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Research Article

Greater Sage-Grouse Vital Rates After Wildfire

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ABSTRACT Greater sage-grouse (*Centrocercus urophasianus*) have been subject to long-term and continuing declines in population and habitat since European settlement of western North America. Increased wildfire activity constitutes a primary threat to the species in western portions of their range, with documented declines in wildfire-affected populations. Following a 187,000-ha wildfire in southeastern Oregon and northern Nevada, USA, we used global positioning system (GPS) telemetry to monitor nest initiation, nest survival, nesting habitat, and adult survival of female sage-grouse during 2013 and 2014. We used known-fate models in Program MARK to estimate daily nest survival and monthly adult survival in relation to temporal patterns, physiological characteristics of females, and habitat and land-cover characteristics. We assessed habitat characteristics using geographic information system (GIS)-derived measures of post-fire habitat condition and land cover. Nest initiation rate following the fire was comparable to that observed in unaltered habitat. We observed nesting rates of 90% and 100% during 2013 and 2014, respectively, and renesting rates of 23% and 57% during the same years. Daily nest survival was consistently low in comparison to rates observed in concurrent studies in the region, for first nests during both years, and for second nests during 2013, but survival markedly increased for second nests during 2014. Sage-grouse generally did not leave the fire perimeter to nest, with 64% and 73% of nests located in the fire boundary during 2013 and 2014, respectively. Approximately 27% of nests were located in burned habitat during 2013, and 20% of nests in 2014 were located in burned habitat. Adult survival varied by month, and although patterns of monthly survival were similar between years, monthly survival rates were significantly reduced from the beginning of the study through the end of the first post-fire growing season. Our results indicate that sage-grouse continue to use fire-affected habitat in the years immediately following wildfire and sage-grouse experienced lower nest survival and adult female survival than other populations during the same period. © 2018 The Wildlife Society.

KEY WORDS annual survival, *Artemisia tridentata*, *Centrocercus urophasianus*, Great Basin, greater sage-grouse, nest success, sagebrush, wildfire.

Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) is a species of conservation concern in western North America, undergoing long-term population declines across their distribution (Garton et al. 2011). These population declines have been linked to widespread habitat loss and degradation (Crawford and Lutz 1985, Klebenow 1985, Connelly et al. 2004, Connelly et al. 2011*a*, Garton et al. 2011). Sage-grouse are a sagebrush (*Artemisia* spp.) obligate species and require sagebrush during every phase of their lifecycle (Patterson 1952). This dependence on sagebrush is acute during the nesting period (Connelly et al. 2011*c*), with most nests located under sagebrush shrubs (Patterson 1952, Popham and Gutiérrez 2003, Connelly et al. 2011*c*). Thus, removal of sagebrush at broad scales can affect vital rates and population persistence (Swenson et al. 1987, Coates et al. 2016).

Early research was predicated on the assumption that productivity limits population growth in sage-grouse (Drut et al. 1994). However, the life-history traits of the species are more consistent with a k-selected species, where population growth rates are more sensitive to changes in adult survival than to changes in reproductive rates (Sæther and Bakke 2000, Stahl and Oli 2006, Taylor et al. 2012, Dahlgren et al.

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2016). Thus, quantifying changes in sage-grouse survival in response to conservation actions or disturbance is an important requirement for predicting the future trajectory of sage-grouse populations. Although nest success has less influence on rates of population change than brood or adult female survival, it is an important factor influencing sage-grouse population stability (Crawford and Lutz 1985, Gregg et al. 1994, Baxter et al. 2008, Taylor et al. 2012). Sage-grouse nest success may be influenced by multiple factors including female age, weather, and nesting habitat (Connelly et al. 2011*b*, *c*). Degradation or disturbance of nesting habitat can alter sage-grouse nesting behavior and reduce nest success (Connelly et al. 2011*b*, *c*).

Although sagebrush habitat degradation and loss due to anthropogenic influences is documented (Schroeder et al. 2004, Connelly et al. 2011*a*, Knick et al. 2011, Leu and Hanser 2011), wildfire is now considered a primary threat to sage-grouse habitat in the western portion of its range (U.S. Fish and Wildlife Service 2015). Wildfire activity across western North America has resulted in sage-grouse habitat alterations at large spatial scales (Baker 2009, 2011), and the number of fires and area burned within the range of sage-grouse has increased annually since 1980 (Miller et al. 2011). Sagebrush habitat regeneration is slow following wildfire (35–120 yr) because most species of sagebrush do not resprout but must regenerate from seed (Baker 2006). Further, if invasive annual grasses successfully dominate sites post-fire, fire return intervals may be shortened to the point of precluding reestablishment of sagebrush and other native vegetation components (Knick and Rotenberry 1997, Brooks et al. 2015).

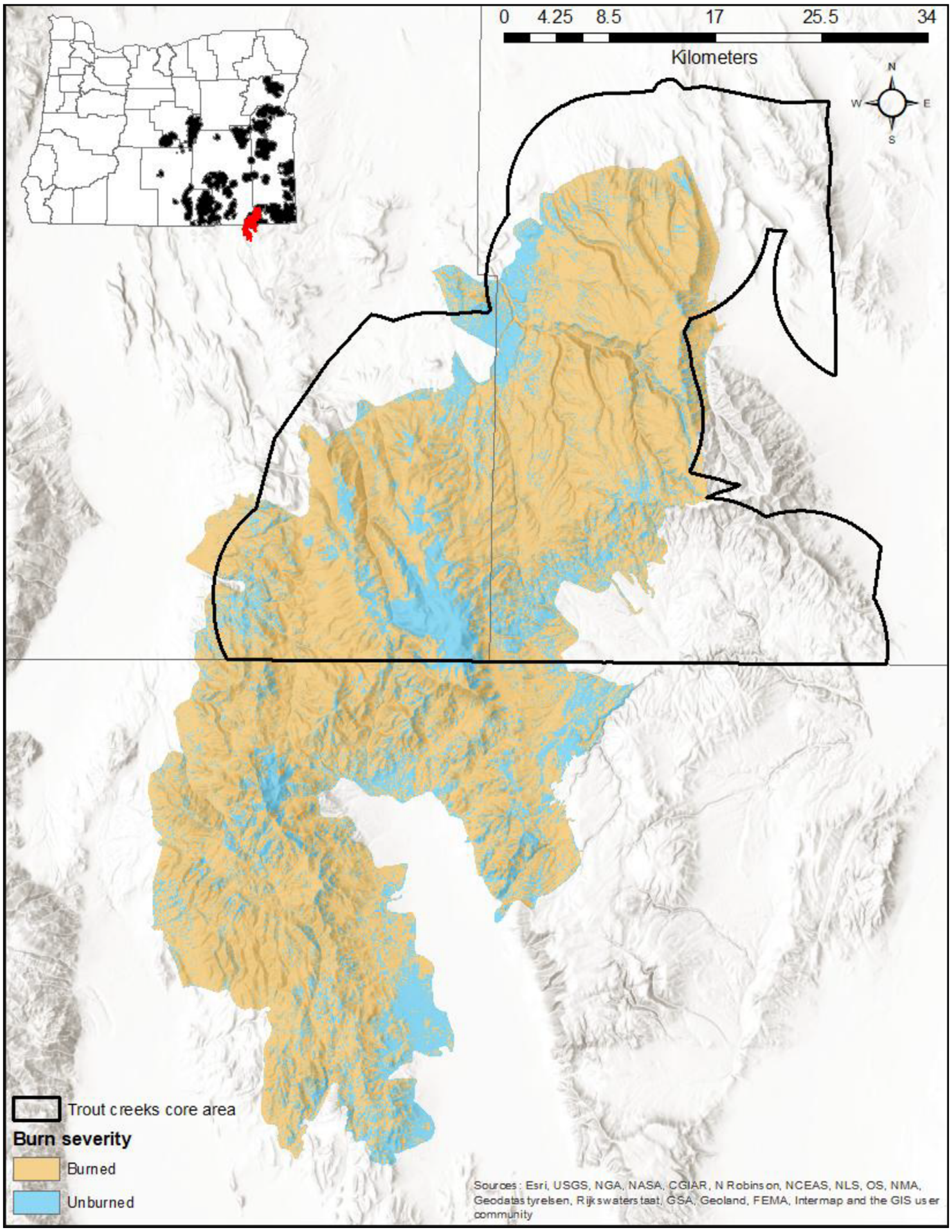
Most studies of the effects of fire on sage-grouse populations and habitat have occurred following prescribed fires or multiple years after small wildfires (Lockyer et al. 2015). Additionally, studies on the effects of fire on sage-grouse habitat and productivity have been biased toward studies of vegetation rather than population response (Davies et al. 2007, Hess and Beck 2012). Prescribed fire, which generally occurs on small spatial scales, appears to have neutral or negative effects on sage-grouse habitat (Pyle and Crawford 1996, Connelly et al. 2000, Nelle et al. 2000, Beck et al. 2009, Rhodes et al. 2010). However, wildfires differ from prescribed fires in timing, intensity, and size and may affect sage-grouse populations more severely (Slater 2003, Baker 2011). Recently, researchers have examined the demographic response of sage-grouse to fire disturbance, and observed generally negative effects of large wildfire or prescribed fire on spring lek counts, recruitment rates, rate of population change (Blomberg et al. 2012, Connelly et al. 2000, Coates et al. 2016), and sage-grouse survival (Lockyer et al. 2015).

