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Greater Sage-Grouse Resource Selection Drives Reproductive Fitness Under a Conifer Removal Strategy☆

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ABSTRACT

The link between individual variation in resource selection (e.g., functional response) and fitness creates a foundation for understanding wildlife-habitat relationships. Although many anthropogenic activities adversely affect these relationships, it is largely unknown whether projects implemented to benefit wildlife populations actually achieve this outcome. For sagebrush (*Artemisia* spp.) obligate species such as the greater sage-grouse (*Centrocercus urophasianus;* sage-grouse), expansion of juniper (*Juniperus* spp.) and pinyon-pine (*Pinus* spp.; conifers) woodlands into sagebrush ecosystems has been identified as a conservation threat. This threat is intensified when a sagebrush ecosystem is bounded by naturally unsuitable habitats. As such, federal, state, and private land managers have implemented landscape-level management to remove conifers on thousands of hectares of sagebrush habitat across the western United States. Despite the scale of contemporary conifer treatments, little was previously known whether sage-grouse will occupy these manipulated landscapes and whether occupancy has consequences on fitness components. To address these questions, we monitored nest and brood success rates for 96 radio-marked sage-grouse from 2012-2015 that inhabited conifer-dominated landscapes in the Box Elder Sage-grouse Management Area in Utah where mechanical conifer removal projects were completed. We then linked sage-grouse resource selection to individual nest ($n = 95$) and brood ($n = 56$) success by incorporating random-slope Resource Selection Functions as explanatory predictors in a logistic brood success model. Using the novel approach of random slope covariates, we demonstrated that sage-grouse selected for nest and brooding sites closer to conifer removal areas and that the probability of individual nest and brood success declined ($\beta = -0.10$ and $\beta = -0.74$, respectively) as sage-grouse females selected sites farther from conifer removal areas. Our research provided the first evidence that mechanical conifer removal treatments can increase suitable available breeding habitats for female sage-grouse and that individuals who occupied these areas experienced enhanced nest and brood success.

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Introduction

The link between resource selection and individual fitness is a key tenet in population ecology (DeCesare et al., 2014). Resource selection is the product of trade-off decisions in which animals address competing demands such as forage acquisition and predator avoidance in an effort to maximize fitness (Beyer et al., 2010; Leclerc et al., 2015). As such, resource selection is a multidimensional ecological process that occurs across both time and space (DeCesare et al., 2012). Furthermore, environmental resources are not distributed evenly across the landscape (Mysterud and Ims, 1998); therefore, individuals are likely to vary in their selection of resources, referred to as a *resource selection functional response* (Mysterud and Ims, 1998). This multidimensional process, depending on resource importance and availability, may drive individual differences in fitness.

In human-altered systems, functional responses in resource selection have been directly linked to reduced fitness (Benson et al., 2015; Hebblewhite and Merrill, 2008). As such, land managers seek to implement habitat improvement projects to mitigate the adverse effects of anthropogenic activities on wildlife populations (Fedy et al., 2014; Williams et al., 2004). However, it is uncertain whether wildlife populations respond to habitat manipulations on temporal and spatial scales that are relevant to managers (Knick et al., 2014). Although wildlife

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may occupy areas where landscapes have been manipulated to increase the available habitat space, little is known how increased habitat availability or space affects individual fitness or population abundance (Cain et al., 2008; Guthery, 1997; Harrington et al., 1999).

In 2010, the greater sage-grouse (*Centrocercus urophasianus;* sage-grouse) was designated as a candidate species by the US Fish and Wildlife Service (USFWS) for protection under the Endangered Species Act (ESA) of 1973 due to range-wide population declines that were attributed to long-term habitat losses and degradation (USFWS, 2010). In 2015, the USFWS determined that ESA protection for the sage-grouse was unwarranted because range wide efforts had sufficiently mitigated the previously identified species conservation threats (USFWS, 2015). These efforts included conifer removal, in particular, pinyon pine (*Pinus* spp.) and juniper (*Juniperus* spp.). The expansion of these conifers into sagebrush (*Artemisia* spp.) ecosystems was identified as a species conservation threat by the USFWS (2013) and several state-specific conservation plans (Idaho Sage-grouse Advisory Committee, 2006; Montana Sage Grouse Work Group, 2005; State of Nevada Sagebrush Ecosystem Council, 2014; State of Wyoming Game and Fish Commission, 2003; Utah Governor's Office, 2013). Stiver et al. (2006) estimated that 60 000 − 90 000 ha of sagebrush habitat across the range of sage-grouse is lost annually to conifer encroachment due to climate change and suppressed fire regimes (Miller and Eddleman, 2000). An estimated 90% of this expansion has occurred in areas that were previously sagebrush ecosystems (Miller et al., 2011).

Because of the impact of conifer expansion on sage-grouse (Baruch-Mordo et al., 2013; Casazza et al., 2011; Commons et al., 1999), managers have increasingly implemented management actions designed to remove or reduce conifer canopy cover in sagebrush habitats. The Natural Resources Conservation Service (NRCS), through its Sage-grouse Initiative (www.sagegrouseinitiative.com), has provided cost-share to landowners to mechanically remove or reduce thousands of hectares of conifer on private lands in the western United States (NRCS, 2015). Similar projects have been implemented range wide on Bureau of Land Management (BLM)- and US Forest Service (USFS)-administered lands. In Utah alone, conifers have been removed from > 200 000 hectares of sagebrush landscapes since 2006 under the Utah Department of Natural Resources (UDNR) Watershed Restoration Initiative (WRI; UDNR, 2014). Despite the scale and cost of these conifer treatments, little was previously known whether sage-grouse will occupy these manipulated landscapes and, if so, whether occupancy had fitness consequences (Connelly et al., 2011).

