MOVEMENT ECOLOGY OF FEMALE SAGE-GROUSE INFORMS SPACE USE, RESOURCE SELECTION, AND DEMOGRAPHY IN SOUTHERN VALLEY COUNTY, MT

by

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NOMENCLATURE

behavior mode: a classification level of animal behavior as determined by a researcher

biplot: multivariate plot illustrating relationships among 2 types of variables

CV: coefficient of variation

eccentricity: index of home range elongation

enclosed points: use points enclosed by a short-term home range

GAM: generalized additive model

GLM: generalized linear model

hull: short-term home range

landscape condition: a habitat condition, environmental variable, or landscape-element property

nearest neighbor point patch: patch with specified area created from nearest neighbor point

nnp: nearest neighbor point – a point from a set of points used to construct a hull

movement property: time-varying characteristic of movement like speed or patch revisitation

MRT: multivariate regression tree

PAM: partitioning around medoids – unsupervised data partitioning/clustering method

partial RDAs examine effects of focus covariates after removing effects of other variables

PCA: principal component analysis

rCD: robust coefficient of determination

RDA: redundancy analysis – multivariate variance partitioning method (direct gradient analysis)

RoV: radius of variance

triplot: multivariate plot illustrating relationships among 3 types of variables

use-intensity: hull enclosed points divided by hull area

ABSTRACT

The greater sage-grouse (*Centrocercus urophasianus*) is a focal species in the effort to conserve imperiled sagebrush ecosystems and associated organisms. Sage-grouse uses of landscapes are modulated by their multilevel movement processes. Understanding the relative contributions of hard-wired and environmental influences on movement processes is necessary for a comprehensive understanding of sage-grouse ecology. Correlates between fitness components and measurable landscape conditions may be of limited value if other influences such as sage-grouse movement and behavior are not accounted for. Movement behaviors may be risky in certain contexts and adaptive in other contexts, and differences in the characteristics of movement and therefore space-use among individuals can have implications for survival and reproductive performance. We collected detailed records of sage-grouse movements for up to 4 years per individual to investigate daily behavioral strategies of sage-grouse and therefore mechanisms driving habitat use and individual performance. During April–May, 2018–2019, we captured 86 (45 in 2018, 41 in 2019) female sage-grouse and outfitted them with GPS transmitters. We collected 192,640 geographic coordinates of 86 female sage-grouse during 2018-04-24 – 2022-04-14 which encompassed 4 complete annual cycles of sage-grouse. We confirmed 185 nest attempts of 76 individuals during the nesting seasons of 2018–2021. Hard-wired or learned seasonal behavior modes appeared to be more influential than vegetation conditions. Sage-grouse can exhibit reactive responses to landscape conditions but also use the landscape as a function of high-level endogenous constraints likely due to memory mechanisms, high temporal predictability of some resources, and moderate spatial heterogeneity of resources. Management prescriptions may ignore important ecological levels such as those responsible for learned-heuristic movement and space use modes. Relationship and magnitude of associations among sage-grouse use-intensity and landscape conditions varied among 7 behavior modes which indicates that behavioral and temporal context is important for understanding habitat and space use by sage-grouse. Our findings also support a fundamental demographic importance of area affinity, fidelity, and familiarity to sage-grouse ecology which has been overlooked in most research on sage-grouse or other birds.

CHAPTER ONE

GENERAL INTRODUCTION

Sagebrush Ecosystems

Sagebrush ecosystems once occupied over 62.7 million hectares of the North America west but are presently one of the most threatened in North America and are continuing to be destroyed and fragmented (West 1988, Knick et al. 2003, Dobkin and Sauder 2004, Schroeder et al. 2004, Welch 2005, Davies et al. 2011, Miller et al. 2011). Most sagebrush ecosystems are shrub steppes which are shrub-dominated ecosystems with climates between deserts and grasslands where subordinate species are largely a mix of those which occupy deserts or grasslands. Intermountain lowland regions of North America currently or historically dominated by sagebrushes (woody *Artemisia* spp) and bunchgrasses are commonly known as sagebrush steppes and once occupied approximately 44.4 x 10^6 ha of the North American west (West 1983c). The sagebrush steppe ecosystem type is present in 9 western states with Wyoming, Idaho, Oregon, Nevada, and Washington accounting for 88 percent of the total. Another major shrub steppe vegetation type characterized by *Artemisia* dominance is Great Basin sagebrush which is found south of the sagebrush steppe and occupies approximately 17.9 x 10^6 ha of the Great Basin and parts of the Colorado Plateau in Nevada, Utah, and Colorado (West 1983a). The Great Basin type is partly characterized by a lesser herbaceous component compared to that of the sagebrush steppe (West 1983a). Numerous biogeographic and ecological regions have been proposed to classify regional generalities regarding climate, physiography, lithology, soil, and potential biotic communities. Regardless of the classification system used to organize and communicate properties of ecosystems in western North America the distribution of sagebrush ecosystems spans multiple types.

While the majority of acreage where sagebrush is considered the dominant potential natural vegetation falls under intermountain sagebrush steppe and Great Basin sagebrush types, sagebrush species are distributed beyond these zones and may attain local dominance in other areas (Johnson 1978, McArthur and Ott 1996). Silver sagebrush (*Artemisia cana*) is sparsely distributed throughout the northern Great Plains and Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) is common in south-central and south-east Montana, reaching its eastern limit in the extreme western Dakotas and the north-west corner of Nebraska. Wyoming big sagebrush is ubiquitous in eastern Wyoming, well beyond the zones considered sagebrush steppe by those who adopt the potential natural vegetation types of Küchler (Küchler 1964, 1970, Johnson 1978, Miller et al. 2011). The intermountain sagebrush steppe and Great Basin sagebrush ecosystem types are often subdivided into finer regional zones based on prevalent landforms (West 1983b, Miller and Eddleman 2000, Miller et al. 2011). Variously termed geographic subdivisions, physiographic provinces, floristic provinces, or ecoregions the subdivisions for the sagebrush steppe include the Columbia Basin, northern Great Basin, Snake River Plain, and Wyoming Basin. The Great Basin sagebrush is split into the southern Great Basin, and Colorado Plateau province. While differences among the biological communities of the physiographic provinces certainly exist, the similarities among and differences within these communities cannot be overstated. Elevational and edaphic properties of a site within a physiographic or ecological subdivision can have a greater influence on the vegetation of a site than the broader ecogeographic context (West 1983b).

The most prevalent climate of sagebrush steppe is similar to semiarid grassland climates which are temperate, semiarid, and continental whereas the more arid climate of Great Basin sagebrush results in a desert like ecosystem type. Mean annual temperatures in the sagebrush steppe range from 4 to 10° C and mean annual precipitation ranges from 20 to 40 cm (West 1998). The climate of the Great Basin is characterized by greater seasonal and diurnal temperature extremes and average annual precipitation from 15.8 cm to 41.9 cm. Cold winters in both sagebrush ecosystem types will generate snowpack and slow melting in the spring will transfer moisture to depth in the soil. Sagebrush steppe is generally more resilient, productive, and diverse than the Great Basin sagebrush type (West 1983c). Perennial grasses and forbs of both types must generally build above-ground biomass in the restricted window between spring and early summer when moisture and temperature are conducive to growth. The shrubs in these systems have long roots which extract moisture in lower soil layers throughout the warm season. Summer precipitation is rarely enough to maintain season-long growth of herbaceous plants (West 1988). Although there are subtle and important differences in soil water dynamics among the sagebrush ecosystem types, they share some consistent patterns. Spring recharge of soil layers and a dry period for top soil layers during the warm season occurs across the entire geographic range of big sagebrush ecosystems (Schlaepfer et al. 2012).

In addition to climatic extremes, shrub steppes are subject to high climatic variation which contributes to poor stability of these ecosystems under disturbance. Dominant organisms that inhabit sagebrush ecosystems are widely distributed but of low abundance which may be owing to the high spatial and temporal variability of environmental conditions (West 1998). The broad distribution of dominant species may represent a spatial bet hedging strategy because adverse conditions like fire or drought are unlikely to occur simultaneously across the entire species' range. The low abundance of dominant species is likely due to modest and unreliable resource availability.

Despite their superficially spartan appearance, sagebrush ecosystems support a wide array of life-forms. A moderate diversity of vascular plant species has been documented with 13 to 41 species per site in the course of 2 separate studies of multiple relatively pristine sites and 54 total species across all sites in another botanical study of intact sagebrush steppe sites (West 1998). Over 1000 species of insects have been found on some sites, 76 on sagebrush alone, and around 100 bird and 70 mammal species occur in sagebrush ecosystems (Baker et al. 1976, Wiens et al. 1991, West 1998). The greater sage-grouse (*Centrocercus urophasianus*), sagebrush sparrow (*Artemisiospiza nevadensis*), Brewer's sparrow (*Spizella breweri*), sage thrasher (*Oreoscoptes montanus*), pygmy rabbit (*Brachylagus idahoensis*), sagebrush vole (*Lemmiscus curtatus*), sagebrush lizard (*Sceloporus graciosus*), and pronghorn (*Antilocapra americana*) are all sagebrush obligate species that require sagebrush as a component of their habitat (Paige and Ritter 1999).

Greater Sage-Grouse Conservation

The greater sage-grouse (hereafter "sage-grouse"), is a gallinaceous bird that has become a focal species in the conservation effort to preserve imperiled sagebrush ecosystems and associated organisms. The range-wide distribution and abundance of sage-grouse populations has been declining since settlers first began exploiting the landscape starting in the 1850's. Population contractions have been attributed to hunting, habitat loss, habitat fragmentation, and habitat degradation (Braun 1998). By the early twentieth century, western rangelands had incurred substantial damage from overgrazing which continued until rangeland degradation became impossible to ignore (Griffiths 1902, Cottam 1947).

To assuage decades of irresponsible rangeland-resource exploitation the Taylor Grazing Act of 1934 facilitated more responsible grazing practices and an increased awareness of declining sage-grouse populations prompted research efforts and regulatory measures to bolster populations (Hornaday 1916, Patterson 1952). Subsequent conservation related laws include the Fish and Wildlife Act of 1934, Fish and Wildlife Act of 1956, Multiple-Use Sustained-Yield Act of 1960, National Wildlife Refuge Administration Act of 1966 (amended by the National Wildlife Refuge System Improvement Act of 1997), National Environmental Policy Act of 1969, Endangered Species Act of 1973, Sikes Act of 1974, Federal Land and Policy Management Act of 1976, and Forest and Rangeland Renewable Resources Research Act of 1978. The collective regulatory measures that have been enacted as law to govern public lands and natural resources must strike a balance between conservation and the needs of an increasing human population. Despite some documented sage-grouse population increases following the cessation of excessive grazing and hunting, sage-grouse are still an imperiled species of substantial conservation concern (Patterson 1952, Connelly and Braun 1997, Schroeder et al. 2004, Aldridge et al. 2008, Connelly et al. 2011c, Allred et al. 2015, Edmunds et al. 2018).

Past and Present Threats

Pervasive contemporary threats to sage-grouse are primarily due to human exploitation of the landscape which comes in the form of agricultural tilling, energy development, urban development, invasive plant introductions, and livestock grazing (Connelly et al. 2004, Connelly et al. 2011c, Doherty et al. 2011, Naugle et al. 2011, Walker and Naugle 2011, Wisdom et al.

2011). Processes such as wildfires and conifer encroachment interact with anthropogenic influences to further imperil sage-grouse and sagebrush ecosystems (Baker et al. 1976, D'Antonio 1992, Miller and Rose 1999, Rhodes et al. 2010, Baruch-Mordo et al. 2013). Climate change may amplify stressors and complicate interactions between stressors of sagebrush ecosystems and sage-grouse populations (Miller et al. 2011).

Stressors to sage-grouse populations are as diverse as the sagebrush ecosystems on which they depend. In the Great Plains and Wyoming Basin provinces previous and future potential energy development represents a substantial cause of current and imminent habitat degradation, disturbance, and loss (Doherty et al. 2011, Allred et al. 2015). In the north-west Great Plains and Columbia Basin substantial areas of sagebrush ecosystems have been lost or degraded due to agricultural tilling (Schroeder and Vander Haegen 2011). Cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherum caput-medusae*) invasion causes sagebrush ecosystem degradation particularly in the warmer lower elevation parts of the Intermountain West where these winter annual grasses have phenologies that exploit winter precipitation and avoid the warm dry summers that limit competition by native grasses and forbs (Davies et al. 2011, Miller et al. 2011). Encroachment into sagebrush ecosystems by conifers in higher elevation regions of the Intermountain West has been substantial after presettlement and has resulted in a loss of herbaceous understory and sagebrush canopy cover (Miller and Rose 1999, Coultrap et al. 2008, Miller et al. 2008, Davies et al. 2011). Each sage-grouse population across the current distribution must cope with novel combinations of stressors making it crucial to identify and understand local threats to which management actions may be tailored. Additionally, a deeper understanding of individual and population-level heterogeneity in sage-grouse behavior and population dynamics may result from basic research of novel populations.

Population- and Individual-Level Heterogeneity

The behavioral and demographic responses of grouse to environmental conditions can vary significantly across space and time (McNew et al. 2013, Fedy et al. 2014, Gregory and Beck 2014, Coates et al. 2017a, Smith et al. 2020). Spatially heterogenous behaviors or fitness may be due to differential habitat conditions interacting with phenotypic plasticity, genetic differences between populations or subpopulations, or even genotype × environment interactions with different degrees of plasticity in sage-grouse ecotypes. Classic common garden experiments by plant ecologists have established that environmental heterogeneity may produce local adaptations that result in species ecotypes or clines (Clausen et al. 1940, Clausen and Hiesey 1958, Aston and Bradshaw 1966, McNeilly and Antonovics 1968, Turkington 1989). Harsh and highly variable conditions across time and space may select for high genetic and ecotypic variability and phenotypic plasticity in species that occupy sagebrush ecosystems. After arrival of sagebrush progenitors to North America from Eurasia substantial speciation has resulted in 13 different *Artemisia* shrub species including 5-6 subspecies of the major species big sagebrush, *Artemisia tridentata* (McArthur 2005). Genetic differentiation in behavior and other adaptive traits among sage-grouse populations is probable given the extent and heterogeneity of sagebrush species and sagebrush ecosystems.

Landscape and Habitat Concepts

Given the broad geographic range of sage-grouse and sagebrush ecosystems and the complex influence of heterogeneous ecosystem structure and function on sage-grouse populations, it is helpful to conceptually frame some research approaches. Ecological sub-disciplines and associated hypotheses rely on simplifying assumptions and restricted viewpoints that require clarification to ensure consistent communication. Three schools of ecology are particularly relevant to the science of sage-grouse. Landscape ecology, wildlife ecology, and rangeland ecology are interrelated fields with distinct perspectives regarding wildlife habitat. Some principles used in landscape ecology and geography provide a sound basis for parsing the landscape into elements that may then be classified and grouped based on the aim of research.

Any attempt to classify a relatively homogeneous area of the landscape into a landscape element should recognize the hierarchical ordering of elements, the scale of observation, and the perspective taken when considering the interrelatedness of elements (Solon 2005). Landscape elements could include rocks, air, water, soil, vegetation, or animals. Landscape elements are hierarchically ordered; high-level elements influence lower-level elements and vise versa. Issues of scale pertain to the extent and resolution of measurement which can alter how we perceive ecosystem structures or processes. Scale of measurement can change the level of a process that we observe or may change what we consider a patch which is a spatially distinct and relatively homogenous assemblage of landscape elements (Turner et al. 2001, Rolstad 2005). The perspective taken when considering interrelatedness of landscape elements pertains to whether we are studying the structural or functional aspect of a landscape. If we are interested in ecological processes such as how sage-grouse are influenced by landscape elements we must first define the landscape in a structural sense by specifying relevant spatial patterns of landscape elements such as vegetation, terrain features, or environmental hazards. Once the structure of the landscape is operationally set then we may adopt a functional approach and analyze the interrelationships between sage-grouse biology and the landscape elements that we suspect compose sage-grouse habitat.

Habitat definitions and conceptualizations of habitat are disjoint and inconsistent (Krausman 1999). Ecologists, wildlife biologists, rangeland ecologists, and the general public often have disparate ideas about what habitat is, where it is, and how it relates to wildlife species. When referring to sagebrush-steppe habitat, or just sagebrush habitat, we are using the term habitat in the structural sense (Gaillard et al. 2010). Structural habitat can be considered a category of land cover such as forest habitat or grassland habitat, in which the term encompasses a broadly similar assemblage of biotic (plant communities) and abiotic (riparian, steppe, mountainous) landscape elements. The structural or habitat-type notion of habitat is often used by land managers, policy makers, and the general public because it is synonymous with a cover type or patch which is a convenient way to thematically inventory the composition of a landscape. The concept of range sites, ecological sites and habitat types have specific meanings to rangeland ecologists and have proven useful for classifying ecogeographic variability on rangelands using known associations between soils and climax plant communities (Shiflet 1975, Hironoka 1987, Brown 2010). Landscape features are synonymous with landscape elements and are characteristic features within a landscape such as sites, soils, patches, vegetation associations, or broader land cover classes (Hall 1987, Wickham et al. 2014). Landscape-feature classification schemes used by rangeland ecologists are based on soils or vegetation associations and are developed as a tool for evaluating the state and variable potential of an explicitly defined area with a mind to livestock production.

Structural habitat types (landscape features) are largely independent of the needs of a given species. By contrast, the term functional habitat originates from a niche-based definition of habitat as proposed by G. Evelyn Hutchinson (Colwell and Rangel 2009, Gaillard et al. 2010). 2010). In this theoretical realm habitat refers to all the resources and environmental factors that determine the presence, performance, and persistence of a species. Here the concept of the niche is inextricably bound to the species; the species' niche is its habitat. The conceptualization of functional habitat aligns with popular definitions of habitat used by wildlife biologists. That is, the physical space used by an animal and all the abiotic and biotic elements in that space are the animal’s habitat. Habitat use refers to the way an animal uses the abiotic and biotic elements (landscape conditions) in the areas that it inhabits (Krausman 1999, Morrison et al. 2006).

Sage-Grouse Ecology

Sage-grouse require large tracts of intact functional habitat which they use in a hierarchical and temporally variable manner to promote individual fitness in the face of variable nutritional needs driven by changing physiologies and substantial risk of predation (Bergerud and Gratson 1988). Vegetation provides food, cover from the weather, and cover from predators. Cover varies with seasonal plant growth, plant population dynamics, and disturbances such as fire, grazing by herbivores, and anthropogenic land use (e.g., tilling, energy development, or urbanization) (Moynahan et al. 2006, Dzialak et al. 2013b, Dahlgren et al. 2015, Gibson et al. 2017, Sianga et al. 2017, Donnelly et al. 2018). The inherent temporal and spatial variability that characterizes sagebrush ecosystems has likely selected for adaptive strategies in sage-grouse that maximize fitness across variable conditions (Miller and Eddleman 2000). Indeed, interseasonal movements of sage grouse are variable among populations and individuals and are influenced by behavioral traditions as well as environmental conditions (Tack et al. 2012, Fedy et al. 2014, Newton et al. 2017).

Sage-grouse have proven to be a species sensitive to anthropogenic disturbances exacted by an ever-increasing human population (Walker et al. 2007, Harju et al. 2010, Lebeau et al. 2014). Individual- and population-level sensitivity to anthropogenic habitat alteration may be due to population dynamics that require consistent production under a suite of landscape-element compositions and interrelationships as well as metapopulation dynamics that bolster local populations via emigration (Crist et al. 2015). The systematic depression of a vital rate such as nesting success due to loss and fragmentation of nesting habitat may narrow the margins of fecundity necessary for sustainable sage-grouse populations. Compared to other prairie-grouse, sage-grouse productivity and rates of population turnover are lower and recovery from population declines may be comparatively slow (Allen 1962, Connelly and Braun 1997, Connelly et al. 2011a). Population performance and component vital rates of sage-grouse have been correlated with climatic conditions (Holloran et al. 2005, Cornelis van Kooten et al. 2007, Coates et al. 2018), predator abundance (Mezquida et al. 2006, Bui et al. 2010, Dinkins et al. 2014), vegetation characteristics (Hagen et al. 2007, Smith et al. 2020), habitat degradation (Coates et al. 2017b, Prochazka et al. 2017), habitat fragmentation (Schroeder et al. 2004, Leu and Hanser 2011), disease (Naugle et al. 2004, Walker et al. 2004, Taylor et al. 2013), and disturbance by anthropogenic activity (Blickley et al. 2012, Taylor et al. 2013, Orning and Young 2016).

Variability among vital rates from different sage-grouse populations and differential vital rate influence on population dynamics underscores the need for population-specific research that links population ecology to habitat in such a way that adaptive monitoring and management of local populations is facilitated. It is important to evaluate critical vital rates such as nesting and female survival for local populations (Taylor et al. 2012, Dahlgren et al. 2016a, Coates et al. 2017a). For adaptive management to be effective, a process based ecological understanding that incorporates spatial and temporal variability will also be necessary (Boyd and Svejcar 2009). Local evaluations of population vital rates may uncover causes of variable population performance but estimates from short-term studies should be interpreted with caution (Dahlgren et al. 2015). When a preponderance of evidence identifies a link between landscape conditions and population performance then management prescriptions are more likely to succeed. For instance, productivity enhancements due to habitat improvements may buffer a population from periodically adverse conditions such as drought or local disease outbreaks. Alternatively, the effects of conservation efforts on population performance may be negated by additional stressors (Taylor et al. 2013). The first step in proper population management is to identify drivers of local population performance which are likely to include some combination of previously documented threats, novel threats, and limiting resources. However, correlates between fitness components and measurable landscape conditions may be of limited value if other influences such as sage-grouse movement and behavior are not accounted for (Piper 2011, Ryan et al. 2012, Sih 2013, Spiegel and Crofoot 2016, Spiegel et al. 2017).

Movement Ecology

Animal distributions arise from individual movements and movements are driven by resource provisioning, shelter seeking, interspecific and interspecific interaction, hard-wired behaviors, predator evasion, and breeding system requirements. Movement patterns play a primary role in individual fitness and population performance (Manly et al. 1993, Turchin 1998, Morales and Ellner 2002). A movement pattern may be risky in certain contexts and adaptive in other contexts and differences in characteristic movements and therefore space-use among individuals can have implications for survival and reproductive performance (Yoder et al. 2004, Prochazka et al. 2017). Analytical techniques that integrate movement patterns and landscape-condition context may provide a more process-based rendering of animal-habitat relationships. For instance, there may be an increase of risk or reward for an animal that periodically adjusts its home range versus one that maintains strong fidelity to a home range (Patten et al. 2011). The same can be said for the complete, partial or null migration of an individual or population of sage-grouse.

Technologies such as GPS transmitters can provide detailed information about animal movements. If patterns in movement data can be reliably attributed to behavioral states then behavior-specific inferences can be garnered from popular analytical techniques such as resource selection functions (Manly et al. 2002) and survival models (Hosmer et al. 2013). In fact, behavior-specific inferences are appearing with greater frequency in the literature due to methodological advances that combine GPS technology with increasingly detailed landscape-condition maps and progressive analytical methods (Gaillard et al. 2010, Dzialak et al. 2013a, Dzialak et al. 2015b, Prochazka et al. 2017). Movement-integrated research promises to parse out increasingly detailed explanations for observed habitat-response patterns for sage-grouse. For example, due to constraints imposed by traditional radiotelemetry monitoring few research efforts have investigated associations between nest survival and detailed movement properties of individual females. Additionally, quantitative descriptions of sage-grouse movements and related space use can inform management agendas by summarizing the timing and extent of landscape use by a population.

Habitat Responses

A comprehensive definition of sage-grouse functional habitat will necessitate the integration of habitat response characteristics at a diverse array of scales, ranging from the immediate vicinity of a grouse to the broader landscape and community scales with which individuals interface. A more mechanistic understanding of habitat selection and fitness gradients will eventually be required to move beyond the inferential limitations imposed by empirical habitat associations derived from phenomenological statistical models. Statistical models describe correlations between resource use or survival and landscape-condition patterns without specifying any cause-and-effect relationships. In contrast, mechanistic models such as spatially explicit population models (SEPM) describe intricate interrelationships between relevant synecological factors and individual life histories within a population. Mechanistic population models are an area of active research but are currently difficult to implement due to vast data requirements, a lack of software implementations, and limited application and assessment in applied settings. Realistic mechanistic models will require that landscape conditions of known importance (e.g., habitat) be dynamically mapped for multiple life history stages and behavior states at an appropriate grain- size; vital rates such as survival and fecundity must be considered in addition to animal movements in response to forage, cover, predation, and abiotic factors (Turner et al. 2001). Mechanistic population models could also incorporate immigration and emigration rates through explicit treatment of animal movement. Comprehensive modeling of functional habitat is not currently feasible but quantified landscape-condition associations can represent some component of the true N-dimensional functional habitat (Gaillard et al. 2010).

We can quantify patterns of disproportionate use of landscape conditions by animals to partially define functional habitat. If landscape conditions are differentially distributed between used areas and available areas then resource use is disproportionate to availability and selection for certain landscape-condition assemblages (habitat) is indicated (Manly et al. 2002, Johnson et al. 2006). Resource selection functions (RSFs) combined with resolute geospatial measures of structural habitat (i.e., landscape features or feature assemblages) offer a flexible modeling approach for estimating the relative probability that a landscape feature is used by an animal given that it is encountered (Johnson et al. 2006, Johnson and Seip 2008, Lele 2009). Relative probability of selection can also be conceptualized as differential space- or time-use intensity of different parcels of the landscape. Directly measuring and modeling use-intensity offers an alternative approach that makes less assumptions about the selection process of an animal (Marzluff et al. 2001, Millspaugh et al. 2006, Barraquand and Benhamou 2008).

An issue related to subjective availability sampling for RSFs is that inferences may be compromised due to incorrect assumptions about movement constraints on habitat availability when behavior modes are aggregated (Cooper and Millspaugh 2001b, Fedy et al. 2012, Northrup et al. 2013). Characterizations of movement behaviors (e.g., migration, learning excursions, foraging) can help account for behavior modes thereby reducing sampling noise introduced by mixing behaviors when conducting habitat response analyses. Entirely objective and biologically justified methods of defining availability for RSFs do not exist and it is currently not possible to fully account for behavior modes. That said, habitat-response research tools such as step-selection functions provide and increasingly mechanistic approach of specifying availability and assessing the importance of landscape conditions to animals (Beyer et al. 2010, Avgar et al. 2016). However, behavior modes are equally relevant to RSF and step-selection function best practices because availability may be different among behaviors but neither method automatically accounts for behavior.

Further research is needed to evaluate whether movements and resultant space use may be driven by behavioral factors other than reactive response to landscape conditions because movement is the mechanism by which differential landscape conditions are encountered. Selection of nest sites has been extensively researched for sage-grouse (Schroeder et al. 1999, Hagen et al. 2007, Connelly et al. 2011d, Smith et al. 2020) and females have been found to prefer sagebrush landcover types. However, at moderate to fine spatial scales preferred landscape conditions are far more equivocal across studies (Smith et al. 2020). Selection of a nest site by a sage-grouse may be influenced by movement constraints during the pre-laying period that are determined by prior knowledge of the nest-site and breeding-lek search area. Some of the selection process may be a function of dynamic response and some may be based on prior knowledge and habits. Ultimate choice of a nest site may be partly informed by vegetation structure at the nest and partly by the quality of the surrounding habitat for incubation break foraging. Evaluations of habitat use patterns at nest sites and at foraging sites may contribute to a more comprehensive understanding of nesting ecology though few researchers have formally evaluated incubation break habitat use (Hagen et al. 2007, Dzialak et al. 2013a) or movements of individual females during nesting.

Due to the extraordinary research efforts put forth to understand range-wide sage-grouse ecology we know that substantial population and individual level variation exists. Intra- and inter-population level variability of vital rates and habitat use could be due to genetic differences among populations and individuals, learned-behavioral differences, or spatially and temporally variable habitat quality and resource availability. Thus, habitat response associations inferred for one population may not be transferable to an alternate population due to fundamental differences between autecological factors and synecological interactions. Regionally specific observational research remains necessary to adequately inform management activities until more mechanistically based and thoroughly validated models of species minimum requirements are developed. Given the complexity of sagebrush ecosystems, prognostic models of population performance based on perturbation scenarios are unlikely to achieve range-wide accuracy in the foreseeable future. That said, limitations to modeling population performance based on the habitat responses of individual animals are being progressively overcome due to improvements in technology that allow vast quantities of data to be collected across multiple spatial and temporal process-levels and resolutions. Improved spatial generality of inferences may be gained by linking habitat response associations with specific behaviors or activity signatures (statistical behaviors) derived from movement data and expert knowledge.

CHAPTER 2

IDENTIFYING LOW-LEVEL BEHAVIOR MODES FOR SAGE-GROUSE USING MOVEMENT PROPERTIES AND STATISTICAL CLUSTERING

Contribution of Authors and Co-Authors

Manuscript in Chapter 2

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Contributions: Robert helped conceive and plan the study, interpret results, and write the manuscript. Robert performed all the analysis. All authors edited the manuscript. All authors read and approved the final manuscript.

Co-Author: Lance B. McNew

Contributions: Lance helped conceive and plan the study, interpret results, and write the manuscript. All authors edited the manuscript. All authors read and approved the final manuscript.

CHAPTER 2

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CHAPTER TWO

IDENTIFYING LOW-LEVEL BEHAVIOR MODES FOR SAGE-GROUSE USING MOVEMENT PROPERTIES AND STATISTICAL CLUSTERING

Background

Movement properties can be used to identify behaviors that are important for understanding the causes of differential habitat use, survival, and reproduction of animals. GPS tracking technology provides detailed movement data that has been used to improve understanding of both obscure and well-known species. The greater sage-grouse (*Centrocercus urophasianus*; hereafter “sage-grouse”) is a gallinaceous bird that has been well studied but is still the focus of substantial conservation concern despite a herculean effort in science-based conservation research and management. Over the course of a year sage-grouse phenology rotates through nesting, brooding, late-summer ranging, migration, and winter ranging. Sage-grouse phenology involves variation in high-level movement modes such as winter ranging or incubating movement behaviors overlying lower-level movements such as transit, searching, foraging, roosting, or predator evasion.

Sage-grouse use landscapes variably across time and space in relation to phenological stage and landscape conditions (Wallestad 1971, Connelly et al. 1988, Walker et al. 2016, Smith et al. 2020). Assessment of population responses to seasonally variable habitats has benefited from research that focuses on the hierarchical and multi-scale nature of both female resource selection and demographic rates during seasonal periods (Doherty et al. 2010, Dzialak et al. 2011, Aldridge et al. 2012, Blomberg et al. 2013, Walker et al. 2016, Coates et al. 2020).

However, drivers of population performance are typically inferred from the evaluation of population-level associations among vital rates and exogenous landscape conditions without regard for individual- or population-level behaviors (Lima and Zollner 1996).

In addition to accounting for multiple spatial scales and seasonal periods, deeper behavioral contexts of habitat responses are also important for valid inference (Owen-Smith et al. 2010). In fact, behavior modes may be largely responsible for the multiscale nature of animal space use (Morales and Ellner 2002, Schick et al. 2008, Van Moorter et al. 2016). Disparate behavior types may confound the interpretation of space-use patterns and related habitat responses if pooled within analyses (Cooper and Millspaugh 2001a, Erickson et al. 2001, Morrison et al. 2006, Abrahms et al. 2016). For instance, associations between home range size and landscape conditions may be confounded by the conflation of individuals that shift as opposed to dilate and contract their home range (searching vs. sedentary types, Mueller and Fagan (2008)).

Understanding movement modes will improve our understanding of interactions between sage-grouse adaptive strategies and habitat conditions. Sage-grouse behavior modes represent endogenous states that likely cause variability in grouse versus habitat relationships. The isolation of endogenous (e.g., sex, age, behavior type) versus exogenous (e.g., weather, landscape patch characteristics, predation risk) causes of variability in the performance of sage-grouse (Coates et al. 2018) will promote more mechanistic and accurate modeling of sage-grouse populations and may therefore improve the efficacy of management prescriptions (Ford 1999, Heglund 2002). When habitat responses such as landscape-condition use or female survival can be attributed to specific movement behaviors then spatial generality and specificity of estimated habitat-performance relationships may improve (Gaillard et al. 2010, Dzialak et al. 2013a, Dzialak et al. 2015a).

Accounting for behaviors in wildlife-environment relationships first requires the identification of behavior modes from movement patterns. Some female sage-grouse behavior modes such as incubating and brood-rearing are readily determined via radio tracking (Wallestad 1971, Wallestad and Pyrah 1974, Dzialak et al. 2011), have been studied extensively (Dahlgren et al. 2016a, Smith et al. 2020), and can substantially influence population dynamics (Taylor et al. 2012, Dahlgren et al. 2016a). Migration and the associated winter-ranging mode are examples of sage-grouse behaviors that have not been as extensively studied but are also important for understanding population performance (Taylor et al. 2012, Dinkins et al. 2017, Newton et al. 2017). Incubation and brood-rearing modes can be identified using radiotracking and direct observation while migration, exploratory movements, and laying behavior can be inferred from remote radiotracking data (Bunnefeld et al. 2011, Dzialak et al. 2011, Edelhoff et al. 2016, Gelling et al. 2022). All behaviors that sage-grouse exhibit may provide insights into their ecology so any that can be identified are worth investigating.

Researchers have successfully identified behavior modes using multivariate partitioning of movement properties (Van Moorter et al. 2010, Abrahms et al. 2017), model-driven analysis of single properties (Owen-Smith et al. 2010, Bunnefeld et al. 2011, Gurarie et al. 2016, Hooten et al. 2017), and ad-hoc criteria with single properties (Dzialak et al. 2015a, Gelling et al. 2022). Many movement properties are useful for behavior-mode identification (Edelhoff et al. 2016, Gurarie et al. 2016, Abrahms et al. 2017) and can be calculated with existing software (Calenge et al. 2009, Bracis et al. 2018, Lyons et al. 2019).

Movement modes identified from individual-level movement properties are most likely to represent low-level movements (e.g., foraging, loafing, roosting) because high-level movements such as brood-rearing are complex amalgamations of numerous ecological factors (e.g., genetic traits, learning, phenology, habitat response). Low-level movement mode identification is often limited to taxis (i.e., movements in response to a stimulus) and area restricted search behavior (two-state models) which are commonly conceptualized as resident vs. migratory, or inter- and intra-patch movements (Patterson et al. 2009, Dzialak et al. 2015a, McClintock et al. 2017, Seidel et al. 2018). High-level movement mode classification is more challenging because these modes are not adequately described by one or two movement properties which increases difficulty of identification and interpretation. However, high-level modes can be inferred from direct observation, phenological context, and association with low-level movement modes.

Objectives

Our goals were to 1) identify high-level movement modes using telemetry observation and field checks, 2) classify low-level inferred movement modes for sage-grouse (e.g., intensive-use foraging, area restricted search, exploratory), and 3) evaluate the biological interpretability and potential utility of the inferred modes for improving inferences from telemetry-based wildlife data. We evaluated inferred modes relative to high-level modes, relative to characteristic movement patterns, and relative to landscape conditions experienced by females during each inferred mode.

Study Area

Our study area was principally on a 425,000-ha area in southern Valley County in north-central Montana, USA (47.66258 N to 48.44968 N, 106.43546 W to 107.44770 W). The area was within Glaciated Northern Grasslands and North Central Highlands as described by (Cleland et al. 1997, McNab et al. 2007), and within the sage-grouse Great Plains Management Zone (Management Zone 1) which corresponds to the Silver Sagebrush Province (Connelly et al. 2004, Stiver et al. 2006). Land cover in the area consisted of approximately 49% big sagebrush steppe, 20% Great Plains mixed-grass prairie, 8% cultivated crops, 6% mat saltbush shrubland, 2% Great Plains riparian, and 2% Great Plains woodland savanna (Anderson et al. 1976, Comer et al. 2003). Additional limited land cover types included greasewood flats, shale badlands, and Great Plains wooded draws and ravines (Anderson et al. 1976, Comer et al. 2003) The area was characterized by high annual variation in average monthly temperature (-10.1 °C to 21.7 °C) and low mean annual precipitation (29.6 cm), with over half occurring May – July (Arguez et al. 2010). Approximately 75% of the study area was in public ownership, managed predominately by the U.S. Bureau of Land Management (BLM), as well as the U.S. Fish and Wildlife Service (USFWS, Charles M. Russell National Wildlife Refuge [CMR]), and the State of Montana. The area was situated just below the northernmost extent of the Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) distribution in Montana with silver sagebrush (*Artemisia cana*) becoming the only woody *Artemisia* species occurring farther north. The area exhibited substantial overlap between a mixed-grass prairie ecosystem and a sagebrush steppe ecosystem which makes it unique in comparison to many other sage-grouse habitats (Dinsmore et al. 2002, Moynahan et al. 2007).

Basic information on the ecology of this sage-grouse population is lacking. The study population represents a core component of the broader northern Montana population (NMP) distributed throughout north-central Montana, southeastern Alberta and southwestern

Saskatchewan (Garton et al. 2011, USFWS 2013). Minimum male counts at leks within the NMP were reported to be approximately 2,700 males and the population is thought to be one of the few remaining stable populations of sage-grouse (Garton et al. 2011). The southern segment of the NMP lies below the Milk River and was designated a Priority Area for Conservation (PAC [corresponds to BLM Priority Habitat Management Area]) which was key habitat identified by state or BLM conservation planning efforts (USFWS 2013).

Methods

Sage-grouse Captures

During April–May, 2018–2019, we captured 89 (48 in 2018, 41 in 2019) female sage-grouse using spotlighting techniques and hoop nets (Giesen et al. 1982, Wakkinen et al. 1992). We attempted a representative sample by spreading captures around 3 separate watersheds in our study area. Upon capture we banded females with uniquely-numbered leg bands. We aged females as adult or yearling by examining the appearance of primary feathers 9 and 10 (Braun and Schroeder 2015). We attached a VHF-equipped 22-g solar powered Global Positioning System (GPS) Platform Transmitter Terminal (PTT; model GT-22GS-GPS, GeoTrak, Inc., Apex, NC, USA) to each of 86 birds (we had 86 PTTs) using a rump-mounted harness (Rappole 1991). PTTs were programmed to collect 4–10 locations every day and upload data every 1.5–3.0 days to the Argos satellite system. PTT performance was specified separately for different seasons and the 2018 programming was slightly adjusted for 2019 based on observed PTT performance. The most aggressive programming for a season was 11 March – 1 September where PTTs obtained up to 10 fixes every day and uploaded data to the Argos system approximately every two days. All animal handing was approved under Montana State University's Institutional Animal Care and Use Committee (protocol # 2017-57).

Sage-grouse Monitoring

The PTTs had an approximate 3-year lifespan and movement data from equipped sage-grouse was recorded until female mortality or loss of a PTT. During the breeding seasons of 2018, 2019 and 2020, females were monitored by downloading GPS fixes and other PTT sensor data from Argos system servers every 3–5 days. During the breeding season of 2021 females were monitored monthly because fewer project resources were available. We used multiple lines of evidence to infer female status. Localization of a PTT indicated either a nesting female, a dead female, or a dropped PTT. The PTTs were equipped with an activity sensor which indicated if the PTT was experiencing motion; static activity sensor readings indicated a mortality or dropped PTT. The visitation of nest sites can lead to observer-induced bias in vital rate estimates (Gibson et al. 2015), therefore we only visited localization sites if a mortality was suspected. In most cases we could differentiate mortalities from nests by reviewing the GPS fix data (Coates and Delehanty 2008, Dzialak et al. 2011). If a mortality was indicated, we verified this with a field visit and recorded the condition of carcass remains including evidence of predation (Blomberg et al. 2013). We estimated the date of incubation initiation for each confirmed nest by reviewing the GPS data. Nest fate was verified in the field when a female had moved off the nest for ≥ 3 days. Nests that failed just prior to incubation were verified in the field if ≥ 2 locations accrued in the same spot due to periodic visits by a female. After nest abandonment, we located nests and recorded evidence regarding nest fate. Hatching was indicated by eggs with detached membranes and eggshells that were consistent with being pipped by chicks (Rearden 1951). We considered a nest successful if we found evidence that ≥ 1 egg had hatched. Nest monitoring allowed us to identify two nesting behaviors for all nests identified: laying and incubating. We labeled points along a female's trajectory as laying if they preceded incubation initiation by ≤ 7 days. Sage-grouse lay an average of ~2 eggs/3 days and average clutch sizes are ~8 eggs (Wallestad 1971, Schroeder et al. 1999). Our specification of 7 days is conservative and ensures that females with small clutches are not erroneously considered laying.

In 2018 and 2019, we monitored females with successful nests and conducted pre-dawn brood counts to ascertain if a female was with a brood. Females with broods were located with recent PTT locations and then Yagi antennas and receivers. All VHF transmitters deployed in 2018 had failed by April 2019 so no brood checks were conducted on females outfitted with PTTs in 2018. Likewise, all VHF transmitters deployed in 2019 had failed by breeding season 2020 so no brood checks took place in 2020 or 2021. Brood checks were conducted at 2-week intervals after hatch date for up to 6 weeks (3 checks). When no chicks were detected, we re-conducted the check within 5 days if the female exhibited defensive behavior consistent with brooding. If females immediately flushed out of the vicinity and no chicks could be located the brood was recorded as unsuccessful. Brood checks were not performed on exact 2-week intervals due to logistical constraints such as weather delays. We labeled points along a female's trajectory as brood-rearing for periods when brood status was known. In cases where females had successful nests, but brood status could not be checked, we labeled all points as potential brood rearing for ≤ 14 days after hatch. Our specification of 14 days was based on our observation of brood survival and our expectation that many of the females with hatched nests would have broods for ≥ 14 days after hatch.

We ultimately gave behavioral labels to all points in a female's trajectory using a combination of PTT data interpretation, field checks, and migration analysis. We identified the following known-behavior modes: laying, incubation, brood, potential brood, exploratory, and winter ranging. See Appendix B for background, methods, and results describing migration research we conducted to delineate winter-range behavior modes using data from 2018–2020. We used identical migration analyses to delineate winter-range behavior during 2020–2022.

Movement Properties

We chose 7 movement properties that we expected would be useful for discriminating among movement modes, such as area-restricted search, transit, or exploratory movements. Our 7 space- and time-use properties (movement properties) were derived from 4 common movement properties: short-term home range area, total residence time, site revisitation, and time-to-return. We calculated variability of residence time and time-to-return and calculated revisitation at two scales which resulted in 7 variables from 4 base movement properties.

Equal-interval sampling is recommended to reduce unbalanced sampling bias for calculating many movement properties (Calenge et al. 2009, Bracis et al. 2018, Lyons et al. 2019). Therefore, we calculated movement properties after subsetting our relocation data to a 6-hour equal-interval temporal resolution. We calculated residence time and revisits at a 100-m patch scale and short-term home range scale which captured fine-scale and coarse-scale space- and time-use for sage-grouse because movement processes can be spatial-scale dependent (Van Moorter et al. 2013, Van Moorter et al. 2016). We calculated the coefficient of variation (CV) of residence time and time-to-return at the 500-m patch scale to capture variation in the periodicity of time-use at a scale intermediate to our 100-m patch and home-range scale. We considered movement ecology of sage-grouse, collinearity among scales, computational feasibility, and GIS-based visual evaluation of different scale options when making movement property selections. Female sage-grouse that had been monitored for fewer than 30 days were excluded from analyses because of limited relocation histories from which to derive the following space- and time-use movement properties:

1. *Short-term home range area* (h-A). Short-term home range area (i.e., hull area) was calculated as the area of each hull polygon derived as a time-local convex hull (short-term home range); hull area provides a geometric delineation of space use and is analogous to a home-range area calculated for brief periods (Lyons et al. 2013, Lyons et al. 2019).
2. *Hull revisits* (h-RV). Hull revisits was calculated as the number of revisits to each short-term home range (Lyons et al. 2013, Lyons et al. 2019). We calculated visitation rate as the number of occurrences in a hull separated by a time gap ≥ 1 week.
3. *Hull duration* (h-D). Hull duration was calculated as the average number of points for visits to each short-term home range; hull duration provides an index to the typical duration of visits to each short-term home range and is therefore similar to mean residence time (Barraquand and Benhamou 2008, Lyons et al. 2019).
4. *Total residence time* (RT). Residence time was calculated as the mean summed duration of all path segments within each 100-m virtual circle (patch) positioned on points used to construct each short-term home range (Bracis et al. 2018, Lyons et al.

2019). Residence time quantified the average total time spent in the vicinity of each point within a short-term home range.

5. *Revisitation* (RV). Revisitation was calculated as the mean of the total number of path segments that intersected each 100-m radius virtual circle (patches) positioned on trajectory points used to construct each short-term home range (Bracis et al. 2018, Lyons et al. 2019).
6. *Variability of time-to-return* (TtoR-CV). Variability of time-to-return was calculated as the coefficient of variation of 500-m time-to-return among the sets of patches created from points used to construct each short-term home range (Bracis et al. 2018, Lyons et al. 2019).
7. *Variability of residence time* (RT-CV). Variability of residence time was calculated as the coefficient of variation of 500-m residence time among the sets of patches created from points used to construct each short-term home range (Bracis et al. 2018, Lyons et al. 2019).

All movement properties were calculated using the tlocoh, recurse, and purr packages (Bracis et al. 2018, Lyons et al. 2019, Henry and Wickham 2020) in R (R Development Core Team 2013). Appendix A describes the tuning parameters that we used to construct time-local convex hulls. Calculation of revisits (RV) and time-to-return (TtoR) are influenced by a time-threshold parameter that defines the time elapsed before a movement outside of a patch is considered a separate visit. We set the time-threshold parameter to 0 to capture recursive movements to nest-sites in addition to broader-scale recursions.

Cluster Analysis

We partitioned 110,024 instances (i.e., objects, hulls, short-term home ranges) of our 7 sage-grouse movement properties (i.e., descriptors variables) into distinct movement modes (groups of similar home ranges) using three clustering methods: 1) k-means partitioning, 2) partitioning around medoids (PAM), and 3) hierarchical clustering (Legendre and Legendre 2012, Borcard et al. 2018). Transformation to attain approximate normality of variables is recommended for k-means and PAM clustering and standardization is recommended whenever Euclidean distances are used to compute similarity properties for clustering (Borcard et al. 2018). Therefore, we normalized all movement property variables using transformations (Table 1) and standardized all variables to zero mean and unit variance using the function decostand of R-package vegan (Oksanen et al. 2019).

K-means clustering We performed k-means analysis (Lance and Williams 1967, MacQueen 1967, Legendre and Legendre 2012) using the kmeans function of the R-package cluster (Maechler et al. 2019). A major limitation of k-means analysis is that *k* number of clusters must be pre-specified by the user. Therefore, we examined the cluster quality of a range of *k* values using function cascadeKM of the R-package vegan and function clusGap of R-package cluster (Maechler et al. 2019, Oksanen et al. 2019). We used the Calinski index, simple structure index, and gap statistic to compare cluster quality and select the number of clusters (Rousseeuw 1987, Kaufman and Rousseeuw 2009, Borcard et al. 2018). We also used function clValid of R-package clValid on a random subset (20,000 observations [reduced computation time]) of our total dataset to examine internal validation and stability validation statistics for a range of *k* values (Brock et al. 2008).

Partitioning around medoids We performed partitioning around medoids (Kaufman and Rousseeuw 2009) using function clara (Clustering Large Applications [PAM for many observations]) of R-package cluster and compared cluster quality with gap statistics calculated using function clusGap. We also used function clValid of R-package clValid on a random subset (20,000 observations) of our total dataset to examine internal validation and stability validation statistics for a range of *k* values (Brock et al. 2008).

Hierarchical clustering Following Husson et al. (2011) we performed hierarchical clustering in two steps (mixed algorithm) because the number of hull instances was too large for available agglomerative clustering algorithms. We first performed k-means analysis using function kmeans (centers = 500) of R-package cluster. We then performed agglomerative hierarchical clustering (Legendre and Legendre 2012) on the 500 centroids using Ward's minimum variance methods (Ward 1963) and R function HCPC of package FactoMineR (method = "ward"). We used the elbow method, silhouette method, and gap statistic to compare cluster quality and select the number of clusters (Rousseeuw 1987, Le et al. 2008, Kaufman and Rousseeuw 2009, Husson et al. 2011). We also used function clValid of R-package clValid on a random subset (20,000 observations) of our total dataset to examine internal validation and stability validation statistics for a range of *k* values (Brock et al. 2008).

Ecological validation After examining the cluster quality, internal validation, and stability validation statistics from the k-means, PAM, and Ward-hierarchical methods we chose a single number of clusters for each method. To further validate and inform our choice of the k-means-based or PAM-based clustering scheme, we created figures illustrating the chosen clustering results relative to the movement properties and known-behavior modes. Combining movement property, inferred-behavior mode, and known-behavior mode visualizations into a comparative multi-panel visualization greatly facilitated interpretation. The first panel employed principal component analysis and illustrated how laying, incubation, brood, potential brood, exploratory, and winter ranging modes correspond to the movement properties. Panel two and four illustrated the clustering results as clouds of objects (hull instances) and group centroids in the plane of the first two principal components derived from the movement properties. The third panel illustrated whether a given movement mode had a significantly ($p \leq 0.05$) higher or lower mean than the overall mean of each of the 7 movement properties (Le et al. 2008). Our k-means and PAM cluster-interpretation plot was created using R packages FactoMineR, factoextra, cluster, vegan, and ggpubr (Le et al. 2008, Maechler et al. 2019, Oksanen et al. 2019).

We further evaluated the Ward-hierarchical clustering scheme using a 3-panel figure illustrating the chosen clusters relative to the movement properties. The first panel employed principal component analysis and illustrated how the 500 cluster centroids were dispersed relative to the movement properties. The second panel simultaneously illustrated the clustering results as a dendrogram (Zuur et al. 2007, Husson et al. 2011, Legendre and Legendre 2012, Borcard et al. 2018) and the cloud of objects (hull instances) in the plane of the first two principal components derived from the movement properties. The third panel illustrated whether a given movement mode had a significantly higher or lower mean than the overall mean of each of the 7-movement properties (Le et al. 2008). The Ward cluster-interpretation plot was created using R packages FactoMineR, factoextra, vegan, grid, and gridExtra (Le et al. 2008, Maechler et al. 2019, Oksanen et al. 2019).

We tested for statistically significant correspondence among levels of the clustering results and known behavior modes using the test.a function provided in Legendre and Legendre (2012), book section 4.10.3. We further examined the association among levels of the clustering results and levels of the high-level modes using Goodman and Kruskal's tau (τ) measure (Pearson 2018).

All our validation methods led us to choose the PAM 8-mode result (PAM-8) as the final clustering scheme. Our final choice was also informed by how we intended to use the clusters in further sage-grouse ecology research and by spatial validation of clusters GIS-mapped relative to sage-grouse movement patterns. We were particularly interested in labeling exploratory or transit movements in our dataset; factor-level 5 of the PAM-8 result appeared to adequately correspond to exploratory or transit movements.

To facilitate interpretation of our final clustering scheme we evaluated correspondence between the PAM-8 clusters and 18 landscape-condition variables (Table 1, Appendix C) standardized to 0 mean and unit variance using a multivariate regression tree (MRT; De'ath (2002)) which partitioned 18 landscape condition variables under control of the PAM-8 inferred movement modes. We included the following landscape conditions that we expected may be related to sage-grouse movements in our study area: daily temperature, daylength, distance from first nest, barren cover, landscape-object height, variability of landscape-object height, radius of variance of landscape-object height, sagebrush cover, variability of sagebrush cover, vegetation biomass, variability of vegetation biomass, radius of variance of vegetation biomass, fine-scale landscape ruggedness derived from LiDAR data, normalized height, variability of normalized height, proximity of water bodies, variability of highly rugged areas derived from digital elevation model data, variability of topographic wetness (Table 1, Appendix C). Our MRT allowed us to explore, test, and describe relationships between landscape conditions and the PAM-8 movement modes. We used statistically significant ($p \leq 0.05$) relationships between our landscape condition variables and our 8 statistically inferred movement modes to gauge biological relevance of the movement modes. MRTs can be viewed and used as a clustering technique as well as a constrained multivariate regression technique (De'ath 2002). Therefore, in addition to explaining variation in PAM-8 modes as a function of landscape conditions, our MRT also defined landscape condition assemblages unique to certain combinations of PAM-8 movement modes. In other words, our MRT provided a framework for aggregating and interpreting clustering results. Aggregation of clustering categories is useful when the statistically optimal number of cluster categories is too many given research objectives. For example, a wildlife researcher might identify numerous land cover classes by clustering multispectral satellite data but then use the MRT approach with ancillary spatial data to reduce the number of classes for subsequent research of wildlife-habitat relationships. We used the tree structure of the MRT to identify landscape conditions which discriminated the split at each node, and we used the cluster structure to identify landscape conditions that were indicative of each terminal node (i.e., tree leaf, cluster). Note that our landscape condition variables were standardized so the usual interpretation of indicator values based on species frequency and abundance (De'ath 2002) is altered. Indicator values for our data are interpreted as variables that have high within-cluster (terminal node) averages compared with overall averages.

Results

Optimal Number of Clusters

All three clustering methods exhibited variability in the optimal number of clusters indicated by each cluster-quality index. Optimal number of clusters for the k-means method was indicated to be 6, 7, and 14 using the Calinski, simple structure index, and gap statistic, respectively (Appendix D, Figure 25). A transition from steep decline to a gentle slope indicates the optimal clusters based on the Calinski method. Optimal number for the PAM method was indicated to be 8 based on the gap statistic (Appendix D, Figure 26) and optimal number for Ward hierarchical was 4, 2, and 9 using the elbow, silhouette, and gap statistic (Appendix D, Figure 27)). Internal validation statistics indicated lowest connectivity (lower is better) using 2 clusters for all three methods (Appendix D, Figure 28). The Silhouette index (higher is better) indicated that for all three methods 2 clusters were optimal (Appendix D, Figure 28). The Dunn index indicated that 20 k-means, 13 PAM, and 7 Ward-hierarchical clusters might be preferred (Appendix D, Figure 28). The stability validation statistics indicated that either 2 or 20 clusters were preferred with k-means and PAM performing similarly and outperforming the Ward-hierarchical method (Appendix D, Figure 29).

Variability in number of clusters identified by each clustering method and cluster-quality index combination indicated that choice of clustering method and evaluation method both introduce subjectivity into the number and nature of clusters identified. High variability in the optimal number of clusters identified also indicated a weak clustering structure in the data. At the 6-hour temporal resolution of our data, female sage-grouse movement properties exhibited a mostly continuous gradient. Nevertheless, our multi-method approach indicated that the preferred number of clusters was > 1 and ≤ 20. We chose 8 PAM clusters (inferred movement modes) as the final method and cluster number combination because it provided a balance between having too many clusters to interpret and too few to be useful for differentiating behaviors. Cluster quality, internal validation, and stability statistics are useful for evaluating potential preferred number of clusters, but interpretability relative to ecological variables is more important.

Cluster Levels vs. Movement Properties

Patterns of clustering relative to movement properties was similar among the k-means, PAM and Ward hierarchical methods as indicated by cluster-membership point cloud plots (Appendix D, Figures 30–32). The dispersion of hull instances and cluster centers along the PC1 axis was primarily due to revisits and residence time at one extreme and hull area, variability in residence time and variability in time-to-return at the other (Appendix D, Figures 30–32). Hull instances and cluster centers along the PC2 axis were organized by hull revisits and hull duration which were negatively correlated (Appendix D, Figures 30–32). Therefore, behavior-mode clusters were mainly organized along a gradient described by high fine-scale time-use intensity at one end and large hull areas and high moderate-scale variability in periodicity of time-use at the other. Clusters were secondarily organized along a gradient contrasting hull revisits with average duration of visits to hulls.

Our principal component analysis triplots further demonstrated that clusters can be described based on extremes along the various gradients of the movement properties (Appendix D, Figures 30–32). For instance, PAM cluster 6 from the 8-mode clustering was high in revisits, residence time and hull duration relative to the respective means of each movement property using the total dataset. In contrast, PAM cluster 5 was high in hull area, variability in residence time and variability in time-to-return relative to the overall means. Mode 3 was similar to mode 6 but lower than 6 in revisits and residence time. Mode 4 was similar to mode 8 but lower than 8 in revisits and residence time, and mode 1 was close to overall means for all movement properties. Mode 7 had relatively higher hull revisits, and mode 2 had relatively lower hull revisits and higher area compared to overall means.

Cluster-by-Behavior Co-occurrence

Presence-absence co-occurrence tests indicated that 31, 19, and 7 cluster by known-behavior pairs exhibited significant ($\alpha = 0.05$) co-occurrence for k-means, PAM, and Ward hierarchical methods, respectively (Appendix D, Figure 33). The Goodman Kruskal tau measure indicated differential correspondence between the known behavior modes and the statistically inferred modes from each method (Appendix D, Figure 34). The k-means 14 mode classification was the most predictive ($\tau = 0.21$) of the 7 known behavior modes, but the PAM 8 classification was a close second (0.17). Furthermore, the known behavior categories were similarly predictive of the PAM-8 classification ($\tau = 0.06$) compared with the k-means-14 classification ($\tau = 0.05$). The Ward-hierarchical 2-mode classification was weakly predictive ($\tau = 0.7$) of the known modes but the known modes were somewhat predictive ($\tau = 0.23$) of the 2 Ward-hierarchical modes.

Cluster Levels vs. Environmental Variables

Our multivariate regression tree analysis resulted in a 3-leaf tree that explained 6.09% of the variability in the 18 landscape-condition variables. The first node explained 4.25% of the variation and the second node explained 1.84% (Figure 1). The first split was defined by a distinction between landscape conditions associated with PAM-8 inferred movement modes 3, 4, 6, and 8 versus 1, 2, 5, and 7. The second split was defined by the difference between landscape conditions associated with mode 6 versus 3, 4, and 8. The discriminant landscape conditions for the first node were daylength, distance to first nest, and mean daily temperature. Modes 3, 4, 6, and 8 were associated with elevated values of daylength and temperature and modes 1, 2, 5, and 7 were associated with elevated values of distance to first nest. The discriminate variables for the second split were variability in vegetation height, variability in sagebrush cover, variability in topographic wetness index, variability in landscape ruggedness, and variability in normalized height. The final partition into 3 leafs (i.e., clusters, terminal nodes) was associated with 18 indicator variables that had statistically significant elevated values for certain clusters (Table 2). Daylength was the top indicator value for the PAM8 = 6 cluster, mean daily temperature was the top indicator value for the PAM8 = 3,4,8 cluster and distance from first nest was the top indicator value for the PAM8 = 1,2,5,7 cluster.

Discussion

Space and resource use by animals is often investigated on seasonal time scales by quantifying home range properties in geographic space or resource selection in environmental space (Boyce and McDonald 1999, Manly et al. 2002, Boyce 2006, Kie et al. 2010, Walter et al. 2011, Powell and Mitchell 2012, Northrup et al. 2013). Historically, studies evaluating resource selection of sage-grouse do not identify or incorporate well-resolved behaviors or activity patterns of individuals (Lima and Zollner 1996, Kirol et al. 2012, Roever et al. 2014, Walker et al. 2016, Coates et al. 2020). Using seasons as grouping levels or subsetting data with blanket seasonal intervals has obvious merit for constraining the spatiotemporal context of space-use or habitat selection research but represents a simplistic and subjective study design.

Arbitrary, ill-conceived, or omitted groupings of any sort may result in inferential issues such as confounding, ecological fallacy, casual ambiguity, or otherwise deficient analyses where the ecological signals being investigated are not properly analyzed, resulting in erroneous interpretation (Gelfand et al. 2010, Plant 2012). Sage-grouse and other animals exhibit differential movement behaviors and habitat selection within seasonal periods (Fedy et al. 2012, Dzialak et al. 2015a, Abrahms et al. 2016, Walker et al. 2016, Bakner et al. 2019) which may represent separate statistical populations of habitat selection events. Estimating single population parameters from a mixture of multiple distinct statistical populations makes interpretation difficult or nonsensical. Habitat selection analyses that use resource selection probability functions (Manly et al. 2002, Lele 2009) may be particularly sensitive to this issue due to the importance of the comparison between use and unused or available distributions in environmental space. Ignoring behavior states may muddle the selection process if animal preference or habitat-element availability are different among states (Bastille-Rousseau et al. 2010, Van Moorter et al. 2016). An example would be the pooling of 2 behaviors with different use and availability processes where the use samples are pooled, and availability is sampled using a single blanket definition. Brooding sage-grouse in our study area were observed using moderate shrub cover on hillsides near the tops of hills or mid-slopes for roosting but during the day would forage or loaf in low-lying areas that generally had denser shrub or herbaceous cover. Conflating roosting (sparser cover than available) and loafing (denser cover than available) samples could ‘average out’ the 2 distinct use-intensity signals.

Seasonal delineations of analysis windows attempt to account for time varying behavioral states and dynamic habitat-element availability (Morrison et al. 2006, Birkett et al. 2012) which are integrally linked (Van Moorter et al. 2016) and can corrode inferences when not properly accounted for (Martin et al. 2008, Forester et al. 2009, Dzialak et al. 2013a, Roever et al. 2014, Dzialak et al. 2015a, Bakner et al. 2019). For instance, it does not make sense to combine summer and winter spatial-location data in a resource selection analysis without specifying a seasonal grouping structure. It is likewise poor practice to combine loafing, foraging and exploratory locations for sage-grouse without strong evidence that the mixing of behavior states is irrelevant to a given question or analysis. Differences in movement patterns among behavior types have implications for pooling data across types in research focused on evaluating wildlife-habitat relationships (Jachowski et al. 2013, Roever et al. 2014, Dzialak et al. 2015a, Abrahms et al. 2016, van Toor et al. 2016, Gelling et al. 2022). Some effort has been made to address behavior specificity of habitat responses for sage-grouse, however, even with detailed movement data researchers rely on simple and subjective ad-hoc criteria to define behavior modes such as within and between patch movement (low-level modes) or broods 0-2 weeks and broods 3-5 weeks (high-level modes) (Dzialak et al. 2015a, Gelling et al. 2022). Repeatable and quantitatively rigorous methods are needed to understand, objectively identify, and delineate behavior modes.

Cluster Analysis

Identification of biologically useful categories from multivariate datasets of animal movement characteristics can be accomplished with a variety of tools but the tool used can influence results (Legendre and Legendre 2012). We designed our analysis to mitigate two important limitations of cluster analysis: 1) clusters are heuristically derived and have no inherent biological relevance, and 2) clusters may change across different cluster analysis methods (Borcard et al. 2018, Pearson 2018). Therefore, we used robust multi-method clustering solutions that identified a clustering structure which appeared repeatedly across multiple clustering efforts. The result was identification of relatively stable groups of short-term home ranges with similar movement properties within groups (i.e., clusters, low-level movement modes). Our results illustrate that detailed analysis of movement data holds promise for identifying and describing movement-behavior modes for sage-grouse that cannot be directly observed or inferred from known phenology. We found that movement modes were largely discriminated along a continuum between movement activity (i.e., hull area, variability in residence time, variability in time-to-return) at one end and use-intensity (i.e., residence time, patch revisits) at the other.

Low-Level Modes vs. High-Level Modes

Our PCA plots of the PAM centroids (multivariate cluster means) demonstrated discrimination among the modes and facilitated interpretation of the inferred PAM modes relative to the known behavior modes (high-level modes). For instance, PAM modes 2, 5, and 7 are associated with exploratory or winter ranging movements, and modes 6 and 8 align with incubating movements. All other modes were intermediate along the continuum between exploratory movements and movements like incubation. Connectivity or overlap among the intermediate modes was substantial but their biological relevance remained interpretable relative to movement property variation and known behavior modes (high-level). Attribution of the PAM modes to each of our hull instances will greatly improve the classification of exploratory movements because we have high confidence that the PAM-5 mode represents a transit or exploratory mode. Our confidence is garnered from the rigorous and multifaceted multivariate analysis that we have presented. We also have high confidence that the PAM-6 mode matches movement patterns of grouse known to be incubating. Attribution of our incubation-like mode to hull instances that do not correspond to incubation could be used to identify intensive-use type movements (e.g., central-place foraging) within higher level modes.

Low-Level Modes vs. Landscape Conditions

Our use of a multivariate regression tree (MRT) to validate the PAM-8 clusters relative to environmental variables was fruitful in 2 important ways: 1) the results of the MRT provided an additional level of validation of our PAM-8 clustering result by testing for association with environmentally relevant variables, and 2) the MRT helped describe the ecological relevance of each inferred behavior mode. Validation of a classification or clustering scheme using subject matter information is arguably more important than internal validation statistics or indices (Legendre and Legendre 2012) and is philosophically analogous to biological validation routines designed to improve statistical clustering of genomic data (Yeung et al. 2001).

Our MRT aggregated the PAM-8 clustering scheme into an MRT-3 clustering scheme which organized the PAM-8 clusters into 3 clusters along the movement activity versus use-intensity movement-property gradient, thereby corresponding with our movement-property clustering results. The MRT-3 clustering scheme was somewhat unexpected because our MRT analysis contained no information about movement properties, only environmental variables. The MRT cluster PAM8 = 1, 2, 5, and 7 corresponded to exploratory, winter ranging and unknown behavior modes whereas the PAM8 = 3, 4, and 8 cluster corresponded to the laying, incubating, brood, potential brood, and unknown categories. The MRT cluster PAM8 = 6 corresponds to the laying and incubating cluster. Our interpretation is that the gradients of variation in the movement properties are sufficiently correlated with the gradients of variation in the environmental variables to reproduce a similar multivariate clustering scheme using only the environmental variables and movement-property based PAM-8 clusters. Given that we included daylength, daily temperature, and distance to first nest and they were the strongest indicator variables for the MRT-3 result, we conclude that the PAM-8 modes are largely defined by seasonality of movement activity.

Seasonality of movement patterns was also associated with differential landscape conditions. For instance, our MRT class PAM8 = 1, 2, 5, and 7 (exploratory, winter range, unknown) was associated with higher values of distance from first nest, bare ground, heterogeneity of vegetation biomass, and variability in terrain ruggedness. Our PAM8 = 6 (reproduction including brood-rearing) cluster was associated with higher values of daylength, normalized height, vegetation biomass, topographic ruggedness, vegetation height, and heterogeneity of vegetation height. Our PAM8 = 3, 4, and 8 cluster was associated with higher values of daily temperature, variability in vegetation biomass, and variability in sagebrush cover relative to the overall mean for all observations combined. Overall, sage-grouse in our study area tended to nest on higher topography (higher normalized height [PAM8 = 6]) but used lower lying areas at other times of year. Also, sage grouse in our study area made distinct movements away from breeding habitat to winter ranges (higher distance from first nest [PAM8 = 1, 2, 5, and 7]). Our primary aim here was not to evaluate and report sage-grouse wildlife-habitat relationships but we stress that multivariate regression tress or a similar biological validation step are important for justifying, defining, and interpreting inferred behavior modes.

Conclusions

The validity of our inferences about statistically inferred behavior modes are compelling because they are based on multiple movement properties, correspondence with known behavior modes, and correspondence with environmental variables. We successfully identified an exploratory-type movement mode and an incubation-type mode that can be used in future research to account for these modes in habitat delineations or female survival models. Moreover, all the PAM-8 inferred low-level modes could be more rigorously defined by future research if ecological processes such as survival or disease risk differ among each mode (Cattarino et al. 2016, Dougherty et al. 2022).

Our results indicate that behaviors such as loafing or incubation breaks are difficult to resolve using 6-hr interval relocations and the 7 movement properties that we used. However, use of similar behavior-mode identification methods with higher temporal-resolution relocation data is likely to identify greater clustering structure and more detailed movement modes (Mills et al. 2006, Rowcliffe et al. 2012). Researchers with finer temporal resolution relocation data have classified diurnal behavior modes such as loafing and night-roosting, patch use and interpatch transit movements, and incubation break behaviors using simple ad-hoc movement-data thresholds and temporal context (Dzialak et al. 2015a, Bakner et al. 2019, Gelling et al. 2022). Behavior modes have also been identified using more objective statistical clustering methods with diverse vertebrate taxa (Abrahms et al. 2017) and we have shown that multivariate clustering of movement properties is useful in objectively parsing behavior for sage-grouse. The volume and sophistication of animal movement datasets will continue to increase, and there exists a call for a unified movement-behavior theory (Nathan et al. 2008). We champion the use of detailed movement data to improve the wildlife-ecology knowledge base but caution that subjective ad-hoc definitions and methods will impede progress just as has occurred for issues of ecological scale and habitat-response research (Krausman 1999, Scott et al. 2002, Wiens and Moss 2005). We expect that species-specific behaviors of importance will become resolved in the scientific literature as more researchers begin inferring movement modes from detailed tracking data. Establishing best practices regarding which behaviors are identified and how they are identified will help promote a unified movement-behavior theory. Behavior-specific investigations of how animals use geographic and environmental space will engender a less biased and more process-based rendering of species-habitat relationships (Lima and Zollner 1996, Morales and Ellner 2002, Roever et al. 2014). Multivariate statistical approaches in combination with movement properties derived from detailed movement data are a viable solution to rigorous and objective behavior classification.

Figures And Tables

Table 1. Description of all variables analyzed to identify sage-grouse behavior modes using 7 movement properties and statistical partitioning of the data. Column 4 indicates either the power by which a variable was transformed or a logit transformation.

Label	Raw Predictor	Computed Summary Statistic	Transformation	Ecological Relevance
		Movement properties		
h.A	hull area	hull area	0.285	size of short-term home range
h.RV	hull revisits	hull revisits	logit	intermittent importance of area
h.D	hull duration	hull-mean number of points per visit	0.1	average time-use intensity
RV	100-m patch revisits	hull-mean revisitations of 100-m patches	0.035	intermittent importance of patches within hull
RT	100-m patch residence time	hull-mean residence time in 100-m patches	0.075	total fine-scale time-use intensity
RT.500CV	CV of 500-m residence time	hull-CV of residence time in 500-m patches	0.45	variability in intermittent importance of patches within hull
TtoR.500CV	CV of 500-m time to return	hull-CV of median time-to-return of patches	(x^-1.25)*-1	variability in intermittent importance of patches within hull
		Landscape Conditions		
prism.tmean.day_mean	temperature	mean of values at nearest neighbor points	1	PRISM estimates of daily mean temperature
lod_mean	length of day	mean of values at nearest neighbor points	1	the time interval between sunrise and sunset
NDnest_mean	distance to first nest	mean of values at nearest neighbor points	1	distance of individual sage-grouse from their first nest
B.100	barren	mean of 100-m patch zonal means	1	bare ground cover estimates
Height	height	mean of 100-m patch zonal means	1	index of the height of objects on the landscape, typically vegetation
Height.rCD	coefficient of determination (rCD) of height	rCD of 100-m patch zonal means	1	heterogeneity of the height of objects on the landscape, typically vegetation
Height.RoV	radius of variance (RoV) of height	mean RoV of 100-m patch zonal means	1	proximal heterogeneity of objects on the landscape, typically vegetation

Sage.100	sage	mean of 100-m patch zonal means	1	sagebrush cover estimates
SAGE.30.CV	sage	hull-CV of 30-m patch zonal means	1	heterogeneity of sagebrush cover estimates
Veg.100	vegetation biomass	mean of 100-m patch zonal means	1	index of vegetation that incorporates digital surface model data
Veg.100.rCD	vegetation biomass	hull-rCD of 100-m patch zonal means	1	heterogeneity of biomass index
Veg.RoV.100	radius of variance (RoV) of biomass	mean RoV of 100-m patch zonal means	1	proximal heterogeneity of biomass index
LiDEM.VRM.30	LiDAR vector ruggedness measure	hull-mean of 30-m patch zonal means	1	index of fine-scale landscape ruggedness due to features such as stream banks
n.H.30	normalized height	hull-mean of 30-m patch zonal means	1	elevation of the land surface normalized by surrounding area
n.H.30.CV	normalized height	hull-CV of 30-m patch zonal means	1	heterogeneity of local-area normalized elevation
WB.100	proximity to water bodies	hull-mean of 100-m patch zonal means	1	proximity to water bodies at a location
VRM.30.CV	DEM vector ruggedness measure	hull-CV of 30-m patch zonal means	1	heterogeneity of topographic ruggedness that highlights severe ruggedness
TWI.30.CV	topographic wetness index	hull-CV of 30-m patch zonal means	1	heterogeneity of expected or potential soil wetness based on topography

Table 2. Table of covariates that had statistically significant indicator values for clusters.