Immediately following the series of large-scale wildfires that occurred in southeastern Oregon and northern Nevada, USA, during summer 2012, in which >400,000 ha of sage-grouse habitat burned in Oregon, we investigated sage-grouse nesting ecology and survival of adult females in response to a 187,000-ha fire in southeastern Oregon and northern Nevada (i.e., Holloway fire). Our study was descriptive, and our objectives were to quantify the effects of wildfire on adult annual survival and sage-grouse nest ecology, including nest initiation and renesting rates, nest habitat characteristics, nest site fidelity, and daily nest survival. We attempted to identify the temporal factors associated with these vital rates within fire-affected areas and nearby unburned habitat.

STUDY AREA

Our study occurred between March 2013 and February 2015, within and adjacent to the 186,972-ha Holloway fire, which burned in 2012 in the Trout Creek Mountains of southeastern Oregon. Elevation in the study area ranged from 1,372–2,438 m (Evenden 1989) and the topography was characterized by mesas, buttes, and fault blocks cut with deep stream canyons (Carlton 1968). The regional climate was semiarid with an average annual precipitation of 39.7 cm, with the majority of that falling between November and May (1981–2010; PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, accessed 14 May 2018). Annual precipitation during 2012, 2013, and 2014 was 32.1 cm, 24.3 cm, and 40.5 cm, respectively (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, accessed 14 May 2018). Average monthly temperature maximum and minimum were 28°C and −6°C occurring in July and December, respectively (1981–2010; PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu). Common predators of sage-grouse nests or adults in the area included badgers (*Taxidea taxus*), common ravens (*Corvus corax*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and golden eagles (*Aquila chrysaetos*). Prior to the Holloway fire, the vegetation communities present in the study area varied based on elevation and topography. At upper elevations (>1,900 m), a mountain big sagebrush (*A. tridentata vaseyana*)–low sagebrush (*A. arbuscula*) mosaic dominated, interspersed with a mountain shrub community of snowberry (*Symphoricarpos* spp.), antelope bitterbrush (*Purshia tridentata*), and buckbrush (*Ceanothus* spp.). Native grasses at higher elevations included Idaho fescue (*Festuca idahoensis*), needlegrass (*Achnatherum* spp.), bluebunch wheatgrass (*Pseudoroegneria spicata*), basin wildrye (*Leymus cinereus*), and Sandberg bluegrass (*Poa secunda*; Freeborn 2006), and following the fire these native grasses greatly increased in areas newly devoid of shrub cover. Additionally, mountain mahogany (*Cercocarpus* spp.) and quaking aspen (*Populus tremuloides*) patches dotted the higher elevations, and cheatgrass (*Bromus tectorum*) and western juniper (*Juniperus occidentalis*) were rare or absent (Freeborn 2006). At lower elevations Wyoming big sagebrush (*A. t. wyomingensis*) dominated prior to the fire, with areas of salt desert shrub present on more alkaline soils (Freeborn 2006). Grasses at lower elevations included bluebunch wheatgrass, needlegrass, Sandberg's bluegrass, bottlebrush squirreltail (*Elymus elymoides*), basin wildrye, and cheatgrass (Freeborn 2006). Following the fire, these grass species rapidly filled areas previously dominated by shrubs. Approximately 95% of the area was managed by the Bureau of Land Management (BLM), a large portion of which was designated as Wilderness Study Area (WSA), with the remaining 5% of land in private holding (Freeborn 2006). The primary land use in the study area was livestock grazing.

A lightning strike ignited the Holloway fire in the Trout Creek Mountains on 5 August 2012. The fire occurred approximately 40 km east of Denio, Nevada, and 210 km southeast of Burns, Oregon (Karges 2013), and was not fully contained until 25 August 2012. The Holloway fire burned 186,972 ha, of which 99,352 ha were in southern Malheur and Harney counties, Oregon, and 87,227 ha were in northern Humboldt County, Nevada (Karges 2013). The sage-grouse core area in the Trout Creeks Mountains (Hagen 2011*a*) was almost completely burned by this fire (Fig. 1). Fire behavior depended on local topographic features, vegetation profiles, and weather conditions, resulting in variable patterns of burned and intact habitat. Fuel loads, wind speeds, and topographic features conducive to fire spread caused the fire to burn intensely in some areas, consuming nearly all vegetation over large areas, while also creating a mosaic of burned and intact vegetation in other areas that burned less intensely. Several large patches of intact habitat existed within the perimeter of the fire, with the largest patch exceeding 4,000 ha. Within the fire boundary, 75% of the land area was burned, and the remaining 25% was composed of unburned, intact habitat patches (Fig. 1; Foster 2016).



Sources: Esri, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community

Figure 1. Holloway fire extent and severity in relation to the sage-grouse core area, Trout Creeks Mountains, Harney and Malheur counties, Oregon, and Humboldt County, Nevada, USA.

