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Multi-scale effects of land cover, weather, and fire on Columbian sharp-tailed grouse

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Abstract

Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) are endemic to grassland and shrub-steppe ecosystems of western North America, yet their distribution has contracted to <10% of their historical range. Primary threats to Columbian sharp-tailed grouse include loss of native habitat and conversion to agriculture, reductions in habitat once provided by the Conservation Reserve Program (CRP), wildfire, and drought conditions, yet population-level consequences of these threats and their spatio-temporal scales of effect are poorly understood. We evaluated multi-scale effects of land cover, weather, and fire histories on patterns of abundance and productivity for Columbian sharp-tailed grouse populations during 1995–2020 in Idaho, USA, using mixed-effects generalized regression and remotely sensed data. We demonstrated negative effects of fire, tree encroachment, and bare ground, positive effects of spring and summer precipitation and cover of shrubs and perennial forbs and grasses, and positive effects of CRP on grouse abundance that changed in magnitude with cover of perennials and shrubs near leks (i.e., strongest effects when average cover of shrubs and perennial forbs and grasses were less abundant). We also demonstrated per capita recruitment of Columbian sharp-tailed grouse is positively associated with late-summer greenness. Our results show that several suspected threats have measurable, population-level impacts to Columbian sharp-tailed grouse

within Idaho. Moreover, our results suggest ongoing changes occurring within the core range of Columbian sharp-tailed grouse, including loss of CRP cover to tilled agriculture and changes to wildfire and precipitation dynamics are likely to have negative effects on populations.

KEYWORDS

agricultural conversion, Conservation Reserve Program (CRP), drought, NDVI, shrub-steppe, tree encroachment, *Tympanuchus phasianellus columbianus*, wildfire

The Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) is an endemic subspecies of sharp-tailed grouse that inhabits grassland, shrub-steppe, and mountain shrub communities of western North America (Connelly et al. 2020). The subspecies was once prolific and ranged from Colorado, USA, to British Columbia, Canada (Aldrich 1963); however, substantial and rapid range contraction occurred during the early twentieth century and Columbian sharp-tailed grouse now occupy <10% of their historical range (Hoffman et al. 2015). Consequently, Columbian sharp-tailed grouse have twice been petitioned for listing under the Endangered Species Act because of concerns about population persistence (U.S. Department of the Interior 2000, 2006). Specific drivers of Columbian sharp-tailed grouse extirpation are believed to be primarily human-caused threats that have caused degradation and elimination of habitat. Past investigators suggested numerous factors contributed to population declines, including conversion of shrubby grasslands for other land uses (e.g., row crops, human development), overgrazing by domestic livestock, invasion of non-native plants, and altered fire regimes (Marshall and Jensen 1937, Buss and Dzedzic 1955, Giesen and Braun 1993, McDonald and Reese 1998, Schroeder et al. 2000). Most extant breeding populations of Columbian sharp-tailed grouse currently persist in 3 areas of North America: southcentral British Columbia, southern Idaho and northern Utah, and northwest Colorado and southcentral Wyoming, USA, although several other isolated populations persist (e.g., north-central WA, USA; Hoffman et al. 2015).

Habitat loss and degradation, weather conditions, and disturbance events such as wildfire are implicated as primary threats to populations of Columbian sharp-tailed grouse (Hoffman et al. 2015, Idaho Department of Fish and Game [IDFG] 2015). Direct loss of native grassland and shrub-steppe to agriculture and other land uses was a driver of past population declines, but other large-scale changes to Columbian sharp-tailed grouse habitat are now considered to be important. For example, continued encroachment by exotic annual grasses and junipers (*Juniperus* spp.) may degrade habitat in some areas (IDFG 2015). Many populations of Columbian sharp-tailed grouse also rely heavily on private lands formerly in production agriculture that have since been removed from production and planted with grassland seed mixes after enrollment in the United States Department of Agriculture Conservation Reserve Program (CRP). These established grasslands enrolled in CRP provide important breeding habitat for Columbian sharp-tailed grouse in some parts of their range (Boisvert 2002, Gillette 2014, Hoffman et al. 2015, IDFG 2015, Proett et al. 2019). The ability of CRP to provide habitat depends on program funding and enrollment levels, which pose a substantial near-term challenge to Columbian sharp-tailed grouse conservation (Hoffman et al. 2015, IDFG 2015). In addition, annual fluctuations in weather can affect vital rates for Columbian sharp-tailed grouse. Drought can limit forb growth and insect production, which serve as important food resources for chicks (IDFG 2015), and therefore chick survival and recruitment can be reduced during drought (Collins 2004, Flanders-Wanner et al. 2004a, Proett et al. 2022). Drought also affects risk of wildfire (Pilliod et al. 2017), which has the potential to rapidly change the composition of shrub-steppe and grassland ecosystems and directly affect cover and food available during the breeding season (Hoffman et al. 2015).

Although researchers have identified threats to Columbian sharp-tailed grouse, empirical assessment of the relative impact of those threats on abundance, or the spatio-temporal scales over which these threats affect the subspecies, is limited (Hoffman et al. 2015). Relative to other sympatric Galliformes in western North America (e.g., greater sage-grouse [*Centrocercus urophasianus*]), few published studies have described population drivers for Columbian sharp-tailed grouse (Hoffman et al. 2015). For example, the effects of fire on Columbian sharp-tailed grouse are poorly understood, as are the cumulative impacts of different types of disturbance (Hoffman et al. 2015). Moreover, lands enrolled in CRP provide important habitat (Hoffman et al. 2015, IDFG 2015), but the degree to which population-level benefits of CRP vary in space and time remains unclear. Some studies suggested that CRP may provide lower-quality breeding habitat relative to native cover (McDonald 1998, Boisvert 2002, Gillette 2014). Yet recent work reported daily nest survival in restored grasslands (similar to grasslands that can be created under CRP or its sub-program CRP-State Acres for Wildlife Enhancement) was comparable to that observed in native habitats and can be improved by increasing forb cover (Proett et al. 2019).

Idaho is important for Columbian sharp-tailed grouse conservation because it contains the majority of extant breeding birds that remain in the United States (Hoffman et al. 2015). For example, 60–65% of breeding Columbian sharp-tailed grouse within the United States reside within the 17 counties of southern Idaho that are the focus of this study (IDFG 2015). Loss of CRP cover is an immediate threat to Columbian sharp-tailed grouse habitat in Idaho, where >43,000 ha of CRP was lost between September 2020 and September 2022 (U.S. Department of Agriculture Farm Services Agency 2020, 2022). Furthermore, large-scale conversion of native shrub-steppe and alteration of fire regimes has occurred across the Columbian sharp-tailed grouse range in Idaho (IDFG 2015). Approximately 70% of Columbian sharp-tailed grouse nesting and brood-rearing habitat in Idaho is located on private land (IDFG 2015), making habitat particularly vulnerable to land use change. Thus, Idaho provides the ideal location to quantify population-level benefits of CRP, cumulative effects of habitat change and disturbance events (e.g., fire), and spatio-temporal scales over which these factors affect Columbian sharp-tailed grouse.

Consequently, our objectives for this study were to describe the relative impacts of land cover, weather, and fire on abundance and productivity for Columbian sharp-tailed grouse, and identify the spatial and temporal scales over which land cover, weather, and fire affect Columbian sharp-tailed grouse populations. We predicted vegetation cover, fire histories, weather, and CRP would affect relative abundance and productivity for Columbian sharp-tailed grouse (Table 1). Specifically, we predicted the following features would benefit Columbian sharp-tailed grouse populations: cover of perennial forbs and grasses, litter cover (including standing dead vegetation), shrub cover, early spring (i.e., pre-hatch) and late summer (i.e., late brood-rearing) precipitation, and late spring (i.e., post-hatch) temperatures (Table 1). We further predicted the following features would be negatively associated with Columbian sharp-tailed grouse populations: fire frequency, cover of annual forbs and grasses, cover of bare ground, tree cover, and late spring (i.e., post-hatch) precipitation. We also predicted a dome-shaped quadratic relationship between Columbian sharp-tailed grouse and area burned by previous fires (i.e., benefits of some intermediate amount of fire) because fire can prevent conifer encroachment (Hoffman et al. 2015, IDFG 2015) but may negatively affect shrub cover and increase cover of annual and invasive forbs and grasses.

STUDY AREA

We studied Columbian sharp-tailed grouse abundance and productivity across their breeding range in Idaho (Figure 1). We used data collected from 1995–2020 at 561 Columbian sharp-tailed grouse leks located within 4 IDFG administrative regions (Southwest, Magic Valley, Southeast, Upper Snake) in southern Idaho (Figure 1). This study spanned the entire Snake River Plain of southern Idaho and covered an irregularly shaped area approximately 465 km from west to east, and 280 km from north to south. The 2020 status of leks sampled at least once from

TABLE 1 Variables considered and their predicted effects for each variable included in the evaluation of spatio-temporal drivers of relative abundance for breeding Columbian sharp-tailed grouse in southern Idaho, USA, 1995–2020. We include an explanation of the biological rationale for each variable and the predicted effects, along with spatial and temporal scales of measurement (combinations of grain and extent) used for each variable. We provide relevant citations justifying each variable and prediction in the footnotes. Spatial extents represent buffered distances around leks where we measured variables.

Variables	Predicted effects	Explanation	Spatial scale (grain/extent)	Temporal scale (grain/extent)
Detection				
Ordinal day ^a	Dome shaped quadratic	Expected counts on leks will peak at some point during breeding season as a function of lek attendance patterns		1 day/1 yr
Time of day (min past sunrise) ^a	(-) or dome shaped quadratic	Expected counts will change across a morning with daily lek attendance patterns, either declining continuously or peaking shortly after sunrise		1 min/1 day
Fire				
Fire frequency ^{b,c}	(-)	Shorter fire return intervals reduce cover for nesting and brood rearing	30 m/1–5 km	1 yr/1–3 yr ^d
Area burned ^{b,c}	Dome shaped quadratic	Some fire prevents woody encroachment and maintains grassland cover, too much fire eliminates nesting and brooding habitat	30 m/1–5 km	1 yr/1–3 yr
Land cover				
Annual forbs and grasses ^{b,c}	(-)	Non-native annuals provide poor quality nesting and brooding habitat and also facilitate more frequent and large-scale wildfire	30 m/1–5 km	1 yr/0–3 yr
Perennial forbs and grasses ^{d,e,f,g}	(+)	Perennial bunchgrasses and forbs improve nesting and brooding habitat	30 m/1–5 km	1 yr/0–3 yr
Bare ground ^{f,h,i,j}	(-)	Bare ground provides little food or cover	30 m/1–5 km	1 yr/0–3 yr

TABLE 1 (Continued)

Variables	Predicted effects	Explanation	Spatial scale (grain/extent)	Temporal scale (grain/extent)
Litter cover ^{e,f,k}	(+)	Increased litter cover (e.g., standing dead brush) increases concealment and escape cover	30 m/1–5 km	1 yr/0–3 yr
Shrub cover ^{d,i,l}	(+)	Shrub cover provides nesting and escape cover, and food during winter	30 m/1–5 km	1 yr/0–3 yr
Tree cover ^{b,c,g}	(-)	Encroachment of trees into shrubby grasslands reduces quality of nesting and brood-rearing habitat	30 m/1–5 km	1 yr/0–3 yr
CRP cover ^{b,c,f,g}	(+)	Restored grassland cover provided by the Conservation Reserve Program (CRP) provides breeding habitat in areas that would otherwise be in agricultural production	30 m/1–5 km	1 yr/0–3 yr
Weather				
Early spring precipitation ^{k,m,n,o}	(+)	Increased concealment cover for nesting and brood rearing, increased food for broods	4 km [†] /4 km	Lay, incubate, hatch [‡] /1–3 yr
Late spring precipitation ^{k,m,n,o}	(-)	Increased exposure decreases survival of young chicks that cannot thermoregulate	4 km/4 km	10, 14, 21 days [†] /1–3 yr
Late spring temperature exposure ^{m,n,p}	(+)	Increased exposure decreases survival of young chicks that cannot thermoregulate	4 km/4 km	10, 14, 21 days/1–3 yr

