energy Information Administration (http://www.eia.gov/cfapps/ipdbproject/IEDIndex3.cfm)
[§]Thousand tons produced. Data obtained from (World Energy Council 2010).
[¶]Million barrels produced. Data obtained from (World Energy Council 2010).

Table 1.2. For each energy development sector, the identified and hypothesized (likely) impacts to wildlife, suggested best management practices (BMPs) and on-site mitigation measures for reducing impacts, and suggested research needs. Identified impacts and suggested BMPS and on-site mitigation measures are listed in order of their frequency in the reviewed literature.

Sector	Identified impacts	Likely impacts	BMPs and on-site mitigation measures	Research needs
Wind	Direct mortality Altered behavior and displacement Decreased fecundity Decreased breeding success Acoustic masking	Altered species composition	Avoid siting near bat colonies or in habitat used for nesting, migration, foraging, soaring for large birds, or other activities that may encourage collisions Curtailment during sensitive seasons, times of high insect activity (bats), low wind (bats), high wind (birds), clear weather and immediately after sunset (bats), and when threatened species are present (birds), Increase cut-in speed Replace older towers (birds) Removal of towers with high mortality rate Move known anthropogenic food sources (scavenging birds) Install shorter towers for bats and fewer, larger towers for birds Habitat offsets (birds) Deploy echolocation devices during assessments Pre-development assessment	Behavioral impacts Economic analyses to optimize cut-in speed and stoppage times Population and demographic information for bats (U.S. and Canada) Greater geographic breadth of bird research Further research into reasons for collisions
Bioenergy	Decreased species richness, diversity, and abundance Altered species composition Increased	Declining populations	Plant native species or high diversity polycultures Maintain mosaic of harvested and unharvested land Maintain native habitat in proximity to	Research on impacts to a greater diversity of species Research on global impacts of bioenergy

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	invasive species Large-scale deforestation Altered space-use patterns		crops Harvest after fledging of bird nestlings Harvest to maintain structural diversity in vegetation Plant woody crops that support nesting habitat Plant larger woody crop plots Plant on degraded or already cultivated lands Promote understory vegetation (epiphytes in oil palm plantations; weeds in herbaceous crops) Habitat offsets Create piles or windrows of coarse woody debris	production in North America Focused research on dedicated bioenergy crops
Unconventional oil and natural gas	Altered behavior, movement, home ranges and territories Altered reproduction Altered species composition Acoustic masking Declining populations Decreased survival Direct mortality Reduced abundance Increased stress Increased hunting pressure	Loss of migratory routes Increased predation Increased illegal hunting	Restricted development in and around critical habitat Maintenance of refuge habitat Re-vegetation and habitat enhancements Traffic and access restrictions Narrow seismic lines Siting of developments in areas obscured by vegetation or topography Noise suppression and barriers Clustered development Helicopter assisted or remote development Habitat offsets Directional drilling Setback distances from critical habitat Remote liquid gathering systems Install predator deterrents around	Assessments of impacts to migratory routes Identification of thresholds above which demographic and population-level impacts occur Untangling of response to multiple activities Noise mitigation methods

		developments	
		Liberal harvest of primary prey	
		Remotely activated deterrents	
		Increased pipeline height	
		Pre-development assessment	
Solar	Displacement	Pre-development assessment	Basic research on
	Altered behavior		impacts to wildlife
	Altered species		
	composition		
	Loss of migratory		
	routes		
Geothermal	Displacement	Pre-development assessment	Basic research on
	Altered behavior		impacts to wildlife
	Altered species		
	composition		

Table 1.3. Top 5 ecoregions with greatest potential for energy development, by sector, for the continental United States. Ecoregions less than 100 km^2 were excluded. Area values indicate total ecoregion area (km^2) in the continental U.S. See Appendix 2 for methodology.

Rank	Unconventional oil and gas (percent overlapped by basins; area km^2)	Wind (percent in wind power class 5 and 6; area km^2)[*]	Bioenergy (mean tons / km^2/ year; area km^2)	Solar (mean kWh potential; area km^2)	Geothermal (percent in class 1 and 2; area km^2)[†]
1	Allegheny Highlands forests (100%; 101,492)	Cascade Mountains leeward forest (93%; 16, 236)	Central tall grasslands (166.83; 259,845)	Mojave desert (7,470; 131,271)	Eastern Cascades forests (84%; 56,208)
2	Western Gulf coastal grasslands (100%; 78,295)	South Central Rockies forests (85%; 159,790)	Willamette Valley forests (156.20; 15,201)	Sonoran desert (7,271; 116,759)	Sierra Madre Occidental pine-oak forests (84%; 7, 267)
3	East Central Texas forests (100%; 55,067)	British Columbia mainland coastal forests (78%; 14,611)	Central Pacific coastal forests (151.53; 41,855)	Sierra Madre Occidental pine-oak forest (7,170; 7,267)	Snake-Columbia shrub steppe (82%; 220,029)
4	Mississippi lowland forests (99%; 121,921)	Wasatch and Uinta montane forests (70%; 41, 481)	Puget lowland forests (126.93, 15,579)	Arizona mountain forests (7,032; 109,135)	Colorado Rockies forests (80%; 133,295)
5	Tamaulipan mezquital (99%, 59,906)	Colorado Rockies forests (68%; 133,295)	Mississippi lowland forests (126.87; 121, 921)	Colorado plateau shrublands (6,777; 326,767)	Great Basin shrub steppe (75%; 337,545)

[*]Power class descriptions obtained from National Renewable Energy Lab (http://www.nrel.gov/gis/data_ wind.html): (5) 7.5-8.0 m/s (excellent potential); (6) 8.0-8.8 m/s (outstanding potential).

[†]Class descriptions obtained from National Renewable Energy Lab (http://www.nrel.gov/gis/data_geothermal.html) and describe geothermal energy potential with class 1 and 2 being the most favorable.
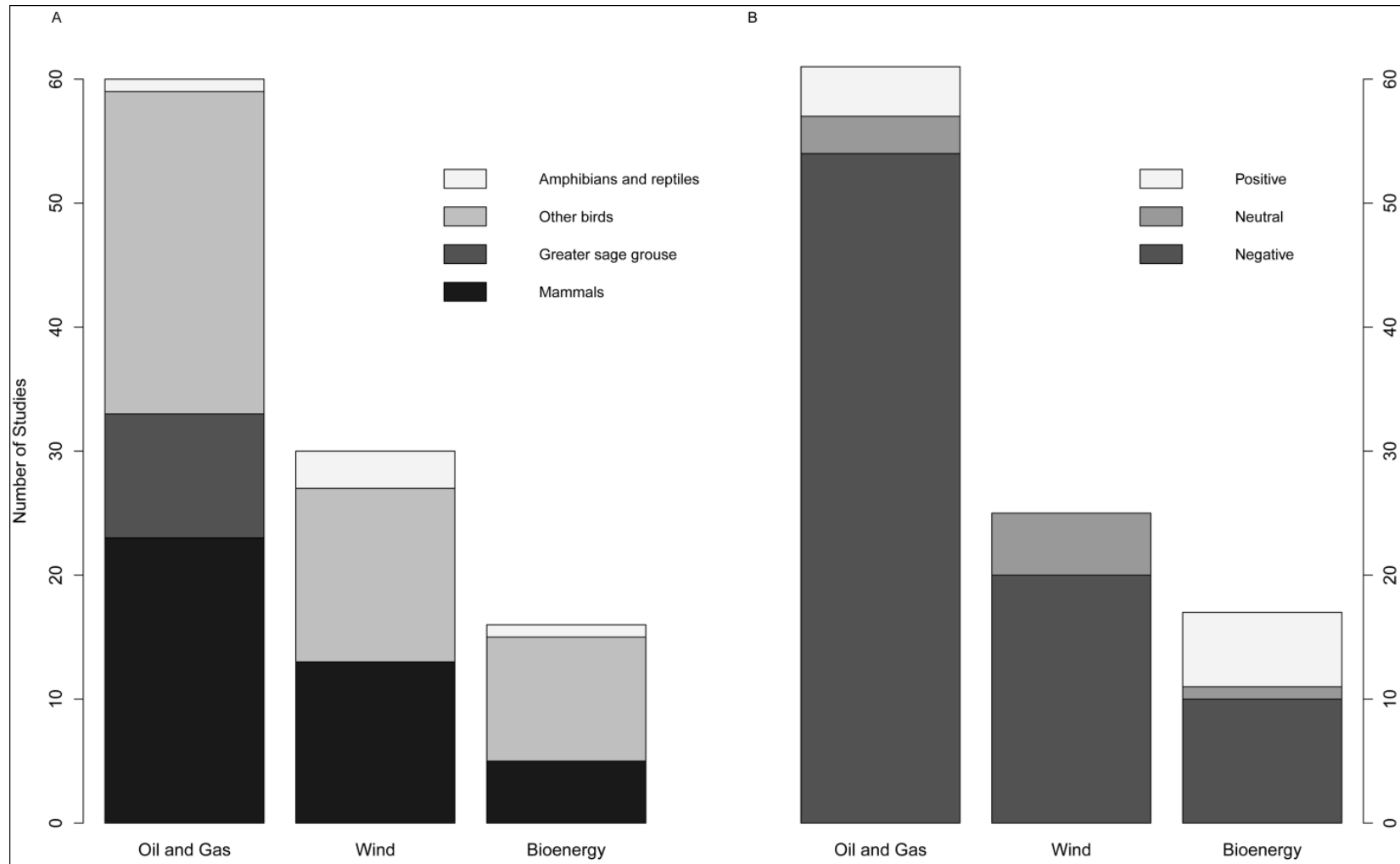
Figure 1.1. Number of U.S. and Canada focused studies summarized by (A) taxonomic group and energy sector and (B) whether they documented negative, neutral, or positive responses by wildlife. Several studies focused on multiple species or treatments (e.g., bioenergy crop type) and thus could have multiple responses.
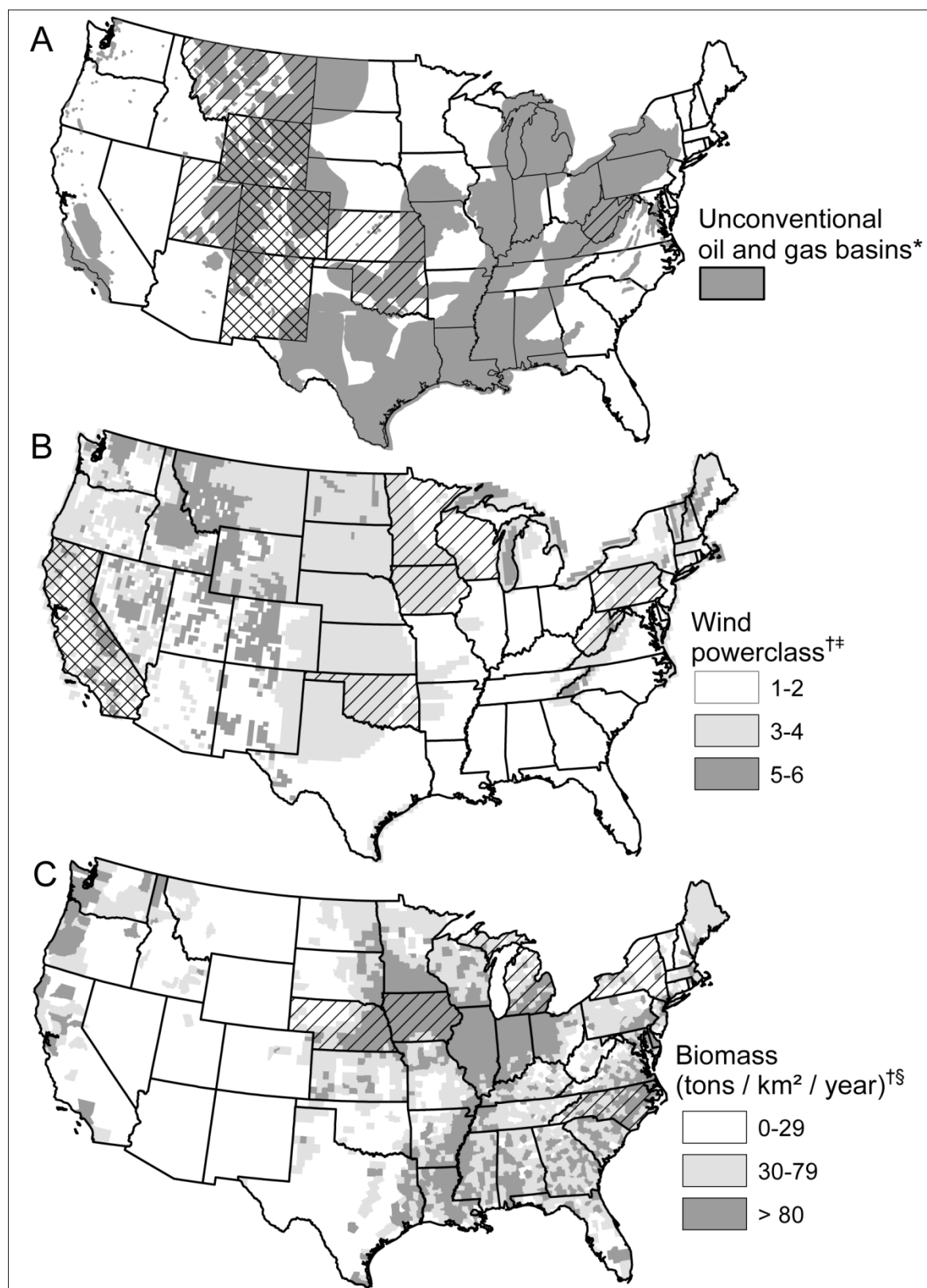
Figure 1.2. Location of reviewed studies and energy potential by sector in the United States for (A) unconventional oil and natural gas, (B) wind energy, and (C) Bioenergy. Diagonal lines

indicate states where 1-5 studies have been conducted, and cross-hatches indicate states where greater than 5 studies have been conducted.

*Unconventional oil and natural gas basin layers obtained from the U.S. Energy Information Administration (http://www.eia.gov/pub/oil_gas/natural_gas/analysis_publications/maps /maps.htm).

[†]Wind and biomass layers obtained from the National Renewable Energy Laboratory (http://www.nrel.gov/gis/).

[‡]Power classes indicate the wind energy potential estimated from 50 m wind speeds, with 1 being the lowest and 6 the highest.

[§]Values for biomass represent potential tons / km^2 / year of both biofuels and biomass burned for heating and electricity.
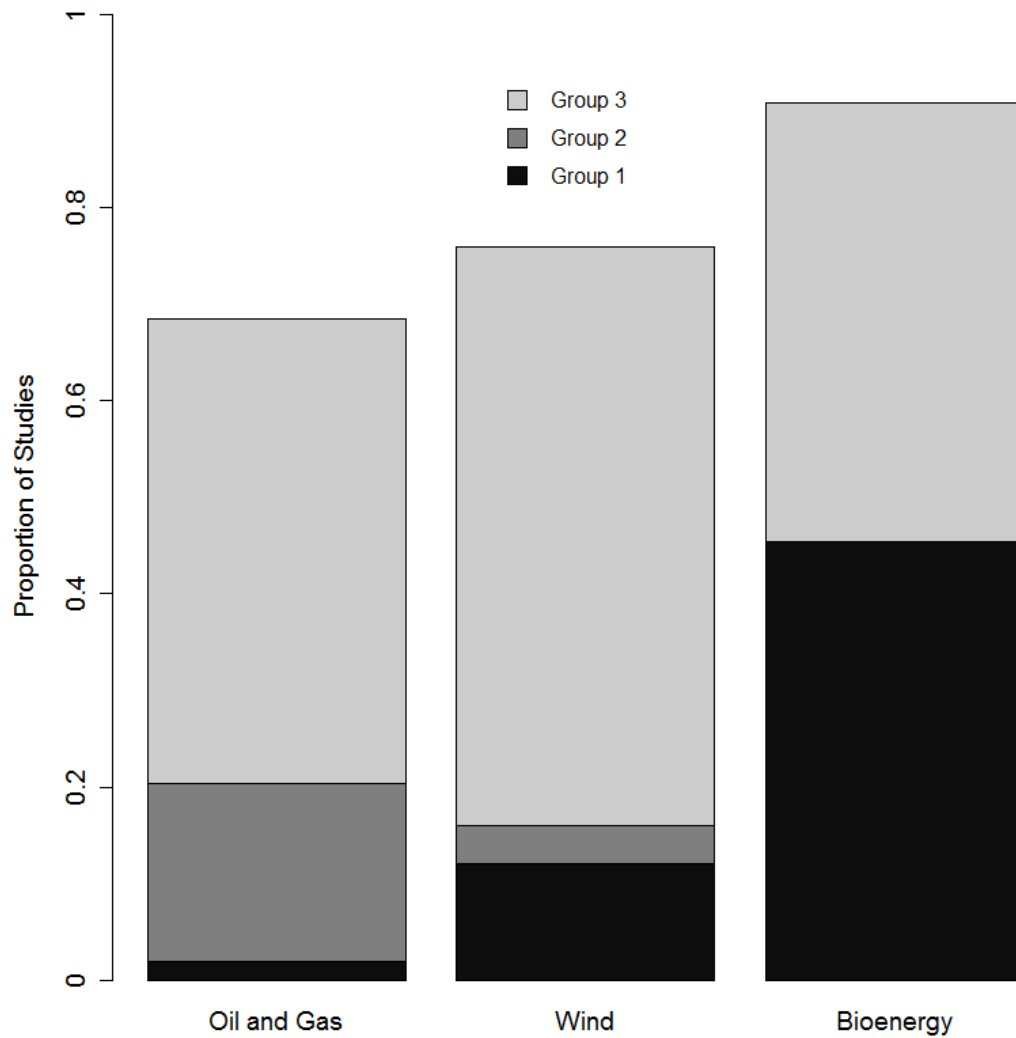
Figure 1.3. Proportion of U.S. and Canada focused studies that discuss mitigation, categorized by study design; (1) studies that explicitly assessed the response of wildlife to the implementation or simulation of a BMP or mitigation measure, with a before-after component (for bioenergy this includes studies examining harvest practices and different plant cultivars), (2) correlative studies that were designed to directly assess the response of wildlife to existing mitigation, and (3) correlative studies that examined the response of wildlife to development and inferred mitigation from their findings.

CHAPTER TWO

EFFECTS OF HELICOPTER CAPTURE AND HANDLING ON MOVEMENT BEHAVIOR

OF MULE DEER

INTRODUCTION

Technological advances such as global positioning system (GPS) radio collars (Cagnacci et al.

2010), heat sensitive vaginal implant transmitters indicating the birth of neonates (Bishop et al.

2007), and advanced physiological monitoring equipment (Laske et al. 2011) allow detailed and

novel research on wildlife. The employment of such approaches necessitates the capture and

handling of animals, which potentially can lead to mortality (Jacques et al. 2009), injury (Cattet

et al. 2008), and altered behavior (Neumann et al. 2011) in focal individuals. As capture

programs continue to become more common, assessment of the impacts of capture and handling

on wildlife is needed to ensure ethical standards and the validity of analyses of movement or

space-use behavior.

Advancements in statistical methods have allowed researchers to use relocation data from

GPS collars to make inferences on complex processes such as habitat selection (Aarts et al.

2008) and behavioral switching (Morales et al. 2004). Such studies typically operate under the

implicit assumption that individual animals exhibit normal behavior after capture, and that these

behaviors can be extrapolated to the greater population. If capture and handling alter these

behaviors, then this assumption is violated, leading to the

potential for biased results. As such, determining the existence of such alterations and subsequently the period over which data are biased by capture and handling is broadly applicable to movement and spatial ecology research and their application for wildlife management objectives.

A number of studies have assessed capture effects on behavioral metrics in free ranging wildlife, and the potential impacts include displacement from areas around capture sites (Chi et al. 1998, Moa et al. 2001), altered space and habitat use (Morellet et al. 2009), and depressed movements (Cattet et al. 2008, Quinn et al. 2012). Defining what constitutes normal behavior for comparison to post-capture behavior is often a difficult task. Using visual observations of collared and uncollared animals, Arzamendia and Villa (2012) found that collared and sheared vicuna (*Vicugna vicugna*) moved significantly more post-capture than unprocessed animals, though they did not determine if the response was due to the shearing or capture. Likewise, Nussberger and Ingold (2006) compared visual observations of collared and uncollared alpine chamois (*Rupicapra rupicapra*) and found no effect of collars, but they did not assess behaviors immediately following capture. Although uncollared animals provide natural controls, they rarely are accessible for comparison because of difficulties in making direct and accurate behavioral observations. In the absence of true controls, Neumann et al. (2011) compared movements of collared moose (*Alces alces*) before and after recapture, finding increased movements for a short time period post- relative to pre-recapture. Although this framework provides useful insight into how capture might cause departures from normal behavior, it is susceptible to erroneously ascribing changes in behavior to capture effects that may be normal seasonal variation (e.g., Ager et al. 2003). Such behavioral changes could obscure or heighten

perceived capture effects and to date have not been accounted for in assessments of capture and handling on animal behavior.

Our objectives were to examine the effect of live capture, handling, and transportation to a central processing site on the movements of mule deer (*Odocoileus hemionus*) that we recaptured between 1 and 4 times, and to compare them to individuals that we did not recapture at the same time. This design allows for understanding capture effects on wildlife behavior and allows for understanding of these effects in the context of typical seasonal behavior.

STUDY AREA

This study took place on mule deer winter range in the Piceance Basin of Northwestern Colorado, near the town of Meeker. Winter range in this area is topographically diverse, with elevation ranging from 1,700 m to 2,300 m. The dominant vegetation type was a mix of pinyon pine (*Pinus edulis*), Utah juniper (*Juniperus osteosperma*), and big sagebrush (*Artemisia tridentata*). Dominant human activity in the area included natural gas extraction and hunting during the fall. Deer in this area were migratory and inhabited winter range between October and May (Lendrum et al. 2012, 2013).

METHODS

Data Collection

We captured adult (>1 yr old) female mule deer between January 2008 and March 2012 as part of ongoing research in the Piceance Basin. Prior to December 2010, we surveyed outlined

capture areas with a helicopter and captured deer opportunistically. Starting in December 2010, we selected a group of deer to recapture every December or March for the following 2 years (Table 2.1). If deer that were scheduled for recapture died, we replaced them with a randomly captured deer. We recaptured deer by locating them via aerial telemetry from a helicopter or fixed-wing aircraft. Upon location, the helicopter capture crew obtained visual confirmation of the focal deer (all collars were fit with unique placards to aid in visual identification of individuals) and captured them using a net gun. We then blindfolded and hobbled the deer, and administered 0.5mg/kg of Midazolam (a muscle relaxant) and 0.25 mg/kg of Azaperone (an anti-anxiety drug) intramuscularly to alleviate capture-related stress (we administered a standard dose of both drugs to each deer based on an average weight of 75 kg). We transported deer to a central processing site typically within 2 km of the capture site (extreme distances were within 5 km) where we took standard measurements and samples. During March captures, we assessed the pregnancy status of all deer and fit a subset ($n = 5$) with vaginal implant transmitters, requiring increased processing times (see Bishop et al. 2007, 2011 for further details). We fit each deer with a GPS radio collar (G2110D, Advanced Telemetry Solutions, Isanti, MN, USA) and released them at the processing site immediately following the collection of samples and collar attachment. We recorded the time the deer arrived at the processing site as the capture time. All procedures were approved by the Colorado State University (protocol ID: 10-2350A) and Colorado Parks and Wildlife (protocol ID: 15-2008) Animal Care and Use Committees.

Deer that we opportunistically captured prior to December 2010 were fit with GPS radio collars set to attempt a relocation once every 5 hours. The group of deer we selected to be recaptured starting in December 2010 were fit with GPS collars set to attempt a relocation once

every 30 minutes or once every hour. We recaptured all of these deer in December 2011, and recaptured a subset in March 2011 and/or March 2012 (see Table 2.1 for further details).

All collars were set to automatically drop off deer after a time period of 12–17 months (i.e., Apr of the year following capture). Once we retrieved collars, we downloaded relocation data. Although we did not explicitly design our capture efforts to assess capture effects, we collected the March data in such a way as to allow a before-after-control-impact (BACI) analysis because of temporally overlapping before-after data from deer that were both recaptured and those that were not. For analysis, we separated these data into 4 groups (Table 2.1). The first included data from deer that were recaptured while wearing GPS collars in March (hereafter March recapture data; Table 2.1). The second group acted as a control for this group and was comprised of deer that were wearing collars during a March capture (i.e., they had been captured and collared the previous December) but were not recaptured in March (hereafter March control; Table 2.1). The third group consisted of deer that were recaptured while wearing a GPS collar in December (i.e., they had been captured previously; hereafter December recapture data; Table 2.1). The final group acted as a control for the December recapture data and was comprised of deer fit with GPS collars that were not recaptured during a December capture (hereafter December control; Table 2.1). The December control deer did not provide a true control as they were not temporally overlapping with the December recapture data, thus we do not make direct quantitative comparisons between December recapture and control data, we only make qualitative comparisons based on the patterns resulting from the models below. In addition, because the December controls were on a 5-hour relocation schedule, whereas December recapture data were on an hourly or 30-minute relocation schedule, we rarefied the finer scale data to match the resolution of the control data for all comparative analyses below.

Analysis focused on movements derived from relocations collected 1 month prior and 1 month following recapture. Captures generally took place during the first week of December or March, and we used the mean capture date across all years to categorize control data for pre- and post-recapture comparisons. Deer in this area are migratory (approx. median winter range leave date is 7 May, approx. median fall winter range arrival date is 22 Oct; C. R. Anderson, Colorado Parks and Wildlife, unpublished data), so we excluded any summer range or migration data falling within this period. We classified spring migration as the time when deer made a directed movement away from their winter range and did not return, and fall migration as when deer made directed movement away from summer range until they ceased directed movement on winter range. We removed any locations with a positional or horizontal dilution of precision (PDOP/HDOP) greater than 10. In addition, we removed erroneous locations identified by unrealistic movements: the largest 95% of movements that upon visual examination in ArcMap 10.1 (Environmental Systems Research Institute, Redlands, CA, USA) were the result of a single outlier location. We used the resulting data to examine the effect of recapture on movement behavior. In all subsequent analyses, the movement data consist of multiple observations from the same individual, and thus are not independent. To account for the nested nature of the data, we used hierarchical (i.e., random effects) models, fit in a Bayesian framework, to assess the effects of recapture on movements. Unless otherwise noted, we fit all models with intercepts varying by individual (i.e., a random effect on intercept). We fit all models in R with the 'rjags' package (Plummer 2013; for JAGS code and specifics on models see online supporting information).

Movement Behavior Analyses

We fit a series of models on combined pre- and post-recapture movements to assess the influence of handling on movement behavior. In cases where analyses indicated a difference between pre- and post-recapture movements, we conducted further analyses directly comparing recapture movements with the control data.

Using the recapture data, we calculated the 24-hour daily displacement (straight-line distance between the first and last location of each day) for every deer 1 month prior to and 1 month after recapture. For post-capture data, we started calculations at midnight on the day of capture, to standardize across deer with different capture times. We fit a model to the displacement distances for the March and December data separately, with a binary covariate for if the displacement was post-recapture (i.e., 1 indicating if the movement was post-recapture and 0 if it was pre-recapture). We allowed both the intercept and the coefficient for pre- versus post-recapture to vary across individuals.

We calculated the movement rate (m/hr) for all locations. We fit a model to movement rates from the December and March recapture datasets (2 models total) examining a single covariate: whether the movement was before or after a recapture. We allowed both the intercept and the coefficient for pre- versus post-recapture to vary across individuals. As these models showed differences between pre- and post-recapture movement rates, we next examined the control data. We fit models to movement rates from the December and March control datasets for comparison with the recapture models. Because the March control data temporally overlapped the March recapture data, allowing for direct comparisons among datasets, we next fit a model to the 1) post-recapture and control data and 2) the pre-recapture and control data for March, with a binary covariate indicating if the movement was a recapture or control movement.

The combination of these models allows us to assess whether the patterns seen in the recapture data differed from those of the control data, which would indicate an effect of capture. If control and recapture data displayed similar patterns, this would indicate no effect of capture.

To further explore the potential for temporal effects of capture and handling on movement rates, we fit a series of additional models to all recapture and control datasets separately, in which the number of days post-recapture was a covariate (see online supporting information). We included the distance moved from the home range as a covariate and tested models with different functional forms for the effect of the number of days since the capture event on movement rates (i.e., linear, quadratic, or log; see online supporting information). We compared models using the deviance information criteria (DIC; Spiegelhalter et al. 2002, but with the effective number of parameters as formulated in Plummer 2012). For all models, the movement rate was natural log transformed to assure proper support (i.e., untransformed movement rates are strictly positive and cannot be modeled using linear regression; see online supporting information for specifics of models).

Home Range Return Analysis

We calculated the time it took for deer to return to their home range following recapture as the number of hours from release to the time when a deer arrived back on the 100% minimum convex polygon (MCP) home range. We calculated MCPs around the data from 1 month prior to recapture using the 'adehabitat' package (Calenge 2006) in the R statistical software (R Core Team 2013), which we then imported into ArcMap 10.1 to calculate return times. To standardize return times across data derived from collars with different relocation schedules, we used linear interpolation to estimate locations every 30 minutes (i.e., the midpoint of the straight line

between hourly locations). For deer whose MCP overlapped the processing site, we set the time to return at 0 hours. We then fit a model to the natural log-transformed home range return times and included covariates for if the capture event took place in March (i.e., December capture was the reference category) and the distance (in meters) between the processing site and the closest point of the MCP.

RESULTS

We recaptured 58 deer at some point throughout the study; we recaptured 26 deer once, 15 deer twice, 7 deer 3 times and 10 deer 4 times for a total of 117 recapture events. Because of capture myopathy (2 deer), poor GPS fix success, and some deer being too far away from the processing site and thus being recaptured and released at the capture location, we were left with 104 recapture events with which we could assess home range return times, and 99 events with which we could assess 24-hour displacements and movement rates. Of the 58 deer that we recaptured, 26 were not subsequently recaptured in March 2011 or March 2012, thus the March control data were comprised of locations from 26 deer. The December control data were comprised of locations from all 61 December control deer.

Movement Analyses

The trend in daily displacement distance suggested that displacement (straight line movement between the first and last location of each day) was shorter during the 30 days prior to recapture than the 30 days post-recapture in both March and December, though the differences were small (pre-recapture Dec: $\bar{x}$ = 745 m, SD = 646; post-recapture Dec: $\bar{x}$ = 757 m, SD = 893; pre-

recapture Mar: $\bar{x}$ = 633 m, SD = 808; post-recapture Mar: $\bar{x}$ = 638 m, SD = 770), and the 95%

credible intervals of the model coefficients for pre- versus post-recapture overlapped 0 (Dec: β =

0.06, 78% of posterior > 0; Mar: β = 0.1, 93% of posterior > 0). Although these values indicate

little departure from pre-recapture behavior when examined in monthly aggregates, daily net

displacement clearly was elevated the first day after recapture (i.e., from midnight on the day of

capture, until the following midnight) and slightly elevated the remainder of the first week (Fig.

2.1).

Mule deer movement rates were substantially greater the day of recapture than during any

other time during the month before or after recapture, and were substantially greater than any

control deer movements (Figs. 2.2 and 2.3). Recapture data movement rates were greater post-

recapture than pre-recapture in March (pre-recapture: $\bar{x}$ = 82 m/hr, SD = 145; post-recapture: $\bar{x}$ =

108 m/hr, SD = 177; β = 0.24, 100% of posterior > 0). In contrast, recapture data movement rates

were lower post-recapture than pre-recapture in December, though only slightly (pre-recapture: $\bar{x}$

= 85 m/hr, SD = 120; post-recapture: $\bar{x}$ = 81 m/hr, SD = 109; β = −0.06, 86% of posterior < 0).

Control data models showed similar patterns; March control movement rates were greater after

the mean March capture date (pre-mean capture date: $\bar{x}$ = 87 m/hr, SD = 143; post-mean capture

date: $\bar{x}$ = 110 m/hr, SD = 164; β = 0.26, 99% of posterior > 0), and December control movement

rates were less after the mean December capture date (pre-mean capture date: $\bar{x}$ = 70 m/hr, SD =

82; post-mean capture date: $\bar{x}$ = 60 m/hr, SD = 69; β = −0.1, 99% of posterior < 0). The models

directly comparing March recapture and control data indicated that both pre- and post-recapture

movements were significantly less than pre- and post-mean capture date control movements

(post-recapture β = −0.14, 100% of posterior < 0; pre-recapture β = −0.09, 100% of posterior <

0).

The model examining movements as a function of the number of days since recapture clarified these patterns, with model predictions showing a slight quadratic relationship with time since recapture, though the 95% credible intervals of the predicted movement rates overlapped at all times (Figs. 2.2 and 2.3). Predicted December recapture movements declined similarly to the December control data, but 95% credible intervals never overlapped. We caution that the December recapture and control data came from different years and thus these results must be interpreted with caution (Figs. 2.2 and 2.3; see online supporting information for detailed model results).

Home Range Return Analysis

The time to return to the MCP was highly variable among deer, ranging from 0 (0.5 when excluding deer whose MCP overlapped the processing site) to greater than 1,800 hours. Mean time for deer to return to their MCP after recapture was 37 hours (SD = 84), with a median of 14 hours. The model of return time also indicated that deer took longer, on average, to return in March than December (Dec median = 14 hours, $\bar{x}$ = 30 hours, SD = 83; Mar median = 13 hours, $\bar{x}$ = 43 hours, SD = 85; β = 0.29, 94% of posterior > 0; see online supporting information for detailed model results). When data from deer whose MCP overlapped the processing site were excluded, these values increased slightly (overall median = 15 hours, $\bar{x}$ = 40 hours, SD = 86; Dec median = 15 hours, $\bar{x}$ = 33 hours, SD = 86; Mar median = 14 hours, $\bar{x}$ = 46 hours, SD = 87). Although the mean times indicate an average of greater than 1 day to return to their MCP, 71% of deer returned within 1 day, 81% within 2 days, 85% within 3 days, and 92% within 4 days. The remaining deer took substantially longer to return, though we note that in several cases, these deer used areas immediately adjacent to the MCP for long periods of time. In effect, these

deer likely had returned to their home range areas, but the 30 days of data we used likely underestimated winter home ranges (post-hoc review of the data confirmed that these deer indeed used these areas during other years or other times during the same winter). The distance we moved a deer from their home range was a strong predictor of the time to return ($\beta = 0.67$, 100% of posterior > 0), with a mean predicted increase in return time of approximately 4 hours for every additional kilometer moved from the home range.

DISCUSSION

We examined movements of GPS collared mule deer following live recapture and transportation to a central processing facility and compared these movements to pre-recapture movements and to movements of control animals that were not recaptured. Deer exhibited substantially elevated movements immediately following recapture, but these movements either returned to pre-capture levels within a few days post-recapture, or showed differences from pre-recapture movements that were similar to control deer.

The control animals allowed us to tease apart the effects of recapture on mule deer movement rates from natural seasonal behavior. Deer in March elevated their movements post-recapture. March represents a time when much of the winter snow in our study area has melted, and spring green-up is in its early stages, when deer likely have used their fat reserves. This interaction between physiology and changing ecological factors likely drove these increased movements. These changes were seen in both the recapture and temporally overlapping control data highlighting that the changes were ecologically driven. Deer in December slightly decreased their movements after recapture. December is the onset of winter, when forage availability is

declining, snow accumulates, and deer decrease their activity to maintain energy stores (Anderson 1981). Thus, the documented decline in movements in December also likely represents natural seasonal patterns. Although the December control and recapture data were not temporally overlapping prohibiting a quantitative comparison, their trends were similar, supporting this assessment. The presence of control deer enabled us to make these connections; we might otherwise have attributed these changes in movement to capture effects.

To return to their home range after capture, deer typically made long movements, causing elevated movement rates and daily displacements in the first days after recapture. The time after recapture that the deer movement rates began to decline was congruous with the time it took for deer to return to their home ranges. Thus, the major impact of our capture methods on deer, at least in terms of movement behavior, seems to have resulted from being removed from areas with which they were familiar. These findings indicate that mule deer behavior is largely unaffected by our capture methods beyond the first few days after capture, and any subsequent behavioral analyses are unlikely to be influenced by capture.

The capture procedure that we employed (helicopter net gunning followed by transport to a central processing site) is only 1 method used to capture ungulates. However, our results are similar to studies of capture effects on other ungulate species captured using different methods. Neumann et al. (2011) examined behavior of moose that were darted from a helicopter and found that individuals increased movement for a short time period following recapture, though animals in their study were fully chemically immobilized. Neumann et al. (2011) also suggested that movements declined from an elevated level shortly after recapture. Arzamendia and Villa (2012) captured vicunas by herding and also found short-term increases in movements following capture, though they attributed this to pelage loss from shearing increasing thermal stress on

captured animals. Neither of the above studies documented any subsequent depression in movements, but Morellet et al. (2009), working with roe deer (*Capreolus capreolus*) captured by driving deer into nets, and Quinn et al. (2012), working with white-tailed deer (*Odocoileus virginianus*) captured via a variety of ground methods, found decreased activity and decreased movement, respectively, following capture, which they interpreted as acclimation to collars and recovery from capture. Their capture protocols did not involve transport from the capture site, so deer in our study may prioritize returning to familiar areas. Despite the differences in capture protocols, the fact that any capture related effects were short lived in our study indicates that helicopter capture via net gunning does not have long-term effects on mule deer behavior beyond the first few days. Because deer behavior was affected for at least the first day by movement to the processing site, we cannot assess the impact of helicopter capture alone. To our knowledge, no literature has assessed the behavioral impacts of helicopter net gunning and release on site, thus we are unable to compare our findings to attempt to isolate the effect of transport to the processing site. However, movement to a processing site as opposed to release on site is likely to affect deer more heavily, and thus the finding of no substantial impact on deer behavior beyond the first few days indicates that capture and release of deer on site probably has minimal behavioral impacts.

Free ranging wildlife clearly are affected by capture and handling, but the nature of these effects depend on the mode of capture and whether animals are processed on-site or transported elsewhere. In capture efforts such as ours, where a large number of individuals are captured (>40 per day on some days), and technical procedures requiring substantial expertise are required, on-site processing might not be an option. However, the most apparent capture effects were short lived, with deer returning to indistinguishable behavior within as little as a day for some

individuals. We did not assess the impact of multiple captures on mule deer because, although we recaptured some individuals multiple times, the sample size of deer recaptured greater than 2 times was not sufficient to test the effects of multiple captures. Such impacts on behavior might exist, but were not obvious in our sample.

Management implications

Capture and handling is a necessary component of any research or monitoring project requiring the instrumentation of animals. These efforts affect animal behavior and thus must be continually assessed and re-evaluated to ensure the best techniques available are being used, and that capture is not affecting animal welfare or the data being collected. For mule deer being captured with helicopter net gunning and transported to a processing site, removal of the first day of data is strongly suggested, and removing the first 4 days of data will likely control for any impacts due to removal from the home range. If deer are recaptured while wearing a GPS collar, eliminating data up until the deer has returned to its pre-capture home range appears to be sufficient for minimizing any such effects. Alternatively, daily movements could be examined to determine when elevated movements have ceased. Where concerns exist over the potential influence of capture on results, analyses could be performed both excluding and including various amounts of data and results could be contrasted.

TABLES

Table 2.1. Details of groups of captured mule deer used in analyses of capture effects in the Piceance Basin, Colorado, 2008–2012.

Group	Details	Number used in analysis
December control	Randomly captured 2008–2009; fix rate 5 hourly; not recaptured	61
March control	Captured December 2010 or 2011; fix rate hourly or half hourly; not recaptured during March 2011 or 2012	26
December recapture	Captured December 2010 or March 2011; fix rate hourly or half hourly; recaptured December 2011	41
March recapture	Captured December 2010 or 2011; fix rate hourly or half hourly; recaptured during March 2011 or 2012, and December 2011	38

FIGURES
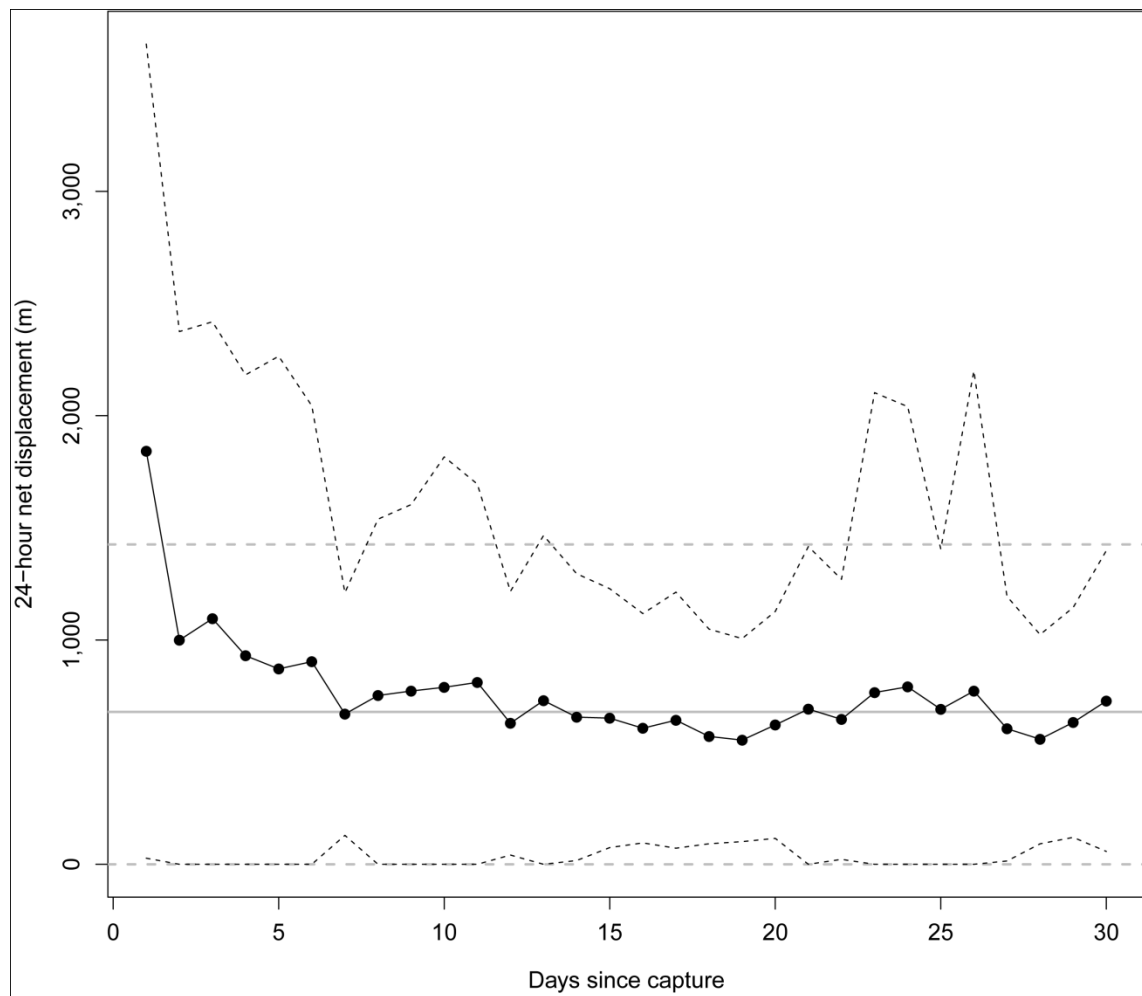
Figure 2.1. Daily displacement (straight line distance between first and last location within each day) as a function of the number of days since recapture for mule deer recaptured in the Piceance Basin, Colorado, 2008–2012. Black lines represent mean daily post-recapture displacement (solid line) ± standard deviation (dashed lines), and gray lines represent overall mean displacement prior to recapture (solid line) ± standard deviation (dashed lines).
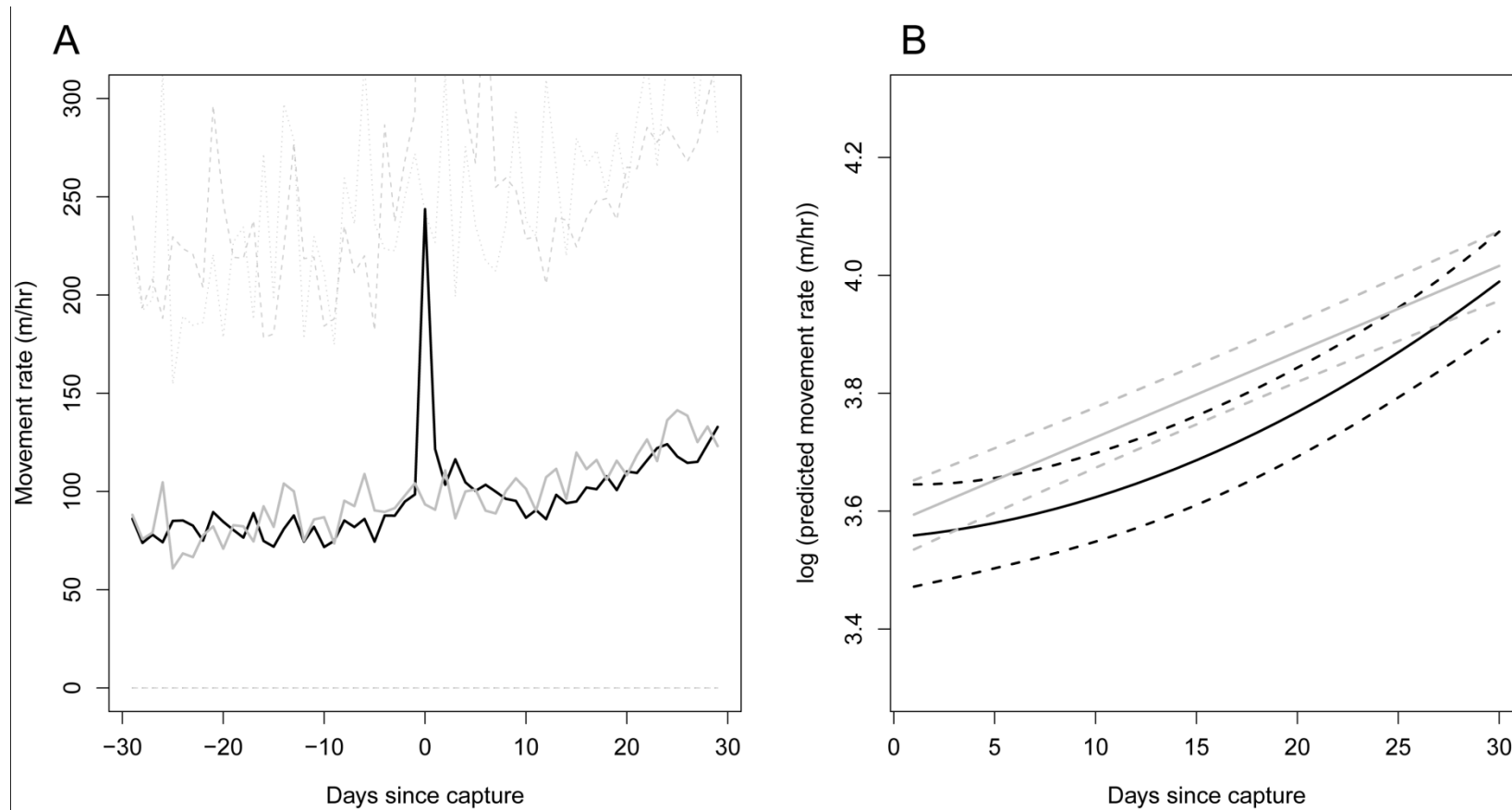
Figure 2.2. (A) Mean movement rates of mule deer in March in the Piceance Basin, Colorado, 2008–2012. Black solid lines represent mean values for recaptured deer and gray for control deer. Dashed lines represent means ± 1 standard deviation for recaptured deer and dotted lines represent means ± 1 standard deviation for control deer. (B) Predicted log movement rates (m/hr) of mule deer in March. Black solid lines represent mean predicted movement rates for recaptured deer and gray for control deer. Dashed lines represent the bounds of 95% credible intervals. For control deer, the number of days since recapture represents the number of days since the mean recapture date.
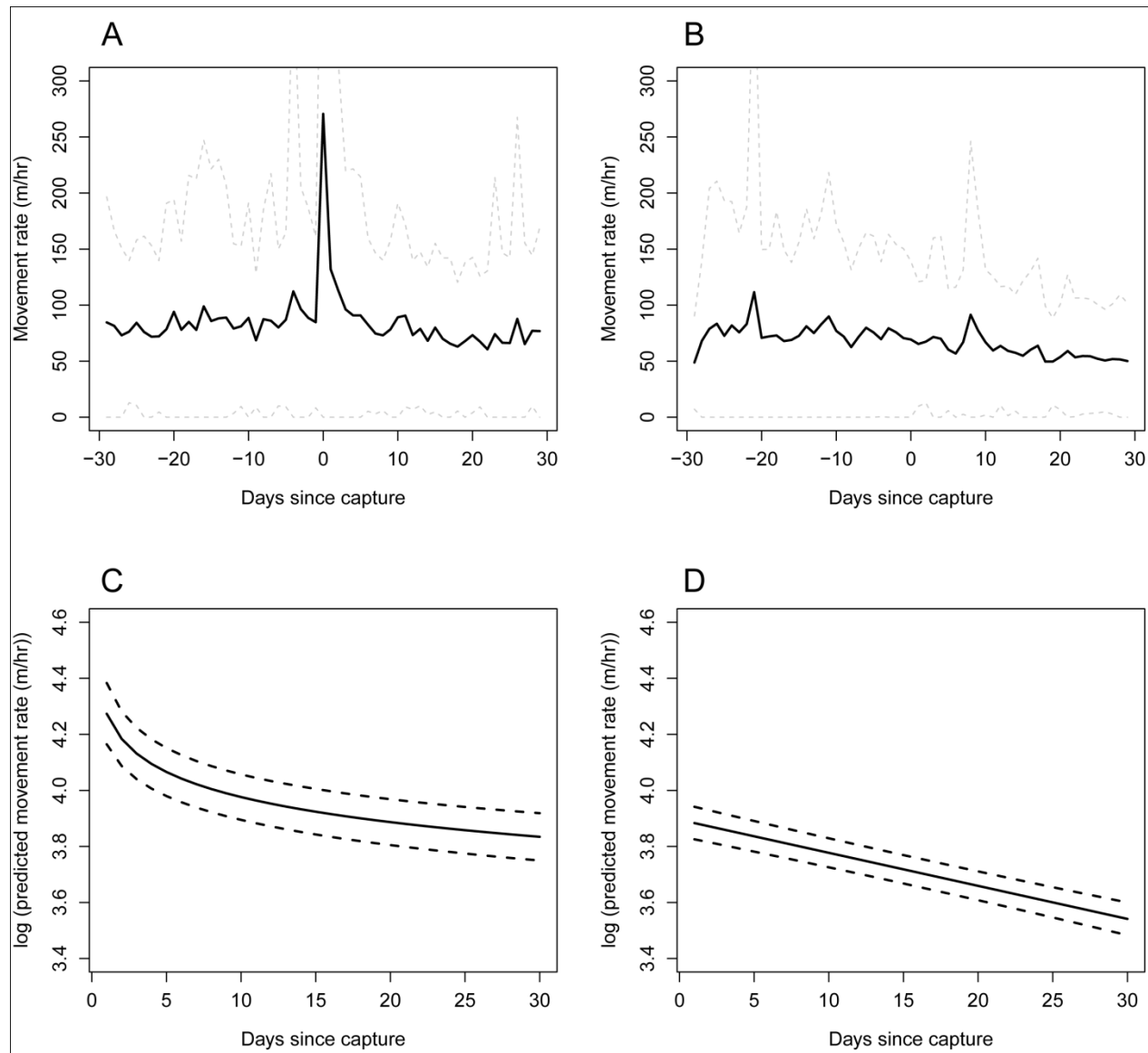
Figure 2.3. December mean movement rates for (A) recaptured mule deer and (B) control mule deer (i.e., deer that were not recaptured) and predicted log movement rates for (C) recaptured mule deer and (D) control mule deer in the Piceance Basin, Colorado, 2008–2012. Solid lines represent mean values and dashed lines represent means ± 1 standard deviation (A and B) or the bounds of 95% credible intervals (C and D). For control deer, the number of days since recapture represents the number of days since the mean recapture date.

CHAPTER THREE

PRACTICAL GUIDANCE ON CHARACTERIZING AVAILABILITY IN RESOURCE

SELECTION FUNCTIONS UNDER A USE-AVAILABILITY DESIGN

INTRODUCTION

Habitat selection is a behavioral process by which animals choose the most suitable locations in

order to maximize fitness (Fretwell and Lucas 1969). Understanding the selection process can

provide insight into population regulation, species interactions, and predator-prey dynamics

(Morris 2003) and thus is fundamental to animal ecology. With advancements in global

positioning system (GPS) radio telemetry and geographic information systems (GIS), the data

required to examine habitat selection patterns of free-ranging animals are increasingly available,

spurring a proliferation of recent studies on this topic.

The most common method for examining habitat selection patterns from GPS radio collar

data is the resource selection function (RSF, see Table 3.1; Manly et al. 2002, Johnson et al.

2006). Resource selection functions typically are fit in a use-availability framework, whereby

environmental covariates (e.g., elevation) at the locations where the animal was present (the used

locations) are contrasted with covariates at random locations taken from an area deemed to be

available for selection (the availability sample; Manly et al. 2002, Johnson et al. 2006). Such

methods are inherently based on models for spatial point processes (as are many species

distribution models; e.g., Warton and Shepherd 2010), however logistic regression, which

asymptotically approximates a point process model (Johnson et al. 2006, Aarts et al. 2012),

typically is used to estimate coefficients (but see Baddeley and Turner 2000, Lele and Keim

2006, Johnson et al. 2008b, and Aarts et al. 2012 for alternate approaches). Logistic regression

allows researchers to easily obtain inference on selection or avoidance of covariates and to

generate maps for use in subsequent analysis (Boyce and McDonald 1999). Such methods have

been used to examine numerous ecological processes and address important management

questions, including the interplay between habitat and dispersal (Shafer et al. 2012), the presence

of ecological traps (Northrup et al. 2012b), and functional responses in wildlife interactions with

anthropogenic development (Hebblewhite and Merrill 2008, Matthiopoulos et al. 2010).

The relative ease of fitting RSFs has made them popular in animal ecology. However,

these methods offer a number of methodological challenges (e.g., Aarts et al. 2008). In

particular, the size and spatial extent of the availability sample can significantly influence

coefficient estimates and subsequent inference (Boyce et al. 2003, Boyce 2006, Warton and

Shepherd 2010). Despite this fact, there is a striking lack of robust guidance for choosing the

availability sample and most applied studies likely are incorrectly sampling availability (Pearce

and Boyce 2006, Warton and Shepherd 2010). Here we illustrate the influence of the availability

sample size and spatial extent on inference from RSFs under the most commonly used sampling

designs, with the goal of offering robust guidance for practitioners. We first review pertinent

literature regarding the availability sample and summarize recognized issues. We then illustrate

the influence of the availability sample on coefficient estimates through simulations and an

empirical analysis of GPS data from mule deer (O*docoileus hemionus*), and provide guidance on

how best to implement robust RSFs.

The use-availability framework and important considerations

For RSFs fit under a use-availability design, the used locations are a realization from the used distribution $f^U(x)$ (see Table 3.1), which can be written as a weighted version of the availability distribution $f^A(x)$ (Johnson et al. 2006, Lele and Keim 2006, Hooten et al. 2013):

$$f^U(x) = \frac{w(x'\beta)f^A(x)}{\int w(x'\beta)f^A(x)\,dx} \tag{1}$$

where x is a vector of environmental covariates, with a corresponding vector of coefficients, β. In this weighted distribution (1), $w(x'\beta)$ is the RSF, and can be interpreted as how the animal selects habitat from $f^A(x)$. The RSF can take a number of functional forms (e.g., probit, logistic; Lele 2009), however Johnson et al. (2006) prove that, provided $w(x'\beta)$ takes the exponential form [i.e., $w(x'\beta) = e^{x'\beta}$], logistic regression can be used to obtain unbiased estimates of β. When using logistic regression, the RSF approximates a spatial point process model and can be interpreted as the expected number of used locations per unit area (Warton and Shepherd 2010, Aarts et al. 2012). Thus, Poisson regression also can be used to obtain unbiased estimates of β in (1), with the dependent variable being the number of used locations within a discrete spatial unit. The intercept in Poisson regression scales the RSF to the number of used locations, but as with logistic regression has no biological meaning (Fithian and Hastie 2012).

The purpose of the availability sample is to approximate the integral in the denominator of (1), and if this sample is too small then the point process model itself is poorly approximated and any inference drawn from the resulting coefficients is incorrect. In determining the size of the availability sample it is the ratio of used to available location that is of paramount importance, with larger ratios providing worse approximations (Fithian and Hastie 2012). Although these factors imply that the availability sample should be as large as possible, there is a

tradeoff between size and computation time, with little guidance on optimal sample size. Manly et al. (2002) suggest sensitivity analyses be conducted to determine the sample size. Several studies have suggested that a minimum of 10,000 locations are required (Lele and Keim 2006, Lele 2009, Barbet-Massin et al. 2012), and Aarts et al. (2012) report that samples of 10,000 locations provide accurate estimates for data simulated from a single covariate. Both Warton and Shepherd (2010) and Aarts et al. (2012) also indicate that regular (as opposed to random) sampling of the availability space can reduce the sample needed to approximate the point process model. Likewise, Fithian and Hastie (2012) show that weighting the availability sample by an arbitrarily large value can accomplish the same. In addition, Barbet-Massin et al. (2012) suggest that the modeling framework (e.g., GLM, GAM or machine learning methods) can influence the number of availability points needed. Despite these suggestions, *ad hoc* approaches to choosing the size of the availability sample appear to be the norm (e.g., 1 point per km2; Hebblewhite and Merrill 2008), and likely under-sample availability, thus poorly approximating the integral in (1) (Warton and Shepherd 2010). However, it is unclear how such under-sampling influences coefficient estimates in a real-world example where researchers assess multiple correlated environmental factors across large landscapes and for multiple individuals.

As with the sample size, the spatial extent over which availability is drawn can substantially influence coefficient estimates and subsequent inference (Johnson 1980, Garshelis 2000, Boyce et al. 2003, Beyer et al. 2010). This extent depends on the scale of inference desired (i.e., 1st, 2nd, 3rd, or 4th order selection; Johnson 1980), and the availability sample must match the scale of inference or there could be strong biases in the interpretation of coefficient estimates (Beyer et al. 2010). This issue has rarely been addressed explicitly from a methodological perspective (but see Beyer et al. 2010). Instead studies typically compare used locations to

availability samples drawn across differing spatial extents (Johnson 1980, Boyce et al. 2003, Boyce 2006), and interpret differences in coefficients as the behavioral response of the animal to habitats at different scales. In most GPS studies, however, animal locations are not independent from one another (i.e., they are autocorrelated), which causes difficulties in inference from RSFs. With the exception of Johnson et al. (2008b) the issue of autocorrelation in habitat selection studies only has been addressed in terms of model assumptions (i.e., independence of errors; Fieberg et al. 2010). When animal locations are sampled at high resolution, the habitat available to be selected also is autocorrelated (Hooten et al. 2013), an issue that has been largely overlooked. Despite this autocorrelation, inference can be obtained at the desired scale through thinning of autocorrelated data, or accounting for autocorrelation explicitly in the model (Hooten et al. 2013). Without proper correction or thinning, comparing used locations to a misinterpreted availability sample (i.e., areas that were not accessible to the animal) complicates the interpretation of coefficients. These coefficients likely represent some mix of a behavioral response to the environmental factors, and noise induced by the distribution of the covariates on the landscape and the movement of the animal (Beyer et al. 2010). The interaction between spatial extent from which availability is drawn, autocorrelation in landscape covariates, and the availability sample size is of critical importance and has not been assessed.

METHODS

We examined the influence of the size and spatial extent of the availability sample on RSF coefficient estimates. Using simulations, we first examined the most common scale of inference in the applied literature: selection of habitat within the home range (3rd order selection; Johnson

1980). Next we examined selection of habitat from within a buffer around each used location (3rd /4th order selection), again using simulation. We also examined the consequences of inaccurately assessing availability in both cases. Finally we examined these scales of selection in an analysis of GPS data from mule deer in the Piceance Basin, Colorado. All analyses herein were conducted in the R statistical software (R Core Team 2012).

3rd order simulation

We simulated used animal locations as an inhomogeneous Poisson spatial point process (IPP) on a true landscape in the Piceance Basin in northwestern Colorado. Locations were simulated as a function of a single environmental covariate (elevation) with $w(x'\beta) = e^{\beta_0 + \beta_1 x}$ across a subset of the study area (here $\beta_1 = 2$, and we varied β_0 to achieve desired used sample sizes). We then drew 1,000,000 random locations across (A) the same spatial extent as the used locations (hereafter the "matched sample") and (B) an area greater than that from which use was simulated (hereafter the "mismatched sample"). The mismatched sample simulates a situation in which what was truly available to be selected by the animal is inaccurately assessed by the researcher. From the larger availability samples, we randomly drew smaller samples ranging in size from 100 to 50,000 (100, 500, 1,000, 2,000, 3,000, 4,000, 5,000, 6,000, 7,000, 8,000, 9,000, 10,000, 30,000, and 50,000) and fit RSFs using logistic regression. We repeated this process 500 times for three different ratios of used to available locations (80, 650 and 3,500 used samples), and calculated the expectation of the coefficient estimator $[E(\hat{\beta}_1)]$ and the 95% simulation envelope.

To assess the interaction between landscape heterogeneity, availability sample size, and spatial extent, we repeated the above analyses on simulated landscapes with varying levels of autocorrelation for a binary and a continuous covariate (see Appendix 3). For the binary

covariate we varied the proportion of the landscape composed of that covariate. We simulated use and fit models as above (with $\beta_1 = 0.5$) for matched and mismatched availability. We calculated the coefficient estimator and 95% simulation envelope for two ratios of use to availability (600 and 6,000 used samples, though only the former for the binary covariate).

3rd/4th order simulation

A common approach to characterizing availability in RSFs entails delineating a buffer around each used location, with the buffer radius determined by the movement of the animal (e.g., the mean Euclidean displacement between locations; Boyce et al. 2003), and assessing availability within each buffer. In this case (1) is then modified such that

$$f_i^{U}(x) = \frac{w(x'\beta)f_i^{A}(x)}{\int w(x'\beta)f_i^{A}(x)\,dx} \qquad (2)$$

where f_i^{A} is the availability distribution for point i. RSFs are fit using conditional logistic regression, with the used points matched to the available points within their respective buffers. To examine the influence of the size of the availability sample on coefficients estimated with this approach, we randomly placed 500 buffers with a 100 m radius (size was chosen arbitrarily) on landscapes simulated with different levels of autocorrelation. We then simulated use as an IPP within each buffer with $w(x'\beta) = e^{\beta_0 + \beta_1 x}$ (a single point was then randomly selected to act as the used location). We then drew 1,000 random locations within each buffer. From this sample we drew availability samples ranging from 1 to 500 points, repeating this process 500 times for each sample size, from which the expectation of the coefficient estimator and 95% simulation envelope were calculated. We repeated this process for a mismatched availability sample, drawn from within a 200 m buffer drawn around the same centroids as above.

Mule deer analysis

We explored the above issues using an empirical dataset from 53 female mule deer captured and fit with GPS radio collars set to attempt a fix once every 5 hours between 2008 and 2010 (C.R. Anderson unpublished data). Though these data arise from a movement process, they are commonly used to fit RSFs, approximating a point process model, and thus all of the same issues apply. We fit RSFs in a use-availability framework separately for each deer, examining a suite of 14 environmental covariates expected to influence deer habitat selection based on preliminary analysis (Appendix 4) and compared 3 approaches for sampling availability. The first two methods were based on home range estimates, where 100,000 random locations were drawn for each animal across both the 100% minimum convex polygon (MCP) and a polygon delineated by buffering all locations for each individual by the mean Euclidean displacement between locations (400 meters), and combining these into a single polygon for each deer. These analyses provide inference at the 3rd order of selection. Aside from controlling for differing availability, we made the assumption that that the GPS locations were independent, following the advice of Otis and White (1999). We next examined location-based availability for a limited number of individuals by buffering each use location by 400 meters and drawing 1,000 random locations within each buffer. For all analyses we extracted and standardized $\left(\frac{x-\bar{x}}{\sigma_x}\right)$ all continuous predictor covariates for every used and available location, and randomly selected subsets of the availability sample; for the MCP and buffered polygon we selected samples ranging from 100 to 50,000 locations, and for the movement buffers between 5 and 500 locations per buffer. We fit RSFs to individual deer using either logistic regression or conditional logistic regression. We repeated this process 1,000 times and recorded the expectation of the coefficient estimator and 95% intervals of the

mean coefficient estimates (i.e., 95% quantiles of the group of all 1,000 $\hat{\beta}$ from the model iterations; note these are not simulation envelopes). For a subset of individuals, we drew 5,000,000 random locations across their MCP and repeated this process, drawing availability samples ranging from 5,000 to 1,000,000 locations.

RESULTS

Simulations

In all matched sample analyses examining 3rd order selection, with true or simulated covariates, coefficient estimates were unbiased and converged to an accurate value at availability samples of 10,000 or less (Fig. 3.1D-F, and Appendix 5). In the mismatched sample analysis, $E(\hat{\beta}_1)$ was consistently biased on the true landscape regardless of sample size and differed substantially between small and large availability samples (Appendix 5). We note that in discussing bias throughout, we are not strictly discussing a statistical bias, as the model is accurately estimating coefficients for the given used and available samples, but rather a bias in inference as results do not reflect the data generating process at this order of selection. With a smaller used sample size, the above issues were less pronounced. In both analyses the simulation envelope was wider with fewer used samples (Fig. 3.1, and Appendix 5). On simulated landscapes, autocorrelation substantially influenced both the bias and the size of the availability sample needed for convergence (Fig. 3.1). For the continuous covariate, when autocorrelation was weak, $E(\hat{\beta}_1)$ was unbiased and converged rapidly, but both bias and the size of the availability sample needed for convergence increased with autocorrelation. This bias is not directly a result of autocorrelation, but rather autocorrelation increases the degree of imbalance between the true and sampled

availabilities in the mismatched sample analysis. Again, a larger availability sample was needed

for convergence with larger ratios of use to availability, and in some cases convergence was not

reached even at very large sample sizes. For the binary covariate, coefficient estimates

converged rapidly. With moderate autocorrelation, estimates were biased but the degree of bias

depended on the proportion of the landscape composed of that covariate (Appendix 3).

Coefficient estimates from RSFs examining $3^{rd}/4^{th}$ order selection converged to a stationary

value at availability samples of 20-100 points per buffer and were unbiased for the matched

sample analysis (Appendix 5). With a mismatched sample, estimates were influenced by

autocorrelation, though bias was only an issue at moderate levels of autocorrelation (Appendix 5)

and estimates converged at similar sample sizes as for the matched sample.

Mule deer analysis

Results varied substantially among individuals and among covariates within individuals. For

many animals, coefficient estimates were highly variable at small availability samples, but

appeared to converge to a consistent value at sample sizes ranging from 1,000 to 10,000

locations, or higher (Fig. 3.2A). However, for many individual and covariate combinations there

were substantial differences between $E(\hat{\beta})$ at small sample sizes and the value to which it

eventually converged (Fig. 3.2B-C). For a few individuals, coefficient estimates did not converge

until extraordinarily large availability samples were used (Fig. 3.2B). These patterns often were

not consistent among covariates within the same individuals, and appeared to be a function of the

individual and covariate combination (though for some individuals these issues persisted across

covariates). In addition, these results were not consistent between availability samples drawn

from the MCP and the buffered polygon. When examining $3^{rd}/4^{th}$ order selection coefficient

estimates were consistent at samples of 20 points per buffer or greater (Fig. 3.2D). We found no cases of extreme differences in $E(\hat{\beta})$ between small and large availability samples as seen in the 3rd order analyses. In addition, the scale of the conditional analysis limited inference to those covariates that the deer interacted with locally, but reduced or eliminated our ability to make inference on interactions at a larger scale (e.g., broad avoidance of a covariate).

DISCUSSION

It has long been recognized that the definition of the availability sample is critical when estimating RSFs in a use-availability framework (Johnson 1980, Manly et al. 2002). However, to date there has been little formal assessment of how coefficient estimates are influenced by the size of this sample, with examinations of spatial extent set in a biological rather than a methodological context (but see Beyer et al. 2010). Thus, there is little guidance for researchers using these methods. Our results indicate that both factors must be carefully considered to avoid analytical and interpretive biases.