METHODS

Capture and Monitoring

We captured female sage-grouse during spring and summer 2013, and spring 2014 using spotlights and long-handled nets (Wakkinen et al. 1992) near roosts or leks within, or near (≤2 km) the boundary of the Holloway fire. We used feather patterns and morphology to determine sex and age of captured individuals (Crunden 1963). We classified sage-grouse as adults (≥2 yr of age), or yearlings (~1 yr of age). We did not capture or mark hatch year individuals during the study. If yearlings survived >1 year of the study, we reclassified them as adults during their second year. We marked all captured individuals with an Oregon Department of Fish and Wildlife (ODFW) numbered aluminum leg band. We attached 30-g solar-powered global positioning system (GPS) platform transmitter terminal (PTT) satellite transmitters (Argos/GPS PTT-100, Microwave Telemetry, Columbia, MD, USA; GPS-PTTs) to captured females using a rump-mount attachment technique (Rappole and Tipton 1991). All animal capture, handling, and instrument attachment procedures were approved under Oregon State University's Institutional Animal Care and Use Committee (protocol number 4465). The GPS-PTTs included ultra-high frequency (UHF) beacons that were turned on for ground tracking from 1 March to 31 July each year. The GPS-PTTs we used during spring and summer 2013 were configured to record locations (±20 m) 6 times daily from 1 March to 31 July, 4 times daily from 1 August to 31 October, and 2 times daily from 1 November to 29 February. The GPS-PTTs deployed in spring 2014 were configured similarly, except that we increased the number of locations collected during the nesting season (10 times daily from 1 Mar to 31 Jul, and 4 times daily from 1 Aug to 29 Feb) to help us determine nest initiation dates more precisely.

We used female behavior as interpreted from the GPS-PTT location data to identify individual nest attempts. If the GPS locations for a female remained stationary for >18 hours during the nesting season (1 Apr–31 May), we considered her to be on a nest. We selected 18 hours for this threshold because it was the shortest period of time an individual remained stationary during the nesting season and we located nest remains upon site visit. Once we identified a nest attempt, we used the location data to approach the general area of the nest and then used a UHF receiver to locate the specific nest site. At that point we approached the nest site to within approximately 3 m, to visually confirm that the female was incubating, while taking care not to flush her. If a nesting female was absent from the nest >8 hours, we assumed nesting activity had ceased, and we revisited the nest to determine its fate. We considered nests successful if ≥1 egg hatched. We characterized nests as failed if no eggs hatched. We identified hatched eggs by the presence of an egg cap, and an intact egg membrane. We identified depredated eggs by crushed or punctured egg shells not exhibiting a distinct egg cap, and intact egg membrane. We assessed nest site fidelity by measuring the distance between first and second nests of individuals, and the distance between nests of individuals in consecutive years. We also characterized nest habitat in terms of whether nests were placed in burned or unburned areas, species of nest cover, size of unburned habitat patches used as nesting cover, and distance from nests to burned areas.

We used movement patterns interpreted from the GPS-PTT location data to identify mortality events of marked females. If the GPS locations of a female remained stationary for >18 hours outside of the nesting season, we assumed that a mortality event had occurred. After the identification of a possible mortality event, we used the satellite location data to locate the general area of the event site. When UHF beacons were active in spring and summer, we used a UHF receiver to pinpoint the location of the transmitter on the ground. We examined the mortality site and transmitter for signs of depredation or mortality, such as feathers and bone fragments, predator scat, a sage-grouse carcass, or damage to the transmitter or harness indicative of depredation (i.e., bite marks or scratches). During periods when the UHF beacon was not active, we approached the last known location of the transmitter and performed grid searches of the surrounding area for the transmitter and signs of mortality. During the nesting season, female movement patterns suggesting mortality were similar to nesting behavior. Thus, we employed maximum caution when conducting mortality searches during this period, to avoid disturbance of females on nests. We classified events as mortalities only if we located a transmitter with conclusive signs of depredation or death. In these cases, we classified the date of mortality as the last known transmission of movement data consistent with live sage-grouse movement patterns (i.e., short between-location movement distances, and locations on top of ridges). We assumed that long straight-line movement distances, and locations at the bottom of draws and canyons immediately prior to transmitters becoming stationary reflected the movement of sage-grouse carcasses and transmitters by predators.

Covariates

Nest survival.—We investigated the relationship between daily nest survival and a variety of covariates, including those reflecting temporal patterns ($n = 2$), inherent characteristics of birds ($n = 3$), and nesting habitat characteristics ($n = 10$; Table 1). We evaluated whether daily nest survival varied between years (2013 vs. 2014) or by the stage of incubation. We allowed year to interact with a number of other covariates to account for the fact that the relationship between some covariates and daily nest survival might change between the first year after the fire and the second because of habitat regeneration.

We characterized nests relative to female age (initiated by adult or yearling), nest attempt (first or second nest attempt), and standardized nest initiation date within each nesting season. We calculated nest initiation dates as the first date on which a female attended its nest location for >18 hours as determined through GPS monitoring. We calculated standardized nest initiation dates in relation to the median nest initiation date in a given year (median nest

Table 1. Covariates, the scales at which they were evaluated, and covariate collection methods, describing sage-grouse nests during 2013 and 2014 in the Trout Creek Mountains, Malheur and Harney counties, Oregon, USA.

Covariate	Description	Scales evaluated[a]	Forms evaluated[b]	Collection method[c]
Year	Year of nest, 2013 or 2014	NA	NA	NA
Time	Day of incubation	NA	D, L, PT	GPS data
Female age	Adult vs. yearling	NA	NA	Capture data
Nesting attempt	First or second nesting attempt	NA	NA	GPS data
Standardized initiation date	Days difference from median nesting date in year	NA	L	GPS data
Nest habitat	Nest placed in an unburned or burned habitat	NA	NA	Site visit
Nest species	Nest under live sagebrush or not	NA	NA	Site visit
Distance to riparian	Straight-line distance from nest site to permanent or semi-permanent stream	NA	L, PT	GIS
Distance to edge	Straight-line distance from nest site to edge between intact and burned habitat	NA	L, PT	GIS
Percent patch cover	Percent of nest site buffer covered by intact patches	100 m, 550 m, 1,500 m	L, PT	GIS
Edge density	Density of burned-intact edges (m/ha) within nest site buffer	100 m, 550 m, 1,500 m	L, PT	GIS

[a] 100 m: 100-m circular buffer around nest site; 550 m: 550-m circular buffer around nest site; 1,500 m: 1,500-m circular buffer around nest site.
[b] NA, not applicable; D, discrete time steps; L, linear; PT, pseudo-threshold.
[c] GPS, global positioning system; GIS, geographic information system.

initiation date: initiation date = 0, nest initiation date prior to mean date: initiation date < 0, nest initiation date following mean date: initiation date > 0). We developed habitat covariates from remotely sensed data and measured them at up to 3 scales around each nest site (100-m circular buffer, 550-m circular buffer, 1,500-m circular buffer; Table 1).

Adult survival.—We investigated the relationship between monthly survival (S_t) and a variety of factors we believed would be associated with survival including those reflecting temporal patterns ($n = 4$), inherent characteristics of birds ($n = 4$), and habitat and land-cover characteristics ($n = 9$; Table 2). We evaluated whether monthly survival varied by biological year (Mar 2013–Feb 2014 vs. Mar 2014–Feb 2015), by month ($n = 24$), or by biological season (breeding = Mar–Jun; summer = Jul–Oct; winter = Oct–Feb). We also investigated whether there was an acute fire effect (AFE) that extended through the end of the first post-fire growing season, July 2013. We measured this effect as a binary temporal covariate, differentiating survival between the first 5 months of the study (Mar 2013–Jul 2013) and the remainder of the study period. Finally, we assessed the effects of age on survival (adult vs. yearling).

