

AN ABSTRACT OF THE THESIS OF

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Title: Greater Sage-Grouse (*Centrocercus urophasianus*) Demographic Rates and Predator Communities in a Degraded Landscape in Modoc County, California.

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The greater sage-grouse (*Centrocercus urophasianus*; hereafter; sage-grouse) population in Modoc County California is geographically isolated and has been subsidized by translocation to prevent inbreeding depression since 2005. Despite significant efforts to increase the population through translocations and habitat improvement by cutting encroaching western juniper (*Juniperus occidentalis*), only a single lek remains (from 56 in the 1940s). Since 2017, several large wildfires have occurred on the area that led to an increase in invasive grasses and a decrease in sagebrush (*Artemisia* sp.) cover that has further degraded important nesting and brooding habitat. In addition to supporting the last known sage-grouse lek, Clear Lake Reservoir is a major stopover point and nesting site for migratory waterfowl and wading birds. This abundance of prey species also attracts a diverse and abundant generalist predator community. I estimated survival for adult females, nests, and chicks and assessed habitat and biotic characteristics that may influence these survival rates to identify factors that may be limiting population growth. I also estimated coyote (*Canis latrans*) probability of use and avian predator densities to evaluate the predation risk to females, nests and chicks on this study area. I monitored 37 female sage-grouse marked with GPS PTTs, 39 nests, and 8 broods during 3 years

(2019-2021). I measured vegetation characteristics for nests at the microsite and landscape scale to evaluate effects on daily nest survival (DNS). I used 70 camera traps to record over 4.9 million photos that I used to estimate coyote probability of use within each season during 2020 and 2021. During these two years I also conducted avian point-count surveys every two weeks at each camera trap location to estimate raven (*Corvus corax*), and raptor (i.e., hawk (*Buteo* sp.), harrier (*Circus hudsonius*), and eagle (*Aquila chrysaetos* and *Haliaeetus leucocephalus*)) densities using distance sampling. Nest success across a 29-day incubation period, the maximum number of incubation days at my field site, was 29% (95% CI: 17.1 to 44.8). Chick survival across a 54 day period was 22% (95% CI: 0.9 to 72.3), and female adult survival across a 12 month period was 29% (95% CI: 17.8 to 43.7). At the microhabitat scale, shrub and medusahead (*Taeniatherum caput-medusae*) cover were the two most supported covariates associated with DNS. Daily nest survival increased as shrub cover increased ($\beta = 3.3$; 95% 0.89 to 5.8) but decreased as medusahead cover increased ($\beta = -2.8$; 95% CI -5.0 to -0.56). At the landscape scale the log-linear structure of annual grass cover at 400m around the nest had the strongest effect on DNS which increased with increasing grass cover to ~35%, where DNS then stabilized ($\beta = 3.0$; 95% CI 0.28 to 5.8). Shrub cover at the landscape scale around nests was 12 % lower than what has been recommended for California and Nevada on the landscape scale, and the amount of annual grasses was 10 % higher than other study sites affected by large wildfires in Oregon, California, and Nevada. My estimated vital rates were 45-55% lower than range-wide estimates. During the course of the sage-grouse breeding season, coyotes used approximately 96 % (95% CI: 0.80 to 0.99) of the camera trap locations and coyote detection probabilities were highest during early brood-rearing for sage-grouse. Raven and raptor densities were 0.29 ravens/km² (95% CI = 0.19 to 0.44) and 0.22 raptors/km² (95% CI = 0.16 to 0.31), respectively. The overlap of brood-rearing with peak coyote activity could explain decreased brood survival within the first two

weeks post-hatch, and why adult predation was the primary cause of brood loss. Ravens and hawks also far outnumber sage-grouse, and the presence of nesting resident predators may be detrimental to this small population of nesting sage-grouse than what might be expected given the estimated density of avian predators. My results suggested recent habitat changes associated with wildfire and the resulting increased distribution of invasive grasses on the study area may have had a detrimental effect on this population across all life stages. The densities and occurrence of predators combined with the reduced availability of vegetation cover used for concealment, and increased perching and nesting structures for avian predators through juniper encroachment, may have increased the risk of sage-grouse females, nests, and chicks to predation. My project is a microcosm of what is occurring across the sage-grouse range in relation to fire, juniper, and invasive grasses and has shown that attention must be given to preventing the transition from sagebrush communities into juniper woodlands or grasslands dominated by invasive annuals if this population and others in degraded landscapes are to persist.

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Greater Sage-Grouse (*Centrocercus urophasianus*) Demographic Rates and Predator
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By

Chelsea E. Sink

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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.

Chelsea E. Sink, Author

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CHAPTER 1
INTRODUCTION

Chelsea E. Sink

The sagebrush (*Artemisia* sp.) biome is one of the largest ecosystems in the coterminous United States, and is home to more than 350 wildlife species (Wisdom et al. 2005). Sagebrush habitats have undergone extensive alteration and loss since the arrival of Europeans to western North America, with as little as 67% percent of the original ecosystem remaining (Noss et al. 1995, Bunting et al. 2002). Historically, sagebrush communities often occurred in large contiguous patches across the western United States and Canada; however, many of these sagebrush patches have been degraded, fragmented, or eliminated due to human disturbance and wildfires (Knick and Connelly 2011, Leu and Hanser 2011). Invasive plant species, weather, and climate change also pose challenges in maintaining this ecosystem (Miller et al. 2011). Significant threats to the western portion of this ecosystem in the Great Basin include large wildfires, and encroachment of western juniper (*Juniperus occidentalis*; hereafter; juniper) where fires have been suppressed. In addition, a variety of non-native grasses (e.g., cheatgrass [*Bromus tectorum*], medusahead rye [*Taeniatherum caput-medusae* hereafter; medusahead]) that respond faster than native plants after a disturbance, and increase future fire severity have invaded and degraded sagebrush ecosystems.

The frequency and severity of wildfires has been increasing in sagebrush ecosystems since the 19080's (Miller et al. 2011, Coates et al. 2016, Pyke et al 2016). Fire disturbance has increased primarily because of climate change, invasion by annual grasses, and human activity (Connelly et al. 2004, Miller et al. 2011). High severity fire kills nearly all sagebrush plants as it is unable to re-sprout from the roots once burned, and sagebrush communities can take up to 50 years to show signs of recovery after a large fire depending on elevation pre-disturbance sagebrush cover (Nelle and Connelly 2000, Baker 2006, Riginos et al. 2019).

In contrast, while the frequency and intensity of fires has increased in recent decades, European settlers began suppressing fire starting in the early 1900's (Agee 1996). Juniper has a

low tolerance to fire due to its thin bark and is highly susceptible to mortality from fire within the first 50 years of growth (Miller and Rose 1999). Thus, fire suppression along with climatic changes that favored juniper growth (Fritts and Xiangdig 1986, Holmes et al. 1986), has allowed the species to expand into open areas of core sagebrush habitat, especially at high elevation sites with cooler temperatures and high moisture content that supports juniper seedling growth (Johnson and Miller 2006, Brooks et al. 2015). Most (90%) of the conifer expansion since European settlement has occurred in sagebrush ecosystems (Davies et al. 2011, Miller et al. 2011) and represents ~3.6 mil ha of the landscape (Miller et al. 2005). Juniper naturally occurred in small stands on rocky ledges or in areas with well-draining soil and sparse vegetation (Miller and Rose 1995, Miller et al. 1999, West 2021) and fire intervals of 15 to 25 years in the sagebrush step are thought to have kept juniper out of sagebrush ecosystems (Houston 1973, Burkhardt and Tisdale 1976, Martin and Johnson 1979). The recent increases in conifer cover and density has caused declines in sagebrush, bunchgrasses, and perennial and annual forbs (Miller et al. 2000, Miller et al. 2005, Roundy et al. 2014).

In comparison to juniper, invasive annual grasses in the sagebrush ecosystems grow quickly, and easily out-compete perennial grasses and forbs after a wildfire (Davies and Svejcar 2008). Cheatgrass has received much of the research focus in the Great Basin as it outcompetes native species for water and soil resources (Melgoza et al. 1990). However, another equally concerning exotic species is medusahead, an annual grass that has been spreading into rangelands in the western U.S. since it was first observed in 1887 (Young 1992). Medusahead has a high silica content which causes it to decompose slowly, causing thick mats of litter to form (Bovey et al. 1961). These mats prevent other plants from becoming established and create fine fuels for wildfire (Young 1992). Sites invaded by medusahead contain lower species

diversity and native plant biomass than uninvaded sites, and both forb and shrub cover is reduced (Davies and Svejcar 2008). Unlike cheatgrass which can be effectively reduced through fall grazing (Schmelzer et al. 2014, Perryman et al. 2020), the timing in which grazing can be used as a control method for medusahead is extremely limited. There is only a two-week window in the spring where the plant is palatable to livestock and susceptible to defoliation, making the plant difficult to manage through conventional rangeland practices (Lusk et al. 1961, Young et al. 1970).

The negative effects these landscape-level changes have had on the sagebrush ecosystem have resulted in declines of sagebrush-obligate species like the greater sage-grouse (*Centrocercus urophasianus*: hereafter, sage-grouse), which forages on sagebrush exclusively during winter and uses it for nesting cover in the spring (Braun et al. 2005, Connelly et al. 2011a). Loss of sagebrush through wildfire can have a negative effect on sage-grouse demography (Foster et al. 2019, Anthony et al. 2022). After a large disturbance like wildfire, invasive grasses can become established and have been found to negatively affect grouse population rates of change (Coates et al. 2016), lek persistence, and male recruitment at leks (Blomberg et al. 2012). Additionally, increased juniper abundance can fragment and displace sagebrush, provide avian predator perches (Coates et al. 2014), and degrade range condition (Miller et al. 2005, Miller et al. 2011). This increase in juniper results in reduced available habitat for sage-grouse, who will avoid using areas of tree cover once it exceeds 4% of the landscape (Baruch-Mordo et al. 2013, Coates et al. 2017, Severson et al. 2017, Olsen et al. 2021), likely because avoiding tree cover mitigates possible predation from avian or mammalian predators for sage-grouse.

As a result of human development and juniper encroachment, trees and anthropogenic structures in sagebrush communities have provided novel nesting and perching sites for ravens (*Corvus corax*) and raptors, allowing their abundance to increase in traditionally open landscapes that otherwise would have low densities of perching structures (Coates et al. 2014, Howe et al. 2014, Dinkins et al. 2014). The increased abundance of ravens is concerning for sage-grouse, as they are an effective sage-grouse nest predator (Coates et al. 2008, Coates and Delehanty 2010, Dinkins et al. 2016). In addition, dramatic shifts in mammalian carnivore distributions throughout North America have been observed (Ritchie and Johnson 2009). The decline in apex predators has influenced changes in the meso-carnivore distribution and abundance in many terrestrial ecosystems (Ritchie and Johnson 2009). For example, as wolf (*Canis lupus*) populations were extirpated or declined across the northern U.S. and Canada, coyote populations (*Canis latrans*) increased rapidly, resulting in declines in red fox (*Vulpes vulpes*) populations (Levi and Wilmsers 2012, Newsom and Ripple 2015).

Understanding this shift in predator communities is important for sage-grouse populations, as avian and mammalian predators affect grouse at different life stages. In Strawberry Valley, Utah, red foxes were frequent predators of adult radio-marked grouse and nests (Bunnell 2000, Baxter et al. 2007, Baxter et al. 2013). Adult survival improved when red foxes were lethally removed from the study area, suggesting foxes may be limiting growth of this small sage-grouse population (Baxter et al. 2007, Baxter et al. 2013). Sage-grouse females selected nest and brood sites with low avian predator densities (Dinkins et al. 2012, 2014), and nest success was negatively correlated with corvid abundance and occupancy (Manzer and Hannon 2005, Bui et al. 2010, Dinkins et al. 2016, Coates et al. 2020). The use of cameras placed at sage-grouse nests has identified ravens, coyotes, and badgers (*Taxidea taxus*) as

frequent sage-grouse nest predators (Coates et al. 2008, Lockyer et al. 2013, Taylor et al. 2017, Conover and Roberts 2017).