The availability sample must be large enough to avoid significant numerical integration error. If a sufficiently large sample is not used then the model does not accurately approximate a point process model, and any inference is compromised. However, a sufficient size is dependent on the animal, the covariates, the ratio of use to availability, and an accurate representation of what is available to the animal. In simulations with matched samples, coefficient estimates were similar at all availability sample sizes and relatively few locations were needed for estimates to converge (<10,000 3rd order analysis, and <100 per buffer for 3rd/4th order analysis). In simulations with a mismatched sample, more locations were needed for convergence in the 3rd

order analysis, but the expectation of the coefficient estimators were biased at all sample sizes and differed substantially between small and large samples.

Attributes of the environmental covariates heavily influenced the interpretational bias of coefficient estimates, but these factors were related to the scale of inference. At the 3rd order, bias was evident for covariates with moderate and high spatial autocorrelation. This issue was only present with moderate autocorrelation when examining the $3^{rd}/4^{th}$ order, with almost no bias at the highest levels of autocorrelation. Autocorrelation induces bias because a mismatch in true and sampled availability in geographic space leads to an imbalance in parameter space. Thus, the level of imbalance appears to result from an interaction between the autocorrelation structure and the extent over which availability is sampled. With the $3^{rd}/4^{th}$ order analysis the spatial extent is such that the imbalance was greatest at moderate levels of autocorrelation, likely relating to the size of the covariate patches relative to the extent of the availability sample. With increasing buffer sizes in this analysis, similar bias likely would occur at higher autocorrelation.

In the deer analysis, estimates often differed substantially between small and large availability samples, but more locations typically were needed for convergence than in simulations. The results of the deer analysis paired with those from the mismatched simulations point to a likely inaccurate assessment of what was available to the animal at the 3rd order, with unclear results for the $3^{rd}/4^{th}$ order (i.e., neither the simulations nor the deer analysis exhibited large differences between coefficient estimates at small and large availability samples). Thus, it is possible that an interpretational bias resulted from incorrectly assessing what was available to be selected by the deer. Beyer et al. (2010) suggest that in such cases the term preference should be used in place of selection to highlight that the behavioral process has not been captured. We agree that some differentiation is needed and our results provide some guidance for conditions

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that are likely to cause a mismatch between the scale of availability and the scale of desired inference (e.g., autocorrelation, and small ratios of use to availability; however we note that these results appear highly context and individual dependent). Although $3^{rd}/4^{th}$ order analyses appear to provide less bias between small and large availability samples, we caution that location based analyses can be more computationally intensive and limit inference regarding interactions that occur at a larger scale than that of the movement process (i.e., avoidance of covariates at the 3rd order will not be captured). In addition, because the spatial extent of availability is reduced with this method, there can be little variation within certain environmental variables leading to high multicollinearity and an ill-posed model. More sophisticated methods for assessing selection and behavior exist that can address the issues described here, including movement-based RSFs that account for temporal autocorrelation (e.g., Johnson et al. 2008b, Hooten et al. 2010, Hooten et al. 2013), hierarchical methods providing robust population-level inference (Duchesne et al. 2010), and methods that explicitly account for the influence of availability (Matthiopoulos et al. 2011). We note that these methods require advanced statistical knowledge and do not guard against interpretational bias.

The results of our analyses highlight the myriad of issues that can influence coefficient estimates in RSF analysis, but the question of the degree to which inference is impacted remains. For studies that use RSFs to strictly draw inference from resulting coefficients, it seems clear that there is the potential for interpretational bias, likely exacerbated by high serial autocorrelation in telemetry locations. However, RSFs often are used solely to produce maps for subsequent analysis or for use in management (Boyce and McDonald 1999, Northrup et al. 2012b, Shafer et al. 2012). Often, such maps are categorized into broad bins and cross validated or validated with

other data (Johnson et al. 2006). In these cases, small biases might have little impact on the

resulting map, particularly if validations indicate a highly predictive surface.

Practical guidance and conclusions

While our results highlight numerous issues that can affect inference from RSF analyses, they

also offer guidance. (1) Most critically, a sufficiently large availability sample must be used. If

this sample is insufficient, then logistic regression does not approximate the point process model

as intended, and no faith can be put in coefficient estimates. A sensitivity analysis of the

availability sample size at the spatial extent of interest should be included in any RSF analysis.

Such assessments could follow the methods presented here, and those suggested elsewhere (e.g.,

Manly et al. 2002, Warton and Shepherd 2010, Aarts et al. 2012) where multiple samples of

varying sizes are tested until coefficient estimates converge.

(2) Provided a sufficiently large sample will be used, how availability is drawn depends directly

on the desired scale of inference. Once this is determined, accurately defining what is available

to the animal and matching the scale of availability to the desired scale of inference is paramount

in studies aimed at obtaining inference on selection behavior. Such definitions are difficult to

obtain, thus, when examining serially autocorrelated GPS data, multiple scales of availability

should be considered and knowledge of the system in question will be critical in interpreting

responses across scales. However, we note that inference is likely prone to bias, which can vary

across covariates relative to differences in autocorrelation structure, and coefficients might not

represent the behavioral process (Beyer et al. 2010).

(3) Where bias in inference is likely, behavioral interpretation should be avoided. In such cases,

mapping applications validated with other data are still useful (Shafer et al. 2012).

(4) Extremely large availability samples will be needed in some systems, which may add computing time, thus researchers will need to decide what level of consistency is desired, assess selection at a different scale, or identify and remove problem individuals (i.e., those for which convergence failed). Otherwise, methods such as regular sampling of availability, or weighting of the availability sample could be explored (Aarts et al. 2012, Fithian and Hastie 2012).

The fields of animal movement and habitat selection are evolving at a rapid pace due to vast improvements in data collection. Analyses of these data increasingly are being used in resource management decision making and planning, making robust analysis and inference critically important. With such an ever-evolving field that has potential societal implications, the need to continually assess methods and assumptions is paramount.

TABLES

Table 3.1. Terms used in RSF analysis and their definitions, adapted from Manly et al. (2002), Johnson et al. (2006), Lele and Keim (2006), Beyer et al. (2010), and Aarts et al. (2012).

Term	Definition
Habitat	The set of biotic and abiotic factors characterizing the space an animal inhabits. In RSF analysis, a set of environmental covariates at discrete locations in space, meant to approximate these factors.
Use	The exploitation of habitat to meet a real or perceived biological need. In RSF analysis, the presence of an animal at a location.
Used distribution	The probability density functions for all animal locations over a specific time period. $f^U(x)$ in the weighted distribution.
Used sample	A measured subset of the used distribution.
Availability	The amount and configuration of habitat over an area of interest.
Availability distribution	The probability density function of all locations available to be selected over an area of interest. $f^A(x)$ in the weighted distribution.
Availability sample	A measured, user-defined subset of the availability distribution (used to approximate the integral in the weighted distribution (1)).
Selection	Use disproportionate to availability.
Resource selection function (RSF)	Any function proportional to the probability of selection of habitat. $w(x'\beta)$ in the weighted distribution.
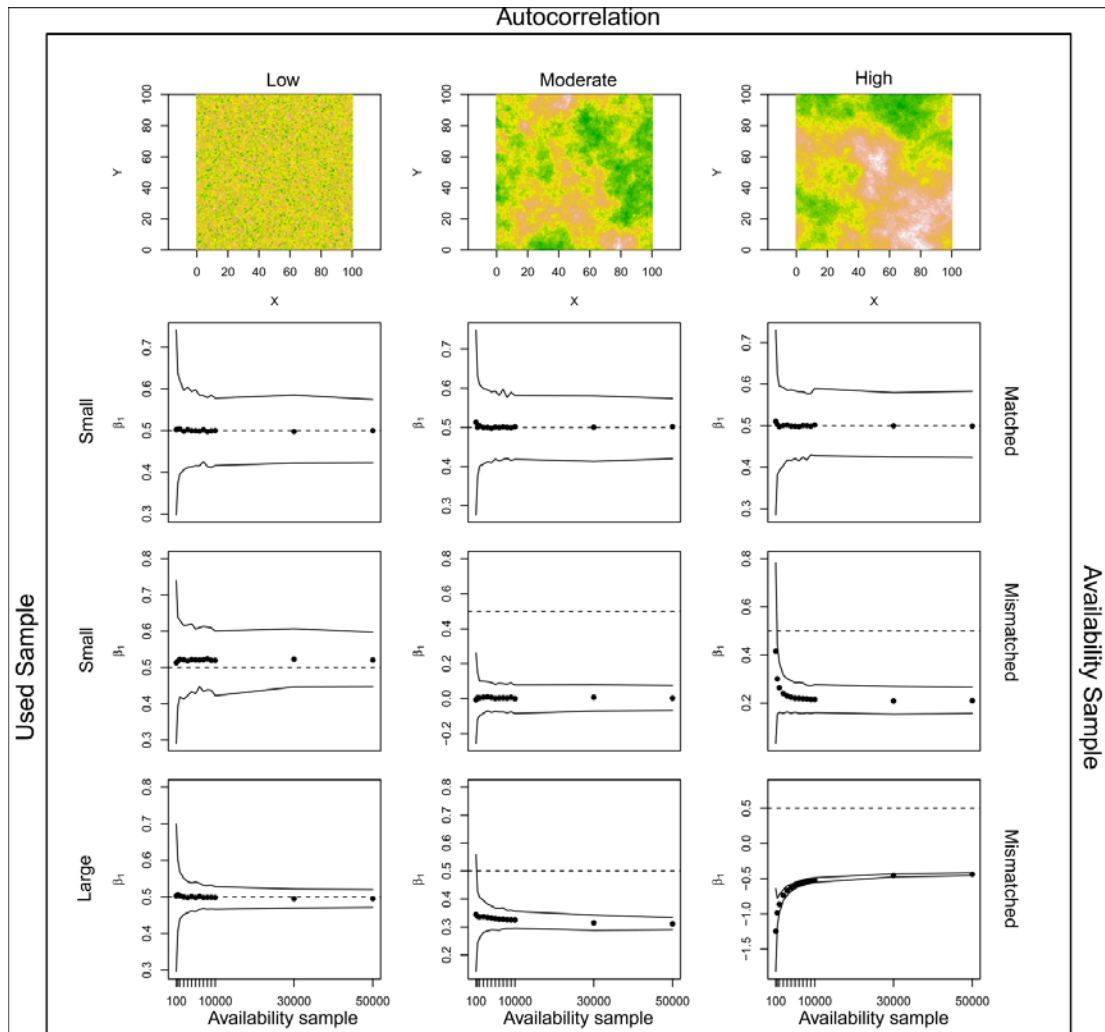
Figure 3.1. Continuous landscape covariates simulated as a Gaussian random field with low ($\phi = 0.001$), moderate ($\phi = 10$) or high ($\phi = 100$) autocorrelation, and expectations of the coefficients (black points) and 95% simulation envelopes (solid lines) from 500 RSF model iterations as a function of availability sample size, with matched or mismatched availability compared to small (600) or large (6,000) used sample sizes. Dotted lines represent the value used for simulation. Models were fit with logistic regression in all cases.
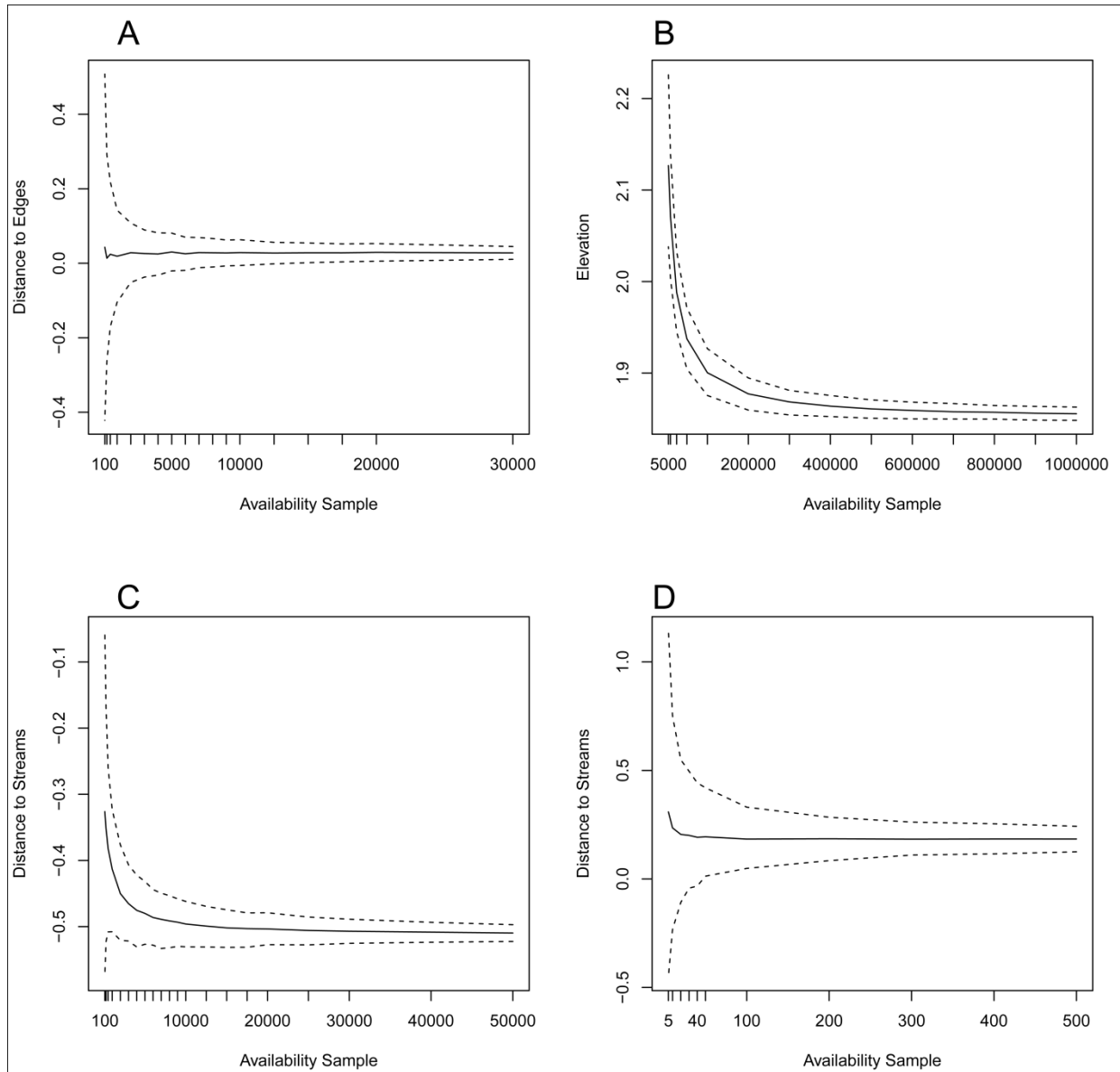
Figure 3.2. Expectation of the coefficients (solid line) and upper and lower 95% intervals (dashed lines) of mean coefficient estimates from 1,000 RSF model iterations as a function of availability sample size, for distance to edges for deer 10 (A) for elevation for deer 62 (B), and for distance to streams for deer 2 (C and D). In A availability was drawn from the buffered polygon, for B and C it was drawn from the MCP, and for D it was drawn from buffers around each location. Models were fit with logistic regression for A-C and with conditional logistic regression for D.

CHAPTER FOUR

IDENTIFYING THRESHOLDS IN HUMAN IMPACTS TO WILDLIFE: HYDROCARBON

DEVELOPMENT ALTERS SPATIAL AND TEMPORAL PATTERNS OF HABITAT

SELECTION IN MULE DEER

INTRODUCTION

Ecological theory predicts that animals distribute themselves across landscapes by selecting

habitats for foraging and resting that maximize their fitness (Fretwell and Lucas 1969).

Examinations of habitat selection provide insight into individual-based ecological processes

(e.g., drivers of site fidelity; Switzer 1997, and tradeoffs between foraging and predation risk;

Creel et al. 2005), but also to larger scale factors influenced by population distribution and

abundance (e.g., speciation; Rice 1987, population dynamics; Pulliam and Danielson 1991, and

dispersal; Shafer et al. 2012). Understanding drivers of habitat selection is fundamental to

ecology, and critical to the management and conservation decision-making process in the face of

global habitat loss and alteration.

Human disturbance can alter habitat selection patterns of animals (e.g., Sawyer *et al.*

2006), but the nature of this response and subsequent ramifications for species is complex.

Humans can cause large-scale displacement of animals, leading to functional habitat loss

disproportionately greater than the area that is directly disturbed (Sawyer *et al.* 2006). Responses

also can be more nuanced, with humans being perceived as akin to predators, driving behavioral

shifts reflecting the tradeoffs between security and other demands such as foraging or

reproduction (Frid and Dill 2002, Hebblewhite and Merrill 2008). Alternatively, animals can be attracted to human developments due to associated resources, or as protection against predation (Berger 2007). This attraction can positively impact animals, but can lead to greater potential for negative encounters with humans (Johnson et al. 2004a) and the formation of ecological traps (e.g., Northrup et al. 2012b). In light of the array of complex responses of animals to human disturbance, research on the mechanisms underlying impacts are critical for developing appropriate mitigation measures.

Over the last decade, Western North America has seen a rapid increase in hydrocarbon (oil and natural gas) exploration and production on public lands (United States Energy Information Administration [USEIA] 2012). This landscape-level disturbance can have a number of negative impacts on animals, detailed information of which is needed to aid in developing mitigation strategies (Northrup and Wittemyer 2013). However, understanding the impact of hydrocarbon development and subsequent mitigation measures is complex as the associated disturbances are spatially variable and temporally dynamic and their cumulative effects not well understood, which can obfuscate animal responses. In light of this complexity, there is a need for more complete information on the ways in which animals respond to development. Specifically, detailed understanding of the distance at which different types of development elicit responses from animals is critical for quantifying habitat impacts and assessing effective mitigation strategies.

During the last decade substantial hydrocarbon development has occurred on mule deer (*Odocoileus hemionus* Rafinesque) winter range, where the species faces acute welfare issues related to decreased access to high quality forage (Parker et al. 1984). Mule deer in western North America experienced major population declines across their range (Unsworth *et al.* 1999)

and recent studies have shown deer to experience alterations of habitat selection patterns and large scale displacement in response to hydrocarbon development (Sawyer et al. 2006, Sawyer et al. 2009a). Obtaining information on the impact of development on deer habitat selection patterns is thus a major management priority throughout areas of the west, as extraction is projected to continue to increase over the next several decades (USEIA 2014).

We fit resource selection functions (RSFs) in a hierarchical Bayesian framework to understand responses of a mule deer population to hydrocarbon development on winter range. Resource selection functions are the most commonly used approach to examine the habitat selection process, but a major methodological and conceptual hurdle to their application is the sensitivity of results to habitat availability definitions (Johnson 1980, Hooten et al. 2013, Lele et al. 2013, Northrup et al. 2013). With technological advances in global positioning system (GPS) radio collars, animal location data are being collected at increasingly fine scales revealing complex temporal autocorrelation structures (Wittemyer et al. 2008, Boyce et al. 2010) that can compound methodological issues related to availability in RSF analyses. Though methods exist for potentially managing this autocorrelation (see Fieberg *et al.* 2010 for a review), approaches for addressing autocorrelation at the scale of the availability sample are limited. Using methods developed in the animal movement literature, Hooten et al. (2013) propose a dynamic movement-based method for determining availability on an individual and location-by-location basis. We apply a similar methodology to address three questions; 1) how does hydrocarbon development (roads and well pads) influence deer habitat selection?, 2) do deer respond to energy development differently at night than during the day?, and 3) at what spatial scale do mule deer most strongly respond to different development features? Our results provide insights into the spatial and temporal factors influencing mule deer habitat selection and the influence of

energy development on this behavior. We offer guidance for the mitigation of development impacts on wildlife.

METHODS

Study Area

We examined mule deer habitat selection on winter range in the Piceance Basin in Northwestern Colorado, USA, (39.954 degrees N, 108.356 degrees W; Fig. 4.1), during a time of ongoing production of natural gas. Deer in this area migrate from high elevations during the summer to low elevation winter range, with winter range occupancy generally occurring between October and May (Lendrum et al. 2013, Northrup et al. 2014b). The area is topographically diverse and dominated by sagebrush (*Artemisia tridentata* Nutt.) and a pinyon pine (*Pinus edulis* Engelm.) and Utah Juniper (*Juniperus osteosperma* Torr.) shrubland complex. The vegetation of the area is described in detail by Bartmann & Steinert (1981) and Bartmann, White & Carpenter (1992). The dominant human activity in the area is natural gas extraction, with winter cattle grazing occurring primarily in the valley bottoms. The area is popular for hunting during the fall, and experiences warm, dry summers and cold winters, with the majority of moisture resulting from snow melt in the spring.

Mule deer data

We monitored adult (>1 year old) female mule deer on their winter range between January 2008 and December 2010. Deer were captured using helicopter net gunning and were fit with store-on-

board global positioning system (GPS) radio collars (G2110D, Advance Telemetry Systems, Istanti, MN, USA and model 4400, Lotek Wireless, Newmarket, ON, Canada) programmed to attempt a relocation once every 5 hours. All procedures were approved by the Colorado State University (protocol ID: 10-2350A) and Colorado Parks and Wildlife (protocol ID: 15-2008) Animal Care and Use Committees. Collars were equipped with timed release mechanisms, set to release after 16 months, at which point collars were recovered, and data were downloaded. Due to the potential behavioral impacts of capture on mule deer (Northrup et al. 2014a), we censored all data for one week following capture. Deer in this area are migratory so we only included data occurring between the termination of fall migration and the initiation of spring migration. Migration termination and initiation were estimated visually in ArcMap 10 (Environmental Systems Research Institute, Redlands, CA, USA). We removed all locations for which the positional dilution of precision (PDOP) was >10 (<1% of locations; D'eon and Delparte 2005, Lewis et al. 2007). We calculated the percent of successful GPS fixes for each individual by dividing the number of total locations by the number of attempted fixes. Overall fix success rate was 93%, which exceeds the threshold commonly used to indicate the need for habitat-bias corrections in habitat modeling (Frair et al. 2004, Hebblewhite et al. 2007). Lastly we divided locations into night and day, with night classified as the time between sunset and sunrise (http://aa.usno.navy.mil/data/docs/RS_OneYear.php).

Predictor variables

We chose a set of covariates for RSF modeling that we hypothesized to be important predictors of deer resource selection based on previous studies (Pierce et al. 2004, Sawyer et al. 2006, Sawyer et al. 2009a, Stewart et al. 2010). We downloaded the location of all oil and natural gas

wells in the study area from the Colorado Oil and Gas Conservation Commission website (cogcc.state.co.us), which maintains a daily updated database of the locations, drilling onset date and drilling completion date of oil and natural gas wells throughout the state. We classified each well in our study area into one of three classes; 1) wells actively being drilled, 2) wells that were actively producing natural gas with no drilling activity, and 3) wells that were abandoned (see Appendix 6 for further details). We created a series of time-specific spatial layers representing the status of each well accurate to the day. These layers were generated for the entire time period during which collared deer were active on winter range in the study area (Oct – May of each year). We grouped individual wells by pad visually using a layer for well pads digitized from aerial imagery from the National Agricultural Imagery Program (NAIP). We then classified each pad as a drilling, producing, or abandoned pad for every day of the study period. If a pad had any wells that were being actively drilled, the entire pad was classified as drilling. Likewise, if the pad had both abandoned and producing wells, it was classified as producing.

Using the resulting data, we created different covariates to represent active natural gas development. Our approach consisted of fitting a single model structure with nested concentric buffers around well pads (Table 4.1). Including concentric buffers in the models allows us to identify the distance at which deer ceased to respond to well pads. We created 8 covariates for this model: the number of well pads within 400 meters of well pad edges (*drill_400* and *prod_400*), the number of pads between 400 and 600 meters (*drill_600* and *prod_600*), the number of pads between 600 and 800 m (*drill_800* and *prod_800*) and the number of pads between 800 and 1,000 m (*drill_1000* and *prod_1000*). The smallest buffer distance assessed (i.e., 400 m) corresponded to the approximate mean distance moved between successful relocations spaced 5 hours apart. We initially attempted to assess responses to the number of

pads within 200 meters but convergence failed for both night and day models that included these

covariates after more than 2 million iterations (traceplots showed poor mixing). On closer

examination, this appeared to result from few used deer locations within 200 m of well pads

classified as drilling (23 locations during the night [0.17% of night time locations] and 17

locations during the day [0.11% of daytime locations]). We excluded abandoned pads from

analysis as there was no extraction activity associated with these pads.

In addition to the well pad covariates, we included the terrain variables slope (*slope*), and

elevation (*elev*), calculated from a digital elevation model. We digitized all roads in the study

area from the NAIP imagery and calculated the distance to the nearest road from each location

(*d_rds*). We obtained land cover data from the Colorado Vegetation Classification

Project (http://ndis.nrel.colostate.edu/coveg/). This land cover database has 69 classes, however

our study area is dominated by two classes (44% sagebrush and 39% pinyon-juniper). Thus, we

classified each pixel as treed or open (*tree*). Lastly we calculated the distance to treed edges

(*d_edge*).

Model formulation

We estimated RSFs separately for night and day locations using hierarchical conditional logistic

regression (sensu Duchesne et al. 2010), in a Bayesian framework where all coefficients varied

by individual. In this framework, each used location is paired with a set of random locations

drawn from an area deemed to be immediately available to the animal at that time (Boyce 2006).

Following Revelt and Train (1998), and Duchesne et al. (2010), the probability that an animal

(n) chooses a resource unit (y) represented by a suite of habitat covariates (x_y) from a set of

available alternative resource units ($\boldsymbol{J}$), represented by suite of habitat covariates ($\boldsymbol{x_j}$) at time t can be written as follows:

$$[y_{tn}|\boldsymbol{\beta}_n] = \frac{\exp(\boldsymbol{x}'_{y_{tn}}\boldsymbol{\beta}_n)}{\sum_{j=1}^{J} \exp(\boldsymbol{x}'_{j_{tn}}\boldsymbol{\beta}_n)}$$

Using this probability mass function we can estimate coefficients for each individual and the population as a whole by placing the model in a Bayesian hierarchical framework as follows:

$$\boldsymbol{\beta}_n \sim normal(\boldsymbol{\mu_\beta}, \sigma_\beta^2 I)$$

$$\boldsymbol{\mu_\beta} \sim normal(\mathbf{0}, 1000000I)$$

$$\log(\sigma_\beta^2) \sim normal(0, 1000000)$$

Characterizing availability

In a RSF fit using conditional logistic regression, each used location is paired with random locations sampled within a distance of the used location presumed to be immediately available to the animal (Boyce 2006). There is no standard approach for determining this distance for drawing availability though methods in the literature include using the distance moved between GPS locations (Boyce *et al.* 2003), or drawing from empirical step length and turn angle distributions (Fortin *et al.* 2005). Although such methods clearly have biological underpinnings, few definitions of availability have accounted for the dynamic movement behavior of animals. Contemporary methods developed in the animal movement literature provide new avenues to do so (e.g., Hooten *et al.* 2013). We used the continuous-time correlated random walk (CTCRW) model described by Johnson et al. (2008a) to categorize availability (*sensu* Hooten *et al.* 2013). The CTCRW model describes movement as an Ornstein-Uhlenbeck process, where the velocity of an animal at the current time step is dependent on its previous velocity, an autocorrelation

parameter, and an error term scaled by the time between known locations (Johnson et al. 2008a). Hooten et al. (2013) use the results of the CTCRW model to characterize resource availability as the predictor distribution for the location and velocity of an animal at any time, which is a description of the uncertainty in the location at the current time given all preceding data.

We fit the a CTCRW model for each individual animal using the 'crawl' package (Johnson et al. 2008a) in the R statistical software (R Core Team 2013). The coordinates of a set of random locations were drawn from the predictor distribution for each used location. To ensure a sufficiently large availability sample (Northrup *et al.* 2013), we explored the stability of covariate estimates from models fit to varying availability sample sizes (5, 25, 50, 100, 250, 500 and 1,000 random locations per used location). Drawing from a set of 10,000 random locations per observed location, we ran 25 models at each availability sample size to examine variation in coefficient estimates as a function of the availability sample. Once the sample size that provided stable covariate estimates had been determined, we drew a single sample of that size for each individual for the hierarchical model described above.

Model fitting

Using the model formulation and data described above, we fit models to deer locations across all years. We first standardized all continuous predictor covariates $\left(\frac{x-\bar{x}}{\sigma}\right)$. We tested for correlations among covariates that appeared in the same model (Appendix 7) to ensure that no covariates were highly correlated ($|r| > 0.7$). Using the Bayesian hierarchical framework described above, we fit RSFs using a Markov-Chain Monte Carlo (MCMC) procedure written in the R programming language. We ran 2 parallel chains for each model for 1,000,000 iterations, discarding the first 100,000 as burn-in. We selected starting values for each parameter chain that

were expected to be overdispersed relative to the posterior distributions and monitored convergence to the posterior distribution by examining traceplots of MCMC samples against iterations to determine if there was proper mixing, and by calculating the Gelman-Rubin diagnostic (mean values < 1.1 indicate convergence; Gelman and Rubin 1992). In addition to fitting the single model structure discussed above, we also fit a set of models each with a single covariate representing the number of well pads within overlapping buffer distances (see Appendix 7 for more details). One of the most basic assumptions of model fitting is that the model is a faithful representation of the data generating process. One method for testing this assumption in Bayesian modeling is the posterior predictive check, which compares a posterior distribution of predicted data to the true data (see examples in Gelman and Hill 2007). We performed a posterior predictive check for our RSF models by first calculating a posterior distribution of the probability of each available location associated with each used location being selected by the deer. We then calculated the proportion of available locations that were predicted to be selected at a higher probability than the used location to which they were associated. If the model was accurately representing the data generating process than the used location would be predicted to be selected at a higher probability than the majority of the available locations.

RESULTS

Model specifications

We monitored 53 adult female mule deer across 3 years, for a total of 29,083 winter range (Oct – May) locations ($\bar{x}$ = 548.7 locations per deer). Between 250 and 500 available locations per used location were needed to provide sufficiently accurate estimation of coefficients. Upon initiation

of model fitting, 500 locations proved to be computationally infeasible on a high-performance

supercomputer. Thus we included 300 available locations per used location. All parameters

converged to their posterior distribution (i.e., all mean Gelman-Rubin values were less than 1.1).

There were strong similarities to the models fit with concentric buffers and those fit with single

covariates representing the number of pads within overlapping buffers (Appendix 7), thus we

only present results of the concentric buffers analysis. Posterior predictive checks indicated that

the model predicted deer would select the used locations with a greater probability than the

majority of the available locations (Appendix 7).

Ecological drivers of selection

Deer selected open areas over treed areas and areas further from edges during the night, although

during the day, deer selected treed areas over open areas and areas closer to edges (Fig. 4.2). In

addition, deer selected areas closer to roads during the night than during the day (Fig. 4.3).

Throughout the day and night, deer selected areas with steeper slopes and at higher elevations,

though the strength of this selection was higher during the night (Table 4.1, Fig. 4.2). Deer

responses to well pads of both types varied by buffer distance (Fig. 4.4). During both night and

day deer avoided drilling well pads at the 0-400 meter buffer and the 400-600 m buffer. During

the night this avoidance persisted to the 600-800 meter and 800-1,000 meter buffers, but was

relatively weak at the furthest buffer distance. Contrarily, deer showed no avoidance of the areas

600-800 meters and 800-1,000 meters from drilling well pads during the day (Fig. 4.4). During

the day, deer also avoided well pads actively producing natural gas at the 0-400 meter buffer and

400-600 meter buffer, while showing no avoidance of the areas between 600 and 1,000 meters

from these pads (Fig. 4.4). During the night deer displayed mild avoidance of producing well

pads at the smallest distance (0-400 meters), while displaying selection for areas at all other buffer distances (Fig. 4.4).

DISCUSSION

The habitat selection patterns of deer in our system were strongly influenced by hydrocarbon development, with deer displaying both spatial displacement and alterations in temporal behavioral patterns relative to these features. The nature of these responses differed depending on disturbance type, time of day, and the distance from development. Our methodology, which accounted for the dynamic nature of deer behavior in the resource availability sample and ensured the sample was conditioned by time and location, distinguished between responses to different development types and how these responses varied by time of day (night and day). These results advance our understanding of how animals perceive and adjust their behavior to minimize exposure to human disturbances, offering important insight for measures to mitigate the impacts of hydrocarbon development.

The drilling stage of development elicited the strongest response by deer in our system. Deer strongly avoided areas within 600 meters of well pads with active drilling at all times, and this avoidance persisted out to 1,000 meters at night (with strongest responses within 800 meters). During both times, the strength of avoidance of drilling well pads increased as distance decreased, with essentially no locations falling within 200 meters of these pads. Sawyer, Kauffman & Nielson (2009a) also documented a greater avoidance of active drilling than other developments by mule deer, indicating that this activity is the predominate stressor during hydrocarbon development. Thus, measures aimed at mitigating impacts from drilling, such as

seasonal drilling stipulations, sound and light barriers, and approaches to reduce truck traffic, are likely to have the greatest benefit to deer.

The other development infrastructure (i.e., roads and producing pads) altered deer behavior, but to a lesser extent. Deer avoided the areas closest to both of these development types to some degree, but the strength and scale of the responses varied between night and day, with stronger avoidance during the day when deer also selected areas with greater vegetative cover. It appears deer temporally modulate their behaviors so as to avoid these features during the most disturbing times of day (e.g., in relation to circadian traffic pulses). Dzialak *et al.* (2011a) documented a similar pattern for elk in a natural gas field, with animals subject to disturbance selecting "security cover" more strongly during the day. This behavior might be a common response by mobile wildlife to disturbance that has any type of temporal signature (e.g., roads; Northrup et al. 2012a).

Understanding the spatial scale at which wildlife behavior is impacted by human disturbance is critical for developing effective mitigation strategies and quantifying the human footprint of development on natural systems. Our analysis design, examining selection or avoidance of concentric buffers around development, allowed us to identify the threshold distance where avoidance ceased. Deer displayed complete avoidance of areas within 200 meters of well pad edges (approximately 2% of the severe winter range used by deer in our study). This distance should be considered the minimum at which indirect habitat loss occurs. However, reductions in use were demonstrated to a distance of at least 800 meters around drilling pads at night, and 600 meters around producing pads during the day. These distances equate to greater than 20% of the severe winter range being impacted by producing pads (area within 600 m) and 2% by drilling pads (area within 600 m; the density of drilling pads is much lower in the study

area), during the day, with 6% impacted by producing pads (area within 200 m) and 6% by

drilling pads (area within 800 m) during the night. In addition, 28% of the severe winter range

fell within 100 m of roads (the area avoided strongly by deer during the day) and 15% fell within

50 m of roads (the area avoided by deer during the night). Although these values do not equate to

complete habitat loss, they do indicate that more than half of the severe winter range was

impacted by development during the day, and more than one quarter of the range was impacted

during the night. The costs of this reduction (avoidance by deer) likely include the time lost

during travel or from foraging in suboptimal areas during times of high human activity (Lima

and Dill 1990, Creel and Christianson 2008), both of which can have impacts on condition and

ultimately reproductive success (Houston et al. 2012). It is important to recognize that fitness

costs of range avoidance likely are compounded during the winter when deer face a negative

energy balance. The spatial scales of reduced use relative to specific types of infrastructure as

defined in this study should be considered by managers when attempting to develop mitigation

strategies.

In a recent published assessment of mule deer response to natural gas development,

Sawyer et al. (2006) found larger-scale displacement of deer from the area around development

than those reported here. Although our results show similar general behavioral responses (i.e.,

alteration of habitat selection patterns), the scale of displacement in the Piceance was less. This

likely relates to differences in the landscapes between the study areas, where the Piceance system

has substantially greater topographic and vegetative diversity than the open, flat areas in the

Pinedale area of Wyoming where Sawyer et al. (2006) conducted their work. We hypothesize

that the structural diversity of the habitat and topography provide refuge areas for deer in our

system at relatively close proximity to infrastructure that allows them to behaviorally mediate

impacts. Such natural structure that can provide refuge for wildlife should be considered and maintained by managers and developers when planning projects, through spacing of roads and pads to ensure sufficient areas outside the 800 meter buffers around drilling pads and 100 meter buffers around roads.

Management Implications

Oil and gas development is projected to continue to increase on public lands in the United States (McDonald *et al.* 2009). Quantifying the spatial extent of development related impacts to wildlife is critical for appropriately gauging the repercussions of negative impacts and identifying potential mitigation measures, which are critical for sustainable development practices (Northrup and Wittemyer 2013). Deer respond most strongly to drilling (in this study and the Pinedale system). This disturbance is temporary, as human activity declines once drilling is complete and wells begin producing (Sawyer et al. 2009a), providing an opportunity to structure development in a manner that allows refuge habitat during the most acute periods of stress. Many drilling pads in an area, as might occur with rapid development, leads to large functional losses in habitat, apparently driving abandonment of areas by deer (e.g., Sawyer *et al.* 2006). Where development is conducted at lower densities, or in a manner that ensures that sufficient area is left undeveloped (i.e., refuge habitat is maintained), impacts are likely to be reduced. Even where drilling occurs in a manner that provides refuge, consideration of the spatial structure of the final footprint of roads, producing wells and facilities is critical in order to ensure adequate space for deer to structure their behaviors in a manner that mitigates negative impacts during the late stage production phase. Coupling spatial patterning of the permanent footprint with approaches that reduce human activity at these areas, such as remote liquid gathering

systems, will reduce the amount of disturbance (e.g., Sawyer et al. 2009a) and subsequently any

negative impacts. Contrasting results from the Piceance Basin and Pinedale provides insight to

features that allow deer to behaviorally mediate disturbance (though this should not be construed

as eliminating all negative impacts; Lima and Dill 1990), though the exact nature of these

components in different systems requires more rigorous examination. Therefore, it is critical for

future studies to identify thresholds to gain better understanding of the disturbance-habitat

relationship and ensure sustainable development in areas with sensitive wildlife.

TABLES

Table 4.1. Covariate names, median (med.) posterior coefficient values and proportion (prop.) of posteriors above and below 0 for resource selection function models fit to GPS data from female mule deer in the Piceance Basin, Colorado, USA during the night and day separately.

Covariate	Night med.	Night Prop. < 0	Night Prop. > 0	Day med.	Day Prop. < 0	Day Prop. > 0
d_edge	0.11	0.00	1.00	-0.17	1.00	0.00
slope	0.17	0.00	1.00	0.05	0.01	0.99
elev	0.91	0.00	1.00	0.69	0.00	1.00
d_rds	-0.35	1.00	0.00	0.17	0.00	1.00
d_rds^2	-0.43	1.00	0.00	-0.30	1.00	0.00
tree	-0.27	1.00	0.00	0.08	0.01	0.99
prod_400_2	-0.06	0.71	0.29	-0.41	1.00	0.00
drill_400_2	-0.73	0.99	0.01	-0.82	1.00	0.00
prod_600_2	0.08	0.19	0.81	-0.14	0.98	0.02
drill_600_2	-0.40	0.96	0.04	-0.28	0.99	0.01
prod_800_2	0.12	0.03	0.97	-0.04	0.77	0.23
drill_800_2	-0.27	0.95	0.05	0.00	0.49	0.51
prod_1000	0.07	0.05	0.95	0.02	0.29	0.71
drill_1000	-0.09	0.78	0.22	0.04	0.29	0.71
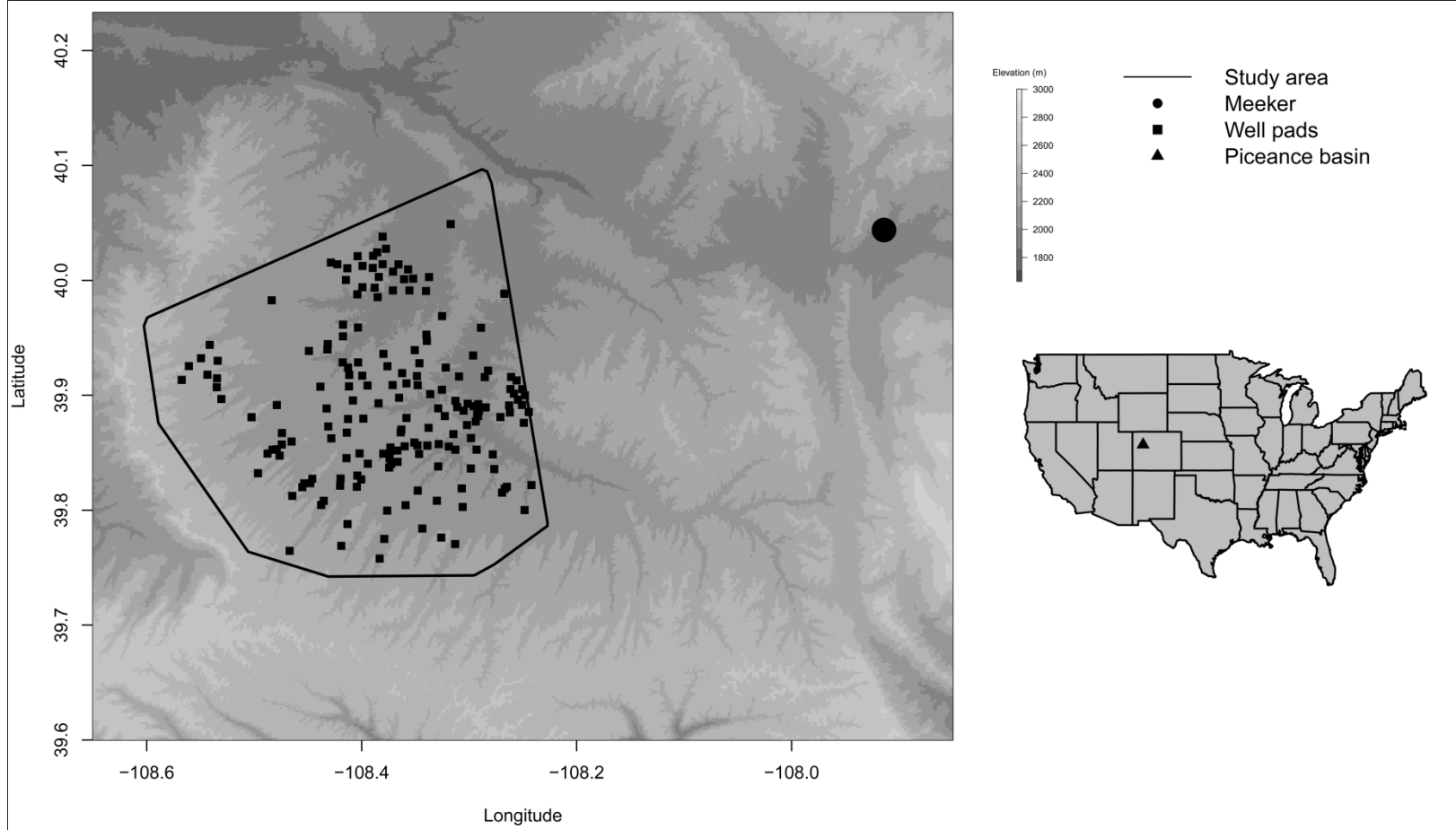
Figure 4.1. Location of study area in the United States, and outline of winter range study area used by female mule deer in the Piceance Basin in Northwest Colorado
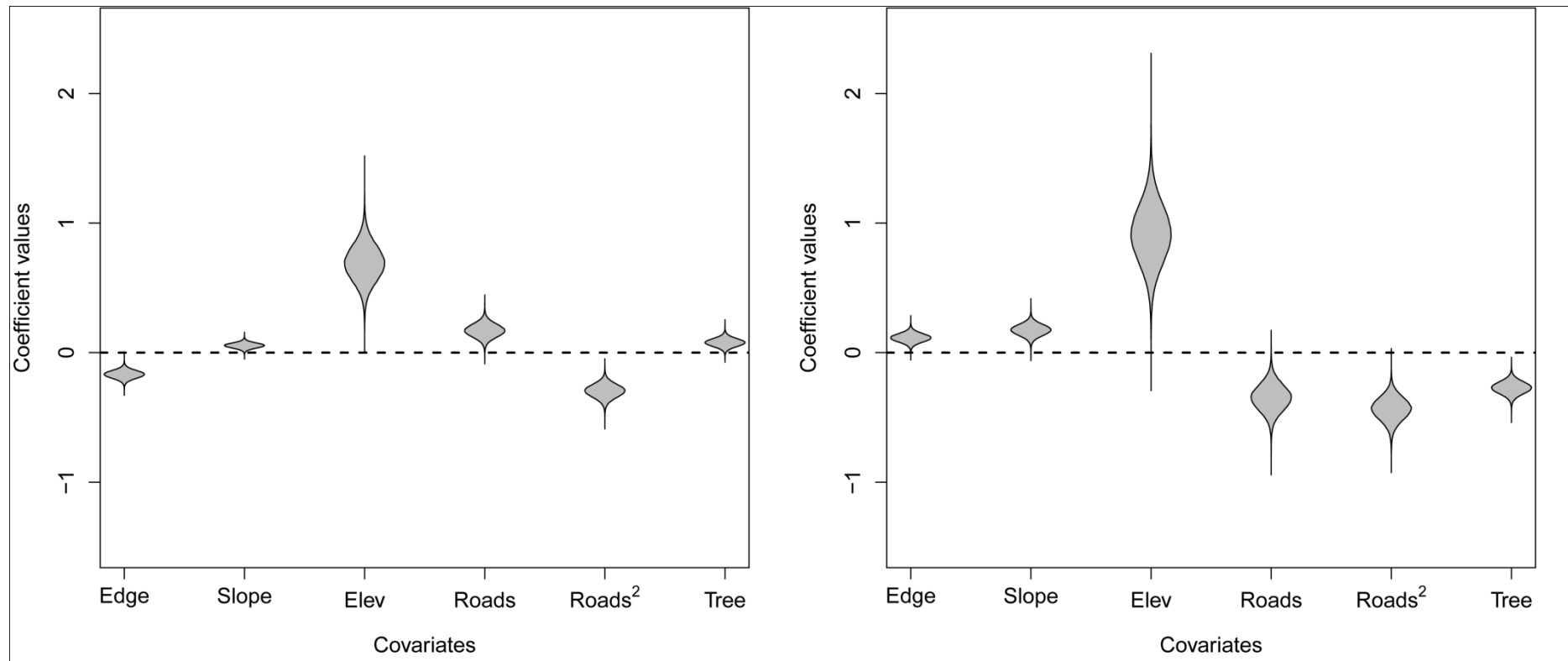
Figure 4.2. Posterior distributions of population-level coefficients for RSF models during the (A) day and (B) night for 53 female mule deer in the Piceance Basin Northwest Colorado. Dashed line indicates 0 selection or avoidance of the habitat features. Displayed coefficients are for non-well pad covariates only, but are taken from models including well pad covariates. 'Edge' refers to the distance to treed edges in meters, 'Slope' was measured in degrees, 'Elev' refers to elevation in meters, 'Roads' refers to the distance to roads in meters, and 'Tree' refers to treed landcover.
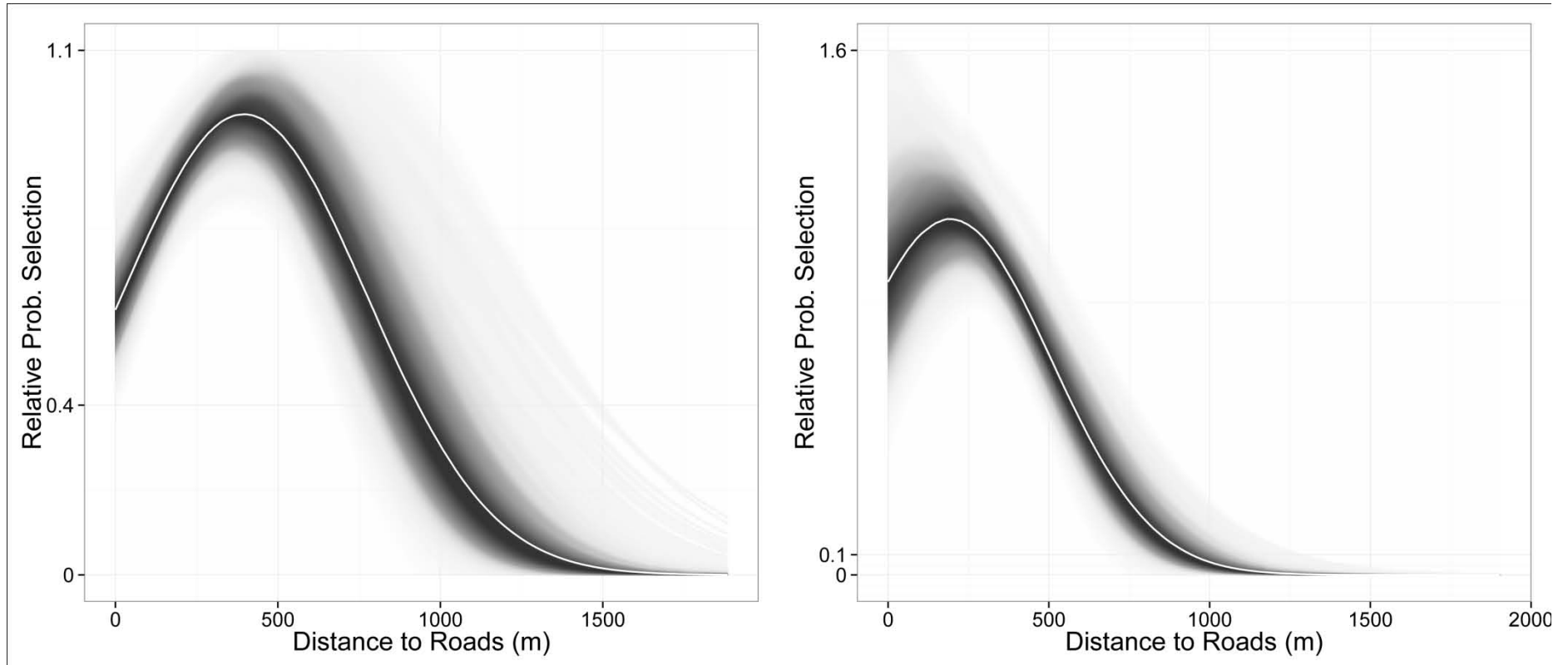
Figure 4.3. Posterior distributions of population-level coefficients related to natural gas development for RSF models during the (A) day and (B) night for 53 female mule deer in the Piceance Basin Northwest Colorado. Dashed line indicates 0 selection or avoidance of the habitat features. 'Drill' and 'Prod' refer to well pads where there was active drilling or not, respectively. The numbers following 'Drill' or 'Prod' represent the concentric buffer over which the number of well pads was calculated (e.g., 'Drill 600' is the number of well pads with active drilling between 400 and 600 meters from the deer location).
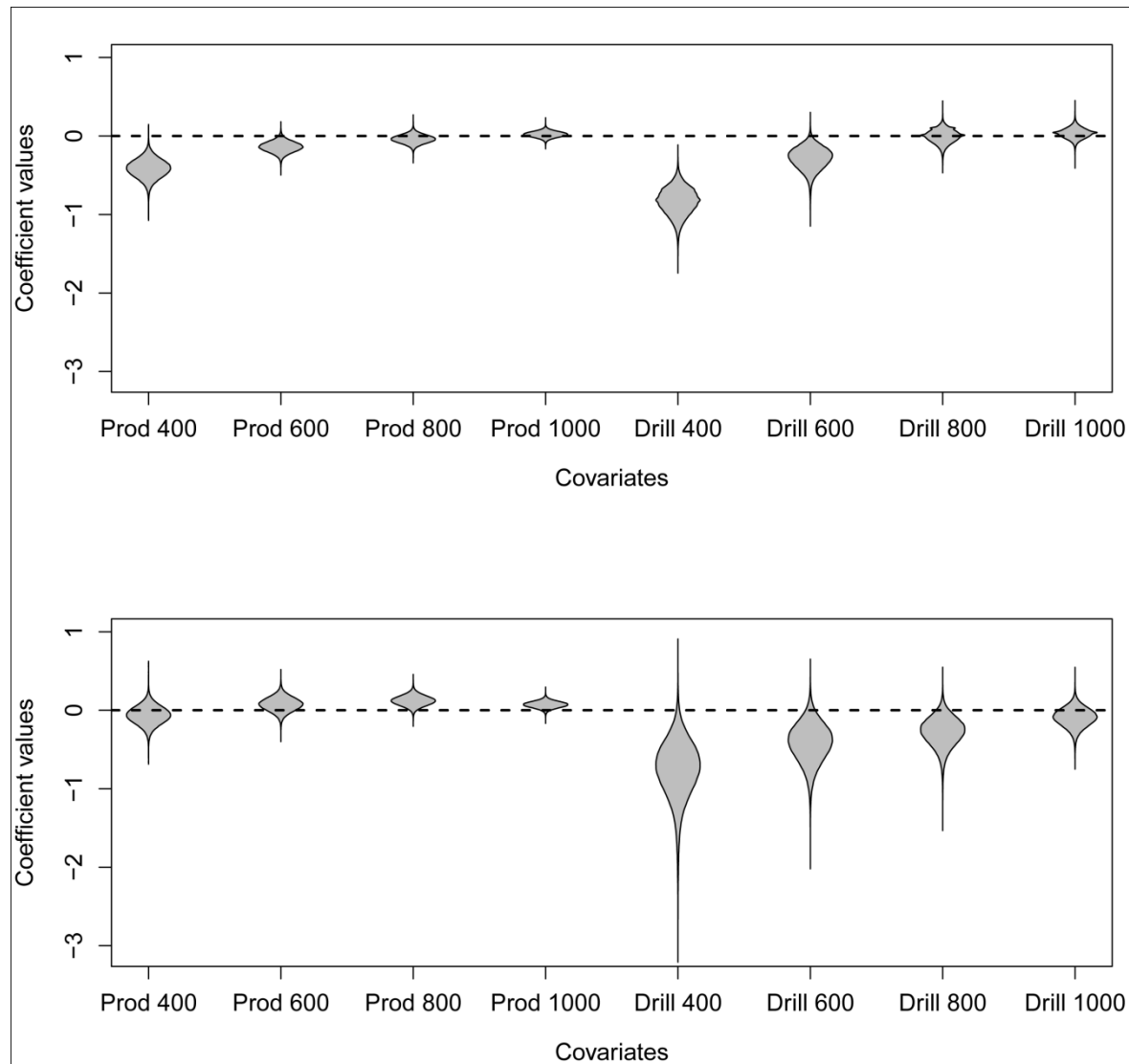
Figure 4.4. Posterior distribution of predicted selection as a function of distance to roads from resource selection functions models fit to data during the (A) day and (B) night for 53 female mule deer in the Piceance Basin Northwest Colorado.

CHAPTER FIVE

ENVIRONMENTAL DYNAMICS AND ANTHROPOGENIC LANDSCAPE CHANGE

ALTER PHILOPATRY AND RANGE SIZE IN A NORTH AMERICAN CERVID

INTRODUCTION

Animals restrict their movements within a given area, or home range (Burt 1943). This range must contain all of the requisite resources for survival and reproduction during a given period and thus information on the dynamics and drivers of range-use provide valuable insight into animal ecology. Understanding how animals use space is fundamental to understanding social structure of populations (Vonhof et al. 2004) and habitat selection (Johnson 1980), as well as broader ecological and evolutionary processes, including ecosystem stability (Makarieva et al. 2005), and the adaptive potential of populations (Stiebens et al. 2013). Furthermore, information on the influence of environmental and anthropogenic perturbations on animal ranges is essential to conservation and management and facilitates prediction of how species might respond to global environmental change.

Two aspects of range-use dynamics that are of primary importance to animal ecology are fidelity to annual and seasonal ranges (range philopatry), and range size. There is ample theoretical work supporting the evolutionary benefits of philopatry. Memory or learning that enhances knowledge of forage resource quality has been shown to be an important factor in optimal foraging (Eliassen et al. 2009, Olsson and Brown 2010, Berger-Tal and Avgar 2012), where the efficiency of future searches increases relative to experience with successful foraging sites (Benhamou 1994). Motor learning allows for animals to better avoid predators and discourage intruders as their familiarity with an area increases (Stamps 1995). In

addition, the degree of philopatry is expected to vary depending on the predictability and spatial heterogeneity of the habitat, the cost of changing ranges, age, and life expectancy (Switzer 1993). The empirical literature demonstrates the broad propensity for philopatric behavior across many species, indicating the importance of this strategy (e.g., pine marten; Phillips et al. 1998, white-tailed deer; Lesage et al. 2000, caribou; Dalerum et al. 2007, elk; Webb et al. 2011c, and wildebeest; Morrison and Bolger 2012). Although some species show high philopatry regardless of variation in environmental or anthropogenic factors (e.g., Lesage et al. 2000, Tracz et al. 2010), variation in philopatry has been related to breeding status (Morrison and Bolger 2012), population density (Lesage et al. 2000) and both natural and anthropogenic disturbance (Linnell and Andersen 1995, Faille et al. 2010, Webb et al. 2011c).

Scaling relationships between range size, body mass and energetics are a fundamental principle of ecology (McNab 1963, Harestad and Bunnell 1979, Swihart et al. 1988), while intraspecific variation in range size often is examined under the framework of optimal foraging theory. This theory predicts that animals will maximize energy intake while minimizing movement (Charnov 1976, Pyke et al. 1977), and thus individuals in areas of greater forage availability should have smaller ranges. Several empirical studies have provided validation for these theoretical underpinnings with higher forage availability being related to smaller ranges in roe deer (Tufto et al. 1996, Kjellander et al. 2004, Said and Servanty 2005), red deer (Rivrud et al. 2010), and moose during certain times of the year (van Beest et al. 2011). However, these predictions are complicated during different life history stages, and by inter and intraspecific interactions (Fretwell and Lucas 1969, Brown et al. 1999, Frid and Dill 2002). Accordingly, range size has been found to vary with multiple environmental, social and individual factors not directly related to forage, including reproductive status (Said et al. 2005, van Beest et al. 2011), age (Said et al. 2009), climate

and weather (Sweanor and Sandegren 1989, Rivrud et al. 2010, van Beest et al. 2011), population density (Tufto et al. 1996), landscape heterogeneity at varying scales (Kie et al. 2002), and anthropogenic development (Walter et al. 2009a, Faille et al. 2010, Webb et al. 2011c).

Anthropogenic disturbance (e.g., roads and settlements) can impact range dynamics (e.g., size and intensity of use) of wild animals by altering habitat selection (Ciuti et al. 2012, Northrup et al. 2012a), or driving displacement (Linnell and Andersen 1995, Stephenson et al. 1996, Webb et al. 2011c), but studies have been infrequent and often show equivocal results (e.g., Edge et al. 1985, Tracz et al. 2010). Assessing such impacts informs our understanding of how animals perceive anthropogenic stressors and can provide insight into the resilience of populations to disturbance that might be otherwise elusive; for example high site philopatry in the face of declining habitat quality might increase the vulnerability of populations (e.g., as has been suggested in caribou; Faille et al. 2010).

Mule deer (*Odocoileus hemionus* Raf.) populations have experienced dramatic declines across much of their range in recent decades (Unsworth et al. 1999), with spatial displacement resulting from energy development being recently identified as a potentially aggravating factor (e.g., Sawyer et al. 2006). Mule deer are recognized to be highly philopatric (Robinette 1966, Garrott et al. 1987). Thus, their range-use dynamics are of particular relevance to management and offer insight into their susceptibility to disturbance from anthropogenic environmental change.

We examined size and annual overlap (philopatry) of individual female mule deer winter and summer ranges in the Piceance Basin in Northwest Colorado, USA (near the town of Meeker at 40.0394 degrees N and 107.9108 degrees W) using data collected from global positioning system (GPS) radio collars. We exploited advances in animal movement modeling that incorporate complexity in the movement process to produce movement-based

estimates of fine-scale space use (e.g., Wall et al. 2014). The incorporation of the movement process into estimates of spatial distribution allows for statistically robust utilization of high resolution movement data. We used these range estimates to compare mule deer seasonal ranges and examine their dynamics across years. Because range-use dynamics are largely determined by foraging behavior, we predicted that the relatively consistent and high quality summer forage would drive greater philopatry. In contrast, the more dynamic nature of winter range, due to snowfall, would lead to lower philopatry. In addition, we examined variation in range size and philopatry in relation to a suite of landscape covariates (primary productivity measured as normalized difference vegetation index [NDVI], snow depth, cover features and the degree of development within an individual deer's range) and individual covariates (deer age and body condition), as well as differences in annual deer density on winter range.

METHODS

Study area

The study was conducted in the Piceance Basin in Northwest Colorado (Fig. 5.1). The area is comprised of a pinyon pine (*Pinus edulis* Engelm.) and Utah Juniper (*Juniperus osteosperma* Torr.) shrubland complex and has a high degree of topographic diversity. For a detailed description of the vegetation of the area see Bartmann & Steinert (1981) and Bartmann, White & Carpenter (1992). The dominant anthropogenic activity was natural gas development, which fluctuated in intensity throughout the study period. The study was focused on two winter range areas, the Ryan Gulch and North Ridge areas (Fig 5.1). The Ryan Gulch area had moderate development related to natural gas extraction, while the North Ridge area was undeveloped, though did contain a minor road network and a number of houses. Deer in the broader study area are migratory and deer in North Ridge migrate to a

different summer range than those in Ryan Gulch. In addition, deer density in North Ridge was greater than that of Ryan Gulch (14.45-22.84 deer km-1 in North Ridge throughout the study and 7.04-8.87 deer km-1 in Ryan Gulch; Anderson Jr. 2014).

Deer data

Adult (> 1 year old) female mule deer were captured in the two study areas using helicopter net gunning. There was an initial capture during March 2010, and subsequent recaptures every December and March between December 2010 and March 2013. Starting in December 2010, capture areas were flown with a helicopter and deer were opportunistically captured to replace any individuals lost from the cohort to establish and maintain a sample of 50 collared individuals (see Appendix 8 for detailed capture data). Throughout the three year study period, 62 individual deer were tracked for multiple years (50 in the Ryan Gulch study area and 12 in the North Ridge study area). For more details on capture procedure see Northrup et al. (2014a).

During capture, deer were weighed using a portable scale, a body condition score was estimated by palpating the rump (Cook et al. 2001, Cook et al. 2007, Cook et al. 2010), the thickness of subcutaneous rump fat and the longissimus dorsi muscle were measured using a portable ultrasound (Stephenson et al. 1998, Cook et al. 2001, Stephenson et al. 2002), and age was estimated using tooth replacement and wear (Robinette et al. 1957, Hamlin et al. 2000). The body condition score, rump fat and longissimus dorsi muscle measurements were used to calculate the percent ingesta-free body fat (hereafter fat) of each deer at the time of capture following Cook et al. (2010). Lastly, each individual was fit with a GPS radio collar (G2110D, Advanced telemetry Systems, Isanti MN, USA) set to attempt a relocation on one of two schedules: 1) hourly between September 1 and June 30 and once every two hours between July 1 and August 31 (deer captured in December 2010 and March 2011); 2) every

30 minutes between September 1 and June 15 and hourly between June 16 and August 31 (deer captured after March 2011). Different duty cycles were used due to a change in the battery capacity of collars between the first and second year of captures. Following recapture, death, or collar release, GPS data were downloaded.

Due to the potential for capture to alter deer behavior, all data occurring 4 days after capture were censored for deer during their first capture, while data between recapture and return to the minimum convex polygon (MCP) from one month prior to capture were censored (Northrup et al. 2014a). In instances where this MCP overlapped the processing site, the data from the first day of following capture were censored. For the remaining data, the speed (distance/time) between all locations was calculated and the fastest 1% of movements was examined to determine if they were induced by erroneous locations (i.e., single outlier locations). In such cases, these outlier locations were removed. The remaining data were categorized as being on either winter or summer range, while data during migration were excluded. Migrations were determined visually in Arcmap 10.1 (Environmental Systems Research Institute, Redlands, CA), with spring migration classified as the time period initiated when deer began directed movement away from winter range without return, until they ceased directed movement on summer range; fall migrations were classified as the time period initiated when deer began directed movement away from summer range without return, until they ceased directed movement on winter range. Because deer returned to winter range prior to the capture date each year (early December), and we opportunistically captured new deer each year, there were unequal winter range samples among deer (i.e., deer that were opportunistically captured each December had shorter datasets). Thus, for winter, all data prior to the capture date in December were removed when estimating ranges. Because GPS locations were collected on different schedules across the study, data were rarefied to the coarsest scale available (1 hour during winter and 2 hours during summer). For any deer that

died, the data for the season during which it died were removed unless their death fell within one month of the median migration time of all other deer. Lastly, one deer made several long movements between winter and summer range throughout the summer. This deer was included in the winter range analyses but excluded from the summer analyses.

Estimation of ranges

A continuous-time correlated random walk (CTCRW) model (Johnson et al. 2008a, Johnson et al. 2008b) was fit to the data from each individual deer, year, and season (summer or winter) combination using the 'crawl' package (Johnson et al. 2008a) in the R statistical software (R Core Team 2013). This model represents an Ornstien-Uhlenbeck process and takes the following form (modified from Johnson et al. 2008a with the mean velocity set to 0 to indicate no drift):

$$v_{c_{t+\Delta}} = e^{-\beta\Delta} v_{c_t} + \epsilon_c \tag{1}$$

$$\epsilon_c | \Delta \sim Normal\left(0, \sigma^2 \frac{1 - e^{-2\beta\Delta}}{2\beta}\right) \tag{2}$$

where v_c is the instantaneous velocity along each coordinate axis (c; longitude or latitude), β is an autocorrelation parameter, Δ is the difference in time between consecutive locations and ϵ_c is a coordinate specific error term (i.e., a single error term for latitude and a single term for longitude). Using the above velocity model, the location of the animal at any point in time can be obtained using integration (modified from Johnson et al. 2008a):

$$s_t = s_0 + \int_0^t v(u)du \tag{3}$$

where s_t is the position at time t and v is the velocity of the animal. Johnson et al. (2008a) describe how the CTCRW model can be used to estimate the probability of an animal being at any location at any point during a sampling period given its recorded positions. Extended

over a specified time period and area, these probabilities can be combined to produce a

utilization distribution (UD) similar to that produced by other home range estimators such as

kernel density estimators (reviewed by Kie et al. 2010). This model is ideal for range

estimation in that the autocorrelation parameter allows incorporation of behavioral dynamics

that are clustered in time (e.g., foraging or resting bouts) and the variance in the estimates of

locations are directly incorporated into the UD, thus addressing concerns over uncertainty in

the UD itself (e.g., as discussed by Fieberg et al. 2005).

The CTCRW model was used to estimate the summer and winter range UDs for each

deer, year and season combination. Although theoretically these utilization distributions are

continuous in space and time, in practice both the sampling area and sampling interval must

be discrete. Thus, deer locations were predicted for every minute between the first and last

location in each dataset, and the probability of use was summed over a 5 meter grid and

weighted to ensure the resulting UDs summed to 1. A sensitivity analysis was conducted to

determine the optimal cell size and sampling interval (see Appendix 9).

Using the resulting UDs (Fig. 5.2), 3 metrics related to home range size and overlap

were calculated. First, polygons representing the smallest area containing 50% and 99% of

the density of the UDs were created and the area of these polygons (hereafter the 50% and

99% highest density ranges) were calculated. Next, the overlap of the UDs coming from any

two years for which we had deer data was calculated. The overlap metric was calculated as:

$$\text{overlap} = \frac{\sum_{i=1}^{I} UD_{1_i} \cap UD_{2_i}}{\sum_{i=1}^{I} UD_{1_i} \cup UD_{2_i}} \qquad (4)$$

Where I represents the number of cells over which the UDs were calculated (see Fig. 5.3 for

illustrative exampled). The result is a value ranging from 0 (no overlap), to 1 (complete

overlap with identical probabilities). As there were three years of data available for some

deer, differences in the distributions of overlap values for ranges separated by one and two

years were assessed using a Wilcox rank sum test. All analyses above were conducted using the R statistical software.

Factors influencing range size and overlap

To examine the factors influencing range size and philopatry, a series of regression models were fit with the size and overlap metrics as the response variables. Temporally dynamic and static covariates of natural, anthropogenic and individual deer characteristics (Appendix 10) were calculated over the outlines of the 50% or 99% highest density ranges. In addition, the annual winter range population density was included as a covariate in all winter models of size, and the difference in density between years was included as a covariate in all winter models of overlap. For the overlap analysis, the outlines of the ranges for the two years of interest were combined and the annual differences in temporally dynamic covariate values were calculated. For NDVI, snow and body fat covariates, the absolute differences between the two years of interest were calculated (assessing if the magnitude of differences in these variables explained changes in range use). For the development covariates, the difference between the second and first year was calculated in order to preserve the direction of the change (i.e., an increase or decrease). In the analysis of range size, the density and number of well pads and facilities (compressor stations, natural gas plants and other non-well pad industrial facilities) were excluded due to artifacts induced by the nature of the analysis. That is, by chance the number of pads will increase as range size increases, causing an artifactual correlation between the number of pads and range size. Although formulating these covariates as density can theoretically ameliorate these issues, all deer had between 1 and 3 pads or facilities in their range, causing an artefactual negative relationship between range size and density. Thus, these covariates were excluded. The body fat of deer was estimated from the regression equation presented in Cook et al. (2010), and thus has uncertainty

associated with estimate. To incorporate this uncertainty into our model, below, we estimated the true fat within the model, putting a normal prior on the true fat with mean equal to the observed fat and standard deviation as presented in Cook et al. (2010; see Appendix 11). For the overlap analysis the uncertainty was incorporated into the fat measures from each year separately and then the difference between years was calculated at each iteration in the algorithm presented below.