Survival Modeling

We developed all habitat and land-cover covariates from geographic information system (GIS) data relating to topography, mesic habitat resources, and post-fire habitat mosaic and recovery (Tables 1 and 2). We modeled all continuous covariates with linear, pseudo-threshold, or quadratic structures depending on *a priori* hypotheses. Pseudo-threshold effects [$\ln(x)$], allowed a covariate to have progressively diminishing effect on nest or adult survival as covariate values increased or decreased. In cases where continuous covariates equaled zero during any interval ($\ln(0)$ = undefined), we used a [$\ln(x+1)$] transformation for all covariates. In the case of adult survival, we hypothesized that a quadratic relationship ($x + x^2$) between habitat covariates and monthly survival rates of sage-grouse would reflect the positive effect of middle-range habitat values.

Because of the large number of covariates included in our analysis, and potential correlation between many of the habitat covariates, we used a sequential modeling procedure to develop multi-factor models rather than running a model set that contained every possible combination of all covariates. This approach alleviates the risk of progressing models with uninformative parameters (Arnold 2010), and generally results in the same outcome as an all-possible combinations modeling approach with the benefits of a much smaller model set (Doherty et al. 2012). We used an information-theoretic approach (Burnham and Anderson 2002) to select competitive models at each modeling stage. We used Akaike's Information Criterion corrected for small sample size (AIC_c), the difference in AIC_c value between each model and the top ranked model (ΔAIC_c), and AIC_c weights (w_i) to rank models (Burnham and Anderson 2002). We evaluated model deviance and 95% confidence limits on covariate model coefficients (β_i) to assess the direction and strength of specific covariate effects, and to identify uninformative parameters in competitive models (Arnold 2010, Dugger et al. 2016). We carried forward models within 2 ΔAIC_c values of the top model from one modeling stage to another, and considered these models in the final model set unless they contained uninformative parameters (Arnold 2010).

We initially evaluated single-factor models in each of 3 categories: temporal effects (e.g., year, season), non-habitat covariates (e.g., age, nest attempt), and habitat covariates. We evaluated temporal effects first to select the most supported temporal structure as the basis for additive models containing other covariates. We then evaluated non-habitat covariates and investigated combinations of those covariates that ranked most highly as additive effects in the best temporal models. Finally, we evaluated habitat covariates across all scales as single factor models, with pseudo-threshold, quadratic, or linear structures depending on

Table 2. Covariates, the scales at which they were evaluated and the covariate forms evaluated, hypothesized to affect greater sage-grouse survival between March 2013 and February 2015 in the Trout Creek Mountains, Malheur and Harney counties, Oregon, USA.

Covariate	Description	Scale[a]	Form[b]
Temporal factors			
Year	Biological year (Mar–Feb)	NA	NA
Time	Monthly intervals	NA	NA
Linear time trend	Linear trend in survival across full study	NA	NA
Month across year	Monthly intervals differ within years, but constant across years.	NA	NA
Season	Three season structure: breeding, summer, winter	NA	NA
Acute fire effect	Acute effect of fire: Mar 2013–Jul 2013	NA	NA
Non-habitat covariates			
Age	Adult vs. yearling	NA	NA
Sex	Female vs. male	NA	NA
Nest status	Number of days within monthly interval that a female spent incubating	NA	L, PT
Range size	Size of Brownian bridge kernel range generated from locations that occurred in an interval's covariate analysis period	95% BBK, 50% BBK	L, PT
Habitat covariates			
Mean distance to water	Mean distance from all points, in a 14-day covariate analysis period within a monthly interval, to a permanent or semi-permanent stream	NA	L, PT, Q
Terrain roughness index	Mean terrain roughness index value calculated following Wilson et al. (2007) within covariate analysis period range	95% BBK, 50% BBK	L, PT
Proportion of locations intact	Proportion of locations within covariate analysis period which occur in intact habitat	NA	L, PT, Q
Percent intact	Percent of covariate analysis period range that is composed of intact habitat	95% BBK, 50% BBK	L, PT, Q
Connectance index – long	Connectance index of patches in covariate analysis period range, calculated in FRAGSTATS using a 1-km connectedness distance	95% BBK, 50% BBK	L, PT
Connectance index – short	Connectance index of patches in covariate analysis period range, calculated in FRAGSTATS using a 0.5-km connectedness distance	95% BBK, 50% BBK	L, PT
Edge density	Amount of intact habitat-burned habitat edge (m/ha) in covariate analysis period range	95% BBK, 50% BBK	L, PT, Q
Mean distance to intact	Mean distance (m) from all points in a covariate analysis period to intact sagebrush habitat, set as 0 m for locations in intact habitat	95% BBK, 50% BBK	L, PT
Mean normalized difference vegetation index	Mean normalized difference vegetation index within covariate analysis period range	95% BBK, 50% BBK	L, PT
Standard deviation normalized difference vegetation index	Standard deviation of normalized difference vegetation index within covariate analysis period range	95% BBK, 50% BBK	L, PT

[a] NA, not applicable; 95% BBK, 95% Brownian bridge kernel range calculated from locations within covariate analysis period; 50% BBK, 50% Brownian bridge kernel range calculated from locations within covariate analysis period.

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

a priori hypotheses. We retained the most supported scale and structure of each continuous habitat covariate in the model set. We included covariates in additive or interactive models, that were within 2 ΔAIC_c of the top single-factor model in their respective category, and that had model coefficients with 95% confidence limits that did not overlap zero or only overlapped zero by <10% (Dugger et al. 2016). We also assessed all habitat covariates in interactions with month because of the changing habitat requirements of sage-grouse throughout the year. We examined correlations among all covariates prior to combining them in additive or interactive models, using the cor function in program R (R Version 3.2.0, www.r-project.org, accessed 1 Oct 2013). Covariates with correlation coefficients >0.6 were not combined in the same model, and we did not investigate models with >1 interaction term or >2 additive effects because the number of individuals included in the analysis was relatively small. Therefore, we combined the best temporal structure with the best non-habitat and habitat covariates from the previous modeling stages to generate the final model set. Because of our interest in the potential presence of acute post-fire impacts on adult survival, we specifically maintained the acute fire effect covariate throughout the modeling process, and carried it forward to additive models regardless of its ranking within the temporal model set.

Analysis

We conducted nest survival analyses in Program MARK (White and Burnham 1999), using known-fate models. We used known-fate models because the GPS telemetry data enabled us to monitor and determine the exact dates of nest initiation and nest fate for all nests. We estimated and used daily nest survival to calculate survival over a 27-day incubation period each year, with year treated as a group effect. We developed *a priori* hypotheses and an associated model set to investigate the effect of each covariate on daily nest survival.

We estimated monthly survival of GPS-instrumented female sage-grouse using known-fate models with a staggered entry design in Program MARK (Pollock et al. 1989, White and Burnham 1999). Monthly survival intervals began on the first day and ended on the last day of each calendar month. We estimated monthly survival during 24 monthly intervals (Mar 2013–Feb 2015). We modeled the effect of habitat covariates following Webb et al. (2012*a*).

