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Fitness consequences of catastrophic wildfire are mitigated by behavioral responses of an iconic bird

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Abstract

Background Drought, human disturbance, and invasive species are reshaping disturbance regimes and increasing the scale, severity, and frequency of wildfire in many ecosystems around the globe, including the sagebrush steppe of western North America. Recent studies suggested greater sage-grouse (*Centrocercus urophasianus*) adhere to strong site fidelity in the aftermath of wildfire, remaining inside fire perimeters for nesting and brood rearing despite negative consequences for survival and reproduction. Sage-grouse in Idaho exhibited context-dependent changes to space use after a large, high-severity fire that burned > 40,000 ha, yet the specific behavioral responses to fire and their fitness consequences remain unclear. We used data collected from 269 hens over a 6-year period under a multi-level before-after-control-impact design to test the hypothesis that sage-grouse mitigated fitness consequences of high-severity wildfire through adaptive behavioral responses and spatial redistribution.

Results We tested predictions deduced from our hypothesis at the population and individual levels using behavioral, demographic, and life history data, including nesting metrics, brood-rearing metrics, hen survival, and body mass at capture. Fifteen of 16 predictions were supported, demonstrating that post-fire space use and avoidance of the burn was adaptive and helped mitigate fitness effects of the fire. Short-term consequences included elimination of nesting and brood rearing habitat and subsequent shifts to the distribution of usable space. Yet fitness consequences were minimal because of behavioral flexibility employed by hens during nesting and brood rearing.

Conclusions Behavioral responses to wildfire by sage-grouse are more flexible than has been described, and sage-grouse demonstrated resilience by rapidly adapting space use to avoid short-term consequences of catastrophic fire when high-quality habitat remained adjacent to the burn and within their seasonal range. Our results imply behavioral and fitness consequences of fire are context-dependent and likely impacted by attributes of the fire and surrounding landscape after disturbance. Furthermore, among-study differences in behavioral and fitness outcomes of sage-grouse after fire supported underappreciated predictions from both fire ecology and site fidelity theory, and suggest conditions where behavioral flexibility should be expressed, and fidelity relaxed, based on severity of disturbance, landscape context, and species mobility.

Keywords Adaptive space use, Behavioral flexibility, Behavioral plasticity, Centrocercus urophasianus, Disturbance, Rapid environmental change, Sage-grouse, Sagebrush, Site fidelity

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Resumen

Antecedentes Las sequías, los disturbios causados por humanos, y las especies invasoras, están reconfigurando los regímenes de disturbio e incrementando la escala, severidad, y frecuencia de incendios en muchos ecosistemas alrededor del mundo, incluyendo la estepa de Artemisia del oeste de los EEUU. Estudios recientes sugieren que el ave "*urogallo de las Artemisas*" (*Centrocercus urophasianus*) se arraiga fuertemente y con gran fidelidad a su hábitat luego de un incendio, permaneciendo dentro de los perímetros del fuego para anidar y luego criar a sus polluelos, a pesar de las consecuencias negativas para su supervivencia y reproducción. El urogallo de las Artemisas en Idaho, exhibió cambios dependientes del uso de espacio luego de un gran fuego de alta severidad que quemó > 40,000 ha, aunque las respuestas específicas sobre su comportamiento al fuego y sus ajustes a consecuencias posteriores continúan siendo poco claras. Usamos datos colectadas de 269 hembras de urogallo en un período de 6 años bajo un diseño multinivel de antes, después y control del impacto (del fuego) para probar la hipótesis en la cual el urogallo mitiga y se ajusta a las consecuencias de un incendio de alta severidad a través de un comportamiento de respuestas adaptativas y de redistribución en el espacio.

Resultados Probamos las predicciones deducidas en nuestra hipótesis a niveles de individuos y de poblaciones usando datos demográficos, de comportamiento, e historias de vida, incluyendo métricas de anidamiento y de cría, supervivencia de hembras y masa corporal al momento de la captura. Quince de las 16 hipótesis fueron corroboradas, demostrando que la ocupación del espacio post fuego y el evitar las quemas, es un aspecto adaptativo que ayudó a mitigar el ajuste a los efectos del fuego. Las consecuencias en el corto plazo incluyeron la eliminación de lugares de anidamiento y cría y los consecuentes cambios en la distribución del espacio de uso. Aún así, las consecuencias del ajuste fueron mínimas dada la flexibilidad en el comportamiento mostrado por las hembras de urogallo durante el período de anidamiento y cría.

Conclusiones Las respuestas comportamentales al fuego por parte del urogallo de Artemisa son más flexibles de lo que se había descripto, y esta ave demostró una gran resiliencia para adaptarse rápidamente al uso del espacio y evitar así las consecuencias a corto plazo de los fuegos catastróficos cuando sitios de alta calidad del hábitat se encuentran dentro de su rango de distribución. Nuestros resultados implican que las consecuencias del comportamiento y de ajuste al fuego son contexto-dependientes, y probablemente impactadas por los atributos del fuego y del paisaje que lo rodea luego de este disturbio. Además, las diferencias entre estudios en cuanto a comportamiento y ajustes al hábitat del urogallo de Artemisa luego de eventos de incendios, apoyan las predicciones subvaloradas tanto de la ecología del fuego como la teoría de la fidelidad al sitio, y sugiere condiciones donde la flexibilidad en el comportamiento debe ser expresada, y la fidelidad al sitio un poco más relajada, basados en la severidad del disturbio, el contexto del paisaje, y la movilidad de las especies.

Background

Fire is an integral part of the ecological and evolutionary history of plants and animals, which are adapted to specific ranges of fire conditions and activity (Hutto et al. 2008; Pausas and Keeley 2009). Fire also creates scale-dependent vegetation patchiness and landscape heterogeneity that can increase species diversity across a range of scales in space and time (He et al. 2019). However, changes to fire regimes substantially impact vegetation structure and composition, often resulting in novel communities, successional trajectories, and habitats for both vertebrate and invertebrate species (Franklin et al. 2016; Keeley and Pausas 2019). Changing fire regimes can therefore decrease or even reverse benefits to biodiversity when fire attributes (e.g., scale, frequency, intensity) move outside their historical range of variation (He et al. 2019; Santos et al. 2022). These changes impact conservation and resilience of animal populations in fire-prone ecosystems, yet there remains substantial uncertainty about species-specific impacts (McKenzie et al. 2004); Jager et al. 2021). Indeed, a mechanistic understanding of species- and population-level responses to fire represents a major knowledge gap impeding conservation in the face of environmental change (Driscoll et al. 2010).

Fire can impact demography and resilience of animal populations both directly and indirectly through changes to vital rates and modification of behavior, habitat, and species interactions (Engstrom 2010; Jolly et al. 2022; Doherty et al. 2022). Changes to habitat choice, movement, and reproductive decisions can be induced by fire through changes to the availability of resources such as food or cover, or by changes to the distribution and abundance of interacting species (Tuomainen and Candolin 2011; Pausas and Parr 2018). Consequently, fire effects can be realized through a variety of processes that influence survival and reproduction (Santos et al. 2022). For example, fire can cause direct mortality or decrease survival indirectly by increasing vulnerability of prey species to predation, but behavioral responses of prey may minimize these impacts (e.g., dispersal into unburned habitats). Behavior and mobility are therefore critical attributes for understanding short- and long-term responses of animals to fire (Nimmo et al. 2019). Attributes of individual fires can also dictate their consequences for animals (e.g., scale, severity; Smucker et al. 2005), yet a lack of empirical data across a range of fire types creates considerable uncertainty surrounding the responses of most species (Pausas and Parr 2018). Understanding demographic consequences of fire and the behaviors that mediate fitness responses in animals across scales are therefore critical for conservation of sensitive species in fire-prone landscapes (Driscoll et al. 2010; Nimmo et al. 2021, 2022), especially with respect to high-severity, large-scale fire events (hereafter catastrophic fires) that are increasingly common in temperate regions (Jolly et al. 2022).

Behavioral changes can provide a buffer for animals against changing conditions and are typically the first responses by individuals to rapid environmental change (Wong and Candolin 2015; Sergio et al. 2018). Behavioral flexibility is a type of phenotypic plasticity that allows individuals to change their behavior in response to changing conditions, and represents a response to environmental variation that can help organisms cope with disturbance and persist under novel conditions (Beever et al. 2017). Flexible behaviors therefore serve as a conduit through which wildfire affects demographic processes of animals and can facilitate population persistence in the face of disturbance (Sergio et al. 2018; Buchholz et al. 2019). However, existing behavioral plasticity evolved in response to past environmental variation, and novel disturbance regimes may exceed those conditions. Resulting mismatches between environmental cues provided by fire and the ensuing responses of animals can cause disconnects between the perceived and real risks and rewards incurred by behavioral decisions, potentially resulting in maladaptive behaviors whereby animals make decisions based on cues that are effectively outdated (e.g., remaining inside fire scar despite increased predation risk; Wong and Candolin 2015; Nimmo et al. 2021). In these situations, environmental change and novel disturbance regimes can result in unique conditions that degrade the value of environmental cues used by animals to adjust behaviors and benefit fitness (Tuomainen and Candolin 2011; Wong and Candolin 2015). Nonetheless, behavioral responses to fire and their fitness outcomes are poorly understood for most species (Nimmo et al. 2019; Jolly et al. 2022).

The sagebrush steppe ecosystem of western North America illustrates the many challenges of conserving a vegetative community and its dependent wildlife in the face of changing fire-regimes and rapid environmental change (Brooks et al. 2004; Abatzoglou and Williams 2016; Abatzoglou et al. 2018; Duane et al. 2021; Pausas and Keeley 2021). Drought and invasive species (e.g., cheatgrass, *Bromus tectorum*) influence both intrinsic (e.g., moisture content) and extrinsic (e.g., landscape pattern and continuity) properties of fuels and interact across the sagebrush biome to produce larger, more severe, and more frequent fires, resulting in conversion of large landscapes to fire-tolerant exotic annual grasses (i.e., the cheatgrass-fire cycle; Whisenant 1990; D'Antonio and Vitousek 1992; Balch et al. 2013; Pilliod et al. 2017). These changes are particularly pronounced in more xeric, lower-elevation ecosystems, as resilience of sagebrush communities varies along moisture and elevational gradients (Davies et al. 2012; Chambers et al. 2014; Ringos et al. 2019). Large fires also complicate recovery and restoration of sagebrush communities because most species of *Artemisia* are killed and do not resprout following fire, and short seed dispersal distances and slow growth make their recolonization and recovery a long process (Reeves et al. 2018). Structural components of sagebrush vegetation that provide important habitat for many native species can take decades to half a century, or longer, to recover from fire (Baker 2006). Thus, changes to fire regimes, fuel continuity, and patterns of ignition have the potential to affect dynamics and persistence of a diverse array of sagebrush-dependent species over long ecological time scales (Knick et al. 2003; Pausas and Keeley 2014; Holbrook et al. 2016).

Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) are an iconic species of western North America and have been used as an umbrella species for conservation of sagebrush-dependent wildlife over broad scales (Rowland et al. 2006; Runge et al. 2019; Smith et al. 2019). The distribution of sage-grouse is linked closely with the distribution of sagebrush vegetation (Schroeder et al. 2004), whereas patterns of population extirpation and persistence have been strongly influenced by elimination of sagebrush cover and conversion of native shrub-steppe for agriculture and other land uses (Aldridge et al. 2008; Wisdom et al. 2011). Fire destroys sagebrush cover and can therefore have long-lasting effects on the quantity, quality, and spatial distribution of sage-grouse habitat (Nelle et al. 2000; Beck et al. 2003; Rhodes et al. 2010). Accordingly, changing fire regimes and the cheatgrass-fire cycle have contributed to population declines for sage-grouse across large portions of their range (Coates et al. 2016, 2020).

Fire can negatively affect sage-grouse over a range of spatial and temporal scales (Connelly et al. 2011b; Lockyer et al. 2015; Smith and Beck 2018; O'Neil et al. 2020), and negative fitness outcomes commonly result when sage-grouse use space inside fire perimeters (i.e., the footprint inside boundaries of a fire that often includes both burned and unburned patches of vegetation) instead of relocating post-burn (Foster et al. 2019; Dudley et al. 2021; Tyrrell et al. 2023). Environmental conditions remaining after wildfire are highly variable and depend on scale and severity of fire (Pausas and Parr 2018). Yet behavioral flexibility and the fitness consequences of sage-grouse responses to severe fire are poorly understood because past work typically studied mixed-severity fires that left patchy sagebrush distributed inside fire perimeters (e.g., Foster et al. 2019; Anthony et al. 2021b), assumed all but the lowest-intensity fires had equivalent consequences for behavior and fitness (e.g., O'Neil et al. 2020; Brussee et al. 2022), or did not address fire severity in their study descriptions, analyses, and conclusions (e.g., Dudley et al. 2021; Tyrrell et al. 2023). Thus, flexibility of behavioral responses by sage-grouse across gradients of fire severity, as well as the acute responses and consequences of catastrophic wildfire, remain unclear.