Large-scale mechanical conifer reduction projects are relatively low cost on a per-hectare basis and may have potential for increasing usable habitat space for sage-grouse and other sagebrush obligate species (Baruch-Mordo et al., 2013; Hanser and Knick, 2011; UDWR, 2009). The best available information shows sage-grouse avoidance of increasing conifer canopy cover (Baruch-Mordo et al., 2013; Commons et al., 1999; Doherty et al., 2008; Frey et al., 2013) and subsequent occupancy of areas where conifers have been removed (Commons et al., 1999; Frey et al., 2013; Cook, 2015; Sandford et al., 2015; Sandford 2016). Concomitantly, Casazza et al. (2011) demonstrated that sage-grouse habitat selection and subsequently fitness were related to conifer encroachment. However, it was unknown whether conifer removal would further increase reproductive fitness. Connelly et al. (2011) suggested that to effectively mitigate sage-grouse conservation threats, managers need better information regarding sage-grouse nest initiation rates, nest and brood success, survival, recruitment, production, seasonal movements, and habitat-use patterns in response to management actions.

To address this knowledge gap, we used a Resource Selection Function (RSF) framework to estimate individually marked female sage-grouse resource selection in relation to conifer removal projects during the reproductive period (nesting and brood-rearing). From this, we estimated how nest and brood success were influenced by individual variation in habitat selection (i.e., functional response in habitat selection). In our study area, conifer removal projects occurred across all phases of conifer-encroached sagebrush landscapes (Miller et al., 2005). These landscapes exhibited relatively intact sagebrush understory communities. Thus, we hypothesized that in these areas, sage-grouse females that selected nest and brood sites in close proximity to large-scale conifer removal areas and areas with lower existing conifer cover would also be more successful because of increased herbaceous cover (Roundy et al., 2014) and reduced predation risks (Commons et al., 1999). Consequently, the female's behavior could contribute to the potential for population level effects.

Methods

Study Area

Our study area was located in the Box Elder Sage-grouse Management Area (SGMA; Fig. 1; Utah Governor's Office, 2013) and the southeast corner of the Snake River Plain Management Zone (Stiver et al., 2006). The Box Elder SGMA encompasses one of the largest and most stable sage-grouse populations in Utah; 577 male sage-grouse were counted on 42 leks in 2013 (Utah Division of Wildlife Resources [UDWR] unpublished data; Western Association of Fish and Wildlife Agencies, 2015). The focal area covers approximately 103 600 ha in the vicinity of the towns of Park Valley (lat. 41°49′16″N, long. 113°24′03″W) and Rosette, as well as the former towns of Rosebud and Dove Creek in western Box Elder County, Utah, and includes all seasonal sage-grouse habitats (Dahlgren et al., 2016a). The sage-grouse population is largely bounded geographically by the Raft River Mountains to the north, the Grouse Creek Mountains to the west, and the Great Salt Lake Desert to the south and east (Cook, 2015). The area is a mix of private and public land and predominantly used for domestic livestock and alfalfa (*Medicago sativa*) hay production. Utah School and Institutional Trust Lands Administration-, BLM-, and USFS-administered lands are interspersed throughout, creating a mosaic of jurisdictions and land uses.

The study area was composed primarily of sagebrush-steppe habitat characterized by big (*A. tridentata* spp.) and small sagebrush (*A. nova* and *A. arbuscula*). Dominant understory grasses included Sandberg's bluegrass *(Poa secunda),* cheatgrass *(Bromus tectorum),* crested wheatgrass *(Agropyron cristatum),* and bluebunch wheatgrass *(Pseudoregnaria spicata).* Common forbs included milkvetch (*Astragalus* spp.), phlox (*Phlox* spp.), hawksbeard (*Crepis* spp.), lupine (*Lupinus* spp.), and western yarrow *(Achillea millefolium).* Native and invading conifer (pinyon-juniper; PJ) woodlands were present throughout the study area. Spruce (*Picea* spp.), fir (*Abies* spp.), quaking aspen *(Populus tremuloides),* and curl-leaf mahogany *(Cercocarpus ledifolius)* communities were found at higher-elevation areas throughout the study area. Elevation ranged from 1 350 m to 2 950 m. Mean annual precipitation was 177 mm at 1 447 m (Western Regional Climate Center [WRCC], 2015) and ranged up to 783 mm at 2 745 m (Utah Climate Center [UCC], 2016). Mean monthly lows of - 12 ° C and – 8 ° C occurred in January at 1 477 and 2 745 m, respectively (Beyer, 2015; Sandford, 2016). Mean monthly highs of 33°C and 21°C occurred in July at 1 477 and 2 745 m, respectively (Beyer, 2015; Sandford, 2016).

Conifer removal projects in the study area were first initiated ~30 yr ago. However, because of little maintenance, conifers have recolonized and expanded beyond the previous removal areas (Box Elder Adaptive Resources Management Working Group, 2007). In 2008, conifer removal projects in the study area increased in both size and frequency. Since 2008, nearly 8 100 ha of conifer canopy cover in the study area have been removed through active management (e.g., one- and two-way chaining, lop-and-scatter, and mechanical mastication). All sites exhibited relatively intact sagebrush communities. The project areas were also reseeded with mixtures of native and introduced high-production grasses and forbs to prevent invasive weeds (e.g., cheatgrass; *Bromus tectorum*) from establishing in newly disturbed soils (UDNR, 2014).