For individuals that died during an interval, we estimated mean habitat covariate values within 95% and 50% Brownian bridge kernel (BBK) ranges generated from all individual locations collected during the 13 days preceding mortality and the date of mortality (covariate analysis period) and applied those estimates to the interval including the mortality event (Webb et al. 2012*a*). For individuals that survived an interval, we randomly selected a 14-consecutive-day period within a single survival interval and used all locations within that period to estimate mean habitat covariates (Webb et al. 2012*a*). We did not allow covariate analysis periods between any 2 intervals to overlap. Thus, we assessed all habitat covariates as time-varying covariates (White and Burnham 1999). We developed *a priori* hypotheses and an associated model set to investigate the effect of each covariate on monthly survival.

RESULTS

We captured and instrumented 58 (adult = 33, yearling = 25) female sage-grouse with GPS-PTTs between 5 March 2013 and 4 April 2014 (i.e., prior to the 2014 nesting season). In 2013, of 35 individuals captured, 21 individuals remained marked and alive until the median first nest initiation date (5 May 2013; 15 adult, 6 yearling). Nineteen of these 21 individuals initiated ≥1 nest, resulting in a nest initiation rate of 0.905 for adults and yearlings combined (adult = 0.867, yearlings = 1.0). Thirteen individuals experienced failure of their first nest during 2013 but survived through initiation of renests (i.e., 22 May 2013; 11 adult, 2 yearlings), 3 of these 13 available individuals initiated a second nest (renesting rate: all individuals = 0.231; adult = 0.273, yearling = 0.0). In 2014, 22 individuals remained marked and alive until the median first nest initiation date (21 Apr 2014; 15 adult, 7 yearling), and all individuals initiated ≥1 nest. Fourteen individuals experienced failure of their first nest but survived through initiation of renests (22 May 2014; 10 adult, 4 yearling), and 8 initiated a second nest (renesting rate: all individuals = 0.571; adult = 0.70; yearling = 0.25).

Nest Characteristics

We monitored 52 nests (2013 = 22, 2014 = 30) with 71% of nests located within the boundary of the Holloway fire. For nests outside of the fire, mean distance to the fire boundary was 767 ± 817 (SD) m (*n* = 15). The mean distance between nests in 2013 and nests in 2014 for individuals that nested within the fire boundary was 1,275 m greater than for individuals that nested outside the fire boundary (inside: $\bar{x} = 1{,}648 \pm 402$ m; outside: $\bar{x} = 373 \pm 49$ m). Additionally, the mean distance between first and second nests for individuals that nested within the fire boundary ($\bar{x} = 1{,}976 \pm 3{,}210$ m) was 1,593 m greater than for individuals that nested outside the fire boundary ($\bar{x} = 383 \pm 151$ m).

Most nests were located in intact sagebrush habitat either within or outside the fire boundary (79%), with 70% of nests inside the fire boundary located within intact sagebrush patches. Of all nests, 71% were located under live sagebrush shrubs (outside fire boundary: 87%; inside fire boundary: 65%). Alternate nest cover species and types within the fire boundary included dead sagebrush (*n* = 3), rabbitbrush (*Ericameria* sp.; *n* = 1), snowberry (*n* = 2), Great Basin wildrye (*n* = 3), bluebunch wheatgrass (*Pseudoroegneria spicata*; *n* = 2), bare-ground (*n* = 1), and a rock outcrop (*n* = 1). Alternate nest cover species and types outside the fire boundary included horsebrush (*Tetradymia* sp.; *n* = 1), and bitterbrush (*n* = 1).

Although nesting habitat use and cover types were similar during 2013 and 2014, the size of intact patches used as nesting habitat was variable during both years. In 2013, mean patch size of intact sagebrush in the interior of the fire used as nesting habitat was 917 ha (*n* = 6, range = 3–4,833 ha). In 2014, mean patch size was 286 ha (*n* = 9, range = 0.01–638 ha). Additionally, although some intact sagebrush patches used as nesting habitat were large (≤4,834 ha), sage-grouse often nested proximate to patch edges. The mean distance to burned habitat for individuals nesting in intact sagebrush patches within the interior of the fire was 39 m (*n* = 6, range = 17–68 m), and 33 m (*n* = 9, range = 2–195 m) during 2013 and 2014, respectively.

Nest Survival

We observed strong support for the effect of nesting attempt on daily nest survival of sage-grouse, but the direction of that relationship varied by year (Table 3). Nineteen of 45 models contained the interaction between year and nesting attempt and received 92% of the model weight, and all competitive models contained this interaction (Table 3). First nests were more likely to survive a given day than re-nests in 2013, but during 2014, re-nests were more likely to survive a given day than first nests (year$_{2013}$: $\widehat{\beta} = -2.83$, 95% CI = −4.75 to −0.91, nest attempt$_{\text{first nest}}$: $\widehat{\beta} = -2.35$, 95% CI = −3.87 to −0.84, year$_{2013}$× nest attempt$_{\text{first nest}}$: $\widehat{\beta} = 3.16$, 95% CI = 1.06 to 5.25; Table 4).

Our best model also supported the positive effect of distance to riparian features (DTR), with diminishing benefits at the farthest distances (ln(DTR); $\widehat{\beta} = 0.47$, 95% CI = 0.127 to 0.814). This was generally consistent with our predictions that daily nest survival increased with distance to riparian features; however, that benefit reached a threshold at approximately 100 m, after which the improvement in daily nest survival began to level off (Fig. 2). An increase in distance to riparian features from the first quartile to the third quartile of observed values (61–284 m, 223-m increase in DTR) increased the likelihood of a nest surviving a given day 2.06 times. When we held distance to riparian features at the mean value (204 m), nesting period survival of first nests decreased slightly between 2013 and 2014, but nesting period survival of second nests in 2014 increased considerably compared to first nests in both years (Fig. 3). Derived estimates based on mean distance to riparian features indicated that on average nest survival (NS) was greater in 2014 than in 2013 (2013: NS = 0.227, 95% CI = 0.098–0.441; 2014: NS = 0.355, 95% CI = 0.195–0.556; Fig. 3).

Two other models were highly competitive with the top model, and 95% confidence limits around model coefficients did not include zero (Table 4). Thus, there was

Table 3. Model selection results for each modeling stage: temporal and biological covariates, landscape and habitat covariates, and the final additive models, relating categorical and continuous nest characteristics to daily survival of sage-grouse nests in the Trout Creek Mountains, Harney and Malheur counties, Oregon, USA, 2013–2014. We ranked models according to Akaike's Information Criterion adjusted for small sample size (AIC_c). The ΔAIC_c, AIC_c weights, number of parameters (K), and model deviance are included for all models. Only models within 2 ΔAIC_c of the top model within each category are displayed, the intercept-only model is also included for comparison during the first 2 steps, and the highest ranked model (year × nesting attempt) from the 2 initial steps is included for comparison in the additive model set.