Compared to other galliformes, sage-grouse have large annual home ranges, high annual survival, and low productivity (Connelly et al. 2011*b*), and population dynamics are largely driven by adult and chick survival (Taylor et al. 2012, Dahlgren et al. 2016). Therefore, high predation rates at the adult and nesting stage can drive population declines (Taylor et al. 2012, Dinkins et al. 2014). Due to their long lifespan (relative to other galliformes), sage-grouse can invest less energy into breeding and may forego renesting if conditions are unfavorable or the first nest is lost late in incubation (Taylor et al. 2012). Thus, annual renesting rates are highly variable but generally low compared to other galliformes (Taylor et al. 2012). Sage-grouse brood survival from 18-50 days post hatch is also highly variable (7-50%) across their range (Connelly et al 2011*b*, Taylor et al. 2012). Both nest and chick survival are regulated by environmental factors that vary annually (Taylor et al. 2012), such as the density of predators (Coates and Delehanty 2010, Conover and Roberts 2017), vegetation cover that mediates predation (Holloran et al. 2005, Coates and Delehanty 2010, Doherty et al. 2010, Hansen et al 2016, Foster et al. 2019), and extreme weather events that cause nest abandonment or death from exposure for chicks (Walker 2007, Huwer et al. 2008, Webb et al 2012, Lundblad et al. 2022).

In the Great Basin, the Clear Lake sage-grouse population is geographically isolated from other nearby populations in south central Oregon, NE California, and NW Nevada (Figure 1). From 1970-1990, the population went through a severe bottleneck and the number of leks was reduced from 56 to one, located on Clear Lake National Wildlife Refuge (CLNWR), with only 5 males attending this lek by 2005. At that time, the USFWS began translocating grouse from both Oregon and Nevada to augment populations on CLNWR. Annual survival for both translocated

and resident adult females during 2007-2011 was similar (Bell and George 2012) and within the range of estimates reported for other populations (Taylor et al. 2012). Nest survival on CLNWR during this time was also within the range of estimates from stable populations across the species range (Bell and George 2012), suggesting translocated females were surviving and successfully rearing young.

Despite observing favorable vital rates in translocated and resident birds in 2011 (Bell and George 2012), the CLNWR sage-grouse population has yet to form additional leks. In fact, lek counts declined from 36 to 17 males after translocation was stopped briefly from 2015-2017. In addition, since the previous research on Clear Lake was published, two additional juniper removal projects (7,572 ha) have been completed, and several large wildfires have occurred (29,946 ha) with ~5,665 ha located in sage-grouse nesting in brooding habitat (Figure 2). Raven populations have also increased across the western US (Ziolkowski et al. 2022, Dinkins et al. 2021), including Modoc County, which could greatly impact sage-grouse nest survival.

In a pilot study completed in 2019, 88 vegetation transects were sampled throughout the study area, and cheatgrass and medusahead were found at the majority of these transects (90% and 71%, respectively), but these invasive grasses are only briefly mentioned by Bell (2011). The pattern observed during the pilot field season suggested that the extent of invasive grasses on CLNWR and Modoc National Forest (MNF) has increased significantly from what was previously recorded (Horney 2010, Bell 2011). These landscape level changes could greatly impact the sage-grouse population as well as the predator community, and updated estimates of resident sage-grouse vital rates are needed. In addition, vegetation characteristics of brood habitats, and the relationship between landscape characteristics and adult survival are currently lacking on CLNWR. Finally, a general understanding as to how landscape scale disturbances,

such as juniper removal and wildfire affect subsequent adult and brood survival is important for directing future management activities on CLNWR.

To address some of the questions needed to effectively manage sage-grouse populations on CLNWR, the objectives of my study were to: 1) estimate seasonal demographic rates including adult survival, daily nest survival, and chick survival for resident sage-grouse on CLNWR and surrounding MNF and determine the association between these vital rates and general landscape characteristics such as shrub cover, juniper cover, and annual grass cover, and 2) determine the probability of use for mammalian predators and the density of avian predators to identify potential causes of sage-grouse population declines on the study area.

CHAPTER 2

METHODS

Chelsea E. Sink

STUDY AREA

Most of the management and research efforts for the Klamath OR-CA population are focused on CLNWR and surrounding MNF, known as the Active Management Unit (AMU; 121,000 ha, Figure 1). Elevation in the AMU ranges from 1200 to 1430 m. The dominant vegetation consists of shrub species such as low sagebrush (*Artemisia arbuscula*), big sagebrush (*A. tridentata* ssp.), green rabbitbrush (*Chrysothamnus viscidiflorus*), and antelope bitterbrush (*Purshia tridentata*), and an herbaceous layer characterized by perennial bunch grasses (Barbour et al. 1997). Annual invasive grasses including cheatgrass, medusahead, Japanese brome (*Bromus japonicas*), and North African wiregrass (*Ventenata dubia* hereafter; wiregrass) are also prevalent.

Recent landscape level changes have drastically altered sage-grouse habitat within the AMU. The USFS has been completing juniper removal in areas identified as breeding and wintering locations used by sage-grouse since 2010. This removal has been completed in 4 stages, creating a patchwork of treatments ranging in age from 1-10 years (Figure 2). In addition, fire has affected 9% of sage-grouse habitat in the AMU. In 2001, the majority of the Clear Lake “U” (i.e., a ~1,618 ha peninsula of sage-grouse habitat) burned, and 1,817 ha just south of the Clear Lake “U” burned in 2017 (The Lake Fire). Both the 2001 and 2017 fires have led to a reduction in shrub species and an increase in invasive annual grasses. On 28 July 2019, a human-caused wildfire (the Tucker Fire) burned 5,753 ha of MNF and CLNWR between HW139 and the shore of Clear Lake Reservoir (Figure 2). The fire boundary for the Tucker Fire contained summer and brood-rearing habitat for sage-grouse. Additionally, two months later a wildfire began after a tree was struck by lightning, burning 2,321 ha directly south of the Lake fire boundary (The Lone Fire).

Average temperature across the 5-month sage-grouse breeding season (from April to August) in Modoc County ranged from lows of -0.6 to 8.9 °C and highs of 15.6 to 30.6 °C, and precipitation ranged from 25.4 to 66.1 mm. Modoc County historically experiences a wet year followed by 4-5 years of drought (Drought.gov). My study began at the beginning of this typical 5-6-year weather cycle, as the first year of my study in 2019 had increased annual precipitation in the winter and spring (31.6 cm), followed by 2 years of moderate to extreme drought in 2020 and 2021 (16.9 cm, 17.9 cm).

METHODS

Adult Capture and Monitoring

I used established spotlighting and hoop-net methods to capture yearling and adult female sage-grouse during November – March of 2019-2021 (Wakkinen et al. 1992). In 2019, I captured females on or near leks in Nevada and translocated them to CLNWR, and also captured resident birds on CLNWR and MNF. Resident and translocated birds received GPS transmitters and were released onto the lek at CLNWR during February-March 2019. In 2020 and 2021, I only captured and instrumented CLNWR resident females (i.e., no birds were translocated). I aged and sexed captured individuals based on body mass and wing characteristics (Braun and Schroeder 2015) and attached 22-g ARGOS/GPS Solar PTTs (GeoTrak, Inc., Apex, NC, USA) with 3g Holohil PD-2 VHF transmitter using a rump-mount technique (Rappole and Tipton 1991). I captured and handled all individuals following protocols approved by the Institutional Animal Care and Use Committee at Oregon State University and permits from the California Department of Fish and Wildlife. I monitored birds fitted with transmitters remotely by downloading GPS locations from the ARGOS satellite system (GeoTrak, Inc., Apex, NC, USA).

If I observed more than 4 consecutive GPS locations in the same place, or the transmitter stopped downloading locations, I visited the last known location to determine the status of the bird.

Nest monitoring

I monitored each nest attempt and nest survival of each nest using a combination of GPS locations and radio telemetry. If GPS locations remained stationary for >18 h during the nesting season (1 April – 31 May) I used GPS and VHF ground tracking to locate and visually confirm a female was incubating a nest. I examined GPS locations daily to identify nest failures and additional potential nest attempts. If a female was absent from the nest for more than 2 consecutive GPS locations, I inspected the nest to determine nest fate. I considered a nest ‘successful’ if a female incubated ≥ 27 days and ≥ 1 egg displayed a distinct egg cap and intact egg membrane, signifying a hatched egg (Webb et al. 2012), and ‘unsuccessful’ if these criteria were not met. Once incubation was confirmed and nest fate determined, I used patterns in GPS locations to identify the date the nest was first incubated and the nest success/failure date.

Weekly brood survival

I estimated brood survival over 10-day intervals using spotlight counts at 14, 24, 34, 44, and 54 days after hatch date. Two observers located and approached broods using a combination of telemetry and a spotlight between the hours of 2200 and 0400. When the observers were close enough to see individual grouse they used binoculars to count the chicks within the spotlight area without flushing them (Dahlgren et al. 2010, Riley et al 2021). If the vegetation was too thick to observe the brood, or the chicks could not be counted because they were under the female, then observers located the adult female the following day using VHF and flushed her chicks in the morning within an hour of sunrise (Dahlgren et al 2010).

Vegetation sampling

I sampled vegetation at nests and GPS-PTT locations of females with broods. I conducted vegetation surveys at each sage-grouse nest location within 3 days of predicted hatch, regardless of ultimate nest fate, to avoid bias in vegetation height measurements between failed and successful nests and account for correlation in herbaceous vegetation growth throughout incubation (Gibson et al. 2016). I centered 2, 10-m transects oriented perpendicular from north to south, and east to west on each nest (Popham and Guierréz 2003, Doherty et al. 2010,). I sampled cover for shrubs, perennial grass, annual grass (down to species for invasive grasses), forb, litter, and bare ground every 1-m using the line-point intercept method (Herrick et al. 2005). I also measured litter depth and the tallest vegetation for each cover type within a 30-cm cylinder at 0, 5, and 10-m (Musil 2011). I measured visual obstruction (VOR; percent obstruction in decimeters) in each cardinal direction using a modified cover board that I viewed from 7-m away and 1m from the ground (Guthery et al. 1981). I recorded shrub line-intercept cover and canopy gap intercept along each transect with canopy gaps of >5 cm not counted as continuous shrub canopy (Canfield 1941, Connelly et al. 2004, Herrick et al. 2005).

I sampled brood locations by assigning each GPS-PTT point location used by females with broods a random number and then I selected the locations assigned numbers 1-3 from each 7-day period after hatch date until the brood was ~54 days old or the brood failed. I centered a single 30-m transect 10-m west of the GPS point and oriented N to S to account for GPS location error. I measured vegetation functional groups, heights, and VOR in the same manner as nests.

Camera Surveys

To estimate the probability of use for mammalian predators on CLNWR, I used GPS locations from female sage-grouse wearing transmitters during 2019 and constructed a 95% kernel density estimate (KDE) to represent the extent of area occupied by grouse within the study site. Within this 250 km² area, I randomly placed 70 infrared motion-activated cameras (Browning Strike Force Extreme, Morgan, Utah) ≥ 1 km from each other to maximize the detection rate of predators low in density (Rovero et al 2013). Private lands within the KDE were not included as available random camera locations. I mounted cameras on 1.1-m tall u-posts, with the camera placed 40-cm off the ground and oriented north to reduce overexposure from the sun. When the motion sensor was activated (a “detection”), cameras were set to take 3 rapid fire pictures with a 1-minute photo delay before a new motion triggered the camera. I deployed cameras continuously from the time female grouse began initiating nests until monitoring of broods ended.