Covariate	**Cluster**	**Indicator Value**	**Probability**
lod__mean	PAM8 = 6	0.4987	0.001
Veg.100	PAM8 = 6	0.2141	0.001
n.H.30	PAM8 = 6	0.2012	0.001
LiDEM.VRM.30	PAM8 = 6	0.1781	0.001
Height.RoV	PAM8 = 6	0.17	0.001
Height	PAM8 = 6	0.0982	0.001
prism.tmean.day_mean	PAM8 = 3,4,8	0.2925	0.001
Veg.100.rCD	PAM8 = 3,4,8	0.2021	0.001
SAGE.30.CV	PAM8 = 3,4,8	0.1816	0.001
NDnest_mean	PAM8 = 1,2,5,7	0.4028	0.001
Height.rCD	PAM8 = 1,2,5,7	0.3214	0.001
n.H.30.CV	PAM8 = 1,2,5,7	0.3014	0.001
TWI.30.CV	PAM8 = 1,2,5,7	0.269	0.001
Veg.RoV.100	PAM8 = 1,2,5,7	0.2585	0.001
B.100	PAM8 = 1,2,5,7	0.2212	0.001
VRM.30.CV	PAM8 = 1,2,5,7	0.2114	0.001
WB.100	PAM8 = 1,2,5,7	0.1627	0.001
Sage.100	PAM8 = 1,2,5,7	0.1236	0.001

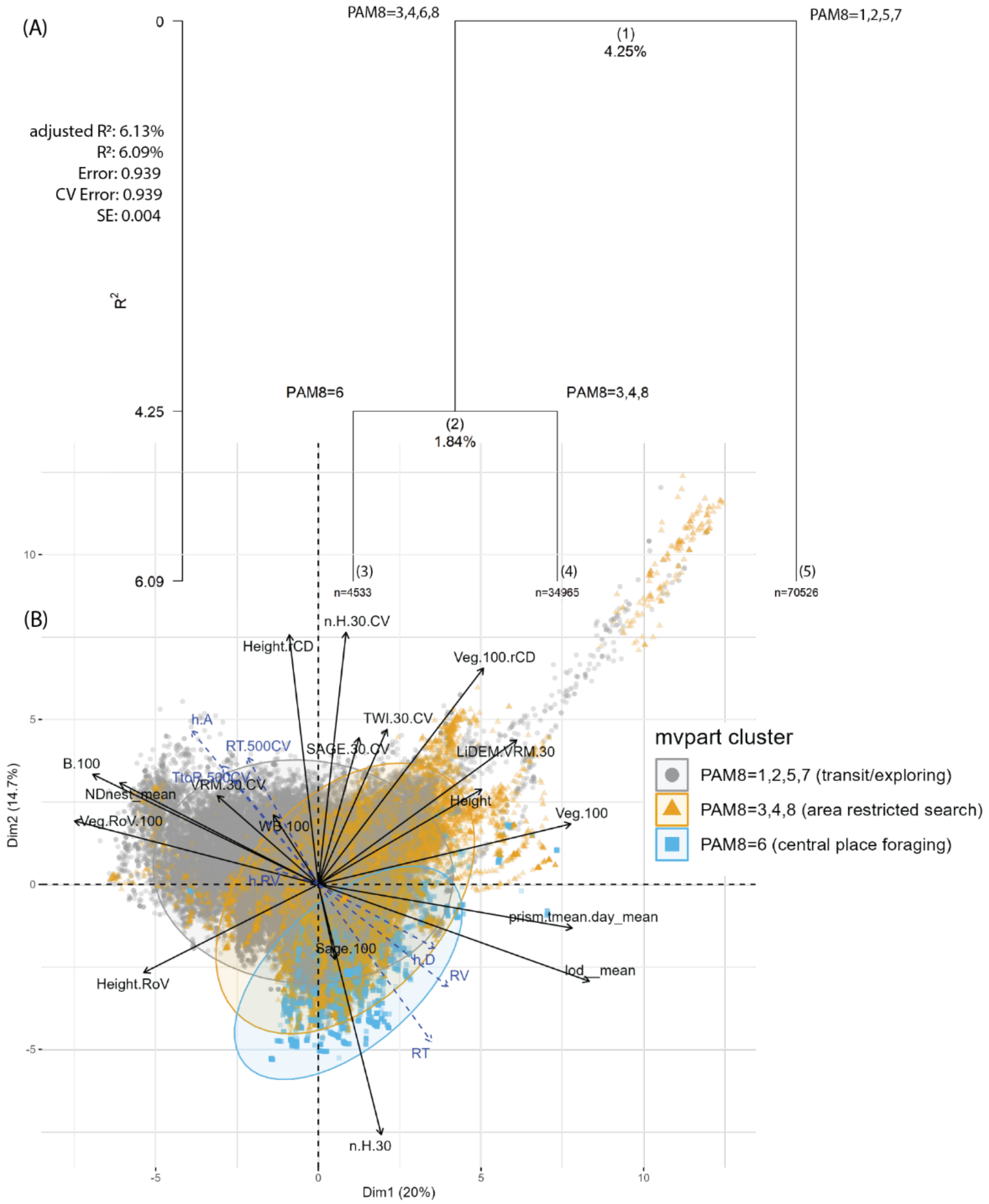

Figure 1. A) Multivariate regression tree (MRT) structure of 18 landscape-condition variables partitioned under control of an 8-mode PAM clustering scheme. The tree has 2 splits (1, 2) and 3 terminal nodes (3, 4, 5) with the first split explaining 4.25% of the variation in the landscape variables and the second spit explaining 1.84%. The tree is labeled with the PAM nodes associated with each split. B) Principal component analysis triplot illustrating MRT terminal-node membership of sage-grouse hull instances relative to the 18 landscape variables and 7 supplementary movement properties.

CHAPTER 3

DECIPHERING PATTERNS OF YEAR-ROUND SPACE- AND TIME-USE INTENSITY IN SAGE-GROUSE OF NORTHEASTERN MONTANA

Contribution of Authors and Co-Authors

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Contributions: Lance helped conceive and plan the study, interpret results, and write the manuscript. All authors edited the manuscript. All authors read and approved the final manuscript.

CHAPTER 3

Manuscript Information

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CHAPTER THREE

DECIPHERING PATTERNS OF YEAR-ROUND SPACE- AND TIME-USE INTENSITY IN SAGE-GROUSE OF NORTHEASTERN MONTANA

Background

Animal distributions are strongly influenced by individual movements which are, in turn, driven by resource provisioning, shelter seeking, interspecific and intraspecific interactions, predator evasion, breeding system requirements, and individual personality traits. Movement behaviors play a primary role in individual fitness and population performance (Millspaugh and Marzluff 2001, Yoder et al. 2004, Prochazka et al. 2017, Bakner et al. 2019) but the integration of movement ecology with population ecology and conservation science is in its infancy (Tear et al. 1997, Turchin 1998, Schick et al. 2008, Morales et al. 2010, Hooten et al. 2017). Discovering the nuanced ways in which movement structures a species' ecology requires detailed observation of the movement process and prior life-history and ecological knowledge of a study organism.

The greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") is a gallinaceous bird with a long history of ecological study resulting from its imperiled conservation status (Patterson 1952, Connelly et al. 2004, Connelly et al. 2011a, Knick and Connelley 2011, Leu and Hanser 2011, Miller et al. 2011, Edmunds et al. 2018). Sage-grouse movements are a response to variable habitat requirements driven by changing physiologies which must be met on a highly variable landscape while maximizing individual fitness in the face of substantial risk of predation (Bergerud and Gratson 1988). Vegetation provides food, cover from the elements, and cover from predators, but varies with seasonal plant growth, plant population dynamics, and disturbances such as fire, grazing by herbivores, and anthropogenic land use (France et al. 2008, Beck et al. 2009, Naugle et al. 2011, Schroeder and Vander Haegen 2011, Allred et al. 2015). Both food resources and the value of cover to an animal can be altered by land management, seasonal climatic phases, and weather events such as hailstorms, drought, and snowfall (Moynahan et al. 2006, Dzialak et al. 2013b, Dahlgren et al. 2015, Gibson et al. 2017, Sianga et al. 2017, Donnelly et al. 2018). The inherent temporal and spatial heterogeneity that characterizes sagebrush ecosystems has likely selected for adaptive movement strategies in sage-grouse that bolster fitness across variable conditions (Miller and Eddleman 2000). An ever-increasing human footprint coupled with the evident sensitivity of sage-grouse populations to endogenous and exogenous environmental stressors necessitate a precise and accurate understanding of sage-grouse ecology on which to base conservation measures.

Spatiotemporal variability in habitat composition and arrangement can translate to variability in habitat use patterns and population vital rates across regions (Wiegand et al. 1999, van Toor et al. 2016, Edmunds et al. 2018). Variability among vital rates from different sage-grouse populations and differential vital rate influences on population dynamics (Taylor et al. 2012, Dahlgren et al. 2016a, Coates et al. 2017a) underscores the need for population-specific research that links space use and demographic processes to habitat in such a way that facilitates adaptive monitoring and management of local populations. Movement-integrated research may be key to understanding the complex relationships between sage-grouse and the landscapes they inhabit (Wallestad 1971, Dunn and Braun 1986b, Connelly et al. 1988).

Movement is integral to space-use and resource selection (Moorcroft and Barnett 2008, Kie et al. 2010, Morales et al. 2010, Van Moorter et al. 2016). Differential use-intensity represents the mechanism by which landscape conditions influence a species' seasonal habitats and population vital rates (Morales et al. 2010, DeCesare et al. 2014, Gibson et al. 2016, Sandford et al. 2017, Mangelinckx et al. 2018, Fierro-Calderón and Martin 2020) and has commonly been measured using utilization distributions (Millspaugh et al. 2006) or resource selection functions that average use-intensity among numerous behaviors (Beyer et al. 2010). A spatiotemporally detailed examination of behavior-specific space- and time-use intensity properties such as residence time and revisits may help identify mechanisms that dictate space use which cannot be isolated when using convolved measures of use-intensity (Barraquand and Benhamou 2008, Moorcroft and Barnett 2008, Benhamou and Riotte-Lambert 2012). Residence time is a movement property that quantifies differential time-use in the vicinity of points along a trajectory. Residence time has been proposed as a movement property useful for segmenting movement trajectories into distinct movement bouts and identifying areas that are profitable to an animal (Barraquand and Benhamou 2008, Kapota et al. 2017). Revisitation is especially useful for identifying repeatedly used zones along a trajectory such as nest sites, roost sites, dens, or point-source resources such as watering holes (Bracis et al. 2018). Movement properties such as residence time, revisitation, time-to-return, ranging area, and directionality of movement are also useful for identifying animal behavior modes (Johnson et al. 2002, Van Moorter et al. 2010, Dzialak et al. 2015a, Abrahms et al. 2017).

Use-intensity varies among and within seasonal (e.g., breeding and non-breeding) use areas through changes in residence time and revisitation rates (Bastille-Rousseau et al. 2010) that result from a combination of innate differences in personality among individuals (Biro and Stamps 2008, Wolf and Weissing 2012, Weiss 2018) and variability in resource distribution and quality experienced by individuals (Van Moorter et al. 2016). Moreover, individuals vary in their preference for certain landscape conditions and therefore modulate the landscape conditions they experience (Mueller and Fagan 2008, Powell and Mitchell 2012, Van Moorter et al. 2016). Thus, documenting associations among environmental factors, and individual-specific movement properties may yield more interpretable management- and conservation-related inferences than identifying correlates with global space use (i.e., home range size) or use-intensity (i.e., resource selection) (Benhamou and Riotte-Lambert 2012, Van Moorter et al. 2016).

A first step for a comprehensive understanding of sage-grouse movement ecology is to parse apparent individual and environmental influences on space- and time-use patterns. Understanding how landscape condition, behavior mode, or individual traits influence space- and time-use intensity patterns will promote the integration of the movement process into our understanding of wildlife-habitat relationships.

Objectives

Our goals were 1) to examine relationships among space- and time-use intensity metrics (movement properties), and 2) parse variability in individual-level movement properties into components due to spatial, temporal, behavioral, and individual-level characteristics. We used a multivariate analysis of 15 movement-metric response variables to estimate and quantify relationships among movement properties. To determine if the movement-property interrelationships are fundamental to sage-grouse ecology, we examined them considering recent movement ecology theory linking residence time and time between revisits to resource selection strength (Van Moorter et al. 2016). To tease apart movement property variation due to landscape conditions while accounting for individual-level status (i.e., age, behavior mode) we: 1) identified laying, incubation, brood-rearing, potential brood-rearing, unclassified (pre-laying, summer, fall), winter ranging, and exploratory behavior modes to control for known behavioral modes, and 2) evaluated the strength of associations between landscape conditions (e.g., terrain, vegetation cover) and temporal modulators (e.g., daily temperature, daily precipitation, daylength) with the 15 movement properties. We employed a multivariate variance partitioning approach (partial redundancy analysis) to isolate variation in individual-level movement properties due to vegetation, terrain, temporal modulators, and behavior modes.

Study Area

Our study area was principally on a 425,000-ha area in southern Valley County in north-central Montana, USA (47.66258 N to 48.44968 N, 106.43546 W to 107.44770 W). The area was within Glaciated Northern Grasslands and North Central Highlands (Cleland et al. 1997, McNab et al. 2007) and within the sage-grouse Great Plains Management Zone 1 which corresponds to the Silver Sagebrush Province (Connelly et al. 2004, Stiver et al. 2006). Land cover in the area consisted of approximately 49% big sagebrush steppe, 20% Great Plains mixed-grass prairie, 8% cultivated crops, 6% mat salt shrubland, 2% Great Plains riparian, and 2% Great Plains woodland savanna (Anderson et al. 1976, Comer et al. 2003). Additional limited land cover types included greasewood flats, shale badlands, and Great Plains wooded draws and ravines (Anderson et al. 1976, Comer et al. 2003). The area was characterized by high annual variation in average monthly temperature (-10.1 °C to 21.7 °C) and low mean annual precipitation (29.6 cm), with over half of annual precipitation occurring May – July (Arguez et al. 2010). Approximately 75% of the study area was in public ownership, managed predominately by the U.S. Bureau of Land Management (BLM), as well as the U.S. Fish and

Wildlife Service (USFWS, Charles M. Russell National Wildlife Refuge [CMR]), and the State of Montana. The area was situated just south of the northernmost extent of the Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) distribution in Montana; silver sagebrush (*A. cana*) becomes the only woody *Artemisia* species further north. The area is a transition zone between a mixed-grass prairie ecosystem and a sagebrush steppe ecosystem which makes it novel in comparison to most sagebrush ecosystems throughout the range-wide sage-grouse distribution.

Our population of sage-grouse represents an important component of a larger metapopulation; however, basic information on the population ecology of this population is lacking. The study population represents a core component of the broader northern Montana population (NMP) distributed throughout north-central Montana, southeastern Alberta, and southwestern Saskatchewan (Garton et al. 2011, USFWS 2013). Minimum male counts at leks within the NMP were ~2,700 males, and the population is thought to be one of the few remaining stable populations of sage-grouse across the species' range (Garton et al. 2011). The southern segment of the NMP lies below the Milk River and was designated a Priority Area for Conservation (PAC [corresponds to BLM Priority Habitat Management Area]) in state and BLM conservation planning efforts (USFWS 2013).

Methods

Sage-grouse Captures

During April–May, 2018–2019, we captured 89 (48 in 2018, 41 in 2019) female sage-grouse using spotlighting and hoop-netting (Giesen et al. 1982, Wakkinen et al. 1992). We attempted to capture a spatially-balanced, representative sample by spreading captures around 3 separate watersheds in our study area. Upon capture, we banded females with uniquely numbered leg bands. We recorded standard morphometrics and collected blood from toenail clippings on Nobuto blood filter strips (Dusek et al. 2014). We aged females as adult or yearling by the appearance of primary feathers 9 and 10 (Braun and Schroeder 2015). We attached a VHF-equipped 22-g solar powered Global Positioning System (GPS) Platform Transmitter Terminal (PTT; model GT-22GS-GPS, GeoTrak, Inc., Apex, NC, USA) to each of 86 birds using a rump-mounted harness (Rappole 1991). All PTTs were programmed to collect 4–10 locations every day and upload data every 1.5–3.0 days to the Argos satellite system. PTT programming was specified separately for different seasons and the 2018 programming was adjusted in 2019 based on prior PTT transmission success. Our most aggressive programming for a season-year was 11 March – 1 September where PTTs obtained up to 10 fixes every day and uploaded data to the Argos system approximately every two days. PTTs attempted to collect ≥ 4 locations per day regardless of season or PTT batch. All animal handling was approved under Montana State University's Institutional Animal Care and Use Committee (protocol # 2017-57).

Sage-grouse Monitoring

The PTTs had an approximate 3-year lifespan and movement data from equipped sage-grouse was recorded until the female died or lost the PTT. During the breeding seasons of 2018, 2019 and 2020, females were monitored by downloading GPS fixes and other PTT sensor data from Argos system servers every 3–5 days. During the breeding season of 2021 PTT data was monitored monthly using a less intensive protocol suitable to a reduced number of live individuals. We used multiple lines of evidence to infer female status. Localization of a PTT indicated either a nesting female, a dead female, or a dropped PTT. The PTTs were equipped with an activity sensor which indicated if the PTT was experiencing motion; static activity sensor readings indicated a mortality or dropped PTT. The visitation of nest sites can lead to observer-induced bias in vital rate estimates (Gibson et al. 2015), therefore we only visited localization sites if a mortality was suspected. In most cases incubation recesses (movements by females off nests) were evident in the GPS fix data and helped separate mortalities from nests (Coates and Delehanty 2008, Dzialak et al. 2011). If a mortality was indicated, we verified this with a field visit and recorded the condition of carcass remains including evidence of predation (Blomberg et al. 2013). We estimated the date of incubation initiation for each confirmed nest by reviewing the GPS data. Nest fate was verified in the field when a female had moved off the nest for ≥ 3 days. Nests that failed just prior to incubation were verified in the field if ≥ 2 locations accrued in the same spot due to periodic visits by a female. After nest abandonment, we located nests and recorded evidence regarding nest fate. Hatching was indicated by eggs with detached membranes and eggshells that were consistent with being pipped by chicks (Rearden 1951). We considered a nest successful if ≥ 1 egg had hatched. Nest monitoring allowed us to identify two nesting behaviors for all nests identified: laying and incubating. We labeled points along a female's trajectory as laying if they preceded incubation initiation by ≤ 7 days. Sage-grouse lay an average of ~2 eggs/3 days and average clutch sizes are ~8 eggs (Wallestad 1971, Schroeder et al. 1999). Our specification of 7 days is conservative and ensures that females with small clutches are not erroneously considered laying.

In 2018 and 2019, we monitored females with successful nests and conducted pre-dawn brood counts to ascertain if a female was with a brood. Females with broods were located with recent PTT locations and then Yagi antennas and receivers using signals from the PTT-attached

VHF transmitters. We conducted brood checks on females only in the year they were first captured and marked because VHF transmitters failed within one year of deployment. Brood checks were conducted at 2-week intervals after hatch date for up to 6 weeks (3 checks). When no chicks were detected, we re-conducted the check within 5 days if the female exhibited defensive behavior consistent with brooding to confirm brood loss. If females immediately flushed out of the vicinity and no chicks were located the brood was recorded as unsuccessful. Logistical constraints (e.g., weather) prevented regular brood checks at 2-week intervals, so broods were flushed to confirm survival every 17 days on average. We labeled points along a female's trajectory as brood-rearing for periods when brood status was known active. In cases where females had successful nests, but brood status could not be checked, we labeled all points as potential brood rearing for ≤ 14 days after hatch. Our specification of 14 days was based on our observation of brood survival an d our expectation that many of the females with hatched nests would have broods for at least 14 days after hatch.

Time-Local Movement Properties

Female sage-grouse monitored for fewer than 30 days were excluded from analyses because of limited relocation histories from which to derive space- and time-use response variables. We segmented space use by each sage-grouse into space-time local hulls (minimum convex polygons [MCPs]). We subset relocations to a 6-hour sampling interval to prevent bias in hull construction due to irregular sampling (Lyons et al. 2013). We used the R package T-LoCoH to process the 6-hr regular-trajectory data and quantify spatiotemporal patterns of sage-grouse movements including: hull-enclosed points, area of hulls, duration of visits (analogous to recursive-based residence time), visitation rate (analogous to recursive-based revisits), hull eccentricity, and mean and standard deviation of nearest neighbor point speeds (Appendix E, Table 11). Appendix A describes the tuning parameters that we used to construct time-local convex hulls. We calculated visitation rate as the number of occurrences in a hull separated by a time gap ≥ 1 week. We calculated visit duration as the mean number of occurrences per visit (Lyons et al. 2019). We calculated eccentricity using the shape parameters of a minimum closing ellipse for each nearest neighbor point set (Lyons et al. 2019). Eccentricity varies from 0 to 1 with 0 being a perfectly round ellipse and 1 being a severely elongated linear ellipse; ellipse elongation indicates directional movements. We calculated hull area as the area of each hull polygon. Hull area provides a geometric delineation of space use and is analogous to a home-range area calculated for brief periods. We calculated hull-enclosed points as the number of points from an individual's trajectory enclosed by each hull. Hull-enclosed points is related to the intensity of a utilization distribution except hull-based intensity is time-local. We also calculated use-intensity (h-UI) as hull-enclosed points divided by area which represents the areal density of used points and approximates the density of a utilization distribution. Other properties associated with the movement mode or activity of an animal are the mean speed and standard deviation of speeds (speed-SD) attributed to the nearest neighbor points from which a hull is constructed. Given hulls of equal area, high movement speeds might indicate that a hull was rapidly traversed over a limited area whereas low movement speeds could indicate a plodding trajectory or high residence time in a few patches. Given similar mean speeds, speed-SD of a highly traversed hull or a hull constructed from a plodding trajectory would be lower than for a hull with multiple rest points connected by rapid directional movements.

Point-Patch Recursive Movement Properties

We calculated point-patch revisitation properties representing movement activity in the vicinity of previously visited points. We subset relocations to a 6-hour sampling interval prior to calculation of recursive movement properties to maintain temporally balanced sampling (Bracis et al. 2018). The calculation of revisits (RV) and time-to-return (TtoR) are influenced by a time-threshold parameter that defines the time elapsed before a movement outside of a patch is considered a separate visit. We set the time-threshold parameter to 0 to capture recursive movements to nest-sites in addition to broader-scale movements. We calculated point-patch revisitation rate (RV) and residence time (RT) to help distinguish among intensity values associated with familiarity versus areas of ephemeral importance. Point-patch revisitation was calculated as the total number of path segments that intersect the virtual circles positioned on trajectory points (Bracis et al. 2018). Residence time was calculated by summing the duration of all path segments within each circle to quantify time spent in the vicinity of each point (Barraquand and Benhamou 2008, Bracis et al. 2018). Residence time has also been calculated as the average duration of each visit to the circle (Barraquand and Benhamou 2008, Van Moorter et al. 2016), so we calculated an average residence time (RTmu) variable for comparison with total residence time (RT). Average residence time may highlight movement patterns that are not well resolved by total residence time. We calculated the median number of hours elapsed between visits which represents the typical periodicity of intermittent patch use (TtoR). We also calculated the net displacement of every relocation away from the first nest site known for each female (ND-nest). If a female never initiated a nest, then the first location in the trajectory is used as the start point. Our ND-nest variable accounts for differential seasonal space use and seasonal home-range fidelity by quantifying movement in relation to the first nesting region (or capture location) of each female.

Previous research indicates that the scale at which variation in movement properties is calculated can influence observed relationships between movement, space-use, and resource selection (Van Moorter et al. 2016). Therefore, we calculated the coefficient of variation (CV) of RT and TtoR at the 100-m and 500-m spatial threshold (extent). We used a 100-m radius extent to calculate all other properties because a 100-m extent is consistent with extents known to be associated with sage-grouse patch use at fine scales (e.g., nest-sites, roosts, loafing sites, mineral deposits) (Doherty et al. 2010, Walker et al. 2016). Our hull-based movement properties represent movement properties at coarser scales that have been associated with sage-grouse region use (Doherty et al. 2008, Doherty et al. 2010, Fedy et al. 2014, Walker et al. 2016).

Behavior Mode Classification

We used individual movement data to classify high-level and low-level behavior modes of each female at each relocation (Chapter 1). High-level behavior modes included those associated laying, incubation, brood-rearing, potential brood-rearing, migration, exploratory movements, and winter ranging. Low-level behavior modes were inferred from statistical clustering of movement properties and represent distinct movement patterns within the high-level modes. Low-level behavior modes might represent patch use and interpatch transit or area-restricted search versus central-place foraging.

Migration high-level mode We used a statistical framework that models the net-squared displacement (NSD) timeseries of a movement path as a function of non-linear regression model parameterizations that represent different movement types (Spitz et al. 2017). We minimally filtered irregular-trajectory raw data where we only removed erroneous locations defined as having step speeds (step length / step interval) ≥ 45 km/day. We based the 45 km/day criteria on our knowledge of errors identified with PTT metadata (e.g., accuracy, direction of anomalous displacement). The models that we considered were migration, mixed-migration, dispersal, resident, and nomadic. See Appendix B for background, methods, and results describing our migration research using data from 2018–2020. Identical migration analyses were used to delineate the individual winter ranging modes for 2020–2021.

<u>Other high-level modes</u> We used a combination of field observation, examining PTT data, and migration classification to classify each hull in a female's trajectory as laying, incubation, brood-rearing, potential brood-rearing, winter ranging, or unclassified. Some exploratory movements were identified from the migration analysis, but shorter duration exploratory movements were relabeled from other known modes based on results of Chapter 1. Additionally, uncertainty in the estimated dates of departure and arrival from NSD migration models caused transit movements between ranges to be initially labeled either winter or unclassified. Our unclassified behavior class was generally a catch-all where distinct breeding or winter-ranging signals were not identified (i.e., pre-laying, late summer, fall). We exclude the unclassified behavior mode from most plots of results to facilitate visualization of the data. Our exploratory high-level mode was inferred from statistical clustering of movement properties (Chapter 1) but represents only 1 of 7 known modes and was based on only 7 of 15 movement properties that we consider herein.

<u>Low-level statistically inferred behavior modes</u> We identified eight statistically inferred behavior modes using statistical clustering (partitioning around medoids [PAM]) on a subset of

our movement properties (Van Moorter et al. 2010, Abrahms et al. 2017). We identified an exploratory mode using the clustering results and we used it to reclassify movement instances within the high-level modes which effectively filtered exploratory movements from modes such as winter or unclassified (Chapter 1). We also used the inferred modes to explore structure in the movement data that was not explained by vegetation, topography, seasonal modulators, high-level known modes, and individuality.

Landscape Condition Predictor Variables

Predictor variables are arguably the most important component of wildlife-habitat research as they represent habitat characteristics, but most regression models used in wildlife-habitat research assume that predictor variables are measured without error. The consequences of violating the measured-without-error assumption include attenuation of observed habitat responses, amelioration of responses, or bias in estimated responses (Davies and Hutton 1975, Meites et al. 1984). To improve scientific inference, we checked correspondence between available geospatial data and our knowledge of the study area. We then developed custom geospatial-layer replacements if available predictor variables were deemed poor quality or had numerous nonsensical values.

Water Sources Water can be an important seasonal resource for sage grouse and may influence distributions and seasonal space use (Donnelly et al. 2016, Donnelly et al. 2018). To quantify the distribution of stream channels on the landscape, we analyzed a 1/3rd arc second scale digital elevation model (DEM) using terrain analysis tools in the System for Automated Geoscientific Analyses (www.saga-gis.org, Version: 7.6.4). We performed a hydrologic analysis of the DEM to generate a stream channel network in our study area. Available water body data layers did not correspond well with recent aerial imagery of our study area so we developed a raster layer delineating water bodies by combining spatial information about water body extents from multiple sources using a multiple criteria analysis (Gao 2009) (Appendix C).

Fine-Scale Landscape Structures We downloaded DNRC LiDAR digital surface model (DSM) and digital elevation model (DEM) data from the Montana State Library site. We processed the DSM with 3 SAGA algorithms that highlighted 3 aspects of fine-scale features on the landscape. We used a terrain-surface texture algorithm to highlight tall objects (e.g., perching substrates). We used a vector ruggedness measure algorithm to create an index for landscape ruggedness which is different from topographic ruggedness because all landscape structures (e.g., vegetation, buildings, fences) contribute to the index values. On the open range, the landscape structure index captures fences, powerlines, isolated trees, and other structures which may be associated with risk to sage-grouse and with the influence of cattle on vegetation characteristics. We used a morphological protection index algorithm to quantify how enclosed and sheltered a unit area was due not only to terrain, but also to vegetation, buildings, or any other surface structures. Finally, we used the vector ruggedness measure algorithm with a LiDAR digital elevation model to quantify fine-scale topographic ruggedness such as stream banks or hoodoos. All four of our LiDAR-derived cover estimate maps were resampled to match the resolution of the 1/3rd arc second DEM and derivative products (Appendix E, Table 12). LiDAR protection, tall objects, and land surface ruggedness (structure) largely represent landscape conditions due to vegetation so we grouped them with vegetation variables. LiDAR DEM vector ruggedness represents fine-scale terrain features.

Vegetation Vegetation characteristics are often associated with space-use and nesting success of female sage-grouse (Holloran et al. 2005, Hagen et al. 2007, Dahlgren et al. 2015), but see (Smith et al. 2020). Available geospatial vegetation data did not correspond well with the ground cover in our study area, so we developed 14 vegetation related variables: normalized difference vegetation index (NDVI), vegetation biomass, radius of variance of vegetation biomass, lowland NDVI, heavy-stature shrub cover, medium-stature shrub cover, forest cover, sagebrush cover, barren ground cover, shelter provided by vegetation (protection), structure due largely to vegetation (landscape structure), tall objects due largely to trees, vegetation height, and radius of variance of vegetation height (Appendix C, Table 12). We also calculated the percent of sagebrush cover class types from LANDFIRE data which is a measure of percent landcover type not a measure of actual sagebrush cover.

Terrain Terrain has been associated with female sage-grouse use of the landscape (Aldridge and Boyce 2007, Aldridge et al. 2012, Walker et al. 2016, Newton et al. 2017). We used a 1/3 arc-second scale digital elevation model (DEM) and System for Automated Geoscientific Analyses (SAGA) GIS to calculate 15 terrain properties (SAGA version 2.3.2, www.saga-gis.org). The terrain properties were terrain ruggedness index, LiDAR DEM vector ruggedness measure, vector ruggedness measure, topographic position index, topographic wetness index, total insolation, mid-slope position, normalized height, standardized height, multi-resolution valley bottom flatness, morphological protection, multi-resolution ridgetop flatness, slope height, valley depth, and wind exposition (Appendix E, Table 12).

Temporal Modulators We calculated mean daily temperature, precipitation (Oregon State PRISM project, Hart and Bell (2015)), and length of day as potential modulating variables to account for movement property variation due to seasonality and weather influences. We also produced a relative-age variable to account for long term trends in the movement data and as a proxy variable representing individual grouse ages (Appendix E, Table 12).

Integrating Space- and Time-Use Intensity and Landscape Condition Data

We calculated summary statistics of all landscape conditions corresponding to the hull and point-patch movement scales for each sage-grouse hull or patch derived from the trajectories. The zonal summary statistics calculated for the hulls were the mean and coefficient of variation of all landscape condition pixels within each hull. We also calculated mean and CV for 30-m and 100-m radius patch footprints from each point-patch visited by a female. The various aggregation scales of the covariates were selected to help represent the multi-scale nature of sage-grouse habitat responses and the differential way alternate summary statistics (e.g., mean, median, CV) represent landscape features at different scales (Appendix E, Table 13). Zonal statistics calculated at the 30-m and 100-m extent were then aggregated by hull nearest neighbor sets of points (nearest neighbor point patches [nnpp]) using the ‘purrr’ package in R (Henry and Wickham 2020). For instance, the CV of heavy shrub index means from 18 100-m radius polygons was calculated to estimate the 100-m hull CV of heavy shrub index. An identical aggregation scheme was used to calculate summary statistics of the 100-m and 500-m patch-level recursive movement estimates. An example recursive movement aggregation would be the mean 100-m nnpp residence time of 18 nnpp attributed to a single hull. Our aggregation scheme based on nearest neighbor sets allowed fine-scale patch use-intensity to be spatially and temporally reconciled with coarser hull movement properties and zonal statistics.

We chose 16 terrain characteristics as base variables for our analyses: midslope position, morphological protection, multi-resolution ridgetop flatness, multi-resolution valley bottom flatness, normalized height, proximity to channels, proximity to water bodies, slope height, solar insolation, standardized height, topographic position index, multi-scale topographic position index, topographic wetness index, valley depth, vector ruggedness measure, and wind exposition. We then further processed the 16 topographic base variables into 55 nnpp summary statistic variables (Appendix E, Table 13). We restricted vegetation base variables to 10 ground-cover and landscape structure characteristics: bare ground, lowland NDVI, LiDAR NDVI, sagebrush, medium shrubs, heavy shrubs, forest, landscape structure, landscape protection, tall objects, and vegetation biomass (Appendix E, Table 13). Daily temperature, precipitation, daylength, and relative age were also aggregated with nnpp means.

Redundancy Analysis of Movement vs Predictor Variables

To understand interrelationships among movement properties (e.g., hull area, visitation) and landscape-condition predictor variables (e.g., vegetation cover, terrain characteristics; Appendix E, Table 13), we used 15, 6-hour movement properties as the response variables (Appendix E, Table 11) in redundancy analyses (RDA) that controlled for 24 predictor variables. Redundancy analysis (Rao 1964) is a two-step constrained ordination procedure in which a multiple regression of each response variable on all explanatory variables is conducted followed by a principal component analysis (PCA) of the fitted values from the regressions (Legendre and Legendre 2012, Borcard, Gillet et al. 2018). To meet assumptions of linear regression, we standardized all variables and normalized highly skewed continuous variables with square root, logarithmic, or Box-Cox power transformations (Faraway 2005; Appendix E, Table 13) using the tools of the ‘MASS’ package in R (Venables and Ripley 2002). We used logistic transformations to normalize highly skewed count data or highly discretized (pseudo-count) data that was first standardized (Faraway 2005). Collinear predictor variables can destabilize regression model estimates and confound interpretation so we calculated Pearson correlation coefficients and variance inflation factors (VIF) for all explanatory variables and sequentially eliminated variables exceeding user specified thresholds (Zuur et al. 2007, Braak and Šmilauer 2012, Legendre and Legendre 2012, Borcard et al. 2018). Collinearities among temporal modulators were easier to interpret, so we set less stringent thresholds for temporal modulators than for terrain and vegetation variables. We specified $r > 0.85$ and VIF > 4 for temporal modulators and $r > 0.6$ and VIF > 2.5 for the terrain and vegetation variable sets. Correlation and VIF-based variable elimination was accomplished with an R script incorporating the auto_cor() and auto_VIF() function which allowed us to prioritize keeping variables that we could easiest interpret from sets of collinear variables (Benito 2021).

To enforce parsimony in our RDA models, we performed a forward selection routine on 3 of the 4 sets of predictor variables: vegetation, topography, and seasonal modulators (Table 3). Forward selection is the standard variable selection method used with RDA (Zuur, Ieno et al. 2007, Legendre and Legendre 2012, Borcard, Gillet et al. 2018) and was executed using the forward.sel() function of packfor (Dray, Legendre et al. 2007, Blanchet, Legendre et al. 2008). The R^2_{adj} stopping criteria that constrained inclusion of explanatory variables in the RDA models was set at the R^2_{adj} of a global RDA model fitted with all candidate variables in a predictor set (e.g., vegetation matrix, topography matrix; Borcard et al. (2018)). All other forward.sel() parameters were left at default values (e.g., $\alpha = 0.05$). Known behavior mode and sage-grouse

ID were the only variables initially included within the fourth predictor set (behavior set). We later added inferred modes to examine residual structure leftover after accounting for data-driven modes based on some of the same movement property data. No forward selection routine was performed for the behavior set because the known mode and individual ID variables were critical for our analysis regardless of variable-and-model selection results. Our known-mode factor levels were laying, incubating, brood-rearing, potential brood-rearing, exploratory movement, and winter ranging; the sage-grouse ID factor had 74 levels.

We implemented our analysis in two phases. First, we used a variance partitioning approach to quantify the movement-property variance explained by 1) vegetation, 2) topography, 3) seasonal modulators, and 4) behavior modes. We further examined the influence of our behavior mode factor with and without an additional factor of sage-grouse identification. The sage-grouse ID factor allowed us to quantify variability in movement characteristics that is explained by individual-based movement tendencies unassociated with our suite of covariates. Sage-grouse ID accounted for a substantial proportion of the variance explained (9.0%) so we included the factor in the behavior-mode matrix to account for within-individual relatedness of movement observations. In the second phase, we performed 6 partial RDA analyses using each predictor-variable set, in turn, as the constraint matrix. Partial RDA analyses allowed us to quantify variation in the movement variables that was solely explained by each focal landscape-condition set (e.g., vegetation, topography), after accounting for variation jointly explained by compliment landscape-condition sets. The six partial RDA analyses were: vegetation, topography, temporal modulators, behavior modes, sage-grouse ID, and a final partial RDA using partitioning around medoids (PAM) movement-mode cluster classes. Separate partial

RDAs for the behavior mode and ID factors facilitated interpretation of the respective influence of known behavior mode and individual by isolating the variance explained by each factor and by simplifying the triplots used to summarize results. Likewise, our partial RDA with the PAM inferred-mode constraint was used to aid interpretation of our statistically inferred behavior modes by isolating the variation explained by the PAM factor and helping link the factor levels to biological behavior modes. Our PAM factor analysis is related to that of Chapter 1 but added here in Chapter 2 to add context to our results.

We used an auxiliary principal component analysis (PCA) to compare with our partial RDA models. Our PCA presents the overall structures in our data for comparison to structures present in our partial RDAs. We included all 15 response variables plus use-intensity (h-UI), mean residence time (RTmu), and CV of mean residence time (RTmu-cov) to allow comparison with hull-enclosed points (h-I), total residence time (RT) and CV of total residence time (RT-cov) (Appendix E, Table 11). We also analyzed and plotted movement versus landscape-condition associations based on the first 2 PCA axes using the seasonal modulator, topography, and vegetation variables that ranked highest for variation explained in our RDA models. We included 12 landscape condition variables: the first- and second-ranked temporal modulator variables and the top five variables from each of the terrain and vegetation predictor sets (see Table 3).

Results

Sage-grouse Monitoring

We collected 192,640 geographic coordinates of 86 female sage-grouse during 2018-04-24 – 2022-04-14 which encompassed 4 complete annual cycles of sage-grouse. The median number and interquartile range (IQR) of locations per female in the complete dataset was 1,410 (IQR = 2,956). After resampling trajectories to 6-hr intervals and removing individuals with inadequate relocation histories, our analysis used 110,360 relocations of 74 females. The median number of locations per female for the RDA analyses was 1156 (IQR = 1968).

Laying, incubating, brooding, potential brooding, winter ranging, and exploratory behaviors were attributed to female sage-grouse relocations whenever these behaviors were known from field observations or migration/cluster analysis for the winter ranging and exploratory mode. The median duration over which brood-rearing was confirmed was 41.4 days (IQR = 31.5, n = 19). Sage-grouse relocations with an unconfirmed behavior state were allocated to a catchall ‘unknown’ behavior category. The median number of relocations per individual attributed to laying was 48 (IQR = 58, n = 69), median locations for incubation 99 (IQR = 112, n = 71), median locations for brooding was 143 (IQR = 79, n = 19), potential brooding 54 (IQR = 11, n = 30), winter range 553 (IQR = 486, n = 43), exploring 72 (IQR = 53.8, n = 4), and 642 (IQR = 1074, n = 74) for the ‘unknown’ category. After reclassification of modes using cluster analysis, the median number of relocations per individual attributed to laying was 48 (IQR = 58, n = 69), median locations for incubation 99 (IQR = 112, n = 71), median locations for brooding was 143 (IQR = 79, n = 19), potential brooding 54 (IQR = 11, n = 30), winter range 442 (IQR = 442, n = 43), exploring 121 (IQR = 126, n = 59), and 585 (IQR = 944, n = 74) for the ‘unknown’ category. All modes were included in all analyses, but the unknown category was the least well discriminated so was excluded it from all plots to improve visualization of the results.

Predictor/Model Selection

Variance inflation factor screening and model selection resulted in 4 seasonal modulator, 10 vegetation, and 10 topography variables at various scales (e.g., hull, point-patch) being included in our RDA models (Table 3). The 4 seasonal modulator variables were precipitation, temperature, length of day, and relative age of the female (Table 3). The 10 topography variables were derived from 9 base variables: LiDAR vector ruggedness measure (VRM), midslope position, normalized height, proximity to channels, proximity to water bodies, LiDAR VRM radius of variance (RoV), proximity to water RoV, topographic wetness index, and vector ruggedness measure (Table 3). The 10 vegetation covariates were derived from 8 base variables: barren, forest, height, LANDFIRE sage, lowland NDVI, sage, vegetation, and vegetation RoV (Table 3).

RDA Variance Partitioning

Variance partitioning of behavior modes without the sage-grouse ID variable indicated that the variance in movement properties explained by each of the 4 explanatory matrices was of similar magnitude (Table 4); behavior mode explained the most overall variation in the movement data ($R^2_{adj} = 0.311$) and vegetation explained the least ($R^2_{adj} = 0.148$). Much of the overall variability explained by a given predictor set was shared among the sets (Table 4). For example, when not considering the contribution of the vegetation, modulators, and behavior-only matrices, the R^2_{adj} for topography was 0.165 (overall variation) but after removing their contribution (shared variation) the R^2_{adj} dropped to 0.035 (pure variation). The analogous situation for behavior mode resulted in a drop from 0.312 (overall) to 0.086 (pure). The vegetation and seasonal modulator predictor sets exhibited similar differences between overall and pure variance explained (Table 4, Figure 2). All 4 predictor sets together accounted for ~ 40.9% ($R^2_{adj} = 0.409$) of the variability present in the response variables (i.e., space- and time-use intensity properties).

The addition of a sage-grouse ID indicator factor to the behavior matrix (behavior/ID predictor set) resulted in a combined R^2_{adj} for the 4 predictor sets of 50% which was an increase of 9.1% (Table 4, Figure 2). The addition of a variable can alter the relative amount of pure explained variation attributed to each variable set. Indeed, 1.2, 0.7, and 1.6% of the pure variation explained by the topography, vegetation, or modulator predictor sets was reattributed to shared variation between the behavior/ID matrix and the other 3 (compliment) matrices (Table 4, Figure 2).

The addition of our PAM class factor to the behavior/ID predictor set resulted in a combined R^2_{adj} for the 4 predictor sets of 62% which was a further increase of 12% (Figure 2). The behavior/ID/PAM matrix had $R^2_{adj =}$ 0.296 which was a combination of movement variation newly explained and variation previously explained by the topography, vegetation, and modulator predictor sets. However, our interest in the PAM classes was not to identify a ‘source’ of movement variation due to the PAM classes but to examine how the PAM factor organizes gradients of movement variation not due to topography, vegetation, seasonal modulators, known behaviors, or individual variability.

Temporal-Modulator Partial RDA

Our partial RDA model which used daily temperature, daily precipitation, length of the day and relative age of female grouse as the predictor matrix had a 1st constrained ordination axis (RDA1) which explained 2.5% of the variation in the movement data, after controlling for all other covariates (total-minus-conditioned variance). The 2nd constrained axis (RDA2) only explained 0.6% of the total-minus-conditioned variance. The 1st unconstrained axis accounted for 25.7% of the total-minus-conditioned variability which shows that there was substantial structure not captured by the constraint (predictor matrix) or conditioning (covariable matrix) variables.

Our seasonal modulator triplot which employed the 1st and 2nd constrained axes (RDA1 and RDA2) indicated that the standard deviation of movement speeds for a nearest neighbor hullset was largely organizing the dispersion of observations along the first axis. The standard deviation of movement speeds in a hullset (h-S-sd) was strongly negatively correlated with the length of day, precipitation, and temperature, which therefore also structure the dispersion of observations along the first axis. Hull-enclosed points, 100-m patch residence time, variability (CV) in 100-m patch residence time, and distance to first nest largely organized dispersion of observations along the 2nd axis. Temperature and day length were the predictor variables most strongly associated with the 2nd axis.

Female age was weaky represented in the triplot indicating that use-intensity is driven mostly by factors other than female age. Day length, and precipitation had a strong-positive correlation with each other and a strong-negative correlation with time-to-return, hull area, and standard deviation of movement speeds indicating that movement properties and precipitation vary seasonally. Day length was also strong-positive correlated with 100-m patch revisitation and the duration of visitation to a hull indicating that high revisitation to 100-m patches and average duration of hull visits are highest during the longest days. Temperature and day length were only moderately positively correlated indicating that they are relevant to sage-grouse movement ecology in unique ways despite being highly correlated in an absolute sense.

Temperature was strongly negatively correlated with the movement activity related variables (i.e., speed, variation in speed, area) and time to return indicating that movement activity is greater during the winter and there is seasonal fidelity to winter ranging areas (see Figure 3). Duration of hull visits, 100-m patch revisitation, residence time, hull-enclosed points, and CV of 100-m patch residence time were strongly negatively correlated with distance to first nest indicating that these movement properties are elevated near nesting areas.

Vegetation Partial RDA

The 1st and 2nd constrained axes from our vegetation-constrained partial RDA explained 1.5 and 0.7% of the total-minus-conditioned variability in the movement data, respectively. The 1st constrained axis (RDA1) was most strongly associated with speed-SD, speed, CV of 100-m residence time, hull area, and CV of 500-m residence time. The 2nd constrained axis largely represented hull-enclosed points, hull revisits, residence time, 100-m revisits, distance to first nest, and time-to-return to 100-m patches. The 1st unconstrained axis (not shown) accounted for 25.8% of the total-minus-conditioned variability which indicates substantial structure not captured by the constraint or conditioning variables.

The vegetation-constrained triplot indicated that the movement activity and space-use variables (speed, speed-SD, area) had a strong-positive correlation with each other but had a moderate-negative correlation with residence time (Figure 4). Movement activity variables were uncorrelated with use-intensity variables such as 100-m revisits, hull-revisits, and hull-enclosed points indicating that movement activity and use-intensity variables represent separate phenomenon in the context of the vegetation-constrained partial analysis. Variability in residence time at both the 100- and 500-m scale were positively correlated with movement activity variables indicating that the RDA1 axis represents various facets of movement activity, space use, and resource selection strength. Hull-enclosed points, hull revisits, 100-m revisits, and residence time had a negative correlation with net displacement away from first nest (ND-nest) and 100-m time-to-return. Therefore, use-intensity variables hull-enclosed points, hull revisits, 100-m revisits, and residence time tend to increase as distance from first nest and time-to-return decrease indicating that the RDA2 axis represents phenomena related to breeding ecology.

Movement-vegetation relationships evident from RDA1 of our triplot indicate a positive correlation among bare ground, coefficient of determination (rCD) of vegetation biomass, vegetation biomass, radius of variance (RoV) of vegetation biomass, and CV of sage. These 5 vegetation variables had a strong-positive correlation with CV of residence time, speed-SD, speed, area and CV of 500-m residence time. Therefore, variability in fine-grain sage and fine-grain NDVI related variables tend to increase as various facets of movement activity, space use, and resource selection strength increase.

Hull forest and hull LANDFIRE sagebrush were positively correlated with 100-m revisits, hull-revisits, hull-enclosed points, and residence time indicating that forest cover increases as use-intensity increases. In contrast, vegetation height and fine-scale sagebrush cover were negatively correlated with the use-intensity variables but positively correlated with distance from first nest and time-to-return indicating that ecological relationships with vegetation height, fine-scale sagebrush cover, forest and LANDFIRE sagebrush vary as a function of distance from nesting areas. Space- and time-use intensity tends to decrease with increasing values of vegetation height and sagebrush cover but increases with increasing vegetation biomass and radius of variance of vegetation biomass.

Terrain Partial RDA

The 1st and 2nd constrained axes from our topography-constrained partial RDA explained 4.3% and 5.5% of the total-minus-conditioned variability in the movement data, respectively. The 1st constrained axis largely represented speed-SD, speed, area, residence time, CV of residence time, CV of 500-m time-to-return, and 100-m revisits. The 2nd constrained axis was most strongly associated with CV of time-to-return, number of hull-enclosed points, hull eccentricity, revisits, and hull revisits. The 1st unconstrained axis accounted for 25.2% of the total-minus-conditioned variability which shows that there was substantial structure not captured by the constraint or conditioning variables.

The topography-constrained triplot showed that speed, speed-SD, area, CV of 100-m residence time, CV of 500-m residence time, time-to-return, CV of time-to-return, and CV of 500-m time-to-return were highly positively correlated with each other but had a strong-negative correlation with residence time, 100-m revisits, duration, and eccentricity (Figure 5). Hull revisits, and hull-enclosed points had a strong-positive correlation between themselves and were negatively correlated with eccentricity.

Variability (CV) of topographic wetness index, and variability of normalized height were the predictor variables most strongly associated with speed, speed-SD, area, CV of 500-m residence time, time-to-return, and CV of 500-m time-to-return. CV of 30-m vector ruggedness measure and water body RoV were strong-positive correlated with hull enclosed points, hull revisits, and CV of time-to-return, negatively correlated with eccentricity, but uncorrelated with most other variables.

Behavior Partial RDA

The 1st and 2nd constrained axes from our behavior-constrained partial RDA explained 11.1% and 1.9% of the total-minus-conditioned variability in the movement data, respectively. The 1st constrained axis was most strongly associated with displacement from first nest (ND-nest), time-to-return, area, speed, hull-enclosed points, 100-m residence time, 100-m revisits, and duration. The 2nd constrained axis was most strongly associated with speed, ND-nest, 100-m variability in residence time, and 500-m variability in residence time. The 1st unconstrained axis accounted for 22.6% of the total-minus-conditioned variability which shows that there was substantial structure not captured by the constraint or conditioning variables.

The behavior-constrained triplot illustrated discrimination among the centroids of the different movement types (Figure 6). Incubating, laying and potential-brood centroids had higher than average 100-m residence time while the exploratory movement centroid is much lower than average. The relationship between the behavior centroids and area was reversed because area and 100-m patch residence time are negatively correlated: exploratory movement was higher than average and laying, incubating, and potential brood were lower than average. The winter range, brood, and unclassified centroids are close to the average of the movement activity variables. The exploring and winter range centroids had higher than average ND-nest, and the laying centroid had lower than average ND-nest. Revisits (100-m) were highest for laying and lowest for exploring, brood, and winter range. Hull-enclosed points were highest for laying and potential brood and lowest for exploring.

Individual ID Partial RDA

The 1st and 2nd constrained axes from our ID-constrained partial RDA explained 9% and 2.4% of the total-minus-conditioned variability in the movement data, respectively. The ID-constrained triplot illustrated discrimination among the centroids of the individual sage-grouse (Figure 7 & Figure 8). The 1st constrained axis was strongly associated with hull-revisits, enclosed points, 100-m revisits, residence time, and time-to-return. The 2nd constrained axis was most strongly associated with displacement from first nest, duration, and variability in 100-m time-to-return. As indicated by their short arrows, individual ID is primarily explaining variability in space- and time-use intensity properties other than speed, speed SD, area, CV of 100-m residence time, and CV of 500-m residence time.

We used our individual ID partial RDA to examine residual structure in the movement data after accounting for the temporal modulator, topography, vegetation, and behavior/ID predictor sets. To examine residual structure in the data we produced a plot of the response variables using the first two unconstrained axes (PC1 & PC2) from the RDA model. The 1st and 2nd unconstrained axis of our PC1 and PC2 plot (Figure 9) represents 22.4 and 13.6% of the total-minus-conditioned variation in the movement data. Hull-enclosed points, 100-m revisits, residence time, time-to-return, and CV of 500-m time-to-return contributed most to the first axis. CV of residence time, hull-enclosed points, CV of 500-m residence time, and area contributed most to the second axis. Movement activity and use-intensity variables were negatively correlated.

PAM Classes Partial RDA

The 1st and 2nd constrained axes from our partitioning around medoids (PAM) constrained partial RDA explained 22.7% and 7.1% of the total-minus-conditioned variability in the movement data, respectively. The PAM-constrained triplot illustrated clear discrimination among the centroids of the inferred movement clusters (Figure 10 & Figure 11). The 1st constrained axis was strongly associated with residence time, hull-revisits, hull-enclosed points, time-to-return, and variability (CV) in 500-m time-to-return. The 2nd constrained axis was strongly associated with hull revisits, hull duration, and CV of 500-m residence time. Residence time, revisits, hull revisits, hull-enclosed points, and CV of time-to-return were positively correlated among themselves and negatively correlated with time-to-return, area, CV of 500-m residence time, and CV of 500-m time-to-return. Net displacement from nest was negatively correlated with residence time, 100-m revisits, hull revisits, hull-enclosed points, and CV of 100-m time-to-return.

To examine residual structure in the data after adding the PAM factor we produced a plot of the response variables using the first two unconstrained axes (PC1 & PC2) from the PAM classes partial RDA model. The 1st and 2nd unconstrained axis of our PC1 and PC2 plot (Figure 12) represents 12.1 and 11% of the total-minus-conditioned variation in the movement data. Hull-enclosed points, hull duration, and hull eccentricity contribute most to the first axis. Speed, speed-SD, CV of 100-m residence time, CV of 500-m residence time, and area contribute most to the second axis.

Principal Component Analysis

The 1st and 2nd axes from our PCA analysis represent 44.4% and 14.7% of the variability in the seventeen space- and time-use intensity variables. Note that two extra 'response' variables (RTmu, RTmu-cov) were included in the PCA (Appendix E, Table 10). Hull use-intensity (h-UI), hull area, residence time, revisits, and time-to-return were strongly associated with the first axis and hull-enclosed points, hull revisits, and variability (CV) of residence time were strongly associated with the second axis.

In our PCA-based PC1 and PC2 biplot, hull use-intensity, residence time, and revisits had a strong positive correlation with each other and a strong negative correlation with ND-nest and time-to-return. Hull enclosed points also had a strong negative correlation with time-to-return and ND-nest. Hull area, speed, speed-SD, and CV of 500-m residence time had a strong positive correlation with each other and a strong-negative correlation with hull use-intensity and residence time. Mean residence time (RTmu) and total residence time (RT) had a weak-positive correlation which was also true for CV of total residence time (RT-cov) and CV of mean residence time (RTmu-cov).

In general, the 12 supplementary environmental variables included in our PCA analysis were not well represented in our PCA-based PC1 and PC2 biplot. Temperature, day length, variability (rCD) of vegetation biomass, CV of topographic wetness index, CV of normalized height, and CV of vector ruggedness index were the most well represented. Temperature and day length were positively correlated with residence time, hull use-intensity and revisits, and negatively correlated with time-to-return, ND-nest, CV of residence time, CV of 500-m time-to-return, and area. Variability (rCD) of vegetation biomass, variability of topographic wetness index, variability of normalized height, and variability of vector ruggedness index were positively correlated with area, variability of residence time, and variability of 500-m time-to-return. The variables representing variation of used landscape conditions were negatively correlated with hull use-intensity, residence time, 100-m revisits, and duration. Therefore, variability of used landscape conditions was generally positively associated with movement activity, space use, and resource selection related variables and negatively associated with use-intensity related variables.

The relationships among the movement properties and between the movement properties and the supplementary environmental variables in our PCA analysis generally corresponded to what we observed with our more rigorous (direct gradient analysis) RDA analyses. However, the dispersion of individual hull 'sites' relative to behavior/phenology modes exhibited a much clearer pattern in our PCA analysis where we were not removing other sources of variation (partial RDAs) in the movement properties (Figure 13). Incubation hulls were below average with respect to both the PC1 and PC2 axes and were well discriminated. Laying hulls occupied the boundary between the incubation cloud of hulls and brood or potential-brood cloud of hulls. Winter range hulls were above averagee relative to the PC1 axis and unclassified hulls were interspersed among all known behavior modes (not shown). Exploratory hulls were always above average with respect to the PC1 axis but often (denser point cloud) below average with respect to the PC2 axis.

Discussion

If sage-grouse movements and space- and time-use are primarily driven by searching and preference for certain landscape conditions, then a large proportion of movement-property variability should be explained by landscape conditions such as vegetation cover. An alternative possibility is that sage-grouse movements and space use are largely determined by innate or learned behavioral patterns or seasonal fidelity to geographic areas and may have only weak response to differential terrain, hydrologic characteristics, surrounding vegetation, or weather. Hard wired space- and time-use would make population-level associations between movement properties and landscape conditions weak and inconsistent among individual sage-grouse. Our results suggest that measurable and manageable vegetation conditions are less influential on movement patterns than terrain conditions or seasonal modulator variables such as day length or temperature. We also observed substantial individual-level variability in movement patterns which further suggest that difficult-to-measure behavioral traits or unobserved experience may structure sage-grouse space use and use-intensity more than differential vegetation conditions in our study area.

Foundational Relationships among Space- and Time-Use Intensity Properties

Recent research investigating the relationships among home-range size (area), resource selection, residence time, time-to-return, and landscape-element arrangement has resulted in a theoretical framework for reconciling these movement-related phenomena (Van Moorter et al. 2016). We have quantified variables similar to those considered by Van Moorter et al. (2016) and can examine our results in the light of their framework. Shorter residence time and longer time-to-return within a home range should be associated with increased home range size which is then associated with greater variability in residence time and time-to-return. Our constrained-axis topography and vegetation triplots indicated strong support for those expected relationships among movement characteristics except that variability of 100-m time-to-return (TtoR-cov) was uncorrelated with area in both cases. Other triplots were mostly consistent with theoretical predictions where 100-m time-to-return, variability of 500-m time-to-return, and variability of 500-m residence time had consistent positive correlations with area. As expected, residence time was always negatively correlated with area; more time spent in patches equates to less time spent maintaining a large home-range. Furthermore, all the aformentioned relationships, except with TtoR-cov, were still supported after we added grouse ID and then statistically inferred low-level behavior modes. Expected relationships (TtoR-cov excluded) were also consistent with the results of our exploratory PCA analysis.

Inconsistent with Van Moorter et al. (2016), the relationship between TtoR-cov and area showed a negative correlation in all plots including our unconstrained axis RDA plots and our PCA-based biplot. This discrepancy may have resulted from scale-dependent relationships between TtoR-cov and area. Theoretically, variability in residence time and time-to-return are positively correlated with the strength of 3rd order habitat selection (Johnson 1980) which is positively correlated with home-range area (Van Moorter et al. 2016). Indeed, at the 500-m extent, increased variability in residence time and time-to-return was positively correlated with hull area which may indicate decreased consistency in use of areas within a hull due to increased 3rd order selection. In contrast, increased TtoR-cov for female sage-grouse appeared to be a result of more intensive use of the broader area which provided greater opportunity for differential visitation to patches within a hull. For instance, hulls with many enclosed points (i.e., high use-intensity) may contain habitat patches used for laying, incubating, and brood rearing in addition to rarely visited patches encountered during taxis or searching, which would result in high variability of 100-m time-to-return. Additionally, increasing the extent by which recursive movement properties are calcualted (e.g., 500-m radius) has the effect of smoothing variability in movements because greater displacements are required to exit patches and to be counted as a separate visits. Greater magnitude movements, associated with large hulls, will then be necessary to exit patches and create variability in time-to-return. Van Moorter et al. (2016) also found that their proposed relationship between variability of time-to-return and home-range area was scale sensitive. The results of Van Moorter et al. (2016) partially motivated our inclusion of multiple extents (i.e., 100-m, 500-m) of variability of time-to-return in our analyses so we were not surprised by our results.

The evident scale sensitivity of the relationship between TtoR-cov and other movement properties warrants further research, but the negative association between TtoR-cov and area may suggest multi-season revisitation patterns at fine spatial scales. For example, TtoR-cov tended to increase as displacement from first nest decreased and this pattern held in all of our partial RDA analyses as well as the PCA analysis. During laying and incubation 100-m time-to-return for the nest site is very low but periphery patches can have high to moderate time to return, partially due to seasonal revisitation, which results in high variability in time-to-return for smaller breeding-related home ranges. The variability in 100-m time-to-return and distance to first nest relationship may also be driven by exploratory movements which tend to have consistently large (low variability) values of 100-m time-to-return and large distances from nesting regions.

The importance of habitat selection and associated landscape-element arrangement proposed by Van Moorter et al. (2016) may help explain why our topography and vegetation triplots most strongly conformed to theoretical expectations. Each of our partial RDAs represent the variation explained by a variable set after removing the contribution of the compliment sets of variables (e.g., movement ~ topography | vegetation, modulators, behavior/ID). Movement, home-range size, and habitat selection relationships are expected to play out in both geographic and environmental space (Mueller and Fagan 2008, Van Moorter et al. 2013, Van Moorter et al. 2016) where topography and vegetation represent environmental space.

Our multivariate movement-integrated RDA that incorporates mean and variability (i.e., CV, rCD, RoV) summary statistics of resources within short-term home ranges can aid interpretation of how and why selection occurs on the landscape. In our topography triplot, variability of 500-m residence time, variability of 500-m time-to-return and variability of 100-m residence time were positively correlated with variability of normalized height, variability topographic wetness index, and radius of variance of fine-scale landcape ruggedness. We attribute the correspondance between variation in the movement properties and variation in the terrain properties as a signal of selection for those aspects of the landscape. Increased within-hull variability in residence time and time-to-return among habitat patches is expected as 3rd order habitat-selection strength increases (Van Moorter et al. 2016). Increased selection strength would then account for increased variability in landscape conditions among visited locations (patches), provided there is sufficient heterogeneity (i.e., low spatial autocorrelation) inside the hull. In other words, profitable patches have high residence time and low time-to-return and less desirable patches have low residence time and high time-to-return. If these two types of visited patches within a hull have divergent values for a predictor variable, then the variability will be high for both the movement characteristics and the predictor variables. The reader should note that we did not explicitly account for spatial autocorrelation but expect that spatial autocorrelation decreases and therefore landscape heterogeneity increases as the magnitude of movements increase (e.g., increased hull area). The positive correlation that we observed between variability of the aforementioned topographic variables and area is likely to be a function of the strength of 3rd order habitat selection but modulated by autocorrelation of landscape elements (Van Moorter et al. 2016). Furthermore, decreasing variability of landscape conditions with increasing residence time and decreasing area may indicate decreased 3rd order selection and increased 2nd order selection (Van Moorter et al. 2016). Incubating sage-grouse exhibited high residence time, small home ranges, and negative associations with variability of landscape conditions within short-term home ranges, and the opposite was true of winter ranging females. Therefore, resource selection appears to operate differently as a function of behavior modes and seasonality. Simplistic assumptions made when using resource selection functions are unlikely to account for spatial, temporal, and behavior fluctuations within the selection process of sage-grouse. Our movement-integrated study design was flexible in evaluating the links among space use, movement properties, and resource selection without incorporating user-defined availability constraints. Gradients of use-intensity were instead generated by the movement process of individual females.

Our partial RDA analyses indicated that the correlation among area (i.e., short-term home range size), speed, and speed-SD was positive and strong. Increased variability in travel speeds may be due to increased diversity of low-order behavior modes such as taxis, searching, and foraging in larger hulls (e.g., winter ranging hulls). Supporting this premise is the fact that variability of 100-m residence time was positively correlated with speed, speed-SD, and area in our vegetation and topography constrained-axis triplots and our PCA. Understanding ecological controls on differential hull areas appears to be largely redundant with understanding drivers of differential speed or speed-SD at the 6-hour temporal scale we examined.

Area was inversely related to the use-intensity related variables hull-enclosed points, use-intensity, revisits, and residence time which indicates consistent and interpretable relationships between space- and time-use. All triplots that we examined indicated a lack of correlation between hull area and hull revisits which demonstrates that similar space-use extents can result from different degrees of visitation to an area. The lack of correspondence between hull-revisits and hull-area indicates the importance of these variables for inferring alternate behavioral mechanisms that result in similar space-use extents. For example, incubation-hull areas are constrained by a central-place foraging strategy (Stephens 1986), but incubation hulls did not necessarily incur numerous revisits by a female. Differences between sage-grouse nesting and brood-rearing habitats (Peterson 1970, Hagen et al. 2007, Dzialak et al. 2011, Walker et al. 2016) indicate that female sage-grouse tend to leave the nest zone (incubation hull) after a failed or successful nest (Berry and Eng 1985, Fedy et al. 2012). Despite well documented nesting region fidelity (Berry and Eng 1985, Fischer et al. 1993, Holloran et al. 2005, Gerber et al. 2019), neither nesting zone (yearly nesting home range) nor nest site fidelity (nest reuse) are thought to be common (Schroeder et al. 1999). Indeed, we observed that upon nesting cessation, females tended to use areas that did not overlap nest sites or zones which is consistent with research examing the distance between nest sites and early brood rearing locations (Connelly et al. 2011d). Therefore, characteristic nesting-hull areas result from high use-intensity for a limited duration but high revisitation is atypical after nesting ends. In contrast, movement in a zone of attractive brood-rearing habitat or nesting-region habitat may result in hulls with a comparable area but that are generated by a different foraging strategy (e.g., area-restricted search) where the area is used repeatedly within, and possibly among, seasons. Our behavior triplot supports this supposition by illustrating that revisits at the hull extent were above average for the potential brood and laying behavior modes.

We found a discrepancy between broods and potential broods which highlights the importance of defining ecologically valid grouping factors in research designs and statistical analyses. Potential broods were more like the incubating mode which exhibited elevated residence time, lower area, and lower distance to first nest relative to overall averages. Confirmed broods were close to average with respect to all movement properties. We attribute the discrepancy between movement properties for broods and potential broods to the fact that we defined potential broods as all locations up to 2 weeks post hatch. Many hatched-nest females (brood status unknown) would have broods with young chicks during those two weeks and would have more restricted average movements than the movements of brood-rearing females (status known) averaged over six weeks; broods gain mobility and can shift to alternate habitats with time (Peterson 1970, Wallestad 1971, Dzialak et al. 2011, Fedy et al. 2012). We did not define early and late brood rearing periods because broods did not make dramatic shifts (Wallestad and Pyrah 1974, Dzialak et al. 2011) to alternate regions during the ≤ 6-week period that we were able to monitor broods after hatch. Our observations and results suggest that brood rearing movement behavior in our study area changes in a gradual manner that would not be well represented by a subjective early and late brood-rearing factor.

None of our constrained-axes triplots indicated that eccentricity was associated with area, speed, and speed-SD. Despite eccentricity values increasing with the directionality of movements, they do not necessarily correspond to increased speeds, variability in speeds, or hull-areas. For instance, we observed (unpublished data) that eccentricity values were highest for large taxis movements as well as recursive travel between 2 patches, such as nests and incubation break sites (Dudko et al. 2019) or roosts and daytime foraging/loafing sites (Dunn and Braun 1986b). Eccentricity values are high in both scenarios but extensive directional movements resulted in large hulls, and to-and-fro movements between a nest site and a foraging site produced relatively small hulls. Therefore, eccentricity seems to provide additional context by which to infer behavioral mechanisms that dictate space-use extents. Eccentricty was poorly represented in all our triplots except the topography triplot (moderately-well represented) but when we added the PAM factor to our RDA the residual structure (PC1 & PC2) plot indicated a strong gradient of variation due to eccentricity. Therefore, we demonstrated that detailed study designs and analyses which recognize the hazards of excluding important grouping factors or variables are important for valid inference. When adequately parsed, eccentricity of short-term home ranges is a relatively novel and useful metric for understanding low-level sage-grouse behaviors.

Importance of Accounting for Behavior Modes

In addition to examining interrelationships between movement characteristics and how temporal, spatial, and individual-level factors affect these characteristics, our explicit accounting of behavior modes also promotes a mechanistic understanding of the movement process. The 7 high-level behavior modes that we included in the RDA analyses accounted for 31.2% overall variation in movement properties, so movement patterns vary substantially among phenological stages. However, only 8.5% pure variation was explained by the high-level modes which indicates that phenological stages are tied to changes in other factors such as day length, terrain characteristics and vegetation. Therefore, it is important to account for behavior modes and thereby evaluate relationships between habitat responses and landscape conditions within individually defined behavior modes. The addition of the 8 statistically inferred behavior modes to our behavior/phenology/ID matrix explained an additional 9.0% of the variability in the movement data, further illustrating that substantial structure remained after accounting for vegetation, topography, sage-grouse high-level behavior modes, and individuality.

Seasonality of Movements and Space Use

Consistent with the literature, our results indicate that sage-grouse exhibit highly variable seasonal movements among populations or subpopulations and among individuals (Eng and Schladweiler 1972, Berry and Eng 1985, Connelly et al. 2000b, Fedy et al. 2012, Orning and Young 2016) and that sage-grouse congregate on, and maintain fidelity to, large winter ranges (Eng and Schladweiler 1972, Berry and Eng 1985, Connelly et al. 2011a). Our seasonal modulator RDA indicated that area had a strong-negative correlation with day length which was itself positively correlated with temperature and precipitation. An increase of hull area with decreasing daylength and temperature is consistent with previous research indicating that sage-grouse movement activity increases as summer progresses into fall and can be maximal during autumn-to-winter and winter-to-spring seasonal range transitions (Dunn and Braun 1986a, Fischer et al. 1996, Bruce et al. 2011, Fedy et al. 2012, Caudill et al. 2015, Dahlgren et al. 2016b, Dinkins et al. 2017). Previous research is inconclusive regarding increased movement activity and home range sizes during winter (Hagen 1999, Orning and Young 2016), but our detailed movement analysis strongly indicates that movements and associated home ranges in our study area are larger during winter. Contributing to the evidence that movements and therefore ranges are more extensive during winter is the fact that most exploratory movements occurred during winter months. Therefore, baseline movement activity appears to be elevated during winter and is accentuated by exploratory type movements.

Modulation of Space- and Time-Use Intensity Properties by Vegetation

Our vegetation RDA model was able to illustrate multiple facets of seasonal wildlife habitat relationships. Sage-grouse in our study area generally use areas with less large stature shrubs and trees, especially during lekking related movements, late summer, fall, and winter. Some individuals used moderately to highly wooded areas (i.e., Rocky Mountain juniper) with a sagebrush component during laying, incubating, and brood rearing.

Although the identification of important landscape elements (e.g., herbaceous cover) is a precursor for prescriptive management (e.g., grazing intensity, energy infrastructure), our results indicate that relatively little (1.9%) of the variation in sage-grouse space- and time-use properties could be explained by our suite of potentially manageable covariates (e.g., lowland NDVI, sagebrush, forest, vegetation biomass). The relative unimportance of vegetation variables is conceptually consistent with Smith et al. (2020) although they examined microhabitat as opposed to our somewhat coarser grain variables. Nevertheless, synthesizing our RDA results allowed us to rank the importance of vegetation components on sage-grouse movements within our study area. Sage-grouse use-intensity was highest in low cover of non-sagebrush shrubs and lowest for high non-sagebrush shrub cover. Our LANDFIRE-based percent sagebrush vegetation type variable corresponds closest with the coarse grain shrub data used in other studies (Moynahan et al. 2007, Doherty et al. 2008) and our results indicate the use-intensity increases with increasing percent sagebrush vegetation type. Direct comparisons to our results using finer grain variables are difficult, but researchers in western Colorado determined that the proportion of xeric shrub and mesic mountain shrub (non-sage shrub categories) negatively affected sage-grouse resource selection during breeding season and winter (Walker et al. 2016). The xeric shrub type also had a negative effect during the summer-fall season. The mesic mountain shrub category in Walker et al. (2016) (serviceberry, antelope bitterbrush, Gambel oak) most closely corresponds to our vegetation height variable which registers juniper and greasewood as having higher values than sagebrush. The negative effects of non-sage vegetation types on habitat selection in Colorado correspond with our observed effects of vegetation height on use-intensity. Contrary to other studies, increased fine-scale sagebrush was also associated with decreased use-intensity. Use-intensity may have been lower for higher cover of fine-scale sagebrush because site fidelity anchored most use to areas in south Valley County. Fine-scale sagebrush cover in Valley County was lower than in the adjacent Phillips County where use was limited and typically occurred during the lower use-intensity winter raging mode. A further contradiction to other studies was that increased forest cover at the hull scale was associated with increased use-intensity. We attribute this relationship to greater tolerance of large junipers of tree stature during breeding. In fact, one female repeatedly nested (often successfully) in dense juniper thickets within a juniper savannah. Consistent with the sage-grouse knowledge base was a complete avoidance of riparian cottonwood forest and ponderosa pine forest.

Conclusions

We examined 15+ (15 primary RDA, 15 + 2 auxiliary PCA) response variables measured at a 6-hour temporal scale across all seasonal stages for up to 4 years per individual and are therefore unsurprised that our predictor variables (PAM factor excluded) only explained 50% of the variability in the response variables. Our RDA models exhibited substantial unexplained structure in the data which indicates that variability in space- and time-use intensity was largely due to unmeasured predictors (e.g., phenotypic traits, interspecific interaction, intraspecific competition, predator evasion, cognitive constraints, or other low-level behavior modes). Unexplained variation is typical of noisy ecological datasets (Zuur et al. 2007, Borcard et al. 2018) and substantial process variance is typical in sagebrush ecosystems (Moynahan et al. 2006, Dahlgren et al. 2015).

