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Research article

Living on the edge: identifying demographic bottlenecks in an isolated sage-grouse population

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The greater sage-grouse (*Centrocercus urophasianus*: hereafter sage-grouse) population in Modoc County California is geographically isolated and contains a single lek (from 56 leks in the 1940s), despite significant efforts to increase the population through translocations and habitat improvement. Repeated wildfire within the landscape has led to an increase in invasive annual grasses and a decrease in sagebrush (*Artemisia* sp.) cover in important nesting and brood-rearing habitat. We estimated survival for adult females, nests, and chicks and assessed biotic characteristics that may influence these survival estimates to identify factors that may be limiting population growth. We monitored 37 female sage-grouse marked with GPS PTTS, 39 nests, and 8 broods for 3 years (2019–2021). We measured vegetation characteristics for nests at the microsite and landscape scale to evaluate effects on daily nest survival (DNS). We used survival rates from all life stages to parameterize matrix models and estimate population growth rate. Mean nest success over 3 years was 29% (95% CI: 17.1–44.8) across a 29-day incubation period and DNS declined as the proportion of both medusahead *Taeniatherum caput-medusae* and Japanese brome *Bromus japonicus* around the nest increased. Across all three years, mean chick survival across a 54-day period was 44% (95% CI: 0.9–72.3) and mean annual survival for adult females was 29% (95% CI: 17.8–43.7). Our estimated vital rates were 45–55% lower than distribution-wide estimates and the projected population growth rate was strongly declining (0.411, 95% CI: 0.30–0.52). Our results suggested recent cover changes associated with wildfire on the study area may have had a detrimental effect on this population across all life stages, and if attention is not given to preventing the transition from sagebrush communities into invasive grasslands, this population and others in degraded landscapes may not persist.

Keywords: California, *Centrocercus urophasianus*, exotic grassland, greater sage-grouse, juniper encroachment, life history, USA, wildfire

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Introduction

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 communities have undergone extensive alteration and loss since the arrival of Europeans to western North America, with as little as 67% of the original ecosystem remaining (Noss et al. 1995, Bunting et al. 2002). Historically, sagebrush communities often occurred in large contiguous landscapes across the western United States and Canada; however, many of these sagebrush landscapes have been degraded, fragmented, or eliminated due to human disturbance and the invasive annual grass-fire cycle (D'Antonio and Vitousek 1992, Eiswerth et al. 2009, Knick and Connelly 2011, Leu and Hanser 2011). High severity fire kills nearly all sagebrush plants as they are unable to re-sprout from the roots once burned, and sagebrush communities can require > 50 years to show signs of recovery after a large fire depending on elevation and pre-disturbance sagebrush cover (Nelle et al. 2000, Baker 2006, Riginos et al. 2019). Significant threats to the western portion of this ecosystem in the Great Basin include large wildfires that are increasing due to continuous fuel beds created by invasive annual grasses, and expansion of western juniper (*Juniperus occidentalis*; hereafter juniper). Fire suppression, along with climatic changes that favored juniper growth (Fritts and Xiangdig 1986, Holmes et al. 1986), has allowed juniper to expand into open areas of core sagebrush habitat (Johnson and Miller 2006, Brooks et al. 2015). Alternatively, a variety of non-native annual grasses (e.g. cheatgrass *Bromus tectorum*, medusahead rye *Taeniatherum caput-medusae* [hereafter medusahead]) that outcompete native plants for resources after a disturbance and increase the likelihood of future fires have invaded and degraded sagebrush ecosystems (Melgoza et al. 1990, Young 1992, Davies and Svejcar 2008).

These landscape-level changes have had negative effects on the sagebrush ecosystem and 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 spring (Braun et al. 2005, Connelly et al. 2011). Invasive annual grasses have been found to negatively affect sage-grouse vital rates (Coates et al. 2016, Foster et al. 2019, Anthony et al. 2022), population dynamics, 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). Expansion of juniper results in reduced available habitat for sage-grouse and may affect their vital rates (Severson et al. 2017, Olsen et al. 2021). This can occur when tree cover exceeds 4% of the landscape (Baruch-Mordo et al. 2013, Coates et al. 2017, Severson et al. 2017, Olsen et al. 2021).

Habitat fragmentation from changes in land-use has isolated populations of sage-grouse on the peripheries of their distribution (Wisdom et al. 2011). 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 demographic stochasticity (Gabriel and Bürger 1992, Garton et al. 2011). For the aforementioned reasons, populations in the periphery of a species distribution typically experience high temporal variation in vital rates and 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 distribution 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 cropland than currently occupied sites (Wisdom et al. 2011).

In the Great Basin, the Clear Lake sage-grouse population is geographically isolated from other nearby populations in south central Oregon, north-eastern California, and north-western Nevada (Fig. 1). Clear Lake National Wildlife Refuge (CLNWR) is at the western edge of the historical distribution of sage-grouse, and the population has been identified as sharing many landscape-level characteristics with extirpated populations (Wisdom et al. 2011). From 1970 to 1990, the population went through a severe bottleneck and the number of leks was reduced from 56 to 1, located on CLNWR, with only five males attending this lek by 2005. At that time, the US Fish and Wildlife Service (USFWS) began translocating grouse from both Oregon and Nevada to augment the population on CLNWR. Annual survival for both translocated and resident adult females during 2005–2010 was similar (Bell and George 2012) and within the range of estimates reported for other populations (Taylor et al. 2012). Nest survival estimates on CLNWR during this time were also within the range of estimates from stable populations across the species distribution (Bell and George 2012), suggesting translocated females were surviving and successfully rearing young. Despite favorable vital rates observed for translocated and resident birds in 2011 (Bell and George 2012), followed by the completion of two juniper removal projects to increase habitat quality (7572 ha), the CLNWR sage-grouse population has yet to form additional leks or expand their seasonal distributions. In fact, after translocating 113 females and 65 males from 2005 to 2019, lek counts have fallen to 13 males attending the single remaining lek in 2023 (Fig. 2).

During a 2019 pilot study (Sink 2023), 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 annual grasses are only briefly mentioned by Bell (2011). Since 2011, several large wildfires (29 946 ha total) have burned ~ 5665 ha of sage-grouse nesting in brooding habitat (Fig. 1). The pattern observed in 2019 suggested that the extent of invasive annual grasses on CLNWR and Modoc