Avian surveys

I used standard distance-sampling techniques (Buckland et al. 1993, Ralph et al. 1995, Thomas et al. 2010) to count and record distance to all corvids and raptors observed during point counts conducted at every location where cameras were placed. Surveys were conducted at each camera location every 14 days starting when the camera was deployed in April and continued until August between 0800 – 1500 hours, for a total of 6-8 surveys per camera station. Approximately 16 surveys could be completed each day, and surveys at all 70 locations were completed within an 8-day time frame. The field site was divided into sections of survey locations that could be completed by one person in a 6-hour day and surveyed in the same order each week. I recorded distance from the observer when standing at the camera to where predators were first located (Ralph et al.

1995, Thomas et al. 2010). I used Rangefinder binoculars (LASERFORCE 10x42, Nikon Inc.,

Melville, NY) in conjunction with a global positioning system unit to estimate distances directly or to validate visually estimated distances.

Estimating demographic rates

Daily Nest Survival

I estimated daily nest survival of sage-grouse using known fate models in Program MARK (White and Burnham 1999) because the exact dates of nest initiation and fate were known from the GPS location data. I estimated daily nest survival (DNS) for a 29-day period, reflecting the longest incubation period across the three field seasons and year was treated as a group effect. Thus, general time effects (day) reflected a standardized day within the 29-day incubation period, rather than date within specific nesting seasons. I investigated the relationship between daily nest survival (DNS) and a variety of covariates, including nesting habitat characteristics and temporal patterns (within season and between years; Table 1). I evaluated whether DNS varied among years (2019 to 2021; YR), by the day of incubation (t), and by nesting attempt (1st or 2nd nest attempt; FIRST; Table 1). Nests were also characterized relative to whether or not they were located in areas treated for conifer encroachment (JUNIPER, Table 1). Habitat covariates (Table 1) were developed from nest site vegetation sampling, or remotely sensed data at the landscape scale. I used a geographic information system to characterize the predominant vegetation around each nest: percentage of shrub, annual grasses and forbs, and trees at 3 buffer distances of 56, 400, and 800-m (Severson et al. 2016). Each 30-m pixel represented the percentage of each variable and was mapped across the landscape using the Rangeland Analysis Platform, which was measured once every year at the end of the growing season (Jones et al. 2018; Table 1). In addition to evaluating linear relationships between DNS and medusahead at the microsite scale and annual forbs and grass at the landscape scale, I also evaluated

pseudothreshold and quadratic structures of each covariate, as I hypothesized that medusahead and annuals may be associated with non-linear increases or decreases in DNS. For example, I hypothesized that medusahead could have a negative linear effect on survival, with survival declining for every unit increase in medusahead, or conversely, medusahead may provide some benefit as cover, up to a certain proportion of the microsite, at which point DNS then levels off (i.e., pseudothereshold) or even declines (i.e., quadratic relationships). If fire and juniper encroachment are negatively affecting sage-grouse nesting habitat through increased predator access to nests and nesting females, I predicted nest sites with less shrub cover, lower visual obstruction, or more trees for perching nearby would be more susceptible to predation and have lower daily nest survival rates.

I developed *a priori* hypotheses and multiple model sets to evaluate factors associated with variation in DNS using a combination of secondary candidate sets and the build-up approach following Bromaghin et al. 2013 and Morin et al 2020. I started by creating single-factor models within 3 different categories resulting in 3 separate model sets including 1) general temporal and biological patterns (year and day within the 29-day incubation period, and nest attempt), 2) microsite covariates, and 3) landscape scale covariates. I then combined covariates that received the most support from each of the covariate categories into a final, multi-factor model set. I 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). I carried covariates forward from the microsite and landscape category model sets and drew inferences from models in the final model set ranked within 5 AIC_c . I also included a few multi-factor models in my final model set that reflected combinations of microsite vegetation covariates that have been shown to have a

significant effect on daily nest survival in previous research such as sage cover (SH.COV) paired with perennial grass height (PG.H), and perennial grass cover (PG.COV; Foster et al 2019, Anthony et al. 2021). In addition to model rankings, I evaluated changes in model deviance and the precision of model coefficients ($\hat{\beta}_i$) to assess the direction and strength of specific covariate effects (Dugger et al. 2016) and identify uninformative parameters in highly ranked models (Arnold 2010).

Chick survival

I estimated chick survival using a modified Mayfield-estimator which accounts for inter-dependence among brood mates (Flint et al. 1995). I modeled the number of chicks lost during intervals equal to the total number of chick days that a brood was observed. There were 5 total intervals of 10 days, from 14-54 days post-hatch. Initial brood size was calculated as the total number of eggs that successfully hatched.

Adult Survival

I used known fate models in Program MARK (White and Burnham 1999) to estimate monthly and annual survival for adult females, model-averaged estimates of monthly and annual survival, and model selection results. Females who slipped their transmitters were right censored starting with the month the slip occurred. Because sample size of instrumented females was small, my model set was focused on general estimates of survival while evaluating temporal variation relative to month, year, and differences in survival between the breeding vs. non-breeding season (March-August, September – February). To generate monthly and annual estimates of survival that incorporated model selection uncertainty I model averaged survival estimates across all models in my model set (Burnham and Anderson 2002).

Mammalian Probability of Use

I estimated the probability of use for coyotes from remote camera data using a single-season occupancy model that accounts for variable detection rates across the sample period (MacKenzie et al. 2018). Each camera location resulted in a sample unit that reflected a 120 m² observation cone around the camera. Cameras were placed randomly throughout the study areas resulting in a density of 0.06 cameras/km². The area sampled by each camera did not reflect discrete coyote home ranges, and were therefore, not “closed” to changes in occupancy during the season. However, because cameras were placed randomly, with none placed adjacent to known coyote dens, I assumed coyote movement into and out of my sampled area was random. For this reason, my estimates of occupancy reflect the probability of use by coyotes, rather than site occupancy (MacKenzie et al. 2018).

I used Program MARK, to estimate the annual probability of use ($\hat{\Psi}$) and detection probability (\hat{p}) within each season, model-averaged estimates, and model selection results (White and Burnham 1999). Sampling periods were weekly within seasons, and I coded each year (2020 – 2021) as a group effect. For the probability of detection (\hat{p}), I also modeled within season temporal variation as general variation by week, as well as a linear, pseudo-threshold, or quadratic trend. I used AIC_c, Δ AIC_c, w_i to rank models containing annual and temporal effects on \hat{p} (Burnham and Anderson 2002). I model-averaged annual estimates of $\hat{\Psi}$ from all models in my model set to account for model-selection uncertainty on estimates of \hat{p} (Burnham and Anderson 2002).

Avian Density Analysis

I estimated raven and raptor density using distance sampling to model counts of individual or groups of birds while taking into account the probability of detection and declines in detection as

distance from the observer increases (Buckland et al. 2001). I conducted analyses with the “*Rdistance*” package in R-statistical software (R Development Core Team, 2012; McDonald, Nielson & Carlisle 2015). For each group I compared the AIC_c values of the hazard rate and half-normal key functions as well as the the Poisson and negative-binomial distributions. For ravens, I right-truncated distance observations beyond 1.4 km, the approximate distance at which detection probability declined below 0.1 (Buckland et al. 2001; Burnham et al. 2004). I also aggregated observations into four distance classes with breakpoints at 350, 700, 1050, and 1400-m (e.g., Sillett et al. 2012; Kéry and Royle 2015.) I specified the hazard-rate key function for the inverse monotonic and curvilinear relationship between distance and detection (Thomas et al. 2010; Fiske and Chandler 2011) and I modeled density with a Poisson distribution (Royle et al. 2004; Sillett et al. 2012).

For raptors, I combined and evaluated density of all species in the Accipitridae family as a single category “raptors.” I right-truncated the distances to 1500-m with observations aggregated into 5 distance classes of 300, 600, 900, 1200, 1500-m. I specified a half-normal key function for the inverse monotonic and curvilinear relationship between distance and detection (Thomas et al. 2010; Fiske and Chandler 2011) and modeled density using a Poisson distribution with cosine adjustments (Royle et al. 2004; Sillett et al. 2012). I determined the number of adjustment terms to add to each function type using AIC_c and evaluated model fit using χ^2 goodness-of-fit statistic and visually inspected histograms of the distance data and the fit of detection function (Buckland et al 2001).

CHAPTER 3

RESULTS

Chelsea E. Sink

Nest Characteristics

From 2019-2021, I caught 37 females and fit them with satellite GPS transmitters. Thirty females initiated 38 nests and 12 females did not attempt a nest ($n = 9$) or were predated ($n = 3$) before nesting season began. Nest initiation dates for first nests ranged from 11 April – 1 May, with the earliest initiation date occurring in 2020 (Table 2). Only a few females (30%) attempted renests in 2019 ($n = 3$), and 2020 ($n = 4$) and no females attempted a second nest in 2021 (Table 2). Only 10 nests were successful, and the primary cause of nest failure was nest predation, but 2 nests failed due to predation of the nesting female. In successful nests, all but one of the 69 total eggs hatched, and of the unsuccessful nests there was one female who incubated for 29 days until her nest was depredated, however the eggs were not fertilized and only filled with yolk.

Nest were mostly placed in sagebrush (68%) but were also observed in slash piles left over from cutting juniper (16%), in clumps of annual grass (5%), rabbitbrush (5%), and small juniper saplings (5%). Only 9 nests (26%) were located in areas where juniper treatments occurred, and only 1 nest was located inside a fire boundary.

Nest Survival

Single covariate microsite models ranked higher than the landscape scale characteristics for their effect on DNS (Table 3). The covariate reflecting the proportion of annual forbs and grasses at 400-m buffer (AN400) around the nest was the only landscape-level covariate selected into the final model set (Table 3). I observed strong support for the additive effect of shrubs (SH.COV) at the microsite scale and AN400 at the landscape scale on daily nest survival. This model received 0.36 of the model weight and received approximately 4.2 times more support than the next best model containing only shrub cover at the microsite scale ($w_i = 0.87$; Table 3). Both shrubs and

annual forbs and grasses had precise positive effects on DNS ($\hat{\beta} = 3.20$; 95% CI: 0.76 to 5.65; $\hat{\beta} = 2.64$; 95% CI: 0.14 to 5.13, Figure 3 and 4), however the positive effect of the amount of annual forbs and grass reached an asymptote at ~32 % average cover, after which DNS increased marginally in association with additional forb and grass cover (Figure 4). Perennial grass cover also had a positive effect on DNS when combined with shrub cover however the confidence interval overlapped zero ($\hat{\beta} = 0.94$; 95% CI: -0.94 to 2.81; Table 3), suggesting little to no support for the effect of perennial grass cover on DNS. At the nest, average shrub cover was 25% (SD = 19.0) and at the landscape scale average cover of annual forbs and grasses at 400-m around the nest was 28% (SD = 5.42).

All species of invasive grasses at the nest site had a negative effect on DNS, however only medusahead and Japanese brome had precise effects (confidence intervals that did not overlap zero) in single covariate models ($\hat{\beta} = 2.80$; 95% CI: -5.04 to -0.56; $\hat{\beta} = -3.85$; 95% CI: -7.13 to -0.56; Table 4, Figure 5 and 6). The model containing shrub cover and medusahead was $<5 \Delta AIC_c$ from the top model, but the beta value for the medusahead covariate was not precise and 95% confidence limits widely overlapped zero (Table 3). Average cover of medusahead and Japanese brome around nests across all three years was 15% (SD = 20) and 5 % (SD = 13%), respectively. In addition to invasive annuals, litter cover around nests was high, and averaged of 68% (SD = 13).