Sage-grouse exhibit strong fidelity to seasonal ranges during key life history events (e.g., breeding and nesting; Fischer et al. 1993) and subsequently may be particularly vulnerable to environmental change induced by catastrophic fire (Merkle et al. 2022). Deeper understanding of behavioral flexibility and the capacity for movements to more suitable areas is therefore needed to assess resilience and persistence of sage-grouse populations under rapid environmental change induced by catastrophic fire. We studied behavioral responses and fitness consequences of sage-grouse breeding in high-elevation mountain big sagebrush (*Artemisia tridentata vaseyana*) communities in eastern Idaho, USA, before and after a catastrophic wildfire that dramatically changed the composition of habitat available for a breeding population of grouse. We previously documented changes to use and selection of multiple components of breeding habitat with landscape-level changes to vegetation (Stevens et al. 2023a), yet the specific behavioral responses and consequences associated with the fire are unknown. Thus, our objective was to assess short-term responses and fitness consequences resulting from catastrophic fire, in terms of the ability of behavior to mitigate consequences of fire for sage-grouse. We developed population- and individual-level predictions under the general hypothesis that sage-grouse responses to catastrophic fire are adaptive, and tested these predictions using a suite of behavioral, demographic, and life history attributes. We also interpret our results relative to general predictions from fire ecology and site fidelity theory, thus providing empirical assessment of existing theory for a species and ecosystem with broad conservation and land management interests.

Methods

Study areas

We studied sage-grouse over a 6-year period (2015–2020) in eastern Idaho, USA (Fig. 1). We monitored distinct breeding subpopulations located in high-elevation

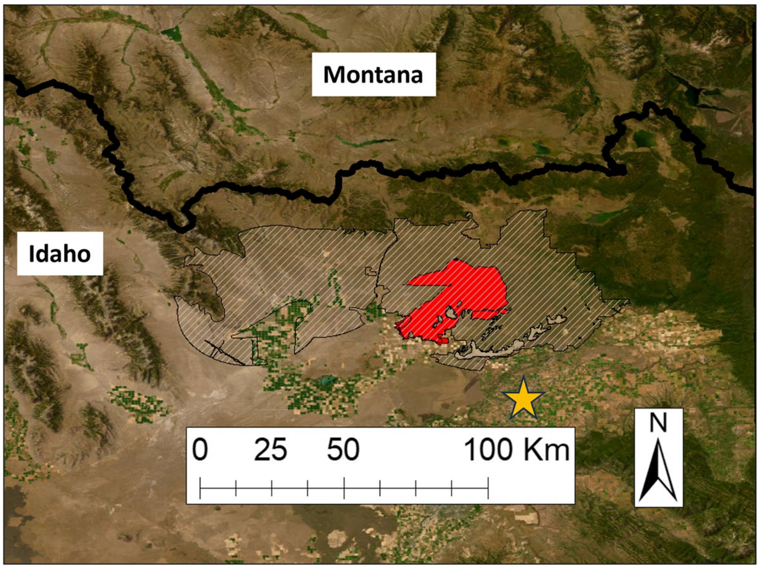

Fig. 1 Map of study areas used to assess fitness consequences of space use behaviors of greater sage-grouse in response to catastrophic wildfire in eastern, Idaho, USA (2015–2020). Study sites are indicated by white cross-hatched areas, with Medicine Lodge (control site) to the west and Sand Creek (impact site) to the east. The area burned by the > 40,000 ha Grassy Ridge Fire during July–August 2018 is indicated by the red polygon within Sand Creek, and the gold star is an indicator for Rexburg, Idaho

mountain big sagebrush communities on the Sand Creek (hereafter impact site) and Medicine Lodge (hereafter control site) study areas, and additional site details are provided by Stevens et al. (2023a). Both sites reside within the Snake River Plain (30.5–50.8-cm precipitation zone) and have an arid continental climate consisting of hot, dry summers (Jun–Aug) and cold winters (Nov–Mar). For example, 30-year average annual precipitation (1991–2020) adjacent to Sand Creek (Ashton, Idaho) was approximately 50 cm, with average summer maximum temperature of 26.3 °C and average winter minimum temperature of − 9.5 °C (http://www.ncdc.noaa.gov/cdo-web/datasets, accessed 2 Mar 2022). Sage-grouse at these sites are separated during the breeding season and exhibit fidelity toward breeding areas, but birds from both sites migrate across seasons and comingle outside of the breeding season (Dalke et al. 1963; Nelle et al. 2000), with a tendency to move to higher elevations to the north-northeast (Sand Creek) and north-northwest (Medicine Lodge) as vegetation desiccates during summer and back to lower elevations to the south-southwest during winter. A > 40,000 ha, high-intensity wildfire (hereafter Grassy Ridge Fire) fueled by strong winds and dry thunderstorms burned a large proportion of sage-grouse nesting habitat on the impact site in July–August of 2018 (Fig. 1), effectively eliminating shrub cover from within the fire perimeter (Stevens et al. 2023a). The Grassy Ridge Fire therefore provided a natural experiment and before-after-control-impact (BACI) design with multiple levels of spatial controls (i.e., control site and unburned portion of impact site) for assessing behavioral responses to the fire and the fitness consequences of those responses. Importantly, shrub growth and recovery at these sites is rapid, with recovery of shrub cover approximately 18–20 years post disturbance (Moffet et al. 2015). These sites have experienced low-moderate fire activity in recent decades, although the control site has experienced larger fires toward its northern reaches (Fig. S1).

General approach

We monitored behavior and demography of sage-grouse hens to test fitness consequences of their responses to catastrophic wildfire. Our goal was to test the overarching hypothesis that changes in sage-grouse behavior and space use arising from a catastrophic wildfire (Stevens et al. 2023a) were adaptive, and therefore served to ameliorate the otherwise negative fitness consequences of fire. We deduced predictions from this hypothesis that specified how spatial–temporal patterns of traits contributing to fitness (behavioral, demographic, life history) would relate to fire at both the population and individual levels (Table 1). These predictions differ from those offered by recent studies from the Great Basin that argued sage-grouse may exhibit maladaptive habitat selection in the aftermath of wildfire, effectively making demographic outcomes worse (O'Neil et al. 2020; Brussee et al. 2022).

The natural experiment provided by the fire and the pre- and post-fire data collection at multiple sites allowed us to test predictions using a BACI design at both the population and individual levels. We used study areas as the control (Medicine Lodge) and impact (Sand Creek) sites for population-level analyses, where the binary variable indicating control or impact observations was shared among individual hens within each site unless otherwise specified. We only considered sage-grouse hens from the Sand Creek study site for individual-level analyses, where the binary variable indicating control or impact for BACI analyses was determined based on spatial location of capture (Table 1). That is, hens captured inside the fire perimeter at Sand Creek were considered impact birds for individual-level analyses, whereas hens captured outside the fire perimeter were considered control birds. We also exclusively used response metrics measured in the same year as capture to assess fire impacts for individual-level analyses to avoid the potential confounding of individual hens moving from inside to outside the fire perimeter across years (or vice versa). This allowed us to focus individual-level analyses on birds from the impact study site that were exposed to the conditions created by catastrophic fire during the breeding season, where interactions between location of capture and time period indicated potential fire effects under the BACI design.

We split the categorical design variable representing before and after periods into 3 categories (before, 1st-year post fire, 2nd-year post fire) for both population- and individual-level analyses, which allowed for time-lagged responses to disturbance that that are common for sage-grouse (e.g., Harju et al. 2010; Smith and Beck 2018) and common for fire effects more generally (e.g., Conway et al. 2010). We sought to identify the significance and directional patterns of site-by-time period interactions to assess fire effects under the BACI design, which provides the evidence that observed patterns were indeed caused by the impact under study. For all analyses that involved model selection, we used Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002) for model ranking, evaluated model support using ΔAIC_c and Akaike model weights (w_i), and used the glmmTMB package (Brooks et al. 2017) in program R (version 4.3.0; R Core Team 2023) to fit models using maximum likelihood unless otherwise specified. We model averaged partial effects of regression coefficients for inference using the model.avg function in the MuMIn R package (Bartón 2022) when model selection uncertainty was high (e.g., multiple models ≤ 2 ΔAIC_c or

Table 1 Population- and individual-level predictions deduced from the hypothesis that sage-grouse mitigate fitness consequences of catastrophic wildfire through adaptive behaviors that help them avoid fitness consequences expected from large-scale disturbance. Support for (+) or against (−) each prediction is indicated based on presented results

Predictions	**Prediction supported**
Population level	
Patterns of resource use and selection will change in response to fire[a]	+
Fewer nest locations will be in close proximity to leks located inside the fire perimeter than outside	+
The fire will have limited or no affect population-level fitness traits across impact and control sites:	
Nest initiation	+
Nest success	+
Brood success	+
42-day brood count	+
Breeding season survival	+
Body mass at capture	+
Individual level[b]	
Nest locations will shift to outside the burned area after fire	+
Hens attending leks near the fire will not go into the fire perimeter to nest	+
Hens attending leks inside the fire perimeter will move outside to nest and will therefore move greater distances to nest	+
Hens attending leks inside and outside the fire perimeter will have a similar:	
Body mass at capture	–
Breeding season survival	+
Nests closer to the fire will not suffer reductions to productivity metrics[c]:	
Nest success	+
Brood success	+
42-day brood count	+

[a] This prediction was demonstrated in a previous analysis by Stevens et al. (2023a)

[b] Measured on impact site only but using a BACI design, with individuals trapped outside of fire perimeter serving as controls

[c] Measured using data from the post-fire period at impact site only

low w_i's). We based inferences on maximum-likelihood estimates of fixed effect model parameters, partial effects, and their confidence intervals from the top model, when model selection uncertainty was low. Lastly, because several population-level analyses included observations from the same hen across multiple breeding periods (e.g., for nest and brood success), we re-fit global models using mixed effects regression with a random intercept for each individual hen to ensure our inferences about fire effects were robust to use of the simpler fixed effects models for analysis.

Fieldwork

We captured and monitored sage-grouse hens during the breeding season at the impact site for the entire study duration (2015–2020) and at the control site for a reduced period before the fire (2017–2020). At each site, we captured sage-grouse March–April on or adjacent to active leks using rocket netting and spotlighting techniques (Wakkinen et al. 1992). Sage-grouse hens were weighed, aged as juvenile or adult using plumage characteristics (Braun and Schroeder 2015), and fitted with Global Positioning System (GPS) platform terminal transmitters ($n = 269$) before release at their capture locations (for additional details see Stevens et al. 2023a). We monitored hen locations daily throughout the breeding season. Transmitters were programmed to collect 6 locations daily (every 4 h), batteries lasted approximately 3 years, and hens were not recaptured after original transmitter deployment. Consequently, a subset of hens provided breeding season data for multiple study years (e.g., 25% of hens that were observed nesting provided nesting data in > 1 year). We used these data to assess predictions about effects of the catastrophic fire on multiple attributes related to sage-grouse behavior and fitness (Table 1), including hen survival and body mass; location, initiation, and success of nests; and brood success and counts at 42 days post hatch. We inferred the initiation of nest incubation when hen locations were observed at the nest location for ≥ 3 days. We visited nest sites to determine fate (success when at least one egg hatched, failure otherwise) based on eggshell characteristics and hatch timing (assuming 27 days of incubation; Schroeder et al. 1999), after hen locations differed from the nest site on several consecutive days. We conducted flush surveys for females with successful nests 42 days after hatching to count the number of chicks and determine brood success (successful brood if ≥ 1 chick survives; Riley and Conway 2020, Riley et al. 2021).

Population-level analyses

The first population-level prediction deduced from the hypothesis that sage-grouse mitigate fitness consequences of catastrophic wildfire through adaptive behavioral responses was that patterns of resource use and selection for important components of nesting habitat will change in response to fire (Table 1). Stevens et al. (2023a) verified this prediction empirically by demonstrating that hen sage-grouse exhibited functional responses in use and selection of key components of nesting habitat via changing patterns of habitat use and selection as a function of available conditions in the environmental space after catastrophic fire. Therefore, evidence supporting prediction 1 was already described and will not be described further here.

A second prediction related to population-level shifts in space use was that fewer nests would be in close geographic proximity to sage-grouse leks located inside the fire perimeter, as compared to outside, as nest locations would shift farther away from burned than unburned leks. We tested this prediction using binomial logistic regression to assess differences in the proportion of nests near leks located inside and outside the fire perimeter, before and after the fire (i.e., a lek location × period interaction model). For this analysis, the response variable was a binomial sample of the number of nests inside a buffered distance around burned (or eventually burned) and unburned sage-grouse leks, given the total number of nests observed on the study site in each year. For example, at the impact site in 2015 the number of nests within 5 km of active leks that would eventually burn was 7, whereas the number of nests within 5 km of leks that remained unburned was 28, given a total of 32 nests (i.e., proportions were 7/32 and 28/32 as an individual nest could be within 5 km of both burned and unburned leks). Similar data were recorded for each study year, pre- and post-fire, and therefore the analysis tested for changes in these ratios before and after the burn, relative to the a priori prediction that the fraction of nests in close proximity to leks inside the fire perimeter would decrease post burn (Table 1). Consequently, support for this prediction was indicated by a reduction in the response ratios across time periods, but only for leks that burned. This proportion is scale-dependent; therefore, we replicated the analysis using 10 buffer distances around leks (1–10 km, by 1 km). Moreover, we treated nests from the control study area (Medicine Lodge) as independent binomial samples of unburned leks for this analysis. The total number of nests for this analysis included 172 during the pre-fire period (2015–2018), 61 during the 1st year post-fire period (2019), and 76 during the 2nd year post-fire period (2020).