Sage-grouse Radio-marking

From 2012 to 2015, we captured, radio-marked, and monitored 96 female sage-grouse in our study area. Sage-grouse trapping occurred

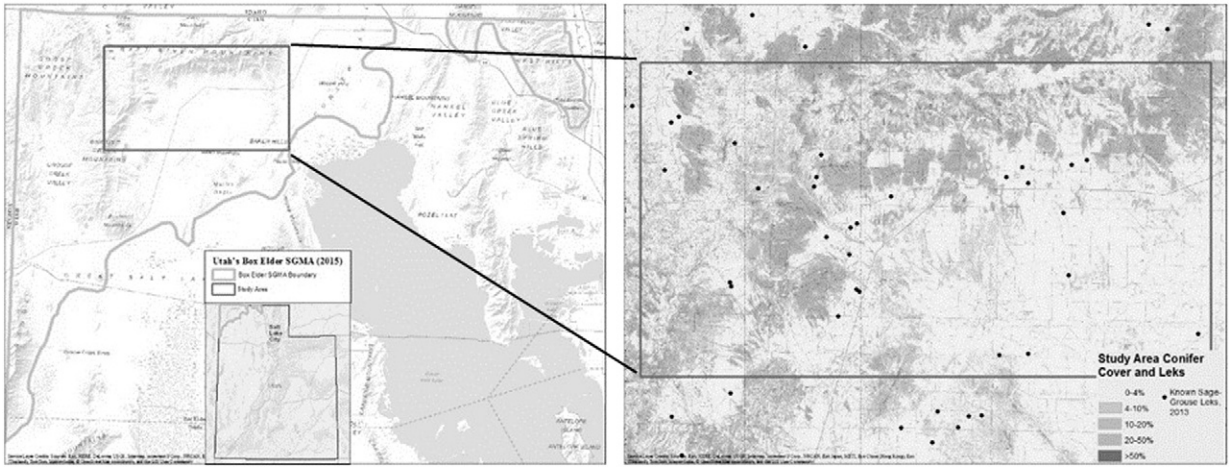

Figure 1. Utah's greater sage-grouse *(Centrocercus urophasianus)* management area 1, located in northwest Box Elder County, Utah (left panel). The proximity of known greater sage-grouse leks to conifer woodlands (*Pinus* spp. and *Juniperus* spp.) in Park Valley, Utah (right panel). The map was adapted from Falkowski et al. (2014).

at night in minimal light conditions, using all-terrain vehicles, spotlights, and dip nets following protocols described by Wakkinen et al. (1992) and Connelly et al. (2003). We determined the ages of female sage-grouse and attached a numbered aluminum leg band and an 18- to 22-g very-high-frequency (VHF) radio-necklace (Advanced Telemetry Systems, Isanti, MN, and Holohil Systems, Ltd., Ontario, Canada).

We predominantly used ground-based radio-telemetry coupled with visual confirmations to relocate radio-marked birds. Each radio-marked bird location was recorded using handheld Global Positioning Systems (GPSs) using UTM Zone 12 N in the NAD 1983 datum. Research protocols were approved by the Utah State University Institutional Animal Care and Use Committee permit #1547 and UDWR Certificate of Registration Number 2BAND8743.

Nest Monitoring

We monitored the radio-marked females (two to three locations per week) during the lekking season and from nest initiation and through nest incubation (Aldridge and Brigham, 2001; Schroeder, 1997). We determined nest success by observing eggshell fragments for signs of successful hatch, including separated membranes, and cupping of shell halves (Rearden, 1951). If a nest was abandoned before the estimated hatch date, and the eggs were crushed, punctured, or absent, the nest was classified as unsuccessful (Patterson, 1952) and the status of the female was immediately investigated. A GPS point was recorded at the exact site of every nest as soon as the nest success was determined. If we determined that a nest failed (due to predation or abandonment), we reduced tracking efforts of the female (one to two locations per week). Despite data range wide that suggests high renesting rates following initial nest failure (Taylor et al., 2012), renesting attempts in our study system were rare (3%; Cook, 2015; Sandford, 2016).

Brood Monitoring

When a female successfully hatched her clutch (i.e., at least one egg hatched), we tracked and recorded GPS locations of her and her brood two to three times per week. Because chick mortality in many of the galliformes slows between 35 and 60 days (Goddard and Dawson, 2009; Guttery, 2011; Jamison, 1996; Kaczor, 2008; Pitman et al., 2006), we determined brood success as a radio-marked female with chick(s) surviving ≥ 50 days. When a brooding female was observed or flushed ≤ 50 days post hatch with ≥ 2 adult sage-grouse and/or no chicks on ≥ 2 consecutive sampling occasions, we determined her brood to be unsuccessful. At 50 days, we located and flushed the female and her chicks to determine brood success (Cook, 2015; Dahlgren et al., 2010b; Schroeder, 1997). To maximize detection probability, sampling occasions of females with chicks were conducted before 0800 to reduce the potential for chick dispersal but have sufficient light to detect, classify, and count adults and chicks. In the event the female flushed without chicks, we repeated flush procedures on the following day. If the second flush still provided inconclusive results, we located the female on the second night with a spotlight and attempted to observe chicks (Dahlgren et al., 2010b). If chicks were still not observed, we classified the female as having an unsuccessful brood. We did not account for brood mixing inflating or detection accuracy, which may have deflated brood success estimates (Dahlgren et al., 2010a). Because of the random nature of these errors, as well as our sufficient sample size, we do not believe either error was over-represented.