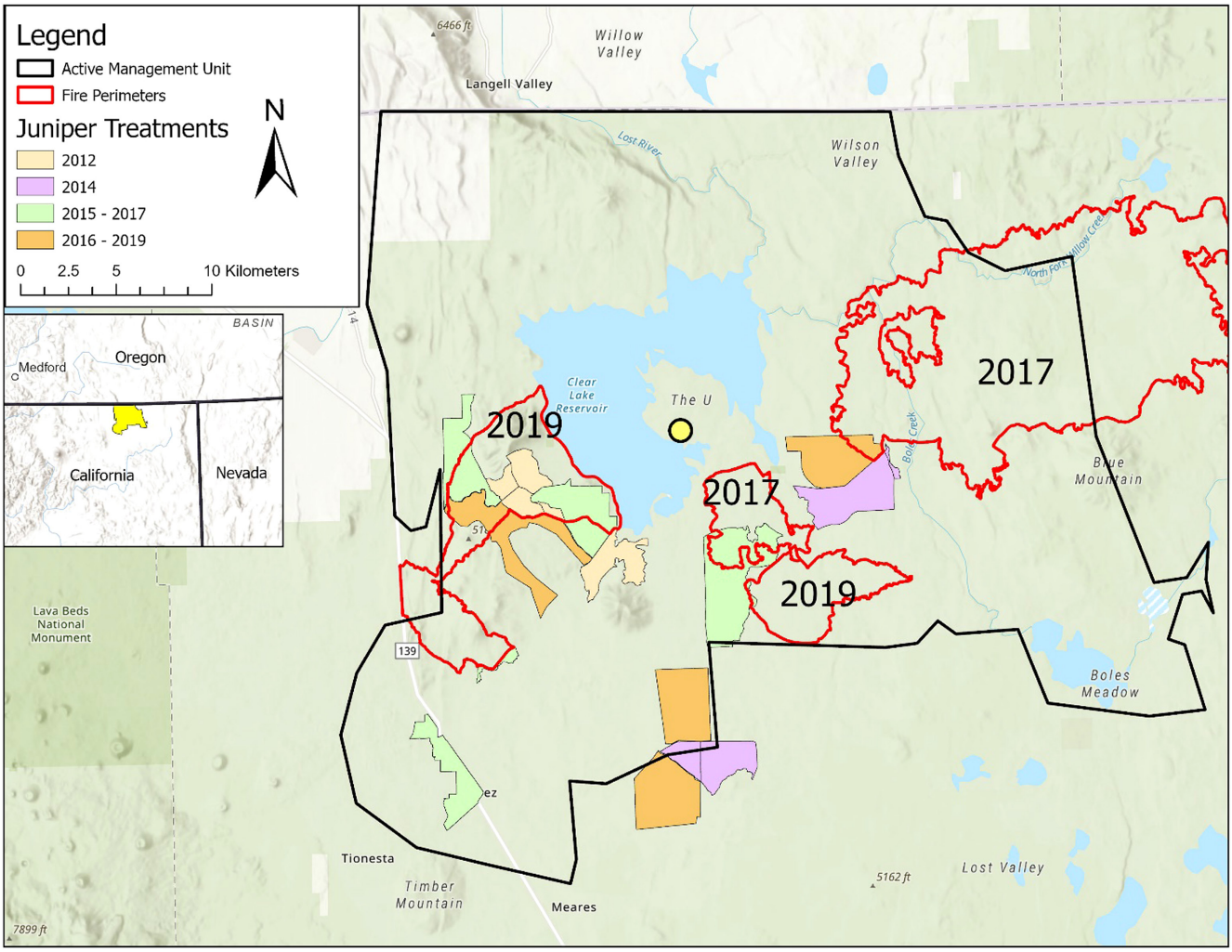


Figure 1. Study area (121 000 ha, active management unit) map, depicting wildfire perimeters occurring from 2017 to 2019 shown in red (30 000 ha), juniper cuts from 2012 to 2019 (beige, purple, green, orange; 24 300 ha), and the last lek (yellow circle) on Clear Lake National Wildlife Refuge, Modoc County, California, USA, 2019–2021.

National Forest (MNF) has increased significantly from what was previously recorded (Horney, unpubl., Bell 2011) and is reflected in remotely sensed data of vegetation cover (Fig. 3, rangeland analysis platform). These landscape-level changes could greatly impact the sage-grouse population, and updated estimates of resident sage-grouse vital rates are needed. In addition, vegetation characteristics of brood habitats are currently lacking on CLNWR. Finally, a general understanding as to how the population vital rates have responded to juniper removal, loss of sagebrush due to repeated wildfire, and increases in invasive grasses is important for directing future management activities on CLNWR and other similarly affected populations.

To address some of the questions needed to effectively manage an isolated sage-grouse population at the edge of the species' distribution, our goal was to identify potential population bottlenecks that may be limiting population growth. Our specific objectives were 1) to estimate demographic rates including daily nest survival, chick survival, and adult survival for resident and translocated sage-grouse on CLNWR and MNF, 2) determine associations between these vital rates and microsite and landscape characteristics, and 3) estimate the rate of population growth (λ) using demographic rates estimated for this population.

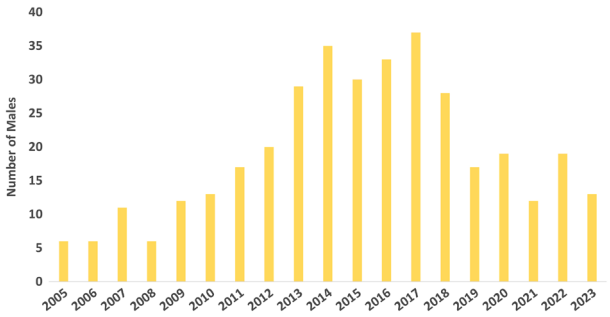


Figure 2. Peak count of male sage-grouse *Centrocercus urophasianus* attendance at the only know lek (breeding ground) in Modoc County, California, 2005–2023.

