AN ABSTRACT OF THE THESIS OF

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Title: Resource Selection and Demographic Rates of Female Greater Sage-Grouse
Following Large-Scale Wildfire

Abstract Approved:

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Understanding the effects of habitat disturbance on a species' habitat selection
patterns, and demographic rates, is essential to projecting the trajectories of
populations affected by disturbance, as well as for determining the appropriate
conservation actions needed to maintain those populations. Greater sage-grouse
(*Centrocercus urophasianus*) is a species of conservation concern in western North
America. The distribution of the species has been reduced by approximately half
since European settlement, with concurrent and continuing population declines across
its occupied range. The primary threats to the species are habitat alteration and loss,
caused by multiple factors. In the western portion of its distribution, increasing
wildfire activity is a primary cause of habitat loss and degradation. Single wildfires
in this area may now reach extremely large sizes (>100,000 ha), and wildfires have
been linked to local population declines. However, no published studies, to date,
have examined the immediate effects of large-scale wildfire on sage-grouse habitat
selection and demographic rates, using modern telemetry methods.

I studied the habitat selection patterns, nest success, and survival of adult, and
yearling female sage-grouse, captured within or near the Holloway fire, using state-
of-the-art GPS-PTT telemetry methods. The Holloway fire burned ~187,000 ha of
highly productive sage-grouse habitat in August, 2012. My study began during the
first spring post-fire (March, 2013), and continued through February, 2015. I
monitored seasonal habitat use patterns, and site-fidelity of sage-grouse, and modeled
third-order seasonal resource selection, using mixed effects resource selection

functions, in relation to characteristics of the post-fire habitat mosaic, terrain, mesic habitat availability, and herbaceous vegetation regeneration. I described sage-grouse nesting habitat use, nesting effort, and modeled daily nest survival in relation to temporal patterns, patch scale vegetation, biological factors, and landscape-scale habitat composition. I modeled adult and yearling female sage-grouse survival in relation to temporal patterns, biological factors, and landscape-scale habitat composition.

Female sage-grouse primarily exhibited a three range seasonal movement pattern, with differentiation between breeding-nesting-early brood-rearing habitat (mean use dates: 8 Mar – 12 Jun), late brood-rearing-summer habitat (13 Jun – 20 Oct), and winter habitat (21 Oct – 7 Mar). However there was variation in seasonal range behavior among individuals. Sage-grouse exhibited considerable fidelity to all seasonal ranges, for individuals which survived >1 yr, mean distance between seasonal range centroids of the same type were 1.80 km, 1.65 km, and 3.96 km, for breeding ranges, summer ranges, and winter ranges, respectively. Within seasonal ranges, sage-grouse exhibited third-order resource selection patterns similar to those observed for populations in undisturbed habitats. Sage-grouse, at the population level, selected for level terrain throughout the year. During the breeding season sage-grouse selected for areas with increased amounts of intact sagebrush land-cover within a 1-km^2 area around used locations, areas of increased NDVI values within a 6.25-km^2 area, an amount of mesic habitat within a 6.25-km^2 area roughly equal to that available on the landscape, and mid-level elevations. During summer, sage-grouse, at the population level, selected for an areas with an intermediate density of burned-intact habitat edge within a 1 km^2 area, areas of increased NDVI values within a 6.25-km^2 area, intermediate distances to mesic habitat, and high elevations. During winter, sage-grouse, at the population level, selected for increased amounts of intact sagebrush land-cover within a 0.089-km^2 area, areas with decreased variation in NDVI within a 0.089-km^2 area, an amount of mesic habitat within a 6.25-km^2 area roughly equal to that available on the landscape, and intermediate elevations. There

was considerable variation in third-order resource selection patterns among individuals during all seasons.

Sage-grouse nest success was consistently low during the study (2013: 19.3%, 2014: 30.1%), and nest initiation rates were average to high (2013: 1st nest initiation = 90.5%, 2nd nest initiation = 23.1%; 2014: 1st nest initiation = 100%, 2nd nest initiation = 57.1%). Daily nest survival rates were influenced by an interaction between year and nesting attempt, and by forb cover within 5 m of the nest. Nest survival over the incubation period was consistently low for 1st and 2nd nests during 2013, and for 1st nests during 2014 (range: 0.131 – 0.212), but increased to 0.744 for 2nd nests during 2014. Forb cover within 5 m of the nest had a positive effect on daily nest survival rates, with a 1% increase in forb cover increasing the probability of a nest surviving a given day by 1.02 times.

We did not detect strong direct effects of habitat or biological characteristics on survival of adult and yearling female sage-grouse. Rather, survival varied by month with lowest survival occurring in April and August of each year, and highest survival occurring during the winter. While patterns of monthly survival were similar between years, there was a strong, negative additive effect on survival which extended from the beginning of the study (March, 2013), through the end of the first post fire growing season (July, 2013). Although monthly survival increased following the end of the 1st post-fire growing season, yearly survival over both the 1st and 2nd biological years post-fire was low (March 2013 – February 2014: 24.0%; March 2014 – February 2015: 37.9%).

These results indicate that female greater-sage grouse do not respond to wildfire related habitat disturbance through emigration, and rather continue to attempt to exist and reproduce in habitats disturbed by wildfire during the immediate years following a fire. While, due to site-fidelity, sage-grouse are not able to leave wildfire affected seasonal ranges, within those seasonal ranges they still attempt to utilize habitat components which most closely match their life-history requirements. However, this behavior appears to have an acute fitness cost to individuals, with reduced nesting success and survival of individuals utilizing fire-affected habitats

during the first two years post-fire. This reduction in demographic rates likely explains observed sage-grouse population declines following wildfire, and indicates that these population declines are not the result of sage-grouse emigration away from fire-affected leks, but rather a true decline in the number of individual sage-grouse on the landscape following large-scale wildfire.

Resource Selection, and Demographic Rates of Female Greater Sage-Grouse
Following Large-Scale Wildfire

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Lee Foster, Author

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AUTHOR CONTRIBUTIONS

Christian Hagen, Katie Dugger and Dave Budeau contributed to this project at most stages, including acquiring funding, assisting with study design and development, and editorial review of chapters. Patrick Donnelly contributed to the development of a detailed map of the Holloway fire, as described in Appendix I.

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CHAPTER 1

GENERAL INTRODUCTION

Lee Foster

CONSERVATION STATUS OF GREATER SAGE-GROUSE

Greater sage-grouse (*Centrocercus urophasianus*; hereafter: sage-grouse) are a sagebrush (*Artemisia* spp.) obligate species of particular conservation concern in western North America (Connelly et al. 2011a). Although still widely distributed, sage-grouse now occupy approximately half of their historic distribution, and long-term population declines have been documented across much of the species distribution (Schroeder et al. 2004, Garton et al. 2011). Population declines and resulting changes in distribution have been linked to a suite of factors including: agricultural conversion, energy development, invasive species, conifer encroachment, unsustainable grazing practices, and altered fire regimes (Connelly et al. 2011b). Declining population trends and distribution changes, along with multiple threats to sage-grouse across their range, have prompted several petitions to list the species under the endangered species act (Stiver 2011). In 2010, the US Fish and Wildlife Service determined that a listing of the species as "threatened or endangered" was warranted but precluded by higher priorities, and scheduled a final listing decision for the species in 2015 (USFWS 2010). This decision prompted widespread conservation efforts to address the threats to the species, and in the fall of 2015 the USFWS determined that a listing of the species was not warranted at that time; in part due to the increase in conservation programs for the species, that had occurred in the intervening five years, to address threats to the species and their habitat (USFWS 2015). However, the USFWS acknowledged that some threats to the species remained unresolved, and the Service committed to a review of their listing decision in 2020 to assess the on-going conservation efforts for the species (USFWS 2015). Increased wildfire activity in the western portion of the species' distribution is one threat to sage-grouse where significant data-gaps still persist.

WILDFIRE IN THE SAGEBRUSH ECOSYSTEM

Fire has been shaping western North American ecosystems for centuries (Kozlowski and Ahlgren 1974). However in the early 20th century Euro-Americans began to view wildfire in a negative light. In the 1930s, a concerted effort to suppress

large wildfires was undertaken, and to a large extent fire was excluded from many ecosystems for the remainder of the century (Kozlowski and Ahlgren 1974, Arno 1996, Keane et al. 2009). However, this wildfire suppression policy (which is still largely in effect today) is widely believed to have increased the accumulation of fine fuels in previously fire prone areas, and instigate larger and more intense fires in many ecosystems of the west (Allen et al. 2002, Miller et al. 2003, Schoennagel et al. 2004, Reinhardt et al. 2008, Miller et al. 2011). In response, there has been increasing demand from land managers and scientists to reduce fuel accumulations and to restore historic fire regimes to western ecosystems, through prescribed burning, fuel reduction programs, and more lenient suppression tactics (Arno 1996, Agee 2002, Finney and Cohen 2003, Reinhardt et al. 2008, Ager et al. 2010). However debate ensues regarding the implementation of these programs, and the role of wildfire in the widely varied habitats of the west (Schoennagel et al. 2004, Baker 2006, Westerling et al. 2006, Sankey et al. 2008).

The discussion surrounding the role of fire in sagebrush ecosystems is a prime example of this debate. Sagebrush is the largest ecosystem type of the intermountain west (West 1983), and is dominated by several species, including big sagebrush (*A. tridentata* ssp.), low sagebrush (*A. arbuscula*), and silver sagebrush (*A. cana*) (West 1983). Sagebrush habitats have undergone extensive alterations and loss since the arrival of Europeans to western North America, with as little as 67% percent of the original ecosystem extent remaining (Noss et al. 1995, Bunting et al. 2002, McIver et al. 2010). There are two competing hypotheses about the historic role of fire in sagebrush ecosystems. It has been suggested that fire was relatively frequent (fire return intervals 30 - 40 years) in some sagebrush ecosystems (Burkhardt and Tisdale 1976), but has been excluded over the past century through a reduction in fuel loads due to livestock grazing, and the intentional suppression of wildfires (Miller and Rose 1999). Recently, this view has been called into question, with evidence that wildfire was historically infrequent in sagebrush (Baker 2006, 2011). Regardless of which hypothesis is correct, the current scientific consensus is that there is insufficient data

to conclusively characterize historical fire regimes in this ecosystem (Romme et al. 2009). Fire return intervals varied, and continue to vary, based on vegetation and soil profiles on a site specific basis (Miller and Rose 1999, Miller et al. 2003, Baker 2006, Miller et al. 2011). Estimates of historic mean fire return intervals range from <30 to 100 years for mountain big sagebrush (*A. t.* ssp. *vaseyana*), 100 to >300 years in Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*), and 100 to 450 years in low sagebrush (Burkhardt and Tisdale 1976, Young and Evans 1978, Miller and Rose 1999, Baker 2006). Fire does not thin sagebrush stands through a reduction in plant density, because even low intensity fire kills nearly all sagebrush plants affected (Sapsis et al. 1991, Baker 2006). Except for silver sagebrush, three-tipped sagebrush (*A. tripartite*), and sand sagebrush (*A filifolia*) (White and Currie 1983, Shariff 1988), most species of sagebrush do not re-sprout from roots following wildfire (Braun 1987, Baker 2006). Thus, relatively long recovery rates are the norm for sagebrush ecosystems: approximately 35 to 100 years for mountain big sagebrush, and 50 to 120 years for Wyoming big sagebrush (Baker 2006, Arkle et al. 2014).

Although variable among floristic provinces, increases in both number of wildfires (0% to 15% per year), and total area burned (3% to 27% per year) occurred in sagebrush habitat between 1980 and 2007 (Miller et al. 2011). Fire disturbance has increased primarily because of climate change, invasion by annual grasses, and human activity (D'Antonio and Vitousek 1992, Connelly et al. 2004, Westerling et al. 2006, Miller et al. 2011). The increase of fire within sagebrush ecosystems is of particular concern due to long-term declines of sage-grouse populations affected by wildfire (Coates et al. 2015). However, the specific demographic causes of these declines, and the habitat selection behavior of sage-grouse affected by wildfire, have remained uninvestigated using modern telemetry methods.

POTENTIAL EFFECTS OF WILDFIRE ON GREATER SAGE-GROUSE

While the specific effects of wildfire on sage-grouse habitat selection, and demographic processes remain unclear, the response of sage-grouse to other forms of

habitat disturbance give some indication of how sage-grouse may respond to wildfire-caused habitat disturbance. Sage-grouse exhibit strong site-fidelity to home and seasonal ranges, and have limited ability to respond to habitat disturbance via emigration (Connelly et al. 2011c). It has been commonly assumed that wildlife species select habitat that most benefits their fitness, however, in the case of highly philopatric species such as sage-grouse, individuals may remain in habitats affected by disturbance rather than move away, which may exact fitness costs (Van Horne 1983, Rettie and Messier 2000). Due to the interplay between the strong philopatry of sage-grouse, and the degradation of habitat following wildfire (Connelly et al. 2000, Nelle et al. 2000, Beck et al. 2009, Rhodes et al. 2010), observed reductions in sage-grouse populations following fire are likely related to reduced survival, or reproduction of sage-grouse, rather than due to emigration of sage-grouse away from fire-affected areas (Coates et al. 2015). Sage-grouse remaining in such habitats likely still attempt to select habitat at the site scale to meet their life-history requirements (Rettie and Messier 2000, Mayer et al. 2009). Thus, description of third-order habitat selection (at the scale of locations within a seasonal range; Johnson 1980), will likely suggest habitat restoration actions in wildfire affected areas to benefit sage-grouse.

As a sagebrush obligate species, sage-grouse require healthy sagebrush ecosystems during every phase of their life-cycle (Connelly et al. 2011a). They primarily nest under sagebrush shrubs. Nesting habitat selection, and nest success are positively influenced by increased shrub and grass cover at the nest site (Connelly et al. 2011a). As wildfire kills all affected shrubs, rather than thinning stands (Sapsis et al. 1991, Baker 2006), and grass cover is reduced following fire during at least the initial growing season (Rhodes et al. 2010), wildfire may reduce nesting habitat availability, and nesting success of sage-grouse. While, nesting success has a smaller impact on sage-grouse population trajectories than adult or juvenile survival, it still may be an important determinate of sage-grouse population trends in some areas (Crawford and Lutz 1985, Gregg et al. 1994, Schroeder et al. 1999, Baxter et al. 2008, Taylor et al. 2012, Dahlgren et al. 2016). Thus reductions in sage-grouse nesting

success, or nesting habitat availability due to wildfire may contribute to observed sage-grouse population declines following fire (Coates et al. 2015).

Sage-grouse can be characterized as a "survivor" or k-selected species, with relatively large body sizes, relatively low reproductive rates, and high adult survival (Sæther et al. 1996, Sæther and Bakke 2000, Stahl and Oli 2006, Taylor et al. 2012, Dahlgren et al. 2016). In such species, population trajectories are more dependent on adult survival than on reproductive output in a given year, (Taylor et al. 2012, Dahlgren et al. 2016). Sage-grouse mortality is primarily caused by predation, however sage-grouse coevolved with their predator community and thus predation should not pose a constraint to sage-grouse population growth in undisturbed habitats with natural levels of predation (Hagen 2011a). In cases where hiding cover or habitat connectivity are reduced, increased predation rates may however influence sage-grouse population dynamics (Hagen 2011a). As both cover and connectivity are reduced by wildfire, adult survival may be negatively affected contributing to observed sage-grouse population declines after a large fire.

CONTEXT OF STUDY

Wildfire activity has been identified as a primary threat to sage-grouse populations in Oregon (Hagen 2011b). During the summer of 2012, > 400,000 ha of sagebrush habitat burned in Oregon. In an effort to quantify the effects of large-scale wildfire on sage-grouse habitat selection and demographic rates, Oregon Department of Fish and Wildlife (ODFW), initiated this research project immediately following these fires in early fall 2012. The study area chosen for this project was within the boundary of the Holloway fire, which burned ~187,000 ha of sage-grouse habitat within the Trout Creeks Sage-Grouse Priority Area of Conservation (PAC; Figure 1.1) during August 2012. We marked female sage-grouse with GPS-PTT transmitters, and VHF radio-transmitters, and used the data generated to address the following objectives:

1. Characterize patterns of female sage-grouse habitat selection and space use in landscape affected by large-scale wildfire.

   1.1. Delineate female sage-grouse seasonal ranges and characterize movement behavior in a post-wildfire landscape.

   1.2. Estimate female sage-grouse site-fidelity in a post-wildfire landscape.

   1.3. Describe habitat composition of female sage-grouse seasonal ranges in a post-wildfire landscape.

   1.4. Describe habitat use and the factors that affect it within seasonal home ranges (i.e., third-order resource selection; Johnson 1980) in a post-wildfire landscape.

2. Describe sage-grouse nesting ecology in a landscape affected by large-scale wildfire.

   2.1. Quantify sage-grouse nest initiation rates following a large-scale wildfire.

   2.2. Describe nesting habitat utilized by sage-grouse within and adjacent to the boundaries of a large-scale wildfire.

   2.3. Estimate daily nest survival (DNS) rates and the spatial and temporal factors associated with DNS within fire affected and associated habitats.

3. Estimate the survival of yearling and adult female sage-grouse in a landscape affected by large-scale wildfire.

   3.1. Estimate survival (S) of GPS marked female sage-grouse, and the spatial and temporal factors associated with survival within fire affected and associated habitats, from March 2013 – February 2015.

3.2. Estimate survival (S) of VHF marked male and female sage-grouse, in relation to time since fire, sex, and age, from November 2012 – September 2014.

3.3. Compare survival rates between individuals marked with VHF vs. GPS transmitters to investigate the possibility of GPS transmitter effects on sage-grouse survival in a cover deficient landscape.

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Figure 1.1. Holloway fire severity in relation to Trout Creeks Sage-Grouse Priority Area of Conservation (PAC), Oregon. Inset depicts Holloway fire (red outline) in relation to all Oregon Sage-Grouse PACs (green polygons).
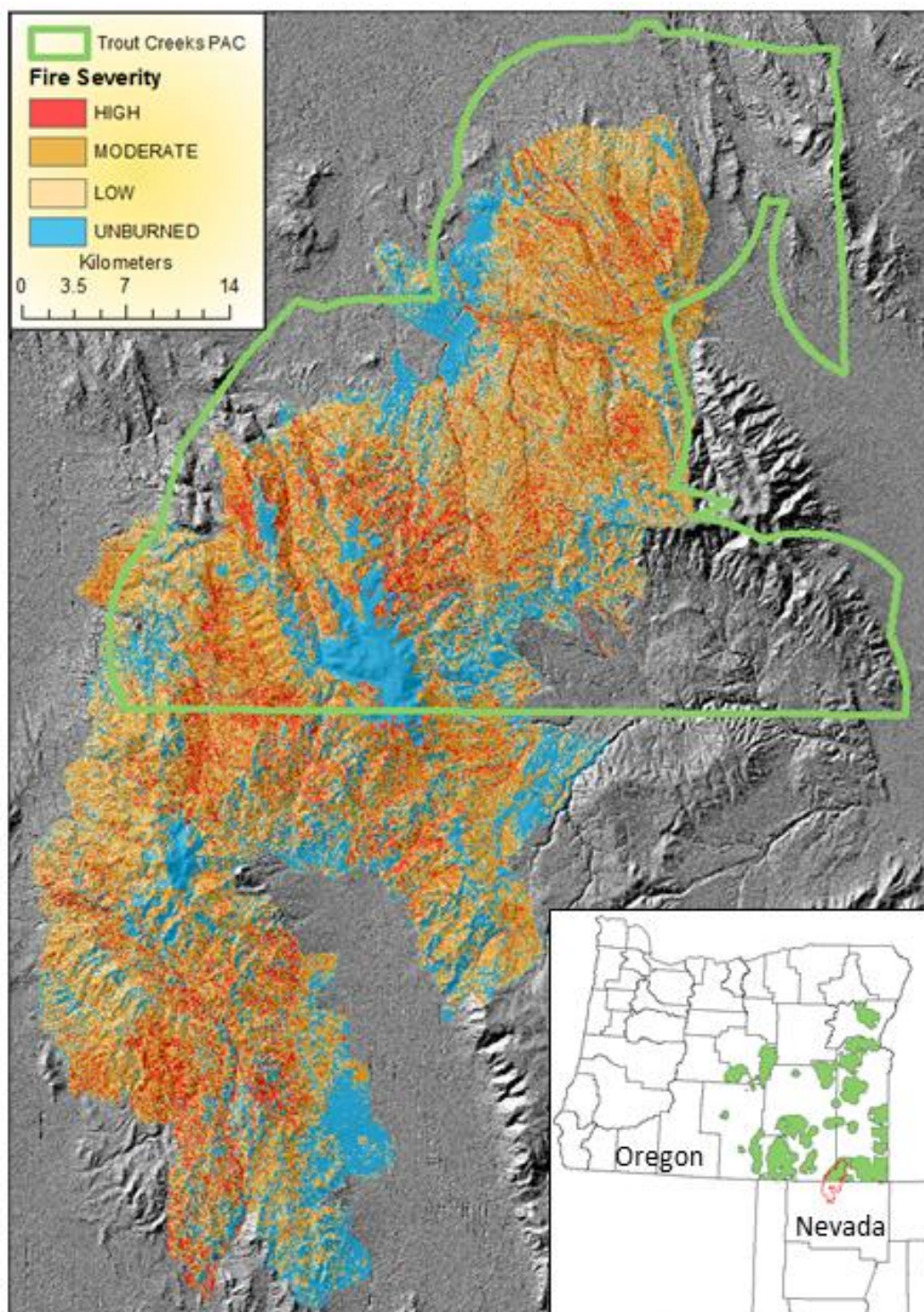
CHAPTER 2

GREATER SAGE-GROUSE RESOURCE SELECTION AND SEASONAL HABITAT COMPOSITION FOLLOWING LARGE-SCALE WILDFIRE

Lee Foster, Christian Hagen, Katie Dugger, Dave Budeau

ABSTRACT

Long-standing tenets of ecology suggest that wildlife species should select habitat that most benefits their fitness; however, this assumption may be incorrect for highly philopatric species affected by infrequent habitat disturbance. Greater sage-grouse (*Centrocercus urophasianus*) are a species of conservation concern in western North America, that exhibit strong site fidelity to breeding and summer ranges. During 2013 and 2014, we attached rump-mounted GPS transmitters to female sage-grouse to investigate the seasonal movement behavior, site-fidelity, seasonal habitat composition, and third-order resource selection patterns of a population affected by a large-scale (~187,000 ha) wildfire in southeastern Oregon. We used the daily location data collected from these birds in a grouping analysis to empirically define sage-grouse seasonal ranges and delineate the dates of movement between seasonal ranges. We used Brownian Bridge Movement Model kernel home ranges and GIS analysis to characterize seasonal range composition and site-fidelity of sage-grouse to breeding, summer, and winter seasonal ranges. Finally, we used mixed effects logistic regression to generate third-order resource selection functions for female sage-grouse in each of the 3 seasonal ranges. The majority of sage-grouse exhibited a three range movement strategy, with differentiation between nesting/early brood-rearing, late brood-rearing/summer, and winter ranges and high site fidelity to all seasonal ranges. Few differences were detected in mean habitat characteristics between seasons, or among seasons between years, except that sage-grouse used summer ranges that occurred at higher elevations than either breeding or winter ranges. Sage-grouse exhibited third-order resource selection patterns consistent with populations existing in undisturbed habitats. Sage-grouse selected strongly against rugged terrain throughout the year. During the breeding and winter seasons sage-grouse selected strongly for increased amounts of intact sagebrush land-cover and selected for intermediate amounts of burnt-intact habitat edge in summer. The patterns of site-fidelity indicated that sage-grouse population declines following wildfire are likely due to true reductions in population size through increased mortality or reduced reproductive output, rather than through emigration of adult

sage-grouse to undisturbed habitat. The third-order resource selection patterns have implications for post-fire habitat restoration methods, and can provide guidance on where to focus habitat restoration projects following wildfire.

INTRODUCTION

Wildlife species differentially select resources across the landscape to meet their various life-history needs (Johnson 1980, Manly et al. 2002). This differential habitat selection generates a hierarchical pattern of resource selection, descending in geographic scale from the range of the species (first-order selection), through the seasonal range of an individual (second-order selection), into the specific habitat components used at individual locations within a home or seasonal range (third-order selection), and finally, to the forage items procured at those locations (fourth-order selection; Johnson 1980, Manly et al. 2002). Within these various scales, it is often assumed that individual animals are selecting those resource units which are most beneficial to their fitness (Fretwell and Lucas 1970, Loegering and Fraser 1995, Manly et al. 2002, Johnson and Seip 2008). However, there are multiple situations wherein animals may not exhibit optimal selection, and instead exist in habitats which may reduce individual fitness (Van Horne 1983). One situation where suboptimal selection may occur, is in species which exhibit considerable site-fidelity to breeding or other areas required during their life-cycle (Van Horne 1983, Knick and Rotenberry 2000). In such cases, individuals may continue occupying habitat which has been rendered unsuitable following disturbance which results in habitat destruction or degradation (Knick and Rotenberry 2000). While site-fidelity to breeding or other seasonal ranges may limit the ability of such species to respond to disturbance via emigration, individuals in this situation should still attempt to select feeding locations within these ranges which most closely match their life-history requirements (Rettie and Messier 2000, Mayer et al. 2009).

The greater sage-grouse (*Centrocercus urophasianus*; hereafter: sage-grouse) is a species which exhibits strong site-fidelity to breeding and summering areas, with

apparently limited ability to respond to disturbance through emigration (Connelly et al. 2011a). It is a lek-breeding species of conservation concern in western North America, and has experienced significant declines in population, now occupying approximately half its historic distribution (Schroeder et al. 2004, Garton et al. 2011). The sage-grouse is a sagebrush (*Artemisia spp.*) obligate species, requiring intact sagebrush habitats during every phase of their life-history (Patterson 1952, Schroeder and Braun 1999). Individual sage-grouse exhibit strong fidelity to lek sites, and nesting areas, with individuals typically returning to the same lek or group of leks, to breed year after year (Dalke et al. 1963, Wallestad and Schladweiler 1974, Emmons and Braun 1984, Dunn and Braun 1985, Connelly et al. 2011a), and female sage-grouse often nest in close proximity to previous year's nest sites (Fischer et al. 1993, Schroeder and Robb 2003, Moynahan et al. 2007, Connelly et al. 2011a, Kaczor et al. 2011). Sage-grouse may also show high fidelity to summer ranges (Hagen 1999), but fidelity to winter ranges may be reduced (Smith 2013). The strong site-fidelity of sage-grouse to some seasonal ranges may decrease their ability to shift those ranges following large-scale habitat disturbance (Knick and Rotenberry 2000, Aldridge and Boyce 2007, Dzialak et al. 2011). However, within disturbance-affected seasonal ranges, sage-grouse should continue to attempt to meet their life-history needs with remaining available intact habitat, and thus, show patterns of resource selection at the third-order similar to populations in undisturbed habitats (Johnson 1980, Rettie and Messier 2000, Mayer et al. 2009).

Sage-grouse face multiple threats to their habitat across their range (Miller et al. 2011), with increasing wildfire activity constituting a significant threat to sage-grouse habitat and populations in the western portion of their distribution (USFWS 2015). Wildfires in the sagebrush ecosystem may rapidly reach large sizes (>100,000 ha), with most large fires burning extensive areas of habitat in ≤ 2 weeks (McGee 1982, Knapp 1995, 1998, Baker 2006). At such sizes, a single wildfire may encompass entire home or seasonal ranges of some sage-grouse populations (Connelly et al. 2011a). The extent of these disturbances and their sudden occurrence

may prompt suboptimal habitat selection by sage-grouse inhabiting landscapes immediately after a large-scale fire. Sagebrush ecosystems are not well adapted to frequent fires. Sagebrush stands are generally not thinned by wildfire, but instead burnt shrubs are killed, and most sagebrush species do not resprout following fire, but must regenerate from seed (Baker 2006). These aspects of sagebrush biology lead to long habitat recovery times, and in the case of significant annual grass invasion, habitats may never recover (Arkle et al. 2014). The strong site-fidelity of sage-grouse may lead to suboptimal selection of seasonal ranges (second-order selection) in populations affected by fire, however most fires in the sagebrush ecosystem leave a mosaic of burned and intact habitat (Boltz 1994). Individual sage-grouse in post-wildfire affected landscapes should attempt to exploit this habitat mosaic to meet their seasonal resource needs at the third-order (i.e., locations within seasonal ranges); fire may thus have a variable effect on sage-grouse habitat availability throughout the annual cycle.

During the summer of 2012, >400,000 ha of sage-grouse habitat burned in Oregon. Beginning in spring 2013, we used rump-mounted GPS PTT transmitters attached to female sage-grouse to investigate sage-grouse habitat selection at the second and third-orders, as well as the seasonal migratory behavior of sage-grouse in the Holloway Fire (~187,000 ha) in southeastern Oregon and northern Nevada. The objectives of our study were to:

1. Delineate female sage-grouse seasonal ranges and characterize movement behavior in a post-wildfire landscape.

2. Estimate female sage-grouse site-fidelity in a post-wildfire landscape.

3. Describe habitat composition of female sage-grouse seasonal ranges in a post-wildfire landscape.

4. Describe habitat use and the factors that affect it within seasonal home ranges (i.e., third-order resource selection; Johnson 1980) in a post-wildfire landscape.

STUDY AREA

This study occurred in the Trout Creek Mountains (hereafter: Trout Creeks) of southeastern Oregon. The Trout Creeks range in elevation from 1372 m to >2438 m (Evenden 1989), and are characterized by mesas, buttes, and fault blocks cut with deep stream canyons (Carlton 1968). Prior to the large-scale wildfire that occurred in southeastern Oregon and northern Nevada during summer 2012, the vegetation communities present in the study area varied based on elevation and topography. At upper elevations (> 1900 m) a mountain big sagebrush (*A. t. vaseyana*) – low sagebrush (*A. arbuscula*) mosaic dominates, interspersed with a mountain shrub community of snowberry (*Albus* spp.), antelope bitterbrush (*Purshia tridentata*), and *Ceanothus* spp. (Freeborn 2006). Native grasses at higher elevations include Idaho fescue (*Festuca idahoensis*), needlegrass (*Achnatherum* spp.), bluebunch wheatgrass (*Pseudoroegneria spicata*), and Sandburg's bluegrass (*Poa secunda*) (Freeborn 2006). Additionally mountain mahogany (*Cercocarpus* spp.) and quaking aspen (*Populus tremuloides*) patches dot the higher elevations, and cheatgrass (*Bromus tectorum*) is generally absent (Freeborn 2006). At lower elevations Wyoming big sagebrush (*A. t. wyomingensis*) dominates, with areas of salt desert shrubs present on more alkaline soils (Freeborn 2006). Grasses at lower elevations include bluebunch wheatgrass, needlegrass, Sandberg's bluegrass, bottlebrush squirreltail (*Elymus elymoides*), basin wildrye (*Leymus cinerius*), and cheatgrass, while western juniper (*Juniperus occidentalis*) is rare or absent from the study area (Freeborn 2006). Approximately 95% of the area is managed by the Bureau of Land Management (BLM), a large portion of which is designated as Wilderness Study Area (WSA), with the remaining 5% of land in private holding (Elmore 2000, Freeborn 2006).

A lightning strike ignited the Holloway fire in the Trout Creek Mountains on August 5, 2012. The fire occurred ~40 km east of Denio, Nevada, and 210 km southeast of Burns, Oregon (Karges 2013), and was not fully contained until August 25, 2012. The Holloway fire burned 186,972 ha, of which 99,352 ha were in southern Malheur and Harney counties, Oregon, and 87,227 ha were in northern Humboldt County, Nevada (Karges 2013). The Trout Creeks sage-grouse Priority Area of Conservation (PAC) was almost completely burned by this fire (Figure 2.1; Hagen 2011). Fire behavior depended on local topographic features, vegetation profiles, and weather conditions. These factors varied considerably in the region, resulting in variable patterns of burned and intact habitat. Increased fuel loads, wind speeds, and topographic features conducive to fire spread caused high fire severity in some areas, consuming nearly all vegetation for square kilometers. In other areas, reduced fuel loads, wind speeds, and topographic features unconducive to fire spread decreased fire severity, leaving a variable mosaic of burned and intact vegetation. Several large patches of intact habitat exist within the perimeter of the fire, with the largest patch exceeding 4,000 ha. Within the fire boundary, 75.3% of the land area was burnt, while the remaining 24.7% was comprised of remnant intact habitat (Figure 2.1; Appendix I).

METHODS

Field Methods

We captured female sage-grouse during both spring and summer of 2013 and 2014 using a spot-lighting technique following Wakkinen et al. (1992). During spring we captured individuals near leks within, or near (≤ 2 km) the boundary of the Holloway fire, and during summer we captured individuals on previously identified roosting areas within the fire boundary. We aged and sexed captured individuals using feather patterns and morphology (Crunden 1963). Females were classified as either adults (≥ 2 years of age), or yearlings (1 year of age) and were marked with individually numbered steel leg bands under the authority of project collaborators, Oregon Department of Fish and Wildlife. All animal capture, handling, and

instrument attachment procedures were approved under Oregon State University's Institutional Animal Care and Use Committee. We attached 30-g ARGOS/GPS Solar PTTs (PTT-100, Microwave Telemetry Inc., Columbia, MD 21045 USA) to all captured females, using a rump-mount technique (Rappole and Tipton 1991). GPS units included Ultra High Frequency beacons which were turned on for ground tracking from 1 March – 31 July each year. The GPS units we used during spring and summer 2013 were configured to record locations (+/- 20m) 6 times daily from 1 March – 31 July, 4 times daily from 1 August – 31 October, and 2 times daily from 1 November – 29 February. GPS units deployed in spring 2014 were configured similarly except that we increased the number of locations collected during the nesting season (10 times daily from 1 March – 31 July, and 4 times daily from 1 August – 29 February). Recorded locations were downloaded weekly from the Argos System website.

Seasonal Range Delineation

We delineated the seasonal ranges of sage-grouse in this study using grouping analysis in ArcGIS 10.1 (ESRI, Inc., Redlands, CA; Assuncao et al. 2006, Duque et al. 2007, Hinde et al. 2007, Jain 2009). For each individual in the study we defined the expected number of distinct location clusters, as the number of visually distinct groups of locations within the pattern of all annual locations collected for each individual. Distances between these groups (i.e. seasonal location clusters) varied, however they were generally separated by 1 – 10 km. We set the expected group value in the Grouping Analysis tool in the ArcGIS 10.1 Spatial Analyst Toolbox, as the number of clusters visually delineated from each individual's location pattern. We then used UTM coordinates and elevation as analysis parameters, and a K-nearest neighbor spatial constraint, with 8 neighbors, to assign locations to a group membership. K-nearest neighbor classification assigns group membership through proximity, where each location is the neighbor of at least one other location in the group, and neighbor relationships are based on the nearest K features (Dudani 1976). If ArcGIS 10.1 K-nearest neighbor classifications suggested more groups than had

been assigned to the data for an individual based on visual observation of clusters within location patterns, the expected number of groups was increased to the level suggested by the program, and we re-ran the analysis. Group membership for each individual was then plotted against date. Seasonal ranges were defined as sets of locations (points) which maintained near constant membership within the same group, or set of groups, within a contiguous range of dates delineating each season. Shifts between seasonal ranges were identified when group membership of locations changed between one group, or a set of groups, to a new group, or a set of groups, and did not revert back to the previous group/groups for 2 – 3 months. We assessed distance between seasonal ranges of individuals by generating 95% Brownian Bridge Movement Model (BBMM) seasonal range polygons (Bullard 1999, Horne et al. 2007), within the seasonal range dates available for an individual. We then calculated the centroid of each seasonal range polygon and calculated the distance between seasonal range centroids to determine mean distance between seasonal ranges for individuals.

Covariate Calculation

To assess seasonal habitat composition, habitat covariates were calculated within seasonal ranges, and distance covariates were not considered in the analysis of seasonal habitat composition. To assess third-order selection (Johnson 1980), habitat covariates were calculated within three point buffers around each analyzed location, or for distance variables, from a location to the habitat feature in question. The buffers we analyzed were 0.169 km (0.089-km^2), 0.564 km (1-km^2), and 1.41 km (6.25-km^2). The 0.169 km buffer corresponds to the 25% quantile of 24 hour straight line movement distances observed within this study. The 0.564 km buffer corresponds to a 1 km^2 area, a common scale at which sage-grouse select habitat (Aldridge and Boyce 2007, Kirol et al. 2015). The 1.41 km buffer corresponds to the 90% quantile of 24 hour straight line movement distances observed within this study. These buffers approximate the scales at which other studies have assessed sage-grouse resource selection, while still being based on empirical information collected

from individuals within our study (Dzialak et al. 2011, Kirol et al. 2015). We analyzed resource selection based on nine covariates, structured into 4 categories: mesic habitat availability, post fire habitat structure, vegetation regeneration, and topography (Table 2.1).

Mesic Habitat Availability

We used the dataset provided by Donnelly et al. (2016), which delineates mesic habitat areas (e.g., wetlands, riparian areas) for sage-grouse across Oregon, California, and northwestern Nevada, to define mesic habitat in the study area. We overlaid sage-grouse location data, and analysis areas (seasonal ranges, or point buffers) generated from that location data, onto this layer to generate a suite of habitat covariates relating to mesic habitat availability, for each location, or analysis area. We quantified mesic habitat availability as the distance from a location to mesic habitat (m; DTM), and as the percentage of mesic habitat (PM) within an analysis area (seasonal range, or point buffer). We assessed distance to mesic habitat with the Near tool in the ArcGIS 10.1 Analysis toolbox. To assess the percentage of mesic habitat, we first converted the polygon data provided by Donnelly et al. (2016) to 10 m resolution raster data using the Polygon to Raster tool in the ArcGIS 10.1 Conversion toolbox, and then calculated percentage of mesic habitat within an analysis area using the Percentage of Landscape metric (PLAND), in FRAGSTATS v4 (McGarigal et al. 2012).