Landscape Classification

We used a baseline surface disturbance map (Manier et al., 2014) of SGMAs (Dahlgren et al., 2016a) in Utah (Gifford et al., 2014) to determine sage-grouse distance (km) from disturbances (Roads > 72 km·h^{-1}, Roads 40 − 72 km·h^{-1}, Roads < 40 km·h^{-1}, Urban and Nonurban Development, Power lines, and Agriculture). Urban development was defined as any building capable of being inhabited or used. Nonurban development was defined as mines (abandoned or used seasonally), pipelines, structures not capable of use (abandoned house trailers, etc.), and miscellaneous unclassified development. Agriculture included irrigated and nonirrigated alfalfa production and pasture, fallow fields, and both irrigated and rangeland pasture (see Gifford et al., 2014 for descriptions). The baseline disturbance map was considered static throughout the study period because there were little to no changes in any anthropogenic disturbance. We used a 10-m resolution Digital Elevation Model (DEM; Utah Automated Geographic Reference Center, 2013) to derive elevation values. Because sage-grouse have previously been shown to select mesic sites (Connelly et al., 2011; Donnelly et al. 2016; Stiver et al., 2015), we derived a spatial distribution of mesic habitat by merging all mesic vegetation types, as well as open water and springs within the LANDFIRE, 2012 (LANDFIRE, 2012) Vegetation Type map. To measure conifer canopy cover, we used Falkowski et al.'s (2013) remotely sensed conifer cover map. The original dataset delineated conifer canopy cover into six classes: 1) 0 − 1%, 2) 1 − 4%, 3) 4 − 10%, 4) 10 − 20%, 5) 20 − 50%, and 6) >50% conifer canopy cover per ha. We merged the 0 − 1% and 1 − 4% classes (see Fig. 1) based on Baruch-Mordo et al.'s (2013) observations and our concerns over the data's ability to accurately detect a 1% difference in cover. To classify conifer removal treatments, we developed maps using WRI data (State of Utah Watershed Restoration Initiative, 2011) and private

landowner data for all known conifer treatments for each year from 2012 to 2015 and corrected conifer cover values to Class I in the canopy cover data where necessary. Because conifer removal projects were implemented annually, we developed annual cover maps to reflect conifer distribution according to each year's nesting and brooding season. All landscape variables except canopy cover and elevation were evaluated as distance-to metrics and calculated in ArcGIS. Distance-to landscape variables, including conifer removal, were calculated as zero for both the landscape variable edge and regions within the landscape variable area (e.g., areas within treatment). Due to a low relocation sample size within individuals, we were unable to estimate canopy cover as a categorical measure (1 − 5) due to model convergence issues; thus, it was evaluated as a continuous measure (1 − 5) of increasing conifer distribution. Further, because the Falkowski et al. (2014) map was derived for sage-grouse, and there is reason to believe that conifer cover greater than Class I (i.e., > 4%) is detrimental to sage-grouse (Baruch-Mordo et al., 2013), the continuous analyses illustrate the increasing negative effect on sage-grouse.

Variables were investigated for correlation using Pearson's correlation test with an $r > |0.6|$ threshold for inclusion for both nest and brood locations (Hosmer and Lemeshow, 2000). Within the nest site analysis, elevation and mesic habitat were correlated ($r = -0.61$); thus, we removed elevation because nest selection could not occur in high elevations due to snowpack. Similarly, agriculture and urban areas were correlated ($r = 0.83$). We removed urban development because most urban development in our study area occurs in association with agriculture, but not all agriculture was associated with urban development.

Within the resource selection analysis, agriculture and roads > 72 km·h^{-1} were correlated. ($r = -0.61$). We removed roads > 40 km·h^{-1} because the majority of roads in the study area > 72 km·h^{-1} are located in proximity to agriculture, but agriculture may be independent of roads > 72 km·h^{-1}. Agriculture and urban areas were correlated ($r = 0.89$); thus, we removed urban areas for the same reason acknowledged in the nest models. Elevation and power lines were also correlated ($r = 0.62$), so we removed powerlines because most power lines were associated with main roads (Gifford et al., 2014). See Table 1 for a summary of used landscape classification variables.

Data Analysis

Nest Success

To evaluate the influence of individual nest site location on nest success, we used Generalized Linear Models (GLMs). We identified our best-fitting population-level model from 32 a priori models built using our aforementioned list of landscape variables (Table S1; Burnham and Anderson, 2002). Models included varying combinations of the landscape variables, but distance to treatments was included in 30/32 models. The two additional models included a null model and a univariate canopy cover model. We evaluated model fit using Akaike Information Criterion scores adjusted for small sample sizes (AICc: Burnham and Anderson, 2002). Although models within two AICc units of the top model were considered to have equal support for influencing nest success (Burnham and Anderson, 2002), we selected the most parsimonious model within 2 ΔAICc of the top model. All analyses were performed using the statistical package lme4 (Bates et al., 2015) in Program R (R version 3.2.2, www.r-project.org, accessed 1 October 2015).