Our combination of time-local convex hull and recursive space- and time-use intensity properties provided a rich matrix of movement information at visited areas. The approach that we have presented is advantageous because derivation of the movement data was done without parametric models which impose difficult to meet assumptions. That is not to say that parametric models do not have advantages (Royle and Dorazio 2008) but most behavior models require further development with respect to capability, reliability, flexibility, and ease of use (Turchin 1998, Barraquand and Benhamou 2008, Hooten et al. 2017).

The fact that much of the explained variation was shared variation indicates substantial multicollinearity among the 4 explanatory variable sets. Had we not made use of variance partitioning and partial RDAs it would be very easy to give an explanatory variable or class of variables more causal credit than deserved. Variables not included in a statistical analysis may account for some or all the pure fraction of variation explained by a variable subset. The influences of multicollinearity on regression modeling results are a concern for all empirical studies but variance partitioning allows a deeper examination of variance fractions by isolating pure explained variation from shared variation. Interpretation of results is paramount to good science and variance partitioning can aid interpretation. Other sage-grouse researchers that employed variance partitioning for resource selection research also observed modest percentages of pure variance explained by their landscape-condition predictor variable sets (Doherty et al. 2010, Kirol et al. 2012).

By simultaneously examining space-use, resource selection (space- and time-use intensity), and multiple facets of movement, our results highlight the minor scope of isolated articles on sage-grouse ecology and should caution managers to constantly monitor the current science and adapt policy as understanding improves. Indeed, generalization of sage-grouse habitat associations within sagebrush ecosystems may be elusive (Hagen et al. 2007, Smith et al. 2020). Due to local (Dahlgren et al. 2015) and range-wide heterogeneity in sage-grouse related ecological processes (Swanson et al. 2013, Coates et al. 2018, Smith et al. 2020) the relationships we have illustrated will be particularly useful for understanding the sage-grouse population that occupies south Valley County, MT. Our detailed movement research will also be valuable for comparison with future wildlife studies that use high-resolution movement data for movement-integrated research.

Our approach of calculating a diverse set of standard movement properties and rendering the structures evident in the data with redundancy analysis lends a degree of objectivity to identifying fundamental components of sage-grouse movement and landscape-condition responses. That said, movement property and landscape-variable associations were of foremost interest; redundancy analysis was just one useful tool among many (Zuur et al. 2007, Legendre and Legendre 2012, Wood 2017, Borcard et al. 2018). The most important facet of a data analysis is interpretability and our integrated approach, though complex, generated numerous useful inferences.

We provide further evidence for some theorized interrelationships among animal movement properties (Van Moorter et al. 2016). The interrelationships we observed among movement properties and landscape conditions indicate that variability in topographic and vegetation characteristics may have a stronger association with resource selection patterns than mean values, even when averages are calculated at multiple scales. Numerous topography and vegetation variables were somewhat associated with female sage-grouse movement properties, but no single landscape-element variable or class of variables appeared to drive the observed movement patterns. Daylength explained the most variation of any single variable and terrain conditions were more strongly associated with variability in movement properties than vegetation conditions but movement associations with non-sage shrubs and tree cover were interpretable. Female sage-grouse in our study area exhibited substantial seasonal variability in movement properties with movement activity (speed, hull area, time-to-return, variability in residence time) being lowest during laying and incubation and then gradually increasing with time through brood-rearing, late summer, fall, and winter. Sage-grouse are a landscape species that have adapted to a spatiotemporally variable landscape through a combination of migration (high-level movements), seasonal modulation of lower-level movements, and strong site fidelity. Sage-grouse do exhibit non-oriented mechanisms of response to environmental conditions (e.g., 4th order selection, predator evasion) but we have highlighted high-level constraints likely due to memory mechanisms, high temporal predictability of landscape conditions, and moderate spatial heterogeneity of landscape conditions (Mueller and Fagan 2008).

Figures And Tables

Table 3. Cumulative effects of redundancy-analysis forward-selection routines performed separately for topography and vegetation matrices with sage-grouse movement properties as the response matrix. Forward selection was performed after correlation and variance inflation factor screening removed variables with $\rho = 0.6$ and $VIF \geq 2.5$. The R^2_{adj} Cum column indicates the cumulative increase in the total sum of the eigenvalues (coefficient of multiple determination) after inclusion of each additional explanatory variable. The p-values are for F-statistic based permutation tests at critical value $\alpha = 0.05$. Global model R^2_{adj} stopping criteria were also implemented in the forward selection routines.

Predictor Label	**Base Predictor**	**Computed Summary Statistic**	**R^2_{adj} Cum**	**p-value**
		Modulator Variables		
day length	length of day	hull-mean of point values	0.143	0.001
temperature	daily temperature	hull-mean of patch zonal means	0.158	0.001
female age	relative age of female	hull-mean of point values	0.166	0.001
precipitation	daily precipitation	hull-mean of patch zonal means	0.169	0.001
		Vegetation Variables		
Veg.100.rCD	Vegetation Biomass	hull-rCD of 100-m patch zonal means	0.056	0.001
Veg.RoV.100	Vegetation Biomass RoV	mean of 100-m patch zonal means	0.101	0.001
Sage.100	Sage	mean of 100-m patch zonal means	0.111	0.001
B.100	Barren	mean of 100-m patch zonal means	0.123	0.001
Sage.30.COV	Sage	hull-CV of 30-m patch zonal means	0.130	0.001
F	Forest	hullwise zonal mean	0.135	0.001
LOW.100	Lowland NDVI	mean of 100-m patch zonal means	0.139	0.001
Li.NDVI.100	Vegetation Biomass	mean of 100-m patch zonal means	0.143	0.001
LFIRE.Sage	LANDFIRE sage	hullwise zonal mean	0.146	0.001
Height.100	Height	mean of 100-m patch zonal means	0.148	0.001
		Topography Variables		
TWI.30.COV	Topographic Wetness Index	hull-CV of 30-m patch zonal means	0.075	0.001
VRM.30.COV	Vector Ruggedness Measure	hull-CV of 30-m patch zonal means	0.113	0.001

n.H.30.COV	Normalized Height	hull-CV of 30-m patch zonal means	0.129	0.001
LiDEM.VRM.30	LiDAR Vector Ruggedness Measure	hull-mean of 30-m patch zonal means	0.141	0.001
WB.100	Proximity to Water Bodies	hull-mean of 100-m patch zonal means	0.151	0.001
n.H.100	Normalized Height	hull-mean of 100-m patch zonal means	0.156	0.001
WB.RoV.100	Radius of Variance to Water Bodies	hull-mean of 100-m patch zonal means	0.159	0.001
C	Proximity to Channels	hull zonal mean	0.162	0.001
LiDEM.VRM.30.RoV	Radius of Variance LiDAR VRM	hull-mean of 30-m patch zonal means	0.163	0.001
m.Slope	Midslope Position	hull zonal mean	0.165	0.001

Table 4. Results of redundancy-analysis variance partitioning for female sage-grouse movement using 4 matrices: seasonal modulators, vegetation, topography, behavior. Columns 4 and 5 are results attained after adding individual ID to the behavior matrix. Column 6 indicates the variance fractions for which a statistical test is available. All testable components were highly significant using permutation tests with 1001 steps and critical value $\alpha = 0.05$. The total sum of the eigenvalues (i.e., R^2_{adj} [coefficient of multiple determination]) was $R^2_{adj} = 0.409$ and $R^2_{adj} = 0.499$ for the behavior only and ID-added analyses, respectively.

Component	**Df**	**R^2_{adj}**	**Df ID added**	**R^2_{adj} ID added**	**Testable**
[aeghklno] = X1 = modulators	4	0.169	4	0.169	TRUE
[befiklmo] = X2 = vegetation	10	0.148	10	0.148	TRUE
[cfgjlmno] = X3 = topography	10	0.165	10	0.165	TRUE
[dhijkmno] = X4 = behavior	6	0.312	79	0.430	TRUE
[abefghiklmno] = X1+X2	14	0.260	14	0.260	TRUE
[acefghjklmno] = X1+X3	14	0.283	14	0.283	TRUE
[adeghijklmno] = X1+X4	10	0.347	83	0.449	TRUE
[bcefgijklmno] = X2+X3	20	0.231	20	0.231	TRUE
[bdefhijklmno] = X2+X4	16	0.340	89	0.454	TRUE
[cdfghijklmno] = X3+X4	16	0.354	89	0.466	TRUE
[abcefghijklmno] = X1+X2+X3	24	0.323	24	0.323	TRUE
[abdefghijklmno] = X1+X2+X4	20	0.374	93	0.471	TRUE
[acdefghijklmno] = X1+X3+X4	20	0.387	93	0.485	TRUE
[bcdefghijklmno] = X2+X3+X4	26	0.376	99	0.482	TRUE
[abcdefghijklmno] = All	30	0.409	103	0.499	TRUE
[a] = X1 | X2+X3+X4	4	0.033	4	0.017	TRUE
[b] = X2 | X1+X3+X4	10	0.022	10	0.015	TRUE
[c] = X3 | X1+X2+X4	10	0.035	10	0.028	TRUE
[d] = X4 | X1+X2+X3	6	0.086	79	0.176	TRUE
[e]	0	0.001	0	0.002	FALSE
[f]	0	0.005	0	0.007	FALSE
[g]	0	0.001	0	0.000	FALSE
[h]	0	0.059	0	0.075	FALSE
[i]	0	0.019	0	0.026	FALSE
[j]	0	0.028	0	0.034	FALSE
[k]	0	0.025	0	0.025	FALSE
[l]	0	0.001	0	0.000	FALSE
[m]	0	0.046	0	0.044	FALSE
[n]	0	0.019	0	0.020	FALSE
[o]	0	0.030	0	0.031	FALSE
[p] = Residuals (1- ALL)	0	0.591	0	0.501	FALSE

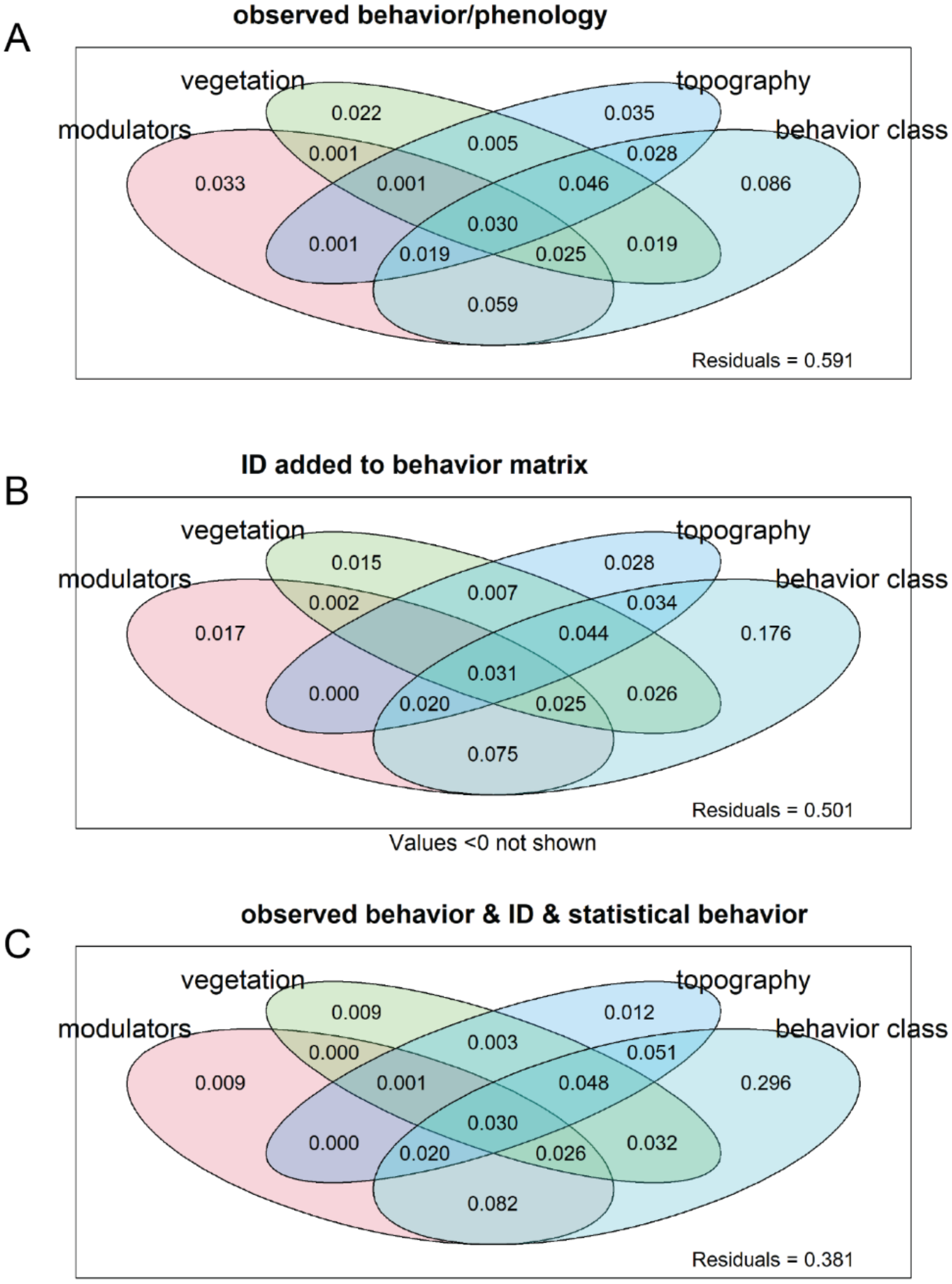


Figure 2. Venn diagrams from a redundancy-analysis partitioning of the variation in female sage-grouse movement properties explained by all combinations of 4 explanatory variable subsets. Coefficients of multiple determination (R^2_{adj}) are provided for each pure (unique) and shared (common) fraction from three separate analyses: A) without a sage-grouse ID indicator variable in the behavior matrix, B) with the ID variable included in the behavior matrix, C) with ID and PAM statistical movement clusters included in the behavior matrix.

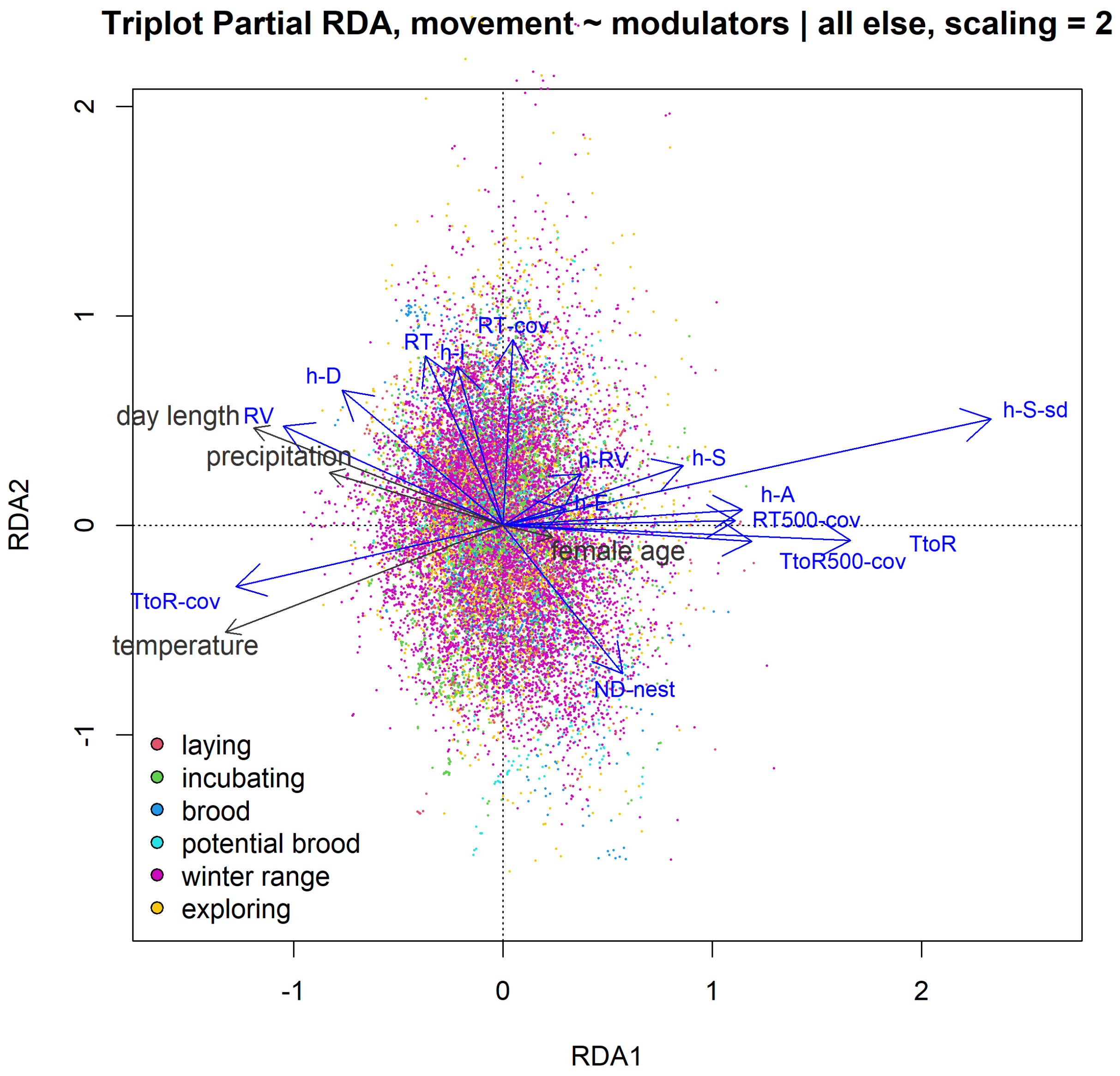


Figure 3. RDA scaling 2 – correlation triplot: The response variables are blue arrows, and the explanatory variables are black arrows. Projecting an object at a right angle on a response or a quantitative explanatory variable approximates the value of the object along that variable. The colored dots represent observations (i.e., records, objects) made for a single female sage-grouse hull. The angles in the triplot between response and explanatory variables, and between response variables themselves or explanatory variables themselves, reflect their correlations. The RDA1 axis represents 2.6% of the total-minus-conditioned variation in the movement data and RDA2 represents 0.6%. The distance a response variable arrow extends along an axis indicates the amount of variation it explains along that axis.

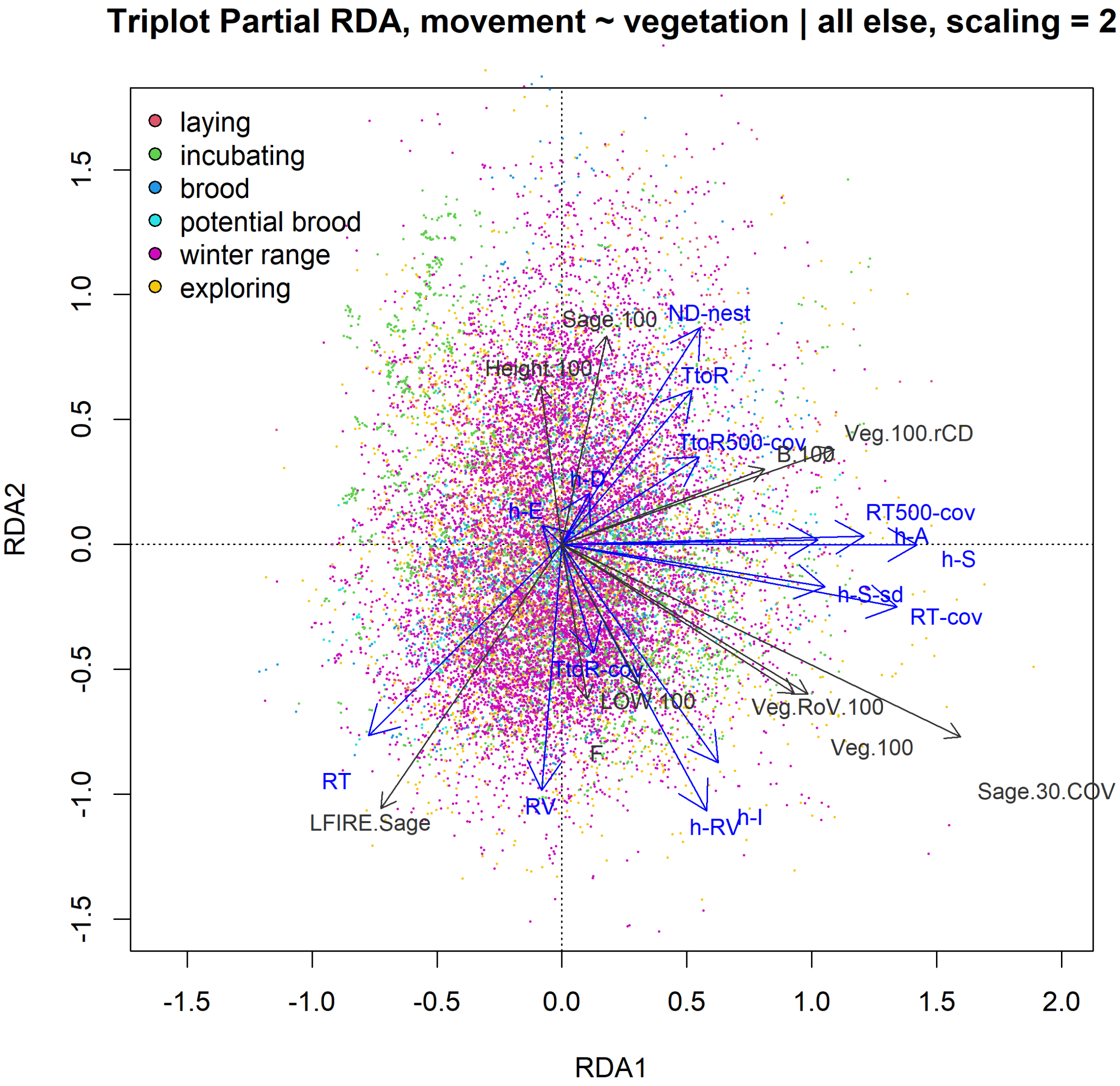


Figure 4. RDA scaling 2 – correlation triplot: The response variables are blue arrows, and the explanatory variables are black arrows. Projecting an object at a right angle on a response or a quantitative explanatory variable approximates the value of the object along that variable. The colored dots represent observations (i.e., records, objects) made for a single female sage-grouse hull. The angles in the triplot between response and explanatory variables, and between response variables themselves or explanatory variables themselves, reflect their correlations, The RDA1 axis represents 1.5% of the total-minus-conditioned variation in the movement data and RDA2 represent 0.8%. The distance a response variable arrow extends along an axis indicates the amount of variation it explains along that axis.

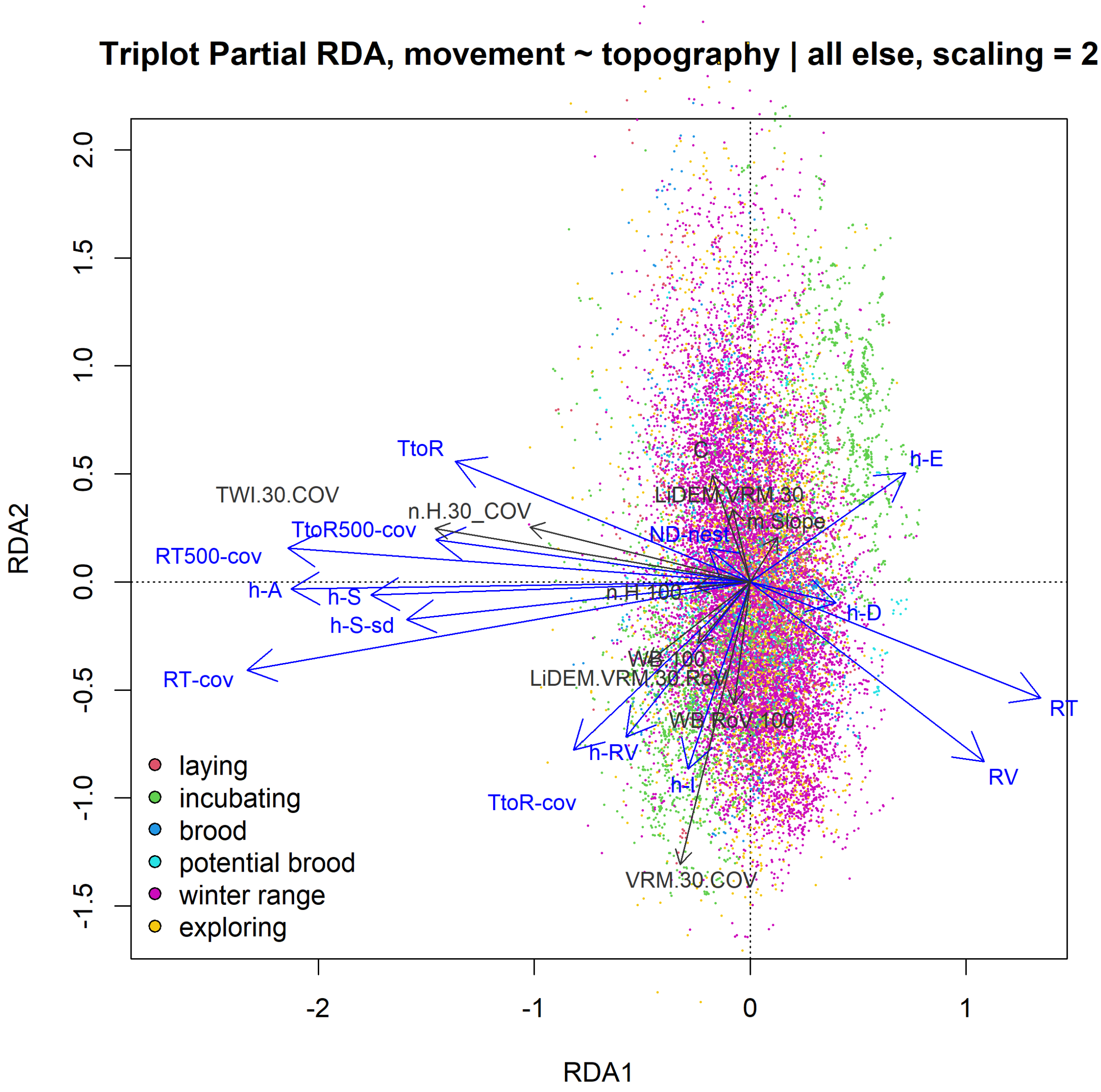


Figure 5. RDA scaling 2 – correlation triplot: The response variables are blue arrows, and the explanatory variables are black arrows. Projecting an object at a right angle on a response or a quantitative explanatory variable approximates the value of the object along that variable. The colored dots represent observations (i.e., records, objects) made for a single female sage-grouse hull. The angles in the triplot between response and explanatory variables, and between response variables themselves or explanatory variables themselves, reflect their correlations. The RDA1 represents 4.3% of the total-minus-conditioned variation in the movement data and RDA2 represents 0.5%. The distance a response variable arrow extends along an axis indicates the amount of variation it explains along that axis.

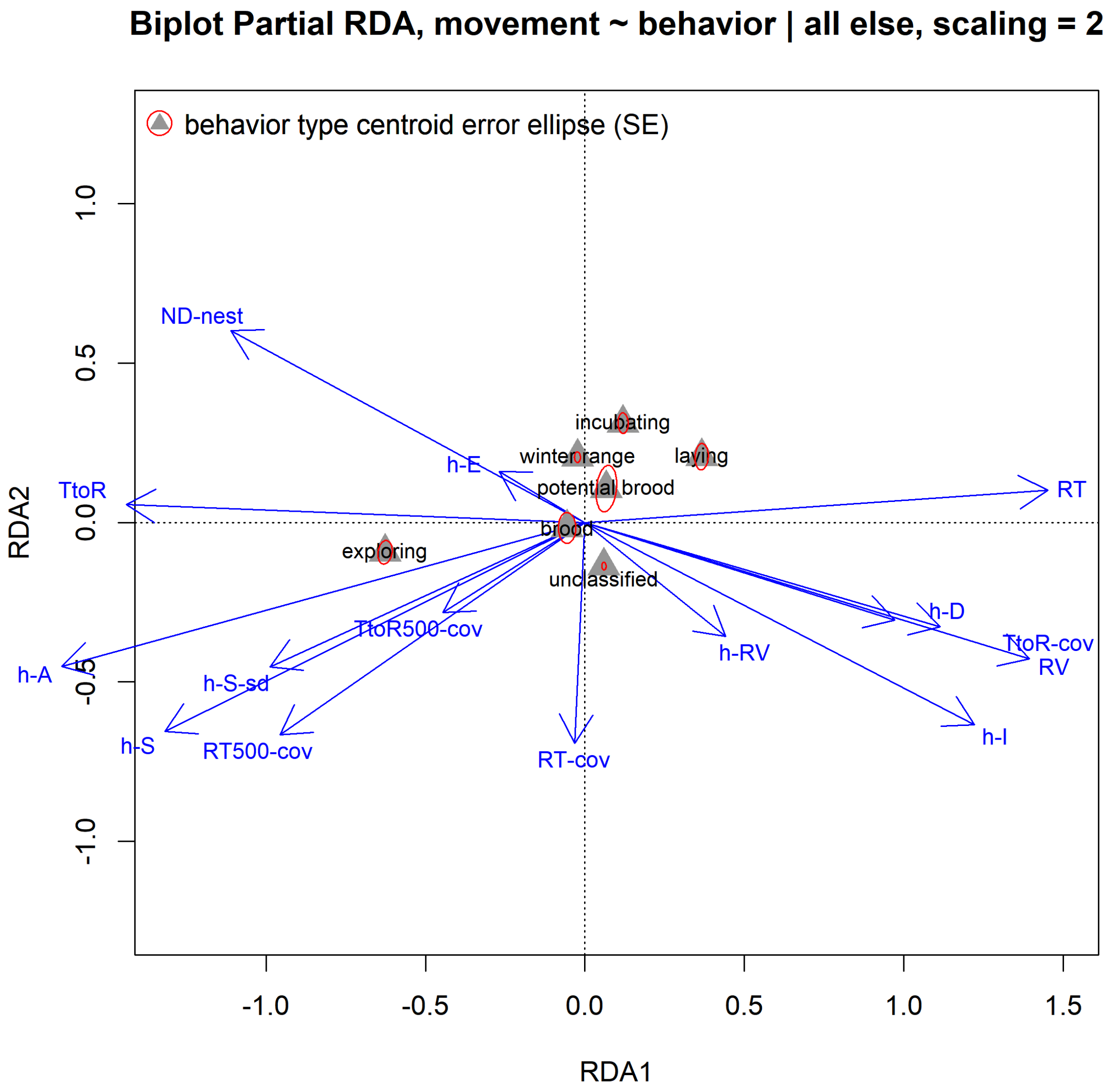


Figure 6. RDA scaling 2 – correlation biplot: The response variables are blue arrows. Projecting an object (black triangle) at a right angle on a response variable approximates the value of the object along that variable. The black triangles represent behavior-mode centroids. The RDA1 axis represents 11.1% of the total-minus-conditioned variation in the movement data and RDA2 represents 1.9%. The distance a response variable arrow extends along an axis indicates the amount of variation it explains along that axis.

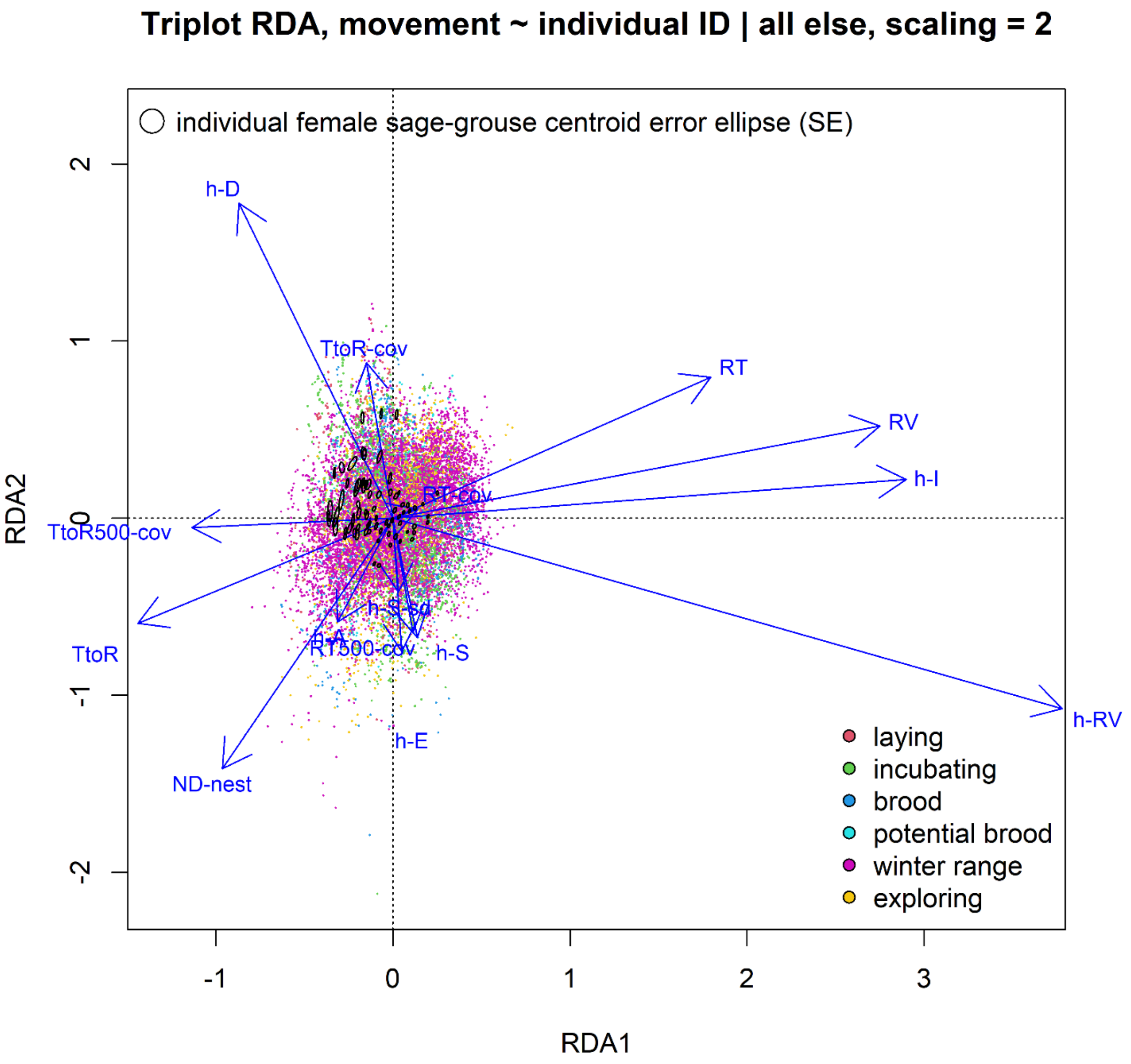


Figure 7. RDA scaling 2 – correlation triplot: The response variables are blue arrows, and the explanatory variables are black arrows. Projecting an ID centroid at a right angle on a response variable approximates the value of the object along that variable. The colored dots represent observations (i.e., records, objects) made for a single female sage-grouse hull. The angles in the triplot between response variables reflect their correlations. The RDA1 axis represents 9.0% of the total-minus-conditioned variation in the movement data and RDA2 represents 2.4%. The distance a response variable arrow extends along an axis indicates the amount of variation it explains along that axis.

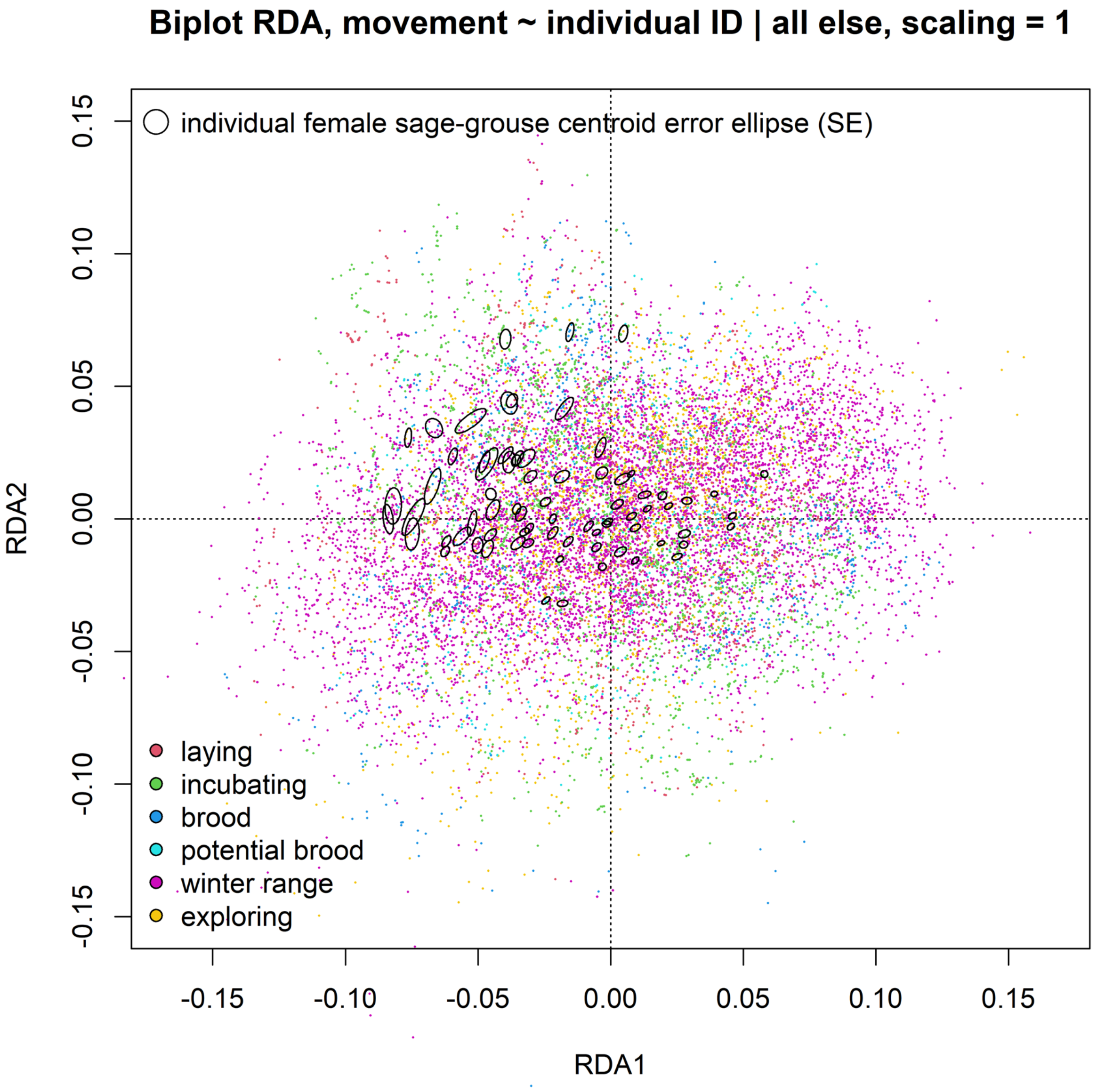


Figure 8. RDA scaling 1 – distance biplot: The colored dots represent observations (i.e., records, objects) made for a single female sage-grouse hull. The RDA1 axis represents 9.0% of the total-minus-conditioned variation in the movement data and RDA2 represents 2.4%. The distance between objects, distance between centroids, and distance between objects and centroids represents how similar or different the elements are from the perspective of the variation represented by that plot.

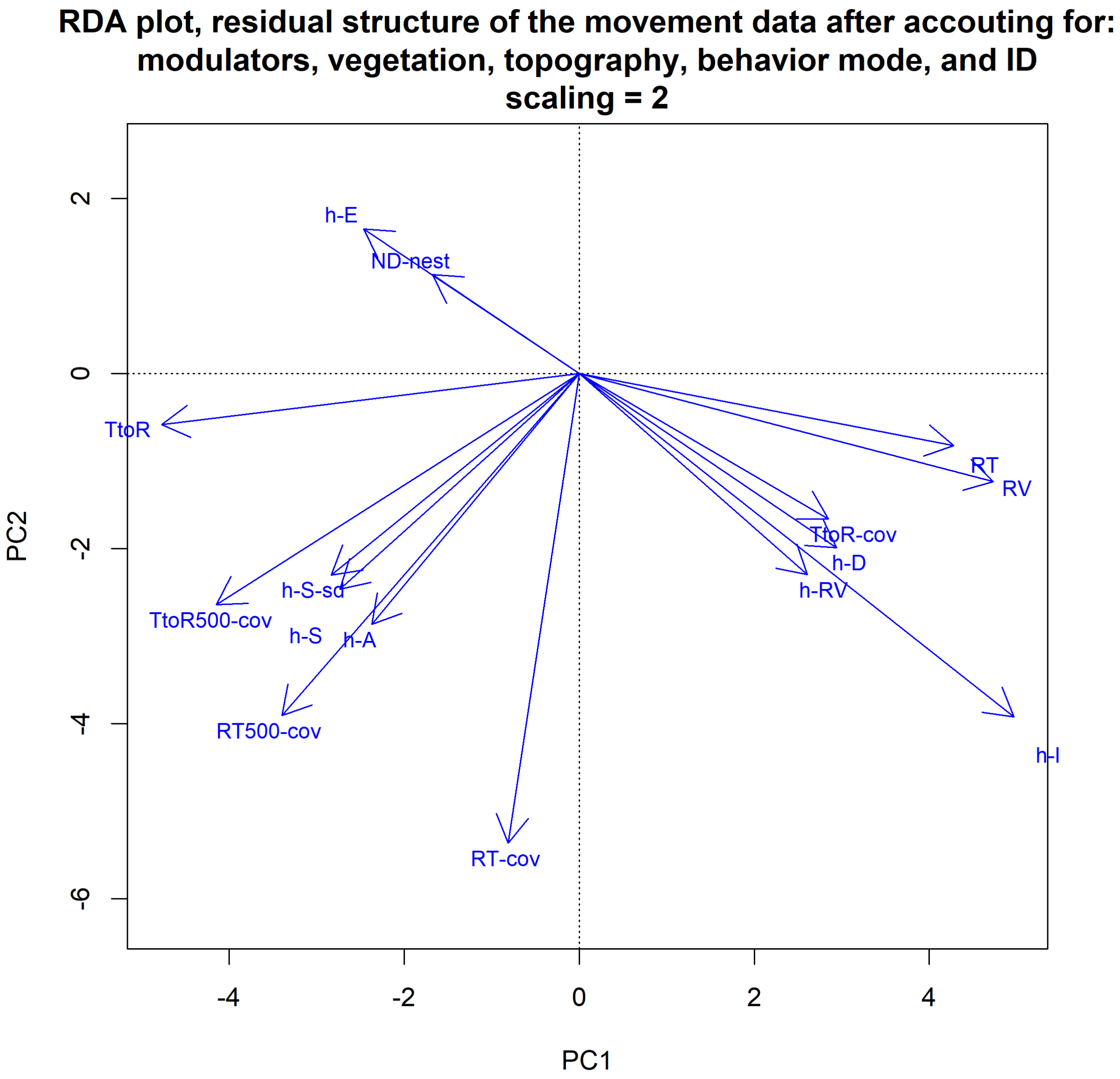


Figure 9. RDA scaling 2 – correlation plot: The response variables are blue arrows and the angles between arrows reflect correlations between variables. The PC1 axis represents 22.4% of the total-minus-conditioned variation in the movement data and PC2 represents 13.6%. The distance a response variable arrow extends along an axis indicates the amount of variation it explains along the axis. The plot illustrates residual structure in female sage-grouse movement data after accounting for temporal modulator, vegetation, topography, observed behavior modes, and individual variability.

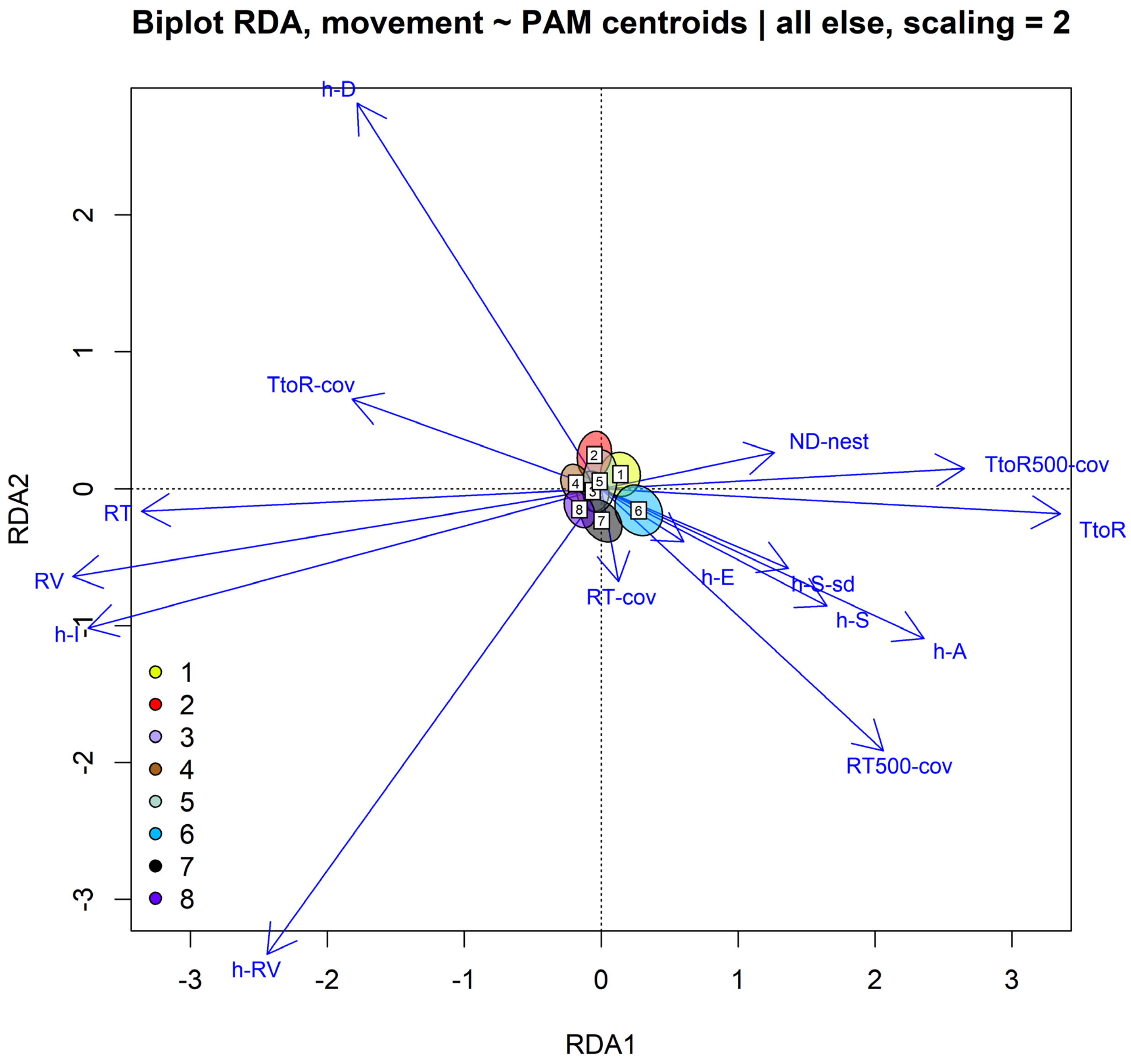


Figure 10. RDA scaling 2 – correlation biplot: The response variables are blue arrows, and the explanatory factor levels are the colored ellipses. Projecting a class-centroid label at a right angle on a response variable approximates the value of the class mean along that variable. The colored ellipses represent the standard deviation of all observations belonging to a factor level. The angles in the triplot between response variables reflect their correlations. The RDA1 axis represents 22.7% of the total-minus-conditioned variation in the movement data and RDA2 represents 7.1%. The distance a response variable arrow extends along an axis indicates the amount of variation it explains along that axis.

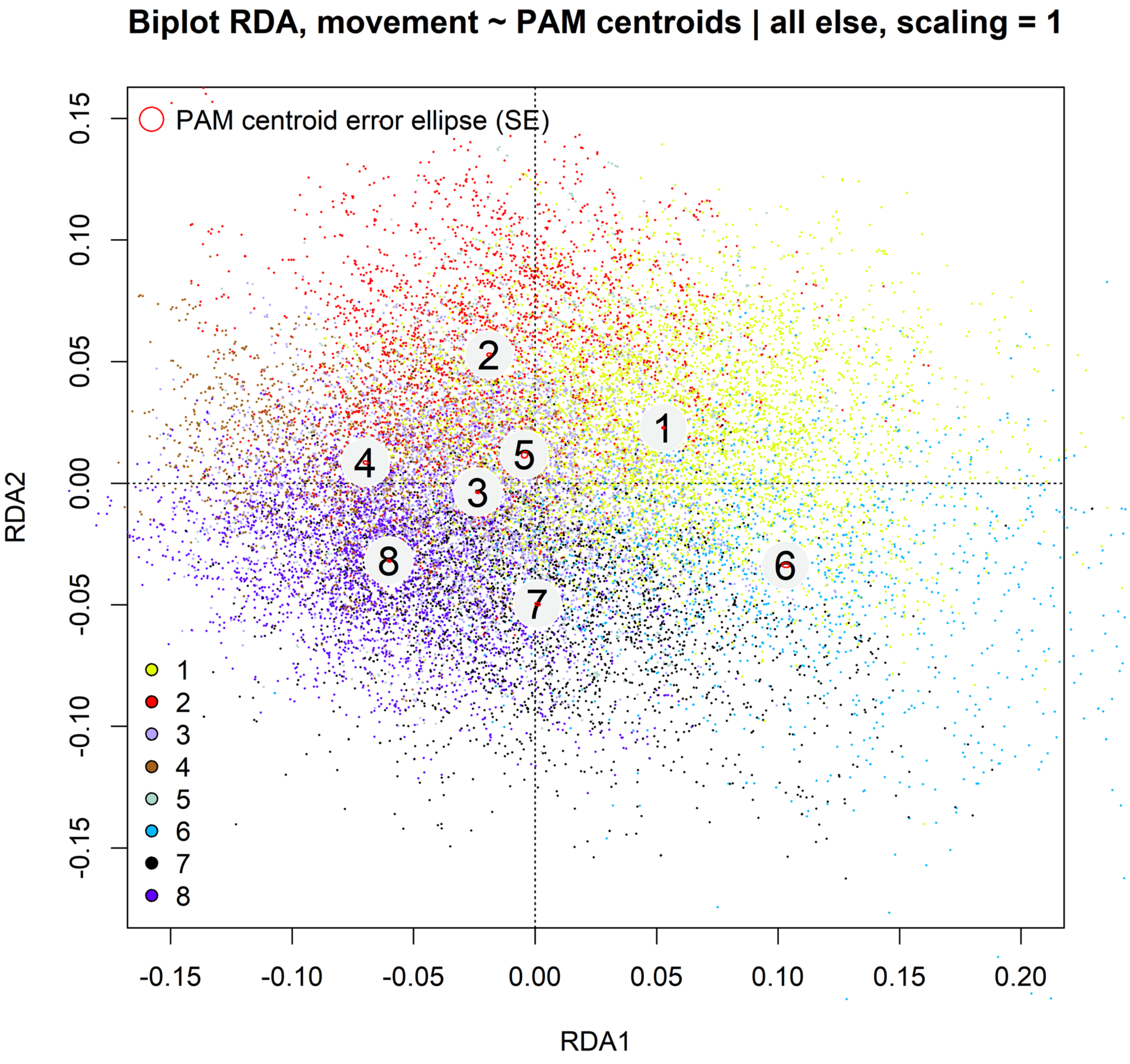


Figure 11. RDA scaling 1 – distance biplot: The colored dots represent observations (i.e., records, objects) made for a single female sage-grouse hull. The numbered circles represent centroids of cluster classes identified using partitioning around medoids (PAM) analysis of movement properties. The RDA1 axis represents 22.7% of the total-minus-conditioned variation in the movement data and RDA2 represents 7.1%. The distance between objects, distance between centroids, and distance between objects and centroids represents how similar or different the elements are from the perspective of the variation in movement properties represented by the plot.

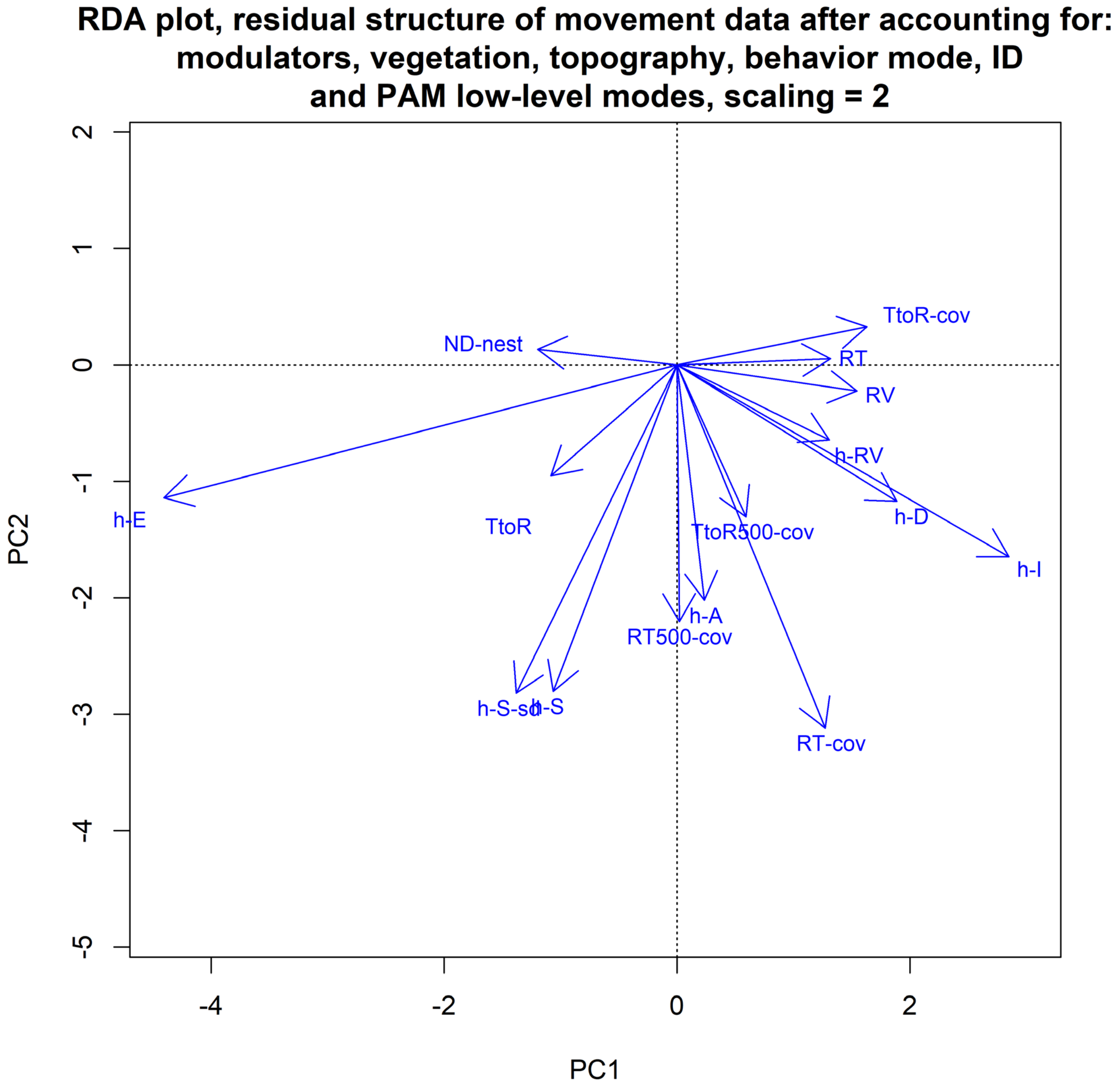
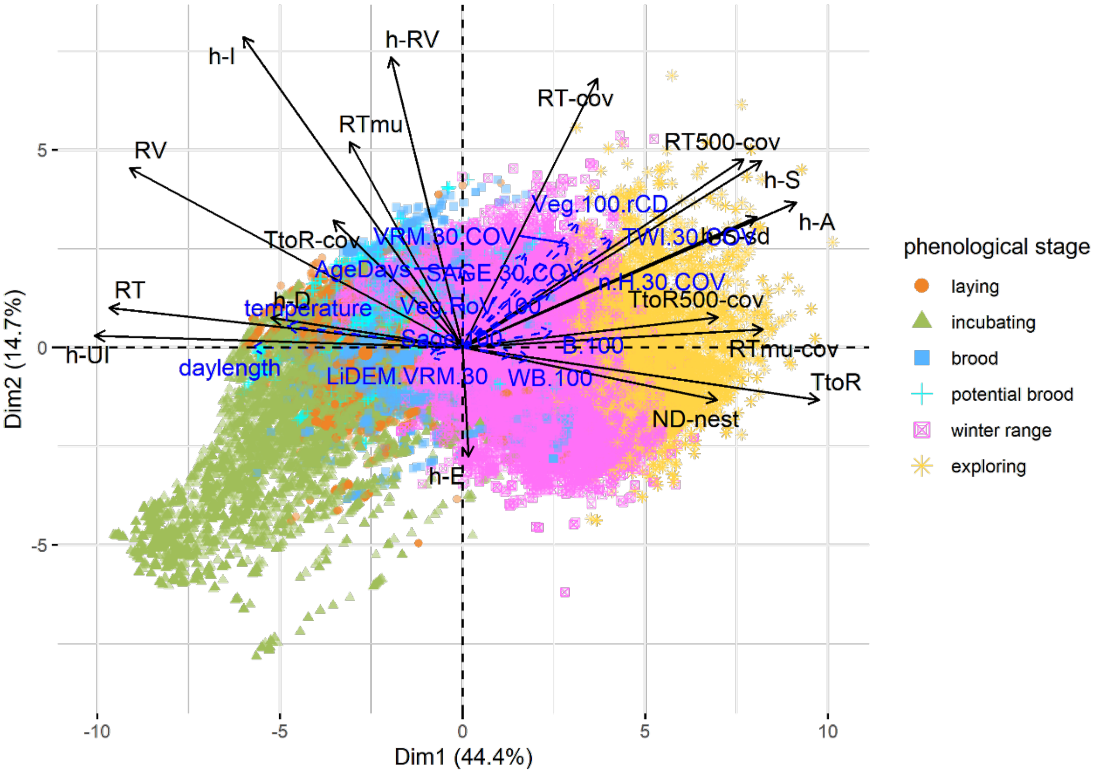


Figure 12. RDA scaling 2 – correlation plot: The response variables are blue arrows and the angles between the arrows reflect correlations between variables. The PC1 axis represents 12.1% of the total-minus-conditioned variation in the movement data and PC2 represents 11.0%. The distance a response variable arrow extends along an axis indicates the amount of variation it explains along the axis. The plot illustrates residual structure in female sage-grouse movement data after accounting for seasonal modulators, vegetation, topography, observed behavior modes, statistically-inferred behavior modes, and individual variability.

A PCA triplot of movement variables, supplementary environmental variables, and hulls



B PCA plot of individual hull observations colored by month

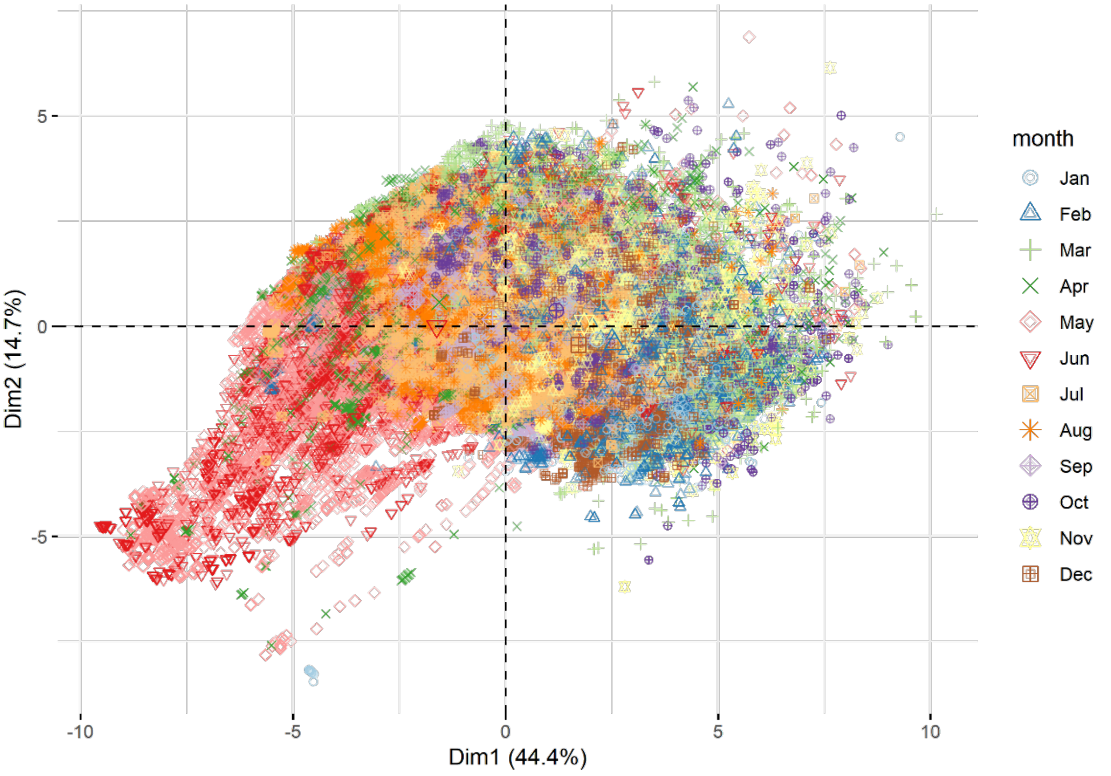


Figure 13. A: PCA biplot of 17 female sage-grouse movement properties and 12 supplementary environmental variables. The movement properties are represented by black arrows and the environmental variables are represented by dashed blue arrows. The angles in the biplot among movement metric variables and supplementary environmental variables, and among movement variables themselves or environmental variables themselves, reflect their correlations. The amount of variance in the movement properties explained by each axis is printed on the PCA component axes. B: PCA plot of individual hull instances colored by month.

CHAPTER 4

BETTER BEHAVED HABITAT DELINEATIONS: A PRACTICAL 21st CENTURY HABITAT MAPPING APPROACH WITH SAGE-GROUSE AS CASE STUDY

Contribution of Authors and Co-Authors

Manuscript in Chapter 4

Author: Robert T. Haynam III

Contributions: Robert helped conceive and plan the study, interpret results, and write the manuscript. Robert performed all the analysis. All authors edited the manuscript. All authors read and approved the final manuscript.

Co-Author: Lance B. McNew

Contributions: Lance helped conceive and plan the study, interpret results, and write the manuscript. All authors edited the manuscript. All authors read and approved the final manuscript.

CHAPTER 4

Manuscript Information

Robert T. Haynam III, Lance B. McNew

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__x__ Prepared for submission to a peer-reviewed journal
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____ Accepted by a peer-reviewed journal
____ Published in a peer-reviewed journal

CHAPTER FOUR

BETTER BEHAVED HABITAT DELINEATIONS: A PRACTICAL 21st CENTURY HABITAT MAPPING APPROACH WITH SAGE-GROUSE AS CASE STUDY

Background

Mankind has valued information about where wildlife are and what they are doing since time immemorial (Bacon et al. 2023). Wildlife researchers and managers have long recognized a seasonality to ecological processes relevant to wildlife (Parker et al. 1984, Berry and Eng 1985, Geir 1986, Garrott et al. 1987) and the value of accurately delineating seasonal wildlife habitats (Craighead et al. 1982, White and Garrot 1990, Falconer 1993, Craighead 1998, Millspaugh and Marzluff 2001, Manly et al. 2002). Published research and mapping efforts often focus on spring, summer, fall or winter occupancy, space use, movements, or demographics (Dunn and Braun 1986a, Homer et al. 1993, Doherty et al. 2008, Dzialak et al. 2013b, Swanson et al. 2013, Smith et al. 2015, Baylis et al. 2017, Dinkins et al. 2017, McMillan et al. 2021) but multi-season efforts are increasingly common (Birkett et al. 2012, Blomberg et al. 2013, Coates et al. 2013, McMillan et al. 2021). Multi-season management and conservation-related habitat delineations (DeCesare et al. 2012, Fedy et al. 2014, Walker et al. 2016, Coates et al. 2020) would have increased ecological relevance, and possibly generality (Dzialak et al. 2013a), if a behavioral focus was substituted for the more common seasonal focus (Ryan et al. 2012). Single-season research based on blanket date thresholds are unlikely to cleanly parse individual and environmental variability in ecological processes.

Seasons and behaviors are often used interchangeably in wildlife ecology, so explicit definitions are important. For instance, it is common for researchers to investigate biological differences due to breeding states (William et al. 2012, Beck et al. 2014, Dzialak et al. 2015a, Coates et al. 2017a, Gelling et al. 2022) or season (Peterson 1970, Dunn and Braun 1986a, Doherty et al. 2008, Bruce et al. 2011, DeCesare et al. 2012, Swanson et al. 2013) but then organize multi-season research by grouping breeding states with seasons (Fedy et al. 2012, Blomberg et al. 2013, Fedy et al. 2014, Walker et al. 2016). Behavior-specific inferences are an ecological gold standard (Cooper and Millspaugh 2001a, Beyer et al. 2010) and season-oriented research organized by coarse seasonal periods may not capture important behavior-by-environment interactions (e.g., process variance). For instance, a subjectively defined wintertime interval is likely to miss or conflate behaviors occurring within a winter period that might be rare but important for survival (Moynahan et al. 2006, Newton et al. 2017). Therefore, we consider season-specific research to be inferior to behavior-specific research and champion individual-based biological specificity (e.g., age, behavior, sex, species) wherever possible. In this article we stress an individual-specific behavioral perspective and present a framework that facilitates behavior-explicit habitat research using detailed animal tracking data.

Modern methods and technologies now afford a greater focus and accounting of individual behaviors in the evaluation of space use and demography (Moorcroft and Barnett 2008, Forester et al. 2009, Cagnacci et al. 2011, Lyons et al. 2013, McClintock et al. 2013, Fleming et al. 2015, Avgar et al. 2016, Signer et al. 2019, Muff et al. 2020). As a result, calls have been made for behavior-integrated research (Lima and Zollner 1996, Millspaugh and Marzluff 2001, Nathan et al. 2008) and recent work has demonstrated the tractability and importance of behavior-specific research based on animal relocation histories (Cooper and Millspaugh 2001a, Marzluff et al. 2001, Morales and Ellner 2002, Sih et al. 2004a, Sih et al. 2004b, Benhamou and Cornelis 2010, McClintock et al. 2013, Roever et al. 2014, Bennitt et al. 2015, Abrahms et al. 2016, Gelling et al. 2022). Our ability to remotely sense behavior modes (Cooke et al. 2004, Gurarie et al. 2009, Van Moorter et al. 2010, Bjørneraas et al. 2012, Langrock et al. 2012, Madon and Hingrat 2014, Gurarie et al. 2016, Hooten et al. 2017) has advanced commensurate with our ability to structure behavior-specific models. In turn, we expect behavior-specific research to proliferate.

Making inference on multiple behaviors is challenging because behavior-specific analyses require statistical models that can efficiently use detailed movement data to estimate spatially explicit and behavior-conditional habitat use predictions. Resource selection analysis (Manly et al. 2002, Johnson et al. 2006, Fieberg et al. 2021) and resource utilization analysis (Millspaugh et al. 2006, Freitas et al. 2008) are two of the prevailing techniques for quantifying and predicting habitat use. Statistical techniques for estimating habitat selection (e.g., resource selection functions [RSFs]) (Manly et al. 2002, Johnson et al. 2006, Lele et al. 2013) commonly compare habitat elements used by animals and habitat elements available or unused (Cooper and Millspaugh 2001a, Northrup et al. 2013). Inferences from habitat selection analyses may be compromised due to incorrect assumptions about movement constraints on habitat availability when behavior modes are aggregated (Cooper and Millspaugh 2001a, Johnson et al. 2002, Fedy et al. 2012, Northrup et al. 2013). For instance, African wild dogs *Lycaon pictus* in northern Bostwana were found to select roads when traveling, ignore roads when running, and avoid roads when resting but none of these useful inferences were apparent when all behaviors were aggregated in a global model that did not account for behavior (Abrahms et al. 2016). Analysis of movement patterns (e.g., migration, learning excursions, foraging) can help separate animal behavior modes thereby reducing bias induced by mixing behaviors. However, the available or unused sample might still cause bias because it introduces a subjective assumption about an animal's perception of the landscape (Erickson et al. 2001, Fauchald and Tveraa 2003, Freitas et al. 2008). A mechanistic definition of availability based on a movement model should reduce bias if the movement model is valid (Beyer et al. 2010) but choice of method, implementation, and statistical assumptions of movement models (e.g., state-space movement models) tend not to be trivial (Van Moorter et al. 2010, Börger 2016, Hooten et al. 2017, Cullen et al. 2022).

Quantifying how intensively animals use areas (Beyer et al. 2010, Van Moorter et al. 2016) is useful for examining differential space use despite an indeterminate correspondence between use-intensity and habitat quality (i.e., fitness contribution) (Marzluff et al. 2001, Millspaugh et al. 2006, Beyer et al. 2010). We define habitat use following Beyer et al. (2010) as the time an animal invests in a particular habitat type. We define habitat types for an animal following Lele et al. (2013) as unique combinations (covariate patterns) of variables in ecological space (e.g., age, behavior, daylength, shrub cover). Habitat-use intensity analyses are therefore related to other habitat selection analyses (e.g., RSFs) but directly model the degree of spatial or temporal use-intensity (i.e., likelihood of visitation) for habitat units (e.g., raster pixels) relative to landscape conditions (Millspaugh et al. 2006, Freitas et al. 2008, Hooten et al. 2013). In fact, habitat selection analyses may appear to consider the binary use status of landscape elements but popular statistical implementations are actually estimating a continuous measure of use-intensity (Fieberg et al. 2021). Directly relating use-intensity to biologically relevant variables eliminates the subjective sampling of availability (Beyer et al. 2010) because the spatial extent of analysis (Johnson 1980) is restricted to observed movements. If the relationship between differential use-intensity and landscape conditions is modeled with sufficient temporal and behavioral context then causes and consequences of animal space use may become apparent. Ultimately, the fitted relationship between use-intensity and landscape conditions can be used to generate habitat maps, an often-desired product of habitat selection analyses.

A variety of radiolocation-derived intensity metrics have been used to quantify use-intensity. A popular metric is the intensity of a point pattern estimated with a kernel smoothing estimator (i.e., utilization distribution via kernel density estimator). Another common metric is first passage time calculated from animal movement trajectories (Fauchald and Tveraa 2003, Millspaugh et al. 2006, Freitas et al. 2008, Benhamou and Riotte-Lambert 2012, Hooten et al. 2017). Estimates of habitat responses can be obtained by using suitable regression models (Faraway 2006, Legendre and Legendre 2012, Harrell 2015, Wood 2017) to relate use-intensity response variables to individual or environmental predictor variables (Pinaud and Weimerskirch 2005, Millspaugh et al. 2006, Freitas et al. 2008, Hooten et al. 2013). Techniques and software developed for detailed tracking data (Calenge 2006, Calenge et al. 2009, Kie et al. 2010, Bracis et al. 2018, Lyons et al. 2019, Joo et al. 2020) facilitate the computation of various use-intensity response variables.

In addition to the behavioral and temporal context of habitat-use intensity it is also important to incorporate the spatially hierarchical nature of habitat selection (Johnson 1980). Therefore, models of use-intensity response to landscape conditions, and corresponding spatial predictions (maps), should integrate the multiscale nature of habitat use (Doherty et al. 2010, Dzialak et al. 2011, Aldridge et al. 2012, DeCesare et al. 2012, Walker et al. 2016). We have previously investigated using the number of use points inside short-term home ranges as a measure of space and time-use intensity (Chapter 2). A time-varying measure of areal density results if we divide the number of use points in each home range by the respective areas. Areal density is a useful measure of use-intensity because it is an intuitive analog to the density of a point pattern (Millspaugh et al. 2006) and accommodates mapping at various grain sizes that correspond to scales evident in the movement process of animals. In other words, multiscale inference and mapping is accomplished using data-driven methods that exploit detailed animal movement data. Furthermore, because regression models that accommodate rate or weighted-count models (e.g., Poisson or negative binomial regression) are implemented in contemporary statistical computing software, no specialized regression tools are necessary to model use-intensity response data.