Model[a,b]	ΔAIC_c	w_i	K	Deviance
Temporal and biological				
Year × nesting attempt	0.00[c]	0.308	4	270.22
Year × standardized initiation date	0.68	0.219	4	270.90
Nesting attempt	1.28	0.162	2	275.54
Intercept only	4.67	0.030	1	280.93
Landscape and habitat				
Intercept only	0.00[d]	0.117	1	280.93
Distance to riparian	0.90	0.074	2	279.57
pt_Distance to Riparian	1.04	0.070	2	279.96
Percent patch cover_1500	1.33	0.060	2	280.25
Edge density_1500	1.37	0.059	2	280.29
pt_Percent patch cover_100	1.39	0.058	2	280.32
Percent patch cover_100	1.41	0.058	2	280.33
pt_Edge density_1500	1.56	0.053	2	280.48
Edge density_100	1.78	0.048	2	280.70
Edge density_550	1.78	0.048	2	280.71
Nest habitat	1.83	0.047	2	280.76
Percent patch cover_550	1.86	0.046	2	280.78
pt_Edge density_100	1.91	0.045	2	280.83
Distance to edge	1.92	0.045	2	280.84
pt_Edge density_550	1.95	0.044	2	280.87
pt_Percent patch cover_550	1.98	0.043	2	280.90
pt_Percent patch cover_1500	1.98	0.043	2	280.90
pt_Distance to edge	2.00	0.043	2	280.92
Additive models				
Year × nesting attempt + pt_distance to riparian	0.00[e]	0.264	5	263.74
Year × nesting attempt + distance to riparian	0.38	0.218	5	264.12
Year × nesting attempt+age	0.41	0.215	5	264.15
Year × nesting attempt	4.45	0.029	4	270.22

[a] Prefix definition: pt = pseudo threshold form of covariate (ln(X)).

[b] Suffix definitions: 100 = covariate measured at 100-m circular buffer scale; 550 = covariate measured at 550-m circular buffer scale; 1,500 = covariate measured at 1,500-m circular buffer scale.

[c] Lowest $\text{AIC}_c = 278.27$.

[d] Lowest $\text{AIC}_c = 282.94$.

[e] Lowest $\text{AIC}_c = 273.82$.

support for the positive additive linear effects of distance to riparian features ($\beta_{\text{DTR}} = 0.003$, 95% CI = 0.000–0.006), and the negative additive effect of age on daily nest survival ($\beta_{\text{adult}} = -0.950$, 95% CI = −1.742 to −0.157), in addition to the interactive effects of year and nest attempt (Table 3). The linear form of distance to riparian was highly correlated with pseudo-threshold form and demonstrated a similar relationship to daily nest survival as the top model. Contrary to predictions, the effect of age suggested nest survival was lower for adults than yearling females, with nests initiated by yearlings having 2.56 times higher likelihood of surviving a given day than nests initiated by adults.

Adult Survival

We monitored 64 individual female sage-grouse between March 2013 and February 2015. We right censored 11 individuals in the data set because of uncertainty about their final fate or date of mortality. We observed strong support for the hypothesis that survival varied by month, but not between years, except for the additional, negative acute effect on survival during the first 5 months of the study (acute fire effect, AFE; Mar 2013–Jul 2013; Table 5). Eighteen of 70 models included monthly variation across years and received 97% of model weight (Table 5). Ten of 70 models contained acute fire effect and received 50% of model weight, and the top 2 models contained both monthly variation and acute fire effect (Table 5). The 95% confidence limit around the model coefficient for acute fire effect only slightly overlapped zero (<1%; $\beta_{\text{AFE}} = -0.985$, SE = 0.505, 95% CI = −1.975 to 0.005) and suggested relatively strong support for lower monthly survival during the second half of the first year post-fire (i.e., Mar 2013–Jul 2013). Probability of survival varied considerably between months within a year, with the lowest probability of survival observed during April and August, and the highest probability of survival observed during November, January, and February (Fig. 4). The likelihood of surviving a given month during March–July 2014 was 2.67 times greater than the likelihood of surviving that month during March–July in 2013 (Fig. 4). When we extrapolated monthly survival estimates, average survival increased by 33% between biological year 2013–2014

Table 4. Coefficient estimates (β) and 95% confidence limits (lower: LCL; upper: UCL) from the 3 best-ranked models of greater sage-grouse nest survival in the Trout Creek Mountains, Harney and Malheur counties, Oregon, USA, 2013–2014.

Model[a]	Parameter	β	LCL	UCL
Year×nesting attempt+pt_distance to riparian				
	Intercept (2014)	2.577	0.610	4.545
	Year (2013)	−2.829	−4.747	−0.911
	Nesting attempt (first nest)	−2.353	−3.872	−0.835
	Year × nesting attempt	3.155	1.057	5.252
	ln(Distance to riparian)	0.470	0.127	0.814
Year×nesting attempt+distance to riparian				
	Intercept (2014)	4.261	2.851	5.671
	Year (2013)	−2.808	−4.737	−0.880
	Nesting attempt (first nest)	−2.263	−3.772	−0.755
	Year × nesting attempt	2.979	0.912	5.046
	Distance to riparian	0.003	0.000	0.006
Year×nesting attempt+age				
	Intercept (2014)	5.281	3.728	6.834
	Year (2013)	−1.874	−3.704	−0.045
	Nesting attempt (first nest)	−2.073	−3.559	−0.588
	Year × nesting attempt	2.143	0.167	4.119
	Age (adult)	−0.950	−1.742	−0.157

[a] Prefix definition: pt = pseudo threshold form of covariate (ln(*X*)).

($\widehat{S} = 0.244$, 95% CI = 0.090–0.398) and biological year 2014–2015 ($\widehat{S} = 0.361$, 95% CI = 0.163–0.558).

There were a number of other competitive models ($\Delta \mathrm{AIC}_c < 2$) that included habitat covariates in addition to the basic structure of the top model (i.e., t + AFE + habitat covariate; Table 5). These included effects of the proportion of locations in intact habitat, the pseudo-threshold form of the amount of intact habitat within an individual's 50% Brownian bridge kernel range, the pseudo-threshold form of the mean terrain roughness index value within an individual's 95% Brownian bridge kernel range, the connectance index using a 1-km threshold within an individual's 50% Brownian bridge kernel range, and an individual's 50% Brownian bridge kernel range size (Table 5). However, estimates of model coefficients on all of these covariates widely overlapped zero (>10%), suggesting these parameters were largely uninformative (Arnold 2010).

DISCUSSION

Our study provides some of the first insights regarding the acute effects of large-scale wildfire on sage-grouse nesting ecology and adult survivorship. Female sage-grouse continued to occupy areas either directly burned, or proximal to burned habitat (Foster 2016), and although they frequently nested either within or proximal to burned habitat, nesting propensity and renesting rates were within the range of natural variation for the species (Connelly et al. 2011*b*). This continued use of the landscape affected by the Holloway fire appeared to have an acute fitness cost in terms of daily nest survival and adult survival during the first 2 years post-fire. Thus, reduced vital rates likely contribute to observed declines in sage-grouse population trend following wildfire (Coates et al. 2016).