Brood Habitat Selection

We used an RSF framework to compare female sage-grouse brood habitat selection from 1 May to 1 August (Manly et al., 2002). We evaluated female sage-grouse resource selection as a function of the landscape variables described earlier using generalized mixed-effects models (GLMMs). We used a GLMM with a random intercept for each individual to allow for interpretation of selection among different individuals (Gillies et al., 2006). This further allowed us to account for autocorrelation among individuals with repeated observations and account for varying numbers of locations among individuals (Gillies et al., 2006). Animal locations were pooled by brooding year (e.g., Female 642_2012, Female 642_2013 were treated as two individuals) to provide a population level estimate of resource selection across the 4-yr study period while also accounting for changing availability as conifers were removed throughout the study period (see Kohl et al., 2013). In this framework the random intercept links year-specific use to the corresponding year-specific habitat availability (e.g., Female 642_2012 use is compared to 2012 habitat availability only).

We estimated brooding female sage-grouse RSFs at the third-order scale (Johnson, 1980) for any individual with more than five brood locations within a given year. A brood location is a point on the landscape where a radio-marked female with chicks is found. We compared recorded sage-grouse use locations to annual-specific habitat availability as identified by 95% Kernel Density Estimates (KDE; Geospatial Modelling Environment; Beyer, 2015) of all brooding locations collected across all individuals within a given brooding year. This produced four annual-specific measures of habitat availability, accounting for changes as conifers were removed. We then generated 1 000 random points within each annual brooding area to quantify habitat availability. As such, availability was identical for all birds within a given year but varied across years.

We constructed GLMMs using the same landscape variables used in the nest success models. To assist with convergence issues, all landscape variables were normalized ($m = 0, sd = 1$) using values corresponding to both used and available locations. We identified our best-fitting population-level model from 28 a priori candidate models (Table S2) using AICc (Burnham and Anderson, 2002). Our candidate models included distance to treatments in every model. We selected the most parsimonious population-level model within two ΔAICcs of the top model. This resulted in a two-level random-effect model (Gillies et al., 2006), in which $g(x)$ is estimated for location i for female j:

$$g(x) = \beta_0 + \beta_1 x_{1ij} + \ldots + \beta_n x_{nij} + \gamma_{0j},$$

where x_n are covariates with fixed regression coefficients β_n,β_0 is the mean intercept, and γ_{0j} is the random intercept calculated as the difference between the mean intercept β_0 for all individuals and the intercept for individual j (Gillies et al., 2006; Skrondal and Rabe-Hesketh, 2004). We estimated confidence intervals for the best-fit population-level RSF model using model-based semiparametric bootstrapping ($n = 1\,000$ iterations) calculated from the bootMer function within the lme4 package.

Employing the population-level model, we imposed a random slope-intercept model to evaluate the individual response of brooding female sage-grouse to annually measured landscape variables. Because of limited sample sizes within individual brood years (range: 6–21 relocations per individual brood year), we were unable to estimate random-coefficients across all variables simultaneously; thus, we employed an iterative

Table 1
Candidate variables and their metrics included in greater sage-grouse *(Centrocercus urophasianus)* nest and brood site selection and success probability models for Park Valley, Utah from 2012 to 2015

	Distance-to									
	Treatment	Roads > 72 kph	Roads 40-72 kph	Roads < 40 kph	Power lines	Agriculture	Urban development	Nonurban development	Canopy cover class	Elevation
Units	Kilometers	Kilometers	Kilometers	Kilometers	Kilometers	Kilometers	Kilometers	Kilometers	Continuous (1-5)	Meters

Female presence in a category was denoted as a "0" in distance-to layers.

process in which we sequentially interacted each landscape variable with the random term for the individual. This resulted in a model in which separate intercepts were fit for each individual while also producing individual-level (conditional) coefficient estimates for each individual according to the specified landscape variable (Benson et al., 2015) and a fixed (marginal) effect for all other variables. For example, if the top model included elevation, distance to treatments, and canopy cover, the first model would consist of an interaction between elevation and each random intercept for the individual. This model would produce a population-level response coefficient estimate for distance to treatments and canopy cover in addition to conditional coefficients (i.e., random slopes) for elevation by individual. In comparison, the second model would consist of an interaction between individual female and variable 2, in this case distance to treatments. We employed the random-slope-intercept model across each landscape variable since habitat selection is a multidimensional process, and as such this allowed us to evaluate fitness according to conifer treatment while also accounting for individual variation in resource selection across all other landscape variables.

Because this random-slope RSF design requires a reference individual from which to calculate conditional coefficients, we selected an "average brooding female." Furthermore, the selection of the average brooding female allowed us to infer the proportional number of individuals that demonstrate similarity in habitat selection (e.g., avoidance of treatments). To identify the reference individual, we calculated the difference between the mean individual-level value of use and the population-level mean value of availability for each landscape variables by individual. The difference value was then averaged across landscape variables but within individuals to provide a single measure of landscape use relative to landscape availability. This value was sorted, and individuals were ranked according to location sample size ($n = 6-21$) and the mean and median difference value. This resulted in the selection of a 2015 female that was the third individual from population mean and median and consisted of the second largest sample size. It is worth noting that this "average" female also raised at least one chick to maturity. The RSF analysis was performed using package lme4 (Bates et al., 2015) in Program R (R version 3.2.2, www.r-project.org, accessed 1 October 2015).

Habitat Selection and Individual Fitness

Individual-specific conditional responses were subtracted from the reference individual conditional response for each landscape variable. These values (maintained in the log-odds form) were extracted for each brooding female sage-grouse and used as predictors in a GLM that included individual brood success or failure. Because we had previously applied model selection to the population-level habitat selection model, no model selection approach was used to evaluate the influence of habitat selection on brood success at the individual level. This methodological decision was necessary because our estimation of random coefficients was only feasible by borrowing statistical power from other individuals from which to estimate individual-level coefficients for each landscape variable. In other words, small sample sizes within individuals would have resulted in model convergence issues across a large number of our sampled individuals, which in turn, would have made model selection within individuals infeasible. As a result, our methodology of using the best-fitting population-level model produced an odds ratio (i.e., probability) of brood success on the basis of the individual-level selection coefficients (i.e., functional response) for a landscape variable of interest once we held the selection preference for all other landscape variables at their population-level mean selection coefficient.