The hypothesis of adaptive responses to fire also predicts changes in space use will serve to ameliorate population-level fitness consequences associated with nesting, and consequently fire should have limited or no effect on nest initiation or nest success (Table 1). We tested these predictions using logistic regression to assess effects of fire on probability of nest initiation and success, where the response variable was binary for initiation (1 = initiated at least 1 nest, 0 = did not initiate nest) for each marked hen in each study year and also for each observed nest (1 = successful, 0 = unsuccessful). This analysis therefore tested for changes in the probability of nesting and apparent nest success at the impact site, compared to the control site, before and after catastrophic fire (site × period effect). For nest initiation analysis, we only included hens that were known to survive until the median date of nest initiation (2 May) because it was generally unclear if hens that went missing or died early in the season had initiated a nest, and hence recording these observations as birds that did not initiate a nest could bias initiation estimates. That is, if a hen either died or went missing (e.g., transmitter failure) prior to 2 May in a given year, the hen was not included in nest initiation analysis. No successful nests were observed hatching prior to 2 May, and therefore it was exceedingly unlikely that this criteria for excluding hens from in nest initiation analyses missed hens that successfully hatched a brood. Sample sizes for these analyses included 305 opportunities for a hen to initiate a nest and 309 unique nests used to measure success (8.4% were renests, $n = 26$).

Although assessing impacts of catastrophic fire was our primary objective, we also sought to control for individual-level attributes and assess the links between space use decisions and fitness metrics. Thus, we considered plausible models for nest success that included control covariates measured for each animal (Stevens et al. 2023b) and habitat variables affecting nest-site selection (Stevens et al. 2023a), in addition to the BACI design variables (site, period, and site × period). We started with 3 individual-level covariates (hen age, body mass at capture, and ordinal day of nest initiation) and all habitat variables from the best performing population-level resource selection function (RSF) for nest sites (details about RSFs and covariates provided by Stevens et al. 2023a): sagebrush cover, heterogeneity of sagebrush cover classes, perennial herbaceous cover, annual herbaceous cover, litter cover, cover of bare ground, compound topographic index, nest-site exposure, distance to nearest mesic patch, and distance to nearest active lek. To reduce the number of covariates considered in our analyses, we conducted a two-stage model selection analysis. In the first stage of model selection, we (1) identified the best individual-level variables, considering both linear and quadratic forms for day of nest initiation, (2) identified the optimal form of relationship between each habitat variable and nest success (linear or quadratic), and (3) identified the best combination of uncorrelated ($r < 0.6$) habitat covariates for modeling nest success (Supplement 1). From the first stage of model selection, we retained ordinal day of nest initiation (quadratic), distance to mesic patch (linear), litter cover (linear), heterogeneity of sagebrush cover classes (quadratic), and nest-site exposure (linear) for the final analysis. In the second stage of model selection, we compared all additive combinations of the design variables and additional variables (design variables always included together as a group), as well as an intercept-only null model, for a total of 64 models of nest success.

Our hypothesis also predicts that changes in space use and avoidance of the burned area by hens with broods (Stevens et al. 2023a) will serve to ameliorate population-level fitness consequences associated with brood rearing. Consequently, catastrophic fire should have had limited or no effect on brood success or total brood counts if behavioral responses were adaptive. We used logistic regression to test for effects of fire on probability of at least one chick surviving to the 42-day brood count, and a negative binomial regression model with a linear variance-mean relationship (NB1 model; Brooks et al. 2017) to test for fire effects on brood counts (number of chicks per brood) for each hen completing a successful nest. These analyses evaluated changes in the probability of apparent brood success and relative brood counts at the impact site, comparing the impact and control sites before and after fire. Sample sizes included 114 broods for the success and 112 for the brood count analyses (2 broods had fate recorded but no count).

As we described for nest success, we also sought to control for individual-level attributes and assess the impacts of space use decisions on brood success and relative brood counts. We started with 3 individual-level covariates (hen age, body mass at capture, and ordinal day of nest initiation) and all habitat variables from the top population-level RSFs for either early (< 21 days post hatch) or late (≥ 21 days post hatch) brood rearing (variables typically optimized at different spatial extents between periods, details about RSFs and covariates provided by Stevens et al. 2023a): sagebrush cover, heterogeneity of sagebrush cover classes, perennial herbaceous cover, annual herbaceous cover, litter cover, cover of bare ground, compound topographic index, terrain ruggedness, nest-site exposure, distance to nearest mesic patch, distance to nearest mesic grass patch, and proportion of brood rearing areas intersecting the burn. To reduce the number of covariates considered in our brood analyses, we again conducted a two-stage model selection analysis. In the first stage of model selection, we focused on brood success and (1) identified the best individual-level variables, considering both linear and quadratic forms for day of nest initiation, (2) identified the optimal spatial scale for variables whose measurement extent differed between early and late brood periods, and optimal form of relationship for each habitat variable (linear or quadratic), and (3) identified the best combination of uncorrelated habitat covariates ($r < 0.6$) for modeling brood success (Supplement 1). From the first stage of model selection that focused on brood success, we retained hen age and ordinal day of nest initiation (linear), as well as cover of perennial herbs and bare ground (both linear and measured during early brood-rearing) for final models for brood success and counts. In the final stage of model selection, we compared all additive combinations of the design variables (site, period, and site × period), animal-level variables, and habitat variables, as well as an intercept-only model, for a total of 24 models each for brood success and brood counts.

The hypothesis of adaptive responses also predicts that catastrophic fire should not affect population-level survival of hens during the breeding season. We used ragged telemetry data (i.e., with staggered entry and potentially unequal time intervals between successful GPS fixes) and the multi-state model (Lebreton and Pradel 2002; Devineau et al. 2014) in program MARK (White and Burnham 1999) to test the effect of fire on survival of marked hens during the spring–summer period (1 March–1 August). We modeled transitions probabilities between the states alive (A) and dead (D) for each observation day (Ψ^{AD}), where Ψ^{DD} was an absorbing state (i.e., $\Psi^{DD} = 1$) because birds cannot transition from dead to alive, and detection probability (p) was fixed at 1 because detection error was not an issue when GPS transmitters recorded location fixes. Days where transmitters failed to record a location (e.g., because solar-powered batteries died) were treated as no data in the encounter histories (".") and therefore did not contribute to the likelihood functions for mortality estimation. We modeled probability of daily mortality (Ψ^{AD}) as a function of design variables (site × period) and control variables (time trend over spring–summer [Stevens et al. 2023b], age [first year or after first year], year) to allow for more precise estimates of fire effects on survival. This analysis tested for changes in hen survival at the severe-fire site, comparing this site to the control site before and after fire. We compared additive combinations of design and control variables, as well as an intercept-only model, for a total of 11 multi-state models. This analysis used 354 unique encounter histories, where each encounter history represented a combination of individual hen and observation year.

Lastly, if behavioral responses to catastrophic fire were adaptive, we would expect limited or no change to body condition at capture for hens exposed to the fire. We did not collect morphometric measurements that would allow standardization of body condition relative to body mass, physical size, and date of capture for individual hens (Blomberg et al. 2014a). However, > 75% of captures occurred over a calendar-day window of only 15 days across years (ordinal days 82–97), and there was no relationship between day of capture and body mass ($P = 0.77$ from linear regression of mass against day). Thus, we used body mass at capture as a surrogate for hen condition and linear regression to test effects of fire on mass at capture before and after the fire. This analysis compared body mass at capture at the impact site to the control site before and after fire using body mass recorded from 275 unique hens with condition measurements. Body mass is also affected by hen age (adult [after first year] or yearling [first year]), and therefore we included a binary indicator variable in our analysis to account for age-related differences in mass. Specifically, we used model selection to evaluate support among four candidate models, including the intercept-only model, and models with design variables only (site × period), additive effects of age and design variables (age + site × period), and full interaction between age and the design variables (age × site × period). Because we were not able to calculate standardized indices of body condition for hens captured at the control and impact sites, this analysis implicitly assumed no structural differences in physical size or growth rates existed for hens breeding on these sites. We believe these are reasonable assumptions given the similarities of background habitat at both sites (Stevens et al. 2023a) and the broad seasonal movements of birds across the region relative to the proximity and size of the control and impact sites (Dalke et al. 1963; Leonard et al. 2000).

Individual-level analyses

The first individual-level prediction deduced from the hypothesis that sage-grouse mitigate fitness consequences of catastrophic wildfire through adaptive responses to space use was that nest locations would shift to outside the fire perimeter after the fire (Table 1). Two related but distinct predictions were that sage-grouse hens attending leks near the fire would not go inside the fire perimeter to nest and hens attending leks inside the fire perimeter would move outside to nest, and therefore would move greater distances between lek of capture and nest sites. To test the first 2 predictions, we made visual comparisons between nest locations (same year as capture) before and after the burn for hens attending leks inside or directly adjacent to (within 1 km) the fire perimeter. Our initial goal was to use logistic regression to test for changes in the proportion of hens caught inside the fire perimeter that nested inside the perimeter before and after the fire, and conversely, the proportion of hens caught adjacent to the fire that moved into the burned area to nest. However, formal statistical analyses were not necessary because of complete separation of nest locations post-fire (see Results). To test the third prediction, we used linear regression to test the effect of fire on natural log of distance moved from lek of capture to nest locations. This analysis therefore tested for changes in distances moved before and after the fire, comparing hens caught inside the fire perimeter to hens caught outside, before and after catastrophic fire. Moreover, we sought to control for potentially confounding variables affecting distances moved between lek locations and nest sites, and therefore included additional variables for hen age, ordinal day of nest initiation, and hen body mass (i.e., earlier nesting, adult, or hens in better condition may preferentially nest closer to leks of capture). This analysis compared all additive combinations of the design variables, age, body mass, and day of nest initiation, as well as an intercept-only model ($n = 15$ models). We also only included hens nesting in the same year as capture in this analysis ($n = 125$), where lek attendance relative to nest locations was known, because hens were not recaptured after initial capture and transmitter deployment.

The 4th and 5th individual-level predictions were that fire would not affect spring–summer survival or body mass of hens attending leks inside the fire perimeter, relative to hens attending leks outside the fire at Sand Creek. We modeled survival using ragged telemetry data and the multi-state model exactly as described above, except we only included hen age as a control variable, based on results of population-level analyses (see Results). Thus, individual-level analyses tested for changes in hen survival before and after the burn, comparing hens caught at leks inside the fire perimeter to hens caught outside the fire perimeter, before and after fire. Sample sizes for this analysis included 101 encounter histories, where each encounter history represented an individual hen in their year of capture. We again used linear regression to test effects of fire on body mass at capture, yet for individual-level analyses hens were assigned to the control and impact groups based on their location of capture at Sand Creek. Thus, we tested for differences in body mass before and after the fire, comparing hens caught inside the fire perimeter to hens caught outside the fire perimeter. Individual-level hen condition analyses included 122 individuals and compared the same model set as population-level analyses described above.

The final individual-level prediction was that hens nesting outside the burned area, but closer to the fire perimeter, would not suffer reductions to nesting and brood-rearing productivity metrics. We used logistic regression to test for an effect of distance outside the fire perimeter of nest locations on subsequent nest or brood success ($n=68$ nests and 36 broods during post-fire period only), while also leveraging important control covariates identified from population-level analyses described above. These analyses each compared 4 models, including an intercept-only model, a model with only distance, and models with control covariates from the top population-level models (with and without distance effects). We also compared 7 models to assess effects of distance outside the fire perimeter on 42-day brood counts, including models with a negative binomial error structure (NB1 structure) and hurdle negative binomial models, with and without distance effects on the hurdle component of the model (i.e., the logistic part of the model characterizing zero vs. non-zero counts). The hurdle models therefore represented a joint model of the zero vs. non-zero counts using a logistic model, and the conditional brood counts for non-zero observations using a NB1 model (Brooks et al. 2017). These analyses allowed us to focus our inference on the effects of nest proximity to the burn by considering only birds that were potentially exposed to severe fire.

Results

Population level

All population-level predictions deduced from our hypothesis were supported by our analyses (Table 1), demonstrating that sage-grouse generally avoided the burn for nesting and brood rearing and fitness consequences of the fire were ameliorated by behavioral responses. First, the proportion of nests located near leks that would eventually burn significantly decreased ($P<0.1$) at 7 of 10 scales by the second-year post-fire (Table 2), with the exception of buffer distances around leks of 1, 2, and 9 km, respectively. Thus, for most spatial extents considered, nests in lekking areas affected by the burn shifted farther away from those leks after the burn, whereas nests in unaffected areas showed no such pattern over time (Fig. 2, upper left).