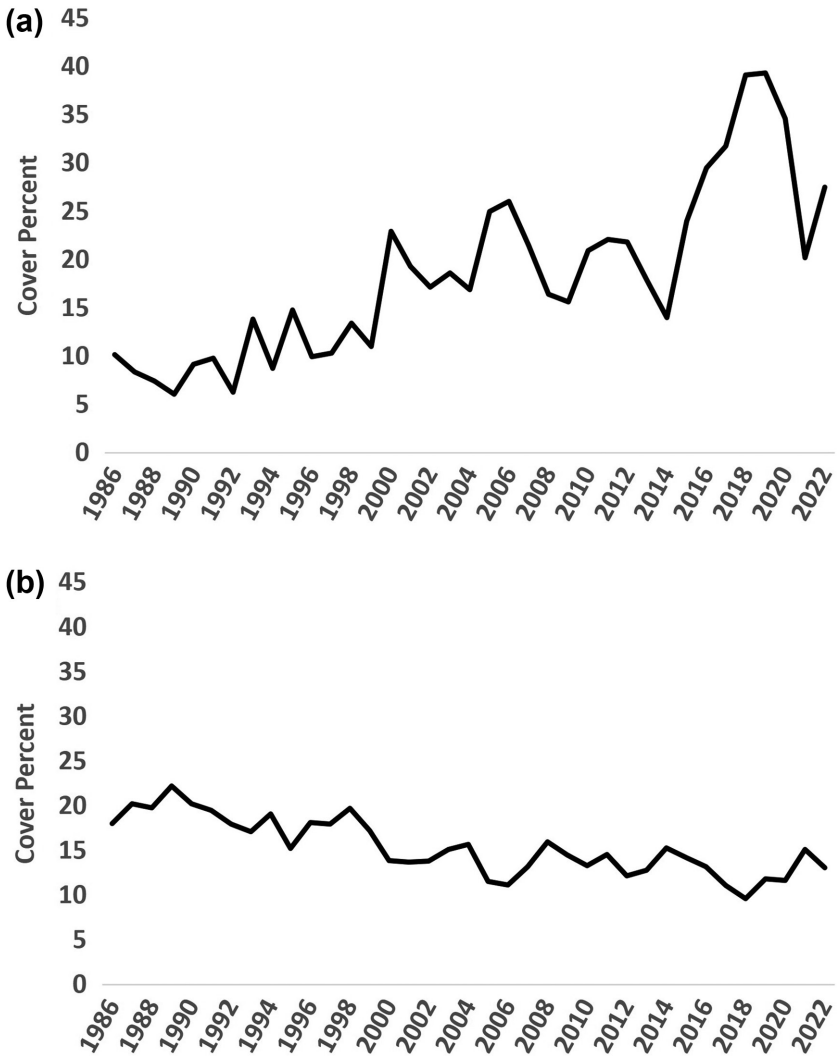


Figure 3. Percent cover of (a) annual forbs and grass and (b) shrub canopy within the AMU (active management unit) for sage-grouse *Centrocercus urophasianus* from 1986 to 2022 in Modoc County, California. Data were obtained from the rangeland analysis platform (https://rangelands.app/).

Material and methods

Study area

Most of the management and research efforts for the Klamath OR-CA population were focused on CLNWR and MNF, known as the active management unit (AMU; 121 000 ha, Fig. 1). Elevation in the AMU ranged from 1200 to 1430 m. The dominant vegetation consisted 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) were also prevalent.

Recent landscape-level changes have drastically altered sage-grouse habitat within the AMU. The US Forest Service (USFS) has been completing juniper removal in areas identified as breeding and wintering locations used by sage-grouse since 2010. Juniper removal has been completed in four stages, creating a patchwork of treatments ranging in age from 1 to 15 years (Fig. 1). In addition, fire has affected 9% of the AMU. In 2001, most of the Clear Lake 'U' (i.e. a ~ 1600 ha peninsula of sage-grouse habitat) burned, and 1817 ha just south of the Clear Lake 'U' burned in 2017 (the Lake Fire). According to remotely sensed data, both the 2001 and 2017 fires have led to a reduction in shrub cover and an increase in invasive annual grasses (Fig. 3, rangeland analysis platform). On 28 July 2019, a human-caused wildfire (the Tucker Fire) burned 5753 ha of MNF and CLNWR between Highway 139 and the shore of Clear Lake Reservoir (Fig. 1). The fire boundary for the Tucker Fire contained summer and brood-rearing habitat for sage-grouse. Additionally, two months later a wildfire (the Lone Fire) began after a tree was struck by lightning, burning 2321 ha directly south of the Lake Fire boundary. Average temperature across the 5-month sage-grouse breeding season (April–August) in Modoc County

during 2019–2021 ranged from lows of −0.6 to 8.9°C and highs of 15.6–30.6°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). Our study began at the beginning of this typical 5–6-year weather cycle, as the first year of our study in 2019 had an increased monthly average of precipitation in the winter and spring (January–May, 29.52 mm), followed by two years of reduced average monthly precipitation in 2020 and 2021 during the same period (14.17, 8.38 mm).

Adult capture and monitoring

We 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, we captured females on or near leks in Nevada and translocated them to CLNWR. We also captured resident females on CLNWR and MNF, and both resident and translocated birds received GPS transmitters and were released onto the lek at CLNWR during February–March 2019. In 2020 and 2021, we only captured and instrumented CLNWR resident females (i.e. no birds were translocated). We aged individuals based on body mass and wing characteristics (Braun and Schroeder 2015) and attached 22-g ARGOS/GPS Solar PTTs with 3 g Holohil PD-2 VHF transmitters using a rump-mount technique (Rappole and Tipton 1991). We captured and handled all birds 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. We monitored birds fitted with transmitters remotely by downloading GPS locations from the ARGOS satellite system (GeoTrak, Inc., Apex, NC, USA). Transmitters collected five locations per day, and we downloaded locations every three days. If we observed more than four consecutive GPS locations in the same place, or the transmitter stopped downloading locations, we visited the last known location to determine the status of the bird.

Nest monitoring

We monitored each nest to determine its fate 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), we used GPS and VHF ground tracking to locate and visually confirm a female was incubating a nest. We examined GPS locations daily to identify nest failures and additional potential nest attempts. If a female was absent from the nest for more than two consecutive GPS locations, we inspected the nest to determine nest fate. We 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, we used patterns in GPS locations to identify the date the nest was first incubated and the nest success/failure date.

Weekly brood survival

We estimated brood survival over 10-day intervals using spotlight counts at 14, 24, 34, 44, and 54 days post-hatch. Two observers located and approached broods using a combination of telemetry and a spotlight between the hours of 22:00 and 04:00. When the observers were close enough to see individual sage-grouse they used binoculars to count the chicks within the spotlight area without flushing them (Dahlgren et al. 2010a, 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. 2010a, b).

Microsite vegetation sampling

We sampled vegetation at nests and GPS-PTT locations of females with broods. We conducted vegetation surveys at each sage-grouse nest location within three days of predicted hatch, regardless of ultimate nest fate, to avoid bias in vegetation height measurements between failed and successful nests, and to account for correlation in herbaceous vegetation growth throughout incubation (Gibson et al. 2016). We centered two, 10-m transects oriented perpendicular from north to south, and east to west on each nest (Popham and Guierrez 2003, Doherty et al. 2010). We 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). We 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). We measured visual obstruction (VOR; percent obstruction in decimeters) in each cardinal direction using a modified cover board that we viewed from 7 m away and 1 m from the ground (Guthery et al. 1981). We 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).

We sampled vegetation at GPS-PTT point locations used by females with broods from each 7-day period after hatch date until the brood was ~ 54 days old or the brood failed. We randomly assigned numbers to brood locations from each period, and chose locations that had been assigned numbers 1, 2, or 3 for vegetation surveys. We centered a single 30-m transect 10-m west of the GPS point and oriented N to S to account for GPS location error. We measured vegetation functional groups, heights, and VOR in the same manner as nests (Supporting information).