Models were fit to the overlap and size metrics using beta and gamma regression respectively in a Bayesian framework in R and JAGS using the 'rjags' package (Plummer 2012). Because there were multiple years of data from individual deer, models were fit with intercepts varying by individual (see Appendix 11 for model specifications). First, all continuous covariates other than fat were standardized $\left(\frac{x-\bar{x}}{\sigma}\right)$ and pairwise correlations among all predictor covariates were calculated. Next, a series of models incorporating all combinations of covariates that were correlated at less than |0.7| were fit. Multiple representations of snow, NDVI, and road density were tested in different models (Appendix 11). The Watanabe-Akaike Information Criteria (WAIC; Watanabe 2010), asymptotically equivalent to leave-one out cross validation and appropriate for hierarchical Bayesian models (Gelman et al. 2013, Hooten and Hobbs 2014), was used to compare models. Each algorithm was run for 125,000 iterations, discarding the first 25,000 as burn-in, to construct posterior distributions for each parameter. Two chains were obtained for each model, using starting values that were expected to be overdispersed relative to the posterior distribution, and convergence was assessed using the Gelman-Rubin diagnostic (Gelman and Rubin 1992) and by examining trace plots of each parameter. The median coefficient value and the proportion of the posterior falling to each side of 0 were calculated for each coefficient. Summer models were fit to the data for deer from the Ryan Gulch study area only, as deer from the North Ridge study area use a summer range for which characterization of anthropogenic features

was infeasible. In addition, these deer use winter range areas that are close in proximity (< 20 km), while their summer ranges are greater than 100 km apart. Winter models were fit to data from both study areas.

To assess whether our data were consistent with our models we performed posterior predictive checks on the best models (Gelman and Hill 2007). Posterior predictive checks are done by producing a posterior realization of the entire dataset at each MCMC iteration and comparing characteristics of the simulated data to the observed data (Gelman and Hill 2007). For all regressions we compared the mean and the squared deviance of the simulated data to the real data at each MCMC iteration and calculated Bayesian p-values as the proportion of iterations for which these parameters were greater in the real data compared to the simulated data.

RESULTS

Utilization distribution overlap

All tracked deer returned to the same general area on both summer and winter range in all years. Overlap values of UDs for both seasons were nearly identical for ranges separated by 1 year and 2 years (1 year winter $\bar{x} = 0.29$ and 2 years $\bar{x} = 0.32$, W = 830, p = 0.31; 1 year summer $\bar{x} = 0.49$, and 2 years $\bar{x} = 0.48$, W = 608, p = 0.88). There was greater overlap in mule deer UDs during summer ($\bar{x} = 0.49$) than winter ($\bar{x} = 0.30$; Wilcox rank sum test W = 6375, p < 0.0001), with some individuals displaying overlap close to 80% on summer range. Posterior predictive checks indicated that the models could reproduce adequate realizations of the data (Bayesian p-values for summer mean = 0.54, winter mean = 0.49, summer squared deviance = 0.59, winter squared deviance = 0.80).

The overlap of the UDs during summer increased with an increase in the number of well pads actively producing natural gas (Fig. 5.4) and the proportion of the range comprised of treed land cover, while overlap weakly declined with greater differences between years in the average NDVI (Table 5.1). During winter, the UD overlap was negatively related to the density of natural gas facilities (Fig. 5.4), the difference in the average NDVI between years, and the proportion of the range comprised of treed land cover, while overlap was positively related to the density of major roads (Table 5.1). Overlap weakly declined with an increase in the number of pads with active drilling and deer age (Table 5.1). There was no relationship between overlap and annual differences in winter range density (Table 5.1).

Range size

Deer used a greater overall area during the winter (99% size $\bar{x} = 5.79$ km^2) than summer (99% size $\bar{x} = 2.27$ km^2; Wilcox rank sum test W = 1203, p < 0.0001) and the area they used most intensively during the winter (50% size $\bar{x} = 0.70$ km^2) also was greater than during summer (50% size $\bar{x} = 0.24$ km^2; Wilcox rank sum test W = 11868, p < 0.0001). Posterior predictive checks indicated that the models could reproduce adequate realizations of the data during the winter, but during the summer the squared deviance of the real data was greater than that of the simulated data during a large proportion of the MCMC iterations (Bayesian p-values for summer 99% range mean = 0.36, summer 50% range mean = 0.36, winter 99% range mean = 0.39, winter 50% range mean = 0.35, summer 99% range squared deviance = 0.92, summer 50% range squared deviance = 0.94, winter 99% range squared deviance = 0.73, winter 50% squared deviance = 0.30). These results likely indicate that the model was not adequately capturing the variance in the data during the summer.

The 99% summer range size was positively related to the body fat of deer in the following December and the density of pipelines and negatively related to terrain ruggedness

and age (Table 5.2). Though weaker, range size also was negatively related to average NDVI (Fig. 5.5) and the density of major roads (Table 5.2). Similarly, the size of the 50% summer range was positively related to the fat of the deer in the following December and the density of all roads, and negatively related to deer age, terrain ruggedness, the density of pipelines, and the average NDVI of the range (Fig. 5.5; Table 5.2).

The 99% winter range size was negatively related to terrain ruggedness, the density of pipelines, and the winter range deer density, while positively related to the proportion of the range comprised of treed land cover (Table 5.2). In addition, range size was weakly negatively related to the average NDVI (Fig. 5.5), and age, while weakly positively related to the total snow on each deer's range (Table 5.2). The size of the 50% winter range was negatively related to terrain ruggedness, and the winter range deer density, and weekly negatively related to the average NDVI (Fig. 5.5), density of major roads, and age (Table 5.2). Similar to summer, fatter deer also had larger 50% highest density winter ranges.

DISCUSSION

An understanding of drivers of space use and philopatry is fundamental to animal ecology. Animals are philopatric for numerous reasons, including the foraging benefits of memory and learned resource locations (Benhamou 1994, Eliassen et al. 2009), enhanced predator avoidance and increased ability to exclude conspecifics (Stamps 1995). Mule deer in our study exhibited a high degree of philopatry to both their summer and winter ranges, highlighting the importance of spatial familiarity and memory to this species. During summer, energy acquisition is likely the primary driver of behavior for deer as they are birthing and rearing fawns, which is an energetically costly activity, as well as accruing fat stores to survive the winter (Tollefson et al. 2010). During this time, deer exhibited high

philopatry within a small, intensively used space. The high philopatry during summer might also be related to past success in raising fawns in an area. During winter, temporal and spatial variation in snow depth makes the landscape much more dynamic and deer are primarily concerned with energy conservation (Torbit et al. 1985). Philopatry in winter was significantly lower than that in summer as predicted (Switzer 1993). At this time, fawns also are more mobile, which might further influence the degree of philopatry during winter.

Environmental and individual factors influenced the degree of philopatry in mule deer. As expected, greater differences in habitat productivity between years decreased the degree of philopatry as deer ranged over larger areas when productivity was lower. During these times, deer still used the same general area, but their intensity of use of specific locations varied as they likely searched farther afield for forage. Importantly, the summer of 2012 was a year of substantial drought in our study area (summer precipitation in 2011 total = 13.84 cm; 2012 total = 5.38 cm; 2013 total = 9.63 cm; http://www.nohrsc.noaa.gov/). which might have driven large differences in habitat productivity and the subsequent responses in range philopatry. Tree cover also was important to overlap in both seasons, though with contrasting effects (positive during summer and negative during winter). During summer, deer are rearing fawns and predation risk for fawns is high (Pojar et al. 2004), and cover thus might be more important than in winter as a result.

Lastly, anthropogenic development was an important predictor of philopatry in line with other studies demonstrating development can drive displacement from preferred areas (Northrup and Wittemyer 2013). There was lower philopatry during the winter on ranges where there were more industrial facilities (natural gas and other), as well as when active drilling increased. During summer, there was a positive relationship between philopatry and the change in well pads actively producing gas (i.e., transitioning from the highly active drilling phase to the relatively inactive producing stage in a gas well lifecycle). Thus, deer

showed greater philopatry when disturbance (i.e., drilling, which is the stage of greatest activity) decreased and lower philopatry when new wells were drilled in their range.

Identification of the factors driving philopatry in our study area align with our understanding of deer behavior and biology. Deer rely heavily on the use of well known areas. Such behavior is expected to be selected for when heterogeneity in sites is low and when the habitat is predictable (Switzer 1993), which supports our findings that departures from high philopatry in our system occur because of environmental or human-induced landscape dynamics. Importantly, changes in philopatric behavioral strategies might occur only after a time lag (Switzer 1993), leaving deer susceptible to detrimental effects of suboptimal behavior. Although development densities are not currently high enough to cause abandonment of ranges (e.g., as seen by Sawyer et al. 2006), our findings showed that higher densities elicited reduced use of the previous year's range (familiar areas), potentially to their detriment. In light of the apparent importance of philopatric space use strategies to deer, our results provide an example of how anthropogenic development and land-use changes alter a fundamental behavior likely to have evolved to enhance deer foraging success and predator avoidance.

Range size

Optimal foraging theory provides a useful theoretical framework for understanding range size dynamics. In areas of high productivity, animals are expected to use smaller areas (Charnov 1976, Pyke et al. 1977) and deer in our study adhered to these predictions, with productivity being a main determinant of (and negatively correlated with) range size. Deer used substantially smaller areas during summer, when range quality is higher, than during winter. Within seasons, individuals also used smaller areas when primary productivity was greater. These results resemble findings for other ungulate species (Tufto et al. 1996, Rivrud et al.

2010, van Beest et al. 2011), supporting the generality of the range size-productivity relationship. In addition, deer in areas with greater terrain ruggedness had smaller ranges, likely reflecting the importance of cover to deer. Our study area is topographically diverse, which serves as an important instrument of cover, particularly from visual stimuli and acoustic disturbances related to natural gas development (e.g., Blickley et al. 2012).

As seen in other studies of ungulate range size (e.g., Tufto et al. 1996), individuals in areas with higher density of deer had smaller ranges. This result suggests that deer in areas of greater density might be more restricted in their space use. Contrarily, the higher density in the North Ridge study area might be a result of higher quality habitat, which would elicit a similar response (i.e., smaller ranges). While these two factors cannot be disentangled, recent work has shown that heavy snow fall during winter causes increased densities in small areas (Bergman et al. 2014b), which might accentuate the density related differences observed on winter range in our system.

The individual animal characteristics of age and body condition also consistently influenced range size. Older deer had smaller ranges, which might indicate that older animals are more experienced and knowledgeable about their ranges (optimally using the area for nutritional and cover requirements) or better able to monopolize preferred range. In contrast, fatter deer had larger ranges supporting other work showing that fatter deer used more energy during the winter (Monteith et al. 2013). Matching summer results indicate that similar dynamics are occurring on both ranges, with fatter deer being able to afford greater movement. These results indicate that there is some benefit to having a larger range potentially linked to access to various welfare factors (i.e., limiting resources, thermal cover) or reducing predation risk. We caution that for the summer result, the post-summer fat of deer in our study might be confounded with the successful rearing of fawns through the summer, as deer with greater fat stores might be more likely to have lost fawns and not incurred the

cost of lactation throughout the summer. Thus, larger ranges during summer might in fact be related to the loss of fawns, though we lack information on reproduction to assess this relationship.

Range estimation

With the increasing sophistication of GPS collar technology, our ability to collect highly detailed and complex movement data is growing. The simultaneous advancement in methods for analyzing these data provides unprecedented ability to understand animal behavior. We used methodology developed in the animal movement modeling literature to take advantage of the complex nature of these data, which enables a movement-based examination of range dynamics at fine spatial and temporal scales (in our case 5 m). Other classic approaches do not incorporate the animal's movement behavior in their estimation approach, resulting in utilization distributions reflecting the assumptions of a point process rather than a movement process. Our approach employing the CTCRW method (Johnson et al. 2008a) ensured that space use estimation based on high resolution location data captured the movement process. It is important to note other methods are available that leverage this strength of high resolution GPS tracking data as well (e.g., Wall et al. 2014). When assessing the relationship between fine-scaled behaviors (such as intensively sampled movement) and landscape dynamics, employing technically appropriate analytical techniques is necessary.

Conclusions

The success of philopatric strategies is based on a certain degree of environmental and landscape-level predictability (Switzer 1993). Environmental and anthropogenic changes can thus negatively impact species that display high philopatry to an area. Climate driven

environmental change is likely to drive variability in precipitation and vegetative productivity. This increase in variability will reduce the predictability of ecological systems thus decreasing the benefits of philopatric strategies. As such, we may expect philopatric species to be particularly susceptible to climate change. However, management options for addressing this issue are limited.

As with climate variation, anthropogenic development clearly influenced range philopatry and size in our study system. In particular, the high degree of philopatry to summer ranges suggests the displacement of deer from their preferred summer range may be of concern. Summer is a critical period for rearing fawns and accruing fat prior to winter, and displacement during this time could be detrimental to deer. However, if much of the summer range is highly productive, there might be little nutritional cost to this displacement. During winter, our results suggest that the lower quality of forage and dynamic nature of the landscape require that deer use a greater amount of space. Increased development on winter range could further exacerbate nutritional stress during this time if it reduces the amount of space deer have available to them. During both seasons, deer displayed decreased philopatry and used larger areas when vegetative productivity was low. This finding indicates that during poor years deer require more area and might be particularly susceptible to anthropogenic impacts. Interestingly, the finding that deer increased their philopatry when development transitioned from drilling to the less disturbing producing stage indicates that deer might be resilient to short-term disturbances and that development impacts can be ameliorated. In respect to these findings, management and mitigations strategies for deer should be focused on reducing the overall density and duration, where possible, of the most disturbing and intensive aspects of development (i.e., drilling and large facilities).

TABLES

Table 5.1. Covariates, median coefficient estimates (coeff.) and proportion of posteriors (prop.) falling above and below 0 for beta regression models fit to the bi-annual overlap (degree of philopatry) in the utilization distributions during summer and winter for female mule deer in the Piceance Basin of Northwest Colorado. Descriptions of all covariates can be found in Appendix 10.

Covariates[a]	Median coeff.	Prop. < 0	Prop. > 0
Summer			
Overall intercept	-0.06	0.64	0.36
difference in *dens_prod*	0.17	0.01	0.99
tree	0.11	0.13	0.87
difference in *avg_NDVI*	-0.06	0.81	0.19
rd_dens_major	-0.04	0.65	0.35
TRI	-0.04	0.63	0.37
age	-0.02	0.58	0.42
fat	0.00	0.53	0.47
Winter			
Overall intercept	-0.91	1.00	0.00
dens_fac	-0.19	1.00	0.00
tree	-0.10	0.91	0.09
rd_dens_major	0.09	0.06	0.94
age	-0.08	0.88	0.12
difference in *dens_drill*	-0.07	0.89	0.11
difference in *avg_NDVI*	-0.07	0.96	0.04
density	0.05	0.23	0.77

difference in *dens_pipe*	-0.02	0.68	0.32
difference in *fat*	0.00	0.43	0.57
difference in *snow_avg*	-0.02	0.62	0.38

[a]See Appendix 10 for descriptions of covariates

Table 5.2. Covariates, median coefficient estimates (coeff.) and proportion of posteriors (prop.) falling above and below 0 for gamma regression models fit to the size of the 99 and 50 percent highest density ranges during summer and winter for female mule deer in the Piceance Basin of Northwest Colorado. Descriptions of all covariates can be found in Appendix 10.

Covariates[a]	Median coeff.	Prop. < 0	Prop. > 0
Summer 99%			
Overall intercept	14.12	0	1
fat	0.04	0.00	1.00
TRI	-0.10	0.94	0.06
dens_pipe	0.05	0.17	0.83
age	-0.08	0.92	0.08
peak_NDVI	-0.06	0.88	0.12
rd_dens_all	0.02	0.37	0.63
tree	-0.06	0.82	0.18
Summer 50%			
Overall intercept	12.05	0.00	1.00
fat	0.03	0.00	1.00
TRI	-0.08	0.95	0.05
avg_NDVI	-0.07	0.98	0.02
dens_pipe	-0.07	0.93	0.07
rd_dens_major	0.03	0.24	0.76
age	-0.06	0.93	0.07
tree	0.03	0.24	0.77
Winter 99%			

Overall intercept	15.41	0.00	1.00
TRI	-0.21	0.99	0.01
density	-0.21	1.00	0.00
dens_pipe	-0.16	0.99	0.01
tree	0.12	0.05	0.95
avg_NDVI	-0.05	0.87	0.13
snow_total	0.06	0.19	0.81
rd_dens_all	0.04	0.26	0.74
age	-0.04	0.81	0.19
fat	0.01	0.24	0.77

Winter 50%

Overall intercept	13.24	0.00	1.00
density	-0.24	1.00	0.00
TRI	-0.14	0.98	0.02
fat	0.02	0.08	0.92
age	-0.04	0.87	0.13
peak_NDVI	-0.02	0.71	0.29
rd_dens_major	-0.04	0.86	0.14
tree	-0.01	0.61	0.39
snow_total	0.02	0.38	0.62

[a]See Appendix 10 for descriptions of covariates
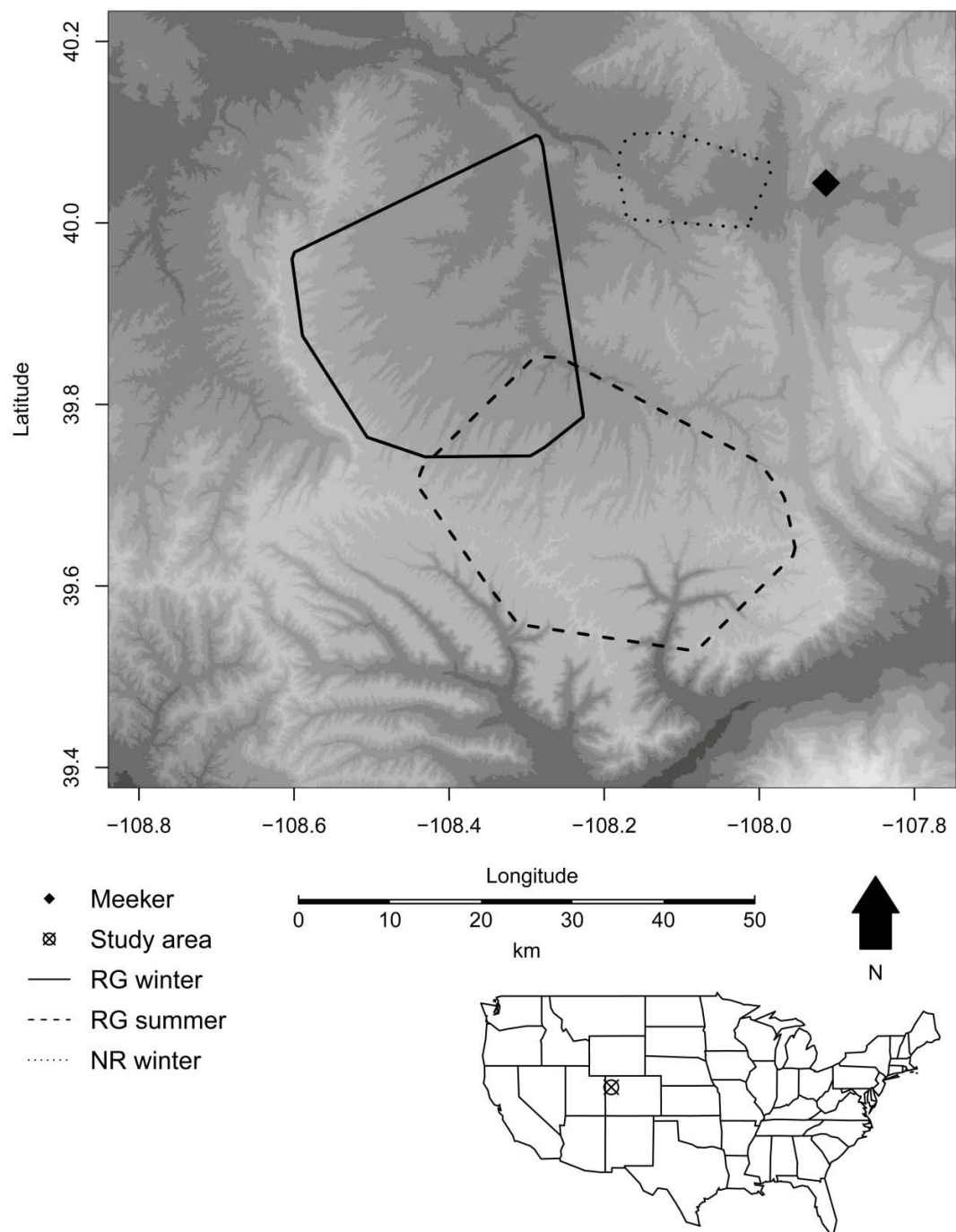
Figure 5.1. Location of study area, nearest town (Meeker, Colorado), and outlines of summer and winter mule deer distribution by study site (RG for Ryan Gulch, and NR for North Ridge). Underlying gray scale represents elevation.
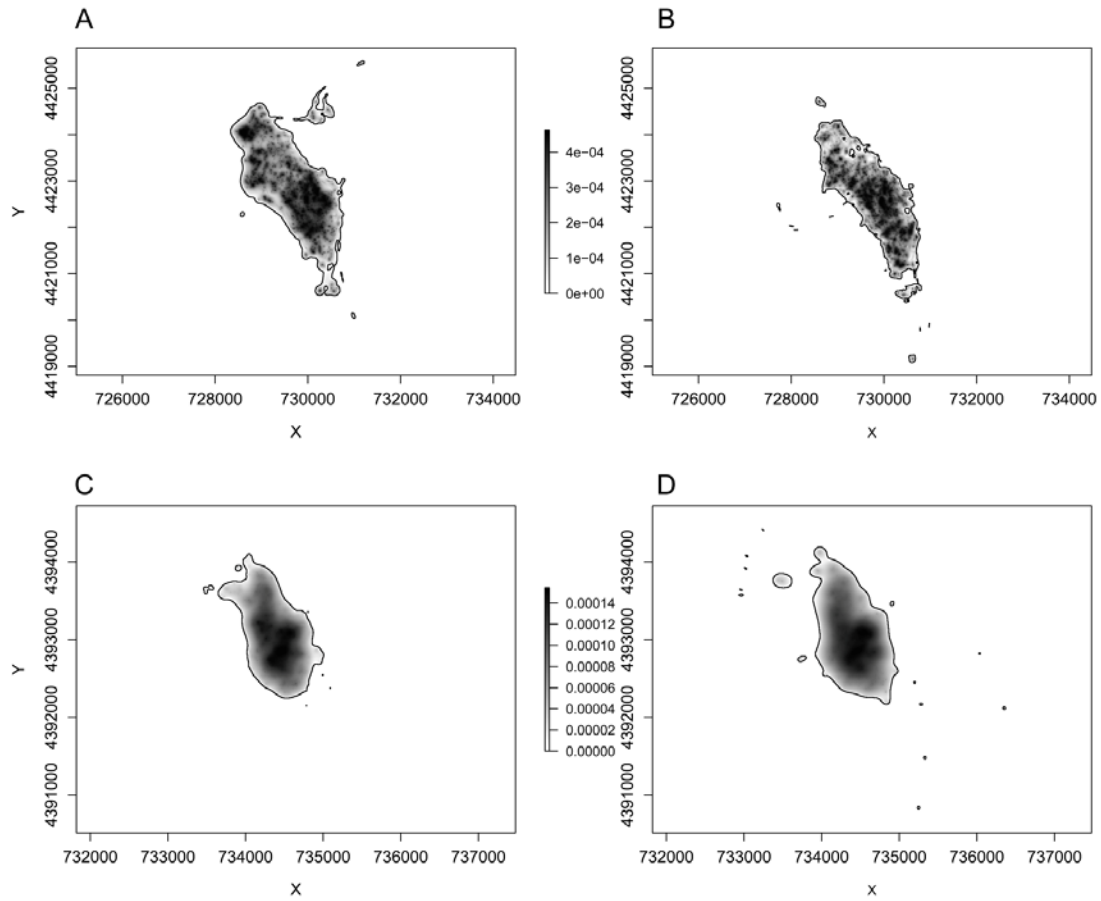
Figure 5.2. Example of utilization distributions for a single female mule deer in the Piceance Basin, Northwest Colorado, USA during (A) winter 2011, (B) winter 2012, (C) summer 2011 and (D) summer 2012. Overlap values were 0.46 and 0.77 in the winter and summer respectively.
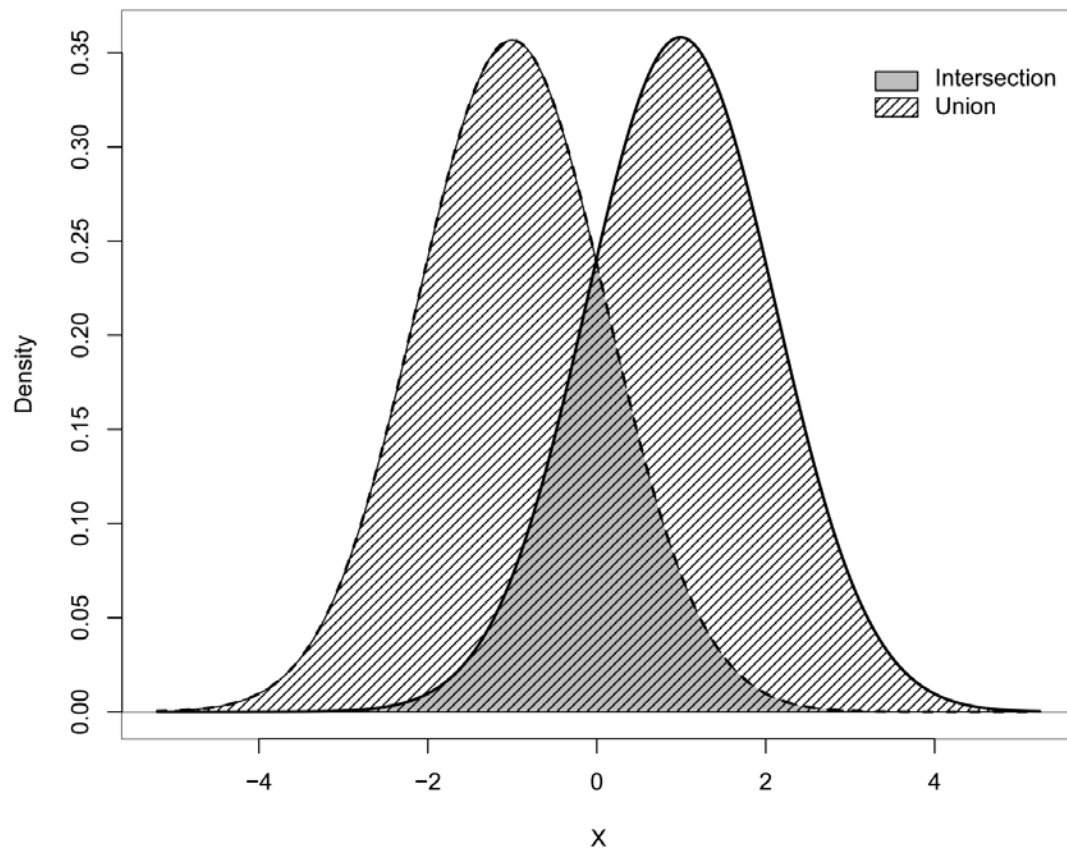
Figure 5.3. Schematic detailing calculation of overlap between utilization distributions used in analyses of mule deer range overlap.
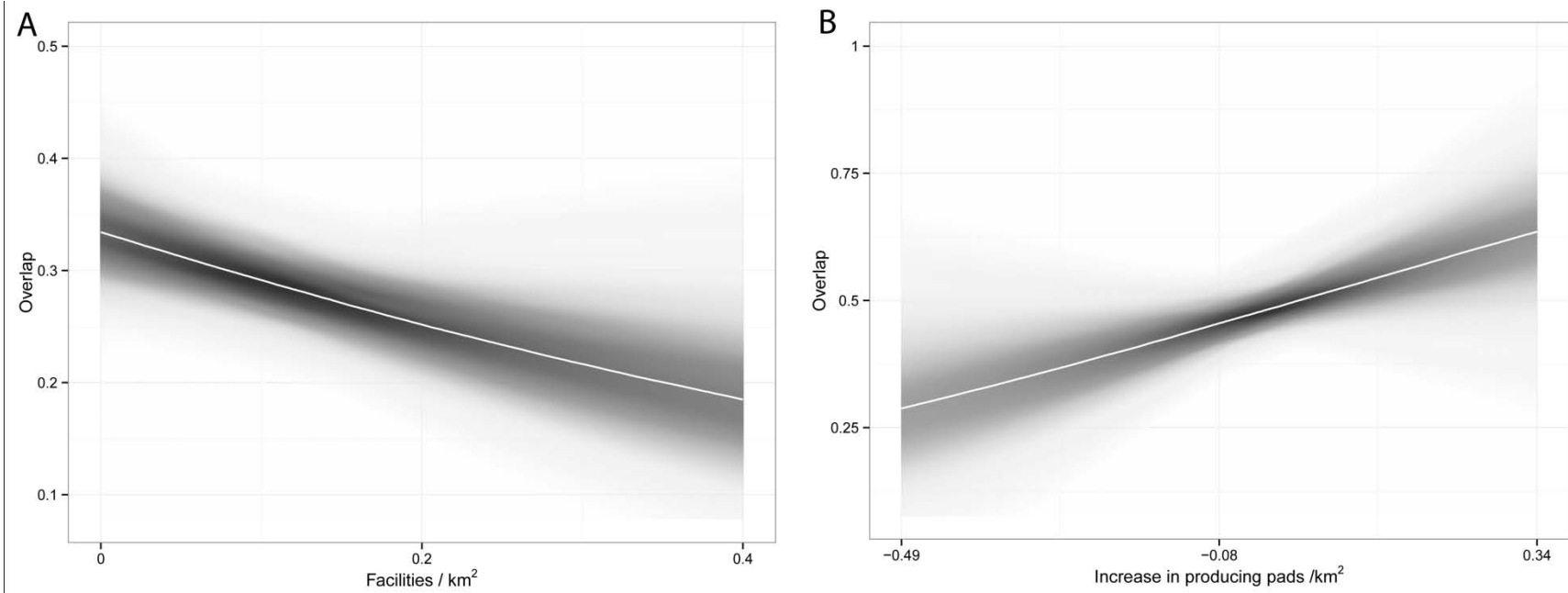
Figure 5.4. Predictions of range overlap with variation in (A) the density of oil and gas and other facilities during winter and (B) the change in density of producing well pads during summer for mule deer in the Piceance Basin, Northwest Colorado, USA. Gradient represents the density of the posterior predicted values.
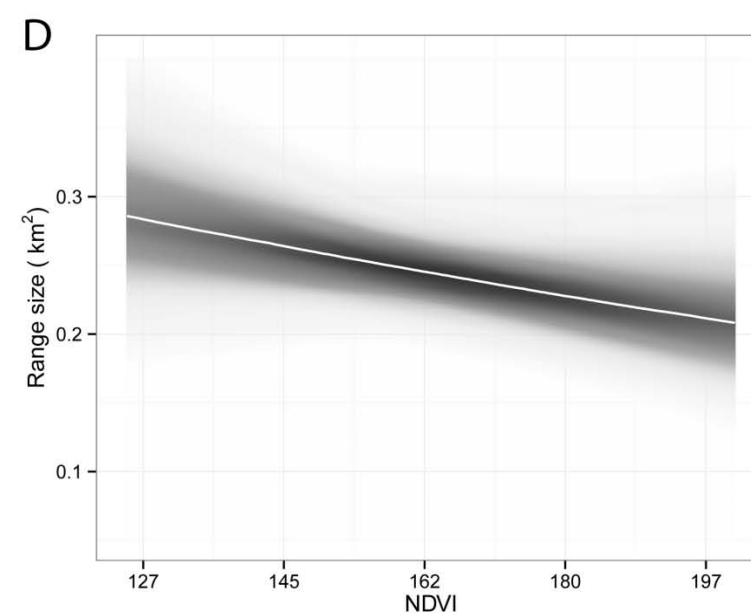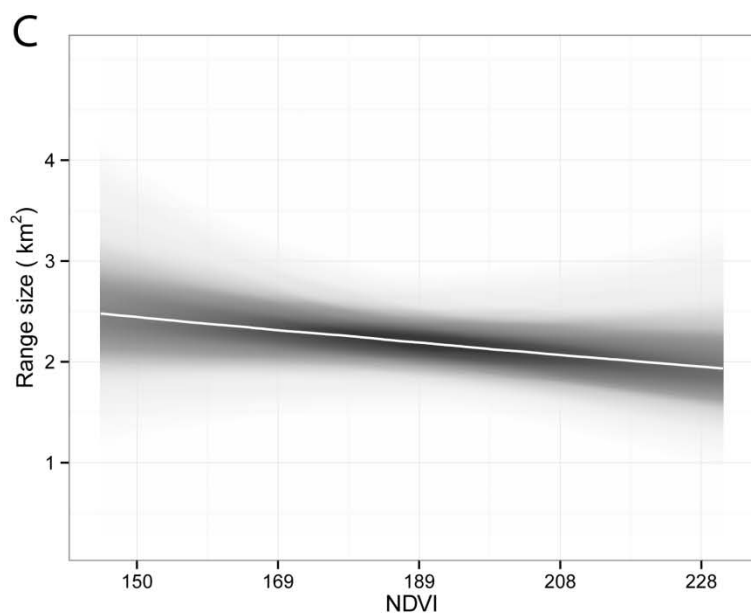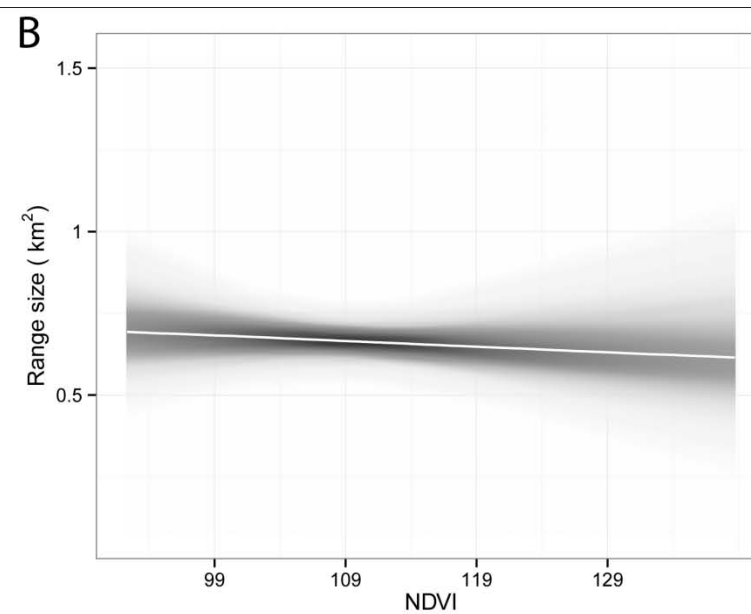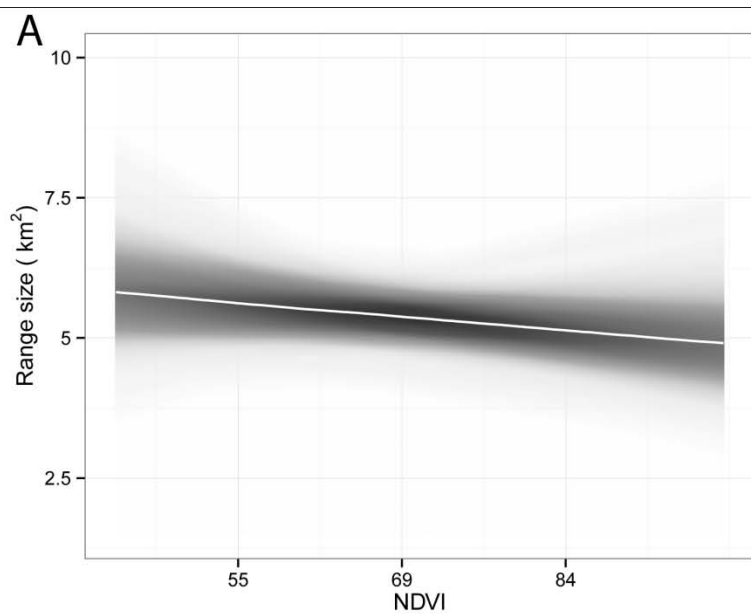
Figure 5.5. Predictions of range size (km^2) against normalized difference vegetation index (NDVI) in the respective season and range size for mule deer in the Piceance Basin, Northwest Colorado, USA for: (A) the winter 99% highest density range, (B) winter 50% highest density range, (C) summer 99% highest density range, and (D) summer 50% highest density range. Gradient represents the density of the posterior predicted values.

CHAPTER SIX

CONDITION-DEPENDENT FORAGING STRATEGIES LEAD TO DIFFERENTIAL LOSS

OF ENERGETIC RESERVES IN A TEMPERATE UNGULATE

INTRODUCTION

Optimal foraging theory predicts that animals will make decisions regarding when and where to

eat to optimize overall resource gain (Macarthur and Pianka 1966, Pyke et al. 1977). Despite the

relative simplicity of this prediction, it has been widely applied to gain insight into behavioral

processes including predator prey interactions (Brown 1988, Brown et al. 1999), the degree of

diet specialization (Macarthur and Pianka 1966), and the value of learning (Berger-Tal and

Avgar 2012). As the foraging decisions of animals also dictate the time spent in different habitats

(Charnov 1976, Wajnberg et al. 2006), these behaviors influence larger scale ecological

processes including community structuring (Petchey et al. 2008), and population distribution and

abundance.

The foraging strategies of temperate ungulates have been shaped by seasonally dynamic

constraints. For these species, winter typically is a time of nutritional limitation (Torbit et al.

1985, Festa-Bianchet et al. 1996, Bishop et al. 2009), when most individuals lose mass while

relying on reserves stored during the previous summer (Torbit et al. 1985, Festa-Bianchet et al.

1996, Parker et al. 1999). Contrastingly, summer is a time of high resource availability but also

high energetic demands due to the need to care for young and build sufficient reserves to survive

the impending winter (Wallmo et al. 1977, Festa-Bianchet et al. 1996, Festa-Bianchet 1998,

Therrien et al. 2008). Thus, during both seasons, the foraging decisions of temperate ungulates are structured by current and future energetic needs (e.g., Festa-Bianchet and Jorgenson 1998). Although the dynamics of the allocation of energy reserves to survival and reproduction have been assessed empirically (Festa-Bianchet and Jorgenson 1998, Monteith et al. 2013), their influence on foraging decisions (and vice versa) are not as well understood outside of theoretical studies. Foraging theory predicts that these decisions will be strongly influenced by current condition (McNamara and Houston 1986, Brown 1988), however the data for assessing these dynamics are difficult to obtain for wide-ranging species.

In addition to endogenous, condition-based drivers, the foraging decisions of animals are structured by exogenous factors. The quality and quantity of forage resources influence when and where animals decide to forage, but the cost of movement between patches alters expected gains (Charnov 1976, Pyke et al. 1977), thereby structuring landscape level space use. These costs likely vary across spatial and temporal scales and are influenced by expected interactions with predators (Lima and Dill 1990) and conspecifics, particularly in highly social species (Polansky et al. 2013). The impact of human activity on foraging decisions can be analogous to that of predators (Frid and Dill 2002), though in some cases humans may serve as predator shields for prey species (Berger 2007). Untangling the factors (endogenous and exogenous) driving the foraging decisions of animals can clarify the relationship between life history strategies and behavior and lend insight into behavioral adaptations to seasonal constraints (e.g., Therrien et al. 2008). Such an approach is increasingly important for understanding the landscape context under which behavioral decisions are made and the influence of human-caused environmental change on those decisions.

Despite the importance of understanding foraging decisions of free ranging animals, often they are difficult to observe in the wild. Thus, much of the research in this field has been theoretical, or focused on species or time periods that are amenable to direct measurement (e.g., during daytime hours in open systems). Technological advances (e.g., global positioning system (GPS) radio collars), provide unprecedented information on animal space use that, when coupled with advances in statistical modeling, provide new avenues for empirical assessments of foraging decisions in species (e.g., McClintock et al. 2012b, Polansky et al. 2013, Louzao et al. 2014). Combining these approaches with detailed information on animal condition can serve to provide insight into the drivers and repercussions of different foraging decisions (Louzao et al. 2014). To date this has been rare with large free ranging animals.

Mule deer (*Odocoileus hemionus*) are predominantly migratory across their range as a result of seasonally variable ecological constraints in their environs (Wallmo et al. 1977). During the winter when forage resources are limited, deer face a net negative energy balance (Torbit et al. 1985), and are susceptible to mortality due to malnutrition (Unsworth et al. 1999). On summer range, resources are abundant (Wallmo et al. 1977), but energetic requirements are high as deer birth and rear between one and three fawns while also gaining sufficient energy stores to survive the impending winter (Wallmo 1981). These seasonal dynamics are critical for management and conservation of this species across Western North America where they have seen large-scale declines across their range in recent decades (Unsworth et al. 1999). Due to the lack of high quality forage on winter range, most management actions focus on improving nutrition during this time using habitat manipulation or supplemental feeding (e.g., Bishop et al. 2009). However, nutritional constraints on summer range might be equally important to the species (Monteith et al. 2013). Understanding what drives foraging decisions, and how these

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decisions interact with and influence mule deer condition can clarify the strategies employed by the species to overcome the constraints they face, providing greater understanding of life history strategies that can inform management actions. Here we examine the spatial and temporal dynamics of foraging behavior and the relationship between this behavior and condition in a wild population of mule deer in the Piceance Basin of Colorado, USA.

METHODS

Deer data

We captured adult (> 1 year old) female mule deer in two winter range areas (North Ridge, and Ryan Gulch; Fig. 6.1) in the Piceance Basin of Colorado, USA (39.954 degrees N, 108.356 degrees W), using helicopter net gunning (see Northrup et al. 2014a for details of capture procedure). From March 2010 through March 2013, uncollared deer were captured opportunistically during March and December of each year to establish and maintain a sample of 50 tracked individuals. All individuals were recaptured each December, and 30 were recaptured each March (see Appendix 12 for details on capture dates of each deer) to weigh them, assess body condition (Cook et al. 2001, Cook et al. 2007, Cook et al. 2010), measure the depth of the longissimus dorsi muscle and the thickness of the subcutaneous rump fat (Stephenson et al. 1998, Cook et al. 2001, Stephenson et al. 2002), and estimate age using tooth replacement and wear. Starting in December 2010, a global positioning system (GPS) radio collar (Advanced Telemetry Systems, Isanti, MN, USA) set to 1 of 2 schedules (Dec. 2010 and Mar. 2011: hourly locations Sep. 1 to Jun. 30 and once every 2 hours otherwise; Dec. 2011/2012 and Mar. 2012/2013: half hourly Sep. 1 to Jun. 15 and hourly otherwise) was fit to each deer and they were released on

site. Different schedules were used due to an upgrade in the collar battery prior to the second

year of the study. The mass, body condition score, rump fat and loin depth measurements were

used to calculate the percent body fat (hereafter fat) following Cook et al. (2010). We also

calculated lean body mass of each deer by first calculating the ingesta-free body mass following

Cook et al. (2007), and subtracting the weight of fat, based on the percent body fat of each deer.

Following mortality of the deer, recapture, or collar release, GPS data were downloaded

from collars. To ensure that data were free from effects of capture, we censored the first 4 days

of data following the first capture (Northrup et al. 2014a). For recaptured deer, we censored all

data between capture and the time when deer returned to an area delineated by a minimum

convex polygon (MCP) drawn around the data one month prior to capture (Northrup et al.

2014a). If deer did not return to this MCP within one week we censored the first week of data. If

the processing site was contained within the MCP, we censored the first day of data. Minimum

convex polygons were calculated using the 'adehabitatHR' package (Calenge 2006) in the R

statistical software (R Core Team 2013), and return to these MCPs was determined by visually

examining data in ArcMap 10.1 (Environmental Systems Research International, Redlands, CA

USA). Using the resulting data, we calculated the speed moved between consecutive locations

(m/hr) and visually examined the fastest 1% of these speeds to determine if they were the result

of single outlier locations, indicating an erroneous fix. Any such locations were censored.

Deer in the Piceance Basin are migratory so we classified data as occurring on winter

range, summer range or during migration. Winter range data were classified as any data falling

between capture (for the first year of data) or arrival on winter range (subsequent years) and

when the deer began directed movement away from the winter range without return. Summer

range data were classified as any data between the cessation of directed movement from winter

range to summer range and when the deer began directed movement away from summer range

without return. Migratory data were classified as all remaining data. Only the resulting summer

and winter range data were used in the analyses presented. In addition, we censored all data

occurring after the median migration initiation date across all deer and before the median

migration termination date across all deer (the latter for summer only) for each of the 3 years of

data. Winter range data were truncated to December 10 (4 days after the typical termination of

capture efforts). Data occurring prior to this date were removed because the majority of deer

initially were captured in December 2010 and thus had no data prior to this date and because the

fix schedule was altered between December 2010 and December 2011. The resulting dataset

comprised 70 deer whose resulting datasets were useable for movement modeling (17 in the

North Ridge study area and 53 in the Ryan Gulch study area), producing 106 and 130 individual

deer and season combinations during summer and winter, respectively.

Estimation of activity budgets

We estimated activity budget using the results of discrete-time correlated random walk models,

formulated as hidden Markov models (hereafter CRW models). We fit these models to step

lengths and turn angles (the distance moved between locations and the relative bearing between

subsequent movements, respectively; Turchin 1998) for each individual deer, year and season

combination. We followed the general approaches discussed by Morales et al. (2004) and

McClintock et al. (2012a). Specifically, our model took the following form:

$$s_t | \mathbf{z_t} \sim \text{gamma}\big(\alpha_j, \beta_j\big)$$

$$\phi_t | \mathbf{z_t} \sim \text{von Mises}\big(\mu_j, \kappa_j\big)$$

$$\mathbf{z_t} | \mathbf{z_{t-1}} \sim \text{multinomial}(\boldsymbol{\psi})$$

$$\boldsymbol{\psi} \sim \text{Dirichlet}(0.5, 0.5)$$

$$\alpha_j \sim \text{uniform}(0, 20000)$$

$$\beta_j \sim \text{uniform}(0, 20000)$$

$$\mu_j \sim \text{uniform}(0, 2\pi)$$

$$\log \kappa_j \sim \text{normal}(0, 1000)$$

where s_t and ϕ_t are the step length and turn angle at time t, $\boldsymbol{z_t}$ is a vector representing the underlying, unobserved behavioral state that dictates which distribution (j) the step length and turn angle originated from. This state vector, $\boldsymbol{z_t}$ is a Markov process where the probability of being in any state (j) depends on the previous state. Thus $\boldsymbol{\psi}$ is a vector of values that sum to 1, with a different vector for each state indicating the probability of remaining in the current state or transitioning to the other state. In general terms, this model indicates that the movements of an animal (step length and turn angle) arise from distributions (in this case a gamma for step length and von Mises for turn angle) that are specific to their underlying behavioral state. This behavioral state changes through time with probability that depends on the previous state. We fit a model with 2 states because acoustic assessments of mule deer behavior in our system have shown that they spend almost the entirety of their days either inactive (resting and ruminating) or foraging (Lynch et al. 2013). All models were fit in a Bayesian hierarchical framework using a Markov Chain Monte Carlo (MCMC) procedure written in R. The algorithm was run twice to obtain two chains for each parameter using starting values that were presumed to be overdispersed relative to the posterior distributions of the parameters. For the state matrices ($\boldsymbol{z}$ above), the two chains were initialized with all movements in one of the two states, with the opposite state chosen for each of the two chains. Algorithms were run for variable numbers of iterations (see Appendix 13 for details) and convergence was assessed using the Gelman-Rubin

diagnostic (Gelman and Rubin 1992) with a value of 1.1 for means used as a threshold for convergence. In addition we examined traceplots of the resulting chains for all parameters to further assess convergence. In several instances the algorithm failed to converge for the dispersion parameter (κ) on one of the two states, due to the separate chains exploring different areas of the posterior that were smaller than 0.01. The convergence issues likely were a result of uniform turning angles for this state. We thus modified the CRW model such that the prior on the concentration parameter κ was a truncated normal with mean = 0, standard deviation = 10,000, upper bound = ∞, and lower bound = 0.01. This algorithm failed to converge for 21 winter models and 15 summer models (see Appendix 13 for details), with the two chains converging to what appeared to be local maxima. These models predominantly were those fit to data from winter and summer 2011 when collars were set to a less frequent fix schedule (hourly during winter and 2 hourly during summer). We refit these models using a Metropolis-Coupled Markov Chain Monte Carlo (MC[3]; Altekar et al. 2004) procedure in R. These MC[3] algorithms converged, however all showed bimodality in the posteriors. This result indicates that these deer were moving in a manner substantially different than the remaining individuals for which the algorithms converged. We thus excluded these individuals from further consideration.

The models as presented above assume that all data are present. However there was variable fix success among the deployed collars. There are several methods that exist for fitting models similar to the CRW model with missing data (see examples in Langrock et al. 2012, McClintock et al. 2012a). We assessed 3 methods using simulation (see Appendix 14), and determined that using linear interpolation but censoring all individuals missing greater than 20% of their data provided the best balance between accuracy and computation time.

After fitting the above models to all deer, year and season combinations we extracted the posteriors of the state vector ($\mathbf{z_t}$) for each location. These vectors provide the probability that the deer was in each of the 2 states for every location. We combined all state vectors across each day to obtain the total proportion of each day that a deer was predicted to be in each state, or their activity budget. We calculated activity budgets incorporating interpolated missing data but excluded all days when greater than 25% of the locations were missing for that day.

Model assessment

We took two separate approaches to assess the performance of the CRW model. First we conducted posterior predictive checks of the autocorrelation structure of the data (Gelman and Hill 2007). For each MCMC iteration, we produced a single realization of the data and calculated the autocorrelation function of the time series across 96 hours. The autocorrelation functions for all MCMC iterations were combined to derive a distribution of the autocorrelation at each time lag. We then calculated the autocorrelation function for the observed data and visually compared the simulated and observed data for each individual.

Next, to verify that our model could accurately identify foraging and resting bouts, we compared the posteriors of the state vectors to acoustical behavior data collected simultaneously on a subset of deer. In December, 2011 we fit collars able to continuously record the acoustic environment on 10 of the deer in our study (Lynch et al. 2013). Lynch et al. (2013) used these data to identify the continuous behaviors that deer engaged in for 5 individuals (a single day was examined for 4 deer, and 5 days were examined for a single deer). The authors identified 9 behaviors: rumination, mastication during rumination, respiration during prolonged resting, browsing, startle events, grooming, and movement. We combined rumination, mastication during

rumination, respiration, and grooming into a single resting behavior, and browsing, startle events and movement into a foraging behavior (movement and startle events were rare and short in duration). We calculated the proportion of time between each GPS location that was spent in each of the two activities and compared these to the CRW model results. We only could compare the results from 3 of the deer, as the remaining 2 had poor fix success and CRW models were not fit for these individuals.

Deer condition and behavior

For deer captured in both December and March of each winter season, we examined the relationship between condition (fat and lean mass) at the start of each season with the seasonal changes in condition (i.e., December fat and mass compared to December-March change and March fat and mass compared to March-December change) using simple linear regression. In addition, we examined the relationship between seasonal activity budgets (derived from state based analyses of movements) and the change in fat and mass. We only examined the relationship between condition and foraging for 2012 and 2013 as the movement data from 2011 were sampled more coarsely resulting in non-comparable activity budget estimates.

Analysis of factors influencing foraging behavior

We next examined the influence of a suite of covariates (Table 6.1; Appendix 15) on activity budgets in each season using hierarchical beta regression in a Bayesian framework (see Appendix 16 for model formulations). The covariates examined were categorized as environmental, anthropogenic or individual characteristics (Table 6.1; Appendix 15), and were

calculated at two scales: the seasonal and daily ranges. The seasonal range was calculated

following the approach in Chapter 5, while daily ranges were assessed by buffering the path of

each animal by their mean movement distance across the entire season. Models were fit to the

proportion of time spent in the resting state. For the analysis at the daily scale, covariates varied

with each day. Thus, the regressions were fit with the intercepts and all coefficients (except the

static variables of fat, age, and study area) varying by individual. For the seasonal range scale,

only the coefficients for temporally dynamic covariates were fit as varying by individual, while

the coefficients for static covariates were fixed across individuals (Table 6.1). Prior to fitting the

regression models we assessed pairwise correlations among covariates and only included

covariates in the same model if they were correlated at $r < |0.7|$. In addition we standardized all

continuous covariates $\left(\frac{x - \bar{x}}{\sigma}\right)$.

We fit a set of models including only uncorrelated covariates (see Appendix 16 for model

structures) and compared models using the Watanabe-Akaike Information Criteria (WAIC;

Watanabe 2010), a Bayesian information criterion that asymptotically approximates leave-one-

out cross validation (Gelman et al. 2013, Hooten and Hobbs 2015). We fit models to each year

and season separately resulting in 6 sets of models (3 years, 2 seasons). We fit all models using

Stan (Stan Development Team 2014b) in the R statistical software using the package 'RStan'

(Stan Development Team 2014a). Stan uses Hamiltonian Monte Carlo (HMC) sampling and the

No U-Turn Sampler to fit Bayesian models with an algorithm that converges with substantially

fewer iterations than models using other platforms such as WinBugs or JAGS (Hoffman and

Gelman 2014). We obtained 5,000 HMC iterations for each model, discarding the first 500 as

burn-in. We ran each algorithm twice for each model with randomly selected starting values and

assessed convergence to the posterior distribution using the Gelman-Rubin diagnostic and by

examining traceplots of the HMC chains. For winter activity budgets we fit models to data from deer in both study areas. For the summer analysis we fit models only to the deer from the Ryan Gulch study area as the deer in North Ridge use a more dispersed summer range, making quantification of anthropogenic covariates infeasible.

RESULTS

Model results and evaluation

The CRW models clustered movements into two states, the first characterized by longer step lengths and the second by shorter step lengths. Turn angles were relatively similar across states (Appendix 17). Providing support for the fit of the model, posterior predictive checks revealed that our models were able to reproduce the autocorrelation structure present in the data, though some highly nuanced structure was not reproduced in all cases (Appendix 17). In addition, validation of behaviors using sound collar data indicated that the two states matched the behaviors of foraging and resting by deer (median difference in classification of behavior = 0.10). Two of the deer had several missing locations overlapping with the sound collar data and the majority of the locations for which the modeled and sound collar behaviors diverged were for these locations (median difference in classification of behavior = 0.16). For the one deer with sound collar data available for 5 full days, there was excellent agreement between the states (median difference in classification of behavior = 0.06; Appendix 17). Upon closer examination, the remaining locations that were poorly classified by the model fell during times when the deer were switching between behaviors, or when they were either foraging but moving very little (i.e.,

the step length for that time period was very short), or ruminating but the step lengths were of moderate distance, indicating the potential for misclassification induced by GPS error.

Deer condition and behavior

Examinations of the activity budgets resulting from the random walk models indicated strong seasonal patterns, with winter activity levels strongly influenced by snow depth (Tables 6.2 & 6.3; Fig. 6.2) and summer activity influenced by NDVI during some years (Table 6.4 & 6.5; Fig. 6.2). There was a strong negative relationship between individual deer body fat at the beginning of winter and the change in fat over the winter (this result was similarly strong when assessed using the proportion of the December fat lost by March; $\beta = -0.82$ $p < 0.0001$; Fig. 6.3), whereby deer that were fatter at the beginning of the winter lost a greater amount of fat and a greater proportion of their body fat over winter than those that had less fat at the beginning of winter. There was a similar negative relationship between body fat in March and fat change over summer ($\beta = -1.26$ $p < 0.001$; Fig. 6.3), whereby deer that had the least fat in March, gained the most fat over summer and gained more fat relative to their March fat. Nearly identical patterns existed for lean body mass, though the summer relationship was relatively weak and appeared to be influenced by a single data point (winter $\beta = -0.48$ $p < 0.0001$; summer $\beta = -0.31$ $p = 0.02$; Fig. 6.3). In addition, deer that had more fat in December lost less lean mass over winter ($\beta = 0.63$ $p < 0.001$; Fig. 6.4). During the summer there was no relationship between March fat and the change in summer body mass ($\beta = -0.1$ $p = 0.87$; Fig. 6.4), though there was a weak relationship between the amount of mass lost over the previous winter and the amount of mass gained over the ensuing summer with deer that had lost more lean mass over the winter putting on more mass over the summer ($\beta = -0.24$ $p = 0.08$; Fig. 6.5). Relative to foraging behavior, deer

that foraged more during the winter lost more fat over the winter but less lean mass (fat β = -13 p = 0.02; mass β = 12.41 p = 0.04; Fig. 6.6). Contrarily, during the summer deer that foraged more gained more fat (β = 12.7 p = 0.01; Fig. 6.6). There was no relationship between activity budget and lean mass gained over the summer (β = -2.74 p = 0.85; Fig. 6.6).

Analysis of landscape factors influencing foraging behavior

During winter, environmental covariates were primary drivers of variation in deer foraging behavior (Tables 6.2 & 6.3, Appendix 16). At both scales and during all years snow was a strong predictor of mule deer activity budgets with deer spending more of their days resting when snow was deeper (Fig. 6.2). Temperature also strongly influenced activity budgets during winter with deer spending more time foraging when temperatures were warmer in 2011 and 2013, though not during 2012. During the winter of 2012, a decoupling of the influence of snow and NDVI demonstrated that NDVI was not an important predictor of deer activity during that winter. Deer also spent more time resting when they were in areas with a greater proportion of treed landcover, and when they were in areas of greater ruggedness, though this covariate varied by year and scale (Tables 6.2 & 6.3; Appendix 16). No consistent patterns emerged relative to the amount of daylight.

Both individual characteristics and development covariates were less influential to deer activity budgets during winter (Tables 6.2 & 6.3; Appendix 16). Deer in the Ryan Gulch study area spent less time resting than deer in the North Ridge study area, while age and fat tended to be unimportant for predicting the daily activity budgets. Deer also did not strongly alter their activity budgets relative to well pads. However, during certain years deer did pattern their activity relative to facilities, pipelines, and roads. During 2011 and 2012, deer with a greater

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number of facilities in their seasonal range spent more time foraging. Deer spent more time foraging when pipeline density was higher at the daily scale in 2012, but more time resting when pipeline density was higher at the annual scale in 2013. Deer also spent more time foraging when road density was higher at the daily scale in 2013, but more time resting when road density was higher at the annual scale in 2011 and 2012.

Environmental factors did not influence deer summer activity budgets as consistently as during winter. Rather, the influence of environmental covariates tended to vary by year and spatial scale (Tables 6.4 & 6.5). Deer rested for more of the day when terrain ruggedness was high. Deer spent more time resting when NDVI was higher during 2011 and 2013 at both scales, but spent less time resting in these areas in 2012 at the annual scale (Tables 6.4 & 6.5). Deer also spent more time resting when temperatures were lower (Tables 6.4 & 6.5). All other environmental covariates were highly variable among years and scales, with no general patterns.

Deer also responded variably to anthropogenic development, with no clear patterns in response to well pads and facilities. However, deer consistently spent more time foraging when pipeline density was higher at the daily scale. Deer also spent more time foraging in all years with higher road density at the daily scale. Both roads and pipelines were not strong predictors at the annual scale. Fat in the following December was strongly related to activity budgets; deer that ended the summer in better condition spent less time resting (i.e., more time foraging) during the preceding summer. As in winter, the age of the deer was important only in certain years and its importance varied across scales indicating it was not a strong predictor of deer activity budgets.

DISCUSSION

The foraging decisions of animals reflect the tradeoffs between the costs and benefits of these decisions (Macarthur and Pianka 1966, Pyke et al. 1977). In seasonally variable environments, ungulates rely on stored energy reserves deposited during the summer to survive through the winter (Parker et al. 1999, Fauchald et al. 2004, Parker et al. 2009). Thus, during both seasons, the current and future need for these reserves must be accounted for when making foraging decisions. Mule deer in our study are clearly responding to these dynamics by adopting seasonally varying condition-dependent behavioral strategies in which the poorest condition individuals prioritized energy conservation during winter and energy acquisition during summer. These strategies were driven by differential availability of fat and protein stores and resulted in differential utilization of these stores depending on individual condition at the beginning of the season. Monteith et al. (2013) found nearly identical dynamics in mule deer in a different study system, and our behavioral analyses provide an underlying mechanism by which these strategies are undertaken. These results provide insight into the general relationship between condition, environment and behavior of long-lived highly mobile animals and elucidate how ungulates alter their behavior to optimize the use of environmental resources and their own reserves.

During winter, mule deer range is nutritionally insufficient to support deer in a positive energy balance (Wallmo et al. 1977) and deer eating poor diets cannot simply consume more to make up for inadequate nutrition (Tollefson et al. 2010). To account for the inability to meet their energetic requirements, deer utilized their energy reserves, relying on both fat and protein up to a certain threshold, at which point no further fat reserves were able to be used and only protein reserves were catabolized. Thus, deer with low fat reserves at the beginning of winter

used more of their protein reserves. These deer were at a nutritional disadvantage and thus adopted an energy conservation strategy, decreasing the amount of time spent foraging and likely reducing their active metabolic rate. Such strategies have been seen in penned white-tailed deer (Ozoga and Verme 1970), where individuals given the poorest diets fed for less time and did so more efficiently.

On the other end of the nutritional spectrum, those deer that came into the winter range with high fat reserves were able to use these reserves to meet their energetic requirements, while conserving more of their protein stores. The existence of different behavioral strategies that are condition-dependent indicates varying benefits to these strategies depending on the nutritional state of the animal. The use of fat and protein reserves in reindeer is sensitive to environmental stochasticity (Fauchald et al. 2004), and we hypothesize that stochasticity is playing an important role in our system as well. Movement during winter is costly, and increases disproportionately with increasing snow depth (Parker et al. 1984). Thus, opting for a behavioral strategy that requires more movement is risky when reserves are low. This hypothesis is supported by theoretical foraging work indicating that when resource are low foregoing foraging can be the optimal strategy, particularly when conservation of energy reserves is important (McNamara and Houston 1986). Deer in better condition might have sufficient reserves to adopt a strategy that is riskier if winter weather becomes severe or foraging resources are unavailable late in the season. For this hypothesis to hold, there would have to be some cost to switching repeatedly between behavioral strategies, otherwise deer would simply use whichever strategy was most effective for the current environmental conditions. In slight contrast to this strategy, the deer that are foraging for a greater amount of time might be able to be more selective in their foraging (as opposed to those in poor condition which might be prioritizing gross intake) or might be prioritizing the

acquisition of micronutrients that are important but not critical for their survival. Deer with fewer reserves simply might not be able to afford the risk of being as selective in their foraging.

That deer in the poorest condition did not use all of their fat reserves prior to catabolizing protein highlights the importance of maintaining some fat stores. Doe body fat is an important predictor of fawn survival (Lomas and Bender 2007). Further, deer might only be able to continue to catabolize protein as long as they have some fat stores remaining (Torbit et al. 1985). Thus, the conservation of fat reserves might be obligatory for deer survival and reproduction. Verme and Ozoga (1980) also showed that in white-tailed deer lipogenesis continued even when deer were near starvation, indicating that this process might be obligatory. If this is the case for mule deer, it would explain why deer with little fat in the beginning of winter did not utilize these stores.

During the summer, the foraging patterns of mule deer in our system were more straightforward, and match predictions of foraging theory in areas where resources are abundant. Deer with the lowest fat reserves foraged the most, and gained the most fat over the summer. However, there was no relationship between lean mass gain and foraging, indicating that all deer forage enough to replenish their protein reserves over the summer, but those that also have depleted their fat reserves must forage more to regain these stores. This interpretation is strengthened by the result that deer that lost more lean mass over winter gained more over the summer. The increased time spent foraging by individuals with the greatest energy deficit from winter could come at a cost to these individuals. Summer is the time when deer are rearing fawns, and if females are prioritizing their own energetic state over that of their fawns (e.g., as has been shown in bighorn sheep Festa-Bianchet and Jorgenson 1998) they could pay a reproductive cost during that season.

An important limitation of the results we present here is the lack of information on the presence of dependent young with does. Although nearly all females were pregnant in our study (~95% each year), fawn mortality likely influenced the patterns we documented. The presence of dependent young strongly influences the condition dynamics of mule deer does during summer (Monteith et al. 2013), and likely is driving the weaker relationship between March condition and change in condition over summer in our study.

Environmental and anthropogenic factors influencing foraging behavior

Although the condition of deer is clearly important in determining their broad-scale foraging patterns, landscape-level factors also influenced how much time deer spent foraging on a daily basis. Understanding these influences provides insight into the effect of dynamic landscapes on the condition-dependent strategies that we documented. During the winter, foraging behavior was most strongly and consistently influenced by climate. At both the daily and seasonal scale deer responded strongly to snow, resting more when snow was deeper. Snow is an important determinant of energy expenditure in mule deer (Parker et al. 1984), and it is not surprising that it is the primary driver of movement-based foraging decisions. Deer also responded strongly to temperature, foraging more when temperatures were higher. Winters in our study area are cold ($\bar{x}$ = 0° C across all years, range -25° – 18° C) and deer forage more when it is warmer, likely prioritizing resting and using thermal cover when it is colder. The influence of these climatic factors on foraging behavior provides a mechanistic link between behavior and population-level processes. During winter deer are susceptible to malnutrition and can face population declines when winter weather is severe (Unsworth et al. 1999). Although conditions during our study were generally favorable, the large decrease in foraging time seen across the population during

large snow events in the spring (Fig. 6.2) highlight that inclement weather can have substantial impacts to deer behavior, which we have shown to subsequently impact their energy budget. Lastly, deer in the Ryan Gulch study area foraged more than those in the North Ridge study area. The North Ridge area has a higher density of animals and thus might have higher habitat quality. If this is the case, deer in the Ryan Gulch area might need to forage more to meet what energetic demands they have during winter.

During the summer, deer also responded to climatic and landscape features. Deer modified their foraging behavior relative to temperature, resting more when temperatures were lower. Although other studies have shown ungulates to forage more during times of lower temperature during the summer due to the potential for heat stress (Aublet et al. 2009), temperatures in our area are moderate during the summer ($\bar{x} = 18.5°$ C across all years, range 0° – 26.7° C) and likely not high enough to elicit similar responses. Interestingly, the patterns of deer response to NDVI during the summer varied across years. We anticipated that deer would forage more during times of high NDVI to maximize resource intake. This was the case during 2012, however deer foraged less during times of high NDVI in 2011 and 2013. This result might indicate that when NDVI is high, deer can meet their nutritional requirements quickly and allocate time to other activities, such as caring for dependent young. Alternatively Wilmhurst et al. (1995) demonstrated that ungulates prefer foraging in areas of intermediate biomass (i.e. when an index such as NDVI would be below its maximum). Thus deer might have been responding to forage quality rather than biomass. During 2012 total summer precipitation was nearly half that of the other years (2011 total = 13.84 cm; 2012 total = 5.38 cm; 2013 total = 9.63 cm; http://www.nohrsc.noaa.gov/). The low precipitation during this year could have resulted in

a different relationship between forage biomass and quality, with deer subsequently increasing their foraging time when NDVI was highest.

Anthropogenic disturbance can greatly impact the foraging behavior of animals (Frid and Dill 2002). Deer in our system altered their foraging behavior relative to natural gas development, though they responded variably by year and season. During both the summer and winter, deer did not alter their behavioral patterns relative to well pads. However, deer in this area avoid well pads (Chapter 4) and thus they might be behaviorally mediating the impact of this development by avoiding them at a larger scale, with no additional effect at the scale of foraging decisions. Also during both seasons, though not all years, deer spent more time foraging when they were in areas with more pipelines and more roads. Both of these features require the removal of vegetation and some degree of reseeding, which could be attracting deer as a foraging resource. The fact that these patterns were stronger at the daily scale and not the annual scale strengthens this hypothesis, as deer moved to the areas with greater road and pipeline density during the days when they were foraging the most. Lastly, deer with more industrial facilities in their winter ranges spent less time foraging. Facilities are highly active features of natural gas development, and their presence might indicate higher overall human activity, leading to behavioral alterations of deer.

Conclusion

The nutritional and environmental context under which animals make their foraging decisions is crucial for understanding the constraints that have shaped their behaviors and ultimately their life history strategies. Deer in our system displayed condition-dependent behavioral strategies that have allowed them to adapt to conditions that vary immensely between and within seasons.