Probability of initiating a nest was unaffected by severe fire (Table S1). Instead, nest initiation was relatively stable over time across the region and was similar between the impact and control areas (Fig. 2, upper middle). Top models for apparent nest success all contained design variables (site + period + site × period), in addition to individual-level and habitat covariates (Table 3). However, model averaged confidence intervals for interaction effects between site and period overlapped zero (Table S2) and partial effects plots demonstrated no effect of the burn on nest success (Fig. 2, upper right). Instead, nest success fluctuated over time but was similar between the control and impact sites. We observed strong model averaged effects on nest success for additional covariates, including dome-shaped quadratic effects for ordinal day of nest initiation and heterogeneity of sagebrush cover within 1000 m of nests (i.e., highest nest success at intermediate levels), positive effects of litter cover within 1000 m and negative effects of site exposure at nest sites (Fig. 3). For example, during the first-year post fire, probability of nest success more than doubled from the smallest observed values of sagebrush heterogeneity (i.e., no cover or homogeneous sagebrush cover) to the peak nest success at intermediate heterogeneity values (Fig. 3). Similarly, probability of nest success increased approximately fourfold during the same period for nests initiated on ordinal day 130 (10 May for non-leap years) as compared to day 100 or 155 (10 April and 4 June). Probability of nest success also increased approximately fourfold from average litter cover values of 10 to 25% during the first-year post fire and decreased approximately 85% from the smallest to largest observed exposure values (Fig. 3).

Top models for brood success and brood counts all contained design variables and additional control covariates (Table 3), model averaged confidence intervals for the site × period interaction overlapped zero (Table S3–S4), and partial effects plots demonstrated no effect of

Table 2 Results of population-level analyses testing for the effects of fire on the proportion of sage-grouse nests from eastern Idaho, USA (2015–2020), located within 10 buffer distances (1–10 km radii) around leks, comparing leks inside ($n=24$) and outside ($n=60$) the perimeter of catastrophic fire. Significant reduction to the proportion of nests (−) near burned leks was found at 7 of 10 buffer distances

Buffer distance (km)	Fire effect[a]
1	+/−
2	+/−
3	−
4	−
5	−
6	−
7	−
8[b]	−
9	+/−
10	−

[a] Significant reduction in proportion of nests was assessed at $\alpha=0.1$ level

[b] Non-significant result was indicated by +/−

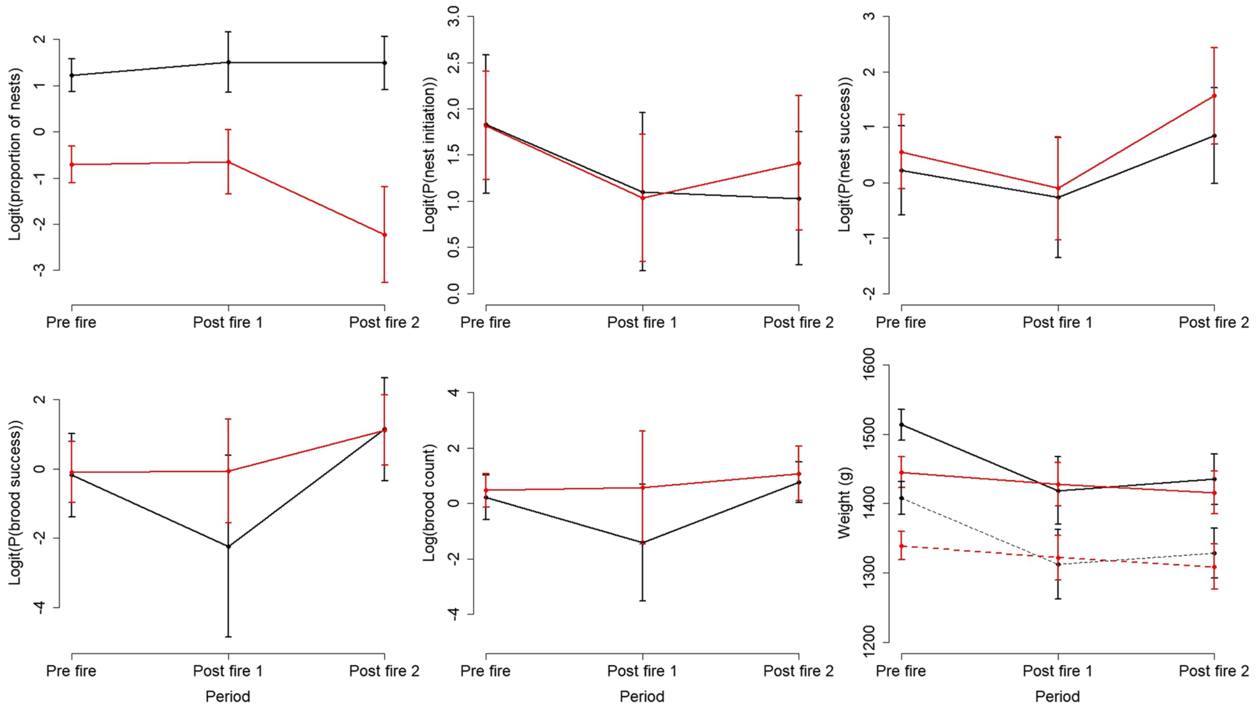

Fig. 2 Results of population-level BACI analyses testing the effects of catastrophic fire on the fitness traits of sage-grouse in eastern Idaho, USA (2015–2020). For all panels, dots represent point estimates and error bars contain 95% confidence intervals, red represents impact (i.e., burned) and black represents control (i.e., unburned) site, and time periods are pre-fire, first year post-fire (Post fire 1), and second year post-fire (Post fire 2). Top left: comparison of the proportion of nests within 5 km of burned and unburned leks, demonstrating that fire caused a reduction in nest density near burned leks 2 years post-fire. The top left panel therefore demonstrates the pattern to be expected in each figure if fire negatively impacted fitness traits at the impact site (i.e., reduction over time at the impact site, but not the control site). Top middle: comparison of the probability of nest initiation at the impact and control sites, demonstrating that fire caused no reduction in probability of nesting. Top right: comparison of the probability of nest success at the impact and control sites, demonstrating that fire did not reduce nest success. Bottom left: comparison of the probability of brood success at the impact and control sites, demonstrating that fire did not reduce brood success. Bottom middle: comparison of the expected 42-day brood counts at the impact and control sites, demonstrating that fire did not reduce brood size. Bottom right: comparison of body mass at capture for sage-grouse hens at the impact and control sites, and by age (dashed lines = juvenile, solid lines = adults), demonstrating that fire did not reduce body mass across the study areas

the burn on population-level brood metrics (Fig. 2, lower left and middle). Instead, brood metrics changed little at the severe-fire site and fluctuated more over time at the control site, but we were unable to detect differences in brood metrics between impact and control sites for any time period. We observed strong model averaged effects of perennial herbaceous cover measured at 200 m extent within early brood-rearing areas on both brood success and brood counts (success: $\beta = -0.750$, 95% CI $= -1.476$ to -0.025; count: $\beta = -0.497$, 95% CI $= -0.930$ to -0.065; Fig. 4). During the first-year post fire, probability of brood success and expected brood count decreased by approximately 75 and 85% when going from 10 to 30% perennial herbaceous cover, respectively. Similarly, probability of brood success decreased approximately 71% when nests were initiated on ordinal day 155 (4 June) as compared to ordinal day 100 (10 April). Hen age effects were included in competitive models for both brood success and brood counts, and directionally implied worse outcomes for yearling hens (Table 3), but model averaged estimates were imprecise, and confidence intervals overlapped zero (Tables S3–S4). Moreover, inferences about fire effects on population-level nest and brood metrics were insensitive to use of fixed effects regression models, instead of the more complex mixed effects models (Tables S2–S4).

We found no evidence that BACI design variables (site × period) affected spring–summer survival of sage-grouse hens (Table 4). The top multi-state model included a time trend over the spring–summer period, yet the null model was highly competitive ($\Delta AIC_c = 0.76$) and the top model provided only weak evidence that daily mortality probability trended over the breeding season ($\beta = 0.006$, 95% CI $= -0.001$–0.013; Table S5). The top model describing body mass at capture included additive effects of design variables and hen age (Table 5), yet a closer look at partial effects and parameter estimates provided no evidence for an effect of fire on body mass. Instead, confidence intervals for the site × period interaction included

Table 3 Model selection results showing top models for population-level analyses testing the effect of catastrophic fire on nest success, brood success, and brood counts for sage-grouse in eastern Idaho, USA (2015–2020). Design variables included in the logistic regression analyses were Site (impact and control sites) and Period (pre-fire, first year post-fire, second year post-fire). Habitat variables used for the nest success analysis included distance to mesic patch (Mesic), litter cover (Litter), heterogeneity of sagebrush cover classes (DI), and nest-site exposure (Exposure), and individual-level attributes included ordinal day of nest initiation (Initiation). Additional variables included in brood models included hen age (Age), perennial herbaceous cover (Perennial), and cover of bare ground (Bare). Models were ranked using Akaike's Information Criterion corrected for small sample sizes (AICc), and only models with ΔAICc ≤ 5 are displayed. Also shown are the Akaike model weights (*w*) and the number of model parameters estimated (*K*)

Model[a]	ΔAIC$_c$	*w*	*K*
Nest success			
Site × Period[b] + DI^{2}[c,d] + Litter + Exposure + Initiation^{2}	0	0.37	12
Site × Period + DI^{2} + Litter + Exposure + Mesic + Initiation^{2}	1.54	0.17	13
Site × Period + DI^{2} + Litter + Initiation^{2}	1.77	0.15	11
Site × Period + DI^{2} + Litter + Mesic + Initiation^{2}	3.04	0.08	12
Site × Period + Litter + Exposure + Initiation^{2}	4.29	0.04	7
Brood success			
Site × Period + Perennial + Initiation	0.00	0.24	8
Site × Period + Perennial	0.43	0.19	7
Site × Period + Perennial + Initiation + Age	1.94	0.09	9
Site × Period + Perennial + Age	2.13	0.08	8
Site × Period + Initiation	2.31	0.07	7
Site × Period + Bare + Initiation	3.51	0.04	8
Perennial	3.81	0.04	2
Site × Period	4.14	0.03	6
Perennial + Initiation	4.18	0.03	3
Site × Period + Initiation + Age	4.31	0.03	8
Site × Period + Bare	4.68	0.02	7
Brood counts			
Site × Period + Perennial	0.00	0.28	8
Site × Period + Perennial + Initiation	1.48	0.13	9
Site × Period + Perennial + Age	1.54	0.13	9
Perennial	2.93	0.06	3
Site × Period + Perennial + Initiation + Age	3.14	0.06	10
Perennial + Age	3.55	0.05	4
Perennial + Initiation	3.82	0.04	4
Perennial + Initiation + Age	4.31	0.03	5
Bare	4.71	0.03	3

[a] Null model ΔAIC$_c$ values were 31.7 (nest success), 7.5 (brood success), and 8.2 (brood counts), respectively

[b] Site × Period denotes the full interaction model including main effects: Site + Period + Site × Period

[c] Measured using Simpson's diversity index calculated on sagebrush cover categories over a 1000-m spatial extent around nest sites (Stevens et al. 2023a)

[d] Squared covariate terms indicate a quadratic function was used to model the relationship. For example, DI^{2} represents a regression model that includes DI + DI^{2} terms

zero (Table S6), and body mass was markedly lower for yearling hens (compared to adult hens) but consistent over time at the impact site (Fig. 2, lower right).

Individual level

All three individual-level predictions related to shifting nest-site locations in response to fire were supported (Table 1). First, the spatial distribution of nest sites relative to the area burned shifted after the burn. Before the fire, nest locations from hens that attended leks within or near the area that would eventually burn were spread across this area (Fig. 5, top row). In contrast, after the burn no hens attending leks inside the fire perimeter or near the burn perimeter moved into the burn to nest (Fig. 5, bottom row). Hens attending leks inside the fire perimeter demonstrated an increase in distance moved between lek site and nest location by the second-year post fire that was not observed for hens attending leks outside the fire perimeter (Table 6, Fig. 6). In addition to the design variables, model selection indicated hen age and ordinal day of nest initiation may impact distance moved between lek and nest (Table 6), but their model averaged 95% confidence intervals overlapped zero (Table S7). While nest sites shifted at the impact site post fire, there was little evidence that fire impacted nest initiation or productivity for hens attending leks inside the fire perimeter (Table S8).

Multi-state models comparing survival of hens based on location of capture demonstrated that fire had little effect on spring–summer survival of sage-grouse. For multi-state model selection, the null model was superior and models with design variables received little support from the data (Table 4). In contrast, individual-level analyses provided evidence that fire impacted mass at capture for birds captured inside the fire perimeter (Table 5). The top body mass model included design variables and an additive effect of hen age, and both site × period interactions and age effects were statistically significant (Table S9). Specifically, juvenile hens were lighter at capture than adult hens, and hens caught within the fire perimeter showed a decreasing body mass at capture over time that was not observed for hens caught outside the burn (Fig. 6).