Post-Fire Habitat Structure

We quantified post-fire habitat structure as the percentage of intact habitat (PI), and edge density (meters of edge per hectare; m/ha) in an analysis area (ED), and distance from a location to the nearest habitat edge (m; DTE). We used a detailed map of the Holloway fire (Appendix I), to quantify post-fire habitat structure. We assessed the percentage of intact habitat (PI), and edge density (ED) using the PLAND and Edge Density metrics respectively, in FRAGSTATS v4 (McGarigal et al. 2012). We extracted the edges of intact habitat from the fire map into a polyline

shape file using the *extractedge* function in program GME (Beyer 2012). We assessed distance to edge using the Near tool in the ArcGIS 10.1 analysis toolbox, and if locations were in intact habitat distance to edge was assigned a negative value, whereas, if locations were in burnt habitat, distance to edge was assigned a positive value.

Vegetation Regeneration

We used the mean and standard deviation of the normalized differential vegetation index (NDVI_MN, NDVI_STD) as an index of vegetation regeneration within the study area. We acquired 1 cloud free Landsat-8 image of the study area for each month of the study, and used the images to generate a NDVI raster of the study area for each month using the NDVI tool in the ArcGIS 10.1 Image Analysis toolbox. We then calculated the mean value of all NDVI rasters contained within a season to generate a seasonal estimate using the *overlay* function in package *raster* in Program R (R Version 3.2.0, www.r-project.org, accessed 1 Oct 2013). We sampled these seasonal rasters of NDVI within the analysis areas, to calculate mean and standard deviation values, using the *isectpolyrst* function in GME (Beyer 2012).

Topography

We assessed the effects of topography on habitat selection as the mean terrain ruggedness index (TRI; Wilson et al. 2007), and mean elevation (EL) within each analysis area. The terrain ruggedness index calculates the mean difference in elevation (in meters) between each cell and its 8 neighboring cells, and reflects heterogeneity of terrain at the 180 m^2 scale (9-pixel blocks; Wilson et al. 2007). We acquired a 10 m digital elevation model (DEM) raster dataset from the National Elevation Dataset (USGS 2015). We generated a TRI raster, from the acquired DEM, for the study area using the *terrain* function of package *raster* in Program R, and then used the *isectpolyrst* function in GME (Beyer 2012) to calculate the mean TRI value for each analysis area. We calculated the mean elevation for each analysis area using the *isectpolyrst* function in GME (Beyer 2012).

Seasonal Habitat Composition and Site Fidelity

Seasonal ranges were generated for each individual as outlined above (*Seasonal Range Delineation*). We compared mean seasonal habitat components, and the 95% confidence intervals around those means, to assess differences in habitat composition between seasons and years.

We calculated two measures of site fidelity to seasonal ranges for individuals that survived between years: percent overlap of seasonal ranges, and distance between seasonal range centroids. We used the Union tool in ArcMap 10.1 to calculate the area of each individual seasonal range which overlapped the other year's seasonal range, and calculated the percent of total seasonal range area accounted for by this overlap. We calculated the centroid of each seasonal range, and measured the distance between these centroids in ArcMap 10.1.

Location Scale Resource Selection

Model Development

We estimated third-order resource selection during the breeding (Mar 8 – Jun 12), summer (Jun 13 – Oct 20), and winter seasons (Oct 21 – Mar 7), using random-effects resource selection functions (RSFs) within a use-availability design (Manly et al. 2002, Gillies et al. 2006). We implemented RSFs using binary logistic regression with the *glmer* function from package *lme4* in Program R. Few individuals were present in the study during both years, so potential changes in habitat selection between years would be confounded with differences in habitat selection among individuals. Therefore, we pooled years and included only individual bird as a random effect. Only diurnal locations were used, as resource selection by sage-grouse has been shown to differ between the day and night (Dzialak et al. 2011, 2012). In addition, we removed incubating locations from the breeding season analysis so as not to bias the RSF towards nest locations. Available diurnal locations were selected at a three to one ratio versus used points within 100% minimum convex polygon seasonal ranges for each individual. If an individual was present in more

than one year, seasonal ranges and available points were generated separately for each year. Individuals were only included in the datasets if they possessed ≥ 100 total used and available locations in a season. We down-weighted available points proportional to used points in the logistic regression analyses in order to correct for any over-representation bias (used point weight = 1.0 vs. available point weight = 0.33; Hirzel et al. 2006, Aldridge and Boyce 2007, Carpenter et al. 2010).

We assessed the probability of selection for specific habitat covariates as linear, pseudo-threshold ($ln(x)$), or quadratic (x^2) relationships (Table 2.2). Psuedo-threshold structures allowed a covariate to have progressively diminishing effect on probability of selection as covariate values increase or decrease. Quadratic structures allowed probability of selection to be greatest or least at a certain middle range of covariate values, to reflect that there may be an optimum level of a covariate, at which selection for or against those factors is strongest. We assessed correlation between covariates using the *cor* function in Program R. Covariates with a Pearson's correlation coefficient >0.6 were not combined in additive models.

We used an information theoretic approach (Burnham and Anderson 2002) to select competitive models, and used Akaike's information criterion corrected for small sample sizes (AIC_c), ΔAIC_c (the difference in AIC_c value between each model and the top ranked model), and AIC_c weights to rank models (Burnham and Anderson 2002). We modeled all covariates univariately, and considered the scale and form of each covariate with the lowest AIC_c value for inclusion in more complex models. We combined covariates with the lowest AIC_c and 95% confidence limits on the model coefficient that did not overlap zero from each covariate category (e.g. Mesic Habitat Availability, Post-Fire Habitat Composition, Vegetation Regeneration, Topography) in additive models. We did not hypothesize interactions between any covariates categories. We considered models within 2 ΔAIC_c of the top model in a set to be competitive. We included "individual bird" as a random intercept, and random slope for all covariates to account for autocorrelation in observations within individuals, an unbalanced sampling design (more locations for some individuals than others), and to

potentially describe differing functional responses of individuals to habitat availability (Gillies et al. 2006).

Model Evaluation

We used variance decomposition to examine the variation explained by the most supported model in each season (Borcard et al. 1992, Lawler and Edwards 2006). We calculated the amount of total process variance explained by the most supported model by dividing the difference between the deviance (-2*log-likelihood) of the null model (intercept-only) and the deviance of the best model by the deviance of the null model ($Dev_{null} - Dev_{best}/Dev_{null}$).

RESULTS

We captured and marked 66 individual female sage-grouse beginning on 8 Mar 2013 through April 2014. After removing locations generated from likely GPS error (i.e., locations >10 km from their preceding and subsequent locations), 52,201 total individual bird locations were collected by the GPS transmitters.

Seasonal Behavior

Of individuals monitored in this study, 31 remained alive long enough after capture to display seasonal migratory behavior between at least two seasonal ranges (n = 44,441 individual locations). A majority of individuals in this study exhibited a three seasonal range movement pattern, with differences between 1) winter range and breeding/early summer range, 2) breeding-early summer range and late summer range, and 3) late summer range and winter range (Table 2.3). However, there was variation in this pattern with no marked differentiation observed for 46%, 21%, 45%, and 14% of monitored individuals between winter and nesting range, breeding and late summer range, early summer and late summer range, and late summer range and winter range, respectively. Additionally, marked differentiation was observed between breeding and early summer range for 26% of individuals. Thus, in addition to the three range movement pattern typical of many birds in the study, some

individuals appeared to be semi-resident, utilizing a central area year round; although direction of movement out of that central area differed seasonally. Additionally, some individuals exhibited a two range movement pattern, with no differentiation between winter and breeding range, a three range movement pattern, with differentiation between breeding and early summer range but no differentiation between early and late summer range, or a four range movement pattern with differentiation between winter, breeding, early summer, and late summer range. Dates of movement between seasonal ranges also varied considerably (Appendix II; Table A2.1). The mean date of movement onto late summer range from breeding/early summer range was 13 Jun, the mean date of movement onto winter range from late summer range was 21 Oct, and the mean date of entrance onto breeding range was 8 Mar (Appendix II; Table A2.1). Distance between seasonal ranges was variable between individuals, but mean distance between seasonal range centroids was consistently between 7 km – 10 km, regardless of seasonal range type (i.e. breeding to summer, summer to winter, etc.; Table 2.4).

Site Fidelity and Seasonal Habitat Composition

Few individuals were alive in both years to compare seasonal fidelity (breeding: n = 6; summer: n = 4; winter: n = 3). However, mean percent overlap of individual seasonal ranges between 2014 and 2013 for those individuals alive in both years was 48.9% (range: 20.3% - 73.1%), 51.1% (range: 7.5% - 73.6%), and 62.6% (range: 21.9% - 99.5%), during the breeding, summer, and winter seasons, respectively. Additionally, the distance between pairs of individual seasonal range centroids were small during each season, with a mean distance of 1.80 km between centroids during the breeding season (range: 0.21 km – 6.76 km), 1.65 km during summer (range: 0.15 km – 3.64 km), and 3.96 km during winter (range: 0.90 km – 8.42 km).

We assessed seasonal habitat composition using only individuals with ≥ 25 locations in a given season, after all nocturnal locations were removed, and

incubating locations were removed from the breeding season (n = 37,417 individual locations). Sixty-one individuals met this criteria during at least one season, and seasonal habitat composition was assessed for 131 individual seasonal ranges (Table 2.5). Across the suite of habitat covariates used to assess seasonal range composition, few differences in mean habitat covariates existed between seasons, or within seasons between years (Table 2.5). Only elevation, edge density, percent mesic habitat, and mean and standard deviation of NDVI exhibited significant differences either between seasons, or between years (Table 2.5).

Breeding Resource Selection

We analyzed resource selection during the breeding seasons of 2013 and 2014, using 15,138 locations comprising 54 seasonal ranges collected from 48 individual female sage-grouse. The most supported model of third-order resource selection during this period contained fixed and random effects of the quadratic forms of mean terrain ruggedness, and percent intact habitat within a 0.564 km buffer, mean NDVI, and percent mesic habitat within a 1.41 km buffer, and mean elevation within a 0.169 km buffer. This model performed significantly better than any other models evaluated, with no other model ranking within 4,000 ΔAIC_c (Table 2.6). Inclusion of random intercepts and slopes for individuals improved model fit over the naïve RSF by thousands of AIC_c values (Table 2.6). All fixed effects included in this model were significant with no 95% confidence intervals on β parameters overlapping zero (Table 2.7). This model explained 34.8% of variance present in the data.

At the population level, sage-grouse during the breeding season selected for level terrain within a 1-km^2 area, and the relative odds of selection peaked at a mean terrain ruggedness index of 0.53 (Table 2.7; Figure 2.2). Sage-grouse selected against burnt habitat, and the relative odds of selection increased after the percentage of intact habitat within a 1-km^2 area exceeded approximately 85% (Table 2.7; Figure 2.2). Sage-grouse selected for a proportion of mesic habitat within a 6.25-km^2 buffer, which was slightly less than that present on the landscape (peak selection: 1.21%

mesic, mean value: 2.56% mesic, range: 0.01% - 26.86%), and the relative odds of selection declined as proportion increased (Table 2.7; Figure 2.2). Sage-grouse selected for mean NDVI values within a 6.25-km^2 area that were near the maximum values available on the landscape, but did not select for mean NDVI when values were <0.23 (Table 2.7; Figure 2.2). Sage-grouse selected for intermediate elevations within a 0.089-km^2 area (Table 2.7; Figure 2.2).

Coefficient estimates for the random effect of individual birds varied considerably for all covariates. Individual selection for terrain ruggedness within a 1-km^2 area was relatively constant, and all but 2 individuals selected for less rugged terrain relative to what was available in the study area (Figure 2.3). In contrast, selection for intact habitat was variable across individuals, with selection peaking for ≥1 individual at values that ranged from <5% to 100% intact habitat within a 1-km^2 area; however a plurality of individuals exhibited the strongest selection at 100% intact habitat (Figure 2.3). Within a 6.25-km^2 area, the majority of individuals selected most strongly for mean NDVI values between 0.10 and 0.20 (Figure 2.3). Likewise, individual selection for mesic habitat within a 6.25-km^2 area was highest for most individuals at values < 5%, and no individuals exhibited strong selection at values > 12% (Figure 2.3). Selection for elevation by individual birds was variable, and selection was high across the entire range of values present in the data (Figure 2.3).

Summer Resource Selection

We analyzed resource selection during the summers of 2013 and 2014 (13 Jun – 20 Oct) using 17,321 points comprising 51 seasonal ranges collected from 45 individuals. The best supported model of third-order resource selection during this period outranked the other models in this model set (no other models within 100 ΔAIC$_c$) and contained fixed and random effects of the quadratic forms of mean terrain ruggedness and edge density within a 0.564 km buffer, mean NDVI within a 1.41 km buffer, and distance to mesic habitat, and fixed effects of the quadratic form

of mean elevation within a 0.169 km buffer (Table 2.8). A model containing random slopes for all covariates was included in the model set, but did not converge (Table 2.8). Inclusion of random intercepts for individuals improved model fit over the naïve RSF by several thousand ΔAIC_c (Table 2.8). For all covariates included in the best model except edge density, 95% confidence limits on at least one model coefficient comprising the quadratic structure did not overlap zero (Table 2.7), and this model explained 26.9% of variance present in the dataset.

At the population level, sage-grouse during the summer selected for level ground within a 1-km^2 area and the relative odds of selection approached zero at terrain ruggedness index values above approximately 1.5 (Table 2.7; Figure 2.4). Sage-grouse selected for intermediate edge density values within a 1-km^2 area with a peak in relative odds of selection observed at approximately 158 m of edge per hectare (Table 2.7; Figure 2.4). Selection for mean NDVI decreased until values exceeded approximately 0.129, at which point relative odds of selection increased, and were highest at the highest available mean NDVI value observed in our data (0.203; Table 2.7; Figure 2.4). At the population level sage-grouse selected intermediate distances to mesic habitat, with relative odds of selection highest at 2.39 km (Table 2.7; Figure 2.4). Sage-grouse primarily selected for higher mean elevations within a 0.089-km^2 area, although relative odds of selection decreased until elevation exceeded 1842 m, after which relative probability of selection increased, peaking at the highest elevation present in the study area (Table 2.7; Figure 2.4).

Random individual coefficient estimates varied considerably for all covariates for which they were estimated, as did covariate values at which peak relative odds of selection occurred (Figure 2.5). The highest relative odds of selection for terrain ruggedness within a 1-km^2 area varied considerably among individual birds (Figure 2.5), however a majority of individuals did exhibit peak selection for terrain ruggedness at the minimum value available to them. The highest individual selection for edge density also varied considerably, from near uniform habitats with 1 m/ha of edge, to highly complex habitat mosaics with 594 m/ha of edge (Figure 2.5). The

pattern of peak individual selection values for mean NDVI during the summer was relatively consistent, and the majority of individuals selected for mean NDVI values between 0.08 and 0.18 (Figure 2.5). In contrast, individual selection for distance to mesic habitat was highly variable, peak selection varied across almost the entire range of values present in the data (Figure 2.5).

Winter Resource Selection

We analyzed resource selection, during the winters of 2013-2014 and 2014-2015 (21 Oct – 7 Mar), using 4,958 points comprising 26 seasonal ranges collected from 22 individuals. The best supported model of third-order resource selection during this period contained fixed and random effects of the quadratic forms of mean terrain ruggedness, percent intact habitat, and standard deviation of NDVI within a 0.169 km buffer, percent mesic habitat within a 1.41 km buffer, and mean elevation within a 0.564 km buffer, as well as a random intercept. This model performed significantly better than any other models evaluated, with no other model in the set ranking within 1,000 ΔAIC_c of it (Table 2.9). Inclusion of random intercepts and slopes for individuals improved model fit over the naïve RSF by several thousand ΔAIC_c (Table 2.9). All fixed effects were significant, with at least one model coefficient for each covariate having 95% confidence intervals which did not overlap zero (Table 2.7). According to variance decomposition this model explained 35.9% of variance present in the dataset.

At the population level, sage-grouse during the winter selected for the most level ground within a 0.089-km^2 area, and the relative odds of selection decreased as terrain ruggedness index values approached ~2.0, after which the relative odds of selection remained near zero (Table 2.7; Figure 2.6). Sage-grouse selected against burnt habitat within a 0.089-km^2 area, with relative odds of selection peaking at 91% intact habitat (Table 2.7; Figure 2.6). Sage-grouse selected against increasing variability in NDVI within a 0.089-km^2 area, with relative odds of selection for standard deviation of NDVI decreasing until values exceeded 0.050, at which point

relative odds of selection increased slightly (Table 2.7; Figure 2.6). Sage-grouse selected for a proportion of mesic habitat, within a 6.25-km^2 area, which was slightly higher than the average proportion present on the landscape (peak selection: 3.55% mesic, mean value: 2.78% mesic, range: 0.00% - 29.65%), and the relative odds of selection declined strongly at greater values (Table 2.7; Figure 2.6). Sage-grouse selected strongly for intermediate elevations within a 1-km^2 area (Table 2.7; Figure 2.6).

While random individual coefficient estimates varied considerably for all covariates, values at which peak relative odds of selection occurred were largely consistent, as we observed considerable variation in peak selection only for percent intact habitat and elevation (Figure 2.7). Individual selection for terrain ruggedness within a 0.089-km^2 area was relatively constant as all but two individuals selected for mean terrain ruggedness index values ≤ 1 (Figure 2.7). Selection for intact habitat was more variable, however there did appear to be a hard threshold of approximately 39% intact habitat within a 0.089-km^2 area, as no individuals exhibited maximum relative odds of selection at lower amounts of intact habitat, and 50% of individuals exhibited maximum selection at > 90% intact habitat (Figure 2.7). The majority of individuals selected for near zero variation in NDVI within a 0.089-km^2 area, whereas individual selection for elevation was variable, with the highest selection observed for ≥ 1 individual across the entire range of values present in the data (Figure 2.7).

DISCUSSION

Our study provides the first examination of sage-grouse resource selection and seasonal migratory behavior in the immediate years following a large-scale wildfire. Sage-grouse continued to occupy the area within and adjacent to the boundaries of the Holloway fire during all seasons throughout our study. Consistent with our hypotheses, sage-grouse selected for high proportions of intact sagebrush land cover during the winter, although at a scale smaller than anticipated. Sage-grouse during our study exhibited variable migratory behavior, as is typical of the species (Dalke et

al. 1960, Connelly et al. 1988, Connelly et al. 2011a), and exhibited considerable site fidelity to all seasonal ranges between 2013 and 2014. At the population level, sage-grouse exhibited patterns of third-order resource selection within fire-affected seasonal ranges consistent with previous observations of resource selection by populations in undisturbed habitats (Connelly et al. 2011b). Seasonal range selection in this study may better describe pre-disturbance habitat selection, while selection at smaller scales reflects attempts by individuals to meet their life-history requirements within current habitat conditions (Rettie and Messier 2000). By including random effects into our models of third-order resource selection we were able to explicitly model individual variation in habitat selection by sage-grouse, and document considerable variation in selection patterns for elevation and intact habitat mosaic during all seasons, and for mesic habitat during the summer.

The fidelity of sage-grouse to leks and nesting areas is well documented in the literature (Connelly et al. 2011a). However, the fidelity of sage-grouse to summer and winter range has received less attention (Hagen 1999, Connelly et al. 2011a, Smith 2013). Hagen (1999) demonstrated fidelity of sage-grouse to summer range, with individuals centering their summer ranges an average of 2.1 km from their previous year's summer range (our study: 1.65 km). However, Smith (2013) observed sage-grouse making atypically large migratory movements during winters of extreme snowfall. Sage-grouse in our study did not appear to respond to reductions in sagebrush cover by wildfire on winter ranges, in the same manner as they responded to extreme snowfall events in another study (Smith 2013). Several factors may have caused this apparent behavioral discrepancy in response to two different types of habitat disturbance. Wildfire in sagebrush ecosystems often leaves intact habitat islands within the fire perimeter, where soil and vegetative conditions, topography, and local weather conditions serve to protect intact vegetation. In contrast, an extreme snowfall event may render nearly all sagebrush unavailable over large areas (Smith 2013). In fact, on average, winter ranges of sage-grouse included in this study were characterized by 40% – 60% intact sagebrush land-cover (Table

2.5). Often these intact patches were composed of low sagebrush, which grows in sites with limited herbaceous production and may provide disproportionately palatable forage to wintering sage-grouse (Remington and Braun 1985, Thacker et al. 2012, Frye et al. 2013). The two years of our study were characterized by mild winters and limited snow fall, which may have allowed sage-grouse to meet their winter habitat requirements with the remaining sagebrush cover present, within, and near the fire perimeter.

At the population level sage-grouse exhibited patterns of third-order resource selection which were generally similar to those documented in populations utilizing undisturbed habitats (Connelly et al. 2011b). During all seasons sage-grouse selected strongly for level terrain, generally inhabiting hill and ridge tops, mesas, and wide valleys, as is characteristic of the species (Musil et al. 1993, Aldridge and Boyce 2007, Dzialak et al. 2011, Fedy et al. 2014). During the breeding season sage-grouse exhibited peak selection for locations which were characterized by 100% intact sagebrush land-cover within a 1-km^2 area. This result is comparable to findings across the range of the species that sage-grouse select for sagebrush cover in nesting and early brood-rearing habitats (Aldridge and Boyce 2007, Doherty et al. 2010, Dzialak et al. 2011, Connelly et al. 2011b, Fedy et al. 2014). At the population level sage-grouse appeared to select for maximum available values of NDVI, but in general, only a limited portion of the range of NDVI available on the study area was available to individuals. Sage-grouse in our study selected against variation in NDVI values at the smallest scale of analysis during winter, contrary to results from Alberta (Carpenter et al. 2010), although this discrepancy may result from differences in vegetation type between Alberta and Oregon.

Similar to the breeding season, resource selection during the summer largely confirmed our hypotheses and sage-grouse selected for landscapes with moderate levels of edge-density. Sage-grouse were presumably selecting for a habitat mosaic which suggested that the responding growth of forbs in the burned areas after the fire provided forage, while sagebrush provided escape and hiding cover. Previous studies

have documented sage-grouse utilizing the edges of meadows and sagebrush patches during the summer (Savage 1969, Dunn and Braun 1985, Klott and Lindzey 1990, Dahlgren 2005). Sage-grouse selected for higher NDVI values, consistent with individuals foraging on herbaceous vegetation (Fischer et al. 1996, Atamian et al. 2010, Connelly et al. 2011b, Fedy et al. 2014). We found that individuals exhibited peak selection at distances approximately 2.4 km from mesic areas, the mean daily straight-line movement distance for sage-grouse during summer in our study was 0.5 km, indicating that at the population level sage-grouse were not preferentially exploiting mesic resources during the summer. Whereas it has commonly been suggested that sage-grouse preferentially exploit mesic habitat resources such as wet meadows, temporary wetlands, riparian areas, and irrigated fields, during the late summer period (Fischer et al. 1996, Atamian et al. 2010, Connelly et al. 2011b, Donnelly et al. 2016), our result suggests that sage-grouse in the Trout Creek Mountains are more likely to exploit persistent forb resources as they become available at progressively higher elevations over the course of the summer (reflecting plant phenology), rather than exploiting lower elevation mesic sites. This indicates that protection of mesic areas alone may not be enough to ensure adequate late summer habitat availability for sage-grouse, and that protection and restoration of high elevation summering areas may be important for the conservation of some populations.

Taken together, these findings support the hypothesis that at the population level, sage-grouse inhabiting disturbed seasonal ranges, are unable to shift habitat selection at the seasonal range scale due to high site-fidelity, but do attempt to select habitat components at the site scale to meet their life-history requirements. However, considerable variation in habitat selection patterns existed in our study between individual sage-grouse, especially for habitat components affected by the fire. Wildlife species inhabiting ecosystems with long disturbance intervals relative to the species' lifespan are likely not well adapted to disturbance, as illustrated by life history characteristics that include high survival, high site fidelity, and low

emigration rates (Hansen and Urban 1992, Drapeau et al. 2016). This lack of adaptation to environmental disturbance events (climate, fire, etc.) may manifest as variability in habitat selection response to disturbance between individuals. In other words, while the majority of individuals may make optimal habitat selection choices at the site scale, other individuals may make a range of non-optimal habitat choices within landscapes recently impacted by disturbance. Some support for this hypothesis exists in the literature regarding sage-grouse, although due to the recent advent of the application of random-effects models to resource selection studies, the ability to quantify selection patterns of individuals will allow more scrutiny of this concept. In a population of sage-grouse affected by recent energy development, individuals exhibited variation in selection patterns against anthropogenic structures (i.e. habitat disturbance), while exhibiting consistent selection patterns towards vegetation and terrain features (i.e. habitat components not affected by disturbance) (Dzialak et al. 2012). Such variation in selection patterns within a population may serve an evolutionary function, by allowing individuals to partition post-disturbance habitat, and by allowing disturbance related selection pressures to select from a range of behaviors, some of which allow behavioral adaptation to the post-disturbance landscape. While selection patterns for post-fire habitat mosaic were highly variable during the breeding season, and summer, sage-grouse appeared to be more constrained during the winter, with no individuals exhibiting peak selection for 0.089 km^2 areas which had less than 39% intact sagebrush land-cover. This reflects the dependence of sage-grouse on sagebrush during this season.

MANAGEMENT IMPLICATIONS

Sage-grouse in our study exhibited considerable fidelity to seasonal ranges, even when those ranges were impacted by wildfire. However, within those fire affected seasonal ranges sage-grouse exhibited third-order resource selection patterns consistent with habitat selection patterns exhibited by sage-grouse populations inhabiting undisturbed habitats. These two findings indicate that wildfire has a limiting effect on sage-grouse habitat availability during the winter, the breeding

season and to a lesser extent the summer, and presumably affects overall carrying capacity of the landscape for sage-grouse. The strong selection for increased intact sagebrush land-cover during the breeding season and winter in particular, and long recovery time of sagebrush after fire (>20 years; Arkle et al. 2014) indicates that wildfire should be suppressed in these habitats, including suppression of interior fire where possible. Invasive annual grasses are widespread throughout the distribution of sage-grouse, and contribute to increased wildfire frequency, size, severity, and intensity (Miller et al. 2011), as well as recovery of sagebrush habitats after fire. Efforts to control annual grasses, are still relatively unproven at the scales which would truly effect sage-grouse populations (Davies et al. 2011). Thus, new developments in the application of green-stripping to prevent fire spread, and in the pre-positioning of fire suppression resources near fire prone sagebrush habitat may be the best hope in limiting wildfire in sage-grouse habitat, until effective methods of cheatgrass and medusahead (*Taeniatherum caput-medusae*) control are developed and proven (Murphy et al. 2013). Following large-scale wildfire, restoration efforts should focus on restoring shrub cover as quickly as possible within breeding and winter ranges, through sagebrush planting and control of invasive annual grasses.

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Table 2.1. Acronyms and brief descriptions of habitat covariates used to analyze resource selection by greater sage-grouse during 2013 and 2014 in the Trout Creek Mountains, Harney and Malhuer counties, Oregon.

Category	Acronym	Description	Units
Mesic Habitat Avaliability	DTM	Distance from location to Mesic Habitat	m
	PM	Percentage of mesic Habitat as identified by Donelly et al. (2016), in analysis area	%
Post-Fire Habitat Composition	PI	Percentage of intact habitat as identified by fire map (Appendix I), in analysis area	%
	ED	Density of intact/burnt habitat edges, in analysis area	m ha^{-1}
	DTE	Distance from location to intact/burnt habitat edge	m
Vegetation Regeneration	NDVI_MN	Mean normalized differential vegetation index (NDVI), in analysis area	0 - 1
	NDVI_STD	Standard deviation of normalized differential vegetation index (NDVI), in analysis area	0 - 1
Topography	TRI	Mean terrain ruggedness index (Wilson et al. 2007), in analysis area	m
	EL	Mean elevation, in analysis area	m

Table 2.2. Hypotheses regarding the relationships between habitat covariates and resource selection of greater sage-grouse in 2013 and 2014 in the Trout Creek Mountains, Harney and Malheur Counties, Oregon. Subscripts denote seasons analyzed, breeding (B), summer (S), winter (W).

Covariate	Third-Order Selection Hypothesis		
	Linear	Psuedo-Threshold	Quadratic
DTM_B	$\beta_{DTM} < 0$	$\beta_{\ln(DTM)} < 0$	$\beta_{DTM} > 0$, $\beta_{DTM}^2 < 0$
DTM_S	$\beta_{DTM} < 0$	$\beta_{\ln(DTM)} < 0$	$\beta_{DTM} > 0$, $\beta_{DTM}^2 < 0$
DTM_W	$\beta_{DTM} = 0$	$\beta_{\ln(DTM)} = 0$	$\beta_{DTM} = 0$, $\beta_{DTM}^2 = 0$
PM_B	$\beta_{PM} > 0$	$\beta_{\ln(PM)} > 0$	$\beta_{PM} > 0$, $\beta_{PM}^2 < 0$
PM_S	$\beta_{PM} > 0$	$\beta_{\ln(PM)} > 0$	$\beta_{PM} > 0$, $\beta_{PM}^2 < 0$
PM_W	$\beta_{PM} = 0$	$\beta_{\ln(PM)} = 0$	$\beta_{PM} = 0$, $\beta_{PM}^2 = 0$
PI_B	$\beta_{PI} > 0$	$\beta_{\ln(PI)} > 0$	$\beta_{PI} > 0$, $\beta_{PI}^2 < 0$
PI_S	$\beta_{PI} < 0$	$\beta_{\ln(PI)} < 0$	$\beta_{PI} > 0$, $\beta_{PI}^2 < 0$
PI_W	$\beta_{PI} > 0$	$\beta_{\ln(PI)} > 0$	$\beta_{PI} > 0$, $\beta_{PI}^2 < 0$
ED_B	$\beta_{ED} > 0$	$\beta_{\ln(ED)} > 0$	$\beta_{PM} > 0$, $\beta_{PM}^2 < 0$
ED_S	$\beta_{ED} > 0$	$\beta_{\ln(ED)} > 0$	$\beta_{PM} > 0$, $\beta_{PM}^2 < 0$
ED_W	$\beta_{ED} < 0$	$\beta_{\ln(ED)} < 0$	$\beta_{ED} > 0$, $\beta_{PM}^2 < 0$
DTE_B	$\beta_{DTE} > 0$	$\beta_{\ln(DTE)} > 0$	$\beta_{DTE} > 0$, $\beta_{DTE}^2 < 0$
DTE_S	$\beta_{DTE} < 0$	$\beta_{\ln(DTE)} < 0$	$\beta_{DTE} > 0$, $\beta_{DTE}^2 < 0$
DTE_W	$\beta_{DTE} < 0$	$\beta_{\ln(DTE)} < 0$	$\beta_{DTE} > 0$, $\beta_{DTE}^2 < 0$
$NDVI\_MN_B$	$\beta_{NDVI\_MN} > 0$	$\beta_{\ln(NDVI\_MN)} > 0$	$\beta_{NDVI\_MN} > 0$, $\beta_{NDVI\_MN}^2 < 0$
$NDVI\_MN_S$	$\beta_{NDVI\_MN} > 0$	$\beta_{\ln(NDVI\_MN)} > 0$	$\beta_{NDVI\_MN} > 0$, $\beta_{NDVI\_MN}^2 < 0$
$NDVI\_MN_W$	$\beta_{NDVI\_MN} = 0$	$\beta_{\ln(NDVI\_MN)} = 0$	$\beta_{NDVI\_MN} = 0$, $\beta_{NDVI\_MN}^2 = 0$
$NDVI\_STD_B$	$\beta_{NDVI\_STD} < 0$	$\beta_{\ln(NDVI\_STD)} < 0$	$\beta_{NDVI\_STD} > 0$, $\beta_{NDVI\_STD}^2 < 0$
$NDVI\_STD_S$	$\beta_{NDVI\_STD} < 0$	$\beta_{\ln(NDVI\_STD)} < 0$	$\beta_{NDVI\_STD} > 0$, $\beta_{NDVI\_STD}^2 < 0$
$NDVI\_STD_W$	$\beta_{NDVI\_STD} < 0$	$\beta_{\ln(NDVI\_STD)} < 0$	$\beta_{NDVI\_STD} > 0$, $\beta_{NDVI\_STD}^2 < 0$
TRI_B	$\beta_{TRI} < 0$	$\beta_{\ln(TRI)} < 0$	$\beta_{TRI} > 0$, $\beta_{TRI}^2 < 0$
TRI_S	$\beta_{TRI} < 0$	$\beta_{\ln(TRI)} < 0$	$\beta_{TRI} > 0$, $\beta_{TRI}^2 < 0$
TRI_W	$\beta_{TRI} < 0$	$\beta_{\ln(TRI)} < 0$	$\beta_{TRI} > 0$, $\beta_{TRI}^2 < 0$
EL_B	$\beta_{TRI} < 0$	$\beta_{\ln(TRI)} < 0$	$\beta_{TRI} > 0$, $\beta_{TRI}^2 < 0$
EL_S	$\beta_{TRI} > 0$	$\beta_{\ln(TRI)} > 0$	$\beta_{TRI} > 0$, $\beta_{TRI}^2 < 0$
EL_W	$\beta_{TRI} < 0$	$\beta_{\ln(TRI)} < 0$	$\beta_{TRI} > 0$, $\beta_{TRI}^2 < 0$

Table 2.3. Yearly sample sizes of marked greater sage-grouse used to assess movement patterns between seasons, and percent of these individuals [n (%)] exhibiting specific seasonal migration patterns, during 2013 and 2014 in the Trout Creek Mountains, Harney and Malheur Counties, Oregon. Initial capture in the study took place on March 8, 2013, during the initial breeding season post-fire, which did not allow us to assess movement patterns between winter 2012 and breeding season 2013.

	2013	2014
Seasonal Transition	n (%)	n (%)
Winter - Breeding	NA	11 (54.5)
Breeding - Early Summer	13 (23.1)	18 (27.8)
Breeding - Late Summer	13 (76.9)	16 (81.3)
Early Summer - Late Summer	13 (53.8)	16 (56.3)
Late Summer - Winter	14 (85.7)	14 (85.7)

Table 2.4. Mean distance (km) between seasonal ranges of female greater sage-grouse, during 2013 and 2014, in the Trout Creek Mountains, Harney and Malheur Counties, Oregon.

		Breeding to Summer			Summer to Winter			Winter to Breeding	
Year	n	Distance (km)	Range	n	Distance (km)	Range	n	Distance (km)	Range
2013	10	8.80	3.79 - 19.40	12	8.38	3.79 - 14.46	-	-	-
2014	13	7.90	2.77 - 15.44	12	9.26	2.49 - 15.85	7	7.18	1.81 - 20.47
Both	23	8.29	2.77 - 19.40	24	8.82	2.49 - 15.85	-	-	-

Table 2.5. Means and 95% confidence intervals [$\bar{x}(95\%CIs)$] of habitat components calculated within seasonal ranges of individual greater sage-grouse (n), during 2013 and 2014, in the Trout Creek Mountains, Harney and Malheur Counties, Oregon.

Season	n	Percent Mesic (%)		Percent Intact (%)		Edge Density (m/ha)		Terrain ruggedness Index (m)		Elevation (m)	
		Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI
Breeding -2013	32	1.19	0.46 - 1.92	47.0	36.9 - 57.1	135	106 - 164	1.28	1.16 - 1.40	1865	1823 - 1906
Breeding -2014	22	1.63	0.80 - 2.46	49.3	37.4 - 61.3	186	142 - 230	1.17	1.01 - 1.33	1801	1759 - 1842
Summer - 2013	28	0.26	-0.11 - 0.63	36.1	27.6 - 44.5	129	108 - 150	1.17	1.07 - 1.28	2137	2080 - 2193
Summer - 2014	23	0.77	-0.04 - 1.58	35.1	25.3 - 44.8	113	92 - 134	1.15	1.04 - 1.25	2130	2040 - 2220
Winter - 2013	14	0.71	0.24 - 1.18	41.2	28.0 - 54.5	131	97 - 165	1.27	1.09 - 1.46	1866	1806 - 1926
Winter - 2014	12	2.26	1.29 - 3.22	57.0	43.2 - 70.7	178	142 - 213	1.24	1.04 - 1.44	1817	1768 - 1866

Table 2.5 *continued.* Means and 95% confidence intervals [$\bar{x}(95\%CIs)$] of habitat components calculated within seasonal ranges of individual greater sage-grouse (n), during 2013 and 2014, in the Trout Creek Mountains, Harney and Malheur Counties, Oregon.

		Mean NDVI		Standard Dev. NDVI	
Season	n	Mean	95% CI	Mean	95% CI
Breeding -2013	31[a]	0.131	0.125 - 0.136	0.026	0.023 - 0.029
Breeding -2014	22	0.141	0.130 - 0.153	0.032	0.027 - 0.036
Summer - 2013	28	0.138	0.131 - 0.146	0.034	0.031 - 0.037
Summer - 2014	23	0.145	0.139 - 0.151	0.035	0.031 - 0.040
Winter - 2013	14	0.074	0.070 - 0.078	0.019	0.017 - 0.021
Winter - 2014	12	0.076	0.072 - 0.079	0.026	0.022 - 0.029

[a]Mean NDVI components during the breeding season of 2013 were calculated using one fewer individual than other mean habitat components during that period.