(Continues)

TABLE 1 (Continued)

Variables	Predicted effects	Explanation	Spatial scale (grain/extent)	Temporal scale (grain/extent)
NDVI ^{b,m}	(+)	Increased greenness of vegetation results in more abundant food and cover and better brood survival	30 m/3–5 km	Late brood period ^u /1–3 yr
<p>^aDrummer et al. (2011). ^bHoffman et al. (2015). ^cIDFG (2015). ^dMeints (1991). ^eBoisvert (2002). ^fProett et al. (2019). ^gStonehouse et al. (2015). ^hBuss and Dziedzic (1955). ⁱMcDonald and Reese (1998). ^jSchroeder et al. (2000). ^kBergerud (1988). ^lGiesen and Braun (1993). ^mFlanders-Wanner et al. (2004a). ⁿGoddard and Dawson (2009). ^oMeasured using 2 different metrics: average daily precipitation, and cumulative number of days with precipitation. ^pMeasured using 2 different metrics: average minimum daily temperatures, and average maximum daily temperatures. ^qTemporal extents of measurement lagged 1 year behind lek counts. For example, 1–3 yr refers to measurements taken the year prior to, or during 2-year or 3-year periods prior to lek counts. Year 0 refers to measurements taken the same year as lek counts. ^rA grain of 1/24° equals an approximately 4-km resolution for the gridMET weather data (Abatzoglou 2013). Grain and extent were equal for most weather variables because we measured them at the year-specific location of each lek (i.e., for the pixel containing each lek) and did not average over moving windows of different extents. ^sThe temporal resolution of raw data was 1 day. We summarized daily weather data for early spring weather variables from 15 Mar to the onset of egg laying (3 May), incubation (15 May), and hatching (8 Jun) for each year. ^tThe temporal resolution of raw data was 1 day. We summarized daily weather data for late spring weather variables from hatch (8 Jun) to 10 (18 Jun), 14 (22 Jun), and 21 days (29 Jun) post hatch for each year. ^uThe temporal resolution of raw data was 1 day. To summarize the normalized difference vegetation index [NDVI] during the late brood period, we averaged daily values from 15 Jul–30 Sep each year.</p>				

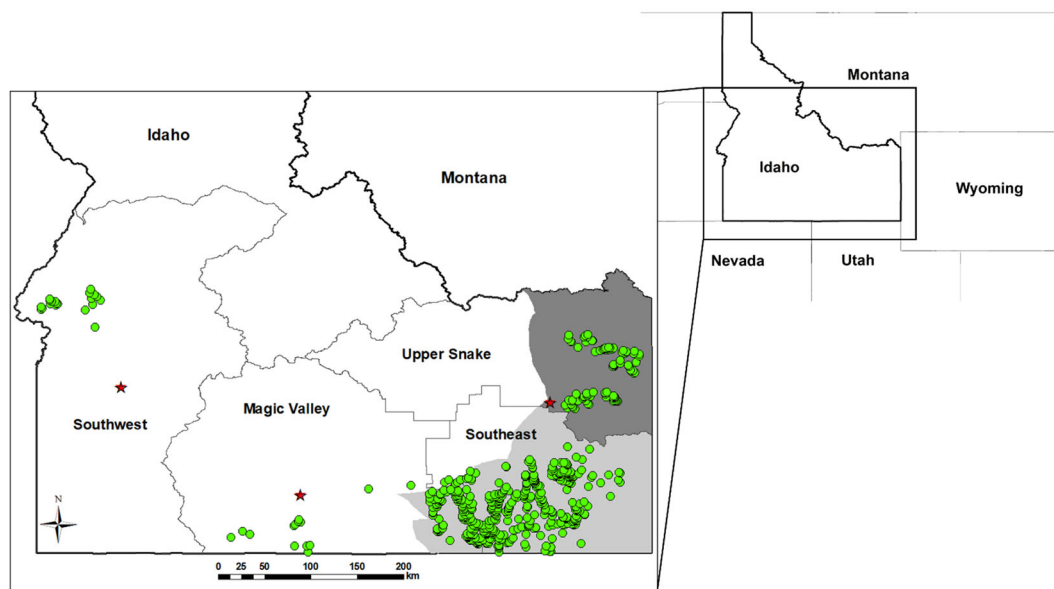


FIGURE 1 Study area showing Columbian sharp-tailed grouse lek locations and hunting regions in Idaho, USA, 1995–2020. Internal boundaries show Idaho Department of Fish and Game administrative regions (Southwest, Magic Valley, Upper Snake, Southeast) and green circles represent locations of leks monitored. Also shown are areas open to hunting in the Upper Snake (dark grey) and Southeast regions (light grey) where we collected age-ratio data from wing samples of hunter-harvested birds (2000–2019). The cities of Boise (Southwest region), Twin Falls (Magic Valley region), and Idaho Falls (Upper Snake region) are indicated with stars.

1995–2020 included 318 leks classified as occupied leks (>1 male counted within previous 5 years), 19 leks classified as unoccupied (0 males observed for 5 consecutive years, or no males observed on all sampling occasions for ≥ 7 of 10 years), 5 leks classified as pending status assignment (>1 male displaying but in a new geographic location), and 219 leks classified as undetermined status (e.g., due to lack of recent sampling). Across all unique lek locations, the average distance to the next nearest lek was $2,075 \pm 2,645$ m (SD). Elevation at Columbian sharp-tailed grouse leks ranged from 935–2,397 m above sea level, and cover near leks varied from native bunchgrass prairie and shrub-steppe communities interspersed with open ground to areas more fragmented by agriculture, including parcels enrolled in CRP. Dominant land uses near leks included agriculture and livestock grazing. Columbian sharp-tailed grouse habitat within the region is predominately associated with moderately sloped topography, although they use ridge tops and bottomlands during winter (IDFG 2015). The Snake River Plain is in the 30.5–50.8-cm precipitation zone and has an arid continental climate with hot, dry summers (Jun–Aug) and cold winters (Nov–Mar). For example, 30-year average annual precipitation (1991–2020) for Ashton, Idaho (northeast portion of study area) was approximately 50 cm, with an average minimum temperature during winter of -9.5°C and average maximum temperature during summer of 26.3°C (<http://www.ncdc.noaa.gov/cdo-web/datasets>, accessed 2 Mar 2022). Harvest of grouse by hunters occurred throughout the study duration but was limited to 2 areas of eastern Idaho (Upper Snake and Southeast; Figure 1).

Common native perennial bunchgrass species found in Columbian sharp-tailed grouse breeding habitat in Idaho included bluebunch wheatgrass (*Pseudoroegneria spicata*), Sandberg bluegrass (*Poa secunda*), and Idaho fescue (*Festuca idahoensis*), whereas common native shrubs included sagebrush (*Artemisia* spp.), bitterbrush (*Purshia tridentata*), and rabbitbrush (*Chrysothamnus* spp.). Common vegetation on CRP parcels included crested wheatgrass (*Agropyron cristatum*), intermediate wheatgrass (*Thinopyrum intermedium*), bluebunch wheatgrass, smooth brome

(*Bromus inermis*), Sandberg bluegrass, cheatgrass (*Bromus tectorum*), basin wild rye (*Leymus cinereus*), yarrow (*Achillea millefolium*), alfalfa (*Medicago sativa*), sainfoin (*Onobrychis viciifolia*), and yellow sweet clover (*Mellilotus officinalis*). Common wildlife species inhabiting the study region included greater sage-grouse, gray partridge (*Perdix perdix*), ruffed grouse (*Bonasa umbellus*), common ravens (*Corvus corax*), golden eagles (*Aquila chrysaetos*), American badger (*Taxidea taxus*), coyote (*Canis latrans*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), elk (*Cervus canadensis*), and moose (*Alces alces*).

METHODS

We used data collected from ongoing IDFG monitoring to assess drivers of Columbian sharp-tailed grouse abundance and productivity. We monitored relative abundance during the breeding season with data from lek counts conducted from 1995–2020 throughout the range of Columbian sharp-tailed grouse in Idaho by IDFG staff and volunteers (Figure 1; Figures S1–S2, available in Supporting Information). We interpreted lek counts as a local index of relative abundance, as is common for prairie grouse (Applegate 2000, Hoffman et al. 2015, Blomberg and Hagen 2020). Surveyors conducted lek counts annually between 9 March and 26 May (Figures S3–S5, available in Supporting Information), sampling intensity varied among leks and years (protocol suggested ≥ 3 visits/year, but the average across leks ranged from 1.5 [1995] to 3.8 [2015] visits), and most leks were not surveyed every year. Crews conducted lek surveys using a standardized protocol, with most counts conducted from 30 minutes before sunrise to 2 hours after sunrise, and on mornings with no precipitation and wind speeds < 16 km/hour. Surveyors flushed birds during lek surveys to obtain an accurate count of all grouse present (zeros were recorded when no grouse were present), but did not attempt to distinguish males from females. Surveyors also recorded the date, time, and location of each survey because lek locations can change through time (Schroeder et al. 2000).

We collected wing samples from Columbian sharp-tailed grouse harvested by hunters during 2000–2019 from the Upper Snake and Southeast hunting regions (Figure 1) to quantify population productivity. Wing samples from hunter-harvested birds are a common approach to monitor production (i.e., juvenile:adult ratios) of Columbian sharp-tailed grouse and other prairie grouse (Flanders-Wanner et al. 2004b, Hoffman et al. 2015), and we aged wing samples based on the wear pattern of primary feathers as described in Amman (1944). To collect wings, IDFG distributed wing collection barrels along major travel routes within primary hunting locations within each region; thus, barrels were located near common hunting areas for Columbian sharp-tailed grouse. Hunters were asked to voluntarily remove 1 wing from harvested birds and deposit the wing in the barrel. To increase wing sample sizes, IDFG mailed self-addressed, pre-paid envelopes to likely Columbian sharp-tailed grouse hunters identified by their purchase of a sage- and sharp-tailed grouse validation on their Idaho hunting license (a requirement to legally hunt those species since 2000). Hunters mailed 1 wing/envelope and also recorded the date, county, and area where the grouse was harvested.

Covariate data

Relative abundance covariates

We predicted that land cover, fire history, and weather before and during the breeding season would affect relative abundance of Columbian sharp-tailed grouse (Table 1). We measured each covariate over a variety of biologically plausible spatial and temporal scales, which allowed us to identify the optimal explanatory scale for each covariate. We linked all covariate data spatially to year-specific lek locations (573 unique locations). We considered shifts in spatial location of < 0.4 km to be the same lek (i.e., the same lek identification number and therefore the same

lek-level random intercept value), whereas we considered larger shifts to be new leks. We used ArcMap 10.5.1 (Esri, Redlands, CA, USA) for analyses measuring covariates around leks.