We explored modeling use-intensity for defining and mapping behavior-conditional habitat using multiyear movement trajectories of female greater sage-grouse (*Centrocercus urophasianus*; hereafter “sage-grouse”). Our main objective was to generate habitat maps for laying, incubating, brood-rearing, potential brood-rearing, unclassified behavior, winter ranging, and exploratory movement modes. Our secondary objective was to evaluate and describe the strengths and weaknesses of our approach relative to common habitat mapping considerations such as workflow reliability, reproducibility, replicability, efficiency, product quality, and product flexibility. Our modeling approach prioritized workflow simplicity; we didn’t create numerous separate models for each behavior that each come with subjective and difficult to document and report modeling decisions such as creating availability sample sets (Johnson 1980, Johnson et al. 2006), choosing size of sampling footprints (Boyce 2006), and choosing analysis scales (2nd order, 3rd order, 4th order (Johnson 1980, Fieberg et al. 2021)). Instead, we used a data-driven approach to define individual behaviors and analysis scales which we integrated into a single model from which spatially and behaviorally explicit predictions could be made using a standard regression modeling framework.

Study Area

Our study occurred over a 425,000-ha area in southern Valley County in north-central Montana, USA (47.66258 N to 48.44968 N, 106.43546 W to 107.44770 W). The area was within Glaciated Northern Grasslands and North Central Highlands (Cleland et al. 1997, McNab et al. 2007) and within the sage-grouse Great Plains Management Zone 1 which corresponds to the Silver Sagebrush Province (Connelly et al. 2004, Stiver et al. 2006). Land cover in the area consisted of approximately 49% big sagebrush steppe, 20% Great Plains mixed-grass prairie, 8% cultivated crops, 6% mat salt shrubland, 2% Great Plains riparian, and 2% Great Plains woodland savanna (Anderson et al. 1976, Comer et al. 2003). Additional limited land cover types included greasewood flats, shale badlands, and Great Plains wooded draws and ravines (Anderson et al. 1976, Comer et al. 2003). The area was characterized by high annual variation in average monthly temperature (-10.1 °C to 21.7 °C) and low mean annual precipitation (29.6 cm), with over half occurring May – July (Arguez et al. 2010). Approximately 75% of the study area was in public ownership, managed predominately by the U.S. Bureau of Land Management (BLM), as well as the U.S. Fish and Wildlife Service (USFWS, Charles M. Russell National Wildlife Refuge [CMR]), and the State of Montana. The area was situated just south of the northernmost extent of the Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) distribution in Montana; silver sagebrush (*A. cana*) becomes the only woody Artemisia species occurring farther north. The area, located at the northeastern edge of the sage-grouse distribution, represents a transition zone between mixed-grass prairie and sagebrush steppe ecosystems which makes it a unique ecotone in comparison to many other sage-grouse habitats (Dinsmore et al. 2002, Moynahan et al. 2007).

Methods

Sage-grouse Captures

During April–May, 2018–2019, we captured 89 (48 in 2018, 41 in 2019) female sage-grouse using spotlights and hoop nets (Giesen et al. 1982, Wakkinen et al. 1992). We made a concerted effort to attain a representative sample by spreading captures around 3 separate watersheds in our study area. Upon capture we banded females with uniquely numbered leg bands. We aged females as adult or yearling by examining the appearance of primary feathers 9 and 10 (Braun and Schroeder 2015). We attached a VHF-equipped 22-g solar powered Global Positioning System (GPS) Platform Transmitter Terminal (PTT; model GT-22GS-GPS, GeoTrak, Inc., Apex, NC, USA) to each of 86 birds using a rump-mounted harness (Rappole 1991). All PTTs were programmed to collect 4–10 locations every day and upload data every 1.5–3.0 days to the Argos satellite system. PTT performance was specified separately for different seasons and the 2018 programming was slightly adjusted for 2019 based on observed PTT performance; PTT programming can affect GPS data transmission success. The most aggressive programming for a season was 15 May – 1 September where 2018-batch PTTs obtained up to 10 fixes every day and uploaded data to the Argos system approximately every two days. At a minimum, location fixes were collected at approximate 6-hr intervals regardless of programming season or PTT batch. All animal handling was approved under Montana State University's Institutional Animal Care and Use Committee (protocol # 2017-57).

Sage-grouse Monitoring

PTTs had an approximate 3-year lifespan and movement data from equipped sage-grouse was recorded until female mortality or loss of a PTT. During the breeding seasons of 2018, 2019 and 2020, females were monitored by downloading GPS fixes and other PTT sensor data from Argos system servers every 3–5 days. During the breeding season of 2021, PTT sensor data was downloaded and reviewed monthly using the sub-daily location histories. We used multiple lines of evidence to infer female status. Localization of a PTT indicated either a nesting female, a dead female, or a dropped PTT. PTTs were equipped with an activity sensor that indicated if it was experiencing motion; static activity sensor readings indicated a mortality or dropped PTT. Visitation of nest sites can lead to observer-induced bias in vital rate estimates (Gibson et al. 2015), therefore we only visited localization sites if a mortality was suspected. In most cases incubation recesses (movements by females off nests) were evident in the GPS fix data and helped separate mortalities from nests (Coates and Delehanty 2008, Dzialak et al. 2011). If a mortality was indicated, we verified this with a field visit and recorded the condition of carcass remains including evidence of predation (Blomberg et al. 2013). We estimated date of incubation initiation for each confirmed nest by reviewing GPS data. Nest fate was verified in the field when a female had moved off the nest for ≥ 3 days. Nests that failed just prior to incubation were verified in the field if ≥ 2 locations accrued in the same spot due to periodic visits by a female. After nest abandonment, we located nests and recorded evidence regarding nest fate. Hatching was indicated by eggs with detached membranes and eggshells that were consistent with being pipped by chicks (Rearden 1951). We considered a nest successful if ≥ 1 egg had hatched. Nest monitoring allowed us to identify two nesting behaviors for all nests identified: laying and incubating. We labeled points along a female's trajectory as laying if they preceded incubation initiation by ≤ 7 days. Sage-grouse lay an average of ~2 eggs/3 days and average clutch sizes are ~8 eggs (Wallestad 1971, Schroeder et al. 1999). Our specification of 7 days is conservative and ensures that females with small clutches are not erroneously considered laying.

In 2018 and 2019, we monitored females with successful nests and conducted pre-dawn brood counts to ascertain if a female was with a brood. Females with broods were located with recent PTT locations and then Yagi antennas and receivers using signals from the PTT-attached VHF transmitters. All VHF transmitters that were deployed in 2018 had failed by April 2019 so no brood checks were conducted on females outfitted with PTTs in 2018. Likewise, all VHF transmitters deployed in 2019 had failed by breeding season 2020 so no brood checks took place in 2020 or 2021. Brood checks were conducted at 2-week intervals after hatch date for up to 6 weeks (3 checks). When no chicks were detected, we re-conducted the check within 5 days if the female exhibited defensive behavior consistent with brood rearing. If females immediately flushed out of the vicinity and no chicks could be located the brood was recorded as unsuccessful. Logistical constraints (e.g., weather) prevented regular brood checks at 2-week intervals and broods were flushed to confirm survival every 17 days on average. We labeled points along a female's trajectory as brood rearing for periods when brood status was known active. In cases where females had successful nests, but brood status could not be checked, we labeled all points as potential brood rearing for ≤ 14 days after hatch. Our specification of 14 days was based on our observation of brood survival and our expectation that many females with hatched nests would have broods for at least 14 days after hatch.

Telemetry quality assurance & quality control We minimally filtered irregular-trajectory raw data by removing locations defined as having step speeds (step length / step interval) ≥ 45 km/day. We based the 45 km/day criteria on our knowledge of errors identified with PTT metadata (e.g., accuracy, direction of anomalous displacement) and sage-grouse ecology. Sage-grouse have been observed moving an average of 80 km over a 11−20-day period when migrating large distances (Newton et al. 2017) and migration is their most rapid directional movement behavior. If a female were to cover 80 km in 11 days her average speed would be 7.27 km/day which is far less than our step speed criteria. Newton et al. (2017) noted a large 27.2 km movement made by a male in a single 6-hour interval which represents an extreme case and is only 2.42 times greater than our filtering threshold. Data transmitted to satellites from PTTs can have errors introduced in the transmission process resulting in corrupted locations. Therefore, we also removed PTT locations that were an anomalous distance away from previous and subsequent points along a single cardinal direction; PTT data corruption typically introduces an error in only the latitude or longitude coordinate.

Use-Intensity Related Movement Properties

Female sage-grouse that had been monitored for fewer than 30 days were excluded from analyses because of limited relocation histories from which to derive space- and time-use variables. We segmented space use by each sage-grouse into space-time local hulls (minimum convex polygons [MCPs]). To prevent bias in hull construction due to irregular sampling we subset relocations to a 6-hour sampling interval (Lyons et al. 2013). We used the R package T-

LoCoH to process the 6-hr regular-trajectory data and quantify spatiotemporal sage-grouse movement properties: hull-enclosed points, area of hulls, hull timespan, and hull revisits. We calculated visitation rate as the number of occurrences in a hull separated by a time gap ≥ 1 week. We calculated hull area as the area of each hull polygon; hull area provides a geometric delineation of space use and is analogous to a home-range area calculated for brief periods. We calculated hull-enclosed points as the number of points from an individual's trajectory enclosed by each short-term home range. Hull-enclosed points was our response variable and is related to the intensity of a utilization distribution except hull-based intensity is time local and sampling-frequency dependent. Hull-enclosed points divided by area represents the areal density of used points in short-term home ranges and is analogous to the density of a utilization distribution.

Movement Mode Classification

We used individual movement data to classify high-level and low-level movement modes (Chapter 1) of each female at each relocation; high-level movement modes included those associated with migration (range shifts), exploratory movements, nest laying, nest incubation, brood-rearing, and winter ranging. We inferred low-level movement modes from statistical clustering of movement properties (Chapter 1). Low-level modes represent distinct movement patterns within the high-level modes and represent patch use and interpatch transit or area-restricted search versus central-place foraging movements.

Winter range high-level mode We identified seasonal range shifts using a statistical framework that models the net-squared displacement (NSD) timeseries of a movement path as a function of non-linear regression model parameterizations that represent different movement types (Spitz et al. 2017). The migration models that we considered were migration, mixed-migration, dispersal, resident, and nomadic. See Appendix B for background, methods, and results describing our migration research using data from 2018–2020. Identical migration analyses were used to delineate our winter ranging modes for 2020–2021.

Non-migratory high-level modes We used a combination of field observation, examining PTT data, and migration classification to label each hull in a female's trajectory as nest laying, incubating, brood-rearing, potential brood-rearing, winter ranging, and unclassified. Some exploratory movements (low-level mode) were identified from our migration analysis, but shorter duration exploratory movements were identified with statistical clustering (Chapter 1). Additionally, uncertainty in the estimated dates of departure and arrival from NSD migration models caused transit movements between ranges to be initially allocated to either the winter range or unclassified behavior class. The unclassified behavior class was generally a catch-all where distinct breeding or winter-ranging statuses were not identified (i.e., pre-laying, late summer, fall).

Low-level statistically inferred movement modes We identified eight statistical movement-behavior modes (Chapter 1) using statistical clustering (partitioning around medoids [PAM]) on a subset of our movement metrics (Van Moorter et al. 2010, Abrahms et al. 2017). We identified an exploratory mode using the clustering results and we used it to reclassify movement instances within the high-level modes which effectively filtered exploratory movements from modes such as winter ranging or unclassified (Chapter 1). Apart from the exploratory mode, we did not label the PAM-based modes with behavioral labels such as area restricted search but we note that this could be done. Our rationale for not relabeling more high-level behaviors was to somewhat reconcile our behavior modes with seasonal periods common in the sage-grouse literature.

Use-Intensity Generalized Additive Model

We conducted initial univariate exploratory analysis of the relationship between use-intensity and predictor variables using pair-wise scatterplots, generalized additive models (GAMs), or loess smoothers. Nearly all relationships between predictor and response variables appeared non-linear. R packages hexbin, Hmisc, lubridate, sf, and tidyverse were used for data manipulation and exploratory data analyses (Grolemund and Wickham 2011, Wickham 2017, Pebesma 2018, Carr et al. 2021, Harrell 2022).

We modeled the non-linear relationships between sage-grouse use-intensity and predictor variables with GAMs (Faraway 2006, Wood 2017). In some cases, predictor variables required log or square root transformations to promote convergence of model fitting algorithms (Table 5). Our response variable, an integer describing the number of hull-enclosed points, was overdispersed relative to Poisson model assumptions so we fit GAMs with a negative binomial distribution and a log link function. We modeled hull enclosed points using rate regression where hull area was used to control for the fact that larger home ranges can encompass more points. Controlling for hull area is analogous to other forms of sampling-effort bias corrections for counts such as controlling for time spent surveying or number of observers (Faraway 2006, Zuur 2012). We included area as a smooth term instead of an offset variable to appropriately model use-intensity (hull enclosed points / hull square kilometers) without assuming that doubling area approximately doubles the number of hull-enclosed points (Zuur 2012).

We selected a set of 42 landscape-condition predictor variables that might influence sage-grouse movements and therefore use-intensity on the landscape (Appendix F, Table 14). Our creation of landscape-condition predictor variables is described in Appendix C. We also included daylength, daily temperature, and female age to control for effects of seasonality and time (Appendix F, Table 14). Female age was calculated as the number of days since 15 June of the previous year for females captured as yearlings and the number of days since 15 June, two years prior, for females captured as adults.

We conducted initial exploratory analysis of predictor characteristics using pairwise scatterplots and Pearson correlation coefficients. Pairwise scatterplots allowed for visualization of both linear and non-linear relationships among predictor variables. More so than generalized linear models, GAMs are sensitive to collinearity among predictor variables which can bias modeled relationships and confound model selection procedures (Wood 2017). We iteratively calculated pairwise Pearson correlations for every predictor variable in the dataset and sequentially removed variables with the maximum correlation until every variable had $r \leq 0.6$. To further quantify non-linear associations among predictors we iteratively calculated variance inflation factors (VIFs) for every predictor variable in the dataset and sequentially removed the variable with the maximum VIF until every variable had a VIF ≤ 3.0 (Zuur et al. 2009). Correlation and VIF-based variable elimination were accomplished with an R script incorporating the auto_cor() and auto_VIF() function which allowed us to prioritize keeping variables that were most amenable to interpretation and generation of spatially explicit predictions (Benito 2021).

Our GAMs were structured with smooth-factor by variable interactions to accommodate behavior-specific habitat mapping. We used a GAM with a separate smooth term for all but three behavior-by-predictor combinations. We split the total sage-grouse movement database in half and used 38,327 records to model use-intensity; subsetting the data reduced computation time and facilitated model validation. Our behavior factor variable had 7 levels: laying, incubating, brood, potential brood, unclassified (summer), winter range, and exploring (Chapter 1). We did not specify an interaction with our behavior factor for the variables daylength, female age, and hull revisits because we expected them to have a consistent influence on use-intensity. Interactions were specified for: barren ground cover, distance to water bodies (km), fine-grain sage, fine-grain topographic ruggedness, LANDFIRE percent sage class, lowland NDVI, normalized height variability, normalized height, radius of variance (RoV) of fine-grain landscape ruggedness, RoV of vegetation biomass index, solar insolation, topographic wetness index, valley bottom flatness, vegetation biomass index, and vegetation height (Table 6). Descriptions of final predictor variables are provided in Appendix F and Table 5.

We included a random intercept to model variability among individual grouse which helps account for both pseudo-replication within an individual and differential sample sizes among individuals (Gillies et al. 2006, Hebblewhite and Merrill 2008, Bolker et al. 2009). All data manipulation and analysis for our GAM model was performed in R largely using packages raster, exactextractr, and mgcv (Wood 2017, Baston 2021, Hijmans 2021). We plotted non-spatial GAM results largely using R-packages mgcViz and gratia (Fasiolo et al. 2018, Simpson 2022).

Model Validation

We calibrated our model following Zuur (2012) using a calibration dataset (n = 27,758) withheld from our total dataset. We adjusted our model after examining model fit (deviance explained) and validation tools such as plots of residuals against fitted values and prediction error calculations (e.g., root mean squared error, mean absolute error) using the calibration dataset. Our calibration procedures included increasing the basis dimensions for some smooth terms, transforming some covariates, and using a Tweedie distribution instead of the negative binomial distribution (Zuur 2012, Wood 2017). We assessed overdispersion using the sum of Pearson residuals divided by the sample size minus the number of parameters (phi-hat) (Zuur 2012).

After model calibration, we validated our model following Zuur (2012) with a hold-out validation dataset (n = 27,677). We compared observed residuals to residuals simulated from our model using function check0D() of R-package mgcViz. We compared deviance residuals to linear predictor values using residuals_linpred_plot() of R-package gratia. We also examined residual patterns by plotting residuals against each covariate using check1D() of R-package mgcViz. However, model diagnostic and validation procedures are difficult to interpret when modeling binary or integer random variables so we also assessed model fit using scaled residuals following Hartig (2022).

Habitat Mapping

We integrated the spatial scale of use-intensity into our model and maps in 3 ways: 1) we defined use area with animal movements at the short-term home range scale (space- and time-local kernels [hulls]), 2) we defined patch use within home ranges as 30-m radius circles

(Appendix F, Table 14), and 3) we made predictions by first aggregating raster-map predictors to a 30-m ‘radius’ (60 x 60-m pixels) and then aggregating again to the median short-term home range area for a given behavior. Landscape-condition maps were used to generate behavior-specific and spatially-explicit conditional effects maps and associated standard errors. We made map predictions at median values of seasonality-related variables such as daylength and median values of female-intrinsic covariates such as age (Appendix F, Table 15). Standard errors were calculated using function predict.bam() of R-package mgcv. We generated a 6-behavior multiscale map of use-intensity by summing (raster algebra) hull-enclosed points and associated standard errors for each behavior-conditional map: laying, incubating, potential brood, unclassified (summer), winter range, and exploring. We excluded the brood behavior mode from the sum due to spatially extensive and large magnitude standard errors. We calculated zonal summary statistics and generated spatial predictions largely using R-packages raster, exactextractr, sf, terra, and mgcv (Hijmans 2022). We used QGIS to sum the 6 behavioral prediction surfaces, examine spatial predictions, and generate cartographic products (QGIS Development Team 2020). Finally, we generated non-spatial conditional and partial effects plots to aid map interpretation using R-packages gratia and ggeffects (Lüdecke 2018).

Results

During May – June 2018 and April 2019, we fitted 86 of 89 captured female sage-grouse with GPS transmitters. We collected 192,640 geographic coordinates of 86 female sage-grouse during 2018-04-24 – 2022-04-14 which encompassed 4 complete annual cycles of sage-grouse. The median and interquartile range (IQR) number of locations per female in the complete dataset was 1,410 (IQR = 2,933). After resampling trajectories to 6-hr intervals and removing individuals with inadequate relocation histories our movement property calculations used 110,024 relocations of 74 females. The median number of locations per female for our year-round movement analysis was 1156 (IQR = 1940).

Laying, incubating, brood-rearing, potential brood-rearing, winter ranging, and exploratory behaviors were attributed to female sage-grouse relocations whenever these behaviors were known from field observations or migration and cluster analysis for the winter ranging and exploratory mode. The median duration over which brood rearing was confirmed was 41.4 days (IQR = 31.5, n = 19). Sage-grouse relocations with an unconfirmed behavior state were allocated to a catch all ‘unknown’ behavior category, which typically occurred during summer. The median number of relocations per individual attributed to laying was 48 (IQR = 65, n = 69), median locations for incubation 99 (IQR = 112, n = 71), median locations for brood rearing was 143 (IQR = 80, n = 19), potential brood rearing 54 (IQR = 11, n = 30), winter range 571 (IQR = 560, n = 42), exploring 72 (IQR = 54, n = 4), and 642 (IQR = 1022, n = 74) for the ‘unknown’ category. After reclassification of exploratory home-range instances using cluster analysis (Chapter 1), the median number of relocations per individual attributed to laying was 48 (IQR = 65, n = 69), median locations for incubation 99 (IQR = 112, n = 71), median locations for brood rearing was 143 (IQR = 79, n = 19), potential brood rearing 53 (IQR = 11, n = 30), winter range 362 (IQR = 452, n = 42), exploring 190 (IQR = 389, n = 70), and 544 (IQR = 900, n = 74) for the ‘unknown’ category.

Correlation and variance inflation factor screening identified 20 minimally correlated continuous-scale predictors (Table 5) that we included in our negative binomial GAM. Our GAM explained 76% of the deviance of the data, indicating good fit. Overdispersion in our

GAM (phi-hat = 1.1) was minimal. Model calibration procedures did not substantially improve model fit or prediction errors. Model validation plots did not identify any diagnostic-data patterns that would indicate serious deficiencies in our model (Appendix F, Figure 52–55). Statistical tests of deviation from model assumptions were significant ($p \leq 0.05$) but given our large sample size that was expected as model checking tests can be significant even when magnitude of departures are of no concern (Appendix F, Figure 55) (Vittinghoff et al. 2012). Overall root mean squared error and mean absolute error for our model was 117 and 73, respectively. Model errors varied by behavior type and were highest for exploratory behavior and lowest for potential brood (Appendix F, Table 16). Model errors were of lower magnitude than the central tendency of number of use points during each behavior mode which indicated reasonable precision of estimates (Appendix F, Table 16).

Our GAM model included 123 smooth terms of which 111 had a p-value ≤ 0.05 (Table 6). Only 7 terms appeared to be linearly related to log(enclosed points) as indicated by the expected degrees of freedom of the smooth terms being > 1 (Table 6). Use-intensity increased nonlinearly with increasing hull revisits and length of day but changed as a smooth periodic function of female age because female age indexes time and therefore seasonality (Appendix F, Figure 35). Partial effects plots indicated that response and predictor relationships often varied by behavior as allowed by the main effects (behavior) plus interaction (landscape condition × behavior) structure of our model (Appendix F, Figure 36-51).

Behavioral differences in use-intensity were evident from our behavior-specific prediction maps (Figures 14–20). Our behavior-specific maps illustrated sage-grouse response to fine- and coarse-scale landscape-condition gradients and features on the landscape. For instance, high uncertainty or very low predicted values were associated with features such as water bodies, hardpan flats, and treed areas that represent distinct landscape features that sage-grouse largely avoid (Figures 14–21). High uncertainty was often associated with very low values of percent LANDFIRE sagebrush cover class at that coarser scale and more smoothed spatial gradient. Spatially-explicit uncertainty estimates varied as a function of geographically differential use among behaviors and different sample sizes among behaviors (Figures 14–21, [Appendix F, Table 16]). Uncertainty estimates appeared to be useful for delineating avoided areas (Figures 14–21) because these areas generally had combinations of covariates (e.g., habitat conditions) that were rare or unobserved in the data. Our brood map had high uncertainty due to our limited sample size for that behavior (Appendix F, Table 16) so we excluded it from our aggregate 6-behavior map (Figure 21).

Our scale-integrated 6-behavior map (Figure 21) delineated areas that were avoided during some or all behaviors and indicates both habitat versus non-habitat areas based on standard errors as well as a multiscale map of geographic use-intensity (predicted use points / pixel area) by female sage-grouse. Our 6-behavior map was effective at integrating multiple behaviors and scales as indicated by the blending of use-intensity values for space use extents unique to each behavior (Figures 14–21).

Non-spatial conditional effects plots can help with map interpretation because predictions are plotted on the response scale so correspond to mapped values. For example, given a fixed home range area, use points were highest for low or intermediate values of proportion bare ground, and vegetation biomass, but declined significantly at high values of vegetation biomass that may represent forays into dense juniper savannah or greasewood flats (Figure 22).

Additional conditional effects plots relevant for evaluating habitat responses can easily be recovered from our fitted model, although that was not our focus here.

Discussion

We demonstrated a flexible framework for modeling habitat distributions with generalized additive models using timeseries of space- and time-use intensity data (areal density) calculated from lifetime trajectories of sage-grouse. We integrated 7 empirically determined behavior modes encompassing all phenological stages of sage-grouse into a single modeling framework to estimate behavior-specific habitat selection in relation to 15 habitat conditions while controlling for use area, use-area timespan, and use area revisits. Our behavior-conditional model predictions of use-intensity were made at biologically meaningful grain sizes (median use area) for each behavior mode which alleviated scale dependance in identifying habitat distributions. We validated our model using accepted standards and incorporated uncertainty estimates into spatial predictions which is necessary for preventing inappropriate inference on habitat distribution, though often neglected by habitat mapping practitioners (Aldridge and Boyce 2007, Doherty et al. 2010, Fedy et al. 2014, Rice et al. 2016, Walker et al. 2016, Coates et al. 2020). Our use-intensity timeseries approach of modeling habitat is consistent with the concept of a temporally-explicit utilization distribution as well as a inhomogeneous point processes which reconciles it with progressive habitat selection methodologies (Kie et al. 2010, Bivand et al. 2013, Hooten et al. 2013, Northrup et al. 2016, Fieberg et al. 2021). Temporally explicit habitat selection analyses are powerful tools in wildlife ecology because they facilitate behavioral specificity of inferences and address temporal-scale dependance of inferences (Schick et al. 2008, Northrup et al. 2016).

Behavior Integration

Behavior analysis workflow Our simultaneous modeling of 7 behavior modes using a behavior-by-predictor interaction indicated that substantial behavioral differences in resource selection occurred for our focal population. Our methodology allowed efficient evaluation of the statistical significance of behavior-conditional effects along with the functional form of the relationship between use-intensity and predictors. We could readily interpret use-intensity response to specific landscape conditions using GAM partial effects plots and conditional effects were easily plotted for specific landscape condition combinations of interest. We produced spatially explicit conditional effects representing prediction maps of use-intensity using GIS predictor maps (landscape conditions) and relevant values for un-mappable covariates (e.g., median age, behavior-specific median daylength). Our use of a single GAM model to make multi-behavior inference greatly alleviated disparate workflows where separate models are fitted to different datasets for different behaviors or seasons.

We were able to generate behavior-specific maps and associated uncertainty estimates in R which lends flexibility, transparency, and repeatability to map production. Historically researchers tend to generate maps in a GIS that is separate from the statistical computing software used to fit habitat distribution models and may not give descriptions of GIS methods adequate for reproducing or replicating methods (Guisan and Zimmermann 2000, Manly et al. 2002, Doherty et al. 2010, DeCesare et al. 2012, DeCesare et al. 2014, Fedy et al. 2014, Walker et al. 2016). Use of a separate GIS makes the workflow more difficult to document and report, reduces mapping efficiency, and introduces opportunity for error when specifying model expressions. Iterative model testing (Guisan and Zimmermann 2000) and computation of prediction uncertainty (Faraway 2006, Vittinghoff et al. 2012, Harrell 2015, Wood 2017) are important modeling procedures so the ability to generate maps using statistical computing software scripts promotes workflow consistency and saves time over executing workflows through the graphical user interface of a standalone GIS (Guisan and Zimmermann 2000). Our GIS-integrated (R has GIS capabilities) statistical modeling framework was of compound benefit as we produced multiple behavior-specific maps.

Rare behaviors Each of our behavior-specific maps had unique characteristics which illuminated methodological considerations in addition to biological phenomena. Brood rearing was under sampled due to technological issues (not true rarity) so its map had generally high standard errors illustrating that uncertainty is a function of frequency of behavior in the dataset. Rare behaviors may also have small sample sizes that will result in less precise prediction surfaces, but rare behaviors are not necessarily the least biologically important. For instance, sage-grouse breed on communal mating grounds and might visit habitat conditions such as food sources, or open ridges with good vantage points when transiting to and from mating locations. A use-intensity map for lek visitation behavior would have ubiquitously large standard errors and limited management applications if a researcher was only able to identify a few instances of mating-taxis behavior per individual. Researchers can consider removing rare-behavior maps when combining maps into an overall map as we did for our confirmed brood-rearing map. However, variable importance or responses to landscape conditions might still be evaluated for a rare behavior despite limited utility of spatially explicit predictions. Furthermore, inferences from other behaviors may be more accurate if rare behaviors are accounted for (filtered from other behaviors) when fitting a model, although we did not assess those effects here. Rare behaviors may be of disproportionate biological importance (e.g., lek visitation, predator evasion, transit flights) and should not be disregarded just because they are inconvenient to research or integrate into habitat distribution maps. The methodology we have outlined promotes use of as many behaviors as can be identified.

Time dependance and behavior The identification of rare behaviors is contingent upon the temporal scale (frequency of relocations) of time-use sampling (e.g., use-intensity, revisitation) because movement analyses is time-scale dependent (Bracis et al. 2018, Lyons et al. 2019). Indeed, recent research has highlighted that spatial and temporal scales both influence resource selection inferences (Johnson et al. 2002, Northrup et al. 2016, Serrouya et al. 2017). Increasing positional sampling rate decreases the likelihood that important behaviors are missed and increases researcher ability to identify behaviors using movement analysis (Rowcliffe et al. 2012). Temporal scale dependance can impact inferences in both VHF-based studies or GPS-based studies (White and Garrot 1990, Mills et al. 2006, Kochanny et al. 2009, Northrup et al. 2016, Serrouya et al. 2017) and represents both a methodological challenge and opportunity to better understand wildlife species (Cagnacci et al. 2010, Kie et al. 2010, Northrup et al. 2016). Our approach can accommodate medium to high positional sampling rates which are necessary for calculating detailed time-series of short-term home ranges and characteristics.

Sampling-frequency inferential dependence can be reduced by controlling for behavior modes. For instance, some sage-grouse in our study used areas with relatively high Rocky Mountain juniper cover during nesting and our incubation-conditional estimates indicated that fact. Predicted areal density during incubation was moderate to high in most juniper areas with low to moderate standard errors for upland juniper savannahs. Strong avoidance of juniper cover would likely have been indicated by a behavior-pooled analysis; avoidance of juniper during non-nesting behaviors would likely dominate the relationship. The methodology we have outlined promotes behavioral, spatial, and temporal process integration so that use-intensity estimates are amenable to nuanced interpretation.

Spatial Scale

We modeled the use of short-term home ranges based on observed movements which had multiple benefits regarding spatial-scale dependence of inferences. Our approach alleviated the need to subjectively define an analysis extent (availability sample), which is problematic but must often be done in resource selection analyses (Johnson 1980, Johnson et al. 2002, Manly et al. 2002, Boyce 2006, Johnson et al. 2006). Users of our approach can select tuning parameters for home-range estimation using published guidelines which reconciles the home range parameters with research objectives and species- or individual-specific movement tendencies (Martin et al. 2008, Lyons et al. 2019). For example, we aggregated our moderate and high-resolution landscape condition variables (e.g., sub-meter NAIP imagery, LiDAR data, 1/3 arc second DEM terrain variables) using 30-m radius use patches within home ranges so that the spatial and temporal scale of our inferences are an integration of fine-scale use within coarser scale home ranges.

We chose a single 30-m radius extent to represent patch-level use because it reconciles with extents commonly used for microhabitat sampling (Herrick et al. 2017), was a coarser extent than the accuracy of our GPS transmitters, and simplified model structure. Our patch-level (30-m radius) sampling at within home range use points (nearest neighbor sets) could be made finer if more resolute and accurate landscape condition maps and GPS locations were available. Alternatively, multiple grain sizes could be evaluated to search for grains with the best fit to the data (Doherty et al. 2010, Laforge et al. 2015). However, we caution against data mining sets of covariates smoothed to different grain sizes and assuming results are confirmatory of important scales. Choice of landscape-condition grain sizes used for evaluating habitat responses should be based on prior evidence unless research is acknowledged as exploratory. Our approach is data driven and inherently multiscale in the sense that scale of analysis is largely a function of animal movements so subjective decisions about scale are reduced. The methodology we have outlined will accommodate use of increasingly detailed landscape condition variables such as very high-resolution or time varying landscape conditions.

We made predictions at median values of home-range timespan and home-range area for each behavior mode, but other biologically relevant values could have been used. We aggregated base covariates to 60-m pixels and then to median home-range area sized pixels to correspond with predictor sampling using nearest neighbor sets in each home range. Spatial reconciliation of sampling and prediction datasets should always be prioritized because aggregation schemes and data footprints can alter results (i.e., alter statistical support, modifiable areal unit problem, Plant (2012)).

Map Interpretation

Prediction maps of use-intensity and prediction uncertainty are both important for delineating space use. Habitat selection theory assumes that animals prefer some landscape condition combinations and avoid others (Manly et al. 2002). Habitat selection analyses based on telemetry data typically conflate use with visitation (Lele et al. 2013). In fact, it is likely that an animal may be briefly located in a position on the landscape that it does not prefer due to a mistake (got lost, poor situational awareness) or irregular operations (predator evasion) where the animal is moving with no regard for landscape conditions.

Our behavior-specific approach helps address the fact that use points and individual instances of time varying use-intensity do not all have the same biological relevance. Use-intensity in commonly visited matrix habitat and preferred habitat will be estimated with relatively low uncertainty and use-intensity of rarely or never visited habitat types (non-habitat) will be estimated with relatively high uncertainty. Therefore, spatial predictions of uncertainty within a study area may largely represent an index of habitat avoidance with low values indicating low avoidance. Uncertainty maps are also helpful in identifying behavioral use-intensity prediction maps where widespread uncertainty degrades the utility of the map due to a limited sample size. In our study, VHF transmitter longevity resulted in a limited sample size and therefore high standard errors for our confirmed-brood map, so we removed it from our combined-behavior map.

A further consideration is that low and moderate use-intensity will be common and extreme use-intensity will be rare, therefore, uncertainty will also increase at extreme degrees of use-intensity. The differential uncertainty we describe is due to movement among patches (low use-intensity) being common and patch use-intensity varying as a function of the use duration and revisitation rate (Lyons et al. 2013). Patches are often used and then abandoned so low or moderate use-intensity is common and can vary upward to moderate-to-high use-intensity if some revisitation elevates the lifetime use-intensity.

Landscape species like sage-grouse, American bison (*Bison* bison), moose (*Alces alces*), or pronghorn (*Antilocapra americana*) will likely exhibit substantial variation in area use over their lifetime (Larter and Gates 1994, Jacques et al. 2009, van Beest et al. 2011, Van Moorter et al. 2013, McMillan et al. 2021) and individuals may rarely have high fidelity to an area used for substantial durations (Van Moorter et al. 2009, Mueller et al. 2011, Lyons et al. 2013, Bracis et al. 2015, Bracis et al. 2018, Geremia et al. 2019) which results in an elevated degree of use-intensity. From a statistical perspective extreme use-intensity is represented as outliers in the extreme right tail of the right-skewed empirical distribution of number of enclosed points in short-term home ranges. We observed the phenomenon of extreme use-intensity values in female sage-grouse due to differential area fidelity among individuals and different lifespans where the longest-lived individuals were obviously rarest. Consequently, very high use-intensity predictions where uncertainty is high required careful interpretation. Interpreting rare events and adequately modeling outliers is challenging. In our study, for example, the highest use-intensity values were observed at nesting areas where short-term home ranges overlapped areas used for prior nesting attempts. Rare behavioral patterns may have substantial ecological importance, but we stress that the highest use-intensity does not necessarily correspond to the most important habitat (Beyer et al. 2010). However, high use-intensity predictions where uncertainty is low or moderate may indicate areas for which individuals have high fidelity which may indeed confer fitness advantages (Chapter 5, Piper (2011)). Habitat conditions with moderate use-intensity are areas which have been used to a degree typical of a behavior mode and areas with lower use-intensity and low uncertainty have habitat conditions that have been used mildly but are not necessarily unimportant. Extremely low use-intensity does indicate avoidance, but care should be taken in selecting transformation thresholds if ranked use-intensity categories (spatial habitat use bins) are desired for habitat mapping; continuous-field discretization can interfere with valid interpretation (Gao 2009). The threshold defining the first and second ranked bin should be chosen to indicate non-habitat and low-use habitat, respectively, though we opted not to create ranked bins because of difficulties defining objective and biologically relevant thresholds. Valid links between use-intensity and fitness are challenging to make and need to be established on a population-by-population basis; even then the relationship may not be stable through time (Hebblewhite and Merrill 2008, Beyer et al. 2010, van Beest et al. 2011, DeCesare et al. 2014, Geremia et al. 2019).

We stress that use-intensity is not necessarily proportional to habitat quality and that low to moderate use-intensity predictions will often be the most reliable. Model validation (Boyce et al. 2002) is important but validation statistics do not indicate spatially variable model performance. Estimates of uncertainty are particularly important when maps are used as covariates in subsequent research (Aldridge and Boyce 2007, Gibson et al. 2016) because predictor data where estimates are unreliable should not be included in analyses. Low to moderate uncertainty estimates will provide an indication of where prediction interpretation is warranted and indicate areas where use of a landscape-condition pattern (covariate pattern) is a rare event (may indicate avoidance). We champion combined interpretation of spatially and behaviorally explicit use-intensity predictions and corresponding uncertainty estimates for understanding animal space use.

Conclusions

Our approach of examining use-intensity as a time-varying quantity over the lifetime of an animal encourages nuanced and biologically realistic interpretation of the causes and consequence of space- and time-use by animals. Attempting to discern habitat responses from static behavior-naïve snapshots of use munges important ecological processes such as time varying and behavior-conditional habitat selection that is fundamental to wildlife ecology. Our behavior-specific modeling approach solves some of the problems with classic habitat mapping approaches and can generate either very specific or somewhat general habitat evaluation products. Spatial and temporal scale dependence is attenuated by use of a behavior-integrated model of a timeseries of use-intensity data. One caveat is that generality of inferences may be limited by sampling design where sampling from the entire range of a species and accounting for geographic variation may not be feasible. Inferences derived from local sampling may be most useful for understanding local populations. However, our approach can be extended with geographic error term correlation structures or predictor term interactions that account for and facilitate interpretation of regional variation.

Figures & Tables

Table 5. List of all predictor variables in our fitted generalized additive model of female sage-grouse use-intensity. Coefficient of variation and radius or variance of a predictor are labeled CV and RoV, respectively.

Variable	Transform	VIF
Barren	1.00	2.10
Female Age	1.00	1.25
Fine-grained Sage	sqrt	1.62
Hull Area	1.00	1.23
Hull Revisits	1	1.20
Hull Timespan	1	1.08
LANDFIRE sage	1.00	1.81
Length of Day	1.00	1.76
LiDAR Vector Ruggedness Measure	1.00	1.88
Lowland NDVI	1.00	2.06
MultiResolution Valley Bottom Flatness	1.00	2.54
Normalized Height CV	1.00	2.42
Normalized Height	1.00	2.00
Proximity to Water Bodies	sqrt	1.48
Solar Insolation	1	1.14
Topographic Wetness Index CV	1.00	1.47
Vegetation Biomass	1.00	2.08
Vegetation Biomass RoV	1.00	1.90
Vegetation Height (LiDAR based)	(x^0.6)*-1	2.41
Water Body Presence RoV	3.00	1.33

Table 6. List of all parametric and smooth terms in our fitted generalized additive model of female sage-grouse use-intensity. The expected degrees of freedom (edf) of smooth terms indicates a nonlinear relationship between use-intensity and a predictor if edf > 1. Ref.df is the degrees of freedom used for hypothesis testing of term significance.

A. parametric coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	5.30	0.27	19.31	< 0.0001
behavior = laying	-1.25	1.22	-1.03	0.3027
behavior = brood	-0.18	0.43	-0.43	0.6708
behavior = potential brood	0.34	0.29	1.16	0.2446

behavior = unclassified	0.15	0.27	0.55	0.5849
behavior = winter range	-0.52	0.28	-1.84	0.0658
behavior = exploring	-1.21	0.27	-4.40	< 0.0001

B. smooth terms	**edf**	**Ref.df**	**F-value**	**p-value**
s(individual ID)	71.94	73.00	103.10	< 0.0001
s(hull revisits)	8.56	8.89	3854.17	< 0.0001
s(area):behavior = incubating	4.54	4.81	57.57	< 0.0001
s(area):behavior = laying	3.89	4.04	39.05	< 0.0001
s(area):behavior = brood	2.63	2.93	5.65	0.0005
s(area):behavior = potential brood	1.00	1.00	42.86	< 0.0001
s(area):behavior = unclassified	5.14	5.72	431.24	< 0.0001
s(area):behavior = winter range	5.13	5.63	317.64	< 0.0001
s(area):behavior = exploring	8.74	8.95	61.07	< 0.0001
s(hull timespan):behavior = incubating	4.43	5.30	6.38	< 0.0001
s(hull timespan):behavior = laying	5.64	6.25	16.64	< 0.0001
s(hull timespan):behavior = brood	6.59	7.42	2.78	0.0045
s(hull timespan):behavior = potential brood	2.02	2.51	9.43	< 0.0001
s(hull timespan):behavior = unclassified	8.56	8.93	97.68	< 0.0001
s(hull timespan):behavior = winter range	6.02	6.61	35.97	< 0.0001
s(hull timespan):behavior = exploring	8.25	8.76	78.98	< 0.0001
s(LANDFIRE sage):behavior = incubating	5.48	6.52	3.63	0.0009
s(LANDFIRE sage):behavior = laying	2.75	3.47	10.24	< 0.0001
s(LANDFIRE sage):behavior = brood	5.33	6.44	5.67	< 0.0001
s(LANDFIRE sage):behavior = potential brood	5.88	6.62	5.36	0.0001
s(LANDFIRE sage):behavior = unclassified	8.76	8.98	34.76	< 0.0001
s(LANDFIRE sage):behavior = winter range	8.47	8.92	12.51	< 0.0001
s(LANDFIRE sage):behavior = exploring	7.75	8.58	25.07	< 0.0001
s(lowland NDVI):behavior = incubating	2.48	3.14	3.54	0.0134
s(lowland NDVI):behavior = laying	5.38	6.32	5.32	< 0.0001
s(lowland NDVI):behavior = brood	1.96	2.42	3.08	0.0566

s(lowland NDVI):behavior = potential brood	5.17	6.07	4.70	0.0001
s(lowland NDVI):behavior = unclassified	8.79	8.98	61.65	< 0.0001
s(lowland NDVI):behavior = winter range	7.17	7.62	28.38	< 0.0001
s(lowland NDVI):behavior = exploring	4.72	5.62	7.08	< 0.0001
s(fine-grain landscape ruggedness rCD):behavior = incubating	7.45	8.24	10.16	< 0.0001
s(fine-grain landscape ruggedness rCD):behavior = laying	1.00	1.00	19.76	< 0.0001
s(fine-grain landscape ruggedness rCD):behavior = brood	3.37	4.25	2.13	0.0764
s(fine-grain landscape ruggedness rCD):behavior = potential brood	3.68	4.58	3.58	0.0037
s(fine-grain landscape ruggedness rCD):behavior = unclassified	8.83	8.99	48.18	< 0.0001
s(fine-grain landscape ruggedness rCD):behavior = winter range	7.28	8.28	7.94	< 0.0001
s(fine-grain landscape ruggedness rCD):behavior = exploring	8.15	8.79	12.84	< 0.0001
s(LiDAR NDVI (biomass index)):behavior = incubating	6.47	6.92	6.07	< 0.0001
s(LiDAR NDVI (biomass index)):behavior = laying	4.58	5.17	3.63	0.0015
s(LiDAR NDVI (biomass index)):behavior = brood	2.13	2.61	11.14	< 0.0001
s(LiDAR NDVI (biomass index)):behavior = potential brood	1.00	1.00	1.79	0.1804
s(LiDAR NDVI (biomass index)):behavior = unclassified	7.70	8.60	19.38	< 0.0001
s(LiDAR NDVI (biomass index)):behavior = winter range	5.03	5.41	14.11	< 0.0001
s(LiDAR NDVI (biomass index)):behavior = exploring	4.76	5.35	8.84	< 0.0001
s(LiDAR NDVI RoV (biomass index RoV)):behavior = incubating	4.86	5.05	19.28	< 0.0001
s(LiDAR NDVI RoV (biomass index RoV)):behavior = laying	5.29	5.73	4.24	0.0002
s(LiDAR NDVI RoV (biomass index RoV)):behavior = brood	1.00	1.00	0.45	0.5049
s(LiDAR NDVI RoV (biomass index RoV)):behavior = potential brood	1.98	2.42	1.62	0.2953
s(LiDAR NDVI RoV (biomass index RoV)):behavior = unclassified	7.73	8.51	35.69	< 0.0001
s(LiDAR NDVI RoV (biomass index RoV)):behavior = winter range	7.35	8.29	11.35	< 0.0001
s(LiDAR NDVI RoV (biomass index RoV)):behavior = exploring	5.43	6.50	17.37	< 0.0001

s(vegetation height):behavior = incubating	5.84	6.90	11.06	< 0.0001
s(vegetation height):behavior = laying	1.00	1.00	0.40	0.528
s(vegetation height):behavior = brood	6.31	7.08	6.51	< 0.0001
s(vegetation height):behavior = potential brood	5.19	6.21	4.98	0.0001
s(vegetation height):behavior = unclassified	8.94	9.00	62.39	< 0.0001
s(vegetation height):behavior = winter range	6.02	7.00	5.26	< 0.0001
s(vegetation height):behavior = exploring	3.18	4.16	1.72	0.1456
s(length of day)	8.71	8.97	80.91	< 0.0001
s(female age)	8.82	8.98	44.21	< 0.0001
s(distance to water bodies (km)):behavior = incubating	6.51	7.47	5.11	< 0.0001
s(distance to water bodies (km)):behavior = laying	2.83	3.59	3.04	0.021
s(distance to water bodies (km)):behavior = brood	4.93	5.75	11.23	< 0.0001
s(distance to water bodies (km)):behavior = potential brood	7.49	8.23	15.56	< 0.0001
s(distance to water bodies (km)):behavior = unclassified	8.74	8.98	96.66	< 0.0001
s(distance to water bodies (km)):behavior = winter range	7.93	8.68	15.15	< 0.0001
s(distance to water bodies (km)):behavior = exploring	4.94	6.05	2.58	0.0164
s(water body presence RoV):behavior = incubating	7.72	8.52	16.92	< 0.0001
s(water body presence RoV):behavior = laying	5.14	6.12	3.42	0.0021
s(water body presence RoV):behavior = brood	4.04	4.91	5.65	0.0001
s(water body presence RoV):behavior = potential brood	1.00	1.00	0.01	0.9295
s(water body presence RoV):behavior = unclassified	8.16	8.80	32.61	< 0.0001
s(water body presence RoV):behavior = winter range	7.47	8.36	6.07	< 0.0001
s(water body presence RoV):behavior = exploring	8.14	8.74	9.78	< 0.0001
s(fine-grain sage (proportion sagebrush)):behavior = incubating	3.21	3.92	15.07	< 0.0001
s(fine-grain sage (proportion sagebrush)):behavior = laying	1.00	1.00	69.75	< 0.0001
s(fine-grain sage (proportion sagebrush)):behavior = brood	4.95	5.57	7.20	< 0.0001
s(fine-grain sage (proportion sagebrush)):behavior = potential brood	2.92	3.55	9.48	< 0.0001

s(fine-grain sage (proportion sagebrush)):behavior = unclassified	8.77	8.98	99.23	< 0.0001
s(fine-grain sage (proportion sagebrush)):behavior = winter range	7.86	8.66	22.05	< 0.0001
s(fine-grain sage (proportion sagebrush)):behavior = exploring	8.02	8.74	18.77	< 0.0001
s(barren index (proportion barren)):behavior = incubating	7.79	8.10	16.48	< 0.0001
s(barren index (proportion barren)):behavior = laying	5.75	6.73	6.42	< 0.0001
s(barren index (proportion barren)):behavior = brood	3.44	4.25	1.22	0.362
s(barren index (proportion barren)):behavior = potential brood	6.14	7.02	6.75	< 0.0001
s(barren index (proportion barren)):behavior = unclassified	7.56	8.34	14.11	< 0.0001
s(barren index (proportion barren)):behavior = winter range	6.72	7.84	7.86	< 0.0001
s(barren index (proportion barren)):behavior = exploring	6.72	7.78	5.66	< 0.0001
s(solar insolation):behavior = incubating	6.78	7.71	15.27	< 0.0001
s(solar insolation):behavior = laying	6.83	7.87	7.29	< 0.0001
s(solar insolation):behavior = brood	5.53	6.28	4.04	0.0014
s(solar insolation):behavior = potential brood	1.00	1.00	32.03	< 0.0001
s(solar insolation):behavior = unclassified	8.32	8.82	23.21	< 0.0001
s(solar insolation):behavior = winter range	6.59	7.40	10.50	< 0.0001
s(solar insolation):behavior = exploring	6.53	7.38	21.62	< 0.0001
s(multiresolution valley bottom flatness):behavior = incubating	7.32	7.90	14.31	< 0.0001
s(multiresolution valley bottom flatness):behavior = laying	7.41	7.91	10.41	< 0.0001
s(multiresolution valley bottom flatness):behavior = brood	3.88	4.83	2.02	0.0781
s(multiresolution valley bottom flatness):behavior = potential brood	1.00	1.00	7.18	0.0074
s(multiresolution valley bottom flatness):behavior = unclassified	7.18	7.92	14.28	< 0.0001
s(multiresolution valley bottom flatness):behavior = winter range	7.78	8.51	56.68	< 0.0001
s(multiresolution valley bottom flatness):behavior = exploring	7.57	8.46	18.74	< 0.0001
s(topographic wetness index (CV)):behavior = incubating	8.36	8.87	20.62	< 0.0001

s(topographic wetness index (CV)):behavior = laying	1.00	1.00	19.37	< 0.0001
s(topographic wetness index (CV)):behavior = brood	5.42	6.31	2.77	0.013
s(topographic wetness index (CV)):behavior = potential brood	3.75	4.61	3.82	0.0026
s(topographic wetness index (CV)):behavior = unclassified	8.71	8.97	22.64	< 0.0001
s(topographic wetness index (CV)):behavior = winter range	6.81	7.74	4.90	< 0.0001
s(topographic wetness index (CV)):behavior = exploring	5.52	6.63	11.35	< 0.0001
s(normalized height):behavior = incubating	7.12	8.12	23.77	< 0.0001
s(normalized height):behavior = laying	6.44	7.43	9.15	< 0.0001
s(normalized height):behavior = brood	4.63	5.52	3.80	0.0015
s(normalized height):behavior = potential brood	1.00	1.00	1.12	0.2905
s(normalized height):behavior = unclassified	8.22	8.83	14.84	< 0.0001
s(normalized height):behavior = winter range	7.39	8.35	19.39	< 0.0001
s(normalized height):behavior = exploring	6.72	7.80	6.37	< 0.0001
s(normalized height CV):behavior = incubating	7.44	8.33	9.67	< 0.0001
s(normalized height CV):behavior = laying	1.00	1.00	47.09	< 0.0001
s(normalized height CV):behavior = brood	5.53	6.45	2.81	0.0067
s(normalized height CV):behavior = potential brood	3.73	4.59	2.47	0.0503
s(normalized height CV):behavior = unclassified	8.01	8.74	67.49	< 0.0001
s(normalized height CV):behavior = winter range	7.59	8.46	11.27	< 0.0001
s(normalized height CV):behavior = exploring	5.14	6.30	12.05	< 0.0001

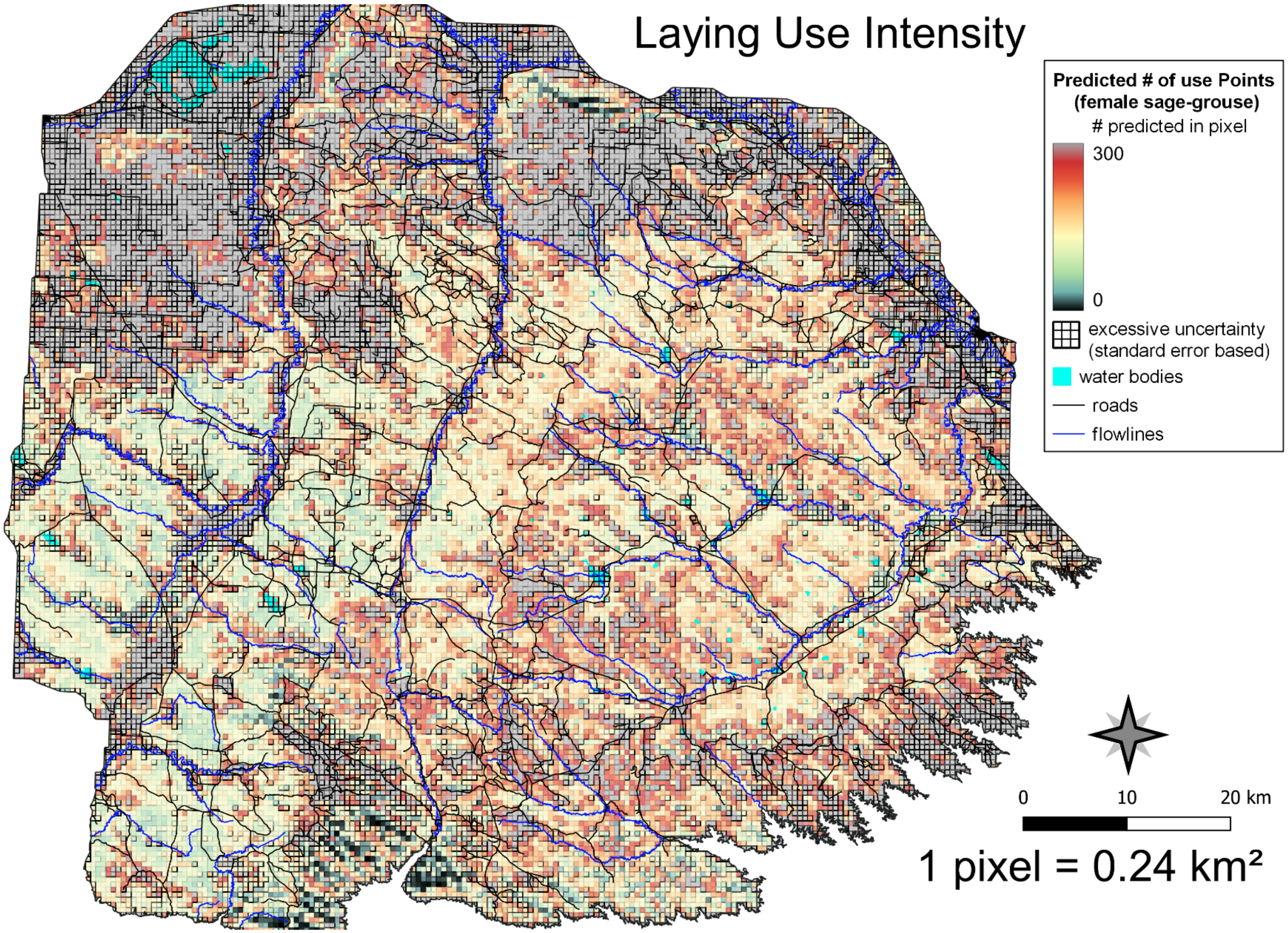


Figure 14. Use-intensity predictions based on number of relocations inside short-term home ranges of laying sage-grouse individuals in our study area near Glasgow, MT, USA. Sage-grouse location data were from 2018–2021.

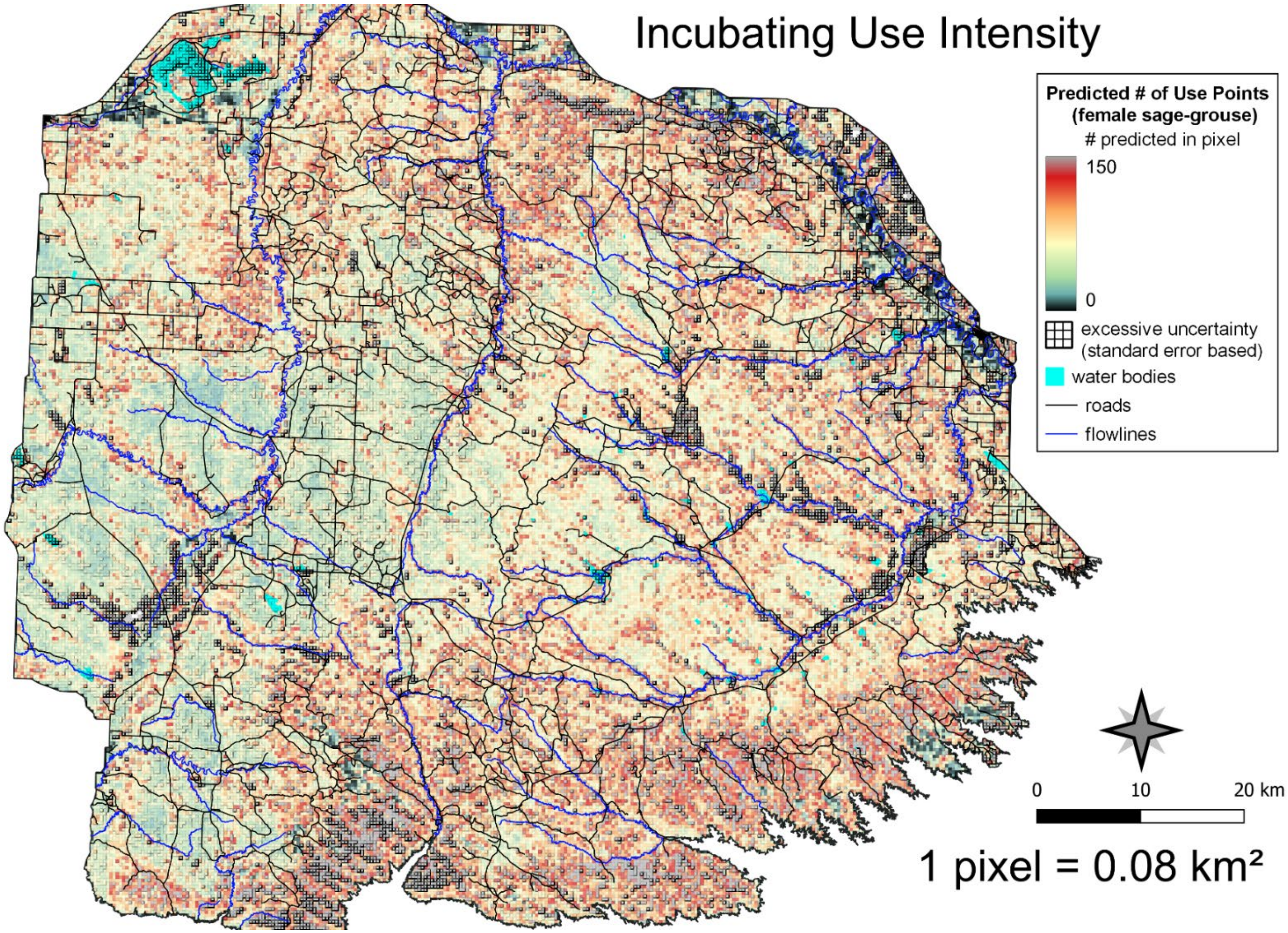


Figure 15. Use-intensity predictions based on number of relocations inside short-term home ranges of incubating sage-grouse individuals in our study area near Glasgow, MT, USA. Sage-grouse location data were from 2018–2021.

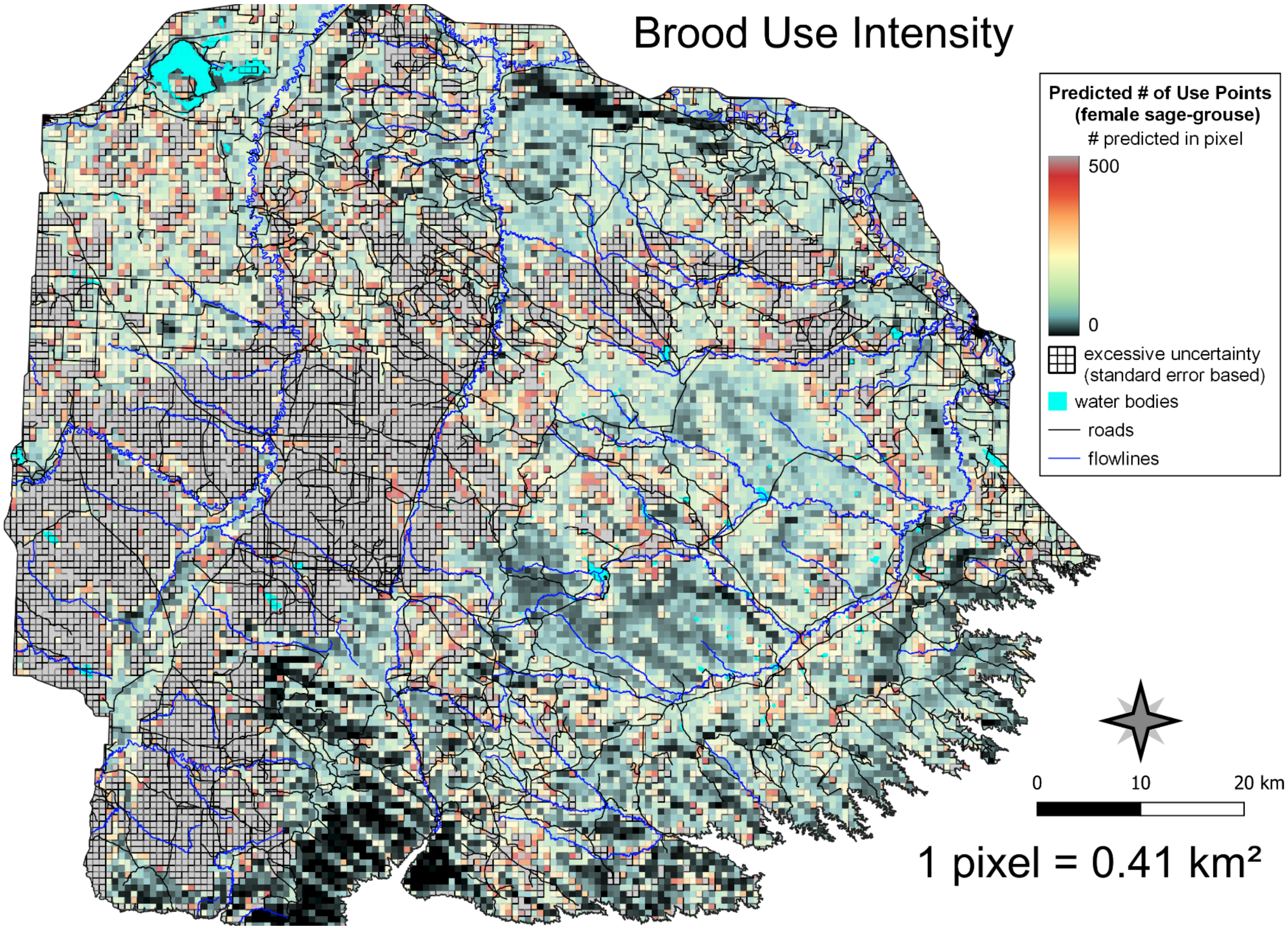


Figure 16. Use-intensity predictions based on number of relocations inside short-term home ranges of brood rearing sage-grouse individuals in our study area near Glasgow, MT, USA. Sage-grouse location data were from 2018–2021.

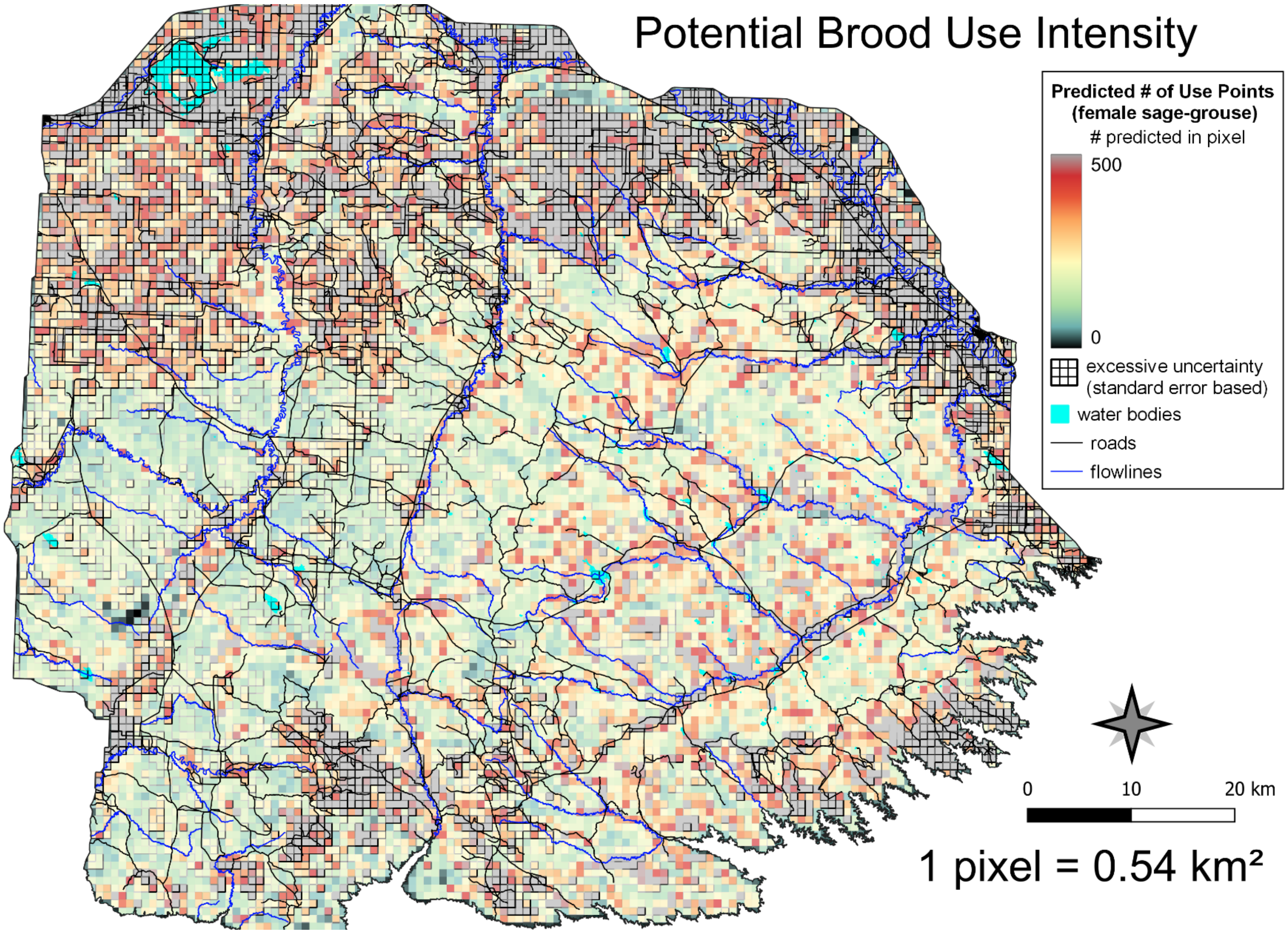


Figure 17. Use-intensity predictions based on number of relocations inside short-term home ranges of potentially brood rearing sage-grouse individuals in our study area near Glasgow, MT, USA. Sage-grouse location data were from 2018–2021.

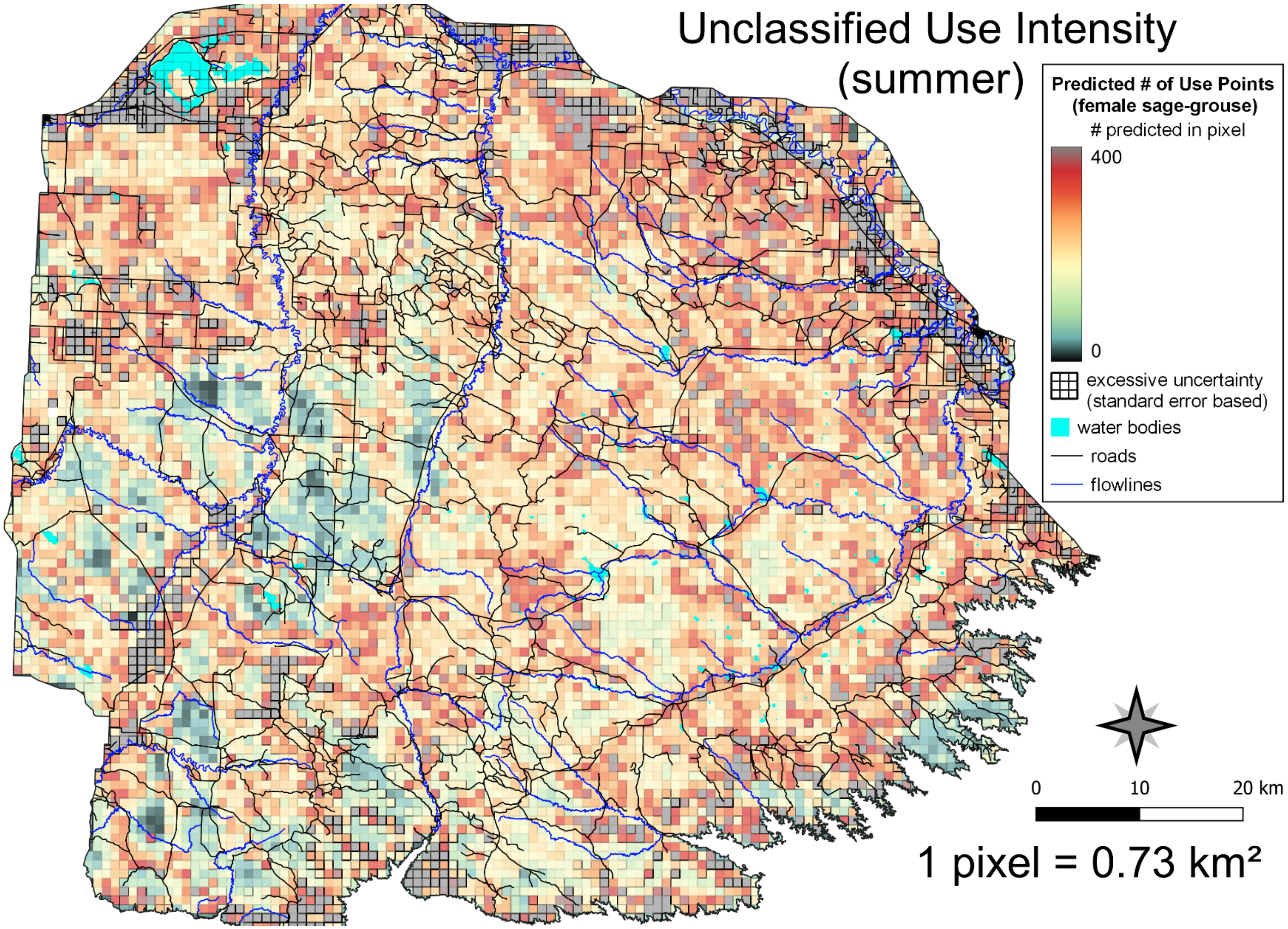


Figure 18. Use-intensity predictions based on number of relocations inside short-term home ranges of female sage-grouse individuals in our study area near Glasgow, MT, USA. Sage-grouse location data were from 2018–2021.

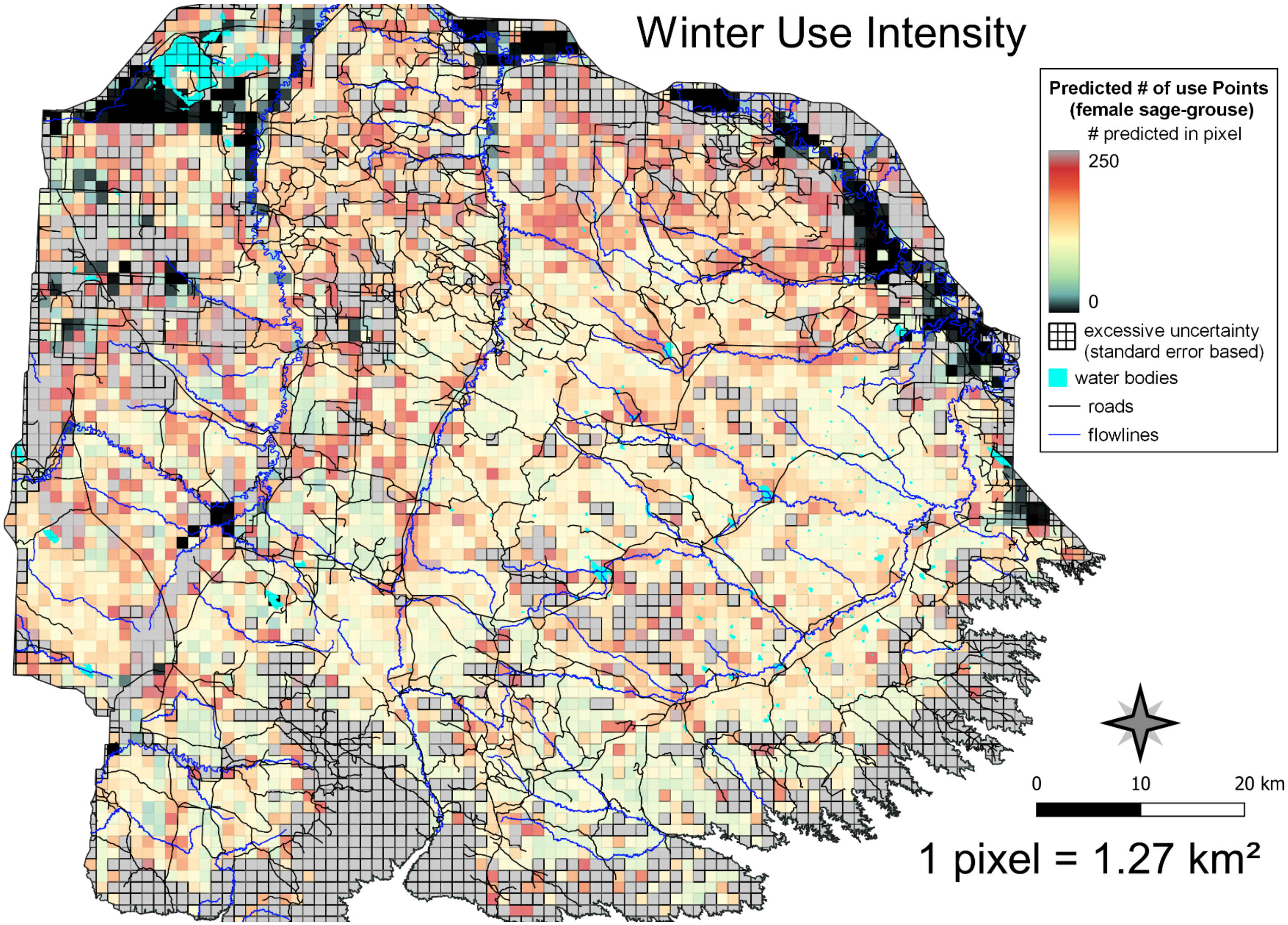


Figure 19. Use-intensity predictions based on number of relocations inside short-term home ranges of female sage-grouse individuals during winter in our study area near Glasgow, MT, USA. Sage-grouse location data were from 2018–2021.