Results

Nesting

We monitored 95 individual sage-grouse nests, of which 61 hatched and brooding was initiated. Some of the individual sage-grouse we monitored nested in more than 1 yr ($n = 16$). Our model selection process identified high model uncertainty with eight models occurring within two ΔAICc (Table 2). We selected the most parsimonious model (ΔAICc = 0.83), which identified distance to treatment as the sole predictor of sage-grouse nest success. This suggests that for every 1 km a nest was located away from a conifer removal area, the probability of nest success was reduced by 9.1% ($\beta = -0.096$, 95% CI: −0.19, −0.001, Fig. 2A). In comparison, a univariate canopy cover model was not a statistically significant predictor of nest success ($\beta = -0.346$, 95% CI: −0.78, 0.08, Fig. 2B), although the population-level response suggested the potential for a negative influence of conifer canopy cover on nest success.

Brooding

We documented 700 brood locations from 56 individual broods. Of these, 43 were successful and fledged at least one chick at 50 days old. Multiple females initiated brooding in more than 1 yr ($n = 7$); however, only one female successfully raised a brood to 50 days in multiple years. Our population-level model selection process identified two models with strong support as our best-fitting model (Table 3). These included a model excluding distance to mesic areas (ΔAICc = 0) and the full model including all variables (ΔAICc = 1.97). The population-level top model indicated that female sage-grouse with broods selected for lesser distances to conifer removal areas ($\beta = -0.524$, 95% CI: −0.63, −0.42) and nonurban development ($\beta = -0.430$, 95% CI: −0.53, −0.34). They also selected for greater distances to roads < 40 km·h^{-1} ($\beta = 0.199$, 95% CI: 0.13, 0.27), roads 40−72 km·h^{-1} ($\beta = 0.104$, 95% CI: 0.03, 0.18), and agriculture ($\beta = 0.364$, 95% CI: 0.27, 0.46). Female sage-grouse with broods also selected for areas of higher elevation ($\beta = 0.318$, 95% CI: 0.24, 0.40) and lower conifer canopy cover ($\beta = -1.341$, 95% CI: −1.48, −1.20). Because landscape variables were normalized, we were able to determine that conifer canopy cover and distance to treatments are the strongest drivers of female sage-grouse resource selection in our study area among variables investigated. This is of note because we observed that more ($n = 48$) successful brooding females selected areas closer to conifer removal areas compared with a few successful brooding females ($n = 7$) that selected areas farther from conifer removal areas (Table 4).

Habitat Selection and Fitness

Of the 56 broods we monitored, 14 demonstrated avoidance of treatment areas when compared with the average female with chicks. Our brood success model demonstrated a 52.6% decrease in probability of brood success for every 1 unit change in the log-odds of selection for distance to treatment; however, the confidence interval did overlap

Table 2
Top-ranking generalized linear candidate models using habitat variables to predict individual greater sage-grouse *(Centrocercus urophasianus)* nest success probability in Park Valley, Utah from 2012 to 2015

Predictor variables	K	AICc	ΔAICc	AICcWt
Treat, Canopy	3	128.11	0.00	0.11
Treat, Mesic, Canopy	4	128.41	0.31	0.10
Treat, Ag	3	128.84	0.74	0.08
Treat, Ag, Canopy	4	129.08	0.98	0.07
Treat, Mesic, Ag, Canopy	5	129.38	1.28	0.06
Treat, Ag, Rds < 40	4	129.56	1.45	0.06
Treat	2	129.67	1.57	0.05
Treat, Mesic, Rds < 40, Canopy	5	129.82	1.71	0.05
Treat, Ag, Power	6	129.97	1.86	0.04
Canopy	2	132.00	3.90	0.02
Null	1	132.46	4.36	0.01

Treat indicates distance (km) to conifer removal area; Power, distance (km) to powerlines; Rds < 40, distance (km) to roads < 40 km·h^{-1}, Ag, distance (km) to agricultural areas; NonUrb, distance (km) to nonurban development; Canopy, canopy cover class (1-5); Mesic, distance (km) to mesic area; Power, distance (km) to powerlines. A "0" in any distance-to category indicated that a nest was at or within the habitat variable.