We used remotely sensed data produced by the Rangeland Analysis Platform (Jones et al. 2018) to measure year- and location-specific rangeland vegetative cover surrounding Columbian sharp-tailed grouse leks. The Rangeland Analysis Platform data provided annual cover estimates (available 1984–2019) for perennial forbs and grasses, annual forbs and grasses, litter, shrubs, bare ground, and trees at a 30-m resolution across the extent of our study area (i.e., each 30-m pixel had a percent cover value for each variable), where each annual cover value was an average of cover estimates produced over 6 64-day periods within each year. We measured the average value of each vegetation variable across pixels within spatial extents of 1–5 km (by 1-km increments) around leks by using moving window analyses (with cropland, development, and water masked out of calculations), which included most nesting and brood-rearing habitat (Hoffman et al. 2015). We also measured vegetation cover variables around each lek at 4 temporal extents, which included years concurrent with and prior to each lek count, and vegetation cover values averaged over the 2- and 3-year periods prior to each count. Growth of vegetation and buildup of fine fuels in sagebrush steppe reflect multi-year sequences of precipitation and drought (Pilliod et al. 2017), and therefore time-lagged effects on Columbian sharp-tailed populations are biologically plausible (e.g., from previous effects on individual vital rates). In summary, we measured each vegetation cover variable over 20 unique spatio-temporal scales (5 spatial extents \times 4 temporal extents) to facilitate multi-scale assessment and allow for biologically plausible time-lagged effects of vegetation.

We obtained spatial data regarding which land parcels were enrolled in CRP directly from the United States Department of Agriculture Farm Services Agency (2020, 2022), as these data are not produced by the Rangeland Analysis Platform. We measured the amount of CRP annually surrounding leks, but these data were only available for more recent years of our study (2012–2020); therefore, we treated CRP values from earlier periods (prior to 2012) as missing covariate data. Approximately 60% of lek surveys were conducted from 2012–2020 (Tables S1–S2, available in Supporting Information) and therefore had paired CRP information available. Also, these data were the only spatially explicit CRP coverage data available at an appropriate spatial resolution for our analyses (i.e., polygons of all CRP parcels instead of county-level summary statistics). We used these data to measure the amount of CRP surrounding leks at the same 20 scales described above for vegetation cover (5 spatial extents \times 4 temporal extents).

We measured fire histories surrounding Columbian sharp-tailed grouse leks by using the remotely sensed Monitoring Trends in Burn Severity (MTBS) data (Eidenshink et al. 2007). The MTBS data provided annual (available 1984–2017) location and ordinal severity measures at a 30-m resolution for fires ≥ 404.7 ha in size. We measured fire frequency (number of unique fires) and area burned around each lek at 5 spatial extents as described above (1–5 km by 1-km increments). We also measured fire histories at 3 temporal extents, which included the year prior to lek counts, and cumulative fire frequency and area burned (for all fires and the most severe burns only [severity category 4]) over the 2- and 3-year periods prior to each lek count. We did not include fires during the year concurrent with lek counts because in this landscape fires typically occur after the spring breeding season and lek counts occur during spring (Mar–May). In summary, we measured each fire variable at 15 unique spatio-temporal scales (5 spatial extents \times 3 temporal extents). The MTBS data do not include coverage of smaller fires (< 404.7 ha), which precluded us from investigating their effects on Columbian sharp-tailed grouse populations (such effects may differ from those of large fires; Hoffman et al. 2015). Unfortunately, no data for coverage of smaller fires were available at appropriate spatial and temporal scales, and therefore our inferences were limited to effects of larger fires. Moreover, because our assessment included only fires near leks that occurred within the 3 years prior to each lek count, we assessed only short-term effects of fire on Columbian sharp-tailed grouse.

We used gridMET climatological data (Abatzoglou 2013; available 1979–present) to measure spring weather conditions surrounding Columbian sharp-tailed grouse leks. The gridMET data set blends the high-resolution spatial attributes of PRISM data (PRISM Climate Group, Oregon State University, <https://prism.oregonstate.edu>) with high temporal resolution remote-sensing information to produce spatial and temporal grids of climatological variables

updated daily for the entire contiguous United States, resulting in a fine spatial ($1/24^\circ$) and temporal (daily) resolution surface of modeled meteorological conditions (Abatzoglou 2013). The gridMET data therefore provided daily precipitation and temperature estimates at an approximately 4-km resolution across the extent of our study area.

We predicted that early spring precipitation, late spring precipitation, and late spring temperature exposure would affect Columbian sharp-tailed grouse populations; however, little information is available to determine the best measures of spring precipitation and temperature exposure *a priori*. Therefore, we derived 2 spring precipitation metrics and 2 temperature metrics from the daily gridMET data: average daily precipitation, cumulative number of days with precipitation, average daily minimum temperature, and average daily maximum temperature (Table 1). We also measured early and late spring weather conditions over multiple temporal resolutions relevant to nesting and brood rearing for Columbian sharp-tailed grouse. Specifically, we measured early spring precipitation over 3 periods, starting 15 March and going through dates that approximate the initiation of egg laying, incubation, and hatching, respectively. We used the midpoint of median hatch dates reported from 4 previous field studies in Idaho (8 Jun; Meints 1991, Apa 1998, Gillette 2014, Proett 2017) to define phenology of these periods because region-specific nesting chronology was not available. We assumed 24 days of incubation and 12 days of laying (i.e., clutch of 12 eggs with 1 egg laid per day) to define timing of incubation and egg laying relative to hatch date. In addition, we measured late spring (i.e., post-hatch) precipitation and temperature metrics over 3 periods, starting with hatch (8 Jun) and going through 10-, 14-, and 21-days post hatch, respectively. We linked all spring weather covariates to year-specific lek locations based on the lek location within a given pixel of the gridMET raster. Lastly, we measured each spring weather covariate at 3 temporal extents to allow for the possibility of time-lagged effects on grouse abundance (i.e., effects of weather on vital rates may not result in immediate changes to abundance). This included the year prior to each lek count, and averaged over 2- and 3-year periods prior to each count. Thus, we measured early and late spring weather at 9 temporal scales (3 temporal resolutions \times 3 temporal extents).

We derived normalized difference vegetation index (NDVI) from 30-m resolution Landsat satellite imagery as a measure of vegetative productivity during the late brood period (15 Jul–30 Sep; Box et al. 1989). We averaged annual NDVI scores for the period using all available Landsat imagery, and acquired Landsat images at 16-day intervals. We summarized NDVI data as an average over 3 spatial extents (within 3–5 km of leks, by 1-km increments) because females with broods may be farther from leks later in the year. We measured NDVI using the same temporal extents described for spring weather variables to allow for time-lagged effects. In summary, we measured greenness at 9 scales (3 spatial extents \times 3 temporal extents).

Productivity covariates

We predicted similar covariates and directional effects for Columbian sharp-tailed grouse productivity (juvenile:adult ratio in the harvest) to those described above for patterns of relative abundance (Table 1). We used the data sets described above to generate land cover, fire history, and weather covariates to explain spatio-temporal patterns of productivity; however, we measured productivity covariates over different scales to reflect the coarser spatial resolution of wing sample data (i.e., IDFG hunting regions; Figure 1) and the inferences gained from abundance modeling described above. For example, we calculated average values of vegetation cover covariates described above across each hunting region for each year but only included areas within 3 km of leks (the max. scale of effect on abundance for any vegetation covariate). This approach allowed us to focus measurement of habitat attributes to breeding areas within each hunting region. Similarly, we measured CRP cover as the cover within each hunting region but only included CRP parcels within 1 km of leks (the optimal scale of effect of CRP on abundance) to reflect the overwhelming support for fine-scaled effects of CRP on Columbian sharp-tailed grouse populations. We also measured land cover covariates in the same year as the age ratios for this analysis. Lastly, we used MTBS

data to measure fire histories across each harvest region. We included fire frequency, area burned, and area of high-severity fire burned within 2 km of leks as covariates in productivity models (the optimal scale of effect of fire variables on abundance). Moreover, we measured fire covariates at 3 temporal extents to reflect the possibility of time-lagged effects on productivity: the year concurrent with each wing sample, and cumulative values over 2- and 3-year periods prior to each hunting season (i.e., including fires from the current year).

We used gridMET data to measure spring weather across each hunting region and included covariates described above, all measured during the year concurrent with wing sample collection. For productivity analyses we used region-specific estimates of median hatch date to define time periods for early- and late-spring precipitation and temperature measures (instead of 8 Jun for all sites) based on recent studies in the Upper Snake (8 Jun; Proett 2017) and Southeast (1 Jun; Gillette 2014) hunting regions. Moreover, we hypothesized additional temporal scales for temperature and precipitation effects on productivity: average minimum and maximum temperatures from 1 March–30 June (i.e., temp over the entire breeding season), and annual precipitation (i.e., overall precipitation may be more important than seasonal precipitation). Annual precipitation could also serve as a proxy to beneficial regional vegetation conditions for the productivity analyses, given the coarse spatial resolution of wing-sample data. This contrasts with the lek count data, which were available at fine resolution and thus could be directly linked with local vegetation data that were also fine resolution (30-m pixels) and updated annually. Consequently, it was appropriate to include annual precipitation as a potential predictor of productivity while excluding it as a predictor of local abundance because local vegetation conditions are already captured by the analyses described above. To reflect the possibility of time-lagged effects of annual precipitation on productivity (where breeding season conditions are determined by the previous years' precipitation), we considered annual precipitation measured over both the year prior to and the year concurrent with age ratio data collection.

Statistical analyses

Relative abundance models

We used mixed-effects log-linear regression to describe patterns of relative abundance while also incorporating effects of survey-level detection covariates on expected lek counts (Sauer and Link 2011, Barker et al. 2018). We used a multi-stage process to eliminate uninformative covariates from consideration because of the large number of hypothesized covariates and biologically relevant scales measured for each (Harrity et al. 2020). Specifically, the sequential stages of our analyses were 1) identify detection covariates to control for differences in lek counts related to the timing of individual surveys, 2) identify the optimal spatio-temporal scale of effect for each covariate predicted to affect local abundance, 3) conduct variable reduction to eliminate uninformative covariates from consideration within the categories of vegetation, fire, and weather variables, 4) identify the optimal stochastic structure for the final models from plausible parameterizations of the Poisson and negative binomial (NB) distributions, and 5) conduct the final model selection using the reduced set of scale-optimized covariates and the optimal distribution identified from previous stages. We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c ; Burnham and Anderson 2002) for all model comparisons, and we used an NB model assuming a linear variance-mean relationship (so-called NB1 distribution; Brooks et al. 2017) as the distribution for lek counts during preliminary analyses (stages 1–3 above). We also used a random-effects structure that included lek-specific random intercepts (i.e., fine-scale spatial variation in counts among leks) and annual random intercepts that were specific to each IDFG administrative management region (i.e., large-scale annual variation in counts that was heterogeneous among regions). We standardized the values of all covariates by subtracting their observed mean and dividing by the standard deviation, and assigned zero values to missing data for individual covariates (e.g., CRP cover prior to 2012) after standardization so that those data points provided no information to estimate the corresponding regression coefficients (Fox 2008; Table S2). Similarly, for covariates that were summarized across

multiple years (e.g., average vegetation cover values for 2 or 3 years prior to a lek count), we assigned values of 0 after standardization if data from any of the component years were missing. We fit all mixed-effects regression models using the `glmmTMB` package (Brooks et al. 2017) in R version 4.0.1 (R Core Team 2020).