Models containing temporal covariates (Table 5) were not well-supported with with model weights $<2\%$. The probability of a sage-grouse nest surviving the entire 29-day incubation period and hatching ≥ 1 egg from the top model including the mean effect of shrubs and annual grasses was 0.292 (95% CI: 0.166 to 0.460).

Brood Survival

I recorded 10 successful nests over the 3 years of my study, but only 9 broods were monitored as one female was censored due to battery failure on her transmitter, and the fate of her brood could not be confirmed. Another female also had a VHF transmitter failure which made it impossible to locate her in real time to confirm whether or not she had chicks. However, I continued to conduct vegetation surveys associated with brood locations for this female because her movements based on GPS locations and examination of roost points for chick fecal pellets suggested she had chicks. I observed this female with 2 chicks at 72-days post-hatch while summer trapping, but ultimately did not include her brood in the survival analysis. Including this female, only 2 other broods survived to 54 days post-hatch from 2019-2021, producing 7 chicks out of the total 69 eggs that hatched from the 9 broods I monitored. The primary cause of brood failure was depredation of the female ($n = 5$), and only in one case was a female observed without her brood on 2 consecutive surveys which I categorized as total brood loss.

Only 8 broods whose fates were confirmed on every survey were included in the survival analysis. Daily brood survival estimated with the modified Mayfield estimator was 0.985 (95% CI: 0.973 to 0.997). The derived estimate of chick survival across the entire 54 days period was 0.441 (95% CI: 0.232 to 0.833).

The dominant vegetation functional group in the canopy at brood points in 2019 and 2020 were shrubs, perennial grasses, and cheatgrass (Table 6). Cheatgrass was the invasive grass with the highest cover at 31.9% (SD = 27.1) and 23.1% (SD = 19.0) in both years; (Table 6). Litter ranged from 30.9-68.1% across the three years of the study and was comprised of mostly medusahead, although live growth of this species was not commonly encountered during

surveys. (Table 6). There was little vegetation growth in 2021 and brood points from this year had the lowest vegetation cover across all functional groups besides forbs (Table 6).

Adult survival

Only 3 of 37 females slipped their transmitters and were censored from the adult survival analysis. One female who slipped her transmitter in 2019 was recaptured in 2021 and identified by her leg band. The primary cause of mortality was predation, with the majority of females predated in April ($n = 19$). The remaining predation occurred during the non-breeding season in September-February ($n = 12$). During the breeding season, 2 females were predated on the nest and 5 were predated while attending a brood.

Adult survival varied by month within the year as the S(month) model received 46% of the total model weight with several top models including interactions with month (Table 7). Survival was lowest in April (0.687, 95% CI: 0.544 to 0.801), followed by October (0.809, 95% CI: 0.588 to 0.927) and January (0.813, 95% CI: 0.552 to 0.938). The second-ranked model contained the effects of year and month and received 34% of the total model weight. However, survival estimates for each year from this model were similar and confidence intervals broadly overlapped zero suggesting little support for yearly differences (Figure 7). The model averaged derived estimate for annual survival for each year from 2019 – 2021 was 0.32 (95% CI: 0.17 to 0.51), 0.33 (95% CI: 0.13 to 0.60), and 0.22 (95% CI: 0.08 to 0.49; Figure 7).

Coyote Probability of Use

I collected 4,435,054 pictures from 70 camera traps over the course of 2 field seasons. Potential sage-grouse predators identified included coyotes (1,532 photos), badgers (47 photos), bobcats

(65 photos), striped skunks (120 photos), and mountain lions (6 photos). Cameras were active from 21 April – 12 August in 2020, and 12 April – 29 July in 2021, resulting 252 calendar days where ≥ 1 camera was deployed.

Coyotes were observed in photos from all but 8 cameras in 2020 and 6 cameras in 2021. My top model explaining coyote detection and probability of use included a quadratic effect of week on the probability of detection, but no differences between years (Table 8). Detection was lowest during the beginning and end of the observation periods and peaked between week 8-10 (late May). Model-averaged derived estimates of coyote probability of use were 0.95 (95% CI: 0.82 to 0.99) in 2020 and 0.96 (95% CI: 0.80 to 0.99) in 2021.

Avian Density

From April – August I completed a total of 1035 surveys. Ravens and red-tailed hawks (*Buteo jamaicensis*) were the most abundant sage-grouse avian predators recorded in both years. Observations of both species declined as the season progressed. For ravens the probability of detection was 0.28 (SE = 0.056) and density was 0.29 ravens/km² (95% CI: 0.19 to 0.44) with an average flock size of 1.6 birds. For hawks, harriers, and eagles, the probability of detection was 0.20 (SE = 0.029) and hawk density was 0.22 birds/km² (95% CI: 0.16 to 0.31).

CHAPTER 4
DISCUSSION AND CONCLUSIONS

Chelsea E. Sink

Discussion

My study estimated the demographic rates of sage-grouse from a small, isolated population in northwestern California that has persisted through active management by translocating individuals from other populations and restoring habitat through juniper removal. I found that estimates of adult annual survival, nest success and brood survival were much lower than estimates from a previous study completed on CLNWR from 2007 – 2009 (Bell 2011, Bell and George 2012) and from stable or increasing populations across the species range (Taylor et al. 2012). CLNWR and MNF have experienced an increase in distribution and abundance of invasive grasses, and my study is one of the first to show a significant and negative effect of medusahead and Japanese brome on the daily nest survival of sage-grouse at the microsite scale. The increased density of invasive grasses over time could be contributing to differences in nest survival that I observed relative to previous estimates on CLNWR and other portions of the sage-grouse range. In addition, the predator community at my study site was diverse and relatively abundant, with peak detections of mammals and avian predators overlapping with peak nesting and brooding activity for sage-grouse which may exacerbate the rate at which this small population is declining.

Small populations that are isolated from a larger metapopulation are more likely to be extirpated due to risks from disease and stochastic events like wildfire and drought (Stacy and Taper 1992). Even without disturbance, small populations with declining growth rates are at higher risk of extinction due to random chance and demographic stochasticity (Gabriel and Bürger 1992). For the aforementioned reasons, populations in the periphery of a species range typically experience high temporal variation in abundance which can increase local extinction rates in contrast to core populations (Vucetich and Waite 2003, Miller et al. 2011). Sage-grouse

extirpation has occurred mostly along the outer portions of their pre-settlement range and their distribution has contracted inward (Schroeder et al. 2004, Aldridge et al. 2008). Sites with extirpated populations have lower sagebrush cover, more edge habitat, lower elevation, higher human and road density, and more agriculture than currently occupied sites (Wisdom et al. 2011). The sage-grouse population on CLNWR is at the western edge of the historic distribution of sage-grouse, and the population has been identified as sharing many landscape-level characteristics with extirpated populations (Wisdom et al. 2011). Adult survival and annual productivity are key vital rates that can have strong impacts on sage-grouse population trajectories (Taylor et al. 2012, Dinkins et al. 2014, Dahlgren et al. 2016, Olsen et al. 2021, Anthony et al. 2022). For the CLNWR population, translocation provided an influx of new individuals while juniper was being removed in areas designated as important breeding or wintering grounds for sage-grouse. This effort should have increased the amount and quality of available habitat and helped the population persist and recover (Severson et al. 2017, Olsen et al. 2021).

However, my nest survival rates (0.292, 95% CI: 0.166 to 0.460) were much lower than those from a previous study on CLNWR (0.450, 95% CI: 0.319 to 0.622; Bell 2011), but similar to other nearby field sites affected by large wildfires in Nevada, Oregon, and California (0.22, 95% CI: 0.13 to 0.33, Lockyer et al. 2015; 0.23, 95% CI: 0.098 to 0.441, Foster et al. 2019; 0.19, 95% CI: 0.06 to 0.42, Dudley et al. 2022), suggesting fire may have had a significant impact on this population. While I found shrub cover had a positive effect on nest survival, cover of sagebrush and other native shrub species is limited at CLNWR and surrounding MNF and the highest mean shrub cover I observed at the landscape scale around nests was 12.2 % (SD = 4.7, Table A3) in 2021. Mean percent shrub cover was higher at the microsite scale, however the

greatest observed mean value was 25% in 2019, which is lower than what is considered suitable for nest survival in California and Nevada (>25.8 %, Coats et al. 2017). However this mean value is higher than other sites affected by wildfire whose shrub cover ranges from 4 – 15 % in burned areas used by sage grouse (Anthony et al. 2020, Lockyer et al. 2015, Coats et al. 2017, Dudley et al. 2022).

I found the opposite pattern for annual grasses, which in some areas accounted for over a third of the total vegetation cover on the landscape scale. Medusahead and cheatgrass ranged from 17-20% cover. Alternatively, litter covered >60% of our vegetation transects around nest sites at the microsite scale (Table A3). Other studies that focused on microsite selection have found sage-grouse actively avoided annual grass cover around nests, however their annual grass cover only ranged from 7 – 10.6 % at nest sites (Lockyer et al. 2015, Coats et al. 2017, Dudley et al. 2022). The progression of exotic grass invasion is likely much greater at CLNWR and MNF than other sites in California and Nevada. Other studies have found sage-grouse may be less tolerant of annual grass cover above thresholds of 5% (Coates et al. 2017), although this threshold may be much higher at a site with a high distribution and abundance of annual grasses, as was the case at CLNWR (Dudley et al. 2022). My results showed a direct and negative effect of medusahead and Japanese brome on daily nest survival that previous studies focused on fire have not observed (Lockyer et al. 2015, Coates et al. 2017, Dudley et al. 2022), likely because my field site was far above the threshold tolerance sage-grouse have for invasive annual grasses, so they can't avoid placing nests in areas with some annual grass component.

As a species with a life history pattern that includes longevity and relatively low annual productivity, adult survival can be the most important factor affecting population change in greater sage-grouse (Taylor et al. 2012, Dahlgren et al. 2016, Anthony et al. 2021). Therefore it

is noteworthy that I found adult female survival in Modoc County (0.290, 95% CI: 0.170 to 0.430) was much lower than range-wide estimates (Taylor et al. 2012) as well as the previous study on CLNWR (0.596, 95% CI: 0.483 to 0.699, Bell and George 2012). My estimates were similar to survival estimates for female grouse the first 2 years after a large (~187,000 ha) wildfire at a nearby site in eastern Oregon in 2012 (0.24, 95% CI: 0.09 – 0.39, Foster et al 2019, Anthony et al. 2021). I observed lower monthly adult survival during the nesting season in April (0.68, 95% CI: 0.54 to 0.80) compared to most of the rest of the year where monthly survival was above 0.9 (except October: 0.81, 95% CI: 0.59 to 0.93 and January: 0.81 (95% CI: 0.55 to 0.94). My estimate of monthly female survival during April was much lower than at other sites across the species range where spring monthly survival estimates range from 0.75 – 0.93 (Blomberg et al 2013, Baxter et al 2013, Severson et al 2019). Reduced adult monthly survival of sage-grouse in autumn and winter was reported in eastern Oregon due to low temperatures (< -15 °C) and mean snow accumulation of up to 7.8 cm (Anthony and Willis). In Oregon, survival was estimated as low as 0.674 (SE = 0.069) during early February and this low rate was observed 4-6 weeks after severe weather conditions (Anthony and Willis 2009). In Modoc County, precipitation in December and January averages 3.68 cm, however in 2019 precipitation in December was 5.5 cm, which might explain the reduced survival I observed in January. While fire is a concern for adult survival, one extreme weather event with above average snowfall or severe cold temperatures could also have detrimental effects on this small population (Anthony and Willis 2009).