Although sage-grouse typically exhibit strong site fidelity to breeding and nesting areas (Dalke et al. 1963, Wallestad and Schladweiler 1974, Emmons and Braun 1984, Dunn and Braun 1985, Connelly et al. 2011*b*), our data suggest that nest site fidelity, at the scale of the individual nest, may have been weaker for individuals in the interior of the fire than for individuals nesting outside of the fire. However, high mortality rates during the first 2 years post-fire reduced our sample to only 6 individuals that survived to nest in both years, limiting our strength of inference. Sage-grouse in

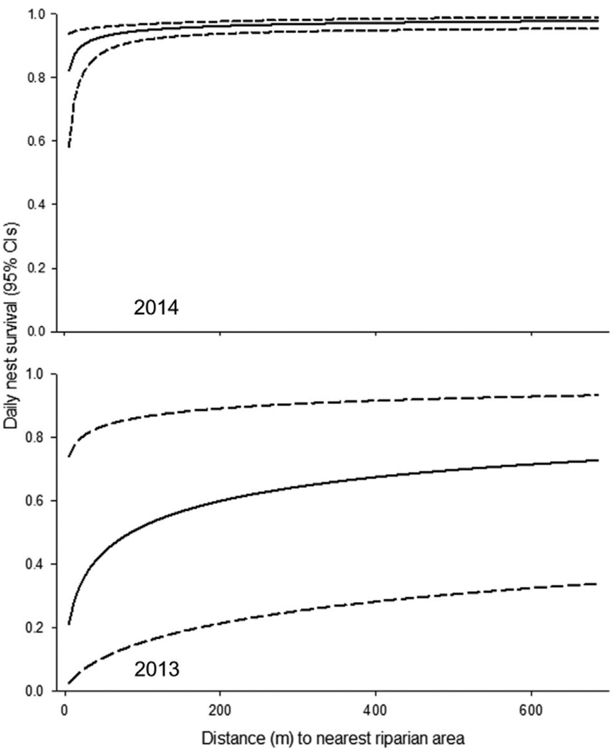


Figure 2. Greater sage-grouse daily nest survival estimates, and 95% confidence intervals, in relation to distance from nest to riparian area, in the Trout Creek Mountains, Harney and Malheur counties, Oregon, USA, 2013–2014.

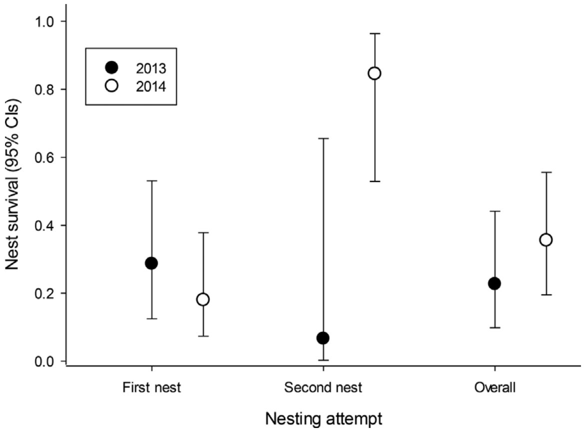


Figure 3. Greater sage-grouse incubation period (27-day) nest survival estimates, and 95% confidence intervals of first nests, second nests, and all nests, while holding distance to riparian area at mean value, in the Trout Creek Mountains, Harney and Malheur counties, Oregon, USA, 2013–2014.

Table 5. Model selection results for models from each modeling stage: temporal covariates, biological covariates, landscape and habitat covariates, and additive models, relating categorical and continuous nest characteristics to monthly survival of greater sage-grouse instrumented with global positioning system platform terminal transmitters (GPS-PTTs) in the Trout Creek Mountains, Harney and Malheur counties, Oregon, USA, during 2013–2014 and 2014–2015. We ranked models according to Akaike's Information Criterion adjusted for small sample size (AIC$_c$). We provide ΔAIC$_c$, AIC$_c$ weights (w_i), number of parameters (K), and model deviance for all models. The intercept-only model is included in each model step for comparison. Temporal and biological steps present all models; because of large model sets, landscape and habitat, and additive steps present competitive models only (ΔAIC$_c < 2$).

Model[a,b]	ΔAIC$_c$	w_i	K	Deviance
Temporal				
Month across year	0.00[c]	0.820	12	241.66
Season	3.58	0.137	3	264.01
Acute fire effect	7.39	0.020	2	269.85
Linear time trend	8.89	0.010	2	271.35
Intercept only	9.40	0.007	1	273.89
Time	10.64	0.004	24	225.81
Year	13.07	0.001	3	273.51
Biological				
Range size_50	0.00[d]	0.338	2	270.62
Intercept only	1.24	0.181	1	273.89
Nest status	1.71	0.144	2	272.33
pt_Range size_50	2.49	0.097	2	273.12
Range size_95	2.61	0.092	2	273.23
pt_Range size_95	2.85	0.081	2	273.47
Age	3.23	0.067	2	273.85
Landscape and habitat				
Proportion locations intact	0.00[e]	0.049	2	271.43
pt_Percent intact_50	0.03	0.048	2	271.47
Connectance index long_50	0.04	0.048	2	271.48
Percent intact_50	0.12	0.046	2	271.55
pt_Proportion locations intact	0.23	0.043	2	271.67
pt_Terrain roughness index_95	0.34	0.041	2	271.77
Intercept only	0.43	0.039	1	273.89
Percent intact_95	0.64	0.035	2	272.07
q_Percent intact_95	0.75	0.034	3	270.15
Terrain roughness index_95	1.00	0.030	2	272.44
Mean distance to intact	1.09	0.028	2	272.52
pt_Terrain roughness index_50	1.16	0.027	2	272.59
pt_Mean normalized difference vegetation index_50	1.23	0.026	2	272.66
pt_Mean normalized difference vegetation index_95	1.23	0.026	2	272.66
Standard deviation normalized difference vegetation index_50	1.23	0.026	2	272.67
pt_Edge density_95	1.25	0.026	2	272.68
pt_Edge density_50	1.28	0.026	2	272.71
pt_Percent intact_95	1.28	0.026	2	272.71
pt_Mean distance to intact	1.29	0.026	2	272.72
pt_ Standard deviation normalized difference vegetation index_95	1.47	0.023	2	272.91
Standard deviation normalized difference vegetation index_95	1.56	0.022	2	272.99
pt_ Standard deviation normalized difference vegetation index_50	1.69	0.021	2	273.12
pt_Connectance index short_95	1.82	0.020	2	273.26
q_Proportion locations intact	1.87	0.019	3	271.28
Terrain roughness index_50	1.95	0.018	2	273.38
Connectance index short_50	1.99	0.018	2	273.43
Edge density_95	2.00	0.018	2	273.43
Combined models				
Month+acute fire effect	0.00[f]	0.145	13	237.44
Month+acute fire effect+year	0.62	0.106	14	235.90
Month+acute fire effect+proportion locations intact	1.24	0.078	14	236.52
Month+acture fire effect+pt_percent intact_50	1.39	0.072	14	236.67
Month+acute fire effect+percent intact_50	1.44	0.070	14	236.73
Month+acute fire effect+pt_terrain roughness index_95	1.50	0.069	14	236.78
Month+acute fire effect+pt_proportion locations intact	1.65	0.064	14	236.93
Month+acute fire effect+connectance index long_50	1.72	0.061	14	237.01
Month+acute fire effect+range size_50	1.94	0.055	14	237.22
Intercept only	11.48	0.000	1	273.89

[a] Prefix definitions: pt = pseudo-threshold form of covariate (ln(X)); q = quadratic form of covariate (X^2).

[b] Suffix definitions: 50 = covariate measured in 50% Brownian bridge kernel range; 95 = covariate measured in 95% Brownian bridge kernel range.

[c] Lowest AIC$_c$ = 266.50.

[d] Lowest AIC$_c$ = 274.65.

[e] Lowest AIC$_c$ = 275.47.

[f] Lowest AIC$_c$ = 264.42.