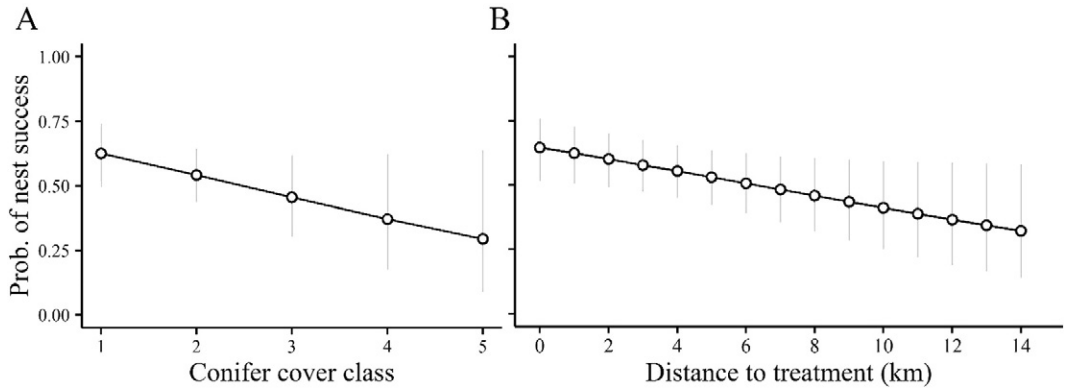

Figure 2. Probability of female sage-grouse *(Centrocercus urophasianus)* nest success as a function of conifer canopy cover class (**A**) and distance to conifer removal area (**B**) in Park Valley, Utah from 2012 to 2015. Probability of nest success decreased by 30% for each unit increase in conifer canopy cover (95% CI = −0.78, 0.08) and decreased by 9.1% (95% CI = −0.096, −0.001) for every 1 km a nest was located away from a conifer removal area. Note: Conifer canopy cover percent divided into five classes: 1) 0−4%, 2) 4−10%, 3) 10−20%, 4) 20−50%, 5) 50+% per acre.

zero ($\beta = -0.75$, 95% CI: −1.60, 0.11, Fig. 3A). Similarly, the probability of brood success declined at a stronger rate (77.2%) as the selection for conifer canopy cover increased ($\beta = -1.48$, 95% CI: −2.74, −0.22, Fig. 3B). In essence, sage-grouse females had a higher likelihood of brood success if they selected brooding locations closer to conifer removal areas and if the brooding area was located in habitat with minimal conifer canopy cover.

Discussion

Our data suggest that the large-scale mechanical conifer removal treatments we studied enhanced sage-grouse nest and brood success. Although links between selection and survival have been previously investigated (Casazza et al., 2011; Lockyer et al., 2015), to our knowledge our research is the first to link individual female sage-grouse selection of nest and brood sites in proximity of conifer removal treatments to increased reproductive success. Our research used data commonly recorded during ecological studies (i.e., VHF-based nest and brood locations and female nest and brood success; Connelly et al., 2003) to evaluate the effect of resource selection on nest and brood success. We also demonstrated a novel approach to using an RSF to investigate the potential effects of habitat manipulations on individuals within a population.

Distance to treatment was the sole predictor of sage-grouse nest success in our GLMs. We confirmed that planned strategic sagebrush ecosystem restoration (i.e., conifer removal via mastication, chaining, and lop-and-scatter) can benefit sage-grouse that select for these manipulated sites. We also recorded multiple sage-grouse nesting attempts ($n = 8$) in treatments < 5 yr old. Our results contradict Knick et al.'s (2014) conclusions that conifer removal projects using mechanical methods are unlikely to increase available habitat for sage-grouse in the short term. The scale of the mechanical treatments we evaluated was larger and located in closer proximity to sage-grouse populations than those studied by Knick et al. (2014). Our results add support to Dahlgren et al.'s (2016a) contention that the sage-grouse population productivity in the area we studied may be limited by habitat availability (Williams et al., 2004).

The sage-grouse population we studied was largely confined by unsuitable and naturally fragmented habitat, and conifer encroachment was further reducing an already limited habitat base (Cook, 2015). Further, the low proportion (14.3%) of sage-grouse we observed that avoided conifer removal reflected the limited habitat availability; these "avoidance" broods used habitat at the far extant of the study area, either in high-elevation sagebrush or low-elevation desert scrub, neither of which are near conifer encroachment or removal. Mechanical conifer removal in areas where the sagebrush understory remains relatively intact but has been encroached by conifers has the potential to immediately restore habitat benefits (Dahlgren et al., 2016a). Sandford et al. (2015) reported the behavior of a female in 2015 that followed a conifer-masticating tractor into a previously phase two- to three-conifer stand, found a remnant patch of sagebrush with acceptable cover, nested, and hatched a brood. This behavior was bolder than previously observed in our study area but demonstrated that sage-grouse immediately recognize newly reopened habitat with an intact sagebrush canopy as usable space.

We evaluated brood success as a function of the log-odds of habitat selection, which limits the capability of back-transforming the data from probability of brood success to a measurable distance from conifer removal. Generally for every 1-unit increase in the resource selection coefficient, such that a female sage-grouse selected areas farther from a conifer removal area, the probability that she would fledge at least one chick to 50 days decreased by 52.6%. Although a direct interpretation of distance was not possible, it is clear that without conifer removal, resource selection of these sites closer to removal areas could not occur, thus eliminating a source of increased fitness. We caution that we analyzed probability of nest and brood success, not survival. Thus, we only report the increased probability of successfully hatching a nest or raising at least one chick to independence; we cannot report whether nest and/or brood survival rates increase.