For sage-grouse broods, the primary cause of chick death is exposure and predation (Dahlgren et al. 2010, Street et al. 2022), however at my field site it was depredation of adult females, which was only listed as a cause of brood failure one time by Dahlgren et al. (2010) for

radio-marked chicks. Females with broods that were not a part of the study were seen each year while traveling about the study area in late summer, and during trapping each winter we continued to find yearlings (8 yearlings : 17 adults). Thus, some production occurred on the study area, however sage-grouse often mix broods and adopt chicks from other females (Street et al 2022), so it is difficult to say how many adults contributed to the juveniles I observed or whether the chicks of depredated hens are adopted by nearby females. It is likely that the presence of Clear Lake Reservoir in the middle of the study site provides mesic habitat and associated food and cover for the current population of adults and chicks in the late summer (Dzialak et al. 2011, Donnelly et al 2018, Lundblad et al. 2022). However lack of overhead cover from sagebrush and other native shrubs may increase the risk of adult predation when with a brood.

While landscape level changes can have significant effects on sage-grouse survival, whether they be positive or negative, predators are the primary cause of sage-grouse mortality (Hagen 2011). Predators of sage-grouse were seen throughout the study area, but detection patterns varied between avian and mammalian species. Coyote detection probabilities peaked during late May through mid-June (weeks 21-26, Figure 8). While detection probability can be influenced by animal activity patterns, there are many other factors that could have influenced the observed patterns in detection probability including precipitation patterns, temperature, wind barometric pressure, etc. However, the timing of peak coyote detection probabilities overlapped with the presence of pups, and typically coyotes exhibit higher activity and increased home range size during pup-rearing (Shivik et al. 1997, Andelt and Gipson 1979). The peak of sage-grouse nest hatching and early brooding rearing for sage-grouse occurs in late May and early June, and is concurrent with increased activity periods for coyotes (Shivik et al. 1997, Figure 8). Sage

grouse broods are the most vulnerable in the first 21 days post-hatch after which survival begins to level off (Dahlgren et al. 2010b). The overlap of brood-rearing with peak coyote activity could explain this pattern in brood survival, and for CLNWR, offer a potential cause for why most broods failed due to adult predation. With the high coyote use rates observed on CLNWR and MNF, sage-grouse were likely to encounter coyotes frequently during nesting and brooding rearing periods. In addition, the reduced complexity in the vegetation community from disturbance combined with the flat topography likely allows scent to travel linearly across the landscape, aiding olfactory predators (e.g., coyote) in efficiently locating nesting females or their broods (Conover et al. 2010, Borgo and Conover 2016).

Ravens also pose the greatest risk to grouse during nesting season, as they are effective nest predators (Coates et al. 2008) and they were most abundant during my study in April and May. Ravens begin nesting by March and fledge their chicks by August (Smith and Murphy 1973, Kristan and Boarman 2007). Ravens activity is centered around nests during the breeding season, but home ranges can vary widely from 1.2 – 9.4 km² depending on the density of ravens and resources available (Linz et al 1992, Scarpignato 2013). Sage-grouse avoid areas where raptors and ravens occur (Conover et al. 2010, Dinkins et al. 2012, Dinkins et al. 2014), but nests were located near avian survey locations, in areas not treated for juniper, where pairs of ravens were frequently observed. Raven density on my study area (0.29 ravens/km², 95% CI = 0.19 - 0.44) was lower than the average reported across the Great Basin (0.54 ravens/km²; 95% CI: 0.42–0.70; Coates et al. 2020). However, based on my density estimates, there are approximately 175 individual ravens annually on CLNWR and MNF. While raven density may be less than the average density identified for the Great Basin, the effect of raven density is linear and negative (Coates et al. 2020). An increase in one raven per 10-km transect survey was associated with a

7.4% increase in the odds that a nest failed (Coates and Delehanty 2010). In addition, predation by ravens is more likely to be carried out by resident individuals (Bui et al 2010). Thus, density of ravens on CLNWR may be less important than the presence of fewer, nesting resident birds. Given the limited sage-grouse nesting habitat on CLNWR and MNF due to juniper encroachment and several wildfires, the observed raven density may be more detrimental to this small population of nesting sage-grouse than what might be expected given the estimated density of avian predators.

Hawks and eagles primarily prey on adult grouse and broods (Hartzler 1974, Conover et al. 2017) and the majority of female grouse in my study died during April and September-October, when females made movements of 2.5 – 13 km between their summer and winter ranges. This pattern is similar to other populations, although movement patterns vary widely between individuals (Connelly et al. 1988, Fedy et al. 2012, Dahlgren et al. 2016). However, the timing of these movements during my study overlapped with the timing of raptor migration (Goodrich and Smith 2008). In the Great Basin, raptor diversity and abundance are greatest September - October and March - April when birds are moving between breeding and wintering areas (Smith and Murphy 1973). Interestingly, I observed higher raptor density than sites used by sage-grouse in Wyoming (0.18 buteos/km², 95% CI: 0.14 to 0.23, Dinkins et al. 2012) and based on my density estimates, there were approximately 133 raptors each year on CLNWR and MNF in 2020 and 2021. Reduced sagebrush cover paired with juniper prevalence on the landscape, may have afforded more perching sites for migrant raptors on my study area, likely putting sage-grouse adults at a higher risk of predation.

Conclusion

CLNWR and MNF serves as important area for many migratory bird species in the Pacific Flyway as a stopover during migration and for some to breed. While Clear Lake Reservoir provides important mesic resources for sage-grouse, particularly in years of extreme drought, it does the same for nesting water birds, and likely increases use of the area by generalist predators who would normally be water-stressed in a high-desert environment. CLNWR and MNF may be a population sink due to high predator use or density and recent landscape level changes. Wildfires have reduced sagebrush cover important for nesting and concealment, and have increased invasive grasses, while juniper encroachment has increased the amount of perching and nesting structures for avian predators, making sage-grouse vulnerable to the diverse array of predators at all life stages. Coyotes use the entire study area, and ravens and raptors far outnumber grouse whose current population likely does not exceed 60 individuals (as indicated by current lek counts; J. Beckstrand, unpubl. data). Control of predators in the landscape is a challenging management dilemma, and active removal of coyotes has not been shown to be effective at increasing sage-grouse survival (Dinkins et al. 2016, Orning et al. 2017). Decreasing raven reproductive success through the oiling of eggs has been shown to effectively decrease raven densities (Brussee and Coates 2018, Sanchez 2022). However, as a protected species under the Migratory Bird Treaty Act, such management activities can only be implemented if raven populations were directly linked to strong, negative effects on sage grouse or waterfowl species around CLNWR. Further research to identify exactly which predator species are the primary cause of nest loss through additional camera surveys and scat analysis of mesocarnivores would be warranted. Due to the small population size of sage-grouse, thresholds for negative effects of predators may occur at lower densities than has been reported elsewhere

due to sage-grouse demographic stochasticity and isolation of this population, which might disrupt natural predator-prey dynamics (Simonis 2012).

The decline of the CLNWR sage-grouse population is likely to continue given the current rates of adult survival and nest success (Johnson and Braun 1999). Management focused on improving conditions during the most important life stages will be paramount to recovering and maintaining this population. Translocation was used in the past to supplement population size and was useful for providing a large influx of breeding individuals but would be required indefinitely to sustain the CLNWR population if resident birds cannot survive and reproduce within the current landscape. Translocation should only be utilized after significant improvements are made to the vegetation community, such that adult, nest, and brood survival are increased to levels that will sustain a population on CLNWR (Reese and Connelly 1997). Due to its location at relatively low elevations, current density and distribution of invasive annual grasses, and recent drought conditions, traditional management methods of prescribed fire would likely not be successful for managing invasive annuals or juniper at this field site. Instead, beneficial management activities to improve food and cover for sage-grouse might include: continued reduction of juniper encroachment on the study area (Frey et al. 2013, Bates et al. 2017, Severson et al. 2017, Olsen et al. 2021), prevention of wildfire that can increase the spread of invasive grasses (Omi 1979; Pellant 1994; Shinneman et al. 2019), decreasing the potential severity of fires that may occur by limiting fine fuels and reducing litter (Schmelzer et al. 2014, Perryman et al. 2020), and active restoration after wildfire through the planting of perennial species that can tolerate future drought conditions (Davies et al 2021). My project is a microcosm of what is occurring across the sage-grouse range in relation to fire, juniper, and invasive grasses and has shown that attention must be given to preventing the transition from

sagebrush communities into juniper woodlands or grasslands dominated by invasive annuals if this population and others in degraded landscapes are to persist.

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Table 1. Covariates with acronyms, measurement unit, measurement scale, and structural forms used to model daily nest survival of female sage-grouse on in Modoc County, California, 2019- 2021.

Covariate	Acronym	Description	Scale ^a	Form ^b	Predicted Relationship
Year (2019, 2020, 2021)	YR		NA	L	NA
Nest Type	FIRST	First nests	NA	L	+
Day	DAY	daily intervals	NA	L,PT, Q	+
Visual obstruction	VOR	Measure at nest bowl	Micro	L,PT	+
Shrub cover	SH.COV	% points hit live shrub	Micro	L	+
Dead shrub cover	DSH	% points hit dead shrub	Micro	L	-
Forb cover	FO.COV	% points hit forb	Micro	L	+
Perennial grass cover	PG.COV	% points hit perennial grass	Micro	L	+
Annual grass cover ^c	AG.COV	% points hit annual grass	Micro	L	-
Medusahead cover	MH.COV	% points hit Medusahead	Micro	L,PT,Q	$\beta_{MH.COV}>0,$ $\beta_{MH.COV}^2<0$
Cheatgrass cover	CG.COV	% points detection Cheatgrass	Micro	L	-
Japanese Brome cover	JB.COV	% points hit Japanese Brome	Micro	L	-
Wiregrass cover	WB.COV	% points hit Wire grass	Micro	L	-
Woody litter cover	WL	% points hit woody litter	Micro	L	+
Tree cover	TR.COV	% points hit trees	Micro	L	-
Litter cover	L	% points hit litter	Micro	L	-
Bare Ground	BARE	% points hit bare ground	Micro	L	-
Shrub height	SH.H	\bar{x} height in cm	Micro	L	+
Forb Height	FO.H	\bar{x} height in cm	Micro	L	+
Perennial grass height	PG.H	\bar{x} height in cm	Micro	L	+
Annual grass height	AG.H	\bar{x} height in cm	Micro	L	-
Litter depth	L.D	\bar{x} depth in cm	Micro	L	-
Annual Forb & Grass Cover	AN56	\bar{x} % cover at 56 m	Landscape	L	-
Shrub Cover	SH56	\bar{x} % cover at 56 m	Landscape	L	+
Tree cover	TR56	\bar{x} % cover at 56 m	Landscape	L	-

Annual Forb & Grass Cover	AN400	\bar{x} % cover at 400 m	Landscape	L,PT,Q	$\beta_{AN400}>0,$ $\beta_{AN400}^2<0$
Shrub Cover	SH400	\bar{x} % cover at 400 m	Landscape	L	+
Tree cover	TR400	\bar{x} % cover at 400 m	Landscape	L	-
Annual Forb & Grass Cover	AN800	\bar{x} % cover at 800 m	Landscape	L	-
Shrub cover	SH800	\bar{x} % cover at 800 m	Landscape	L	+
Tree cover	TR800	\bar{x} % cover at 800 m	Landscape	L	-
Juniper treatment	JUNIPER	Nests in boundaries	Landscape	L	+

^a Scale includes the microsite measured at the nest using vegetation surveys, and the landscape scale measured using 30m resolution GIS rasters from the Rangeland analysis platform, and averaging them across 56, 400, and 800m around each nest.

^bStructural forms included linear (L); pseudo-threshold (PT); and Quadratic (Q)

^cAnnual grasses that could not be identified to species, or were not cheatgrass, medusahead, Japanese brome, or *Ventanata dubia*.