These strategies likely evolved to maximize over-winter survival when deer have a negative energy balance and are susceptible to mortality from malnutrition (Unsworth et al. 1999). Any impacts that alter the environment could reduce the effectiveness of these strategies. In our study area deer primarily altered their behavior in response to climatic factors and secondarily to human development. If development becomes more intense, there could be greater behavioral alterations than we documented. These issues will be more salient during winters with consistently low temperatures and/or deep snow as nutritional constraints will be more severe, reducing the amount of time available for foraging, and consequently causing a further reduction in condition. Although summer range appeared to have sufficient forage to meet nutritional needs of deer in our study, years of high drought, particularly following harsh winters, could impact deer at a population level. These issues are likely to become more pertinent as climate change alters moisture regimes and changes yearly temperature patterns.

TABLES

Table 6.1. Names, descriptions, sources, pixel size (when available), and the unit of time over which the covariates were available for covariates used in regression models examining foraging behavior of female mule deer in the Piceance Basin of Colorado, USA.

Covariate	Description	Pixel size	Temporal scale	Source
Environmental				
Light	Number of hours of between sunrise and sunset	NA	Daily	http://aa.usno.navy.mil/data/docs/RS_OneYear.php
NDVI	Normalized Difference Vegetation Index averaged over range	1 km × 1 km	Every 10 days	http://www.vito-eodata.be/
Snow	Snow depth averaged over range	30 m × 30 m	Daily	See Appendix 15
Tree	Proportion of range comprised of treed land cover	25 m × 25 m	NA	http://ndis.nrel.colostate.edu/coveg/
TRI	Terrain ruggedness index. Squared difference between elevation in each	30 m × 30 m	NA	Calculated from digital elevation model from http://seamless.usgs.gov

	cell and 8 neighbors averaged over entire range			
Temp	Average temperature at weather station closest to study site	NA	Daily	http://www.nohrsc.noaa.gov
Anthropogenic				
Drill	Density of well pads with wells being actively drilled	NA	NA	See Appendix 15
Prod	Density of well pads with producing wells only	NA	NA	See Appendix 15
Facilities	Density of industrial facilities	NA	Annual	See Appendix 15
All rds	Density of all roads	NA	NA	See Appendix 15
Major rds	Density of primary roads	NA	NA	See Appendix 15
Pipelines	Density of pipelines	NA	NA	See Appendix 15
Individual				
Age	Age at capture	NA	Annual	Measured during capture

Fat	Percent ingesta-free body fat	NA	Annual	Measured during capture
Study	Study are (North Ridge, or Ryan Gulch) in which the animal was captured	NA	NA	NA

Table 6.2. Covariates, median posterior coefficient values and the proportion (Prop.) of posteriors falling above and below 0 for beta regression models with lowest WAIC values fit to activity budgets of mule deer in the Piceance Basin of Colorado during winter, with covariates calculated at the daily range scale.

Covariate	Median	Prop. < 0	Prop. > 0
M1 2011			
Intercept	-0.28	0.98	0.02
Facilities	0.00	0.61	0.39
Snow	0.04	0.00	1.00
TRI	0.00	0.57	0.43
Pipelines	-0.01	0.77	0.23
Tree	0.01	0.11	0.89
All rds	0.00	0.58	0.42
Light	-0.02	0.58	0.42
Temp	-0.05	1.00	0.00
Age	0.02	0.40	0.60
Fat	0.13	0.08	0.92
Study	-0.59	1.00	0.00
M1 2012			
Intercept	0.24	0.03	0.97
Facilities	-0.01	0.82	0.18
Snow	0.12	0.00	1.00
TRI	0.06	0.00	1.00
Pipelines	-0.03	0.89	0.11

Tree	0.06	0.00	1.00
All rds	0.00	0.56	0.44
Light	-0.01	0.56	0.44
NDVI	0.00	0.37	0.63
Temp	0.01	0.23	0.77
Age	-0.04	0.80	0.20
Fat	0.00	0.52	0.48
Study	-0.40	1.00	0.00

M2 2013

Intercept	0.02	0.42	0.58
Facilities	0.00	0.34	0.66
Snow	0.21	0.00	1.00
TRI	0.06	0.00	1.00
Tree	0.06	0.00	1.00
Major rds	-0.02	1.00	0.00
Light	-0.14	0.98	0.02
Temp	-0.08	1.00	0.00
Age	-0.06	0.83	0.17
Fat	-0.01	0.60	0.40
Study	-0.12	0.83	0.17

Table 6.3. Covariates, median posterior coefficient values and the proportion (Prop.) of posteriors falling above and below 0 for beta regression models with lowest WAIC values fit to activity budgets of mule deer in the Piceance Basin of Colorado during winter, with covariates calculated at the annual range scale.

Covariate	Median	Prop. < 0	Prop. > 0
M1 2011			
Intercept	-0.33	0.94	0.06
Drill	-0.01	0.69	0.31
Prod	-0.06	0.67	0.33
Snow	0.03	0.00	1.00
Light	-0.08	0.73	0.27
Temp	-0.05	1.00	0.00
Major rds	0.15	0.08	0.92
TRI	-0.16	0.88	0.12
Age	0.00	0.51	0.49
Fat	0.06	0.28	0.72
Tree	0.20	0.03	0.97
Facilities	-0.17	0.93	0.07
Study	-0.54	0.97	0.03
M2 2012			
Intercept	0.19	0.16	0.84
Prod	0.01	0.44	0.56
Snow	0.13	0.00	1.00
NDVI	0.01	0.28	0.72

Light	-0.04	0.71	0.29
Temp	0.01	0.29	0.71
All rds	0.13	0.03	0.97
TRI	-0.04	0.70	0.30
Age	-0.08	0.93	0.07
Fat	-0.02	0.65	0.35
Tree	0.12	0.08	0.92
Facilities	-0.08	0.88	0.12
Pipelines	-0.05	0.72	0.28
Study	-0.29	0.90	0.10

M3 2013

Intercept	-0.09	0.66	0.34
Prod	0.01	0.46	0.54
Snow	0.24	0.00	1.00
Light	-0.24	1.00	0.00
Temp	-0.08	1.00	0.00
Pipelines	0.18	0.08	0.92
TRI	0.22	0.10	0.90
Age	-0.05	0.72	0.28
Fat	-0.03	0.70	0.30
Tree	0.07	0.29	0.71
Facilities	-0.05	0.68	0.32

Study	0.03	0.46	0.54

Table 6.4. Covariates, median posterior coefficient values and the proportion (Prop.) of posteriors falling above and below 0 for beta regression models with lowest WAIC values fit to activity budgets of mule deer in the Piceance Basin of Colorado during summer, with covariates calculated at the daily range scale.

Covariate	Median	Prop. < 0	Prop. > 0
M2 2011			
Intercept	-0.83	0.96	0.04
Facilities	-0.02	0.72	0.28
TRI	0.13	0.00	1.00
Pipelines	-0.06	0.95	0.05
Tree	-0.09	0.94	0.06
Major rds	-0.08	0.94	0.06
NDVI	0.08	0.01	0.99
Light	0.45	0.22	0.78
Temp	-0.05	0.98	0.02
Age	0.11	0.40	0.60
Fat	-0.87	0.97	0.03
M2 2012			
Intercept	0.49	0.00	1.00
Facilities	-0.04	0.71	0.29
TRI	0.12	0.00	1.00
Pipelines	-0.07	0.94	0.07
Tree	0.00	0.46	0.54
Major rds	-0.03	0.87	0.13

NDVI	0.00	0.58	0.42
Light	-0.44	1.00	0.00
Temp	-0.02	0.95	0.05
Age	-0.13	0.92	0.08
Fat	-0.46	1.00	0.00

M2 2013

Intercept	0.24	0.29	0.71
Facilities	-0.02	0.85	0.15
TRI	-0.02	0.72	0.29
Pipelines	-0.06	0.96	0.04
Tree	-0.02	0.63	0.37
Major rds	-0.10	0.99	0.01
NDVI	0.06	0.03	0.97
Light	0.08	0.42	0.58
Temp	-0.01	0.76	0.24
Age	-0.40	0.82	0.18
Fat	-0.45	0.85	0.15

Table 6.5. Covariates, median posterior coefficient values and the proportion (Prop.) of posteriors falling above and below 0 for beta regression models with lowest WAIC values fit to activity budgets of mule deer in the Piceance Basin of Colorado during summer, with covariates calculated at the seasonal range scale.

Covariate	Median	Prop. < 0	Prop. > 0
M2 2011			
Intercept	-0.69	0.92	0.08
Prod	1.30	0.05	0.95
NDVI	0.07	0.04	0.96
Light	-0.22	0.64	0.36
Temp	-0.05	0.96	0.04
Age	-0.86	0.90	0.10
Fat	-0.97	0.96	0.04
Facilities	0.54	0.20	0.80
TRI	0.97	0.11	0.89
Tree	-0.30	0.66	0.34
All rds	0.29	0.30	0.70
Pipelines	-1.33	0.96	0.04
M2 2012			
Intercept	0.60	0.00	1.00
Prod	-0.21	0.89	0.11
NDVI	-0.02	0.80	0.20
Temp	-0.41	1.00	0.00
Light	-0.01	0.81	0.19

Age	-0.10	0.76	0.24
Fat	-0.43	1.00	0.00
Facilities	0.17	0.15	0.85
TRI	0.04	0.40	0.60
Tree	-0.28	0.93	0.07
All rds	-0.12	0.81	0.19
Pipelines	0.18	0.17	0.83

M2 2013

Intercept	0.79	0.00	1.00
Prod	-0.32	0.70	0.30
NDVI	0.11	0.00	1.00
Light	-0.13	0.62	0.38
Temp	-0.01	0.79	0.21
Age	-0.03	0.53	0.47
Fat	-0.05	0.56	0.44
Facilities	-0.50	0.93	0.07
TRI	-0.25	0.77	0.23
Tree	0.58	0.04	0.96
All rds	-0.26	0.82	0.18

FIGURES
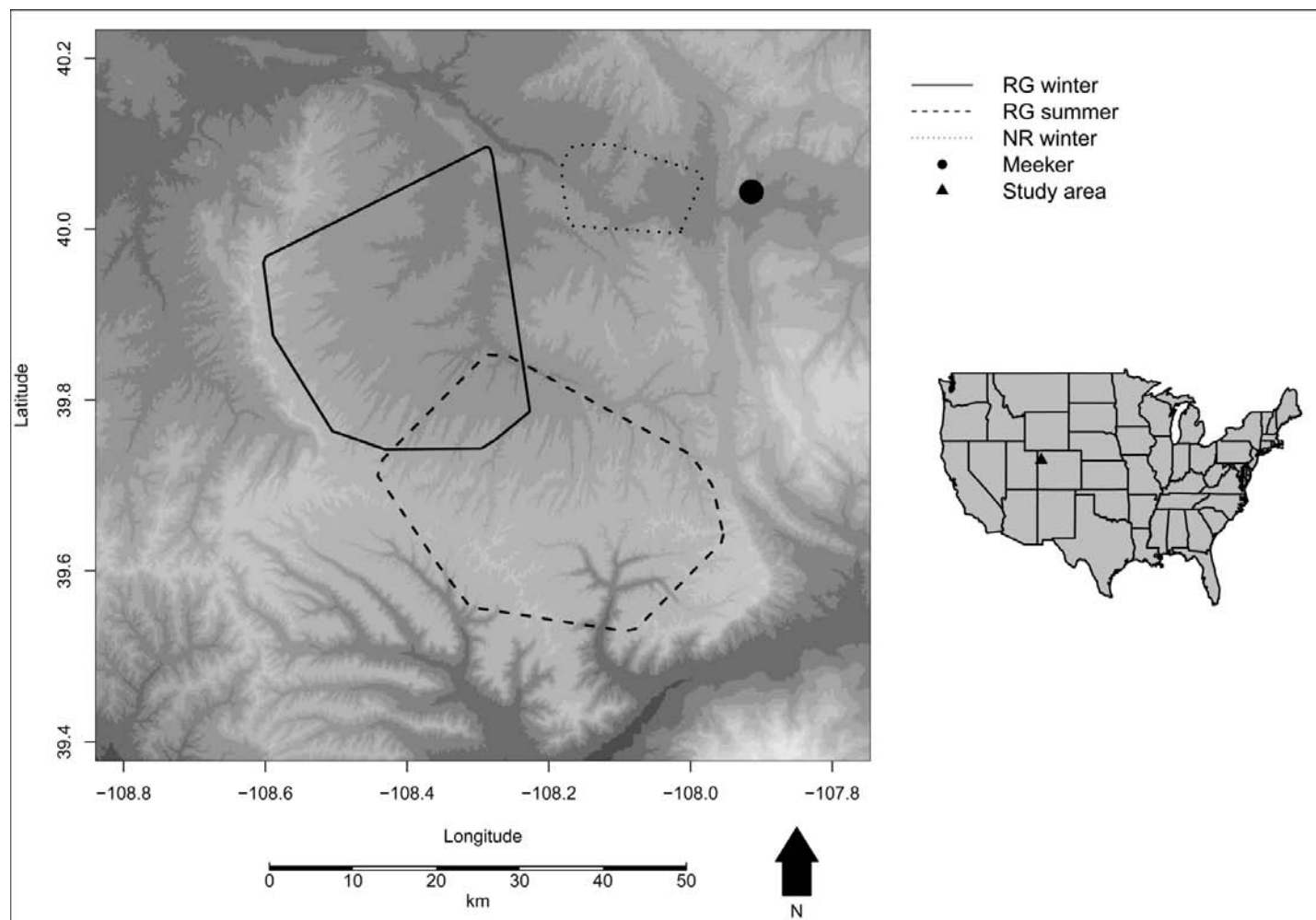
Figure 6.1. Location of study area within the United States, map of study area, and summer and winter range outlines for mule deer in the Piceance Basin, Colorado, USA.
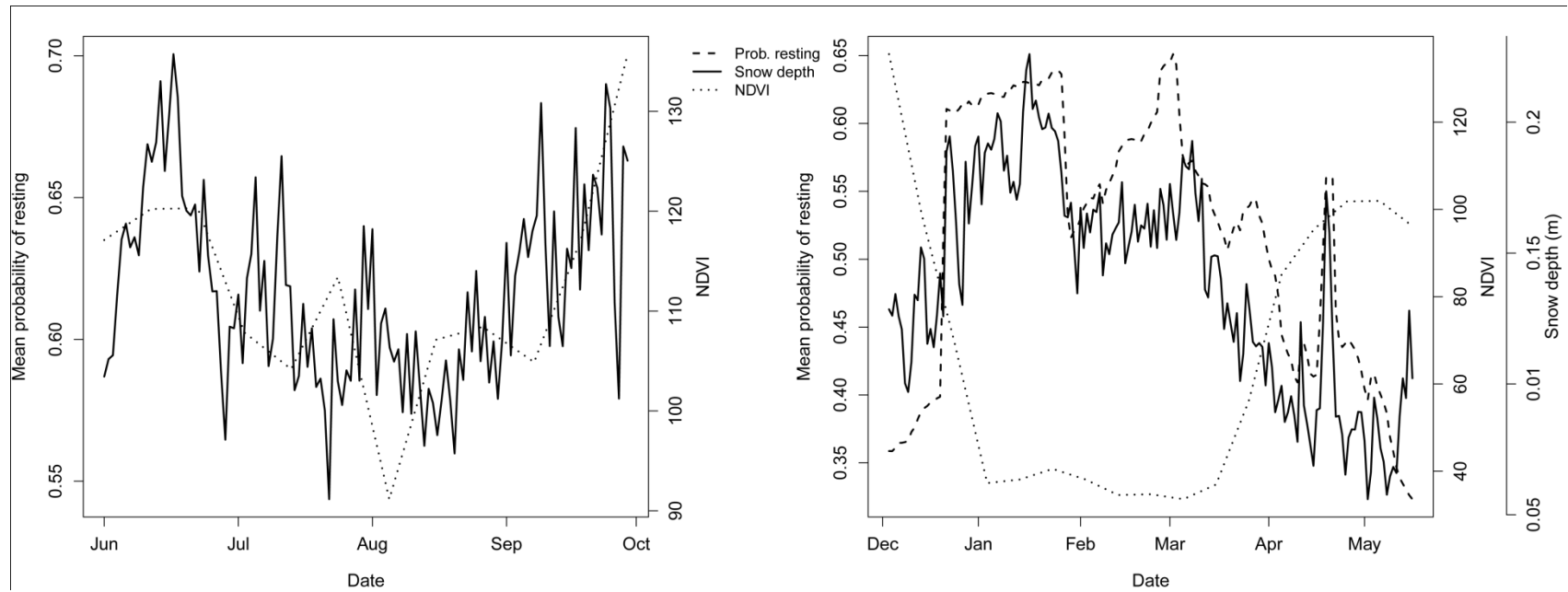
Figure 6.2. Probability of being in the resting state averaged across all individuals and locations during 2013 as a function of date during the (A) summer, and (B) winter plotted with average snow depth as a function of date. Probabilities were estimated using a discrete-time correlated random walk model fit to adult female mule deer movement data.

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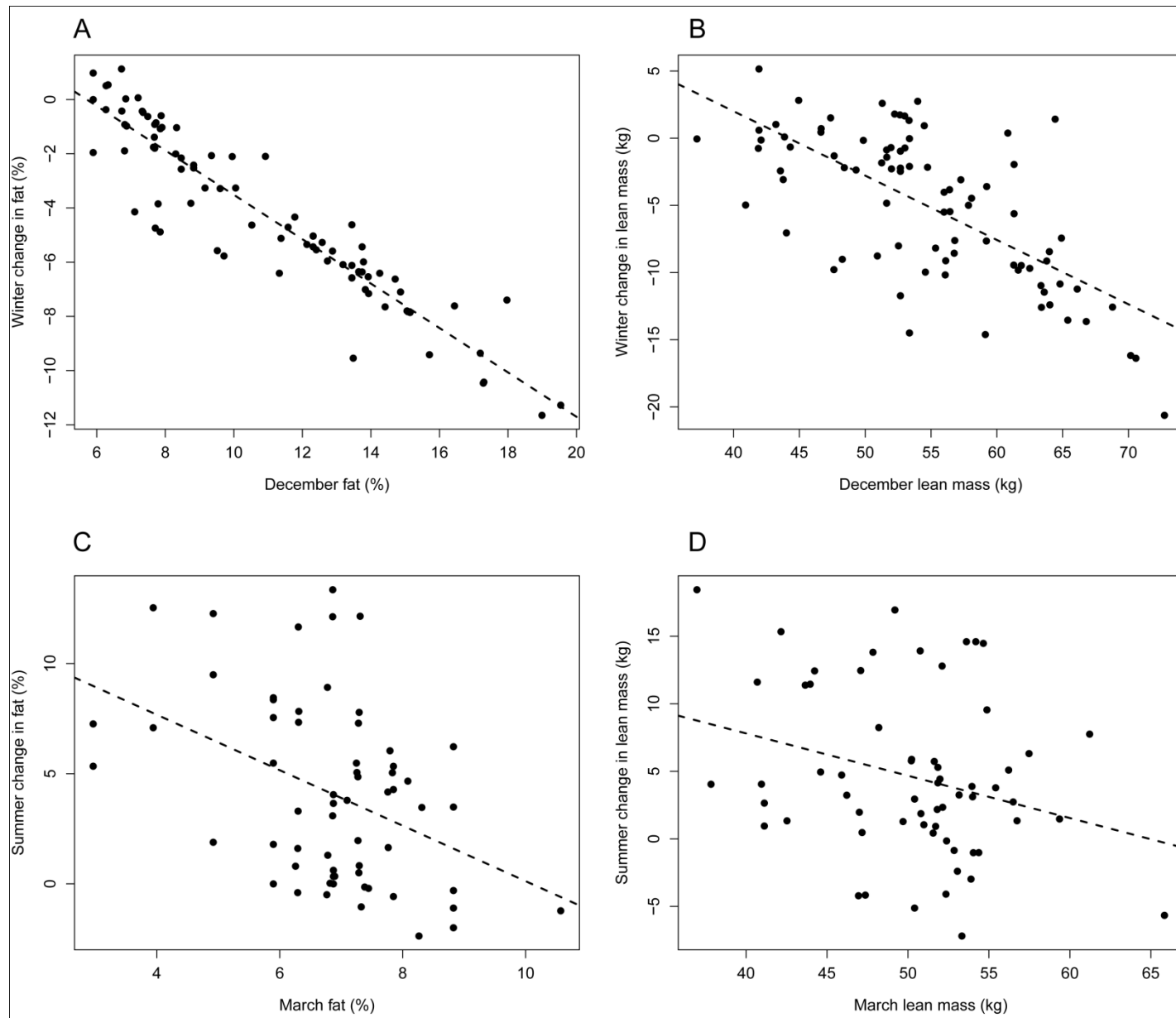
Figure 6.3. Change in (A) over-winter percent body fat as a function of December body fat (β = -0.82, $p < 0.0001$), (B) over-winter lean body mass as a function of December lean body mass (β = -0.48, $p < 0.0001$), (C) over-summer percent body fat as a function of March body fat (β = -1.26, $p < 0.001$), and (D) over-summer lean body mass as a function of March lean body mass (β = -.31, $p < 0.05$), along with lines of best fit for female mule deer in the Piceance Basin, Colorado, USA.
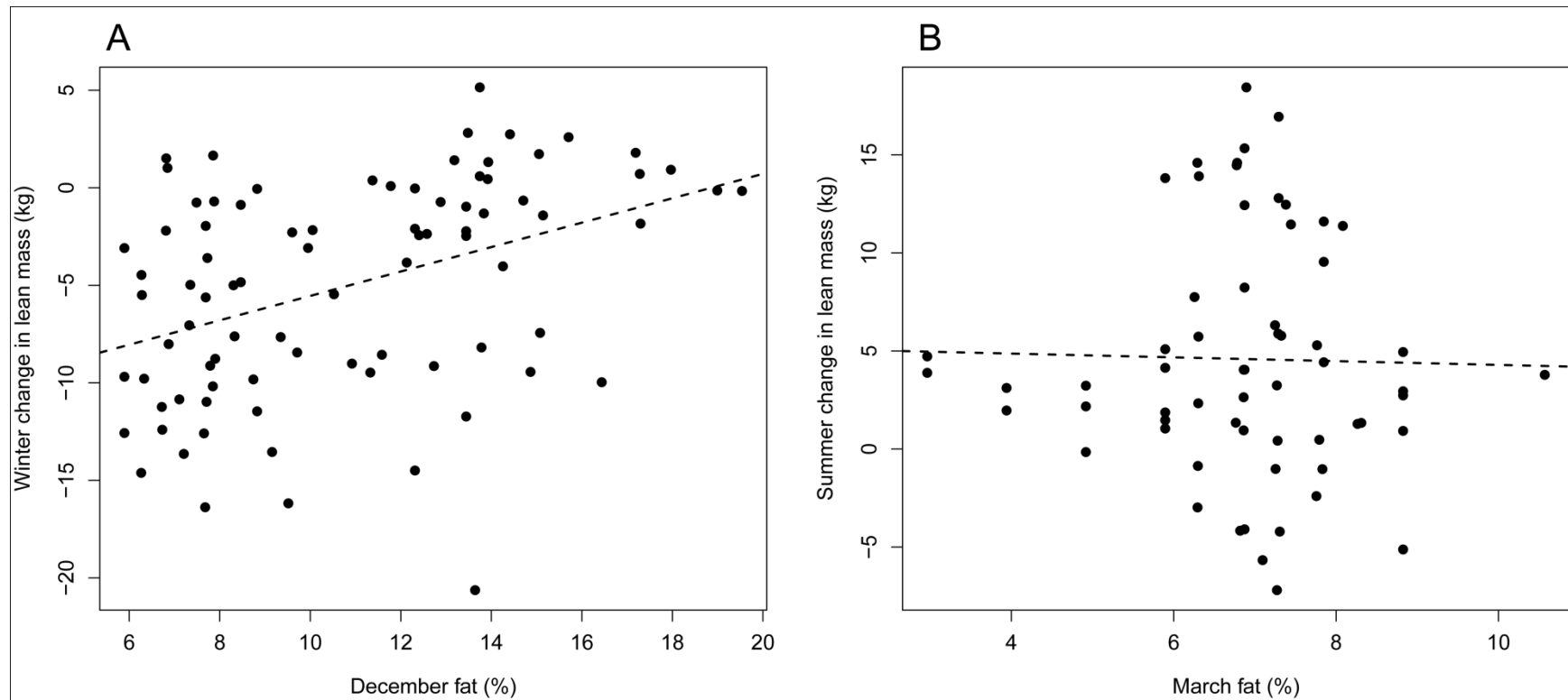
Figure 6.4. Change in (A) over-winter lean body mass as a function of December percent body fat ($\beta = 0.63$, $p < 0.001$), and (B) over-summer lean body mass as a function of March percent body fat ($\beta = -.1$, $p = 0.87$), along with lines of best fit for female mule deer in the Piceance Basin, Colorado, USA.
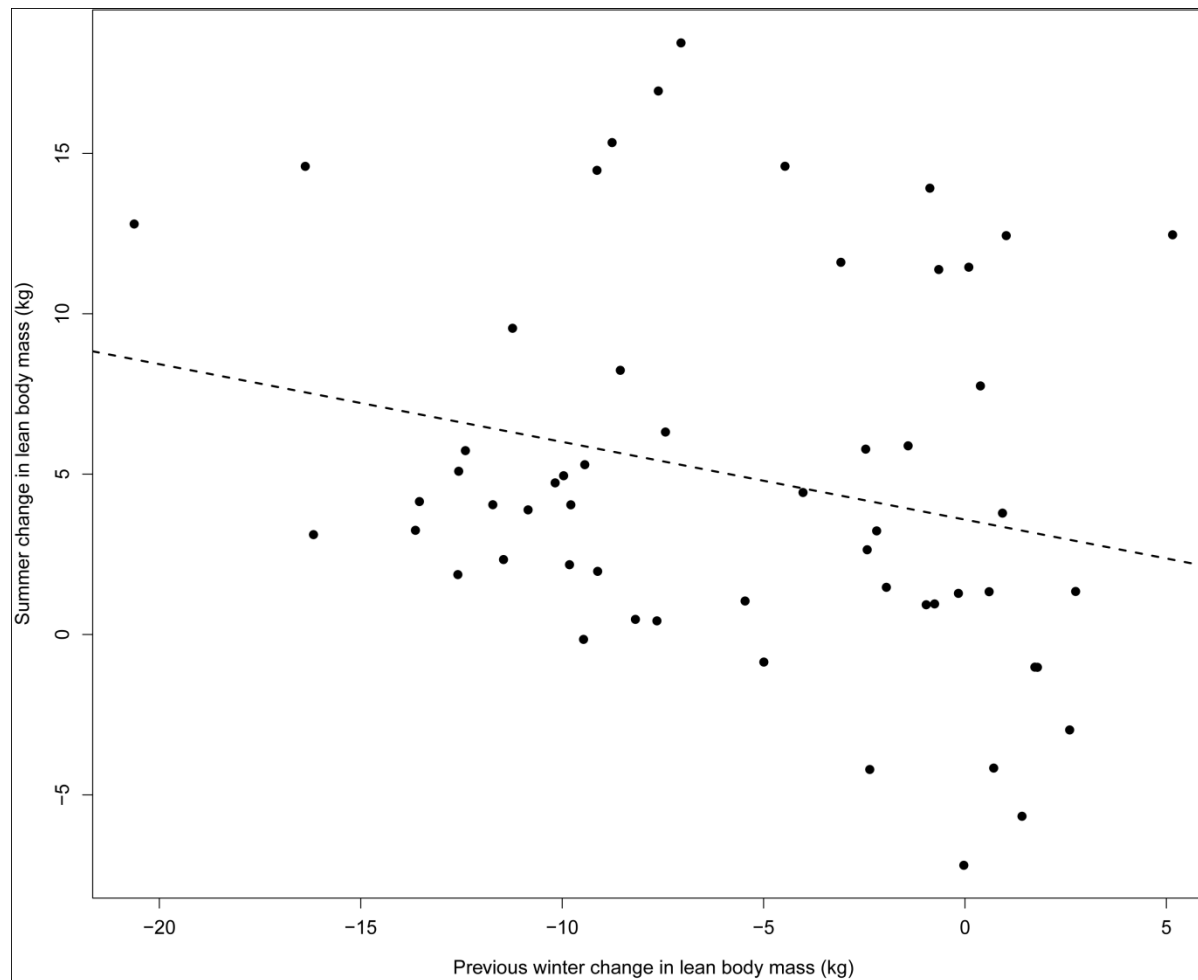
Figure 6.5. Change in over-summer lean body mass as a function of previous winter's change in lean body mass (β = -0.24, p = 0.075) and line of best fit for female mule deer in the Piceance Basin, Colorado, USA.
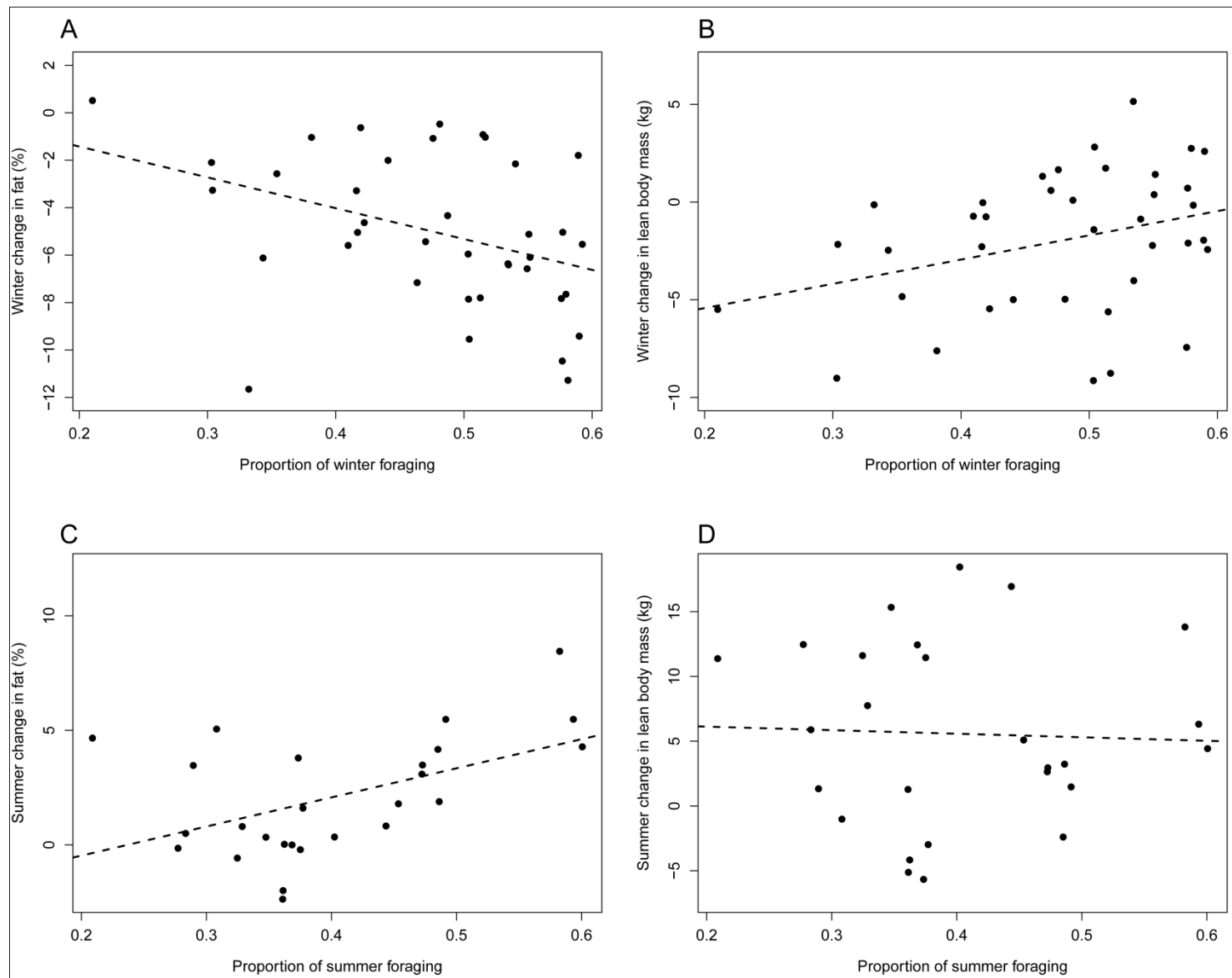
Figure 6.6. Change in (A) over-winter change in body fat percent as a function of the proportion of the winter spent in the foraging state ($\beta = 13$, $p < 0.05$), (B) over-winter change in lean body mass as a function of the proportion of the winter spent in the foraging state ($\beta = 12.41$, $p < 0.05$), (C) over-summer change in body fat percent as a function of the proportion of the summer spent in the foraging state ($\beta = 12.70$, $p < 0.05$), (D) over- summer change in lean body mass as a function of the proportion of the summer spent in the foraging state ($\beta = -2.74$, $p = 0.85$), along with lines of best fit for female mule deer in the Piceance Basin, Colorado, USA. Proportion of time spent foraging was estimated from discrete-time correlated random walk models fit to step length and turn angle data.

CHAPTER SEVEN

FINE-SCALE GENETIC CORRELATES TO CONDITION AND MIGRATION IN A WILD

CERVID

INTRODUCTION

Understanding variation in phenotypic traits related to fitness in wild populations is fundamental

to the study of evolution and ecology. Such traits can be related to genetic variation at relatively

fine spatial scales, and knowledge of these relationships can provide insight into important eco-

evolutionary processes such as inbreeding depression, local adaptation, population structure, and

speciation (Kupper et al. 2010, Olano-Marin et al. 2011, Shafer and Wolf 2013, Shafer et al.

2014). Moreover, these relationships can have implications for developing and implementing

conservation and management plans that strive to account for evolutionary processes (e.g.,

maintenance of gene flow through protection of corridors, or minimizing possible effects of

inbreeding).

Relationships between fine-scale genetic variation and phenotypic traits have been

identified using a variety of methods. Chief among these in wild populations are heterozygosity-

fitness correlations (HFCs; see Chapman et al. 2009), and correlations amongst genetic

differentiation and phenotypic or ecological divergence (Shafer and Wolf 2013). Heterozygosity-

fitness correlations are typically calculated between

heterozygosity at neutral loci and phenotypic traits presumed to be proxies for fitness (Szulkin et

al. 2010). Correlations can occur with a multi-locus heterozygosity (MLH) metric, indicating a

general genome-wide effect of inbreeding, or heterozygosity at a single locus (single-locus heterozygosity; SLH), indicating local (either direct or indirect) effects due to linkage to a gene that affects fitness (Hansson et al. 2004). For the latter, individual neutral markers are hypothesized to show associative overdominance as a result of the consequences of deleterious alleles or a fitness advantage at those linked loci (Frydenberg 1963, Houle 1989, David et al. 1995, David 1997, Pamilo and Palsson 1998). Screening for HFCs can be described as a tantalizing pursuit; significant relationships are rarely found and care must be used with interpretation as overall effect sizes often are variable and small (Chapman et al. 2009, Kardos et al. 2013), and numerous concerns (but also caveats) related to the HFC exist (Szulkin et al. 2010). Given the potential for false positives with SLH correlations, confidence in these relationships can be bolstered by appropriate statistical analyses and by examining the location of loci on the annotated genome of a related species that might provide post-hoc links to causative agents (e.g., Von Hardenberg et al. 2007, Kupper et al. 2010, Kardos et al. 2013).

In slight contrast, correlations between genetic differentiation and phenotypic (or ecological) divergence have been identified across taxa and appear to be relatively robust (Shafer and Wolf 2013, Sexton et al. 2014). Although this pattern is generally regarded as evidence for local adaptation (Nosil 2012), ancestral (allopatric) divergence and secondary contact can confound interpretations of this correlation (Bierne et al. 2013) and, similar to HFCs, must be factored into interpretations and models. But beyond these caveats, correlations between phenotypic traits and both genetic diversity and differentiation can provide important indications of inbreeding and local adaptation that should be considered by managers (Shafer et al. 2014).

Mule deer ecology and evolution

Cervids (family *Cervidae*) are an ecologically important group of ungulate that have been the focus of numerous investigations into the relationship between genetic variation and phenotypic traits. Da Silva et al. (2009) showed that juvenile roe deer (*Capreolus capreolus* L.) survival was correlated with MLH; likewise, red deer (*Cervus elaphus* L.) birth weight, neonatal survival, and lifetime breeding success increased significantly with heterozygosity (Coulson et al. 1998, Slate et al. 2000), and individuals with the smallest antlers tended to have lower heterozygosity (Perez-Gonzalez et al. 2010). Furthermore, studies have shown correlations between genetic differentiation and social groups in white-tailed deer (Odocoileus virginianus Zimm.; Miller et al. 2010), and niche overlap in mule deer (Odocoileus hemionus Raf.; Pease et al. 2009).

Among cervids, mule deer present an interesting species for which to examine correlations between phenotypic traits and genetic variation. Latch et al. (2009, 2014) showed that across their range there are multiple phylogeographic lineages that presumably represent different refugia, though the species shows minimal population-level genetic structure at large geographic scales (Cullingham et al. 2011b, Powell et al. 2013). Female mule deer also display fine-scale genetic structuring, likely due to the existence of related social groups (Cullingham et al. 2011b, Colson et al. 2013). In addition, hybridization can occur with white-tailed deer, with fairly widespread genetic introgression resulting (Carr et al. 1986, Cathey et al. 1998). Mule deer also exhibit substantial variation in important phenotypic traits such as body size and migratory behavior, both across their range (Anderson 1981, Wallmo 1981), and within populations (Monteith et al. 2011, Lendrum et al. 2013). Lastly, mule deer are the subject of extensive management programs throughout North America, due to their importance as a game species (e.g., it was estimated that over 30,000 mule deer were harvested in the state of Colorado in 2013 [Colorado Parks and Wildlife 2014]).

Both the aforementioned phenotypic traits are of paramount importance for survival and reproduction in this species. Condition is a fitness proxy as individuals rely heavily on fat and protein stores for survival on winter range when forage quality is low (Wallmo et al. 1977, Torbit et al. 1985). Body fat also influences annual survival of adult females (Bender et al. 2007), pregnancy and twinning rates (Johnstone-Yellin et al. 2009, Tollefson et al. 2010), and the probability of a female rearing a fawn through the summer (Johnstone-Yellin et al. 2009). Deer across much of their range migrate from high altitude, productive summer range to low altitude winter range and back again in the spring. Migrations typically match changes in resource availability (Fryxell and Sinclair 1988), with mule deer attempting to optimize migratory timing relative to both plant productivity and weather (snow depth and temperature) on their summer range (Monteith et al. 2011, Lendrum et al. 2013). The timing of migratory onset is clustered around a few weeks each year, but individuals show different strategies in terms of early or late onset dates (Monteith et al. 2011, Lendrum et al. 2013). Thus migration timing is of clear interest in understanding the ecology of this species and, importantly, recent work has identified a clear genetic component to differences in this trait in other taxa (Ruegg et al. 2014, Toews et al. 2014).

Both individual condition and migration are of interest to wildlife managers as recent anthropogenic development may threaten migratory routes for mule deer (Sawyer et al. 2005, Sawyer et al. 2009b), and climate change could cause trophic mismatches (Post and Forchhammer 2008), with phenotypic plasticity in migration being suggested as a potential buffer for mule deer against this process (Monteith et al. 2011). The importance of winter condition to deer survival has led to active research into means of improving winter condition through habitat manipulation and supplemental feeding (Bishop et al. 2009, Bergman et al. 2014a). The existence of genetic correlations to these traits could provide insight into the

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effectiveness of management programs and aid managers in making decisions in light of evolutionary processes.

Here, we examined the relationship between genetic variability and phenotypic traits in a wild mule deer population of the Piceance Basin, Colorado. Using an extensive dataset consisting of over 100 individual animals, we combined phenotypic, behavioral (global positioning system [GPS]), and genetic data to: (i) examine whether genetic differentiation was correlated to migration timing; (ii) screen for specific mitochondrial haplotypes associated with migration timing; and (iii) test if heterozygosity (multi-locus and single locus) was associated with body mass and fat. We discussed the results in light of the phylogeographic history of mule deer and the metabolic role of the mitochondrion, and highlight the importance of considering evolutionary processes in the management of this species.

METHODS

Sample collection and DNA extraction

We captured adult (>1 year old) female mule deer using helicopter net gunning in four winter range study areas in the Piceance Basin of Northwestern Colorado (Fig. 7.1). Deer were captured in either December 2010 or March 2011. These dates were chosen because during December deer have recently migrated from summer range and typically are in their best physical condition, while March represents the end of winter when deer typically are in their worst condition. Deer were transferred to processing sites where we weighed them using a portable scale, estimated body condition by palpating the rump (Cook et al. 2001, 2007, 2010) and measured the thickness of their subcutaneous rump fat and longissimus dorsi muscle using a

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portable ultrasound (Stephenson et al. 1998, Cook et al. 2001, Stephenson et al. 2002). The above measurements were used to calculate the percent ingesta-free body fat (hereafter fat) of each deer following Cook et al. (2010). Deer were fit with store-on-board GPS radio collars (Advanced Telemetry Systems, Isanti MN, USA) set to attempt a relocation on one of three schedules (once every 5 hours, once every 60 minutes, or once every 30 minutes - meaning the relocation schedules varied by individual). Blood samples were taken for genetic analysis and DNA was extracted using the DNeasy™ Blood and Tissue Kit (Qiagen, Inc., Valencia, CA, USA) following the manufacturer's protocol.

Microsatellite genotyping and DNA sequencing

We amplified 17 microsatellite loci using a previously optimized multiplex reaction from Cullingham et al. (2011a) and single PCRs. The mitochondrial control region was sequenced using both the primers from Latch et al. (2009) and LGL215 and ISM015 from Purdue et al. (2006). PCR conditions and basic population genetic analyses are available in Appendices S1, S2.

For the microsatellite data, we first used STRUCTURE 2.3.3 (Pritchard et al. 2000) to assess genetic structure (1,000,000 iterations with 25% removed as a burn-in repeated five times for each number of possible populations (*k*) ranging from 1 to 5). We assumed an admixed model with correlated allele frequencies (Falush et al. 2003) and used the LOCPRIOR parameter to allow location information to assist in the clustering. Next, we calculated overall MLH as the average of heterozygosity at each locus, and SLH as binary variables indicating heterozygosity (1) or homozygosity (0) at each locus. Pairwise relatedness between all individuals was estimated with the Queller and Goodnight (QG) relationship coefficient using the software

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SPAGEDI v.1.3 (Hardy and Vekemans 2002). We also constructed a coancestry matrix using the software MOL_COAN v.3 (Fernandez and Toro 2006). Here, a simulated annealing approach was used to create virtual common ancestors of the genotyped individuals, producing pedigree-like relationship coefficients. Model parameters consisted of 200 steps with 5,000 solutions tested per step, an initial temperature of 0.01 and increase of 0.75. We simulated 2 previous generations, each consisting of 1,000 males and 1,000 females.

For mitochondrial DNA (mtDNA; conducted on a subset of individuals), we constructed a minimum-spanning tree among haplotypes using ARLEQUIN v. 3.5.1.3 (Excoffier and Lischer 2010) and edited it with HapStar v0.7 (Teacher and Griffiths 2011). Neighbor-joining analysis using pairwise deletion and both *P* and *K2* distances was conducted using the software package MEGA v.5 (Tamura et al. 2011). Bayesian analysis was conducted in MrBayes v.3.1.2 (Huelsenbeck and Ronquist 2001) with a model of nucleotide substitution determined from Modeltest v.3.07 (Posada and Crandall 1998). For the Bayesian phylogenetic analysis we used default priors with two independent runs of four chains (three heated) run for 10,000,000 generations, with the first 25% discarded as a burn-in. Confidence in topologies was evaluated based on 1,000 bootstrap replicates (for the neighbor-joining) or posterior distributions. All three methods were compared to identify common mitochondrial haplogroups.

Genetic correlates to phenotypic traits

Both migration and body condition are phenotypic traits that are important to the fitness of mule deer. However, only condition can be thought of as a proxy for fitness. Thus, we used two separate analytical frameworks to examine genetic correlations with these traits. For migration we examined the relationship between mitochondrial haplotypes and genetic differentiation to

determine if there was a genetic component to the timing of migration (an isolation-by-ecology analysis, sensu Shafer and Wolf 2013). For body condition, a fitness proxy, we followed the general HFC framework discussed in Chapman et al. (2009).

Genetic-migration correlates

After GPS radio collars were recovered and data were downloaded, we calculated the initiation and termination dates of spring and fall migration (i.e., the dates at which deer started or finished their migration) in ArcMap 10.1 (Environmental Systems Research Institute, Redlands, CA, USA). Migration was demarcated as the time period during which deer traveled between their winter and summer home ranges. Home ranges were determined by outlining a minimum convex polygon around all locations that occurred prior to directed movement, without return, away from the summer or winter range areas.

We first examined the relationship between mtDNA haplogroup (derived from haplotype and phylogenetic analyses) and the dates of spring and fall migrations. For this analysis, we corrected the Julian date of migration to the earliest date among all individuals. The resulting data represented a count of the number of days since the earliest arriving or leaving migrant had terminated or initiated their migration. These data were analyzed using negative binomial regression (see Appendix 20 for model formulation). We included covariates for the mtDNA haplogroup to which each deer was assigned (categorical) as well as a covariate for the age of the animal and binary covariates indicating winter range study area (i.e., three separate covariates indicating if the deer was from a winter range study area [1] or not [0]). Before models were fit, correlations among covariates were examined to assess collinearity (no predictors were correlated at $|r| > 0.7$) and age was standardized $\left(\frac{x - \bar{x}}{\sigma_x}\right)$, a common procedure in regression to aid

in interpretability of coefficient estimates (Gelman and Hill 2007). We fitted all models under a Bayesian framework in JAGS (Plummer 2012) and R 3.0.1 (R Core Team 2013), using the 'rjags' package (Plummer 2013). See Appendix 20 for specifics of model runs and assessment of convergence. To assess the fit of the models we calculated residuals (observed – predicted values) and plotted them against the fitted values to examine any potential patterns in residuals.

Secondly, we examined correlations between genetic relatedness metrics and similarity in migration using Mantel tests. For this analysis, we calculated absolute pairwise distances (calculated in days) between each individual's migration termination or initiation dates leaving us with four matrices representing differences in migration timing for spring and fall. The relationships between relatedness indices (QG and coancestry) and migratory behavior (dates) were evaluated in R 3.0.1 (R Core Team 2013) using Mantel tests (Mantel 1967) under 10,000 permutations as implemented by the Ecodist library (Goslee and Urban 2007). Here a comparison is made between relatedness and the difference in migration timing and thus a negative relationship is expected if there is a genetic signature (i.e., more closely related individuals have more similar migration timing). To account for similarities among individuals inhabiting similar areas or grouping together we ran two partial Mantel tests controlling for the distance between the centroids of individuals' winter range and summer range (Fig. 7.1). Significance was assessed by examining 95% confidence intervals.

Genetic-condition correlates

We next examined if there was a relationship between either MLH or SLH and condition metrics (mass and fat) using the HFC framework. We fit hierarchical (i.e., random effects) models in a Bayesian framework. The presence or absence of a relationship was determined by examining the posterior probability distributions of each coefficient to determine the probability that either MLH or heterozygosity at any single locus was related to condition. In all models we included covariates for either MLH or SLH, the age of the animal, a binary variable for if the data came from a March capture (both mass and fat are expected to be lower in March), and binary variables indicating which of the four winter range areas the deer was captured in (as in the migration analysis, above). We tested between models with solely a linear effect or a quadratic effect of age using the deviance information criteria (DIC; Spiegelhalter et al. 2002, but with the effective number of parameters calculated as in Plummer 2012). Identity disequilibrium among loci (i.e., covariance of heterozygosity among loci) was used to infer the validity of MLH correlation: accordingly we calculated g^2 where a value of zero means no variance in inbreeding (Szulkin et al. 2010).

We examined the relationship between heterozygosity and mass or fat using linear regression and beta regression respectively. Mass was natural log transformed to ensure proper support (i.e., untransformed mass is strictly positive, while linear regression allows for negative values; log transformation addresses this issue), while beta regression was used because it is proper for dependent variables ranging between 0 and 1 as percent body fat does. Because there were multiple condition measures for certain deer (i.e., those captured in both March and December), for both analyses we allowed the intercept to vary by individual, estimating a population-level intercept (i.e., we fit a random intercept by individual), with all other coefficient

values fixed. See Appendix 20 for details of model parameters and convergence assessment. To assess the fit of the models we calculated residuals (observed – predicted values) and plotted them against the fitted values to examine any potential patterns in residuals.

RESULTS

Genotype and mitochondrial sequence data

A total of 134 adult female deer were captured with 30 captured in the NM area, 30 in the NR area, 44 in the RG area, and 30 in the SM area (102 in December, and 79 in March, with 47 caught during both capture periods; see Appendix 22 for details). Deer ranged in age from yearlings to over 11 years old, with a median age of 5.5 years old (See Appendix 22). All 134 deer were genotyped at 17 loci producing a data set that was 99% complete (data available from the Dryad Digital Repository: http//:dryad.org/resource/doi:10.5061/dryad3vc1b). All markers were in Hardy-Weinberg Equilibrium and there was no evidence of linkage (diversity statistics by loci are presented in Appendix 19). The STRUCTURE-based analysis of the microsatellites suggested a single, homogenous population was most likely (i.e., had the lowest likelihood score). Based on winter range, F_{IS} values were: NR = -0.05 ($P = 0.02$), NM = -0.02 ($P = 0.16$), RG = -0.03 ($P = 0.07$), and SM = 0.01 ($P = 0.31$). The MOL_COAN analysis produced a matrix of pedigree-like coefficients for all individuals; we note the one suspected mother-daughter pairing had a coefficient of 0.50 suggesting the results were indeed reflective of pedigree data. We sequenced the mitochondrial control region in a subset of animals ($n = 81$). For comparison with data from Latch et al. (2009), we parsed the data set down to 545 base pairs (GenBank submission KM061069-KM061151). Examining the mtDNA, 37 unique haplotypes were

observed (Fig. 7.2). The neighbor joining and Bayesian phylogeny (based on a GTR+I+G substitution model) produced essentially the same topology (Appendix 21): a major split between two clades was highly supported, while a third, more tenuous clade was evident in the neighbor analysis with some support in the Bayesian analysis (posterior probability = 0.60). The three groupings are identified in the haplotype network (Fig. 7.2).

Genetic correlates to phenotypic traits

We obtained mass and fat measures on 134 adult female mule deer. Migration data were not obtained for all deer due to mortalities, collar failure, or because some deer were not collared during capture. Thus, our total sample for microsatellites analyses examining relationships with migration consisted of 104 and 95 deer for spring and fall migration, respectively. Our total sample for mtDNA analyses consisted of 65 and 59 deer for spring and fall migration, respectively. In addition, two deer did not leave summer range while collars were still attached and thus were excluded from the fall migration analyses. During spring, deer initiated migration between April 11 and June 1, and terminated migration between April 19 and June 21. During the fall, deer initiated migration between October 4 and November 8 and terminated migration between October 6 and November 14.

For all regression models hereafter we made inference based on the proportion of the posterior distributions that fell to one side of 0. Winter range area was related to fall migration termination and initiation dates, while age was not related to migration timing in any of the analyses (Table 7.2; Appendix 22). The mtDNA haplogroups were related to both fall termination and initiation, though both the effect itself and the probability of an effect were lower for fall initiation (Table 7.2; Appendix 22). For haplogroups identified by the Bayesian

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phylogenetic analysis, our models predicted that deer in haplogroup 2 terminated migration 6 days earlier on average than those in haplogroup 1 (see Fig. 7.2 for haplogroups), while for the neighbor joining analysis models predicted that deer in haplogroups 2 and 3 terminated migration on average 7 and 9 days earlier than those in haplogroup 1. Plots of residuals against fitted values showed no trend, though the 6 largest negative residuals were all from the NR winter range area, indicating the potential for a missing covariate (Appendix 22). The microsatellites analyses showed that related individuals generally migrated at similar times regardless of the distance between them on summer or winter range (Table 7.3).

There was weak evidence for identity disequilibrium ($g^2 = 0.01$, $P = 0.07$); however, MLH was a poor predictor of both body mass and fat in all models (Appendix 22 Table 7.2), while heterozygosity at individual loci were strongly related to condition measures (Table 7.2; Appendix 22 Table A22.2). Because heterozygosity at individual loci were the only significant correlates to the phenotypic traits we continued with this model only. When examining the relationship between SLH and body mass, models with a quadratic term for age fit the data slightly better than those with a linear term, with evidence for greater body mass for middle aged deer compared to young or old deer (Appendix 22 Table 7.2). When examining fat, models with a linear effect of age fit the data slightly better, and age was a poor predictor of fat (Table 7.1; Appendix 22 Table A22.2). Winter range area was weakly related to both body mass and fat (<95% of posterior on one side of 0; Table 7.1; Appendix 22 Table A22.2). Heterozygosity at two loci (RT30, and P) were strongly related to fat (>95% of posterior on one side of 0; Table 7.1; Fig. 7.3). Plots of residuals against fitted values showed a positive trend, with all of the largest fitted values showing positive residuals (Appendix 22). To guard against false positives, we refit the models with a strong 0 multivariate normal prior (with means set to 0) on the

coefficients, which shrinks coefficient estimates towards 0 (the standard deviation on the prior was taken as the standard deviation of the median coefficient values; approximately 0.14; Gelman et al. 2012).

DISCUSSION

We documented relationships between phenotypic traits recognized as being critical to fitness and genetic variation at a very fine spatial scale in female mule deer. These results provide insight into the genetic structuring of the population and the possible genetic drivers shaping the diversity of phenotypes and migration strategies seen in this important game species. These findings have potential implications for conservation and management, particularly in light of contemporary climatic changes and white-tailed deer expansion (Latham et al. 2011), as both migration timing and body condition are influential traits for mule deer survival and reproduction that vary among individuals in a population (Monteith et al. 2011, Monteith et al. 2013). Examining these traits conjointly provided a more complete picture of the genetic contributions to important phenotypic traits in this population and cervids in general.

Genetic-migration correlations

Fall and spring migration dates were more similar among related females. An individual's mtDNA haplogroup also was a stronger predictor of fall than spring migration - even when controlling for winter or summer range. The mtDNA haplotype effect is particularly striking given there appears to be virtually no spatial clustering of haplotypes (Fig. 7.2). Female philopatry and relatedness among social groups would explain the pattern in the form of learning

(e.g., the majority of white-tailed deer fawns follow their mother's migration route; Nelson 1998); however, our model accounted for such effects through the range covariates (i.e., if daughters were following their mother's migration path they would also share a winter and summer range), and the diversity of haplotypes suggests many different matrilines. In addition, upon examination of individual migratory routes, we found only 2 deer that shared an identical route. An analysis including males could test this hypothesis (sensu Nielsen et al. 2013) or at least be viewed as an independent replicate as males are more prone to disperse (Nelson 1993).

Interestingly, Colorado represents a confluence of several different refugial lineages (Latch et al. 2009), with recolonization routes and so-called hybrid hot-spot clusters falling directly in Northwestern Colorado (Swenson and Howard 2005). We hypothesize that the mtDNA effect we documented is either: i) reflective of different refugial histories and biogeography of the mtDNA lineages (Latch et al. 2009), where for example, mule deer originating in northern regions would have locally adapted phenotypes and distinct haplotypes linked to earlier migration times than those from the south (a carry-over effect); or ii) due to differences in energetics related to mtDNA, where for example Toews et al. (2014) showed that mitochondrial introgression (where different haplotypes had different energetic output) was responsible for differing migratory behavior in a warbler transition zone.

Monteith et al. (2011) and Lendrum et al. (2013) showed that spring migration timing is closely linked to plant phenology, as deer aim to arrive on their summer range close in time of peak plant productivity. Spring arrival dates are more likely to follow plant phenology on individual deer summer ranges whereas fall migration is linked to weather (temperature and snow on summer range), and individual characteristics such as age and condition. Monteith et al. (2011) suggested that prime age individuals in the best condition can adopt a strategy by which

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they stay on summer range for longer time periods to consume higher quality vegetation despite the potential for being caught in adverse weather, while poorer quality individuals cannot take on such risks. The individual characteristics hypothesis of Monteith et al. (2011) provide support for the energetics scenario (ii above), whereby individuals with certain haplotypes might be better suited for taking on the risks associated with remaining on summer range later in the season due to associated differences in energetics.

Fine-scale natal dispersal has been shown to have a heritable basis in albatross (Charmantier et al. 2011), and genotype-phenotype associations are thought to be important next steps in migration studies (Liedvogel et al. 2011). For the carry over effect to be true, the mtDNA lineages must reflect nuclear differences that (at least partially) encode for differences in migratory behavior or have a physiological effect. Although our results cannot tease apart a specific nuclear or mitochondrial effect, given the mtDNA migration effect shown in warblers (Toews et al. 2014), we think this is worth following up on using both biochemical modeling and genome-wide scans (i.e., with mtDNA haplotype as the response measure or interaction term). Importantly, recent development in the western United States has raised concerns over the sustainability of mule deer migratory routes (Sawyer et al. 2005, Sawyer et al. 2009b), and under climate change there is the potential for trophic mismatch for migratory species, whereby migrations occur asynchronously with plant phenology (Post et al. 2008). Monteith et al. (2011) suggested that plasticity in mule deer migration might allow the species to avoid such mismatches; however, if there is a genetic basis for the variability in migration among individuals, there may be less plasticity and more natural selection at work (Nelson 1998). Mitochondrial introgression with white-tailed deer is likely to be unidirectional (Carr et al. 1986), which could jeopardize the adaptive potential if hybridizations increase. However, we

note that there is no evidence of white-tailed deer presence in our study area, and thus hybridization is not a concern at this point. Thus, the potential for loss of migratory routes to development, combined with climate change and hybridization highlight the importance of maintaining the existing genetic variability in diverse migratory phenotypes.

Genetic-condition correlations

Fat is an important determinant of fitness for mule deer (Bender et al. 2007, Johnstone-Yellin et al. 2009, Tollefson et al. 2010). We identified two genetic markers as having relationships with fat, though the relationships were antagonistic (i.e., one had a positive relationship with fat and the other negative). Similar results have been seen in studies of both the Kentish plover (Charadrius alexandrinus L.; Kupper et al. 2010) and the blue tit (Parus caeruleus L.; Olano-Marin et al. 2011). With the contrasting signals of the two markers, interpretations of what these relationships represent become muddled. Olano-Marin et al. (2011) viewed the negative correlation as evidence for direct effects of the neutral loci, with the positive correlation due to inbreeding. Inbreeding in our study area is not supported by the F_{IS} values, and difficult to imagine given the population size and deer ecology.

Based on the evidence for a mixing of different mitochondrial lineages and effect sizes, the negative relationship to body fat of RT30 (0.99 probability and nearly double the effect size as all other loci) is the most likely to be genuine. However, given the concern over spurious HFCs we must still consider the possibility of Type I errors (i.e., false positives). The potential for Type I errors is of particular concern when detecting local effects and examining multiple models (Szulkin et al. 2010). In light of this concern, we highlight three points of support for the recorded relationship. First, the effect sizes of the significant coefficients were substantially

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greater than those of the other loci (Fig. 7.3). Second, we refit all models that had significant coefficients, but with a strong multivariate normal prior (with means set to 0) on the coefficients. This approach shrinks all estimates towards 0, acting as a penalty and reducing the number of significant covariates (Gelman et al. 2012). In the case of the SLH – fat correlation, all significant results (probability of an effect >0.95) remained. Lastly, the proximity of a locus in question relative to genes of known effect can be taken as supportive evidence for understanding single-locus HFCs (Von Hardenberg et al. 2007, Kupper et al. 2010). Slate et al. (2002) observed considerable synteny in ruminants, and more than half of the microsatellites used in their deer linkage map had been used for the same purposes in cow and sheep. When we screened RT30 against the annotated cow genome (using BLAST), both primers co-localized with 100% identity to a region with the closest known gene being that of TBC1D1. Interestingly, this gene regulates cell growth and differentiation, and has been shown to influence fat metabolism in mice and humans (Stone et al. 2006, Chadt et al. 2008). Given the combination of divergent mtDNA lineages in our study area and panmixia ($k = 1$), a slight disruption of co-adapted alleles that are linked to fat metabolism could explain the negative correlation between this locus and fat (we emphasize these results represent a small effect as body fat was predicted to decrease body fat by < 0.2% in the model). This is predicted to outcome when locally adapted lineages mix, and it has been recently suggested for grizzly bears in an area where they are subject to large-scale human assisted migration (Shafer et al. 2014).

Although the above lines of evidence offer support to the effect of RT30 on fat being genuine, given the small number of loci examined we must remain skeptical about this relationship. Rather, we present these findings as noteworthy and in need of confirmation by studies with larger samples and with genomic methods.

Conclusions and evolutionary applications

We have shown fine-scale relationships between genetic variation and phenotypic traits in mule deer that have not been found in previous work on this species. Our study identified fine-scale genetic correlates to both migration timing and body fat that are likely overlooked (and probably unexpected) in this species. These results have potential management implications for mule deer, which are under substantial human pressure from a multitude of stressors (e.g., Sawyer et al. 2006). The genetic polymorphisms in this population that are linked to phenotypic traits related to phenology and metabolic variation could prove important in the face of climate change and other anthropogenic stressors that are likely to affect both optimal timing of migration and the role of fat stores in survival and reproduction. Monitoring hybridization with white-tailed deer should also be considered with respect to the mtDNA effect, as introgression is likely to go from white-tailed to mule deer (Carr et al. 1986) and could alter the adaptive potential. Efforts should be made to better characterize additional drivers behind this phenotypic and genetic variation in an effort to maintain a diversity of phenotypes that might best be able to adapt to novel conditions. Screening for similar associations in more imperiled deer populations (and Cervid species) may help shed light on local population dynamics and better inform management decisions.

TABLES

Table 7.1. Covariates, median coefficient (coeff.) values, and the probability (prob.) of either a negative or positive effect of the covariate from multi-level beta regression on the percent body fat of mule deer in the Piceance Basin, Colorado.

Covariate	Median coeff. value	Prob. coeff. is negative	Prob. coeff. positive
Intercept	-2.15	1	0
Age	-0.05	0.89	0.11
March Capture	-0.52	1	0
Winter range			
NR[*]	-0.10	0.80	0.20
RG[†]	-0.11	0.82	0.18
SM[‡]	-0.06	0.69	0.31
Microsatellite loci			
INRA011	-0.13	0.93	0.07
RT30	-0.24	0.99	0.01
BBJ	0.08	0.22	0.78
K	-0.03	0.65	0.35
BL25	0.07	0.27	0.73
BM6438	-0.001	0.50	0.50
BM848	-0.11	0.87	0.13
RT7	-0.08	0.72	0.28
N	0.09	0.22	0.78

ETH152	-0.004	0.52	0.48
BM6506	0.02	0.40	0.60
P	0.18	0.04	0.96
D	0.092	0.13	0.87
BM4107	0.05	0.32	0.68
RT5	0.15	0.13	0.87
OCAM	0.02	0.41	0.59
R	-0.08	0.81	0.19

[*]Indicates deer captured in the NR winter range, with NM as the reference category
[†]Indicates deer captured in the RG winter range, with NM as the reference category
[‡]Indicates deer captured in the SM winter range, with NM as the reference category

Table 7.2. Covariates, median coefficient (coeff.) values, and the probability (prob.) of either a negative or positive effect of the covariate from negative binomial regression model on mule deer fall migration termination dates from deer in the Piceance Basin, Colorado.

Neighbor joining clades

Covariate	Median coeff. value	Prob. coeff. is negative	Prob. coeff. positive
Intercept	3.08	0.00	1.00
Age	-0.09	0.88	0.12
Winter range			
NR[*]	0.16	0.22	0.78
RG[†]	-0.38	0.96	0.04
SM[‡]	-0.56	0.99	0.01
mtDNA			
Haplogroup 2[§]	-0.46	0.99	0.01
Haplogroup 3[§]	-0.33	0.94	0.06

Bayesian clades			
Intercept	2.932	0.000	1.000
Age	-0.095	0.90	0.10
Winter range			
NR[*]NR[A]	0.1768	0.22	0.78
RG[†]RG[B]	-0.270	0.90	0.10
SM[‡]SM[C]	-0.440	0.97	0.03

<u>mtDNA</u>

Haplogroup 2[§]	-0.350	0.97	0.03

[*]Indicates deer captured in the NR winter range, with NM as the reference category
[†]Indicates deer captured in the RG winter range, with NM as the reference category
[‡]Indicates deer captured in the SM winter range, with NM as the reference category
[§]mtDNA haplogroup 1 is the reference category

Table 7.3. Mantel test models, Mantel's *r* and lower and upper confidence limits (CL), calculated through randomization, for models examining correlation between relatedness metrics (Queller-Goodnight (QG) and coancestry) and migration dates, for mule deer in the Piceance Basin, Colorado. End spring and end fall indicate the termination of spring and fall migration, respectively. Start spring and start fall indicate the initiation of spring and fall migration, respectively. Winter and summer distance indicate the distance between winter and summer range centroids. All values are presented as Mantel *r* (lower CL, upper CL). Vertical lines (|) indicate partial Mantel tests with the covariate that is controlled for following the vertical line.