Lastly, individual-level analyses provided no evidence that hens nesting in close proximity to the fire perimeter suffered reductions in productivity (Table 1). The top model for nest success was the null model (Table 7), and the effect of distance from burn in the second-best model was not different from zero (Table S10). The top models for both brood success and brood counts included effects of distance of nest site outside the burn perimeter (Table 7), yet directional effects

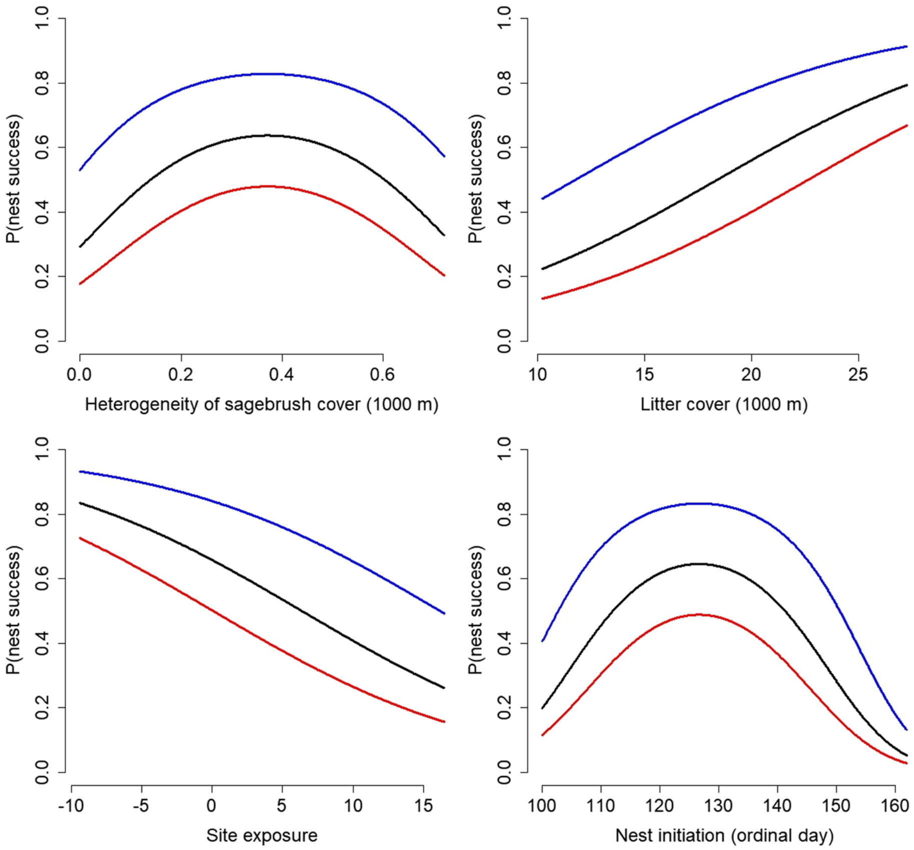

Fig. 3 Partial effects of control covariates from population-level BACI analyses testing the effects of catastrophic fire on probability of nest success by sage-grouse in eastern Idaho, USA (2015–2020). Model-averaged partial effects from logistic regression models are shown for the heterogeneity of sagebrush cover classes (Simpson's diversity index, measured at 1000 m spatial extent; top left), litter cover (measured at 1000 m; top right), nest-site exposure (bottom left), and ordinal day of nest initiation (bottom right). Additive effects showing how time period shifts the observed relationships are indicated by line color (pre-fire = black, first year post-fire = red, second year post-fire = blue)

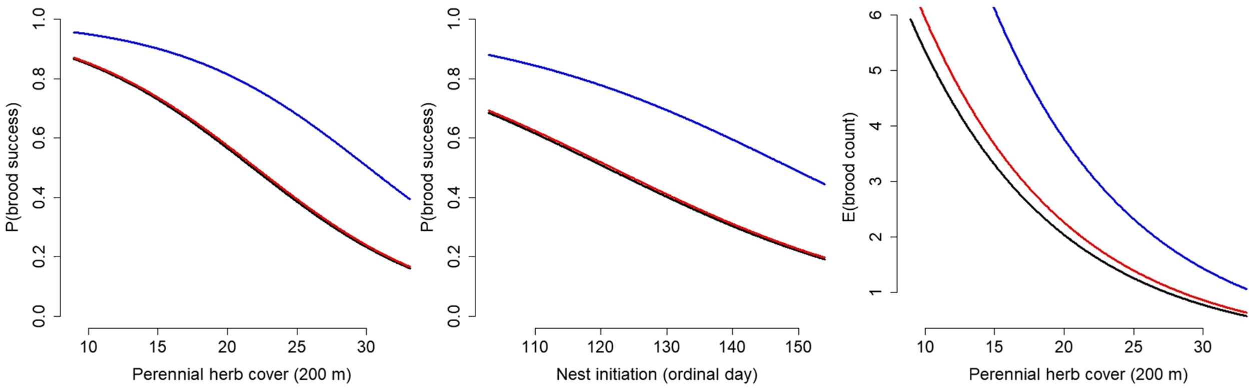

Fig. 4 Partial effects of control covariates from population-level BACI analyses testing the effects of catastrophic fire on probability of brood success and 42-day brood counts by sage-grouse in eastern Idaho, USA (2015–2020). Model-averaged partial effects from regression models are shown for the effects of perennial herbaceous percent cover (measured at 200 m extent; left) and ordinal day of nest initiation (middle) on brood success, as well as the effect of perennial herbaceous percent cover on 42-day brood counts (right). Additive effects showing how time period shifts the observed relationships are indicated by the line color (pre-fire = black, first year post-fire = red, second year post-fire = blue)

Table 4 Model selection results for analyses testing for effects of catastrophic fire on breeding season survival of sage-grouse hens in eastern Idaho, USA (2015–2020). Results are presented for population- and individual-level analyses, where the multi-state models were used to estimate daily mortality probability as a function of covariates. Design variables included Site (impact and control sites for population-level analyses) or Location (hen captured inside or outside the fire perimeter for individual-level analyses) and Period (pre-fire, first year post-fire, second year post-fire), whereas control variables included a time trend over the breeding season (Trend), a categorical year effect (population-level only), and age (juvenile or adult). These results provide no evidence that fire affected hen survival. Models were ranked using Akaike's Information Criterion corrected for small sample sizes (AICc). Also shown are the Akaike model weights (*w*) and the number of model parameters estimated (*K*)

Model	ΔAIC_c	*w*	*K*
Population level			
Trend	0	0.47	2
Null	0.76	0.32	1
Age	2.75	0.12	2
Year + Trend	6.34	0.02	7
Site × Period[a] + Trend	6.37	0.02	7
Site × Period	7.06	0.01	6
Year	7.12	0.01	6
Year + Age + Trend	8.32	0.01	8
Site × Period + Trend + Age	8.34	0.01	8
Site × Period + Age	9.06	0.01	7
Year + Age	9.12	0.01	7
Individual level			
Null	0	0.89	1
Location × Period[b]	4.82	0.08	6
Location × Period + Age	6.55	0.03	7

[a] Site × Period denotes the full interaction model including main effects: Site + Period + Site × Period

[b] Location × Period denotes the full interaction model including main effects: Location + Period + Location × Period

Table 5 Model selection results for analyses testing the effect of catastrophic fire on body mass at capture for sage-grouse hens in eastern Idaho, USA (2015–2020). Design variables included Site (impact and control sites for population-level analyses) or Location (hen captured inside or outside of fire perimeter for individual-level analyses) and Period (pre-fire, first year post-fire, second year post-fire), whereas age (juvenile or adult) was used as a control variable. Models were ranked using Akaike's Information Criterion corrected for small sample sizes (AICc). Also shown are the Akaike model weights (*w*) and the number of model parameters estimated (*K*)

Model	ΔAIC_c	*w*	*K*
Population level			
Site × Period[a] + Age	0	0.98	7
Site × Period × Age	7.65	0.02	12
Site × Period	81.68	0.00	6
Null	108.08	0.00	1
Individual level			
Location × Period + Age	0	0.97	7
Location × Period × Age	7.19	0.03	12
Null	29.07	0.00	1
Location × Period	35.84	0.00	6

[a] All interactions are represented by the full interaction models including main effects and lower-order interactions. For example, Site × Period denotes the model including main effects (Site + Period + Site × Period), and Site × Period × Age includes main effects and lower order interactions (Site + Period + Age + Site × Period + Site × Age + Period × Age + Site × Period × Age)

were opposite to those expected if nesting close to the burn negatively affected broods (Table S10). That is, coefficients for distance effects were negative (success: $\beta = -0.828$, 95% CI $= -1.624$ to -0.032; counts: $\beta = -0.650$, 95% CI $= -1.057$ to -0.242), indicating that hens nesting farther from the fire perimeter had reduced brood success and brood counts. However, increased distance of nest sites outside the burn perimeter was also associated with increased perennial herbaceous cover in early brood-rearing areas (Fig. S2), which negatively affected brood success and brood counts (Fig. 4).

Discussion

Large-scale and high-intensity disturbances are becoming a defining characteristic of modern ecology with the capacity to rapidly reshape the structure and function of ecosystems and challenge conservation of sensitive species around the globe (Sergio et al. 2018). This study provided a rare opportunity to leverage catastrophic wildfire as a natural experiment for studying behavioral responses and resilience of wildlife to rapid and large-scale environmental change. This allowed us to study fire effects using a BACI design with multiple levels of spatial controls and a continuous data stream that spanned pre- and post-fire periods. We demonstrated the potential of behavioral responses by an iconic species of the sagebrush biome to mitigate fitness consequences in response to rapid change induced by catastrophic fire. Short-term responses were generally adaptive, and our results demonstrated that sage-grouse have the capacity to adjust breeding-season space use to avoid immediate consequences of fire. These novel results demonstrate behavioral flexibility by breeding sage-grouse when cues provided by the fire are strong and high-quality habitat remains adjacent to the fire perimeter.

Behavioral flexibility is predicted by theory for habitat specialists like sage-grouse (Tuomainen and Candolin 2015) and also supported by rapid responses of sage-grouse to other types of disturbance (e.g., conifer removal; Sandford et al. 2017; Olsen et al. 2021), but contradicts recent claims that sage-grouse are behaviorally inflexible in the face of environmental change due to strong site fidelity (O'Neil et al. 2020; Brussee et al. 2022; Tyrrell et al. 2023). Our results suggest variation in behavioral responses to fire has been underestimated in the literature and highlight challenges of inferring adaptiveness of behaviors from observations after a single fire or using only a single fitness metric. Our results also provide empirical support to underappreciated predictions from site fidelity theory and fire ecology that suggest expression of behavioral flexibility and relaxation of fidelity after major disturbance is influenced by disturbance severity, availability and quality of remaining habitat within the surrounding landscape, reliability of environmental cues provided by the disturbance event, and species-specific traits such as mobility. Moreover, these results highlight the role of behavioral flexibility in mitigating short-term consequences of fire and have strong implications for understanding resilience and population persistence in a rapidly changing environment.

Behavioral responses to wildfire

Behavioral flexibility can provide a mechanism by which animals cope with changing conditions, as altering behavior provides a way for animals to increase their adaptive capacity, persistence, and resilience in response to environmental change (Beever et al. 2017; Buchholz et al. 2019). Understanding plasticity of behavioral responses is therefore vital to conservation in the presence of an altered fire regime that includes more catastrophic fires. Changes to behavior can be affected by both intrinsic (e.g., species traits) and extrinsic factors (e.g., environmental conditions), and understanding the forces shaping those responses is therefore needed to predict population- and species-level consequences of wildfire (Tuomainen and Candolin 2011; Wong and Candolin 2015). Our results demonstrated that behavioral flexibility and the intrinsic and extrinsic factors shaping sage-grouse responses to fire are more complex than previously suggested; therefore, results of past studies of mixed severity fire may not generalize to more severe burns.

Mobility is an intrinsic trait predicted to impact ecological and evolutionary consequences of fire for animals (Pausas and Parr 2018; Jolly et al. 2022). Movement is used to avoid negative impacts of fire, where movements can occur in situ or ex situ with respect to the fire perimeter, and the capacity for movement needed to leave burned areas is an important adaptation in fire-prone landscapes (Pausas and Parr 2018). Sage-grouse in eastern Idaho are highly mobile and move hundreds of kilometers annually to distinct seasonal ranges across broad elevational and moisture gradients (Dalke et al. 1963; Leonard et al. 2000). Thus, despite the large extent of the fire (>40,000 ha), its extent was smaller than the extent of movements used by sage-grouse among their traditional seasonal ranges. Moreover, sage-grouse remained in situ for acts of lek attendance and breeding after the fire. That is, hens were captured at or near active leks inside the fire perimeter and were also observed flying in to attend leks inside the burned area from the surrounding unburned landscape. In contrast, hens altered their patterns of space use to nest and raise broods, moving longer distances from capture leks to nest at unburned locations outside the fire perimeter. Thus, mobility likely increased the flexibility of breeding season space use by sage-grouse, but the specific responses changed with life history state (i.e., lek attendance versus nesting). Consequently, short-term responses to fire are complex and may change among different components of life history.