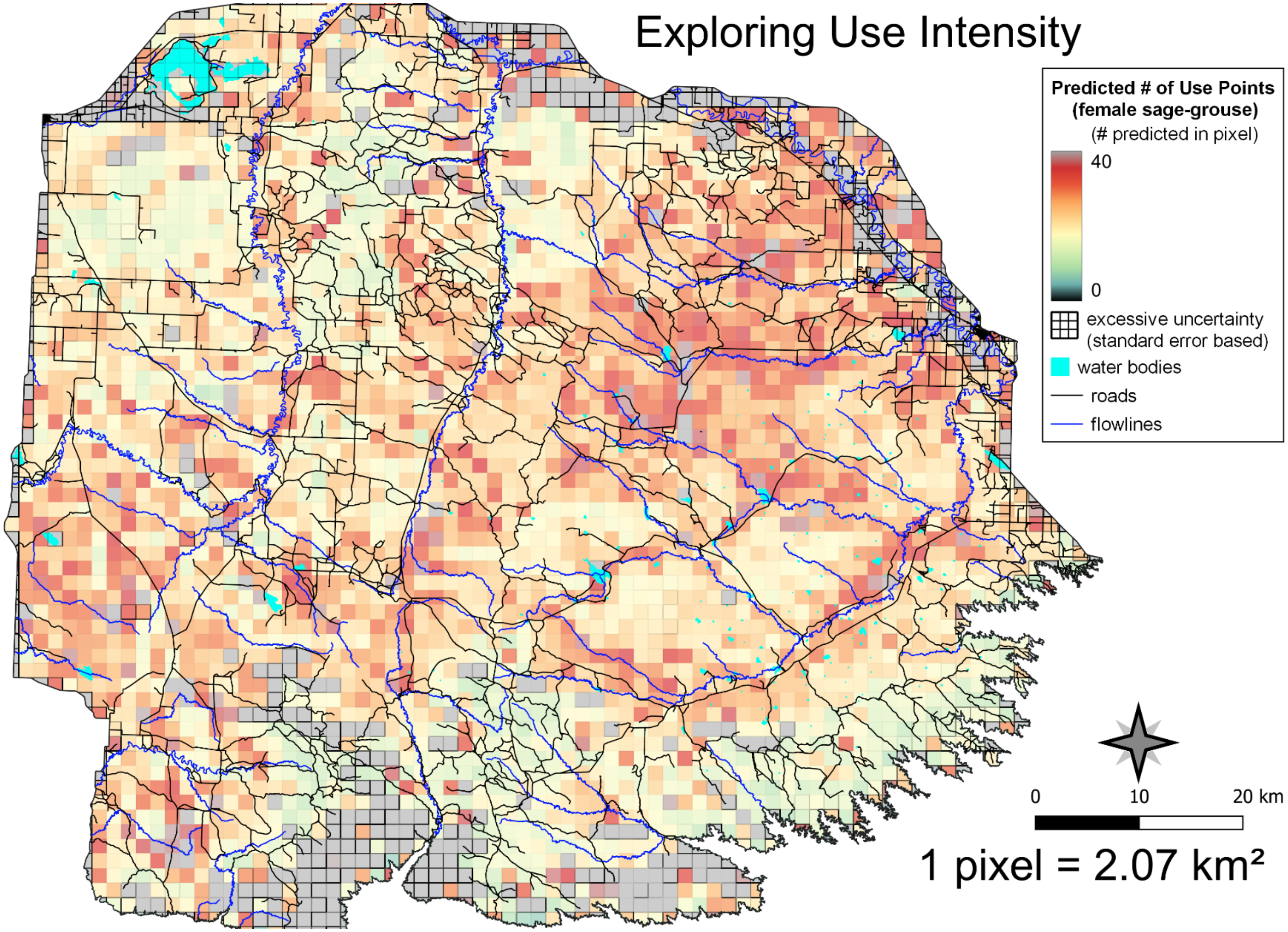


Figure 20. Use-intensity predictions based on number of relocations inside short-term home ranges of exploring or transiting female sage-grouse individuals in our study area near Glasgow, MT, USA. Sage-grouse location data were from 2018–2021.

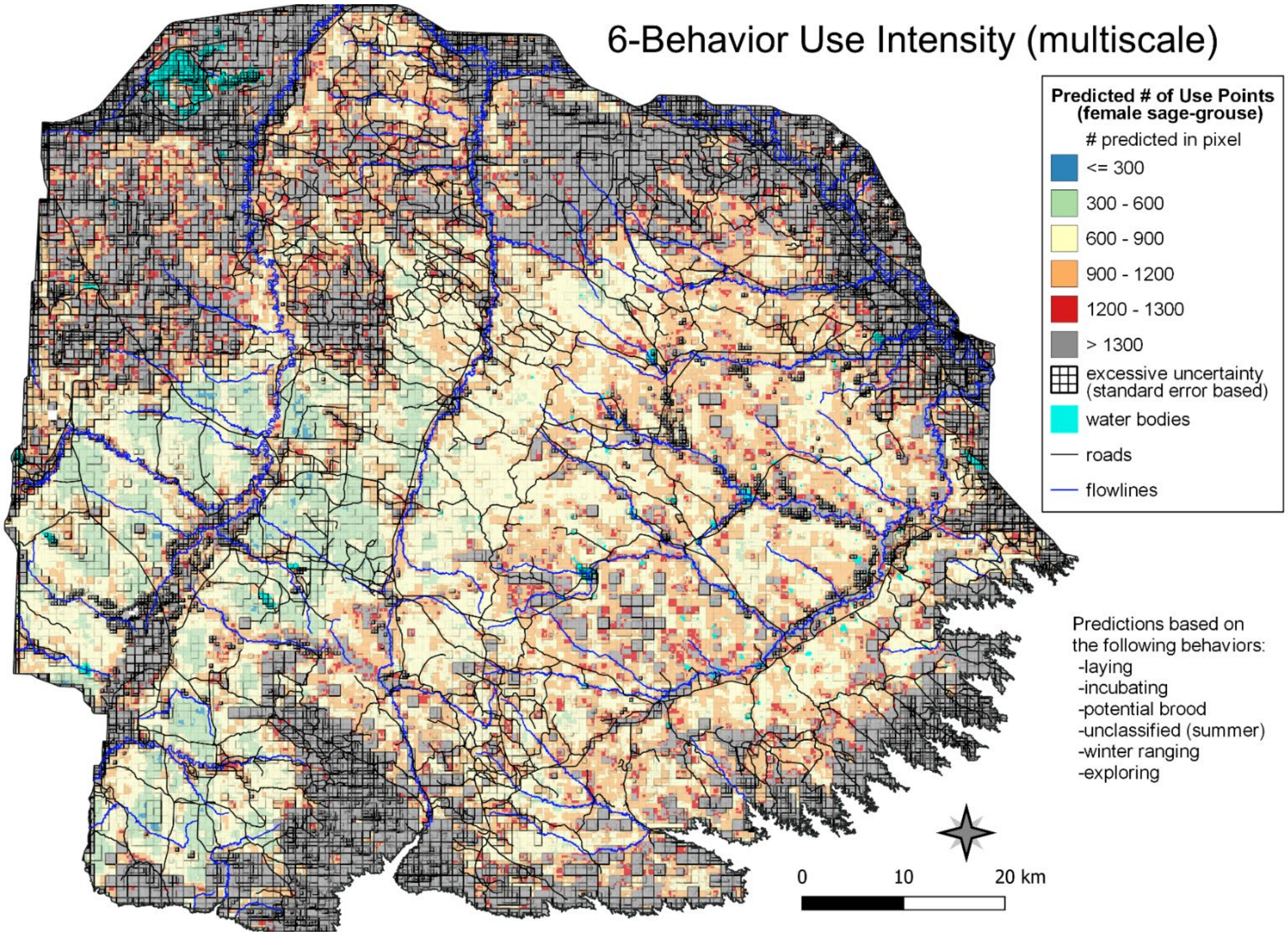


Figure 21. Integrated 6-behavior use-intensity predictions based on number of relocations inside short-term home ranges of female sage-grouse individuals in our study area near Glasgow, MT, USA. Behavior mode integration was achieved by summing use-intensity predictions and associated standard errors for 6 behavior modes. Sage-grouse location data were from 2018–2021.

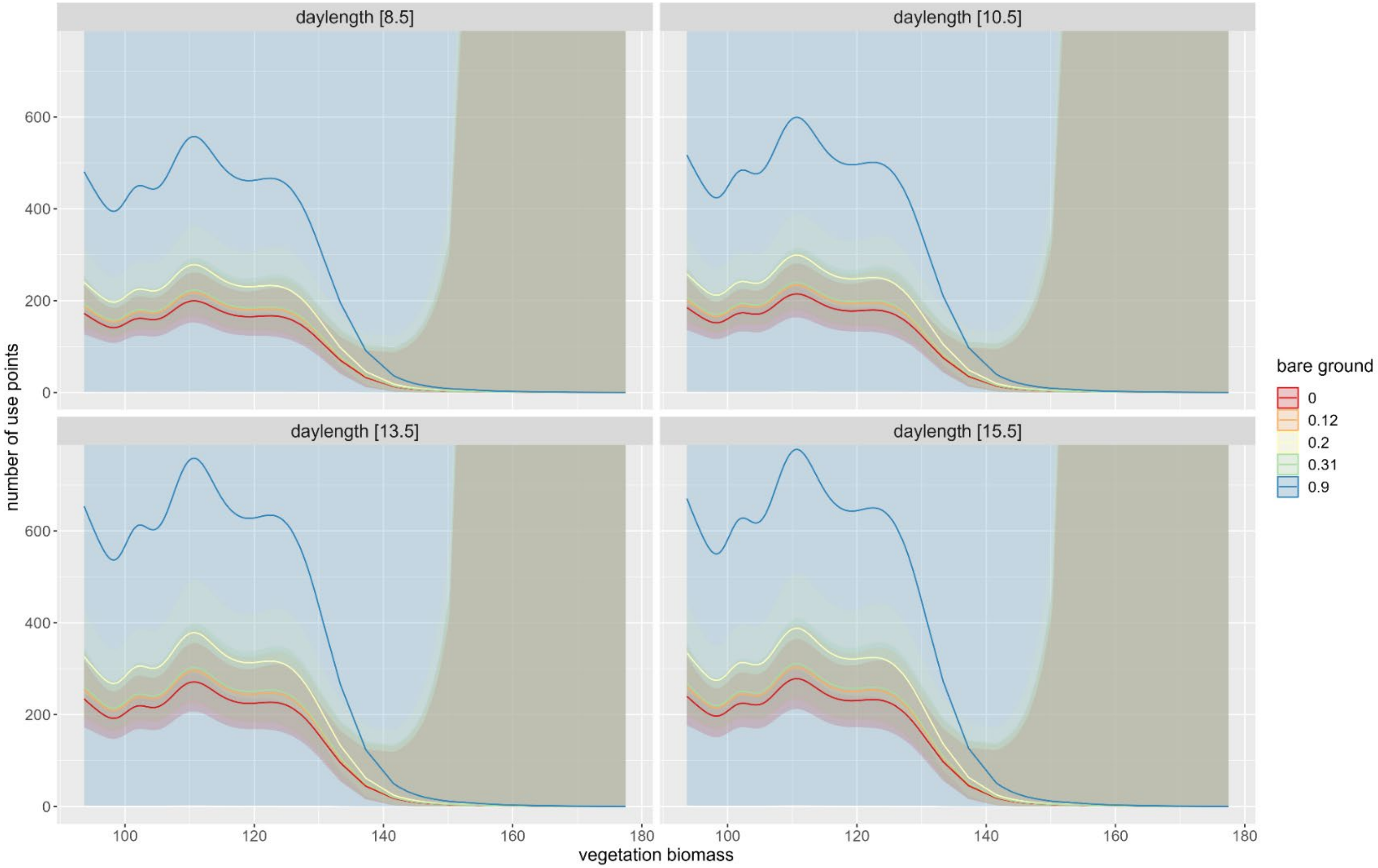


Figure 22. Conditional effects plot from a negative binomial generalized additive model indicating how counts of home-range enclosed points for incubating female sage-grouse vary as a function of vegetation biomass for quartiles of proportion bare ground at four different daylengths. Other covariates were held at median values. Shaded areas represent 95% confidence bands.

CHAPTER 5

NESTING AREA FIDELITY AND MOVEMENT STRATEGIES SUPERSEDE LANDSCAPE CONDITIONS IN DETERMINING NEST SUCCESS IN SAGE-GROUSE

Contribution of Authors and Co-Authors

Manuscript in Chapter 5

Author: Robert T. Haynam III

Contributions: Robert helped conceive and plan the study, interpret results, and write the manuscript. Robert performed all the analysis. All authors edited the manuscript. All authors read and approved the final manuscript.

Co-Author: Lance B. McNew

Contributions: Lance helped conceive and plan the study, interpret results, and write the manuscript. All authors edited the manuscript. All authors read and approved the final manuscript.

CHAPTER 5

Manuscript Information

Robert T. Haynam III, Lance B. McNew

Status of Manuscript:
__x__ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-reviewed journal
____ Accepted by a peer-reviewed journal
____ Published in a peer-reviewed journal

CHAPTER FIVE

NESTING AREA FIDELITY AND MOVEMENT STRATEGIES SUPERSEDE LANDSCAPE CONDITIONS IN DETERMINING NEST SUCCESS IN SAGE-GROUSE

Background

Familiarity with the surrounding landscape is thought to be beneficial to animals through mechanisms such as increased spatial awareness of foraging resources, sheltering cover, specialized breeding habitat, and predator occurrence (Spencer 2012, Gerber et al. 2019). Site fidelity would therefore be expected as a common strategy to promote fitness. Indeed, site fidelity is well documented for many animal species (Craighead et al. 1973, Berry and Eng 1985, Fischer et al. 1993, Baylis et al. 2017, Smedley et al. 2019, McLaren and Patterson 2021) but documented associations between fidelity and fitness measures are rarer (Bradshaw et al. 2004, Forrester et al. 2015). If spatial fidelity is a fundamental adaptive trait for a wildlife species, then fitness consequences of differential fidelity should be evident.

Various factors can modulate the degree of site fidelity including landscape disturbance, habitat degradation, weather conditions, and phenological status. The strength and consistency of site fidelity at the population level may be weakened by anthropogenic disturbance impacting individual animals in seasonal home ranges (Webb et al. 2011). Energy development and associated roads have been shown to alter movement and space use of a variety of taxa, including sage-grouse (Doherty et al. 2008, Gibson et al. 2018), prairie-chickens (Winder et al. 2014), elk (Webb et al. 2011) and caribou (Tracz et al. 2010). Timber harvest can influence calving site fidelity in moose possibly via a response to prior reproductive success (Welch et al.

2000) and anthropogenic landscape disturbance can attenuate otherwise strong site fidelity of elk (Edge et al. 1985, Webb et al. 2011). When experiencing disturbances on the landscape individuals may alter patterns of use-intensity (use points per unit area) within established home ranges or shift ranges entirely (Andersen 1991, Linnel and Andersen 1995, Tracz et al. 2010, Little et al. 2016). During severe winters, for example, animals may relocate to areas with more suitable conditions that may be fully or partially outside of typical seasonal home ranges, thereby altering patterns of site fidelity (Parker et al. 1984, Miquelle et al. 1992, Newton et al. 2017).

Site fidelity is a fundamental ecological phenomenon that is entangled with but conceptually distinct from much habitat selection theory and can vary in a complex fashion due to several factors (Piper 2011). Animals may exhibit differential fidelity to landscape features such as roosts, bedding sites, watering holes, salt licks, dens, or nest sites within seasonal home ranges or territories. In some cases the degree of fidelity among seasonal use areas may be similar and in other cases the degree may differ substantially among seasons (Lafontaine et al. 2017). Consequently, site fidelity can operate at multiple ecological levels ranging from home range maintenance to the reuse of specific forging sites (Wolf et al. 2009). Therefore, changes in patch-level fidelity relative to landscape disturbance or weather may be due to the same trait which drives higher-level and higher profile movement phenomena such as seasonal migration. Seasonal or behavioral patterns of habitat use may also be influenced by biological factors such as body size or the reproductive status of females (Miquelle et al. 1992, Bjorneraas et al. 2011, Bjørneraas et al. 2012, Gelling et al. 2022) which may cause site fidelity to vary over time for the same individual.

Despite the established importance of site fidelity for wildlife, fidelity is often ignored when characterizing and evaluating the quality of habitat for conservation and management (Piper 2011). Tools commonly used to evaluate wildlife-habitat associations, such as resource selection functions, do not incorporate site fidelity through integral model structure and end users rarely attempt to extend models and account for site fidelity (Piper 2011). Without understanding how fidelity modulates wildlife responses to landscape conditions we may misinterpret associations between habitat conditions and population performance which are important for effective population management (Morrison et al. 2006). For instance, beyond documenting site fidelity for sage-grouse (Berry and Eng 1985, Dunn and Braun 1985, Fischer et al. 1993), further links with space use or fitness are needed because sage-grouse are a species of substantial conservation concern.

Sage-grouse have proven to be a species sensitive to anthropogenic disturbances exacted by an ever-increasing human population (Walker et al. 2007, Harju et al. 2010, Lebeau et al. 2014). Individual- and population-level sensitivity to anthropogenic habitat alteration is likely owing to population dynamics that require optimal performance under a suite of landscape-condition compositions and interrelationships as well as metapopulation dynamics that bolster local populations via immigration (Crist et al. 2015). If strong site fidelity exists for a sage-grouse population then individuals may become anchored to areas where habitat quality has become poor after disturbance which could result in depressed vital rates (Fischer et al. 1997, Connelly et al. 2000a, Lockyer et al. 2015, Foster et al. 2019). In other words, fidelity to a particular site may result in an ecological trap after a disturbance (Robertson and Hutto 2006, Hale and Swearer 2016). Compared to other prairie-grouse, sage-grouse productivity and rates of population turnover are lower and recovery from population declines may be comparatively slow (Allen 1962, Connelly and Braun 1997, Connelly et al. 2011a). Therefore, to maintain viable populations it is important to understand if and how site fidelity influences vital rates for sage-grouse. Furthermore, a greater effort to document the fitness consequences of site fidelity on wildlife populations will result in a more comprehensive understanding of wildlife ecology.

We hypothesized that spatial fidelity that is common in sage-grouse would influence reproductive success. Specific predictions that resulted from our hypothesis were that: 1) spatial fidelity would be evident in our sage-grouse population during breeding, 2) fidelity would influence breeding success, and 3) explicit modeling of fidelity would attenuate or alter the apparent effects of commonly evaluated landscape conditions. Disturbance, habitat quality, and individual variability or plasticity in fidelity behavior are expected to cause heterogeneity of nesting area fidelity among individuals. However, no substantial anthropogenic disturbances occurred in our study area before or during our research, so we did not expect any major fidelity-fitness mismatches. We quantified individual-level space- and time-use and examined 3 facets of fidelity-related movement properties to establish fidelity behavior in sage-grouse. Differential use-intensity across the landscape indexed where sage-grouse were spending their time. Our main objective was to test the following statistical hypothesis that derives from our conceptual hypothesis and predictions: nesting-area fidelity, as measured by indices of space- and time-use, should be positively associated with daily nest survival and the influences of landscape conditions (e.g., habitat) on survival may be diminished after accounting for fidelity.

Study Area

Our study occurred over a 425,000-ha area in southern Valley County in north-central Montana, USA (47.66258 N to 48.44968 N, 106.43546 W to 107.44770 W). The area was within Glaciated Northern Grasslands and North Central Highlands (Cleland et al. 1997, McNab et al. 2007) and within the sage-grouse Great Plains Management Zone 1 which corresponds to the Silver Sagebrush Province (Connelly et al. 2004, Stiver et al. 2006). Land cover in the area consisted of approximately 49% big sagebrush steppe, 20% Great Plains mixed-grass prairie, 8% cultivated crops, 6% mat salt shrubland, 2% Great Plains riparian, and 2% Great Plains woodland savanna (Anderson et al. 1976, Comer et al. 2003). Additional limited land cover types included greasewood flats, shale badlands, and Great Plains wooded draws and ravines (Anderson et al. 1976, Comer et al. 2003). The area was characterized by high annual variation in average monthly temperature (-10.1 °C to 21.7 °C) and low mean annual precipitation (29.6 cm), with over half occurring May – July (Arguez et al. 2010). Approximately 75% of the study area was in public ownership, managed predominately by the U.S. Bureau of Land Management (BLM), as well as the U.S. Fish and Wildlife Service (USFWS, Charles M. Russell National Wildlife Refuge [CMR]), and the State of Montana. The area was situated just south of the northernmost extent of the Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) distribution in Montana; silver sagebrush (*A. cana*) becomes the only woody Artemisia species occurring farther north. The area, located at the northeastern edge of the sage-grouse distribution, represents a transition zone between mixed-grass prairie and sagebrush steppe ecosystems which makes it unique in comparison to many other sage-grouse habitats (Dinsmore et al. 2002, Moynahan et al. 2007).

Our population of sage-grouse represents an important component of a larger metapopulation; however, basic information on the population ecology of this population is lacking. The study population represents a core component of the broader northern Montana population (NMP) distributed throughout north-central Montana, southeastern Alberta and southwestern Saskatchewan (Garton et al. 2011, USFWS 2013). Minimum male counts at leks within the NMP were reported to be approximately 2,700 males and the population is thought to be one of the few remaining stable populations of sage-grouse (Garton et al. 2011). The southern segment of the NMP lies below the Milk River and was designated a Priority Area for Conservation (PAC [corresponds to BLM Priority Habitat Management Area]) which was key habitat identified by state or BLM conservation planning efforts (USFWS 2013).

Methods

Field Methods

Sage-grouse Captures During April–May, 2018–2019, we captured 89 (48 in 2018, 41 in 2019) female sage-grouse using spotlighting techniques (Giesen et al. 1982, Wakkinen et al. 1992). We made a concerted effort to attain a representative sample by spreading captures around 3 separate watersheds in our study area. Upon capture we banded females with uniquely numbered leg bands. We aged females as adult or yearling by examining the appearance of primary feathers 9 and 10 (Braun and Schroeder 2015). We attached a VHF-equipped 22-g solar powered Global Positioning System (GPS) Platform Transmitter Terminal (PTT; model GT-22GS-GPS, GeoTrak, Inc., Apex, NC, USA) to each of 86 birds using a rump-mounted harness (Rappole and Tipton 1991, Bedrosian and Craighead 2007). All PTTs were programmed to collect 4–10 locations every day and upload data every 1.5–3.0 days to the Argos satellite system. PTT performance was specified separately for different seasons and the programming was slightly adjusted for 2019 based on observed 2018 PTT performance; PTT programming can affect GPS data transmission success. Our most aggressive programming for a season was 15 March – 1 September where 2018-batch PTTs obtained up to 10 fixes every day and uploaded data to the Argos system approximately every two days. At a minimum, location fixes were collected at approximate 6-hr intervals regardless of programming season or PTT batch. All animal handling was approved under Montana State University's Institutional Animal Care and Use Committee (protocol # 2017-57).

Sage-grouse Monitoring The PTTs had an approximate 3-year lifespan and movement data from equipped sage-grouse was recorded until female mortality or loss of a PTT. During the breeding seasons of 2018, 2019 and 2020, females were monitored by downloading GPS fixes and other PTT sensor data from Argos system servers every 3–5 days. During the breeding season of 2021, PTT sensor data were downloaded and reviewed monthly using the sub-daily location histories. We used multiple lines of evidence to infer female status. Localization of a PTT indicated either a nesting female, a dead female, or a dropped PTT. The PTTs were equipped with an activity sensor which indicated if the PTT was experiencing motion; static activity sensor readings indicated a mortality or dropped PTT. Visitation of nest sites can lead to observer-induced bias in vital rate estimates (Gibson et al. 2015), therefore we only visited localization sites if a mortality was suspected. In most cases incubation recesses (movements by females off nests) were evident in the GPS fix data and helped separate mortalities from nests (Coates and Delehanty 2008, Dzialak et al. 2011). If a mortality was indicated, we verified this with a field visit and recorded the condition of carcass remains including evidence of predation

(Blomberg et al. 2013). We estimated the date of incubation initiation for each confirmed nest by reviewing the GPS data. Nest fate was verified in the field when a female had moved off the nest for ≥ 3 days. Nests that failed just prior to incubation were verified in the field if ≥ 2 locations accrued in the same location due to periodic visits by a female. After nest abandonment, we located nests and recorded evidence regarding nest fate. Hatching was indicated by eggs with detached membranes and eggshells that were consistent with being pipped by chicks (Rearden 1951, Sargeant et al. 1998). We considered a nest successful if we found ≥ 1 egg had hatched.

Nest Survival Predictor Variables

Movement Properties Spatial fidelity of animals has previously been quantified as the mean distance between consecutive locations within a period or the distance between mean coordinates of different periods (Garrott et al. 1987, Fischer et al. 1993, Popp et al. 2011, Brough et al. 2017, McLaren and Patterson 2021). Additionally, nest-site fidelity has been examined by comparing observed distances among consecutive nests to a statistical null distribution representing random nest placement (Holloran and Anderson 2005). We chose to use more formalized movement properties including number of points accrued in short-term home ranges, elongation of home ranges, and overall use-intensity to evaluate site fidelity because detailed movement properties are interpretable in the context of the time-series movement process of animals (Barraquand and Benhamou 2008, Benhamou and Riotte-Lambert 2012, Lyons et al. 2013, Bracis et al. 2018).

Use-intensity captures both the degree of revisitation and total residence time in areas and represents a time-varying utilization distribution which is related to space use and resource selection (Millspaugh et al. 2006, Hooten et al. 2013, Van Moorter et al. 2016, Fieberg et al.

2021). Moreover, use-intensity is an index of site familiarity (time spent in an area) which is a hypothesized link between spatial fidelity and fitness (Yoder et al. 2004). Individual-level use-intensity increases as more time is spent in a unit area so major fluctuations in use-intensity are also due to the size of short-term home ranges during nesting with smaller home ranges resulting in higher use-intensity, given a fixed degree of fidelity. Therefore, examination of other movement properties can help differentiate between areas with elevated use-intensity due to revisitation vs. due to contracted space use at nest sites. Differential counts of previously visited points in short-term home ranges (enclosed points) may indicate switching between space-use strategies (larger or smaller use area) which would increase exposure to predators (greater spatial dispersion) and may indicate lower quality incubation recess habitats. Furthermore, lower number of enclosed points for a given use-intensity may indicate coarser spatial- and temporal-scale aspects of fidelity such as switching nesting areas entirely, thereby diminishing familiarity (use-intensity). Eccentricity of home ranges further discriminates among movement behaviors at nest sites by quantifying fine-scale fidelity. For instance, high eccentricity indicates a consistent vector of movement to and from a nest and incubation break area. Fidelity to an incubation break area may also restrict a female's use area which would limit exposure to predators (Coates and Delehanty 2008).

Unless otherwise noted, we used the statistical computing software R for data manipulation and analyses (R Development Core Team 2013). To quantify coarse-scale movement properties we segmented space use by each sage-grouse into space-time local hulls (minimum convex polygons [MCPs]). To prevent bias in hull construction due to irregular sampling we subset relocations to 6-hour sampling intervals (Lyons et al. 2013). We used the R package T-LoCoH to process the 6-hr regular-trajectory data and quantify spatiotemporal patterns of sage-grouse movements including: hull-enclosed points, area of hulls, and hull eccentricity. We calculated eccentricity using the shape parameters of a minimum closing ellipse for each nearest-neighbor-point set (Lyons et al. 2019). Eccentricity varies from 0 to 1 with 0 being a perfectly round ellipse and 1 being a severely elongated linear ellipse; ellipse elongation indicates directional movements. We calculated hull area as the area of each hull polygon; hull area provides a geometric delineation of space use and is analogous to a home-range area calculated for brief periods. We calculated number of enclosed points accrued up to the maximum time of each home range observation; every short-term home range has a timespan and we calculated enclosed points as all prior and current points enclosed by each home range. We calculated use-intensity by dividing enclosed points by the short-term home range area. Our method of calculating number of enclosed points is a modification of standard T-LoCoH output (Lyons et al. 2019) which counts the enclosed points that have accrued over the period of a trajectory (duration an individual is monitored).

We also calculated the net distance of every relocation away from the first nest site known for each female. If a female never initiated a nest, then we used the first location in the lifetime trajectory as the start point. First locations were near nesting areas because females were captured during breeding season. Our net distance variable accounts for differential seasonal space use and seasonal home-range fidelity by quantifying distance from the initial nesting region of each female. We used distance from first nest to quantify breeding season fidelity with the expectation that distance from the nesting region would remain relatively low during the reproductive phase of female sage-grouse.

Previous research indicates that the scale at which variation in movement properties are calculated can influence observed relationships between movement, space-use and resource selection (Van Moorter et al. 2016). Our hull-based (home range) movement metrics represent movement properties at coarser scales that have been associated with sage-grouse region use (Doherty et al. 2008, Doherty et al. 2010, Fedy et al. 2014, Walker et al. 2016). However, the scale of our analysis is largely dictated by the movement behavior of individuals which in this case is restricted to sage-grouse nesting behavior.

Hydrology Water can be an important seasonal resource for sage grouse and may influence distributions and seasonal space use (Donnelly et al. 2016, Donnelly et al. 2018). Water also shapes the landscape and may create terrain features such as runnels used for loafing or larger gullies with steep banks in which coyotes place dens. To quantify the distribution of stream channels on the landscape, we analyzed a 1/3rd arc second scale digital elevation model (DEM) using terrain analysis tools in the System for Automated Geoscientific Analyses (www.saga-gis.org, Version: 7.6.4). We performed a hydrologic analysis of the DEM to generate a stream channel network in our study area. Stock ponds were abundant in our study area and can influence vegetation structure by influencing grazing patterns of cattle. Available water body data layers did not correspond well with recent aerial imagery of our study area so we developed a raster layer delineating water bodies by combining spatial information about water body extents from multiple sources using a multiple criteria analysis (Gao 2009) (see Appendix G, Table 17, and Appendix C).

Vegetation Vegetation characteristics are often associated with space-use and nesting success of female sage-grouse (Holloran et al. 2005, Hagen et al. 2007, Doherty et al. 2010, Dahlgren et al. 2015), but see (Smith et al. 2020). Available geospatial vegetation data did not correspond well with the ground cover in our study area, so we developed 8 vegetation related variables: barren cover, LANDFIRE sage cover, lowland NDVI, medium shrub cover, radius of variance of vegetation biomass, sagebrush cover, vegetation biomass, and vegetation height (see Appendix G, Table 17, and Appendix C).

Terrain Intensity of landscape area use by female sage-grouse has been associated with terrain features during multiple seasons (Aldridge and Boyce 2007, Aldridge et al. 2012, Walker et al. 2016, Newton et al. 2017). Terrain-analysis landscape condition variables most used by wildlife researchers include slope, aspect, topographic position, ruggedness, and relative elevation but other terrain related variables may be more biologically interpretable. We used a 1/3 arc-second scale digital elevation model (DEM) and SAGA GIS to calculate 14 terrain metrics (SAGA version 2.3.2, www.saga--gis.org). Variables derived from terrain analyses tend to be highly collinear, so we did not expect to use all 14 but created them to have a comprehensive set to evaluate. Our terrain metrics were topographic ruggedness index, vector ruggedness measure, topographic position index, topographic wetness index, total insolation, mid-slope position, normalized height, standardized height, multi-resolution valley bottom flatness, morphological protection, multi-resolution ridgetop flatness, slope height, valley depth and wind exposition (see Appendix G, Table 17, and Appendix C).

Temporal Modulators Female age, nest age, nesting attempt, and year are commonly hypothesized to influence daily nest-survival rates (Dinsmore et al. 2002, Rotella et al. 2004, Moynahan et al. 2007, Webb et al. 2012, Doherty et al. 2014) and used to model time-dependent process variance in nest survival. Effects of female age, nest age, nesting attempt, and year are not easily interpreted with respect to biological mechanisms influencing nest survival because the mechanism is not observed. However, a well-supported candidate model with one or more of these predictors may hint at processes influencing nest survival. For instance, nests for precocial birds in a risk set may see risk decrease through time (as nests age) because nests in riskier environments fail earlier (Klett and Johnson 1982, Dinsmore et al. 2002). More importantly, female age, nest age, and year may be positively collinear with residence time, revisits, duration, and therefore use-intensity at various temporal scales. Consequently, we evaluated or controlled for female age, nest age, and year to prevent confounding of statistical associations between space- and time-use movement properties and daily nest-survival rates. We calculated female age in daily increments by assuming an individual was hatched June 15 one or two years prior dependent on being identified a yearling or adult at capture. We did not expect daily aging during nesting would influence nest survival, so we discretized daily ages into four categories ranging from one to six years of age using cluster analysis. Ages were therefore underestimated for many females captured as adults because they were specified as 2 years old but could have been > 2 years old. We also calculated mean daily temperature, precipitation (Oregon State PRISM project, Hart and Bell (2015)) and length of day as variables to account for variation in daily nest-survival rates due to weather and seasonality.

Confirming Fidelity Behavior

We evaluated breeding-season fidelity behavior in our sage-grouse population by fitting a generalized additive model to a time series of log-transformed distances from first nests of individuals (NDnest) using our complete year-round dataset of short-term home ranges. NDnest within and among individuals should not exhibit seasonal periodicity if seasonal fidelity behavior is not operating. Sage-grouse females that move according to the ideal free distribution (Fretwell and Lucas 1969, Piper 2011) or correlated random walks (Turchin 1998) would not be expected to consistently return to the same breeding patches. For instance, a nomadic sage-grouse might exhibit temporally increasing or other non-seasonal changes in distance from a reference point (Bunnefeld et al. 2011).

We modeled NDnest as a function of study time (hour of study) while covariate correcting for precipitation, normalized height, home range area, number of home-range enclosed points, fine-scale sagebrush cover, bare ground, and NDVI. All predictor variables were modeled with thin plate spline smooths and we included a random effect of individual ID to help account for repeated measures on individuals. We evaluated the complexity of our smooth terms by iteratively fitting our model and using function gam.check() of R package mgcv to check adequacy of basis dimension (k) choices. We increased k until increasing it did not substantially change the expected degrees of freedom of the smooth terms (Wood 2017).

Reconciling Movement Properties and Landscape Conditions

We calculated landscape-condition summary statistics for each sage-grouse short-term home range at multiple scales. We calculated zonal summary statistics as the mean, coefficient of variation (standard deviation/mean [CV]), and robust coefficient of determination (median absolute deviation/median [rCD]) of all landscape condition pixels within each home range. We calculated CV and rCD because either may better represent landscape-condition variability and we had no a priori information. We also calculated mean values for 30-m and 100-m radius patch footprints centered on the points from which each home range was delineated, thereby capturing finer grain use within the home ranges. We selected the three aggregation scales of the covariates (home range, 100 m, 30 m) to help represent the multiscale nature of sage-grouse habitat responses. Zonal statistics calculated at the 30-m and 100-m extent for sets of points composing each home range were aggregated by home range using the 'purrr' package in R (Henry and Wickham 2020). For instance, the CV of sagebrush cover means from 18 100-m radius polygons representing use patches in a home range was calculated to estimate the 100-m home range CV of sagebrush cover use in a single home range. Our hull-wise aggregation scheme was based on nearest neighbor sets associated with each short-term home range (Lyons et al. 2019) and allowed multiple landscape-condition grain sizes (home range, 100 m, 30 m) and summary statistics (mean, CV, rCD) to be evaluated.

Statistical Analysis

Modeling Strategy We lagged the hull-wise (short-term home range) summary statistics of all landscape conditions and movement properties by 20 home range observations to ensure that the timespan of home ranges did not exceed the endpoint of an observation interval. In cases where no female sage-grouse fixes were missing, the 20-observation lag represents a $20 \times 6 = 120$-hour time lag of home range parent points and if there were missing locations the time lag is somewhat longer. Time intervals represented by each home range observation always temporally bracket a home range parent point and are a function of female movements and T-LoCoH tuning parameters (Appendix A). Our time lag helped ensure that landscape conditions and movement properties sampled at each home range observation represent spatial and temporal aggregates (smooths) of landscape use and movement behavior just prior to and generally not beyond observation timestamps. In other words, space- and time-local smoothing represented the local past and present instead of the local past and future relative to observation timestamps.

Sub-daily changes in movement properties were minor given central-place foraging behavior of nesting females because we calculated movement properties with 6-hr regular-trajectory data that updated at 6-hr increments based on space- and time-use of individual females. Therefore, we calculated single mean home range observations from the ≤ 4 lagged movement and landscape condition observations typically available each day. Aggregating to achieve daily observations eased the computational burden of modeling the effects of time-varying predictor variables and modeling 6-hr nest-survival rates was not necessary to evaluate our hypothesis.

We modeled daily nest survival response to time-varying predictors using a standard regression modeling strategy where we first performed variable selection and then model selection to identify the best supported model from a candidate set. We deviated from standard regression modeling strategy by fitting sets of generalized linear models (GLM) and generalized additive models (GAM). In both cases our models were logistic regression models modified to logistic-exposure models that modeled daily nest survival data (0 = failure, 1 = success) as a function of variables hypothesized to influence survival. We modified the logit link function to model daily nest survival following Shaffer (2004). We matched daily predictor observations to daily nest-survival data using function tmerge(), and tdc() of R package Survival. We used both GLM and GAM model types because each have respective strengths and weaknesses which we assessed against our dataset and objectives (Faraway 2006, Zuur et al. 2007, Van Der Burg et al. 2010, Harrell 2015, Wood 2017). For instance, the relationship between movement properties and daily nest survival might not be linear on the log odds scale as is assumed by GLMs. Conversely, GLMs provide standard coefficient estimates (i.e., effect sizes and uncertainty estimates [e.g., dot-and-whisker plots]) and conditional effects plots; GAMs do provide nonstandard alternatives and parametric terms can be included. Furthermore, some datasets are not substantial enough to accommodate complex model structures facilitated by GAMs, but ours was.

Variable Selection Collinear predictor variables can destabilize regression model estimates and confound interpretation so we calculated Pearson correlation coefficients and variance inflation factors (VIF) for all explanatory variables and sequentially eliminated variables exceeding user specified thresholds (Zuur et al. 2007, Braak and Šmilauer 2012, Legendre and Legendre 2012, Borcard et al. 2018). We accomplished correlation and VIF-based variable elimination using an R script incorporating the auto_cor() and auto_VIF() function which allowed us to prioritize keeping variables of primary interest and highest interpretability from sets of collinear variables (Benito 2021). For instance, we chose to specify that use-intensity be included with higher priority than other movement properties because it integrates multiple aspects of space- and time-use and can therefore highlight areas where fidelity was occurring. We specified $r < |0.6|$ and VIF < 2.5 and acknowledge that our thresholds are somewhat aggressive but we do not consider collinearity to be a trivial impediment to sound regression inference and GAMs are particularly sensitive to collinearity issues (Wood 2017). In some cases, we transformed predictor variables after initial variable selection because of model convergence problems (Table 7). We reconducted our variable selection procedure after transforming variables because transformations can alter collinearity.

Model Selection All 103 predictors that we calculated to represent landscape conditions and movement properties during nesting could influence nest survival and many are based on published evidence (See Appendix G, Table 17, and Appendix C). VIF and Pearson correlation screening reduced the number of variables in our GLM and GAM models but retained 16 predictors. An all-subsets regression would result in 2^n models where n is the number of predictors considered. However, fitting $2^{16} = 65{,}536$ models is not recommended (Burnham and Anderson 2002) or computationally reasonable so we conducted all-subsets regression separately for movement, temporal modulator, vegetation mean, vegetation variability, and terrain predictors. We then merged the all-subsets results of each predictor-type set and examined variable importance and model ranks using the 95% confidence sets (Burnham and Anderson 2002) of the merged GLM and GAM sets. Finally, our interpretation of the 95% confidence sets informed our construction of a final model.

We made multi-model inference using model weights, and variable importance scores from the GLM and GAM merged sets. We employed model selection and multi-model inference methods based on Kullback-Leibler information loss (Akaike's information criterion [AIC]), small-sample AIC ($\mathrm{AIC_c}$), difference-transformed $\mathrm{AIC_c}$ values (Δ_i), and normalized Akaike weights (w_i) (Burnham and Anderson 2001, Burnham and Anderson 2002). We summed w_i across candidate models that contain a given predictor (j) to quantify variable importance ($w_+(j)$). We also used Akaike weights to select a GLM and a GAM 95% confidence set of models (Burnham and Anderson 2002). We used function dredge(), merge(), mod.avg(), and sw() of R package MuMIn to calculate $\mathrm{AIC_c}$, Δ_i, w_i, and $w_+(j)$ for the GLM and GAM model sets.

An important regression modeling consideration is whether predictors represent fixed or random effects. We initially used function glmer() of R package lme4 to include a random intercept for individual ID in some candidate GLM models because many females had > 1 nest within and across years which represents repeated measures on individuals (Rotella et al. 2004). Many GLM model structures did not accommodate random intercept terms for individual because the models did not converge. However, we explicitly modeled individual heterogeneity in daily nest-survival rate due to nesting attempt, weather, movement activities, vegetation, and terrain. Modeling factors that can contribute to individual heterogeneity helps alleviate issues due to nonindependence of data for females that contribute more than one nest within and across years (Rotella et al. 2004). We fitted all GLM models without random intercept terms for individual using function glm() of R package stats. We used function bam() of R package mgcv to fit all GAMs. We used bam() instead of gam() because the fitting procedure accommodated use of a modified link function without extensive custom coding. We withheld using an individual-ID random effect from GAM all-subsets regression to limit computational burden but included it in the GAM final model.

Finally, we considered biologically justified interaction terms for variables identified for inclusion in our final model. Specifically, we included an interaction between number of enclosed points and use-intensity to help explain how different combinations of the movement properties affect daily nest survival. We added the interaction between use-intensity and enclosed points because finer temporal-scale revisitation and residence time, that largely drive use-intensity (Chapter 2), may differentially influence daily nest survival depending on the degree of coarser temporal-scale revisitation (intermittent use). Enclosed points can help differentiate use-intensity fluctuations due to fine-scale movements (contracted home ranges) versus coarser scale recursive movements (revisitation).

Results

During May – June 2018 and April 2019, we fitted 86 of 89 captured female sage-grouse with GPS transmitters. We collected 192,640 geographic coordinates of 86 female sage-grouse during 2018-04-24 – 2022-04-14 which encompassed 4 complete annual cycles of sage-grouse. The median (IQR) number of locations per female in the complete dataset was 1,410 (2,933). After resampling trajectories to 6-hr intervals and removing individuals with inadequate relocation histories our movement property calculations used 110,024 relocations of 74 females. The median (IQR) number of locations per female for our year-round movement analysis was 1156 (1940).

We located 185 nests of 76 individuals during the nesting seasons of 2018 – 2021. Mean number of nests per female-year was 1.37 (SD = 0.53, n = 135). Mean date of incubation initiation for firsts nests was 04 May (range = 17 April – 03 June, n = 135). Mean date of incubation initiation for second nests was 24 May (range = 05 May – 08 June, n = 47). Mean date of incubation initiation for third nests was 02 June (range = 25 May – 07 June, n = 3).

Evaluating Fidelity Behavior

Our fitted GAM model that evaluated the relationship between distance from first nest (NDnest) and study time was consistent with a regular seasonal pattern of change in NDnest and fidelity to nesting areas (Appendix G, Figure 56). Model fit (adjusted $R^2 = 0.78$) and model diagnostics were good (Appendix G, Figure 60). Study time and home range area required the highest basis dimensions (*k*) indicating that those variables have a complex relationship (seasonality) with NDnest (Appendix G, Table 18). All smooth terms except precipitation were statistically significant (Appendix G, Table 18). NDnest decreased as number of enclosed points increased, normalized height increased, vegetation biomass increased, and area decreased (Appendix G, Figures 57–59). NDnest increased as proportion bare ground became very low or became very high (Appendix G, Figures 58 & 59).

Nest Survival

We linked lagged movement properties from our year-round tracking data to daily nest survival observations. Five individuals, representing 5 first nests, were completely removed from analysis because movement data was lagged to a time prior to GPS deployment (no movement properties) and the individuals never contributed another nest. Two other individuals each had a nest removed due to data lagging but future nests by those individuals were included. One nest was removed because a female vanished during nesting so lagging resulted in an incomplete record (missing movement property data).

Correlation and variance inflation factor screening identified 16 suitable continuous-scale predictors (Table 7) that we included in both the GLM and GAM all-subsets model sets. To control for potential confounders, we also included female age, nest age, and nesting attempt in both sets. Our female-age factor had 4 age-range levels and was collinear with year, so inclusion of female age precluded using year to represent the passage of time.

The 95% confidence set of models from our GLM and GAM merged sets both indicated that models containing use-intensity, enclosed points, and eccentricity had relatively high Akaike weights ($\boldsymbol{w_i}$). Models with use-intensity, number of enclosed points, and eccentricity ranked the same (1, 2, 3) in GLM and GAM merged candidate sets (Table 8). The GLM model with the most support in the data ($\boldsymbol{w_i} = 0.47$) was a movement model with use-intensity as the only variable (Table 8). The GAM model with the most support in the data ($\boldsymbol{w_i} = 0.39$) was a movement model with a smooth term for use-intensity (Table 8). No landscape conditions were supported as influential on daily nest survival (Table 8). For instance, the vegetation model with most support in the data ($\boldsymbol{w_i} = 0.021$) was a model with a smooth term for radius-of-variance of vegetation height, radius-of-variance of vegetation biomass, and variability of vegetation biomass. The season and nest phenology model with most support in the data ($\boldsymbol{w_i} = 0.006$) had a smoothing term for daylength, precipitation, and nest age.

All competing models in both 95% confidence sets were within 2 $\mathrm{AIC_c}$ units of the top model (use-intensity). Additional variables were uninformative in our GLM confidence set; one additional variable penalized $\mathrm{AIC_c}$ by ≤ 2 units (Arnold 2010). However, one additional variable in GAM models contributed more degrees of freedom per variable (≈ 5–6) so being within 2 $\mathrm{AIC_c}$ units was not indicative of noninformative variables. In other words, adequately capturing non-linear functional forms of the predictors changed eccentricity and enclosed points from uninformative to informative (Table 8). Nevertheless, $\mathrm{AIC_c}$ values and model rankings were similar in all GLM and GAM 95% confidence set models (Table 8).

Because we also detected non-linear functional forms during model checking of the final GLM model, we make inference primarily from our final GAM model: log(s/1-s) = s(ID random effect) + s(nest age) + s(eccentricity) + s(enclosed points) + s(use-intensity) + ti(use-intensity, enclosed points), where s, s(x) and ti(x_a, $\mathrm{x_b}$) represent survival rate, thin-plate spline smoothing terms, and tensor product spline terms, respectively. For comparison of GLM and GAM models we present results from our final GLM model in Appendix G, Figure 61.

Daily nest survival rate was strongly influenced by sage-grouse movements where use-intensity, and eccentricity of nesting home ranges had a positive association with daily nest survival (Figure 23). Holding other covariates constant (number of enclosed points = 104, nest age = 15, eccentricity = 0.62), daily nest survival changed from 0.91 (CI = 0.85 – 095) to 0.98 (CI = 0.96 – 0.99) when log(use-intensity) was 5 or 10, respectively (Figure 24). Nest age was not well supported as influencing daily nest survival rate but we include nest age in our final model to control and illustrate its influence on use-intensity. Nest attempt and female age were not well supported (Table 8).

Discussion

Our results demonstrate that 1) female sage-grouse have strong fidelity to nesting locations, and 2) nest survival of sage-grouse is strongly associated with movement properties that indicate fidelity. Our study is the first to identify a positive relationship between fidelity to nesting locations and daily nest survival of sage-grouse. We also documented a positive association between increased directionality of movement away from nests and increased daily nest survival rates which demonstrates the importance of movement patterns at nest sites. Moreover, the positive association between fidelity and nest survival was a function of individual- and time-varying space use strategies of females while incubating and not vegetation related habitat conditions. The effects of landscape vegetation conditions often deemed important for sage-grouse nesting ecology were not well supported; a result that challenges contemporary sage-grouse management that ignores the consequences of fidelity.

Affinity, Fidelity, Familiarity and Fitness

Area fidelity is synonymous with area familiarity if repetitive use occurs in regions that do not change drastically between or during visits. Elevated values of use-intensity in nesting home ranges partly result from repeated and extended use of an area within and among years. Therefore, the positive association between use-intensity and daily nest survival supports our hypothesis that nesting area fidelity has a positive influence on breeding success.

A behavioral driver of fidelity is affinity, an unobservable trait which results in observed fidelity. We define affinity as the presumed liking and draw that an animal experiences for a place independent of repeated evaluations of a place. Therefore, affinity enforces fidelity which promotes familiarity and consequent fitness advantages. A positive influence of nesting-area fidelity on daily nest survival may result from familiarity due to consistent repeated use, return to use from an alternate nesting area, or movement to a previously used non-nesting area. Consistent repeated use was the most common form of fidelity for our study population and is clearly distinguished from an active area-selection decision process (non-oriented movement) where site switching would be common, assuming other suitable areas are available. We generally cannot discern the degree of spatial fidelity exhibited by sage-grouse in other studies but caution that if fidelity behavior is exhibited then ignoring it may compromise study designs where space use is assumed to be solely a function of active resource selection decisions by sage-grouse (Doherty et al. 2008, Doherty et al. 2010, Aldridge et al. 2012, Fedy et al. 2014, Smith et al. 2014, Kirol et al. 2015, Gibson et al. 2016, Walker et al. 2016, Gibson et al. 2017).

Consistent repeated use of nesting areas indicates that female sage-grouse developed affinity for their nesting areas prior to induction into our study. Highly unsuitable grouse-area matches may have been largely eliminated during natal dispersal (Yoder et al. 2004) which is generally prior to capture of subjects for research. Further research is needed regarding when and how sage-grouse females complete natal dispersal (Thompson 2012). We propose that natal dispersal in sage-grouse involves an individual's development of affinity for a breeding area which results in area familiarity and subsequent influence on future reproductive output. If natal dispersal involves attraction to areas proximal to natal areas (prior familiarity), then successful breeding areas could represent production hotspots where positive feedback in reproductive output exists across generations (Freedberg et al. 2005).

In contrast to previous research, female age and landscape conditions, including vegetation, terrain, precipitation events and seasonality, were not strongly linked to nest success and females hatched nests in highly variable environments within the sagebrush-steppe on our study area. Therefore, our results indicate that the influence of familiarity on reproductive success may have to do with an interaction between individual quality and site quality that is not driven by typically measured landscape conditions. Our results offer a possible reason that recent syntheses have noted major problems with simplistic interpretation and acceptance of standard habitat evaluation studies for sage-grouse (Dahlgren et al. 2015, Smith et al. 2020). Our results also have implications for appropriately managing areas to maintain or promote increases in important vital rates (Taylor et al. 2012), particularly if natal dispersal involves attraction to natal areas (Freedberg et al. 2005, Thompson 2012, Dahlgren et al. 2016a).

Identification of nesting home ranges may represent breeding habitat units for sage-grouse. We propose a nesting-area home range conceptualization of breeding habitat as an alternative to the notion that breeding habitat is best inventoried by habitat suitability models that ignore individual-level fidelity behavior. Destruction of areas where there is a synergistic area-by-individual interaction may have a disproportionate influence on population performance particularly if site-dependent population regulation is operating (Rodenhouse et al. 1997).

Individuals of high quality may drive population dynamics and such individuals may achieve high quality through life experience (Carrete et al. 2006) which for philopatric individuals equates to experience with an area. Further research is needed to decipher, clarify and expand upon the importance of fidelity behavior for the ecology of sage-grouse.

Presumably, affinity is plastic and can be modulated by landscape conditions or other cues such as prior reproductive performance or landscape disturbance (Faille et al. 2010). Plasticity in affinity would be adaptive because fidelity does not represent familiarity if landscape conditions change drastically due to factors such as land use change, changing predator densities, conspecific densities, resource distributions, weather, or anthropogenic disturbance. Animals may search out a new use area or change how an area is used as affinity diminishes due to either decreased familiarity or familiarity with now undesirable properties of an area. Indeed, an inverse relationship between fidelity and disturbance is supported for many animal species including sage-grouse (Doherty et al. 2008, Tracz et al. 2010, Webb et al. 2011, Winder et al. 2014, Gibson et al. 2018). However, low to moderate degrees of fidelity attenuation in response to disturbance may not be enough to compensate for negative impacts. Affinity and resultant fidelity behaviors may be deleterious if coarse- and fine-scale habitat destruction and degradation create poor habitat in areas where fidelity has been established.

Consequently, it is important to take landscape heterogeneity and disturbance into account when interpreting the ecological significance of fitness impacts due to seasonal spatial fidelity. We suggest that sage-grouse and other animals could have evolved individual-level plasticity in spatial affinity to promote fitness on landscapes of varying spatial and temporal heterogeneity. A related hypothesis is that fidelity genotypes exist that can regulate populations in the face of landscape disturbance in a manner analogous to density genotypes theorized to induce density-dependent population regulation (Bergerud and Gratson 1988). Spatial fidelity is thought to be advantageous in environments where spatial and temporal heterogeneity of resources or risks is low or in environments that are spatially heterogeneous but certain areas have predictably high habitat quality (Mueller and Fagan 2008, Wolf et al. 2009, Fagan et al. 2013). An “always stay” strategy has been suggested for sage-grouse breeding ranges where vegetation conditions are heterogeneous but breeding area vegetation can be relatively spatially and temporally predictable (Gerber et al. 2019). Predation pressure in breeding ranges may further promote area fidelity because predation risk is spatially homogeneous but temporally unpredictable so there may be costs or no benefit to seeking an alternate home range (Schmidt et al. 2010, Gerber et al. 2019).

Our data were gathered from a sage-grouse population that was not experiencing substantial or recent disturbance which could decouple landscape conditions from otherwise adaptive area fidelity. Cattle grazing was the dominant land use in our study area, minimal energy development was present, and no substantial wildfires occurred. Cattle grazing at moderate intensity is not thought to be a severe disturbance for sage-grouse (Beck and Mitchell 2000, Crawford et al. 2004, Boyd et al. 2014, Smith et al. 2018). Our results indicate that nesting area fidelity confers fitness advantages for the local population under low disturbance regimes. Conversely, major disturbances may result in severe declines in population performance if extreme site fidelity by individuals causes persistent use of unpredictably altered areas (Connelly et al. 1991, Fischer et al. 1993, Connelly et al. 2000a, Lockyer et al. 2015, Abrahms et al. 2018, Gerber et al. 2019). In fact, population persistence might only be promoted by area fidelity when coupled with moderate to high temporal autocorrelation of important landscape conditions in used areas (Schmidt 2004).

A commonly invoked alternative to an “always stay” strategy is the “win-stay:lose-switch” strategy (Switzer 1993, Schmidt et al. 2010, Gerber et al. 2019) which proposes that fidelity is only maintained if outcomes promoting fitness occur. Presumably, animals exhibiting the “win-stay:lose-switch” strategy should achieve increased fitness from the behavior. Previous research indicates that sage-grouse may move larger distances among consecutive nest sites if a nest fails but that nest success is initially lower after moving (Bergerud and Gratson 1988, Fischer et al. 1993, Schroeder and Robb 2003, Holloran and Anderson 2005, Gerber et al. 2019). Initial movement to new nesting areas would result in initially low use-intensity which we found is associated with lower nest success. Furthermore, back-to-back nest success in the same area would strengthen the positive relationship between use-intensity and daily nest survival. Our results are therefore consistent with prior research on fitness consequences of sage-grouse nesting area fidelity, but we modeled detailed movement property influences on daily nest survival rates. In contrast, most previous nesting area fidelity research has relied on evaluating apparent nest success or performing univariate statistical tests (Schroeder and Robb 2003, Holloran and Anderson 2005) which are not as rigorous (Mayfield 1961, Dinsmore et al. 2002, Rotella et al. 2004, Shaffer 2004). Additionally, most prior research has been concerned with distances among nest sites as opposed to our more resolute and biologically complete examination of nesting home range use patterns based on multiple movement properties. Simply checking for statistical differences in nest proximities grouped by prior fate may miss the pertinent scale and timing of fidelity influences on nest success. Despite documentation of somewhat larger distances among nest sites after nest failure we are aware of no evidence that nest survival is higher after moving. The dominant pattern in the literature is that fine scale philopatric modulation by sage-grouse, if occurring, is not adaptive (Gerber et al. 2019). Female sage-grouse have never been documented reusing a nest site (finest scale) but at moderate and coarse scales breeding area fidelity is pronounced regardless of prior nest fate. Therefore, the fine scale at which the "win-stay:lose-switch" strategy has typically been examined in sage-grouse has an unresolved mechanism but appears to be neutral or detrimental to the fecundity of individuals. Further research is needed to understand why some female sage-grouse sometimes move nest sites farther after nest failure and why the behavior does not appear to be adaptive. Gerber et al. (2019) review interesting possibilities for why "win-stay:lose-switch" is consistently documented but has not been linked to fitness advantages. We hypothesize that some individuals more aggressively override philopatry based on prior nest success and these individuals represent a personality type that is only adaptive under certain circumstances. In other words, most females "always stay" but some "win-stay:lose-switch" so that not all the population's eggs are in the same basket after a major landscape change.

Stressors to sage-grouse populations are as diverse as the sage-brush ecosystems on which they depend. In the Great Plains and Wyoming Basin provinces, previous and future potential energy development represents a substantial cause of current and imminent habitat degradation, disturbance, and loss (Doherty et al. 2011, Allred et al. 2015). In the northwestern Great Plains and Columbia Basin substantial areas of sagebrush ecosystems have been lost or degraded due to agricultural tilling (Schroeder and Vander Haegen 2011). Cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherum caput-medusae*) invasion causes sagebrush ecosystem degradation particularly in the warmer, lower elevation parts of the Intermountain West where these winter annual grasses have phenologies that exploit winter precipitation and avoid the warm dry summers that limit competition by the native grasses and forbs (Davies et al. 2011, Miller et al. 2011). Encroachment into sagebrush ecosystems by conifers in more mesic and often higher elevation areas of western North America has been substantial after presettlement and has resulted in a loss of herbaceous understory and sagebrush canopy cover (Miller and Rose 1999, Coultrap et al. 2008, Miller et al. 2008, Davies et al. 2011). Each sage-grouse population across the current distribution must cope with novel combinations of stressors making it crucial to identify and understand local threats to which management actions may be tailored. We have demonstrated that site fidelity may be integral to sage-grouse response to stressors so incorporating fidelity behavior into wildlife-habitat response research is crucial. Additionally, some individuals may be able to capitalize on their site familiarity to achieve high reproductive success in areas that do not appear to be of high quality based on conventional standards.

An implication of moderate- and coarse-scale fidelity being positively associated with fitness when landscape processes and conditions are suitable is that it can integrate multiple fitness components and may be a valuable proxy to habitat quality (Blums et al. 2002, Schroeder and Robb 2003). Habitat performance is often evaluated via resource selection analyses (Manly et al. 2002, Lele 2009, Fieberg et al. 2021) which assume that resources visited disproportionately to available resources are indicative of habitat quality. However, the assumed link between disproportionate use of resources and fitness benefits is tenuous and contrary to the concept of ecological traps (Robertson and Hutto 2006, Aldridge and Boyce 2007, Hale and Swearer 2016). Furthermore, fidelity may be a more reliable indicator of habitat suitability than associations between landscape conditions and fitness components. For instance, demonstrating a statistical association between shrub cover and nest success is only useful if the biological significance can be interpreted and results from replicated studies are consistent (Smith et al. 2020). Associations among landscape conditions and daily nest survival could be unrepresentative of stable and robust populations if disturbances or population decline alter habitat responses that promote population persistence (Taylor et al. 2012, Dahlgren et al. 2016a). Given that most local sagebrush ecosystems and respective sage-grouse populations are unique and under duress it is often difficult to demonstrate universal importance of research results (Schroeder et al. 1999, Connelly et al. 2004, Hagen et al. 2007, Connelly et al. 2011a, Miller et al. 2011, Smith et al. 2020). In contrast, differential nesting area fidelity may be judged relative to established baselines if strong fidelity is fundamental to sage-grouse ecology, as it appears to be. Breakdown or perturbation of established fidelity patterns may indicate a toxic relationship with the environment. Regionally weak associations between fidelity and vital rates may indicate poor habitat suitability and regions with strong associations between fidelity and vital rates may indicate high habitat suitability. Failure to account for area fidelity in conservation and management related research is troubling because fidelity may confer fitness advantages or disadvantages independent of habitat selection (Piper 2011, Patrick and Weimerskirch 2017, Catlin et al. 2019, Nordberg et al. 2021). The link between fidelity and fitness has not been well researched for sage-grouse but a study of a threatened population of Gunnison sage-grouse (*Centrocercus minimus*) found no association between breeding or brooding area fidelity and fitness components, despite high area and patch-level fidelity (Gerber et al. 2019). Similar results have been found for other declining bird populations (Pyle et al. 2001). Our results may indicate relatively high habitat suitability in our study area because fidelity was predictive of fitness.

Landscape Conditions We included 8 vegetation and 2 terrain variables in our model sets and none of these landscape conditions had notable support based on our model selection criteria. Vegetation conditions are often touted as critical to sage-grouse nest success (Beck and Mitchell 2000, Stiver et al. 2006, Hagen et al. 2007, Connelly et al. 2011b, Doherty et al. 2014, Stiver et al. 2015, Smith et al. 2018) but were not the dominant influence in this case. Discrepancies in the literature regarding the importance of vegetation conditions for nesting (Herman-Brunson et al. 2009, Smith et al. 2020) may be partly owing to rote focus on assumed proactive preference decisions by sage-grouse without accounting for other fundamental drivers of space use such as affinity for areas where individuals have familiarity that benefits their fitness.

GLM and GAM Approaches

Our use of two modeling approaches to evaluate consistency of results given differential model-type strengths and weaknesses was only partially warranted. Use-intensity, enclosed points, and eccentricity had similar support between the 2 modeling approaches although support for enclosed points and eccentricity was greater using the GAM approach. Our approach provides another example of generalized additive model (GAM) advantages such as robust automatic smoothing term selection and alternative random effects extensions (Van Der Burg et al. 2010, Wood 2017, Muff et al. 2020). The GAM function gam() of the R package mgcv appropriately selected linear terms where appropriate (use-intensity, enclosed points) and facilitated fitting of random intercepts for individuals which we could not easily accomplish using function glmer() of R-package lme4. Fitting 2-dimensional smooths (interactions [use-intensity × enclosed points]) was also facilitated with package mgcv. If we had used only the generalized linear models (GLM) we would have arrived at largely the same conclusions except that no support for enclosed points or eccentricity would have been indicated. It would have been difficult to adequately evaluate non-linear transformations for all the terms in the various GLM models so we would be less convinced that we adequately transformed the covariates. Despite flexibility of GLMs in modeling non-linear relationships with transformations or polynomials of independent variables the flexibility can be inadequate to capture even moderately complex relationships (Van Der Burg et al. 2010, Wood 2017).

Conclusions

We modeled the influence of 3 movement, 8 vegetation, 2 terrain, and 2 seasonality related variables using 2 modeling approaches to evaluate predictor-variable associations with daily nest survival and found that movement related variables were well supported. Use-intensity was the variable with the most support in the data even after controlling for female age and nest age and its contribution was robust to model type. We assert that use-intensity and eccentricity of short-term nesting home ranges both represent different facets and scales of area fidelity and therefore familiarity. Movement properties derived from detailed relocation histories offer a flexible means of studying sage-grouse space and time-use and therefore fidelity patterns. Further research is needed to refine our understanding of which movement properties best describe fidelity patterns and their consequences. Research is also needed to understand how fidelity benefits or harms sage-grouse population performance in different landscape-disturbance contexts. Our findings support the fundamental importance of nesting area affinity, fidelity, and familiarity to sage-grouse ecology which has been overlooked in most nesting ecology research for sage-grouse or other birds.

Figures and Tables

Table 7. Predictor variables included in generalized linear model and generalized additive model daily nest survival merged-model sets after variance inflation factor screening and Pearson's correlation screening of 103 initial predictor variables.

Raw Predictor	Computed Summary Statistic	Transformation
barren	hull-mean of 30-m patch zonal means	1
daily precipitation (PRISM)	mean of values at nearest neighbor points	1
female age	age category of female	1
hull eccentricity	index to the elongation of a hull	3
hull enclosed points	number of current and prior points in a hull	1
hull use-intensity	hull enclosed points / hull area	log
length of day	mean of values at nearest neighbor points	1
medium shrub	hull-mean of 100-m patch zonal means	1
nest age	age of nest in days since incubation began	1
nest number	sequence of nesting attempts for the year (1 - 3)	1
normalized height	hull-mean of 30-m patch zonal means	1
normalized height CV	hull-CV of 30-m patch zonal means	1
proximity to flow channels (km)	hull zonal mean	1
radius of variance (RoV) of veg biomass	hull-mean of 100-m patch zonal means	1
radius of variance (RoV) of veg height	hull-mean of 100-m patch zonal means	1
sage	hull-rCD of 30-m patch zonal means	1
vegetation biomass	hull-mean of 30-m patch zonal means	1
vegetation biomass	hull-rCD of 100-m patch zonal means	1
vegetation height	hull-mean of 30-m patch zonal means	1

Table 8. A) Model support table based on 68 generalized linear model (GLM) candidate sage-grouse nest survival models, B) sum of weights for each predictor variable based on GLM 95% confidence set, C) model support table based on 79 candidate generalized additive model (GAM) sage-grouse nest survival models and, D) sum of weights for each predictor variable based on GAM 95% confidence set. Number of models containing each variable is listed under ***n*** in sub-table B and D.

A. Nest Survival Models (GLM) 95% confidence set	**df**	**logLik**	**AICc**	**Δ_i**	**w_i**
intercept + hull use-intensity	2	-430.1	864.21	0	0.47
intercept + hull use-intensity + hull enclosed points	3	-429.55	865.1	0.9	0.3
intercept + hull use-intensity + hull eccentricity	3	-429.78	865.57	1.36	0.24

B. Model Terms (GLM)	**Model Term Descriptions**	**$w_{+}(j)$**	***n***
hull use-intensity	additive effect of hull enclosed points / hull area	1	3
hull enclosed points	additive effect of total points accrued in a hull footprint	0.3	1
hull eccentricity	additive effect of index to directional movement	0.24	1

C. Nest Survival Models (GAM) 95% confidence set	**df**	**logLik**	**AICc**	**Δ_i**	**w_i**
intercept + s(use-intensity)	2	-430.1	864.21	0	0.39
intercept + s(use-intensity) + s(hull enclosed points)	3	-429.55	865.1	0.9	0.25
intercept + s(use-intensity) + s(hull enclosed points) + s(eccentricity)	4.76	-428.11	865.76	1.55	0.18
intercept + s(use-intensity) + s(eccentricity)	6.22	-426.64	865.76	1.56	0.18

D. Model Terms (GAM)	**Model Term Descriptions**	**$w_{+}(j)$**	***n***
s(hull use-intensity)	smooth of hull enclosed points / hull area	1	4
s(hull enclosed points)	smooth of total points accrued in a hull footprint	0.43	2
s(eccentricity)	smooth of index to directional movement	0.36	2

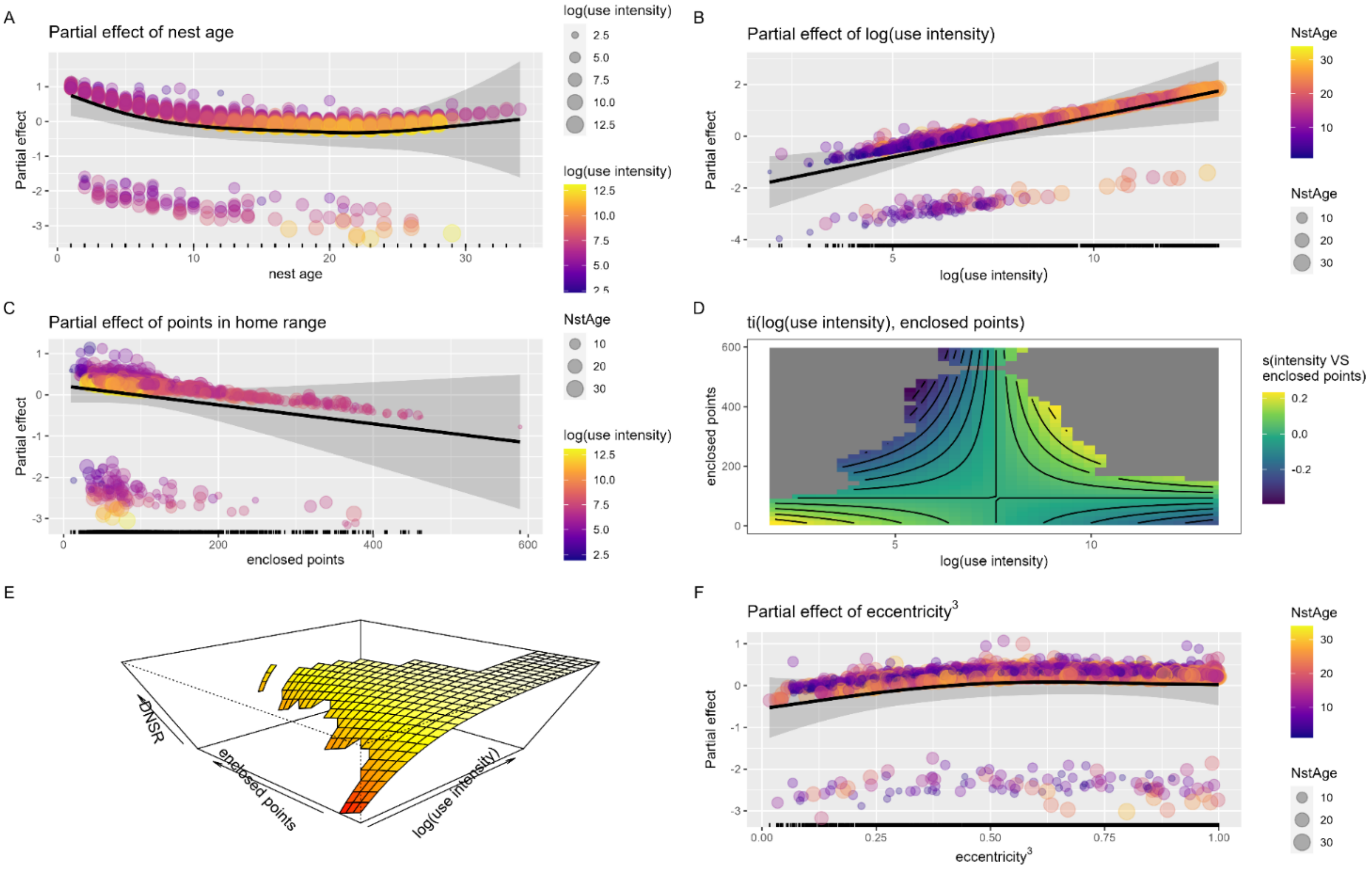


Figure 23. Partial effects plots for variables included in final logistic-exposure generalized additive model of sage-grouse daily nest survival rates (DNSR). Final model was constructed after collinearity screening and multi-model inference methods that indicated predictor suitability and importance. Subplots A and F represent partial effects of nest age and incubation recess movement directionality. Subplots B, C, and D represent main effects and the interaction of use-intensity and number of enclosed points based on marginal basis main effects and a tensor product smooth. Plot E illustrates the overall interaction of use-intensity and enclosed points in 3 dimensions.