Migratory metric	QG	Coancestry
End spring	-0.04 (-0.06, -0.01)	-0.06 (-0.09, -0.01)
End spring | winter distance	-0.02 (-0.04, -0.001)	-0.07 (-0.10, -0.03)
End spring | summer distance	-0.03 (-0.05, -0.01)	-0.05 (-0.08, -0.02)
End fall	-0.04 (-0.06, -0.01)	-0.02 (-0.05, 0.02)
End fall | winter distance	-0.04 (-0.06, -0.01)	-0.02 (-0.05, 0.02)
End fall | summer distance	-0.04 (-0.06, -0.01)	-0.02 (-0.05, 0.01)
Start spring	0.002 (-0.02, 0.02)	-0.03 (-0.07, 0.01)
Start spring | winter distance	0.01 (-0.02, 0.02)	-0.03 (-0.06, 0.01)
Start spring | summer distance	0.01 (-0.01, 0.04)	-0.02 (-0.06, 0.01)
Start fall	-0.05 (-0.07, -0.03)	-0.05 (-0.08, -0.03)
Start fall | winter distance	-0.05 (-0.06, -0.01)	-0.05 (-0.08, -0.03)
Start fall | summer distance	-0.05 (-0.07, -0.03)	-0.05 (-0.08, -0.03)
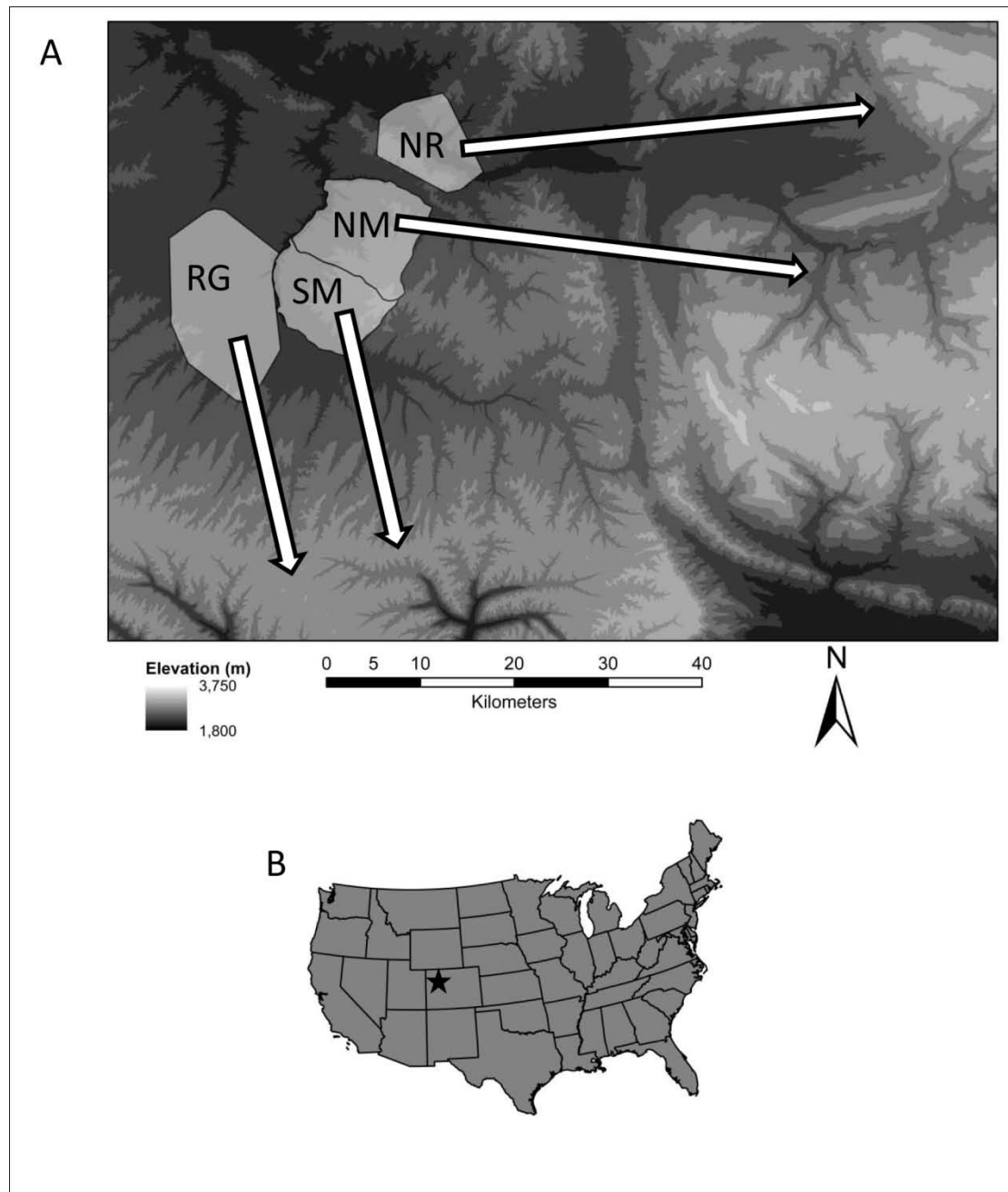
Figure 7.1. (A) Winter range areas (1=Ryan Gulch (RG), 2=South Magnolia (SM), 3=North Magnolia (NM) and 4=North Ridge (NR)) and simplifications of migratory routes, with arrows indicating general location of summer ranges for mule deer in the Piceance Basin, and (B) Location of study within the United States. Adapted with permission from Lendrum et al. (2013).
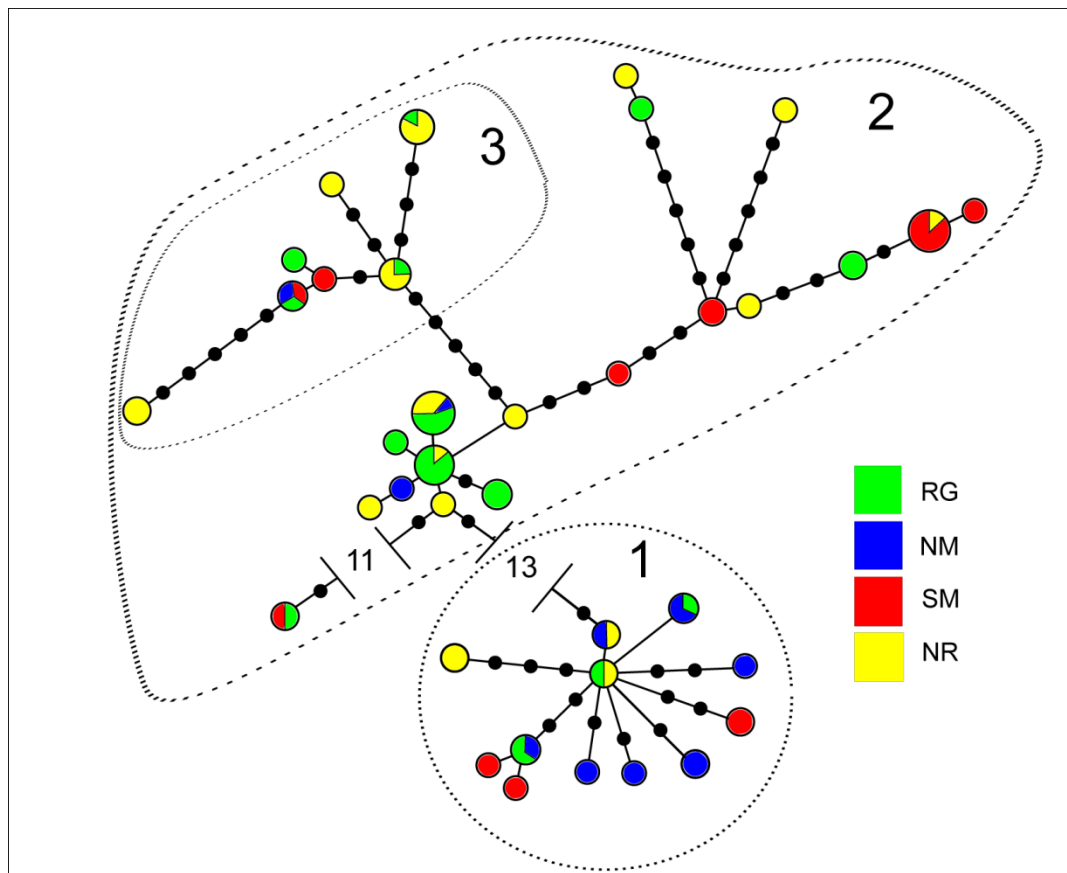
Figure 7.2. Mitochondrial control region haplotype network and winter range area assignments. Circle size is proportional to the haplotype frequency with small black circles representing undetected, intermediate haplotypes. Haplotypes are colored according to winter range area. The dashed-circle outlines and corresponding numbers are in reference to the phylogenetic clades (Appendix 21).
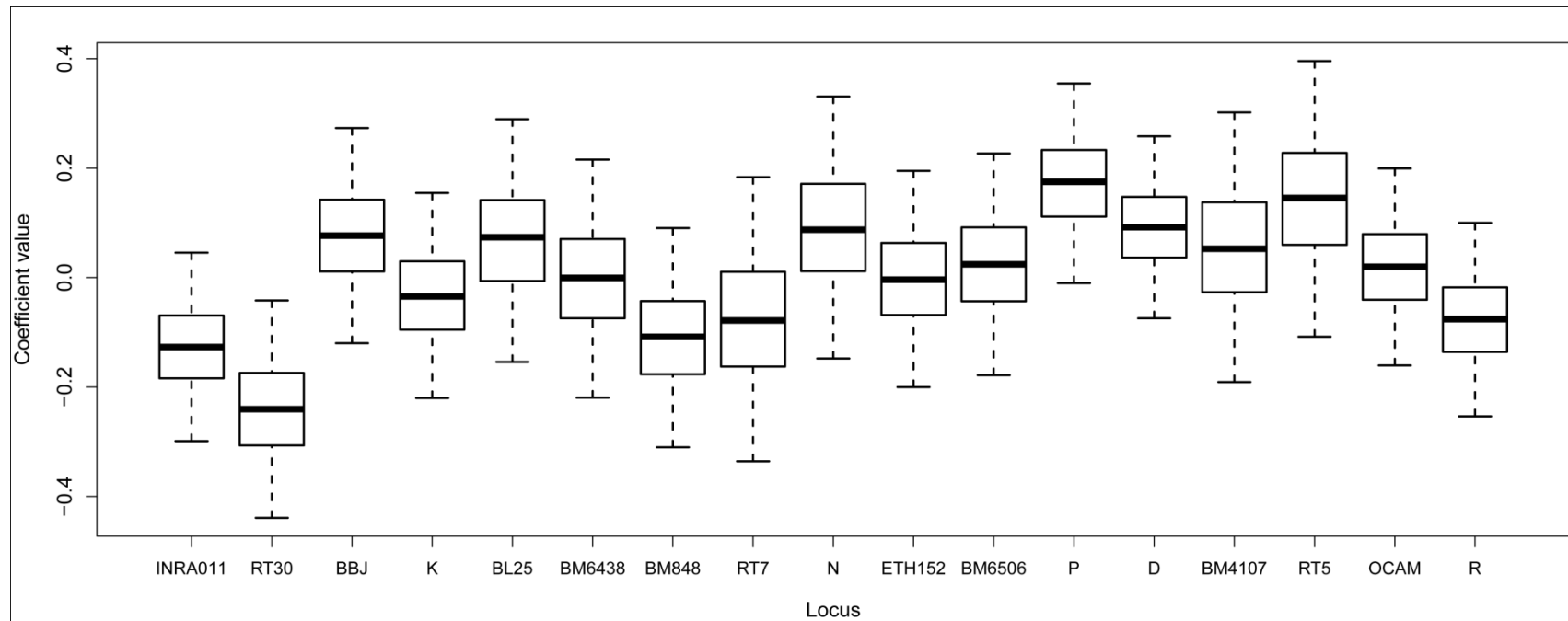
Figure 7.3. Box plots of coefficients for effect of microsatellite loci on mule deer body fat percent. Coefficients were obtained through beta regression model in a Bayesian hierarchical framework. Box plots represent median (black line) interquartile range (box bounds) and upper and lower 95% bounds (whiskers) of coefficient values.

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APPENDIX 1

REVIEW PROTOCOL, MITIGATION ASSESSMENT AND TABLES OF LITERATURE

REVIEWED IN CHAPTER ONE

REVIEW PROTOCOL

We systematically reviewed the literature on wildlife impacts from unconventional oil and natural gas, wind, bioenergy, solar and geothermal energy development through standardized searches of Google Scholar and the Thomas Reuters Web of Knowledge. Searches were conducting using combinations of the terms "wildlife" or "environmental impact" and all of the following:

- Energy development

- Industrial development

- Resource extraction

- Petroleum

- Oil

- Natural gas

- Wind

- Wind energy

- Biofuels

- Bioenergy

- Biomass energy

- Ethanol

- Geothermal

- Solar

We reviewed peer reviewed publications on empirical research published between January 1, 2000 and July 1, 2012. Studies that were not related to energy resource development

(i.e., did not address any aspect of development of unconventional oil and natural gas, wind, bioenergy, solar, or geothermal energy development as determined from the title) were excluded. Further screening was conducted by reviewing the abstracts of all other publications and excluding simulation studies and modeling exercises that lacked empirical data. Formal meta-analyses and reviews (for reviews only in the case of solar and geothermal, for which there were no empirical studies) were included. Literature that examined wildlife responses to impacts hypothesized to be similar to those caused by the wind and unconventional oil and gas sectors but did not directly assess an energy development impact were excluded. This included studies reporting on pre-development assessments and making predictions on expected impacts.

For literature on oil and gas research outside the U.S. and Canada the type of oil and gas resources (i.e., conventional versus unconventional) was not reported in the literature arising from our search. Unconventional oil production is limited to only a few countries, while unconventional gas resources are only known in certain regions and production is largely limited to the U.S. and Canada (World Energy Council 2010, 2012). Public production data are unavailable for most countries outside of North America. Thus, we assumed most, if not all global research on oil and natural gas development was conventional, and we exclude this research from Table A1.2, below (of note: our search produced less than ten global studies on oil and gas impacts). However, in the main text, we review select global literature on oil and gas development to provide context for likely impacts with the expected increase in unconventional development outside of the U.S. and Canada.

Although there is a rich literature throughout the world on wildlife response to agriculture that might be directly relevant to impacts of bioenergy development, many of these studies do not report on the end use of the crops and it is difficult to determine if the documented responses

are germane to bioenergy. Thus, we excluded studies of agricultural impacts to wildlife unless

they were directly assessing the response to dedicated bioenergy crops and reported that these

crops were used for bioenergy or were set in the context of bioenergy production (e.g., studies

assessed the impact of crops that are projected to be used in bioenergy production). This issue is

particularly salient to oil palm research. Not all oil palm plantations are used for the production

of bioenergy, and a number of studies have been published on the impacts of oil palm cultivation

to wildlife that do not mention bioenergy. These studies were not reviewed.

For the papers which fit the above criteria, we reviewed the references and citations and

included the resulting literature that met the above criteria. The selected literature from the

United States and Canada is summarized in Table A1.1 and global literature is summarized in

Table A1.2. No first-hand research was found for solar and geothermal energy sectors, therefore

we include reviews focusing on the impacts of these sectors.

QUANTIFICATION OF SPECIES, GEOGRAPHIC LOCATIONS, IMPACTS AND

MITIGATION FROM THE U.S. AND CANADA

To further quantify research in the U.S. and Canada we extracted and summarized the following

information from studies conducted in these regions: taxonomic group studied, geographic

location, impact (negative, positive, neutral), implication for mitigation and if mitigation was

directly assessed by the study (Table A1.1). To assess the proportion of studies offering

mitigation suggestions, and the robustness of study design relative to these suggestions, we

assigned each of these studies to one of four groups based on study design and mitigation

suggestions. Group 1 consisted of studies that explicitly assessed the response of wildlife to the

implementation, or simulation of a BMP or mitigation measure, with a before-after component. For bioenergy this included studies examining harvest practices and different plant cultivars. Group 2 consisted of correlative studies that were designed to directly assess the response of wildlife to existing mitigation. Group 3 consisted of correlative studies that examined the response of wildlife to development and inferred mitigation from their findings. Lastly, group 4 consisted of studies that made no mitigation suggestions.

TABLES

Table A1.1. Peer-reviewed literature on the impacts of unconventional oil and natural gas, wind and bioenergy development on wildlife in Canada and U.S. The species and taxonomic group studied, processes and variables examined, documented impacts, inferred potential population-level impacts, implications for mitigation, and if the study discussed these impacts explicitly is summarized for each sector.

Taxonomic group	Common name	Process(es) examined	Variables examined	Impact or results	Potential population-level impacts	Implications of findings for BMPs and mitigation	Implications discussed in paper?	Citation
Oil and gas								
Birds	Greater sage grouse	Nest and brood success; habitat selection	Distance to roads and wells	Avoid development; nest far from development; brood near development; higher brood loss near development	Decreased abundance; decreased reproductive output	Enhance habitat in nesting and brooding areas*	Yes	(Aldridge and Boyce 2007)
Birds	Ovenbird	Home range size; territory size; overlap with seismic lines;	Seismic line width	Reduced territory size with wider seismic lines	Decreased abundance	Use narrow seismic lines	Yes	(Bayne et al. 2005a)

		density						
Birds	Ovenbird	Territory overlap with seismic lines; abundance	Seismic line density	Reduced abundance at high density; singing further from seismic lines	Decreased abundance; decreased reproductive output	Use narrow seismic lines	Yes	(Bayne et al. 2005b)
Birds	Various	Density and occupancy	Noise from compressor stations	Species specific decline in density near compressor stations	Decreased pairing success and reproductive output; decreased abundance	Install noise suppression equipment	Yes	(Bayne et al. 2008)
Mammals	Pronghorn (*Antilocapra americana*)	Habitat selection	Distance to roads and well pads	No response to roads or well pads; decreased number of high use patches with increasing development	Increased energy expenditure; decreased abundance	Reduce development	No	(Beckmann et al. 2012)
Birds	Greater sage grouse	Lek attendance	Recorded drilling and road noise	Lower attendance at noisy leks. Lower male attendance at leks with road noise than drilling noise	Decreased reproductive output	Expansion of seasonal drilling restrictions	Yes	(Blickley et al. 2012)
Birds	Common raven; greater	occupancy and density;	Type of habitat (towns vs.	High occupancy but low density in oil field; decreased	Declining population	Install raven deterrents; harass and control	Yes	(Bui et al. 2010)

	sage grouse	grouse nest and brood success	oil field vs. sagebrush)	sage grouse nest and brood success with higher raven occupancy		nesting ravens; reduce raven density in source areas (cities and towns)		
Birds	Greater sage grouse	Habitat selection	Distance to wells; well density	Avoid areas near wells	Decreased abundance	Restrict development in critical winter habitat	Yes	(Carpenter et al. 2010)
Birds	Sprague's pipit; Baird's sparrow; savannah sparrow	Abundance	Well density	Decline in Sprague's pipit and Baird's sparrow; increase in savannah sparrow	Decreased abundance	Reduce development	No	(Dale et al. 2008)
Birds	Greater sage grouse	Winter habitat selection	Well density	Avoid development	Decreased abundance	Set aside suitable habitat within project area	Yes	(Doherty et al. 2008)
Birds	Greater sage grouse	Male lek attendance; lek persistence	Well density	Decreased lek attendance and persistence with increased density	Declining population	Offset habitat; enhance productivity of habitat; cluster developments	Yes	(Doherty et al. 2010)
Birds	Northern bobwhite	Habitat and nest site selection	Distance to oil structures	No response	-	-	No	(Dunkin et al. 2009)
Mammals	Moose, deer, bear,	Crossing rate	Pipeline; pipeline	Moose avoid crossing higher	Increased energy	Construct crossing	Yes	(Dunne and

	coyote, lynx, wolf		height	pipelines; moose use crossing structures; no impact on other species	expenditure; population fragmentation	structures; raise pipeline height		Quinn 2009)
Mammals	Caribou	Habitat selection	Distance to roads, seismic lines, and wells	Avoid roads, seismic lines and wells; avoid new developments more than old	Decreased abundance	Limit development in caribou range; replant seismic lines; reduce traffic	Yes	(Dyer et al. 2001)
Mammals	Caribou	Road and seismic line crossing	Roads and seismic lines; road traffic	Avoid crossing roads; cross roads least when traffic highest; no influence of seismic lines	Increased energy expenditure; population fragmentation	Reduce traffic	No	(Dyer et al. 2002)
Birds	Greater sage grouse	Habitat selection; nest success; brood success	Distance to anthropogenic features (includes well pads)	No impact on habitat selection or nest success; lower brood success closer to wells	Declining population	Restrict development in critical habitat; maintain distance between nesting habitat and development	Yes	(Dzialak et al. 2011b)
Mammals	Elk	Habitat selection and survival	Road density; area disturbed by industrial footprint	Decreased survival of individuals near development; temporal avoidance of industrial footprint	Declining population	Reclaim, restore and avoid critical habitat	Yes	(Dzialak et al. 2011c)

				and roads				
Mammals	Elk	Habitat selection	Road density; distance to development footprint	Avoid development during the day	Increased energy expenditure; decreased abundance	Maintain refuge habitat within developed areas	Yes	(Dzialak et al. 2011a)
Birds	Greater sage grouse	Habitat selection	Distance to natural gas wells and roads	Avoided roads during night and day; avoided wells during day but not night	Altered behavior	Mitigation should incorporate landscape scale component	Yes	(Dzialak et al. 2012)
Birds	Ash-throated flycatcher; grey flycatcher	Habitat use; vocal frequency	Noise amplitude	Decreased grey flycatcher occupancy with more noise; vocal frequency unaffected; ash-throated flycatcher occupancy unaffected; increased vocal frequency	Decreased mating success; increased predation	-	No	(Francis et al. 2011d)
Birds	Various	Species composition; density; nest predation	Wells with different levels of noise	Altered community structure; altered species interactions; no decline in density	Decreased abundance of sensitive species; increased reproductive output for	Install noise barriers; place compressor stations in centralized locations	No	(Francis et al. 2009)

					some individuals			
Birds	Plumbeous vireo; Gray vireo	Occupancy; song frequency and duration	Noise amplitude	Increased minimum frequency and decreased duration for plumbeous vireo; increased maximum frequency for gray vireo; no impact on occupancy	Decreased mating success; increased predation	Install noise barriers; site compressor stations in centralized locations	No	(Francis et al. 2011a)
Birds	Gray flycatcher; Western scrub jay	Occupancy and nest survival	Wells with different levels of noise	Reduced occupancy rate but increased nest success with more noise	Decreased abundance; increased reproductive output for some individuals	Install noise barriers; site compressor stations in centralized locations	Yes	(Francis et al. 2011b)
Birds	Various	Nest frequency; bird abundance	Noisy vs. quiet areas	Lower nest frequency and bird abundance in noisy areas for species with low frequency vocalizations; positive response for birds with high frequency vocalizations	Decreased reproductive output and abundance for birds with low frequency vocalizations	-	No	(Francis et al. 2011c)

Birds and small mammals	Black-chinned humming bird; various small mammals	Flower visitation; pollen transfer; occurrence; seed removal	Noisy vs. quiet areas	Greater flower visitation by hummingbirds and greater pollen transfer in noisy areas; greater presence of some small mammal species and greater seed removal in noisy areas	Altered plant community structure	-	No	(Francis et al. 2012)
Birds	Tree swallow	Thyroid hormone levels	Presence in reclaimed oil sands wetlands versus reference	T4 hormones greater in birds inhabiting nest boxes in reclaimed sites	Decreased survival	-	No	(Gentes et al. 2007)
Birds	Brewer's sparrow; vesper sparrow; sage sparrow; horned lark; sage thrasher	Abundance and species richness	Well density	Species richness unaffected; decreased abundance of Brewer's, sage, and vesper sparrow with increasing density; no response by sage thrasher; increased abundance of horned lark with increasing density at one site	Decreased abundance of sensitive species	Reduce development	No	(Gilbert and Chalfoun 2011)

Birds	Mallard	Growth; toxicant exposure	Exposure to reclaimed oil sands wetlands versus reference	Birds in reclaimed wetlands had less growth and greater exposure to toxicants	Decreased survival	-	No	(Gurney et al. 2005)
Birds	Ovenbird	Pairing success and age distribution	Noise from compressor stations	Decreased pairing success; younger age distribution relative to noiseless controls	Decreased reproductive output; inhibited predator detection; decreased mating success	Install noise suppression equipment	Yes	(Habib et al. 2007)
Birds	Lesser prairie-chicken	Range and habitat selection	Before vs. after power line construction; number of wells, roads, power lines, and buildings in monthly range	Range overlap with roads, wells, and power lines less than random; home range centroids further than random from roads, wells, power lines and buildings	Increased energy expenditure	Do not develop within certain distances of summer and breeding habitat (i.e., setbacks)	Yes	(Hagen et al. 2011)
Birds	Savannah sparrow; Sprague's pipit;	Occurrence and abundance	Well density	Decreased abundance and probability of occurrence for	Decreased abundance of sensitive species	Reduce development	No	(Hamilton et al. 2011)

	Chestnut collared longspur			Sprague's pipit; increased probability for savannah sparrow; no change for chestnut collared longspur				
Birds	Greater sage grouse	Male lek attendance	Well density; presence of wells within various buffer distances	Results varied among locations but general decrease in lek attendance with increasing development	Declining population	Restrict development around leks (i.e., setbacks)	No	(Harju et al. 2010)
Mammals	Elk	Habitat selection	Distance to roads and well pads	Avoided roads and well pads	Increased energy expenditure; decreased abundance	Reduce development; maintain refuge habitat within developed area	No	(Harju et al. 2011)
Birds	Greater sage grouse	Nest site selection; survival; lek recruitment; lek attendance	Distance to industrial roads and wells	Decreased lek recruitment and survival in developed areas; avoid nesting near development	Decreased abundance; reduced reproductive output; declining population	Maintain suitable habitat within developed area	Yes	(Holloran et al. 2010)
Birds	Various	Density	Distance to	Altered species	Decreased	Decrease traffic;	No	(Ingelfing

		and abundance	roads and pipelines	composition; decline in sage brush obligates near roads; greater decline near roads with more traffic	abundance of sensitive species	cluster development		er and Anderson 2004)
Mammals	Caribou and wolves	Habitat selection; predation and mortality sites	Distance to linear features (roads, seismic lines, pipelines)	Caribou avoid linear features; mortalities closer to linear features; wolves closer than random to roads when in caribou range	Increased energy expenditure; declining population	Remote technology for wells; use of helicopter for seismic exploration; rollback of trees onto linear features; reclamation of linear features	Yes	(James and Stuart-Smith 2000)
Birds	Lesser prairie chicken	Lek occurrence	Distance to anthropogenic features (includes oil and gas wells)	Decreased lek habitat suitability near anthropogenic features	Decreased abundance; declining populations	Restrict development in areas of high lek occurrence probability	No	(Jarnevich and Laubhan 2011)
Mammals	Caribou; white-tailed deer; moose; wolves	Caribou population rate of change and survival; wolf diet; density; proportion	Before vs. after intensive development for oil	Declining caribou population; increase in caribou and deer in wolf diets, decrease in moose; increase in deer and wolf density; increased	Declining caribou population	Liberalized harvest of deer	Yes	(Latham et al. 2011)

		of overlap between caribou and wolves		overlap between caribou and wolves				
Mammals	Grizzly bear	Habitat selection	Distance to seismic lines; habitat patch size	No response to seismic lines; indirect impact on habitat selection	Increased energy expenditure; decreased abundance	Use narrow seismic lines	No	(Linke et al. 2005)
Birds	Greater sage grouse	Nest site selection; nest success; nest initiation rate	Developed (< 3 km from well or road) vs. undeveloped	Lower nest initiation rate and greater distance moved between lek and nest in developed areas	Increased energy expenditure; declining population	Restrict traffic during nesting	Yes	(Lyon and Anderson 2003)
Birds	Various	Territory size; seismic line crossing; distance to lines; territory overlap with lines	Before vs. after construction of seismic lines	At community level territory size increased but no other impacts; species specific declines in number of territories, avoidance of lines, and decline in territory overlap with lines	increased energy expenditure; decreased abundance	Use narrow seismic lines	Yes	(Machtans 2006)
Amphibians and reptiles	Salamanders	Capture proportion	Distance from well pad edge	Capture proportion highest closer to edges	-	-	No	(Moseley et al. 2009)

Mammals	Grizzly bear	Habitat selection; mortality risk	Distance to industry roads	Select areas near roads; higher risk of mortality near roads	Declining population	Reduce traffic and access; reduce quality of habitat near roads	Yes	(Nielsen et al. 2006)
Birds	Lesser prairie chicken	Nest location and success	Distance to anthropogenic features (includes oil wells)	Avoid nesting near development in one study area; no impact of wells on nest success	Decreased abundance	Avoid development in nesting habitat; develop on already disturbed lands	Yes	(Pitman et al. 2005)
Birds	Various	Mortality	Wastewater fields	Direct mortality	Declining population	Deep well injection of wastewater; separate petroleum and surfactants from wastewater; place nets over open wastewater	Yes	(Ramirez 2010)
Mammals	Mule deer	Habitat selection	Distance to wells; road density	Avoidance of development increased over time with more development	Increased energy expenditure; decreased abundance	Employ directional drilling; limit public access	Yes	(Sawyer et al. 2006)
Mammals	Mule deer	Habitat selection	Distance to wells with different levels of human activity	Avoid all wells; stronger avoidance with more activity	Increased energy expenditure; decreased abundance	Install remote liquid gathering systems; employ directional drilling	Yes	(Sawyer et al. 2009a)

Mammals	Caribou	Population rate of change	Area within 250 m of industrial features	Populations declining more rapidly in areas with more development	Declining population	Maintain sufficient proportion of range undeveloped; use narrow seismic lines and remote well monitoring;	Yes	(Sorensen et al. 2008)
Birds	Various	Mortality	Tailings ponds	Direct mortality	Declining population	Create "compensation ponds" to provide clean water alternative for birds	Yes	(Timoney and Ronconi 2010)
Mammals	Caribou	Annual home range fidelity and overlap	Well density	No change in home range overlap or fidelity	Declining population (high fidelity despite degraded habitat)	Reduce development	No	(Tracz et al. 2010)
Birds	Greater sage grouse	Lek attendance; lek persistence	Inside vs. outside of developed areas	Lek attendance and persistence lower in developed areas	Declining population	Restrict development around leks (i.e., setbacks); ensure sufficient sage brush habitat around leks	Yes	(Walker et al. 2007a)
Mammals	Caribou	Habitat	Distance to	Caribou avoid	Increased	Cluster human	Yes	(Wasser

	and moose	selection; nutritional and psychological stress	roads of different activity levels (primary, secondary, tertiary)	roads; greater avoidance of busier roads; no avoidance of seismic lines; moose avoid all linear features; higher psychological stress for caribou near roads and with more activity; higher nutritional stress for caribou in most selected areas	energy expenditure; decreased abundance; decreased survival	activity along roads; construct developments in areas with visual and auditory barriers; minimize secondary roads		et al. 2011)
Mammals	Pine marten	Trapline activity; marten taken	Human access (roads and seismic lines)	Declining harvest	Declining population	Reduce number of roads and seismic lines by coordinating construction among companies	Yes	(Webb and Boyce 2009)
Mammals	Elk	Movement distance; tortuosity; home range size	Distance to anthropogenic features; inside vs. outside developed area	Smaller home ranges in developed area; greater tortuosity and movement distance in more developed areas	Increased energy expenditure	Avoid development in critical habitat; maintain refuge habitat within developed areas; construct developments in areas that are	Yes	(Webb et al. 2011b)

						obscured from view		
Mammals	Elk	Survival	Proportion of industrial footprint within area used the week prior to mortality	Non-significant decline in survival probability with increasing development	Declining population	Maintain refuge habitat within developed areas	Yes	(Webb et al. 2011a)
Mammals	Elk and mule deer	Pellet occurrence	Distance to roads and wells	Decreased probability of pellets near roads for both species	Increased energy expenditure; decreased abundance	Maintain refuge habitat within developed areas	Yes	(Webb et al. 2011d)
Mammals	Elk	Home range size; annual home range overlap	Proportion of home range developed	Decrease in home range size and annual overlap with increasing development	Increased energy expenditure; decreased abundance	Restrict development in critical habitat; maintain refuge habitat in developed areas; construct developments in areas that are obscured from view	Yes	(Webb et al. 2011c)
Birds	Sage grouse	Daily nest survival	Distance to oil and gas wells; distance to	Lower probability of survival near oil and gas wells; greater probability	Declining population	Reduce water discharge to avoid predator subsidization near	Yes	(Webb et al. 2012)

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Wind

Bats	Various	Mortality	Cut-in speed	Decreased mortality with increasing cut-in speed	Declining population	Increase cut-in speeds	Yes	(Arnett et al. 2010)
Bats	Hoary bats; silver-haired bats	Mortality and activity	Temperature; wind speed; turbine height; mortality relative to activity	Greater mortality at taller turbines and with greater activity at taller turbines	Declining population	Install shorter turbines	No	(Baerwald and Barclay 2009)
Bats	Various	Mortality	Cut-in speed	Decreased mortality with increasing cut-in speed and with stoppage during low winds	Declining population	Increase cut-in speeds	Yes	(Baerwald et al. 2009)
Bats	hoary and silver-haired bats	Mortality and activity	Activity; wind speed and direction; barometric pressure;	Activity and mortality peaked in mid-august but differed by species; activity peaked at dusk and	Declining population	Reduce northern exposure of wind farms; stop turbines during falling barometric pressure and high	Yes	(Baerwald and Barclay 2011)

			moon illumination; temperature; turbine position	dawn; higher mortalities at northern end of facility; greater mortality during high moon illumination and falling barometric pressure; no relation to turbine position in rows or lighting; species specific responses to weather		moon illumination		
Birds and bats	Various	Mortality	Area swept by rotors; turbine height; megawatt capacity of turbines	Higher mortality of bats with taller turbines; higher mortality with greater megawatt capacity	Declining population	Replace several small turbines with single large turbines (birds); install shorter turbines (bats)	Yes	(Barclay et al. 2007)
Birds	Raptors	Abundance and behavior	Flight height; land cover; weather	Avoid turbines; decreased abundance; birds flew within rotor zone	Decreased abundance; displacement	-	No	(Garvin et al. 2011)
Birds	Red tailed hawk	Behavior	Elevational and topographic characteristi	Variation in behavior by season, wind and topography;	-	Stop turbines when winds are strong and perpendicular to	Yes	(Hoover and Morrison 2005)

			cs; wind conditions; seasons; weather; time of day	perched and soared more during light winds; kited during high winds; kiting most on west facing slopes with inclines > 20% and at higher elevations		steep slopes; paint blades to accentuate them		
Bats	Various	Activity	Turbine height; wind speed and direction; temperature; turbine rotation speed; pressure; insect activity	Bats foraging in turbine sweep zone; bat activity proportional to insect activity; greater activity with greater turbine speed and just after sunset	-	Stop turbines during times of greater insect activity, just after sunset, and during times predicted to have high bat activity	Yes	(Horn et al. 2008)
Bats	Various	Mortality and activity	Activity in areas with turbines and without; distance to woodlots; presence of lights; wind speed	All mortalities and activity peak during summer or fall; no influence of lighting on mortality; no differences in activity related to turbines or distance to woodlot	Declining population	Stop turbines during certain seasons	No	(Jain et al. 2010)

Birds	Various	Mortality	None	Mortalities greater during later phases of development	Declining population	Conduct pre-development assessments	Yes	(Johnson et al. 2002)
Birds	Various	Mortality	Mortality during different development phases	Non-significant but greater mortalities at taller turbines	Declining population	Install shorter towers	No	(Johnson et al. 2003)
Bats	Various	Mortality and activity	Land cover; turbine lighting; season	Activity and mortality peaked in mid-August; greater activity close to woodlands; no influence of nightly activity, lighting or cover on mortality	Declining population	Stop turbines during certain months	No	(Johnson et al. 2004b)
Amphibians and reptiles	Desert tortoise	Burrow location	Distance to roads and turbines	Burrows located closer to roads and turbines than random locations	-	-	No	(Lovich and Daniels 2000)
Amphibians and reptiles	Desert tortoise	Growth; sex ratio; mortality	Study population in a wind farm compared to other studies in	No impact	-	-	No	(Lovich et al. 2011b)

				undisturbed sites				
Amphibians and reptiles	Desert tortoise	Mortality	Presence of culverts	Mortality documented in a culvert	Decreased Survival	Install larger culverts or excluder devices	Yes	(Lovich et al. 2011a)
Birds	Various	Mortality	Areas with turbines vs. reference; habitat type; position of turbine in turbine rows; season	No influence of habitat type; turbines at the end of turbine rows had greater mortality; greater mortality than random during spring	Declining population	Avoid building in areas with large bird concentrations	Yes	(Osborn et al. 2000)
Bats	Various	Mortality	Land cover; topography	More mortalities of Brazilian free-tailed bats near ravine topography in one year; hotspots of mortality located near ravine	Declining population	Stop turbines during certain conditions (not specified)	Yes	(Piorkowski and O'Connell 2010)
Mammals	California ground squirrels	Behavior	Noisy vs. quiet areas	No response to conspecific alert calls at noisy site; closer to burrows and more alert at noisy site	Increased energy expenditure	Site turbines away from burrows	No	(Rabin et al. 2006)
Birds and bats	Various	Mortality	Type of turbine	more mortalities for birds at newer	Declining population	Upgrade to newer and more	Yes	(Smallwood and

				and more powerful turbines; increased mortalities for bats		powerful turbines		Karas 2009)
Birds	Various	Mortality	None	Direct mortality	Declining population	Habitat offsets; upgrade to newer, more powerful, and taller turbines; design safer turbines; develop remote collision detection technology	Yes	(Smallwood and Thelander 2008)
Birds	Various	Mortality and behavior	Mortality relative to behavior; behavior relative to flock size, time, season, number of turbines operating	Flew closer to turbines when not spinning; increasing mortalities with increasing flights through rotor zone; greater mortalities of some species with greater winds	Declining population	Synchronize turbine activity within turbine rows; maintain sufficient gaps between turbines; stop turbines during certain seasons and high winds	Yes	(Smallwood et al. 2009b)
Birds	Various	Mortality	Energy capacity of turbines	More mortalities at turbines with lower capacity	Declining population	Upgrade to newer and more powerful turbines; move turbines to areas with higher winds	Yes	(Smallwood et al. 2010)

Birds	Burrowing owl	Mortality and behavior	Behavior; rodent management activity; season; turbine type	More mortalities Sept.-Dec., and at turbines in areas with rodent control, in areas with more rodents and near owl burrows; more mortalities at vertical axis turbines, tubular towers, and with slower moving and smaller turbines	Declining population	Terminate rodent control; install flight diverters; upgrade to newer, more powerful, and taller turbines; site turbines closer together; site turbines in areas where owls do not frequent; stop turbines during winter	Yes	(Smallwood et al. 2007)
Birds	Burrowing owl	Mortality	Predicted likelihood of owl burrows	More burrowing owl mortalities in areas with more burrows	Declining population	Upgrade to newer and more powerful turbines	Yes	(Smallwood et al. 2009a)
Birds	Various	Abundance	Number of turbines; power of turbines; size of wind farm; time since operation	Greater declines with low-power turbines; greater declines with longer operating times	Decreased abundance	Long-term monitoring post development	Yes	(Stewart et al. 2007)
Mammals	Elk	Home range size; forage quality	Pre-construction versus during	No impact	None	Pre-development assessment to ensure infrastructure not	Yes	(Walter et al. 2006)

		from pellets	construction versus post-construction of a wind farm			built on areas with high quality forage		
Bats	Various	Nightly presence	Wind speed and direction; moon illumination; temperature; date	Increased presence with low wind speed, higher temperature and greater moon illumination; highly variable by season with lowest activity during winter	Declining population	Deploy echolocation detectors to determine when changes in turbine operation will be beneficial	Yes	(Weller and Baldwin 2012)

Bioenergy

Birds	Various	Nest site selection; nest success	Clone type and diversity; year	Selection by some species of certain clones; altered preference with time	-	Plant clones that support nesting	Yes	(Dhondt et al. 2004)
Birds	Various	Species richness; nest density; nest success	Number of clones; proximity to forest; year; size; compared to richness in BBS	Greater richness and nest density in larger and older plots; results similar to BBS; change in species composition over time	-	Plant larger plots to increase richness and nest success	Yes	(Dhondt et al. 2007)

Birds	Various	Abundance, density, diversity	Crops likely to be used for biofuels vs. reference	Lower abundance and diversity in crops, particularly row crops	Decreasing abundance and diversity	Replace row crops with perennials; harvest native prairies	Yes	(Fletcher et al. 2010)
Small mammals	Various	Abundance, diversity, sex ratio, recruitment	Treatment of post-harvest coarse woody debris; presence of switchgrass in forest plots	No impact on diversity, sex ratio, or recruitment; species specific abundance responses with invasive rodent more abundant in plots with switchgrass	Decreased abundance of native rodent	-	No	(Marshall et al. 2012)
Birds	Various	Species richness	Low input high diversity crops (LIHD; e.g., hay, alfalfa, pasture land) vs. high input low diversity crops (HILD e.g., corn, soy)	Increased richness with small amounts of HILD crops but decline with increasing proportion; greater richness with increase in LIHD crops	Decreased abundance	Plant low input high diversity crops	Yes	(Meehan et al. 2010)

Birds	Various	Abundance and nest success	Different levels of harvest in switchgrass field (fully harvested, partially harvested, unharvested); width of harvested strips	No impact of strip width; no overall impact on abundance; different impacts by species leading to altered species composition; greater nest success and lowest predation in unharvested fields;	Decreased abundance for sensitive species; decreased reproductive output	Maintain mosaic of harvested and unharvested crops	Yes	(Murray and Best 2003)
Birds and small mammals	Various	Species diversity and abundance	Short-rotation woody crops vs. reference	Lower diversity and abundance of birds and mammals in crops; altered species composition for birds; effects decreased with time	Decreased abundance	-	No	(Riffell et al. 2011)
Birds	Various	Species density, richness and abundance	Type of potential crop (native prairie, switchgrass, corn); surrounding land cover; patch size; vegetative	Greater species richness, abundance, and density in prairie and switchgrass than corn; positive relationship between patch size and richness, abundance, and	Decreased abundance, richness, and diversity	Plant perennial crops; harvest native prairies	Yes	(Robertson et al. 2011b)

			characteristics (e.g., forb cover, litter density)	density in prairie and switchgrass but not corn				
Birds	Various	Species richness; density; occurrence; abundance	Switchgrass crops vs. native prairie; vegetative characteristics (e.g., density, height); patch size	Greater species richness in prairie; greater richness in larger patches; greater density and abundance with greater structural heterogeneity in vegetation	Decreased abundance in switchgrass vs. native prairie and with certain vegetative characteristics	Implement harvest strategies that create within-crop structural diversity; maintain mosaic of harvested and unharvested crops	Yes	(Robertson et al. 2011a)
Birds	Various	Bird richness and abundance	Harvested fields vs. unharvested fields	No change in abundance but altered community structure in harvested fields	Decreased abundance of sensitive species	Maintain mosaic of harvested and unharvested crops; delay harvest until after fledging	Yes	(Roth et al. 2005)
Small mammals	Red-backed vole (*Myodes gapperi*)	Abundance	Post-logging treatment of coarse woody debris	Greater abundance with more coarse woody debris; greater abundance when debris pushed into piles or windrows	Decreased abundance without mitigation	Maintain coarse woody debris and put into piles or windrows	Yes	(Sullivan et al. 2011)
Birds; mammals	Various	Species diversity	Reference forest vs.	Overall positive impact of thinning	Decreased abundance	Thin forests but develop species	Yes	(Verschuyl et al.

; reptiles; amphibians		and abundance	thinned forests	on birds, mammals and reptiles; guild specific responses; no overall impact of thinning on amphibians but negative guild level responses; negative response with more intensively thinned plots	of sensitive species	and site-specific guidelines		2011)
Mammals	White-tailed deer	Home range size; mean annual home range overlap	Percent of crops in home range	Percent of crops in home range increased over time; home range size decreased; high site fidelity	Altered range use patterns	-	No	(Walter et al. 2009b)

Solar

Review	-	-	-	-	-	-	-	(Lovich and Ennen 2011)
Review	-	-	-	-	-	-	-	(Pimental 2008)

Geothermal

Review	-	-	-	-	-	-	-	(Pimental 2008)

Table A1.2. Global peer-reviewed literature on the impacts of wind and bioenergy development on wildlife, excluding the United States and Canada. The country where the study took place, species and taxonomic group are reported for each sector. No studies were found on the impacts of geothermal or solar energy, and oil and natural gas studies were excluded (see text above).

Taxonomic group	Common name	Country	Citation
Wind			
Birds	Various	Spain	(Barrios and Rodríguez 2004)
Birds	Egyptian vulture	Spain	(Carrete et al. 2009)
Birds	Griffon vulture	Spain	(Carrete et al. 2012)
Birds	White-tailed eagle	Norway	(Dahl et al. 2012)
Birds	Various	Spain	(de Lucas et al. 2004)
Birds and small mammals	Various	Spain	(de Lucas et al. 2005)
Birds	Various raptors	Spain	(de Lucas et al. 2008)
Birds	Griffon vulture	Spain	(de Lucas et al. 2012)
Birds	Various	United Kingdom	Devereux 2008-JAE
Birds	Red Grouse and Golden Plover	United Kingdom	(Douglas et al. 2011)
Birds	Various	Spain	(Farfán et al. 2009)
Birds	Various	Spain	(Ferrer et al. 2012)
Bats	*Pipistrellus pipistrellus,* and *Hypsugo savii*	Italy	(Ferri et al. 2011)
Mammals	Reindeer	Norway	(Flydal et al. 2004)
Birds	Various	Netherlands	(Krijgsveld et al. 2009)
Birds	Pink-footed geese	Denmark	(Larsen and Madsen 2000)
Birds	White-tailed sea eagle	Germany	(Krone and Scharnweber 2003)
Birds	Pink-footed geese	Denmark	(Madsen and Boertmann 2008)
Birds	Eurasian griffon vulture	Spain	(Martinez-Abrain et al. 2012)
Birds	Golden Plover	United Kingdom	(Pearce-Higgins et al. 2008)
Birds	Various	United Kingdom	(Pearce-Higgins et al. 2009)
Birds	Various	United Kingdom	(Pearce-Higgins et al. 2012)

Bats	various	Meta-analysis	(Rydell et al. 2010)
Mammal and amphibians and reptiles	Various	Portugal	(Santos et al. 2010)
Birds	Golden Eagle	United Kingdom	(Walker et al. 2005)

Bioenergy

Birds	Various	United Kingdom	(Bellamy et al. 2009)
Birds and small mammals	Various	United Kingdom	(Clapham and Slater 2008)
Birds	Various	Sweden	(Berg 2002)
Birds and reptiles and mammals	Various	Meta-analysis	(Danielsen et al. 2009)
Birds	Various	Borneo	(Edwards et al. 2010)
Birds	Various	United Kingdom	(Fry and Slater 2011)
Small mammals	Various	Italy	(Giordano and Meriggi 2009)
Birds	Various	Borneo	(Koh 2008)
Birds	Various	Guatemala	(Najera and Simonetti 2010)
Birds	Various	United Kingdom	(Sage et al. 2006)
Birds	Various	United Kingdom	(Sage et al. 2010)
Birds and small mammals	Various	United Kingdom	(Semere and Slater 2007)
Birds	Various	Malaysia	(Sheldon et al. 2010)
Birds	Skylark	Finland	(Vepsalainen 2010)

APPENDIX 2

QUANTIFYING ENERGY POTENTIAL BY ECOREGIONS

DESCRIPTION OF PROTOCOL

We quantified the resource potential present in each ecoregion (Olson et al. 2001) for the

continental United States, as this region had comprehensive spatial data on each of the five

energy sectors reviewed. We overlaid each ecoregion (Olson *et al.* 2001; Fig. A2.1F) with

spatially explicit data on the resource potential for each of the 5 energy sectors: unconventional

oil and natural gas, wind, bioenergy, solar, and geothermal. For wind, bioenergy, solar, and

geothermal, resource potential maps were downloaded from the National Renewable Energy

Laboratory website (http://www.nrel.gov/gis/; Fig. A2.1B-E). We downloaded shapefiles

representing the extent of unconventional oil and natural gas basins from the Energy Information

Administration (http://www.eia.gov/pub/oil_gas/natural_gas/analysis_

publications/maps/maps.htm; Fig. A2.1A). In Arcmap 10.0 (Environmental Systems Research

Incorporated, Redlands, CA), we used the Intersect and Zonal Statistics tools to quantify the

resource potential overlap with each of the ecoregions. Results of this analysis are presented in
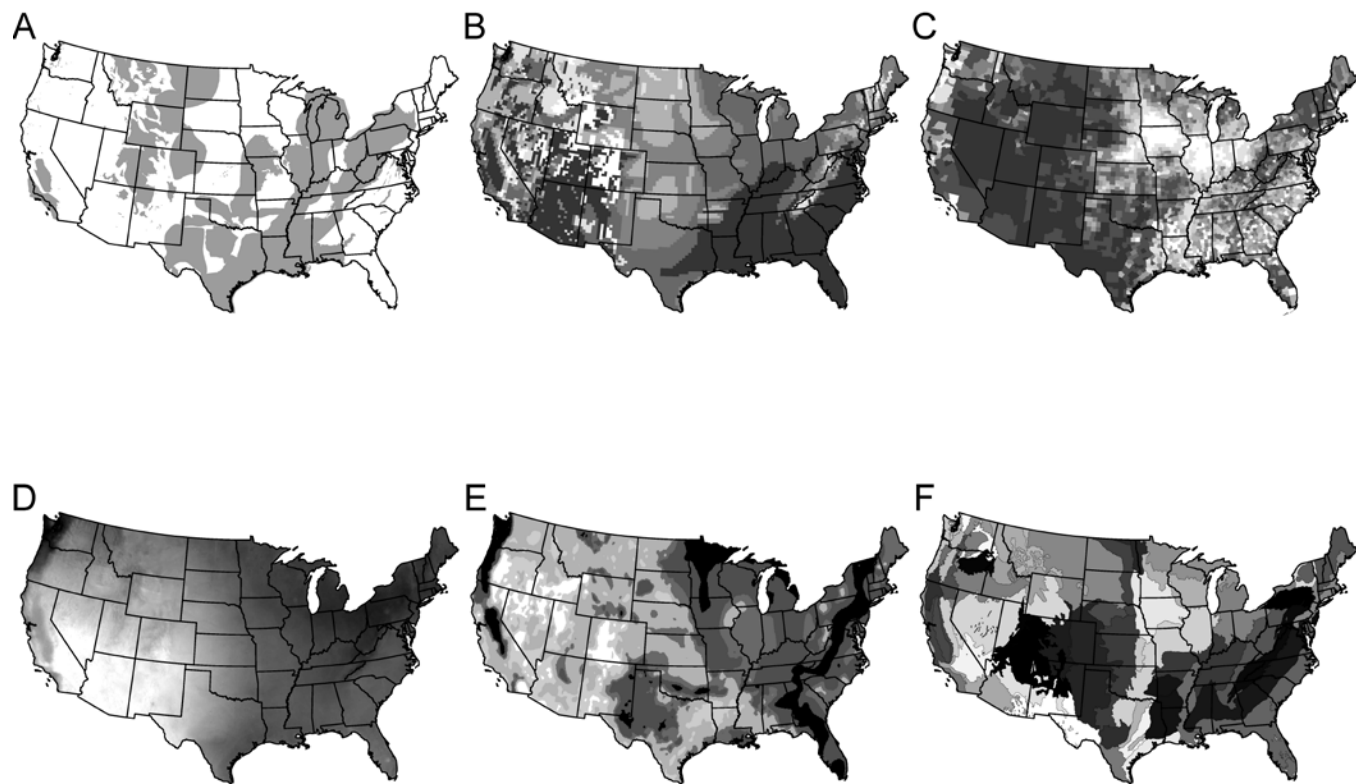
FIGURES

Figure A2.1. Energy potential in the 48 contiguous United States for (A) unconventional oil and natural gas (geographic extent of basins), (B) wind energy (wind power class defined using 50 m wind speed; http://www.nrel.gov/gis/data_ wind.html), (C) bioenergy (tons / km2 / year biomass potential; http://www.nrel.gov/gis/data_biomass.html), (D) solar (kWh / year), and (E) geothermal (energy potential class; http://www.nrel.gov/gis/data_geothermal.html), and (F) ecoregions represented. For A, basin extents are highlighted in gray. For B-E lighter colors indicate greater energy potential.

APPENDIX 3

SIMULATION OF LANDSCAPE COVARIATES USED IN CHAPTER 3

SIMULATION PROTOCOL

To assess how resource selection function (RSF) coefficient estimates were influenced by the interaction between spatial autocorrelation in environmental covariates and the size and spatial extent of the availability sample we fit RSFs to data simulated from environmental covariates that were themselves simulated as a Gaussian random field, using the grf function in the package 'geoR':

$$x \sim Normal(\mathbf{0}, \Sigma) \qquad (A.1)$$

$$\Sigma_{ij} = \sigma^2 e^{\left(\frac{-d_{ij}}{\phi}\right)} \qquad (A.2)$$

where x is a simulated environmental covariate, Σ is a covariance matrix, d_{ij} is the distance between cells i and j, and ϕ is the range parameter controlling the level of correlation among cells. At larger values of ϕ the landscape is more spatially autocorrelated, while small values produce a more random landscape (Fig. A3.1). We set $\sigma^2 = 1$ and varied ϕ from 0.001 to 100 (0.001, 0.05, 1, 2.5, 5, 10, 20, 40, 100). Using these covariates we simulated used data as an inhomogeneous Poisson spatial point process, and fit RSFs with both matched and mismatched availability samples (see main text). Results are presented in Figures A3.2-A3.4.

The above analysis provided an assessment of how autocorrelation interacts with the size and spatial extent of the availability sample to influence RSF coefficient estimates for a continuous covariate. For binary covariates, the proportion of the landscape composed of that covariate also has the potential to influence this interaction. To examine this potential we again simulated environmental covariates as a Gaussian random field with ϕ parameters of 0.001 and

10. We then converted these covariates to binary covariates by selecting a threshold above which all values were converted to 1s and below which they were converted to 0s. We chose thresholds to simulate 2.5%, 25%, and 50% of the landscape being composed of the binary variable (Fig. A3.6). Using these covariates we simulated used data as an inhomogeneous Poisson spatial point process and fit RSFs with both matched and mismatched availability sample (see main text). Results are presented in Figure A3.6.
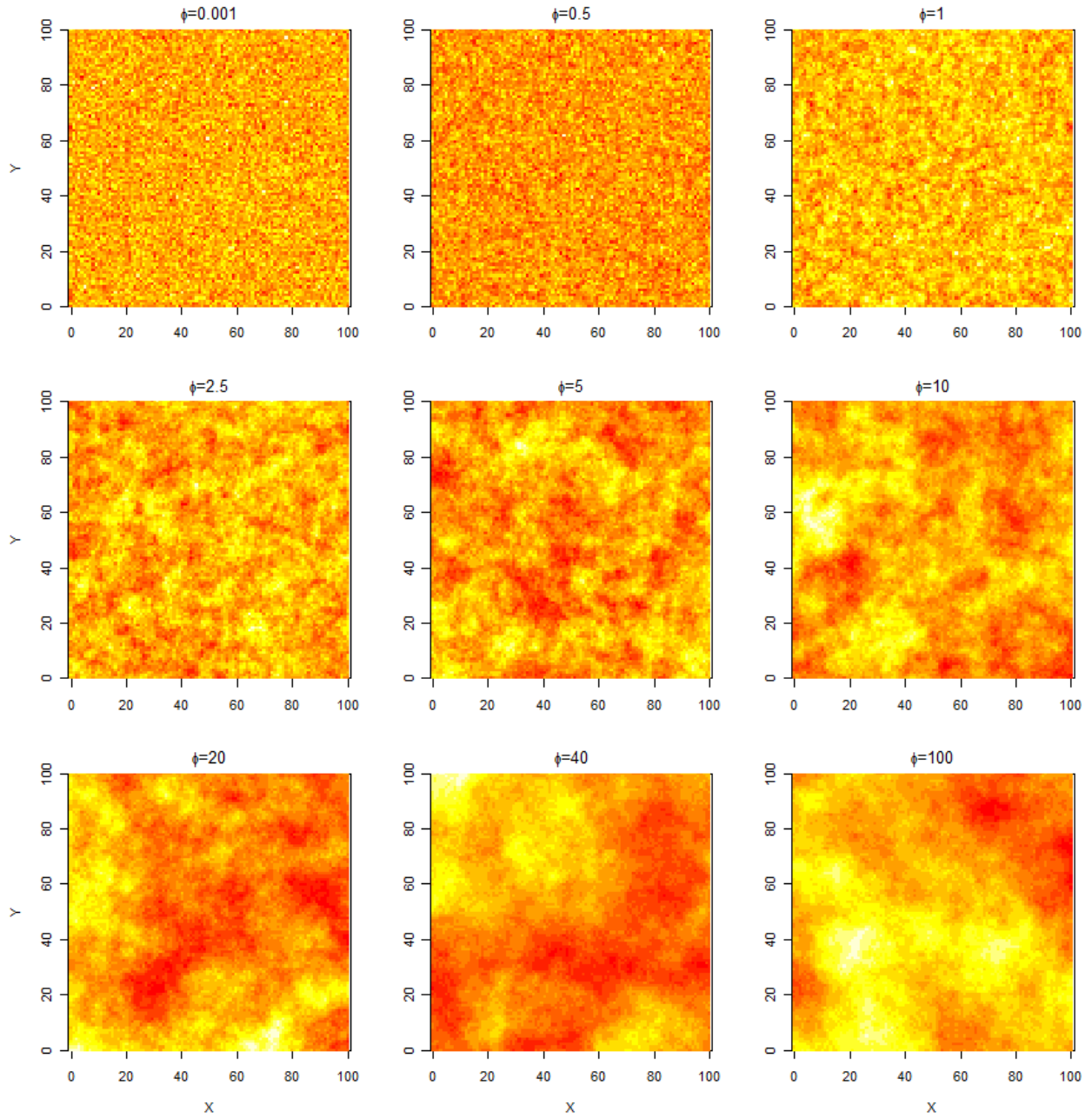
Figure A3.1. Continuous environmental covariate simulated as a Gaussian random field, with varying ϕ parameters.
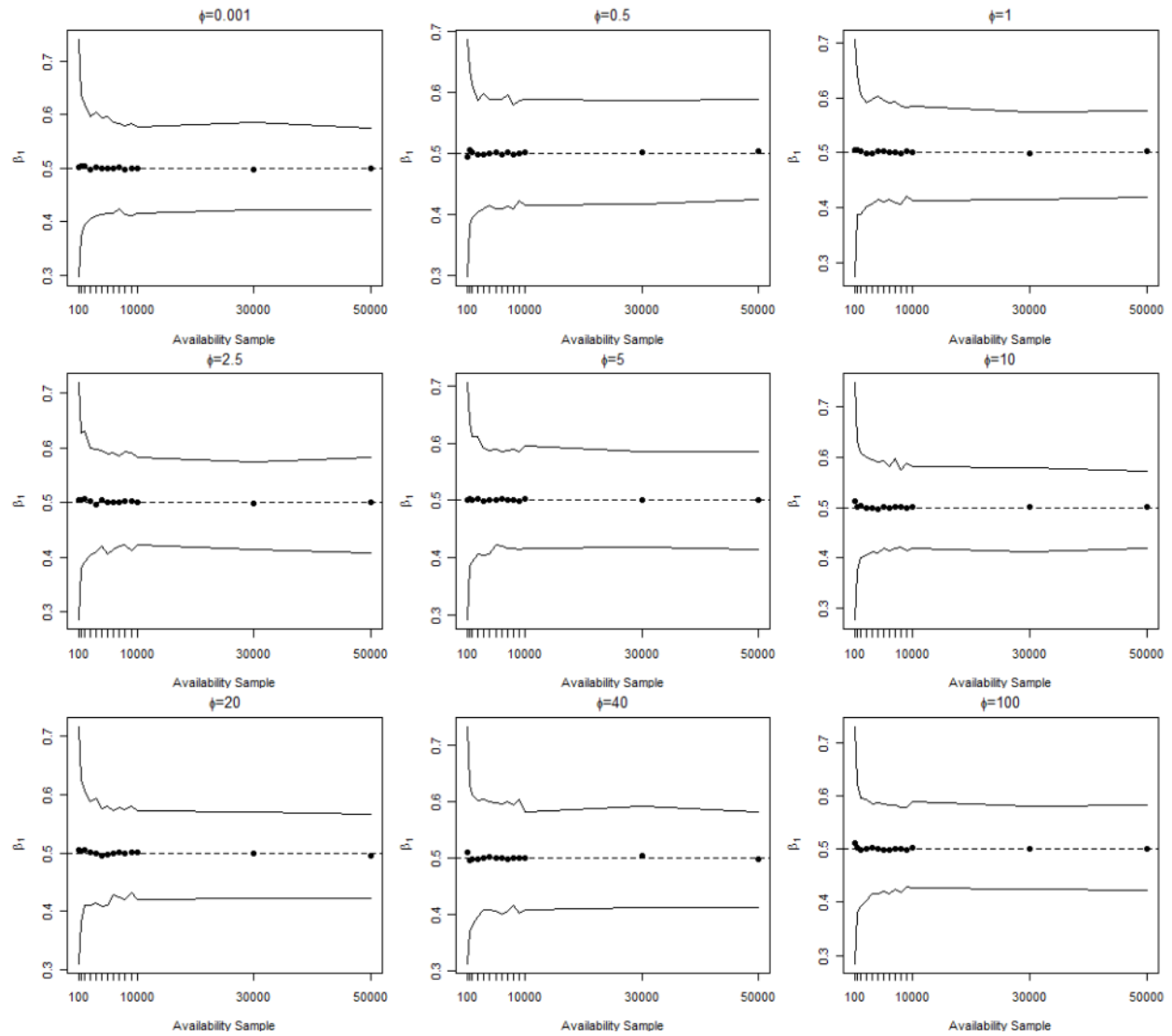
Figure A3.2. Coefficient estimator (black points) and 95% simulation envelopes (solid lines) from 500 RSF model iterations fit to data simulated from covariates generated as Gaussian random fields with varying ϕ parameters. Availability was drawn from the same spatial extent as use. Dashed lines represent the coefficient value from which the used data were simulated.
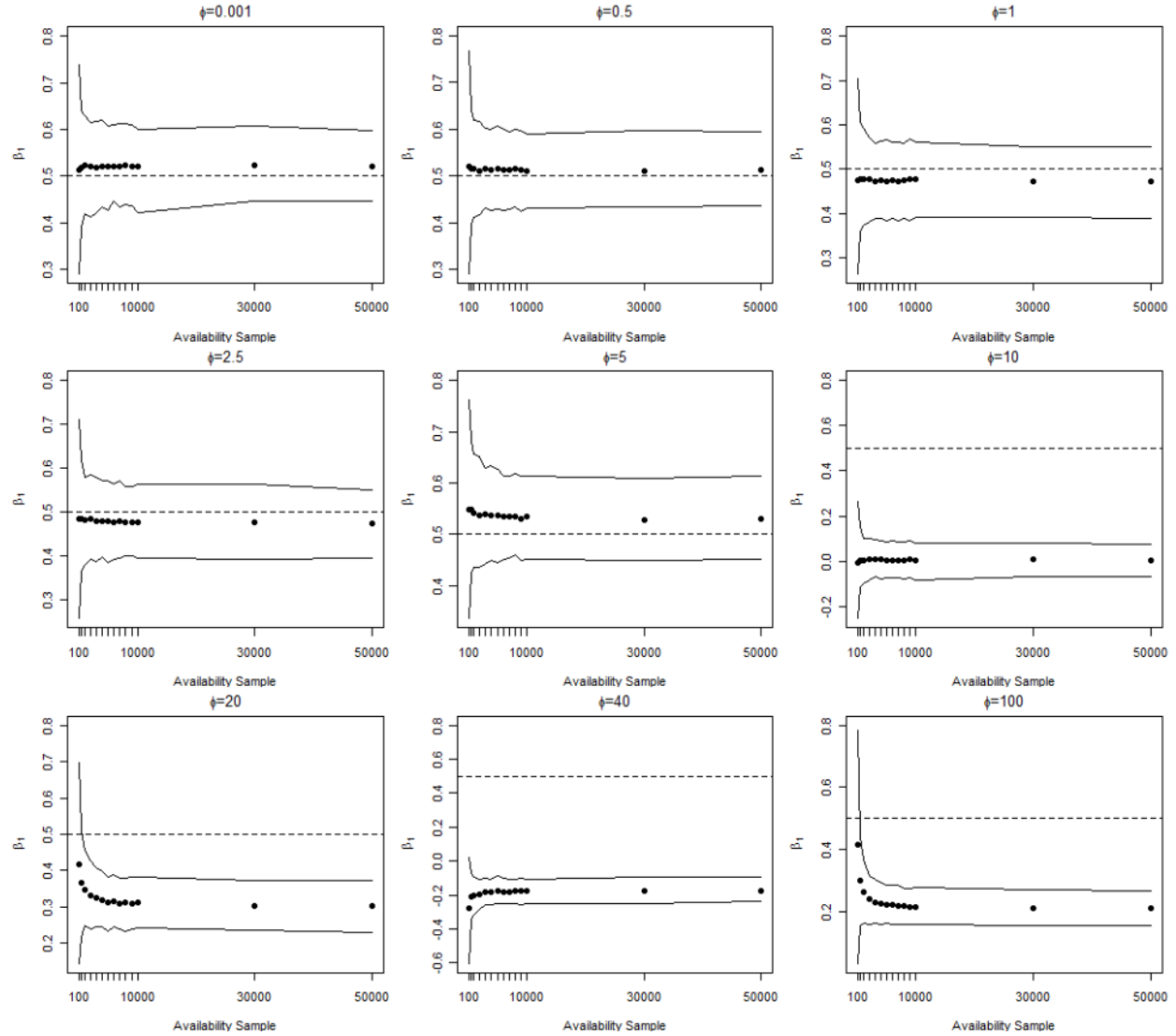
Figure A3.3. Coefficient estimator (black points) and 95% simulation envelopes (solid lines) from 500 RSF model iterations fit to data simulated from covariates generated as Gaussian random fields with varying ϕ parameters. Availability was drawn from a different spatial extent as use. Dashed lines represent the coefficient value from which the used data were simulated. Approximately 600 used locations were simulated for each iteration.
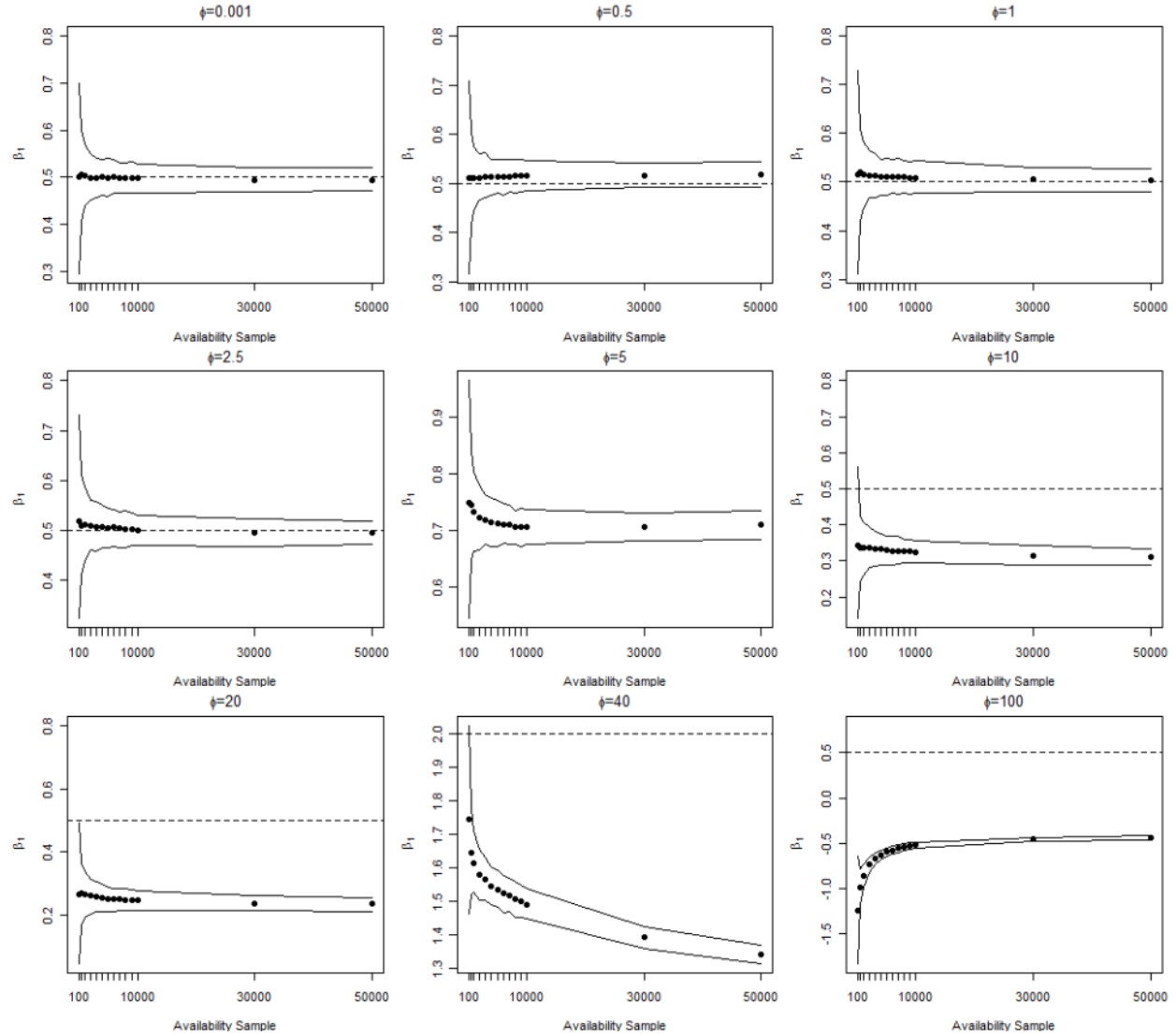
Figure A3.4. Coefficient estimator (black points) and 95% simulation envelopes (solid lines) from 500 RSF model iterations fit to data simulated from covariates generated as Gaussian random fields with varying ϕ parameters. Availability was drawn from a different spatial extent as use. Dashed lines represent the coefficient value from which the used data were simulated. Approximately 6,000 used locations were simulated for each iteration.
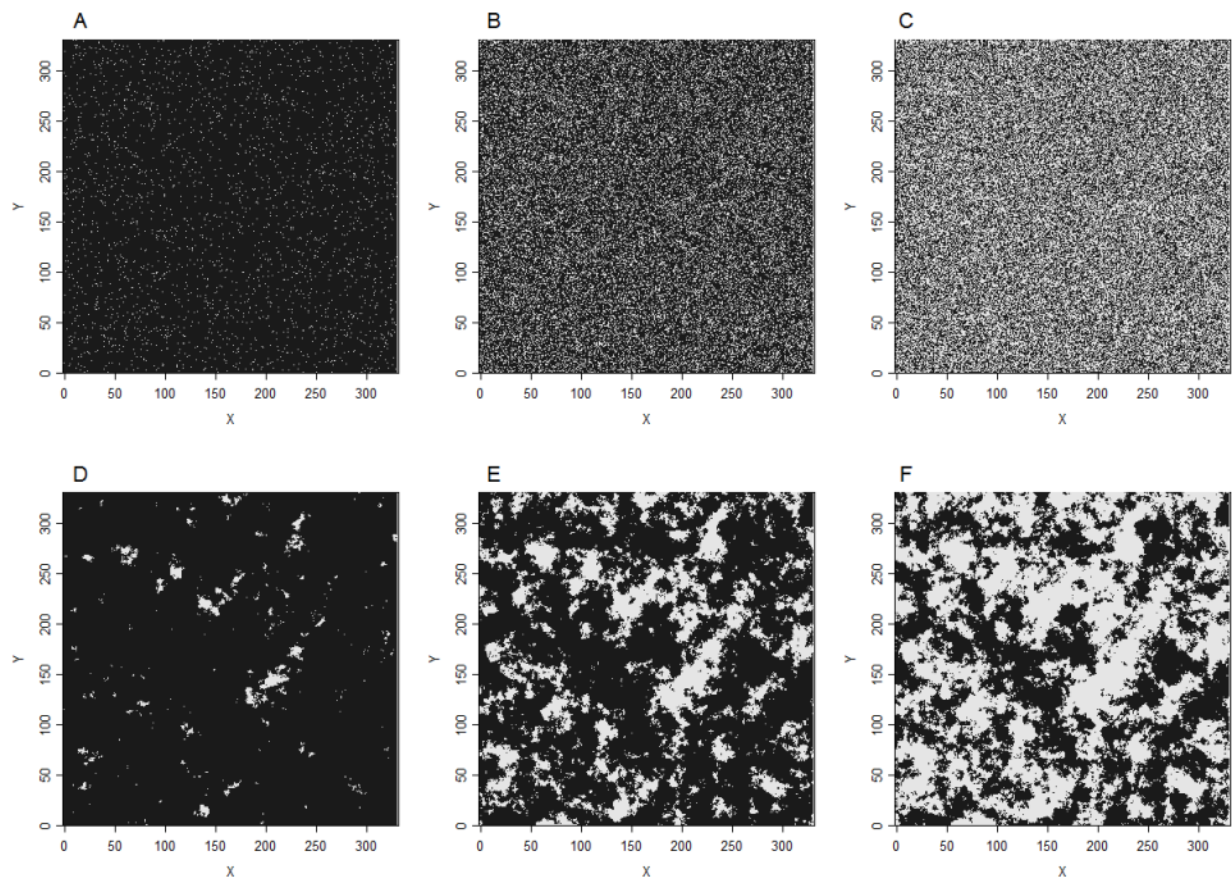
Figure A3.5. Binary environmental covariate simulated as a Gaussian random field with $\phi = 0.001$ (A-C) or $\phi = 10$ (D-F), and converted to a binary covariate composing 2.5% (A and D), 25 % (B and E) or 50% (C and F) of the landscape.
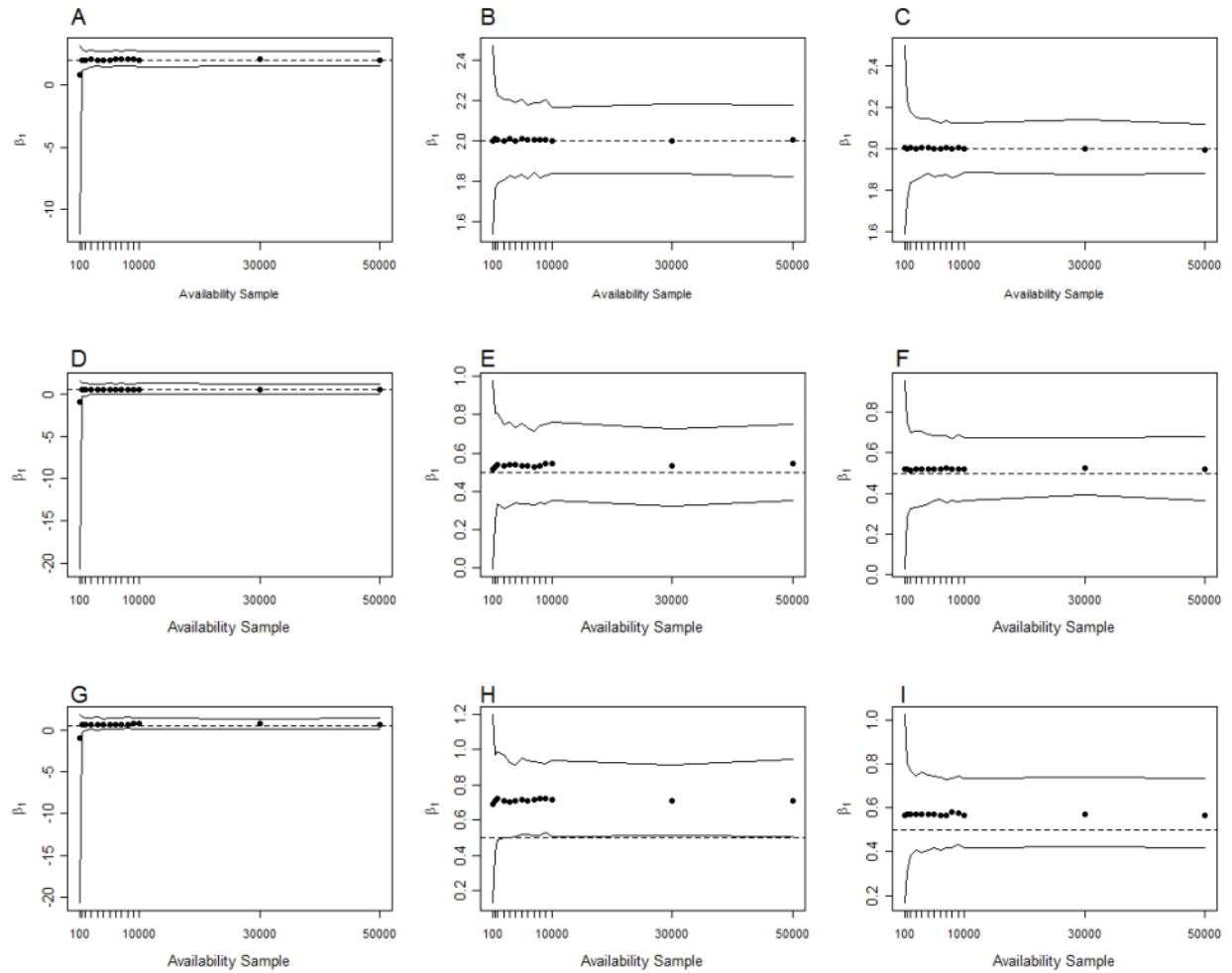
Figure A3.6. Coefficient estimator (black points) and 95% simulation envelopes (solid lines) from 500 RSF model iterations fit to data simulated from covariates generated as Gaussian random fields with $\phi = 0.001$ (D-F) or $\phi = 10$ (A-C and G-I), and converted to a binary covariate composing 2.5% (A, D & G), 25 % (B, E & H) or 50% (C, F & I) of the landscape. Availability was drawn from either the same spatial extent as use (A-C) or a greater spatial extent (D-I). Dashed lines represent the coefficient value from which the used data were simulated. Approximately 600 used locations were simulated at each iteration.