Table 2.6. Model selection results for additive models of breeding season resource selection by sage-grouse during 2013 and 2014, in the Trout Creek Mountains, Harney and Malheur Counties, Oregon. Models were ranked according to Akaike's information criterion corrected for small sample size (AIC_c). Number of parameters (k), ΔAIC_c, log-likelihood, and model deviance are given for all models. Covariate acronyms are described in Table 1. Prefixes indicated sampling scale _S = 0.169 km point buffer, _M = 0.564 km point buffer, _L = 1.41 km point buffer. All covariates in supported models were assessed under a quadratic structure. Subscripts indicate whether random individual slopes were included for that covariate.

Model	k	ΔAIC_c	Log-Likelihood	Deviance
$M\_TRI^2_{RE} + M\_PI^2_{RE} + L\_NDVI\_MN^2_{RE} + L\_PM^2_{RE} + S\_ELEV^2_{RE}$	23	0	–41061	82123
$M\_TRI^2_{RE} + M\_PI^2_{RE} + L\_NDVI\_MN^2_{RE} + L\_PM^2_{RE}$	19	4856	–43493	86986
$M\_TRI^2_{RE} + M\_PI^2_{RE} + L\_NDVI\_MN^2_{RE}$	15	9327	–45733	91465
$M\_TRI^2_{RE} + M\_PI^2_{RE} + L\_PM^2_{RE}$	15	9894	–46017	92033
$M\_TRI^2_{RE} + M\_PI^2_{RE}$	11	14771	–48459	96917
$M\_TRI^2_{RE} + L\_NDVI\_MN^2_{RE}$	11	16175	–49161	98321
$M\_TRI^2_{RE} + L\_PM^2_{RE}$	11	16345	–49246	98492
$M\_TRI^2 + M\_PI^2 + L\_NDVI\_MN^2 + L\_PM^2 + S\_ELEV^2$	11	35422	–58785	117569

Table 2.7. Fixed effects model coefficient estimates and lower (LCL) and upper (UCL) 95% confidence limits for the effects of habitat covariates on breeding, summer, and winter resource selection by sage-grouse during 2013 and 2014, in the Trout Creek Mountains, Harney and Malheur Counties, Oregon. Covariate acronyms are described in Table 1. Prefixes indicate sampling scale _S = 0.169 km point buffer, _M = 0.564 km point buffer, _L = 1.41 km point buffer.

Habitat Covariate	Model Coefficient	LCL	UCL
Breeding			
M_TRI	1.301	1.150	1.450
M_TRI^2	−1.222	−1.280	−1.160
M_PI	−0.007	−0.012	−0.003
M_PI^2	0.001	0.001	0.001
L_NDVI_MN	−184.772	−186.080	−183.460
L_NDVI_MN^2	1069.801	1062.860	1076.740
L_PM	0.632	0.600	0.670
L_PM^2	−0.284	−0.290	−0.280
S_ELEV	0.097	0.097	0.097
S_ELEV^2	−0.00003	−0.00003	−0.00003
Summer			
M_TRI	−3.428	−4.780	−2.080
M_TRI^2	0.406	−0.450	1.270
M_ED	0.007	−0.002	0.016
M_ED^2	0.00002	0.00005	0.00000
L_NDVI_MN	−90.954	−105.990	−75.920
L_NDVI_MN^2	352.829	266.330	439.330
DTM	0.004	0.003	0.004
DTM^2	−0.0000008	−0.0000009	−0.0000006
S_ELEV	−0.012	−0.013	−0.011
S_ELEV^2	0.000003	0.000003	0.000004
Winter			
S_TRI	−0.017	−0.055	0.510
S_TRI^2	−0.730	−0.970	−0.490
S_PI	0.042	0.026	0.058
S_PI^2	−0.0002	−0.0003	−0.0001
S_NDVI_STD	−58.646	−82.670	−34.620
S_NDVI_STD^2	590.511	−204.410	1385.430
L_PM	0.453	0.270	0.640
L_PM^2	−0.064	−0.076	−0.052

M_ELEV	0.071	0.071	0.072
M_ELEV^2	−0.00002	−0.00002	−0.00002

Table 2.8. Model selection results for additive models of summer resource selection by sage-grouse during 2013 and 2014, in the Trout Creek Mountains, Harney and Malheur Counties, Oregon. Models were ranked according to Akaike's information criterion corrected for small sample size (AIC$_c$). Number of parameters (k), ΔAIC$_c$, log-likelihood, and model deviance are given for all models. Covariate acronyms are described in Table 1. Prefixes indicated sampling scale _S = 0.169 km point buffer, _M = 0.564 km point buffer, _L = 1.41 km point buffer. All covariates in supported models were assessed under a quadratic structure. Subscripts indicate whether random individual slopes were included for that covariate.

Model	k	ΔAIC$_c$	Log-Likelihood	Deviance
$M\_TRI^2_{RE} + M\_ED^2_{RE} + L\_NDVI\_MN^2_{RE} + DTM^2_{RE} + S\_ELEV^2$	21	0	–52865	27877
$M\_TRI^2_{RE} + M\_ED^2_{RE} + L\_NDVI\_MN^2_{RE} + DTM^2_{RE}$	19	117	–52926	28155
$M\_TRI^2 + M\_ED^2_{RE} + L\_NDVI\_MN^2_{RE} + DTM^2_{RE} + S\_ELEV^2_{RE}$	21	433	–53081	29609
$M\_TRI^2_{RE} + M\_ED^2_{RE} + DTM^2_{RE}$	15	2847	–54295	108589
$M\_TRI^2_{RE} + L\_NDVI\_MN^2_{RE} + DTM^2_{RE}$	15	3585	–54664	109327
$M\_TRI^2_{RE} + DTM^2_{RE}$	11	7224	–56487	112974
$M\_TRI^2_{RE} + L\_NDVI\_MN^2_{RE}$	11	10408	–58079	116158
$M\_TRI^2_{RE} + M\_ED^2_{RE}$	11	10621	–58186	116371
$M\_TRI^2 + M\_ED^2 + L\_NDVI\_MN^2 + DTM^2 + S\_ELEV^2$	11	27225	–66488	132975

Table 2.9. Model selection results for additive models of winter resource selection by sage-grouse during 2013 and 2014, in the Trout Creek Mountains, Harney and Malheur Counties, Oregon.   Models were ranked according to Akaike's information criterion corrected for small sample size (AIC$_c$). Number of parameters (k), ΔAIC$_c$, log-likelihood, and model deviance are given for all models. Covariate acronyms are described in Table 1. Prefixes indicated sampling scale _S = 0.169 km point buffer, _M = 0.564 km point buffer, _L = 1.41 km point buffer. All covariates in supported models were assessed under a quadratic structure. Subscripts indicate whether random individual slopes were included for that covariate.

Model	k	ΔAIC$_c$	Log-Likelihood	Deviance
$S\_TRI^2_{RE} + S\_PI^2_{RE} + S\_NDVI\_STD^2_{RE} + L\_PM^2_{RE} + M\_ELEV^2_{RE}$	23	0	−13270	26541
$S\_TRI^2_{RE} + S\_PI^2_{RE} + S\_NDVI\_STD^2_{RE} + L\_PM^2_{RE}$	19	1328	−13938	27877
$S\_TRI^2_{RE} + S\_PI^2_{RE} + L\_PM^2_{RE}$	15	1598	−14077	28155
$S\_TRI^2_{RE} + S\_PI^2_{RE} + S\_NDVI\_STD^2_{RE}$	15	2665	−14611	29222
$S\_TRI^2_{RE} + S\_PI^2_{RE}$	11	3044	−14804	29609
$S\_TRI^2_{RE} + L\_PM^2_{RE}$	11	3363	−14964	29928
$S\_TRI^2_{RE} + S\_NDVI\_STD^2_{RE}$	11	4379	−15472	30944
$S\_TRI^2 + S\_PI^2 + S\_NDVI\_STD^2 + L\_PM^2 + M\_ELEV^2$	11	4502	−15534	31067

Figure 2.1. Holloway fire severity in relation to Trout Creeks Sage-Grouse Priority Area of Conservation (PAC), Oregon. Inset depicts Holloway fire (red outline) in relation to all Oregon Sage-Grouse PACs (green polygons).
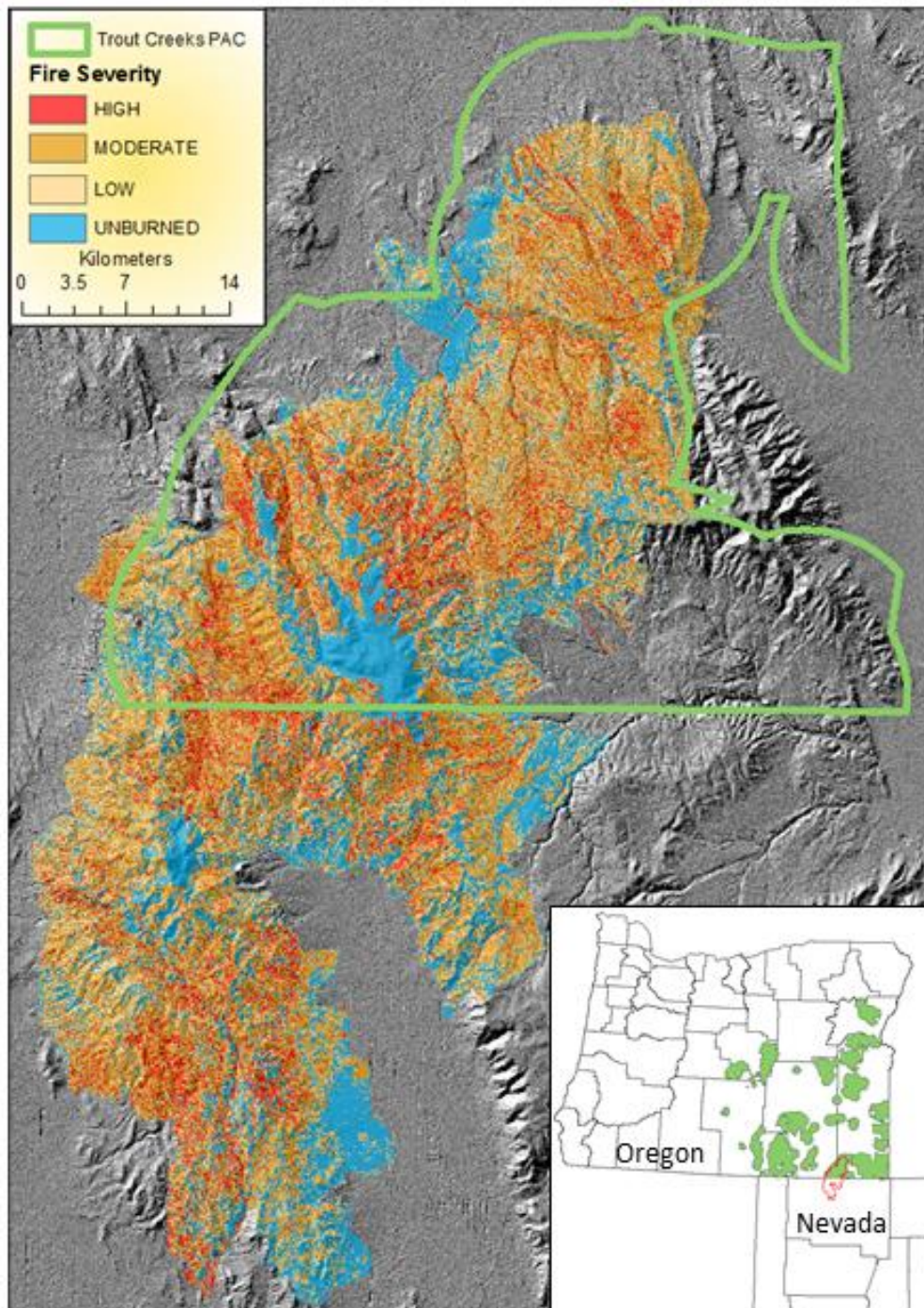
Figure 2.2. Population level (marginal) estimates of scaled relative odds of selection for each habitat covariate included in the top model of sage-grouse resource selection during the breeding seasons of 2013 and 2014 in the Trout Creek Mountains, Harney and Malheur Counties, Oregon. Relative odds of selection were calculated while holding the remaining covariates at mean values, and then plotted against the range of covariate values included in the analysis.
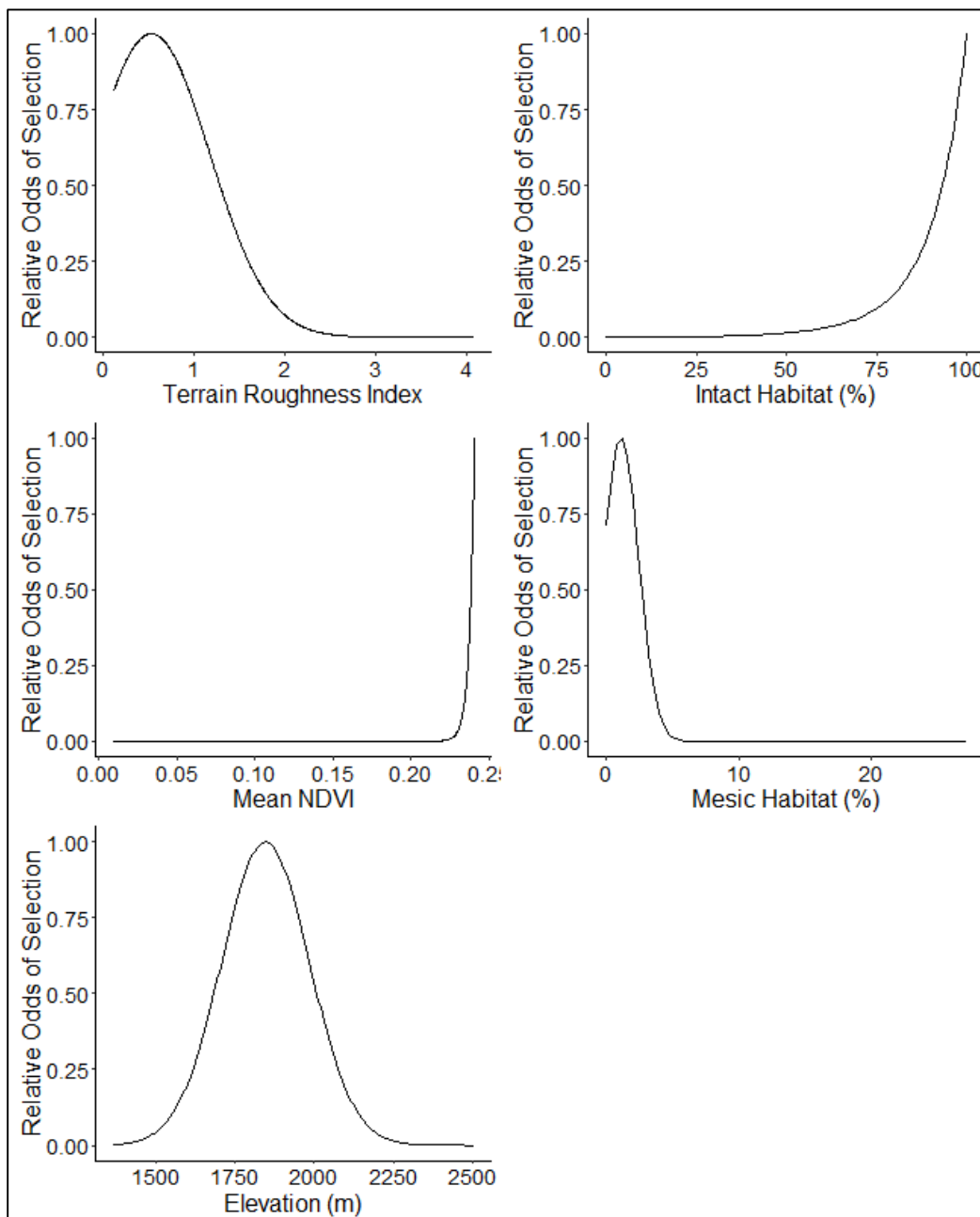
Figure 2.3. Conditional and marginal estimates of covariate values at which relative odds of selection peaked for sage-grouse during the breeding season, while holding all other covariates at mean values, during 2013 and 2014, in the Trout Creek Mountains, Harney and Malheur Counties, Oregon. Values are plotted within the range of observed values for both used and available points. X axis corresponds to estimates, pink circles denote individual conditional estimates, blue triangles and dashed lines denote marginal estimates (i.e., population means). Conditional estimates were generated within the range of covariate values present for each individual, marginal estimates were generated within the complete range of covariate values present in the data.
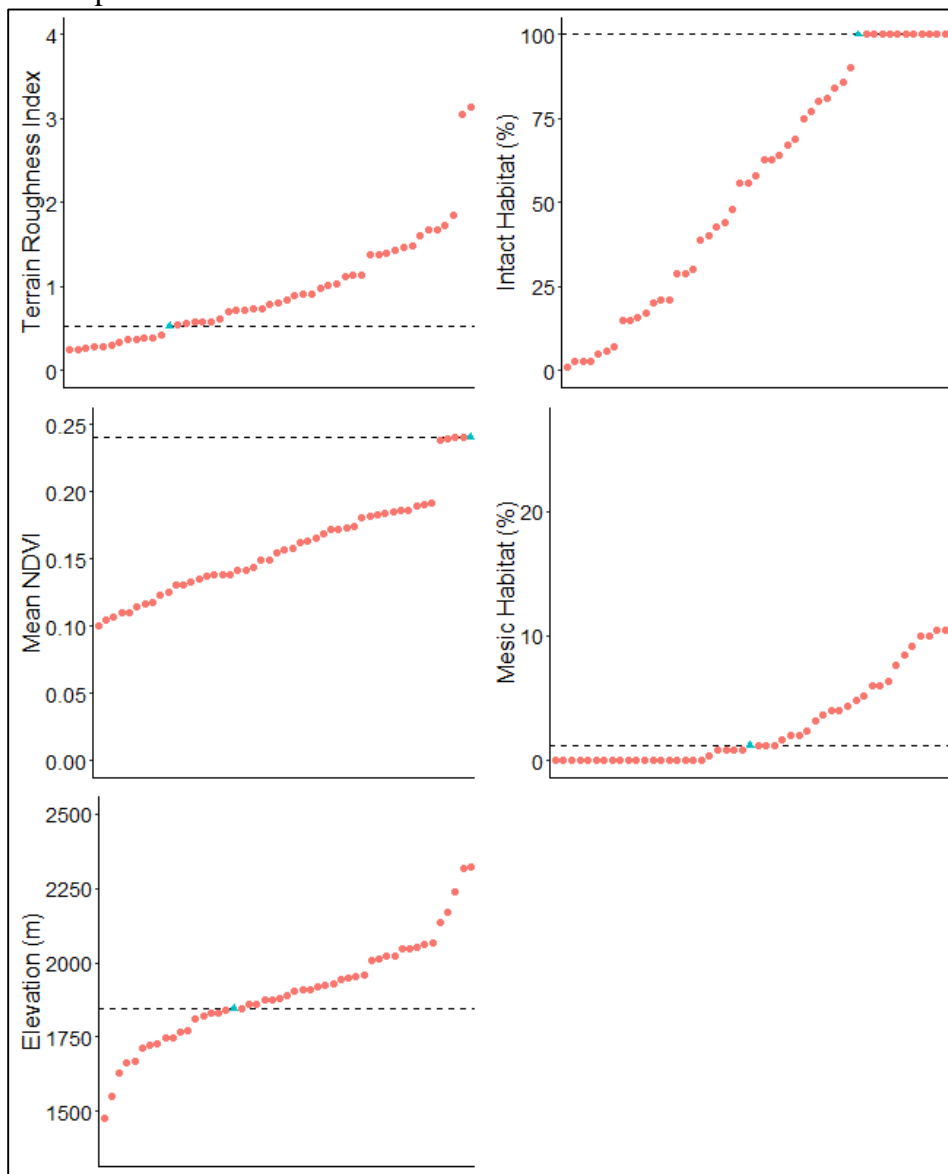
Figure 2.4. Population level (marginal) estimates of scaled relative odds of selection for each of the covariates included in the top model of sage-grouse summer resource selection, while holding the remaining covariates at mean values, during 2013 and 2014 in the Trout Creek Mountains, Harney and Malheur Counties, Oregon.
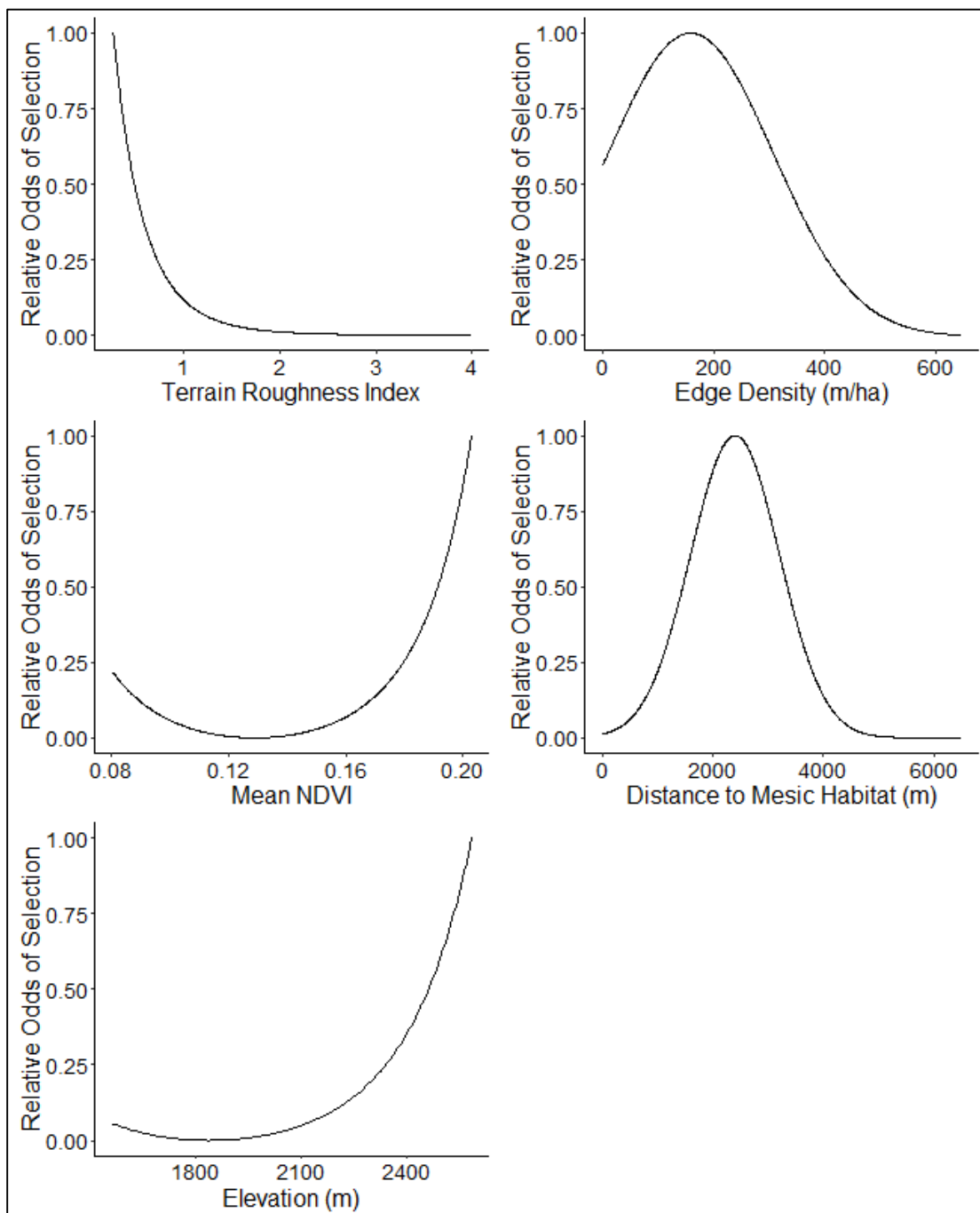
Figure 2.5. Conditional and marginal estimates of covariate values at which relative odds of selection peaked for sage-grouse during the summer, while holding all other covariates at mean values, during 2013 and 2014, in the Trout Creek Mountains, Harney and Malheur Counties, Oregon. Values are plotted within the range of observed values for both used and available points. X axis corresponds to estimates, pink circles denote individual conditional estimates, blue triangles and dashed lines denote marginal estimates (i.e., population means). Conditional estimates were generated within the range of covariate values present for each individual, marginal estimates were generated within the complete range of covariate values present in the data.
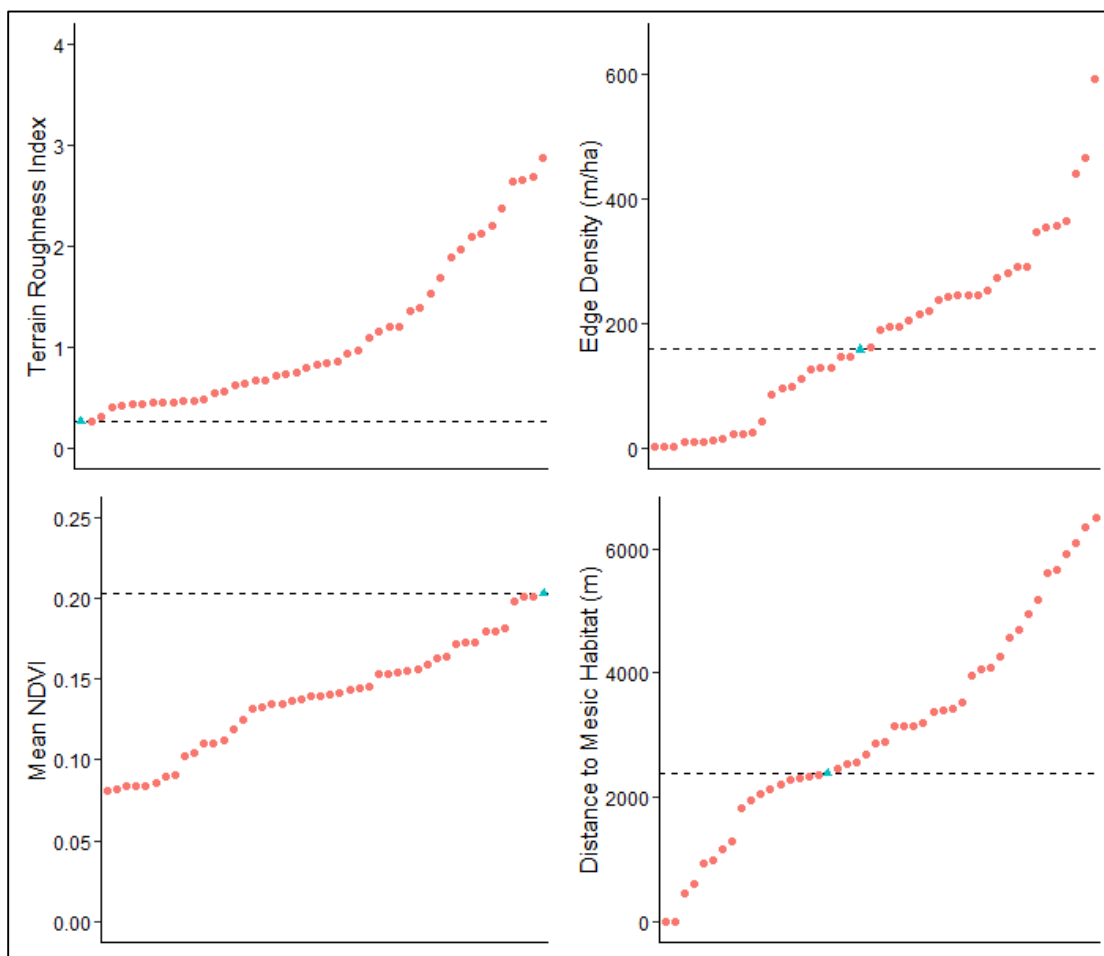
Figure 2.6. Population level (marginal) estimates of scaled relative odds of selection for each of the covariates included in the top model of sage-grouse resource selection, while holding the remaining covariates at mean values, during the winters of 2013-2014 and 2014-2015 in the Trout Creek Mountains, Harney and Malheur Counties, Oregon.
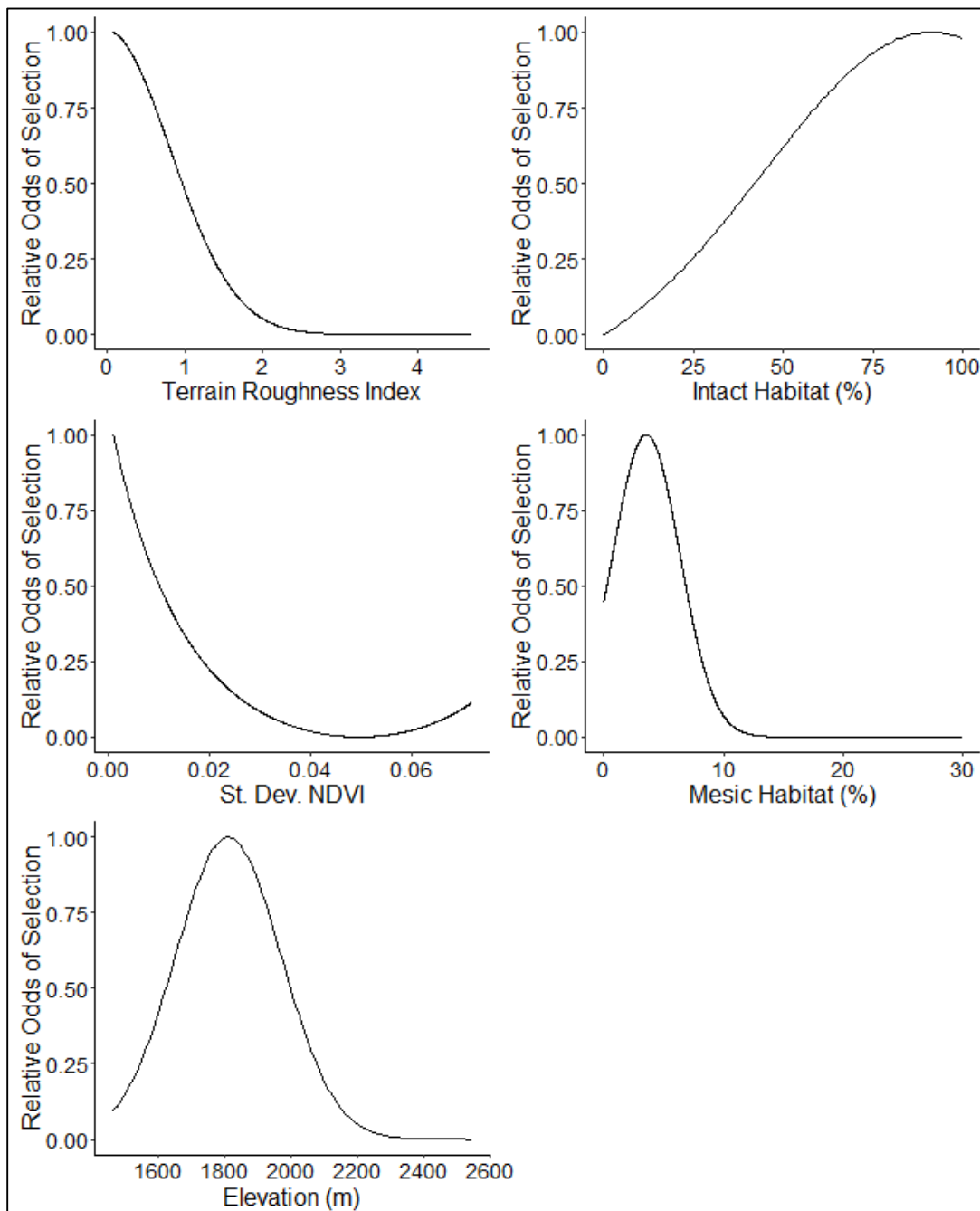
Figure 2.7. Conditional and marginal estimates of covariate values at which relative odds of selection peaked for sage-grouse during the winter, while holding all other covariates at mean values, during 2013-2014 and 2014-2015, in the Trout Creek Mountains, Harney and Malheur Counties, Oregon. Values are plotted within the range of observed values for both used and available points. X axis corresponds to estimates, pink circles denote individual conditional estimates, blue triangles and dashed lines denote marginal estimates (i.e., population means). Conditional estimates were generated within the range of covariate values present for each individual, marginal estimates were generated within the complete range of covariate values present in the data
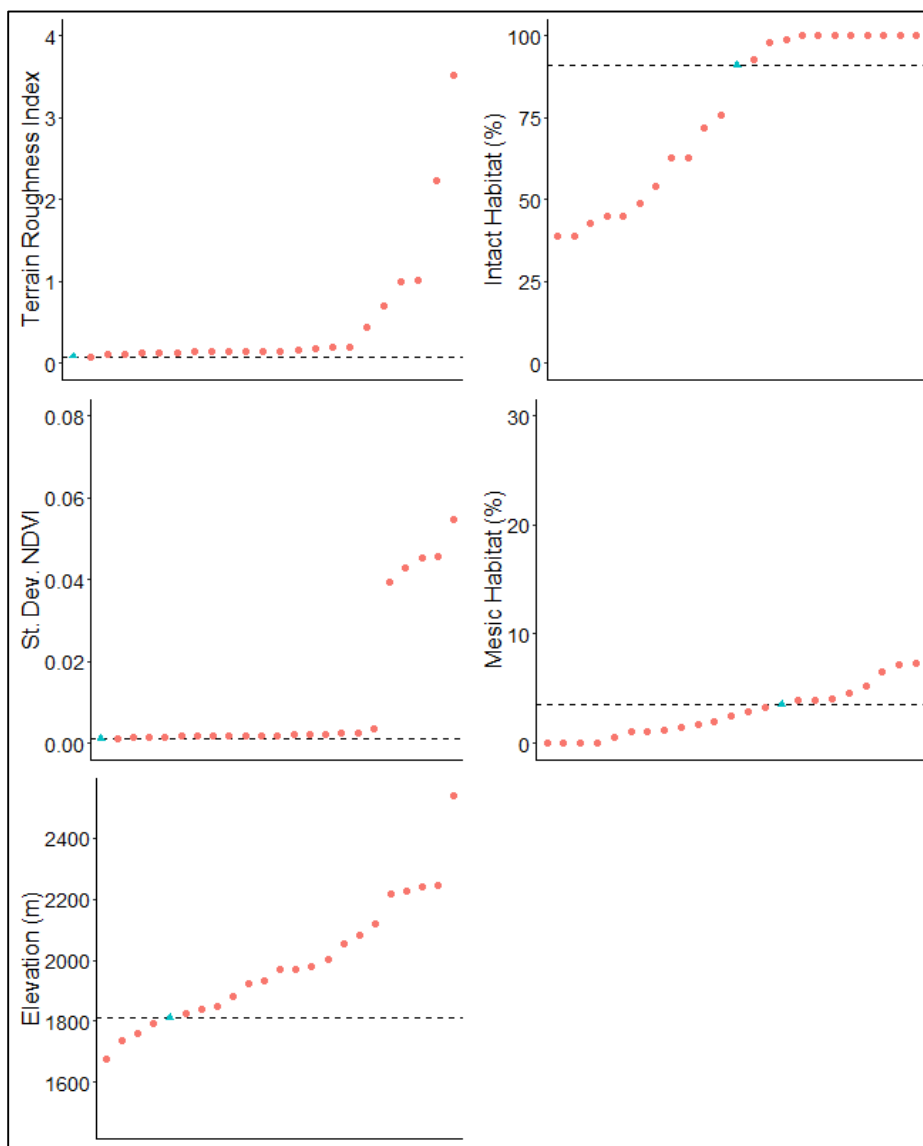
CHAPTER 3

GREATER SAGE-GROUSE NEST SURVIVAL AND NESTING
HABITAT FOLLOWING LARGE-SCALE WILDFIRE

Lee Foster, Katie Dugger, Christian Hagen, Dave Budeau

ABSTRACT

Greater sage-grouse (*Centrocercus urophasianus*) have been subject to long-term and continuing declines in population and habitat since European settlement of western North America. Increased wildfire activity constitutes a primary threat to the species in western portions of their range, with documented population declines following wildfire. We investigated, nesting effort, nest survival, and nesting habitat use of female sage-grouse following a large-scale (~187,000 ha) wildfire in southeastern Oregon. We used GPS telemetry to monitor female sage-grouse for nest initiation and nest-fate during 2013 and 2014, during the first two breeding seasons following the fire. We used known-fate models in Program MARK to estimate daily nest survival in relation to temporal patterns, physiological characteristics of females, and habitat characteristics of nest sites. We assessed nesting habitat characteristics using line-point intercept, gap-intercept, and visual obstruction habitat survey methods. Nest initiation rate did not appear to decrease following the fire, we observed nesting rates of 90% and 100%, during 2013 and 2014 respectively, and renesting rates of 23% and 57% during the same years. Daily nest survival was affected by nesting chronology and year, with consistently low nest survival rates for 1st nests during both years, and 2nd nests during 2013, but markedly increased survival for second nests during 2014. Sage-grouse did not leave the fire, in large numbers, to nest, with 64% and 73% of nests located in the fire, during 2013 and 2014 respectively. Approximately 27% of nests were located in burnt habitat during 2013, and 20% of nests in 2014 were located in burnt habitat. Our results indicate that sage-grouse continue to nest within fire-affected habitat in the immediate years following wildfire, and that this behavior potentially has fitness costs for sage-grouse during at least the first year following wildfire.