Table 2. Number of first nests and renests, mean (\bar{x}) nest initiation date (standard deviations; SD) for both nest types and mean clutch size across all nests for female sage-grouse in Modoc County, California 2019 -2021.

	2019		2020		2021	
	<i>n</i>	\bar{x} (SD)	<i>n</i>	\bar{x} (SD)	<i>n</i>	\bar{x} (SD)
Initiation 1 st nest	10	1 May (8)	13	11 Apr (4)	10	21 Apr (5)
Initiation 2 st nest	3	15 May (7)	5	28 Apr (9)	3	n/a
Average clutch size	13	7.60 (0.5)	18	6.92 (1.9)	13	7.29 (1.5)

^aIn 2020 there was a 3rd nest attempt on 22 May not included in these totals.

Table 3. Model selection results for models within 5 AIC_c from the final multi-factor model set relating nest characteristics at the microsite and landscape levels to daily nest survival for female greater sage-grouse instrumented with GPS transmitters in Modoc County, California, during 2019-2021. Models were ranked according to Akaike's information criterion adjusted for small sample size (AIC_c). The difference in AIC_c between each model and the model with the lowest AIC_c (ΔAIC_c), Akaike model weights ($AIC_c w_i$), number of parameters (k), and model deviance are given for all models. The intercept-only model is included for comparison.

Model ^a	ΔAIC_c	w_i	k	Deviance
lnAN400+SH.COV	0.00	0.36	3	195.32
SH.COV	2.89	0.09	2	200.23
FIRST	2.92	0.08	2	200.26
MH.COV+SH.COV	3.37	0.07	3	198.69
PG.COV+SH.COV	3.90	0.05	3	199.22
PG.H+SH.COV	4.78	0.03	3	200.10
lnAN400	4.95	0.03	2	202.29
Intercept-only	8.41	0.01	1	207.76

^a Prefixes to nest characteristics: SH.COV = Shrub cover; AN400 = average Annual grass and forb cover at 400m around the nest; FIRST = first vs. second nest attempt; MH.COV = Medusahead cover; PG.COV = Perennial grass cover.

^b Lowest $AIC_c = 201.36$

Table 4. Model coefficients from the highest ranking known fate models relating the percent cover of invasive grasses such as Medusahead, Japanese brome, cheatgrass, and Wiregrass observed at 10-m around sage grouse nests to daily nest survival, 2019-2021.

Covariate	β	SE	LCI	UCI	ΔAIC_c
AG.COV	-5.40	3.71	-12.68	1.87	3.64
MH.COV	-2.80	1.14	-5.04	-0.56	2.35
JB.COV	-3.85	1.67	-7.13	-0.56	3.35
CG.COV	-0.70	1.24	-3.14	1.73	3.64
WG.COV	7.66	23.66	-38.70	54.03	3.64

Table 5. Model selection results for models within 5 AIC_c relating time and biotic characteristics to daily survival of nests belonging to female greater sage-grouse instrumented with GPS transmitters in Modoc County, California, during 2019-2021. Models were ranked according to Akaike's information criterion adjusted for small sample size (AIC_c). The difference in AIC_c between each model and the model with the lowest AIC_c (ΔAIC_c), Akaike model weights (w_i), number of parameters (k), and model deviance are given for all models. The intercept-only model is included for comparison.

Model ^a	ΔAIC_c	w_i	k	Deviance
FIRST	0.00	0.76	2	200.26
TT	4.33	0.08	3	202.56
T	5.42	0.05	2	205.68
Intercept	5.49	0.04	1	207.76
Year	6.39	0.03	3	204.63
lnT	7.06	0.02	2	207.32
DAY	31.04	0.00	29	174.26
Year+DAY	32.76	0.00	31	171.53

^a Prefixes to nest characteristics: FIRST = First nests; T = linear time trend across days within seasons; lnT = pseudo-threshold time trend across days within seasons; TT= quadratic time trend across days within seasons; YEAR = variation in daily nest survival rates by year (2019, 2020, 2021); DAY = general daily variation within season .

^b Lowest AIC_c = 204.28

Table 6. Mean percent cover (standard deviation; SD) categorized by vegetation type from line-point intercept transects centered over a sample of used female sage-grouse brood points (*n*) in Modoc County, California, during 2019-2021.

Vegetation Type	2019 (<i>n</i> = 12)	2020 (<i>n</i> = 47)	2021 (<i>n</i> = 39)
Shrub	17.5 (15.6)	25.8 (14.9)	7.4 (7.8)
Forb	17.1 (19.7)	9.7 (7.6)	11.8 (8.7)
Perennial Grass	50.2 (34.1)	24.8 (15.9)	10.3 (8.6)
Annual Grass ^a	0.83 (2.2)	2.8 (4.9)	NA
Medusahead	1.3 (4.3)	10.8 (12.8)	9.8 (11.0)
Cheatgrass	31.9 (27.1)	23.1 (19.0)	8.1 (6.3)
Japanese Brome	3.5 (12.3)	11.9 (17.7)	2.2 (4.9)
Wiregrass	0.62 (2.2)	1.9 (4.5)	1.0 (2.5)
Litter	68.1 (25.4)	60.7 (17.7)	30.9 (12.4)
Woody Litter	NA	3.1 (4.4)	0.26 (1.1)
Bare	15.0 (22.5)	9.6 (7.9)	5.6 (5.2)

Table 7. Model selection results from known fate models evaluating temporal patterns in monthly survival of female greater sage-grouse instrumented with GPS transmitters in Modoc County, California, during 2019-2021. Models were ranked according to Akaike's information criterion adjusted for small sample size (AIC_c). The difference in AIC_c between each model and the model with the lowest AIC_c (ΔAIC_c), Akaike model weights (w_i), number of parameters (k), and model deviance are given for all models. The intercept-only model is included for comparison.

Model ^a	ΔAIC_c	w_i	k	Deviance
Month	0.00	0.46	12	26.56
YEAR+Month	0.61	0.34	14	22.78
Yr19, Yr20=Yr21+Month	1.66	0.20	13	26.04
Yr19=20, Yr21	13.83	0.00	2	61.47
Yr19, Yr20=Yr21*Month	14.58	0.00	24	13.78
Intercept-only	14.92	0.00	1	64.58
YEAR	15.57	0.00	3	61.17
Yr19=Yr21, Yr20	15.70	0.00	2	63.34
YEAR*Season	16.10	0	6	55.49
Season	16.31	0	2	63.95
Yr19, Yr20=Yr21	16.56	0	2	64.20
YEAR+Season	17.29	0	4	60.83
YEAR*Month	30.72	0	36	0

^aMonth = general variation by month; YEAR = survival differed across all 3 years, 2019, 2020, and 2021; Yr19 = 2019; Yr20 = 2020; Yr21= 2021 to denote models that evaluated whether survival was the same for some years (“=”); Season = variation between months occurring in the breeding (March - August) vs. the non-breeding (September - February) seasons.

^bLowest AIC_c = 193.35

Table 8. Model selection results for temporal patterns in weekly detection and occupancy for Coyotes in Modoc County, California, during 2020-2021. Models were ranked according to Akaike's information criterion adjusted for small sample size (AIC_c). The difference in AIC_c between each model and the model with the lowest AIC_c (ΔAIC_c), Akaike model weights (w_i), number of parameters (k), and model deviance are given for all models. The intercept-only model is included for comparison.

Model ^a	ΔAIC_c	w_i	k	Deviance
p(TT) Psi(Intercept)	0	0.69	4	685.81
p(TT) Psi(Year)	1.62	0.31	5	685.28
p(Week) Psi(Intercept)	25.41	0.00	19	675.14
p(T) Psi(Intercept)	27.09	0.00	3	715.02
p(Week) Psi(Year)	27.62	0.00	20	674.61
p(Year+Week) Psi(Intercept)	28.15	0.00	20	675.13
p(T) Psi(Year)	28.41	0.00	4	714.22
Intercept-only	28.47	0.00	2	718.49
p(Year) Psi(Intercept)	30.16	0.00	3	718.09
p(year+Week) Psi(Year)	30.34	0.00	21	674.55
p(lnT) Psi(Intercept)	30.53	0.00	3	718.45
p(Year) Psi(Year)	31.60	0.00	4	717.41
p(Year*Week) Psi(Year)	58.30	0.00	35	657.94

^aWeek = general variation by week; Year = survival differed across all 3 years, 2019, 2020, and 2021; T = linear time trend across weeks within seasons; lnT = pseudo-threshold time trend across weeks within seasons; TT= quadratic time trend across days within seasons

^bLowest $AIC_c = 1830.56$

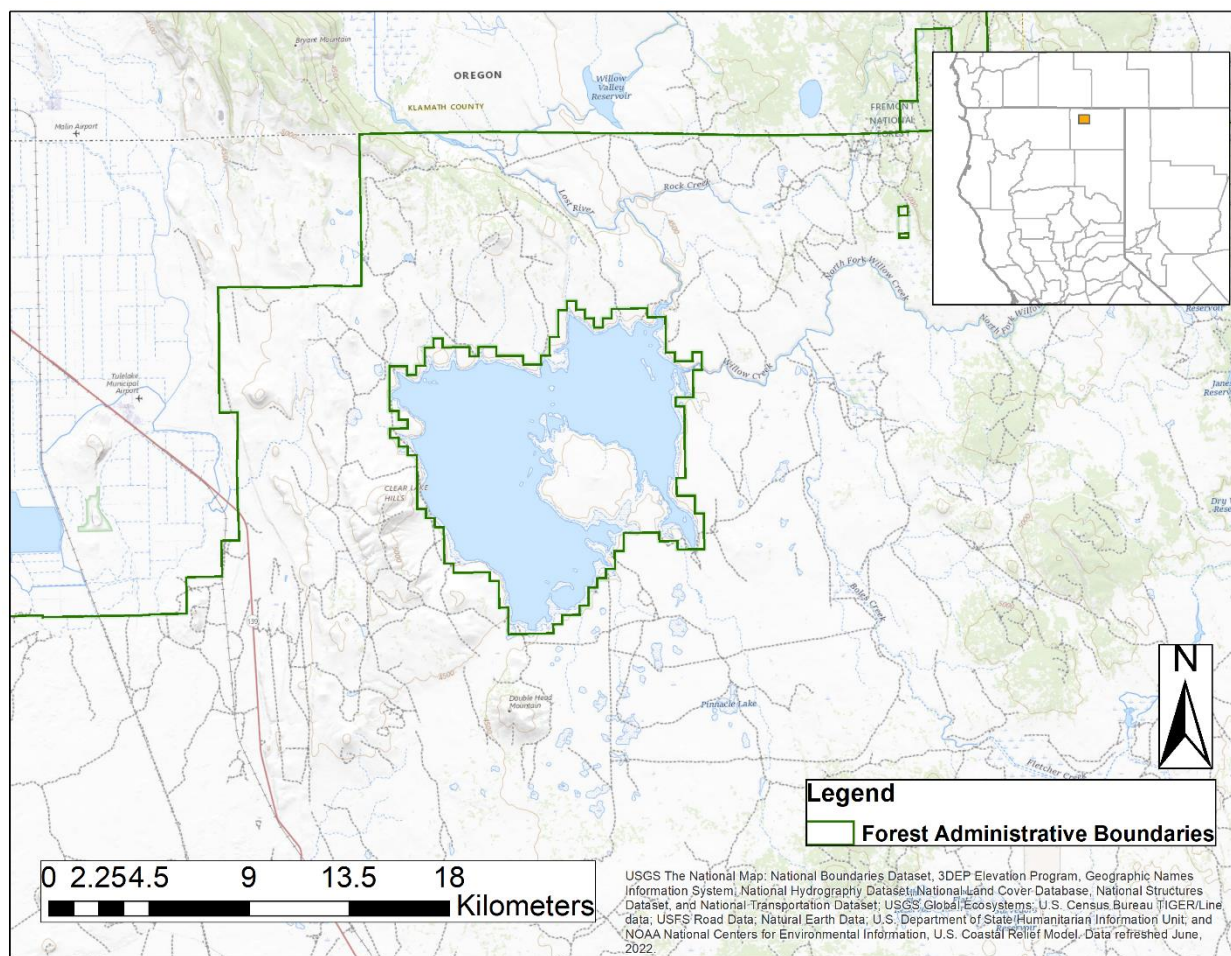


Figure 1. Study area (121,000 ha) of Clear Lake National Wildlife Refuge and surrounding Modoc National forest (green), where sage-grouse research was conducted in Modoc County, California, USA, 2019–2021.