Estimating demographic rates

Daily nest survival

We estimated daily nest survival during incubation of sage-grouse using known fate models in Program MARK (White

and Burnham 1999) because the exact dates of the onset of incubation and nest fate were known from the GPS location data. We estimated daily nest survival (DNS) for a 29-day incubation period, reflecting the longest incubation period across the three field seasons and assumed, therefore, that daily survival during egg-laying was 1.0. Year was treated as a group effect so general time effects (day) reflected a standardized day within the 29-day incubation period, rather than date within specific nesting seasons. We investigated the relationship between DNS and a variety of covariates, including characteristics of nesting cover and temporal patterns (within season and between years; Table 1). We did not explore the effect of female age as a covariate due to the limited captures of yearlings in 2020 and 2021 (Table 2). We evaluated whether DNS varied among years (2019–2021; 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). Vegetation covariates (Table 1) were developed from nest site vegetation sampling at the microsite scale, or remotely sensed data at the landscape scale. We used remotely sensed 30-m^2 annual rangeland fractional plant cover from the rangeland analysis platform (RAP, https://rangelands.app/; Jones et al. 2018, Allred et al. 2021) to characterize the predominant vegetation around each nest: percentage of shrub, annual grasses and forbs, and trees at three circular buffers with radii of 56, 400, and 800 m (Table 1, Severson et al. 2017, Olsen et al. 2021). Each 30 × 30 m resolution pixel represents the percentage of each variable and is measured once every year at the end of the growing season (Jones et al. 2018, Allred et al. 2021). In addition to evaluating linear relationships between DNS and the four invasive grass species present on the study site (medusahead, cheatgrass, Japanese brome, and wiregrass)

Table 1. Covariates with acronyms, measurement unit, measurement scale, and structural forms used to model daily nest survival of female sage-grouse *Centrocercus urophasianus* (n = 38) 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 wiregrass	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 and 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 and 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 and 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 30 m resolution GIS rasters from the rangeland analysis platform (https:// rangelands.app/), and averaging them across 56, 400, and 800 m around each nest.
[b]Structural forms included linear (L); pseudo-threshold (PT); and Quadratic (Q).
[c]Annual grasses that could not be identified to species, or were not cheatgrass, medusahead, Japanese brome, or *Ventanata dubia*.

Table 2. Summary statistics for yearling and adult (after second year) female sage-grouse (n = 37) *Centrocercus urophasianus*, nests (n = 38), and broods (n = 10) monitored in Modoc County, California during 2019–2021.

	2019	2020	2021
Females captured	25	4	7
Translocated	18	N/A	N/A
Resident	7	4	7
Yearling	11	0	4
Adult	14	4	3
Total females monitored (April–July)	26	13	13
Yearling	11	N/A	4
Adult	15	13	9
Females monitored through nesting[a]	21	13	8
Translocated	13	N/A	N/A
Resident	8	13	8
Yearling	10	N/A	3
Adult	11	13	5
Nesting females	10	13	7
Translocated	5	N/A	N/A
Resident	5	13	7
Yearling	4	N/A	2
Adult	6	13	5
Nests monitored	13	18	7
1st nests	10	13	7
2nd nests	3	4	0
3rd nests	0	1	0
Successful nests/broods monitored	2	5	3
Successful broods at 54 days	1	1	1

[a]Number of females with active GPS transmitters at time of first nest.

at the microsite scale, and annual forbs and grass at the landscape scale, we also evaluated pseudo-threshold and quadratic structures of each covariate, as we hypothesized that annual grasses may be associated with non-linear increases or decreases in DNS. For example, we hypothesized that invasive annuals could have a negative linear effect on survival, with survival declining for every unit increase in invasive annuals; or, conversely, invasive annuals may provide some benefit as cover up to a certain proportion of the microsite, at which point DNS then leveled off (i.e. pseudo-threshold) or even declined (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, we predicted nest sites with less shrub cover, lower visual obstruction, or high tree cover would be more susceptible to predation and have lower daily nest survival rates.

We 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). We started by creating single-factor models within three different categories resulting in three 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. We then combined covariates that received the most support from each of the covariate categories into a final, multi-factor model set. 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 carried covariates forward from the microsite and landscape category model sets and drew inferences from models in the final model set ranked within five AIC_c. We used an AIC_c cut-off of five to draw inference because we had small sample sizes and did not want to discount models and associated covariates that may still be informative (Richards 2005). We also included a few multi-factor models in our 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 sagebrush 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, we 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

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

Adult survival

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

Population matrix model

We used methods developed by Caswell (2001) to create an annual, 2-age, female stochastic population matrix models for yearlings and adults using vital rates estimated for each

age class to estimate λ. Nest initiation is typically reported as the proportion of females that began incubating a nest; however, these estimates may not accurately reflect nesting efforts, as females that failed to begin incubation may have attempted a nest but lost it prior to the onset of incubation, and nests lost during egg-laying are difficult to identify using GPS data (Blomberg et al. 2015, Weiser 2021). To highlight this potential bias in reported vital rates, we hereafter refer to nest initiation rates as nest incubation rates (NI). We estimated mean age-specific NI for first nests (across all three years) as the number of females that began incubating, divided by the number of females that were monitored and alive through the first nesting period (i.e. last individual to begin incubation for first nests). Sample sizes for re-nests by age class were small each year, so we pooled yearlings and adults and estimated annual nest incubation rate as the proportion of all females that were monitored through the second nesting period (i.e. last individual to begin incubation for re-nests) and began incubating a second nest, given the first nest failed. Therefore, we had a single annual re-nesting rate that was used to reflect re-nesting of both age classes. We estimated SEs for nest incubation rate based on the variance of the sample proportion ($\sigma^2 = pq/n$), where p = number of females that incubated a nest, q = 1–p, and n = number of females that were monitored through the entire nesting period.

We estimated age-specific mean annual clutch size (CS) for first nests as the total number of eggs counted after the nest was terminated or during nesting if the female was flushed during monitoring, divided by the number of total nests for yearlings and adults. For CS estimates of re-nests, we used results from a meta-analysis of CSs across the distribution of sage-grouse (Taylor et al. 2012) that reported the mean difference between mean CS for first nests and re-nests (1.39 eggs for yearlings; 1.63 eggs for adults). Therefore, to estimate CS for re-nests we subtracted 1.39 eggs (yearlings) and 1.63 eggs (adults) from mean annual clutch size estimates of first nests (Anthony et al. 2022).

We estimated egg hatching success rate (i.e. hatchability; H) for all years as the total number of eggs hatched divided by the number of total eggs laid for all nests that were successful. We estimated SEs for hatchability based on the variance of the sample proportion.

We did not have data on the survival of juveniles (54-days post hatch to first breeding; ~ April); therefore, we derived estimates of juvenile survival (S_{juv}) from annual adult survival estimates. We used an adjustment rate based on Apa et al. (2017) who examined juvenile survival (0.53) relative to adult survival (0.83) for 183 individuals over 7 months in Colorado from 2005 to 2008. Therefore, we scaled adult survival from our study area to a 7-month time period comparable to the juvenile survival period by raising annual adult survival to the 0.58th power (7/12 = 0.58). Then, we multiplied the scaled 7-month adult survival by 0.64 (0.53/0.83). We calculated SE for juvenile survival following Apa et al. (2017).

We constructed annual 2 × 2 population matrix models using the pre-birth-pulse format, because we began monitoring annual female survival in March of each year, and we included fecundity (F) and survival (S) for both yearlings (SY) and adults (ASY; Caswell 2001); however, these age classes were set as equal in our model due to small sample sizes and our inability to estimate age-specific fecundity or survival:

$$A = \begin{bmatrix} F_{SY}S_{juv} & F_{ASY}S_{juv} \\ S_{SY} & S_{ASY} \end{bmatrix}$$

We developed age-specific fecundity (F) estimates using the following equation:

$$F_j = [\{(NI_1 \times CS_1 \times NS_1) + \left((1 - NS_1) \times NI_2 \times CS_2 \times NS_2\right)\} \times H] \times \left(0.5 \times S_{chick}\right)$$

where subscript j represents age class, subscripts 1 and 2 indicate first nests and re-nests, respectively, and 0.5 = portion of offspring that are female (Atamian and Sedinger 2010).