We first selected survey-level covariates affecting detection of Columbian sharp-tailed grouse to control for the effects of survey timing on observed lek counts. We did not attempt to separate nuisance parameters for the distinct processes of animals being available for detection and conditional detection of animals given their presence during surveys (Pollock et al. 2004), but rather we considered covariates that could affect either of these processes and therefore shift expected counts during a given survey. We predicted that ordinal day and time of each survey (measured in min after sunrise) would directly affect expected counts of Columbian sharp-tailed grouse through seasonal and daily lek attendance patterns or displaying behavior. We predicted dome-shaped quadratic effects for both variables, predicting lek attendance would likely peak in April, and shortly after sunrise for a given day of the breeding season (Drummer et al. 2011). We considered 9 detection-covariate models that included additive combinations of ordinal day and time of survey, both linear and quadratic effects for each variable, and an intercept-only null model to evaluate the need to consider these control variables further. We included detection covariates from the top model ($\Delta AIC_c = 0$) in all subsequent analyses to control for their effects on lek counts.

Next, we optimized the scale for each covariate predicted to affect Columbian sharp-tailed grouse abundance (Jackson and Fahrig 2015, McGarigal et al. 2016, Stevens and Conway 2019). We used AIC_c to compare all measured scales for each variable and retained the optimal measurement scale for each covariate for further analyses. During the scale-optimization step, we also optimized the shape (linear vs. quadratic relationship) of individual variables that we predicted had nonlinear relationships with lek counts (Table 1). Moreover, because we measured early spring precipitation, late spring precipitation, and late spring temperature exposure in multiple ways (e.g., average daily precipitation vs. cumulative daily precipitation), the scale optimization stage for these variables also included selecting the optimal metric for measuring each of these attributes. From this stage, we retained scale-optimized measures of each land cover and fire covariate, and NDVI during the late brood period, the cumulative number of days with precipitation up to incubation as a measure of early spring precipitation, the cumulative number of days with precipitation up to 21 days post hatch as a measure of late-spring precipitation, and average maximum temperature up to 21 days post hatch as a measure of late-spring temperature exposure.

For stage 3, we conducted variable reduction analyses to eliminate uninformative covariates from further consideration by comparing all combinations of uncorrelated covariates ($r < 0.65$) within each category (vegetation, fire, weather). For example, we compared all combinations of scale-optimized vegetation covariates to reduce the number of vegetation variables used in the final model selection. We used the `CombPairs` function within the `DescTools` R package (Andri et al. 2021) to generate the appropriate variable combinations within each covariate group, which resulted in comparison of 63, 3, and 9 models within the vegetation, fire, and weather categories, respectively. From this analysis, we retained covariates within each group if they were contained within the top model, or if they were contained within a competitive model ($\Delta AIC_c \leq 2.0$) and their 90% confidence interval excluded zero. Models for weather covariates at this step also included an interaction term between late-spring precipitation and late-summer NDVI because we predicted that benefits of late-summer greenness would be stronger after periods of low spring precipitation.

After reducing the number of covariates within each group, we next used the global fixed-effects model with all remaining covariates to select the optimal stochastic distribution for the final models. In this stage, we selected an optimal count distribution by comparing 7 statistical distributions for the lek count data: the Poisson distribution, 3 parameterizations of the NB distribution with a linear variance-mean relationship (NB1 model), and 3 parameterizations of the NB distribution with a quadratic variance-mean relationship (i.e., variance increases nonlinearly with mean; NB2 model; Brooks et al. 2017). Changes in animal behavior across a breeding season can cause changes in the variance-mean relationship of count data across time (Lindén and Mäntyniemi 2011, Harrity

et al. 2020). Therefore, we predicted the NB dispersion parameter (θ) would change over the Columbian sharp-tailed grouse breeding season. Specifically, we predicted that dispersion would have a U-shaped quadratic relationship with ordinal day of the survey. Thus, we predicted overdispersion of the lek counts would be smallest during the middle of the lekking season because of more consistent lek attendance (Drummer et al. 2011), and consequently counts from the middle of the season would have a smaller variance than counts early or late in the season (i.e., conditioned on the same expected count). Thus, we considered 3 models of θ for each of the NB1 and NB2 distributions, including a constant model and models with linear and quadratic effects of ordinal day, and modeled heterogeneity in θ using the log link function (Brooks et al. 2017).

For the final stage of analysis, we selected a model for inference by comparing fixed-effects covariates describing patterns of abundance as a function of vegetation cover, fire history, weather, and CRP. We considered models where vegetation, fire, weather, and CRP covariates were either included collectively or not. For example, models with vegetation included all of the scale-optimized vegetation covariates retained from stage 3, whereas models without vegetation included none of them. Because we predicted the effects of CRP would depend on the amount of native cover surrounding leks (i.e., stronger positive effects in areas with less natural habitat close to leks), we also included 2-way interaction terms between CRP and cover of perennial forbs and grasses, and between CRP and cover of shrubs. In total, we considered 16 models for the final stage of model selection, which included combinations of the covariate groups and the null model with none of these covariates. We created partial-effects plots for each variable with all others held at their mean values to visually portray biological effects of covariates in the final model. We also generated 95% confidence intervals for real-scale partial-effects plots using nonparametric bootstrapping, with 1,000 bootstrapped samples of the original data and the top model re-fitted to each bootstrapped sample. Because many lek surveys lacked corresponding CRP covariate data (i.e., surveys prior to 2012, approximately 40% of lek counts), we also conducted a sensitivity analysis to ensure our conclusions about the effects of CRP on Columbian sharp-tailed grouse abundance were robust to exclusion of data from prior to 2012. Specifically, we re-fit the top model using only data from 2012–2020 and compared the estimated effects of CRP with reduced data to that of the original analyses.

Productivity models

We used weighted mixed-effects logistic regression to model Columbian sharp-tailed grouse productivity derived from annual wing samples. The number of wings in a sample served as the weights in this analysis, whereas the response variable was a binomial sample of the number of juveniles in the wing sample for each region. Therefore, this analysis modeled the proportion of juveniles in the wing sample as the response, where a proportion >0.5 indicated juvenile:adult ratios that were greater than 1:1. We again used a multi-stage process to arrive at a final model for inference because of the large number of covariates predicted to affect Columbian sharp-tailed grouse, and we used a random-effects structure with annual random intercepts that were specific to each hunting region. We standardized observed covariate values as described above and assigned missing data values of zero after standardization.

We used a multi-stage model selection process similar to that described above to identify covariates affecting Columbian sharp-tailed grouse productivity. First, we identified the optimal shape (linear vs. quadratic) for fire covariates predicted to have nonlinear effects, and identified the optimal scale for those covariates measured over multiple temporal scales (i.e., fire and spring weather effects). Second, we conducted a variable reduction analysis to reduce the number of covariates within each group (vegetation, fire, weather), by comparing all combinations of covariates in each group that were not strongly correlated ($r < 0.65$). The variable reduction step compared 31, 3, and 31 models within the vegetation, fire, and weather categories, respectively. For each variable group, we retained covariates found in the top model for the final model set. For the last stage, we compared all combinations of remaining covariates (vegetation, CRP, fire, and weather) that were not strongly correlated ($r < 0.65$; $n = 64$

models). We created partial-effects plots for variables in the top models to visually portray results of this analysis and we used nonparametric bootstrapping of the original data ($n = 1,000$ bootstrap samples) to generate 95% confidence intervals for real-scale partial effects of each covariate.

RESULTS

We used data from 6,114 lek surveys conducted at 561 leks ($n = 573$ unique locations) from 1995–2020 (Table S1; Figures 1, S1–S2), with individual surveys conducted as early as 9 March and as late as 26 May ($\bar{x} = 17$ Apr). Lek counts were skewed toward smaller values ($\bar{x} = 8.5$ birds/count, range = 0–115 birds), approximately 76% of counts were <15 birds (31% of surveys resulted in 0 counts), and intensity of lek sampling varied among years (Figures S1–S5). Preliminary modeling indicated a dome-shaped quadratic effect of ordinal day on expected lek counts, which peaked near the observed average survey date, and a linear decline in lek counts with time elapsed after sunrise (Figure 2; Table S3, available in Supporting Information). We used 10,281 wing samples collected from hunter-harvested birds during 2000–2019 (Southeast region: $n = 5,857$; Upper Snake region: $n = 4,424$) to estimate age ratios and assess patterns of productivity (Table S4, available in Supporting Information). The proportion of juveniles in wing samples ranged from a low of 0.27 in the Upper Snake region in 2003 to a high of 0.67 in the Upper Snake region in 2019 and averaged 0.49 across both regions during the study duration (Southeast region: $\bar{x} = 0.47$; Upper Snake region: $\bar{x} = 0.52$).

Relative abundance models

The optimal scales of effect on lek counts differed (in both space and time) for disturbance, land cover, and weather covariates (Tables S5–S8, available in Supporting Information). For example, a 2-km radius around leks was the optimal spatial scale and the 2 years prior to a lek count was the optimal temporal scale for the relationships between Columbian sharp-tailed grouse abundance and both fire variables in the final model. In contrast, a 1-km radius around leks was the optimal spatial scale for the relationships between abundance and cover of bare ground,

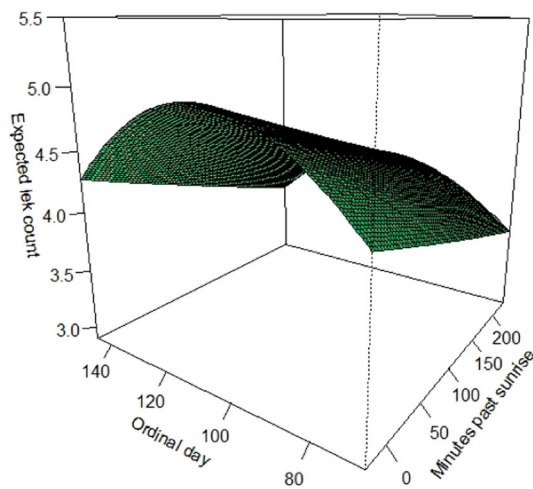


FIGURE 2 Effects of survey timing on expected lek counts during field surveys for Columbian sharp-tailed grouse in southern Idaho, USA, 1995–2020. Figures show the interactive effects of survey time (minutes past sunrise) and date (ordinal day) on expected counts. The median ordinal day of sampling was 105 and the median time of sampling was 59 minutes past sunrise.

trees, perennial forbs and grasses, and CRP, but 3-km and 4-km radii were optimal for shrubs and annual forbs and grasses, respectively. The optimal temporal scale was the year concurrent with lek counts (bare ground, shrubs, and CRP), the year prior to lek counts (trees), or the average cover over the 3 years prior to lek counts (perennial forbs and grasses, annual forbs and grasses). The optimal temporal scale for measuring early spring precipitation was up to median onset of incubation and during the year prior to lek counts, whereas the optimal temporal scale for late-spring precipitation was during the first 21 days post hatch and over the 3 years prior to lek counts. Moreover,

TABLE 2 Top models for the effects of vegetation, weather, fire, and area of Conservation Reserve Program (CRP) lands on relative abundance of Columbian sharp-tailed grouse in southern Idaho, USA, 1995–2020. All models contained survey-level detection variables (ordinal day and time of day), random intercept terms for individual leks and region-specific annual effects, and effects of ordinal day on the negative binomial dispersion parameter; the global model was the top model in this analysis. We present the difference in Akaike's Information Criterion corrected for sample size (ΔAIC_c), model weight (w_i), and number of parameters (K).