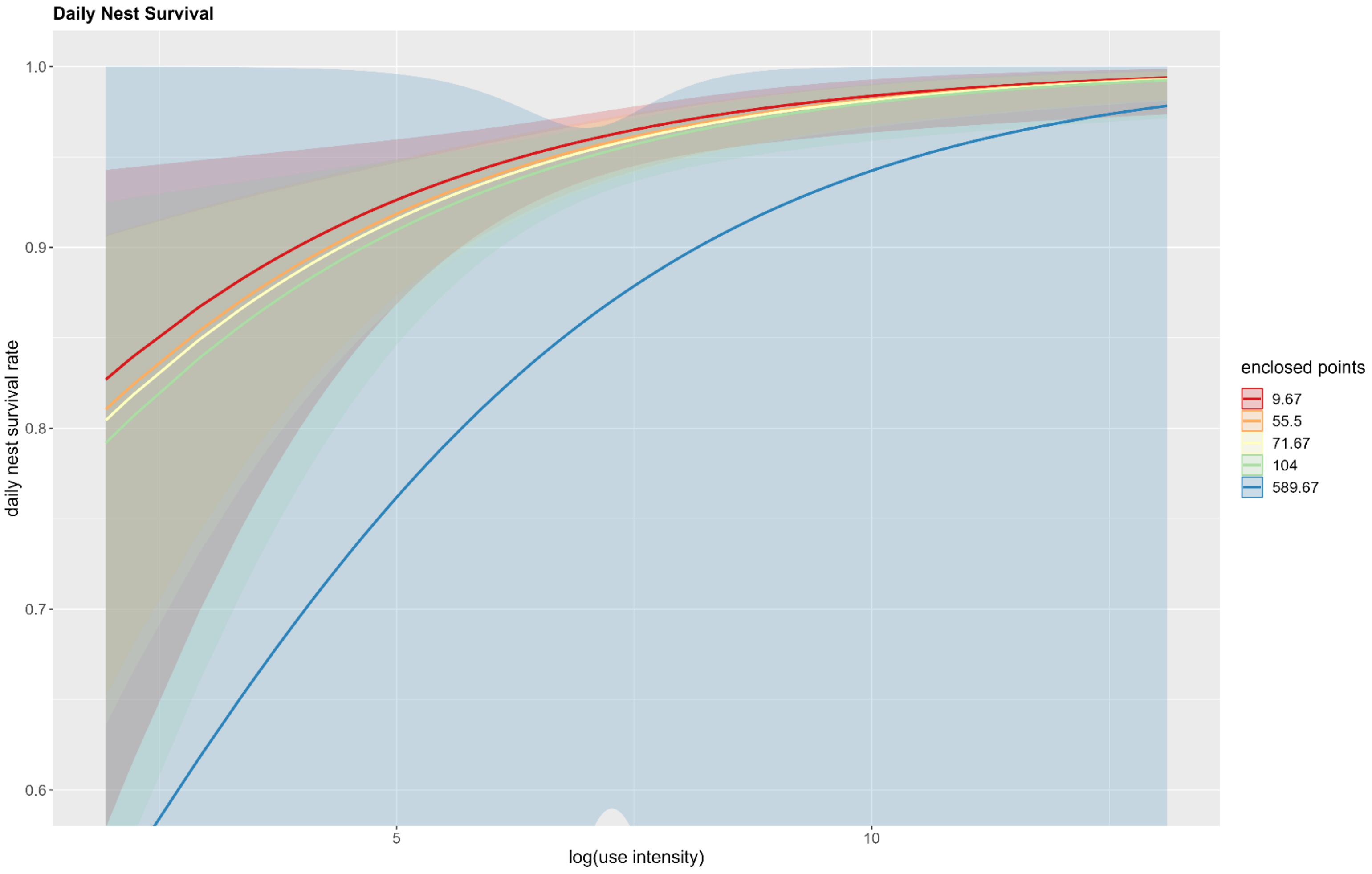


Figure 24. Conditional effects plot generated from a logistic-exposure generalized additive model indicating how daily nest survival rate changes as a function of log(use-intensity) for quartiles of home range enclosed points, holding nest age at 15 days and all other variables at median values. The other terms in the model were hull eccentricity (directional movement tendency) and an interaction between log(use-intensity) and enclosed points. Shaded areas represent 95% confidence bands.

CHAPTER SIX

GENERAL CONCLUSIONS

Detailed animal movement properties and related behavior modes have been difficult to integrate into applied research because technology and tools have only recently been available to collect and analyze sub-daily movement data. We fitted female sage-grouse with GPS transmitters that collected relocations approximately every 6 hours over the lifetime of individuals. We processed relocations to generate a suite of contemporary space- and time-use movement properties. We asked questions of our data related to identifying behavior modes, reconciling multiple movement properties with sage-grouse ecology, creating behavior-specific habitat maps, and evaluating the influence of movement properties on daily nest survival.

We found that applying multivariate statistical approaches to our movement data was a viable solution for rigorous and objective behavior classification. Our statistically inferred behavior modes had a compelling biological interpretation because they were based on multiple movement properties, correspondence with known behavior modes, and correspondence with environmental variables. We successfully identified an exploratory movement mode that we integrated into other sections of our research.

Our multivariate examination of movement properties versus potential predictors for females provided further evidence supporting theorized interrelationships among facets of space- and time-use of the landscape by animals (Van Moorter et al. 2016). We also found that much variation in movement properties explained by our predictor-variable sets was shared variation indicating that substantial multicollinearity exists among behavior modes, temporal modulators, terrain, and vegetation. Without using variance partitioning and partial RDAs we could easily give an explanatory variable or class of variables more causal credit than deserved which may help explain the prevalence of equivocal results in sage-grouse habitat-response research. Multiple terrain and vegetation variables were somewhat associated with female sage-grouse movement properties, but no single landscape-condition variable or class of variables appeared to drive variation in movement properties. Daylength explained the most variation of any single covariate which is consistent with high seasonal process variance of sage-grouse movement patterns.

We created behavior-specific habitat maps for our study area by modeling use-intensity as a lifetime timeseries which encouraged nuanced and biologically realistic interpretation of the causes and consequence of space- and time-use by females. Our individual-level and behavior-specific modeling approach helped resolve some problems with classic habitat mapping approaches such as relying on user specified habitat-availability delineations and seasonal periods. Our reliance on a use-intensity timeseries also helped alleviate spatial- and temporal-scale dependence by integrating scale via observed female movements. We found that landscape use varied substantially among behavior modes both with respect to range size and landscape conditions experience by females.

Our daily nest survival research identified use-intensity as the variable with greatest support in the data. We interpreted use-intensity at nest sites as being a strong proxy to site fidelity which highlights the fact that movement properties derived from detailed relocation histories offer a flexible means of studying sage-grouse space and time-use and therefore fidelity patterns. Increased site fidelity and therefore familiarity with a site appeared to have a positive influence on daily nest survival. Further research is needed to refine our understanding of which movement properties best describe fidelity patterns and their consequences. Research is also needed to understand how fidelity benefits or harms sage-grouse population performance in different landscape-disturbance contexts. Our findings support the fundamental importance of nesting area affinity, fidelity, and familiarity to sage-grouse ecology which has been largely overlooked in nesting ecology research for sage-grouse or other birds.

APPENDICES

APPENDIX A

SCALING OF T-LOCOH HULLS

T-LoCoH uses a scaling parameter *s* to control the degree to which local hulls are local in time versus space. We plotted the distribution of *s* for various time scales (Δt), and the proportion of time selected hulls for various values of *s*, to identify a value for *s* that achieved approximate parity of time and space influence on hull construction (Lyons et al. 2013, Lyons et al. 2019). A value of $s = 0.005$ was near the median parity for most sage-grouse where time scaling and displacement in two-dimensional space have balanced influence on hull construction, given a sub-monthly time scale. We set the scaling parameter *s* the same for all sage-grouse. Custom analysis and choices of *s* for each individual might optimize the hull construction for each female but would exorbitantly complicate processing and eliminate standardization, which complicates interpretation. Nearest neighbor sets of points were identified using the *a*-method which uses a cumulative time-scaled-distance (TSD) and a threshold parameter that dictates the cutoff for inclusion of points in a nearest-neighbor set. A value of $a = 26000$ TSD units was chosen after examining simulation generated plots of *a* vs. isopleth area for a sequence of *a* values (Lyons et al. 2013, Lyons et al. 2019).

APPENDIX B

MIGRATION CLASSIFICATION

Background

Migration has evaded a single objective definition by researchers and is known to operate along a continuum which indicates that it may arise from an amalgamation of factors (Dingle and Drake 2007). Sage-grouse migration has manifested differently among populations but has typically been reported as to-and-fro movements between breeding and winter ranges or breeding to summer and then winter range (Eng and Schladweiler 1972, Connelly et al. 1988, Fedy et al. 2012, Dinkins et al. 2017, Newton et al. 2017, Pratt et al. 2017). Generally, sage-grouse maintain fidelity to individual seasonal use areas but interseasonal movements of sage-grouse are variable within and among populations; individuals are influenced by behavioral traditions (use area fidelity) as well as environmental conditions (Tack et al. 2012, Fedy et al. 2014, Newton et al. 2017, Pratt et al. 2017). As a result, sage-grouse populations are known to exhibit multiple patterns of migration including null, obligate, facultative, partial, and irruptive migration (Tack et al. 2012, Fedy et al. 2014, Newton et al. 2017, Pratt et al. 2017). In some cases, sage-grouse migration is altitudinal or latitudinal and topography and sagebrush cover often differs between seasonal ranges (Dinkins et al. 2017, Newton et al. 2017, Pratt et al. 2017).

Promoted by an early publication on sage-grouse migration events, researchers have been subjectively classifying migration for individuals based on minimum distances between ranges (10 km) using roughly estimated seasonal range boundaries (Connelly et al. 1988, Fedy et al. 2012, Dinkins et al. 2017). The recent availability of GPS transmitters for sage-grouse has provided the data necessary for more accurate seasonal range estimates and more detailed definitions of migration have been attempted (Pratt et al. 2017). Although a standard method of classifying migratory status has not been adopted, progressively sophisticated methods are being developed which recognize migration as one behavior type among multiple broad-scale movement behaviors that ultimately shape population distributions (Mueller and Fagan 2008, Bunnefeld et al. 2011, Abrahms et al. 2017). The primary variables used by ecologists to describe migratory behavior are 1) the proportion of migratory individuals, 2) the distance traveled between stable ranges, 3) the timing of migratory movements, 4) the duration of range use, 5) and the fidelity of individuals to stable ranges (Bunnefeld et al. 2011, Cagnacci et al. 2016). Variables such as distance between stable seasonal ranges, fidelity to ranges, and duration on distinct ranges can be used to distinguish migration from resident (e.g., home range, sedentary), mixed migration, dispersal, and nomadic movement behaviors. Resident behavior is evident when an individual maintains a single ranging area (home-range) that occupies a small area relative to the population distribution (Roshier and Reid 2003, Mueller and Fagan 2008). Mixed migration occurs when spatially disparate ranges are used on a seasonal basis but fidelity is not maintained to the breeding range, non-breeding range, or both. Nomadism is distinguished by a lack of fixed breeding grounds, breeding and non-breeding range overlap, irregular timing of movements, irregular directionality to movements, and movements that are extensive and persistent (Roshier and Reid 2003, Mueller and Fagan 2008). Dispersal has been variously defined as movement by an individual from its birthplace to a site of potential reproduction, movement leading to spatial gene flow, or a three-stage process including departure from a natal area, movement through a matrix environment, and settlement in a novel area (Clobert 2012). Dispersal does not require successful reproduction and is therefore characterized by spatial displacement and social context (Roshier and Reid 2003). Though the classification of migration and disentanglement from other behaviors remains a challenge, recent research has found evidence of some ecological causes and consequences of sage-grouse migration including increased survival for non-migratory females and the initiation of migration due to environmental cues (Dinkins et al. 2017, Pratt et al. 2017). Methodologies for classifying migration with more objectivity and corroboration by other studies will be needed to establish generalities about migratory behavior in sage-grouse. In the meantime, model-driven classification and quantification of migratory behavior will be helpful for understanding the characteristics of migratory behavior for local populations.

Methods

We constructed movement trajectories from the relocation histories of each female using the R package adehabitatLT (R Version 4.0.0, www.r-project.org; Calenge et al. (2009)). Descriptive parameters included the distance and turning angles between successive locations as well as the net squared displacement (i.e., NSD, displacement from start) of each location. We analyzed the trajectories of each female to classify migratory behavior and quantify the timing and extent of migration. We used a statistical framework that models the NSD timeseries of a movement path as a function of non-linear model parameterizations that represent different movement types. The models that we considered were migration, mixed-migration, dispersal, resident, and nomadic. For migratory female sage-grouse, we expected a stable NSD near zero while nesting, increase rapidly for a brief period sometime during fall or early winter, and then stabilize at an elevated level on a winter range until breeding season when NSD would drop back to stable levels near zero. In the case of mixed migration, NSD should increase from near zero and stabilize at higher winter levels with a subsequent drop to a lower level that is distinctly greater than zero. A dispersing animal has an NSD profile that dramatically increases from initial low levels and permanently stabilizes at elevated levels. A resident individual exhibits consistently stable NSD values. A nomadic individual would likely have steadily increasing NSD values. Non-linear models for migrants and mixed migrants are double sigmoid functions whereas dispersal can be modeled with a logistic model (Bunnefeld et al. 2011, Spitz 2019). An asymptotic regression model has been shown to perform well for representing resident behavior and a linear model captures the expected pattern for nomadic behavior (Börger and Fryxell 2012, Spitz et al. 2017).

The migratory and mixed-migratory NSD models fit the data best when stable ranging behavior is evident before and after seasonal home range shifts (Spitz et al. 2017). Therefore, we subset the relocation data from the 86 females into animal-year movement paths that represent yearly relocation histories for females that were alive with functional PTTs for > 300 days during 2018-06-01 to 2019-07-01 or during 2019-06-01 to 2020-07-01. We further subset the relocation data from each trajectory to one position per day to establish a 24-hour sampling interval using the amt package version 0.0.7 in R. A 24-hour sampling interval represents a sufficient temporal scale for analyzing migration behavior and can eliminate fine-scale noise in the NSD signature while also improving computational efficiency (Bunnefeld et al. 2011, Spitz et al. 2017). We calculated the NSD for each animal-year trajectory using the adehabitatLT package version 0.3.25 in R and then fit NSD models to each animal-year NSD timeseries using the migrateR package version 1.0.9 (Börger and Fryxell 2012, Spitz et al. 2017).

We were not able to successfully fit all movement models with default starting values and parameter constraints for the movement timing parameters. Therefore, we plotted fitted model predictions on top of time-series scatterplots of NSD values to determine possible causes for poor or failed model fits (Spitz et al. 2017). We then used the refine() function in migrateR to specify parameter starting values or constraints that might improve or promote model fit (Spitz et al. 2017). For instance, if the parameter estimates for a migration or mixed migration model appeared to be fitted to an earlier and less substantial increase in NSD values then we would specify the initial value of the midpoint of starting movement, theta, as a later date. Iterative visual checks of plotted models and manual specification of model parameters allowed all 5 movement models to be fitted to each of 59 animal-year NSD data sets. We used the topmvmt() function in migrateR to calculate Akaike's Information Criterion (AIC), which we used to evaluate support for each of the five NSD-based models fit to each animal-year NSD dataset (Appendix B, Tables 9 & 10) (Anderson and Burnham 2002, Spitz 2019). AIC can favor more complicated models (e.g., migratory) over resident-behavior models so topmvmt() applies Arnolds Rule to further penalize model complexity (Arnold 2010, Spitz et al. 2017).

We imposed prespecified movement parameter constraints to eliminate consideration of models that have biologically unreasonable parameter estimates (Burnham and Anderson 2002, Spitz et al. 2017). To highlight discrepancies in movement patterns among animal-years, we imposed a constraint on the migration and mixed migration models which required winter-range occupancy to be greater or equal to 30 days (Spitz et al. 2017). The 30-day constraint highlighted the erroneous classification of animal-year NSD patterns as being migratory due to short duration displacement bouts that are associated with breeding or exploratory movement behavior and not migratory movements. If a classification change from migrant or mixed migrant was observed, then we determined the classification by visualizing the NSD time series plots with movement-model fitted lines in concert with the spatio-temporal context of sage-grouse locations which were visualized in QGIS. Sage-grouse classified as dispersers exhibited some exploratory movements which caused the linear model (disperser) to fit better than the constant model (resident) but no sage-grouse exhibited actual dispersal behavior. In all such cases we manually reassigned dispersers to the resident category. We calculated the mean and standard deviation of the movement parameters for the most well supported migrant and mixed migrant models for each animal-year to make population-level inference about the yearly extent, and timing of migration for female sage-grouse in our study area.

Results

In 2018 and 2019, 63% (n = 19) and 97% (n = 34) of female sage-grouse were classified as migratory, respectively (Appendix B, Table 10). For migratory females, the median (± SD) midpoint of the departing movement from summer-fall range to winter range was 20 October in 2018 (± 46 days, n = 12) and 26 October (± 40 days, n = 33) in 2019. The median time to complete ½ to ¾ of the departing movement was 3.5 days (± 7 days) in 2018 and 1.7 days (± 8 days) in 2019. The median distance traveled from summer-fall to winter range was 30.6 km (± 28 km) in 2018 and 17.5 km (± 21 km) in 2019. The median duration spent on the winter range in 2018 and 2019 was 141 days (± 48 days) and 120 days (± 40 days), respectively. The median midpoint of the return movement from winter range to breeding range was 25 March in 2018 (± 10 days) and 11 March (± 35 days) in 2019. The median time to complete ½ to ¾ of the return movement was 1 day (± 8 days) in 2018 and 1 day (± 5 days) in 2019.

Table 9. Table of Δ AIC values for each of five NSD models fit to each animal-year dataset of greater sage-grouse in south Valley County, Montana.

	Δ AIC				
grouse-year	**disperser**	**migrant**	**mix-migrant**	**nomad**	**resident**
004 2018	953.21	0	71.57	996.13	997.91
006 2018	752.64	0	33.14	775.12	769.08
006 2019	325.75	0	3.91	412.37	373.43
007 2018	370.42	12.53	0	574.39	389.43
012 2018	559.71	0	12.44	585.2	582.21
014 2018	513.21	0	34.37	538.91	519.87
014 2019	113.84	0	2.03	176	152.81
015 2018	791.29	0	40.06	829.37	820.35
015 2019	966.09	0	20.87	1105.53	1041.43
016 2018	781.7	0	13.79	1024.71	1023.68
017 2018	626.22	0	7.17	800.37	724.01
017 2019	913.64	0	7.74	1103.11	989.52
018 2018	881.58	0	30.23	1075.99	979.11
018 2019	903.33	0	16.57	1050.31	1003.97
020 2018	1114.55	0	27.92	1281.17	1210.24
021 2018	0	1.4	3.65	247.16	37.25
025 2018	618.18	0	8.76	677.94	662.13
025 2019	1223.54	0	42.06	1340.91	1289.94
029 2018	566.38	0	3.82	827.97	587.64
031 2018	219.6	15.51	0	255.9	259.67
032 2018	1685.63	0	113.38	1833.56	1771.77
035 2018	678.53	0	0.9	987.03	711.38
035 2019	1090.86	0	21.24	1416.89	1112.95
037 2018	467.83	0	2.32	578.62	476.99
037 2019	262.51	92.12	0	575.31	598.54
039 2018	556.79	0	26.08	589.36	588.64
039 2019	14.25	5.49	0	31.68	27.47
040 2019	890.63	4.42	0	1034.06	977.61
041 2019	309.52	3.62	0	473.34	375.36
042 2019	973.27	0	12.78	1115.6	1058.11
045 2019	932.41	0	3.46	1056.25	972.51
046 2018	416.58	0	8.19	706.74	710.65
049 2018	1722.45	0	134.86	1897.88	1807.54
049 2019	1905.92	0	181.29	2002.83	1939.52
055 2018	734.95	0	15.65	857.23	821.86
055 2019	511.56	0	8.97	790.09	810.89
056 2018	1392.54	27.92	0	1573.01	1496.32
056 2019	911.07	87.37	0	1340.84	1375.51
057 2019	1126.91	0	198.35	1142.1	1133.06

060	2019	1082.15	0	27.26	1193.41	1143.21
061	2019	1394.38	0	67.78	1504.54	1466.44
062	2019	735.19	0	3	976.93	766.34
063	2019	903.78	0	23.68	1015.85	963.95
064	2019	237.08	6.1	0	338.2	273.75
065	2019	1386.44	0	30.27	1541.28	1470.56
066	2019	645.65	0	12.83	743.91	691.39
068	2019	3.83	7.28	2.39	9.96	0
069	2019	795.35	0	12.65	942.63	866.05
070	2019	715.47	3.88	0	887.31	881.6
071	2019	548.03	3.08	0	636.64	588.02
072	2019	308.57	0	2.94	429.02	423.2
073	2019	1579.31	0	87.38	1707.55	1581.63
076	2019	93.79	43.58	0	301.29	212.2
077	2019	826.52	0	27.04	930.68	833.64
078	2019	682.45	0	3.97	937.92	688.39
081	2019	325.11	2.46	0	390.06	349.05
084	2019	1249.17	0	39.79	1404.87	1352.21
085	2019	503.67	0	41.12	516.36	504.43
088	2019	78.6	3.15	0	136.79	131.81

Table 10. Sequence of migration classification refinements for NSD model analysis evaluating migratory behavior for greater sage-grouse in south Valley County, Montana. Sage-grouse 068 was not classified because gaps in the relocation history precluded a final determination.

id	year	initial NSD classification	30-day constraint	mixed migration = migration	final determination
004	2018	migrant	disperser	disperser	resident
006	2018	migrant	disperser	disperser	migrant
006	2019	migrant	migrant	migrant	migrant
007	2018	mixmig	mixmig	migrant	migrant
012	2018	migrant	disperser	disperser	migrant
014	2018	migrant	disperser	disperser	migrant
014	2019	migrant	migrant	migrant	migrant
015	2018	migrant	disperser	disperser	migrant
015	2019	migrant	migrant	migrant	migrant
016	2018	migrant	migrant	migrant	migrant
017	2018	migrant	migrant	migrant	migrant
017	2019	migrant	migrant	migrant	migrant
018	2018	migrant	migrant	migrant	migrant
018	2019	migrant	migrant	migrant	migrant
020	2018	migrant	migrant	migrant	migrant
021	2018	disperser	disperser	disperser	migrant

025	2018	migrant	disperser	disperser	migrant
025	2019	migrant	migrant	migrant	migrant
029	2018	migrant	migrant	migrant	migrant
031	2018	mixmig	disperser	disperser	migrant
032	2018	migrant	migrant	migrant	migrant
035	2018	migrant	migrant	migrant	migrant
035	2019	migrant	migrant	migrant	migrant
037	2018	migrant	migrant	migrant	migrant
037	2019	mixmig	mixmig	migrant	migrant
039	2018	migrant	disperser	disperser	resident
039	2019	mixmig	migrant	migrant	migrant
040	2019	mixmig	mixmig	migrant	migrant
041	2019	mixmig	mixmig	migrant	migrant
042	2019	migrant	migrant	migrant	migrant
045	2019	migrant	migrant	migrant	migrant
046	2018	migrant	disperser	disperser	resident
049	2018	migrant	migrant	migrant	migrant
049	2019	migrant	migrant	migrant	migrant
055	2018	migrant	migrant	migrant	migrant
055	2019	migrant	migrant	migrant	migrant
056	2018	mixmig	mixmig	migrant	migrant
056	2019	mixmig	mixmig	migrant	migrant
057	2019	migrant	disperser	disperser	resident
060	2019	migrant	migrant	migrant	migrant
061	2019	migrant	migrant	migrant	migrant
062	2019	migrant	migrant	migrant	migrant
063	2019	migrant	migrant	migrant	migrant
064	2019	mixmig	mixmig	migrant	migrant
065	2019	migrant	migrant	migrant	migrant
066	2019	migrant	migrant	migrant	migrant
068	2019	resident	resident	resident	rejected
069	2019	migrant	migrant	migrant	migrant
070	2019	mixmig	mixmig	migrant	migrant
071	2019	mixmig	mixmig	migrant	migrant
072	2019	migrant	migrant	migrant	migrant
073	2019	migrant	migrant	migrant	migrant
076	2019	mixmig	mixmig	migrant	migrant
077	2019	migrant	migrant	migrant	migrant
078	2019	migrant	migrant	migrant	migrant
081	2019	mixmig	disperser	disperser	migrant
084	2019	migrant	migrant	migrant	migrant
085	2019	migrant	migrant	migrant	migrant
088	2019	mixmig	mixmig	migrant	migrant

APPENDIX C

REMOTE SENSING LANDSCAPE CONDITIONS

Existing Geospatial Products

We downloaded annual 30-m resolution ground cover metrics from the Rangeland Analysis Platform (RAP; (Jones et al. 2018)) and Multi-Resolution Land Characteristics (MRLC) 30-m resolution vegetation layers (Homer et al. 2012, Xian et al. 2015). We evaluated ground cover data from both sources because the different modeling methods may result in differing, yet unknown, accuracies and correspondence with ground cover in our study area. We checked for correspondence between univariate movement-cover response curves for matched RAP and MRLC cover types (e.g., shrubs, perennial herbaceous/forbs). The RAP and MRLC layers did not correspond well with each other, especially for shrubs. The RAP and MRLC layers also exhibited poor correspondence to our cover expectations inferred from NAIP imagery and familiarity with the study area.

Distance to Channels

We used a digital elevation model (DEM) to synthesize a distance to stream channel variable which represents potential water sources in our study area. First, we used the Sink Drainage Route Detection tool with default settings (no threshold) to generate a sink route input layer which leads flow through closed depressions. Second, we calculated the Strahler stream order for use as the stream initiation grid. Third, we generated a stream channel network layer using the Channel Network algorithm with the DEM, sink route grid, and Strahler stream order grid as inputs. We specified channels to be initiated at Strahler order > 4; minimum segment length was left at the default 10 cells. Finally, using QGIS, we subset the resulting channel network to channel segments with Strahler order > 5, rasterized the resulting channel layer with the vector to raster tool, and calculated the distance to channel cells using the raster distance tool.

Channels with Strahler order > 5 were chosen by overlaying a Strahler-order-labeled channel network on terrain and aerial imagery data and choosing a threshold that generally corresponded to actual eroded gullies or channels where flow would accumulate during typical rain events.

Distance to Water Bodies

Water can have a distinct image texture, so we used a texture analysis to extract water body zones from National Agriculture Imagery Program (NAIP) imagery captured during June and July of 2017. Our texture analysis was performed with the multi-band variation (MBV) algorithm of the System for Automated Geoscientific Analysis (SAGA) GIS with the default 1-pixel neighborhood radius (SAGA version 2.3.2, www.saga-gis.org, Conrad et al. (2015)). Using values from all the NAIP raster cells in a neighborhood (moving window) the algorithm calculates distances from the feature space (spectral values) centroid to each individual cell. Feature space distance is the basis for three spectral variation metrics that are calculated and mapped to the center cell in each neighborhood to create three new images. The three outputs are the mean distance of all cells, the standard deviation of distances for all cells, and the distance of the center cell from the centroid. The standard deviation of distances (MBV SD) best seemed to highlight water bodies. We derived water body information by transforming the MBV SD texture image with a fuzzy raster linear membership function. Using the NAIP imagery we also calculated a normalized difference water index (NDWI) using SAGA GIS and transformed it with a fuzzy raster linear membership function. The fuzzy raster linear membership function transformed the values of the MBV SD and NDWI into a continuous gradient from 0 to 1 representing our determination of the proportion water body membership represented by original values of the layers. We determined the specific parameters for "fuzzifying" the MBV SD and

NDWI layers by examining them in QGIS to decide on an acceptable balance between certain membership and fuzzy (partial) membership. We additionally rasterized vector feature water bodies from the High Resolution National Hydrography Dataset Plus (NHDPlus HR) by burning the value of 0.45 into pixels where a water body was present and 0 otherwise. We used the raster algebra algorithm in QGIS to add together the fuzzy MBV SD layer, fuzzy NDWI and NHDPlus water body raster. The sum-layer pixels were binary reclassified to 1 if greater than 1.15 and 0 otherwise. Finally, we masked any areas where a topographic slope layer generated from a digital elevation model (DEM) was ≤ 10.15 because pillowy coarse clay ridgetops in our study area had a smooth texture and gray spectral profile that indicated water in both the NDWI and MVB SD layers. The expression used in QGIS raster calculator to generate the raster layer of water bodies in the study area was ((MBV_SDfuz + NDWIfuz + NHDwater)>1.15) * slope <= 10.15. The proximity algorithm in QGIS was used to generate our final product which represents the Euclidean distance from water bodies in our study area. To quantify landscape heterogeneity of water bodies we also calculated the radius of variance (RoV) of proximity to water bodies using the SAGA radius of variance algorithm (search radius = 120, SD = 0.15).

NDVI-Based Non-Sage Shrub Layers

Sage-grouse may be attracted to or repelled by structural-habitat types such as mesic creek margins, shrublands, juniper savannas, and forest. Landscape-element GIS products that have broad-extent coverage may not have a sufficient signal-to-noise ratio at moderate scales to realistically represent mesic creek margins, shrublands, juniper savannas, and forest habitat elements to which sage-grouse respond. To fill the gap in available data, we adopted an image-texture analysis approach to derive indices for mesic meadows along creeks, medium-sized shrubs, large shrubs, and forest zones. Our methodology for creating these structural habitat indices (vegetation indices) was also motivated by a need to distinguish upland vegetation types from lowland types. Sage-grouse in our study area tended toward use of upland sites for nesting and visited mesic or lowland sites to different degrees during other phenological stages.

We extracted vegetation-based texture signals in a NDVI image derived from 2017 NAIP imagery using the structural feature set (SFS) application in Orfeo ToolBox as the key tool (Grizonnet et al. 2017). The 2017 NAIP image was captured in July of 2017 which was a year of particularly low rainfall in July. Drought conditions during image capture aided discrimination of persistent vegetation from more seasonally ephemeral vegetation which cannot be mapped with high reliability. The 2017 NAIP imagery also captured image texture better (i.e., was sharper) than the 2019 NAIP imagery. While we relied on the 2017 NAIP imagery for extracting image texture features we exploited information in the 2015, 2017, and 2019 NAIP imagery to calculate an average NDVI image from all three years. Averaging NDVI values across the 3 years was a further effort to map persistent vegetation and attenuate noise from ephemeral vegetation. We calculated average NDVI values using the fast non-local means algorithm in Orfeo ToolBox. Non-local means is a noise reduction procedure that preserves image texture better than most smoothing algorithms. The fast version of the algorithm takes computational shortcuts to facilitate processing of large images. Our general strategy for extracting information about landscape elements useful to sage-grouse was to weight NDVI values from the 2015-2017-2019 NDVI image using textural information contained in the 2017 NDVI image and topographic context derived from a DEM.

We preprocessed the raw data prior to calculating SFS texture features by rescaling the NDVI image to the range 0–255 and resampling the rescaled image from a 0.6-m resolution to a 2-m resolution. We generated 2 base images during rescaling by using a nearest neighbor interpolation on one and a cubic polynomial interpolation on the other. The nearest neighbor resampled image captured texture ranging from medium shrubs (e.g. black greasewood *[Sarcobatus vermiculatus*], skunkbrush sumac [*Rhus trilobata*], western snowberry [*Symphoricarpos occidentalis*]) to trees (e.g. ponderosa pine [*Pinus ponderosa*]) while the cubic polynomial resampled image captured texture from larger junipers (e.g. creeping juniper [*Juniperus horizontalis*], Rocky Mountain juniper [*Juniperus scopulorum*]) to trees. Therefore, resampling allowed us to isolate the medium-sized shrub texture signal from the total-shrub texture signal. We processed each rescaled-resampled NDVI image with the Orfeo ToolBox SFS application (spectral threshold = 20, spatial threshold = 20, number of directions = 20) to generate 6 texture feature layers for each NDVI image. Of the 6 texture feature layers, we identified the SFS-length feature as discriminating the image textures (shrubs and trees) that we needed to isolate. We processed the two SFS-length texture images with the Orfeo ToolBox Haralick feature extraction tool (x radius = 10, y radius = 10, x offset = 1, y offset = 1) to generate 8 Haralick simple texture features for each image and selected the second Haralick feature (“entropy”) which adequately highlighted the zones where the SFS-length texture values were high. Our intermediate result was a heavy-shrub and tree (e.g. juniper, ponderosa) index and a total-woody index (e.g. greasewood, juniper, ponderosa).

Isolating upland shrubland texture from lowland mesic creek zones required us to discount both the medium-shrub index and the heavy-shrub and tree index by geomorphon (terrain form), valley bottom flatness, distance to higher order (higher flow) stream channels, water bodies and a riparian mask extracted from the LANDFIRE 2016 existing vegetation type layer. Geomorphon terrain forms were reclassified from 10 forms into 4 broader terrain classes composed of 1) flats and footslopes, 2) valleys and depressions, 3) hollows and 4) all other upland forms including slopes, ridges, and summits. We rescaled our multi resolution valley bottom flatness layer so that extremely flat areas had a value of 0 and ridges had a value near 1. Our distance to stream channel and water body layers were converted to a binary image such that distance values within 50 meters of a feature were given a value of 0 and all other features were given a value of 1. All continuous field and binary mask images were then multiplied with the total-woody index and a 0–255 rescaled 0.6-m resolution NDVI image to weight the magnitude of 2015-2017-2019 NDVI values by the masks and the total-woody index. The exact same procedure was executed on the heavy-shrub and tree index. The result was a weighted total-woody index and a weighted heavy-shrub and tree index.

A lowland-NDVI index was calculated by inverting the weighted total-woody index and multiplying it by the unweighted 0–255 rescaled 0.6-m resolution 2015-2017-2019 NDVI image. A medium-shrub index was calculated by inverting the heavy-shrub and tree index, multiplying it by the total-woody index and then weighting the resultant medium-shrub index using the same procedure as for the weighted total-woody index. To isolate heavy shrubs (e.g. juniper) we masked trees out of the weighted heavy-shrub and tree index using Rangeland Analysis Platform version 2 tree data. Due to implausible fluctuations in RAP tree layer values among years we averaged 4 tree cover images representing yearly estimates for 2016 – 2019. Image averaging was accomplished using the dimensionality reduction algorithm in Orfeo toolbox to dampen prediction error-noise while maintaining the central tendency of predictions. A principal component analysis (PCA) was performed on the 4-band multiyear image (RAP tree 2016 – 2019) and the first principal component was then inverse transformed back to the original scale of the data. The PCA-averaged image was then examined to identify a threshold value whereby values above the threshold were mostly woodlands and values below the threshold were not. We created a binary mask using the forest threshold to mask forested areas out of the weighted heavy-shrub and tree index. We then inverted the mask and multiplied it by the PCA-averaged tree cover estimates and the 2015-2017-2019 NDVI image to produce our woodland (forest) index.

Mesic creek floodplains and valley bottoms are captured by our lowland-NDVI index. Upland greasewood patches and Rocky Mountain juniper groves of smaller stature are captured by the weighted medium-shrub index. Larger stature juniper-savannah zones are captured by the weighted heavy-shrub and tree index and ponderosa pine woodlands are captured by the forest index. Shrubs or subshrubs such as Wyoming big sagebrush (*Artemisia tridentata Nutt. ssp. wyomingensis*), rabbitbrush (e.g., *Ericameria nauseosa*), longleaf wormwood (*Artemisia longifolia*), field sagewort (*Artemisia campestris*), and tarragon (*Artemisia dracunculus*) were generally too small and spectrally ambiguous to produce a substantial textural signal. Therefore, our shrub indices represent medium and large stature shrubs only.

Sagebrush Cover Estimation

Sagebrush cover is an unequivocally important habitat element for sage-grouse, so we developed a method of estimating sagebrush cover by combining an image classification of sagebrush with the NDVI-based textural information described above. We also attempted to develop a sagebrush index to use either as a final product or as an ancillary layer in our classification. Ultimately, we developed or identified 5 NAIP-derived indices to use as image classification explanatory layers in place of the raw spectral bands (i.e., red, green, blue, NIR). Our strategy was to exploit the unique characteristics of sagebrush as recorded by biannual 1-m or 0.6-m 4-band NAIP imagery. The sagebrush characteristics that worked to our advantage were the among-band homogeneity of reflectance values, temporal consistency of sagebrush cover, distinct image texture at a 0.6-m resolution and low NDVI values relative to other plant cover. To capitalize on the gray color of sagebrush we calculated the per-pixel coefficient of variation (CV) of the red, green, and blue bands of NAIP imagery (RGB-CV). To capture temporal consistency of sagebrush cover and attenuate the signature of shadows we calculated the average of the RGB-CV index from the 2015, 2017, and 2019 imagery. Image averaging of the 3 RGB-CV images was accomplished with the fast non-local means (patch radius = 3, search radius =3) algorithm in Orfeo toolbox.

Our second index weighted the absolute magnitude of summed deviations from the mean for each cell of a 4-band NAIP image by the coefficient of variation in the per-pixel set of 4 spectral bands. Therefore, the index registers an interaction between the intensity of the spectral reflectance values and the variability among spectral bands. High intensity (bright) colored pixels or pixels with high or low near-infrared reflectance, relative to the mean, receive high values while pixels on a gray scale, including black or white, receive low values, regardless of their intensity. Bright cells with slight coloring will have higher index values than dark pixels with slight coloring. Henceforth, we will refer to our second index as the vegetation color index (V-COLOR). The V-COLOR index was a variation of the RGB-CV index that highlighted water, green vegetation and senesced vegetation while generally preserving the low CV values of sagebrush. Sagebrush with a substantial green or recently senesced (red) grass or herbaceous understory will have moderate V-COLOR index values. The distribution of the V-COLOR index was very compact and right skewed so we square root transformed the index. To capture temporal consistency of sagebrush cover and attenuate the signature of shadows we calculated the average of the V-COLOR index from 2015, 2017, and 2019 imagery. Image averaging of the 3 V-COLOR images was accomplished with the fast non-local means algorithm (patch radius = 3, search radius =3) in Orfeo toolbox.

We developed two vegetation indices from 2015, 2017, and 2019 NAIP imagery. NDVI was calculated from each year of NAIP imagery and then the average was taken with the fast non-local means algorithm (patch radius = 3, search radius =3) in Orfeo toolbox. In addition to NDVI we also calculated leaf area index from reflectances with linear combination (LAIfromRefLinear [LAI]) using the Radiometric Indices application in Orfeo toolbox. Based on visual comparison to the NAIP images, the NDVI and LAI images each captured unique aspects of the non-vegetated land surface where discrimination of barren areas generally appeared better for the LAI.

The final index that we generated was a textural feature layer derived from the 2017 NAIP imagery. We used the multi-band variation (MBV) application in SAGA GIS (weighting = none, radius = 3 cells) to generate a textural feature set (Palmer 2002, Conrad et al. 2015). The MBV application calculates pixel variability statistics using information in every input band (e.g., NAIP 4-band imagery) and returns 3 images based on feature space distances between focal pixels and neighborhood pixels. The MBV-distance image appeared to best highlight sagebrush texture and we further processed it to enhance the textural signal using the PanTex application in Orfeo toolbox (window radius x = 4, window radius y = 4) (Pesaresi et al. 2008). PanTex is texture-derived built-up presence index originally created to identify built-up (developed) areas on the landscape. PanTex preserves the grainy texture created by stands of shrubs but attenuates the MBV distance signal that is due to natural and manmade edge effects (e.g. streambanks, road margins).

The next phase of our sagebrush classification required delineating image classification training polygons for 17 land-cover classes that we could reliably discern from NAIP imagery. We reduced variability within the training classes by choosing land-cover classes that were readily evident in the NAIP imagery and that had a relatively stable occurrence and spectral signature across years. For instance, we did not delineate irrigated agricultural fields or lake margins which can incur substantial changes from year to year. To increase accuracy of delineations, we examined a 1-m NAIP image from 2015 and 0.6-m NAIP imagery from 2017 and 2019. A weakness of both field-based and GIS-based training data delineations is that spectrally unique cover classes may be hard to identify and can be compromised by imprecise delineations, image anomalies, or image noise. To reduce noise introduced by imprecise delineations or our inability to visualize the multispectral uniqueness of training zones we segmented subsets of the training image using the large-scale mean shift segmentation algorithm in Orfeo ToolBox. Segmentation allowed us to select spatially adjacent and spectrally similar sets of pixels (super-pixels) overlying the footprint of targeted land-cover classes. We selected super-pixel training polygons for 1) shadowed terrain, 2) clear water bodies, 3) moderately turgid water, 4) highly turgid water, 5) barren coarse-clay zones, 6) bright barren zones, 7) moderately bright barren zones, 8) barren-zone vegetation islands, 9) xeric non-irrigated pastures, 10) xeric sparse-sagebrush zones, 11) Wyoming big sagebrush, 12) silver sagebrush, 13) greasewood, 14) juniper, and 3 tiers of progressively higher green leafy biomass. Our three green-leafy tiers roughly corresponded to 15) mesic meadows near creek margins, 16) snowberry groves near creek margins or seeps, and 17) wet-mesic meadows, or broadleaf cattail (*Typha latifolia*) monocultures.

We conducted image classification using the machine learning applications in Orfeo toolbox. We trained classifiers with the training polygons and the 5 NAIP-derived indices. We fitted classifiers using multiple classifier types and then chose the classifier with the best performance based on confusion matrices. The confusion matrices may give an overly optimistic accounting of classifier performance because they were calculated with subsets of the training data and not independent validation datasets. Nevertheless, the confusion matrices provided a useful criterion by which to choose among multiple classifiers. The classifiers that we fitted were the support vector machine classifier, boost classifier, decision tree (DT), normal bayes, random forest, and k nearest neighbors classifier. We chose the decision tree classifier because it had the highest global performance ($\kappa = 0.95$) and highest f-scores for the xeric sparse-sagebrush (f-score = 0.95) and Wyoming big sagebrush (f-score = 0.95) cover classes.

We binary reclassified the DT classified image such that xeric sparse-sagebrush and Wyoming big sagebrush pixels had values of 1 and all other classes had a value of 0. We then threshold masked the binary reclassified sage-class image using our MBV-based textural feature layer and our total-woody index. Threshold masking removed pixels classified as sagebrush in areas without valid sagebrush textural values such as wooded areas or flat areas with minimal vegetation structure. We mean resampled the sagebrush cover product to match the resolution of the 1/3rd arc second DEM and derivative products. Resampling resulted in continuous-field cover estimates of sagebrush based on the binary 0.6-m DT sagebrush image.

Bare Ground Cover Estimation

We derived bare ground cover estimates by binary reclassifying the DT classified image (see above) such that classes 5, 6, and 7 were given a value of 1 and all other categories were given a value of 0. The bare ground cover product was mean resampled to match the resolution of the 1/3r arc second DEM and derivative products. Resampling resulted in continuous-field cover estimates of bare ground based on the binary 0.6-m DT bare ground image.

LiDAR-Based Vegetation Estimation

We downloaded DNRC LiDAR digital surface model (DSM) and digital elevation model (DEM) data from the Montana State Library site: http://msl.mt.gov/gis/lidarinventory. We used a vector ruggedness measure algorithm on the DSM to create an index for landscape ruggedness which is different from topographic ruggedness because all landscape structures (e.g., vegetation, buildings, fences) contribute to the index values. We used the same vector ruggedness algorithm on the DEM to create an index for landscape ruggedness. We then subtracted the two indices to create an index of non-terrain height of objects on the landscape. On the open range, our height index largely corresponds to an index of vegetation height and the landscape ruggedness index corresponds to fine-scale landscape features such as gullies, headcuts, or cliffs. To quantify landscape heterogeneity of vegetation height and ruggedness we calculated the radius of variance (RoV) of each variable using the SAGA radius of variance algorithm (search radius = 120, SD = 1).

We also created a LiDAR-enhanced vegetation index by performing a principal component analysis on NAIP-imagery NDVI from 2015, 2017 and 2019 as well as the LiDAR DSM image. The first principal component effectively captured a gradient of variation due to NDVI values and height values which positively covaried. Our LiDAR enhanced NDVI product better represents vegetation biomass because verdant pastures or wetlands have lower values than verdant forest canopies. We refer to our LiDAR enhanced NDVI product as vegetation biomass. To quantify landscape heterogeneity of vegetation biomass we calculated the RoV of biomass using the SAGA radius of variance algorithm (search radius = 120, SD = 1).

APPENDIX D

BEHAVIOR MODE CLUSTER QUALITY VALIDATION

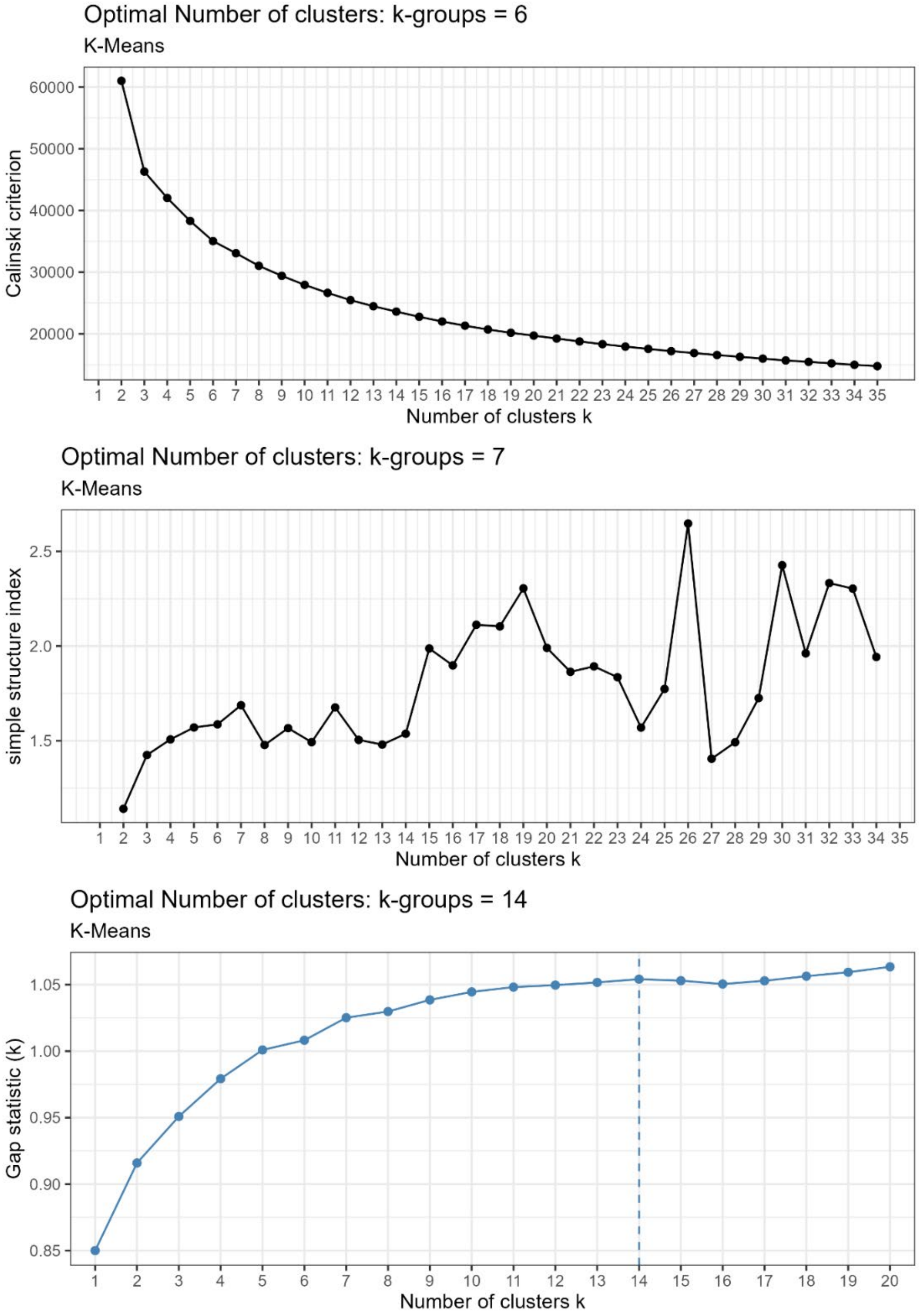


Figure 25. Cluster quality statistics for k-means partitioning.

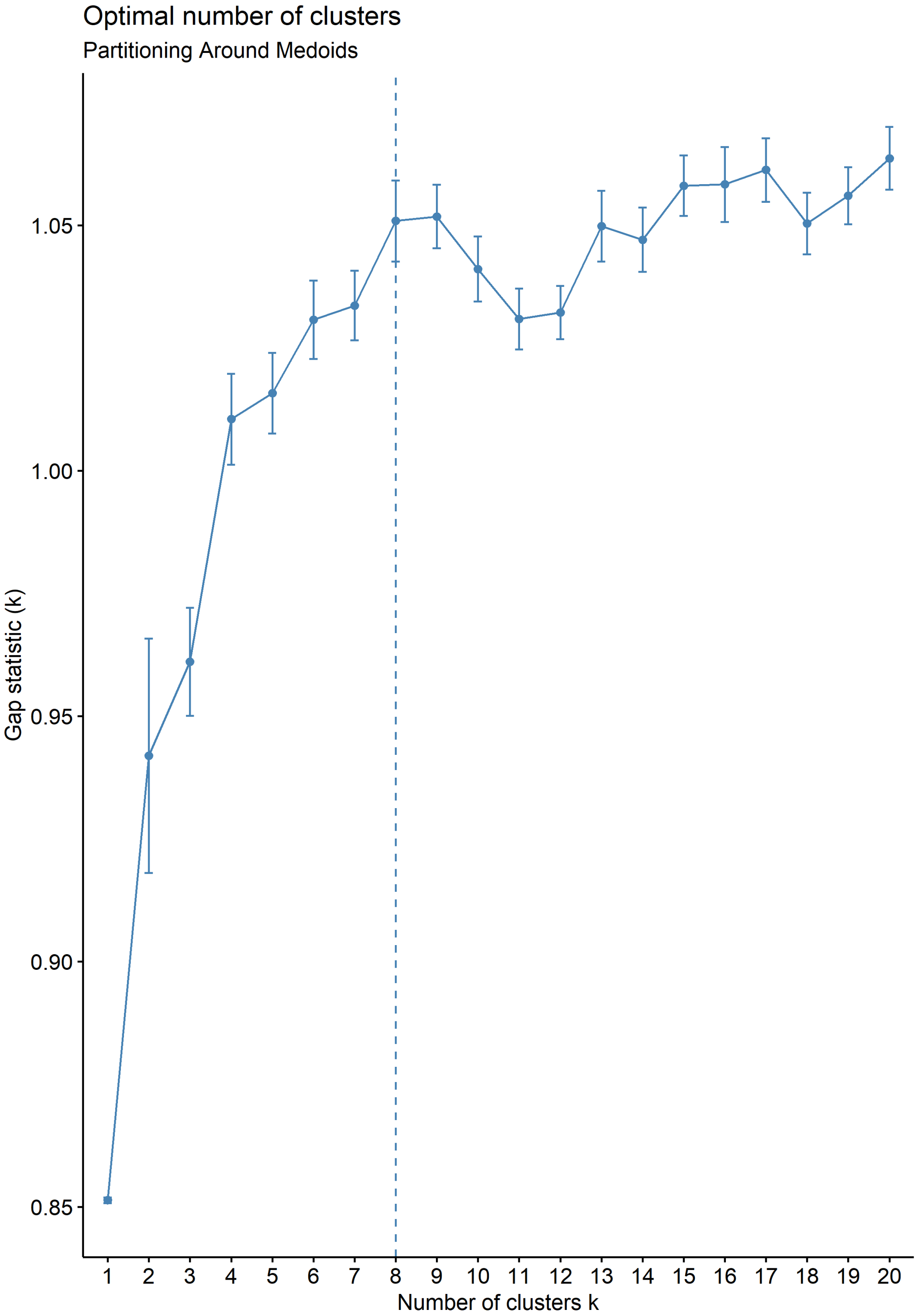


Figure 26. Cluster quality statistics for PAM partitioning.

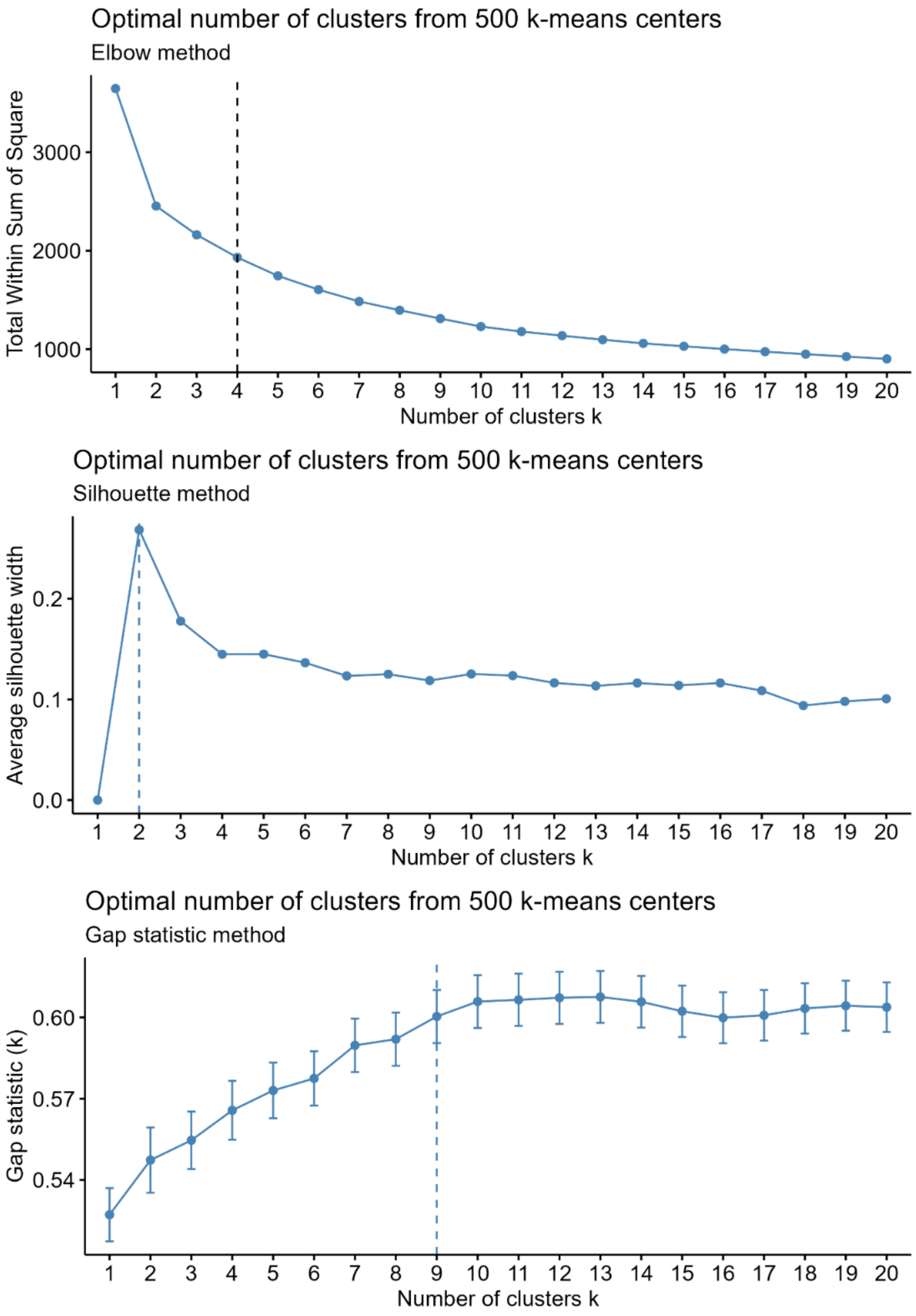


Figure 27. Cluster quality statistics for Ward-hierarchical partitioning.

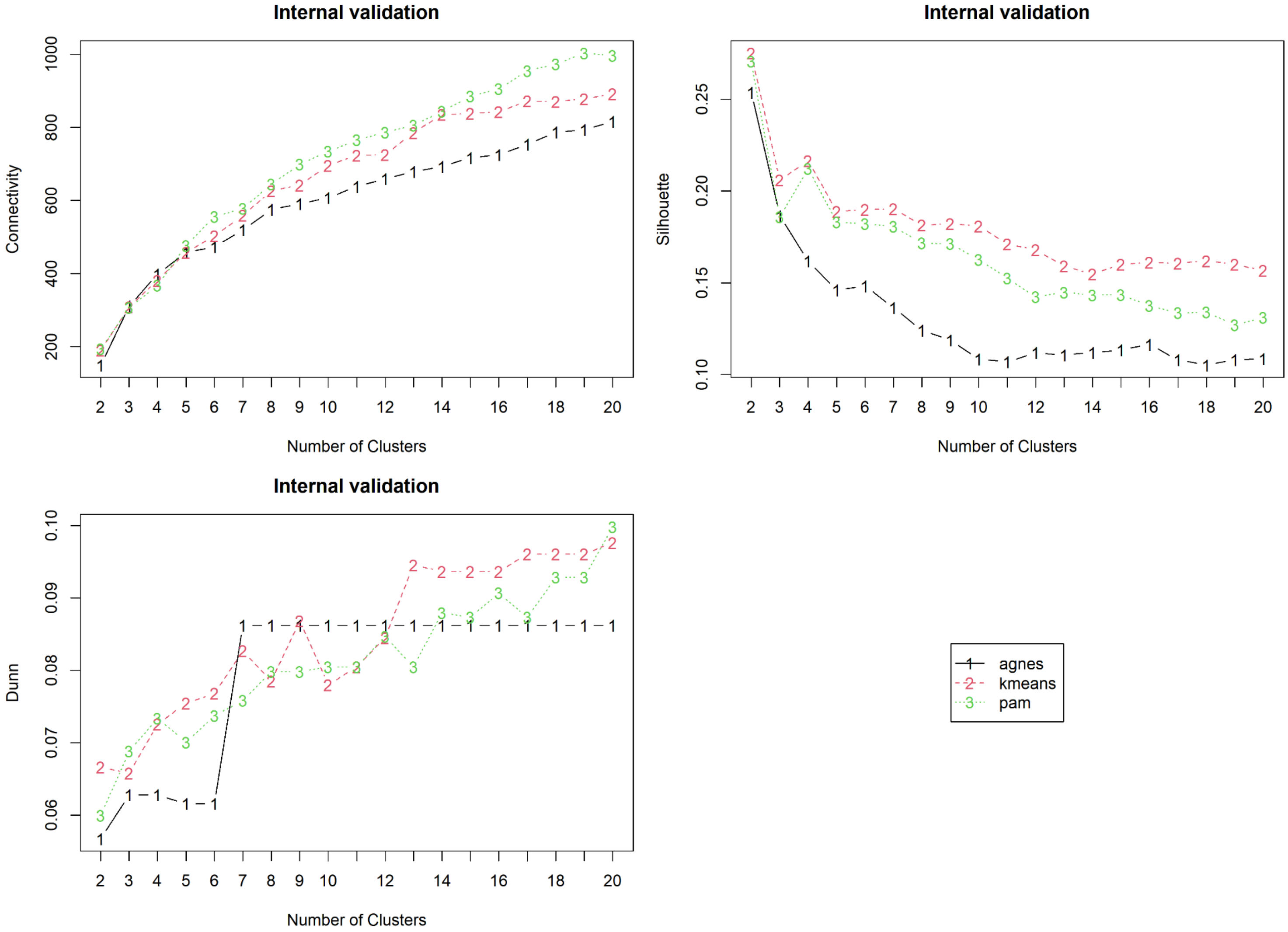


Figure 28. Internal validation statistics for k-means, partitioning around medoids (PAM), and Ward-hierarchical partitioning of 7 movement metrics for sage-grouse. The term agnes in the legend refers to the Ward-hierarchical partitioning method; agnes is the R statistical computing function used.

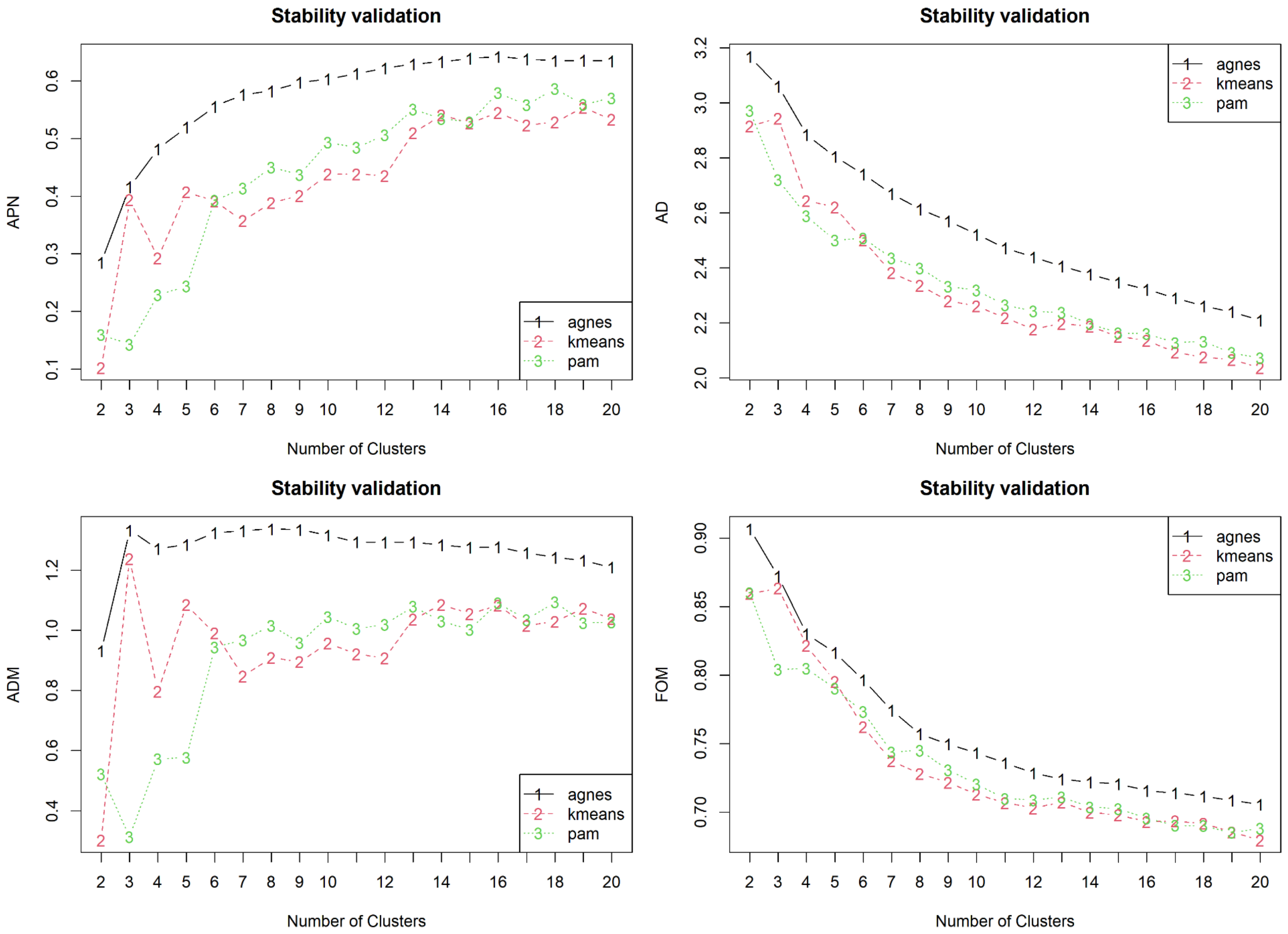


Figure 29. Stability validation statistics for k-means, partitioning around medoids (PAM), and Ward-hierarchical partitioning of 7 movement metrics for sage-grouse. The term agnes in the legend refers to the Ward-hierarchical partitioning method; agnes is the R statistical computing function used.

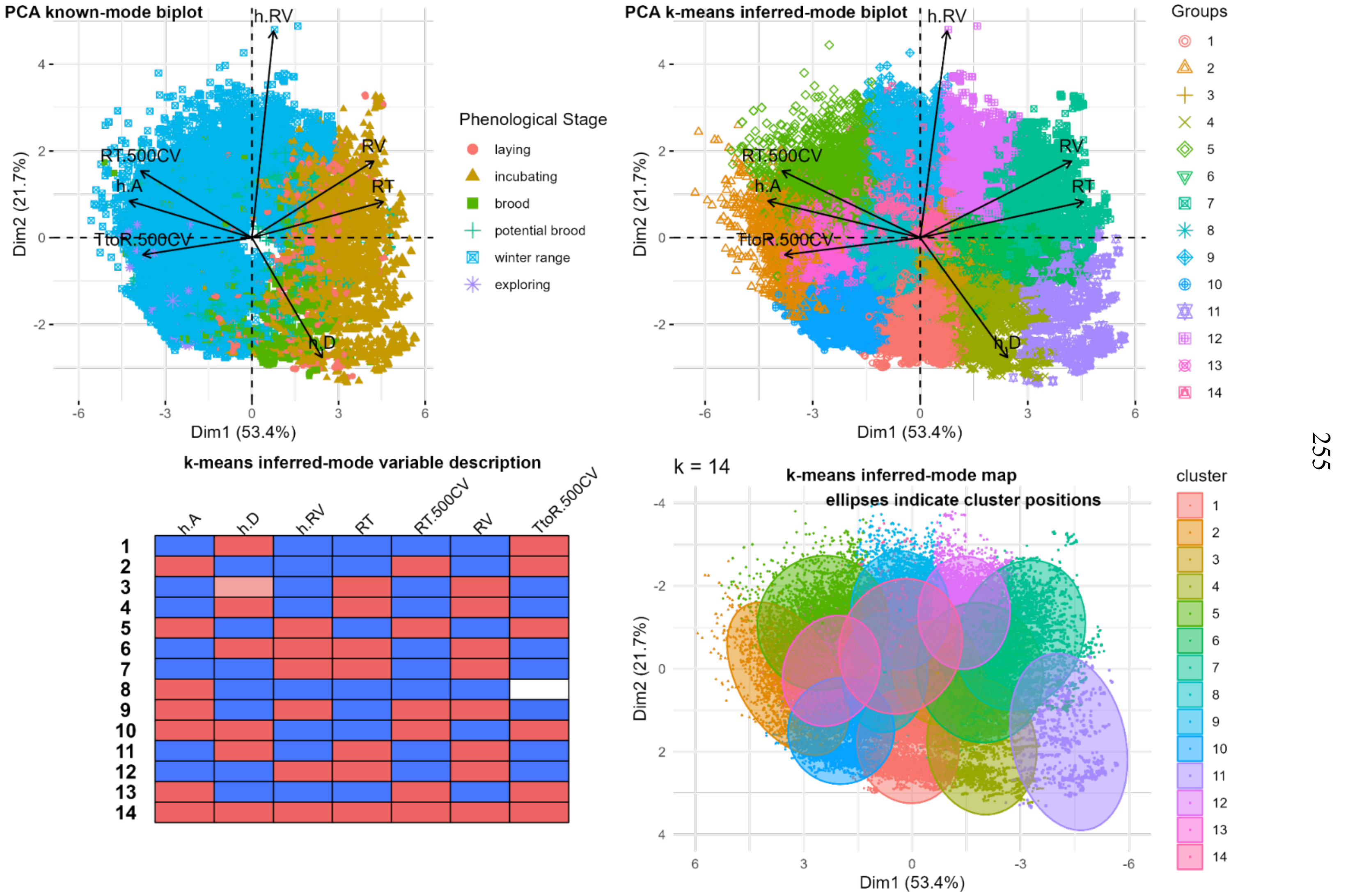
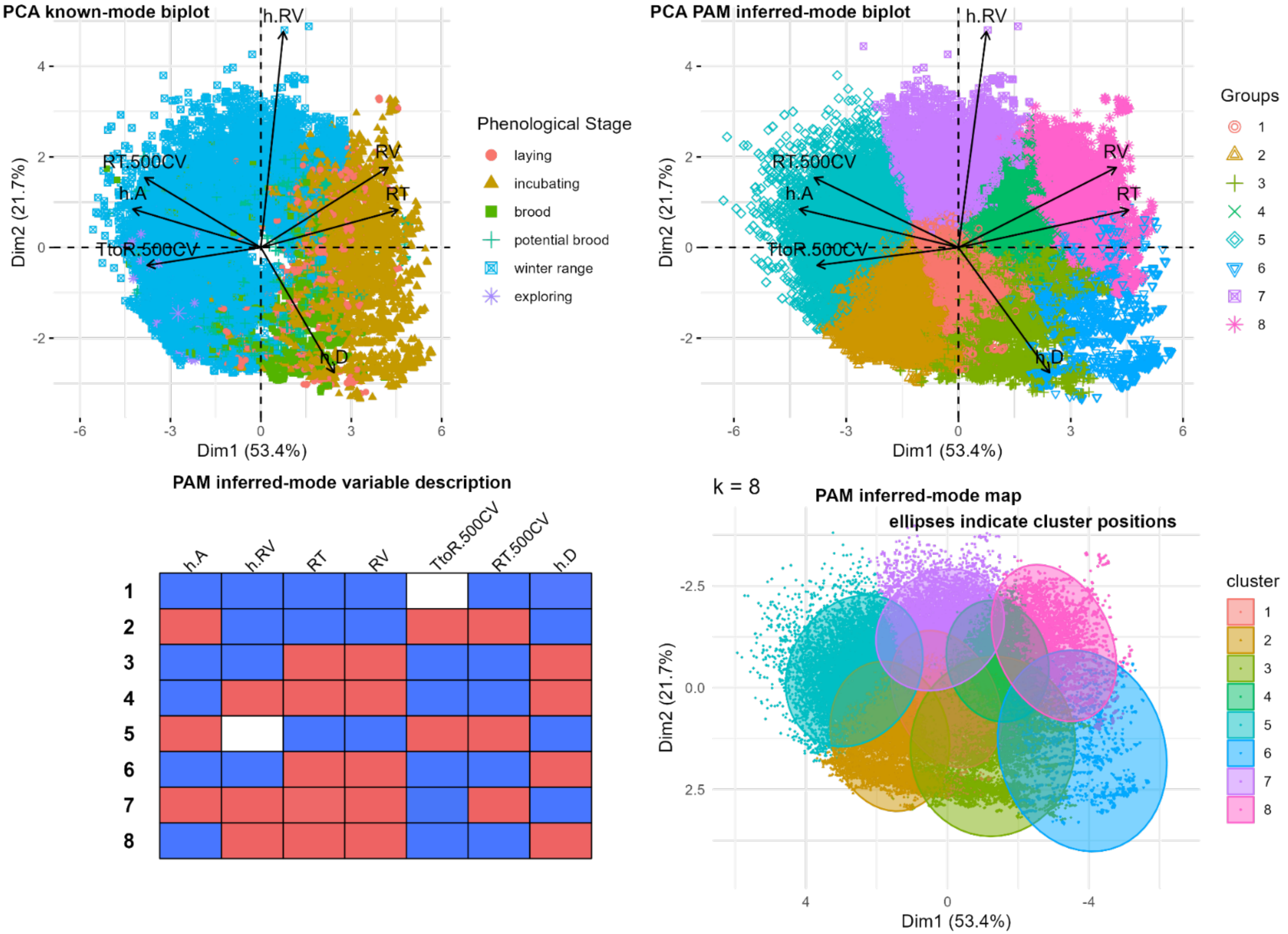


Figure 30. Multipaneled figure illustrating 14 k-means clusters relative to known behavior modes and movement metrics for sage-grouse.



	h.A	h.RV	RT	RV	TtoR.500CV	RT.500CV	h.D
1	🟦	🟦	🟦	🟦	⬜	🟦	🟦
2	🟥	🟦	🟦	🟦	🟥	🟥	🟦
3	🟦	🟦	🟥	🟥	🟦	🟦	🟥
4	🟦	🟥	🟥	🟥	🟦	🟦	🟥
5	🟥	⬜	🟦	🟦	🟥	🟥	🟦
6	🟦	🟦	🟥	🟥	🟦	🟦	🟥
7	🟥	🟥	🟥	🟥	🟦	🟥	🟦
8	🟦	🟥	🟥	🟥	🟦	🟦	🟥

Figure 31. Multipaneled figure illustrating 8 PAM clusters relative to known behavior modes and movement metrics for sage-grouse.