We parameterized annual matrices with bootstrapped estimates of fecundity and annual survival by resampling lower-level vital rates 10 000 times from beta distributions for probabilities (e.g. nest survival) and normal distributions for clutch size. We estimated λ and 95% confidence intervals (CIs) by taking 10 000 replicates from parameterized matrices (Meyer et al. 1986). We used bootstrap estimates of λ and 95% CIs to assess whether the population was increasing ($\lambda \geq 1.0$), stable ($\lambda = 1.0$), or decreasing ($\lambda \leq 1.0$) annually. We performed all analyses in program R ver. 4.2.1 (www.r-project.org).

Sensitivity analysis

Sensitivity and elasticity estimates were calculated with the *vitalsens* function in the 'popbio' package in R, which calculates sensitivities and elasticities of λ to lower-level vital rates (Stubben and Milligan 2007). All parameters were set at mean values for these analyses.

Identifying vital rates necessary to achieve population stability

We also conducted a post hoc analysis to calculate the minimum value of each vital rate needed to reach a stable level of population growth ($\lambda = 1.0$) to help inform future management decisions regarding this population. We re-ran the original analysis using the distribution-wide estimates of adult survival and survival of first nests (and associated SEs) from Taylor et al. (2012). We chose to adjust both adult survival and survival of first nests, because both these vital rates were well below distribution-wide averages in our study (Taylor et al. 2012), and both can have impacts on population trajectories of sage-grouse (Taylor et al. 2012, Dahlgren et al. 2016, Anthony et al 2022). We retained our estimate of chick survival as it was higher than distribution-wide estimates

(Taylor et al. 2012). This initial vital rate adjustment did not predict a stable population, so we then calculated lambda four more times, and for each subsequent calculation we increased survival by 0.05. After our initial adjustment of both nest success and adult survival did not result in estimates of $\hat{\lambda} \approx 1.0$, we focused on increasing adult survival because that is the vital rate that has the greatest potential to influence λ in sage-grouse (Dahlgren et al. 2016, Anthony et al. 2022). Juvenile survival was scaled to match adult survival using the adjustment rate based on Apa et al. (2017), and similar to the original analysis we set yearling survival and associated vital rates equal to adults.

Results

Nesting ecology

From 2019 to 2021, we caught 37 females and fit them with satellite GPS transmitters (Table 2). Of these females, 1 was translocated in 2018 (and considered a resident in 2019), 18 were translocated from Nevada in 2019, and 18 were captured on Clear Lake NWR. Female age was determined at capture, with 15 captured as yearlings and 22 captured after their second year (hereafter 'adults'). In 2019, mean incubation initiation rate was 47% for 21 females alive when incubation was initiated for the first nest, as only five resident and five translocated females initiated nests, and 13 translocated females either did not attempt to nest (n = 8) or were predated (n = 5) before nesting season began. Thus, breeding propensity for translocated females was substantially lower than it was for residents in 2019. Of the 13 yearlings alive during nesting, six initiated nests, while 24 adult females initiated nests, making breeding propensity higher for adults compared to yearlings (0.82, 0.46, Table 2). In 2020, mean incubation rate was 100%, and in 2021 only one female did not attempt a nest (Table 2). Nest incubation dates for first nests ranged from 11 April to 1 May, with the earliest incubation initiation date occurring in 2020. Thirty percent of females available to re-nest attempted to re-nest 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 two 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 she abandoned it when her nest was partially depredated, and after candling the remaining eggs we determined they were not fertilized and only filled with yolk.

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). We 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:0.76–5.65; $\hat{\beta} = 2.64$; 95% CI:0.14–5.13, Fig. 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 annual forb and grass cover (Fig. 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 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, Fig. 4). Average cover of medusahead and Japanese brome around nests across all three years was 15% (SD = 20%) and 5% (SD = 13%), respectively. Cheatgrass was the most abundant invasive annual grass species around nests, with an average cover of 24% (SD = 18%). In addition to invasive annuals, litter cover around nests was high, and averaged 68% (SD =13).

Table 3. Model selection results for models within five AIC_c from the final multi-factor model set relating nest characteristics at the microsite and landscape levels to daily nest survival (n = 38) for female greater sage-grouse *Centrocercus urophasianus* 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[b]	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 400 m around the nest; FIRST = first versus second nest attempt; MH.COV = medusahead cover; PG.COV = perennial grass cover.
[b]Lowest AIC_c = 201.36.