INTRODUCTION

Greater sage-grouse (*Centrocercus* urophasianus; hereafter: sage-grouse) are a species of conservation concern in western North America, undergoing long-term population declines across their distribution (Garton et al. 2011). These population declines have been linked to widespread habitat loss and degradation across its distribution (Crawford and Lutz 1985, Klebenow 1985, Connelly et al. 2004, Connelly et al. 2011a, Garton et al. 2011). While having less influence on rates of population change than brood or adult female survival, nest success is an important factor influencing sage-grouse population stability (Crawford and Lutz 1985, Gregg et al. 1994, Baxter et al. 2008, Taylor et al. 2012). Sage-grouse nest success is influenced by multiple factors including female age, weather, and nesting habitat (Connelly et al. 2011a, 2011c). Degradation or disturbance of nesting habitat can alter sage-grouse nesting behavior, and reduce nest success (Connelly et al. 2011a, 2011c).

Sage-grouse are a sagebrush (*Artemisia spp.*) obligate species and require sagebrush habitats during every phase of their lifecycle (Patterson 1952). This dependence on sagebrush is acute during the nesting period (Connelly et al. 2011c), with 60% to 100% of sage- grouse nests located under sagebrush shrubs (Patterson 1952, Popham and Gutiérrez 2003, Connelly et al. 2011c). In addition, preferred sagebrush nesting habitat includes taller sagebrush plants (Wallestad and Pyrah 1974, Sveum et al. 1998, Holloran et al. 2005, Connelly et al. 2011c) and greater canopy cover (Klebenow 1969, Fischer 1994, Sveum et al. 1998, Aldridge and Brigham 2002, Hagen et al. 2007). The response of sage-grouse nesting behavior to habitat fragmentation and disturbance can vary, and the scale of disturbance may be important in predicting post-disturbance nesting behavior (Klebenow 1970, Schroeder 1997). Ultimately, sage-grouse nest success is dependent on the interaction between

nest site vegetation and the density and composition of local predator communities (Connelly et al. 2011c).

While sagebrush habitat degradation and loss due to anthropogenic influences is well documented (Schroeder et al. 2004, Connelly et al. 2011b, Knick et al. 2011, Leu and Hanser 2011), wildfire is now considered a primary threat to sage-grouse habitat in the western portion of its range (USFWS 2015). Wildfire activity across western North America has resulted in sage-grouse habitat alterations at large spatial scales (Baker 2009, 2011), and both the total number of fires and total area burned within the range of sage-grouse has increased annually since 1980 (Miller et al. 2011). The effects of wildfire in sagebrush ecosystems can linger because habitat regeneration is slow (35 – 120 yrs), as most species of sagebrush do not resprout following fire but must regenerate from seed sources (Baker 2006).

Most studies of the effects of fire on sage-grouse populations, and habitat, have occurred either following prescribed fires or multiple years after small wildfires (Lockyer et al. 2015). Additionally, research on the effects of fire on sage-grouse habitat and productivity has been biased towards studies of vegetation response rather than population response. Prescribed burning, which generally happens on small spatial scales, has neutral or negative effects on sage-grouse habitat associated with reduced sagebrush cover and structure after burning (Pyle and Crawford 1996, Connelly et al. 2000, Nelle et al. 2000, Beck et al. 2009, Rhodes et al. 2010). However, wildfires differ from prescribed fires in timing, intensity, severity, and size (Slater 2003, Baker 2011) and may affect sage-grouse more severely.

A long-history of research on the effect of habitat disturbance on sage-grouse populations exists in the literature and can be characterized in general as attempts to: 1) understand the structure of habitat alterations, and the recovery of habitat components identified as critical to sage-grouse persistence (Pyle and Crawford 1996,

Connelly et al. 2000, Nelle et al. 2000, Beck et al. 2009, Rhodes et al. 2010); 2) quantify patterns of habitat selection following habitat disturbance (Martin 1990, Byrne 2002, Holloran et al. 2005, Harju et al. 2011); and 3) estimate survival, productivity, or population growth in relation to habitat disturbance (Holloran et al. 2005, Dzialak et al. 2011, Coates et al. 2015). Early research concerning fire effects on sage-grouse populations was focused primarily on the structure of habitat alterations and recovery after fire. However, more recently, researchers have examined the demographic response of sage-grouse to fire disturbance, and observed generally negative effects of large wildfire or prescribed burns observed for lek populations, recruitment and population rate of increase (Blomberg et al. 2012, Connelly et al. 2000, Coates et al. 2015) and survival (Lockyer et al. 2015). To fully understand the potential consequences of wildfire on sage-grouse populations it is necessary to not only understand the effects of fire on sage-grouse habitat, but also the habitat selection response of sage-grouse to fire, and the consequences of habitat selection on sage-grouse productivity following fire.

Immediately following the fire season of 2012, during which >400,000 ha of sage-grouse habitat burned in Oregon, we utilized GPS PTT technology to investigate sage-grouse nest locations and daily survival in response to one ~187,000 ha fire in southeastern Oregon and Northern Nevada. The objectives of our study were to:

1. Quantify sage-grouse nest initiation rates following a large-scale wildfire.

2. Describe nesting habitat utilized by sage-grouse within and adjacent to the boundaries of a large-scale wildfire.

3. Estimate daily nest survival (DNS) rates and the spatial and temporal factors associated with DNS within fire affected and associated habitats.

STUDY AREA

      This study took place in the Trout Creek Mountains of southeastern Oregon. The Trout Creeks range in elevation from 1372 m to over 2438 m (Evenden 1989), and are characterized by mesas, buttes, and fault blocks cut with deep stream canyons (Carlton 1968). Prior to the large-scale wildfire that occurred in southeastern Oregon and northern Nevada during summer 2012 (hereafter known as the "Holloway fire"), the vegetation communities present in the study area varied based on elevation and topography. At upper elevations (> 1900 m) a mountain big sagebrush (*A. t. vaseyana*) – low sagebrush (*A. arbuscula*) mosaic dominates, interspersed with a mountain shrub community of snowberry (*Albus* spp.), antelope bitterbrush (*Purshia tridentata*), and *Ceanothus* spp. (Freeborn 2006). Native grasses at higher elevations include Idaho fescue (*Festuca idahoensis*), needlegrass (*Achnatherum* spp.), bluebunch wheatgrass (*Pseudoroegneria spicata*), and Sandburg's bluegrass (*Poa secunda*) (Freeborn 2006). Additionally mountain mahogany (*Cercocarpus* spp.) and quaking aspen (*Populus tremuloides*) patches dot the higher elevations, and cheatgrass (*Bromus tectorum*) is generally absent (Freeborn 2006). At lower elevations Wyoming big sagebrush (*A. t. wyomingensis*) dominates, with areas of salt desert shrubs present on more alkaline soils (Freeborn 2006). Grasses at lower elevations include bluebunch wheatgrass, needlegrass, Sandberg's bluegrass, bottlebrush squirreltail (*Elymus elymoides*), basin wildrye (*Leymus cinerius*), and cheatgrass, while western juniper (*Juniperus occidentalis*) is rare or absent from the study area (Freeborn 2006). Approximately 95% of the area is managed by the Bureau of Land Management (BLM), a large portion of which is designated as Wilderness Study Area (WSA), with the remaining 5% of land in private holding (Elmore 2000, Freeborn 2006).

      A lightning strike ignited the Holloway fire in the Trout Creek Mountains on August 5, 2012. The fire occurred approximately 40 km east of Denio, Nevada, and

210 km southeast of Burns, Oregon (Karges 2013), and was not fully contained until August 25, 2012. The Holloway fire burned 186,972 ha total, of which 99,352 ha were in southern Malheur and Harney counties, Oregon, and 87,227 ha were in northern Humboldt County, Nevada (Karges 2013). The Trout Creeks sage-grouse Priority Area of Conservation (PAC) was almost completely burned by this fire (Figure 3.1; Hagen 2011). Fire behavior depended on local topographic features, vegetation profiles, and weather conditions. These factors varied considerably in the region, resulting in variable patterns of burned and intact habitat. Increased fuel loads, wind speeds, and topographic features conducive to fire spread caused the fire to burn severely in some areas, consuming nearly all vegetation for square kilometers. In other areas, reduced fuel loads, wind speeds, and topographic features unconducive to fire spread decreased fire severity, leaving a variable mosaic of burned and intact vegetation. Several large patches of intact habitat exist within the perimeter of the fire, with the largest patch exceeding 4,000 ha. Within the fire boundary, 75.3% of the land area was burnt, while the remaining 24.7% was comprised of remnant intact habitat (Figure 3.1; Appendix I). Within potential nesting habitat affected by the Oregon half of the fire (defined as a 5 km buffer around leks within 3 km of the fire boundary), 59.9% of the land area was burnt, with 40.1% remaining as intact habitat either outside the fire boundary or within remnant intact patches (Figure 3.1; Appendix I). Considering only potential nesting habitat within the fire boundary, 78.4% of the land area was burnt, with the remaining 21.6% persisting as intact habitat (Figure 3.1).

Recently formulated concepts concerning the resilience of sagebrush habitats to disturbance, and resistance to invasive species invasion (R&R concept), allow the prediction of potential habitat recovery within post-fire landscapes (Chambers et al. 2014b, Maestas et al. 2016). The R&R concept describes habitat gradients within the larger sagebrush ecosystem, which mediate the response of habitats to disturbance. These concepts also describe the potential for habitats to be invaded by annual

grasses both preceding and following wildfire (Chambers et al. 2014b, Maestas et al. 2016). Sites within the sagebrush ecosystem exist along interacting gradients of elevation, slope aspect, precipitation, soil temperature regime, and productivity. The various plant communities comprising the larger sagebrush ecosystem lie at distinct points along these gradients, and thus exhibit differential responses to disturbance, i.e. differential resistance and resilience (Chambers et al. 2014b, Maestas et al. 2016). The resistance and resilience of sites in the sagebrush ecosystem are commonly classified into three categories: low R&R, moderate R&R, and high R&R (Chambers et al. 2014b, Maestas et al. 2016).

Within the coverage of the fire, 35.0% of the land area was categorized as low R&R habitat, 45.3% was categorized as moderate R&R habitat, and 19.6% was categorized as high R&R habitat, with the remaining 0.1% classified as wetland or riparian habitat (Chambers et al. 2014b, Maestas et al. 2016). When considering only potential nesting habitat within the Oregon portion of the fire, as delineated above, 10.9% of the land area was categorized as low R&R, 57.9% was categorized as moderate R&R, and 31.0% was categorized as high R&R, with the remaining 0.2% classified as wetland or riparian habitat (Chambers et al. 2014b, Maestas et al. 2016). These figures suggest that 35.0% of the total land area of the fire, and 10.9% of the potential nesting habitat in the Oregon portion of the fire, have a high likelihood of permanent annual grass conversion, while 19.6% of the total land area of the fire, and 31.0% of potential nesting habitat have a high likelihood of recovering to a state of optimum habitat function given appropriate management. The remaining 45.3%, and 57.9%, of the total land area, and potential nesting habitat, respectively, exist in a state which could either be converted to annual grasses, or functional sage-grouse habitat, depending on site-scale factors, management regimes, and time. Habitat required for every phase of sage-grouse life history was available within the area of the Holloway fire. On the Oregon side of the fire, 77 sage-grouse leks were located within, or in close proximity to, the fire boundary (ODFW, unpublished data).

METHODS

Capture and Instrument Attachment

We captured female sage-grouse during spring 2013, summer 2013, and spring 2014 using a spotlight (Wakkinen et al. 1992) near leks within, or near ($\leq$ 2 km) the boundary of the Holloway fire, and near previously identified roost sites within the fire boundary. We used feather patterns and morphology to determine sex and age of captured individuals (Crunden 1963). Sage-grouse were either classified as adults ($\geq$2 years of age), or yearlings (1 year of age), no hatch year individuals were captured during the study. If yearlings survived more than 1 year of the study, they were reclassified as adults during their second year. Under the authority of project collaborators, Oregon Department of Fish and Wildlife, we marked all captured individuals with a numbered steel leg band. We also attached 30-g ARGOS/GPS Solar PTTs (PTT-100, Microwave Telemetry Inc., Columbia, MD 21045 USA) to captured females using a rump-mount attachment technique (Rappole and Tipton 1991). All animal capture, handling, and instrument attachment procedures were approved under Oregon State University's Institutional Animal Care and Use Committee. GPS units included Ultra High Frequency (UHF) beacons which were turned on for ground tracking from 1 March – 31 July each year. The GPS units we used during spring and summer 2013 were configured to record locations (+/- 20m) 6 times daily from 1 March – 31 July, 4 times daily from 1 August – 31 October, and 2 times daily from 1 November – 29 February. GPS units deployed in spring 2014 were configured similarly, except that we increased the number of locations collected during the nesting season (10 times daily from 1 March – 31 July, and 4 times daily from 1 August – 29 February), to help us determine nest initiation dates more accurately. We also measured weight (kg), wing length (cm), culmen length (mm), and tarsus length (mm) for all captured individuals.

Nest Monitoring

We used female behavior as interpreted from the GPS PTT location data to identify individual nest attempts. If the GPS locations for a female remained stationary for >18 h during the nesting season (1 April – 31 May) she was considered to be on a nest. Once we identified a nest attempt we used the location data to approach the general area of the nest and then we used a UHF receiver to locate the specific nest site. At that point we approached the nest site to within ~3 m, to visually confirm that the female was incubating, while taking care not to flush her. If a nesting female was absent from the nest >8 h, nesting activity was assumed to have ceased, and we revisited the nest to determine its fate. We considered a nest to be successful if a female incubated for >23 days, and hatched ≥1 egg. We identified hatched eggs by the presence of an egg cap, and an intact egg membrane. We characterized nests as "failed" if the female incubated for ≤25 days and either eggs did not hatch, or were depredated. We distinguished a depredated egg from a hatched egg if the egg was broken but a distinct egg cap and intact egg membrane was absent.

Vegetation Sampling

We sampled vegetation characteristics at all nests during July and August 2013, and June and July 2014 after we determined nest fate. For nests within unburned habitat (hereafter referred to as "intact" habitat), we laid 3 parallel 50-m transects along a randomly chosen azimuth within each habitat patch containing a nest, with the center transect centered on the nest site. A "patch" of intact habitat was defined as all unburned vegetation within a contiguous area separated from any other patch of unburned vegetation by ≥ 50 m. If more than 50% of the transect occurred outside of intact sagebrush we moved it to the opposite side of the nest. If three transects did not fit within a single patch then we only sampled transects with ≥ 50% of their length in intact vegetation. We did this to restrict our sample to habitat within intact patches only, (i.e., sampling stopped at the edge of intact habitat). We also

sampled a single 50-m transect centered on the nest site for nests located outside of intact habitat.

We collected data on the amount of foliar and basal shrub, herbaceous cover, the percent bare ground, and species composition along transects using the line-point intercept method (Elzinga et al. 1998, McCord 2013). We recorded every species of shrub and genus of herbaceous plant at 1-m intervals, and height of both woody and herbaceous cover and a measure of visual obstruction (VOR; Robel et al. 1970) every 5 m along each transect. We also recorded the length of gaps >20 cm between both shrub canopies and shrub bases to the nearest 1 cm along the length of each transect following McCord (2013) to gather information about the proportion of transect covered by large gaps between shrubs.

Nest Initiation Rate

We defined nest initiation rate based on the proportion of individuals alive and present on the study area through the median nest initiate date for first nests each year that made at least one nesting attempt in a given year. Renesting rate was the proportion of individuals available for renesting that made a second nesting attempt in a given year, given they attempted a first nest and were alive and present on the study areas until the date of the final second nesting attempt each year.

Covariates

We investigated the relationship between daily nest survival (DNS) and a variety of covariates, including those reflecting temporal patterns (2), inherent characteristics of birds (3), and nesting habitat characteristics (28) (Table 3.1; Appendix III). We evaluated whether daily nest survival varied between years (2013 vs. 2014; YR), or by the stage of incubation (standardized nest incubation day; Table 3.1). Year was allowed to interact with a number of other covariates, to account for the possiblity that the relationship between some covariates and DNS might change

between the first year after the fire and the second, primarily due to potential habitat regeneration (Table 3.2).

We characterized nests relative to female age (initiated by adult or yearling; FA), nest attempt (1st or 2nd nest attempt; NAT), and standardized nest initiation date (SID) within each nesting season (Table 3.1). Nest initiation dates were calculated as the first date on which a female attended its nest location for >18 h as determined through GPS monitoring.

Habitat covariates (Table 3.1; Appendix III) were developed from nest site vegetation sampling, or remotely sensed data, and measured at up to 4 scales around each nest site (Table 3.1). All covariates were evaluated as either linear effects, or pseudothreshold effects [$\ln(x)$], which allowed a covariate to have progressively diminishing effect on DNS as covariate values increase or decrease. In cases where continuous covariates possessed a value of zero at any nest site, we rescaled all covariate values by adding "1" [i.e., $\ln(x+1)$] because the natural-log of zero is undefined.

Analyses

We conducted nest survival analyses in program MARK (White and Burnham 1999), using known fate models. Known fate models were utilized because the GPS telemetry data enabled us to monitor and determine the exact dates of nest initiation and nest fate for all nests. Daily nest survival (DNS) was estimated for a 27 day nesting season each year, with year treated as a group effect. We developed *a priori* hypotheses and an associated model set to investigate the effect of each covariate on DNS (Table 3.2).

Because of the large number of covariates included in our analysis, and potential correlation between many of the habitat covariates, we used a hierarchical modeling procedure to conduct the analysis rather than running a model set that

contained every possible combination of all covariates. This approach generally results in the same outcome as an all-possible combinations approach, with the benefits of a much smaller model set and fewer models with uninformative parameters (Doherty et al. 2012). We used an information theoretic approach (Burnham and Anderson 2002) to select competitive models at each modeling stage, and we used Akaike's information criterion corrected for small sample size (AIC$_c$), ΔAIC$_c$ (the difference in AIC$_c$ value between each model and the top ranked model), and AIC$_c$ weights (w_i) to rank models (Burnham and Anderson 2002). Models within 4 ΔAIC$_c$ values of the top model were carried forward from one modeling stage to another and models within 2 ΔAIC$_c$ values of the top model were considered competitive in the final model set. We evaluated model deviance and 95% confidence limits on covariate model coefficients (β_i) to assess the direction and strength of specific covariate effects, and to identify uninformative parameters in competitive models (Arnold 2010).

During the first step of modeling, we evaluated all non-habitat covariates as single factor models. Covariates in models within 4 ΔAIC$_c$ of the top model were then assessed with an interactive effect of year. Differences in habitat regeneration were apparent between years (L. Foster, *personal observation*). Thus, we hypothesized that the effects of some covariates on DNS might not be the same across years (i.e., additive), but rather vary in relation to habitat regeneration or changes in population density due to acute effects of the fire (Table 3.2). Following the addition of year interactions, models within 2 ΔAIC$_c$ of the top model were retained in the model set.

During the second step of modeling, we evaluated habitat covariates across all scales as single factor models with both linear and pseudo-threshold structures. The most supported scale and structure of each continuous covariate was then retained in the model set. The effect of a year interaction was evaluated for covariates in single

factor models within 4 ΔAIC$_c$ of the top model, if an interaction with year was thought to be biologically important (Table 3.2). The most supported model for each of these single factor and interactive model pairs was then retained. We examined correlations among all covariates prior to combining them in additive or interactive models, using the *cor* function in Program R (R Version 3.2.0, www.r-project.org, accessed 1 Oct 2013). Covariates with correlation coefficients >0.6 were not combined in the same model, and we did not investigate models with >1 interaction term or >1 additive effect because of the small number of nests included in the analysis. Therefore habitat covariates contained in single factor habitat models within 4 ΔAIC$_c$ of the top model were combined in turn with the best non-habitat covariate model from the previous modeling stage to generate the final model set.

RESULTS

Nest Initiation Rate

During 2013 and 2014, we captured and instrumented 58 female sage-grouse with GPS PTTs. In 2013, 21 individuals remained marked and alive until the median first nest initiation date (5 May 2013; 15 adult, 6 yearling). Nineteen of these 21 individuals initiated at least one nest resulting in a nest initiation rate of 90.5% for adults and yearlings combined (adult = 86.7%, yearlings = 100%). First nests of 13 individuals failed during 2013, but these females survived through initiation of renests (i.e., 22 May 2013; 11 adult, 2 yearlings). Three of these 13 available individuals initiated a second nest (renesting rate: all individuals = 23.1%; adult = 27.3%, yearling = 0%).

In 2014, 22 individuals remained marked and alive until the median first nest initiation date (21 April 2014; 15 adult, 7 yearling), and all 22 individuals initiated at least 1 nest. The first nests of 14 individuals failed, yet these 14 females survived through initiation of all renests (22 May 2014; 10 adult, 4 yearling), and 8 initiated a

second nest (renesting rate: all individuals = 57.1%; adult = 70.0%; yearling = 25.0%).

Nest Characteristics

In 2013, we monitored 22 nests, with 63.6% of nests located within the boundary of the Holloway Fire. Nests located outside the fire all occurred in intact sagebrush habitat and mean distance to the fire boundary was 941 m (n = 8, SD = 944 m). The majority of all nests were located in intact sagebrush (72.7%), with 57.1% of nests inside the fire boundary located within intact sagebrush patches. All nests in intact sagebrush habitat were located under live sagebrush shrubs and all nests located in burnt habitat were located under one of the following: dead sagebrush, or rabbitbrush (*Ericameria* spp.), live snowberry (*Symphiocarpus* spp.), or Great Basin wildrye (*Leymus cinereus*), or on bare-ground (Figure 3.2).

In 2014, we monitored 30 nests, with 73.3% of nests located within the fire boundary. For nests outside the fire, mean distance to fire boundary was 557 m (n = 8, SD = 455 m). Eighty percent of all nests were located within intact sagebrush patches and 69.5% of nests located within the fire were located in intact sagebrush patches. Of all nests, 66.7% were located under sagebrush. Species providing nest cover in burned habitats included dead sagebrush, live snowberry, horsebrush (*Tetradymia* spp.), bitterbrush (*Purshia tridentata*), Great Basin wildrye, and bluebunch wheatgrass (*Pseudoroegneria spicata)*; and one nest was located under a rock outcrop (Figure 3.3).

The size of intact patches used as nesting habitat was variable during both years. In 2013, mean patch size of intact sagebrush in the interior of the fire used as nesting habitat was 916.6 ha (n = 6, range: 3.3 ha – 4833.9 ha). In 2014, mean patch size was 285.9 ha (n = 9, range: 0.01 ha – 638.7 ha). Additionally while some intact sagebrush patches used as nesting habitat were large (≤4780 ha), sage-grouse often

nested in proximity to patch edges. The mean distance to burnt habitat for individuals nesting in intact sagebrush patches within the interior of the fire was 38.6 m (n = 6, range: 16.9 m – 67.8 m), and 33.0 m (n = 9, range: 1.9 m – 195.1 m), during 2013 and 2014 respectively.

Vegetation surveys and GIS analyses were conducted at 22 and 28 nest sites respectively, during 2013 and 2014 (Appendix IV; Tables A4.1 – A4.2). In 2013, 16 of the nests we surveyed were in intact habitat patches or outside of the fire boundary, and 6 nests were located in burnt habitat. In 2014, 23 of the nests we surveyed were in intact habitat patches or outside the fire boundary, and 5 nests were located in burnt habitat. Vegetation characteristics around nests sites varied between intact and burnt habitat during each year, and between years (Appendix IV; Tables A4.1 – A4.2).

Nest Survival

We observed strong support for the effect of nesting attempt (1st nest vs. re-nest) on daily nest survival of sage-grouse, but the direction of that relationship varied by year (Table 3.3). Models containing the interaction between year and nest type (YR*NAT) received 62% of the model weight, with both of the two top models containing this interaction (Table 3.3). First nests were more likely to survive a given day than re-nests in 2013, but during 2014, re-nests were more likely to survive a given day than first nests (YR$_{2013}$: $\hat{\beta} = -1.96$, 95%CI: -3.79 to -0.13, NAT$_{1st\ nest}$: $\hat{\beta} = -1.81$, 95%CI: -3.29 to -0.33, YR$_{2013}$*NAT$_{1st\ nest}$: $\hat{\beta} = 2.09$, 95% CI: 0.11 to 4.08; Figure 3.4). The effect of forb cover on DNS, in addition to the YR*NAT interaction, was also supported by our best model, but that effect was relatively small, and 95% CIs on the model coefficient slightly overlapped zero (FC: $\hat{\beta} = 0.017$, 95%CI: -0.005 to 0.039). However, an increase of 1% in forb cover at the nest vicinity scale increased the likelihood of a nest surviving a given day 1.02 times (Figure 3.5). When forb cover was held at the mean value, DNS of first nests

decreased slightly between 2013 and 2014, but DNS of 2nd nests in 2014 increased considerably compared to 1st nests in both years (Table 3.4; Figure 3.4). When DNS estimates were extrapolated to the entire 27 day nesting period the interaction between year and nest type became more apparent (Table 3.4; Figure 3.6). Derived estimates of nest survival for all nests based on mean forb cover in each year indicated that average nest survival in 2014 was greater than in 2013 (Table 3.4).

DISCUSSION

Our study provides the first examination of factors affecting nest survival of sage-grouse in a post-wildfire landscape, immediately following the fire. At the broad scale, our work indicates that sage-grouse exhibited strong site fidelity and continued to occupy and attempt reproduction in a fire-disturbed landscape. This behavior had an acute fitness cost in context of nest success during the first breeding season following the fire. The factors that influenced nest survival most strongly in this study were an interaction between study year and nesting attempt, with weaker evidence that increased forb cover had positive effects on nest success across nest types and years. While we did not document direct effects of post-fire habitat on nest survival, we observed potential indirect effects of habitat through the interaction between year (i.e. a coarse reflection of time since fire) and nesting attempt (i.e. a coarse reflection of nest initiation date in relation to growing season progression). Unfortunately, our ability to accurately characterize nest site vegetation used by sage-grouse may have been limited due to the timing of vegetation surveys conducted during this study. Vegetation surveys during this study were conducted between late June through August in 2013, and early July through late July in 2014 after females left nests and most of the brood survival monitoring was done. The growing season in Great Basin sagebrush communities occurs from approximately April to early July (Comstock and Ehleringer 1992, Dysart 2001, Wrobleski and Kauffman 2003) and sage-grouse initiate nests during the initial months of the growing season. Therefore, by sampling

vegetation at the end of the growing season, we likely did not sample the actual vegetative conditions that characterize sage-grouse nest sites during incubation. In addition, herbaceous species continued to grow during the period between nesting and vegetation sampling, potentially leading to the overestimation of grass and forb cover. These issues were especially severe at nests in burnt habitat. For example, forb cover estimates at the first four nests sampled in 2013 (sampling dates: 9 Jul – 11 Jul) were 15.2% lower on average than those at the last three nests sampled (sampling dates 21 Aug – 28 Aug). Burning of sagebrush increases herbaceous vegetation and bunchgrass production during the first two years following fire (Wrobleski and Kauffman 2003, Davies et al. 2007), and may extend the length of the growing season for herbaceous species (Wrobleski and Kauffman 2003). However, these issues likely only apply to measurements of herbaceous vegetative components because shrub characteristics (if present) should not change measurably between sage-grouse nest initiation and vegetation surveys. For example, visual obstruction, which was primarily provided by shrubs in this system, was not markedly different between nest which were sampled early in the summer of 2013, and nests which were sampled late in the summer.

The nest initiation rate we observed during the first year post-fire was similar to average reported in the literature, but daily nest survival was on the extreme low end of the range previously reported for sage-grouse (Connelly et al. 2011a). However in 2014, the interplay between increased nesting and renesting rates, and increased daily nest survival of second nests allowed nest survival to approach a level more typical for this species (This study: 30.1%: literature range: 15% - 86%; Connelly et al. 2011a). Few hypotheses explaining increased survival for second nests compared to first nests have been put forth for sage-grouse in the literature, however it has been suggested that this pattern may be related to warmer temperatures or increased forb cover during the period of second nest incubation (Sika 2006). Availability of forbs has also been posited as a major influence on sage-

grouse renesting rates (Barnett and Crawford 1994, Schroeder 1997). Reduced forb cover was reported during the first year following prescribed fire in Oregon, however it increased by the second year (Pyle and Crawford 1996). Although we did not quantify these changes during our study because of the timing of our vegetation surveys, early in the first spring post-fire (i.e., April - May) little vegetation remained in burned areas, but vegetation increased through the first post fire growing season (April – June) and into the second spring post-fire.

The nest survival rates we observed in this study were considerably lower than those observed by concurrent studies of sage-grouse nest survival in Oregon, and elsewhere in the Great Basin. Nesting survival rates for the 27-day nesting period in the Warner Mountains, approximately 140 km west of our study area, were 50.8% and 53.3%, in 2013 and 2014, respectively (Severson 2016). At the Sheldon-Hart Mountain National Wildlife Refuge complex, approximately 110 km west of our study area, 28 day nesting period survival rates were 0.45 during both 2013 and 2014 (Street et al. 2014). Additionally, the mean 27 day nesting period survival rates across 8 study areas in northern Nevada, and eastern California were 39.9%, and 42.5%, in 2013 and 2014 respectively (P. Coates, U.S. Geological Survey, unpublished data). The marked increase (56%) in nesting period survival between 2013 and 2014 that we observed in the Trout Creeks was not reported in these concurrent studies. This supports our conclusion that nest survival rates in our study were reduced by the fire affected habitat, and that the increase in nest survival we witnessed between the two years of the study was likely influenced by vegetation regeneration between the first and second post-fire nesting seasons.

Interestingly, we observed little evidence that sage-grouse attempted to leave the fire perimeter to nest. Throughout the study 85.7% of nesting individuals were captured within the fire boundary, and 73.2% of first nest attempts by these birds were also located within the fire perimeter. Additionally, individuals that did nest

outside the fire generally nested within 1 km of the fire perimeter, with no individuals nesting more than 3.1 km from the fire. Sage-grouse exhibit strong site fidelity to breeding and nesting areas (Dalke et al. 1963, Wallestad and Schladweiler 1974, Emmons and Braun 1984, Dunn and Braun 1985, Connelly et al. 2011a). This strong site fidelity appears to reduce the ability of sage-grouse to respond to the post-fire landscape through emigration. Additionally, yearling sage-grouse were commonly captured near leks associated with the fire during both 2013 and 2014, and were confirmed to have nested in association with the fire during each year of the study, indicating that juvenile dispersal away from the fire affected area did not occur at a significant rate.

However, there were indications that nest site fidelity at the scale of the individual nest, may have been weaker for individuals in the interior of the fire than for individuals nesting outside of the fire. The mean distance between nests in 2013 ($\bar{x}$ = 373 m, SD = 49 m, n = 3) and nests in 2014 ($\bar{x}$ = 1,648 m, SD = 402 m, n = 3) for individuals which nested within the fire was 1,275 m greater than for individuals which nested outside the fire. Additionally, the mean distance between first and second nests for individuals that nested within the fire ($\bar{x}$ = 1,976 m, SD = 3,210 m, n = 6) was 1,593 m greater than for individuals that nested outside the fire ($\bar{x}$ = 383 m, SD = 151 m, n = 4). However, due to high mortality rates the first 2 years post-fire (Chapter 4, Foster 2016), only six marked individuals survived to nest in both years of the study. Sage-grouse in Washington inhabiting a highly fragmented landscape have been shown to exhibit diminished nest site fidelity in comparison to sage-grouse inhabiting intact landscapes (Schroeder and Robb 2003). The effects of large-scale wildfire may be similar to fragmentation, resulting in reduced nest site fidelity for females that survive to breed is subsequent years.

Most sage-grouse nests occur under live sagebrush shrubs (Patterson 1952, Drut et al. 1994, Gregg et al. 1994, Sveum et al. 1998, Connelly et al. 2011c),

however sage-grouse can utilize non-sagebrush species as nesting cover (Patterson 1952, Klebenow 1969, Wakkinen 1990, Connelly et al. 1991, Popham and Gutierrez 2003). In our study approximately 30% of nests were located under non-sagebrush species in each year, primarily in burnt habitat. Interestingly, throughout the study the mean distance between nests in burnt habitat and available intact habitat was just 107 m (range: 2.7 m – 272.8 m), although presumably, sage-grouse were aware of available intact habitat which could have been utilized as nesting cover. During 2014 increased prevalence of bunch grasses in burnt habitats appeared to provide attractive nesting habitat to some females. However during 2013 little herbaceous cover was available during the nesting season in burnt habitats. Potentially, residual sagebrush patches within burned landscapes must be of some minimum size before they become disproportionately attractive nesting habitat for sage-grouse, however evaluation of this hypothesis was beyond the scope of this study.

We were unable to document any effects of the pattern of habitat mosaic around nest sites, on nest survival. Nest survival did not appear to be affected by the amount of intact habitat near nest sites, the amount of edge habitat present, or the distance from a nest to the edge of intact habitat. These covariates described sagebrush land-cover and configuration, and the effect of shrub characteristics on nest survival has been equivocal in the literature (Connelly et al. 2011c). Herbaceous characteristics of nest sites have been shown to have more consistent effects on nest survival than shrub characteristics, and thus may be more important in determining the likelihood of nest survival (Connelly et al. 2011c). Additionally, sage-grouse select nest sites based on micro-scale vegetation (Connelly et al. 2011c), thus micro-site habitat characteristics may likewise have a greater influence on survival than landscape scale habitat configuration (Baxter et al. 2008, Webb et al. 2012, Lockyer et al. 2015). In addition to this potential dynamic, the sampled nests in my study may not have had enough variation in landscape level habitat covariates to detect an effect on nest survival. Sage-grouse did appear to disproportionately place nests in intact

habitat, thus, remnant intact habitat and the structure of the habitat mosaic following fire may influence nest site selection to a greater extent than they influence nest survival.

Ecosystem resilience and resistance (R&R) is a growing consideration in management of sagebrush ecosystems (Chambers et al. 2014a, Maestas et al. 2016). These ecosystems exist along strong environmental gradients which contribute to resilience to disturbance and resistance to invasive species (Chambers et al. 2014a, Maestas et al. 2016). Sage-grouse utilize different habitats within these gradients during different time periods, and thus may be affected more strongly by wildfire and cheatgrass encroachment during certain life-history stages. The majority of sage-grouse nests within our study were located in low or moderate R&R classes (Low: n = 7; Moderate: n = 34; High: n = 12). Sites within low R&R classes are the least resilient to disturbance, and least resistant to cheatgrass invasion (Chambers et al. 2014a, Maestas et al. 2016). Such sites are also the least responsive to vegetation manipulation, and if the cheatgrass-fire cycle progresses may cross thresholds rendering restoration virtually impossible (Chambers et al. 2014a, Maestas et al. 2016). Sites within moderate R&R classes may also become cheatgrass dominated without appropriate invasive annual grass management such as herbicide application and seeding of perennial bunchgrasses (Chambers et al. 2014a, Maestas et al. 2016).

MANAGEMENT IMPLICATIONS

Sage-grouse in our study experienced lower nest survival during the first 2 years after the fire relative to averages for the species in intact ecosystems. In addition, we observe strong fidelity to nesting areas, even those within the burn and females primarily nested within intact sagebrush patches, even within the interior of the fire. This suggests that fire suppression in intact sage-grouse habitat may be the most important management activity in fire-prone landscapes, currently available to managers. Suppression efforts in sage-grouse habitat should be focused on limiting

fire within intact sage-grouse nesting habitat, particularly in ecosystems where recovery and resilience after disturbance may be low.   In addition, suppression efforts should not be limited to suppressing fire spread but also extend to the suppression of interior fire and the protection of interior habitat islands whenever possible. Following large-scale wildfire in sagebrush habitat, restoration efforts should focus on reestablishing native shrub and grass communities as quickly as possible. Additionally, invasive annual grasses, such as cheatgrass should be controlled wherever possible. Annual grass invasions promote more frequent fire, which may preclude the reestablishment of sagebrush, and burn additional intact areas further reducing sage-grouse nesting habitat (Murphy et al. 2013). Forb recovery within fires in sagebrush habitat will likely progress naturally following wildfire. However efforts to speed native forb recovery may be beneficial, as this study indicated that forb cover may positively influence sage-grouse nest survival.

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Table 3.1. The factors hypothesized to affect daily nest survival or characterize nest sites of female sage-grouse during 2013 and 2014 in the Trout Creek Mountains, Malheur and Harney Counties, OR. Covariate acronyms, a description of the effect, the scales at which the covariate was evaluated (Scale), the structural form evaluated (Form) and the method of data collection (Method) is included.