APPENDIX 4

ENVIRONMENTAL COVARIATES USED IN RSF MODELING

Table A4.1. Covariates, descriptions of covariates, pixel size, and source of data for environmental covariates used in habitat selection modeling

Covariate	Description	Pixel Size (m)	Data Source
num_drill	Number of drilling natural gas well pads within 800 m	30 × 30	Colorado Oil and Gas Conservation Commission (http://cogcc.state.co.us/)
num_prod	Number of actively producing natural gas well pads within 800 m	30 × 30	Colorado Oil and Gas Conservation Commission (http://cogcc.state.co.us/)
elev	Elevation (m)	30 × 30	United States Geological Survey seamless data warehouse (http://seamless.usgs.gov)
heat	Heat load index, a standardized index of incoming solar radiation, corrected for latitude (McCune and Keon 2002)	30 × 30	Calculated from elevation layer, above using ArcMap 10
slope	Slope (degrees)	30 × 30	Calculated from elevation layer, above using ArcMap 10
barren	Non-vegetated land cover	30 × 30	Colorado Vegetation Classification Project (http://ndis.nrel.colostate.edu/coveg/)
shrub	Shrub land cover	30 × 30	Colorado Vegetation Classification Project (http://ndis.nrel.colostate.edu/coveg/)
grass	Grass land cover	30 × 30	Colorado Vegetation Classification Project (http://ndis.nrel.colostate.edu/coveg/)
d_edge	Distance to edge of treed land cover	30 × 30	Colorado Vegetation Classification Project (http://ndis.nrel.colostate.edu/coveg/), calculated using ArcMap 10
d_rds	Distance to roads	30 × 30	United States Geological Survey seamless data warehouse (http://seamless.usgs.gov)
traffic	Traffic volume class of the nearest road	30 × 30	J.M. Northrup, C.R. Anderson and G. Wittemyer unpublished data
d_stream	Distance to rivers and streams	30 × 30	Colorado Division of Water Resources (http://water.state.co.us/DataMaps/GISandMaps/Pages/GISDownloads.aspx)

APPENDIX 5

RESULTS OF BASIC SIMULATIONS AND LOCATION-BASED AVAILABILITY

SIMULATIONS IN CHAPTER 3

FIGURES
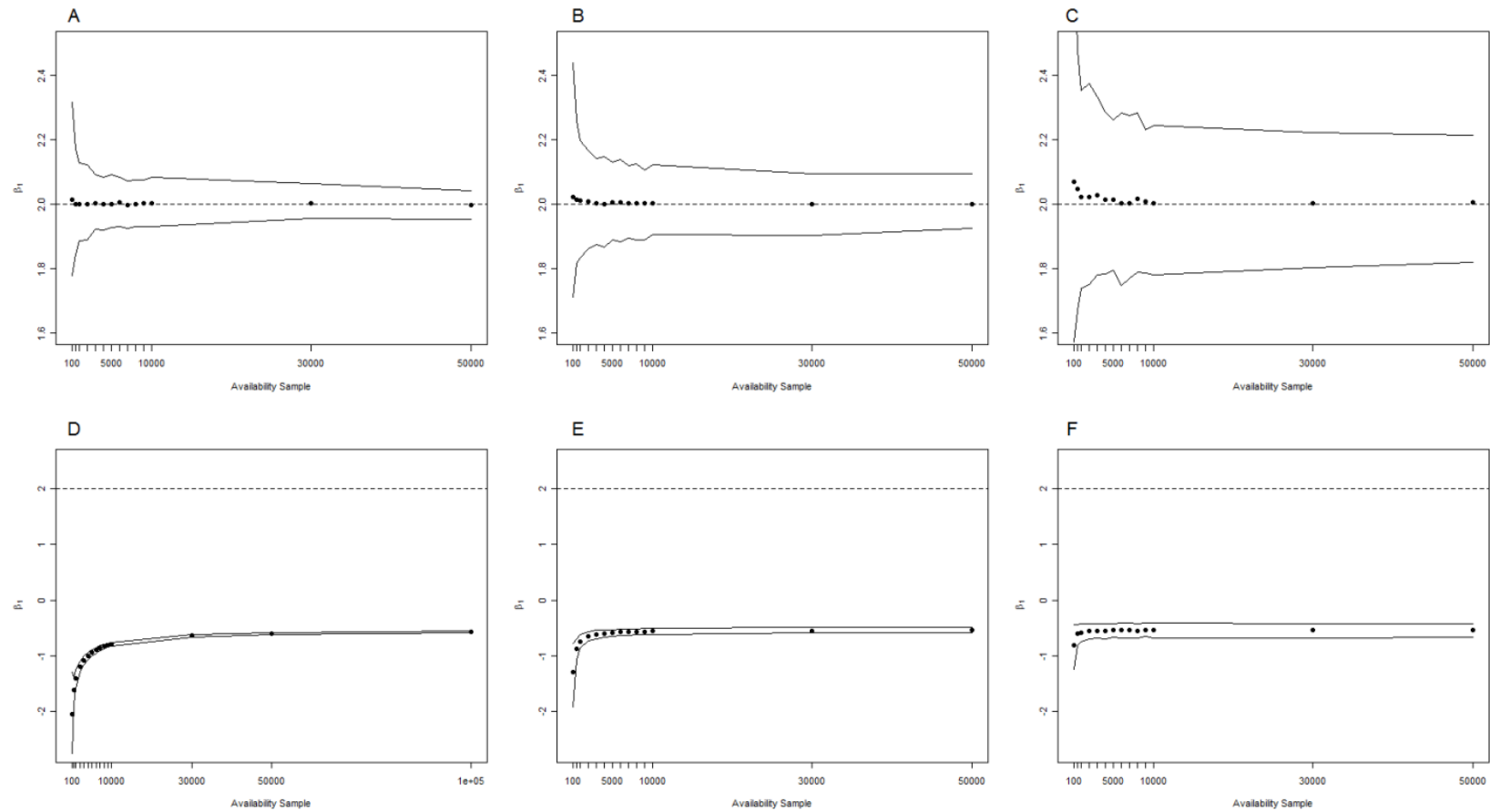
Figure A5.1. Coefficient estimator (black points) and 95% simulation envelopes (solid lines) from 500 RSF model iterations as a function of availability sample size, with availability drawn from the same spatial extent as use, for high (A), medium (B) and low (C)

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used sample sizes, and availability drawn from a greater spatial extent than use for high (D), medium (E), and low (F) used sample sizes. Dotted line represents the value used for simulation. Models were fit with logistic regression in all cases.
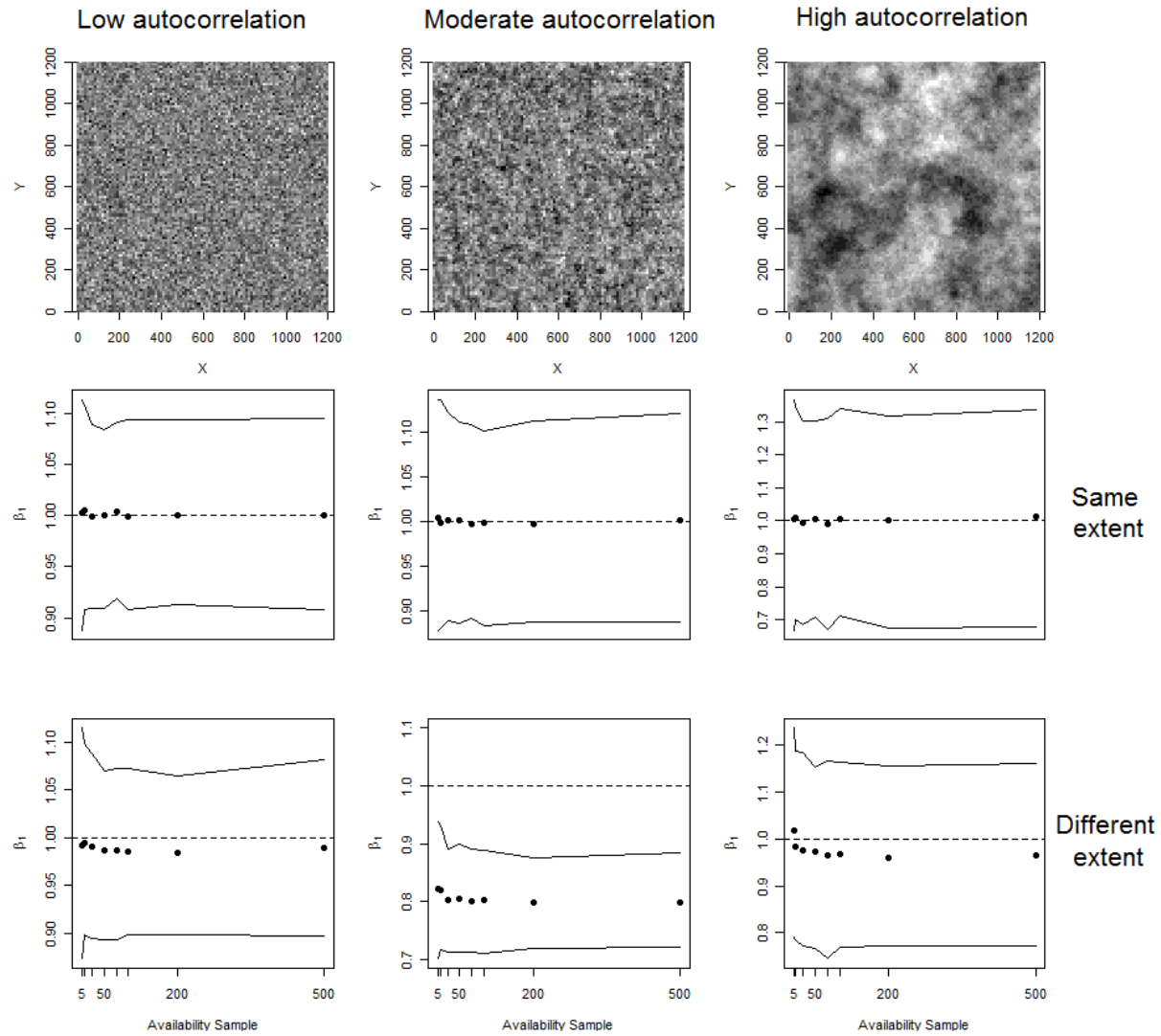
Figure A5.2. Continuous landscape covariates simulated as a Gaussian random field with low($\phi = 0.001$), moderate ($\phi = 10$) or high ($\phi = 100$) autocorrelation, and expectations of the coefficients (black points) and 95% simulation envelopes (solid lines) from 500 RSF model iterations as a function of availability sample size. Used data were simulated within 100 meter buffers and models were fit with conditional logistic regression with availability drawn from the same or different (200 m buffers with identical centroids) spatial extents as use.

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APPENDIX 6

DETAILED DESCRIPTION OF WELL CLASSIFICATIONS

The Colorado Oil and Gas Conservation Commission data provide the location of every well drilled in the state, the current status of each well, and the dates drilling began (spud date), the date that drilling reached its deepest depth (total depth date), and the date that the well was completed (the test date). We first attempted to categorize each well into one of 3 classes for every day during which we had deer GPS data. Wells were classified as drilling on every day between the spud date and the test date. Wells were classified as producing on days after the test date until the well was listed as abandoned. Wells were listed as abandoned from the time their status was listed as abandoned. In several cases the status of the well could not be directly categorized as one of these three statuses, and instead had a status of temporarily abandoned, injection well (wells where fluids are injected underground), shut in (wells that have been drilled but are not producing natural gas), or waiting on completion (wells that have been drilled but not completed). These instances were infrequent, and typically it was impossible to determine the date of any activity associated with the well as listed dates were prior to the onset of the study or were missing. In light of these difficulties, we categorized all of these wells as producing. In addition to the above statuses, the COGCC database includes a number of records for permitted locations that were never drilled. To ensure that these classifications were accurate we overlaid the well data with aerial imagery from the National Agriculture Imagery Program (NAIP) to assess if these records were indeed abandoned locations or if there was evidence of disturbance.

APPENDIX 7

OVERLAPPING BUFFERS ANALYSIS, MODEL STRUCTURES AND RESULTS OF ALL

FITTED MODELS FROM CHAPTER 4

In addition to the single model structure discussed in the main text, where the number of well pads within concentric buffers was analyzed, we also fit a set of models including covariates for the number of well pads within overlapping buffers (Table A7.1). For this analysis we created 8 separate covariates representing active natural gas development. We first calculated the distance to the closest well pad classified as either drilling or producing (*d_drill* and *d_prod* respectively). We next calculated the number of well pads of each type falling within buffers of different sizes (400 m; *drill_400_2* and *prod_400_2*, 600 m; *drill_600_2* and *prod_600_2*, and 800 m; *drill_800_2* and *prod_800_2*). These 8 variables (continuous distance and the four buffers) represent separate hypotheses for the scale and nature of mule deer responses to well pads. Model fitting proceeded as in the main text but the total number of iterations for which algorithms were run and the number of iterations removed as burn-in varied by model (Table A7.1). We compared models using the Watanabe-Akaike Information Criteria (Watanabe 2010, see Hooten and Hobbs 2014 for a discussion of applications in ecology).

TABLES

Table A7.1. Model numbers, covariates included in each model, Watanabe-Akaike Information Criteria (WAIC), total MCMC iterations, and burn-in for resource selection functions fit to GPS radio collar data from 53 adult female mule deer in the Piceance Basin winter range, Northwest Colorado, Jan 2008—Dec 2010.

Model	Covariates	WAIC	Total iterations	Burn-in
Night				
M1	d_edge + $slope$ +$elev$ +d_rds +d_rds^2 +$prod\_800\_2$ +$drill\_800\_2$ + $tree$	218,163.50	200,000	50,000
M2	d_edge + $slope$ +$elev$ + d_rds + d_rds^2 +$prod\_600\_2$ +$drill\_600\_2$ + $tree$	219,770.30	200,000	50,000
M3	d_edge + $slope$ +$elev$ + d_rds + d_rds^2 +$prod\_400\_2$ +$drill\_400\_2$ + $tree$	219,601.10	400,000	100,000
M4	d_edge + $slope$ +$elev$ + d_rds + d_rds^2 +d_prod + d_prod^2 + d_drill + d_drill^2 + $tree$	251,666.30	1,800,000	700,000
Day				
M1	d_edge + $slope$ +$elev$ + d_rds + d_rds^2 +$prod\_800\_2$ +$drill\_800\_2$ + $tree$	227,247.40	200,000	50,000
M2	d_edge + $slope$ +$elev$ + d_rds + d_rds^2 +$prod\_600\_2$ +$drill\_600\_2$ + $tree$	226,333.10	200,000	50,000

M3	$d\_edge + slope + elev + d\_rds + d\_rds^2 + prod\_400\_2 + drill\_400\_2 + tree$		400,000	50,000
		225,421.00		
M4	$d\_edge + slope + elev + d\_rds + d\_rds^2 + d\_prod + d\_prod^2 + d\_drill + d\_drill^2 + tree$		1,800,000	700,000
		239,439.00		

Table A7.2. Covariates, median coefficient values, and the proportion (prop.) of the posterior falling above or below 0 for resource selection function models, fit to separate night and day GPS radio collar data from 53 adult female mule deer in the Piceance Basin winter range, Northwest Colorado, Jan 2008—Dec 2010.

Covariate	Median	Prop. < 0	Prop. > 0
Night			
M1			
d_edge	0.11	0.00	1.00
slope	0.18	0.00	1.00
elev	0.90	0.00	1.00
d_rds	-0.36	1.00	0.00
d_rds²	-0.45	1.00	0.00
prod_800_2	0.07	0.14	0.86
drill_800_2	-0.36	0.99	0.01
tree	-0.29	1.00	0.00
M2			
d_edge	0.11	0.00	1.00
slope	0.17	0.00	1.00
elev	0.85	0.00	1.00
d_rds	-0.38	1.00	0.00
d_rds²	-0.47	1.00	0.00
prod_600_2	-0.05	0.77	0.23
drill_600_2	-0.58	1.00	0.00
tree	-0.28	1.00	0.00
M3			
d_edge	0.11	0.00	1.00
slope	0.17	0.00	1.00
elev	0.81	0.00	1.00
d_rds	-0.40	1.00	0.00
d_rds²	-0.47	1.00	0.00
prod_400_2	-0.21	0.99	0.01
drill_400_2	-0.78	1.00	0.00
tree	-0.28	1.00	0.00
M4			
d_edge	0.11	0.00	1.00
slope	0.17	0.00	1.00
elev	1.07	0.00	1.00
d_rds	-0.37	1.00	0.00
d_rds²	-0.45	1.00	0.00
d_prod	-0.67	1.00	0.00
d_prod²	-0.63	1.00	0.00
d_drill	-1.51	1.00	0.00
d_drill²	-1.37	1.00	0.00
tree	-0.29	1.00	0.00
Day			
M1			

d_edge	-0.18	1.00	0.00
slope	0.06	0.00	1.00
elev	0.65	0.00	1.00
d_rds	0.19	0.00	1.00
d_rds²	-0.30	1.00	0.00
prod_800_2	-0.12	0.98	0.02
drill_800_2	-0.18	0.99	0.01
tree	0.08	0.01	0.99
M2			
d_edge	-0.18	1.00	0.00
slope	0.05	0.01	0.99
elev	0.63	0.00	1.00
d_rds	0.16	0.00	1.00
d_rds²	-0.32	1.00	0.00
prod_600_2	-0.23	1.00	0.00
drill_600_2	-0.50	1.00	0.00
tree	0.08	0.01	0.99
M3			
d_edge	-0.18	1.00	0.00
slope	0.05	0.01	0.99
elev	0.61	0.00	1.00
d_rds	0.16	0.00	1.00
d_rds²	-0.30	1.00	0.00
prod_400_2	-0.36	1.00	0.00
drill_400_2	-0.84	1.00	0.00
tree	0.09	0.00	1.00
M4			
d_edge	-0.17	1.00	0.00
slope	0.05	0.01	0.99
elev	0.73	0.00	1.00
d_rds	0.18	0.00	1.00
d_rds²	-0.27	1.00	0.00
d_prod	-0.21	0.90	0.10
d_prod²	-0.55	1.00	0.00
d_drill	0.13	0.33	0.67
d_drill²	-0.88	1.00	0.00
tree	0.08	0.01	0.99
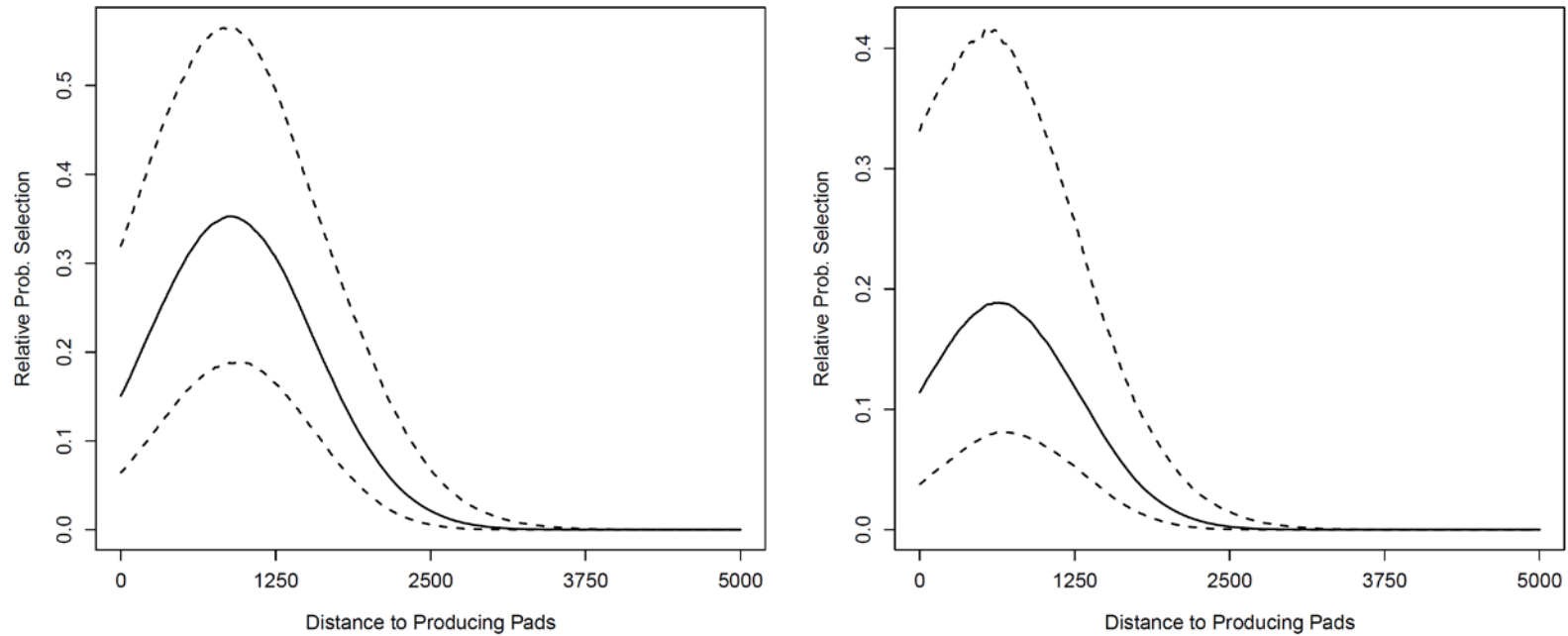
Figure A7.1. Predicted relative probability of selection as a function of distance to well pads actively producing natural gas in meters from resource selection function models fit to 53 adult female mule deer in the Piceance Basin, Colorado, USA. The left panel is for the model from the day time and the right panel for the model from the night. Solid lines represent median posterior predicted values and dashed lines represent the 95% credible intervals.
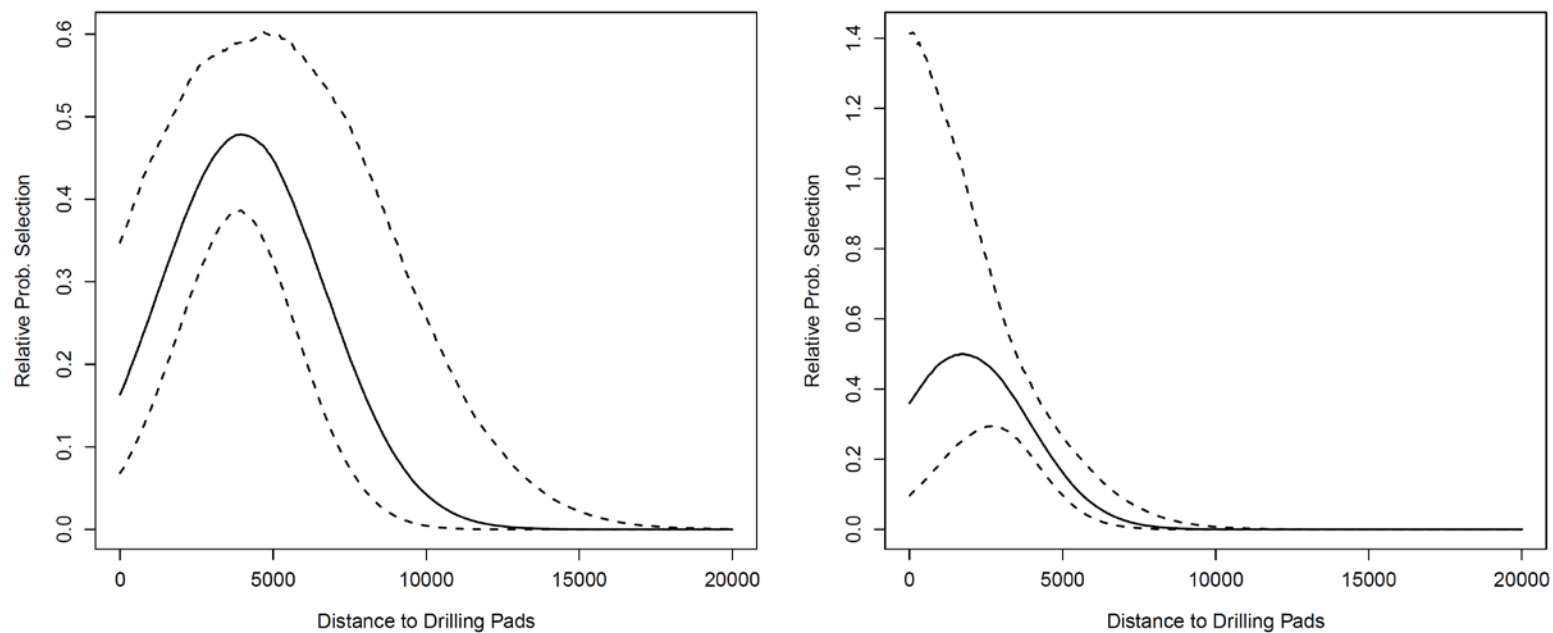
Figure A7.2. Predicted relative probability of selection as a function of distance to well pads with active drilling in meters from resource selection function models fit to 53 adult female mule deer in the Piceance Basin, Colorado, USA. The left panel is for the model from the day time and the right panel for the model from the night. Solid lines represent median posterior predicted values and dashed lines represent the 95% credible intervals.
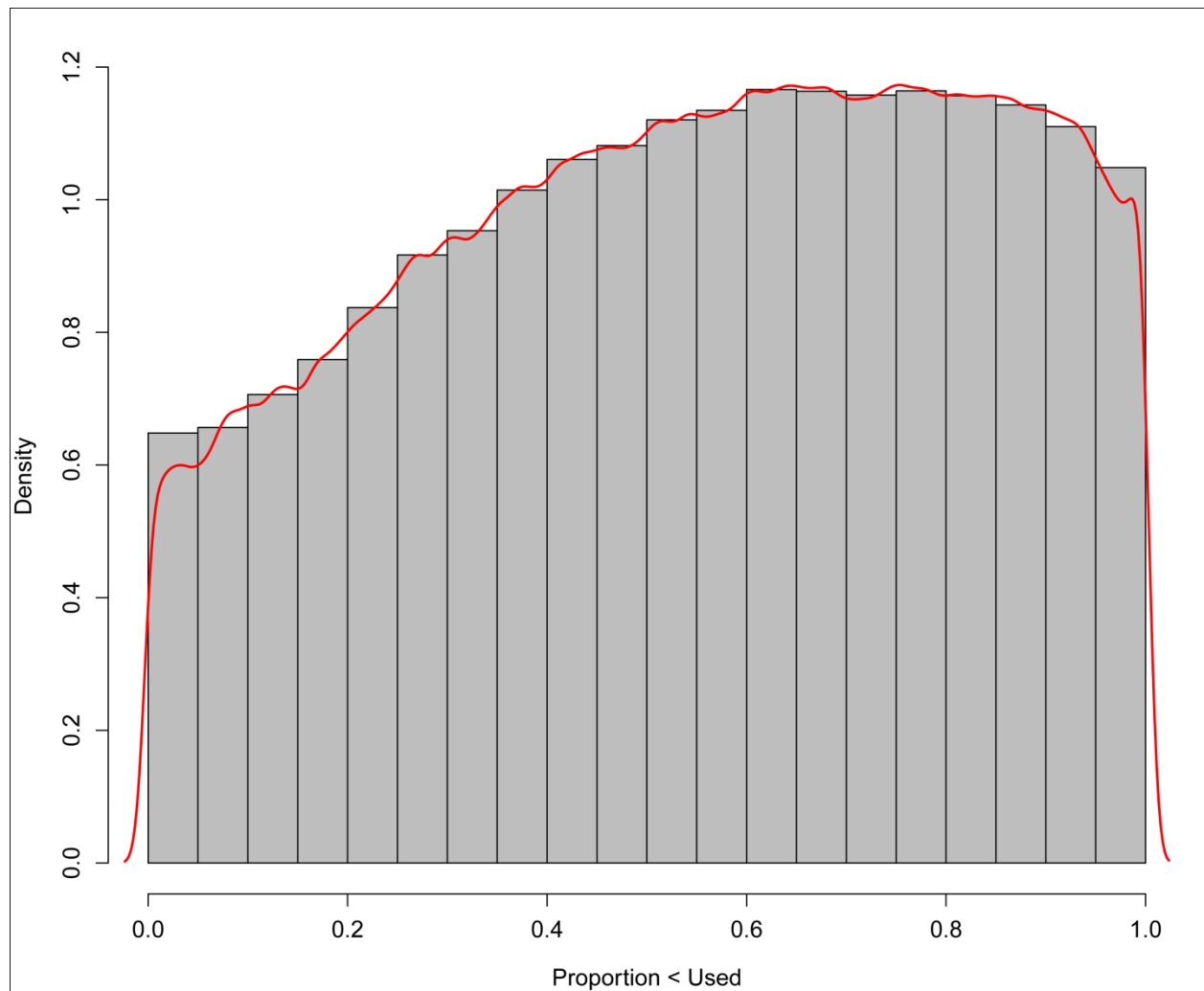
Figure A7.3. Results of posterior predictive check on day time RSF model with concentric buffers fit to winter range GPS data from 53 female mule deer. X-axis represents the proportion of available locations that were predicted to be selected at a lower probability than the used locations.
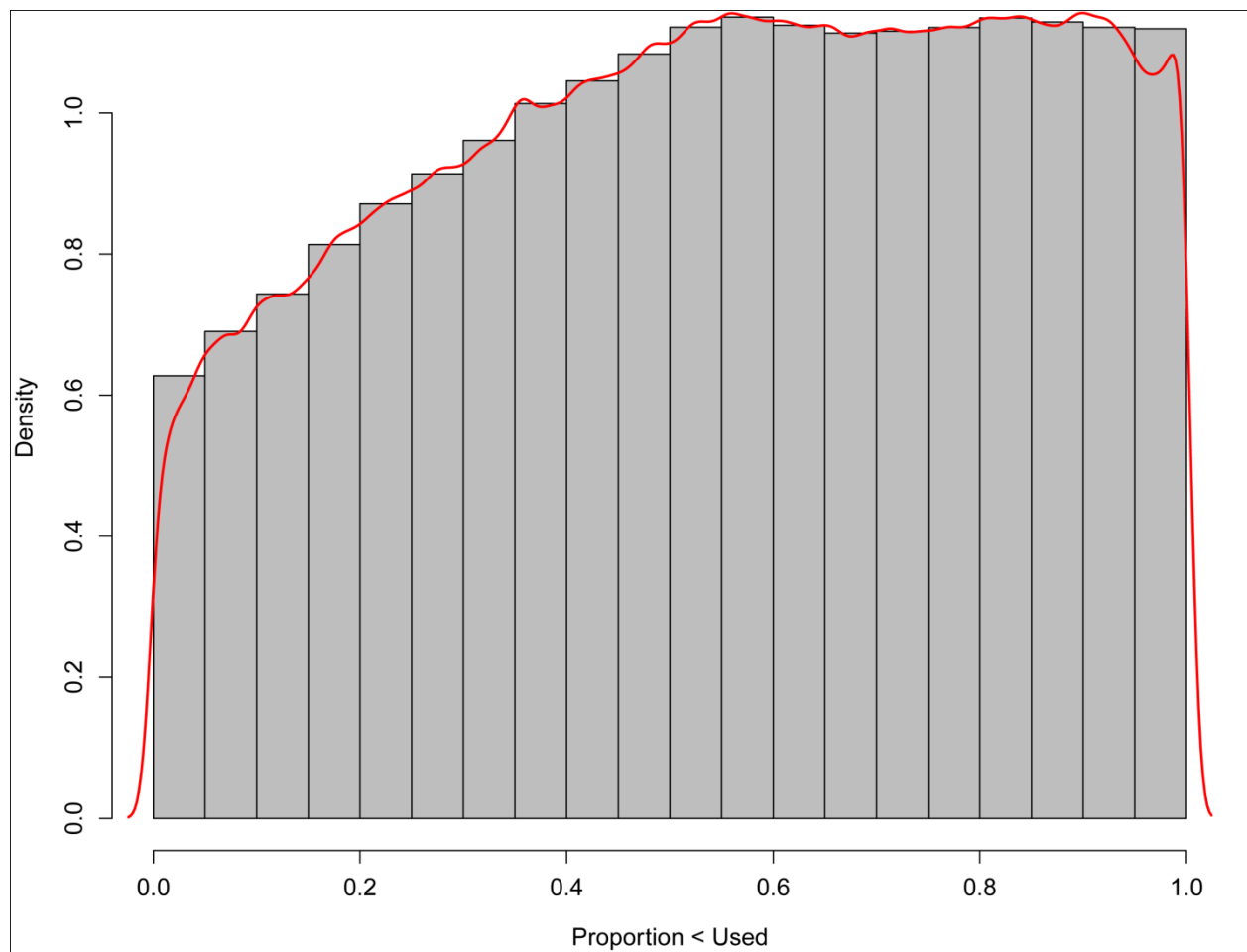
Figure A7.4. Results of posterior predictive check on night time RSF model with concentric buffers fit to winter range GPS data from 53 female mule deer. X-axis represents the proportion of available locations that were predicted to be selected at a lower probability than the used locations.

APPENDIX 8

MULE DEER CAPTURE DATA FOR DEER USED IN CHAPTER FIVE

Table A8.1. Deer unique identifiers (ID), the study area in which they were captured, the date of first capture, and number of summers and winters with complete datasets that could be used for estimating ranges of adult female mule deer in the Piceance Basin of Northwest Colorado, USA.

Deer ID	Study area[a]	Date of first capture	# summers of complete data	# winters of complete data
NR110	NR	December 2012	NA	1
NR111	NR	December 2012	NA	1
NR44	NR	March 2010	NA	1
NR45	NR	March 2010	NA	2
NR47	NR	March 2010	NA	3
NR48	NR	March 2010	NA	3
NR51	NR	March 2010	NA	1
NR70	NR	December 2010	NA	3
NR71	NR	December 2010	NA	2
NR74	NR	December 2010	NA	2
NR75	NR	December 2010	NA	1
NR79	NR	March 2011	NA	1
RG1	RG	March 2010	3	3
RG100	RG	March 2012	2	1
RG101	RG	December 2012	1	1
RG102	RG	December 2012	1	1
RG103	RG	December 2012	1	1
RG104	RG	December 2012	1	1
RG105	RG	December 2012	1	1
RG106	RG	December 2012	0	1
RG13	RG	March 2010	3	3
RG15	RG	March 2010	2	3
RG19	RG	March 2010	3	3
RG24	RG	March 2010	3	3
RG25	RG	March 2010	0	1
RG3	RG	March 2010	3	3
RG4	RG	December 2010	3	3
RG5	RG	March 2010	2	3
RG65	RG	December 2010	2	3
RG66	RG	December 2010	1	1
RG67	RG	December 2010	1	1
RG68	RG	December 2010	1	1
RG69	RG	December 2010	1	1
RG7	RG	March 2010	0	3
RG70	RG	December 2010	1	2
RG71	RG	December 2010	3	3
RG72	RG	December 2010	3	3
RG73	RG	December 2010	3	3
RG74	RG	December 2010	3	3
RG75	RG	December 2010	3	3
RG76	RG	December 2010	3	3

RG77	RG	December 2010	3	3
RG78	RG	December 2010	3	3
RG79	RG	December 2010	3	3
RG8	RG	March 2010	1	1
RG80	RG	December 2010	3	3
RG82	RG	December 2010	3	3
RG83	RG	December 2010	3	3
RG84	RG	December 2010	3	3
RG85	RG	December 2010	2	3
RG86	RG	December 2010	1	1
RG87	RG	December 2010	2	2
RG89	RG	December 2010	3	3
RG9	RG	December 2010	2	2
RG90	RG	December 2010	3	3
RG91	RG	December 2010	2	2
RG94	RG	December 2011	2	2
RG95	RG	December 2011	2	2
RG96	RG	December 2011	1	1
RG98	RG	March 2012	2	1
RG99	RG	March 2012	1	0

[a]NR refers to the North Ridge study area, while RG refers to the Ryan Gulch study area (Fig. 5.1 in main text).

APPENDIX 9

ANALYSIS OF SENSITIVITY OF UTILIZATION DISTRIBUTIONS TO SAMPLING

INTERVAL AND CELL SPACING

Although the continuous-time correlated random walk (CTCRW) model described by Johnson et al. (2008a, 2008b) is continuous in both time and space, to develop utilization distributions from these models in practice requires discrete sampling in both dimensions. To ensure that these discrete representations accurately represented the continuous process we assessed the sensitivity of our analysis to variation in the time between predicted animal locations and the size of the grid over which we estimated the utilization distribution. We chose the overlap in consecutive year's ranges as the metric over which we would assess sensitivity. We first chose 100 animal locations from two separate years that were broadly overlapping in space. We fit the CTCRW model (Johnson et al. 2008a) to both datasets and estimated locations at every 2.5 seconds, 5 seconds, 10 seconds, 30 seconds, 1 minute, 2 minutes, 3 minutes, 5 minutes, and 10 minutes. We then predicted the probability of being at any point on a grid of points spaced 5 meters apart, calculated the overlap between the two years of data and examined the difference in the overlap value across time scales (Fig. A9.1). Using only 100 locations the computer time required to create the utilization distributions was substantial at the finer time scales (several hours at 2.5 seconds between locations). Thus, we attempted to balance computer time with accuracy of the representation of the utilization distribution and selected the 1 minute time scale to use in further assessment of the sensitivity of the utilization distributions to the size of the grid over which they were calculated (Fig. A9.1).

To assess the sensitivity of the utilization distributions to the size of the grid over which they were calculated we next estimated the utilization distributions over grids with varying distances between points (0.05, 0.1, 0.5, 1, 2, 3, 4, 5, 10, 20 and 30 meters). This analysis showed that at a grid size of 5 m or less there was less than a 5% difference between the overlap values (Table A9.1).

To further assess the sensitivity of the utilization distributions to the size of the grid we estimated utilization distributions for two full winter seasons for a single deer. We fit the CTCRW model as above and estimated locations every minute. We then attempted to estimate the utilization distribution over the same grid sizes as above. At grid sizes of less than 1 m the computation time became prohibitive (greater than 1 day). Thus we assessed the sensitivity of the overlap in utilization distributions to a reduced set of grid sizes (Table A9.2).

The results of the above analyses allowed us to make a decision concerning the tradeoff between computation time and accuracy of the approximation of the continuous process. We decided that predicting locations every minute and estimating the utilization distribution over a 5 m grid was the optimal set of conditions. We note that these conditions still required substantial computational time. To fit all models and estimate all utilization distributions required over 1 month of processing time on the Colorado State University ISTeC Cray High Performance Computing System, a supercomputer housed at Colorado State University.

TABLES

Table A9.1. Grid cell size, resulting overlap value and the percent difference between the calculated overlap value and that calculated on the grid with the smallest cell size for utilization distributions calculated for 100 locations from consecutive years of mule deer data in the Piceance Basin Northwest Colorado.

Cell size	Overlap value	Percent difference from smallest grid
0.05	0.194	0
0.1	0.194	<0.001
0.5	0.194	0.002
1	0.195	0.006
2	0.196	0.01
3	0.198	0.021
4	0.2	0.031
5	0.202	0.043
10	0.213	0.09
20	0.269	0.281
30	0.311	0.378

Table A9.2. Grid cell size, resulting overlap value and percent difference between the calculated overlap value and that calculated on the grid with the smallest cell size for utilization distributions calculated for two complete winter seasons from consecutive years of mule deer data in the Piceance Basin Northwest Colorado.

Cell size	Overlap value	Percent difference from smallest grid
1	0.373	0
2	0.378	0.014
5	0.384	0.028
10	0.384	0.028
20	0.387	0.036
30	0.367	-0.017

FIGURES
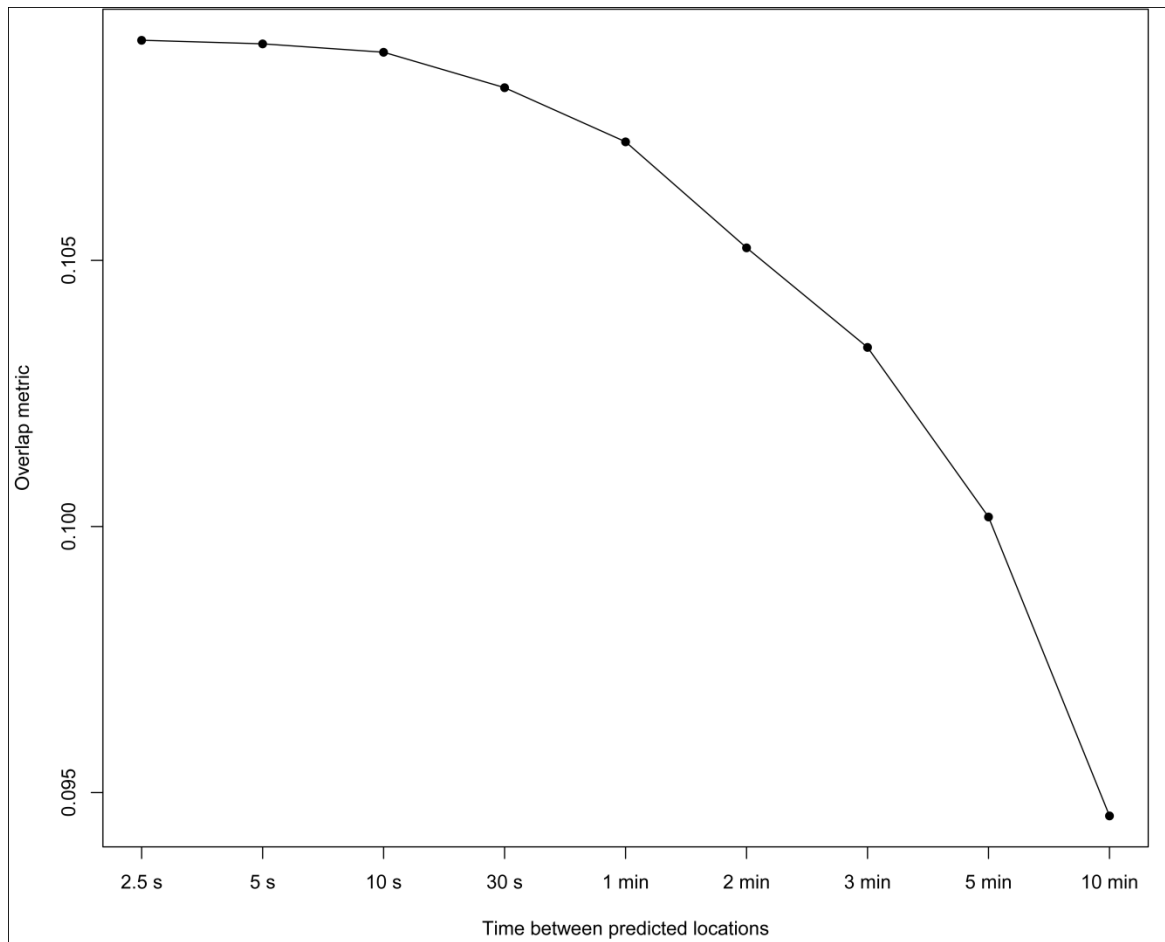
Figure A9.1. Results of analysis assessing sensitivity of overlap in utilization distributions to the time between predicted animal locations assessed using the continuous time correlated random walk model.

APPENDIX 10

COVARIATES USED IN REGRESSION MODELS AND DESCRIPTION OF THEIR

DERIVATION

NATURAL GAS WELL PADS

To obtain information on natural gas activity we downloaded publicly available data from the

Colorado Oil and Gas Conservation Commission website (http://cogcc.state.co.us/). These data

provide the location of every well drilled in the state, the current status of each well, and the

dates drilling began (spud date), the date that drilling reached its deepest depth (total depth date),

and the date that the well was completed (the test date). We first categorized each well into one

of 4 classes for every day between March 1, 2010 and December 1, 2013. Wells were classified

as drilling on every day between one week prior to the spud date and one week after the total

depth date (one week was an arbitrary time added to account for moving the substantial amount

of equipment required for drilling onto and off of the pad). Wells were classified as being

between the drilling phase and producing phase on days between one week after the total depth

date and the test date. Wells were classified as producing on days after the test date until the well

was listed as abandoned. Wells were listed as abandoned from the time their status was listed as

abandoned. In addition to these four statuses the COGCC database includes a number of records

for permitted locations that were never drilled. To ensure that these classifications were accurate

we overlaid the well data with aerial imagery from the National Agriculture Imagery Program

(NAIP) to assess if these records were indeed abandoned locations or if there was evidence of

disturbance. We next overlaid all remaining records that were classified as abandoned,

producing, drilling or in the completion phase with the NAIP imagery to group wells onto well

pads. We then classified each well pad by the status of the well undergoing the most intensive

process for every day of the study period. Thus a pad was only classified as producing if all wells

on the pad were producing or abandoned, was classified as between drilling and producing if any

wells were in this phase and all other wells were either producing or abandoned, and was classified as drilling if any wells were being drilled.

SNOW DEPTH

We predicted snow depth using a spatially distributed snow-evolution modeling system designed for fine spatial and temporal scale snow modeling, called SnowModel (Liston and Elder 2006). This model takes inputs of land cover type, elevation, latitude, temperature, relative humidity, precipitation, wind speed and direction and can predict snow depth at time scales as fine as 10 minutes, and spatial scales as small as 1 m. This model accounts for numerous factors influencing snow depth, including sublimation, redistribution from blowing snow, forest canopy interception, snow density evolution, and snowpack melt (Liston and Elder 2006). We obtained freely available meteorological data from 14 weather stations near our study area (data obtained from http://www.nohrsc.noaa.gov/interactive/html/map.html and http://www.wcc.nrcs.usda.gov/snotel/Colorado/colorado.html). We used these data to predict snow depth at a daily time scale over a 30×30 m cell size between October 1 and May 31 of every year of the sampling period. During the first two years of the study (winters 2011 and 2012) we placed 4 measuring stakes at locations in the study area and opportunistically measured the snow depth at these stakes. During winter 2013 we deployed two weather stations equipped with ultrasonic depth sensors (Judd Communications LLC, Salt Lake City UT, USA) which provided daily snow depth measurements. The snow stake and ultrasonic depth measurements were used to assess the performance of the SnowModel and to adjust input values of precipitation to best match on-the-ground measurements.

ROAD NETWORK

To characterize the road network we digitized all roads in the study area using the NAIP imagery from both 2011 and 2013. There were few new roads built in the area between these years, and with no imagery available in 2012 we chose to create a single road network layer representing conditions during the summer of 2013. This area receives little traffic other than that associated with natural gas development, though during the fall hunting seasons (September through November) traffic increases. Thus we further classified the road network into primary and secondary roads. Primary roads included all major thoroughfares (based on width), and all roads leading to well pads. Secondary roads included all roads that appeared to be two tracks, trails or little traveled roadways, based on their appearance in the NAIP imagery.

TABLES

Table A10.1. Names, descriptions, sources, pixel size (when available), and the unit of time over which the covariates were available for covariates used in regression models examining range size and bi-annual range overlap for summer and winter ranges of female mule deer in the Piceance Basin of Northwest Colorado, USA.

Covariate	Description	Source	Pixel size	Time scale
Environmental				
tree	Proportion of range comprised of treed land cover	Colorado Vegetation Classification Project (http://ndis.nrel.colostate.edu/coveg/)	25 m × 25 m	NA
TRI	Terrain ruggedness index. Squared difference between elevation in each cell and 8 neighbors averaged over entire range	DEM from http://seamless.usgs.gov	30 m × 30 m	
avg_NDVI	Normalized difference vegetation index (NDVI) averaged over area and time period of range	Calculated from layers available at http://www.vito-eodata.be/	1 km × 1 km	Every 10 days
peak_NDVI	Maximum value of NDVI averaged over the area of the range for every 10 day period	Calculated from layers available at http://www.vito-eodata.be/	1 km × 1 km	Every 10 days
snow_total	Total winter snow fall summed for each pixel and averaged over entire range	See above	30 × 30 m	Daily
snow_avg	Average winter snow fall per pixel and averaged over entire range	See above	30 × 30 m	Daily
Anthropogenic				
rd_dens_all	Density of all roads within range	See above	NA	NA
rd_dens_major	Density of all primary roads within range	See above	NA	NA
dens_prod	Density of well pads with producing wells only	See above	NA	Daily
dens_drill	Density of well pads with wells being actively drilled	See above	NA	Daily
dens_pipe	Density of pipelines	Bureau of Land Management	NA	Annual

dens_fac	Density of compressor stations, natural gas plants, and other industrial facilities	See above	NA	Annual
Individual				
fat	Percent ingesta-free body fat	Measured during capture	NA	Annual
Age	Age of deer at capture	Measured during capture	NA	Annual[a]
Area-specific				
density	Mule deer density (deer km^{-1})	(Anderson and Bishop 2012, Anderson Jr. 2014)	NA	Annual

[a]While age varied by year, when assessing overlap a difference in age was not calculated. Rather the age covariate was calculated as the average age between the two years of interest.

APPENDIX 11

MODEL STRUCTURES AND FORMULATION AND RESULTS TABLES FOR CHAPTER 5

The range size regression was conducted using gamma regression with intercepts varying by individual. The model for this analysis took the following form:

$$y_{ij} \sim gamma(\gamma, \omega_{ij})$$

$$\gamma \sim gamma(0.0001, 0.0001)$$

$$\omega_{ij} = \frac{\gamma}{\mu_{ij}}$$

$$\mu_{ij} = e^{\alpha_j + x_i'\beta + fat'_{true_i}\gamma}$$

$$\alpha_j \sim normal(\mu_\alpha, \sigma_\alpha^2)$$

$$\mu_\alpha \sim normal(0, 1000)$$

$$\sigma_\alpha^2 = \frac{1}{\sqrt{\tau}}$$

$$\tau \sim gamma(0.0001, 0.0001)$$

$$\beta \sim normal(\mathbf{0}, 1000I)$$

$$fat_{true_i} \sim normal(fat_{obs_i}, 1.471)$$

The range overlap regression was conducted using beta regression with intercepts varying by individual. The model for this analysis took the following form:

$$y_{ij} \sim beta(a_{ij}, b_{ij})$$

$$a_{ij} = \phi\mu_{ij}$$

$$b_{ij} = (1 - \mu_{ij})\phi$$

$$\mu_{ij} = \frac{e^{\alpha_j + x_i'\beta + fat'_{true_i}\gamma}}{1 + e^{\alpha_j + x_i'\beta + fat'_{true_i}\gamma}}$$

$$\phi \sim gamma(0.0001, 0.0001)$$

$$\alpha_j \sim normal(\mu_\alpha, \sigma_\alpha^2)$$

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$$\mu_\alpha \sim normal(0, 1000)$$

$$\sigma_\alpha^2 = \frac{1}{\sqrt{\tau}}$$

$$\tau \sim gamma(0.0001, 0.0001)$$

$$\boldsymbol{\beta} \sim normal(\mathbf{0}, 1000\mathrm{I})$$

$$fat_{true_i} \sim normal(fat_{obs_i}, 1.471)$$

TABLES

Table A11.1. Model numbers, structure, Watanabe-Akaike Information Criteria value (WAIC) and effective number of parameters (PD) for gamma regression models fit to the size of the 99 percent highest density ranges during summer for female mule deer in the Piceance Basin of Northwest Colorado.

Model	Model structure	WAIC	PD
M1	*tree + dens_pipe + rd_dens_all +TRI + avg_NDVI + fat +*		
	age	2810.04	54.74
M2	*tree + dens_pipe + rd_dens_all +TRI + peak_NDVI + fat*		
	+ age	2806.89	53.66
M3	*tree + dens_pipe + rd_dens_major +TRI + avg_NDVI +*		
	fat +age	2820.88	58.86
M4	*tree + dens_pipe + rd_dens_major +TRI + peak_NDVI +*		
	fat + age	2819.41	58.68

Table A11.2. Covariates, median coefficient estimates and proportion of posteriors falling above and below 0 for gamma regression models fit to the size of the 99 percent highest density ranges during summer for female mule deer in the Piceance Basin of Northwest Colorado.

M1

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	14.12	0	1
tree	-0.06	0.82	0.18
dens_pipe	0.06	0.15	0.85
rd_dens_all	0.02	0.37	0.63
TRI	-0.10	0.94	0.06
avg_NDVI	-0.05	0.86	0.14
fat	0.04	0.00	1.00
age	-0.08	0.92	0.08

M2

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	14.12	0	1
tree	-0.06	0.82	0.18
dens_pipe	0.05	0.17	0.83
rd_dens_all	0.02	0.37	0.63
TRI	-0.10	0.94	0.06
peak_NDVI	-0.06	0.88	0.12
fat	0.04	0.00	1.00
age	-0.08	0.92	0.08

M3

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	14.08	0	1
tree	-0.05	0.77	0.23
dens_pipe	0.09	0.08	0.93
rd_dens_major	-0.06	0.78	0.22
TRI	-0.12	0.98	0.02
avg_NDVI	-0.06	0.88	0.12
fat	0.05	0.00	1.00
age	-0.08	0.94	0.06

M4

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	14.10	0	1
tree	-0.05	0.79	0.21
dens_pipe	0.09	0.09	0.91
rd_dens_major	-0.06	0.78	0.22
TRI	-0.13	0.97	0.03
peak_NDVI	-0.06	0.90	0.10
fat	0.05	0.00	1.00
age	-0.08	0.93	0.07

Table A11.3. Model numbers, structure, Watanabe-Akaike Information Criteria value (WAIC) and effective number of parameters (PD) for gamma regression models fit to the size of the 50 percent highest density ranges during summer for female mule deer in the Piceance Basin of Northwest Colorado.

Model	Model structure	WAIC	PD
M1	*tree + dens_pipe + rd_dens_all +TRI + avg_NDVI + fat + age*	2364.66	56.27
M2	*tree + dens_pipe + rd_dens_all +TRI + peak_NDVI + fat + age*	2366.08	56.96
M3	*tree + dens_pipe + rd_dens_major +TRI + avg_NDVI + fat + age*	2363.77	55.42
M4	*tree + dens_pipe + rd_dens_major +TRI + peak_NDVI + fat + age*	2363.98	55.79

Table A11.4. Covariates, median coefficient estimates and proportion of posteriors falling above and below 0 for gamma regression models fit to the size of the 50 percent highest density ranges during summer for female mule deer in the Piceance Basin of Northwest Colorado.

M1

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	12.04	0.00	1.00
tree	0.03	0.27	0.73
dens_pipe	-0.06	0.95	0.05
rd_dens_all	0.06	0.10	0.90
TRI	-0.07	0.90	0.10
avg_NDVI	-0.07	0.98	0.02
fat	0.03	0.00	1.00
age	-0.06	0.92	0.08

M2

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	12.05	0.00	1.00
tree	0.02	0.31	0.69
dens_pipe	-0.06	0.96	0.04
rd_dens_all	0.06	0.07	0.93
TRI	-0.07	0.92	0.08
peak_NDVI	-0.06	0.96	0.04
fat	0.03	0.00	1.00
age	-0.06	0.90	0.10

M3

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	12.05	0.00	1.00
tree	0.03	0.24	0.77
dens_pipe	-0.07	0.93	0.07
rd_dens_major	0.03	0.24	0.76
TRI	-0.08	0.95	0.05
avg_NDVI	-0.07	0.98	0.02
fat	0.03	0.00	1.00
age	-0.06	0.93	0.07

M4

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	12.05	0.00	1.00
tree	0.03	0.27	0.73
dens_pipe	-0.07	0.94	0.06
rd_dens_major	0.04	0.19	0.81
TRI	-0.08	0.96	0.04
peak_NDVI	-0.06	0.96	0.04
fat	0.03	0.00	1.00
age	-0.06	0.92	0.08

Table A11.5. Model numbers, structure, Watanabe-Akaike Information Criteria value (WAIC) and effective number of parameters (PD) for gamma regression models fit to the size of the 99 percent highest density ranges during winter for female mule deer in the Piceance Basin of Northwest Colorado.

Model	Model structure	WAIC	PD
M1	*TRI + avg_NDVI + tree + dens_pipe + rd_dens_all + snow_avg + fat + age + density + density*	4169.91	114.42
M2	*TRI + peak_NDVI + tree + dens_pipe + rd_dens_all + snow_avg + fat + age + density*	4182.28	120.53
M3	*TRI + avg_NDVI + tree + dens_pipe + rd_dens_all + snow_total + fat + age + density*	4157.05	107.56
M4	*TRI + peak_NDVI + tree + dens_pipe + rd_dens_all + snow_total + fat + age + density*	4173.32	115.58
M5	*TRI + avg_NDVI + tree + rd_dens_major + snow_avg + fat + age + density*	4222.72	141.73
M6	*TRI + peak_NDVI + tree + rd_dens_major + snow_avg + fat + age + density*	4245.74	152.75
M7	*TRI + avg_NDVI + tree + rd_dens_major + snow_total + fat + age + density*	4208.75	135.07
M8	*TRI + peak_NDVI + tree + rd_dens_major + snow_total + fat + age + density*	4226.75	143.21

Table A11.6. Covariates, median coefficient estimates and proportion of posteriors falling above and below 0 for gamma regression models fit to the size of the 99 percent highest density ranges during winter for female mule deer in the Piceance Basin of Northwest Colorado.

M1

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	15.41	0.00	1.00
TRI	-0.23	1.00	0.00
avg_NDVI	-0.06	0.92	0.08
tree	0.12	0.04	0.96
dens_pipe	-0.16	0.99	0.02
rd_dens_all	0.04	0.25	0.75
snow_avg	0.01	0.43	0.57
fat	0.01	0.26	0.74
age	-0.04	0.83	0.17
density	-0.18	0.99	0.02

M2

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	15.43	0.00	1.00
TRI	-0.23	1.00	0.00
peak_NDVI	-0.05	0.89	0.11
tree	0.13	0.04	0.96
dens_pipe	-0.15	0.98	0.02
rd_dens_all	0.04	0.30	0.70
snow_avg	0.04	0.24	0.76
fat	0.01	0.33	0.67
age	-0.05	0.84	0.16
density	-0.16	0.97	0.03

M3

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	15.41	0.00	1.00
TRI	-0.21	0.99	0.01
avg_NDVI	-0.05	0.87	0.13
tree	0.12	0.05	0.95
dens_pipe	-0.16	0.99	0.01
rd_dens_all	0.04	0.26	0.74
snow_total	0.06	0.19	0.81
fat	0.01	0.24	0.77
age	-0.04	0.81	0.19
density	-0.21	1.00	0.00

M4

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	15.42	0.00	1.00
TRI	-0.21	0.99	0.01

Covariate	Median	Prop. below 0	Prop. above 0
peak_NDVI	-0.05	0.86	0.14
tree	0.13	0.04	0.96
dens_pipe	-0.15	0.99	0.01
rd_dens_all	0.04	0.26	0.74
snow_total	0.08	0.09	0.91
fat	0.01	0.27	0.73
age	-0.04	0.84	0.16
density	-0.20	0.99	0.01

M5

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	15.37	0.00	1.00
TRI	-0.20	1.00	0.00
avg_NDVI	-0.06	0.95	0.05
tree	0.12	0.04	0.96
rd_dens_major	-0.15	0.99	0.01
snow_avg	0.03	0.34	0.66
fat	0.01	0.17	0.83
age	-0.03	0.75	0.25
density	-0.19	0.99	0.01

M6

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	15.39	0.00	1.00
TRI	-0.20	1.00	0.00
peak_NDVI	-0.06	0.91	0.09
tree	0.13	0.03	0.97
rd_dens_major	-0.15	1.00	0.01
snow_avg	0.06	0.18	0.83
fat	0.01	0.20	0.80
age	-0.04	0.79	0.21
density	-0.17	0.98	0.02

M7

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	15.37	0.00	1.00
TRI	-0.19	0.99	0.01
avg_ndvi	-0.05	0.86	0.14
tree	0.13	0.04	0.97
rd_dens_major	-0.16	0.99	0.01
snow_total	0.07	0.16	0.84
fat	0.01	0.17	0.83
age	-0.03	0.76	0.24
density	-0.22	1.00	0.00

M8

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	15.37	0.00	1.00
TRI	-0.19	0.99	0.01
peak_NDVI	-0.05	0.87	0.13
tree	0.13	0.04	0.96
rd_dens_major	-0.15	1.00	0.00
snow_total	0.10	0.05	0.95
fat	0.01	0.16	0.84
age	-0.03	0.78	0.22
density	-0.21	1.00	0.00

Table A11.7. Model numbers, structure, Watanabe-Akaike Information Criteria value (WAIC) and effective number of parameters (PD) for gamma regression models fit to the size of the 50 percent highest density ranges during winter for female mule deer in the Piceance Basin of Northwest Colorado.

Model	Model structure	WAIC	PD
M1	*TRI + avg_NDVI + tree + dens_pipe + rd_dens_all + snow_avg + fat + age + density*	3504.22	53.19
M2	*TRI + peak_NDVI + tree + dens_pipe + rd_dens_all + snow_avg + fat + age + density*	3512.26	58.61
M3	*TRI + avg_NDVI + tree + dens_pipe + rd_dens_all + snow_total + fat + age + density*	3525.25	65.66
M4	*TRI + peak_NDVI + tree + dens_pipe + rd_dens_all + snow_total + fat + age + density*	3525.05	66.21
M5	*TRI + avg_NDVI + tree + rd_dens_major + snow_avg + fat + age + density*	3477.83	36.61
M6	*TRI + peak_NDVI + tree + rd_dens_major + snow_avg + fat + age + density*	3479.20	36.99
M7	*TRI + avg_NDVI + tree + rd_dens_major + snow_total + fat + age + density*	3481.16	38.80
M8	*TRI + peak_NDVI + tree + rd_dens_major + snow_total + fat + age + density*	3475.64	35.99

Table A11.8. Covariates, median coefficient estimates and proportion of posteriors falling above and below 0 for gamma regression models fit to the size of the 50 percent highest density ranges during winter for female mule deer in the Piceance Basin of Northwest Colorado.