Model	ΔAIC_c	w_i	K
Fire ^a + vegetation ^b + weather ^c + CRP ^d	0.00	0.97	23
Vegetation + weather + CRP	7.07	0.03	21
Fire + vegetation + CRP	35.12	0.00	19
Vegetation + CRP	40.79	0.00	17
Fire + vegetation + weather	137.53	0.00	20
Vegetation + weather	139.15	0.00	18
Fire + weather + CRP	155.39	0.00	16
Weather + CRP	166.12	0.00	14
Fire + vegetation	174.21	0.00	16
Vegetation	174.78	0.00	14
Fire + CRP	194.98	0.00	12
CRP	203.79	0.00	10
Fire + weather	250.90	0.00	15
Weather	263.83	0.00	13
Fire	299.63	0.00	11
Null ^e	309.93	0.00	9

^aFire variables included were area burned within 2 km of leks (year prior to lek counts) and fire frequency within 1 km of leks (cumulative over 2 years prior to lek counts).

^bVegetation variables included were perennial forb and grass cover within 1 km of leks (average over 3 years prior to lek counts), annual forb and grass cover within 4 km of leks (average over 3 years prior to lek counts), bare ground cover within 1 km of leks, shrub cover within 3 km of leks, and tree cover within 1 km of leks (year prior to lek counts).

^cWeather variables included were normalized difference vegetation index [NDVI] within 5 km of leks (calculated during the late brood-rearing period, averaged over 2 years prior to lek counts), early-spring precipitation (measured as number of days with precipitation from 15 Mar until onset of nest incubation in year prior to lek counts), and late-spring precipitation (measured as number of days with precipitation from the median hatch date until 21 days post hatch, averaged over 3 years prior to lek counts). Models with weather variables also included an interaction between NDVI and late-spring precipitation.

^dCRP was measured within 1 km of leks in the year concurrent with lek counts, and models that contained both vegetation and CRP effects included interactions between CRP and cover of shrubs and perennial forbs and grasses.

^eNull model contained only the survey-level detection variables, random effects, and quadratic effects of ordinal day on the negative binomial dispersion parameter.

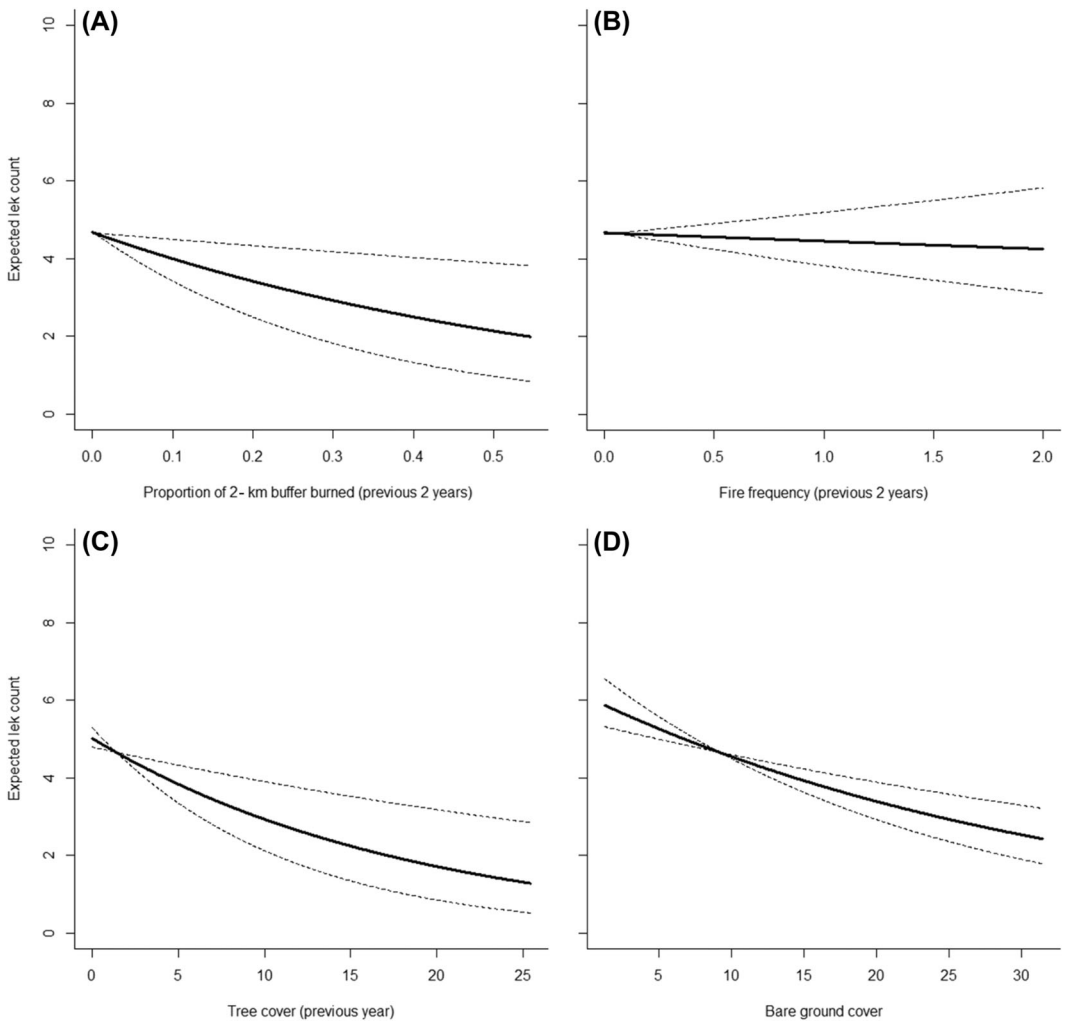


FIGURE 3 Effects of fire and land cover on expected counts of Columbian sharp-tailed grouse at leks in southern Idaho, USA, 1995–2020. Figures show partial effects from the top model: A) area burned (proportion within 2 km of leks, measured during the previous year), B) frequency of fires (number within 2 km of leks, measured during previous 2 years), C) tree cover (%; within 1 km of leks, measured during the previous year), and D) bare ground cover (%; within 1 km of leks, measured during the year concurrent with lek counts). Dashed lines represent 95% confidence intervals for each relationship.

scale-optimization analyses demonstrated clear sensitivity to choice of scale, where inferences about covariate effects often changed among the measurement scales that we considered (Figure S6, available in Supporting Information).

We documented multi-scale effects of disturbance, land cover, weather, and CRP on patterns of Columbian sharp-tailed grouse abundance (Table 2; Figures 3–5; Tables S5–S12, available in Supporting Information). We observed strong negative effects of area burned, cover of bare ground, and cover of trees (Figure 3), and positive effects of shrubby-grassland cover (perennial forbs and grasses, shrubs; Figure 4) and early-spring precipitation (cumulative days with precipitation up to incubation; Figure 5). For example, when holding all other covariates at their mean values, expected lek counts decreased by 57.5% with area burned, 8.9% with fire frequency, 74.5% with tree cover, and 58.7% with bare ground, from low to high values of the observed data

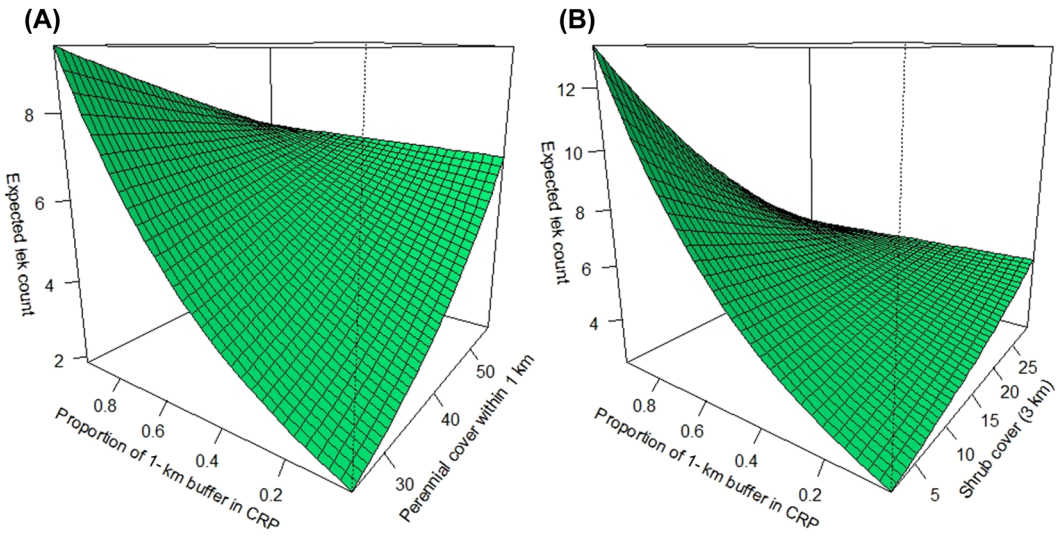


FIGURE 4 Interactive effects of shrubby-grassland cover and cover of lands enrolled in the Conservation Reserve Program (CRP) on expected counts of Columbian sharp-tailed grouse at leks in southern Idaho, USA, 1995–2020. Figures show interactions between A) proportional coverage of CRP (within 1 km of leks; measured during the year concurrent with lek counts) and perennial forb and grass cover (% within 1 km of leks, averaged over the 3 previous years), and B) proportional coverage of CRP (within 1 km of leks, measured during the year concurrent with lek counts) and shrub cover (% within 3 km of leks, measured during the year concurrent with lek counts).

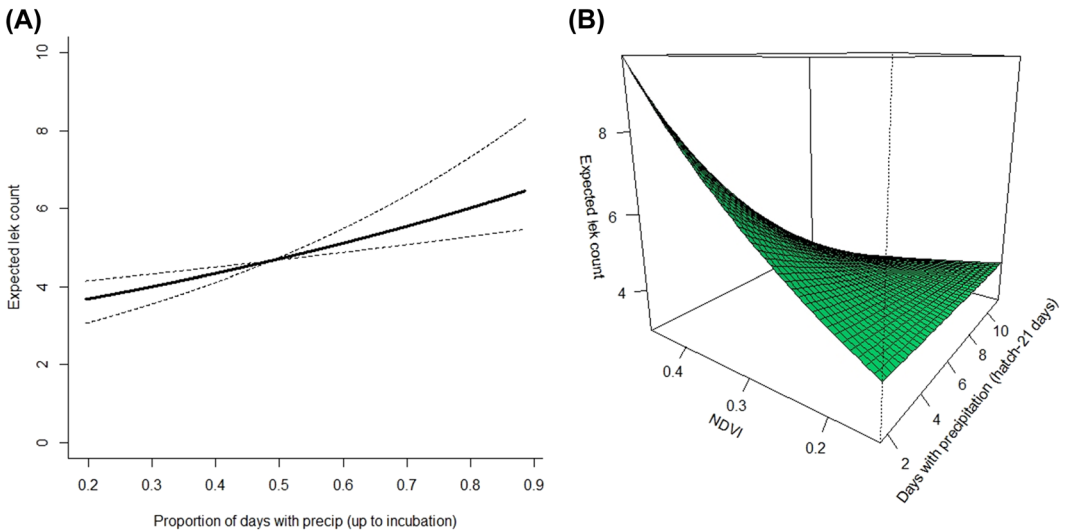


FIGURE 5 Effects of spring precipitation and summer greenness on expected counts of Columbian sharp-tailed grouse at leks in southern Idaho, USA, 1995–2020. Figures show partial effects of A) early spring precipitation (proportion of days with precipitation from 15 Mar to incubation onset, measured the year prior to lek counts), with 95% confidence intervals (dashed lines), and B) interactive effects between late-spring precipitation (proportion of days with precipitation from hatch to 21 days post hatch, averaged over previous 3 years) and greenness (normalized difference vegetation index [NDVI] within 5 km of leks, averaged over 2 years prior to lek counts) during the late brood-rearing period.