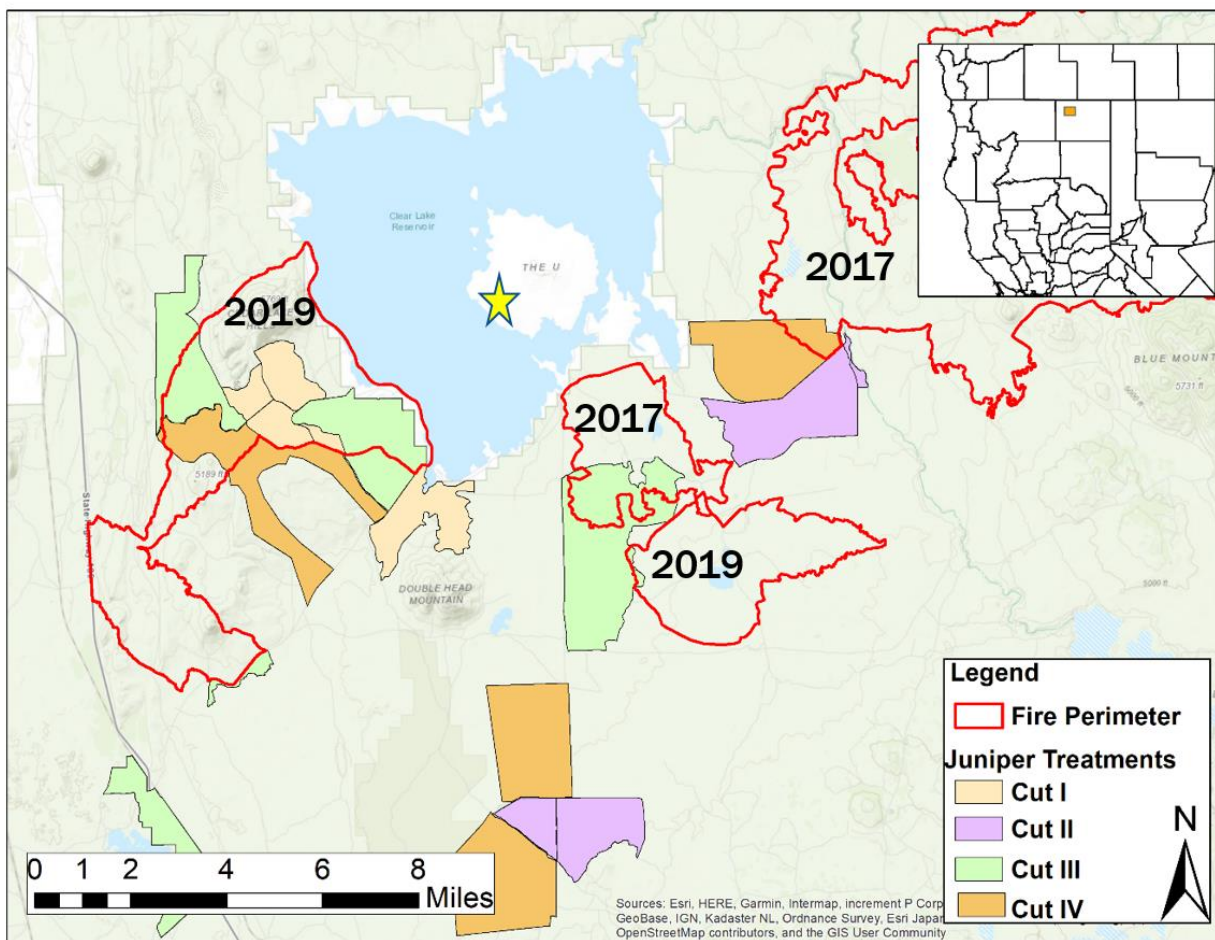


Figure 2. Study area (121,000 ha) map, depicting wildfire perimeters occurring from 2017 – 2020 are shown in red (30,000 ha), Juniper cuts from 2005 – 2019 (beige, purple, green, orange; 24,300 ha), and the last lek (yellow star) on Clear Lake National Wildlife Refuge, Modoc County, California, USA, 2019–2021.

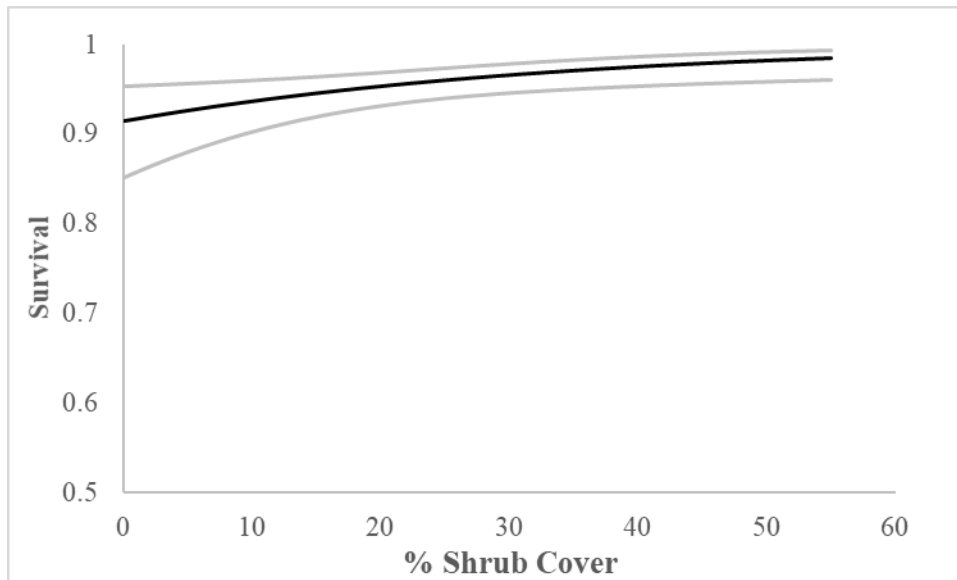


Figure 3. Estimates (solid black line) and 95% confidence limits (solid gray lines) of daily nest survival relative to mean percent shrub cover measured around nests of female sage-grouse in Modoc County California, 2019-2021.

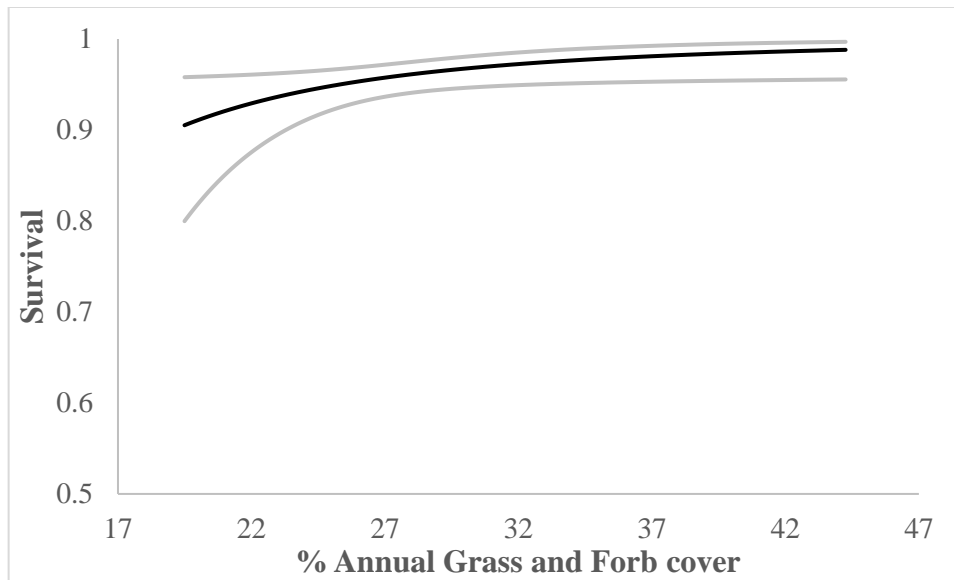


Figure 4. Estimates (solid black line) and 95% confidence limits (solid gray lines) of daily nest survival relative to the log of mean percent annual grass and forb cover averaged across a 400-m buffer around nests of female sage-grouse in Modoc County California, 2019-2021.

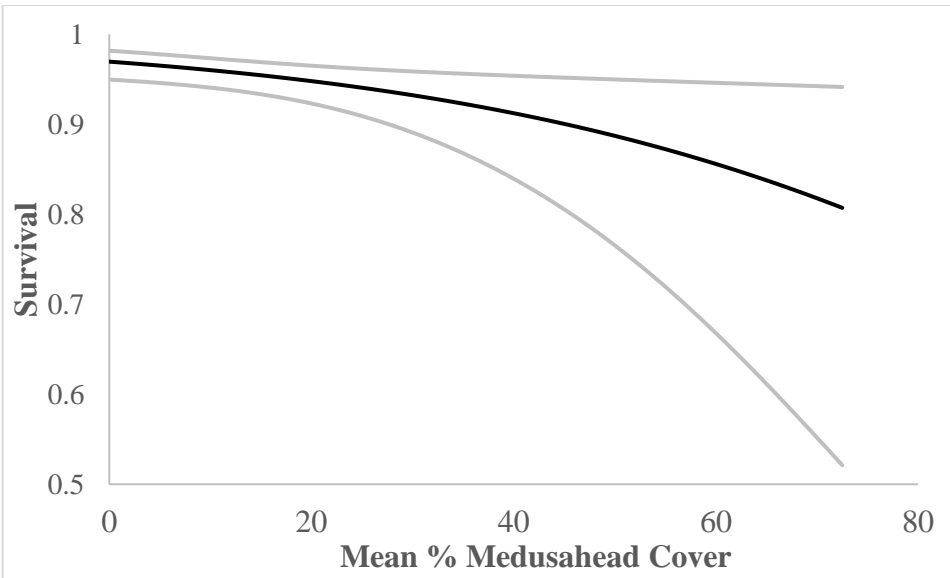


Figure 5. Estimates (solid black line) and 95% confidence limits (solid gray lines) of daily nest survival relative to mean percent medusahead cover measured around nests of female sage-grouse in Modoc County California, 2019-2021.