M1

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	13.25	0.00	1.00
TRI	-0.17	1.00	0.00
avg_NDVI	-0.03	0.77	0.23
tree	-0.02	0.67	0.33
dens_pipe	-0.06	0.92	0.09
rd_dens_all	-0.09	0.97	0.03
snow_avg	0.00	0.53	0.47
fat	0.01	0.10	0.90
age	-0.04	0.87	0.13
density	-0.23	1.00	0.00

M2

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	13.28	0.00	1.00
TRI	-0.17	1.00	0.00
peak_NDVI	-0.01	0.60	0.41
tree	-0.02	0.66	0.34
dens_pipe	-0.07	0.94	0.06
rd_dens_all	-0.08	0.96	0.04
snow_avg	0.01	0.43	0.57
fat	0.01	0.17	0.83
age	-0.05	0.90	0.10
density	-0.23	1.00	0.00

M3

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	13.25	0.00	1.00
TRI	-0.16	1.00	0.00
avg_NDVI	-0.02	0.67	0.33
tree	-0.03	0.69	0.31
dens_pipe	-0.06	0.92	0.08
rd_dens_all	-0.09	0.98	0.02
snow_total	0.03	0.28	0.72
fat	0.01	0.10	0.90
age	-0.04	0.87	0.14
density	-0.25	1.00	0.00

M4

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	13.28	0.00	1.00
TRI	-0.15	0.99	0.01

Covariate	Median	Prop. below 0	Prop. above 0
peak_NDVI	0.00	0.54	0.46
tree	-0.03	0.68	0.32
dens_pipe	-0.06	0.92	0.08
rd_dens_all	-0.09	0.97	0.03
snow_total	0.04	0.21	0.79
fat	0.01	0.16	0.84
age	-0.04	0.89	0.11
density	-0.26	1.00	0.00

M5

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	13.23	0.00	1.00
TRI	-0.15	1.00	0.00
avg_NDVI	-0.03	0.77	0.23
tree	-0.01	0.61	0.39
rd_dens_major	-0.04	0.87	0.13
snow_avg	0.00	0.53	0.47
fat	0.02	0.08	0.92
age	-0.04	0.88	0.12
density	-0.22	1.00	0.00

M6

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	13.23	0.00	1.00
TRI	-0.16	0.99	0.01
peak_NDVI	-0.03	0.74	0.26
tree	-0.01	0.59	0.41
rd_dens_major	-0.04	0.87	0.13
snow_avg	0.00	0.50	0.50
fat	0.02	0.07	0.93
age	-0.05	0.90	0.10
density	-0.21	1.00	0.00

M7

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	13.24	0.00	1.00
TRI	-0.14	0.98	0.02
avg_NDVI	-0.02	0.71	0.29
tree	-0.01	0.61	0.39
rd_dens_major	-0.04	0.86	0.14
snow_total	0.02	0.38	0.62
fat	0.02	0.08	0.92
age	-0.04	0.87	0.13
density	-0.24	1.00	0.00

M8

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	13.24	0.00	1.00
TRI	-0.14	0.98	0.02
peak_NDVI	-0.02	0.71	0.29
tree	-0.01	0.61	0.39
rd_dens_major	-0.04	0.86	0.14
snow_total	0.02	0.38	0.62
fat	0.02	0.08	0.92
age	-0.04	0.87	0.13
density	-0.24	1.00	0.00

Table A11.9. Model numbers, structure, Watanabe-Akaike Information Criteria value (WAIC) and effective number of parameters (PD) for beta regression models fit to the bi-annual overlap of the utilization distributions during summer for female mule deer in the Piceance Basin of Northwest Colorado.

Model	Model structure	WAIC	PD
M1	difference in *avg_NDVI* + difference in *dens_prod* + *tree* + *dens_pipe* + *rd_dens_all* + *TRI* + difference in *fat* + *age*	-53.85	22.63
M2	difference in *peak_NDVI* + difference in *dens_prod* + *tree* + *dens_pipe* + *rd_dens_all* + *TRI* + difference in *fat* + *age*	-54.75	22.92
M3	difference in *avg_NDVI* + difference in *dens_prod* + *tree* + *dens_pipe* + *rd_dens_major* + *TRI* + difference in *fat* + *age*	-55.06	22.71
M4	difference in *peak_NDVI* + difference in *dens_prod* + *tree* + *dens_pipe* + *rd_dens_major* + *TRI* + difference in *fat* + *age*	-54.41	22.23

Table A11.10. Covariates, median coefficient estimates and proportion of posteriors falling above and below 0 for beta regression models fit to the bi-annual overlap in utilization distributions during summer for female mule deer in the Piceance Basin of Northwest Colorado.

M1

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.09	0.71	0.29
difference in *avg_NDVI*	-0.07	0.83	0.17
difference in *dens_prod*	0.17	0.01	0.99
tree	0.10	0.16	0.84
dens_pipe	-0.04	0.66	0.34
rd_dens_all	0.06	0.29	0.72
TRI	0.00	0.49	0.51
fat	0.00	0.46	0.54
age	-0.01	0.54	0.46

M2

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.05	0.63	0.37
difference in *peak_NDVI*	-0.02	0.61	0.39
difference in *dens_prod*	0.17	0.01	0.99
tree	0.10	0.16	0.84
dens_pipe	-0.05	0.69	0.31
rd_dens_all	0.05	0.33	0.67
TRI	-0.02	0.57	0.43
fat	0.00	0.55	0.45
age	-0.01	0.53	0.47

M3

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.06	0.64	0.36
difference in *avg_NDVI*	-0.06	0.81	0.19
difference in *dens_prod*	0.17	0.01	0.99
tree	0.11	0.13	0.87
rd_dens_major	-0.04	0.65	0.35
TRI	-0.04	0.63	0.37
fat	0.00	0.53	0.47
age	-0.02	0.58	0.42

M4

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.04	0.59	0.41
difference in *peak_NDVI*	-0.01	0.54	0.46
difference in *dens_prod*	0.16	0.02	0.99
tree	0.12	0.12	0.88
rd_dens_major	-0.07	0.74	0.26
TRI	-0.07	0.69	0.31

fat	-0.01	0.59	0.41
age	-0.01	0.56	0.44

Table A11.11. Model numbers, structure, Watanabe-Akaike Information Criteria value (WAIC) and effective number of parameters (PD) for beta regression models fit to the bi-annual overlap of the utilization distributions during winter for female mule deer in the Piceance Basin of Northwest Colorado.

Model	Model structure	WAIC	PD
M1	difference in *dens_drill* + *dens_fac* + difference in *avg_NDVI* + *tree* + difference in *dens_pipe* + *rd_dens_all* + difference in *fat* + difference in *snow_avg* + *age* + *density*	958.94	611.96
M2	difference in *dens_drill* + *dens_fac* + difference in *peak_NDVI* + *tree* + difference in *dens_pipe* + *rd_dens_all* + difference in *fat* + difference in *snow_avg* + *age* + *density*	1068.04	665.21
M3	difference in *dens_drill* + *dens_fac* + difference in *avg_NDVI* + *tree* + difference in *dens_pipe* + *rd_dens_major* + difference in *fat* + difference in *snow_avg* + *age* + *density*	715.06	491.91
M4	difference in *dens_drill* + *dens_fac* + difference in *peak_NDVI* + *tree* + difference in *dens_pipe* + *rd_dens_major* + difference in *fat* + difference in *snow_avg* + *age* + *density*	976.40	621.61
M5	difference in *dens_drill* + *dens_fac* + difference in *avg_NDVI* + *tree* + difference in *dens_pipe* + *rd_dens_all* + difference in *fat* + difference in *snow_total* + *age* + *density*	1079.15	671.19
M6	difference in *dens_drill* + *dens_fac* + difference in *peak_NDVI* + *tree* + difference in *dens_pipe* + *rd_dens_all* + difference in *fat* + difference in *snow_ total* + *age* + *density*	1300.26	780.57
M7	difference in *dens_drill* + *dens_fac* + difference in *avg_NDVI* + *tree* + difference in *dens_pipe* + *rd_dens_major* + difference in *fat* + difference in *snow_ total* + *age* + *density*	885.34	576.60

M8	difference in *dens_drill* + *dens_fac* + difference in *peak_NDVI* + *tree* + difference in *dens_pipe* + *rd_dens_major* + difference in *fat* + difference in *snow_ total* + *age* + *density*	1163.04	713.94
M9	difference in *dens_drill* + difference in *avg_NDVI* + *TRI* + difference in *dens_pipe* + *rd_dens_all* + difference in *fat* + difference in *snow_avg* + *age* + *density*	876.04	565.05
M10	difference in *dens_drill* + difference in *peak_NDVI* + *TRI* + difference in *dens_pipe* + *rd_dens_all* + difference in *fat* + difference in *snow_avg* + *age* + *density*	960.85	606.44
M11	difference in *dens_drill* + difference in *avg_NDVI* + *TRI* + difference in *dens_pipe* + *rd_dens_major* + difference in *fat* + difference in *snow_avg* + *age* + *density*	724.63	489.76
M12	difference in *dens_drill* + difference in *peak_NDVI* + *TRI* + difference in *dens_pipe* + *rd_dens_major* + difference in *fat* + difference in *snow_avg* + *age* + *density*	901.90	577.20
M13	difference in *dens_drill* + difference in *avg_NDVI* + *TRI* + difference in *dens_pipe* + *rd_dens_all* + difference in *fat* + difference in *snow_total* + *age* + *density*	974.86	613.51
M14	difference in *dens_drill* + difference in *peak_NDVI* + *TRI* + difference in *dens_pipe* + *rd_dens_all* + difference in *fat* + difference in *snow_ total* + *age* + *density*	1021.55	635.41
M15	difference in *dens_drill* + difference in *avg_NDVI* + *TRI* + difference in *dens_pipe* + *rd_dens_major* + difference in *fat* + difference in *snow_ total* + *age* + *density*	890.93	572.50

| M16 | difference in *dens_drill* + difference in *peak_NDVI* + *TRI* + difference in *dens_pipe* + *rd_dens_major* + difference in *fat* + difference in *snow_ total* + *age* + *density* | 1026.95 | 638.55 |

Table A11.12. Covariates, median coefficient estimates and proportion of posteriors falling above and below 0 for beta regression models fit to the bi-annual overlap in the utilization distributions during winter for female mule deer in the Piceance Basin of Northwest Colorado.

M1

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.89	1.00	0.00
difference in *dens_drill*	-0.08	0.93	0.07
dens_fac	-0.17	0.99	0.01
difference in *avg_NDVI*	-0.05	0.90	0.10
tree	-0.08	0.86	0.14
difference in *dens_pipe*	0.00	0.53	0.47
rd_dens_all	-0.06	0.80	0.20
difference in *fat*	0.00	0.54	0.46
difference in *snow_avg*	-0.01	0.55	0.45
age	-0.08	0.87	0.13
density	0.01	0.43	0.57

M2

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.88	1.00	0.00
difference in *dens_drill*	-0.09	0.95	0.06
dens_fac	-0.18	0.99	0.01
difference in *peak_NDVI*	-0.02	0.66	0.34
tree	-0.09	0.88	0.12
difference in *dens_pipe*	0.02	0.37	0.64
rd_dens_all	-0.07	0.86	0.14
difference in *fat*	0.00	0.59	0.41
difference in *snow_avg*	0.02	0.36	0.64
age	-0.07	0.83	0.17
density	-0.01	0.56	0.44

M3

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.91	1.00	0.00
difference in *dens_drill*	-0.07	0.89	0.11
dens_fac	-0.19	1.00	0.00
difference in *avg_NDVI*	-0.07	0.96	0.04
tree	-0.10	0.91	0.09
difference in *dens_pipe*	-0.02	0.68	0.32
rd_dens_major	0.09	0.06	0.94
difference in *fat*	0.00	0.43	0.57
difference in *snow_avg*	-0.02	0.62	0.38
age	-0.08	0.88	0.12
density	0.05	0.23	0.77

M4

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.90	1.00	0.00
difference in *dens_drill*	-0.08	0.93	0.08
dens_fac	-0.19	1.00	0.00
difference in *peak_NDVI*	-0.02	0.67	0.33
tree	-0.10	0.92	0.08
difference in *dens_pipe*	0.00	0.48	0.52
rd_dens_major	0.08	0.08	0.92
difference in *fat*	0.00	0.51	0.49
difference in *snow_avg*	0.02	0.40	0.61
age	-0.07	0.84	0.16
density	0.02	0.39	0.61

M5

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.88	1.00	0.00
difference in *dens_drill*	-0.08	0.94	0.06
dens_fac	-0.17	1.00	0.00
difference in *avg_NDVI*	-0.06	0.95	0.05
tree	-0.08	0.85	0.15
difference in *dens_pipe*	-0.02	0.65	0.35
rd_dens_all	-0.04	0.75	0.25
difference in *fat*	0.00	0.58	0.42
difference in *snow_total*	-0.06	0.85	0.15
age	-0.09	0.90	0.10
density	0.04	0.23	0.77

M6

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.86	1.00	0.00
difference in *dens_drill*	-0.10	0.96	0.04
dens_fac	-0.17	1.00	0.01
difference in *peak_NDVI*	-0.04	0.80	0.20
tree	-0.08	0.85	0.16
difference in *dens_pipe*	0.00	0.52	0.48
rd_dens_all	-0.05	0.77	0.23
difference in *fat*	-0.01	0.67	0.33
difference in *snow_total*	-0.06	0.85	0.15
age	-0.08	0.89	0.11
density	0.05	0.25	0.75

M7

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.90	1.00	0.00
difference in *dens_drill*	-0.07	0.91	0.09
dens_fac	-0.19	1.00	0.00

Covariate	Median	Prop. below 0	Prop. above 0
difference in *avg_NDVI*	-0.07	0.97	0.03
tree	-0.10	0.92	0.08
difference in *dens_pipe*	-0.04	0.80	0.20
rd_dens_major	0.09	0.06	0.94
difference in *fat*	0.00	0.47	0.53
difference in *snow_total*	-0.06	0.86	0.14
age	-0.09	0.90	0.10
density	0.07	0.12	0.88

M8

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.88	1.00	0.00
difference in *dens_drill*	-0.09	0.96	0.04
dens_fac	-0.19	1.00	0.00
difference in *peak_NDVI*	-0.04	0.81	0.19
tree	-0.10	0.91	0.09
difference in *dens_pipe*	-0.01	0.60	0.40
rd_dens_major	0.07	0.11	0.89
difference in *fat*	0.00	0.60	0.40
difference in *snow_total*	-0.06	0.84	0.16
age	-0.09	0.91	0.09
density	0.07	0.15	0.85

M9

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.87	1.00	0.00
difference in *dens_drill*	-0.09	0.94	0.06
difference in *avg_NDVI*	-0.06	0.93	0.07
TRI	0.03	0.33	0.67
difference in *dens_pipe*	-0.02	0.68	0.32
rd_dens_all	-0.04	0.73	0.27
difference in *fat*	0.00	0.58	0.42
difference in *snow_avg*	-0.03	0.67	0.33
age	-0.08	0.88	0.12
density	0.03	0.31	0.69

M10

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.86	1.00	0.00
difference in *dens_drill*	-0.09	0.95	0.05
difference in *peak_NDVI*	-0.02	0.68	0.32
TRI	0.05	0.28	0.72
difference in *dens_pipe*	0.00	0.50	0.50
rd_dens_all	-0.06	0.82	0.18
difference in *fat*	-0.01	0.66	0.34
difference in *snow_avg*	0.01	0.46	0.54

age	-0.07	0.85	0.16
density	0.01	0.46	0.54

M11

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.88	1.00	0.00
difference in *dens_drill*	-0.08	0.92	0.08
difference in *avg_NDVI*	-0.07	0.97	0.03
TRI	0.05	0.30	0.70
difference in *dens_pipe*	-0.04	0.79	0.21
rd_dens_major	0.06	0.18	0.82
difference in *fat*	0.00	0.49	0.51
difference in *snow_avg*	-0.04	0.75	0.25
age	-0.09	0.91	0.09
density	0.06	0.18	0.82

M12

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.87	1.00	0.00
difference in *dens_drill*	-0.09	0.95	0.05
difference in *peak_NDVI*	-0.03	0.71	0.29
TRI	0.05	0.26	0.74
difference in *dens_pipe*	-0.01	0.59	0.41
rd_dens_major	0.04	0.26	0.74
difference in *fat*	-0.01	0.63	0.37
difference in *snow_avg*	-0.01	0.54	0.46
age	-0.08	0.87	0.13
density	0.03	0.33	0.68

M13

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.86	1.00	0.00
difference in *dens_drill*	-0.09	0.94	0.06
difference in *avg_NDVI*	-0.07	0.95	0.05
TRI	0.05	0.27	0.73
difference in *dens_pipe*	-0.04	0.78	0.22
rd_dens_all	-0.03	0.71	0.29
difference in *fat*	0.00	0.63	0.37
difference in *snow_total*	-0.08	0.89	0.11
age	-0.09	0.92	0.08
density	0.06	0.18	0.82

M14

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.84	1.00	0.00
difference in *dens_drill*	-0.10	0.97	0.03

difference in *peak_NDVI*	-0.04	0.79	0.21
TRI	0.05	0.25	0.75
difference in *dens_pipe*	-0.02	0.65	0.35
rd_dens_all	-0.04	0.72	0.28
difference in *fat*	-0.01	0.74	0.27
difference in *snow_total*	-0.07	0.88	0.12
age	-0.09	0.90	0.10
density	0.06	0.20	0.80

M15

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.87	1.00	0.00
difference in *dens_drill*	-0.08	0.94	0.06
difference in *avg_NDVI*	-0.07	0.96	0.04
TRI	0.05	0.28	0.72
difference in *dens_pipe*	-0.05	0.85	0.15
rd_dens_major	0.05	0.19	0.81
difference in *fat*	0.00	0.58	0.42
difference in *snow_total*	-0.08	0.92	0.08
age	-0.10	0.94	0.06
density	0.08	0.11	0.89

M16

Covariate	Median	Prop. below 0	Prop. above 0
Overall intercept	-0.85	1.00	0.00
difference in *dens_drill*	-0.10	0.96	0.04
difference in *peak_NDVI*	-0.04	0.79	0.21
TRI	0.06	0.24	0.76
difference in *dens_pipe*	-0.03	0.73	0.27
rd_dens_major	0.04	0.30	0.71
difference in *fat*	-0.01	0.70	0.30
difference in *snow_total*	-0.08	0.91	0.09
age	-0.09	0.91	0.09
density	0.07	0.15	0.85

APPENDIX 12

MULE DEER CAPTURE DATA FOR DEER USED IN CHAPTER 6

Table A12.1. Deer unique identifiers (ID), the study area in which they were captured, the date of first capture, and number of summers and winters with complete datasets that could be used for movement modeling of adult female mule deer in the Piceance Basin of Northwest Colorado.

Deer ID	Study area[a]	Date of first capture	# summers of complete data	# winters of complete data
NR110	NR	December 2012	NA	1
NR111	NR	December 2012	NA	1
NR112	NR	December 2012	NA	1
NR113	NR	December 2012	NA	1
NR37	NR	December 2012	NA	1
NR44	NR	March 2010	NA	1
NR45	NR	March 2010	NA	2
NR47	NR	March 2010	NA	3
NR48	NR	March 2010	NA	3
NR51	NR	March 2010	NA	2
NR54	NR	December 2010	NA	1
NR66	NR	December 2010	NA	1
NR70	NR	December 2010	NA	3
NR71	NR	December 2010	NA	3
NR74	NR	December 2010	NA	3
NR75	NR	December 2010	NA	2
NR79	NR	March 2011	NA	2
RG1	RG	March 2010	3	3
RG100	RG	March 2012	2	2
RG101	RG	December 2012	1	1
RG102	RG	December 2012	1	0
RG103	RG	December 2012	1	1
RG104	RG	December 2012	1	1
RG105	RG	December 2012	1	1
RG106	RG	December 2012	0	1
RG13	RG	March 2010	3	3
RG15	RG	March 2010	3	3
RG18	RG	March 2010	0	1
RG19	RG	March 2010	3	3
RG24	RG	March 2010	3	2
RG25	RG	March 2010	0	1
RG3	RG	March 2010	2	1
RG4	RG	December 2010	3	2
RG5	RG	March 2010	3	2
RG65	RG	December 2010	3	3
RG66	RG	December 2010	1	1
RG67	RG	December 2010	1	1
RG68	RG	December 2010	1	1
RG69	RG	December 2010	1	1
RG7	RG	March 2010	3	2
RG70	RG	December 2010	2	1

RG71	RG	December 2010	3	3
RG72	RG	December 2010	3	3
RG73	RG	December 2010	3	3
RG74	RG	December 2010	3	3
RG75	RG	December 2010	3	3
RG76	RG	December 2010	3	3
RG77	RG	December 2010	3	1
RG78	RG	December 2010	3	3
RG79	RG	December 2010	3	3
RG8	RG	March 2010	1	1
RG80	RG	December 2010	3	3
RG82	RG	December 2010	3	1
RG83	RG	December 2010	3	2
RG84	RG	December 2010	3	3
RG85	RG	December 2010	3	3
RG86	RG	December 2010	1	1
RG87	RG	December 2010	2	1
RG88	RG	December 2010	0	1
RG89	RG	December 2010	3	2
RG9	RG	December 2010	2	3
RG90	RG	December 2010	3	2
RG91	RG	December 2010	2	2
RG92	RG	December 2010	0	1
RG94	RG	December 2011	2	2
RG95	RG	December 2011	2	2
RG96	RG	December 2011	1	1
RG97	RG	December 2011	0	1
RG98	RG	March 2012	2	2
RG99	RG	March 2012	1	2

[a]NR refers to the North Ridge study area, while RG refers to the Ryan Gulch study area (Fig. 6.1 in main text).

APPENDIX 13

DETAILS OF NUMBER OF ITERATIONS RUN AND MODELS USED FOR EACH DEER

AND SEASON USED IN CHAPTER 6

Table A13.1. Deer unique identifiers (ID), season during which the data were collected, the prior distribution used for the dispersion parameter (κ), number of iterations run, total burn-in removed, and whether the algorithms ultimately converged for discrete-time correlated random walk models fit to adult female mule deer movement data from summer range in the Piceance Basin of Colorado, USA.

Deer ID	Year	Prior on κ	No. iterations	Burn-in	Converged
RG1	2011	Truncated normal	200000	25000	Y
RG1	2012	Uniform	400000	25000	Y
RG1	2013	NA	NA	NA	N
RG100	2012	Uniform	100000	25000	Y
RG100	2013	Truncated normal	200000	25000	Y
RG101	2013	Uniform	100000	25000	Y
RG102	2013	Truncated normal	200000	25000	Y
RG103	2013	Truncated normal	200000	25000	Y
RG104	2013	Truncated normal	200000	25000	Y
RG105	2013	NA	NA	NA	N
RG13	2011	Truncated normal	200000	25000	Y
RG13	2012	Uniform	100000	25000	Y
RG13	2013	Uniform	100000	25000	Y
RG15	2011	Truncated normal	200000	25000	Y
RG15	2012	Uniform	100000	25000	Y
RG15	2013	NA	NA	NA	N
RG19	2011	Truncated normal	400000	50000	Y
RG19	2012	Uniform	100000	25000	Y
RG19	2013	NA	NA	NA	N
RG24	2011	NA	NA	NA	N
RG24	2012	Uniform	100000	25000	Y
RG24	2013	Truncated normal	200000	25000	Y
RG3	2012	Uniform	100000	25000	Y
RG3	2013	Uniform	100000	25000	Y
RG4	2011	Truncated normal	200000	25000	Y
RG4	2012	Uniform	100000	25000	Y
RG4	2013	Uniform	100000	25000	Y
RG5	2011	Uniform	400000	25000	Y
RG5	2012	Uniform	100000	25000	Y
RG5	2013	Truncated normal	200000	25000	Y
RG65	2011	Truncated normal	200000	75000	Y
RG65	2012	Truncated normal	200000	25000	Y
RG65	2013	Uniform	100000	25000	Y
RG66	2011	Uniform	100000	25000	Y
RG67	2011	Truncated normal	200000	25000	Y
RG68	2011	NA	NA	NA	N
RG69	2011	NA	NA	NA	N
RG7	2011	NA	NA	NA	N
RG7	2012	Uniform	100000	25000	Y
RG7	2013	Uniform	100000	25000	Y

RG70	2011	Truncated normal		200000	25000	Y
RG70	2012	Truncated normal		200000	25000	Y
RG71	2011	Truncated normal		400000	50000	Y
RG71	2012	Uniform		100000	25000	Y
RG71	2013	Uniform		100000	25000	Y
RG72	2011	NA	NA		NA	N
RG72	2012	Truncated normal		200000	25000	Y
RG72	2013	Truncated normal		400000	50000	Y
RG73	2011	Truncated normal		200000	25000	Y
RG73	2012	Uniform		100000	25000	Y
RG73	2013	Truncated normal		200000	25000	Y
RG74	2011	Truncated normal		200000	25000	Y
RG74	2012	Truncated normal		200000	25000	Y
RG74	2013	Truncated normal		400000	50000	Y
RG75	2011	Truncated normal		400000	50000	Y
RG75	2012	Truncated normal		200000	25000	Y
RG75	2013	Uniform		100000	25000	Y
RG76	2011	Truncated normal		400000	100000	Y
RG76	2012	Truncated normal		200000	25000	Y
RG76	2013	Uniform		100000	25000	Y
RG77	2011	Truncated normal		200000	25000	Y
RG77	2012	Truncated normal		200000	25000	Y
RG77	2013	Truncated normal		200000	25000	Y
RG78	2011	Truncated normal		400000	50000	Y
RG78	2012	Truncated normal		200000	25000	Y
RG78	2013	Truncated normal		200000	25000	Y
RG79	2011	NA	NA		NA	N
RG79	2012	Truncated normal		200000	25000	Y
RG79	2013	Uniform		100000	25000	Y
RG8	2011	Truncated normal		200000	25000	Y
RG80	2011	NA	NA		NA	N
RG80	2012	Truncated normal		200000	25000	Y
RG80	2013	Truncated normal		200000	25000	Y
RG82	2011	NA	NA		NA	N
RG82	2012	Uniform		100000	25000	Y
RG82	2013	Truncated normal		200000	25000	Y
RG83	2011	NA	NA		NA	N
RG83	2012	Truncated normal		200000	25000	Y
RG83	2013	Truncated normal		200000	25000	Y
RG84	2011	Truncated normal		200000	25000	Y
RG84	2012	Uniform		100000	25000	Y
RG84	2013	Uniform		100000	25000	Y
RG85	2011	Truncated normal		200000	25000	Y
RG85	2012	Truncated normal		200000	25000	Y
RG85	2013	Truncated normal		200000	25000	Y
RG86	2011	Truncated normal		200000	25000	Y

RG87	2011	Truncated normal		200000	25000	Y
RG87	2012	Uniform		100000	25000	Y
RG89	2011	Truncated normal		200000	25000	Y
RG89	2012	Truncated normal		200000	25000	Y
RG89	2013	Truncated normal		200000	25000	Y
RG9	2011	NA	NA		NA	N
RG9	2012	Truncated normal		200000	25000	Y
RG90	2011	Truncated normal		200000	25000	Y
RG90	2012	Uniform		100000	25000	Y
RG90	2013	Truncated normal		200000	25000	Y
RG91	2011	Truncated normal		200000	25000	Y
RG91	2012	NA	NA		NA	N
RG94	2012	Truncated normal		200000	25000	Y
RG94	2013	Truncated normal		200000	25000	Y
RG95	2012	Truncated normal		200000	25000	Y
RG95	2013	Uniform		100000	25000	Y
RG96	2012	Uniform		100000	25000	Y
RG98	2012	Uniform		100000	25000	Y
RG98	2013	Uniform		100000	25000	Y
RG99	2012	Uniform		100000	25000	Y

Table A13.2. Deer unique identifiers (ID), season during which the data were collected, the prior distribution used for the dispersion parameter (κ), number of iterations run, total burn-in removed, and whether the algorithms ultimately converged for discrete-time correlated random walk models fit to adult female mule deer movement data from winter range in the Piceance Basin of Colorado, USA.

Deer ID	Year	Prior on κ	No. iterations	Burn-in	Converged
NR110	2013	Uniform	100000	25000	Y
NR111	2013	Uniform	100000	25000	Y
NR112	2013	Uniform	100000	25000	Y
NR113	2013	Uniform	100000	25000	Y
NR37	2011	Uniform	100000	25000	Y
NR44	2011	Uniform	100000	25000	Y
NR45	2011	Uniform	100000	25000	Y
NR45	2012	NA	NA	NA	N
NR47	2011	Uniform	100000	25000	Y
NR47	2012	NA	NA	NA	N
NR47	2013	Uniform	100000	25000	Y
NR48	2011	NA	NA	NA	N
NR48	2012	Uniform	100000	25000	Y
NR48	2013	Uniform	100000	25000	Y
NR51	2011	Truncated normal	200000	25000	Y
NR51	2012	Uniform	100000	25000	Y
NR54	2011	Uniform	100000	25000	Y
NR66	2011	Uniform	100000	25000	Y
NR70	2011	Uniform	100000	25000	Y
NR70	2012	Uniform	100000	25000	Y
NR70	2013	Truncated normal	200000	25000	Y
NR71	2011	Uniform	100000	25000	Y
NR71	2012	Uniform	100000	25000	Y
NR71	2013	Uniform	100000	25000	Y
NR74	2011	Uniform	100000	25000	Y
NR74	2012	Uniform	100000	25000	Y
NR74	2013	Uniform	100000	25000	Y
NR75	2011	Uniform	100000	25000	Y
NR75	2012	Uniform	100000	25000	Y
NR79	2012	Uniform	100000	25000	Y
NR79	2013	Truncated normal	200000	25000	Y
RG1	2011	NA	NA	NA	N
RG1	2012	Truncated normal	200000	25000	Y
RG1	2013	Uniform	100000	25000	Y
RG100	2012	NA	NA	NA	N
RG100	2013	Truncated normal	200000	25000	Y
RG101	2013	Uniform	100000	25000	Y
RG103	2013	NA	NA	NA	N
RG104	2013	Uniform	100000	25000	Y
RG105	2013	Uniform	100000	25000	Y

RG106	2013	NA	NA		NA	N
RG13	2011	Uniform		100000	25000	Y
RG13	2012	Uniform		100000	25000	Y
RG13	2013	NA	NA		NA	N
RG15	2011	Truncated normal		400000	50000	Y
RG15	2012	Truncated normal		2000000	25000	Y
RG15	2013	Uniform		100000	25000	Y
RG18	2011	Uniform		100000	25000	Y
RG19	2011	Uniform		100000	25000	Y
RG19	2012	Uniform		100000	25000	Y
RG19	2013	Uniform		100000	25000	Y
RG24	2011	Uniform		100000	25000	Y
RG24	2012	Uniform		100000	25000	Y
RG25	2011	NA	NA		NA	N
RG3	2013	Uniform		100000	25000	Y
RG4	2011	Truncated normal		200000	25000	Y
RG4	2012	Uniform		100000	25000	Y
RG5	2011	Uniform		100000	25000	Y
RG5	2013	Uniform		100000	25000	Y
RG65	2011	NA	NA		NA	N
RG65	2012	Uniform		100000	25000	Y
RG65	2013	NA	NA		NA	N
RG66	2011	Uniform		100000	25000	Y
RG67	2011	Uniform		100000	25000	Y
RG68	2011	Uniform		100000	75000	Y
RG69	2011	Uniform		100000	25000	Y
RG7	2011	Uniform		100000	25000	Y
RG7	2012	Uniform		100000	25000	Y
RG70	2011	NA	NA		NA	N
RG71	2011	Uniform		100000	25000	Y
RG71	2012	Uniform		100000	25000	Y
RG71	2013	Uniform		100000	25000	Y
RG72	2011	Uniform		100000	25000	Y
RG72	2012	Uniform		100000	25000	Y
RG72	2013	NA	NA		NA	N
RG73	2011	Truncated normal		200000	25000	Y
RG73	2012	Uniform		100000	25000	Y
RG73	2013	Uniform		100000	25000	Y
RG74	2011	Uniform		100000	25000	Y
RG74	2012	Uniform		100000	25000	Y
RG74	2013	Truncated normal		200000	25000	Y
RG75	2011	NA	NA		NA	N
RG75	2012	Uniform		100000	25000	Y
RG75	2013	Uniform		100000	25000	Y
RG76	2011	Uniform		100000	25000	Y
RG76	2012	Uniform		100000	25000	Y

RG76	2013	Uniform		100000	25000	Y
RG77	2011	NA	NA		NA	N
RG78	2011	Truncated normal		200000	25000	Y
RG78	2012	Uniform		100000	25000	Y
RG78	2013	Truncated normal		200000	25000	Y
RG79	2011	Uniform		100000	25000	Y
RG79	2012	Uniform		100000	25000	Y
RG79	2013	Truncated normal		200000	25000	Y
RG8	2011	Uniform		100000	25000	Y
RG80	2011	Uniform		100000	25000	Y
RG80	2012	Truncated normal		200000	25000	Y
RG80	2013	Uniform		100000	25000	Y
RG82	2011	NA	NA		NA	N
RG83	2011	Truncated normal		400000	50000	Y
RG83	2013	NA	NA		NA	N
RG84	2011	Uniform		100000	25000	Y
RG84	2012	Truncated normal		200000	25000	Y
RG84	2013	Uniform		100000	25000	Y
RG85	2011	Truncated normal		200000	25000	Y
RG85	2012	Uniform		100000	25000	Y
RG85	2013	Uniform		100000	25000	Y
RG86	2011	Truncated normal		200000	25000	Y
RG87	2011	Uniform		100000	25000	Y
RG88	2011	Uniform		100000	25000	Y
RG89	2011	NA	NA		NA	N
RG89	2012	Truncated normal		200000	25000	Y
RG9	2011	Uniform		100000	25000	Y
RG9	2012	Uniform		100000	25000	Y
RG9	2013	Uniform		100000	25000	Y
RG90	2011	NA	NA		NA	N
RG90	2013	Uniform		100000	25000	Y
RG91	2011	Uniform		100000	25000	Y
RG91	2012	Truncated normal		200000	25000	Y
RG92	2012	Uniform		100000	25000	Y
RG94	2012	Uniform		100000	25000	Y
RG94	2013	NA	NA		NA	N
RG95	2012	Uniform		100000	25000	Y
RG95	2013	Uniform		100000	25000	Y
RG96	2013	NA	NA		NA	N
RG97	2012	Truncated normal		200000	25000	Y
RG98	2012	Uniform		100000	25000	Y
RG98	2013	Uniform		100000	25000	Y
RG99	2012	Truncated normal		200000	25000	Y
RG99	2013	Uniform		100000	25000	Y

APPENDIX 14

ASSESSMENT OF METHODS FOR INTERPOLATING MISSING DATA

To assess the most efficient method for interpolating missing data in the discrete time correlated random walk model we simulated 3,000 movements (paired turn angles and step lengths) from the model outlined in the main text (parameter values used in simulation can be found in Table A14.1). This model takes the following form:

$$s_t | \mathbf{z_t} \sim \text{gamma}(\alpha_j, \beta_j)$$

$$\phi_t | \mathbf{z_t} \sim \text{von Mises}(\mu_j, \kappa_j)$$

$$\mathbf{z_t} | \mathbf{z_{t-1}} \sim \text{multinomial}(\boldsymbol{\psi})$$

$$\boldsymbol{\psi} \sim \text{Dirichlet}(0.5, 0.5)$$

$$\alpha_j \sim \text{uniform}(0, 20000)$$

$$\beta_j \sim \text{uniform}(0, 20000)$$

$$\mu_j \sim \text{uniform}(0, 2\pi)$$

$$\log \kappa_j \sim \text{normal}(0, 1000)$$

We chose values for the simulation so that there was some degree of overlap between the two states (Fig. A14.1). We assigned a starting location at arbitrary coordinates (1,000,000, 1,000,000) and then forward calculated each subsequent location using the simulated turn angles and step lengths. We then randomly removed portions of the data, leaving 95%, 90%, 80%, 70%, and 60% of the dataset intact. Next, we assessed three separate methods for estimating the missing locations for each of the datasets. The first method was simple linear interpolation, in which missing locations were calculated as the average of the previous and following location. In this procedure, the missing locations were calculated prior to fitting the model and were included as the data without error. The second method was to estimate the mean and variance of the missing locations prior to fitting the hidden Markov models using the continuous-time correlated random walk model (CTCRW) described by Johnson et al. (2008a). The model described by

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Johnson et al. (2008a) can be used to estimate a location at any point in time. We used the 'crawl' package (Johnson et al. 2008a) in R to fit the CTCRW models and estimate a mean and variance for each missing location. We then fit our CRW model, randomly drawing a realization of each missing location from the means and variances and recalculating the missing step lengths and turn angles prior to each iteration in the Markov Chain Monte Carlo procedure. Finally we estimated the missing locations within the model, following the general procedure of McClintock et al. (2012a). This model took the following form:

$$s_t | \mathbf{z_t}, x_{t-1}, x_{t+1} \; y_{t-1}, y_{t+1} \sim \text{gamma}(\alpha_j, \beta_j)$$

$$\phi_t | \mathbf{z_t}, x_{t-1}, x_{t+1} \; y_{t-1}, y_{t+1} \sim \text{von Mises}(\mu_j, \kappa_j)$$

$$\mathbf{z_t} | \mathbf{z_{t-1}} \sim \text{multinomial}(\boldsymbol{\psi})$$

$$\boldsymbol{\psi} \sim \text{Dirichlet}(0.5, 0.5)$$

$$x_t \sim \text{normal}(\gamma_x, \epsilon_x)$$

$$y_t \sim \text{normal}(\gamma_y, \epsilon_y)$$

$$\gamma_x = \frac{x_{t-1}}{2} + \frac{x_{t+1}}{2}$$

$$\gamma_y = \frac{x_{t-1}}{2} + \frac{x_{t+1}}{2}$$

$$\log \epsilon_x \sim \text{normal}(0, 1000)$$

$$\log \epsilon_y \sim \text{normal}(0, 1000)$$

$$\alpha_j \sim \text{uniform}(0, 20000)$$

$$\beta_j \sim \text{uniform}(0, 20000)$$

$$\mu_j \sim \text{uniform}(0, 2\pi)$$

$$\log \kappa_j \sim \text{normal}(0, 1000)$$

In the above model, the coordinates of the missing locations are assumed to be normally distributed with mean equal to the linearly interpolated missing locations, and variance as formulated above.

First, we fit the original model to the complete simulated dataset. We then used each of the three data interpolation methods outlined above to estimate parameters from each of the datasets with missing data. All simulations and model fitting were conducted in R and we fit two chains for each analysis using initial values that were expected to be overdispersed relative to the posterior. We assessed convergence to the posterior using the Gelman-Rubin diagnostic (Gelman and Rubin 1992). As our main interest was the classification of the states, we assessed the performance of the different methods by calculating a residual for the states, or the difference in the estimated probability of being in each state and the actual simulated state. These residuals range from 0 (complete agreement between the estimated state and the simulated state), to 1 (complete disagreement). In addition, and to ensure at least near approximation of the state parameters, we examined the difference between the simulated and estimated state parameter values.

For models fit to linearly interpolated data, and for models in which the locations were estimated within the MCMC, convergence was achieved for all datasets missing 20% or less of the data. For both of these missing data estimation methods, algorithms fit to datasets missing 30% or more of the data did not converge. All algorithms fit to datasets for which the missing locations were interpolated using the CTCRW model converged. In the cases where there was a lack of convergence, the large amount of missing data appeared to be inundating the model with turn angles that were 0. Thus the model was categorizing all the missing data and all non-missing data with turn angles near 0 as a single state and the step lengths were providing no information

to the classification of states. All other movements were categorized as the other state and the dispersion parameter for this state was failing to converge to the posterior distribution because both chains were estimating extremely small values that were not overlapping but still providing similar probabilities. Even estimating the missing data within the model did not ameliorate this situation, as the most likely values for these turn angles were still 0, because of the large amount of missing data.

The model fit to the complete dataset recovered the simulated values (i.e., 95% credible intervals covered the true value of each parameter; Table A14.2). Regardless of the method used to assess missing data, most models failed to recover simulated values for certain parameters even with most of the dataset intact (Table A14.2). For example, the only occasion in which the simulated value for α_1 fell within the 95% credible intervals of the posterior was when 95% of the data were present and the CTCRW model was used to interpolate the missing data. However, below 95% of the dataset being present, this model failed to recover simulated values, similar to the other two missing data estimation methods (Table A14.2).

Examining the residuals of the estimated states, all of the missing data estimation methods performed similarly for datasets with 5 and 10% of the data removed (Table A14.3). The models using linear interpolation and interpolation within the MCMC performed similarly to one another for the dataset with 20% missing data, and outperformed the CTCRW method. None of the methods performed well for datasets with greater than 20% of the data missing, and there was a noticeable increase in the residuals at this point. When examining residuals of only the non-missing data, all models performed similarly well, and residuals were similar to those from the model fit to the complete dataset. Considering the performance of the models, we chose to use linear interpolation while censoring all deer datasets missing more than 20% of the data.

TABLES

Table A14.1. Parameters and parameter values used in simulation of discrete-time correlated random walk model.

Parameter	Value
α_1	1
α_2	9
β_1	0.02
β_2	0.06
μ_1	0
μ_2	π
κ_1	0.5
κ_2	0.5
$\psi_{1,1}$	0.7
$\psi_{1.2}$	0.3
$\psi_{2,1}$	0.6
$\psi_{2,2}$	0.4

Table A14.2. Median parameter estimates (95% credible interval) for discrete-time correlated random walk models fit to simulated movement datasets with various amounts of missing data.

Interpolation method	α_1	α_2	β_1	β_2	μ_1	μ_2	κ_1	κ_2	$\psi_{1,1}$	$\psi_{1.2}$	$\psi_{2,1}$	$\psi_{2,2}$
Complete dataset	1.029 (0.958, 1.111)	9.62 (7.707, 12.335)	0.022 (0.018, 0.028)	0.063 (0.052, 0.079)	6.252 (6.091, 0.128)	3.239 (3.02, 3.454)	0.43 (0.356, 0.508)	0.501 (0.351, 0.679)	0.685 (0.63, 0.739)	0.315 (0.261, 0.370)	0.645 (0.578, 0.716)	0.355 (0.284, 0.422)
Linear interpolation												
95% complete	1.076 (1.008, 1.15)	9.43 (7.493, 11.857)	0.022 (0.019, 0.026)	0.062 (0.051, 0.077)	6.258 (6.13, 0.105)	3.224 (2.989, 3.454)	0.528 (0.454, 0.603)	0.512 (0.335, 0.710)	0.728 (0.677, 0.774)	0.272 (0.223, 0.323)	0.666 (0.599, 0.732)	0.334 (0.268, 0.401)
90% complete	1.12 (1.05, 1.18)	9.65 (7.36, 12.51)	0.021 (0.018, 0.024)	0.064 (0.051, 0.081)	6.21 (6.10, 0.04)	3.22 (3, 3.45)	0.59 (0.51, 0.66)	0.62 (0.38, 0.89)	0.77 (0.72, 0.81)	0.23 (0.19, 0.28)	0.71 (0.63, 0.78)	0.29 (0.22, 0.37)
80% complete	1.21 (1.14, 1.3)	6.07 (4.84, 7.59)	0.024 (0.020, 0.029)	0.044 (0.036, 0.053)	0.005 (6.21, 0.08)	3.35 (3.09, 3.66)	0.93 (0.83, 1.02)	0.56 (0.21, 0.97)	0.77 (0.71, 0.82)	0.23 (0.18, 0.29)	0.65 (0.55, 0.74)	0.35 (0.26, 0.45)
70% complete	1.16 (1.09, 1.22)	1.95 (1.78, 2.14)	0.016 (0.015, 0.017)	0.035 (0.032, 0.039)	3.93 (3.13, 2.82)	6.28 (6.28, 0.003)	0.0015 (0, 0.0017)	170.15 (151.98, 29+99)	0.68 (0.66, 0.70)	0.32 (0.3, 0.34)	0.67 (0.63, 0.70)	0.33 (0.3. 0.36)
60% complete	1.23 (1.16, 1.31)	2.03 (1.88, 2.2)	0.017 (0.016, 0.018)	0.039 (0.036, 0.043)	0.44 (2.69, 2.37)	0.0008 (6.28, 0.004)	0 (0,0)	275.51 (250.91, 300.85)	0.60 (0.58, 0.63)	0.4 (0.37, 0.42)	0.54 (0.51, 0.57)	0.46 (0.43, 0.49)
CTCRW												
95% complete	1.05 (0.98,	8.05 (6.48,	0.023 (0.018,	0.055 (0.046,	6.27 (6.09,	3.25 (3.003,	0.41 (0.32,	0.44 (0.29,	0.66 (0.59,	0.34 (0.28,	0.52 (0.54,	0.38 (0.31,

	1.13)	10.08)	0.028)	0.068)	0.16)	3.51)	0.48)	0.60)	0.72)	0.40)	0.69)	0.46)
90% complete	1.09 (1.01, 1.17)	7.52 (5.91, 9.38)	0.022 (0.018, 0.028)	0.053 (0.043, 0.065)	6.24 (6, 0.19)	3.29 (3.012, 3.58)	0.34 (0.25, 0.43)	0.40 (0.26, 0.58)	0.64 (0.70, 0.56)	0.36 (0.298, 0.44)	0.599 (0.51, 0.68)	0.40 (0.32, 0.49)
80% complete	1.1 (1.01, 1.2)	5.41 (1.46, 6.6)	0.02 (0.019, 0.033)	0.042 (0.036, 0.049)	0.096 (6.1, 0.38)	3.35 (3.05, 3.65)	0.36 (0.25, 0.47)	0.34 (0.21, 0.49)	0.53 (0.45, 0.61)	0.47 (0.39, 0.55)	0.46 (0.37, 0.56)	0.54 (0.44, 0.63)
70% complete	1.15 (1.05, 1.27)	4.63 (3.86, 5.5)	0.025 (0.019, 0.035)	0.038 (0.033, 0.044)	6.23 (5.77, 0.43)	3.11 (2.8, 3.43)	0.25 (0.12, 0.38)	0.33 (0.2, 0.47)	0.47 (0.37, 0.57)	0.53 (0.43, 0.63)	0.41 (0.31, 0.52)	0.59 (0.48, 0.69)
60% complete	1.21 (1.09, 1.34)	4.36 (3.64, 5.3)	0.023 (0.018, 0.032)	0.035 (0.03, 0.04)	6.26 (5.76, 0.49)	3.18 (2.93, 3.43)	0.26 (0.10, 0.42)	0.41 (0.28, 0.56)	0.43 (0.34, 0.54)	0.56 (0.46, 0.66)	0.36 (0.26, 0.48)	0.64 (0.52, 0.74)
Estimation online												
95% complete	1.07 (1, 1.14)	9.45 (7.5, 11.9)	0.022 (0.018, 0.026)	0.062 (0.051, 0.077)	6.18 (6.12, 0.13)	3.24 (2.99, 3.49)	0.47 (0.39, 0.54)	0.46 (0.27. 0.41)	0.72 (0.67, 0.77)	0.28 (0.23, 0.33)	0.66 (0.59, 0.73)	0.34 (0.27, 0.41)
90% complete	1.12 (1.06, 1.19)	9.95 (7.45, 12.85)	0.021 (0.018, 0.024)	0.066 (0.051, 0.084)	6.19 (6.04, 0.04)	3.23 (2.96, 3.52)	0.47 (0.399, 0.55)	0.51 (0.29, 0.76)	0.77 (0.71, 0.81)	0.23 (0.19, 0.29)	0.70 (0.62, 0.78)	0.296 (0.22, 0.38)
80% complete	1.22 (1.14, 1.3)	7.03 (5.41, 9.14)	0.023 (0.0198, 0.28)	0.049 (0.0398, 0.062)	0.01 (6.20, 0.09)	3.40 (3.09, 3.84)	0.77 (0.69, 0.85)	0.51 (0.26, 0.97)	0.79 (0.72, 0.84)	0.21 (0.16, 0.28)	0.67 (0.56, 0.77)	0.33 (0.23, 0.44)
70% complete	-	-	-	-	-	-	-	-	-	-	-	-
60% complete	-	-	-	-	-	-	-	-	-	-	-	-

Table A14.3. Datasets with various amounts of missing data and mean residuals calculated as the mean difference between the simulated states and the posterior probabilities for three different methods used for missing data interpolation. Mean residuals of non-missing data are in parentheses.

Dataset	Mean residual for linear interpolation	Mean residual for CTCRW	Mean residual for location estimated within model
95% complete	0.19 (0.17)	0.20 (0.18)	0.19 (0.18)
90% complete	0.21 (0.18)	0.24 (0.19)	0.21 (0.18)
80% complete	0.23 (0.19)	0.32 (0.21)	0.23 (0.19)
70% complete	0.44* (0.35)	0.39 (0.25)	-
60% complete	0.52* (0.45)	0.44 (0.25)	-

	Mean residual		
Complete	0.17		

*Residuals were calculated for algorithms that had not converged for a single dispersion parameters for means of comparison
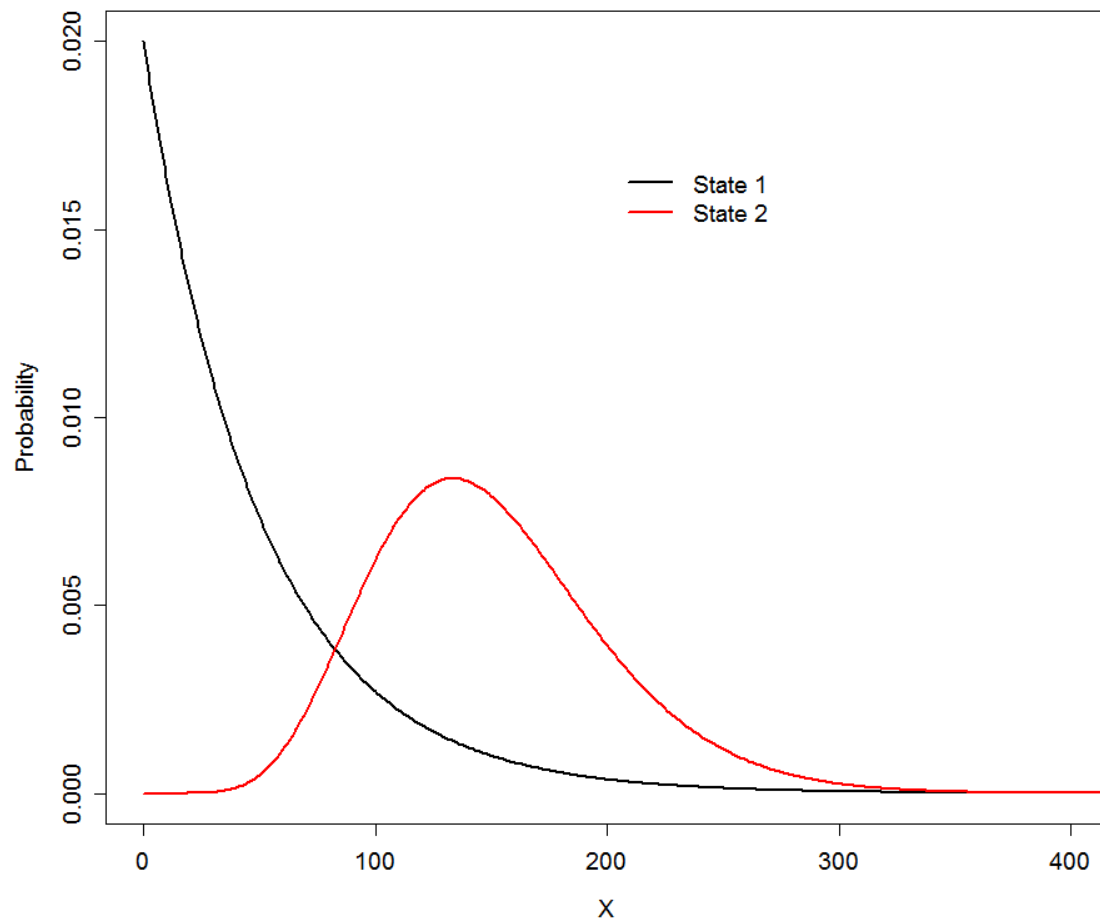
Figure A14.1. Step length distributions used in simulation of movement data from discrete-time correlated random walk models.

APPENDIX 15

DERIVATION OF COVARIATES USED IN REGRESSION MODELS

ANTHROPOGENIC COVARIATES

The anthropogenic covariates used in the regression modeling fell into one of 4 categories: pipelines, roads, industrial facilities (natural gas and other), and natural gas well pads. We obtained a pipeline spatial layer from the Bureau of Land Management White River Office and verified the existence of the pipelines in this layer by overlaying them with National Agricultural Imagery Program (NAIP) aerial imagery in ArcMap 10.1 (Environmental Systems Research Institute, Redlands, CA, USA). To examine the road network we digitized all roads in the area using the NAIP imagery. We further classified roads as major roads or secondary roads. Major roads were those that appeared to be paved or improved roads (based on their apparent width in the NAIP imagery), or roads that led to well pads or facilities. Natural gas and other facilities were identified using the NAIP imagery and through ground truthing a portion of the study area. Facilities in this area include natural gas plants and compressor stations and are easily identifiable from the NAIP imagery. We created polygonal features by digitizing the outlines of the facilities. To categorize natural gas well pads in our study area, we downloaded publicly available data on oil and natural gas wells from the Colorado Oil and Gas Conservation Commission (http://cogcc.state.co.us/). The Commission maintains a daily-updated database that contains information on the location of all wells in the state and their current status as well as the dates on which their status changed (e.g., from being drilled to producing natural gas). We categorized each well in the study area as either abandoned, producing, actively being drilled, or between the drilling and producing stages for all days for which we had mule deer location data. Wells were categorized as abandoned if their status was listed as abandoned in the database. Wells were categorized as producing starting on the test date. Wells were categorized as drilling

starting 1 week prior to the spud date, until one week after the total depth date. Wells were categorized as being between the drilling and producing stages starting one week after the total depth date, until the test date. To provide some validation of the status of the wells in the study area we overlaid all wells onto the NAIP imagery and assessed whether the locations provided were accurate. In addition, we assessed whether or not the abandoned wells were in fact abandoned, or if there was some infrastructure still at these sites. We next grouped wells onto well pads using polygonal well pad features digitized from the NAIP imagery. Pads were the final unit of measure used in regression models and thus we categorized each well pad into one of the four classes mentioned above. Pads were considered to be in the drilling phase if any wells were being actively drilled. Pads were considered to be in the phase between drilling and producing if any wells were in this phase and no wells were being drilled. Pads were considered to be in the producing phase if any well was producing and no wells were being drilled or were in the phase between drilling and producing. Pads only were considered abandoned if all wells on the pad were abandoned.

SNOW DEPTH

To examine the response of mule deer to snow on their winter range we obtained predictions of snow depth using a using a spatially distributed snow-evolution modeling system designed for fine spatial and temporal scale snow modeling, called SnowModel (Liston and Elder 2006). This model can predict snow depth at high temporal and spatial resolution using freely available meteorological inputs. Specifically the model uses relative humidity, precipitation, temperature, wind speed and direction to predict the amount of snow-water equivalent present on the

landscape. We downloaded meteorological data from 14 weather stations in or near the study area (data obtained from http://www.nohrsc.noaa.gov/ interactive/html/map.html and http://www.wcc.nrcs.usda.gov/snotel/Colorado/colorado.html) for every day between October 1 and May 31 of each of the three winters for which we had deer GPS data. We ran the model on a daily time scale, producing predictions over 30×30 meter pixels. To validate the predictions of the model, during winter 2011 and 2012 we placed 4 measuring stakes throughout the study area and opportunistically recorded snow depths. During the winter of 2013 we deployed two weather stations equipped with ultrasonic depth sensors (Judd Communications LLC, Salt Lake City UT, USA). These data were used to assess the performance of the model and to correct values to match conditions seen in the study area.

APPENDIX 16

BETA REGRESSION MODEL FORMULATIONS, MODEL STRUCTURES AND

REGRESSION RESULTS

$$y_{ij} \sim \text{beta}(a_{ij}, b_{ij})$$

$$a_{ij} = \phi\mu_{ij}$$

$$b_{ij} = \frac{1 - \mu_{ij}}{\phi}$$

$$\mu_{ij} = \frac{\exp(\alpha_j + \boldsymbol{x}_i'\boldsymbol{\beta}_j + \boldsymbol{z}_i'\boldsymbol{\gamma})}{1 + \exp(\alpha_j + \boldsymbol{x}_i'\boldsymbol{\beta}_j + \boldsymbol{z}_i'\boldsymbol{\gamma})}$$

$$\phi \sim \text{cauchy}(0,50)$$

$$\alpha_j \sim \text{normal}(\mu_\alpha, \sigma_\alpha^2)$$

$$\beta_{j_k} \sim \text{normal}(0, \sigma_{\beta_k}^2)$$

$$\gamma_l \sim \text{normal}(0, \sigma_{\gamma_l}^2)$$

$$\sigma_\alpha^2 \sim \text{cauchy}(0,50)$$

$$\sigma_{\beta_k}^2 \sim \text{cauchy}(0,50)$$

$$\sigma_{\gamma_l}^2 \sim \text{cauchy}(0,50)$$

TABLES

Table A16.1. Model names, year during which data were collected, model structure, Watananbe-Akaike information criteria (WAIC) and effective number of parameters (PD) for beta regression models fit to activity budgets of mule deer in the Piceance Basin of Colorado during the winter. Covariates were calculated at the scale of the daily range. Activity budgets were derived from discrete-time correlated random walk models.

Model	Year	Structure	WAIC	PD
M1	2011	*Facilities + snow + TRI + pipelines + tree + all rds + light + temp + age + fat + study*	-10492.5	144.11
M2	2011	*Facilities + snow + TRI + pipelines + tree + major rds + light + temp + age + fat + study*	-10486.3	135.90
M1	2012	*Facilities + snow + TRI + pipelines + tree + all rds + light + ndvi + temp + age + fat + study*	-8417.58	180.88
M2	2012	*Facilities + snow + TRI + tree + major rds + light + ndvi + temp + age + fat + study*	-8375.1	171.91
M1	2013	*Facilities + snow + TRI + pipelines + tree +all rds + light + temp + age + fat + study*	-9088.97	141.47
M2	2013	*Facilities + snow + TRI + tree + major rds + light + temp + age + fat + study*	-9094.21	124.70

Table A16.2. Covariates, median posterior coefficient values and the proportion (Prop.) of posteriors falling above and below 0 for beta regression models fit to activity budgets of mule deer in the Piceance Basin of Colorado during winter, with covariates calculated at the daily scale.

Covariate	Median	Prop. < 0	Prop. > 0
M1 2011			
Intercept	-0.28	0.98	0.02
Facilities	0.00	0.61	0.39
Snow	0.04	0.00	1.00
TRI	0.00	0.57	0.43
Pipelines	-0.01	0.77	0.23
Tree	0.01	0.11	0.89
All rds	0.00	0.58	0.42
Light	-0.02	0.58	0.42
Temp	-0.05	1.00	0.00
Age	0.02	0.40	0.60
Fat	0.13	0.08	0.92
Study	-0.59	1.00	0.00
M2 2011			
Intercept	-0.28	0.98	0.02
Facilities	0.00	0.59	0.41
Snow	0.04	0.00	1.00
TRI	0.00	0.52	0.48
Pipelines	0.00	0.64	0.36
Tree	0.01	0.12	0.88
Major rds	-0.01	0.72	0.28
Light	-0.01	0.55	0.45
Temp	-0.04	1.00	0.00
Age	0.02	0.39	0.61
Fat	0.13	0.09	0.91
Study	-0.58	1.00	0.00
M1 2012			
Intercept	0.24	0.03	0.97
Facilities	-0.01	0.82	0.18
Snow	0.12	0.00	1.00
TRI	0.06	0.00	1.00
Pipelines	-0.03	0.89	0.11
Tree	0.06	0.00	1.00
All rds	0.00	0.56	0.44
Light	-0.01	0.56	0.44
NDVI	0.00	0.37	0.63
Temp	0.01	0.23	0.77
Age	-0.04	0.80	0.20
Fat	0.00	0.52	0.48

Study	-0.40	1.00	0.00

M2 2012

Intercept	0.27	0.02	0.98
Facilities	-0.02	0.90	0.10
Snow	0.12	0.00	1.00
TRI	0.05	0.01	0.99
Tree	0.06	0.00	1.00
Major rds	0.00	0.64	0.36
Light	0.00	0.49	0.51
NDVI	0.01	0.34	0.66
Temp	0.01	0.32	0.68
Age	-0.05	0.82	0.18
Fat	0.00	0.54	0.46
Study	-0.42	1.00	0.00

M1 2013

Intercept	0.01	0.46	0.54
Facilities	0.00	0.39	0.61
Snow	0.21	0.00	1.00
TRI	0.06	0.00	1.00
Pipe	-0.03	0.99	0.01
Tree	0.06	0.00	1.00
All rds	-0.01	0.72	0.28
Light	-0.13	0.98	0.02
Temp	-0.08	1.00	0.00
Age	-0.05	0.81	0.19
Fat	-0.01	0.60	0.40
Study	-0.12	0.83	0.17

M2 2013

Intercept	0.02	0.42	0.58
Facilities	0.00	0.34	0.66
Snow	0.21	0.00	1.00
TRI	0.06	0.00	1.00
Tree	0.06	0.00	1.00
Major rds	-0.02	1.00	0.00
Light	-0.14	0.98	0.02
Temp	-0.08	1.00	0.00
Age	-0.06	0.83	0.17
Fat	-0.01	0.60	0.40
Study	-0.12	0.83	0.17

Table A16.3. Model names, year during which data were collected, model structure, Watananbe-Akaike information criteria (WAIC) and effective number of parameters (PD) for beta regression models fit to activity budgets of mule deer in the Piceance Basin of Colorado during the summer. Covariates were calculated at the scale of the daily range. Activity budgets were derived from discrete-time correlated random walk models.

Model	Year	Structure	WAIC	PD
M1	2011	*Facilities + TRI + pipelines +tree + all rds + NDVI + light + age + fat*	-5292.12	187.31
M2	2011	*Facilities + TRI + pipelines + tree + major rds + NDVI + light + age + fat*	-5298.52	153.27
M1	2012	*Facilities + TRI + pipelines + tree + all rds + NDVI + light + age + fat*	-9438.16	208.28
M2	2012	*Facilities + TRI + pipelines + tree + major rds + NDVI + light + age + fat*	-9457.07	200.34
M1	2013	*Facilities + TRI + pipelines + tree + all rds + NDVI + light + age + fat*	-4985.43	170.67
M2	2013	*Facilities + TRI + pipelines + tree + major rds + NDVI + light + age + fat*	-4985.6	154.13

Table A16.4. Covariates, median posterior coefficient values and the proportion (Prop.) of posteriors falling above and below 0 for beta regression models fit to activity budgets of mule deer in the Piceance Basin of Colorado during summer, with covariates calculated at the daily scale.

Covariate	Median	Prop. < 0	Prop. > 0
M1 2011			
Intercept	-0.89	0.97	0.03
Facilities	0.00	0.58	0.42
TRI	0.12	0.00	1.00
Pipelines	-0.11	0.98	0.02
Tree	-0.12	0.98	0.02
All rds	-0.02	0.69	0.31
NDVI	0.07	0.01	0.99
Light	0.50	0.19	0.81
Temp	-0.05	0.98	0.02
Age	0.06	0.45	0.55
Fat	-0.85	0.97	0.03
M2 2011			
Intercept	-0.83	0.96	0.04
Facilities	-0.02	0.72	0.28
TRI	0.13	0.00	1.00
Pipelines	-0.06	0.95	0.05
Tree	-0.09	0.94	0.06
Major rds	-0.08	0.94	0.06
NDVI	0.08	0.01	0.99
Light	0.45	0.22	0.78
Temp	-0.05	0.98	0.02
Age	0.11	0.40	0.60
Fat	-0.87	0.97	0.03
M1 2012			
Intercept	0.50	0.00	1.00
Facilities	-0.06	0.77	0.23
TRI	0.12	0.00	1.00
Pipelines	-0.06	0.95	0.05
Tree	0.00	0.46	0.54
All rds	-0.01	0.81	0.19
NDVI	-0.01	0.63	0.37
Light	-0.43	1.00	0.00
Temp	-0.02	0.95	0.05
Age	-0.13	0.91	0.09
Fat	-0.47	1.00	0.00
M2 2012			
Intercept	0.49	0.00	1.00

Facilities	-0.04	0.71	0.29
TRI	0.12	0.00	1.00
Pipelines	-0.07	0.94	0.07
Tree	0.00	0.46	0.54
Major rds	-0.03	0.87	0.13
NDVI	0.00	0.58	0.42
Light	-0.44	1.00	0.00
Temp	-0.02	0.95	0.05
Age	-0.13	0.92	0.08
Fat	-0.46	1.00	0.00

M1 2013

Intercept	0.21	0.32	0.68
Facilities	-0.02	0.81	0.19
TRI	-0.02	0.70	0.30
Pipelines	-0.11	0.99	0.01
Tree	-0.02	0.64	0.36
All rds	-0.05	0.92	0.08
NDVI	0.06	0.03	0.97
Light	0.05	0.46	0.54
Temp	-0.02	0.84	0.16
Age	-0.35	0.79	0.21
Fat	-0.36	0.79	0.21

M2 2013

Intercept	0.24	0.29	0.71
Facilities	-0.02	0.85	0.15
TRI	-0.02	0.72	0.29
Pipelines	-0.06	0.96	0.04
Tree	-0.02	0.63	0.37
Major rds	-0.10	0.99	0.01
NDVI	0.06	0.03	0.97
Light	0.08	0.42	0.58
Temp	-0.01	0.76	0.24
Age	-0.40	0.82	0.18
Fat	-0.45	0.85	0.15

Table A16.5. Model names, year during which data were collected, model structure, Watananbe-Akaike information criteria (WAIC) and effective number of parameters (PD) for beta regression models fit to activity budgets of mule deer in the Piceance Basin of Colorado during the winter. Covariates were calculated at the scale of the seasonal range. Activity budgets were derived from discrete-time correlated random walk models.

Model	Year	Structure	WAIC	PD
M1	2011	*Drill + prod + snow + light + major roads + TRI + age + fat + tree + facilities + study*	-10495.90	92.13
M2	2011	*Drill + prod + snow + light + all roads + TRI + age + fat + tree + facilities + pipe + study*	-10494.90	92.96
M1	2012	*Prod + snow + NDVI + light + major roads + TRI + age + fat + tree + facilities + study*	-8058.57	104.14
M2	2012	*Prod + snow + NDVI + light + all roads + TRI + age + fat + tree + facilities + pipe + study*	-8058.87	103.92
M1	2013	*Prod + snow +light +major roads + TRI +age +fat +tree + facilities + study*	-8871.57	67.30
M2	2013	*Prod + snow +light +all roads + TRI +age +fat +tree + facilities + study*	-8871.64	67.67
M3	2013	*Prod + snow +light +pipe + TRI +age +fat +tree + facilities + study*	-8877.95	67.61

Table A16.6. Covariates, median posterior coefficient values and the proportion (Prop.) of posteriors falling above and below 0 for beta regression models fit to activity budgets of mule deer in the Piceance Basin of Colorado during winter, with covariates calculated at the seasonal range scale.

Covariate	Median	<0	>0
M1 2011			
Intercept	-0.33	0.94	0.06
Drill	-0.01	0.69	0.31
Prod	-0.06	0.67	0.33
Snow	0.03	0.00	1.00
Light	-0.08	0.73	0.27
Temp	-0.05	1.00	0.00
Major rds	0.15	0.08	0.92
TRI	-0.16	0.88	0.12
Age	0.00	0.51	0.49
Fat	0.06	0.28	0.72
Tree	0.20	0.03	0.97
Facilities	-0.17	0.93	0.07
Study	-0.54	0.97	0.03
M2 2011			
Intercept	-0.41	0.97	0.03
Drill	-0.01	0.69	0.31
Prod	-0.04	0.61	0.39
Snow	0.03	0.00	1.00
Light	-0.10	0.76	0.24
Temp	-0.05	1.00	0.00
All rds	0.10	0.13	0.87
TRI	-0.12	0.80	0.20
Age	0.02	0.42	0.58
Fat	0.08	0.23	0.77
Tree	0.19	0.05	0.95
Facilities	-0.17	0.91	0.09
Pipelines	0.08	0.27	0.73
Study	-0.43	0.92	0.08
M1 2012			
Intercept	0.34	0.04	0.96
Prod	-0.02	0.60	0.40
Snow	0.13	0.00	1.00
NDVI	0.01	0.29	0.71
Light	0.00	0.51	0.49
Temp	0.01	0.29	0.71
Major rds	0.09	0.10	0.90
TRI	-0.05	0.74	0.26
Age	-0.05	0.80	0.20

Fat	-0.03	0.68	0.32
Tree	0.09	0.14	0.86
Facilities	-0.12	0.94	0.06
Study	-0.47	0.98	0.02

M2 2012

Intercept	0.19	0.16	0.84
Prod	0.01	0.44	0.56
Snow	0.13	0.00	1.00
NDVI	0.01	0.28	0.72
Light	-0.04	0.71	0.29
Temp	0.01	0.29	0.71
All rds	0.13	0.03	0.97
TRI	-0.04	0.70	0.30
Age	-0.08	0.93	0.07
Fat	-0.02	0.65	0.35
Tree	0.12	0.08	0.92
Facilities	-0.08	0.88	0.12
Pipelines	-0.05	0.72	0.28
Study	-0.29	0.90	0.10

M1 2013

Intercept	0.01	0.47	0.53
Prod	0.07	0.22	0.78
Snow	0.24	0.00	1.00
Light	-0.17	0.99	0.01
Temp	-0.08	1.00	0.00
Major rds	0.03	0.37	0.63
TRI	0.18	0.13	0.87
Age	-0.03	0.66	0.34
Fat	-0.02	0.63	0.37
Tree	0.05	0.34	0.66
Facilities	0.02	0.42	0.58
Study	-0.09	0.67	0.33

M2 2013

Intercept	0.04	0.41	0.59
Prod	0.10	0.11	0.89
Snow	0.24	0.00	1.00
Light	-0.17	0.99	0.01
Temp	-0.08	1.00	0.00
All rds	-0.05	0.75	0.25
TRI	0.14	0.19	0.81
Age	-0.04	0.72	0.28
Fat	-0.02	0.65	0.35
Tree	0.07	0.26	0.74

Facilities	0.04	0.30	0.70
Study	-0.12	0.72	0.28

M3 2013

Intercept	-0.09	0.66	0.34
Prod	0.01	0.46	0.54
Snow	0.24	0.00	1.00
Light	-0.24	1.00	0.00
Temp	-0.08	1.00	0.00
Pipelines	0.18	0.08	0.92
TRI	0.22	0.10	0.90
Age	-0.05	0.72	0.28
Fat	-0.03	0.70	0.30
Tree	0.07	0.29	0.71
Facilities	-0.05	0.68	0.32
Study	0.03	0.46	0.54

Table A16.7. Model names, year during which data were collected, model structure, Watananbe-Akaike information criteria (WAIC) and effective number of parameters (PD) for beta regression models fit to activity budgets of mule deer in the Piceance Basin of Colorado during the summer. Covariates were calculated at the scale of the seasonal range. Activity budgets were derived from discrete-time correlated random walk models.