(Figure 3). In contrast, when holding all other covariates at their mean values, expected lek counts increased by 75.5% from low to high values of early spring precipitation (Figure 5). Expected lek counts decreased by 15.1% over low to high values of cover of annual forbs and grasses. We had little model selection uncertainty in the top abundance model ($w_i = 0.97$), which included an NB1 distribution with nonlinearly increasing dispersion (i.e., variance increased relative to the mean count) over the breeding season (Table S13 and Figure S7, available in Supporting Information). Most covariates in the top abundance model were estimated precisely, with 95% confidence intervals for main effects or interaction terms that did not overlap zero (all variables except fire frequency and annual forb and grass cover; Table S9), and the top model demonstrated a good fit to the observed count data (Figure S8, available in Supporting Information).

There was strong evidence for interactive effects; CRP cover within 1 km of leks produced increases in expected lek counts (and the largest expected counts) when local cover of perennial forbs and grasses (within 1 km) and shrubs (within 3 km) were low, but the relationships between expected lek counts and CRP cover were flat when perennial forb and shrub cover in the surrounding area were high (Figure 4). Similarly, the benefits of increased NDVI during the late-brood period were most important during periods with little precipitation during the 21-day period after median hatch, and considerably less pronounced when post-hatch precipitation was high (Figure 5). Interactive effects between CRP and cover of perennial forbs and grasses, and cover of shrubs, changed minimally in the sensitivity analyses that excluded data from prior to 2012 (Figures S9–S10, available in Supporting Information) and suggested the largest expected lek counts when both CRP and cover of perennials were highest.

Productivity models

Productivity modeling revealed positive effects of greenness (NDVI) during the late-brood period on Columbian sharp-tailed grouse but weak evidence for the effect of other variables (Table 3; Figure 6; Tables S14–S18, available in Supporting Information). Productivity models had a higher degree of model selection uncertainty ($w_i = 0.12$ for the top models), but the effects of NDVI were consistent among the most-competitive models (3 models with $\Delta AIC_c < 2.0$; Figure 6) and the 95% confidence intervals for NDVI did not overlap zero in those models (Table S14). There was also some evidence that productivity was negatively associated with bare ground and positively associated with early-spring precipitation (average daily precipitation up to onset of egg laying; Table 3; Figure S11, available in Supporting Information), but these effects were less precise and their 95% confidence intervals contained zero (Table S14). Nonetheless, the top productivity model demonstrated a close association between the observed and fitted proportions of juveniles in wing samples ($\rho = 0.99$; Figure S12, available in Supporting Information).

DISCUSSION

Our analyses suggested effects of land cover, fire, and weather on abundance of Columbian sharp-tailed grouse, and identified spatial and temporal scales over which these factors affected populations. Our results supported our *a priori* predictions for positive effects of land cover (perennial forbs and grasses, shrubs, CRP) and weather (early spring precipitation, late brood NDVI) on Columbian sharp-tailed grouse, and our predictions for negative effects of bare ground and tree cover. In contrast, our results did not support the predicted positive effects of litter cover or late spring temperature, nor did they support the predicted negative effects of annual forbs and grasses and late spring precipitation on Columbian sharp-tailed grouse. Similarly, our prediction that having some intermediate amount of burned area near leks would benefit Columbian sharp-tailed grouse was not supported, as the effects of area burned were consistently negative. These results reduce uncertainty about the joint effects of environmental conditions on Columbian sharp-tailed grouse populations and provide clear evidence for the benefits of maintaining shrubby, perennial grassland cover while minimizing local disturbances that degrade or eliminate breeding habitat.

TABLE 3 Top models for the effects of vegetation, weather, and fire on Columbian sharp-tailed grouse productivity (proportion of juveniles in wing sample) in southern Idaho, USA, 2000–2019. Variables considered were early-spring precipitation as measured using average daily precipitation from 15 March until onset of egg laying (average precipitation), normalized difference vegetation index measured during the late brood-rearing period (NDVI), cover of bare ground (bare ground) and annual forbs and grasses (annuals) within 3 km of leks, fire frequency within 2 km of leks (fire frequency), and cover of Conservation Reserve Program lands within 1 km of leks (CRP). All models included annual random intercept terms that were unique to each hunting region. We present the difference in Akaike's Information Criterion corrected for sample size (ΔAIC_c), model weight (w_i), and number of parameters (K).

Model	ΔAIC_c	w_i	K
Average precipitation + NDVI	0.00	0.12	4
NDVI	0.02	0.12	3
NDVI + bare ground	0.20	0.11	4
Average precipitation + NDVI + bare ground	2.06	0.04	5
NDVI + annuals	2.30	0.04	4
NDVI + fire frequency	2.43	0.04	4
NDVI + CRP	2.46	0.04	4
Average precipitation + NDVI + CRP	2.59	0.03	5
NDVI + bare ground + annuals	2.60	0.03	5
Average precipitation + NDVI + fire frequency	2.62	0.03	5
Average precipitation + NDVI + annuals	2.62	0.03	5
NDVI + bare ground + CRP	2.75	0.03	5
NDVI + bare ground + fire frequency	2.82	0.03	5
Average precipitation	3.99	0.02	2
Bare ground + annuals	4.25	0.01	4

We also provide empirical evidence for context-dependent benefits of CRP cover on Columbian sharp-tailed grouse populations, which suggests CRP may result in the largest gains to local populations in areas where perennial grassland and shrub cover are locally sparse near leks, but it would be of less benefit to abundance in areas where native perennial grassland and shrub cover are higher. Our results also demonstrate that productivity and abundance are affected by precipitation during nesting and brood rearing. Moreover, land cover, fire, and weather affected Columbian sharp-tailed grouse over a variety of spatial and temporal scales, including lagged and multi-year time effects and spatial extents larger than has typically been examined in the literature (i.e., ≤ 2 km distance from leks; Hoffman et al. 2015). Collectively, these results imply short-term (e.g., loss of CRP) and long-term changes (e.g., shifts in climate and fire regimes) that affect Columbian sharp-tailed grouse will likely have detrimental effects within the core of their United States range.

Abundance of Columbian sharp-tailed grouse was positively associated with the amount of perennial forb and grass cover, and to a lesser degree with shrub cover. Columbian sharp-tailed grouse breed in shrub-steppe and perennial bunchgrass rangelands with shrub cover (Connelly et al. 2020, Hoffman et al. 2015, IDFG 2015, Stonehouse et al. 2015), and as such this result was anticipated. Nest selection and survival were shown to be related to the amount of grassland with $>30\%$ cover of forbs within the core-use area of nesting females in southeast Idaho (Proett et al. 2019). Dense shrub patches are also commonly used by Columbian sharp-tailed grouse as escape cover during the breeding season (Hoffman et al. 2015) and can provide visual obstruction around

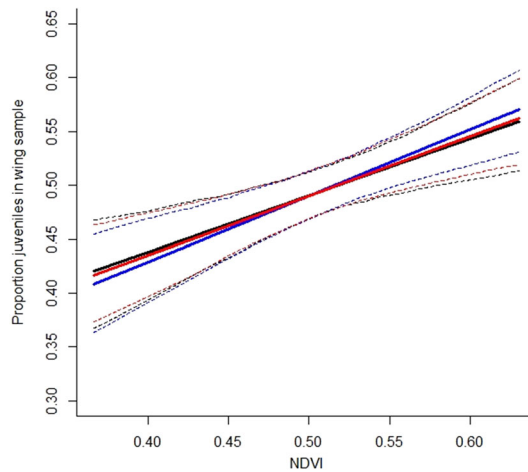


FIGURE 6 Effects of greenness (normalized difference vegetation index [NDVI]) during the late brood-rearing period on Columbian sharp-tailed grouse productivity (proportion of juveniles in wing sample) in southern Idaho, USA, 2000–2019. Figure shows partial effects of NDVI from the top models ranked using Akaike's Information Criterion corrected for small sample sizes (AIC_c ; black: $\Delta AIC_c = 0$; blue: $\Delta AIC_c = 0.02$; red: $\Delta AIC_c = 0.20$) with 95% confidence intervals (dashed lines) for each relationship.

ests that improves nest survival (Proett et al. 2019). Moreover, past studies indicated loss of quantity and quality of native vegetation cover as responsible for declines in distribution and abundance of Columbian sharp-tailed grouse near the periphery of their range (Geisen and Braun 1993, McDonald and Reese 1998, Schroeder et al. 2000). We quantified relationships between breeding abundance and vegetation cover and show key components of native cover were beneficial to local populations within their core range.

Factors that reduced shrubby grassland cover were associated with lower abundance of breeding Columbian sharp-tailed grouse. Detrimental effects stemmed from cover of trees and bare ground, and cover of recently burned areas. Forest encroachment has been identified as a potential threat to Columbian sharp-tailed grouse breeding habitat (IDFG 2015). Columbian sharp-tailed grouse in Washington preferentially used areas within their spring-summer home ranges that were farther from trees (Stonehouse et al. 2015), yet we are unaware of prior studies that quantified effects of forest cover on local abundance. Our results also suggest that bare ground is detrimental to Columbian sharp-tailed grouse, which corroborates results of Buss and Dziedzic (1955), Meints et al. (1992), McDonald (1998), Hoffman et al. (2015), and Proett et al. (2019). For example, fall and spring plowing were believed to be a direct cause of extirpation of Columbian sharp-tailed grouse in Washington (Buss and Dziedzic 1955), and percent cover of bare ground was greater at unsuccessful nests than at successful ones (McDonald 1998). Areas with little visual obstruction or vegetation cover have little value to breeding Columbian sharp-tailed grouse (Meints et al. 1992, Hoffman et al. 2015, Proett et al. 2019), and our analyses show this result is manifested in the expected abundance of breeding birds on leks.

The effects of disturbance from fire on Columbian sharp-tailed grouse populations and habitat are poorly understood. Larger and more frequent fires have been predicted to be the most detrimental to breeding Columbian sharp-tailed grouse (Hoffman et al. 2015). Our results support the first prediction, whereby increased coverage of recent fires within 2 km of leks reduced local abundance. Our results failed to provide strong support for the fire frequency prediction, as short-term fire frequencies had little impact on local abundance of Columbian sharp-tailed grouse. Our data revealed little evidence of a meaningful effect of fire severity on Columbian sharp-tailed grouse abundance; however, effects of fire severity could be context-dependent and change with amount of native cover (Hoffman et al. 2015). We also caution that any longer-term effects of fires on Columbian sharp-tailed grouse

habitat quality would not be captured directly by our analyses of short-term fire effects (i.e., <3 yr). Nonetheless, we suspect any longer-term benefits of fire would be realized through improvements to vegetation cover variables, which were already included in our analyses.

We found context-dependent benefits of the amount of CRP near leks for breeding Columbian sharp-tailed grouse, where gains in local abundance were realized most strongly when perennial forb and grass cover and shrub cover within 1–3 km of leks was less abundant. Hoffman et al. (2015) suggested CRP provides vegetation that maintains connectivity and provides food and escape cover when native habitat is small in area or geographically isolated (e.g., because of fragmentation by agriculture). Translocated Columbian sharp-tailed grouse in Washington preferentially used restored grassland cover within their spring-summer home ranges and selected restored grassland patches at very fine scales (10 × 10-m pixels) for nesting (Stonehouse et al. 2015). We provide evidence that increasing the amount of CRP cover translated into increases in local abundance of Columbian sharp-tailed grouse within the core of their United States range, and this benefit of CRP on abundance was also among the strongest effects we observed (e.g., when cover of perennials and shrubs were low). These results provide further evidence CRP cover can increase local abundance when native habitat surrounding leks has been lost, as has been commonly suggested (Hoffman et al. 2015, IDFG 2015). Nonetheless, future studies are needed to evaluate the implications of CRP plantings and mid-contract management strategies. Data on parcel-level CRP attributes were not widely available, yet prior researchers suggested the composition of plantings may affect demography of Columbian sharp-tailed grouse (Proett et al. 2019). More work is also needed to understand how configuration of CRP juxtaposed near patches of native cover and cropland may affect local abundance of Columbian sharp-tailed grouse. Our study focused on the amount of CRP and components of native vegetation cover near leks but did not address questions of their configuration or the potential impacts of cropland cover on local abundance.