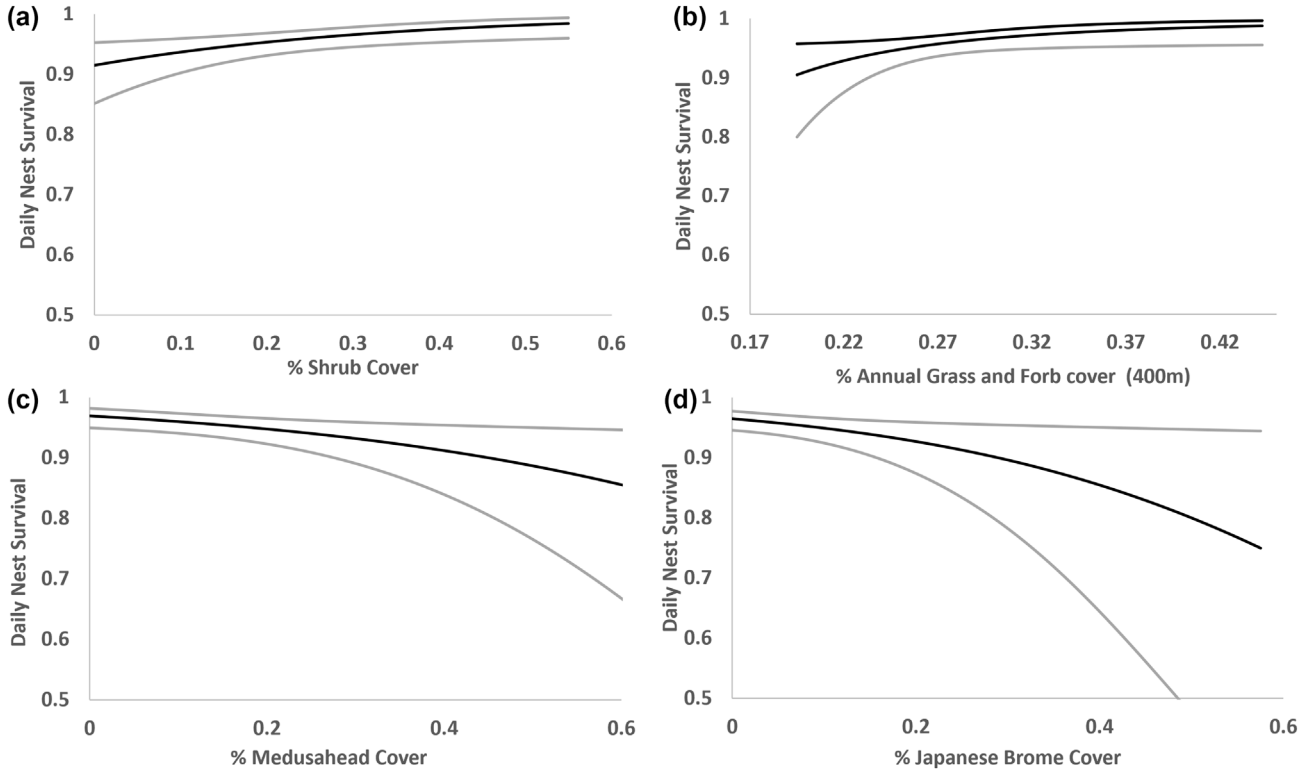


Figure 4. Estimates (solid black line) and 95% confidence limits (solid gray lines) of daily nest survival relative to mean proportion of shrub (a), annual grass averaged across a 400 m buffer (b), medusahead *Taeniatherum caput-medusae* (c), and Japanese brome *Bromus japonicus* (d), measured around nests of female sage-grouse *Centrocercus urophasianus* in Modoc County, California, 2019–2021.

Models containing tree cover at the landscape scale were not competitive (AIC_c Wt. < 0.01), as well as models differentiating between nests located within or outside of a juniper treatment (AIC_c Wt. < 0.01, Supporting information). Temporal variation (Table 5) was also not well supported. Apparent nest survival was 26% across all three years (n = 38, Table 2), while the estimated probability of a sage-grouse nest surviving the entire 29-day incubation period and hatching > 1 egg from the top model that included the mean effect of shrubs and annual grasses on DNS was 0.292 (95% CI: 0.166–0.460).

Chick survival

We recorded 10 successful nests over the three years of our study, but only nine 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 meant we could not locate her in real time to confirm presence of chicks.

Table 4. Model coefficients from known fate models with $\Delta AIC_c < 5$ (Akaike's information criterion), relating the percent cover (COV) of invasive grasses such as medusahead *Taeniatherum caput-medusae* (MH), Japanese brome *Bromus japonicus* (JB), cheatgrass *B. tectorum* (CG), and wiregrass *Ventenata dubia* (WG) observed at 10 m around sage-grouse *Centrocercus urophasianus* nests (n = 38) 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 relating time and biotic characteristics to daily survival of nests (n = 38) belonging to female greater sage-grouse *Centrocercus urophasianus* 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[b]	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.

Thus, only eight 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: 0.973–0.997). The derived estimate of chick survival across the entire 54-day brood-rearing period was 0.441 (95% CI: 0.232–0.833).

Adult survival

Three 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 encounter history for this bird was censored ('00') for the months she was without a transmitter, but she was re-added to the monitored population once she was recaptured and refit with a new transmitter. 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, two females were predated on the nest and five were predated while attending a brood.

Adult survival varied by month as the S(month) model received 46% of the total model weight with several top models including interactions with month (Table 6). Survival was lowest in April (0.687, 95% CI: 0.544–0.801), followed by October (0.809, 95% CI: 0.588–0.927) and January (0.813, 95% CI: 0.552–0.938). 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 (Fig. 5). The model-averaged derived estimates of annual survival each year were 0.32 (95% CI: 0.17–0.51) in 2019, 0.33 (95% CI: 0.13–0.60) in 2020, and 0.22 (95% CI: 0.08–0.49) in 2021 (Fig. 5).

Finite rate of population change and sensitivity

Our estimate of λ based on vital rates estimated during 2019–2021 (Table 7) indicated that the CLNWR sage-grouse population was declining markedly ($\lambda \leq 1.0$) as projected population growth was 0.425 (95% CI: 0.32–0.55). Sensitivity analyses indicated that changes in adult survival have the greatest potential to influence λ, followed by chick survival (Fig. 6). Similar patterns held true for elasticities, with adult survival having the largest influence on λ. However, when we summed elasticities over lower-level vital rates it indicated that first nests had more potential effect on λ than brood survival. We conducted a post hoc analysis and found that the population would stabilize with $\lambda = 1$ if annual adult survival was increased to 0.68, survival of juveniles was 0.55, chick survival was 0.49, and nest success of first nests was 0.49 (Table 8).

Table 6. Model selection results from known fate models evaluating temporal patterns in monthly survival of female greater sage-grouse *Centrocercus urophasianus* instrumented with GPS transmitters (n = 37) 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[b]	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

[a]Month = general variation by month; YEAR = survival differed across all three 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) versus the non-breeding (September–February) seasons.
[b]Lowest $AIC_c = 193.35$.

Discussion

Our study estimated the demographic rates of sage-grouse from a small, isolated population in north-western California that has persisted through active management by translocating individuals from other populations and restoring habitat through juniper removal. We 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 to 2009 (Bell 2011, Bell and George 2012) and from stable or increasing populations across the species distribution (Taylor et al. 2012). CLNWR and MNF have experienced an increase in distribution and abundance of invasive annual grasses, and our study suggests there may

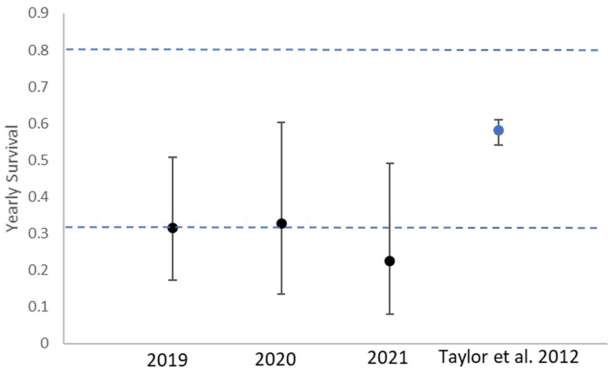


Figure 5. Model-averaged derived estimates of annual survival of female sage-grouse *Centrocercus urophasianus* in Modoc County, California, 2019–2021, compared to range-wide estimates of annual survival for female sage-grouse (Taylor et al. 2012, blue). The minimum and maximum estimates of survival from across the distribution of sage-grouse are represented by the dashed lines (blue).

Table 7. Mean vital rate estimates and SE of female greater sage-grouse *Centrocercus urophasianus* at Clear Lake National Wildlife Refuge and Modoc National Forest, Modoc County, Oregon, USA, 2019–2021.

Vital rate	n	$\bar{x}$ (SE)
$NI_{1\ Adult}$	29	0.82 (0.004)
$NI_{1\ y}$	13	0.46 (0.019)
NI_2	8	0.26 (0.08)
$CS_{1\ Adult}$	17	7.41 (0.40)
$CS_{2\ Adult}$	8	5.78 (0.86)
$CS_{1\ y}$	3	7.00 (0.00)
$CS_{2\ y}$	0	NA
H	38	0.99 (0.014)
NS_1	30	0.29 (0.08)
NS_2	8	0.001 (0.08)
S_{chick}	8	0.44 (0.006)
S_{juv}	38	0.34 (0.067)
S_y	38	0.29 (0.067)
S_{Adult}	38	0.29 (0.067)

Abbreviations: 1, first attempt; 2, re-nest; CS, clutch size; H, egg hatchability; NI, nest incubation rate; NS, 29-day nest survival; S_{chick}, 54-day chick survival; S_{juv}, juvenile survival.

be a negative effect of medusahead and Japanese brome on the daily nest survival of sage-grouse at the microsite scale. The increased cover of invasive grasses over time (Fig. 4) could be contributing to differences in nest survival that we observed relative to previous estimates on CLNWR and other portions of the sage-grouse distribution.