External factors such as the environmental conditions remaining after disturbance can also affect responses by providing cues that trigger changes in behavior, yet the cues triggering changes in movement and space use after catastrophic fire are poorly understood (Nimmo et al. 2019). The removal of vegetation by severe disturbance is a likely cue for dispersal of mobile species, thereby providing the impetus to shift territories or activity centers to better quality habitat (Buchholz et al. 2019). Thus, spatial heterogeneity of vegetation and post-fire resource availability over a range of scales are expected to shape local and regional distributions of animals in burned landscapes, and changes to fire severity may induce different behavioral responses through changes to the distribution and availability of key components of habitat (Sergio et al. 2018; Nimmo et al. 2019). High-severity fire that results in broad-scale loss of habitat likely provides a strong cue for behavioral responses by animals, thereby providing an impetus to alter space use to maintain the same contributions to fitness. Further, habitat specialists like sage-grouse are expected to exhibit a high degree of plasticity in space use in response to the extreme changes in habitat induced by severe disturbance, as their ability to remain in the same geographic location and exploit different resources is limited (Tuomainen and Candolin 2015).

Our observations before and after severe fire are consistent with predictions that high-severity disturbance should elicit a strong response through patterns of movement and space use. Physical relocation and changes to resource use and selection represent types of behavioral

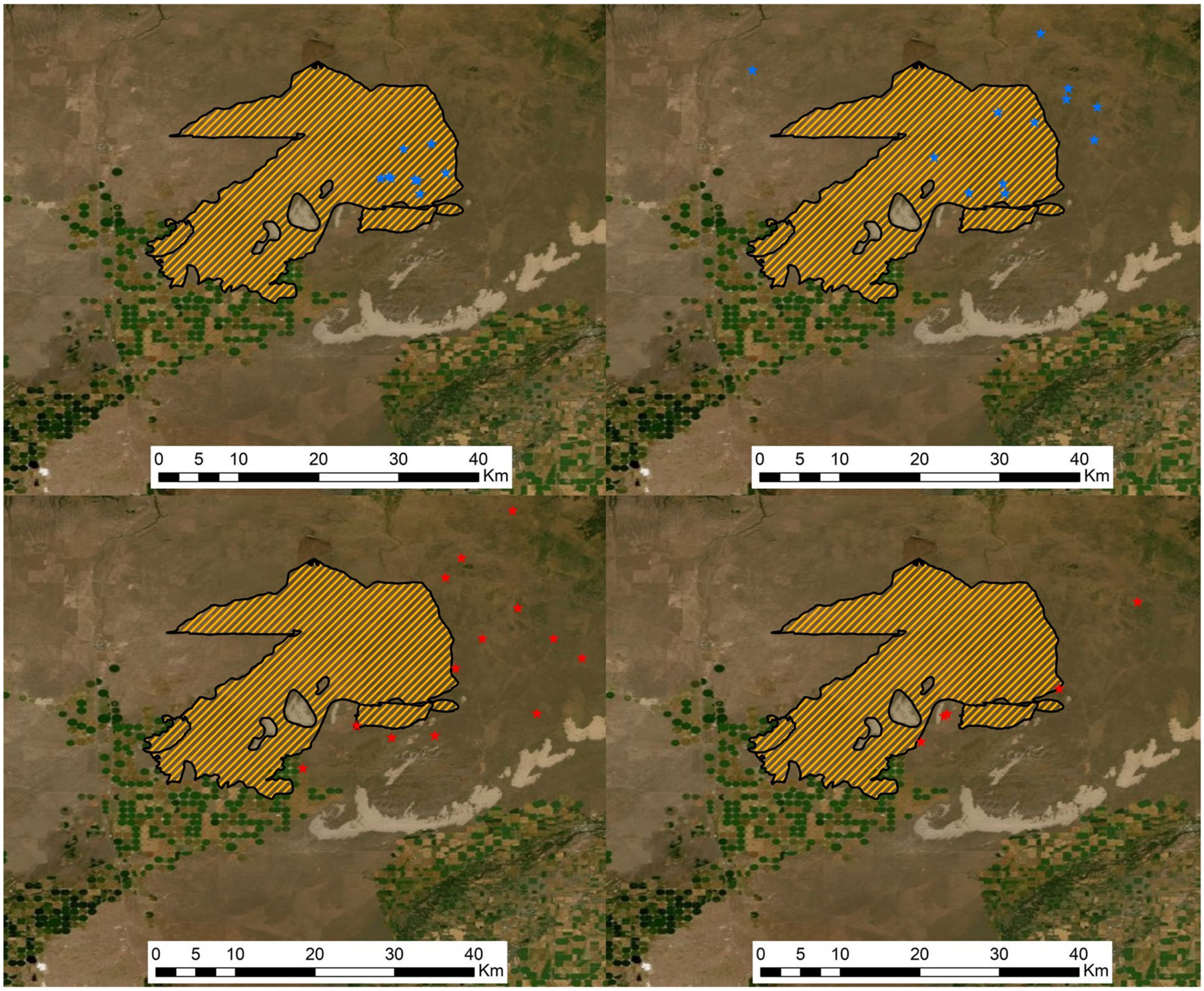

Fig. 5 Comparison of pre-fire (top row) and post-fire (bottom row) nest locations for sage-grouse hens in eastern Idaho, USA (2015–2020). The left column represents hens whose location of capture was inside the fire perimeter, whereas the right column shows hens whose capture location was outside but within 1 km of the fire perimeter. Pre-fire nest locations are indicated by blue stars, whereas post-fire nest locations are indicated by red stars. The orange hashed area represents the area burned by the Grassy Ridge Fire in summer of 2018. These maps demonstrate that nesting activity ceased inside the burn perimeter after the fire

flexibility that can confer fitness benefits in the presence of environmental change (Beever et al. 2017). We provide evidence of such responses for nesting sage-grouse in the aftermath of catastrophic fire. Elimination of nesting sites via the elimination of sagebrush resulted in complete avoidance of the fire perimeter by nesting sage-grouse (this study), as well as the intensification of selection for sagebrush cover in the surrounding landscape by nesting hens (Stevens et al. 2023a). Thus, when sagebrush was effectively removed over > 40,000 ha, the distribution of nesting hens shifted to areas outside of the fire perimeter where quality shrub cover remained.

Comparison of our results to previous studies of mixed-severity fire also supports the role of fire severity in shaping behavioral responses. For example, the 187,000-ha mixed-severity Holloway Fire in Oregon left 25% of the landscape inside the fire perimeter as unburned, intact habitat, and therefore remnant sagebrush patches inside the fire perimeter were available (so-called fire refugia; Robinson et al. 2013). Under these conditions, sage-grouse hens remained in situ and utilized remnant habitat patches for nesting (Foster et al. 2019; Anthony et al. 2021b). Thus, fire severity may affect cues that trigger decisions about spatial relocation by nesting hens and likely played a role in shaping differences in space use and movement observed in eastern Idaho. However, a more complete understanding of environmental cues and population- and individual-level attributes shaping space use

Table 6 Model selection results for individual-level analyses testing effects of catastrophic fire on distance moved from lek of capture to nest sites for sage-grouse hens captured in eastern Idaho, USA (2015–2020). Design variables included Location of capture (inside or outside of fire perimeter at the impact site) and Period (pre-fire, first year post-fire, second year post-fire), whereas control variables included age (Age = juvenile or adult), body mass at capture (Mass), and ordinal day of nest initiation (Initiation). Models were ranked using Akaike's Information Criterion corrected for small sample sizes (AICc). Also shown are the Akaike model weights (*w*) and the number of model parameters estimated (*K*)

Model	ΔAIC_c	*w*	*K*
Location × Period[a] + Initiation	0	0.32	7
Location × Period	0.84	0.21	6
Location × Period + Age + Initiation	1.80	0.13	8
Location × Period + Mass + Initiation	2.31	0.10	8
Location × Period + Age	2.82	0.08	7
Location × Period + Mass	2.93	0.07	7
Location × Period + Age + Mass + Initiation	3.86	0.05	9
Location × Period + Age + Mass	4.48	0.03	8
Initiation	13.39	0.00	2
Mass + Initiation	14.88	0.00	3
Age + Initiation	15.17	0.00	3
Null	17.33	0.00	1
Mass	18.12	0.00	2
Age + Mass	18.64	0.00	3
Age	19.09	0.00	2

[a] Location × Period denotes the full interaction model including main effects: Location + Period + Location × Period

by breeding sage-grouse over a gradient of fire severities is needed. More specifically, cues triggering relaxation of nest-site fidelity and their dependence on disturbance severity and landscape context are poorly understood.

Site fidelity to a particular location in geographic space can complicate responses to disturbance and environmental change. Strong site fidelity can make adaptation to rapidly changing conditions difficult because responses to changing habitat may be delayed, and at its most extreme can result in a fidelity-induced ecological trap where geographic affinity supersedes effects of changing habitat on animal space use to the detriment of fitness (Merkle et al. 2022). Yet animals capable of relaxing fidelity in the face of changing conditions can increase short-term population resilience (Beever et al. 2017; Merkle et al. 2022).

Sage-grouse have a strong tendency toward site fidelity during key life history events, which may leave them vulnerable to catastrophic wildfire. While the concept of a fidelity-induced ecological trap had not yet been articulated, this basic idea was proposed > 25 years ago as a potential mechanism that may increase vulnerability of breeding sage-grouse to habitat degradation induced by wildfire (Fischer et al. 1997). Site fidelity has therefore been commonly invoked as a mechanism to explain why birds still nest in fire-affected areas after habitat has been degraded by fire (O'Neil et al. 2020; Dudley et al. 2021; Tyrrell et al. 2023). Yet past studies did not consider the role of fire severity, were embedded within landscapes with much greater habitat degradation than eastern Idaho (i.e., from past fires and prominence of exotic annual grasses), and did not collect data immediately

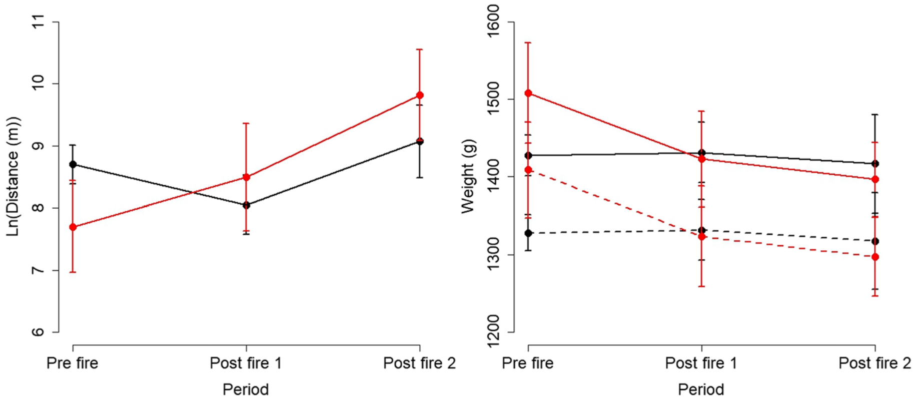

Fig. 6 Results of individual-level BACI analyses testing for the effects of catastrophic fire on fitness traits of sage-grouse at the Sand Creek study area in eastern Idaho, USA (2015–2020). For both panels, dots represent model averaged point estimates and error bars contain 95% confidence intervals, red represents impacted hens (i.e., captured inside fire perimeter) and black represents control hens (i.e., captured outside fire perimeter), and time periods are pre-fire, first year post-fire (Post fire 1), and second year post-fire (Post fire 2). Left: comparison of the distance traveled from lek of capture to nest sites for sage-grouse hens caught inside and outside the fire perimeter, demonstrating that fire increased the distance hens moved from lek of capture to nest sites over time. Right: comparison of the body mass at capture for sage-grouse (solid lines: adults; dashes lines: juveniles) captured inside and outside of the fire perimeter, demonstrating that body mass at capture was reduced post-fire for hens attending leks inside the fire perimeter, but not for hens attending leks outside the fire perimeter

Table 7 Model selection results for individual-level analyses testing effects of nest distance outside the fire perimeter (Distance), habitats, and ordinal day of nest initiation (Initiation) on nest success, brood success, and 42-day brood counts for sage-grouse in eastern Idaho, USA (2015–2020), after the Grassy Ridge Fire. Habitat variables included cover of perennial herbs (Perennial), heterogeneity of sagebrush cover (DI; calculated as Simpson's diversity index), litter cover (Litter), and nest-site exposure (Exposure). Competing models for brood counts included hurdle negative binomial regression models that conditioned expected 42-day counts on top logistic regression models of brood success (also a function of distance outside of burn). Models were ranked using Akaike's Information Criterion corrected for small sample sizes (AICc). Also shown are the Akaike model weights (*w*) and the number of model parameters estimated (*K*)

Model	ΔAIC_c	*w*	*K*
Nest success			
Null	0.00	0.52	1
Distance	1.32	0.27	2
$DI^{2,a}$ + Litter + Exposure + $Initiation^2$	2.52	0.15	7
DI^2 + Litter + Exposure + $Initiation^2$ + Distance	4.51	0.05	8
Brood success			
Distance	0.00	0.62	2
Null	2.68	0.16	1
Perennial + Initiation	3.31	0.12	3
Perennial + Initiation + Distance	3.75	0.10	4
Brood counts			
Distance	0.00	0.57	2
Perennial + Distance	2.18	0.19	3
Distance | $Distance^b$	3.32	0.11	4
Perennial + Distance | Distance	4.71	0.05	5
Perennial	4.99	0.05	2
Null | Distance	6.24	0.03	3
Perennial | Distance	8.93	0.01	4

[a] Squared covariate terms indicate a quadratic function was used to model relationship. For example, DI^2 represents a regression model that includes DI + DI^2 terms

[b] Hurdle component sub-models are indicated as negative binomial model (log link) for expected 42-day counts | logistic model (logit link) of brood success

prior to and after fire in both burned and control areas (but see Tyrrell et al. 2023). Our conclusions about the degree of behavioral flexibility in sage-grouse space use differ strongly from these studies. We demonstrated that sage-grouse are not necessarily trapped by fixed behavioral patterns that prioritize site fidelity indefinitely, but instead may rapidly adjust space use in response to catastrophic wildfire by locating their nests and raising their broods in adjacent unburned habitat (this study), and by intensifying their strength of nest-site selection for unburned sagebrush at the population level (Stevens et al. 2023a). These results imply past research has underestimated the likelihood that behavioral responses of sage-grouse vary based on cues left after a fire (e.g., from fire intensity, context of surrounding landscape, etc.).