Abundance and productivity of Columbian sharp-tailed grouse were related to precipitation during the nesting and brood-rearing periods. We also found evidence for cross-period interactions in the effects of precipitation and greenness on abundance. Specifically, the benefit of increased greenness during the late brood-rearing period depended on the precipitation that fell in the 21-day period after hatch, suggesting that consistent precipitation over time during the brood-rearing period may buffer negative impacts of consistently reduced precipitation during early brood rearing. Greenness during late brood rearing also had the strongest effect on management-unit scale measures of productivity. Clearly the effects of spring and summer weather on grouse populations are complicated and depend on both timing and magnitude of weather events during the breeding season. For instance, warmer temperatures during nesting and brood rearing can benefit production of Columbian sharp-tailed grouse, unless temperatures are extreme and result in heat stress for young chicks (Flanders-Wanner et al. 2004a). Precipitation prior to and during nesting benefits production, but studies reported mixed results regarding the effects of precipitation directly after hatch on chick survival or production (negative, Flanders-Wanner et al. 2004a, Goddard and Dawson 2009, positive, Proett et al. 2022). Exposure to cold and wet conditions can act as a mortality source on young chicks (Manzer and Hannon 2007), but the mixed results of past studies suggest regional conditions (e.g., vegetation composition and condition, aridity) might dictate whether post-hatch precipitation has beneficial or detrimental effects on recruitment. In addition, while we did consider possible effects of precipitation throughout the entire annual cycle on productivity, we did not consider annual precipitation effects on relative abundance. We suspect any carryover effects from total precipitation during the previous year would arise through vegetation conditions, which were already included in our models.

Land cover, fire, and weather affected Columbian sharp-tailed grouse populations over a variety of spatial and temporal scales. Our data demonstrated that population drivers affected local abundance over a variety of time scales, including several whose influence was in the year concurrent with lek counts (bare ground, shrubs, CRP), and others whose influence was in the year prior (trees, early spring precipitation), cumulative over the previous 2 years (area burned), or via average conditions over the previous 2- (NDVI) or 3-year periods (perennial forbs and grasses, late spring precipitation). Little work has attempted to identify the optimal temporal scales for environmental effects on Columbian sharp-tailed grouse populations, yet our results imply this may be an important consideration

for understanding population dynamics. Our results suggest maintaining consistent conditions over time may be more important for some variables (e.g., perennial forbs and grasses), whereas the effects of other variables may be more acute and year specific (e.g., early spring precipitation).

Explicit optimization of spatial scales of effect for environmental variables affecting Columbian sharp-tailed grouse is another novel contribution of our study. Past investigators have commonly used a single measurement scale for each variable when evaluating habitat relationships (e.g., Stonehouse et al. 2015). Most nesting and brood-rearing activities occur within 2 km of where females were bred (Apa 1998, Collins 2004, Boisvert et al. 2005), and thus management of habitat and disturbance is typically focused within 2 km of leks (Hoffman et al. 2015). Most, but not all (e.g., shrub cover), of our variables affected local abundance of Columbian sharp-tailed grouse within this threshold, but a few were more influential at spatial scales other than 2 km. The optimal scale for most covariates was far superior to the other scales that we considered, although NDVI had a consistent effect across all measurement scales. These findings, paired with the scale sensitivity of many observed vegetation cover relationships, strongly suggest that arbitrarily selecting a single measurement scale for making inferences could yield incorrect conclusions about effects and importance of covariates. Regardless, identification of optimal scales of effect is important for both understanding and predicting the distribution and abundance of animals (Jackson and Fahrig 2015, McGarigal et al. 2016, Stevens and Conway 2019), and our results suggest explicit consideration of scales of effect for environmental variables may improve our understanding of the factors that influence Columbian sharp-tailed grouse populations.

Our results also suggest ongoing changes affecting habitat and climate across the western United States will likely be detrimental to Columbian sharp-tailed grouse. For example, large-scale reductions in CRP contracts are already occurring within southern Idaho, which is the core of the United States range. Given the CRP program takes land out of agricultural production, many of these areas will likely go back into row-crop production and restored grasslands will be plowed and eliminated. This eliminates the benefit of CRP grasslands to breeding Columbian sharp-tailed grouse in areas where native cover may already be limited. Plowing grasslands produces more bare ground, at least seasonally during the breeding season, and was directly responsible for past extirpation of Columbian sharp-tailed grouse (Buss and Dziedzic 1955, McDonald and Reese 1998, Schroeder et al. 2000). Loss of CRP thus poses a significant risk to conservation of Columbian sharp-tailed grouse in the near term. In addition, our results suggest widespread encroachment of conifer forests into sagebrush steppe ecosystems may pose a threat to Columbian sharp-tailed grouse. Thus, ongoing efforts to remove encroaching conifers in sagebrush steppe (Miller et al. 2017) may benefit sympatric Columbian sharp-tailed grouse, in addition to the benefits described for greater sage-grouse and shrub-steppe songbirds (Donnelly et al. 2017, Holmes et al. 2017, Severson et al. 2017).

The benefits of precipitation and negative impacts of area burned by large wildfires also implies that complicated relationships between climate change, invasive species, and wildfire may exacerbate effects of habitat loss on Columbian sharp-tailed grouse. Frequency and intensity of drought conditions (Strzepek et al. 2010, Williams et al. 2020, Chiang et al. 2021) and frequency of wildfires (Westerling et al. 2006, Abatzoglou and Williams 2016) are increasing in western North America. Within the Great Basin region, which includes our study area, a complicated fire cycle has emerged with the potential to increase area burned and cover of bare ground near leks. This cycle is driven by growth of invasive cheatgrass and native herbs during periods of high winter-spring precipitation, which increases the prevalence, severity, and scale of fires when that growth is followed by drought years (Pilliod et al. 2017). This cycle also facilitates the further spread and establishment of cheatgrass, often to the detriment of habitat for shrub-steppe wildlife (e.g., greater sage-grouse; Coates et al. 2016). Therefore, the same precipitation that directly benefits Columbian sharp-tailed grouse by promoting herbaceous cover could interact with increased frequency of drought to increase the threat posed by wildfire. Consequently, our results suggest long-term changes in climate may have complex effects on Columbian sharp-tailed grouse that challenge efforts to maintain and restore populations. Efforts to conserve Columbian sharp-tailed grouse within their remaining core areas are therefore likely to benefit from identification of conservation strategies that are robust to large-scale environmental changes affecting fire regimes, vegetation cover, and spring weather conditions.

Lastly, while lek counts can be a difficult index of abundance to interpret given variable lek attendance and conditional detection probabilities, our inferences about factors affecting Columbian sharp-tailed grouse appear robust. Count-based generalized regression models (e.g., Poisson and NB regression) can adequately describe patterns of relative abundance for animal populations in the absence of systematic structure in detection processes that can confound inferences (Barker et al. 2018, Monroe et al. 2019, Blomberg and Hagen 2020). Given that our focus was to identify relationships between relative abundance and environmental covariates, and not to assess temporal trends in abundance, we do not believe such systematic changes in detection confounded our inferences. We accounted for the effects of survey timing (which affect detection because of temporal changes in lek attendance; Drummond et al. 2010) on lek counts in multiple ways, including through the model of expected counts but also via effects on the NB dispersion parameter (i.e., the variance-mean relationship for lek counts). Moreover, if habitat or disturbance variables affected survey-level detection, their effects would be largely predictable (e.g., positive for bare ground and negative for shrub cover) and opposite our *a priori* predictions and results. Therefore, we believe that if unmodeled heterogeneity in attendance and detection had any effect on our inferences, it would have been to increase the stochasticity of lek counts, and consequently decrease our ability to detect effects of environmental conditions on abundance (i.e., make our inferences more conservative). Nonetheless, our results should aid in the development of more mechanistic hypotheses to explain observed population patterns, which could be tested using field studies.

MANAGEMENT IMPLICATIONS

Maintaining perennial forb, grass, and shrub cover near leks, and minimizing forest encroachment and disturbances that result in increased cover of bare ground within breeding habitat should benefit local populations of Columbian sharp-tailed grouse. Increased CRP cover benefits grouse populations, particularly when areas near leks contain sparse perennial grassland and shrub cover. Therefore, increasing restored grassland cover in Columbian sharp-tailed grouse breeding areas through CRP or other private-lands conservation programs may provide a useful mechanism to offset regional habitat losses caused by other factors (e.g., forest encroachment, climate-fire interactions). Ongoing losses of CRP, in conjunction with changing climate and weather, may pose near- and long-term threats to Columbian sharp-tailed grouse conservation. Thus, conservation strategies that address these changes while also maintaining key components of breeding habitat may be most beneficial for Columbian sharp-tailed grouse populations within the core of their United States range.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

No animals were directly handled during this study. Lek flush counts and wing collections were conducted by Idaho Department of Fish and Game personnel, protocols for these activities were approved by the Idaho Department of Fish and Game wildlife health lab, and survey methods followed typical ethical standards for monitoring birds (<https://birdnet.org/info-for-ornithologists/guidelines-english-3rd-edition-2010/>).

DATA AVAILABILITY STATEMENT

The data that support this study are available on request from the corresponding author or from IDFG. The data are not publicly available because of privacy restrictions.