Despite major habitat improvements with a total of 24 000 ha of juniper removed from identified nesting and wintering grounds, the Clear Lake sage-grouse population has yet to see improvements in lek attendance since 2017 (Fig. 2). Juniper removal can increase the area and quality of habitat (Severson et al. 2017, Olsen et al. 2021), and for a short period of time lek attendance at CLNWR began to

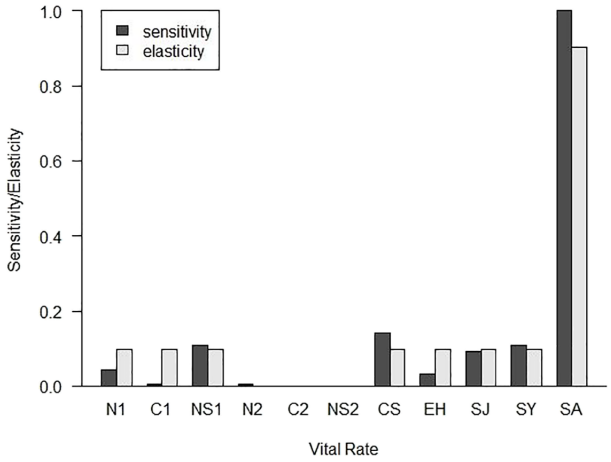


Figure 6. Estimates of sensitivity and elasticity of sage-grouse *Centrocercus urophasianus* vital rates on λ in Modoc County, California, 2019–2021. Abbreviations: 1, first attempt; 2, re-nest; C, clutch size; N, nest initiation rate; NS, 29-day nest survival; CS, 54-day chick survival; EH, egg hatchability; SJ, juvenile survival; SY, yearling survival; SA, after hatch-year survival.

Table 8. Summary of post hoc analysis for adult survival (S_{ASY}), juvenile survival (S_{JUV}), chick survival (S_{chick}), first nest survival (NS1), and projected estimates of λ for sage-grouse at Clear Lake National Wildlife Refuge and Modoc National Forest, Modoc County, Oregon, USA. Values start with vital rates from our study, and then raised to averages from Taylor et al. (2012) if below the national average. Each round one vital rate is increased 0.05 (bolded).

S_{ASY}	S_{JUV}	S_{chick}	NS1	λ	95% CI
0.29	0.34	0.44	0.29	0.43	0.32–0.55
0.58	0.51	0.44	0.44	0.86	0.81–0.91
0.63	**0.53**	0.44	0.44	0.91	0.86–0.97
0.63	0.53	**0.49**	0.44	0.96	0.89–1.01
0.63	0.53	0.49	**0.49**	0.99	0.93–1.05
0.68	**0.55**	0.49	0.49	1.05	0.99–1.12

increase (high of 36 males; Fig. 2). However, 21% of the total area of juniper treatments have burned (Fig. 1), and in these areas, vegetation regrowth the following years after a wildfire consisted of mostly annuals while perennials have yet to recover. Annual grasses and forbs have increased by ~ 15% while shrub cover has decreased by ~ 4% across the study area compared to when the population was last monitored 10 years previous (Bell 2011, Fig. 3). The increase in annual grasses is a potential explanation for why nest survival (0.292, 95% CI: 0.166–0.460) was much lower than estimates from previous work on CLNWR (0.450, 95% CI: 0.319–0.622; Bell 2011), but similar to other nearby field sites affected by large wildfires in Nevada, Oregon, and California (0.22, 95% CI: 0.13–0.33, Lockyer et al. 2015; 0.23, 95% CI: 0.098–0.441, Foster et al. 2019; 0.19, 95% CI: 0.06–0.42, Dudley et al. 2022). The area of the Tucker Fire was a known nesting and brooding area with several nests located there in 2009–2011 (n = 11, Bell 2011). However, we only observed one nest in the post-fire area (2019), so females appeared to generally avoid the area for nesting, further limiting the amount of available nesting habitat. Our nest survival estimates suggested fire may have had a significant impact on the CLNWR population by significantly reducing the amount of perennial understory and available nesting habitat, which may have outpaced increases in sagebrush habitat gained from juniper treatments and suppressed demographic performance.

While we found shrub cover had a positive effect on nest survival, the magnitude of the overall effect on DNS was small, likely because our sample of nests was small and the majority (68%) of nests had an average shrub cover between 0 and 10% (n = 12) or 15 and 25% (n = 14), although maximum shrub cover did reach 55% for one nest (Fig. 4). However, this range in the proportion of sagebrush and other native shrub cover is generally reflective of the limited shrub cover available at CLNWR and surrounding MNF. Shrub cover averaged 15% across the entire AMU in 2021 (Fig. 3) with roughly 14% of the AMU containing shrub cover > 20% (Jones et al. 2018, Allred et al. 2021). Mean percent shrub cover around nests was higher at the microsite scale and ranged from 18 to 25% when averaged across the three years of the study, which is at the lower end of what is considered suitable for nest survival in California and Nevada

(> 25.8%, Coates et al. 2017). However, this mean value is higher than other sites affected by wildfire whose shrub cover ranges from 4 to 15% in burned areas used by sage-grouse (Lockyer et al. 2015, Coates et al. 2017, Anthony et al. 2020, Dudley et al. 2022).

We found the opposite pattern for annual grasses, with cover being greatest at the landscape scale, which in some areas accounted for over a third of the total vegetation cover (Jones et al. 2018, Allred et al. 2021). Medusahead and cheatgrass ranged from 17 to 20% cover at the microsite scale. Alternatively, litter which was predominately from medusahead on average covered > 60% of the total length of our vegetation transects around nest sites at the microsite scale (Supporting information). Medusahead decomposes slowly, and the dense litter present at the field site may prevent perennial forbs and grass from growing, and provide additional visual obstruction for nests in future years (Melgoza et al. 1990, Young 1992, Davies and Svejcar 2008). Other studies that focused on microsite selection have found sage-grouse actively avoided annual grass cover around nests, however annual grass cover in these studies only ranged from 7.0 to 10.6% at nest sites (Lockyer et al. 2015, Coates et al. 2017, Dudley et al. 2022). Other studies have found sage-grouse may be less tolerant of annual grass cover above thresholds of 5% (Coates et al. 2017), although this avoidance behavior has not been observed in sites with a high distribution and abundance of annual grasses, as was the case at CLNWR (O'Neil et al. 2020, Dudley et al. 2022). While our results showed medusahead and Japanese brome had a negative effect on daily nest survival at the microsite scale, these models were not competitive when compared to other vegetation metrics (Table 3), consistent with previous studies focused on fire effects in sagebrush systems (Lockyer et al. 2015, Coates et al. 2017, Anthony et al. 2021, Dudley et al. 2022). Conversely, at the landscape scale annual forbs and grass had a positive effect on DNS and were ranked highly in our model set when paired with shrub cover, likely because post-wildfire annuals provide the only cover for nest concealment when perennial and shrub species are reduced (O'Neil et al. 2020, Dudley et al. 2022).