Site-fidelity theory has also generated testable predictions for when fidelity should be stronger or weaker (Switzer 1993), and these predictions reinforce observed behavioral differences between this and past studies. First, site-fidelity should be inversely related to spatial heterogeneity in habitat quality, such that spatially homogeneous habitats should see stronger fidelity, whereas spatially heterogeneous habitats should see weaker fidelity. Thus, catastrophic fire events that generate strong spatial structure in habitat quality across a populations' breeding range, like we observed in this study, are expected to weaken fidelity. Under these conditions, stronger differences in expected fitness gains among potential nesting sites inside and outside the fire perimeter means that fitness costs of relocation are likely to be compensated for. More severe fires should also increase the lifetime fitness benefits of relocation because of the prolonged recovery period of key components of habitat (e.g., sagebrush cover), which should weaken tendencies toward site fidelity. In contrast, if large-scale fire eliminates existing heterogeneity of habitat quality across the breeding range, and instead spatially homogenizes the breeding range with poor-quality habitat inside and outside the fire perimeter, stronger site fidelity is predicted because the expected lifetime fitness gains of relocating to unburned areas are negligible.

Additional relevant predictions from site-fidelity theory relate to the predictability of habitat quality, in terms of the reliability of environmental cues perceived and used by animals to guide site selection in heterogeneous environments (Switzer et al. 1993). Specifically, if there are spatial differences in habitat quality among sites that are correctly perceived by sage-grouse based on environmental cues, then an experiential strategy should be employed where relocation to better sites is triggered by reproductive failure (e.g., the win-stay/lose-switch hypothesis based on success of first nests; Bergerud and Gratson 1988). In contrast, if spatial differences in habitat quality are more subtle and therefore effectively unpredictable to the animal (i.e., cues are less reliable), then site fidelity should be favored. Thus, strength of site fidelity should be weaker when environmental cues provided by fire are stronger, but fidelity should be stronger when environmental cues provided by fire are weaker. In other words, elimination of sagebrush over large scales by catastrophic fire likely provides a stronger cue of fitness consequences, and hence result in weaker fidelity, whereas mixed-severity fires that leave remnant patches of intact sagebrush distributed across the burned landscape may provide weaker cues of fitness consequences, and hence result in stronger site fidelity. The context of fire severity within the fire perimeter but also the interplay between environmental cues, habitat quality, and heterogeneity of the broader breeding range are therefore predicted by theory to affect when sage-grouse will relax fidelity and move to adjacent unburned habitats. Site-fidelity theory therefore offers plausible mechanisms explaining differences in behavioral responses to fire observed among studies (e.g., this study; Foster et al. 2019; Anthony et al. 2021b).

The focus of our study was not to test site-fidelity theory explicitly, yet this and other studies provided empirical evidence that disturbance intensity may affect sage-grouse site fidelity. For example, strong temporal changes in habitat structure that include removal of sagebrush over large areas (this study) and removal of conifers encroaching into sagebrush-steppe (Sandford et al. 2017; Olsen et al. 2021) have triggered rapid changes to the distribution of usable space by nesting sage-grouse, suggesting rapid and intense environmental change may weaken fidelity to a specific location. Moreover, internest distances were 4.4–5.2 times greater for birds that nested inside the Holloway Fire boundary in Oregon, as compared to birds nesting outside the burn perimeter (Foster et al. 2019), suggesting fidelity may begin to break down even after mixed-severity fire. These results demonstrated that sage-grouse hens have behavioral flexibility and are capable of adjusting nest locations under changing conditions. Yet we are unaware of prior studies that considered disturbance severity, shrub cover, and other variables (e.g., prior nest fate, landscape composition, etc.) may interact to influence the strength of site fidelity by sage-grouse, despite the relevance of these questions for population resilience in the face of large-scale disturbances.

Fitness consequences of wildfire

Understanding fitness consequences and adaptiveness of flexible behaviors is critical for species conservation in the face of rapid environmental change, and few studies have assessed demographic consequences of high-severity fire on vertebrates (Jolly et al. 2022). Movement can offset survival and reproductive costs of fire (Santos et al. 2022), and we demonstrated that post-fire space use largely mitigated negative short-term consequences expected after large-scale fire (e.g., Foster et al. 2019; Tyrrell et al. 2023). Indeed, we observed few measurable impacts of fire on metrics related to fitness despite our study design that included multiple spatial control areas (unburned areas of the impact site and the entire control site) and multiple levels of analysis (individual and population).

Fire-induced changes in vegetation structure and availability affect predation risk in burned landscapes (Doherty et al. 2022), and consequently sage-grouse that remain inside fire perimeters during breeding may experience increased mortality for hens, their nests, and broods (Foster et al. 2019; Anthony et al. 2021b; Dudley et al. 2021; Tyrrell et al. 2023). Alternatively, hens could minimize risk when faced with the prospect of nesting and raising broods in extremely poor habitat by avoiding nesting all together and instead allocating resources to self-maintenance, or by relocating to areas with improved habitat. We found the proportion of hens initiating a nest was generally high, as is typical for sage-grouse (Connelly et al. 2011a; Blomberg et al. 2017), but also that hens minimized risk by moving away from the burned area to nest and raise broods, even as they were observed attending leks inside the fire perimeter.

Nest success was unaffected by fire but varied among years, the latter of which is common for sage-grouse (e.g., Moynahan et al. 2007; Stevens et al. 2023b). We also found little evidence that spring–summer survival of hen sage-grouse was affected by fire or varied measurably over space and time. In contrast, across the Great Basin hens have commonly responded in situ to mixed-severity fires by seeking out remaining shrub patches within fire perimeters for nesting; this behavior has likely improved nest success, but success is often lower than in adjacent unburned areas (Lockyer et al. 2015; Anthony et al. 2021b; Dudley et al. 2021). Short-term reductions to hen survival have also been reported after fire (Foster et al. 2019; Anthony et al. 2021a, Tyrell et al. 2023), again resulting from in situ utilization of burned areas. We observed different behavior that translated to different fitness consequences, where in situ patches of nesting cover were largely unavailable (Stevens et al. 2023a) and hens responded ex situ by moving to adjacent high-quality habitats (i.e., long unburned areas; Nelle et al. 2000; Beck et al. 2003) that remained outside of the fire perimeter, offsetting fitness impacts.

Similarly, we detected no effect of fire on sage-grouse broods, as brood success and 42-day counts were stable-to-increasing at the severe-fire site but exhibited stronger temporal fluctuations at the control site. Fewer studies have addressed impacts of fire on sage-grouse broods, yet increased burned area around nests decreased brood survival in Nevada when cover of annual grasses was high (Brussee et al. 2022); although the opposite was true when cover of annual grasses was low, where brood survival increased with area burned. At the impact site, nesting hens avoided the burn and those with broods rarely entered the fire perimeter (Stevens et al. 2023a, this study). Even hens that moved just outside the burn to nest did not suffer reduced success due to their close proximity. Hens with broods in this region generally move to higher elevations as lower elevations desiccate (i.e., north-northwest at control site and north-northeast at impact site; Dalke et al. 1963; Leonard et al. 2000), making the area burned (southwest portion of impact site; Fig. 1) less relevant to breeding sage-grouse as the summer progresses. Interestingly, distance to fire perimeter and brood metrics were negatively associated, which would seem to imply broods benefitted from proximity to the fire even though they rarely entered the burned area. However, a closer look reveals this pattern to be an artifact of the spatial patterning of an important covariate affecting brood success. Specifically, nests farther from the fire were in locations with greater cover of perennial herbs during early brood-rearing (Fig. S2), which reduced brood success (Fig. 4). Thus, apparent benefits of proximity to the burn for broods were unsubstantiated.

Our results strongly suggest behavioral responses of breeding sage-grouse served to mitigate negative fitness consequences of fire, yet we did find some evidence of decreased pre-nesting body mass based on location of capture from individual-level analyses. Specifically, we observed decreased body mass at capture for hens caught inside the burn at the impact site but not for hens caught outside the burn. The specific mechanisms underlying this pattern are not clear, yet we speculate these birds may have required more movement to fulfill their breeding activities and explore potential nest sites outside the burn, contributing to a reduced mass at capture. Field crews observed hens regularly flying into the burned area to attend leks from the surrounding unburned landscape. Nonetheless, body mass differences did not translate into measurable changes in fecundity or survival, whereas past research has provided mixed results for effects of condition on fitness, depending on the fitness metric and life stage (e.g., Hausleitner 2003; Blomberg et al. 2014). Moreover, long distance movements (e.g., > 5 km) between lek visits by individual females and from leks to nests have been observed in both intact and fragmented landscapes, but may be more common in disturbed areas (Lyon and Anderson 2003; Schroeder and Robb 2003; Holloran and Anderson 2005; Connelly et al. 2011a). Also, population-level analyses showed no effects of fire on body mass when comparing the control and impact study areas but instead indicated hens on the control site were slightly heavier for reasons unrelated to the fire. Sage-grouse breeding on both sites exhibit large annual movements and can comingle across seasons, however, and consequently the observed differences in body mass may have been affected by factors operating outside of the breeding season.

While not related to the fire, we also observed quadratic effects of ordinal nest initiation day on nest success (i.e., highest success for hens initiating nests in middle of season) and linear effects of nest timing on brood success (i.e., greater brood success for nests initiated earlier in season). Quadratic timing effects on sage-grouse nest success were recently reported from other areas of Idaho (Stevens et al. 2023b), yet we are unaware of studies that assessed timing of nest initiation on brood success. We suspect that reduced success for broods hatched later in the year reflect early-brood rearing during periods of desiccated vegetation. Regardless, these findings are novel and suggest selective pressures for timing of sage-grouse nest initiation that favor early brood rearing but intermediate nesting dates, and hence life-history tradeoffs between nest and brood success in terms of timing of nest initiation.

We demonstrated that behavioral flexibility was important for moderating impacts of environmental change on sage-grouse, yet responses to changing conditions are not always adaptive (Wong and Candolin 2015). For breeding season space use to be adaptive, locations of nest sites and use points for females with broods should reflect environmental conditions benefitting their survival and success (Misenhelter and Rotenberry 2000; Chalfoun and Schmidt 2012). In other words, habitat selection should favor resources that result in positive fitness outcomes. An understanding of the interplay between space use and demography therefore facilitates a deeper understanding of ecological and evolutionary consequences of wildfire. Sage-grouse responses generally mitigated effects of fire, yet effects of selection for individual components of habitat were more nuanced and included adaptive and neutral selection of nesting resources, and potentially maladaptive selection of perennial herbaceous cover during early brood rearing, but only by individuals that chose nest sites in areas with more herbaceous cover (additional details in Supplement 1). These patterns suggest that sage-grouse hens respond in real time to dynamically changing resource availability (Gibson et al. 2016, 2017), but not always in optimal ways. Nonetheless, the apparently maladaptive use of perennial herbaceous cover by some hens did not translate into measurable effects of fire on brood productivity, which was stable to increasing over time at the impact site.