Covariate	Acronym	Description	Scale[a]	Form[b]	Method
Year	YR	Year of nest, 2013/2014	NA	NA	NA
Time	T	Day of incubation	NA	D, L, PT	NA
Female Age	FA	< 2 years of age, ≥ 2 years of age	NA	NA	Capture Data
Nesting Attempt	NAT	1st or 2nd nesting attempt	NA	NA	GPS Data
Standardized Initiation Date	SID	Days difference from median nesting date in year	NA	L	GPS Data
Nest Habitat	NHA	Nest placed in an intact habitat patch or burnt habitat	NA	NA	Site Visit
Nest Species	NSP	Nest under live sagebrush or not	NA	NA	Site Visit
Total Shrub Cover	TSC	Percent of points detecting a live or dead shrub	P, C, NV	L, PT	Line Point Intercept
Live Shrub Cover	LSC	Percent of points detecting a live shrub	P, C, NV	L, PT	Line Point Intercept
Perennial Grass Cover	PGC	Percent of points detecting a perennial grass	P, C, NV	L, PT	Line Point Intercept
Total Grass Cover	TGC	Percent of points detecting a perennial or annual grass	P, C, NV	L, PT	Line Point Intercept
Forb Cover	FC	Percent of points detecting a forb species	P, C, NV	L, PT	Line Point Intercept
Bare Ground	BG	Percent of points not detecting any plant species	P, C, NV	L, PT	Line Point Intercept

Litter Cover	LC	Percent of points detecting woody litter	P, C, NV	L, PT	Line Point Intercept
Total Shrub Height	TSH	Mean height of live and dead shrubs	P, C, NV, N	L, PT	Line Point Intercept
Live Shrub Height	LSH	Mean height of live shrubs	P, C, NV, N	L, PT	Line Point Intercept
Perennial Grass Height	PGH	Mean height of perennial grasses	P, C	L, PT	Line Point Intercept
Total Grass Height	TGH	Mean height of perennial and annual grasses	P, C	L, PT	Line Point Intercept
Herbaceous Height	HH	Mean height of all non-shrub plants	P, C, NV, N	L, PT	Line Point Intercept
Canopy Gap - 20 - 50 cm	CG20_50	Mean percent of transects covered by shrub canopy gaps 20 -50 cm wide	P, C, NV	L, PT	Gap Intercept
Canopy Gap - 51 - 100 cm	CG51_100	Mean percent of transects covered by shrub canopy gaps cm wide	P, C, NV	L, PT	Gap Intercept
Canopy Gap - 101 - 200 cm	CG101_200	Mean percent of transects covered by shrub canopy gaps 101 - 200 cm wide	P, C, NV	L, PT	Gap Intercept
Canopy Gap - >200 cm	CG200+	Mean percent of transects covered by shrub canopy gaps > 200 cm wide	P, C, NV	L, PT	Gap Intercept
Basal Gap - 20 - 50 cm	BG20_50	Mean percent of transects covered by shrub basal gaps 20 -50 cm wide	P, C, NV	L, PT	Gap Intercept
Basal Gap - 51 - 100 cm	BG51_100	Mean percent of transects covered by shrub basal gaps cm wide	P, C, NV	L, PT	Gap Intercept

Basal Gap - 101 - 200 cm	BG101_200	Mean percent of transects covered by shrub basal gaps 101 - 200 cm wide	P, C, NV	L, PT	Gap Intercept
Basal Gap - >200 cm	BG200+	Mean percent of transects covered by shrub basal gaps > 200 cm wide	P, C, NV	L, PT	Gap Intercept
Basal Shrub Cover	BSC	Mean percent of transects covered by shrub bases	P, C, NV	L, PT	Gap Intercept
Visual Obstruction	VO	Mean Robel pole reading	P, C, NV, N	L, PT	Robel Pole
Distance to Riparian	DTR	Straight line distance from nest site to permanent or semi-permanent stream	NA	L, PT	GIS
Distance to Edge	DTE	Straight line distance from nest site to edge between intact and burnt habitat	NA	L, PT	GIS
Percent Patch Cover	PPC	Percent of nest site buffer covered by intact patches	100 m, 550 m, 1500 m	L, PT	GIS
Edge Density	ED	Density of burnt/intact edges (m/ha) within nest site buffer	101 m, 550 m, 1500 m	L, PT	GIS

[a]Scale of evaluation: P - patch scale, mean values across all vegetation sampling transects; C - center scale, mean values for transect bisecting nest sites; NV - nest vicinity scale, mean value within 5 m of nest site; N - nest scale, measurement at nest site; 100 m - 100 m circular buffer around nest site; 550 m - 550 m circular buffer around nest site; 1500 m - 1500 m circular buffer around nest site.

[b]Structural forms: L – linear; PT – pseudo-threshold

Table 3.2. Hypotheses regarding relationships between nest covariates and daily nest survival (S) of sage-grouse nests during 2013, and 2014, in the Trout Creek Mountains, Harney and Malheur counties, Oregon, and the literature sources from which hypotheses were derived. [a] Potential interaction with year hypothesized.

| Model | Structure of predicted effects | | Source |
	Linear	Psuedothreshold	
S_{YR}	$\beta_Y > 0$	-	Moynahan et al. 2007, Connelly et al. 2011a
S_T	$\beta_T > 0$	-	Moynahan et al. 2007
S_{HA}	$\beta_{HA} > 0$	-	Wallestad and Pyrah 1974, Connelly et al. 2011a
S_{NAT}[a]	$\beta_{NAT} > 0$	-	Moynahan et al. 2007, Taylor et al. 2012
S_{SID}[a]	$\beta_{SID} > 0$	$\beta_{ln(SID)} > 0$	Moynahan et al. 2007, Taylor et al. 2012
S_{NHA}[a]	$\beta_{NHA} > 0$	-	Connelly et al. 2011b
S_{NSP}	$\beta_{NSP} > 0$	-	Connelly et al. 1991
S_{TSC}[a]	$\beta_{TSC} > 0$	$\beta_{ln(TSC)} > 0$	Klebenow 1969, Wallestad and Pyrah 1974, Gregg 1991, Fischer 1994, Sveum et al. 1998, Aldridge and Brigham 2002
S_{LSC}[a]	$\beta_{LSC} > 0$	$\beta_{ln(LSC)} > 0$	Klebenow 1969, Wallestad and Pyrah 1974, Gregg 1991, Fischer 1994, Sveum et al. 1998, Aldridge and Brigham 2002
S_{PGC}[a]	$\beta_{PGC} > 0$	$\beta_{ln(PGC)} > 0$	Wakkinen 1990, Gregg et al. 1994, Sveum et al. 1998, Aldridge and Brigham 2002, Hausleitner 2003, Holloran et al. 2005, Woodward 2006, Moynahan et al. 2007
S_{TGC}[a]	$\beta_{TGC} > 0$	$\beta_{ln(TGC)} > 0$	Wakkinen 1990, Gregg et al. 1994, Sveum et al. 1998, Aldridge and Brigham 2002, Hausleitner 2003, Holloran et al. 2005, Woodward 2006, Moynahan et al. 2007
S_{FC}	$\beta_{FC} > 0$	$\beta_{ln(FC)} > 0$	Holloran 1999, Hausleitner 2003
S_{BG}	$\beta_{BG} < 0$	$\beta_{ln(BG)} < 0$	Klebenow 1969, Wakkinen 1990, Sveum et al. 1998, Holloran 1999, Lyon 2000, Slater 2003, Hagen et al. 2007

S_{LC}	$\beta_{LC} < 0$	$\beta_{ln(LC)} < 0$	Kaczor et al. 2011
S_{TSH}[a]	$\beta_{TSH} > 0$	$\beta_{ln(TSH)} > 0$	Wallestad and Pyrah 1974, Sveum et al. 1998, Holloran et al. 2005, Connelly et al. 2011b
S_{LSH}[a]	$\beta_{LSH} > 0$	$\beta_{ln(LSH)} > 0$	Wallestad and Pyrah 1974, Sveum et al. 1998, Holloran et al. 2005, Connelly et al. 2011b
S_{PGH}[a]	$\beta_{PGH} > 0$	$\beta_{ln(PGH)} > 0$	Wakkinen 1990, Gregg et al. 1994, Sveum et al. 1998, Aldridge and Brigham 2002, Hausleitner 2003, Holloran et al. 2005, Woodward 2006, Moynahan et al. 2007
S_{TGH}[a]	$\beta_{TGH} > 0$	$\beta_{ln(TGH)} > 0$	Wakkinen 1990, Gregg et al. 1994, Sveum et al. 1998, Aldridge and Brigham 2002, Hausleitner 2003, Holloran et al. 2005, Woodward 2006, Moynahan et al. 2007
S_{HH}	$\beta_{HH} > 0$	$\beta_{ln(HH)} > 0$	Wakkinen 1990, Gregg et al. 1994, Sveum et al. 1998, Aldridge and Brigham 2002, Hausleitner 2003, Holloran et al. 2005, Woodward 2006, Moynahan et al. 2007
S_{CG20_50}	$\beta_{CG20\_50} > 0$	$\beta_{ln(CG20\_50)} > 0$	Klebenow 1969, Wakkinen 1990, Gregg 1991, Fischer 1994, DeLong et al. 1995, Sveum et al. 1998, Aldridge and Brigham 2002
S_{CG51_100}	$\beta_{CG51\_100} < 0$	$\beta_{ln(CG51\_100)} < 0$	Klebenow 1969, Wakkinen 1990, Gregg 1991, Fischer 1994, DeLong et al. 1995, Sveum et al. 1998, Aldridge and Brigham 2002
S_{CG101_200}	$\beta_{CG101\_200} < 0$	$\beta_{ln(CG101\_200)} < 0$	Klebenow 1969, Wakkinen 1990, Gregg 1991, Fischer 1994, DeLong et al. 1995, Sveum et al. 1998, Aldridge and Brigham 2002
S_{CG200+}	$\beta_{CG200+} < 0$	$\beta_{ln(CG200+)} < 0$	Klebenow 1969, Wakkinen 1990, Gregg 1991, Fischer 1994, DeLong et al. 1995, Sveum et al. 1998, Aldridge and Brigham 2002
S_{BG20_50}	$\beta_{BG20\_50} > 0$	$\beta_{ln(BG20\_50)} > 0$	Klebenow 1969, Wakkinen 1990, Gregg 1991, Fischer 1994, DeLong et al. 1995, Sveum et al. 1998, Aldridge and Brigham 2002

S_{BG51_100}	$\beta_{BG51\_100} < 0$	$\beta_{ln(BG51\_100)} < 0$	Klebenow 1969, Wakkinen 1990, Gregg 1991, Fischer 1994, DeLong et al. 1995, Sveum et al. 1998, Aldridge and Brigham 2002
S_{BG101_200}	$\beta_{BG101\_200} < 0$	$\beta_{ln(BG101\_200)} < 0$	Klebenow 1969, Wakkinen 1990, Gregg 1991, Fischer 1994, DeLong et al. 1995, Sveum et al. 1998, Aldridge and Brigham 2002
S_{BG200+}	$\beta_{BG200+} < 0$	$\beta_{ln(BG200+)} < 0$	Klebenow 1969, Wakkinen 1990, Gregg 1991, Fischer 1994, DeLong et al. 1995, Sveum et al. 1998, Aldridge and Brigham 2002
S_{BSC}	$\beta_{BSC} > 0$	$\beta_{ln(BSC)} > 0$	Klebenow 1969, Wakkinen 1990, Gregg 1991, Fischer 1994, DeLong et al. 1995, Sveum et al. 1998, Aldridge and Brigham 2002
S_{VO}	$\beta_{VO} > 0$	$\beta_{ln(VO)} > 0$	Wakkinen 1990, Popham 2000, Slater 2003
S_{DTR}	$\beta_{DTR} > 0$	$\beta_{ln(DTR)} > 0$	Bider 1968, Harris and Gallagher 1989, Conover 2007, Dzialak et al. 2011
S_{DTE}	$\beta_{DTE} > 0$	$\beta_{ln(DTE)} > 0$	Bider 1968, Harris and Gallagher 1989
S_{PPC}	$\beta_{PPC} > 0$	$\beta_{ln(PPC)} > 0$	Connelly et al. 2011a
S_{ED}	$\beta_{ED} < 0$	$\beta_{ln(ED)} < 0$	Connelly et al. 2011a

Table 3.3. Model selection results for 10 best-ranked models relating categorical and continuous nest characteristics to daily survival of sage-grouse nests in the Trout Creek Mountains, Harney and Malheur counties, Oregon, during 2013 and 2014 after the introduction of additive models to the set. Models were ranked according to Akaike's information criterion adjusted for small sample size (AIC_c) and ΔAIC_c, AIC_c weights, number of parameters (k), and model deviance are included for all models. The intercept-only model is also included for comparison. Nest characteristic acronyms are described in Table 2.

Model[a]	ΔAIC_c[b]	AIC_c Weight	k	Deviance
YR*NAT+FC_NV	0.00	0.25	5	267.72
YR*NAT	0.47	0.20	4	270.22
YR*SID	1.15	0.14	4	270.90
NAT	1.75	0.10	2	275.54
YR*NAT+pt_BG_NV	2.04	0.09	5	269.75
YR*NAT+PGH_P	2.32	0.08	5	270.04
pt_BG_NV	3.19	0.05	2	276.98
FC_NV	3.86	0.04	2	277.64
PGH_P	3.96	0.03	2	277.74
SID	4.33	0.03	2	278.11
Intercept Only	5.14	0.01	1	280.93

[a]Prefixes to nest characteristics indicate structural form: pt_ = pseudothreshold, no prefix = linear structure. Suffixes indicate sampling scale: _NV = nest vicinity, _P = patch scale, no suffix = scale not applicable.
[b] The lowest AIC_c for this analysis is 277.80.

Table 3.4. Daily, and incubation period (27 day) nest survival rates, with standard errors (SE), and 95% confidence intervals (95% CI), with forb cover held at mean values, for greater sage-grouse 1st nests, 2nd nests, and combined estimates for both nest types, during 2013 and 2014, in the Trout Creek Mountains, Harney and Malheur Counties, Oregon.

Parameter	Year	1st Nests	95% CI	SE	2nd Nests	95% CI	SE	All Nests	95% CI	SE
Daily Nest Survival	2013	0.944	0.906 - 0.967	0.015	0.927	0.796 -0.997	0.041	NA	NA	NA
Daily Nest Survival	2014	0.937	0.899 - 0.961	0.015	0.989	0.957 - 0.997	0.008	NA	NA	NA
27 Day Nest Survival	2013	0.212	0.084 - 0.440	0.091	0.131	0.010 - 0.687	0.156	0.193	0.080 - 0.395	0.080
27 Day Nest Survival	2014	0.171	0.068 - 0.367	0.075	0.744	0.369 - 0.935	0.156	0.301	0.157 - 0.499	0.090

Figure 3.1. Holloway fire severity in relation to Trout Creeks Sage-Grouse Priority Area of Conservation (PAC), Oregon. Inset depicts Holloway fire (red outline) in relation to all Oregon Sage-Grouse PACs (green polygons).
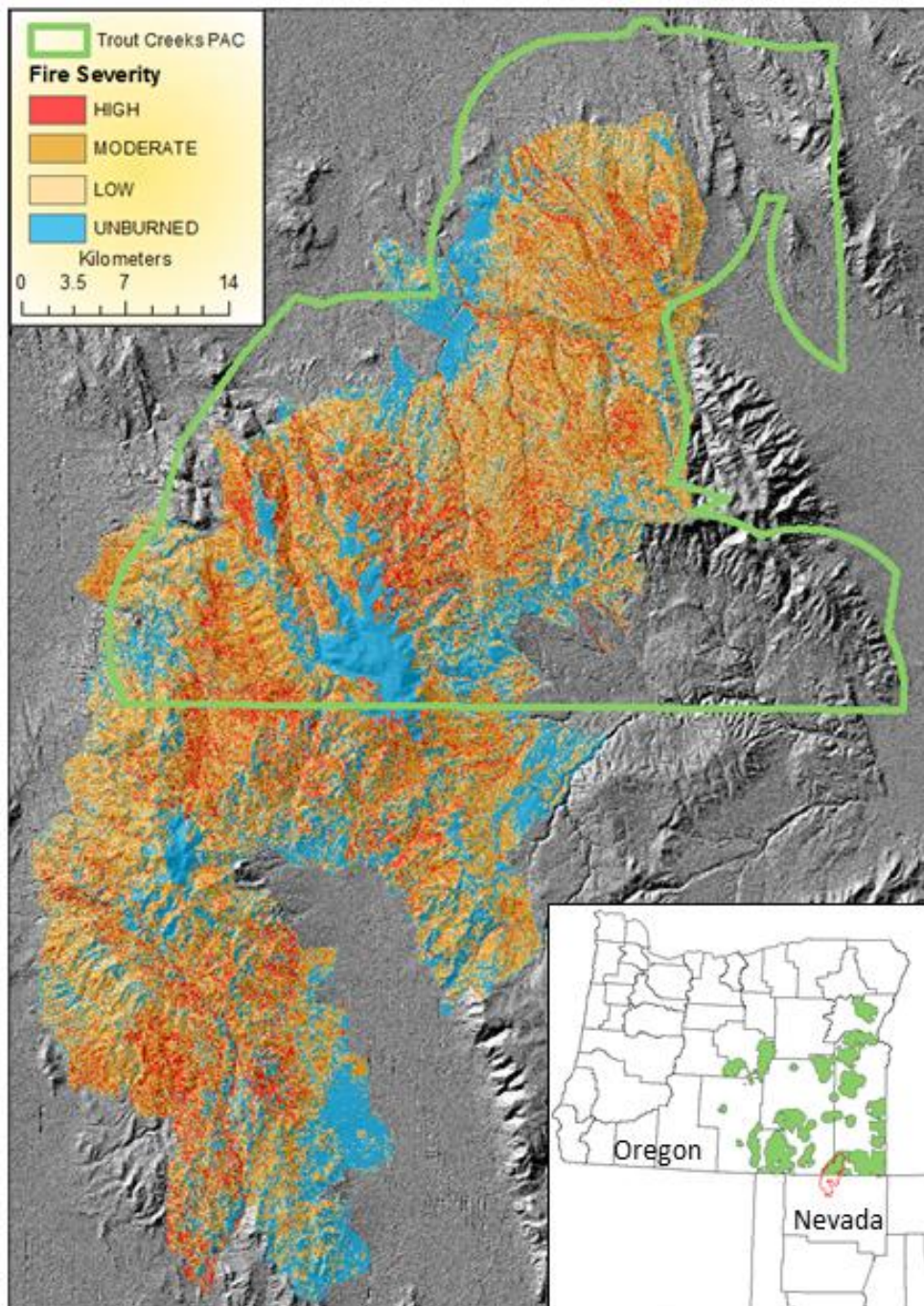
Figure 3.2. Examples of non-sagebrush sage-grouse nesting cover used by ≥1 female for nest placement during 2013 in the Trout Creek Mountains, Harney and Malheur counties, Oregon. A) dead mountain big sagebrush; B) snowberry; C) dead rabbitbrush; D) bare ground with no vegetative cover; E) great basin wild rye.
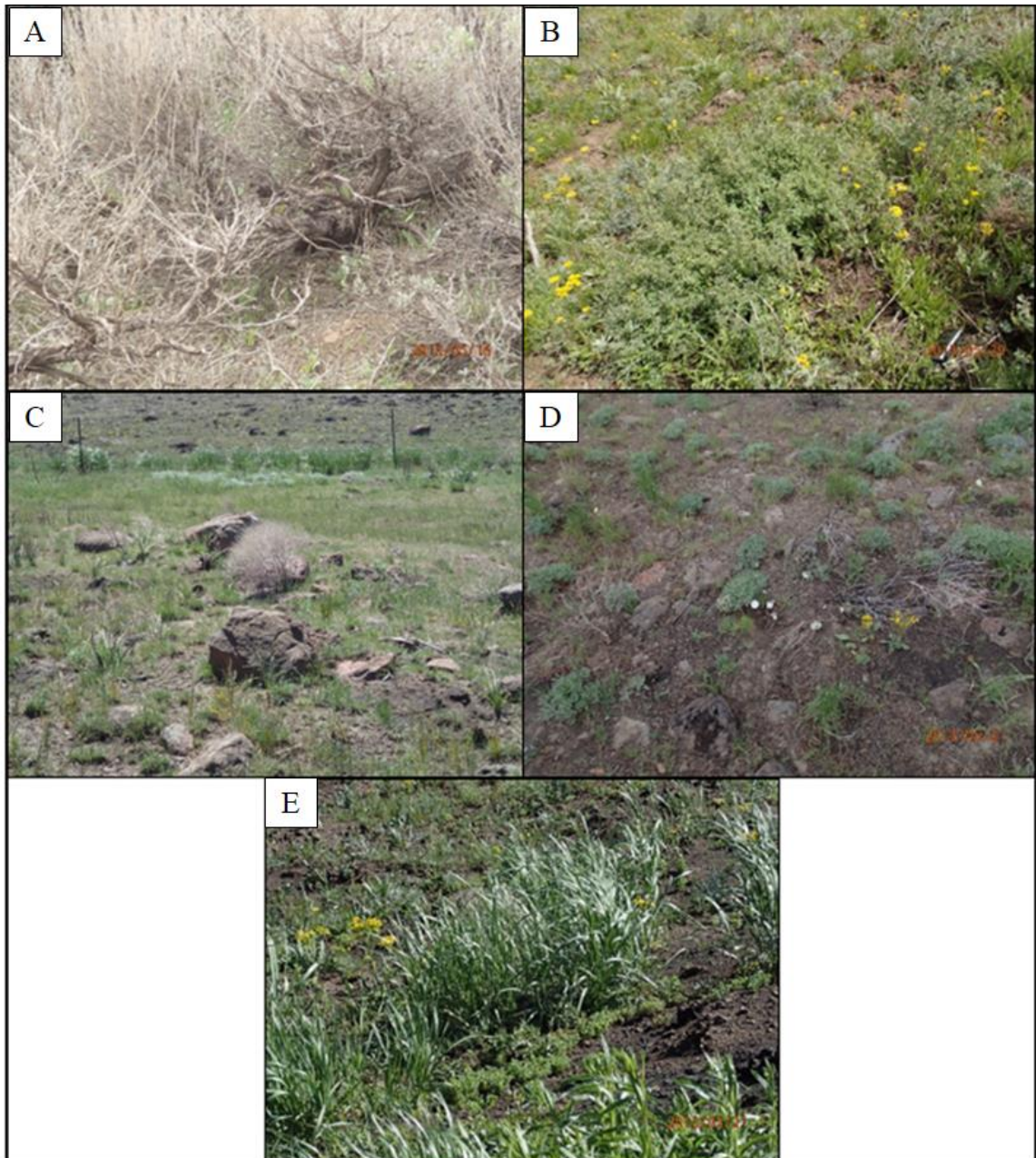
Figure 3.3. Examples of non-sagebrush sage-grouse nesting cover used by ≥1 female for nest placement during 2014 in the Trout Creek Mountains, Harney and Malheur counties, Oregon. A) great basin wild rye; B) dead snowberry; C) rocks; D) horsebrush; E) dead sagebrush; E) blue bunch wheatgrass; F) bitterbrush.
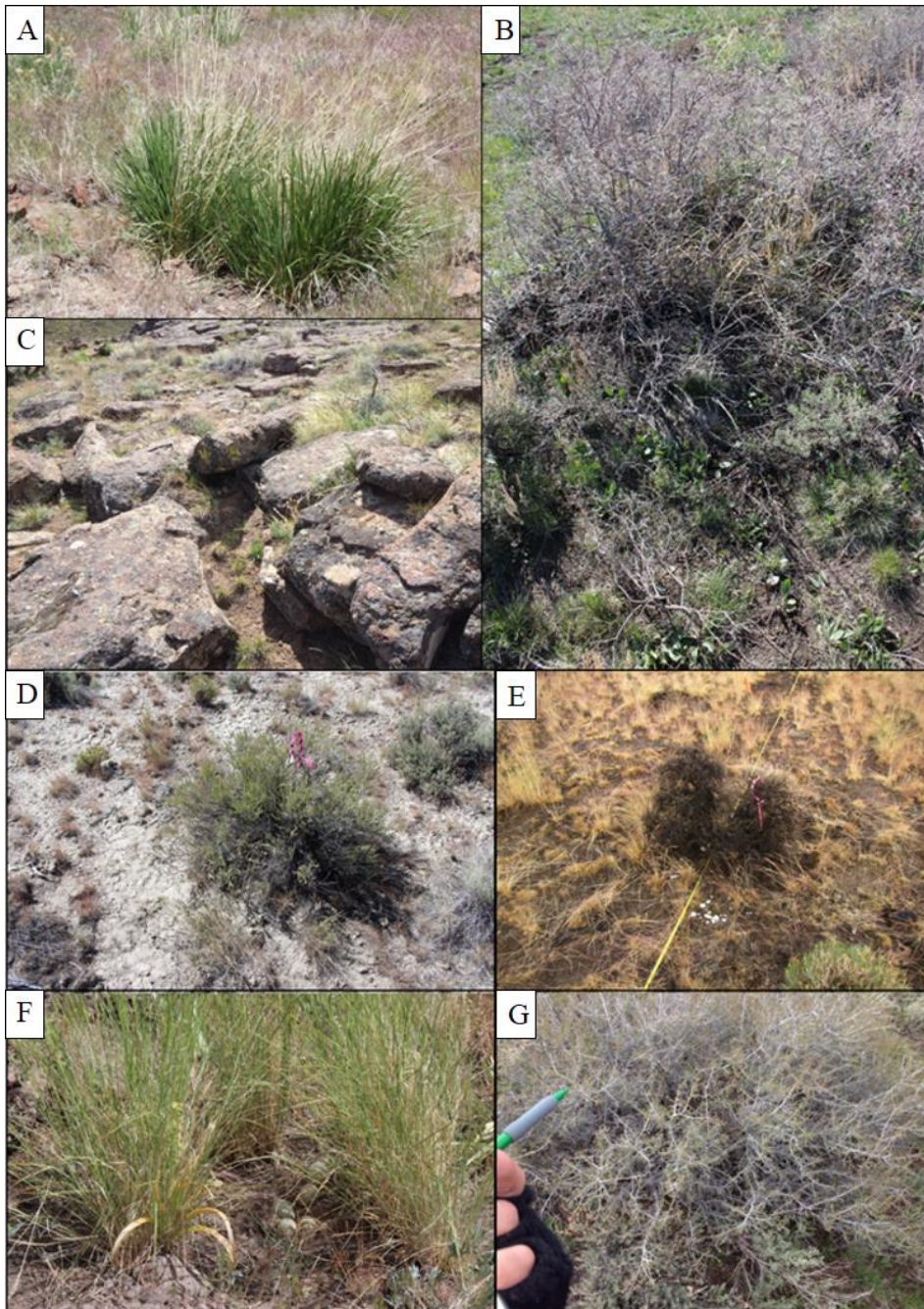
Figure 3.4. Greater sage-grouse daily nest survival estimates, and 95% confidence intervals of first and second nests, with forb cover held at mean values, during 2013 and 2014, in the Trout Creek Mountains, Harney and Malheur counties, Oregon.
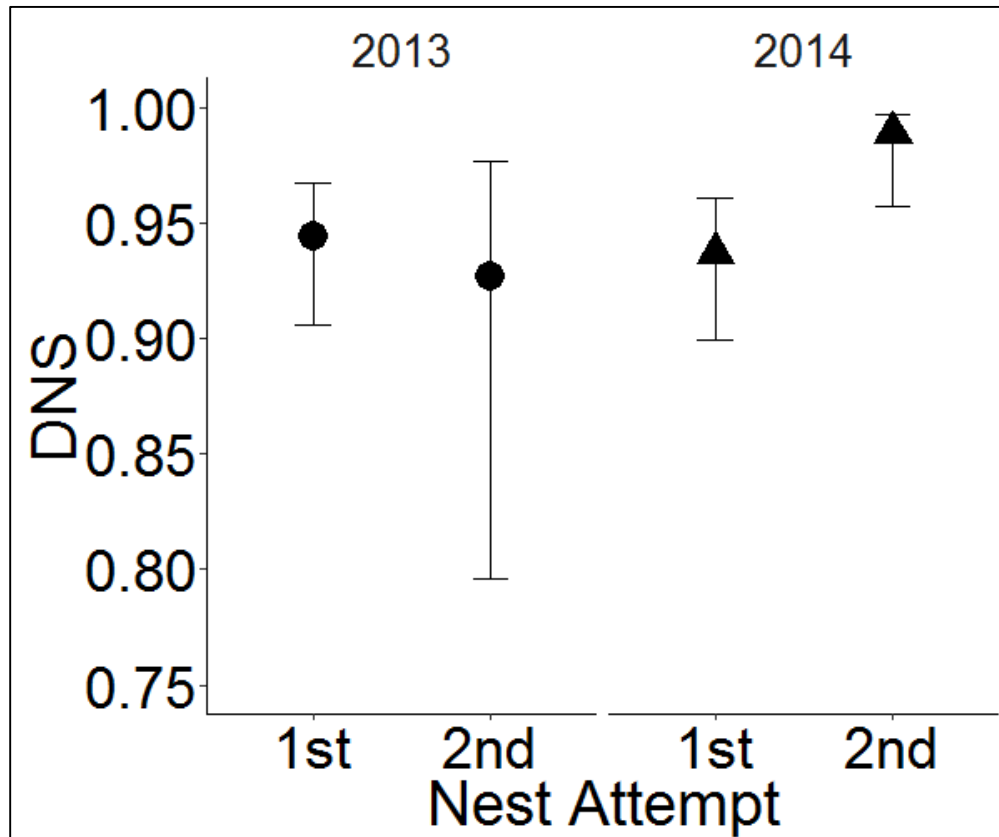
Figure 3.5. Estimates of daily sage-grouse nest survival from the best model including percent forb cover at the nest vicinity scale (FC_NV) and an interaction between year and nest attempt (YR*NAT) plotted against percent forb cover at the nest vicinity scale by year.   Survival estimates were generated for each sage-grouse nest where vegetation surveys were conducted in 2013 (n = 22), and 2014 (n = 28) in the Trout Creek Mountains, Harney and Malheur counties, Oregon.
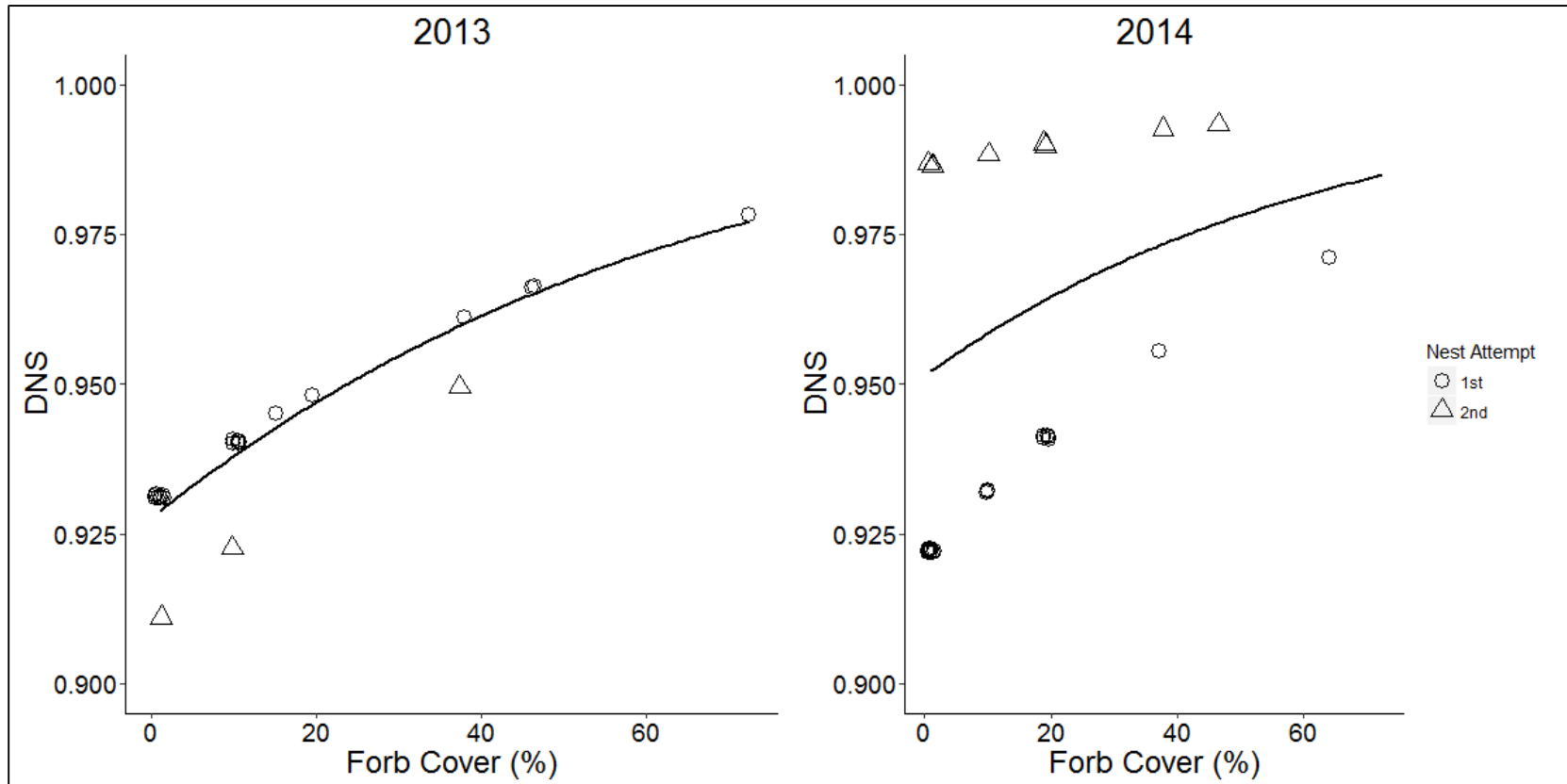
Figure 3.6. Greater sage-grouse incubation period (27 day) nest survival estimates, and 95% confidence intervals of first and second nests, with forb cover held at mean values, during 2013 and 2014, in the Trout Creek Mountains, Harney and Malheur counties, Oregon.
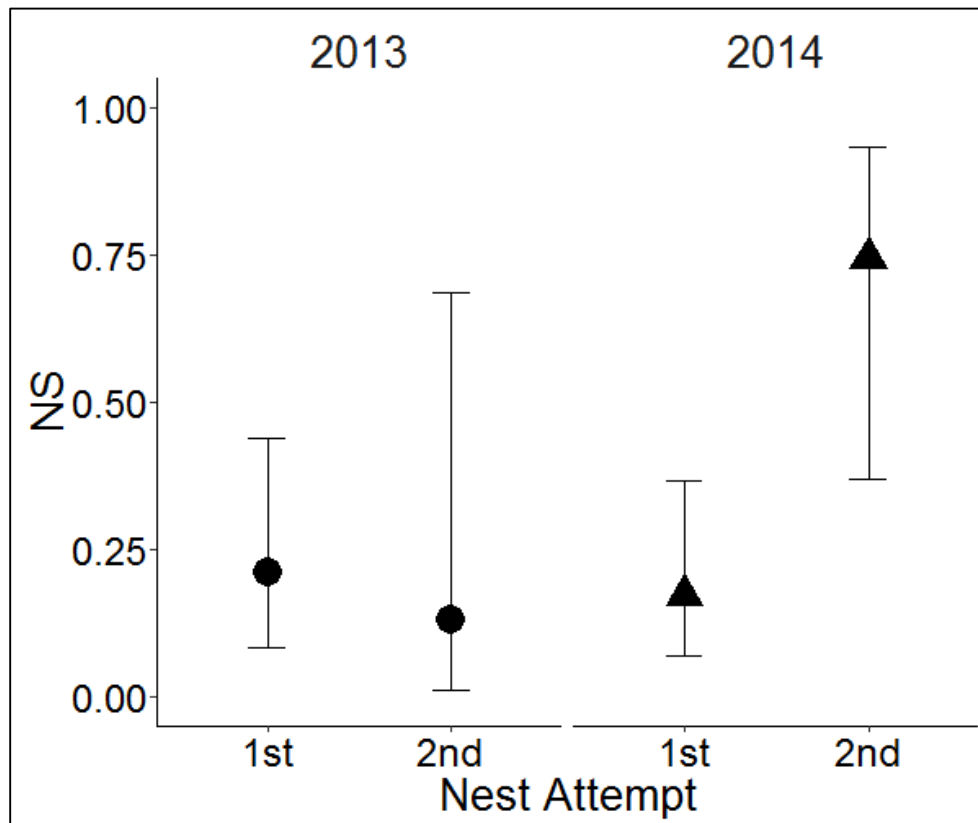
CHAPTER 4

ADULT AND YEARLING SURVIVAL OF GREATER SAGE-GROUSE IMMEDIATELY FOLLOWING LARGE-SCALE WILDFIRE

Lee Foster, Katie Dugger, Christian Hagen, Dave Budeau

ABSTRACT

Understanding species vital rates and the factors that affect them is necessary to arrest or reverse population declines in threatened or vulnerable species. Greater sage-grouse (*Centrocercus urophasianus*) are a long-lived species of North American grouse, characterized by relatively low productivity and high survival rates. The species has experienced long-term population declines, and currently faces multiple threats to its habitat. In the western portion of the sage-grouse's range local population declines have been observed following recent wildfire. We investigated the survival of a population of sage-grouse following a large-scale (~187,000 ha) wildfire in southeastern Oregon. We monitored sage-grouse captured in or near the Holloway Fire and marked with VHF or GPS telemetry transmitters, beginning 3 months following the suppression of the fire (November 2012) until February 2015. We estimated survival of VHF marked individuals, in relation to temporal patterns, and physiological factors, and survival of GPS marked individuals in relation to temporal patterns, physiological factors, and habitat, in Program MARK. Individuals sampled with both transmitter types exhibited severely reduced survival from the beginning of the study until the end of the first post-fire growing season (approximately July or August, 2013). GPS marked individuals exhibited seasonal patterns of survival consistent with previous studies, albeit at reduced levels. Monthly survival of VHF marked individuals was 0.830 from November 2012 through August 2013, and 0.963 from September 2013 through September 2014. Annual survival of this group during the first year of the study (November 2012 – October 2013) was 0.160, among the lowest rates ever reported for the species. Survival of GPS marked individuals was lowest during April and August, and relatively high during the winters of 2013 and 2014 (Monthly S = 0.729 – 1.0). Annual survival of this group increased between the biological years (March – February) of 2013-2014 and 2014-2015 ($S_{2013-2014} = 0.240$, $S_{2014-2015} = 0.379$). The survival rates we observed indicate that a severe die-off of sage-grouse affected by

the Holloway Fire occurred during the first winter post-fire and extended through the end of the first post-fire growing season.

INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*; hereafter: sage-grouse) are a species of conservation concern in western North America. The distribution of the species has declined by approximately half since European settlement, and long-term population declines continue in the remaining distribution (Schroeder et al. 2004, Garton et al. 2011). For threatened and vulnerable species, the first step in arresting population declines is to estimate key demographic parameters and identify the factors that affect them (Wisdom et al. 2000, Reed et al. 2002, Taylor et al. 2012, Dahlgren et al. 2016). Significant work has occurred since the 1950's to describe sage-grouse habitat requirements and demographic rates (Patterson 1952, Connelly et al. 2011a, Connelly et al. 2011b). This work has formed the basis for more recent efforts to quantitatively model sage-grouse population trajectories (Garton et al. 2011), and to identify those vital rates which most limit sage-grouse population growth (Taylor et al. 2012, Dahlgren et al. 2016). While early research was predicated on the assumption that productivity limits population growth in sage-grouse (e.g. Drut et al. 1994), the life-history traits of the species are more consistent with a k-selected species, where adult survival has more impact on population growth rates than reproduction (Sæther et al. 1996, Sæther and Bakke 2000, Stahl and Oli 2006, Taylor et al. 2012, Dahlgren et al. 2016). Recent sensitivity analyses have supported this hypothesis, indicating that adult female survival and chick survival have the greatest effect on sage-grouse population growth rates (Johnson and Braun 1999, Taylor et al. 2012, Dahlgren et al. 2016). Thus, quantifying changes in sage-grouse survival in response to conservation actions or disturbance is an important requirement for predicting the future trajectory of sage-grouse populations.

The advancement of sage-grouse marking and tracking technologies, and statistical methods, has greatly increased knowledge regarding the seasonal patterns, and causes of sage-grouse mortality, and those factors that influence adult survival in the species (Connelly et al. 2011a). Sage-grouse mortality peaks during the breeding season (Mar – Jun) (Connelly et al. 2000, Moynahan et al. 2006), and potentially again during the late summer (Davis et al. 2014), with high overwinter survival (Robertson 1991, Connelly et al. 2000, Beck et al. 2006, Battazzo 2007, Connelly et al. 2011a). Sage-grouse mortality is primarily caused by predation (Connelly et al. 2000, Connelly et al. 2011a, Hagen 2011a), however sage-grouse mortality may also result from collisions with fences and other anthropogenic structures, and disease (Connelly et al. 2011a, Stevens et al. 2012). Sage-grouse co-evolved with their predator community and as evidenced by high annual survival, predation should not act as a limiting factor on sage-grouse populations in a natural setting (Hagen 2011a). However, in cases where habitat has been altered to reduce hiding cover or connectivity, anthropogenic sources of mortality are prevalent, or predator populations are artificially increased due to human subsidies, predation may negatively influence sage-grouse population dynamics (Hagen 2011a).

Across their distribution sage-grouse face multiple threats to their habitat (Miller et al. 2011), and a primary threat to the species in Oregon is increasing wildfire activity (Hagen 2011b). Wildfires in the sagebrush (*Artemisia* spp.) ecosystem may exceed 100,000 ha, and burn large areas in short time periods with most fires burning for $\leq$ 2 weeks (McGee 1982, Knapp 1995, Knapp 1998, Baker 2006). Sage-grouse are a sagebrush obligate species, and require intact sagebrush habitats throughout their lifecycle (Schroeder and Braun 1999, Connelly et al. 2011b). Individuals utilize sagebrush as hiding cover throughout the year, as well as subsisting almost entirely on sagebrush leaves during the winter (Connelly et al. 2011b). The increasing size of fires in the sagebrush ecosystem is exceeding the range of natural variation (Baker 2006), and coupled with the fact that almost all

burned sagebrush is killed, may lead to drastic reductions in sagebrush land-cover across entire seasonal ranges of sage-grouse populations (Boltz 1994, Chapter 2, Foster 2016). Reduction in sagebrush cover may lead to increased predation on sage-grouse due to a reduction in concealment cover or due to food stress during winter, either of which may negatively affect survival. Because sagebrush is slow to regenerate following wildfire, the carrying capacity of the system may be greatly reduced resulting in lag effects in population recovery (Baker 2006). Indeed, sage-grouse populations affected by wildfires have been observed to have reduced population growth rates when compared to populations inhabiting undisturbed habitat (Coates et al. 2015). Identifying sage-grouse demographic rates that are negatively impacted by wildfire will help increase understanding of post-fire population declines, and may suggest management actions to mitigate the effects of large-scale wildfire on sage-grouse populations.

During the summer of 2012, >400,000 ha of sage-grouse habitat burned in Oregon. We utilized GPS-PTT, and VHF radio-transmitters to monitor adult and yearling sage-grouse survival and the acute effects of the Holloway Fire, which burned ~ 187,000 ha in southeastern Oregon and northern Nevada. We also compared survival rates between birds wearing the newer, GPS-PTT rump-mounted instruments and traditional necklace-style VHF transmitters. The specific objectives of our study were to:

1. Estimate survival (S) of GPS marked female sage-grouse, and the spatial and temporal factors associated with survival within fire-affected and associated habitats, from March 2013 – February 2015.

2. Estimate survival (S) of VHF marked male and female sage-grouse, in relation to time since fire, sex, and age, from November 2012 – September 2014.

3. Compare survival rates between individuals marked with VHF vs. GPS transmitters to investigate the possibility of GPS transmitter effects on sage-grouse survival in a cover deficient landscape.

STUDY AREA

Our study was conducted in the Trout Creek Mountains of southeastern Oregon. The Trout Creeks range in elevation from 1372 m to over 2438 m (Evenden 1989), and are characterized by mesas, buttes, and fault blocks cut with deep stream canyons (Carlton 1968). Prior to the Holloway fire, vegetation communities varied based on elevation and topography. At upper elevations (> 1900 m) a mountain big sagebrush – low sagebrush (*A. arbuscula*) mosaic dominated, interspersed with a mountain shrub community of snowberry (*Albus* spp.), bitterbrush (*Purshia tridentata*), and *Ceanothus* spp. (Freeborn 2006). Native grasses at higher elevations included Idaho fescue (*Festuca idahoensis*), needlegrass (*Achnatherum* spp.), bluebunch wheatgrass (*Pseudoroegneria spicata*), and Sandburg's bluegrass (*Poa secunda*) (Freeborn 2006). Additionally mountain mahogany (*Cercocarpus* spp.), and aspen (*Populus tremuloides*) patches dot the higher elevations, and cheat grass (*Bromus tectorum*) was generally absent (Freeborn 2006). At lower elevations Wyoming big sagebrush (*A. t. wyomingensis*) dominated, with areas of salt desert shrub present on more alkaline soils (Freeborn 2006). Grasses at lower elevations included bluebunch wheatgrass, needlegrass, Sandberg's bluegrass, bottlebrush squirreltail (*Elymus elymoides*), basin wildrye (*Leymus cinerius*), and cheat grass, while western juniper (*Juniperus occidentalis*) was rare or absent from the study area (Freeborn 2006). Approximately 95% of the area is managed by the Bureau of Land Management (BLM), a large portion of which is designated as Wilderness Study Area (WSA), with the remaining 5% of land in private holding (Elmore 2000, Freeborn 2006).

A lightning strike ignited the Holloway fire in the Trout Creek Mountains on 5 August 2012. The fire occurred approximately 40 km east of Denio, Nevada, and 210 km southeast of Burns, Oregon (Karges 2013), and was not fully contained until 25 August 2012. The Holloway fire burned 186,972 ha total, of which 99,352 ha were in southern Malheur and Harney counties, Oregon, and 87,227 ha were in northern Humboldt County, Nevada (Karges 2013). The Trout Creeks sage-grouse Priority Area of Conservation (PAC) was almost completely burned by this fire (Figure 4.1; Hagen 2011b). Fire behavior depended on local topographic features, vegetation profiles, and weather conditions. These factors varied considerably in the region, resulting in variable patterns of burned and intact habitat. Increased fuel loads, wind speeds, and topographic features conducive to fire spread caused the fire to burn severely in some areas, consuming nearly all vegetation for square kilometers. In other areas, characterized by reduced fuel loads, wind speeds, and topographic features unconducive to fire spread, fire severity was reduced, leaving a variable mosaic of burned and intact vegetation. Within the fire boundary, 75.3% of the land area was burnt, while the remaining 24.7% was comprised of remnant intact habitat (Figure 4.1; Appendix I). However, several large patches of intact habitat exist within the perimeter of the fire, with the largest patch exceeding 4,000 ha (Figure 4.1; Appendix I).

METHODS

Capture and Instrument Attachment

We captured male and female sage-grouse during October 2012, and female sage-grouse only during both spring and summer of 2013 and 2014 using spotlights and long-handled nets (Wakkinen et al. 1992) near leks or roost sites within, or near ($\leq$ 2 km) the boundary of the Holloway fire. We used feather patterns and morphology to determine sex and age of captured individuals (Crunden 1963). Sage-grouse were either classified as adults ($\geq$2 years of age), or yearlings (1 year of age),

and no hatch year individuals were captured during the study. If yearlings survived more than 1 year of the study, they were reclassified as adults during their second year. Under the authority of project collaborators, Oregon Department of Fish and Wildlife, we marked all captured individuals with an individually numbered steel leg band. We attached 30-g ARGOS-GPS Solar PTTs (PTT-100, Microwave Telemetry Inc., Columbia, MD 21045 USA) to females captured in 2013 and 2014 using a rump-mount attachment technique (Rappole and Tipton 1991). GPS units included Ultra High Frequency (UHF) beacons which were turned on for ground tracking from 1 March – 31 July each year. The GPS units we used during spring and summer 2013 were configured to record locations (± 20m) 6 times daily from 1 March – 31 July, 4 times daily from 1 August – 31 October, and 2 times daily from 1 November – 29 February. GPS units deployed in spring 2014 were configured similar to the previous year's units except that we reconfigured them to collect more locations during the nesting season (10 times daily 1 March – 31 July). All sage-grouse captured in fall 2012, and female sage-grouse captured in summer 2013 received 18 g VHF radio-transmitters (A4000, ATS Inc., Isanti, MN 55040 USA). VHF transmitters were attached with a PVC covered cable neck collar, and contained a mortality switch which increased signal pulse rate if transmitters had not moved for 12 h. We also measured weight (kg), wing length (cm), culmen length (mm), and tarsus length (mm) for all captured individuals. All animal capture, handling, and instrument attachment procedures were approved under Oregon State University's Institutional Animal Care and Use Committee.

Survival Monitoring

We used movement patterns interpreted from the GPS-PTT location data to identify mortality events of marked females. If the GPS locations for a female remained stationary for >18 h outside of the nesting season we assumed that a mortality event had occurred. After the identification of a possible mortality event we

used the satellite location data to locate the general area of the event site. When UHF beacons were active in spring/summer we used a UHF receiver to pinpoint the location of the transmitter on the ground. We examined the mortality site and transmitter for signs of depredation or mortality, such as feathers and bone fragments, predator scat, a sage-grouse carcass, or damage to the transmitter or harness indicative of depredation (i.e., bite marks or scratches). During periods when the UHF beacon was not active, we approached the last known location of the transmitter and performed grid searches of the surrounding area for the transmitter and signs of mortality. During the nesting season female movement patterns suggesting mortality were similar to nesting behavior, thus we employed caution during mortality searches during this period, to avoid disturbance to females on nests. Mortalities were only classified as such if we located a transmitter with conclusive signs of depredation or death (i.e. feather piles or bone fragments near transmitters, damage to transmitter or harness). In these cases we classified the date of mortality as the last known transmission of movement data consistent with live sage-grouse movement patterns (i.e. short between-location movement distances, and locations on top of ridges). Long straight line movement distances, and locations at the bottom of draws and canyons immediately prior to transmitters becoming stationary were assumed to reflect the movement of a sage-grouse carcass and transmitter by predators.

We monitored VHF-marked individuals monthly using aerial VHF telemetry from Oct 2012 – May 2013, and from Oct 2013 – May 2014. We monitored these individuals weekly using handheld VHF telemetry from Jun 2013 – Sep 2013, and from Jun 2014 – Sep 2014. Mortality events were considered to have occurred when we detected the activation of mortality switches.

Covariate Development

We investigated the relationship between monthly survival (S) and a variety of factors we believed would be associated with survival including those reflecting

temporal patterns (n = 4), inherent characteristics of birds (n = 4), and habitat and land-cover characteristics (n = 9) (Table 4.1; see Appendix V for details regarding calculation of covariates).

We evaluated whether monthly survival varied by biological year (YR: Mar 2013 – Feb 2014 vs. Mar 2014 – Feb 2015), by month (t; 24 total), or by biological season including Breeding (March – June), Summer (July – October), Winter (October – February) (SEAS; Table 4.1). We also investigated whether there was an acute effect of the fire on survival which extended through the end of the first post-fire growing season, approximately Jul or Aug 2013 (AFE; Table 4.1). We assessed the effects of age on survival of GPS instrumented birds (AGE; Yearling vs. Adult; Table 4.1). We put VHF transmitters on both males and females, and investigated the effect sex on survival of VHF instrumented birds only (SEX; Table 4.1). We calculated the number of days a female spent on a nest during an analysis interval, to determine whether a female's nesting status impacted survival. This covariate was only applied to time periods when females were on nests (Apr – Jun; NS; Table 4.1). We investigated the effect of movement patterns immediately before mortality on survival, by calculating the size of size of 95% and 50% Brownian bridge kernel ranges (Bullard 1999, Horne et al. 2007), during the 14 days preceding mortality, or during a random 14 day interval within the analyzed month for individuals which survived a given month (RS; Table 4.1).

Habitat and land-cover covariates were developed from GIS data relating to topography, mesic habitat resources, and post-fire habitat mosaic and recovery (Table 4.1; Appendix V). All continuous covariates were modeled with linear, pseudo-threshold, or quadratic structures depending on *a priori* hypotheses (Table 4.2). Pseudo-threshold effects [ln(x)], allowed a covariate to have progressively diminishing effect on S as covariate values increase or decrease. In cases where continuous covariates equaled zero during any interval, we increased all covariate

values by one [ln(x+1)]. We hypothesized that a quadratic relationship ($x + x^2$) between habitat covariates and monthly survival rates of sage-grouse would reflect the positive effect of middle-range habitat values, with negative effects of too much, or too little of a particular habitat covariate.

Analyses

GPS-Instrumented Individuals

We estimated monthly survival of GPS-instrumented female sage-grouse using known fate models with a staggered entry design in program MARK (Pollock et al. 1989, White and Burnham 1999). Monthly survival intervals began on the 1st and ended on 30th or 31st of each calendar month. We estimated monthly survival (S) during 24 monthly intervals (Mar 2013 – Feb 2015) and we assessed the effect of all covariates except sex, as all GPS marked individuals were female. We modeled the effect of habitat covariates following Webb et al. (2012). For individuals which died during an interval, we estimated mean habitat covariate values within 95% and 50% Brownian bridge kernel (BBK) ranges generated from all individual locations collected during the 13 days preceding mortality and the date of mortality (Covariate Analysis Period), and applied those estimates to the interval including mortality (Webb et al. 2012). For individuals which survived an interval, we randomly selected a 14-consecutive-day period within a single survival interval and all locations within that period were used to estimate mean habitat covariates (Webb et al. 2012). Covariate analysis periods between any two intervals were not allowed to overlap. Thus, all habitat covariates were assessed as time varying covariates (White and Burnham 1999). We developed *a priori* hypotheses and an associated model set to investigate the effect of each covariate on monthly survival (Table 4.2).

Due to the large number of covariates included in our analysis, and potential correlation between many of the habitat covariates, we used a hierarchical modeling

procedure to conduct the analysis rather than running a model set that contained every possible combination of all covariates. The hierarchical modeling approach generally results in the same outcome as an all-possible combinations modeling approach, with the benefits of a much smaller model set and fewer models with uninformative parameters (Doherty et al. 2012). We used an information theoretic approach (Burnham and Anderson 2002) to select competitive models at each modeling stage, and we used Akaike's information criterion corrected for small sample size (AIC_c), ΔAIC_c (the difference in AIC_c value between each model and the top ranked model), and AIC_c weights (w_i) to rank models (Burnham and Anderson 2002). We evaluated model deviance and 95% confidence limits on covariate model coefficients (β_i) to assess the direction and strength of specific covariate effects, and to identify uninformative parameters in competitive models (Arnold 2010). Models within 2 ΔAIC_c values of the top model were carried forward from one modeling stage to another, and considered competitive in the final model set unless they contained uninformative parameters (Arnold 2010).

During the first step of modeling, we evaluated temporal effect to select the most supported temporal structure as the basis for additive models containing other covariates. During the second step of modeling, we evaluated non-habitat covariates as single factor models. During the third step of modeling, we evaluated habitat covariates across all scales as single factor models, with pseudo-threshold, quadratic, or linear structures depending on *a priori* hypotheses (Table 4.2). The most supported scale and structure of each continuous habitat covariate was retained in the model set. Covariates included in models within 2 ΔAIC_c of the top model and that had model coefficients with 95% confidence limits that did not overlap zero or only overlapped zero by <10% , were considered for inclusion in additive models. We also assessed all habitat covariates in interactions with month, due to the changing habitat requirements of sage-grouse throughout the year. We examined correlations among all covariates prior to combining them in additive or interactive models, using

the *cor* function in Program R (R Version 3.2.0, www.r-project.org, accessed 1 Oct 2013). Covariates with correlation coefficients >0.6 were not combined in the same model, and we did not investigate models with >1 interaction term or >1 additive effect because of the small number of individuals included in the analysis. Therefore the best temporal structure was combined with the best non-habitat or habitat covariate from the previous modeling stages to generate the final model set.

VHF-Instrumented Individuals

Due to ragged telemetry data (i.e. an uneven schedule of telemetry checks), we analyzed survival of VHF marked individuals in Program MARK (White and Burnham 1999) using Nest Survival models with a staggered entry design (Pollock et al. 1989). Nest Survival models are useful when analyzing ragged telemetry data, because they do not require a regular schedule of transmitter status checks, and do not require knowledge of the exact date of mortality, only the last date an individual was known to be alive, and the first date an individual was known to be dead (White and Burnham 1999, Hartke et al. 2006, Mong and Sandercock 2007, McNew et al. 2011). Nest survival models allow for staggered entry of individuals into the study, right censoring, and the use of individual covariates (White and Burnham 1999, Hartke et al. 2006). Monthly survival (S) was estimated for 23 monthly intervals (Nov 2012 – Sep 2014), and we assessed the temporal structure of survival, and the effects of age and sex on VHF marked individuals. We used Akaike's information criterion corrected for small sample size (AIC_c), ΔAIC_c (the difference in AIC_c value between each model and the top ranked model), and AIC_c weights (w_i) to rank models (Burnham and Anderson 2002). Models within 2 ΔAIC_c values of the top model were considered competitive in the final model set. We evaluated model deviance and 95% confidence limits on covariate model coefficients (β_i) to assess the direction and strength of specific covariate effects, and to identify uninformative parameters in competitive models (Arnold 2010).

RESULTS

Survival of GPS-Instrumented Individuals

We monitored 64 individual female sage-grouse, for varying amounts of time (range: 1 – 24 months) between Mar 2013 and Feb 2015. Eleven individuals were right censored in the data set due to uncertainty about their final fate, or date of mortality. Within the sample of individuals instrumented with GPS transmitters we observed strong support for the hypothesis that survival varied by month, but not between years, except for the additional, negative acute effect on survival during the first five months of the study (AFE; Mar 2013 – Jul 2013; Table 4.3).   Models that included monthly variation across years received 97% of model weight (Table 4.3). Models containing AFE received 50% of model weight, and the top two models in the set contained both monthly variation and AFE (Table 4.3). The 95% confidence limit around the model coefficient for AFE (β) only slightly overlapped zero (<1%; β_{AFE} = –0.985, SE = 0.505, 95% CI: –1.975 to 0.005) suggesting relatively strong support for lower monthly survival during the first 5 months of the study, which corresponded to the second half of the first year post-fire. Probability of survival varied considerably between months within a year, with the lowest probability of survival observed during Apr and Aug, and the highest probability of survival observed during the winter months (Table 4.4; Figure 4.2). The likelihood of surviving a given month during Mar – Jul 2014 was 2.67 times greater than the likelihood of surviving that month during Mar – Jul in 2013 (Figure 4.2). When monthly survival estimates were extrapolated across biological years average survival increased between 2013-2014 and 2014-2015 (Mar 2013 – Feb 2014: S = 0.244, 95% CI = 0.090 – 0.398; Mar 2014 – Feb 2015: S = 0.361, 95% CI = 0.163 – 0.558).

There were a number of other competitive models within the set ($\Delta AIC_c < 2$) that included habitat covariates in addition to the basic structure of the top model (i.e., t + AFE + hab cov) (Table 4.3). These included effects of the proportion of locations

in intact habitat (PLI), the pseudo-threshold form of the amount of intact habitat within an individual's 50% BBK range (LN_PI_50), the pseudo-threshold form of the mean terrain roughness index value within an individual's 95% BBK range (LN_TRI_95), the connectance index, using a 1 km threshold, within an individual's 50% BBK range (CONNL_50), and an individual's 50% BBK range size (RS_50) (Table 4.3). However, estimates of model coefficients on all of these covariates widely overlapped zero (>10%), suggesting these parameters were largely uninformative (Arnold 2010).

Survival of VHF-Instrumented Individuals

We monitored 33 VHF marked individual sage-grouse (7 male, 26 female), marked with VHF radio-collars, for varying lengths of time between Nov 2012 and Sep 2014. We right censored four individuals from the sample due to transmitter failure. We found strong support for constant survival between months, with an additive negative temporal effect on survival during the first 10 months that VHF marked individuals were monitored (AFE; Nov 2012 – Aug 2013; Table 4.5). The two best models contained AFE for 77% of the total model weight (Table 4.5). The 95% confidence interval on the model coefficient for AFE did not overlap zero, suggesting this was a strong effect ($\beta_{AFE} = -1.832$, SE = 0.537, 95% CI: –2.884 to –0.781). The likelihood of surviving a month after Aug 2013 was 6.25 times greater than the likelihood of surviving a month between Nov 2012 and Aug 2013 (Monthly S: Nov 2013 – Aug 2013 = 0.830, Sep 2013 – Sep 2014 = 0.968). When monthly survival estimates were extrapolated across years, or portions thereof, mean survival increased between 2012-2013 and 2013-2014 (Nov 2012 – Oct 2013: S = 0.160, 95% CI = 0.012 – 0.308; Nov 2013 – Sep 2014: S = 0.685, 95% CI = 0.451 – 0.919). Models including additive effects of age, and sex, in addition to AFE were competitive ($\Delta AIC_c < 2$), however, the model coefficients for these covariates widely overlapped zero, suggesting these parameters were uninformative (Arnold 2010).

Comparison of Transmitter Types

We observed considerable overlap of 95% confidence limits on both monthly and annual survival estimates during the biological year of 2013-2014 (Mar 2013 – Feb 2014) (Figure 4.3 – Figure 4.4). During the period of the biological year of 2014-2015 when both transmitter types were monitored (Mar 2014 – Sep 2014), there was considerable overlap of 95% confidence limits on monthly survival estimates for all months except August 2014 (GPS: $S_{Aug-14} = 0.754$, 95% $CI_{Aug-14} = 0.567 – 0.877$; VHF: $S_{Aug-14} = 0.966$, 95% $CI_{Aug-14} = 0.919 – 0.986$; Figure 4.3). The derived survival estimate for the entire interval from March to September 2014 (7 months) was higher for sage-grouse of both sexes marked with VHF transmitters, than for female sage-grouse marked with GPS transmitters, however 95% confidence limits on these estimates overlapped and this interval corresponds to only 7 months of the biological year (GPS: S= 0.453, 95% CI = 0.252 – 0.654; VHF: S = 0.785 95% CI = 0.615 – 0.957; Figure 4.4).

DISCUSSION

Our study provides the first detailed examination of acute effects of large-scale wildfire on adult and yearling sage-grouse survival. Survival of sage-grouse was severely reduced from the time of fire until the post-fire growing season of 2013 (circa July or August). Survival of GPS and VHF marked individuals was comparable during throughout much of the study, but survival between the instrument groups diverged during August 2014, a period when the sample of VHF marked sage-grouse in the study had declined to eight individuals and mortality on GPS marked birds was unusually high. Consistent with previous research, we observed considerable variation in survival throughout the year for GPS instrumented individuals, with lowest survival occurring during April and August (Connelly et al. 2000, Baxter et al. 2008, Blomberg et al. 2013a, Caudill et al. 2014, Davis et al. 2014). Increased mortality of sage-grouse during the spring (Connelly et al. 2000,

Wik 2002, Baxter et al. 2008, Blomberg et al. 2013a, Davis et al. 2014), and late summer-autumn (Blomberg et al. 2013a, Caudill et al. 2014, Davis et al. 2014) is well documented. Similar to other studies, we observed generally high survival during the winter (Robertson 1991, Connelly et al. 2000, Beck et al. 2006, Connelly et al. 2011a), however we did observe declines in survival in December during each year. Potentially, this mid-winter decline in survival may have reflected reductions in sagebrush cover within the study area or an influx of avian predators on winter migration.

In contrast to other studies, we did not find support for the effects of age, nesting status, or habitat covariates on survival (Zablan et al. 2003, Blomberg et al. 2013b, Davis et al. 2014, Dinkins et al. 2014). However, the strong decline in survival immediately following the fire was indicative of the general large-scale loss of sagebrush habitat within the fire boundary (~75% of pre-fire sagebrush cover lost). Understanding habitat effects on survival after a large-scale disturbance event can be difficult. The overall carrying capacity of the landscape was likely dramatically altered (Swenson et al. 1987, Braun 1998, Connelly et al. 2000b, Crawford et al. 2004, Walker et al. 2007) and the immediate death of birds due to the fire itself or shortly afterwards (i.e., between Aug – February 2013 before the study began) may have reduced the population within the fire boundary to a level that allowed survival of remaining individuals through their use of required habitats still available within the fire boundary. Also, linking habitat use within time/space to the survival of individual animals is difficult and while we addressed this by developing time-varying habitat covariates on individual sage-grouse, another study using this approach also failed to identify landscape effects on survival (Webb et al. 2012), suggesting we still may not be measuring habitat characteristics and use in a way that is meaningful to the survival of individual sage-grouse.

The growing season in Great Basin sagebrush communities occurs from approximately April to August (Comstock and Ehleringer 1992, Dysart 2001, Wrobleski and Kauffman 2003). During the period between a summer wildfire in this ecosystem, and the end of the following growing season, vegetation in wildfire affected areas is drastically reduced, and prior to the commencement of the first post-fire growing season, vegetation in burned areas is essentially non-existent (Wrobleski and Kauffman 2003). Due to these patterns, approximately 75% of the area of the fire provided sparse to no cover or forage for sage-grouse between September 2012 and April 2013, with herbaceous cover and forage increasing slowly between April 2013 and August 2013 (L. Foster, *personal observation*). Within the sample of VHF marked individuals, overwinter survival during 2012-2013 was reduced (Monthly S, Winter 2012-2013: 0.830) when compared to estimates from other populations inhabiting intact sagebrush areas (Monthly S, Winter: 0.917 – 0.973, Moynahan et al. 2006; 0.96 – 0.98, Battazzo 2007). The pre-fire population of sage-grouse in our study area was thought to be one of the densest concentrations of sage-grouse in the Oregon (ODFW, *unpublished data*). The fire itself may have resulted in the direct mortality of some individuals, reducing the overall population. However, the concentration of individuals remaining, and the sudden removal of sagebrush and herbaceous cover following the fire, likely "reset" the carrying capacity for sage-grouse in the region. During the months immediately following the fire we observed high mortality rates as birds returned to, or remained within the fire-boundary during the first winter post-fire, and this effect extended until herbaceous cover had reestablished following the first post-fire growing season. Increases in sage-grouse survival following the summer of 2013 likely reflected an end to this period of pronounced mortality, as populations inhabiting the fire boundary fell below carrying capacity of the remaining habitat, and as herbaceous cover within burned areas increased to the point where it provided hiding cover and forage for the remaining sage-grouse population. Predation is the primary cause of sage-grouse mortality

(Hagen 2011a), thus probability of mortality of sage-grouse may be more affected by the habitat conditions occurring at a small temporal scale prior to predation than by the larger scale habitat conditions characterizing an individual's locations during the 2 weeks preceding mortality. Conversely, predation may be random, and not measurably affected by habitat conditions, thus making reducing our ability to model habitat effects on sage-grouse survival.

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Table 4.1. Covariates, the scales at which they were evaluated, and the covariate forms evaluated, hypothesized to affect greater sage-grouse survival between Oct 2012 and Feb 2015 in the Trout Creek Mountains, Malheur and Harney counties, Oregon.

Covariate	Acronym	Description	Scale[a]	Form[b]
Temporal Factors				
Year	YR	Biological year (Mar - Feb)	NA	NA
Time	t	Monthly intervals	NA	NA
Linear time trend	T	Linear trend in survival across full study	NA	NA
Month across year	MONTH	Monthly intervals differ within years, but constant across years.	NA	NA
Season	SEAS	Three season structure: breeding, summer, winter	NA	NA
Acute Fire Effect	AFE	Acute effect of fire: Mar 2013 - Jul 2013	NA	NA
Non-Habitat Covariates			NA	NA
Age	AGE	Adult (>2 yrs) vs yearling (1 yr)	NA	NA
Sex	SEX	Female vs. male	NA	NA
Nest Status	NS	Number of days within monthly interval that a female spent incubating	NA	L, PT
Range Size	RS	Size of Brownian bridge kernel range generated from locations that occurred in an interval's covariate analysis period	95% BBK, 50% BBK	L, PT
Habitat Covariates				
Mean Distance to Water	DTW	Mean distance from all points, in a 14 day covariate analysis period within a monthly interval, to a permanent or semi-permanent stream	NA	L, PT, Q

Terrain Roughness Index	TRI	Mean terrain roughness index value calculated following Wilson et al. (2007) within covariate analysis period range	95% BBK, 50% BBK	L, PT
Proportion of Locations Intact	PLI	Proportion of locations within covariate analysis period which occur in intact habitat	NA	L, PT, Q
Percent Intact	PI	Percent of covariate analysis period range which is composed of intact habitat	95% BBK, 50% BBK	L, PT, Q
Connectance Index - Long	CONNL	Connectance index of patches in covariate analysis period range, calculated in FRAGSTATS using a 1 km connectedness distance	95% BBK, 50% BBK	L, PT
Connectance Index - Short	CONNS	Connectance index of patches in covariate analysis period range, calculated in FRAGSTATS using a 0.5 km connectedness distance	95% BBK, 50% BBK	L, PT
Edge Density	ED	Amount of intact habitat/burnt habitat edge (m/ha) in covariate analysis period range	95% BBK, 50% BBK	L, PT, Q
Mean Distance to Intact	DTI	Mean distance (m) from all points in a covariate analysis period to intact sagebrush habitat, set as 0 m for locations in intact habitat	95% BBK, 50% BBK	L, PT
Mean NDVI	NDVI_MN	Mean normalized difference vegetation index within covariate analysis period range	95% BBK, 50% BBK	L, PT
Standard Deviation NDVI	NDVI_STD	Standard deviation of normalized difference vegetation index within covariate analysis period range	95% BBK, 50% BBK	L, PT

[a]Scale: 95% BBK – 95% Brownian bridge kernel range calculated from locations within covariate analysis period, 50% BBK – 50% Brownian bridge kernel range calculated from locations within covariate analysis period.

[b]Form: L – linear; PT – pseudo-threshold, Q - quadratic.

Table 4.2. Hypotheses regarding relationships between covariates and survival (S) of greater sage-grouse between Oct 2012 and Feb 2015, in the Trout Creek Mountains, Harney and Malheur counties, Oregon, and the literature sources from which hypotheses were derived.

| Covariate | Structure of Predicted Effects | | | Support For Hypothesis |
	Linear	Psuedothreshold	Quadratic	
YR	$\beta_{YR} > 0$	-	-	Zablan et al. 2003, Swanson 2009, Blomberg et al. 2012
T	$\beta_{T} > 0$	-	-	Swanson 2009, Blomberg et al. 2012, Davis et al. 2014
AFE	$\beta_{AFE} < 0$	-	-	-
AGE	$\beta_{AGE} > 0$	-	-	Blomberg et al. 2013a, Davis et al. 2014
SEX	$\beta_{female} > 0$	-	-	Zablan et al. 2003
NS	$\beta_{NS} > 0$	$\beta_{ln(NS)} > 0$	-	Swanson 2009, Blomberg et al. 2013b, Dinkins et al. 2014
RS	$\beta_{RS} < 0$	$\beta_{ln(RS)} < 0$	-	Erikstad 1985, Thompson and Fritzell 1989.
DTW	$\beta_{DTW} > 0$	$\beta_{ln(DTW)} > 0$	$\beta_{DTW} > 0, \beta_{DTW}^2 < 0$	-
TRI	$\beta_{TRI} < 0$	$\beta_{ln(TRI)} < 0$	-	Dinkins et al. 2014, Kirol et al. 2015
PLI	$\beta_{PLI} > 0$	$\beta_{ln(PLI)} > 0$	$\beta_{PLI} > 0, \beta_{PLI}^2 < 0$	-
PI	$\beta_{PI} > 0$	$\beta_{ln(PI)} > 0$	$\beta_{PI} > 0, \beta_{PI}^2 < 0$	-
CONNL	$\beta_{CONNL} > 0$	$\beta_{ln(CONNL)} > 0$	-	-
CONNS	$\beta_{CONNS} > 0$	$\beta_{ln(CONNS)} > 0$	-	-
ED	$\beta_{ED} < 0$	$\beta_{ln(ED)} < 0$	$\beta_{ED} > 0, \beta_{ED}^2 < 0$	-
DTI	$\beta_{DTI} < 0$	$\beta_{ln(DTI)} < 0$	-	-
NDVI_MN	$\beta_{NDVI\_MN} > 0$	$\beta_{ln(NDVI\_MN)} > 0$	-	Kirol et al. 2015
NDVI_STD	$\beta_{NDVI\_STD} < 0$	$\beta_{ln(NDVI\_STD)} < 0$	-	Kirol et al. 2015

Table 4.3. Model selection results for models relating categorical and continuous nest characteristics to monthly survival of greater sage-grouse instrumented with GPS transmitters in the Trout Creek Mountains, Harney and Malheur counties, Oregon, during 2013/2014 and 2014/2015 after the introduction of additive models to the set. Models were ranked according to Akaike's information criterion adjusted for small sample size (AIC$_c$). ΔAIC$_c$, AIC$_c$ weights (AIC$_c$ Wts), number of parameters (k), and model deviance are given for all models. Covariate acronyms are described in Table 4.1 and the intercept-only model is included for comparison.

Model[a]	ΔAIC$_c$	AIC$_c$ Wts	k	Deviance
MONTH + AFE	0.00	0.09	13	237.44
YR + MONTH + AFE	0.06	0.08	14	235.35
MONTH + AFE + PLI	1.24	0.05	14	236.52
MONTH + AFE + pt_PI__50	1.39	0.04	14	236.67
MONTH + AFE + pt_TRI_95	1.50	0.04	14	236.78
MONTH+AFE+CONNL_50	1.72	0.04	14	237.01
MONTH + AFE + CONNL_50	1.72	0.04	14	237.01
MONTH+AFE+HRS_50	1.94	0.03	14	237.22
MONTH + AFE + HRS_50	1.94	0.03	14	237.22
MONTH	2.08	0.03	12	241.66
MONTH*PLI + AFE	2.64	0.02	14	237.93
MONTH*pt_PI_50	2.85	0.02	14	238.14
MONTH*CONNL_50 + AFE	3.00	0.02	14	238.28
YR+MONTH	3.55	0.01	14	238.83
AFE	9.47	0.00	2	269.85
Intercept-only model	11.48	0.00	1	273.89

[a]Prefixes to nest characteristics indicate structural form: pt_ = pseudo-threshold, no prefix = linear structure. Suffixes indicate sampling scale: _50 = 50% BBK range, _95 = 95% BBK range, no suffix = scale not applicable. Only models within 10 ΔAIC$_c$ of the top model displayed.