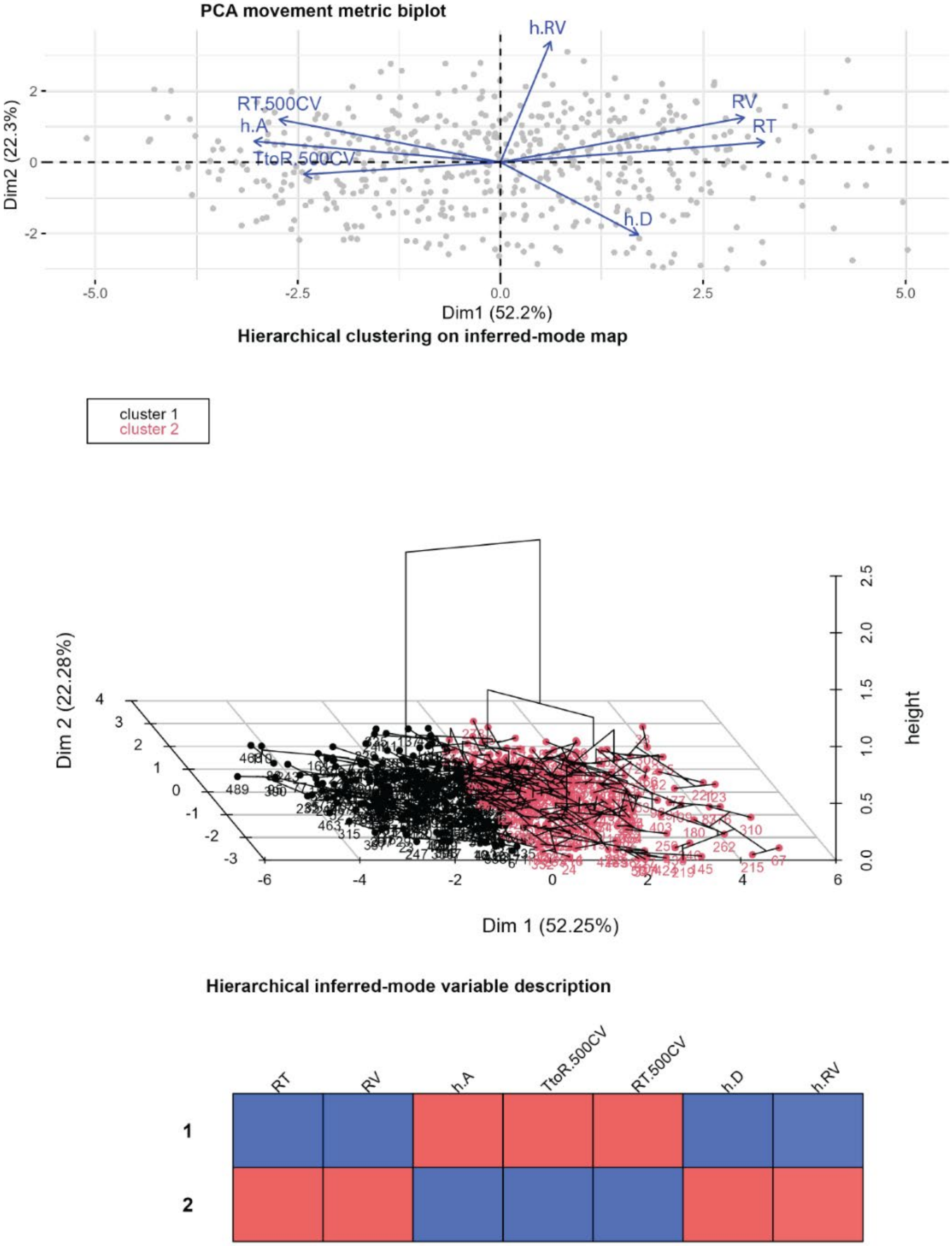


Figure 32. Multipaneled figure illustrating 2 Ward-hierarchical clusters relative to known behavior modes and movement properties for sage-grouse.

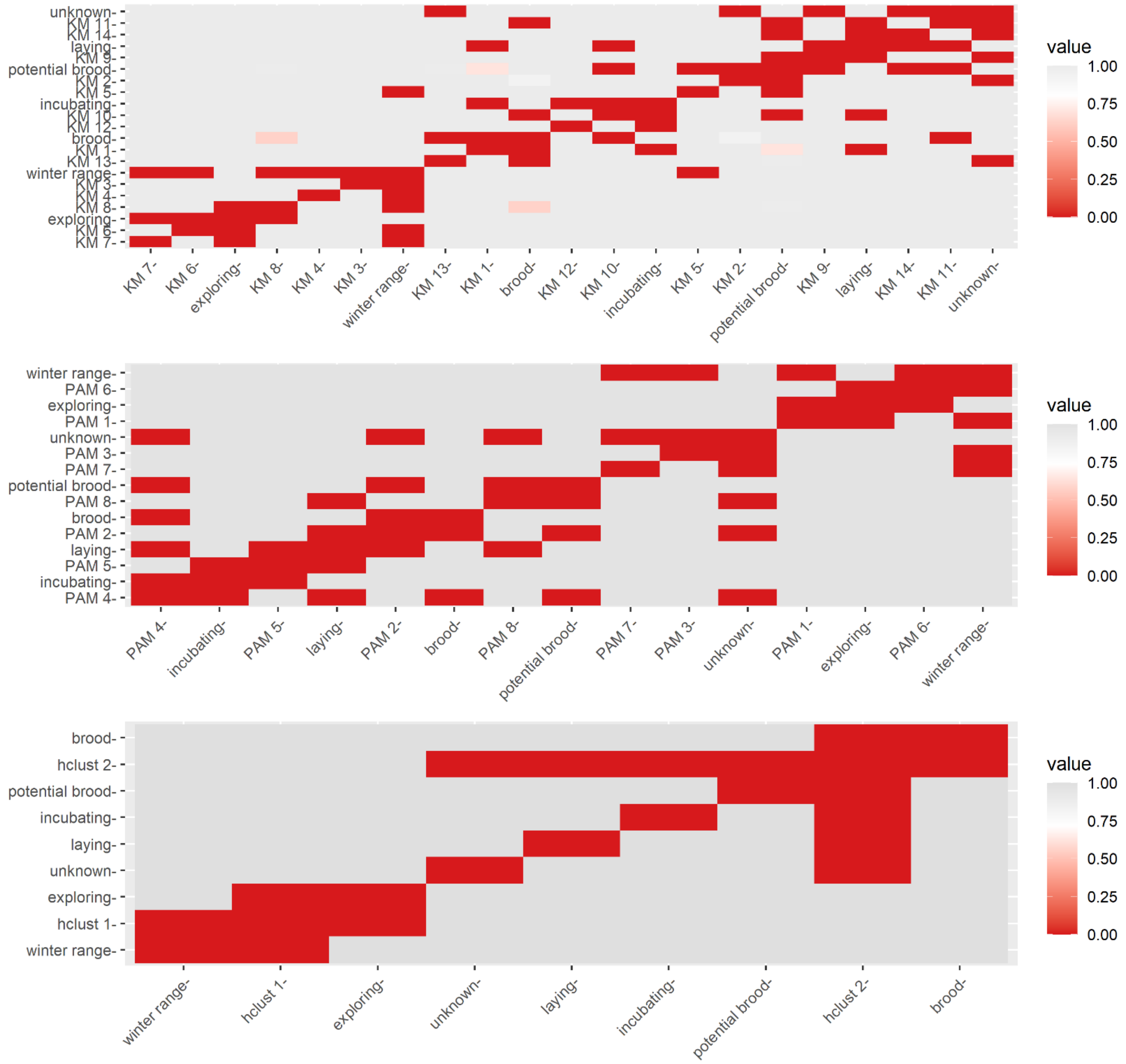


Figure 33. Similarity matrices for presence-absence co-occurrence tests of correspondence between partition results and known behavior modes. From top to bottom, the matrices are for k-means, PAM, and Ward-hierarchical partitioning. Statistically significant correspondence is indicted by red cells (low p-values).

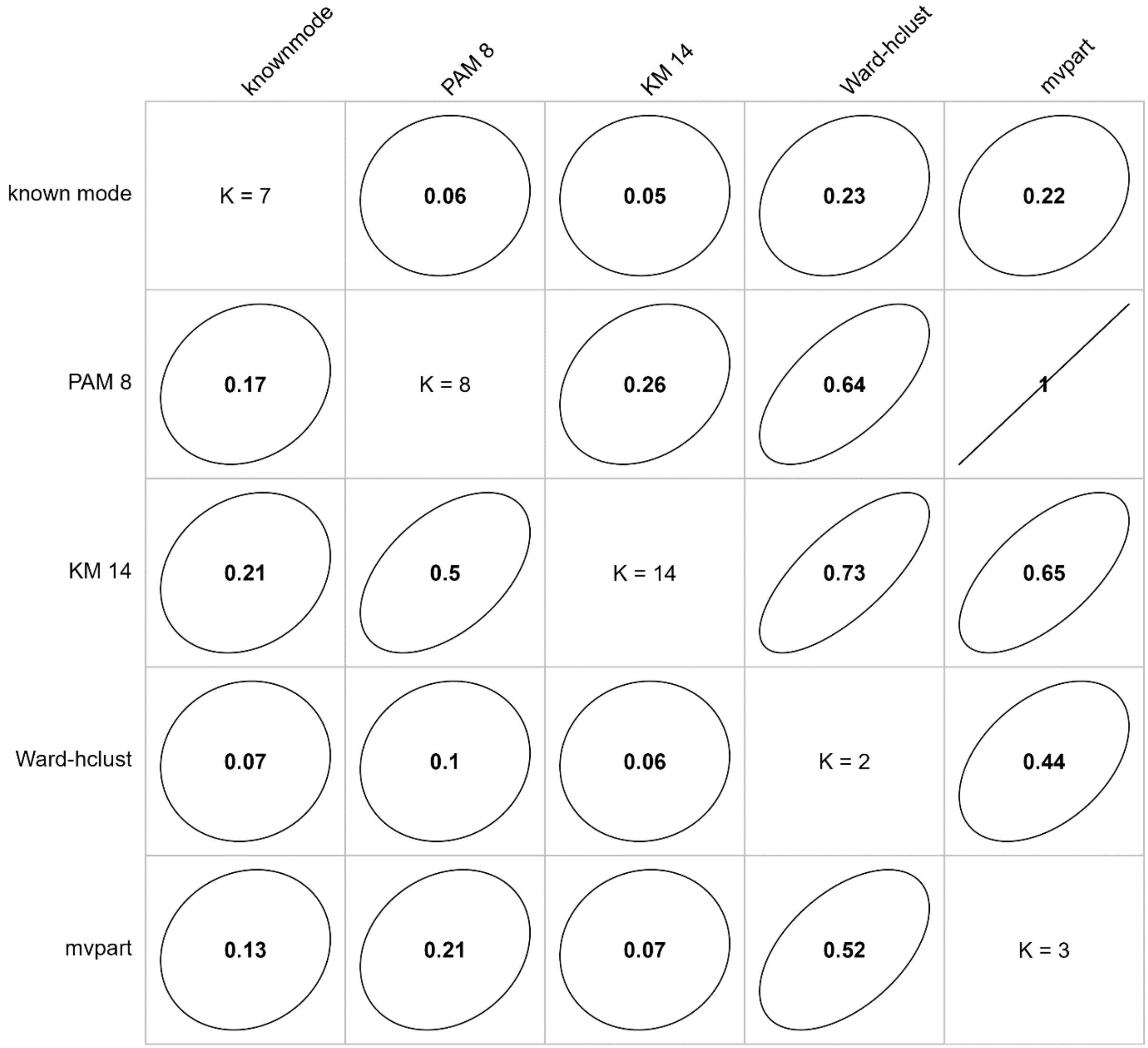


Figure 34. Similarity matrix illustrating correspondence among known sage-grouse behavior modes, a k-means partitioning scheme (KM 14), a partitioning around medoids (PAM 8) partitioning scheme, a Ward-hierarchical partitioning scheme, and the results of multivariate-regression-tree (mvpart) partitioning of the 8-mode PAM scheme based on 18 landscape condition variables relevant to sage-grouse.

APPENDIX E

SUPPLEMENTARY MATERIAL FOR MOVEMENT PROPERTY CHAPTER

Table 11. Description of 15 redundancy-analysis response variables and additional 3 variables (h-UI, RTmu, RTmu-cov) used in PCA analysis.

Movement Property	Label	Description	Ecological Relevance
hull area	h-A	size of hull	short-term home range
hull duration	h-D	average time spent in a hull per visit	average time-use intensity
hull eccentricity	h-E	elongation of hull	index to directional movement
hull enclosed points	h-I	number of points accrued in a hull footprint	index of global use-intensity
hull enclosed points / hull area	h-UI	areal density of used points enclosed by a hull	analogous to global use-intensity
hull revisits	h-RV	number of visits to a hull	intermittent importance of area
hull speed	h-S	average speed of ‘steps’ among points in a hull	average movement magnitude
hull speed (SD)	h-S-sd	variability of step speeds among points in a hull	variability in movement magnitudes
100-m patch residence time (total)	RT	hull-wide mean of total residence time in used 100-m radius patches	total fine-scale time-use intensity
100-m patch residence time (mean per visit)	RTmu	hull-wide-mean of average residence time per visit to used 100-m radius patches	average fine-scale time-use intensity
CV of 100-m patch residence time (total)	RT-cov	hull-wide variability in residence time per visit to used 100-m radius patches	variability in total fine-scale time-use intensity within hull
CV of 100-m patch residence time (mean)	RTmu-cov	hull-wide variability in average residence time per visit to used 100-m radius patches	variability in average fine-scale time-use intensity within hull
100-m patch revisits	RV	hull-wide mean of number of revisits to used 100-m radius patches	intermittent importance of patches within hull
100-m patch time-to-return	TtoR	hull-wide mean of median time-to-return among visits to used 100-m radius patches	intermittent importance of patches within hull
CV of 100-m patch time-to-return	TtoR-cov	hull-wide variability of median time-to-return among visits to used 100-m radius patches	variability in intermittent importance of patches within hull
CV of 500-m patch residence time	RT500-cov	hull-wide variability in residence time per visit to used 500-m radius patches	variability in intermittent importance of patches within hull

CV of 500-m patch time-to-return	TtoR500-cov	hull-wide variability of median time-to-return among visits to used 500-m radius patches	variability in intermittent importance of patches within hull
net displacement from first nest	ND-nest	distance from first nest	related to seasonal movements

Table 12. Description of all predictor variables used or seriously considered for redundancy-analysis based female sage-grouse movement ecology research.

Geospatial Layer Description	**Data Source >> Processing**	**Raw Grain Size**	**Ecological Relevance**
mean(2016–2019) annual forbs and grasses	RAP >> QGIS	30 m	annual forbs and grasses percent cover
mean(2016–2019) bare ground	RAP >> QGIS	30 m	bare ground percent cover
mean(2016–2019) litter	RAP >> QGIS	30 m	litter percent cover
mean(2016–2019) perennial forbs and grasses	RAP >> QGIS	30 m	perennial forbs and grasses percent cover
mean(2016–2019) shrubs	RAP >> QGIS	30 m	shrubs percent cover
mean(2016–2019) trees	RAP >> QGIS	30 m	trees percent cover
MSU LANDFIRE sage	LANDFIRE	30 m	percent sagebrush cover class type
MRLC annual herbaceous	USGS NLCD	30 m	annual plant percent cover
MRLC bare ground	USGS NLCD	30 m	bare ground percent cover
MRLC big sagebrush	USGS NLCD	30 m	big sagebrush percent cover
MRLC herbaceous	USGS NLCD	30 m	herbaceous plants percent cover
MRLC litter	USGS NLCD	30 m	litter percent cover
MRLC sagebrush	USGS NLCD	30 m	sagebrush percent cover
MRLC shrub height	USGS NLCD	30 m	average height of shrubs
MRLC shrub	USGS NLCD	30 m	shrub percent cover
NDVI (resampled from 1-m resolution)	2017 NAIP >> QGIS	1/3 arc second	green vegetation cover
MSU LiDAR NDVI (biomass index)	2015 -- 2019 NAIP + DSM	0.6m	index of vegetation that incorporates digital surface model data

MSU LiDAR NDVI RoV	2015 -- 2019 NAIP + DSM	0.6m	heterogeneity of biomass index
MSU lowland NDVI	2015-2017-2019 NAIP	0.6 m	index of lowland vegetation cover
MSU heavy shrubs	2015-2017-2019 NAIP	0.6 m	index of large shrubs (e.g., juniper)
MSU medium shrubs	2015-2017-2019 NAIP	0.6 m	index of medium shrubs (e.g., sagebrush, greasewood)
MSU forest	2015-2017-2019 NAIP	0.6 m	index of trees
MSU sagebrush	2015-2017-2019 NAIP	0.6 m	sagebrush cover estimates
MSU bare ground	2015-2017-2019 NAIP	0.6 m	bare ground cover estimates
MSU protection	DSM >> SAGA GIS	0.9 m	index of how landscape objects shelter an area
MSU landscape structure	DSM >> SAGA GIS	0.9 m	index of how rugged the landscape surface is due to all surface objects
MSU tall objects	DSM >> SAGA GIS	0.9 m	index of the density of tall or prominent objects on the landscape
MSU vegetation height	DSM-DEM >> SAGA GIS	0.9m	index of the height of objects on the landscape, typically vegetation
MSU vegetation height RoV	DSM-DEM >> SAGA GIS	0.9m	proximal heterogeneity of the height of objects on the landscape, typically vegetation
MSU fine-scale landscape ruggedness	DEM>> SAGA GIS	0.9m	index of fine-scale landscape ruggedness due to terrain features such as stream banks
MSU fine-scale landscape ruggedness RoV	DEM>> SAGA GIS	0.9m	heterogeneity of fine-scale landscape ruggedness
proximity to hydrologic channels	DEM >> SAGA GIS	1/3 arc second	distance to areas where surface water may persist
proximity to water bodies	DEM >> SAGA GIS	1/3 arc second	distance to areas where surface water is present

proximity to water bodies RoV	DEM >> SAGA GIS	1/3 arc second	proximal heterogeneity of water bodies
fence line density	BLM >> QGIS	1/3 arc second	density of fences
multiresolution ridge top flatness	DEM >> SAGA GIS	1/3 arc second	index of highland area flatness
multiresolution valley bottom flatness	DEM >> SAGA GIS	1/3 arc second	index of bottomland flatness
mid-slope position	DEM >> SAGA GIS	1/3 arc second	index of middle slopes between ridges and valleys
normalized height	DEM >> SAGA GIS	1/3 arc second	elevation of the land surface normalized by surrounding area
standardized height	DEM >> SAGA GIS	1/3 arc second	elevation of the land surface standardized by all heights in the study area
wind exposition	DEM >> SAGA GIS	1/3 arc second	exposure to wind
morphometric protection	DEM >> SAGA GIS	1/3 arc second	index of how topographic relief shelters and area
slope height	DEM >> SAGA GIS	1/3 arc second	height of slopes relative to relief in the immediate vicinity
valley depth	DEM >> SAGA GIS	1/3 arc second	vertical distance an area is from the basal channel below
vector terrain ruggedness	DEM >> SAGA GIS	1/3 arc second	index of topographic ruggedness that highlights severe ruggedness
terrain ruggedness index	DEM >> SAGA GIS	1/3 arc second	common index of the ruggedness of the landscape in an area
topographic position index multiscale	DEM >> SAGA GIS	1/3 arc second	multiscale index of landscape topographic position, (e.g., valley, midslope, ridge)
topographic position index	DEM >> SAGA GIS	1/3 arc second	standard index of landscape topographic position, (e.g., valley, midslope, ridge)
topographic wetness index	DEM >> SAGA GIS	1/3 arc second	index of the expected or potential soil wetness based on topography

total insolation	DEM >> SAGA GIS	1/3 arc second	index of the total solar insolation that a parcel of the landscape receives
daylength	PTT timestamp >> R	daily	the time interval between sunrise and sunset
daily precipitation	PRISM >> R	daily, 4 km	PRISM estimates of daily mean precipitation
daily mean temperature	PRISM >> R	daily, 4 km	PRISM estimates of daily mean temperature
age of female sage-grouse	PTT timestamp >> R	daily	approximate age of female based on age at capture plus days elapsed

Table 13. List of predictor and response variables selected for inclusion in redundancy analysis (RDA) models of female sage-grouse movements, prior to variance inflation factor screening and forward selection routines. All response variables and modulating variables were included in all the RDA models. Column 3 indicates either the power by which a variable was transformed, a natural log transformation (log), or a logit transformation. The 75th quartile is labeled Q75 for some summary statistics.

Raw Predictor	Computed Summary Statistic	Transformation
Response Variables		
speed (h-S)	average speed of nearest neighbor points (nnp)	0.3
standard deviation of speed (h-S-SD)	standard deviations of nnp speeds	0.165
area (h-A)	hull area	0.285
enclosed points (h-I)	number of hull-enclosed points	0.066
revisits (h-RV)	hull revisits	logit
duration (h-D)	hull-mean number of points per visit	0.1
eccentricity (h-E)	hull eccentricity	logit
net displacement from start (ND-nest)	net displacement from start at first-known nest site	0.12
100-m patch revisits (RV)	hull-mean revisitations of 100-m nnp-patches	0.035
100-m patch residence time (RT)	hull-mean residence time in 100-m nnp-patches	0.075
RT coefficient of variation (RT-cov)	hull-CV of residence time in 100-m nnp-patches	0.615
500-m patch RT-cov (RT500-cov)	hull-CV of residence time in 500-m nnp-patches	0.45
100-m patch time-to-return (TtoR)	hull-mean of median time-to-return of nnp-patches	0.255
TtoR coefficient of variation (TtoR-cov)	hull-CV of median time-to-return of nnp-patches	0.585
500-m TtoR-cov (TtoR500-cov)	hull-CV of median time-to-return of nnp-patches	0.35
Modulator Variables		
day length	mean of values at nearest neighbor points	2.5
female age in days	age at hull parent point	1
precipitation	mean of values at nearest neighbor points	0.3
temperature	mean of values at nearest neighbor points	$(x+27)^{1.5}$
Vegetation Covariates		

Barren	hullwise zonal mean	logit
Barren	hullwise zonal CV	log+1
Barren	mean of 100-m patch zonal means	0.357
Barren	hull-CV of 100-m patch zonal means	0.315
Barren	mean of 30-m patch zonal means	0.41
Forest	hullwise zonal mean	logit
Forest	hullwise zonal CV	logit
Forest	mean of 100-m patch zonal means	logit
Forest	mean of 30-m patch zonal means	logit
Heavy Shrub	hullwise zonal mean	((x+1)^-0.73) *-1
Heavy Shrub	hullwise zonal CV	log+1
Heavy Shrub	mean of 100-m patch zonal means	logit
Heavy Shrub	mean of 30-m patch zonal means	0.18
Height	hullwise zonal mean	0.045
Height	mean of 30-m patch zonal means	0.155
Height	mean of 100-m patch zonal means	(x^-0.123) *-1
LANDFIRE sage	mean of 100-m patch zonal means	1.92
LANDFIRE sage	hullwise zonal mean	(x+0.01)^1.665
Landscape Structure	mean of 30-m patch zonal Q75s	((x+1)^-0.057) *-1
Lowland NDVI	hullwise zonal mean	log+1
Lowland NDVI	hullwise zonal CV	0.077
Lowland NDVI	mean of 100-m patch zonal means	1
Lowland NDVI	mean of 30-m patch zonal means	log+1
Lowland NDVI	hull-CV of 30-m patch zonal means	0.01
Medium Shrub	hullwise zonal mean	((x+1)^-0.24) *-1
Medium Shrub	hullwise zonal CV	log+1
Medium Shrub	mean of 100-m patch zonal means	0.164
Medium Shrub	mean of 30-m patch zonal means	0.145
Protection	mean of 30-m patch zonal Q75s	log
Protection	hull-CV of 30-m patch Q75s	log
Ruggedness	hull-CV of 30-m patch Q75s	log
Sage	hullwise zonal mean	logit
Sage	hullwise zonal CV	log+1
Sage	mean of 100-m patch zonal means	0.055
Sage	mean of 30-m patch zonal means	0.1375
Sage	hull-CV of 30-m patch zonal means	log+1
Structure	mean of 30-m patch zonal Q75s	logit
Tall Objects	hull-CV of 30-m patch Q75s	logit
Vegetation Biomass	hullwise zonal mean	(x^-9.5) *-1
Vegetation Biomass	mean of 100-m patch zonal means	(x^-10.4) *-1

Vegetation Biomass	hull-CV of 100-m patch zonal means	0.23
Vegetation Biomass	hull-rCD of 100-m patch zonal means	0.23
Vegetation Biomass	mean of 30-m patch zonal means	(x^-10.4) *-1
Vegetation Biomass	hull-CV of 30-m patch zonal means	0.23
Vegetation Biomass	hull-rCD of 30-m patch zonal means	0.23
Radius of Variance of Biomass	mean of 30-m patch zonal means	(x^-1.77) *-1
Radius of Variance of Biomass	mean of 100-m patch zonal means	(x^-1.63) *-1
Topography Covariates		
LiDAR Vector Ruggedness Measure	hull-mean of 30-m patch zonal means	log + 0.0001
Midslope Position	hull zonal mean	1
Midslope Position	hull-mean of 30-m patch zonal means	log + 1
Midslope Position	hull-mean of 100-m patch zonal means	log + 1
Morphometric Protection Index	hull zonal mean	sqrt
Morphometric Protection Index	hull-mean of 30-m patch zonal means	log + 1
Morphometric Protection Index	hull-mean of 100-m patch zonal means	log + 1
Multiresolution Ridge Top Flatness	hull zonal mean	sqrt
Multiresolution Ridge Top Flatness	hull-mean of 30-m patch zonal means	log + 1
Multiresolution Ridge Top Flatness	hull-mean of 100-m patch zonal means	log + 1
MultiResolution Valley Bottom Flatness	hull zonal mean	sqrt
MultiResolution Valley Bottom Flatness	hull-mean of 30-m patch zonal means	log + 1
MultiResolution Valley Bottom Flatness	hull-mean of 100-m patch zonal means	log + 1
Multiscale Topographic Position Index	hull-mean of 30-m patch zonal means	log + 1
Multiscale Topographic Position Index	hull-mean of 100-m patch zonal means	log + 1
Normalized Height	hull zonal mean	1
Normalized Height	hull-mean of 30-m patch zonal means	log + 1
Normalized Height	hull-CV of 30-m patch zonal means	sqrt
Normalized Height	hull-mean of 100-m patch zonal means	log + 1

Proximity to Channels	hull zonal mean	sqrt
Proximity to Channels	hull-mean of 30-m patch zonal means	log + 1
Proximity to Channels	hull-mean of 100-m patch zonal means	log + 1
Proximity to Water Bodies	hull zonal mean	sqrt
Proximity to water bodies	hull-mean of 30-m patch zonal means	log + 1
Proximity to Water Bodies	hull-mean of 100-m patch zonal means	log + 1
Radius of Variance of LiDAR VRM	hull-mean of 30-m patch zonal means	(1/*x*) *-1
Radius of Variance of Water Bodies	hull-mean of 100-m patch zonal means	(1/*x*) *-1
Slope Height	hull zonal mean	sqrt
Slope Height	hull-mean of 30-m patch zonal means	log + 1
Slope Height	hull-CV of 30-m patch zonal means	sqrt
Slope Height	hull-mean of 100-m patch zonal means	log + 1
Solar Insolation	hull zonal mean	1
Solar Insolation	hull-mean of 30-m patch zonal means	log + 1
Solar Insolation	hull-mean of 100-m patch zonal means	log + 1
Standardized Height	hull zonal mean	sqrt
Standardized Height	hull-mean of 30-m patch zonal means	log + 1
Standardized Height	hull-CV of 30-m patch zonal means	sqrt
Standardized Height	hull-mean of 100-m patch zonal means	log + 1
Topographic Position Index	hull zonal mean	1
Topographic Position Index	hull zonal mean	1
Topographic Wetness Index	hull zonal mean	1
Topographic Wetness Index	hull-mean of 30-m patch zonal means	log + 1
Topographic Wetness Index	hull-CV of 30-m patch zonal means	sqrt
Topographic Wetness Index	hull-mean of 100-m patch zonal means	log + 1
Valley Depth	hull zonal mean	log
Valley Depth	hull-mean of 30-m patch zonal means	log + 1
Valley Depth	hull-CV of 30-m patch zonal means	sqrt
Valley Depth	hull-mean of 30-m patch zonal means	log + 1
Vector Ruggedness Measure	hull zonal mean	sqrt
Vector Ruggedness Measure	hull-mean of 30-m patch zonal means	sqrt
Vector Ruggedness Measure	hull-CV of 30-m patch zonal means	sqrt
Vector Ruggedness Measure	hull-mean of 100-m patch zonal means	sqrt

Wind Exposition	hull zonal mean	1
Wind Exposition	hull-mean of 30-m patch zonal means	log + 1
Wind Exposition	hull-CV of 30-m patch zonal means	log + 1

APPENDIX F

SUPPLEMENTARY MATERIAL FOR HABITAT MAPPING CHAPTER

Table 14. List of all ecological variables considered for our behavior-specific model of female sage-grouse use-intensity. Our model was a negative-binomial generalized additive model of number of hull-enclosed points as a function of landscape conditions, conditional on behavior modes, and covariate correcting for pertinent movement properties. Predictor variable screening was conducted with Pearson correlation and variance inflation factor screening.

Base Variable	Summary Statistic	Transform	Ecological Relevance
Barren	hull-mean of 30-m patch zonal means	1.00	bare ground cover estimates
Daily Temperature	mean of hull nearest neighbor points	1.00	PRISM estimates of daily mean temperature
Female Age	female age at hull parent point	1.00	approximate age of female based on age at capture plus days elapsed
Fine-grain Ruggedness (LiDAR based)	hull-mean of 30-m patch zonal means	log	index of how rugged the landscape surface is due to all surface objects
Fine-grain Ruggedness (LiDAR based)	hull-CV of 30-m patch zonal means	1.00	variability of index of how rugged the landscape surface is due to all surface objects
Fine-grain Ruggedness (LiDAR based)	hull-rCD of 30-m patch zonal means	1.00	variability of index of how rugged the landscape surface is due to all surface objects
Fine-grained Sage	hull-mean of 30-m patch zonal means	sqrt	actual sagebrush areal cover estimates (not percent coarse sagebrush cover class)
Hull Area	hull area	1.00	area of short-term home range
Hull Revisits	number of hull revisits	1.00	relatively coarse temporal scale revisitation to prior short-term home ranges
Hull Timespan	timespan of hull nearest neighbor points	1.00	time span of short term-home range giving home range temporal context
Hull-enclosed Points (response variable)	number of hull-enclosed points	1.00	number of use points accrued by an individual inside a short-term home range
LANDFIRE sage	hull-mean of 30-m patch zonal means	1.00	percent LANDFIRE vegetation data that is sagebrush class
LANDFIRE sage	hull-CV of 30-m patch zonal means	1.00	variability of percent LANDFIRE vegetation data that is sagebrush class
LANDFIRE sage	hull-rCD of 30-m patch zonal means	1.00	variability of percent LANDFIRE vegetation data that is sagebrush class
Length of Day	mean of hull nearest neighbor points	1.00	the time interval between sunrise and sunset
LiDAR Vector Ruggedness Measure	hull-mean of 30-m patch zonal means	1.00	index of fine-grain landscape ruggedness due to terrain features such as stream banks
LiDAR Vector Ruggedness Measure	hull-rCD of 30-m patch zonal means	1.00	variability of fine-grain landscape ruggedness

Lowland NDVI	hull-CV of 30-m patch zonal means	1.00	variability of index of lowland vegetation cover
Lowland NDVI	hull-mean of 30-m patch zonal means	1.00	index of lowland vegetation cover
Lowland NDVI	hull-rCD of 30-m patch zonal means	1.00	variability of index of lowland vegetation cover
Medium Shrub	hull-mean of 30-m patch zonal means	sqrt	index of medium shrubs (e.g., sagebrush, greasewood)
MultiResolution Valley Bottom Flatness	hull-CV of 30-m patch zonal means	1.00	variability of index of bottomland flatness
MultiResolution Valley Bottom Flatness	hull-mean of 30-m patch zonal means	1.00	index of bottomland flatness
MultiResolution Valley Bottom Flatness	hull-rCD of 30-m patch zonal means	1.00	variability of index of bottomland flatness
NED Vector Ruggedness Measure	hull-CV of 30-m patch zonal means	1.00	variability of index of topographic ruggedness that highlights severe ruggedness
NED Vector Ruggedness Measure	hull-rCD of 30-m patch zonal means	1.00	variability of index of topographic ruggedness that highlights severe ruggedness
NED Vector Ruggedness Measure	hull-mean of 30-m patch zonal means	sqrt	common index of the ruggedness of the landscape in an area
Normalized Height	hull-CV of 30-m patch zonal means	1.00	variability of elevation of the land surface normalized by surrounding area
Normalized Height	hull-mean of 30-m patch zonal means	1.00	elevation of the land surface normalized by surrounding area
Normalized Height	hull-rCD of 30-m patch zonal means	1.00	variability of elevation of the land surface normalized by surrounding area
Proximity to Channels	hull-CV of 30-m patch zonal means	1.00	distance to areas where surface water may persist
Proximity to Water Bodies	hull-mean of 30-m patch zonal means	sqrt	distance to areas where surface water is present
Slope Height	hull-mean of 30-m patch zonal means	log	height of slopes relative to relief in the immediate vicinity
Slope Height	hull-CV of 30-m patch zonal means	1.00	variability of height of slopes relative to relief in the immediate vicinity
Solar Insolation	hull-mean of 30-m patch zonal means	1.00	index of the total solar insolation that a parcel of the landscape receives
Topographic Wetness Index	hull-CV of 30-m patch zonal means	1.00	variability of the expected or potential soil wetness based on topography
Topographic Wetness Index	hull-mean of 30-m patch zonal means	1.00	index of the expected or potential soil wetness based on topography
Topographic Wetness Index	hull-rCD of 30-m patch zonal means	1.00	variability of the expected or potential soil wetness based on topography
Valley Depth	hull-mean of 30-m patch zonal means	1.00	vertical distance an area is from the basal channel below

Vegetation Biomass	hull-mean of 30-m patch zonal means	1.00	index of vegetation that incorporates digital surface model data
Vegetation Biomass RoV	hull-mean of 30-m patch zonal means	1.00	proximal heterogeneity of biomass index
Vegetation Height (LiDAR based)	hull-mean of 30-m patch zonal means	(x^0.6)*-1	index of the height of objects on the landscape, typically vegetation
Vegetation Height (LiDAR based)	hull-mean of 30-m patch zonal means	1.00	proximal heterogeneity of the height of objects on the landscape, typically vegetation
Water Body Presence RoV	hull-mean of 30-m patch zonal means	3.00	proximal heterogeneity of surface water presence
Wind Exposition	hull-mean of 30-m patch zonal means	1.00	exposure to wind

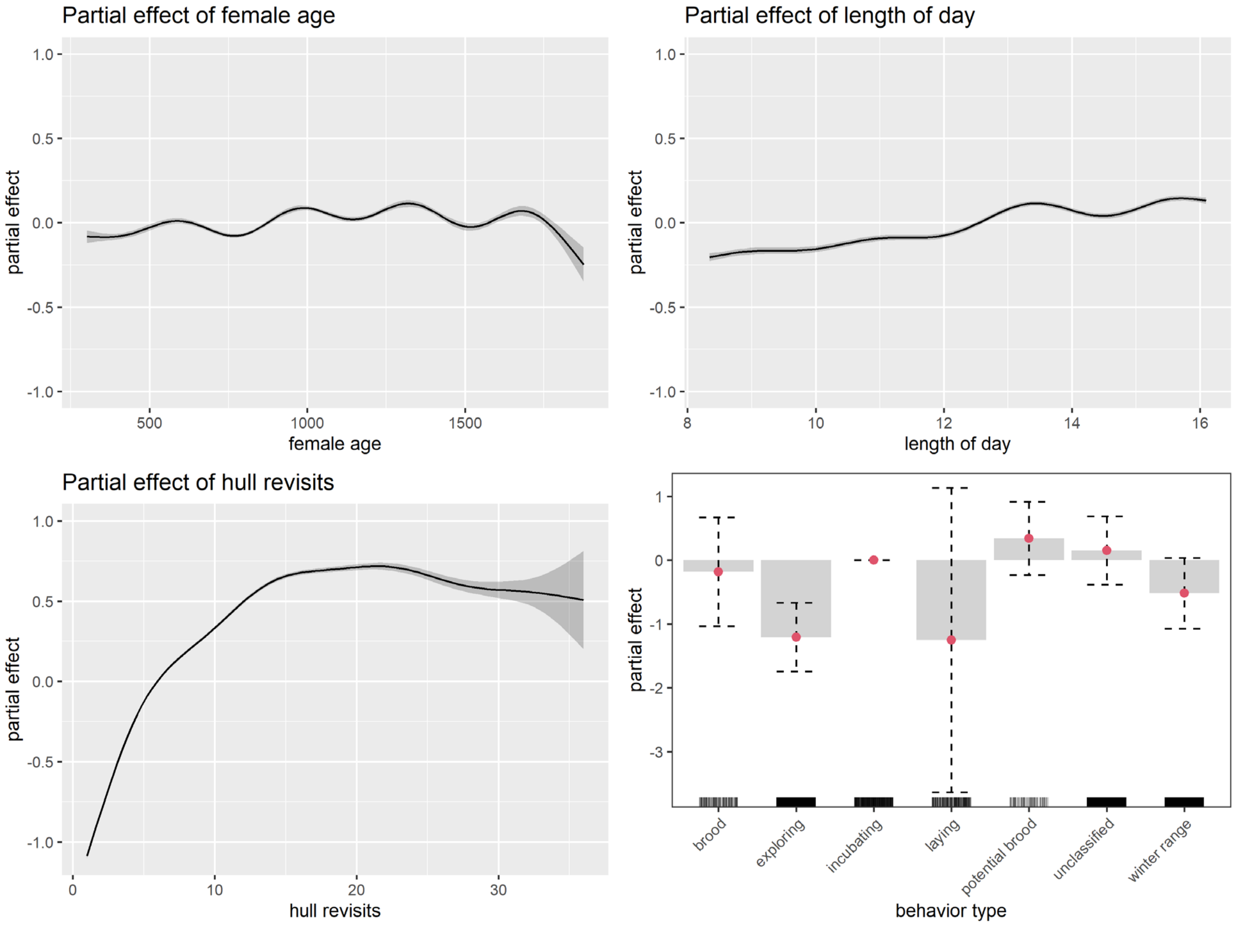


Figure 35. Estimates of partial effects of age, length of day, hull revisits, and behavior type on female sage-grouse use-intensity. The y axis represents the contribution of the terms to the linear predictor of log(use-intensity). A rug plot is provided at the bottom of the behavior forest plot to indicate relative sample sizes among the 7 behavior modes.

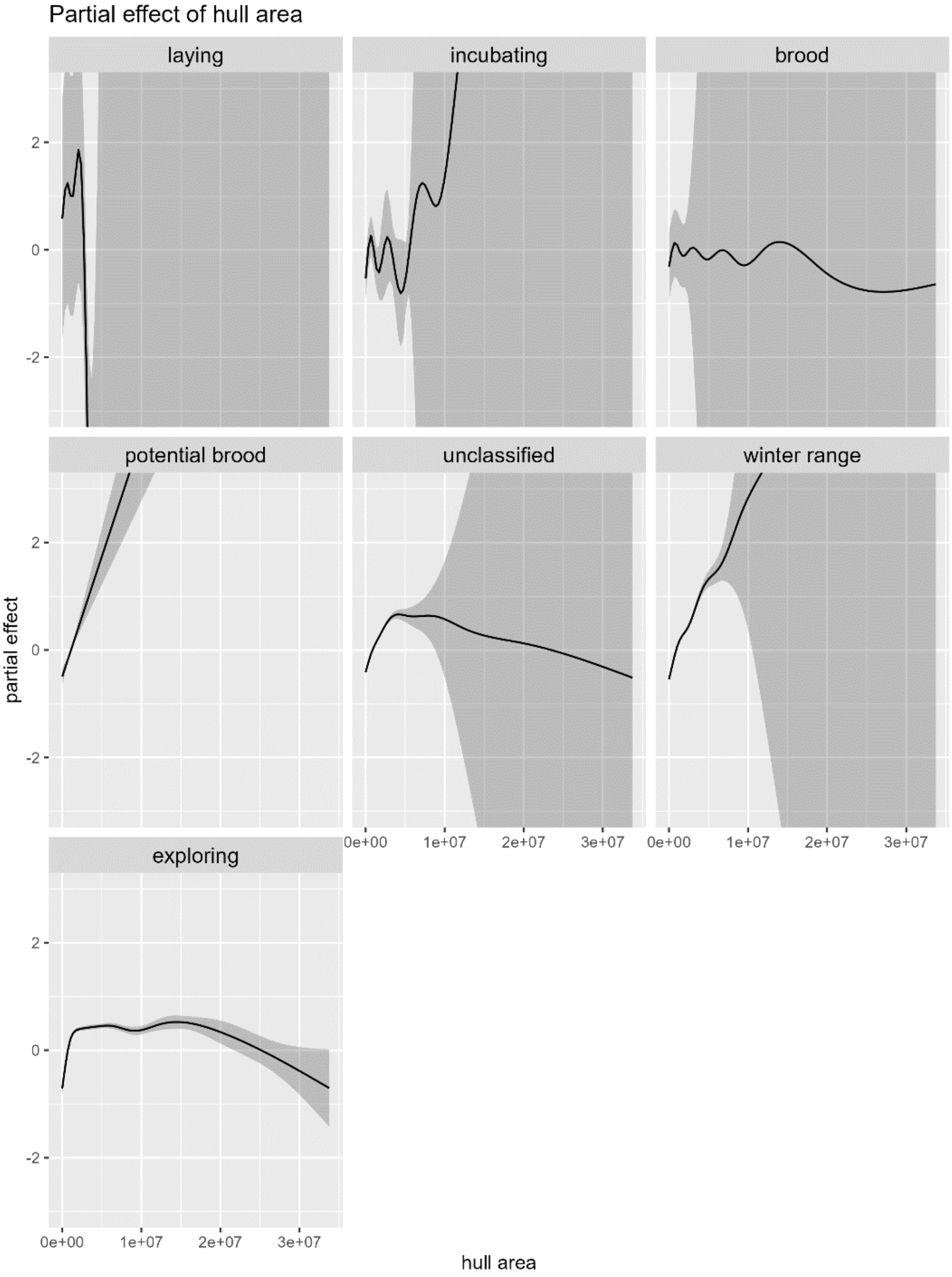


Figure 36. Estimates of smooth functions, s(x), of the effect of a predictor variable on female sage-grouse use-intensity for smooth-factor interactions with different levels of behavior-season types. The y axis represents the contribution of the smooth term to the linear predictor of log(use-intensity).

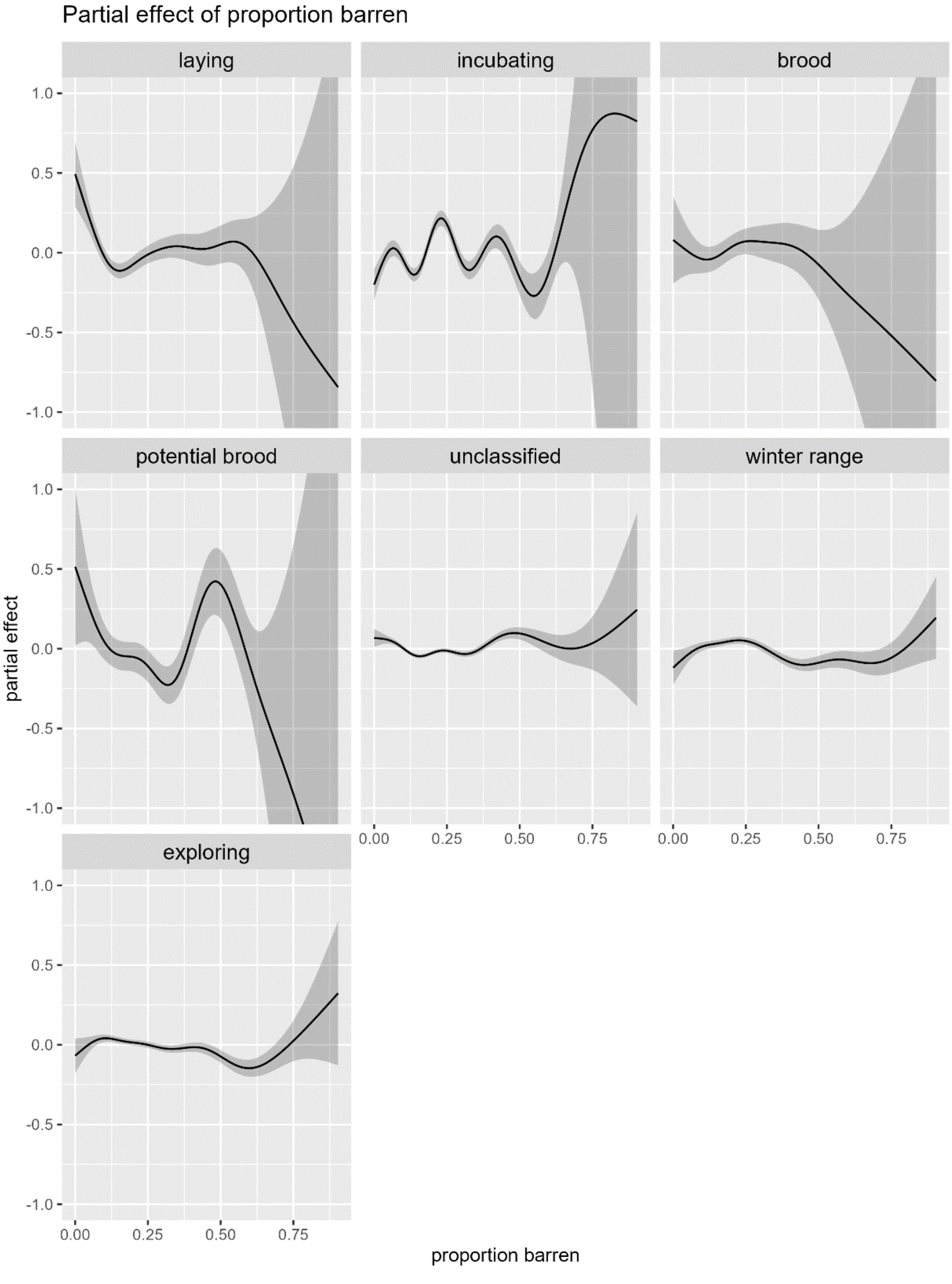


Figure 37. Estimates of smooth functions, s(x), of the effect of a predictor variable on female sage-grouse use-intensity for smooth-factor interactions with different levels of behavior-season types. The y axis represents the contribution of the smooth term to the linear predictor of log(use-intensity).

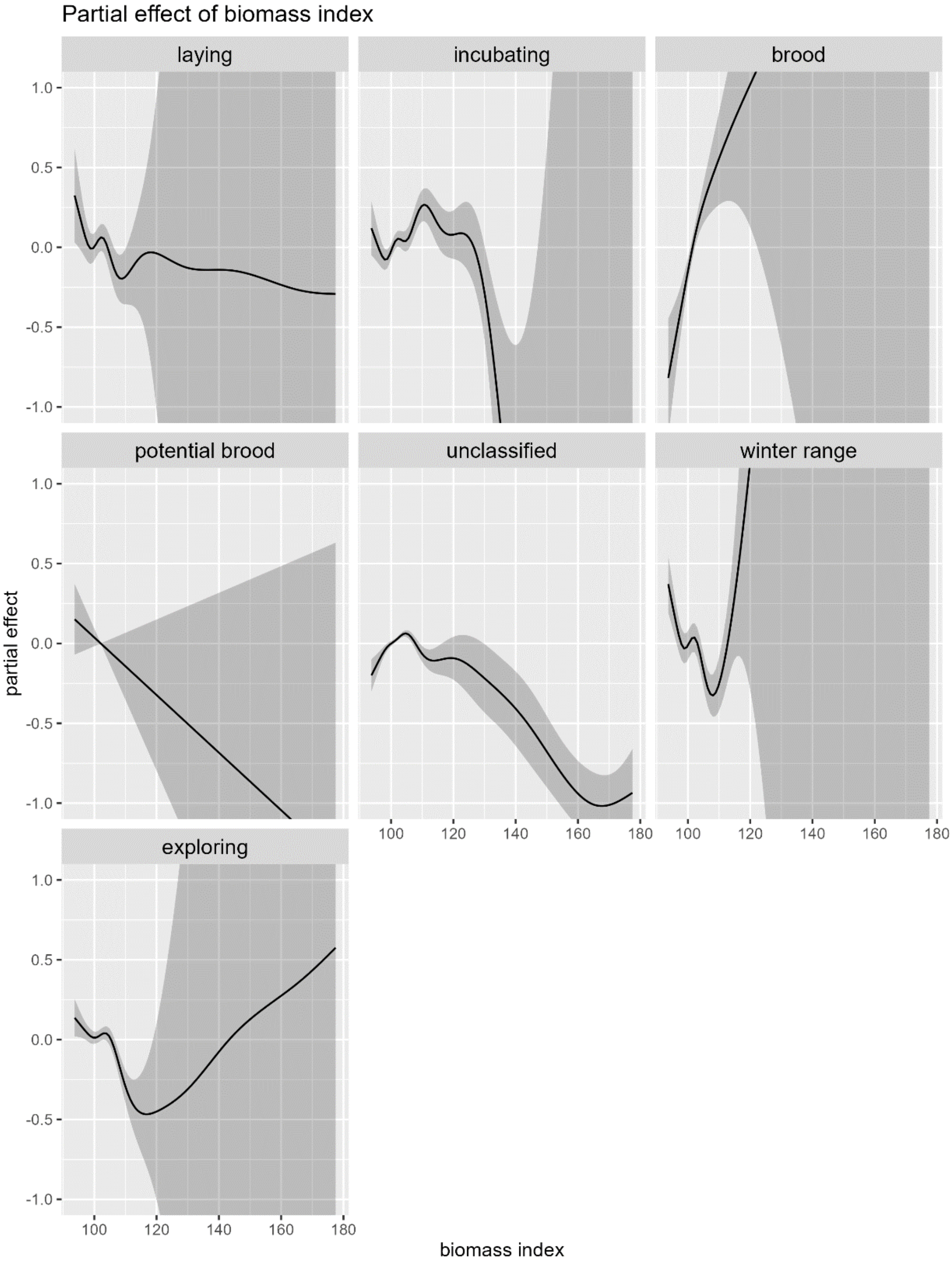


Figure 38. Estimates of smooth functions, s(x), of the effect of a predictor variable on female sage-grouse use-intensity for smooth-factor interactions with different levels of behavior-season types. The y axis represents the contribution of the smooth term to the linear predictor of log(use-intensity).

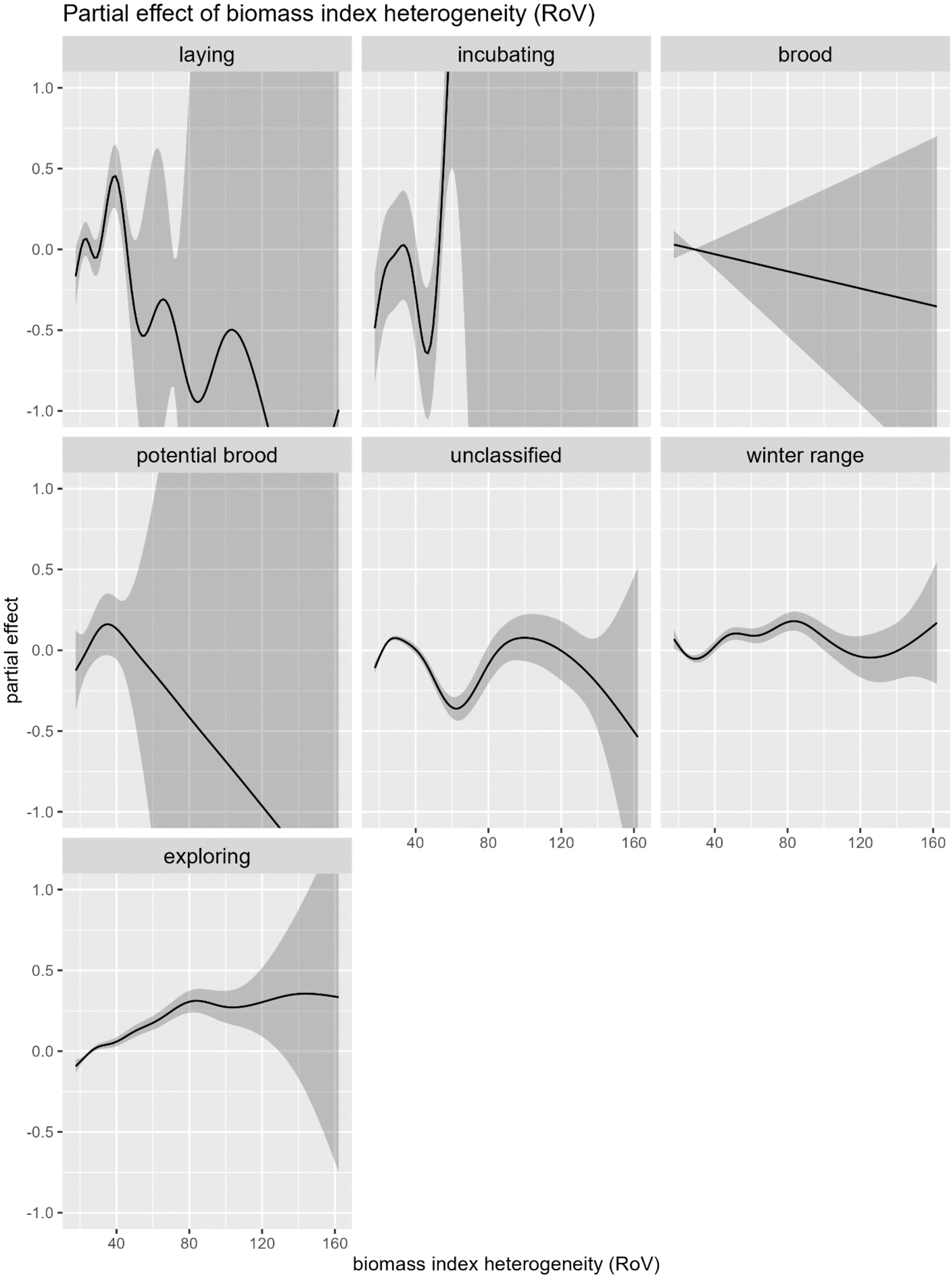


Figure 39. Estimates of smooth functions, s(x), of the effect of vegetation biomass RoV on female sage-grouse use-intensity for smooth-factor interactions with different levels of behavior-season types. The y axis represents the contribution of the smooth term to the linear predictor of log(use-intensity).

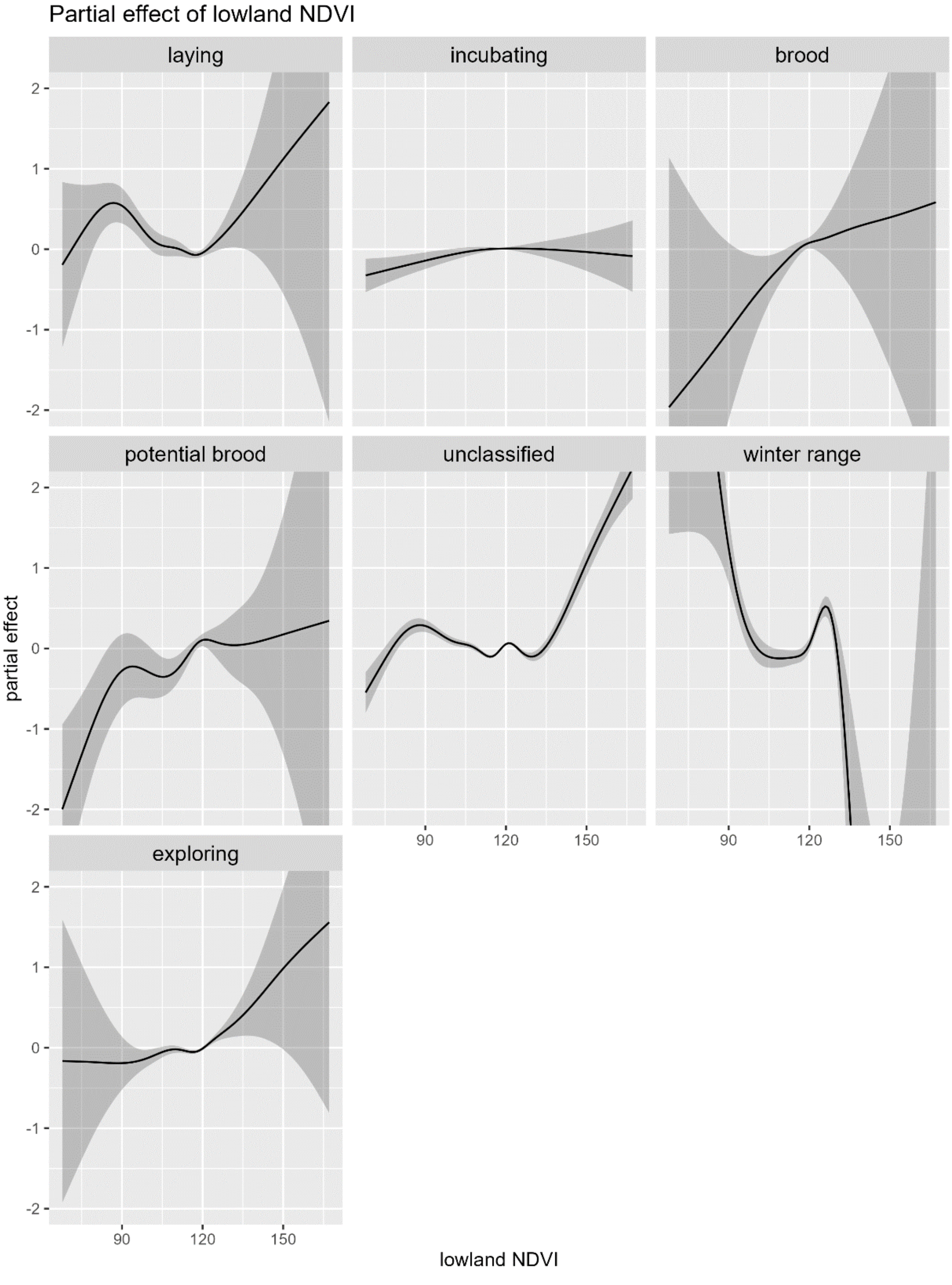


Figure 40. Estimates of smooth functions, s(x), of the effect of a predictor variable on female sage-grouse use-intensity for smooth-factor interactions with different levels of behavior-season types. The y axis represents the contribution of the smooth term to the linear predictor of log(use-intensity).

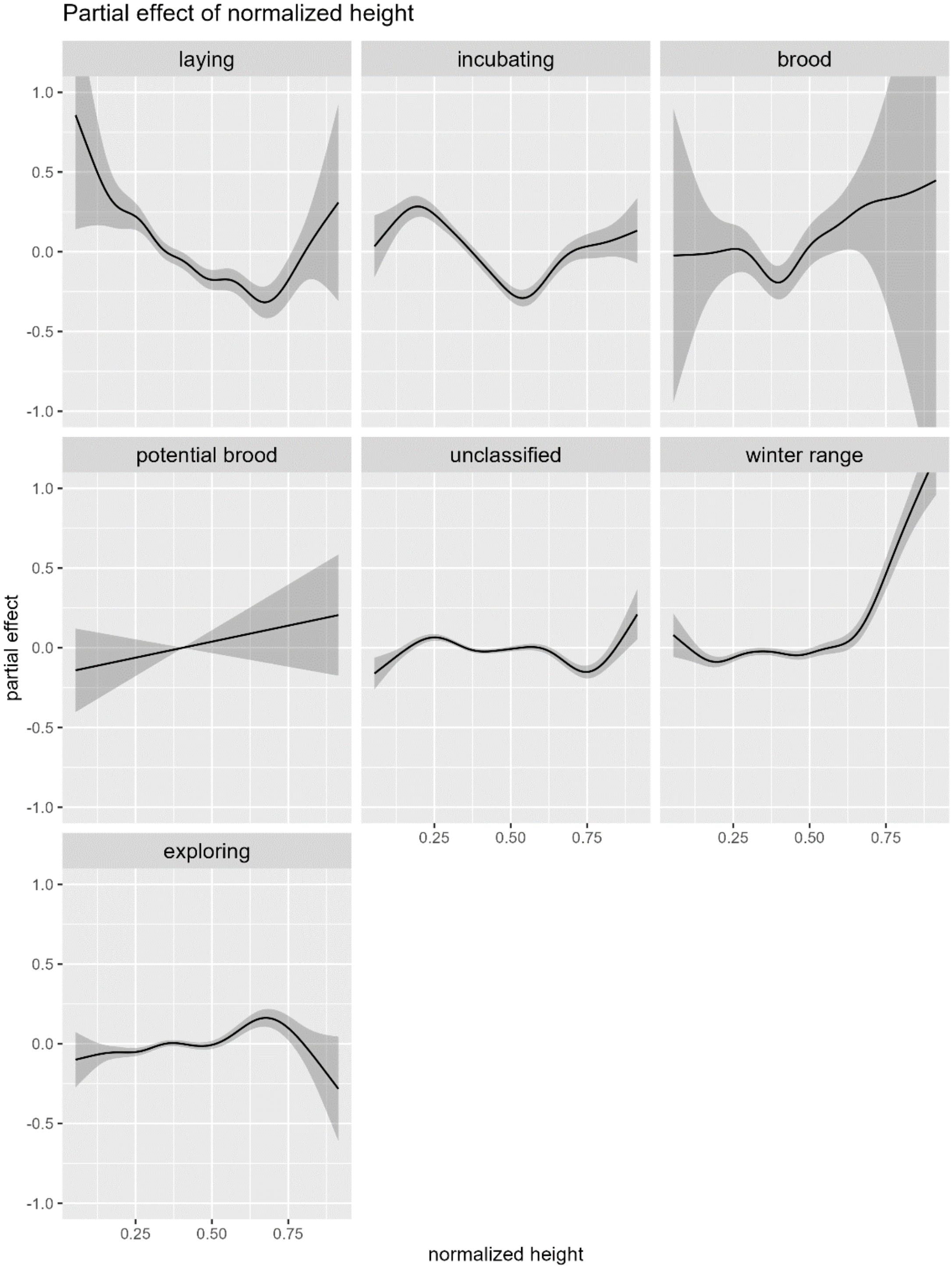


Figure 41. Estimates of smooth functions, s(x), of the effect of a predictor variable on female sage-grouse use-intensity for smooth-factor interactions with different levels of behavior-season types. The y axis represents the contribution of the smooth term to the linear predictor of log(use-intensity).

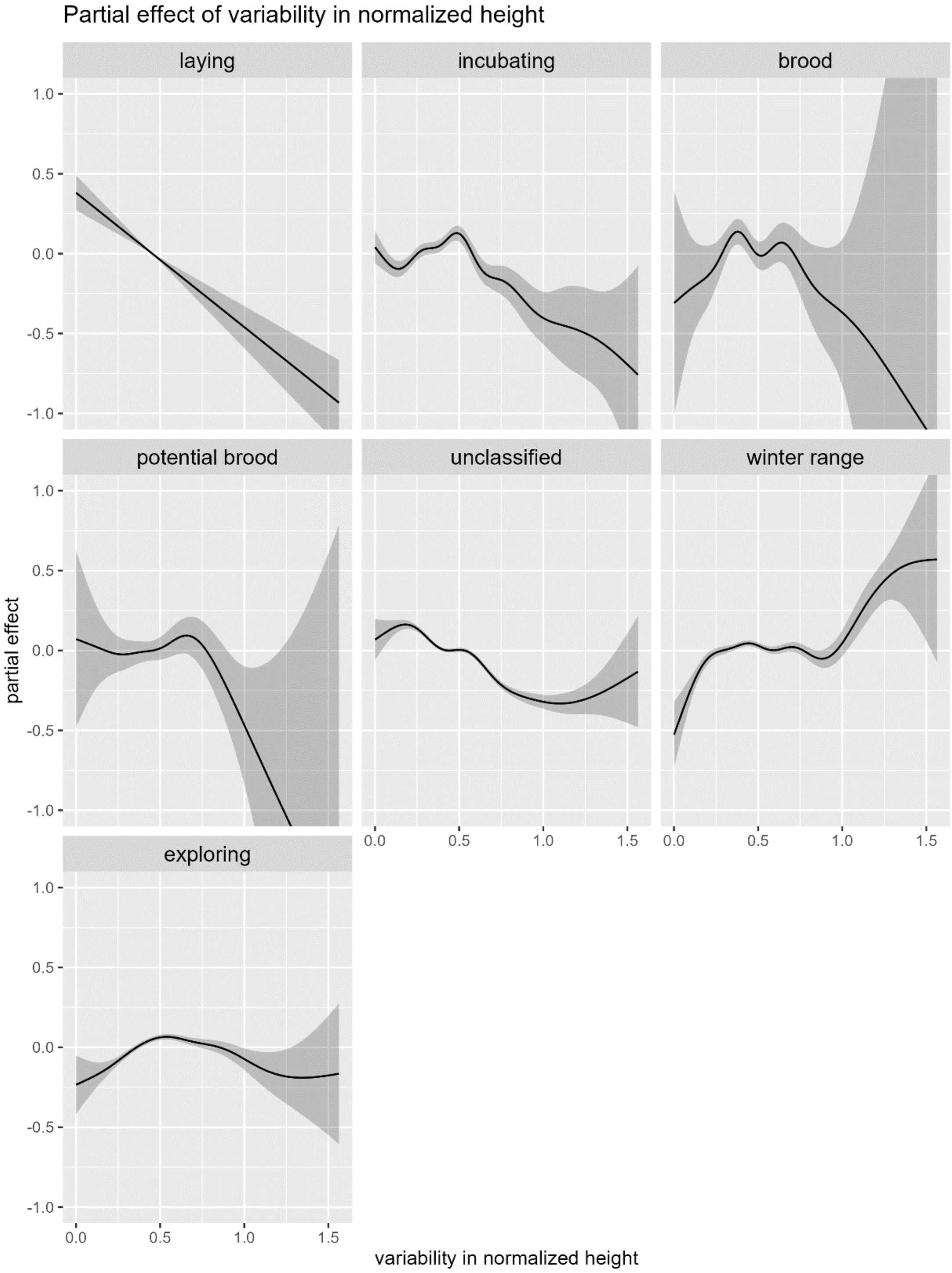


Figure 42. Estimates of smooth functions, s(x), of the effect of normalized height coefficient of variation on female sage-grouse use-intensity for smooth-factor interactions with different levels of behavior-season types. The y axis represents the contribution of the smooth term to the linear predictor of log(use-intensity).

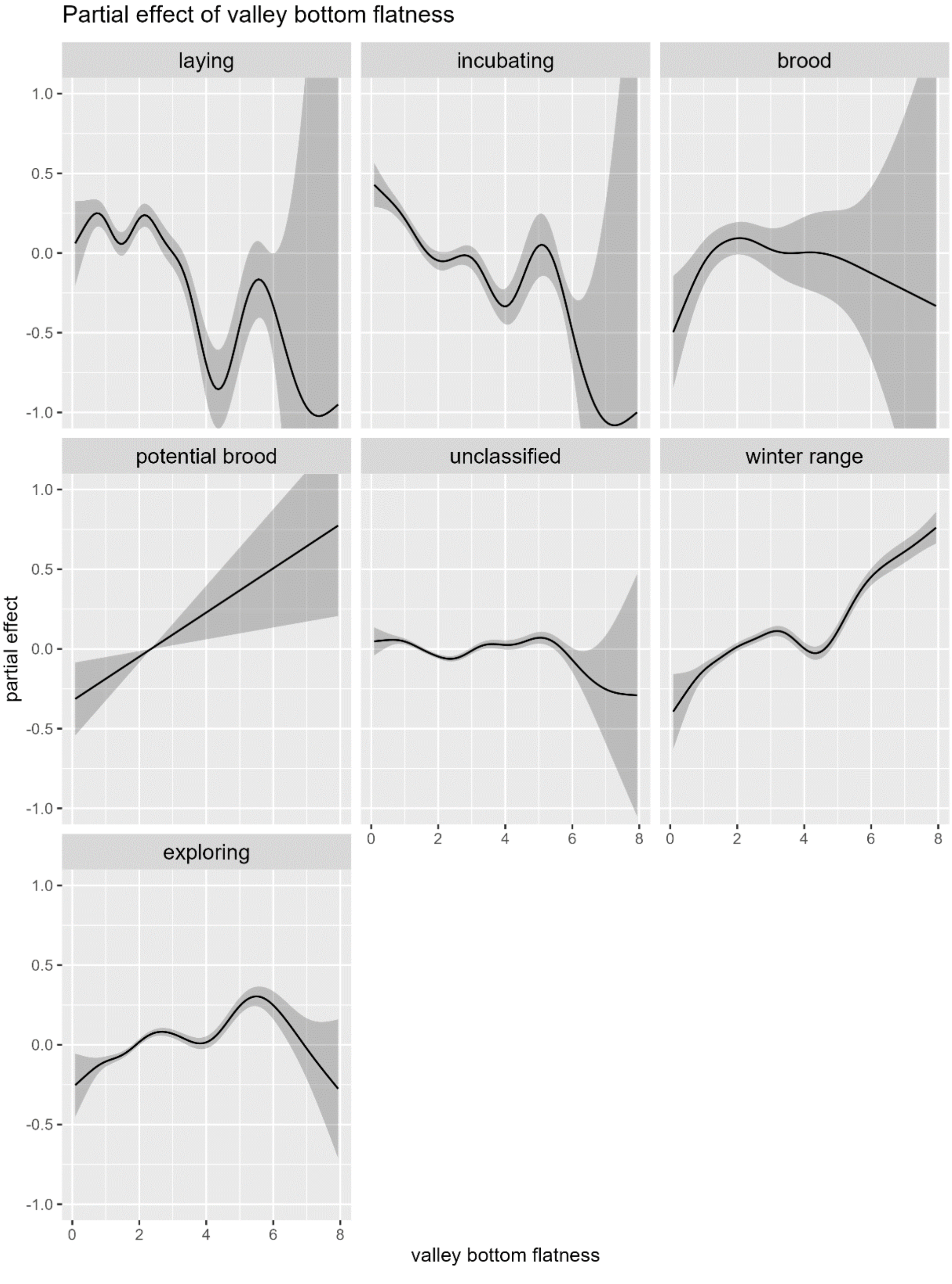


Figure 43. Estimates of smooth functions, s(x), of the effect of MultiResolution valley bottom flatness on female sage-grouse use-intensity for smooth-factor interactions with different levels of behavior-season types. The y axis represents the contribution of the smooth term to the linear predictor of log(use-intensity).

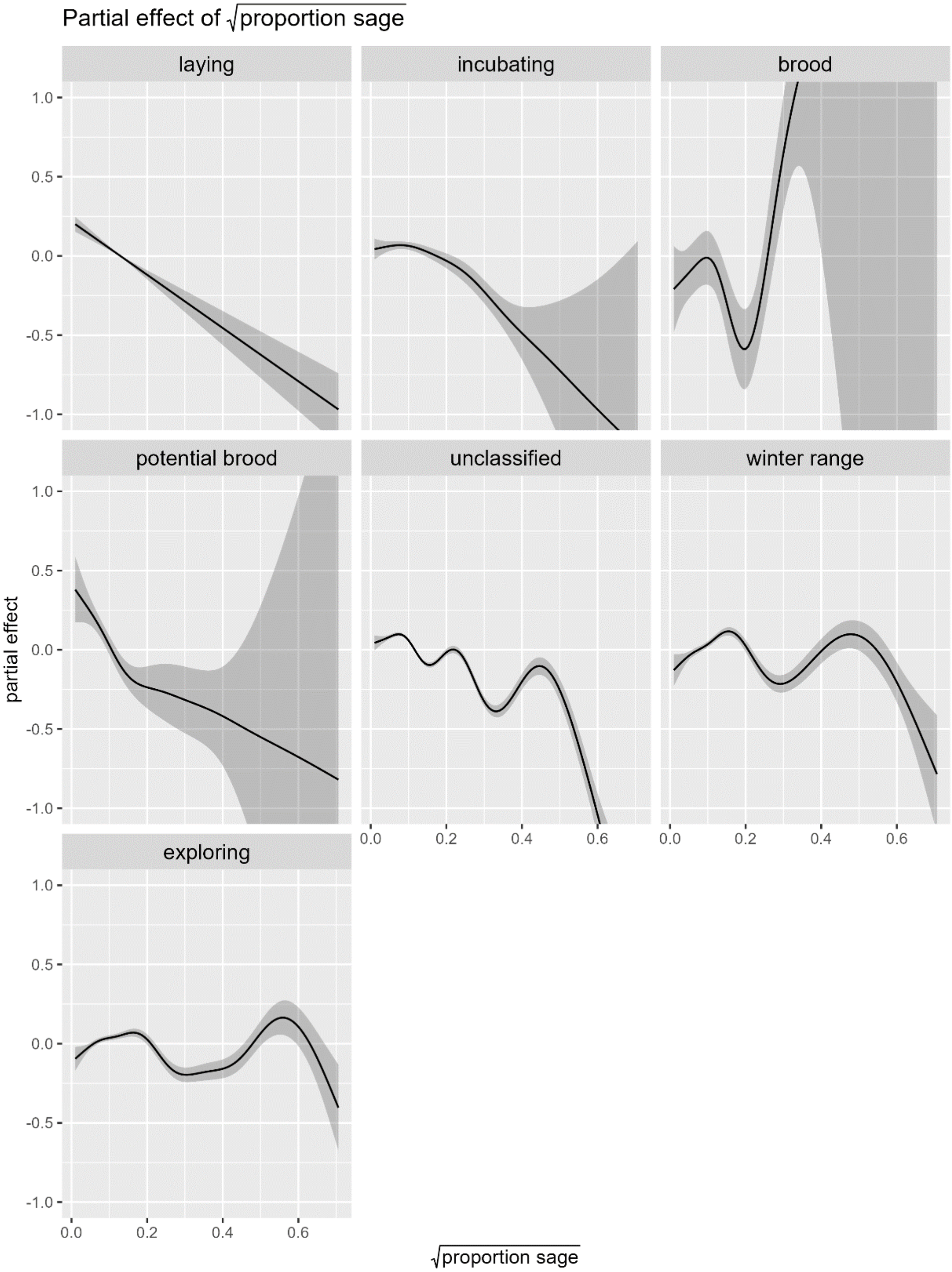


Figure 44. Estimates of smooth functions, s(x), of the effect of fine-grained sage on female sage-grouse use-intensity for smooth-factor interactions with different levels of behavior-season types. The y axis represents the contribution of the smooth term to the linear predictor of log(use-intensity).