REFERENCES

- Abatzoglou, J. T. 2013. Development of gridded surface meteorological data for ecological applications and modelling. *International Journal of Climatology* 33:121–131.
- Abatzoglou, J. T., and A. P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western U.S. forests. *Proceedings of the National Academy of Sciences* 113:11770–11775.
- Aldrich, J. W. 1963. Geographic orientation of American Tetraonidae. *Journal of Wildlife Management* 27:529–545.
- Amman, G. A. 1944. Determining the age of pinnated and sharp-tailed grouse. *Journal of Wildlife Management* 8:170–171.
- Andri, S., K. Aho, A. Alfons, N. Anderegg, T. Aragon, C. Arachchige, A. Arppe, A. Baddeley, K. Barton, B. Bolker, et. al. 2021. DescTools: tools for descriptive statistics. R package version 0.99.44. <https://cran.r-project.org/package=DescTools>
- Apa, A. D. 1998. Habitat use and movements of sympatric sage and Columbian sharp-tailed grouse in southeastern Idaho. Dissertation, University of Idaho, Moscow, USA.
- Applegate, R. D. 2000. Use and misuse of prairie-chicken lek surveys. *Wildlife Society Bulletin* 28:457–458.
- Barker, R. J., M. R. Schofield, W. A. Link, and J. R. Sauer. 2018. On the reliability of N-mixture models for count data. *Biometrics* 74:369–377.
- Bergerud, A. T. 1988. Increasing the numbers of grouse. Pages 686–731 in A. T. Bergerud and M. W. Gratson, editors. *Adaptive strategies and population ecology of northern grouse, volume II: theory and synthesis*. University of Minnesota Press, Minneapolis, USA.
- Blomberg, E. J., and C. A. Hagen. 2020. How many leks does it take? Minimum sample sizes for measuring local-scale conservation outcomes in greater sage-grouse. *Avian Conservation and Ecology* 15:9.
- Boisvert, J. H. 2002. Ecology of Columbian sharp-tailed grouse associated with Conservation Reserve Program and reclaimed surface mine lands in northwestern Colorado. Thesis, University of Idaho, Moscow, USA.
- Boisvert, J. H., R. W. Hoffman, and K. P. Reese. 2005. Home range and seasonal movements of Columbian sharp-tailed grouse associated with Conservation Reserve Program and mine reclamation lands. *Western North American Naturalist* 65:36–44.
- Box, E. O., B. N. Holben, and V. Kalb. 1989. Accuracy of the AVHRR vegetation index as a predictor of biomass, primary productivity and net CO₂ flux. *Vegetation* 80:71–89.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal* 9:378–400.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. Second edition. Springer-Verlag, New York, New York, USA.
- Buss, I. O., and E. S. Dziedzic. 1955. Relation of cultivation to the disappearance of Columbian sharp-tailed grouse in southeastern Washington. *Condor* 57:185–187.
- Chiang, F., O. Mazdiyasi, and A. AghaKouchak. 2021. Evidence of anthropogenic impacts on global drought frequency, duration, and intensity. *Nature Communications* 12:e2754.
- Coates, P. S., M. A. Ricca, B. G. Prochazka, M. L. Brooks, K. E. Doherty, T. Kroger, E. J. Blomberg, C. A. Hagen, and M. L. Casazza. 2016. Wildfire, climate, and invasive grass interactions negatively impact an indicator species by reshaping sagebrush ecosystems. *Proceedings of the National Academy of Sciences* 113:12745–12750.
- Collins, C. P. 2004. Ecology of Columbian sharp-tailed grouse breeding in coal mine reclamation and native upland cover types in northwestern Colorado. Thesis, University of Idaho, Moscow, USA.
- Connelly, J. W., M. W. Gratson, and K. P. Reese. 2020. Sharp-tailed grouse (*Tympanuchus phasianellus*). Version 2.0 A. Poole and F. Gill, editors. *Birds of the World*. Cornell Laboratory of Ornithology, Ithaca, New York, USA. <https://birdsoftheworld.org/bow/historic/bna/shtgro/2.0/introduction>. Accessed 26 Jan 2022.
- Donnelly, J. P., J. D. Tack, K. E. Doherty, D. E. Naugle, B. W. Allred, and V. J. Dreitz. 2017. Extending conifer removal and land protection strategies from sage-grouse to songbirds, a range-wide assessment. *Rangeland Ecology and Management* 70:95–105.
- Drummer, T. D., R. G. Coracelli, and S. J. Sjogren. 2011. Sharp-tailed grouse lek attendance and fidelity in Upper Michigan. *Journal of Wildlife Management* 75:311–318.
- Eidenshink, J., B. Schwind, K. Brewer, Z. L. Zhu, B. Quayle, and S. Howard. 2007. A project for monitoring trends in burn severity. *Fire Ecology* 3:3–21.

- Flanders-Wanner, B. L., G. C. White, and L. L. McDaniel. 2004a. Weather and prairie grouse: dealing with effects beyond our control. *Wildlife Society Bulletin* 32:22–34.
- Flanders-Wanner, B. L., G. C. White, and L. L. McDaniel. 2004b. Validity of prairie grouse harvest-age ratios as production indices. *Journal of Wildlife Management* 68:1088–1094.
- Fox, J. 2008. *Applied regression analysis and generalized linear models*. Second edition. Sage Publications, Thousand Oaks, California, USA.
- Giesen, K. M., and C. E. Braun. 1993. Status and distribution of Columbian sharp-tailed grouse in Colorado. *Prairie Naturalist* 25:237–242.
- Gillette, G. L. 2014. Ecology of Columbian sharp-tailed grouse in southern Idaho: evaluating infrared technology, the Conservation Reserve Program, statistical population reconstruction, and the olfactory concealment theory. Dissertation, University of Idaho, Moscow, USA.
- Goddard, A. D., and R. D. Dawson. 2009. Factors influencing the survival of neonate sharp-tailed grouse *Tympanuchus phasianellus*. *Wildlife Biology* 15:60–67.
- Harrity, E. J., B. S. Stevens, and C. J. Conway. 2020. Keeping up with the times: mapping range-wide habitat suitability for endangered species in a changing environment. *Biological Conservation* 250:e108734.
- Hoffman, R. W., K. A. Griffin, J. M. Knetter, M. A. Schroeder, A. D. Apa, J. D. Robinson, S. P. Espinosa, T. J. Christiansen, R. D. Northrup, D. A. Budeau, et. al. 2015. Guidelines for the management of Columbian sharp-tailed grouse populations and their habitats. Sage and Columbian Sharp-tailed Grouse Technical Committee, Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.
- Holmes, A. L., J. D. Maestas, and D. E. Naugle. 2017. Bird responses to removal of western juniper in sagebrush-steppe. *Rangeland Ecology and Management* 70:87–94.
- Idaho Department of Fish and Game. 2015. Management plan for the conservation of Columbian sharp-tailed grouse in Idaho 2015–2025. Idaho Department of Fish and Game, Boise, USA.
- Jackson, H. B., and L. Fahrig. 2015. Are ecologists conducting research at the optimal scale? *Global Ecology and Biogeography* 24:52–63.
- Jones, M. O., B. W. Allred, D. E. Naugle, J. D. Maestas, P. Donnelly, L. J. Metz, J. Karl, R. Smith, B. Bestelmeyer, C. Boyd, et al. 2018. Innovation in rangeland monitoring: annual, 30 m, plant functional type percent cover maps for U.S. rangelands, 1984–2017. *Ecosphere* 9:e02430.
- Lindén, A., and S. Mäntyniemi. 2011. Using the negative binomial distribution to model overdispersion in ecological count data. *Ecology* 92:1414–1421.
- Manzer, D. L., and S. J. Hannon. 2007. Survival of sharp-tailed grouse *Tympanuchus phasianellus* chicks and hens in a fragmented prairie landscape. *Wildlife Biology* 14:16–25.
- Marshall, W. H., and M. S. Jensen. 1937. Winter and spring studies of sharp-tailed grouse in Utah. *Journal of Wildlife Management* 1:87–89.
- McDonald, M. W. 1998. Ecology of Columbian sharp-tailed grouse in eastern Washington. Thesis, University of Idaho, Moscow, USA.
- McDonald, M. W., and K. P. Reese. 1998. Landscape changes within the historical distribution of Columbian sharp-tailed grouse in eastern Washington. *Northwest Science* 72:34–41.
- McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecology* 31:1161–1175.
- Meints, D. R. 1991. Seasonal movements, habitat use, and productivity of Columbian sharp-tailed grouse in southeastern Idaho. Thesis, University of Idaho, Moscow, USA.
- Meints, D. R., J. W. Connelly, K. P. Reese, A. R. Sands, and T. P. Hemker. 1992. Habitat suitability index (HSI) procedure for Columbian sharp-tailed grouse. University of Idaho Forest, Wildlife, and Range Experimental Station Bulletin 55, Moscow, USA.
- Miller, R. E., D. E. Naugle, J. D. Maestas, C. A. Hagen, and G. Hall. 2017. Special issue: targeted woodland removal to recover at-risk grouse and their sagebrush-steppe and prairie ecosystems. *Rangeland Ecology and Management* 70:1–8.
- Monroe, A. P., G. T. Wann, C. L. Aldridge, and P. T. Coates. 2019. The importance of simulation assumptions when evaluating detectability in population models. *Ecosphere* 10:e02791.
- Pilliod, D. S., J. L. Welty, and R. S. Arkle. 2017. Refining the cheatgrass-fire cycle in the Great Basin: precipitation timing and fine fuel composition predict wildfire trends. *Ecology and Evolution* 7:8126–8151.
- Pollock, K. H., H. Marsh, L. L. Bailey, G. L. Farnsworth, T. R. Simons, and M. W. Allredge. 2004. Separating components of detection probability in abundance estimation: an overview with diverse examples. Pages 43–58 in W. L. Thompson, editor. *Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters*. Island Press, Washington, D.C., USA.
- Proett, M. C. 2017. The influence of wind energy development on Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) breeding season ecology in eastern Idaho. Thesis, Utah State University, Logan, USA.

- Proett, M., S. B. Roberts, J. S. Horne, D. N. Koons, and T. A. Messmer. 2019. Columbian sharp-tailed grouse nesting ecology: wind energy and habitat. *Journal of Wildlife Management* 83:1214–1225.
- Proett, M., S. B. Roberts, and T. A. Messmer. 2022. Columbian sharp-tailed grouse brood success and chick survival in a wind-energy landscape. *Journal of Wildlife Management* 86:e22287.
- R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Sauer, J. R., and W. A. Link. 2011. Analysis of the North American Breeding Bird Survey using hierarchical models. *Auk* 128: 87–98.
- Schroeder, M. A., D. W. Hays, M. A. Murphy, and D. J. Pierce. 2000. Changes in the distribution and abundance of Columbian sharp-tailed grouse in Washington. *Northwestern Naturalist* 81:95–103.
- Severson, J. P., C. A. Hagen, J. D. Maestas, D. E. Naugle, J. T. Forbes, and K. P. Reese. 2017. Short-term response of sage-grouse nesting to conifer removal in the northern Great Basin. *Rangeland Ecology and Management* 70:50–58.
- Stevens, B. S., and C. J. Conway. 2019. Predicting species distributions: unifying model selection and scale optimization for multi-scale occupancy models. *Ecosphere* 10:e02748.
- Stonehouse, K. F., L. A. Shipley, J. Lowe, M. T. Atamian, M. E. Swanson, and M. A. Schroeder. 2015. Habitat selection and use by sympatric, translocated greater sage-grouse and Columbian sharp-tailed grouse. *Journal of Wildlife Management* 79:1308–1326.
- Strzepek, K., G. Yohe, J. Neumann, and B. Boehlert. 2010. Characterizing changes in drought risk for the United States from climate change. *Environmental Research Letters* 5:e044012.
- United States Department of Agriculture Farm Services Agency. 2020. Conservation Reserve Program Monthly Summary: September 2020. <https://www.fsa.usda.gov/Assets/USDA-FSA-Public/usdfiles/Conservation/PDF/Summary-September-2020-1.pdf>. Accessed 12 Dec 2022.
- United States Department of Agriculture Farm Services Agency. 2022. Conservation Reserve Program Monthly Summary: September 2022. <https://www.fsa.usda.gov/Assets/USDA-FSA-Public/usdfiles/Conservation/PDF/Summary%20September%202022%20CRPMonthly.pdf>. Accessed 12 Dec 2022.
- U.S. Department of the Interior. 2000. Endangered and threatened wildlife and plants; 12-month finding for a petition to list the Columbian sharp-tailed grouse as threatened. *Federal Register* 65:60391–60396.
- U.S. Department of the Interior. 2006. Endangered and threatened wildlife and plants; 90-day finding on a petition to list the Columbian sharp-tailed grouse as threatened or endangered. *Federal Register* 71:67318–67325.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313:940–943.
- Williams, A. P., E. R. Cook, J. E. Smerdon, B. I. Cook, J. T. Abatzoglou, K. Bolles, S. H. Baek, A. M. Badger, and B. Livneh. 2020. Large contribution from anthropogenic warming to an emerging North American megadrought. *Science* 368: 314–318.

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