Adaptive habitat selection should favor selection of attributes that benefit fitness outcomes, yet inferring adaptiveness of space use after fire is difficult. Sage-grouse habitat selection can change rapidly in the aftermath of large fires (e.g., within 1–2 years) and likely depends on the composition of available vegetation (Poessell et al. 2022; Schuyler et al. 2022; Stevens et al. 2023a). Lack of data collection immediately prior to and after a fire may therefore provide an incomplete picture of the extent of behavioral change. Moreover, many areas are already degraded by past fires, invasive annual grasses, or both, and therefore the value of remaining habitats may be suboptimal both inside and outside the fire perimeter. In these situations, it is difficult to infer an in situ response as maladaptive if potential nesting or brood-rearing locations available outside the fire perimeter are of similarly poor quality. For example, Dudley et al. (2021) reported the area burned by the 107,000 ha Rush Fire along the California-Nevada border experienced a stronger reduction in nest survival post-fire as compared to the unburned area adjacent to the fire, and interpreted sage-grouse nesting inside the burned area as maladaptive (data were collected $\geq$ 3 years pre- and post-fire, and thus no data were available immediately before or after). However, the Rush Fire reduced the quality of better nesting habitat inside the burned area (pre-burn) to a level equivalent with the reduced quality habitat contained in their adjacent control area (post-burn) and therefore burned and control sites were not functionally equivalent before the fire but were after. Consequently, it appears the Rush Fire homogenized the landscape to poorer quality nesting habitat, and this homogeneity meant that hens nesting in situ after the fire was not maladaptive; it effectively made no difference whether a bird stayed or moved, and the observed response was predicted by site fidelity theory (see *Behavioral Responses to Wildfire*). Our results also show the possibility of minor differences in pre-fire functionality between treatment and control areas for some metrics (i.e., body mass and lek-to-nest distances; Fig. 2 and Fig. 6), yet these differences did not affect our conclusions about population- or individual-level effects or the adaptiveness of behavioral responses to fire.

Interpretation of adaptiveness of habitat selection is further challenged because space use decisions can appear adaptive for some fitness metrics but maladaptive for others (Pratt and Beck 2021, this study). Thus, the adaptiveness of space use is difficult to infer in isolation using only a resource selection function and a single or small number of fitness metrics (Chalfoun and Schmidt 2012). Previous studies clearly demonstrated the capacity of wildfire to degrade breeding habitat over large scales (O'Neil et al. 2020; Brussee et al. 2022), yet suggestions that sage-grouse frequently demonstrate maladaptive behavior after wildfire appear less supported. Importantly, decisions that appear maladaptive for a single fitness metric may be adaptive within the context of other decisions and existing environmental and ecological constraints (see Fig. 2 of Chalfoun and Schmidt 2012; this study). Studies conducted in contexts other than fire have also reported habitat selection by breeding sage-grouse was generally adaptive, but that selection of some components of habitat may have little impact on reproductive success (e.g., Gibson et al. 2016). Our results support this conclusion, where we leveraged spatially replicated data from immediately before and after fire and a broad suite of metrics to demonstrate that decisions by breeding sage-grouse in the aftermath of catastrophic wildfire were generally adaptive and served to offset negative fitness outcomes.

Context-dependent outcomes

The contexts under which flexible behaviors are expressed are poorly understood for most species, representing a key knowledge gap for conservation (Beever et al. 2017). We highlight important but unresolved questions regarding expression of flexible behaviors and fitness consequences resulting from wildfire. For example, why did we observe discrepancies in comparison to earlier studies, and under what circumstances do sage-grouse exercise behavioral flexibility and abandon their tendencies toward site fidelity? If site-fidelity theory is correct and expression of fidelity is affected by strength and reliability of environmental cues (e.g., availability of shrub cover), individual experience (e.g., past reproductive success), or their interaction, a number of factors should determine context-dependent behaviors and resilience of sage-grouse in the face of increasing scale and severity of wildfire.

First, context-specific outcomes of wildfire likely depend on habitat quality and availability within the surrounding landscape, which constrains post-disturbance behavioral change (Beever et al. 2017) and imposes limits on the ability of behavior to offset fire effects on fitness. Remaining inside a fire perimeter to nest and raise broods in sagebrush islands while suffering reduced fitness may be a neutral behavior if habitat available outside the fire perimeter is of similar quality. Under this situation, the only truly adaptive strategy may be to disperse to a new breeding population. On the other hand, if fire eliminates nesting cover within the burn perimeter, then abandonment of fidelity in search of nesting cover would be adaptive if high-quality habitat was available to the same population, as we observed in this study. Landscape context and habitat quality after a fire will vary among populations, complicating interpretation of behavior for studies that lump data from widely varying geographies (e.g., O'Neil et al. 2020). As such, behavioral responses and fitness outcomes may not generalize well across populations and landscapes. Moreover, details concerning availability and structure of remaining habitat in burned landscapes are needed for interpreting fire effects within a landscape context, but are lacking for many studies of sage-grouse and fire.

Fire severity and its role in leaving refugia habitat in the form of intact shrub patches is a second likely driver of context-specific outcomes for sage-grouse. Fire refugia has typically described island of habitat that remain post-burn within fire perimeters that reduce mortality during fire events, provide habitat post-burn, or facilitate reestablishment of populations into burned areas as habitat recovers (Robinson et al. 2013). Compositional and structural attributes of refugia patches are affected by scale and intensity of fire. Mixed-severity fires may result in more remnant shrub refugia and in situ habitat use, yet these islands of unburned shrubs appear functionally less valuable than unburned habitat outside fire perimeters (see *Fitness Consequences of Wildfire*). In contrast, avoidance of burned areas with subsequent recolonization from the surrounding landscape is generally expected for high-severity fires that provide less ambiguous environmental cues (Pausas 2019). Our results demonstrated that nesting hens can adjust their space use when in situ refugia are not available, provided there is high-quality habitat adjacent to the burn. Therefore, changes to environmental cues resulting from severity of fire provide a potential mechanistic link to context-dependent behavior and fitness consequences of fire.

Fire refugia concepts originally referred to in situ patches of habitat remaining unburned inside a fire perimeter (Robinson et al. 2013), yet we demonstrate how these concepts also apply across broader areas (Meddens et al. 2018). Refugia concepts can be used to understand the value of unburned regions across broader landscapes within the seasonal range of a population and therefore unify landscape context and fire severity effects on wildfire outcomes described above. Across a broader seasonal range, ex situ habitat may function like source habitat in a biogeographic sense, supporting local populations immediately after fire and facilitating recolonization of burned areas in future years as habitat recovers. We demonstrate that at this broader extent, quality unburned habitat adjacent to severe fire can facilitate short-term resilience and adaptive behavioral responses by sage-grouse. Thus behavior can facilitate movement to regional refugia that offset otherwise negative fitness outcomes expected from local habitat destruction caused by wildfire.

Context-specific outcomes of fire are also mediated by the spatiotemporal distribution of fire relative to key life history periods of animals (Driscoll et al. 2010; Sergio et al. 2018; Pausas 2019). Thus, the spatial location, landscape context, severity, and timing of fire must be considered relative to the phenology of important events within the annual cycle of a species. Sage-grouse populations in eastern Idaho are migratory, and direct mortality from the Grassy Ridge Fire was therefore not an issue because the fire burned breeding habitat that sage-grouse had mostly left by the time of the burn (July–August 2018). Thus, migratory status may provide important context, as the likelihood of finding appropriate habitats elsewhere and the costs and benefits of knowledge acquisition in nearby areas are both hypothesized to affect post-fire redistribution of animals (Nimmo et al. 2019). Migratory sage-grouse are highly mobile and even large burns like the Grassy Ridge Fire may cover a spatial extent smaller than movements of populations that undergo seasonal migrations. Nonetheless, location, timing, and scale of fire relative to core areas and seasonal movements of sage-grouse are not described by most studies, and therefore the relationships between migration and resilience to fire are poorly understood.

We describe a number of factors expected to generate context dependent outcomes from wildfire, yet disturbance events do not act in isolation, but rather realized responses can result from the interaction of multiple disturbances and environmental change agents (Didham et al. 2007; Driscoll et al. 2010; Krawchuk et al. 2020). Fire attributes, landscape composition and arrangement, and invasive species can act in concert to affect behavioral and fitness outcomes after wildfire (Nimmo et al. 2019). For example, if the burned area recovers to annual grassland, the landscape as a whole will be functionally degraded (Blomberg et al. 2012) and more vulnerable to future fires (Balch et al. 2013). Degradation of sage-grouse habitat by annual grasses and fire is common across the Great Basin (Blomberg et al. 2013; Coates et al. 2016), particularly at lower elevations and drier locations dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*). Similarly, adaptiveness of behaviors could differ in regions where the surrounding unburned landscape is more degraded by other factors affecting sage-grouse demography (e.g., where predators are anthropogenically subsidized; O'Neil et al. 2018). Thus, the rapid distribution shifts we observed in eastern Idaho likely does not reflect the dynamics of less resilient sites that are drier, lower elevation, or more generally degraded (Chambers et al. 2014). Furthermore, broad-scale cover and fragmentation of sagebrush affect occupancy of potential breeding habitat (Shirk et al. 2017), and therefore the breeding population at Sand Creek is also more vulnerable in the near term to further degradation and disturbance while sagebrush vegetation recovers.

Our study also focused exclusively on females and did not evaluate changes in male behavior or abundance pre- and post-fire. We note that males were observed attending leks inside the fire perimeter post burn. Hence lek-site fidelity likely affected scale-specific population responses across the area, and we suspect that over time lek-based analyses would reflect a time-lagged process of population redistribution to unburned areas, and possibly a decline in regional carrying capacity after the fire (Coates et al. 2016; Dinkins et al. 2021). Preliminary assessment of raw lek counts immediately before and after the Grassy Ridge Fire provided limited evidence for a regionwide decline in the number of males across both study areas (i.e., considering leks at the control site and both inside and outside the fire perimeter at the impact site; Table S12), but did not provide evidence this resulted from the fire. Nonetheless, our results suggest a direct and rapid change in the area of usable space available to nesting and brood-rearing sage-grouse hens in eastern Idaho.

Conclusions

Detailed information about life-history traits, behavior, and demographic responses are needed to develop a mechanistic understanding of wildlife responses to wildfire, yet in practice such data and the understanding they support are rare (Driscoll et al. 2010). This is partly because pulse disturbances like wildfire are transient events that make attempts at a priori study design and experimentation dubious, and nearly impossible for large-scale fire events. We were able to leverage spatially replicated field studies that were ongoing at the time of a catastrophic fire into a natural experiment with a BACI design that involved multiple levels of spatial controls for before-after comparison to a fire that effectively eliminated shrub habitat across > 40,000 ha. This study allowed us to observe previously unrecorded behavioral flexibility by breeding sage-grouse and that flexibility served to mitigate fitness consequences and thereby increase resiliency of sage-grouse in eastern Idaho. This work provides empirical support for predictions related to animal behavior and site fidelity theory and suggests that sage-grouse responses to rapid environmental change are likely influenced by a number of factors, including disturbance severity, landscape context, and mobility of the population under study. Thus, future work that links spatial variation in habitat quality to population growth (Kane et al. 2017) would strongly benefit context-specific interpretation of fire effects on sage-grouse by describing the functional value of remaining and lost habitats, and further assist with broad-scale conservation planning (Doherty et al. 2016), restoration of native sagebrush communities (Davies et al. 2014), and strategic targeting of fire suppression efforts (Meddens et al. 2018). Additional work is also needed to further clarify the roles of environmental cues (e.g., remaining shrub cover), individual-level attributes (e.g., experience), and their interactions in shaping behavioral responses to rapid habitat loss. Despite the responses we observed, their benefits to sage-grouse could still fall short of the pace of ongoing change if additional disturbances materialize, or invasive annual grasses proliferate, prior to sagebrush recovery. Nonetheless, we demonstrate that flexible behavioral responses to catastrophic fire include rapid alteration of space use that can mitigate short-term fitness impacts on an iconic species that is vulnerable to ongoing changes in habitat and fire regimes.

Abbreviations

BACI	Before-after-control-impact
AIC_c	Akaike's Information Criterion corrected for small sample size
GPS	Global Positioning System
RSF	Resource selection function
NB1 model	Negative binomial regression with a linear variance-mean relationship

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-025-00391-2.

Supplementary Material 1: Supplemental description and interpretation of analyses for nest and brood success models

Supplementary Material 2: Additional tables and figures for assessing the behavioral and fitness consequences of catastrophic wildfire on greater sage-grouse in eastern Idaho, USA

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Authors' contributions

BSS, CJC, and SJR conceived of the analyses and study questions, DKE and SJR conceived of field studies, supervised fieldwork, and compiled original location and capture-related datasets. BSS conducted all spatial and statistical analyses, led interpretation of results, wrote the first manuscript draft, and led all manuscript editing. CJC and SJR provided supervision of the research. All authors provided critical feedback and editing of the manuscript and read and approved the final manuscript.

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Data availability

The datasets analyzed during the study are available from the corresponding author on reasonable request.

Declarations

Ethics approval

This study was performed under the auspices of University of Idaho Institutional Animal Care and Use Committee protocols #2014–4, 2019–81, and #2022–03.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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