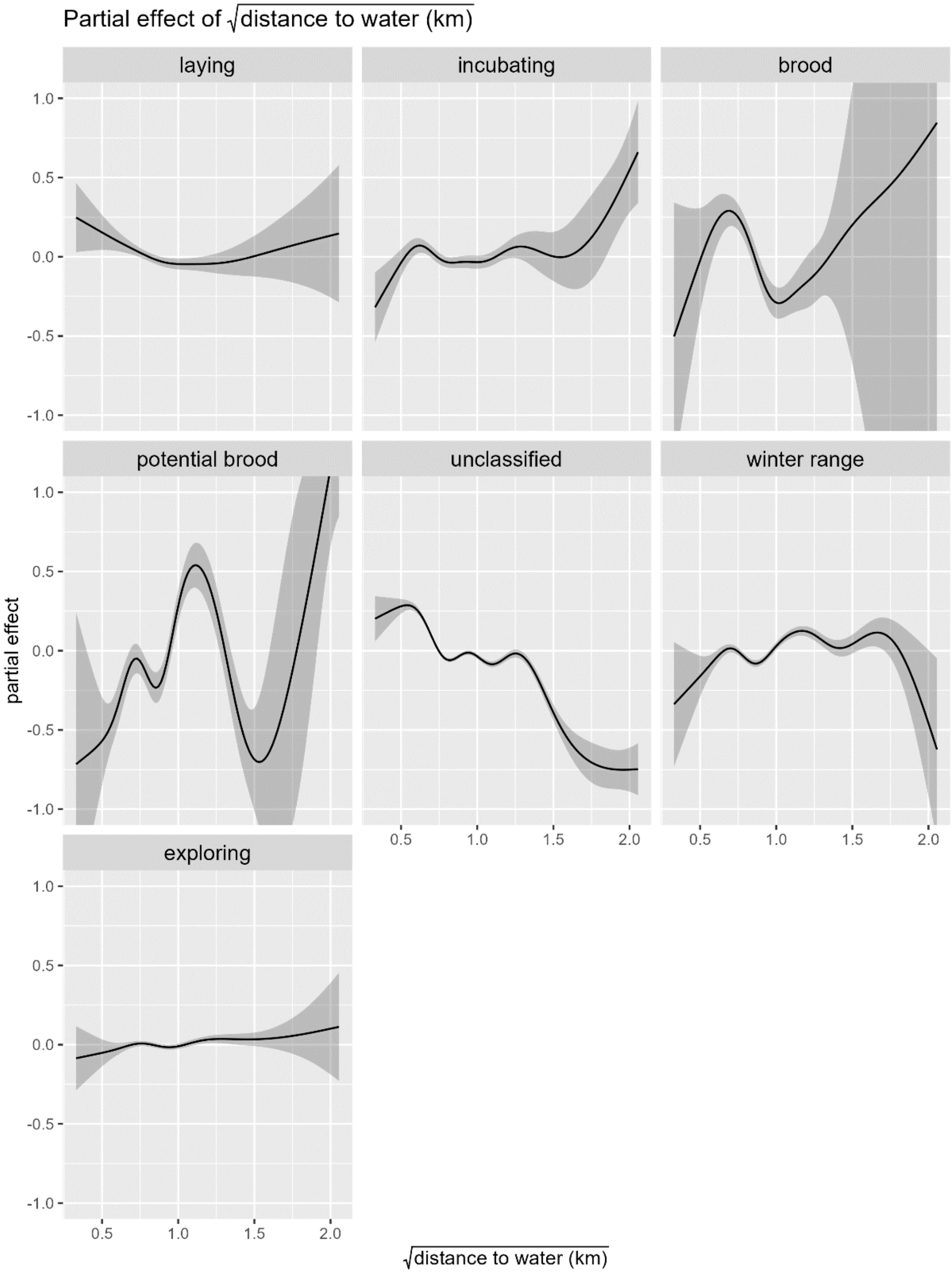


Figure 45. Estimates of smooth functions, s(x), of the effect of a predictor variable on female sage-grouse use-intensity for smooth-factor interactions with different levels of behavior-season types. The y axis represents the contribution of the smooth term to the linear predictor of log(use-intensity).

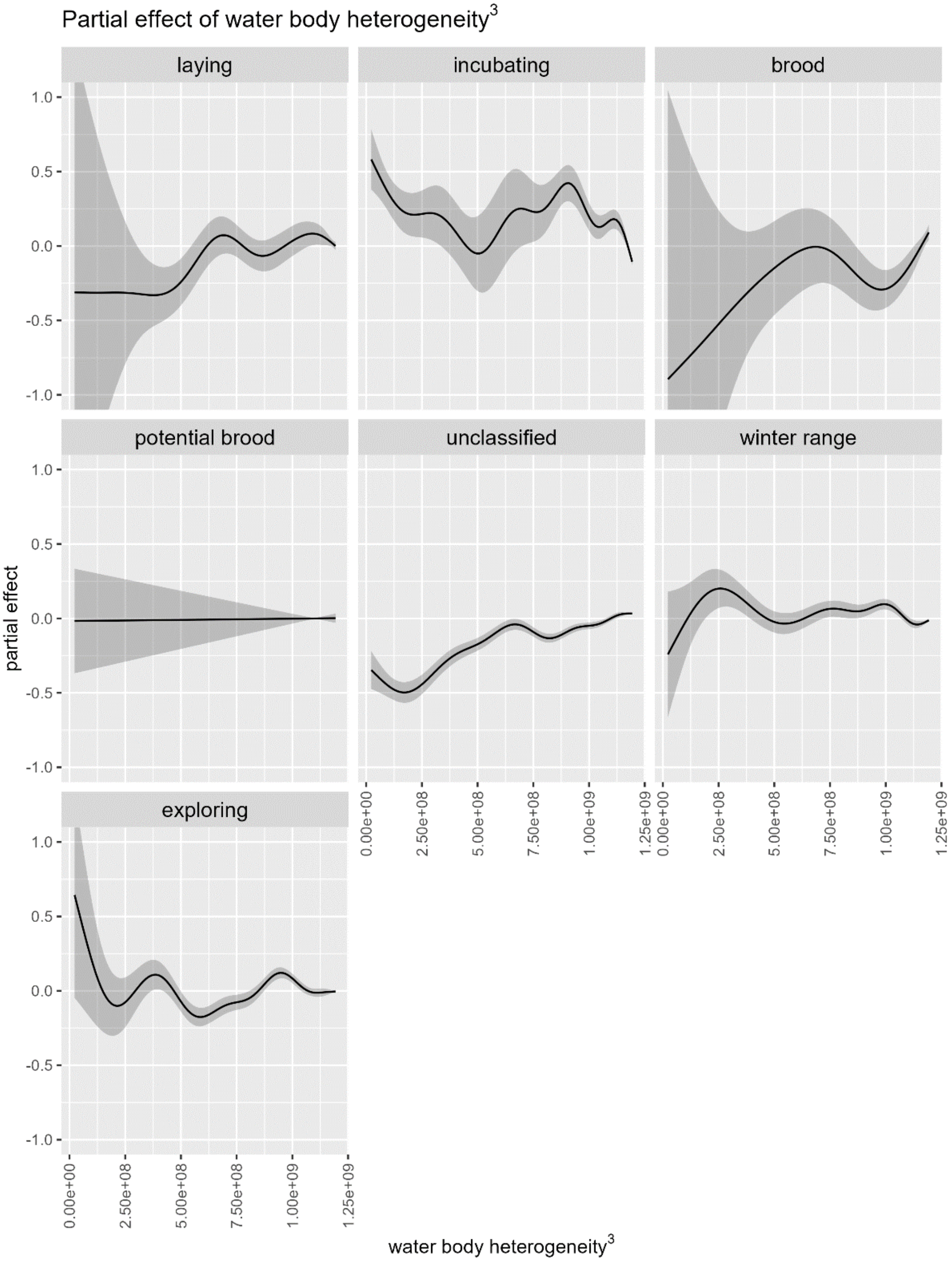


Figure 46. Estimates of smooth functions, s(x), of the effect of water body presence radius of variance (RoV) on female sage-grouse use-intensity for smooth-factor interactions with different levels of behavior-season types. The y axis represents the contribution of the smooth term to the linear predictor of log(use-intensity).

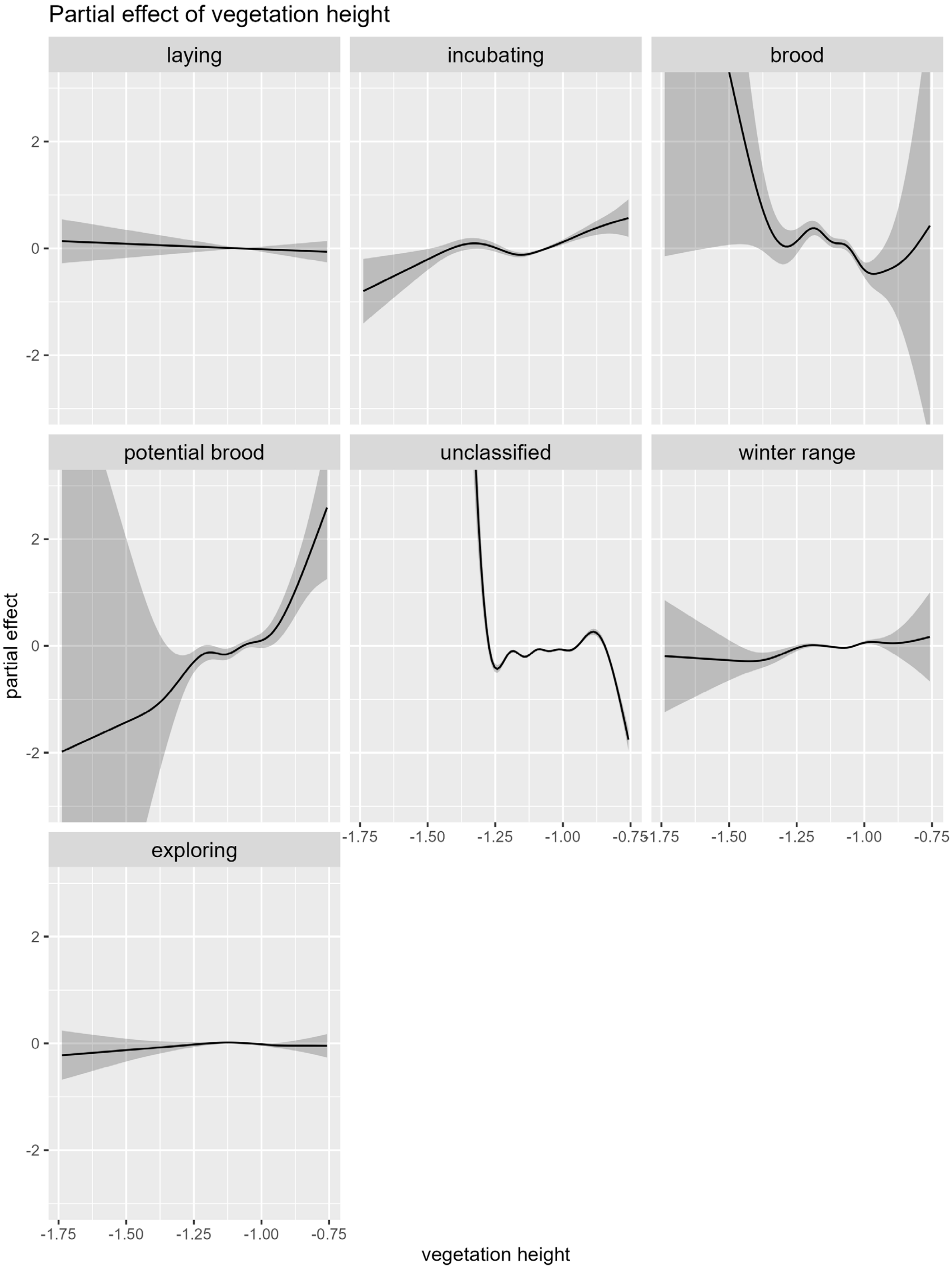


Figure 47. Estimates of smooth functions, s(x), of the effect of a predictor variable on female sage-grouse use-intensity for smooth-factor interactions with different levels of behavior-season types. The y axis represents the contribution of the smooth term to the linear predictor of log(use-intensity).

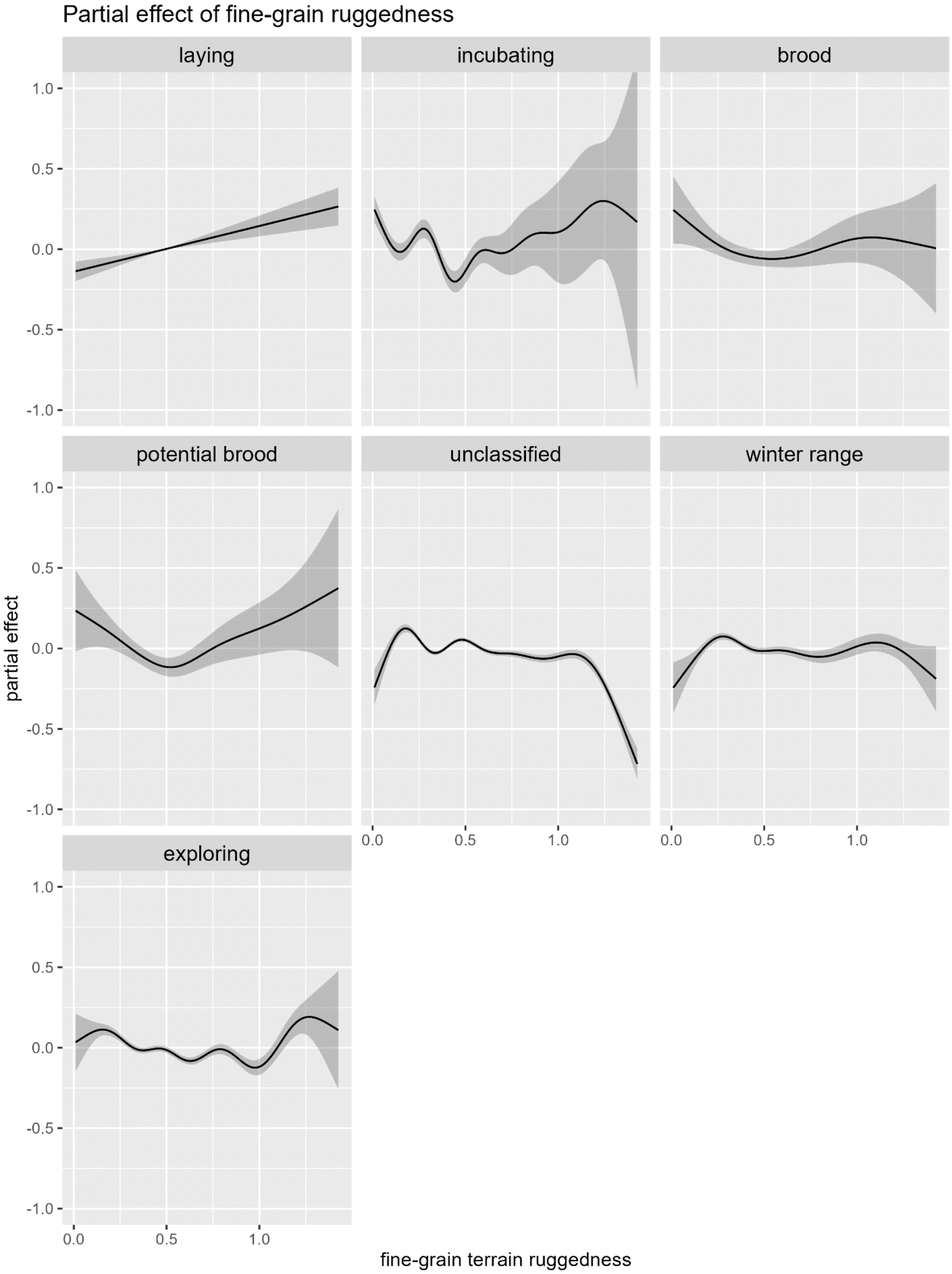


Figure 48. Estimates of smooth functions, s(x), of the effect of LiDAR vector ruggedness measure on female sage-grouse use-intensity for smooth-factor interactions with different levels of behavior-season types. The y axis represents the contribution of the smooth term to the linear predictor of log(use-intensity).

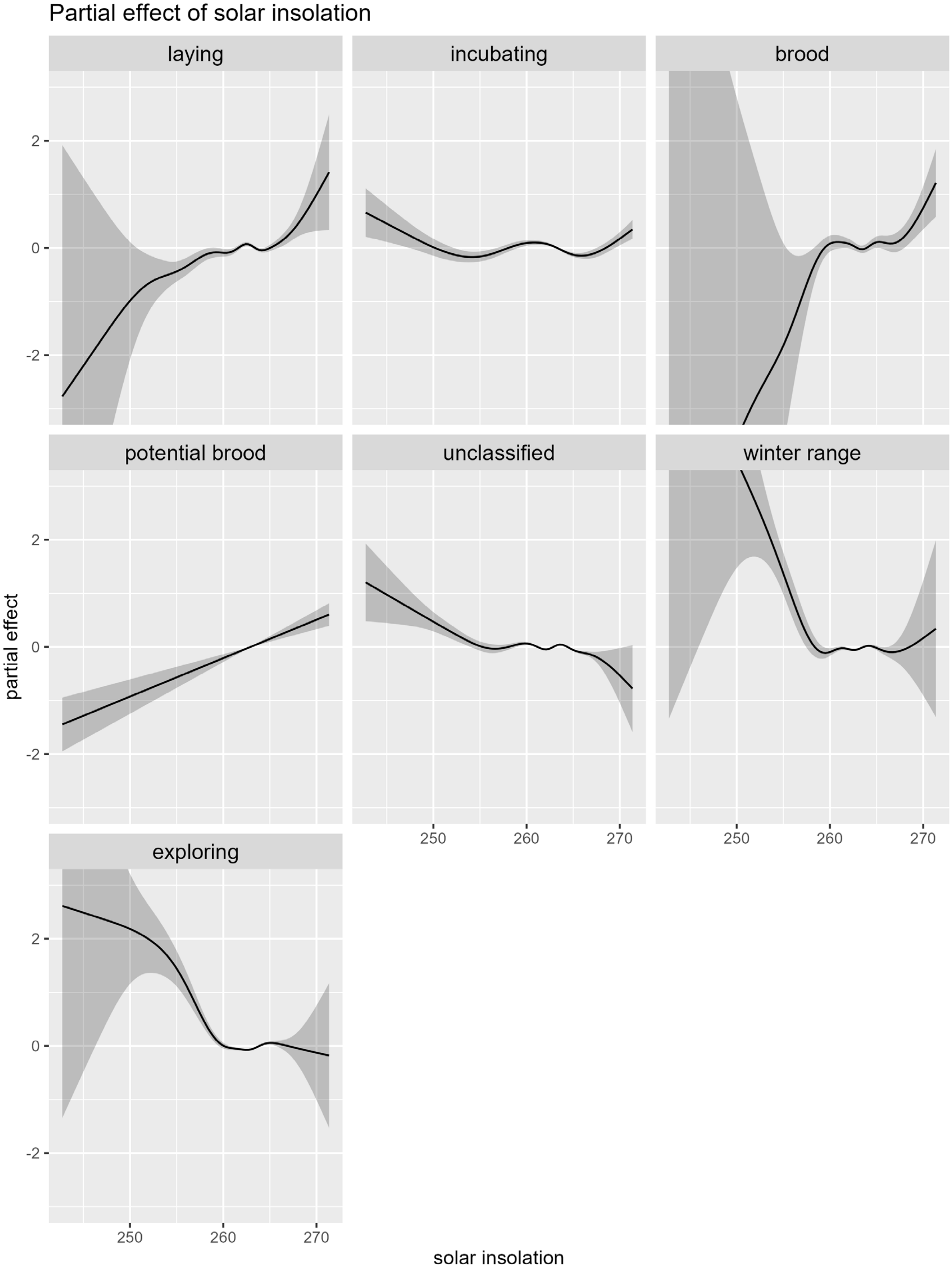


Figure 49. Estimates of smooth functions, s(x), of the effect of a predictor variable on female sage-grouse use-intensity for smooth-factor interactions with different levels of behavior-season types. The y axis represents the contribution of the smooth term to the linear predictor of log(use-intensity).

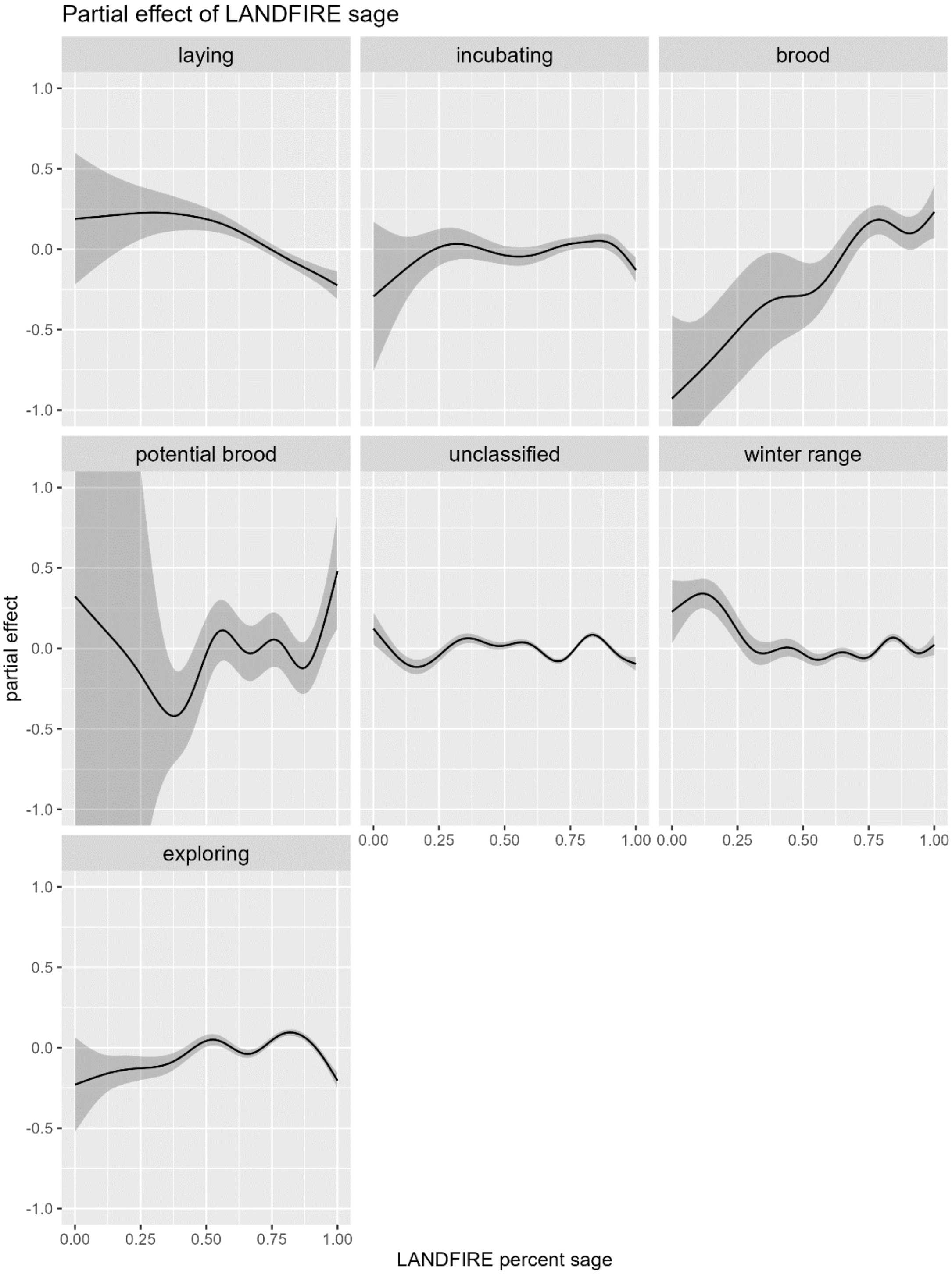


Figure 50. Estimates of smooth functions, s(x), of the effect of a predictor variable on female sage-grouse use-intensity for smooth-factor interactions with different levels of behavior-season types. The y axis represents the contribution of the smooth term to the linear predictor of log(use-intensity).

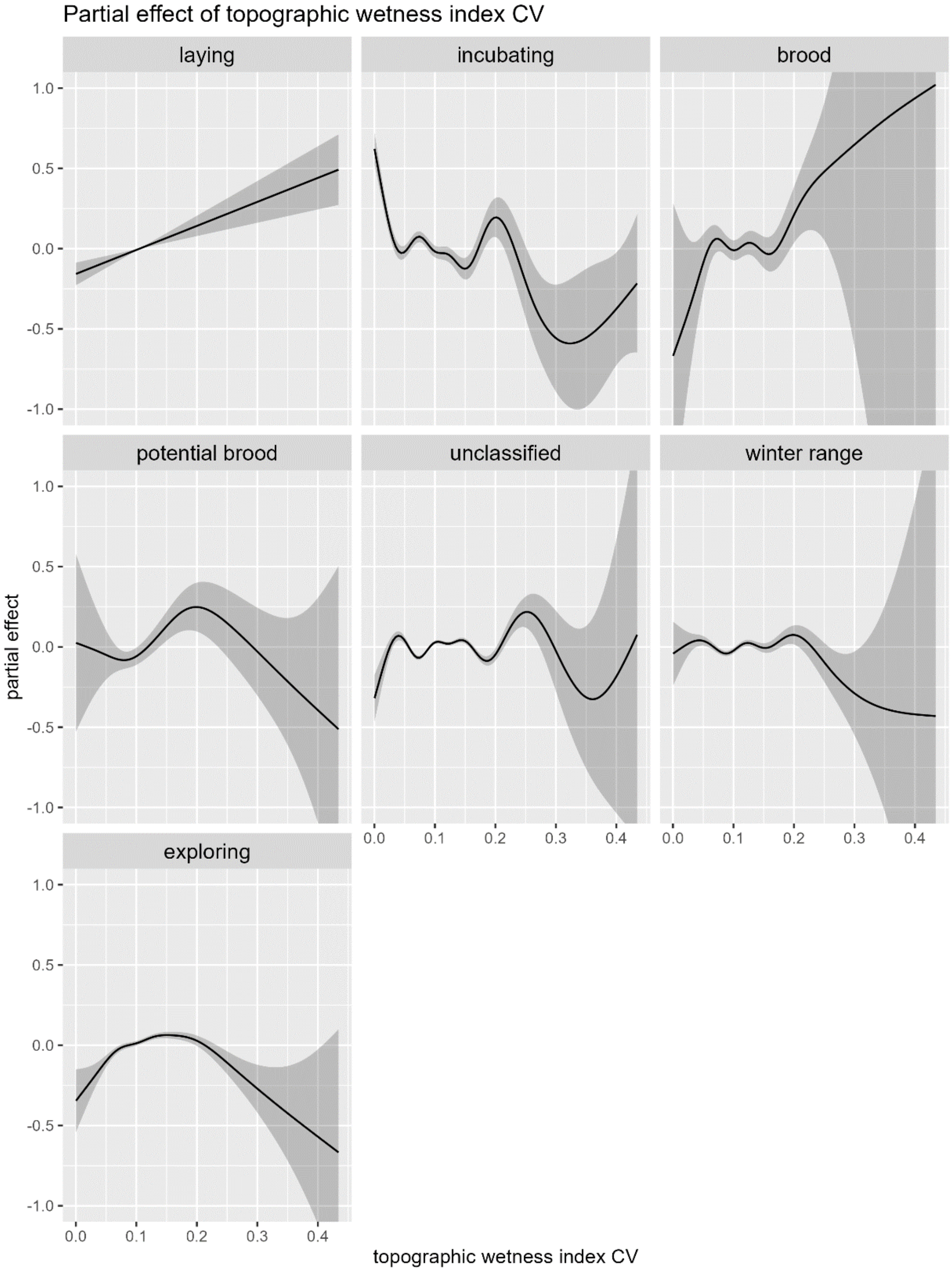


Figure 51. Estimates of smooth functions, s(x), of the effect of a predictor variable on female sage-grouse use-intensity for smooth-factor interactions with different levels of behavior-season types. The y axis represents the contribution of the smooth term to the linear predictor of log(use-intensity).

Table 15. List of covariate values used to generate behavior-specific conditional effects maps that we combined into a multi-behavior multiscale habitat map for female sage-grouse.

Behavior	**Area (m^2)**	**Tspan**	**Hull Revisits**	**Female Age (days)**	**Daylength**
laying	235824	48	8	1000	14.8
incubating	81430	54	4	1000	15.3
brood	411235	54.9	3	1000	16
potential brood	541327	46	11	1000	16
unclassified	727283	46	8	1000	14
exploring	2065277	47	1	1000	11.3
winter	1270735	46	8	1000	9.5

Table 16. Behavior specific statistics from our dataset and fitted generalized additive model of female sage-grouse use-intensity. Table illustrates prediction error and sample properties using the hold-out validation dataset randomly subset from our total dataset. Statistics are based on 25% of our total data so are only roughly representative of the complete dataset. However, qualitive comparisons are informative. For example, our brood behavior included the fewest individuals and our potential brood behavior had the fewest observations.

Behavior	**R2**	**RMSE**	**MAE**	**Mean_obs**	**Median_obs**	**SD_obs**	**Min_obs**	**Max_obs**	**females**	**n_obs**
laying	0.69	87.04	61.61	236.95	193.00	154.79	25	929	65	926
incubating	0.63	71.21	43.63	151.15	108.00	115.36	32	738	71	2128
brood	0.78	92.63	55.00	231.01	148.00	197.31	30	960	19	628
potential brood	0.83	93.67	69.90	338.10	306.00	223.95	45	1373	30	414
unclassified	0.60	149.06	103.49	287.39	212.00	235.42	4	1556	74	13423
winter range	0.78	85.32	52.71	201.89	134.00	181.09	6	1415	43	4806
exploring	0.39	58.42	35.37	89.33	70.00	74.53	4	970	68	5352

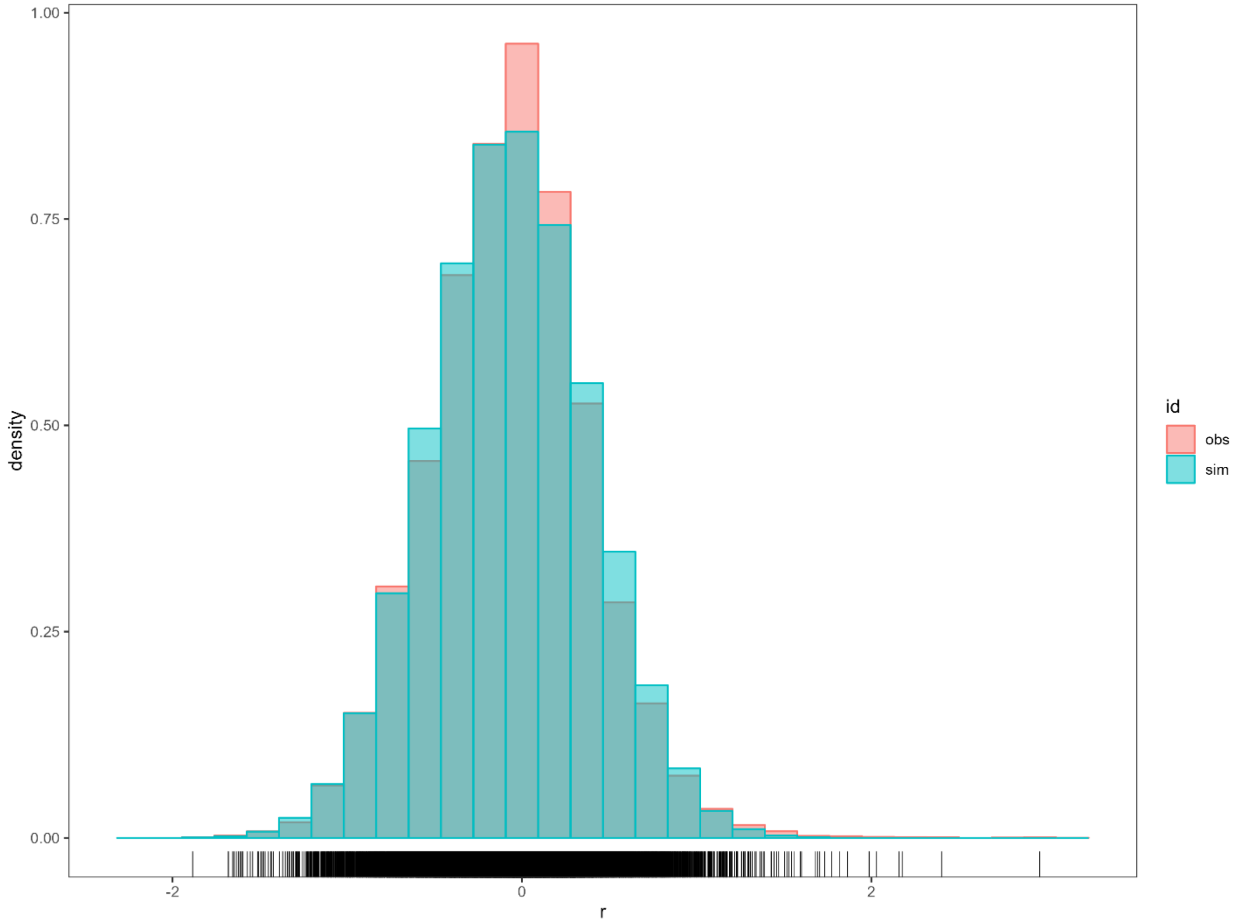


Figure 52. Model diagnostic plot comparing the distribution of observed residuals to those simulated from our fitted generalized additive model of female sage-grouse use-intensity.

Figure 53. Model diagnostic plot from our fitted generalized additive model of female sage-grouse use-intensity.

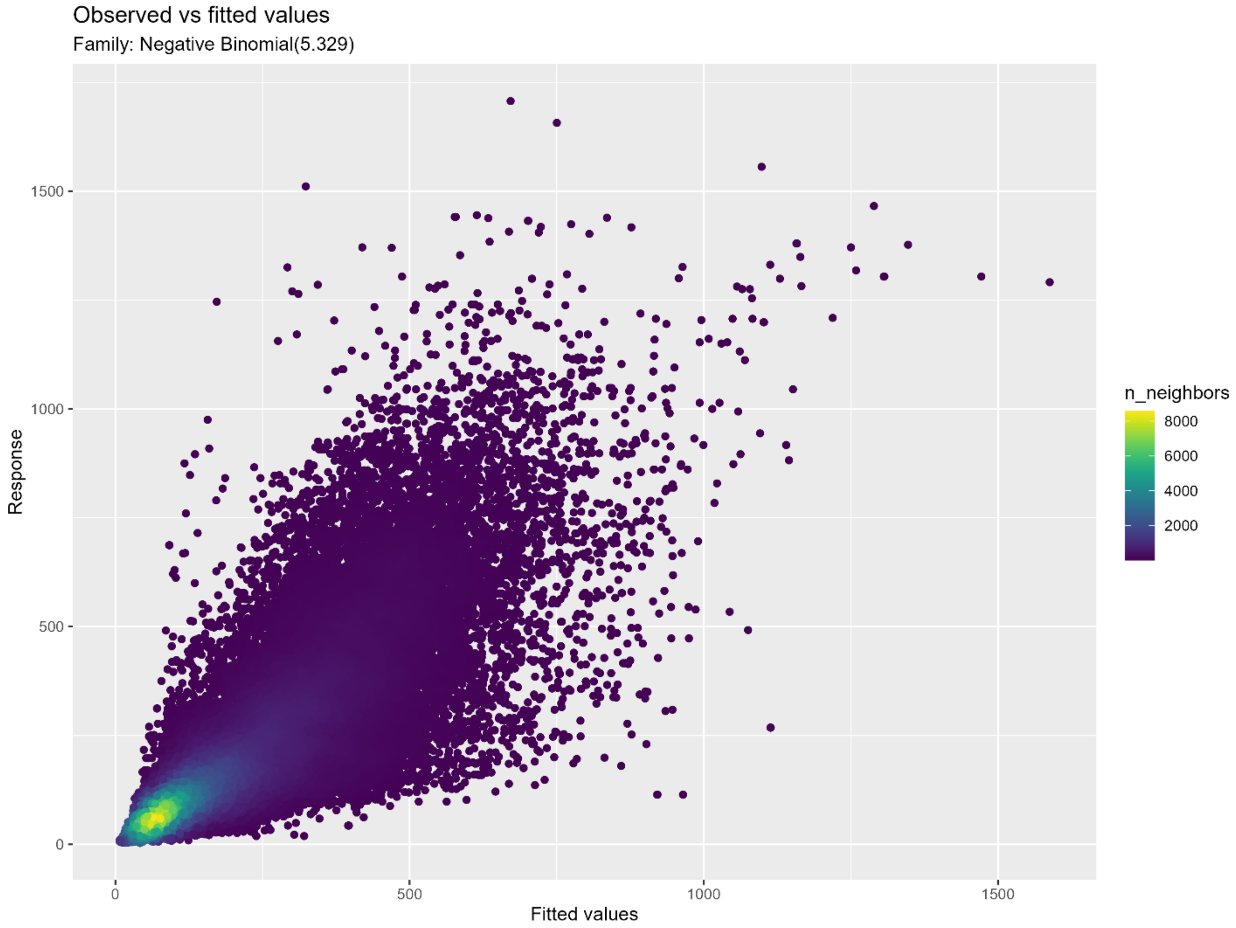


Figure 54. Indication of how predicted use-intensity corresponds to observed use-intensity for our generalized additive model of female sage-grouse use-intensity.

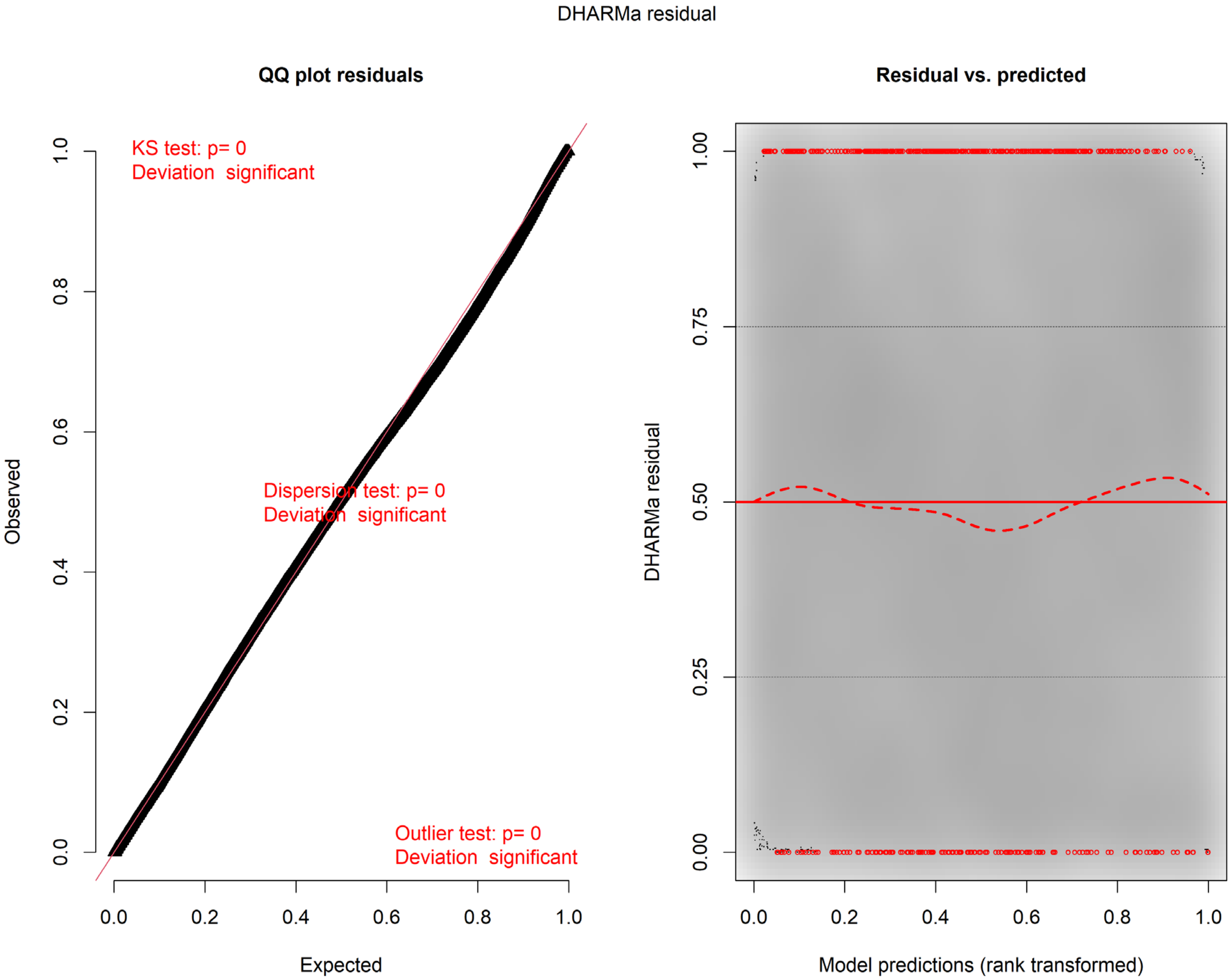


Figure 55. Model diagnostic plot of scaled residuals from our generalized additive model of female sage-grouse use-intensity. Gray shading indicates distribution of residuals in the residual vs. predicted plot.

APPENDIX G

SUPPLEMENTARY MATERIAL FOR NEST SURVIVAL CHAPTER

Table 17. Description of all predictor variables used for sage-grouse daily nest survival nesting ecology research.

Raw Predictor	Computed Summary Statistic	Transform	Ecological Relevance
Movement Properties			
hull eccentricity	index to the elongation of a hull	1	index to directional movement
hull enclosed points	number of points accrued in a hull footprint	1	use-intensity of home range
hull use-intensity	hull enclosed points / hull area	1	areal density of points in home range
net displacement from first nest	hull-mean displacement from first nest	1	indicates proximity to initial nesting area
Season and Time			
daily precipitation (PRISM)	mean of values at nearest neighbor points	1	PRISM estimates of daily mean precipitation
daily temperature (PRISM)	mean of values at nearest neighbor points	1	PRISM estimates of daily mean temperature
female age category	a factor indicating female age	1	nest survival may vary due to female experience
female age discretized	age category of female	1	female may gain experience with age which may increase nest survival
female age in days	age at hull parent point	1	age at hull parent point
length of day	mean of values at nearest neighbor points	1	the time interval between sunrise and sunset
nest age	age of nest in days since incubation began	1	nest survival may change as the exposure period lengthens
nest number	sequence of nesting attempts for the year (1 - 3)	1	first, second, or third nesting attempts may have different survival
Terrain and Water			
LiDAR vector ruggedness measure (VRM)	hull-mean of 30-m patch zonal means	1	index of surface roughness in topography (LiDAR grain size)
midslope position	hull zonal mean	1	has a topoclimatic association with warmer zones of slopes
midslope position	hull-mean of 30-m patch zonal means	1	has a topoclimatic association with warmer zones of slopes

midslope position	hull-mean of 100-m patch zonal means	1	has a topoclimatic association with warmer zones of slopes
morphometric protection index	hull zonal mean	1	index of how topographically protected a unit of land is (e.g., from wind)
morphometric protection index	hull-mean of 30-m patch zonal means	1	index of how topographically protected a unit of land is (e.g., from wind)
morphometric protection index	hull-mean of 100-m patch zonal means	1	index of how topographically protected a unit of land is (e.g., from wind)
multi-resolution valley bottom flatness	hull zonal mean	1	index of openness and flatness of valley bottoms
multi-resolution valley bottom flatness	hull zonal mean	1	index of openness and flatness of valley bottoms
multi-resolution valley bottom flatness	hull-mean of 30-m patch zonal means	1	index of openness and flatness of valley bottoms
multi-resolution valley bottom flatness	hull-mean of 30-m patch zonal means	1	index of openness and flatness of valley bottoms
multi-resolution valley bottom flatness	hull-mean of 100-m patch zonal means	1	index of openness and flatness of valley bottoms
multi-resolution valley bottom flatness	hull-mean of 100-m patch zonal means	1	index of openness and flatness of valley bottoms
NED vector ruggedness measure (VRM)	hull zonal mean	logit	indicates terrain ruggedness of a unit of land
NED vector ruggedness measure (VRM)	hull-mean of 30-m patch zonal means	logit	index of surface roughness in topography (NED grain size)
NED vector ruggedness measure (VRM)	hull-mean of 100-m patch zonal means	logit	index of surface roughness in topography (NED grain size)
NED vector ruggedness measure (VRM)	hull-CV of 30-m patch zonal means	1	local variability of surface roughness in topography (NED grain size)
normalized height	hull zonal mean	1	topographic height normalized by heights in the immediate vicinity
normalized height	hull-mean of 30-m patch zonal means	1	topographic height normalized by heights in the immediate vicinity

normalized height	hull-CV of 30-m patch zonal means	1	local variability of the land surface normalized by surrounding area
normalized height	hull-mean of 100-m patch zonal means	1	topographic height normalized by heights in the immediate vicinity
proximity to flow channels (km)	hull zonal mean	1	distance to channels that provide loafing sites, puddles, mesic areas
proximity to flow channels (km)	hull-mean of 30-m patch zonal means	1	distance to channels that provide loafing sites, puddles, mesic areas
proximity to flow channels (km)	hull-mean of 100-m patch zonal means	1	distance to channels that provide loafing sites, puddles, mesic areas
proximity to water bodies	hull zonal mean	1	distance to water bodies near where grazing may be more intensive
proximity to water bodies	hull-mean of 30-m patch zonal means	sqrt	distance to water bodies near where grazing may be more intensive
proximity to water bodies	hull-mean of 100-m patch zonal means	1	distance to water bodies near where grazing may be more intensive
radius of variance (RoV) of LiDAR VRM	hull-mean of 30-m patch zonal means	1	local heterogeneity of surface roughness in topography (LiDAR grain size)
radius of variance (RoV) to water bodies	hull-mean of 100-m patch zonal means	1	local heterogeneity of distance to water bodies
slope height	hull zonal mean	1	height of a slope above flow channels
slope height	hull-mean of 30-m patch zonal means	1	height of a slope above flow channels
slope height	hull-CV of 30-m patch zonal means	1	local variability of slope heights above flow channels
slope height	hull-mean of 100-m patch zonal means	1	height of a slope above flow channels
solar insolation	hull zonal mean	1	how much solar flux a unit of land will receive based on topography
solar insolation	hull-mean of 30-m patch zonal means	1	how much solar flux a unit of land will receive based on topography
solar insolation	hull-mean of 100-m patch zonal means	1	how much solar flux a unit of land will receive based on topography

standardized height	hull zonal mean	1	absolute height weighted by normalized height
standardized height	hull-mean of 30-m patch zonal means	1	absolute height weighted by normalized height
standardized height	hull-CV of 30-m patch zonal means	1	local variability of absolute height weighted by normalized height
standardized height	hull-mean of 100-m patch zonal means	1	absolute height weighted by normalized height
topographic position index	hull zonal mean	1	indicates if a unit of land has a low, moderate, or high position
topographic position index	hull zonal mean	1	indicates if a unit of land has a low, moderate, or high position
topographic position index (multiscale)	hull-mean of 30-m patch zonal means	1	indicates if a unit of land has a low, moderate, or high position
topographic position index (multiscale)	hull-mean of 100-m patch zonal means	1	indicates if a unit of land has a low, moderate, or high position
topographic wetness index	hull zonal mean	1	index of the expected or potential soil wetness based on topography
topographic wetness index	hull-mean of 30-m patch zonal means	1	index of the expected or potential soil wetness based on topography
topographic wetness index	hull-CV of 30-m patch zonal means	1	local variability of expected or potential soil wetness based on topography
topographic wetness index	hull-mean of 100-m patch zonal means	1	index of the expected or potential soil wetness based on topography
valley depth	hull zonal mean	1	indicates how recessed a unit of land is on the landscape
valley depth	hull-mean of 30-m patch zonal means	1	indicates how recessed a unit of land is on the landscape
valley depth	hull-CV of 30-m patch zonal means	1	local variability of how topographically recessed a unit of land is
valley depth	hull-mean of 30-m patch zonal means	1	indicates how recessed a unit of land is on the landscape
wind exposition	hull zonal mean	1	indicates how exposed to wind a unit of land is

wind exposition	hull-mean of 30-m patch zonal means	1	indicates how exposed to wind a unit of land is
wind exposition	hull-CV of 30-m patch zonal means	1	local variability of how exposed to wind a unit of land is
wind exposition	hull-mean of 100-m patch zonal means	1	indicates how exposed to wind a unit of land is
Vegetation			
barren	hull zonal mean	1	bare ground cover estimates
barren	hull zonal CV	1	local variability of bare ground cover estimates
barren	hull-mean of 100-m patch zonal means	1	bare ground cover estimates
barren	hull-CV of 100-m patch zonal means	1	local variability of bare ground cover estimates
barren	hull-mean of 30-m patch zonal means	1	bare ground cover estimates
LANDFIRE sage	hull-mean of 30-m patch zonal means	1	coarse-scale sagebrush cover type estimates
LANDFIRE sage	hull-CV of 30-m patch zonal means	1	local variability of coarse-scale sagebrush cover type estimates
LANDFIRE sage	hull-mean of 100-m patch zonal means	1	coarse-scale sagebrush cover type estimates
LANDFIRE sage	hull zonal mean	1	coarse-scale sagebrush cover type estimates
lowland NDVI	hull zonal mean	1	topographically low-lying vegetation index
lowland NDVI	hull zonal CV	1	local variability of topographically low-lying vegetation index
lowland NDVI	hull-mean of 100-m patch zonal means	1	topographically low-lying vegetation index
lowland NDVI	hull-mean of 30-m patch zonal means	1	topographically low-lying vegetation index
lowland NDVI	hull-CV of 30-m patch zonal means	1	local variability of topographically low-lying vegetation index
medium shrub	hull zonal mean	1	medium stature shrub cover estimates

medium shrub	hull zonal CV	1	local variability of medium stature shrub cover estimates
medium shrub	hull-mean of 30-m patch zonal means	1	medium stature shrub cover estimates
medium shrub	hull-mean of 100-m patch zonal means	1	medium stature shrub cover estimates
radius of variance (RoV) of veg biomass	hull-mean of 30-m patch zonal means	1	vegetation index that incorporates digital surface model data
radius of variance (RoV) of veg biomass	hull-mean of 100-m patch zonal means	1	vegetation index that incorporates digital surface model data
sage	hull zonal mean	1	fine-scale sagebrush cover type estimates
sage	hull zonal CV	1	local variability of fine-scale sagebrush cover
sage	hull-mean of 30-m patch zonal means	sqrt	fine-scale sagebrush cover type estimates
sage	hull-mean of 100-m patch zonal means	1	fine-scale sagebrush cover type estimates
sage	hull-mean of 30-m patch zonal means	1	fine-scale sagebrush cover type estimates
sage	hull-rCD of 30-m patch zonal means	1	local variability of fine-scale sagebrush cover
vegetation biomass	hull zonal mean	1	vegetation index that incorporates digital surface model data
vegetation biomass	hull-mean of 100-m patch zonal means	1	vegetation index that incorporates digital surface model data
vegetation biomass	hull-CV of 100-m patch zonal means	1	local variability of biomass index
vegetation biomass	hull-rCD of 100-m patch zonal means	1	heterogeneity of biomass index
vegetation biomass	hull-mean of 30-m patch zonal means	1	vegetation index that incorporates digital surface model data
vegetation biomass	hull-CV of 30-m patch zonal means	1	local variability of biomass index

vegetation biomass	hull-rCD of 30-m patch zonal means	1	heterogeneity of biomass index
vegetation height	hull zonal mean	1	index of the height of objects on the landscape, typically vegetation
vegetation height	hull-mean of 30-m patch zonal means	1	index of the height of objects on the landscape, typically vegetation
vegetation height	hull-mean of 100-m patch zonal means	1	index of the height of objects on the landscape, typically vegetation
vegetation height	hull-mean of 30-m patch zonal means	1	index of the height of objects on the landscape, typically vegetation
vegetation height	hull-mean of 30-m patch zonal means	1	index of the height of objects on the landscape, typically vegetation

Table 18. List of predictor variables and smooth-term results from fitted generalized additive model evaluating how distance from first nest for a female sage-grouse varies as a function of study time and other covariates. The estimated degrees of freedom (edf) indicate the degree of non-linearity of the model terms with a value around 1 indicating a linear relationship with distance from first nest and larger values indicating progressively more ‘wiggly’ relationships.

GAM Term	**edf**	**Ref.df**	**F**	**p-value**
s(study time)	137.06	144.00	1195.99	0.00
s(daily precipitation)	0.46	9.00	0.04	0.37
s(number of enclosed points)	7.30	9.00	13733.69	0.00
s(hull area)	150.07	164.00	394.55	0.00
s(sage)	86.02	94.00	451.66	0.00
s(barren)	80.60	94.00	335.34	0.00
s(vegetation biomass)	65.06	69.00	223.12	0.00
s(normalized height)	42.27	44.00	243.80	0.00
s(individual ID)	72.81	73.00	867.86	0.00

Figure 56. Scatterplot illustrating the relationship between study time and distance from first nest for female sage-grouse. Each point represents an observation of a short-term home range for an individual. Observation histories span up to 4 years. The blue line represents a generalized additive model fitted to the time series of distance from first nest and study time.

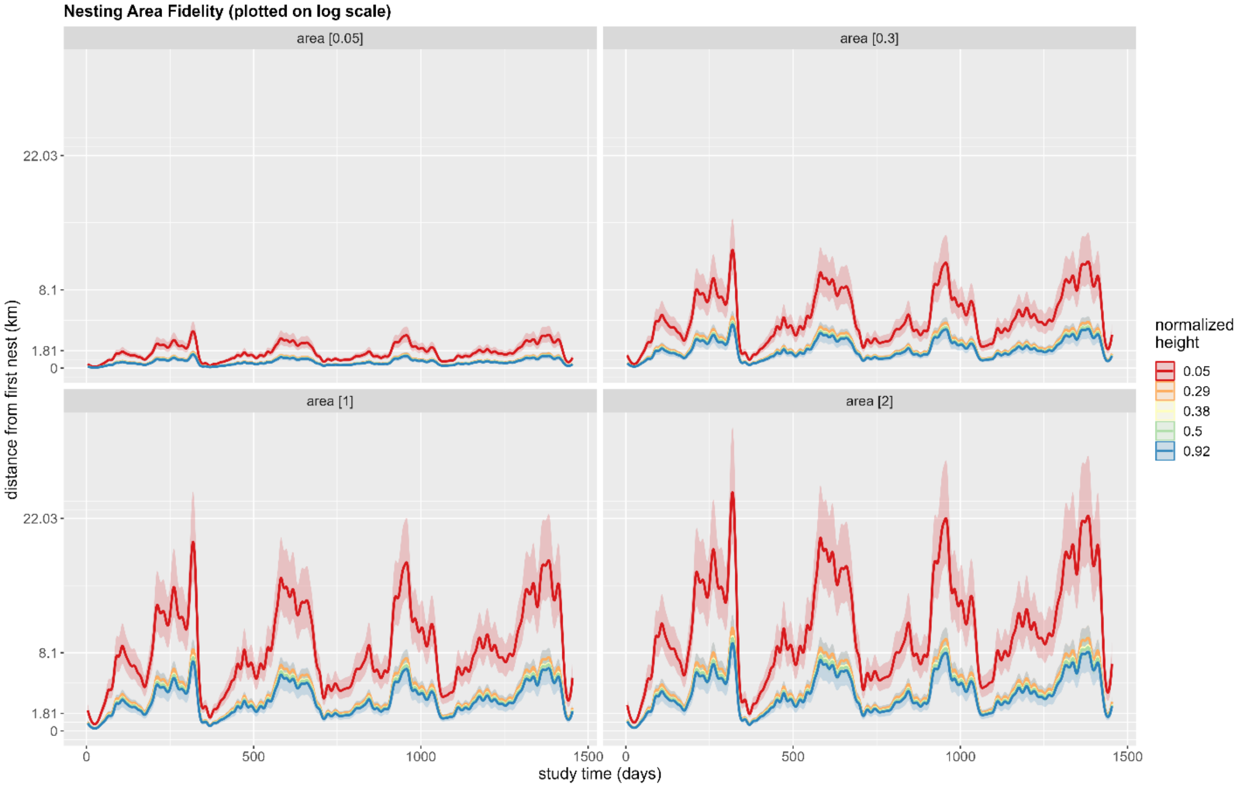


Figure 57. Conditional effects plot indicating how distance from first nest for female sage-grouse varies as a function of study time, short-term home range area (km^2), and normalized height. Normalized height is an index of topographic position with greater values indicating higher elevations relative to those in the local area.

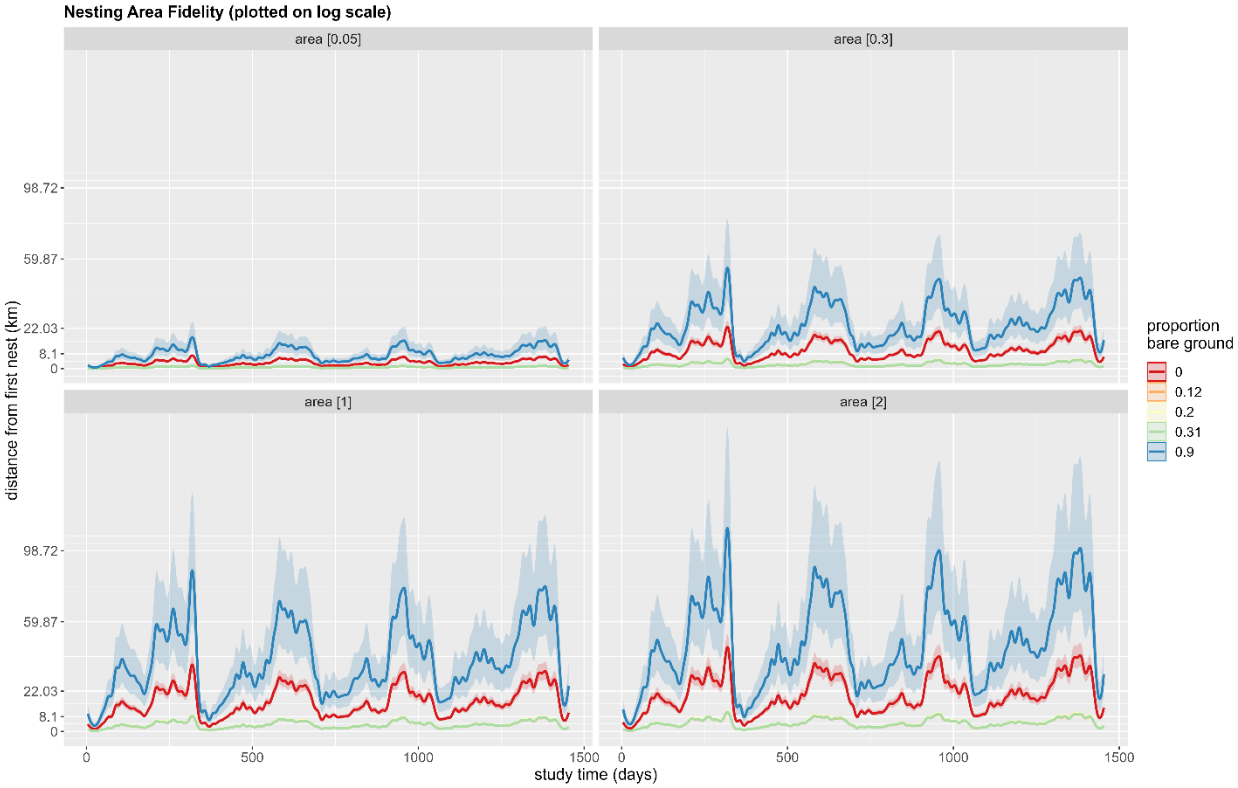


Figure 58. Conditional effects plot indicating how distance from first nest for female sage-grouse varies as a function of study time, short-term home range area (km^2), and proportion bare ground.

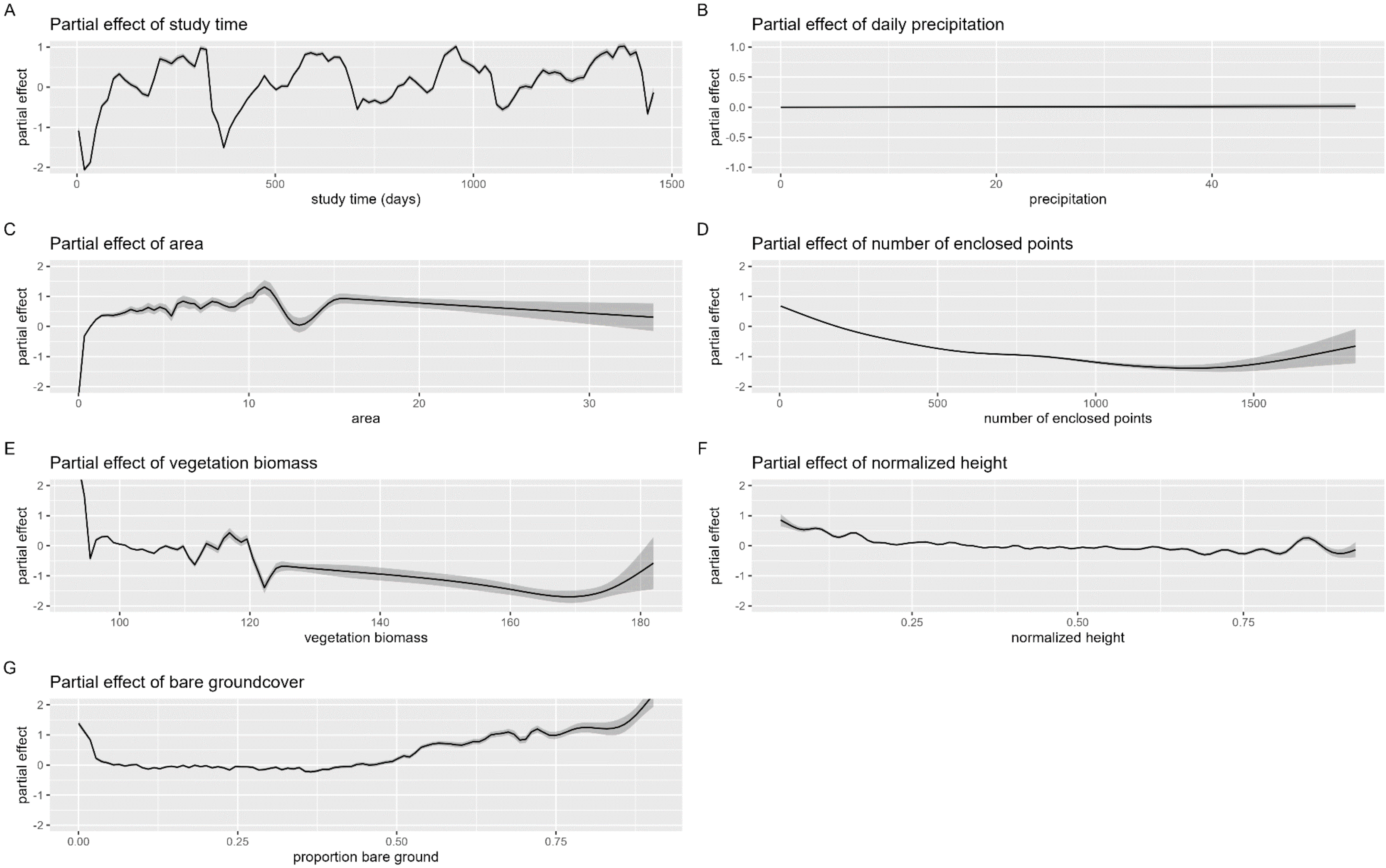


Figure 59. Partial effects plots from fitted generalized additive model evaluating how distance from first nest for a female sage-grouse varies as a function of study time and other covariates. The effect size of each variable can be discerned by examining the range of effect on the y-axis of each plot.

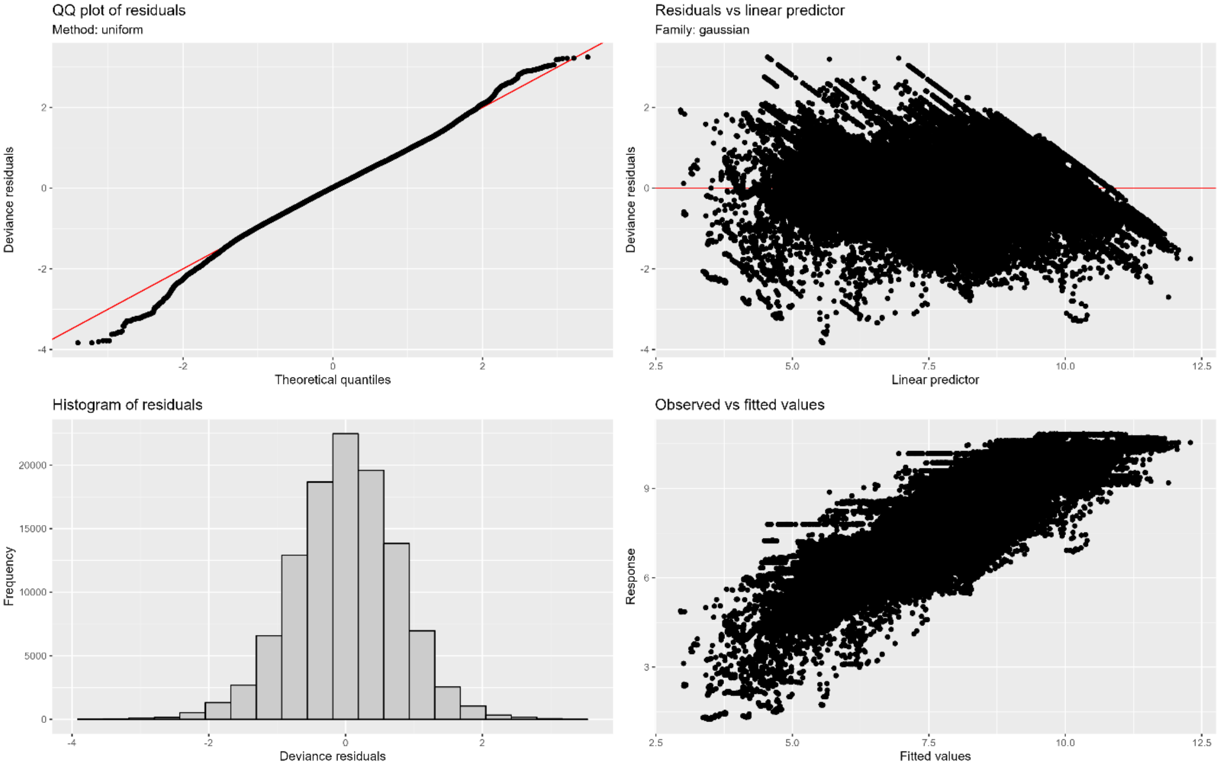
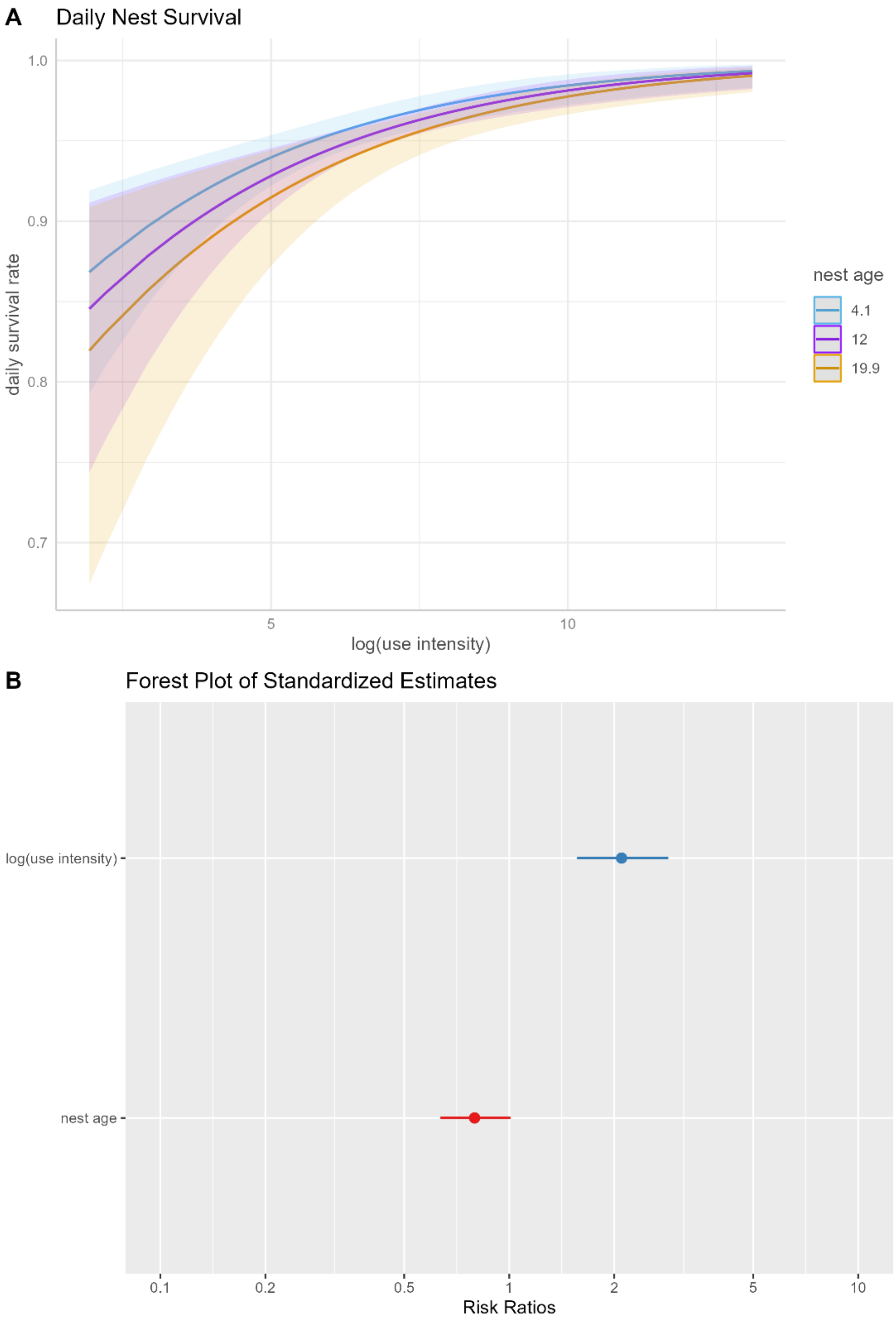


Figure 60. Model diagnostics plot from fitted generalized additive model evaluating how distance from first nest for a female sage-grouse varies as a function of study time and other covariates. The residuals versus fitted values plot does not show concerning patterns (e.g., non-constant variance) and the normality assumption is reasonable, although the deviance residuals are somewhat lite tailed.



A Daily Nest Survival

B Forest Plot of Standardized Estimates

Figure 61. Subplot A is a conditional effect plot generated from our final logistic-exposure generalized linear model indicating how daily nest survival rate changes as a function of log(use-intensity) over quantiles of nest age. Subplot B indicates the magnitude and direction of effects for log(use-intensity) and nest age.

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