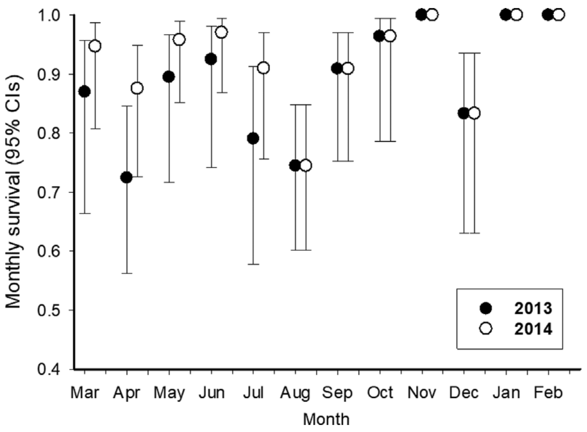


Figure 4. Model averaged estimates, and 95% confidence intervals, of greater sage-grouse monthly survival in the Trout Creek Mountains, Harney and Malheur counties, Oregon, USA, 2013–2014 and 2014–2015.

Washington, USA, inhabiting a highly fragmented landscape exhibited diminished nest site fidelity in comparison to sage-grouse inhabiting intact landscapes (Schroeder and Robb 2003). The effects of large-scale wildfire provide a mechanism for habitat fragmentation, and may thus result in reduced nest site fidelity although we could not document that clearly in our study.

The nest initiation rate we observed in 2013 was similar to reported averages for the species (Taylor et al. 2012, Dahlgren et al. 2016), but daily nest survival was on the extreme low end of the reported range (15–86%; Connelly et al. 2011*b*). In 2014, the interplay between increased nesting and renesting rates, and increased daily nest survival of second nests resulted in a higher estimate of nest survival (36%), although it was still at the lower end of the range reported for the species (Connelly et al. 2011*b*). In addition, although nest survival of sage-grouse was not monitored prior to the Holloway fire, the rates we observed in this study were considerably lower than those observed by concurrent studies of sage-grouse nest survival in Oregon and elsewhere in the Great Basin. Nest survival for the 27-day incubation period in the Warner Mountains, approximately 140 km west of our study area, were 51% and 53%, in 2013 and 2014, respectively (Severson 2016). At the Sheldon-Hart Mountain National Wildlife Refuge complex, approximately 110 km west of our study area, 28-day nest survival was 45% during 2013 and 2014 (Street et al. 2014). Additionally, 27-day nest survival averaged between 40% and 43% in 2013 and 2014, respectively, across 8 study areas in northern Nevada, and eastern California, USA (P. S. Coates, U.S. Geological Survey, unpublished data). The marked increase (56%) in nest survival between 2013 and 2014 that we observed in our study area was not apparent across these concurrent studies. This supports our conclusion that nest survival was reduced because of the fire, and that the increase in nest survival between the 2 years of the study was likely influenced by changes in vegetation structure and abundance. By 2014, the amount of herbaceous vegetation in burned habitats increased compared to the 2013 nesting season, and continued to increase as the 2014 nesting season progressed. However, we cannot rule out the effect potential changes in predator communities might have had on nest survival post-fire (Howe et al. 2014) because we did not survey for mammalian or avian predators during our study.

Although we did not document direct effects of post-fire land cover on nest survival, we observed potential indirect effects of habitat and land cover through the interaction between year (i.e., a coarse reflection of time since fire) and nesting attempt (i.e., a coarse reflection of nest initiation date in relation to growing season progression). Sage-grouse select nest sites based on micro-scale vegetation (Connelly et al. 2011*c*); thus, micro-site habitat characteristics may have a greater influence on survival than landscape-scale habitat configuration (Baxter et al. 2008, Webb et al. 2012*b*, Lockyer et al. 2015). In addition to this potential dynamic, the sampled nests in our study may not have had enough variation in landscape-level habitat covariates to detect an effect on nest survival. Sage-grouse did appear to disproportionately place nests in intact habitat; thus, remnant intact habitat and the structure of the habitat mosaic following fire may influence nest site selection to a greater extent than they influence nest survival. Although we measured micro-site vegetation during our study, we collected those measurements following the end of the growing season, which likely resulted in micro-scale vegetation data that had changed considerably compared to conditions during incubation, limiting the utility of those data in describing patterns of nest success (Foster 2016).

Contrary to previous research, we did not find support for the effects of age, nesting status, or habitat covariates on adult survival (Zablan et al. 2003, Blomberg et al. 2013, Davis et al. 2014, Dinkins et al. 2014). However, the strong decline in survival immediately following the fire was likely indicative of the general large-scale loss of sagebrush habitat within the fire boundary (~75% of pre-fire sagebrush cover lost). The growing season in Great Basin sagebrush communities occurs from approximately April to August (Comstock and Ehleringer 1992, Dysart 2001, Wrobleski and Kauffman 2003). In this system, vegetation is almost completely removed in areas directly burned by wildfire, and during the period following summer wildfire and prior to the first growing season, vegetation in burned areas remains essentially non-existent (Wrobleski and Kauffman 2003). We observed this pattern of habitat loss and regeneration during this study, and immediately following the fire we observed high mortality rates as birds returned to, or remained within the fire boundary. This period of high mortality extended until herbaceous cover had reestablished following the first post-fire growing season (Foster 2016). Within a sample of conventional radio-marked individuals collared immediately following the fire (Oct 2012), overwinter survival during 2012–2013 was less than (S_t, winter 2012–2013 = 0.830; Foster 2016) estimates from populations inhabiting intact habitat (monthly S_t, winter = 0.917–0.973, Moynahan et al. 2007; 0.96–0.98, Battazzo 2007; 0.623–1.00, Anthony and Willis 2009). Increases in sage-grouse survival following summer 2013 likely reflected an end to this period of pronounced mortality as populations inhabiting the fire boundary fell below carrying capacity of the remaining habitat and as herbaceous cover within burned areas increased to the point where it provided hiding cover and forage for the remaining sage-grouse population.

Predation is the primary mechanism influencing sage-grouse mortality in intact ecosystems (Hagen 2011*b*). However, there are a number of indirect mechanisms that may increase the likelihood of predation, including lack of concealment cover, changes in food availability, and challenges to thermoregulation (Wiebe and Martin 1998). The latter 2 factors are perhaps more obvious indirect effects leading to increases in predation, whereby birds may be in poor condition because of limited diet or increased physiological stress while trying to thermoregulate effectively in a highly variable thermal environment (Hovick et al. 2014). Clearly, reductions in concealment cover are more directly related to predation at broad and local scales. As patch size is reduced, predator efficiency can increase (Chalfoun et al. 2002) and lack of shrub cover reduces the effectiveness of cryptic plumage. We are only able to speculate as to which of these mechanisms was most important in explaining the increased mortality rates. Regardless, there was a measurable fitness cost to sage-grouse attempting to persist in the post-fire landscape through reduced survival of adult females and nests the first year post-fire compared to the second year post-fire.

MANAGEMENT IMPLICATIONS

The acute and generalized reductions in sage-grouse nest and adult survival we observed following the Holloway fire suggest that fire suppression (e.g., fuel breaks, direct attack) to maintain patches of intact sage-grouse habitat may be the most important management activity currently available to managers of fire-prone landscapes. Suppression efforts in sage-grouse habitat are likely to be most beneficial if focused on limiting fire within intact sage-grouse nesting habitat, particularly in ecosystems where recovery and resilience after disturbance may be low. In addition, suppression efforts that are not limited to suppressing fire spread but also extend to the suppression of interior fire and the protection of interior habitat islands whenever possible are likely to be the most effective at preserving sage-grouse habitat.

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