Model	Year	Structure	WAIC	PD
M1	2011	*Prod + NDVI + light + age + fat + facilities + TRI + tree + major rds*	-5115.32	85.47
M2	2011	*Prod + NDVI + light + age + fat + facilities + TRI + tree + all rds + pipelines*	-5116.61	85.87
M1	2012	*Prod + NDVI + light + age + fat + facilities + TRI + tree + major*	-8864.71	104.91
M2	2012	*Prod + NDVI + light + age + fat + facilities + TRI + tree + all rds + pipelines*	-8872.38	105.04
M1	2013	*Prod + NDVI + light + age + fat + facilities + TRI + tree + major rds*	-4752.18	75.73
M2	2013	*Prod + NDVI + light + age + fat + facilities + TRI + tree + all rds + pipelines*	-4752.86	75.70

Table A16.8. Covariates, median posterior coefficient values and the proportion (Prop.) of posteriors falling above and below 0 for beta regression models fit to activity budgets of mule deer in the Piceance Basin of Colorado during summer, with covariates calculated at the seasonal range scale.

Covariate	Median	<0	>0
M1 2011			
Intercept	-0.74	0.92	0.08
Prod	0.73	0.14	0.86
NDVI	0.07	0.04	0.96
Light	-0.27	0.68	0.32
Temp	-0.05	0.96	0.04
Age	-0.59	0.80	0.20
Fat	-1.01	0.96	0.04
Facilities	0.09	0.44	0.56
TRI	0.66	0.21	0.79
Tree	-0.43	0.71	0.29
Major rds	-0.52	0.81	0.19
M2 2011			
Intercept	-0.69	0.92	0.08
Prod	1.30	0.05	0.95
NDVI	0.07	0.04	0.96
Light	-0.22	0.64	0.36
Temp	-0.05	0.96	0.04
Age	-0.86	0.90	0.10
Fat	-0.97	0.96	0.04
Facilities	0.54	0.20	0.80
TRI	0.97	0.11	0.89
Tree	-0.30	0.66	0.34
All rds	0.29	0.30	0.70
Pipelines	-1.33	0.96	0.04
M1 2012			
Intercept	0.60	0.00	1.00
Prod	-0.17	0.89	0.11
NDVI	-0.02	0.85	0.15
Light	-0.34	1.00	0.00
Temp	-0.01	0.79	0.21
Age	-0.18	0.92	0.08
Fat	-0.42	1.00	0.00
Facilities	0.13	0.16	0.84
TRI	0.21	0.11	0.89
Tree	-0.28	0.96	0.04
Major rds	0.28	0.07	0.93
M2 2012			

Intercept	0.60	0.00	1.00
Prod	-0.21	0.89	0.11
NDVI	-0.02	0.80	0.20
Temp	-0.41	1.00	0.00
Light	-0.01	0.81	0.19
Age	-0.10	0.76	0.24
Fat	-0.43	1.00	0.00
Facilities	0.17	0.15	0.85
TRI	0.04	0.40	0.60
Tree	-0.28	0.93	0.07
All rds	-0.12	0.81	0.19
Pipelines	0.18	0.17	0.83

M1 2013

Intercept	0.83	0.00	1.00
Prod	-0.16	0.62	0.38
NDVI	0.12	0.00	1.00
Light	-0.13	0.63	0.37
Temp	-0.01	0.79	0.21
Age	-0.05	0.57	0.43
Fat	0.01	0.49	0.51
Facilities	-0.54	0.98	0.02
TRI	-0.33	0.79	0.21
Tree	0.62	0.02	0.98
Major rds	-0.25	0.69	0.31

M2 2013

Intercept	0.79	0.00	1.00
Prod	-0.32	0.70	0.30
NDVI	0.11	0.00	1.00
Light	-0.13	0.62	0.38
Temp	-0.01	0.79	0.21
Age	-0.03	0.53	0.47
Fat	-0.05	0.56	0.44
Facilities	-0.50	0.93	0.07
TRI	-0.25	0.77	0.23
Tree	0.58	0.04	0.96
All rds	-0.26	0.82	0.18
Pipelines	-0.07	0.55	0.45

APPENDIX 17

RESULTS OF DISCRETE-TIME CORRELATED RANDOM WALK MODELS, MODEL

EVALUATION AND ASSESSMENTS

Figure A17.1. Summer range empirical turn angle (A and B) and step length (C and D) distributions for foraging (A and C) and resting (B and D) states identified from a discrete-time correlated random walk model fit to GPS data from adult female mule deer in the Piceance Basin of Colorado. Histograms and density plots include all movements regardless of state, weighted by the probability of being in each state.
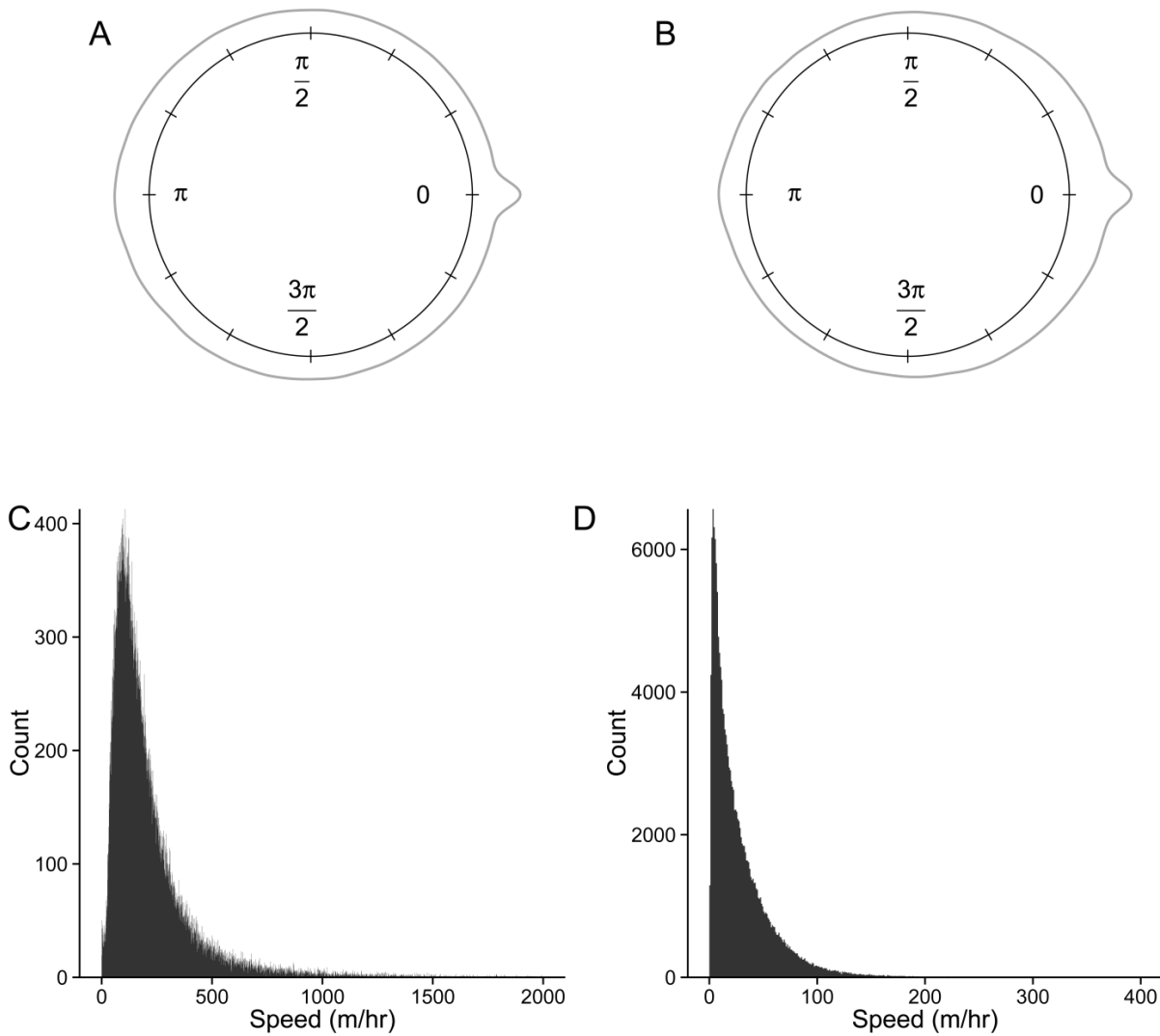
Figure A17.2. Winter range empirical turn angle (A and B) and step length (C and D) distributions for foraging (A and C) and resting (B and D) states identified from a discrete-time correlated random walk model fit to GPS data from adult female mule deer in the Piceance Basin of Colorado. Histograms and density plots include all movements regardless of state, weighted by the probability of being in each state.
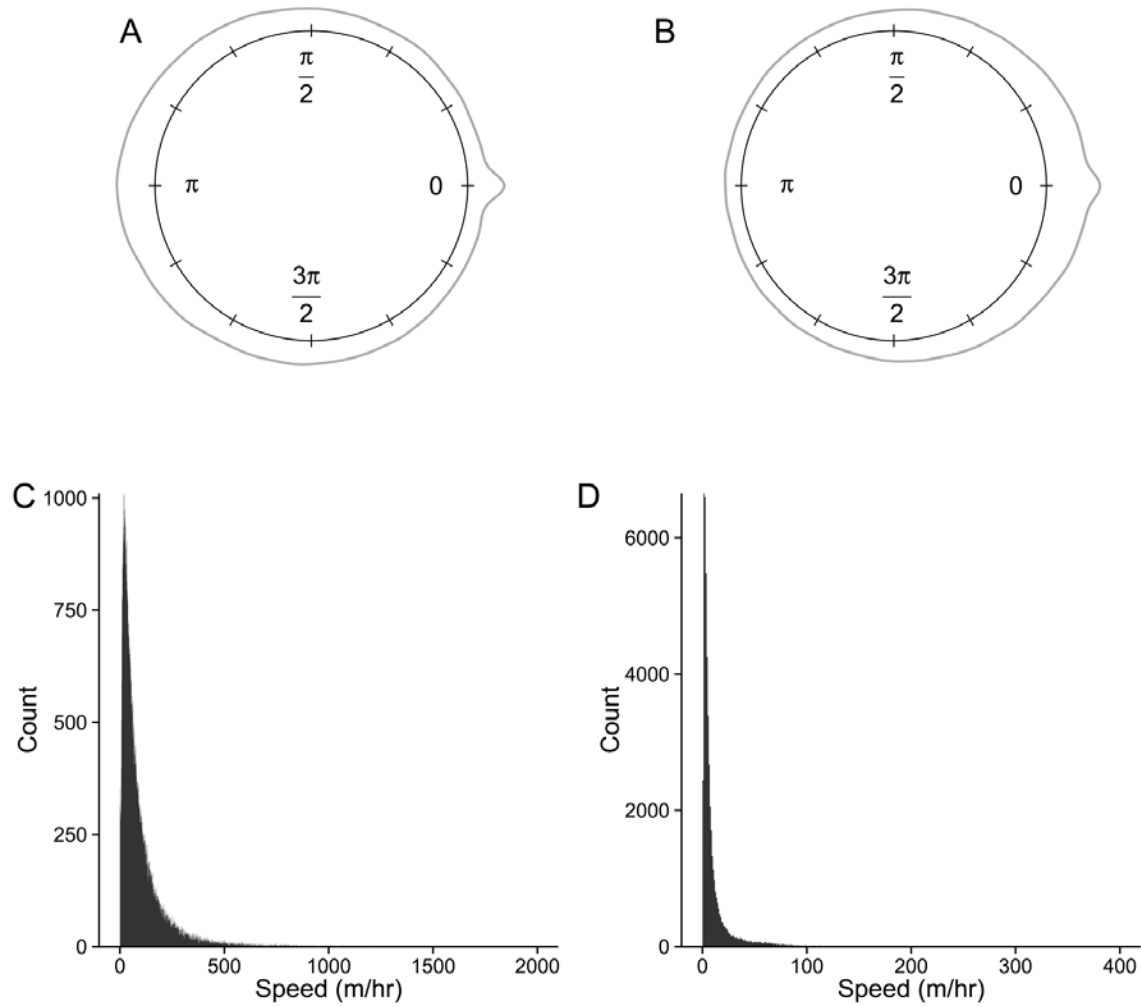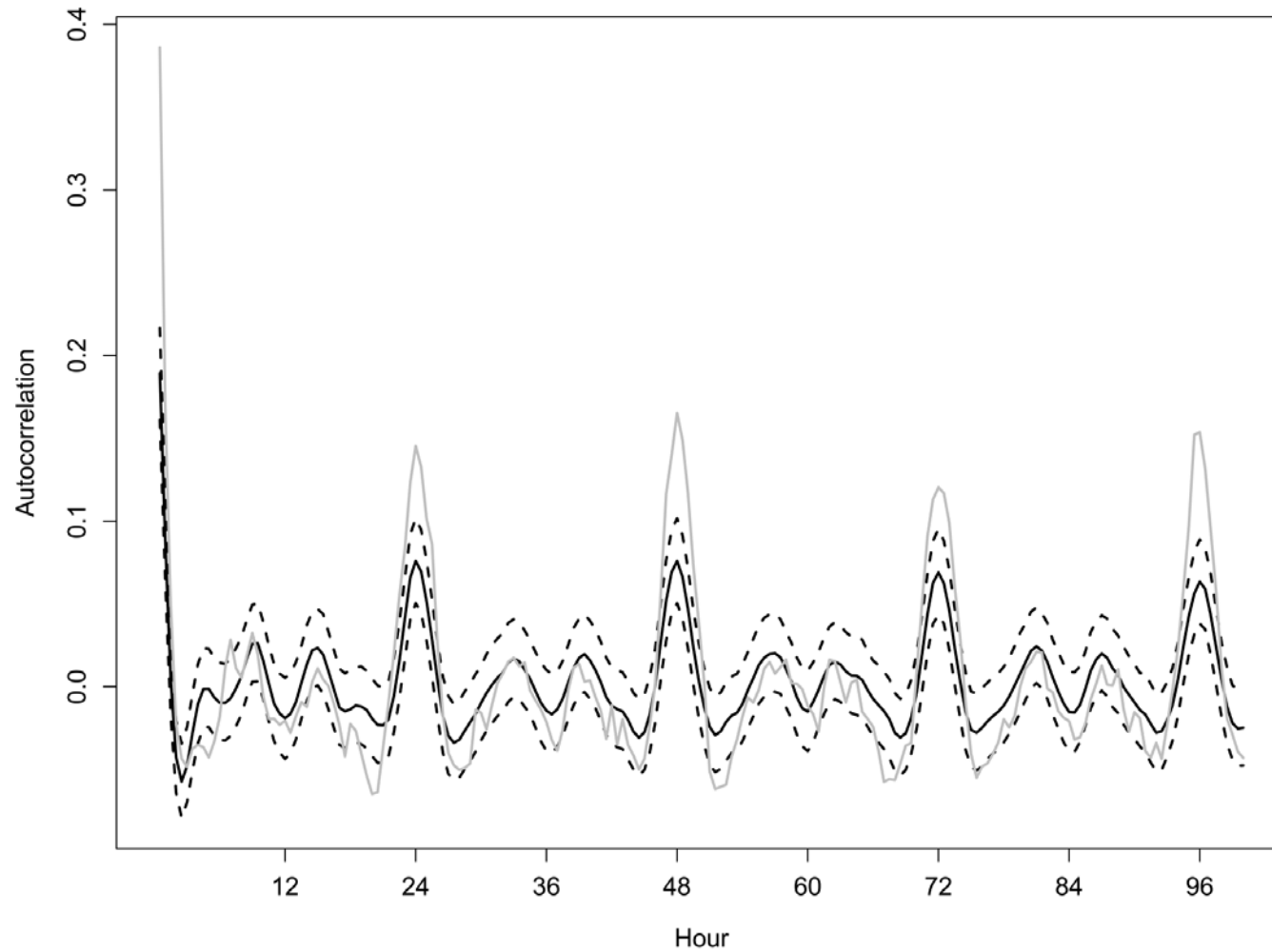
Figure A17.3. Representative result of posterior predictive check on the autocorrelation structure in consecutive step lengths for a single mule deer doe during the winter in the Piceance Basin of northwest Colorado. Black lines represent the median (solid line) and 95% credible interval (dashed lines) of autocorrelation structure produced from the results of discrete-time correlated random walk model, while grey lines represent the true autocorrelation structure estimated from the data.
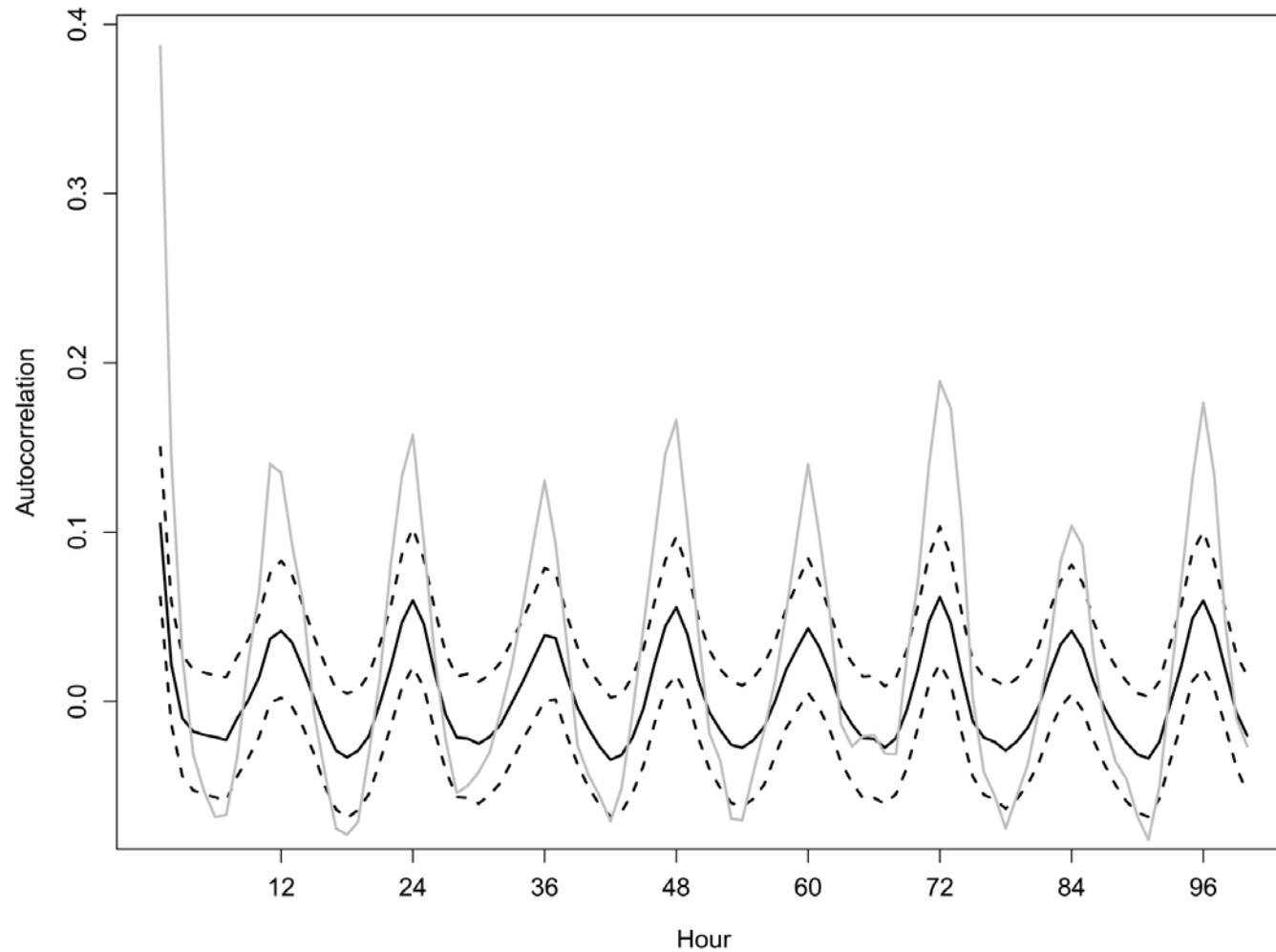
Figure A17.4. Representative result of posterior predictive check on the autocorrelation structure in consecutive step lengths for a single mule deer doe during the summer in the Piceance Basin of northwest Colorado. Black lines represent the median (solid line) and 95% credible interval (dashed lines) of autocorrelation structure produced from the results of discrete-time correlated random walk model, while grey lines represent the true autocorrelation structure estimated from the data.
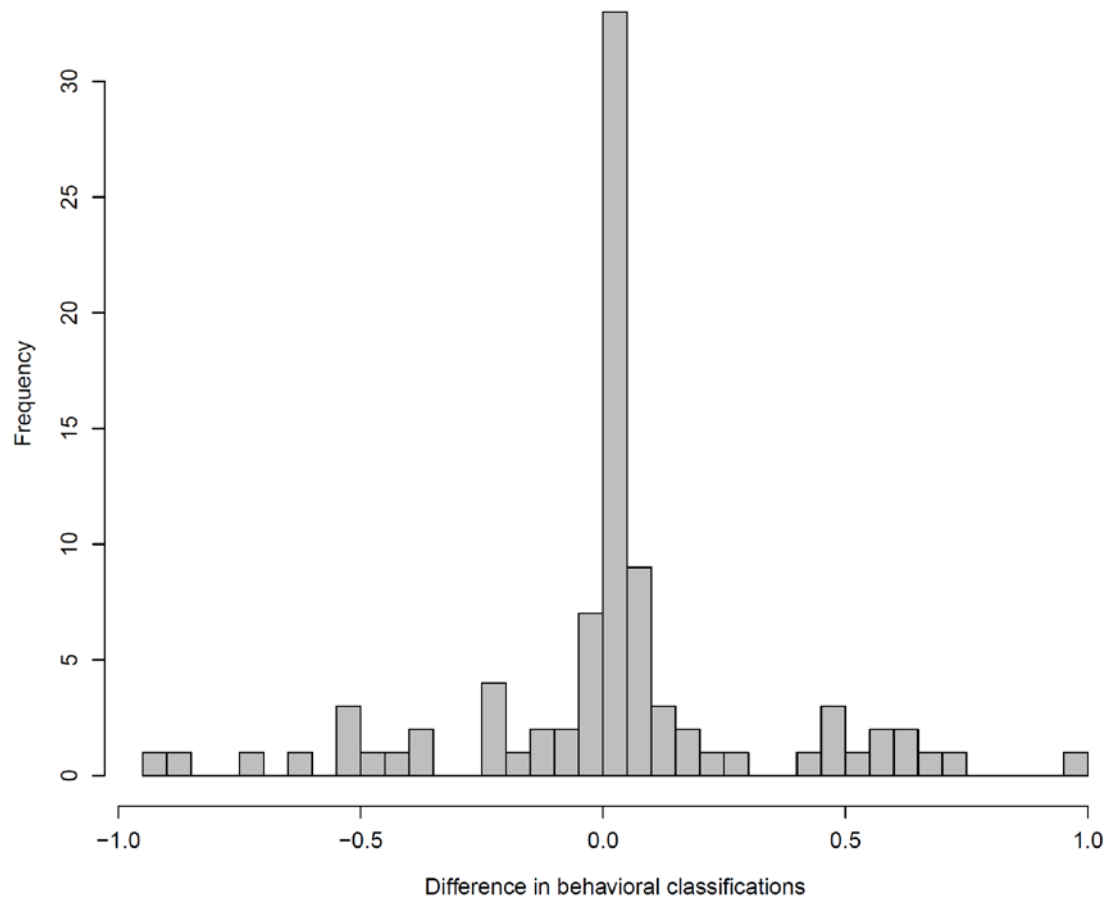
Figure A17.5. Histogram of residuals calculated as the difference between the probability of the animal being in the resting state, as classified by the discrete-time correlated random walk, and the proportion of time spent resting as calculated using acoustic behavioral data.

Figure A17.6. Histogram of residuals calculated as the difference between the probability of the animal being in the resting state, as classified by the discrete-time correlated random walk, and the proportion of time spent resting as calculated using acoustic behavioral data.

Figure A17.7. Histogram of residuals calculated as the difference between the probability of the animal being in the resting state, as classified by the discrete-time correlated random walk, and the proportion of time spent resting as calculated using acoustic behavioral data.
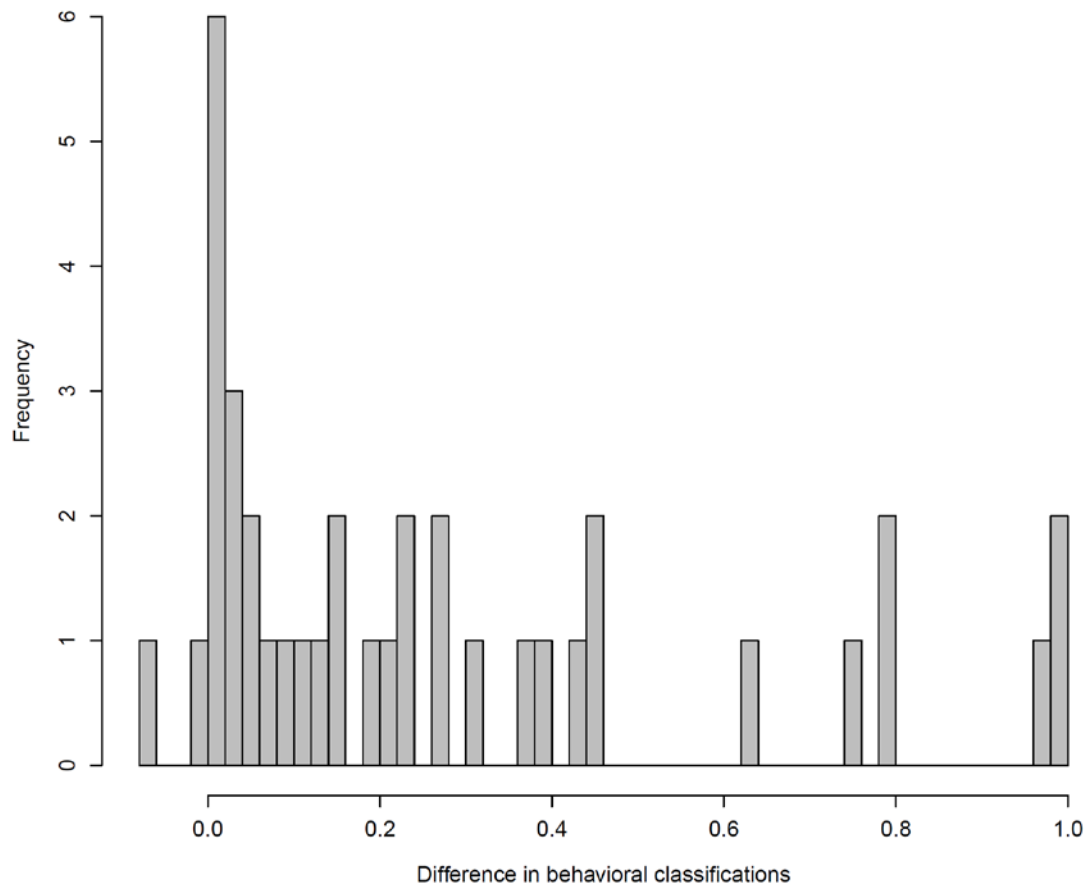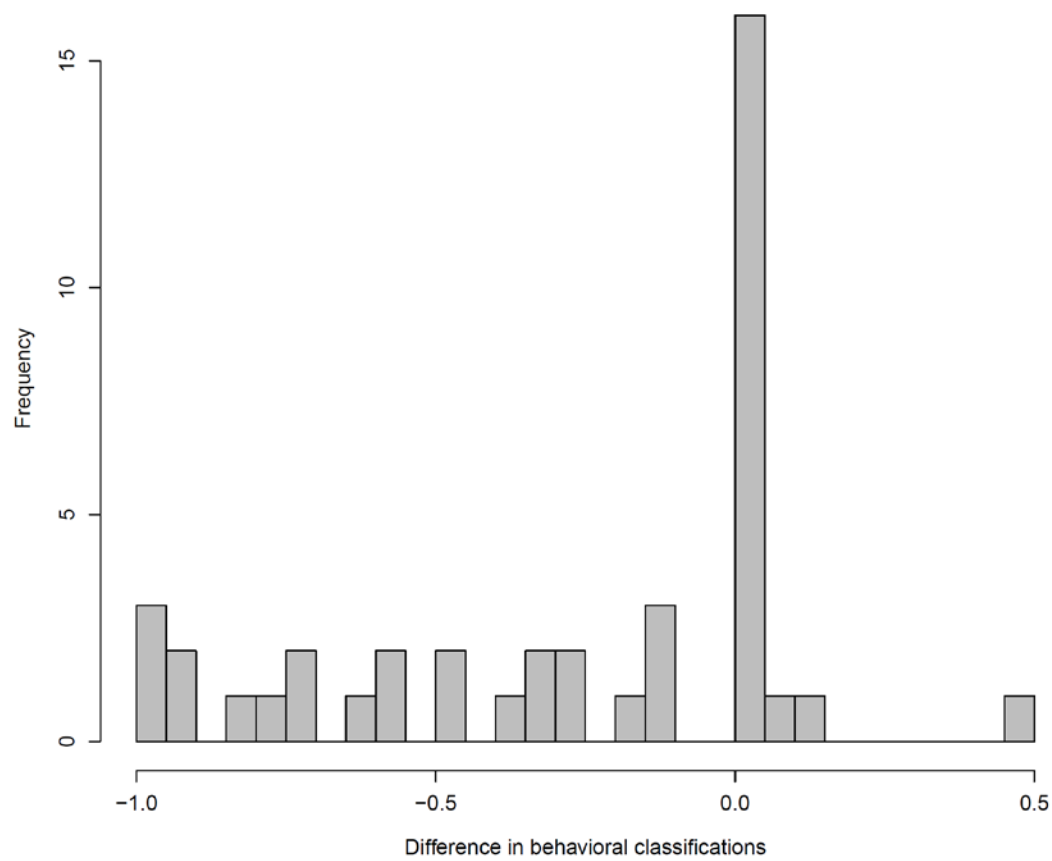
APPENDIX 18

PCR CONDITIONS

DESCRIPTION OF PCR CONDITIONS

The following describes the polymerase chain reaction (PCR) conditions for chapter four. The

multiplex microsatellite reaction consisted of 25 ng DNA, 5 μL 2× Qiagen Multiplex mix, 2 μL

primer mix, and 0.5 μL distilled water. The 10 μl single reactions contained 0.8 μL of $MgCl_2$ (20

mM), 1 μL 10× PCR buffer, 2 μL of dNTPs (0.2 mM each), a 20× primer mix diluted to between

0.24 and 0.34 μL each, 0.08 μL of Taq (0.5 units), 1 μL of DNA template (~10 ng) and Milli-Q

water. One primer per pair was fluorescently labeled. The multiplex PCR parameters followed

Cullingham et al. (2011a) and the single-PCRs began with an initial 3-minute denaturation at

95°C, followed by 38 cycles of 30 seconds denaturation at 94°C, 90 seconds annealing at 49°C,

and 30 seconds extension at 72°C. The microsatellite amplicons were loaded on an ABI 3730

DNA sequencer (Applied Biosystems, Foster City, CA, USA) with a GS500LIZ size standard

(Applied Biosystems). Microsatellite alleles were scored using GENEMAPPER version 4.0

(Applied Biosystems) and deviations from Hardy-Weinberg equilibrium (HWE) were tested

using the exact test (Guo and Thompson 1992) implemented in Genepop v.4.0 (Rousset

2008)and FSTAT v.2.9.3 (Goudet 1995)was used to test for linkage disequilibrium.

The mitochondrial control region was amplified in a 25 μl PCR reaction containing ~50

ng of template DNA, 0.2 mM each dNTP, 1× PCR buffer, 0.2 μM each primer, 1.6 mM $MgCl_2$,

0.1 U Taq DNA polymerase, and Milli-Q water. The PCR profile was as follows: hot-start

followed by an initial 2-minute denaturation at 94°C, followed by 38 cycles of 30 seconds

denaturation at 94°C, 58°C, 72°C. The run concluded after 5 minutes at 72°C. PCR success was

determined from gel electrophoresis. PCR product (10 μl) was treated with 5 μl of ExoSAP

(USB Corporation, OH, USA) and incubated at 37°C for 15 minutes followed by 80°C for 15

minutes. The ExoSAP treated PCR product was used in a sequencing reaction. Amplicons were directly sequenced in both directions using a Big Dye Terminator Kit (Applied Biosystems, Foster City, CA) and generated on an ABI 3730. Sequences were aligned using the ClustalW algorithm (Thompson et al. 1994).

APPENDIX 19

MICROSATELLITE DIVERSITY STATISTICS

Table A19.1. Microsatellite loci, number of individuals genotyped (N), number of alleles present at each loci (Na), observed heterozygosity (Ho), expected heterozygosity (He), and fixation index (F).

Locus	N	Na	Ho	He	F
INRA011a	134	6.000	0.500	0.489	-0.023
RT30a	132	14.000	0.788	0.794	0.008
BBJ2a	134	8.000	0.739	0.781	0.054
Ka	135	5.000	0.748	0.725	-0.032
BL25a	133	6.000	0.767	0.706	-0.086
BM6438a	134	10.000	0.784	0.732	-0.071
BM848a	135	9.000	0.748	0.755	0.010
RT7a	133	8.000	0.827	0.786	-0.052
Na	135	12.000	0.852	0.881	0.033
ETH152a	134	10.000	0.791	0.803	0.015
BM6506a	135	5.000	0.741	0.701	-0.056
Pa	132	7.000	0.538	0.550	0.021
Da	132	6.000	0.462	0.463	0.001
BM4107a	134	11.000	0.828	0.838	0.011
RT5a	134	10.000	0.836	0.777	-0.075
OCAMa	129	8.000	0.628	0.558	-0.125
Ra	131	6.000	0.634	0.619	-0.024
Mean	133.294	8.294	0.718	0.703	-0.023
SE	0.400	0.629	0.029	0.030	0.012

APPENDIX 20

MODEL FORMULATION FOR MODELS USED IN CHAPTER 7

The following is the model formulation for the regression models used in chapter four.

Multi-level linear regression model:

$$\log(mass_{ij}) \sim Normal(\mu_{ij}, \sigma^2)$$

$$\mu_{ij} = \alpha_i + x'_{ij}\beta$$

$$\alpha_i \sim Normal(\mu_\alpha, \sigma_\alpha^2)$$

$$\mu_\alpha \sim Normal(0, 300)$$

$$\sigma_\alpha = \frac{1}{\sqrt{\tau_\alpha}}$$

$$\tau_\alpha \sim gamma(0.001, 0.001)$$

$$\beta \sim Normal(\mathbf{0}, 10\,000I)$$

$$\sigma = \frac{1}{\sqrt{\tau}}$$

$$\tau \sim gamma(0.001, 0.001)$$

Multi-level beta regression model:

$$fat_{ij} \sim beta(a_{ij}, b_{ij})$$

$$a_{ij} = \mu_{ij} \times \phi$$

$$b_{ij} = (1 - \mu_{ij})\phi$$

$$logit(\mu_{ij}) = \alpha_i + x'_{ij}\beta$$

$$\alpha_i \sim Normal(\mu_\alpha, \sigma_\alpha^2)$$

$$\mu_\alpha \sim Normal(0, 300)$$

$$\sigma_\alpha = \frac{1}{\sqrt{\tau_\alpha}}$$

$$\tau_\alpha \sim gamma(0.001, 0.001)$$

$$\boldsymbol{\beta} \sim Normal(\mathbf{0}, 10\ 000I)$$

$$\phi \sim gamma(0.0001, 0.0001)$$

Negative binomial regression model:

$$days_j \sim Negative\ binomial(p_j, r)$$

$$p_j = \frac{r}{r + \lambda_j}$$

$$\log(\lambda_j) = \boldsymbol{x}_j' \boldsymbol{\beta}$$

$$\boldsymbol{\beta} \sim Normal(\mathbf{0}, 10\ 000I)$$

$$r \sim Uniform(0,100)$$

In all models, i indexes the individual, j indexes the observation, $\boldsymbol{x}_{ij}$ is vector of covariates for the ith individual and j^{th} observation with corresponding vector of coefficients, $\boldsymbol{\beta}$. The above formulations include priors, which were formulated to be diffuse.

For all models 2 Markov Chain Monte Carlo (MCMC) algorithms were run, with initial values that were expected to be overdispersed relative to the posterior distribution. Convergence to the posterior distribution was assessed using the Gelman-Rubin diagnostic (Gelman and Rubin 1992), and by examining trace plots of the MCMCs. We ran the negative binomial models of migration timing for 400,000 iterations, discarding the first 100,000 as burn-in. We ran the MLH models for condition for 300,000 iterations, discarding the first 100,000 as burn-in. We ran the SLH models for condition for 400,000 iterations discarding the first 100,000 as burn-in. Once convergence was reached we calculated the median of the posterior distributions for all coefficients, as well as the probability that each coefficient was above and below 0.

APPENDIX 21

PHYLOGENETIC TREES
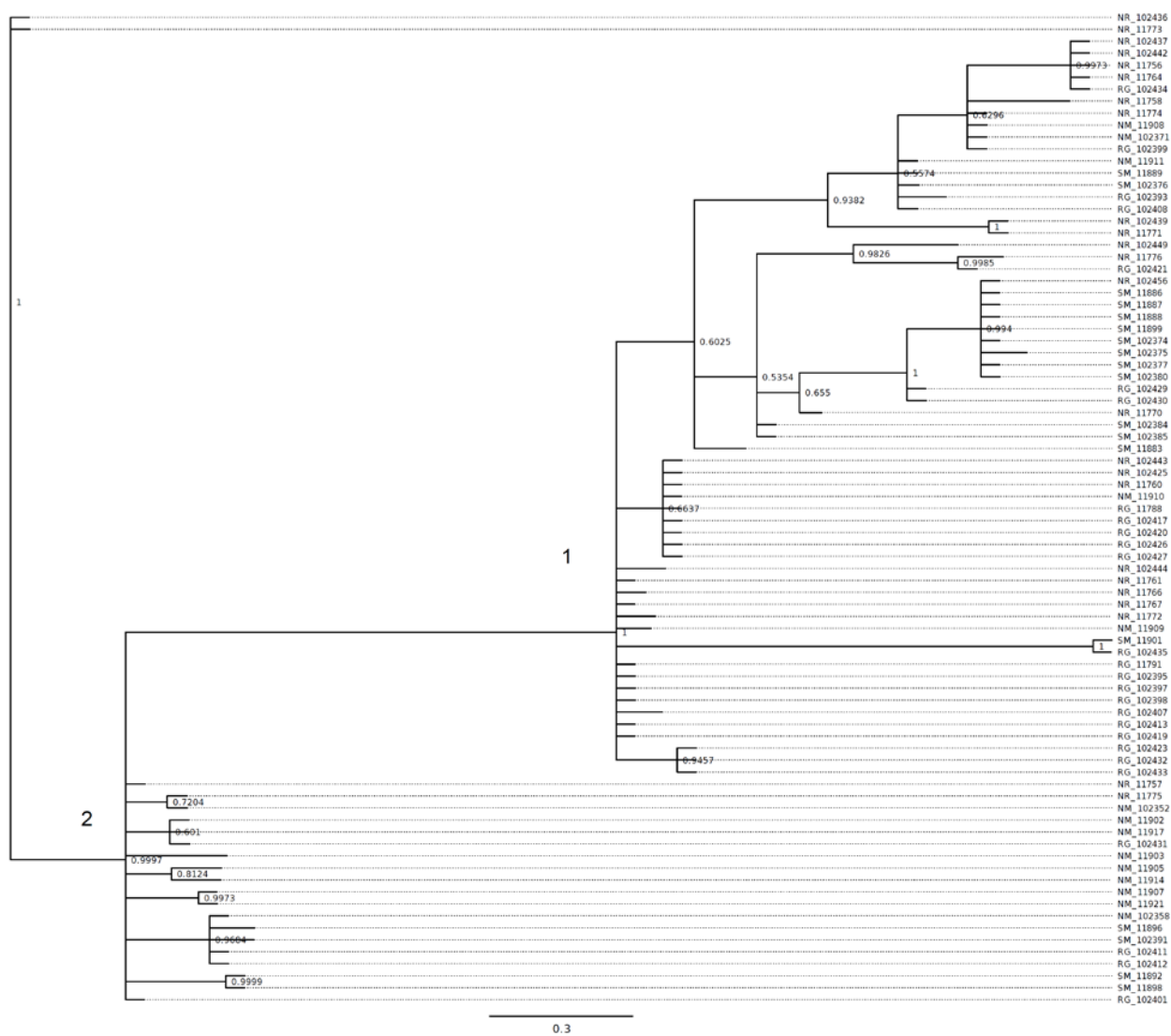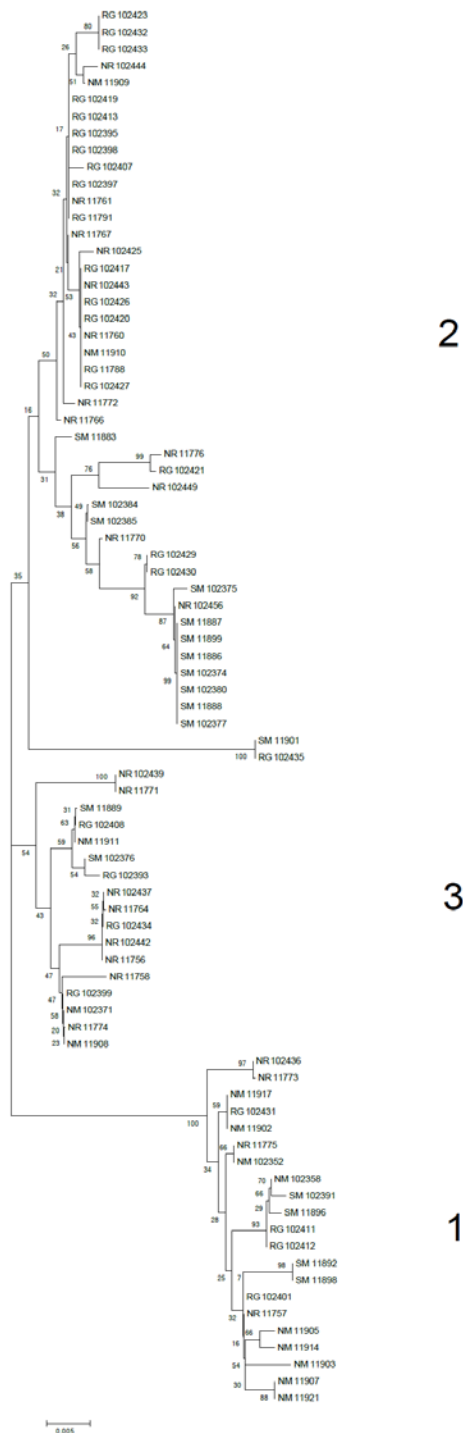
Figure A21.1. Phylogenetic trees for female mule deer in the Piceance Basin, Northwest Colorado.

APPENDIX 22

SUPPLEMENTAL RESULTS FOR CHAPTER 7

Table A22.1. Identification (ID) numbers, ages, study area, and whether individual was captured in December, March or both for mule deer captured in the Piceance Basin of Colorado.

ID number	Age	Study area	Capture period
11890	4.5	SM	December
102352	5.5	NM	December
102353	9.5	NM	December
102354	5.5	NM	December
102357	10.5	NM	December
102358	2.5	NM	December
102363	5.5	NM	December
102365	5.5	NM	December
102368	3.5	NM	December
102370	3.5	NM	December
102371	10.5	NM	December
102374	8.5	SM	December
102375	2.5	SM	December
102376	10.5	SM	December
102377	5.5	SM	December
102380	2.5	SM	December
102384	7.5	SM	December
102385	1.5	SM	December
102386	4.5	SM	December
102390	7.5	SM	December
102391	4.5	SM	December
102392	4.5	RG	December
102396	7.5	RG	December
102398	3.5	RG	December
102407	9.5	RG	December
102408	6.5	RG	December
102409	4.5	RG	December
102410	1.5	RG	December
102411	4.5	RG	December
102412	7.5	RG	December
102413	4.5	RG	December
102416	3.5	RG	December
102417	6.5	RG	December
102418	3.5	RG	December
102419	5.5	RG	December
102420	4.5	RG	December
102421	10.5	RG	December
102423	2.5	RG	December
102426	7.5	RG	December
102427	9.5	RG	December
102429	7.5	RG	December
102430	9.5	RG	December
102431	10.5	RG	December

102434	5.5	RG	December
102435	4.5	RG	December
102436	7.5	NR	December
102442	7.5	NR	December
102443	10.5	NR	December
102444	4.5	NR	December
102448	6.5	NR	December
102449	3.5	NR	December
102452	2.5	NR	December
102455	3.5	NR	December
102456	4.5	NR	December
102457	8.5	NR	December
11758	9.5	NR	Both
11760	5.5	NR	Both
11761	2.5	NR	Both
11767	4.5	NR	Both
11768	6.5	NR	Both
11769	8.5	NR	Both
11771	3.5	NR	Both
11772	8.5	NR	Both
11778	5.5	RG	Both
11779	5.5	RG	Both
11780	4.5	RG	Both
11781	4.5	RG	Both
11782	6.5	RG	Both
11783	4.5	RG	Both
11784	5.5	RG	Both
11787	8.5	RG	Both
11788	3.5	RG	Both
11789	6.5	RG	Both
11791	4.5	RG	Both
11792	3.5	RG	Both
11885	2.5	SM	Both
11886	5.5	SM	Both
11887	6.5	SM	Both
11888	3.5	SM	Both
11889	5.5	SM	Both
11891	10.5	SM	Both
11894	10.5	SM	Both
11899	4.5	SM	Both
11903	3.5	NM	Both
11905	3.5	NM	Both
11906	2.5	NM	Both
11908	3.5	NM	Both
11910	8.5	NM	Both
11911	4.5	NM	Both

11913	6.5	NM	Both
11916	10.5	NM	Both
11919	2.5	NM	Both
11920	2.5	NM	Both
102393	6.5	RG	Both
102395	8.5	RG	Both
102397	6.5	RG	Both
102399	4.5	RG	Both
102401	3.5	RG	Both
102432	3.5	RG	Both
102433	9.5	RG	Both
102437	5.5	NR	Both
11756	7.5	NR	March
11759	7.5	NR	March
11762	1.5	NR	March
11764	7.5	NR	March
11765	2.5	NR	Both
11766	5.5	NR	Both
11770	6.5	NR	March
11773	6.5	NR	March
11774	5.5	NR	March
11775	3.5	NR	March
11776	2.5	NR	March
11777	11.5	RG	March
11882	5.5	SM	March
11883	7.5	SM	March
11884	8.5	SM	March
11892	4.5	SM	March
11893	8.5	SM	March
11895	10.5	SM	March
11896	4.5	SM	March
11897	3.5	SM	March
11898	6.5	SM	March
11900	7.5	SM	March
11901	3.5	SM	March
11902	7.5	NM	March
11904	3.5	NM	March
11907	7.5	NM	March
11909	4.5	NM	March
11912	6.5	NM	March
11914	4.5	NM	March
11915	8.5	NM	March
11917	4.5	NM	March
11918	8.5	NM	March
11921	6.5	NM	March

Table A22.2. DIC values for multi-level linear regression models on mule deer body mass, and multi-level beta regression models on mule deer body fat relative to MLH (multi-locus heterozygosity) or SLH (single-locus heterozygosity). Body mass and fat were calculated from deer captured via helicopter net-gunning on their winter range.

Dependent variable	Model	Model structure	DIC
Mass	M1	MLH + Age + March Capture + Study area	-338.9
Mass	M2	MLH + Age + Age^2 + March Capture + Study area	-339.2
Mass	M3	SLH* + Age + March Capture + Study area	-334.5
Mass	M4	SLH* + Age + Age^2 + March Capture + Study area	-334.6
Fat	F1	MLH + Age + March Capture + Study area	-695.9
Fat	F2	MLH + Age + Age^2 + March Capture + Study area	-695.8
Fat	F3	SLH* + Age + March Capture + Study area	-691.6
Fat	F4	SLH* + Age + Age^2 + March Capture + Study area	-690.9

*SLH indicates a set of 17 dummy variables indicating if the individual was heterozygous (1) or not (0) at a specific locus.

Table A22.3. Covariates, median coefficient (coeff.) values, and the probability (prob.) of either a negative or positive effect of the covariate on mule deer body mass and body fat estimated from multi-level linear or beta regression respectively. Models presented are lowest DIC models for both MLH and SLH models of mass and body fat.

Mass model M2

Covariate	Median coeff. value	Prob. coeff. is negative	Prob. coeff. positive
MLH	0.117	0.24	0.76
Age	0.036	0.03	0.97
Age^2	-0.021	0.91	0.09
March Capture	-0.1	1	0
NR[*]	-0.014	0.61	0.39
RG[†]	-0.02	0.67	0.33
SM[‡]	-0.007	0.56	0.44

Mass model M4

Covariate	Median coeff. value	Prob. coeff. is negative	Prob. coeff. positive
Age	0.033	0.06	0.94
Age^2	-0.021	0.89	0.11
March Capture	-0.100	1	0
NR[*]	-0.014	0.60	0.40
RG[†]	-0.027	0.69	0.31
SM[‡]	-0.027	0.69	0.31
INRA011	-0.024	0.73	0.27
RT30	-0.060	0.90	0.10
BBJ	0.024	0.30	0.70
K	0.036	0.20	0.80
BL25	-0.004	0.53	0.47
BM6438	0.010	0.42	0.58
BM848	0.028	0.27	0.73
RT7	0.030	0.29	0.71
N	0.085	0.06	0.94
ETH152	-0.034	0.77	0.23
BM6506	0.036	0.21	0.79
P	0.002	0.48	0.52
D	0.010	0.40	0.60
BM4107	0.044	0.21	0.79
RT5	0.032	0.27	0.73
OCAM	0.027	0.25	0.75
R	-0.038	0.82	0.18

Fat model F1

Covariate	Median coeff. value	Prob. coeff. is negative	Prob. coeff. positive
MLH	0.094	0.39	0.61
Age	-0.043	0.87	0.13

March Capture	-0.515	1	0
NR[*]	-0.078	0.74	0.26
RG[†]	-0.026	0.60	0.4
SM[‡]	0.041	0.36	0.64

Fat model F3

Covariate	Median coeff. value	Prob. coeff. is negative	Prob. coeff. positive
Age	-0.051	0.89	0.11
March Capture	-0.518	1	0
NR[*]	-0.104	0.80	0.20
RG[†]	-0.105	0.82	0.18
SM[‡]	-0.059	0.69	0.31
INRA011	-0.127	0.93	0.07
RT30	-0.240	0.99	0.01
BBJ	0.077	0.22	0.78
K	-0.034	0.65	0.35
BL25	0.074	0.27	0.73
BM6438	-0.001	0.50	0.50
BM848	-0.108	0.87	0.13
RT7	-0.078	0.72	0.28
N	0.087	0.22	0.78
ETH152	-0.004	0.52	0.48
BM6506	0.024	0.40	0.60
P	0.175	0.04	0.96
D	0.092	0.13	0.87
BM4107	0.053	0.32	0.68
RT5	0.145	0.13	0.87
OCAM	0.020	0.41	0.59
R	-0.076	0.81	0.19

[*]Indicates deer captured in the NR study area, with NM as the reference category
[†]Indicates deer captured in the RG study area, with NM as the reference category
[‡]Indicates deer captured in the SM study area, with NM as the reference category

Table A22.4. Covariates, median coefficient (coeff.) values, and the probability (prob.) of either a negative or positive effect of the covariate on mule deer Spring migration termination date estimated from negative binomial regression model from mule deer captured in the Piceance Basin, Colorado.

Neighbor joining clades

Covariate	Median coeff. value	Prob. coeff. is negative	Prob. coeff. positive
Intercept	3.48	0	1
Age	0.01	0.45	0.55
NR[*]	-0.23	0.93	0.07
RG[†]	-0.01	0.52	0.48
SM[‡]	-0.02	0.56	0.44
mtDNA cluster 2[§]	0.04	0.38	0.62
mtDNA cluster 3[§]	0.04	0.39	0.61

Bayesian clades

Covariate	Median coeff. value	Prob. coeff. is negative	Prob. coeff. positive
Intercept	3.49	0	1
Age	0.01	0.44	0.56
NR[*]	-0.23	0.93	0.07
RG[†]	-0.02	0.55	0.45
SM[‡]	-0.03	0.58	0.42
mtDNA cluster 2[§]	0.03	0.41	0.59

[*]Indicates deer captured in the NR study area, with NM as the reference category
[†]Indicates deer captured in the RG study area, with NM as the reference category
[‡]Indicates deer captured in the SM study area, with NM as the reference category
[§]mtDNA cluster 1 is the reference category

Table A22.5. Covariates, median coefficient (coeff.) values, and the probability (prob.) of either a negative or positive effect of the covariate on mule deer Spring migration initiation date estimated from negative binomial regression model from mule deer captured in the Piceance Basin, Colorado.

Neighbor joining clades

Covariate	Median coeff. value	Prob. coeff. is negative	Prob. coeff. positive
Intercept	3.41	0	1
Age	-0.03	0.7	0.3
NR[*]	-0.67	1	0
RG[†]	-0.14	0.79	0.21
SM[‡]	-0.08	0.67	0.33
mtDNA cluster 2[§]	0.01	0.48	0.52
mtDNA 3	-0.12	0.76	0.24

Bayesian clades

Covariate	Median coeff. value	Prob. coeff. is negative	Prob. coeff. positive
Intercept	3.36	0	1
Age	-0.04	0.76	0.24
NR[*]	-0.66	1	0
RG[†]	-0.11	0.74	0.26
SM[‡]	-0.05	0.32	0.38
mtDNA cluster 2[§]	0.04	0.38	0.62

[*]Indicates deer captured in the NR study area, with NM as the reference category
[†]Indicates deer captured in the RG study area, with NM as the reference category
[‡]Indicates deer captured in the SM study area, with NM as the reference category
[§]mtDNA cluster 1 is the reference category

Table A22.6. Covariates, median coefficient (coeff.) values, and the probability (prob.) of either a negative or positive effect of the covariate on mule deer Fall migration initiation date estimated from negative binomial regression model from mule deer captured in the Piceance Basin, Colorado.

Neighbor joining clades

Covariate	Median coeff. value	Prob. coeff. is negative	Prob. coeff. positive
Intercept	3.07	0	1
Age	-0.17	0.92	0.08
NR[*]	-0.1	0.62	0.38
RG[†]	-0.44	0.91	0.09
SM[‡]	-0.78	0.98	0.02
mtDNA cluster 2[§]	-0.52	0.96	0.04
mtDNA cluster 3[§]	-0.55	0.95	0.05

Bayesian clades

Covariate	Median coeff. value	Prob. coeff. is negative	Prob. coeff. positive
Intercept	2.84	0	1
Age	-0.18	0.93	0.07
NR[*]	-0.08	0.59	0.41
RG[†]	-0.28	0.81	0.19
SM[‡]	-0.59	0.95	0.05
mtDNA cluster 2[§]	-0.35	0.9	0.1

[*]Indicates deer captured in the NR study area, with NM as the reference category
[†]Indicates deer captured in the RG study area, with NM as the reference category
[‡]Indicates deer captured in the SM study area, with NM as the reference category
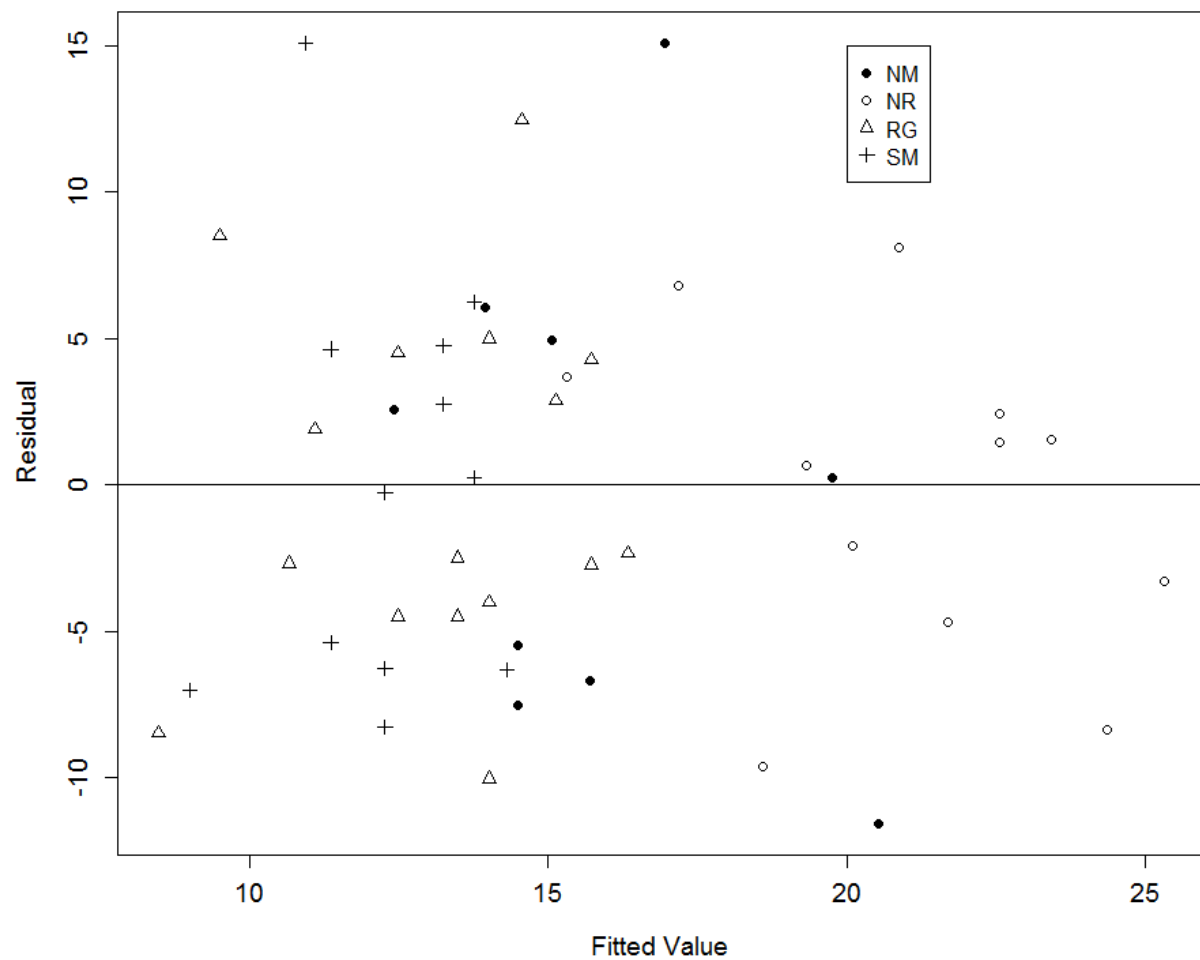[§]mtDNA cluster 1 is the reference category

Figure A22.1. Fitted values versus residuals from negative binomial model fit to migration timing of mule deer in the Piceance Basin of Colorado. The residuals were calculated from the model including mtDNA clades determined from the Bayesian analysis.
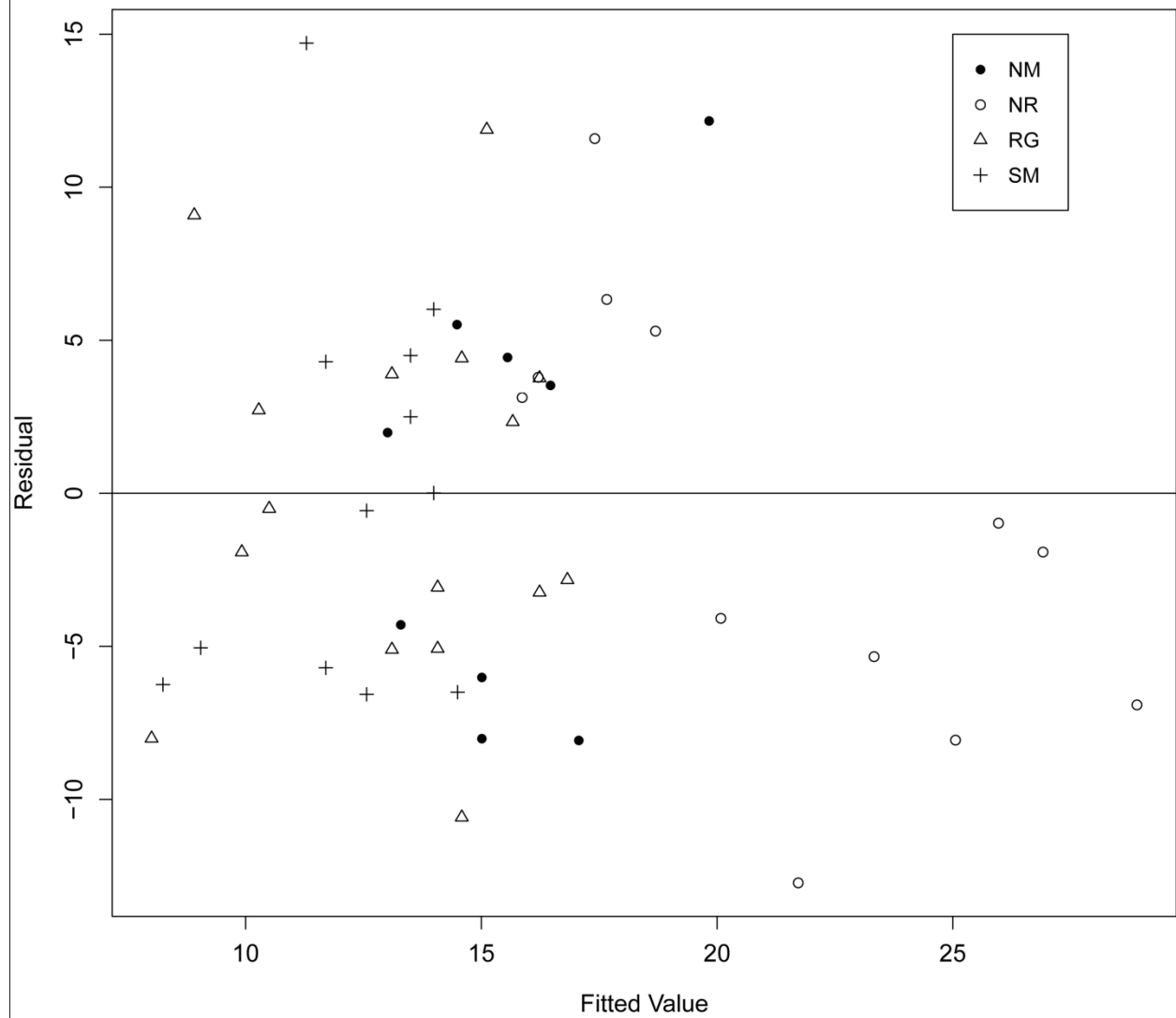
Figure A22.2. Fitted values versus residuals from negative binomial model fit to migration timing of mule deer in the Piceance Basin of Colorado. The residuals were calculated from the model including mtDNA clades determined from the neighbor joining analysis.
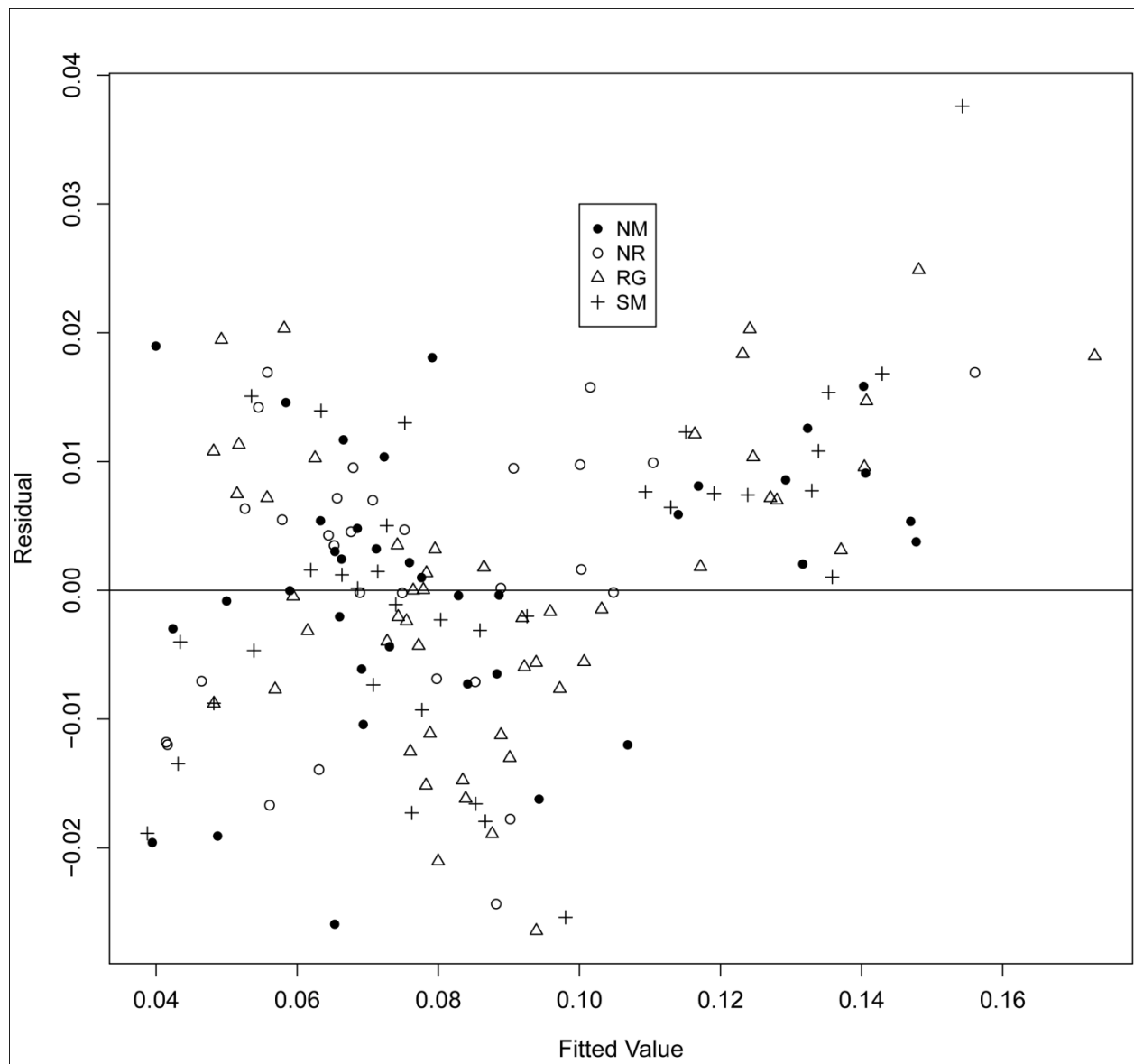
Figure A22.3. Fitted values versus residuals from hierarchical beta regression fit to percent body fat of mule deer in the Piceance Basin of Colorado. Residuals are from best model as determined by DIC (deviance information criteria).