Table 4.4. Model averaged estimates of GPS instrumented greater sage-grouse monthly survival, during 2013/2014 and 2014/2015 in the Trout Creek Mountains, Harney and Malheur counties, Oregon.

| Month | 2013-2014 | | | 2014-2015 | | |
	S	SE	95% CI	S	SE	95% CI
March	0.868	0.075	0.647 - 0.960	0.944	0.047	0.747 - 0.990
April	0.745	0.080	0.562 - 0.869	0.864	0.063	0.689 - 0.948
May	0.900	0.058	0.719 - 0.969	0.949	0.035	0.817 - 0.987
June	0.923	0.056	0.719 - 0.983	0.961	0.034	0.805 - 0.993
July	0.810	0.086	0.587 - 0.928	0.893	0.061	0.703 - 0.967
August	0.761	0.077	0.582 - 0.879	0.753	0.080	0.567 - 0.877
September	0.911	0.051	0.748 - 0.973	0.906	0.055	0.732 - 0.971
October	0.963	0.036	0.779 - 0.995	0.960	0.039	0.769 - 0.994
November	0.998	0.013	0.972 - 1.000	0.998	0.013	0.972 - 1.000
December	0.844	0.082	0.616 - 0.948	0.834	0.087	0.595 - 0.945
January	0.998	0.013	0.972 - 1.000	0.998	0.013	0.972 - 1.000
February	0.998	0.013	0.972 - 1.000	0.998	0.013	0.972 - 1.000

Table 4.5. Model selection results for models relating categorical and continuous nest characteristics to monthly survival of greater sage-grouse marked with VHF radio-collars in the Trout Creek Mountains, Harney and Malheur counties, Oregon, during 2012-2013, 2013-2014, and 2014-2015 after the introduction of additive models to the set. Models were ranked according to Akaike's information criterion adjusted for small sample size (AIC_c). ΔAIC_c, AIC_c weights, number of parameters (k), and model deviance are given for all models. Covariate acronyms are described in Table 4.1 and the intercept-only model is included for comparison.

Model	ΔAIC_c	AIC_c Wts	k	Deviance
AFE	0.00	0.33	2	107.81
SEX+AFE	0.79	0.23	3	106.55
AGE+AFE	1.95	0.13	3	107.72
SEX+AGE+AFE	2.69	0.09	4	106.39
Intercept-only	11.68	0.00	1	121.53
Month+AFE	19.07	0.00	13	103.38
Month	27.28	0.00	12	113.81
t	36.01	0.00	23	96.92
t+AFE	38.47	0.00	24	96.92

Figure 4.1. Holloway fire severity in relation to Trout Creeks Sage-Grouse Priority Area of Conservation (PAC), Oregon. Inset depicts Holloway fire (red outline) in relation to all Oregon Sage-Grouse PACs (green polygons).
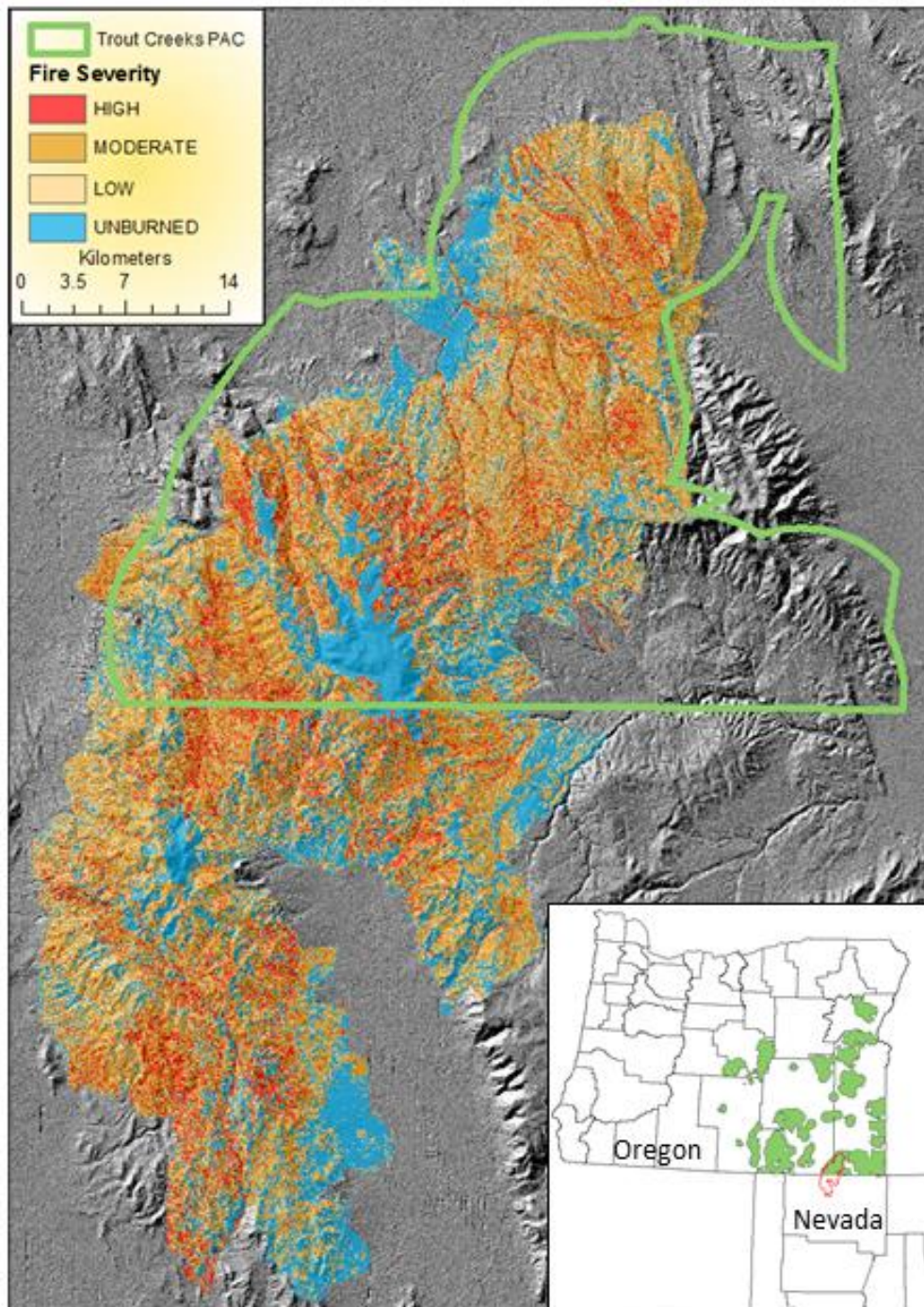
Figure 4.2. Model averaged estimates, and 95% confidence limits, of greater sage-grouse monthly survival during 2013-2014 and 2014-2015, in the Trout Creek Mountains, Harney and Malheur counties, Oregon.
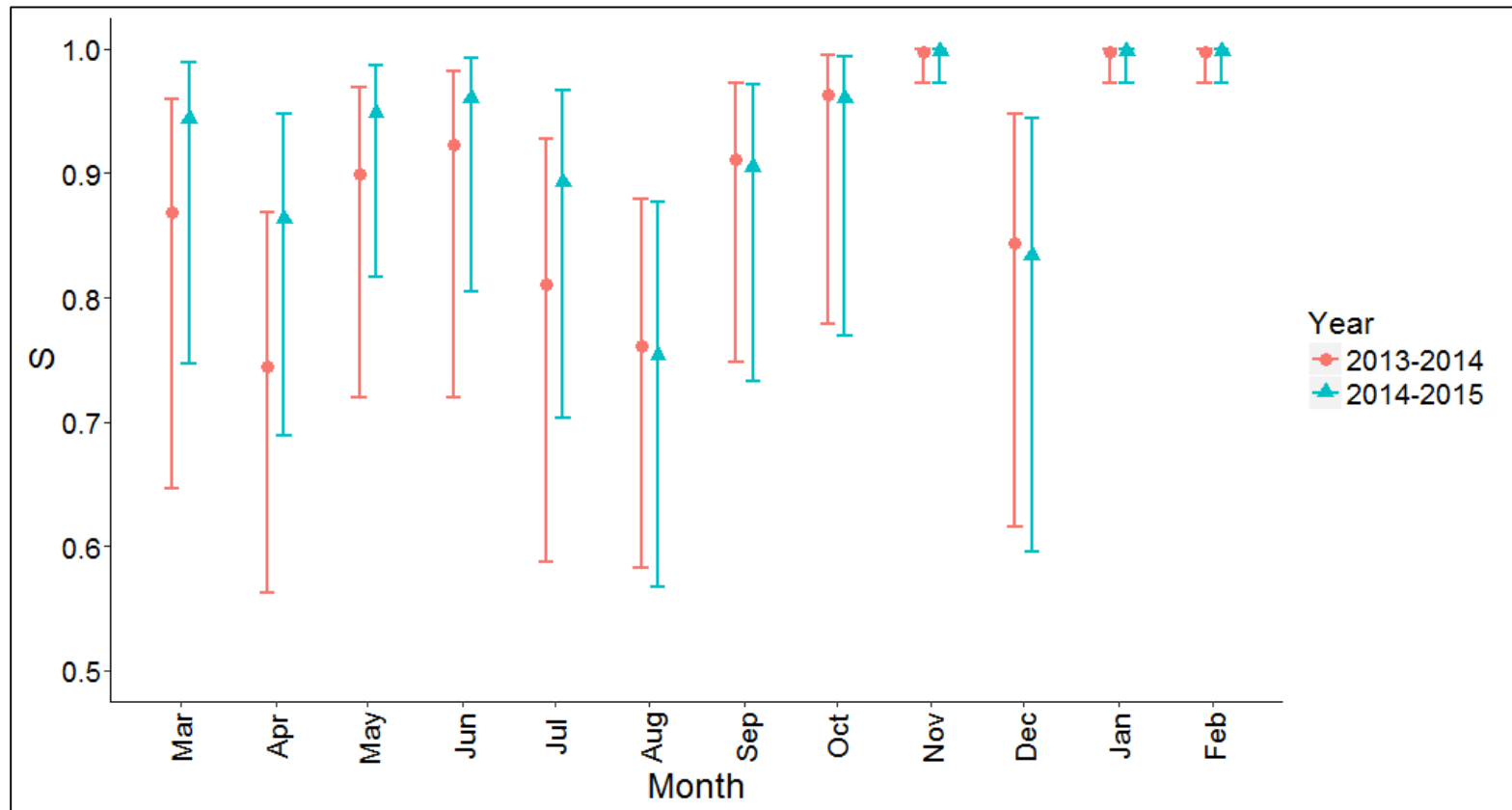
Figure 4.3. Model averaged estimates, and 95% confidence limits, of adult survival of GPS and VHF marked sage-grouse between November 2012 and February 2015, in the Trout Creek Mountains, Harney and Malheur Counties, Oregon.
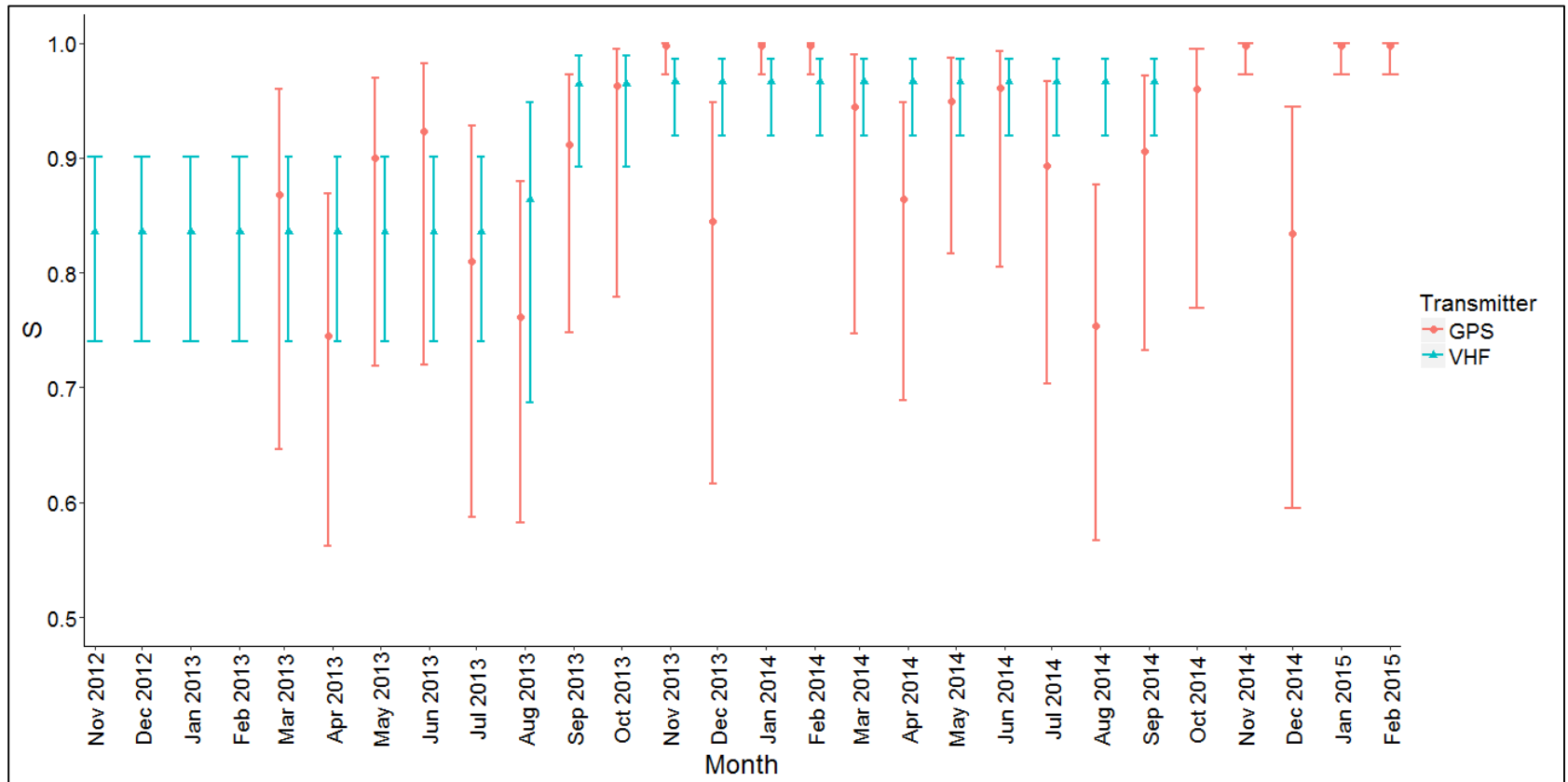
Figure 4.4. Model averaged derived estimates, and 95% confidence intervals, of adult survival of GPS and VHF marked sage-grouse, during the periods of March 2013 – February 2014, and March 2014 – September 2014, in the Trout Creek Mountains, Harney and Malheur Counties, Oregon.
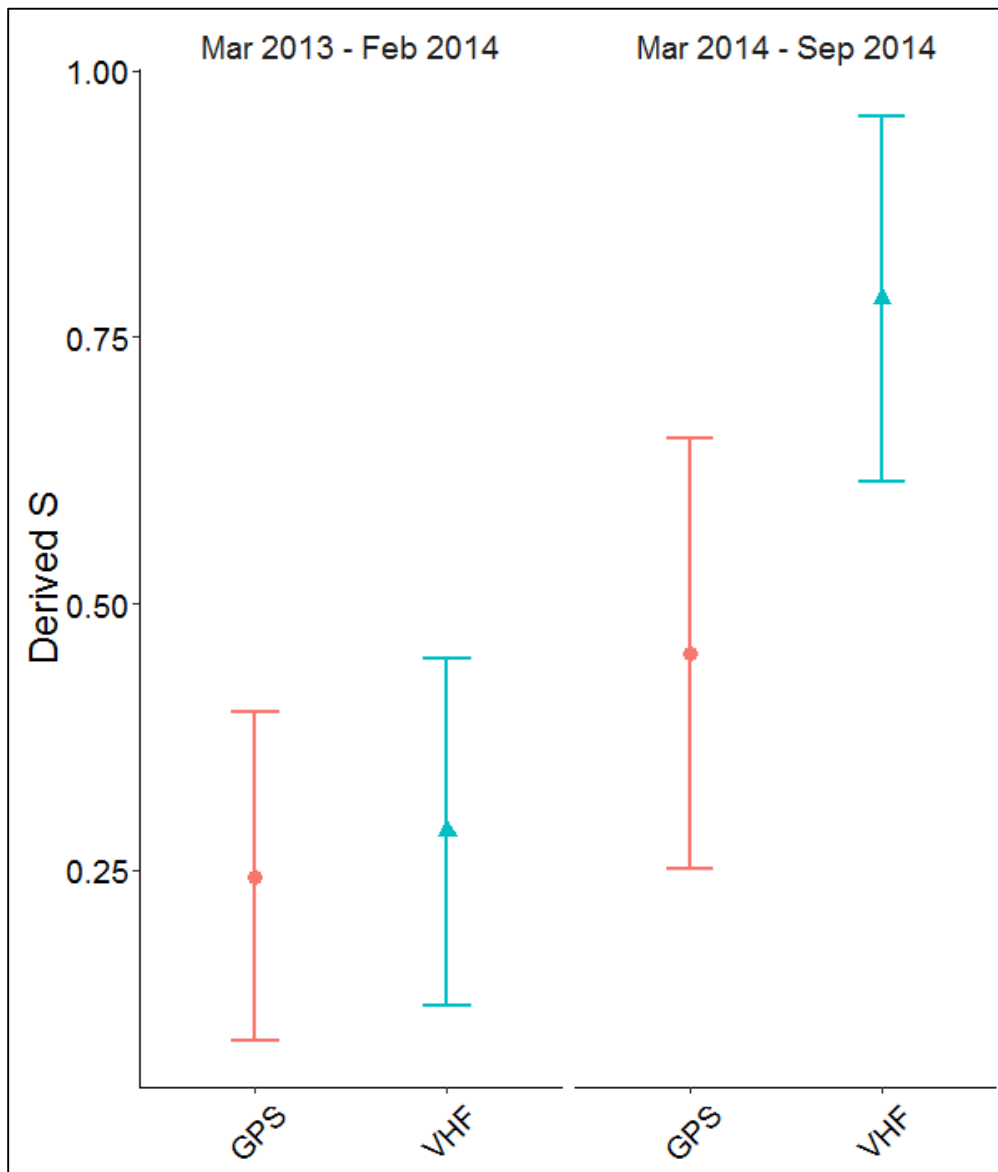
CHAPTER 5

SYNTHESIS AND CONCLUSIONS

Lee Foster

SUMMARY OF KEY FINDINGS

Female sage-grouse in our study occupied and attempted to reproduce in habitat affected by wildfire during the initial 2 years following the Holloway Fire, even in areas with extremely limited residual sagebrush cover. Sage-grouse in undisturbed habitat exhibit extremely strong site-fidelity to seasonal ranges (Hagen 1999, Connelly et al. 2011a). We found that this pattern of behavior persisted following large-scale wildfire, indicating that sage-grouse do not respond to habitat disturbance through emigration. While sage-grouse seasonal ranges did not appear to shift in response to the fire, sage-grouse still attempted to select habitat at the third-order (Johnson 1980), in a similar manner to populations in undisturbed habitat (Connelly et al. 2011b). During the breeding and winter seasons, sage-grouse selected strongly for increasing amounts of intact sagebrush land-cover around used locations, and during the summer selected for increased density of intact-burnt habitat edge around used locations. Presumably, these selection patterns indicate that sage-grouse were attempting to utilize the habitat available to them, although constrained by seasonal range philopatry, in a manner most beneficial to their fitness.

However, our results also suggest that the sage-grouse occupying the Holloway Fire suffered acute fitness costs during the first two years post-fire. Nesting success throughout our study was consistently low, and during the first nesting season post-fire was among the lowest rates reported for sage-grouse (2013 Nesting Success: 19%; Previously Reported Range: 15% - 86%, Connelly et al. 2011a). Similarly, survival of adult and yearling sage-grouse was consistently low throughout the study, and from the time of the fire through the end of the first post-fire growing season was drastically reduced. These results suggest there was significant mortality of adult sage-grouse during the first winter and spring post-fire, concurrent with a period of reduced reproduction. Following this initial demographic

trough, survival and reproduction increased, but through the 2nd year post-fire remained low in comparison with populations existing in undisturbed habitat.

IMPLICATIONS FOR SAGE-GROUSE POPULATIONS AFFECTED BY FIRE

Wildfire has long been posited as a primary threat to sage-grouse populations and habitat (Brooks and Pyke 2001, Connelly et al. 2011c, Coates et al. 2015). However, until recently the effects of wildfire on sage-grouse population trajectories, and demographic rates remained uninvestigated (Coates et al. 2015). To fully assess the consequences of habitat disturbance on wildlife populations, it is necessary not only to quantify habitat changes, and resource selection of wildlife species affected by disturbance, but to also quantify the demographic rates of affected populations (Van Horne 1983). Sage-grouse population trajectories, as measured by trends in male sage-grouse lek counts, have declined in areas affected by wildfire (Coates et al. 2015). If wildfire continues to impact sage-grouse habitat at current levels, persistent population declines in the species are predicted (Coates et al. 2015). However, the specific changes in demographic rates or behavior associated with sage-grouse population declines after large-scale wildfire have not been previously investigated. The lack of evidence for sage-grouse emigration away from fire affected areas indicates that any sage-grouse population declines following wildfire are likely due to reduced sage-grouse survival and reproductive output, rather than due to avoidance of disturbed habitats. Thus, wildfire suppression and management activities that increase the resilience of sage-grouse habitats are likely the types of activities that will have the best chance of counteracting wildfire effects on grouse populations.

We were not able to conclusively document direct effects of habitat composition on sage-grouse survival or reproductive output; however, third-order sage-grouse resource selection patterns do suggest there are resource management actions that can benefit sage-grouse following wildfire. In species exhibiting considerable site fidelity, selection of home or seasonal ranges likely reflects

historical (pre-disturbance) habitat composition, whereas third-order resource selection likely reflects efforts by individuals to fully meet their life-history requirements within the habitat that remains (Rettie and Messier 2000, Mayer et al. 2009). Thus, third-order resource selection patterns exhibited in our study provide guidance regarding the appropriate habitat management actions that should take place prior to, and following wildfire. First, we suggest that efforts be undertaken to limit the size and spread of wildfires in sage-grouse habitat, to reduce the chances of entire sage-grouse home or seasonal ranges being consumed by fire. Efforts to pre-position suppression resources in sage-grouse habitat prone to fire should be prioritized. Additionally, the judicious use of fire-breaks (i.e. "green-stripping") along existing roads should be promoted so as to ensure that individual fires do not reach catastrophic sizes (Murphy et al. 2013). Following the occurrence of wildfire, efforts should be made, through the application of herbicide and perennial grass seeding (Booth et al. 2003, Chambers et al. 2007, Blank and Morgan 2012), to limit annual grass invasion into burnt sites so as to reduce the risk of further fire, and conversion of sites to deleterious annual grassland (Chambers et al. 2014). Sagebrush planting efforts following fire should be prioritized in breeding and wintering habitat, due to the strong selection of sage-grouse for intact sagebrush land-cover during these life-stages. Finally, efforts to maintain habitat mosaic and forb availability should be made in high elevation sage-grouse summer habitat, where the risk of annual grass invasion is reduced.

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APPENDICES

APPENDIX I – HOLLOWAY FIRE MAP DEVELOPMENT METHODS AND
ACCURACY ASSESSMENT RESULTS

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Methods

Remote sensing in semiarid sage steppe rangelands must consider presence of
bare ground and high soil reflectance characteristic of open shrub and grassland
canopies (Okin et al. 2001). The influence of high soil reflectance on remote sensing
interpretation of vegetation is well documented (Huete 1988, 1989, Qi et al. 1994,
Bannari et al. 1995, Schmidt and Karnieli 2001). We accounted for these system
characteristics by applying a soil adjusted vegetation index (SAVI; Huete 1988) to
Satellite Pour l'Observation de la Terre 5 (SPOT 5), 10 meter resolution satellite
imagery as a transformation technique to minimize soil reflectance:

$$SAVI = \frac{(1 + L)(NIR - Red)}{NIR + Red + L}$$

where L is a constant soil adjustment factor, NIR is near infrared SPOT 5 band 3
(0.78 – 0.89 μm), and Red is red SPOT 5 band 2 (0.61 – 0.68 μm). We applied a
constant soil adjustment factor of 0.5 to our transformation, as this value is known to
best reduce soil noise across a range of different vegetation densities and soil types
found in the study area (Huete 1988).

The most recent post fire cloud free images available were used in our
analysis. Satellite imagery acquired closer to post fire dates provide better
estimations of ecological condition when evaluating fire burn severity (Weber et al.
2009). The study area boundary was defined by the Holloway fire burn perimeter
polygon produced and obtained from the Bureau of Land Management (Figure A1.1).
Four separate SPOT 5 satellite images were required to cover the burn extent. Image
acquisition dates ranged from 28 August to 13 September 2012 (Figure A1.2).

Images were attained through download from the United States Geological Survey Earth Explorer website (available from http://earthexplorer.usgs.gov/). Prior to SAVI transformation, all images were processed to at-ground reflectance in order to normalize atmospheric variability between scenes. Image processing was completed using the Raster Calculator feature in software ArcGIS 10.1 (Environmental Systems Research Institute, Redlands California) as follows:

$$Radiance = \frac{Digital\ number}{Absolute\ claibration\ gain}$$

$$Reflectance = \frac{\Pi\ (Radiance)(sun - earth\ distance^2)}{(Solar\ equivalent\ irradiance)((cos)\ Solar\ angle)}$$

Where:

Radiance = spectral radiance at SPOT 5 sensor's aperture

Digital number = the digital number of each image pixel ranging from 0 – 255

Absolute Calibration Gain = SPOT 5 sensor processing procedure to maximize the instrument's radiometric resolution without saturating the detectors; each band's gain is provided by the imagery metadata

Sun-Earth Distance = Earth-sun distance in astronomical units

Solar Equivalent Irradiance = mean solar exoatmospheric irradiances in watts/(meter squared * μm) provided by the imagery metadata for each band

Solar Angle = solar zenith angle in degrees unique to each image

Burn severity types were defined by correlating pixel threshold values to each class through visual interpretation of burn patterns from SPOT 5 satellite imagery.Model outputs were classified by five burn severity types; high, moderate,

low, low/unburned, and unburned. Burn severity types were correlated to rates of above ground vegetation removal during the fire. For example, high burn severity areas are representative of near complete removal of surface vegetation, while moderate, low and low/unburned areas contain greater proportions of unconsumed fuels. Unburned areas indicate no direct vegetative impact from fire.

Model accuracy was assessed using 391 grid based field observation points collected within the study area boundary (Fig A1.2). Points were collected approximately two years post fire (August - September 2014) and indicate presence or absence of vegetative fire effects (i.e. burn or no burn). Only model outcomes indicating presence or absence of fire were assessed. Burn severity classes; high, moderate, and low indicated presence. Classes; low/unburned and unburned indicated absence. Three different accuracy assessment approaches were used to account for potential geometric misalignment between observational points and satellite imagery. Mean GPS error for field observation points (4.5 meters) and satellite level 1G systematic geometric accuracy estimates (±30 meters) were considered (http://landsat.usgs.gov/geometric_accuracy.php).

Our initial accuracy assessment approach assumed complementary alignment (i.e. no geometric error) between observation points and satellite imagery. Observations and model outcomes were compared by intersecting point locations to the burn severity class of the single 10 meter pixel it fell within. Next we buffered observational point locations by 30 meters to account for estimated geometric error. In our second approach we applied a majority function to burn severity pixels within the 30 meter buffer around each point. The burn severity class representing the majority of pixels within each buffer was used to conduct the assessment. A fuzzy logic was applied in our third approach. We assumed validation of field observation by presence of any complimentary burn severity class (i.e. model pixel = to field

observation) within the estimated geometric error (30 meter buffer; mean pixel count by buffer = 20).

Results

   SAVI burn severity results indicate patterns of heterogeneity within the study area boundary (Figure A1.3). Upper (> 2,500 meters) and lower elevations (< 1,500 meters) contained large patches of low/unburned and unburned vegetation. High and moderate burn severities occurred largely in mid and upper elevations within areas of more complex topographic relief. High burn severity areas were confined to steeper north facing slopes and canyon bottoms (Figure A1.3). Burned versus unburned areas made up 75% and 25% of the study area respectively (Table A1.1). Overall model accuracy ranged from 83.6% to 100% (Tables A1.2 – A1.4). Model accuracy was higher using assessment techniques accounting for geometric error, suggesting some level of misalignment in observational and satellite data.

Table A1.1. Holloway fire burn severity area and abundance by type, Trout Creek Mountains, Harney and Malheur counties, Oregon, and Humboldt County, Nevada.

Burn severity	km²	% Total
High	223.2	12.0%
Moderate	685.1	36.7%
Low	496.2	26.6%
Low/Unburned	203.2	10.9%
Unburned	258.5	13.9%

Table A1.2. Holloway fire map point intersect burn severity error matrix, Trout Creek Mountains, Harney and Malheur counties, Oregon, and Humboldt County, Nevada. Model output was evaluated using 391 grid based field observation points indicating presence or absence of fire (i.e. burn or no burn).   Complementary alignment (i.e. no geometric error) between observation points and satellite imagery was assumed. Evaluations were made by comparing point locations to the single 10 meter satellite pixel they intersect.

	Burned	Unburned	Total	Commission	
Burned	288	19	307	93.8%	
Unburned	45	39	84	53.6%	
Total	333	58	391		
Omission	86.5%	32.8%		**83.6%**	**Overall**

Table A1.3. Holloway fire map majority function burn severity error matrix, Trout Creek Mountains, Harney and Malheur counties, Oregon, and Humboldt County, Nevada. Model output was evaluated using 391 grid based field observation points indicating presence or absence of fire (i.e. burn or no burn).   Observational point locations were buffered by 30 meters to account for estimated geometric error. A majority function was applied to burn severity pixels within the 30 meter buffer around each point. The burn severity class containing the majority of pixels within each buffer was used to compare field observations and model output.

	Burned	Unburned	Total	Commission	
Burned	305	24	329	92.7%	
Unburned	28	34	62	45.2%	
Total	333	58	391		
Omission	91.6%	41.4%		**86.7%**	**Overall**

Table A1.4. Holloway fire map fuzzy logic burn severity error matrix, Trout Creek Mountains, Harney and Malheur counties, Oregon, and Humboldt County, Nevada. Model output was evaluated using 391 grid based field observation points indicating presence or absence of fire (i.e. burn or no burn). Observational point locations were buffered by 30 meters to account for estimated geometric error. A fuzzy logic approach was applied to burn severity pixels within the 30 meter buffer around each point. Validation of field observations were assumed by presence of any complimentary burn severity class within the estimated geometric error (30 meter buffer; mean pixel count by buffer = 20).

	Burned	Unburned	Total	Commission	
Burned	333	0	333	100%	
Unburned	0	58	58	100%	
Total	333	58	391		
Omission	100%	100%		**100%**	**Overall**

Figure A1.1. Holloway fire extent and U.S. Fish and Wildlife Service greater sage-grouse priority areas of conservation (PACs).
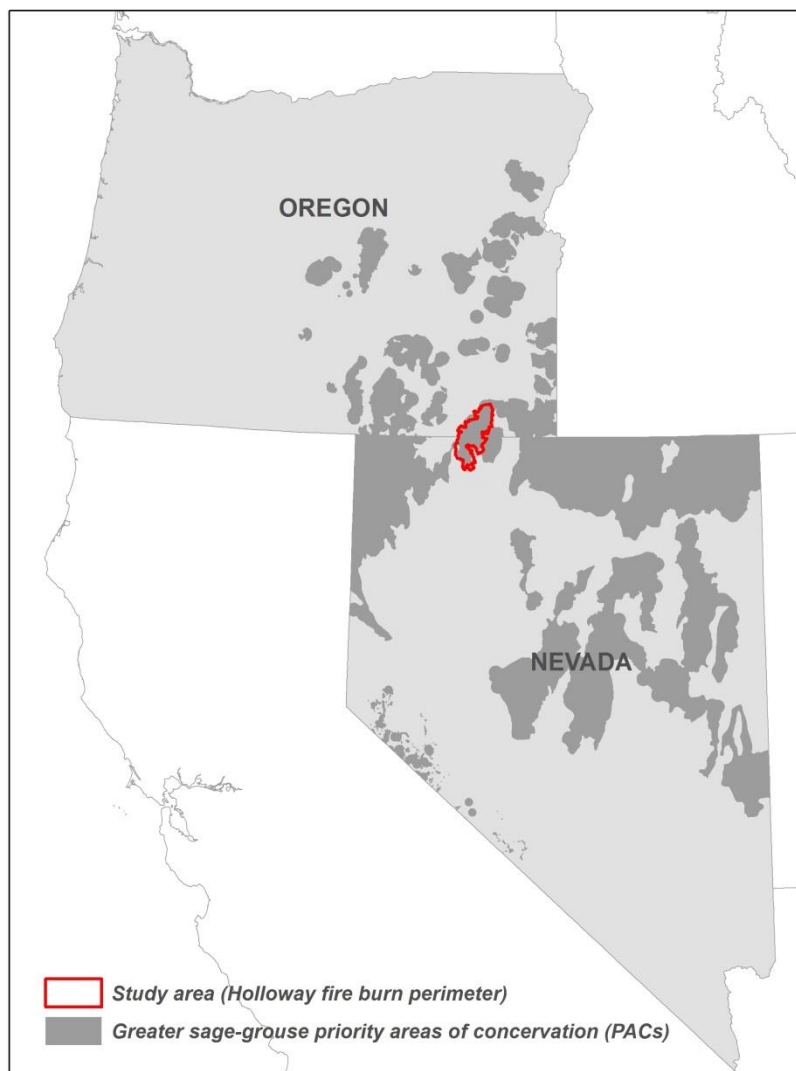
Figure A1.2. Holloway fire field observation points indicating presence or absence of fire (i.e. burned or unburned) and Satellite Pour l'Observation de la Terre 5 (SPOT 5) satellite images used in SAVI model. Image acquisition dates range from 28 August to 13 September, 2012. Images shown in color infrared.
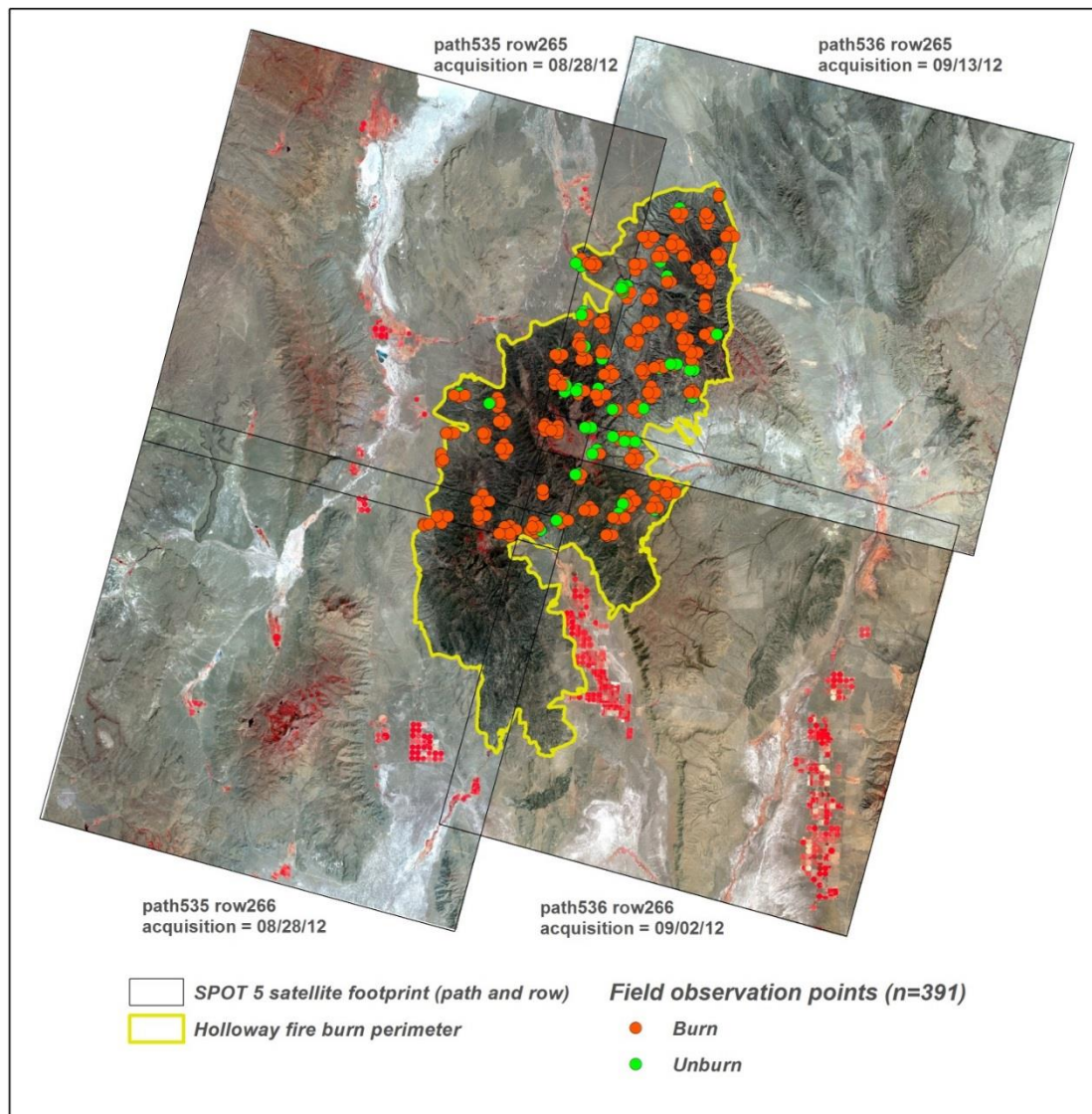
Figure A1.3. Holloway fire burn severity estimation. Model derived from soil adjusted vegetation index (SAVI; constant soil adjustment factor = 0.5) applied to Satellite Pour l'Observation de la Terre 5 (SPOT 5), 10 meter resolution satellite imagery.
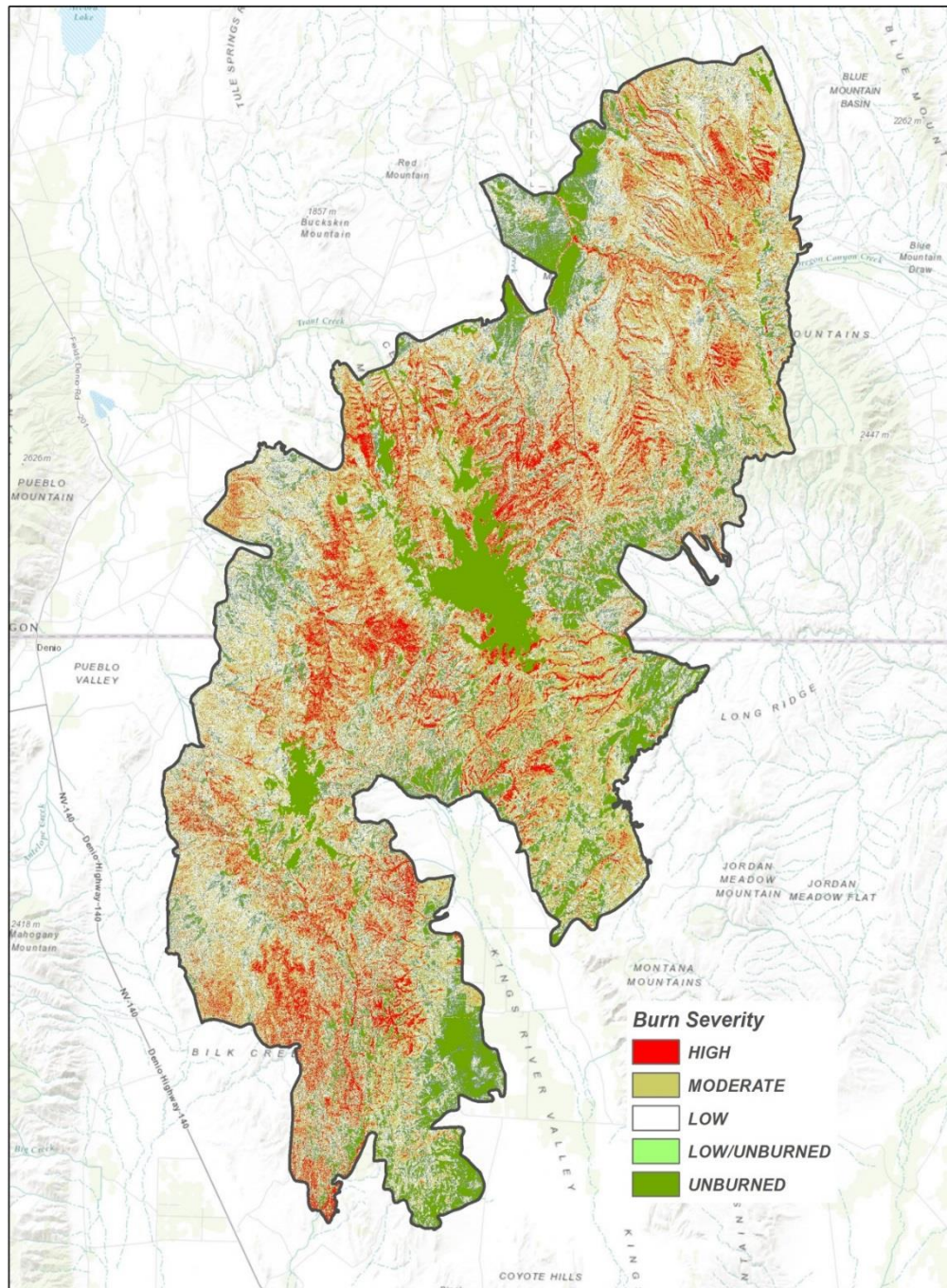
APPENDIX II – CHAPTER 2 SUPPLEMENTARY INFORMATION

Table A2.1. Mean population entrance dates onto nesting/early brood rearing, summer, and winter range, and ranges of individual entrance dates, by female greater sage-grouse during 2013, 2014, and both years combined, in the Trout Creek Mountains, Harney and Malheur counties, Oregon.