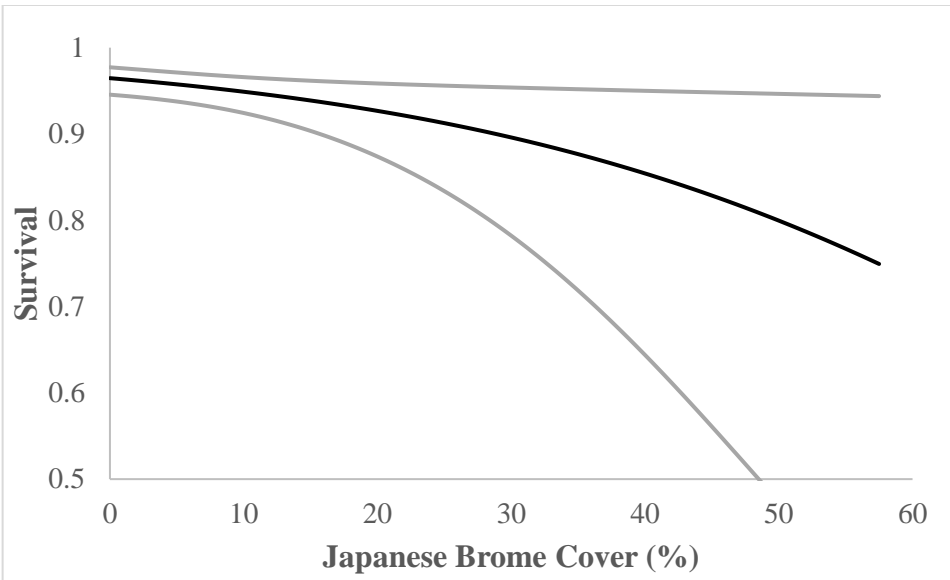


Figure 6. Estimates (solid black line) and 95% confidence limits (solid gray lines) of daily nest survival relative to mean percent Japanese Brome cover measured around nests of female sage-grouse in Modoc County California, 2019-2021.

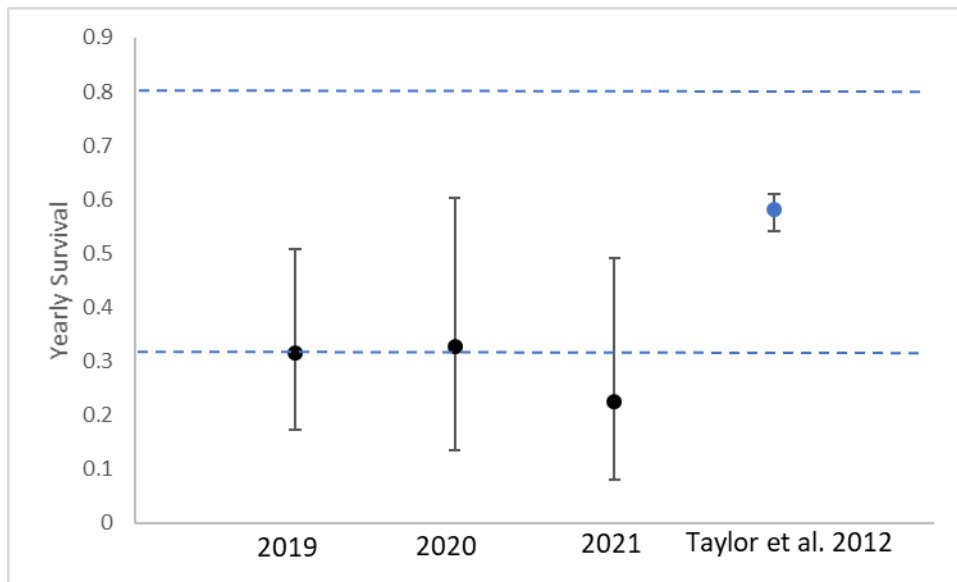


Figure 7. Model-averaged derived estimates of annual survival of female sage-grouse in Modoc County California, 2019-2021, compared to range-wide estimates of annual survival for female sage-grouse (Taylor et al. 2012, blue). The minimum and maximum of survival estimates from across the range of sage-grouse is represented by the dashed lines (blue).

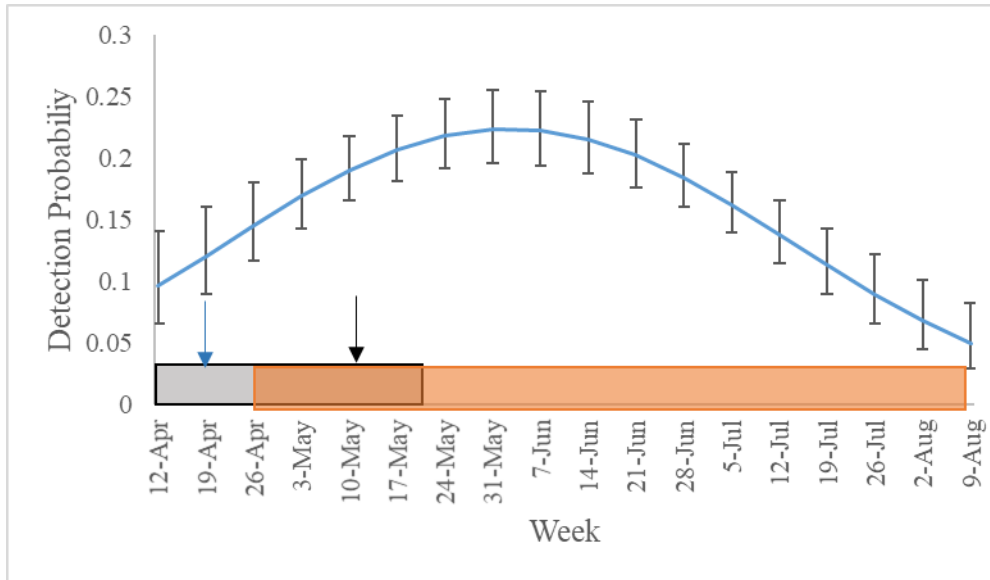


Figure 8. Weekly estimates of the probability of detection (\hat{p}) for coyotes starting in April 12th through August 15th, overlaid with sage-grouse nest incubation (gray) and brooding (orange) periods in Modoc County, California 2020 – 2021. Arrows represent peak nesting (blue) and hatch (black) periods.

APPENDICES

Table A1. Model selection results for models relating continuous nest characteristics at the microhabitat scale to daily survival of nests belonging to female greater sage-grouse instrumented with GPS transmitters in Modoc County, California, during 2019-2021. Models were ranked according to Akaike's information criterion adjusted for small sample size (AIC_c). The difference in AIC_c between each model and the model with the lowest AIC_c (ΔAIC_c), Akaike model weights (AIC_c Wts), number of parameters (k), and model deviance are given for all models. The intercept-only model is included for comparison.

Model	ΔAIC_c	w_i	k	Deviance
SH.COV	0.00	0.21	2	200.23
MH.COV+SH.COV	0.48	0.17	3	198.69
PG.COV+SH.COV	1.01	0.13	3	199.21
PG.H+SH.COV	1.89	0.08	3	200.10
MH.COV	2.35	0.07	2	202.58
lnVOR	2.71	0.06	2	202.93
JB.COV	3.35	0.04	2	203.58
MH.COV+MH.COV ²	3.39	0.02	3	201.60
AG.COV+CG.COV+JB.COV+WG.COV+MH.COV	3.64	0.04	6	195.74
VOR	3.73	0.03	2	203.96
lnMH.COV	4.14	0.03	2	204.37
Intercept	5.52	0.01	1	207.76

^aPrefixes to nest characteristics: SH.COV = Shrub cover; MH.COV = Medusahead cover; PG.COV = Perennial grass cover; VOR = Visual Obstruction; JB. COV = Japanese Brome Cover; AG.COV = Annual Grass Cover (not Cheatgrass, Medusahead, Japanese Brome, or Wiregrass); CG.COV = Cheatgrass; WG.COV = Wiregrass.

^bLowest AIC_c = 204.25

Table A2. Mean height (cm) with standard deviations (SD) of shrub, perennial grasses, forbs, annual grasses, and litter depth from line point intercept transects centered over female sage-grouse nests on Clear Lake National Wildlife Refuge in Modoc County, California 2019-2021.

Vegetation Type	2019	2020	2021
Shrub	23.0 (17.9)	57.4 (21.2)	54.0 (40.5)
Perennial Grass	41.2 (12.0)	41.2 (13.3)	24.7 (7.3)
Forb	16.6 (6.5)	18.0 (10.7)	18.29 (6.0)
Annual Grass	17.1 (7.0)	22.2 (5.1)	21.3 (7.5)
Litter Depth	0.9 (0.6)	1.0 (0.3)	0.7 (0.2)

Table A3. Mean percent cover and standard deviations (SD) of annual forbs and grasses, shrubs, and trees calculated from 30m resolution GIS rasters of vegetation cover, from the Rangeland Analysis Platform, in buffers of varying size (m; 50,400,800) around female sage-grouse nests on Clear Lake National Wildlife Refuge in Modoc County, California 2019-2021.

Buffer Distance	Cover Type		
	Annual Grass and Forbs	Shrubs %	Trees
56	26.56 (7.57)	12.16 (4.68)	0.33 (0.28)
400	27.70 (5.42)	11.49 (2.58)	0.44 (0.15)
800	28.27 (3.95)	10.31 (2.37)	0.47 (0.22)

Table A4. Mean percent cover and standard deviations (SD) categorized by vegetation type from line-point intercept transects centered over a sample of female sage-grouse nests (n) on Clear Lake National Wildlife Refuge in Modoc County, California, during 2019-2021.

	2019 ($n = 13$)	2020 ($n = 18$)	2021 ($n = 7$)
Vegetation Type			
Shrub	25.2 (18.7)	19.2 (9.7)	18.3 (11.4)
Forb	14.6 (7.6)	9.2 (8.2)	8.2 (4.9)
Perennial Grass	53.3 (30.6)	27.8 (20.9)	20.8 (14.2)
Annual Grass ^a	1.9 (2.7)	2.3 (5.4)	2.1 (5.7)
Litter	65.8 (19.8)	74.3(11.3)	66.7 (19.2)
Woody Litter	N/A	4.1 (5.4)	3.9 (6.3)
Bare	5.0 (6.5)	6.4 (5.8)	21.5 (12.6)
Medusahead	13.8 (22.1)	16.8 (21.3)	15.8 (20.8)
Cheatgrass	22.1 (23.4)	29.9 (12.6)	26.4 (15.7)
Japanese Brome	12.9 (19.4)	2.0 (6.8)	0.0 (0.0)
Wiregrass	0.0 (0.0)	0.4 (0.9)	0.1 (0.4)
Dead Shrub	N/A	1.1 (2.4)	1.9 (3.2)
Tree	N/A	0.6 (2.0)	0.8 (2.2)

^aAnnual grasses that could not be identified to species, or were not cheatgrass (*Bromus tectorum*), medusahead (*Taeniatherum caput-medusae*), Japanese brome (*Bromus japonicus*), or *Ventanata dubia*.

Table A5. Model selection results for models relating continuous and categorical nest characteristics at the landscape scale to daily survival of nests belonging to female greater sage-grouse instrumented with GPS transmitters in Modoc County, California, during 2019-2021. Models were ranked according to Akaike's information criterion adjusted for small sample size (AIC_c). The difference in AIC_c between each model and the model with the lowest AIC_c (ΔAIC_c), Akaike model weights (AIC_c Wts), number of parameters (k), and model deviance are given for all models. The intercept-only model is included for comparison.

Model	ΔAIC_c	w_i	k	Deviance
lnAN400	0.00	0.23	2	202.29
AN400	0.44	0.18	2	202.73
SH56*lnAN400	1.21	0.12	4	199.45
AN400+AN400 ²	1.46	0.11	3	201.73
TR56*lnAN400	2.28	0.07	4	200.52
JUNIPER	2.63	0.06	2	204.92
Intercept	3.46	0.04	1	207.76
AN800	3.90	0.03	2	206.18
SH56	4.53	0.02	2	206.81
TR56	4.96	0.01	2	207.25

^aPrefixes to nest characteristics: AN400 = average Annual grass and forb cover at 400m around the nest; SH56 = average shrub cover 56m around the nest; TR56 = average tree cover 56m around the nest; AN800 = average Annual grass and forb cover at 800m around the nest; JUNIPER = Nests located in in areas with juniper removal

^bLowest AIC_c = 206.31