Adult survival has a strong influence on the population change for greater sage-grouse (Taylor et al. 2012, Dahlgren et al. 2016, Anthony et al. 2022). Therefore, it is noteworthy that mean adult female survival across all three years in Modoc County (0.290, 95% CI: 0.170–0.430) was much lower than distribution-wide estimates (Taylor et al. 2012) as well as in the previous study on CLNWR (0.596, 95% CI: 0.483–0.699, Bell and George 2012). All our females were outfitted with rump-mounted GPS transmitters which may have lowered our observed survival (Foster et al. 2018, Severson et al. 2019); however, when accounting for transmitter effect (5% higher or 1.19 greater than the GPS survival rate), estimates of annual survival would be ~ 0.34, which is still much lower than local and distribution-wide estimates (Bell and George 2012, Taylor et al. 2012). Translocated birds were included in survival estimates for 2019, but we did not include a translocation effect in our model set because we only had a single year of translocations, and differences in survival between years, particularly 2019 and 2020, were minimal. Thus, we believe translocation did not significantly affect adult survival in 2019 as has been observed in other studies (Bell and George 2012, Duvuvuei et al. 2017), but due to small sample sizes we did not test this directly. Our estimates of annual adult female survival were similar to estimates for female grouse the first two 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. 2022). Within the annual cycle, our estimates of monthly female survival during early spring (April: 0.68, 95% CI: 0.54–0.80) were much lower than at other sites across the species distribution where spring monthly survival estimates range from 0.75 to 0.93 (Baxter et al 2013, Blomberg et al 2013, Severson et al 2019). Spring and fall have been found to be the lowest periods of survival for breeding sage-grouse due to the increased risk of predation and energy demands during nesting and brooding (Baxter et al 2013, Blomberg et al 2013).

For sage-grouse broods, the two primary causes of chick mortality are exposure and predation (Dahlgren et al. 2010a, b, Street et al. 2022), however at our field site it was predation of adult females (n = 5, 62%); and only in one case was a female observed without her brood on two consecutive surveys, which we categorized as total brood loss. Predation of an adult brooding female was listed as a cause of brood failure only once prior to our work (Dahlgren et al. 2010a, b) for radio-marked chicks. Unmarked females with broods were observed each year while traveling about the study area in late summer, and during trapping each winter we continued to capture 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), therefore it is difficult to say how many adults contributed to the juveniles we observed or whether the chicks of depredated females 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, despite reductions in perennials and shrubs elsewhere (Dzialak et al. 2011, Donnelly et al 2018, Lundblad et al. 2022). However, lack of overhead cover typically provided by sagebrush and other native shrubs may increase the risk of adult predation when with a brood, and would limit the amount the thermal buffering available to young chicks who cannot thermoregulate (Fischer et al. 1996, Anthony et al. 2022). While our estimates of perennial grass and shrub cover at brood sites are similar to distribution-wide estimates (Hagen et al. 2007), the mean percent cover of cheatgrass across brood locations each year ranged from 8 to 31%, and the subsequent litter from annual grass species ranged from 30 to 68% (Supporting information). While we were unable to determine chick survival in relation to vegetation cover, cover of annual grasses has strong implications for early brood survival (0–3 weeks), as Hymenoptera, an important dietary source during

early brood rearing (Thompson et al. 2006) are known to avoid areas of high cheatgrass abundance (Robertson and Robertson 2020).

In combination, the demographic rates we observed indicated that the CLNWR population is currently declining by ~ 60% annually, with a growth rate of 0.425. We found, in order of importance, low adult, chick, and nest survival were contributing to this decline. Several studies have reported λ to be most sensitive to changes in adult female survival, juvenile (fledging to 1-year old) survival, and chick survival (Johnson and Braun 1999, Taylor et al. 2012, Dahlgren et al. 2016, Olsen et al. 2021, Anthony et al. 2022). Considering that adult survival may have been negatively affected by use of GPS transmitters, our estimate of juvenile survival may also be an underestimate, therefore underestimating the population growth rate. For comparison, we estimated $\bar{\lambda}=0.55$ for the four years post-translocation (2020–2023 mean male lek count = 15.8, SE = 2.2) in relation to the prior four years (2016–2019 mean male lek count = 28.8, SE = 5.0) from the lek count data for male sage-grouse on Clear Lake (Fig. 2). Although λ calculated for males from lek counts from the 2020–2023 interval was somewhat higher than our estimate based on female vital rates, both estimates indicated a dramatically declining population. To reverse the declining population trend on CLNWR and achieve a $\lambda \geq 1$, both adult and nest success need to increase (Fig. 5, Table 8). The population would stabilize with $\lambda = 1$ if annual adult survival was increased to 0.68, survival of juveniles was 0.55, chick survival was 0.49, and nest success of first nests was 0.49. However, these estimates may not be obtainable with the amount of habitat restoration needed to double the current adult survival rate, due to the current limitations in shrub cover and extent of annual grass and juniper at the field site.

The near-term projection is that the CLNWR sage-grouse population is likely to continue in steep decline. Management focused on improving habitat conditions, increasing the amount of sagebrush cover, and reducing predation during the nesting and brooding life stages will be paramount to recovering and maintaining this population. Translocation was used in the past to supplement the population 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 at rates far higher than we estimated in the current landscape. Translocation might be a viable consideration after significant improvements are made to the vegetation communities, such that adult, brood, and nest 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 annual grasses or juniper at this field site. Instead, there are many other management activities that may well defend or expand current cover and food for sage-grouse and other sagebrush-dependent species, including the continued reduction of juniper encroachment through mechanical means (Frey et al. 2013, Bates et al. 2017, Severson et al. 2017, Olsen et al. 2021), suppressing future wildfires by limiting their ability to spread (Omi 1979, Pellant 1994, Shinneman et al. 2019), and limiting the amount of fine fuels on the landscape (Schmelzer et al. 2014, Perryman et al. 2020). Finally, actively restoring sagebrush communities after wildfire through the planting of perennial species that can tolerate future drought conditions could be beneficial to sagebrush-dependent species by reducing the likelihood of invasive annuals gaining a competitive advantage (Davies et al. 2021). Our research represented a microcosm of concurrent conditions across the sage-grouse distribution in relation to fire, juniper, and invasive annual grasses, and has shown that when sagebrush communities are degraded by juniper woodland encroachment or grasslands dominated by invasive annuals, sage-grouse populations cannot persist.

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Chelsea E. Sink: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Katie M. Dugger**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (supporting); Methodology (equal); Project administration (equal); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Christian A. Hagen**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (supporting); Methodology (equal); Project administration (equal); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (supporting); Writing – original draft (equal); Writing – review and editing (equal). **John N. Vradenburg**: Conceptualization

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Data availability statement

Data are available from Science Base: https://doi.org/10.5066/P14HV5XD (Sink et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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