	Nesting/Early Brood Rearing		Summer		Winter	
Year	Mean Entrance Date	Range	Mean Entrance Date	Range	Mean Entrance Date	Range
2013	-	-	12-Jun	14-May to 26-Jul	26-Oct	15-Sep to 6-Dec
2014	8-Mar	1-Mar to 16-Mar	14-Jun	7-May to 3-Aug	17-Oct	15-Sep to 2-Nov
Both	-	-	13-Jun	7-May to 3-Aug	21-Oct	15-Sep to 6-Dec

APPENDIX III – NESTING HABITAT COVARIATE CALCULATION
METHODS

We calculated all cover covariates for the patch, center, and nest vicinity
scale. These were calculated as the percentage of total LPI points surveyed where the
pin came in contact with the cover type in question (hereafter: where cover type was
detected). Cover covariates included: total shrub cover (TSC) – percentage of
sampled points where either a live or dead shrub was detected; live shrub cover (LSC)
– percentage of sampled points where a live shrub was detected; perennial grass cover
(PGC) – percentage of sampled points where a perennial grass species was detected;
total grass cover (TGC) – percentage of sampled points where either an annual or
perennial grass species was detected; forb cover (FC) – percentage of sampled points
where a forb species was detected; bare ground (BG) – percentage of sampled points
where no vegetative species was detected; litter cover (LC) – percentage of sampled
points where woody litter was detected. General shrub cover was measured as
opposed to specifically sagebrush cover due to the lack of sagebrush, but presence of
non-sagebrush shrubs, at some nest sites within the study. Additionally, both live and
total shrub cover were investigated due to the prevalence of fire-killed shrubs in some
portions of the study area. Both covariates were assessed to determine whether dead
shrubs provided similar benefits as live shrubs. Perennial grass cover and total grass
cover were separated due to a large amount of cheatgrass (*Bromus tectorum*)
regrowth present during the second year of the fire; a question of interest was the
influence of native grasses on nest survival as opposed to the influence of cheatgrass
cover.

Height covariates were calculated for the patch, center, nest vicinity, and nest
scales, excepting perennial and total grass height which were only calculated at the
patch, and center scales. Height covariates were calculated as the mean height of the
cover type in question at all height survey points contained within a given scale.
Height covariates included: total shrub height (TSH) – mean height of both live and

dead shrubs; live shrub height (LSH) – mean height of live shrubs; perennial grass height (PGH) – mean height of perennial grasses; total grass height (TGH) – mean height of both annual and perennial grasses; herbaceous height (HH) – mean height of all herbaceous species. Perennial and total grass height were only calculated at the larger scales due to the methodology employed in measuring herbaceous heights. Herbaceous height measurements were made on the tallest herbaceous species every five meters along each transect. At the smaller nest vicinity and nest scales, a significant number of height measurements were made on non-grass species, causing NA values to be recorded for grass height at these points. Grasses may have been present at these points, but at heights lower than the maximum herbaceous height. Therefore a height of NA for grass species did not always correspond to a height of 0, i.e. no grass present. Therefore grass heights were only averaged at the larger scales where enough measured heights were recorded to generate a robust mean value.

We calculated GI covariates at the patch, center, and nest vicinity scales. Both canopy (CG_) and basal gaps (BG_) were labeled under 4 categories: 20 – 50 cm (20_50), 51 – 100 cm (51_100), 101 – 200 cm (101_200), and >200 cm (200+). The percentage of each transect characterized by each gap category was then calculated. Patch scale gap covariates were calculated as the mean of each gap category across all transects within a plot. The effect varying canopy gap values might have on sage-grouse nest survival is unclear. The method was originally designed to assess site susceptibility to wind erosion and invasive species encroachment (McCord 2013). However this method may provide information on shrub patch structure and visual obstruction. Basal shrub cover (BSC) was also calculated from GI measurements as the percentage of each transect not covered by a basal gap. We calculated visual obstruction (VO) at the patch, center, nest vicinity, and nest scales as the mean Robel pole reading across all VO survey points within each scale.

We derived 4 nest location covariates using remotely sensed data and GIS analysis: distance to riparian (DTR), distance to edge (DTE), percent patch cover (PPC), and edge density (ED) (Table 2). Distance to riparian was calculated as the straight line distance (m) from each nest site to a permanent or semi-permanent stream. A GIS layer depicting permanent and semi-permanent streams within the study area was acquired from the National Hydrography Dataset. The Near tool within the ArcGIS 10.1 (ESRI, Inc., Redlands, CA) Analysis Toolbox was then used to calculate the nearest straight line distance between nests and riparian features. Distance to edge was calculated as nearest straight line distance (m) between nests and intact/burnt habitat edges. Using a detailed map of Holloway fire severity (Appendix I), raster cells classified as burnt or intact were converted to 2 polygon shape files, corresponding to each habitat class, using the Raster to Polygon tool within the ArcGIS 10.1 Conversion Toolbox. The Near tool within the ArcGIS 10.1 Analysis Toolbox was then used to calculate the nearest straight line distance between nests in a given class to the polygon shape file of the opposite class. Percent patch cover, and ED were calculated within 3 circular buffers around each nest site with radii of 100 m, 550 m, and 1500 m. These buffer radii were chosen to reflect patterns previously observed in sage-grouse nest selection, predator behavior, and landscape scale processes. Several studies have shown that sage-grouse select nest sites based on habitat features within 100 m of the nest site (Doherty et al. 2010, Dzialak et al. 2011). The 550 m buffer was chosen to reflect potential raven (*Corvus corax*) foraging behavior within the study area. Ravens are a primary nest predator of sage-grouse (Coates et al. 2008), and Dinkins (2013) demonstrated that sage-grouse nest success decreased by 50% if a raven was detected within 550 m of a nest. Mean nearest neighbor distance between first nesting attempts within the study area was approximately 1800 m over the course of the study. The 1500 m radius buffer was chosen to reflect approximate spacing of known sage-grouse nests within the study area, as well as landscape scale patterns in habitat structure following the fire.

Percent patch cover, and ED were calculated from the raster fire map using FRAGSTATS v4 (McGarigal et al. 2012). Raster cell locations containing nest sites were calculated in ArcGIS 10.1, and input into FRAGSTATS v4 as user provided points. Percent patch cover was then calculated in the buffers surrounding each nest point using the class metric Percentage of Landscape (PLAND) for intact habitat cells (McGarigal et al. 2012). Edge density (m/ha) was calculated in the buffers surrounding each nest point using the landscape metric Edge Density (ED) (McGarigal et al. 2012).

APPENDIX IV – CHAPTER 3 SUPPLEMENTARY INFORMATION

Table A4.1. Means, standard deviations, and ranges of continuous vegetation and GIS covariates at sage-grouse nests in intact and burnt habitat in 2013 in the Trout Creek Mountains, Harney and Malheur counties, Oregon.

Covariate	Scale	All Nests					Intact Nests					Burnt Nests				
		N	Mean	SD	Min	Max	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max
TSC (%)	P	22	29.3	17.0	0.0	62.3	16	34.3	13.0	17.3	62.3	6	16.0	20.2	0.0	53.8
	C	22	31.7	18.5	0.0	62.0	16	37.6	14.4	20.0	62.0	6	16.2	20.2	0.0	53.8
	NV	22	34.9	22.4	0.0	81.8	16	40.4	18.5	9.1	81.8	6	20.4	27.0	0.0	71.4
LSC (%)	P	22	25.5	15.3	0.0	59.2	16	31.7	12.4	16.0	59.2	6	9.0	8.2	0.0	20.6
	C	22	27.9	17.7	0.0	59.3	16	35.3	14.3	16.0	59.3	6	8.1	6.9	0.0	15.4
	NV	22	30.2	20.8	0.0	81.8	16	38.1	18.5	9.1	81.8	6	9.3	7.8	0.0	18.2
PGC (%)	P	22	24.6	13.6	4.7	52.7	16	24.3	14.8	4.7	52.7	6	25.3	11.1	8.0	38.5
	C	22	26.0	17.1	4.0	69.3	16	26.9	19.3	4.0	69.3	6	23.6	10.4	8.0	38.5
	NV	22	26.1	21.4	0.0	72.7	16	28.4	24.1	0.0	72.7	6	19.9	10.8	0.0	28.6
TGC (%)	P	22	32.9	13.9	4.7	56.0	16	32.7	14.8	4.7	56.0	6	33.6	12.5	14.0	50.0
	C	22	33.6	17.4	6.0	69.3	16	34.2	19.1	6.0	69.3	6	31.9	13.2	14.0	50.0
	NV	22	35.6	20.4	0.0	72.7	16	35.8	21.4	0.0	72.7	6	35.1	19.3	0.0	54.5
FC (%)	P	22	15.3	13.3	1.1	40.0	16	11.6	12.0	1.1	40.0	6	25.2	11.9	12.0	40.0
	C	22	15.3	14.3	0.0	40.7	16	11.9	13.5	0.0	40.7	6	24.4	13.1	7.7	40.0
	NV	22	14.7	19.8	0.0	71.4	16	10.8	15.3	0.0	45.5	6	24.9	27.6	0.0	71.4
BG (%)	P	22	42.7	15.1	12.0	70.0	16	43.7	16.5	12.0	70.0	6	39.9	11.3	23.1	52.0
	C	22	41.2	14.8	16.0	62.0	16	41.3	16.0	16.0	62.0	6	41.2	12.5	23.1	53.8
	NV	22	35.3	17.2	0.0	63.6	16	36.4	19.1	0.0	63.6	6	32.3	11.6	14.3	45.5
LC (%)	P	22	12.3	8.7	0.0	30.8	16	14.3	8.4	4.0	30.8	6	7.1	7.9	0.0	16.0
	C	22	13.5	11.3	0.0	36.0	16	16.1	11.4	2.0	36.0	6	6.5	7.7	0.0	16.0
	NV	22	15.1	18.9	0.0	63.6	16	19.9	20.0	0.0	63.6	6	2.4	5.8	0.0	14.3

		N	Mean	SD	Min	Max	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max
TSH (cm)	P	22	44.1	17.7	0.0	81.1	16	46.8	15.4	27.0	81.1	6	37.0	23.0	0.0	65.0
	C	22	49.6	21.4	0.0	94.6	16	54.0	19.9	26.8	94.6	6	37.8	22.4	0.0	65.0
	NV	22	51.4	27.3	0.0	118.7	16	58.1	24.6	27.5	118.7	6	33.5	27.9	0.0	65.0
	N	22	61.5	29.9	0.0	114.0	16	70.2	25.4	18.0	114.0	6	38.3	30.3	0.0	65.0
LSH (cm)	P	22	44.3	21.3	0.0	81.1	16	50.6	17.1	27.6	81.1	6	27.4	23.7	0.0	57.7
	C	22	47.9	24.0	0.0	94.6	16	54.8	20.6	26.8	94.6	6	29.3	23.9	0.0	57.7
	NV	22	50.6	30.1	0.0	118.7	16	60.0	25.4	27.5	118.7	6	25.5	29.1	0.0	60.0
	N	22	55.9	34.9	0.0	114.0	16	66.6	30.8	0.0	114.0	6	27.5	30.5	0.0	60.0
PGH (cm)	P	22	36.9	12.5	18.2	61.0	16	32.8	10.5	18.2	50.6	6	48.1	11.0	35.3	61.0
	C	22	36.2	13.2	14.3	61.0	16	31.3	10.8	14.3	48.5	6	49.4	9.5	37.0	61.0
TGH (cm)	P	22	35.5	12.7	18.2	61.0	16	31.1	10.4	18.2	50.6	6	47.2	11.2	35.3	61.0
	C	22	34.3	13.1	14.3	61.0	16	29.0	9.8	14.3	46.1	6	48.4	9.9	35.4	61.0
HH (cm)	P	22	34.0	11.0	16.9	53.5	16	30.5	9.7	16.9	48.1	6	43.5	8.9	29.7	53.5
	C	22	32.3	11.2	13.7	53.5	16	27.7	8.8	13.7	41.7	6	44.5	7.1	36.0	53.5
	NV	22	32.4	14.0	9.5	71.0	16	27.4	9.8	9.5	44.5	6	45.7	15.5	26.5	71.0
	N	22	32.2	20.6	0.0	77.0	16	25.4	17.5	0.0	60.0	6	50.3	18.0	22.0	77.0
CG20_50 (%)	P	22	2.9	1.9	0.0	6.5	16	3.5	1.4	0.9	6.5	6	1.2	2.0	0.0	5.1
	C	22	2.9	2.0	0.0	6.2	16	3.6	1.5	0.9	6.2	6	1.0	2.0	0.0	5.1
	NV	22	4.2	4.6	0.0	17.9	16	5.1	5.0	0.0	17.9	6	1.6	1.7	0.0	3.4
CG51_100 (%)	P	22	8.5	5.3	0.0	17.7	16	9.9	3.5	2.0	15.0	6	4.8	7.8	0.0	17.7
	C	22	9.5	7.1	0.0	26.7	16	10.7	5.0	1.0	18.7	6	6.3	11.0	0.0	26.7
	NV	22	12.5	11.3	0.0	39.7	16	14.5	10.2	0.0	39.7	6	7.1	13.2	0.0	33.0
CG101_200 (%)	P	22	15.7	8.6	0.0	27.0	16	19.4	5.5	10.9	27.0	6	5.6	7.2	0.0	18.0
	C	22	14.9	9.9	0.0	33.6	16	18.5	8.5	8.0	33.6	6	5.5	7.1	0.0	17.7
	NV	22	15.5	12.7	0.0	36.2	16	15.9	12.9	0.0	36.2	6	14.4	13.4	0.0	32.4
CG200+ (%)	P	22	48.5	24.6	8.7	98.9	16	38.9	14.3	8.7	70.9	6	74.2	29.2	32.7	98.9
	C	22	46.0	26.1	15.1	98.9	16	35.5	15.1	15.1	70.9	6	73.8	29.9	30.1	98.9

		n	mean	SD	min	max	n	mean	SD	min	max	n	mean	SD	min	max
	NV	22	36.2	32.0	0.0	100.0	16	29.7	24.2	0.0	75.0	6	53.7	45.2	0.0	100.0
BG20_50	P	22	0.4	0.7	0.0	2.0	16	0.5	0.7	0.0	2.0	6	0.2	0.5	0.0	1.2
(%)	C	22	0.5	1.0	0.0	3.1	16	0.7	1.1	0.0	3.1	6	0.0	0.0	0.0	0.0
	NV	22	0.5	1.7	0.0	7.3	16	0.5	1.8	0.0	7.3	6	0.6	1.5	0.0	3.6
BG51_100	P	22	1.8	2.7	0.0	12.5	16	1.7	1.1	0.0	3.5	6	2.1	5.1	0.0	12.5
(%)	C	22	1.9	3.0	0.0	13.2	16	1.7	1.7	0.0	5.9	6	2.2	5.4	0.0	13.2
	NV	22	1.6	5.1	0.0	22.6	16	0.8	2.2	0.0	6.6	6	3.8	9.2	0.0	22.6
BG101_200	P	22	6.5	7.2	0.0	33.0	16	6.4	4.0	0.0	14.8	6	6.9	13.0	0.0	33.0
(%)	C	22	6.9	9.1	0.0	38.0	16	6.6	6.4	0.0	16.3	6	7.8	15.0	0.0	38.0
	NV	22	9.0	14.3	0.0	48.7	16	8.1	12.3	0.0	34.0	6	11.4	19.9	0.0	48.7
BG200+	P	22	88.0	12.6	42.6	100.0	16	87.8	7.0	74.4	99.2	6	88.5	22.7	42.6	100.0
(%)	C	22	88.1	13.4	41.9	100.0	16	87.9	8.7	72.1	99.0	6	88.4	23.0	41.9	100.0
	NV	22	80.7	29.8	0.0	100.0	16	81.3	26.8	0.0	100.0	6	79.0	39.6	0.0	100.0
BSC (%)	P	22	3.3	2.8	0.0	10.8	16	3.7	2.1	0.8	7.1	6	2.3	4.2	0.0	10.8
	C	22	2.7	2.0	0.0	6.9	16	3.1	1.6	1.0	6.4	6	1.6	2.7	0.0	6.9
	NV	22	8.2	21.3	0.0	100.0	16	9.3	24.5	0.0	100.0	6	5.2	9.9	0.0	25.1
VO (dm)	P	22	1.8	1.4	0.0	6.0	16	2.2	1.4	0.4	6.0	6	0.8	0.7	0.0	1.5
	C	22	2.0	1.5	0.0	5.9	16	2.4	1.4	0.6	5.9	6	0.7	0.6	0.0	1.5
	NV	22	3.1	2.3	0.0	9.5	16	3.7	2.3	1.2	9.5	6	1.3	1.1	0.0	2.5
	N	22	4.4	2.6	0.0	9.5	16	5.2	2.5	0.5	9.5	6	2.3	1.9	0.0	4.0
DTR (m)	-	22	235.1	203.9	5.3	684.9	16	255.6	183.4	17.4	670.7	6	180.5	262.2	5.3	684.9
DTE (m)	-	22	383.8	730.8	0.5	3098.6	16	486.8	838.4	0.5	3098.6	6	109.2	100.4	16.9	272.8
PPC (%)	100 m	22	63.5	38.2	0.0	100.0	16	79.1	27.4	32.2	100.0	6	21.8	31.6	0.0	69.7
	550 m	22	50.0	38.6	0.5	100.0	16	64.7	34.8	11.3	100.0	6	10.9	9.4	0.5	22.3
	1500 m	22	46.3	32.2	2.9	100.0	16	59.3	27.5	19.6	100.0	6	11.8	10.6	2.9	29.2
ED (m/ha)	100 m	22	176.4	246.6	0.0	738.2	16	198.3	272.8	0.0	738.2	6	117.8	162.5	0.0	406.9
	550 m	22	152.8	143.9	0.0	461.0	16	169.6	161.9	0.0	461.0	6	107.9	70.8	18.5	195.8

| | 1500 m | 22 | 147.9 | 106.3 | 0.0 | 378.7 | 16 | 170.1 | 112.6 | 0.0 | 378.7 | 6 | 88.9 | 60.4 | 34.1 | 173.6 |

Table A4.2. Means, standard deviations, and ranges of continuous vegetation and GIS covariates at sage-grouse nests in intact and burnt habitat in 2014 in the Trout Creek Mountains, Harney and Malheur counties, Oregon.

Covariate	Scale	All Nests					Intact Nests					Burnt Nests				
		N	Mean	SD	Min	Max	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max
TSC (%)	P	28	27.6	16.5	0.0	72.0	23	32.5	13.7	14.0	72.0	5	5.2	5.9	0.0	14.0
	C	28	33.5	21.4	0.0	72.0	23	39.7	18.3	14.0	72.0	5	5.2	5.9	0.0	14.0
	NV	28	41.1	23.4	0.0	90.9	23	47.2	20.6	9.1	90.9	5	12.7	12.2	0.0	27.3
LSC (%)	P	28	24.1	15.2	0.0	60.0	23	28.4	12.9	10.0	60.0	5	4.0	6.2	0.0	14.0
	C	28	29.3	19.8	0.0	64.0	23	34.8	17.2	14.0	64.0	5	4.0	6.2	0.0	14.0
	NV	28	34.0	21.5	0.0	81.8	23	39.8	18.6	9.1	81.8	5	7.3	11.9	0.0	27.3
PGC (%)	P	28	28.6	13.7	4.7	54.0	23	28.1	13.2	4.7	50.0	5	30.8	17.2	14.0	54.0
	C	28	29.8	14.9	6.0	62.0	23	29.6	14.7	6.0	62.0	5	30.8	17.2	14.0	54.0
	NV	28	32.4	21.4	0.0	72.7	23	29.8	20.8	0.0	72.7	5	44.5	21.9	18.2	72.7
TGC (%)	P	28	34.4	19.3	6.0	90.0	23	30.3	14.4	6.0	58.7	5	53.6	28.4	14.0	90.0
	C	28	36.1	19.8	6.0	90.0	23	32.3	15.8	6.0	67.3	5	53.6	28.4	14.0	90.0
	NV	28	36.3	25.1	0.0	100.0	23	31.0	21.1	0.0	72.7	5	60.9	30.1	18.2	100.0
FC (%)	P	28	11.1	9.4	1.3	50.0	23	9.5	5.9	1.3	21.0	5	18.4	18.1	6.0	50.0
	C	28	12.3	9.9	2.0	50.0	23	11.0	7.1	2.0	26.0	5	18.4	18.1	6.0	50.0
	NV	28	12.3	16.3	0.0	63.6	23	10.7	13.9	0.0	45.5	5	20.0	25.2	0.0	63.6
BG (%)	P	28	39.3	12.3	6.0	61.3	23	41.7	11.0	12.0	61.3	5	28.4	13.4	6.0	38.0
	C	28	33.9	13.8	6.0	60.0	23	35.1	13.9	12.0	60.0	5	28.4	13.4	6.0	38.0
	NV	28	28.6	20.3	0.0	72.7	23	31.6	20.8	0.0	72.7	5	14.6	10.4	0.0	27.3
LC (%)	P	28	2.7	2.5	0.0	10.0	23	3.3	2.4	0.0	10.0	5	0.0	0.0	0.0	0.0
	C	28	3.4	3.7	0.0	14.0	23	4.1	3.7	0.0	14.0	5	0.0	0.0	0.0	0.0

	NV	28	2.9	6.1	0.0	18.2	23	3.6	6.6	0.0	18.2	5	0.0	0.0	0.0	0.0
TSH (cm)	P	28	38.5	14.3	0.0	61.0	23	40.2	11.1	21.2	59.7	5	31.0	24.9	0.0	61.0
	C	28	42.9	19.1	0.0	80.5	23	45.5	17.2	22.9	80.5	5	31.0	24.9	0.0	61.0
	NV	28	48.0	24.7	0.0	103.0	23	50.0	19.8	16.0	86.3	5	38.8	42.8	0.0	103.0
	N	28	49.3	25.7	0.0	103.0	23	52.9	18.1	0.0	79.0	5	32.8	47.3	0.0	103.0
LSH (cm)	P	28	37.4	15.0	0.0	56.6	23	41.1	10.7	24.0	56.6	5	20.4	21.3	0.0	51.0
	C	28	41.3	19.8	0.0	80.5	23	45.9	16.7	22.9	80.5	5	20.4	21.3	0.0	51.0
	NV	28	45.9	27.3	0.0	103.0	23	50.5	20.7	16.0	86.3	5	24.8	44.7	0.0	103.0
	N	28	45.0	28.5	0.0	103.0	23	50.3	21.2	0.0	79.0	5	20.6	46.1	0.0	103.0
PGH (cm)	P	28	40.5	18.0	19.3	99.8	23	34.8	9.7	19.3	52.6	5	66.3	25.4	38.2	99.8
	C	28	41.6	18.6	22.1	99.8	23	36.2	11.9	22.1	60.2	5	66.3	25.4	38.2	99.8
TGH (cm)	P	28	38.4	13.6	19.3	70.6	23	34.2	9.4	19.3	52.6	5	57.5	14.5	38.2	70.6
	C	28	39.8	14.7	22.1	70.6	23	35.9	11.9	22.1	60.2	5	57.5	14.5	38.2	70.6
HH (cm)	P	28	36.2	12.8	14.7	66.6	23	32.4	9.1	14.7	49.9	5	53.7	14.0	38.2	66.6
	C	28	38.0	14.6	15.9	66.6	23	34.7	12.6	15.9	57.1	5	53.7	14.0	38.2	66.6
	NV	28	36.0	18.0	8.3	77.3	23	30.9	12.2	8.3	60.0	5	59.9	22.2	28.0	77.3
	N	28	39.9	31.2	0.0	139.0	23	32.3	19.6	0.0	70.0	5	75.0	51.0	21.0	139.0
CG20_50 (%)	P	28	3.4	3.1	0.0	14.9	23	4.1	3.0	0.3	14.9	5	0.2	0.4	0.0	0.8
	C	28	3.6	3.2	0.0	14.9	23	4.3	3.1	0.0	14.9	5	0.2	0.4	0.0	0.8
	NV	28	5.4	4.4	0.0	14.5	23	6.5	3.9	0.0	14.5	5	0.0	0.0	0.0	0.0
CG51_100 (%)	P	28	7.8	5.7	0.0	20.5	23	9.4	4.9	3.1	20.5	5	0.3	0.6	0.0	1.3
	C	28	7.2	5.9	0.0	20.5	23	8.7	5.4	1.9	20.5	5	0.3	0.6	0.0	1.3
	NV	28	7.3	8.5	0.0	25.6	23	8.9	8.6	0.0	25.6	5	0.0	0.0	0.0	0.0
CG101_200 (%)	P	28	14.8	9.1	0.0	33.1	23	17.9	6.6	5.0	33.1	5	0.4	0.9	0.0	2.0
	C	28	17.4	11.2	0.0	39.7	23	21.1	8.6	2.1	39.7	5	0.4	0.9	0.0	2.0
	NV	28	20.7	15.7	0.0	51.8	23	25.2	13.6	0.0	51.8	5	0.0	0.0	0.0	0.0
	P	28	47.8	28.6	0.0	100.0	23	37.4	18.7	0.0	83.3	5	96.1	6.6	84.5	100.0

CG200+	C	28	42.0	32.6	0.0	100.0	23	30.2	22.1	0.0	88.4	5	96.1	6.6	84.5	100.0
(%)	NV	28	31.8	36.7	0.0	100.0	23	19.0	25.6	0.0	74.7	5	90.6	14.6	65.1	100.0
BG20_50	P	28	0.1	0.2	0.0	0.6	23	0.1	0.2	0.0	0.6	5	0.0	0.0	0.0	0.0
(%)	C	28	0.1	0.3	0.0	1.0	23	0.1	0.3	0.0	1.0	5	0.0	0.0	0.0	0.0
	NV	28	0.2	0.8	0.0	3.5	23	0.3	0.9	0.0	3.5	5	0.0	0.0	0.0	0.0
BG51_100	P	28	0.6	0.7	0.0	2.2	23	0.7	0.7	0.0	2.2	5	0.0	0.0	0.0	0.0
(%)	C	28	0.7	1.0	0.0	2.8	23	0.8	1.0	0.0	2.8	5	0.0	0.0	0.0	0.0
	NV	28	1.2	3.7	0.0	16.4	23	1.4	4.0	0.0	16.4	5	0.0	0.0	0.0	0.0
BG101_200	P	28	2.1	2.1	0.0	6.4	23	2.5	2.1	0.0	6.4	5	0.0	0.0	0.0	0.0
(%)	C	28	2.6	2.8	0.0	11.1	23	3.2	2.8	0.0	11.1	5	0.0	0.0	0.0	0.0
	NV	28	4.8	9.2	0.0	36.2	23	5.8	9.9	0.0	36.2	5	0.0	0.0	0.0	0.0
BG200+	P	28	96.0	3.6	87.9	100.0	23	95.2	3.4	87.9	99.8	5	99.8	0.3	99.3	100.0
(%)	C	28	95.0	4.3	83.5	100.0	23	94.0	4.1	83.5	99.7	5	99.8	0.3	99.3	100.0
	NV	28	91.4	12.0	51.5	100.0	23	89.8	12.7	51.5	100.0	5	99.0	1.5	96.7	100.0
BSC (%)	P	28	1.3	1.1	0.0	4.2	23	1.5	1.1	0.3	4.2	5	0.2	0.3	0.0	0.7
	C	28	1.6	1.4	0.0	7.2	23	1.9	1.4	0.3	7.2	5	0.2	0.3	0.0	0.7
	NV	28	2.4	5.4	0.0	28.9	23	2.7	5.9	0.0	28.9	5	1.0	1.5	0.0	3.3
VO (dm)	P	28	1.6	0.7	0.5	3.1	23	1.6	0.8	0.5	3.1	5	1.4	0.7	0.6	2.4
	C	28	2.0	1.4	0.5	5.5	23	2.1	1.5	0.5	5.5	5	1.4	0.7	0.6	2.4
	NV	28	2.4	1.5	0.2	5.3	23	2.5	1.6	0.2	5.3	5	2.0	0.7	1.0	3.0
	N	28	3.0	2.0	0.0	6.5	23	2.9	2.1	0.0	6.5	5	3.5	1.3	2.0	5.0
DTR (m)	-	28	179.0	117.3	24.1	376.2	23	188.6	118.7	38.9	376.2	5	134.7	111.3	24.1	289.9
DTE (m)	-	28	186.9	348.0	0.0	1647.7	23	211.9	379.6	0.0	1647.7	5	72.0	68.8	2.7	174.8
PPC (%)	100 m	28	61.9	36.9	0.0	100.0	23	69.6	32.9	1.6	100.0	5	26.2	36.2	0.0	79.5
	550 m	28	57.7	36.0	0.3	100.0	23	63.4	34.0	4.8	100.0	5	31.3	36.3	0.3	73.9
	1500 m	28	46.2	32.2	2.2	100.0	23	50.8	31.8	2.9	100.0	5	25.0	27.7	2.2	56.3

ED (m/ha)	100 m	28	210.6	215.3	0.0	709.8	23	211.4	214.8	0.0	709.8	5	207.0	243.2	0.0	517.4
	550 m	28	168.4	125.6	0.0	422.2	23	160.5	119.1	0.0	384.1	5	204.7	162.3	7.6	422.2
	1500 m	28	178.2	111.3	0.0	428.1	23	171.4	103.2	0.0	428.1	5	209.4	153.6	50.9	421.2

APPENDIX V – ADULT SURVIVAL HABITAT COVARIATE CALCULATION
METHODS

We assessed the effect of three classes of habitat covariates on survival of
GPS marked female sage-grouse: topography, mesic habitat resources, and post-fire
mosaic and recovery. Covariates relating to topography, land-cover, and habitat
recovery were calculated within 95% and 50% Brownian Bridge Kernel (BBK)
ranges generated within 14 day analysis periods, and applied to the survival interval
during which an analysis period occurred. Distance covariates relating to mesic
habitat resources, and habitat edge effect, were calculated as the mean distance from
each location in an analysis period to the habitat feature in question.

We assessed the effect of topography on survival using terrain ruggedness
index (TRI; Wilson et al. 2007). The terrain ruggedness index calculates the mean
difference in elevation (m) between each cell and its eight neighboring cells,
reflecting heterogeneity of terrain at the scale of 9 pixels (Wilson et al. 2007). We
acquired a 10 m digital elevation model (DEM) from the National Elevation Dataset
(USGS 2015). We generated a TRI raster for the study area using the *terrain* function
of package *raster* in Program R (R Version 3.2, www.r-project.org, accessed 20 Oct
2013). We calculated the mean TRI value within each analysis period BBK range
using the *isectpolyrst* function in GME (Beyer 2012).

We assessed the effect of mesic habitat resources on survival using mean
distance to water (m; DTW), for all locations in an analysis period. We subset each
set of used locations within an analysis period from the complete sage-grouse location
dataset, and used the "Near" tool in ArcGIS 10.1, to calculate the distance from each
location to a permanent or semi-permanent stream, as depicted by the National
Hydrologic Dataset. The mean value of DTW for all points within an analysis period
was then generated using the *mean* function in Program R.

We assessed the effects of post-fire habitat mosaic, and recovery, on survival using eight covariates: proportion of locations in intact habitat (PLI), percent intact habitat in analysis period BBK range (%; PI), connectance index using a 1 km connectance threshold (CONNL), connectance index using a 0.5 km connectance threshold (CONNS), edge density (m/ha; ED), mean distance from intact habitat (m; DTI), mean normalized difference vegetation index (NDVI_MN), and standard deviation of NDVI (NDVI_SD). We used the rasterized map of burnt and intact habitat within the fire boundary (Appendix I) to calculate the proportion of locations in intact habit. We used the "Extract Value to Points" tool in ArcGIS 10.1 to classify each point in analysis period as either occurring in intact or burnt habitat, the proportion of locations in intact habitat was then calculated as the number of points in intact habitat divided by the number of total points occurring in an analysis period. We calculated the percent of each analysis period BBK range that was composed of intact sagebrush land-cover using the rasterized map of burnt and intact habitat in the fire, and the metric Percentage of Landscape (PLAND) in FRAGSTATS v4 (McGarigal et al. 2012). We clipped the intact-burnt habitat map to the extent of each analysis period BBK range in ArcGIS 10.1, then input those clipped rasters into FRAGSTATS v4, and used the PLAND metric to calculate the percent of each analysis period BBK range which was composed of intact sagebrush land-cover. Using the same clipped fire map rasters we calculated the connectance index for all intact habitat patches within an analysis period BBK range using the Connectance Index Metric (CONNECT) in FRAGSTATS v4. The CONNECT metric calculates the proportion of habitat patches in an area which are within a specified distance to another patch of the same type (i.e. connected). We utilized the threshold distances of 1 km, and 0.5 km to define connectedness. Using the same clipped fire map rasters we calculated the density of intact-burnt habitat edges within an analysis period BBK range using the Edge Density Metric (ED) in FRAGSTATS v4. The ED metric calculates the density of habitat edge (m/ha) in an area. We calculated the distance

from each location in an analysis period to intact habitat using the "Near" tool in
ArcGIS 10.1. We created a polygon layer of intact habitat in the fire boundary using
the "Raster to Polygon" tool in ArcGIS 10.1, then implemented the near tool on all
analysis period locations to calculate the distance from each location to an intact
habitat feature, where locations within intact habitat were assessed with a DTI value
of zero. We then calculated the mean distance for all analysis period points using the
mean function in Program R. We generated NDVI rasters in ArcGIS 10.1 using one
cloud free Landsat 7 or Landsat 8 image of the study area during each month of the
study. We calculated mean and standard deviation of NDVI within each analysis
period using the *isectpolyrst* function in GME, using the monthly NDVI raster
collected during the month in which an analysis period occurred.

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