We hypothesize that the reduction in conifer cover may have contributed to increased fitness through a combination of factors that may include removing avian nest and perch sites for potential sage-grouse nest and brood predators (Commons et al., 1999; Fedy et al., 2014), providing a release of forbs and grasses (Miller and Eddleman, 2000; Roundy et al., 2014; Schaefer et al., 2003; Vaitkus and Eddleman, 1987), and reestablishing mesic areas (Deboodt et al., 2008) critical to early brood success (Stiver et al., 2015). Frey et al. (2013) found that

Table 3
Top-ranking generalized linear mixed-effects candidate models using habitat variables to predict population-level habitat selection of greater sage-grouse *(Centrocercus urophasianus)* females with broods in Park Valley, Utah from 2012 to 2015

Predictor variables	K	AICc	ΔAICc	AICcWt
Treat, Elev, Roads > 40 , Roads < 40, Ag, NonUrb, Canopy	9	6759.73	0	0.73
Treat, Elev, Roads > 40, Roads < 40, Ag, NonUrb, Canopy, Mesic	10	6761.7	1.97	0.27
Treat, Elev, Roads > 40, Ag, NonUrb, Canopy, Mesic	9	6788.07	28.34	0
Canopy	2	7055.97	296.25	0
Null	2	7526.63	766.91	0

Treat indicates distance (km) to conifer removal area; Elev, elevation (m); Roads > 40, distance to roads 40−72 km·h^{-1}; Roads < 40, distance (km) to roads < 40 km·h^{-1}; Ag, distance (km) to agricultural areas; NonUrb, distance (km) to nonurban development; Canopy, canopy cover class (1-5); Mesic, distance (km) to mesic area. A "0" in any distance-to category indicated that a nest was at or within the habitat variable.

Table 4
Population level—based best-model estimates showing the individual-level marginal response (selection coefficient) for 56 individual female sage-grouse *(Centrocercus urophasianus)* in Park Valley, Utah from 2012 to 2015

Distance-to																				
Sign	Treatment			Roads 40-72 km·h^{-1}			Roads < 40 km·h^{-1}			Agriculture			Nonurban			Canopy			Elevation		
	n	b	p	x	b	p	x	b	p	x	b	p	x	b	p	x	b	p	x	b	p
+	8	7	0	20	13	20	32	22	6	36	29	12	22	15	22	55	40	16	37	29	2
−	48	34	37	36	28	23	24	18	13	20	12	9	34	26	6	1	1	1	19	12	14

n indicates the number of female sage-grouse with a brood according to selection coefficient; b, the number of sage-grouse females that fledged a brood regardless of coefficient significance in each sign category; p, the number of females regardless of brood success that displayed a statistically significant selection coefficient ($P < 0.05$). Negative coefficient signs for "distance-to" variables indicate a selection for a distance closer to the landscape variable. Negative coefficients for conifer canopy indicate an aversion to higher canopy class. Negative coefficients for elevation indicate a selection for lower elevation.

when conifers were removed, sage-grouse selected for mulched and seeded conifer removal sites over previously favored agricultural areas. Previous research in our study area suggested that sage-grouse immediately recognized and used conifer removal areas depending on a suite of factors including proximity to treeless sagebrush cover occupied by sage-grouse, intact sagebrush cover within treated areas postconifer removal, and distance to mesic sites (Cook, 2015; Wing, 2014).

Cook (2015), Sandford et al. (2015), and Wing (2014) noted that sage-grouse in our study area readily expanded when suitable (Fig. 4) habitat was reopened, suggesting that the population may be space limited. Dahlgren et al. (2016a) observed that across Utah, sage-grouse populations with less habitat space made smaller brood movements from nest sites while populations in large areas made larger movements. They suggested that increasing usable space could increase habitat availability and movements.

We suggest the methods and spatial scale of conifer removal may also affect sage-grouse use of treatment sites, particularly as it relates to distance to open occupied sagebrush habitat, remaining intact sagebrush canopy cover within conifer removal areas, and distance to mesic areas. Prescribed fire would likely have a negative impact on the shrubs and herbaceous understory plants important for sage-grouse (Connelly et al., 2011; Knick et al., 2014; Roundy et al., 2014), whereas mechanical conifer removal can maintain sufficient understory to attract sage-grouse use depending on preremoval conditions (Frey et al., 2013; Sandford et al., 2015).

The prescribed fire treatments studied by Knick et al. (2014) exhibited a remaining 6—24% PJ cover, and woodland canopy cover > 4% has been implicated as being associated with sage-grouse lek extirpation and avoidance (Baruch-Mordo et al., 2013; Fedy et al., 2014). Mechanical treatments are likely to obtain higher conifer removal percentages than prescribed fire because they involve more human control in the outcome (A. Clark, UDNR, personal communication; Frey et al., 2013). Because sage-grouse are a landscape species, the scale of treatments may also affect the probability of sage-grouse use (Doherty et al., 2010; Frey et al., 2013). The conifer removal treatments we studied were completed in an SGMA that exhibited some of the highest sage-grouse densities reported in Utah (UDWR, 2009).

Population-level investigations are often used to compare species (Kohl et al., 2013) or relate habitat manipulation or disturbance to population-level fitness (Benson et al., 2015; Cain et al., 2008; Harrington et al., 1999). Dahlgren et al. (2016b) provided evidence that telemetry-based studies can provide unbiased demographic information for analysis and monitoring, and male-based lek counts of sage-grouse can be an effective index to overall population change. Population-level variation in vital rates can be highly informative of landscape-scale demographic rates (DeCesare et al., 2014). The integration of these data in concert with our RSF approach to assessing sage-grouse fitness could provide new insight into population dynamics in response to management actions at greater temporal and spatial scales. Studies based on long-term demographic data are needed to enhance scientific rigor for prioritization of the most cost-effective species conservation and management actions. These studies could provide the basis for using male-based lek counts to track the effect of conservation actions on long-term population stability (Dahlgren et al., 2016b; Utah Governor's Office, 2013). In view of our results, we suggest that mechanically removing conifers at a landscape scale (< 57 ha) may increase not only habitat availability but also reproductive fitness and population stability.

Management Implications

We demonstrated that the removal of conifer canopy cover on large areas by mechanical methods adjacent to occupied sage-grouse habitat

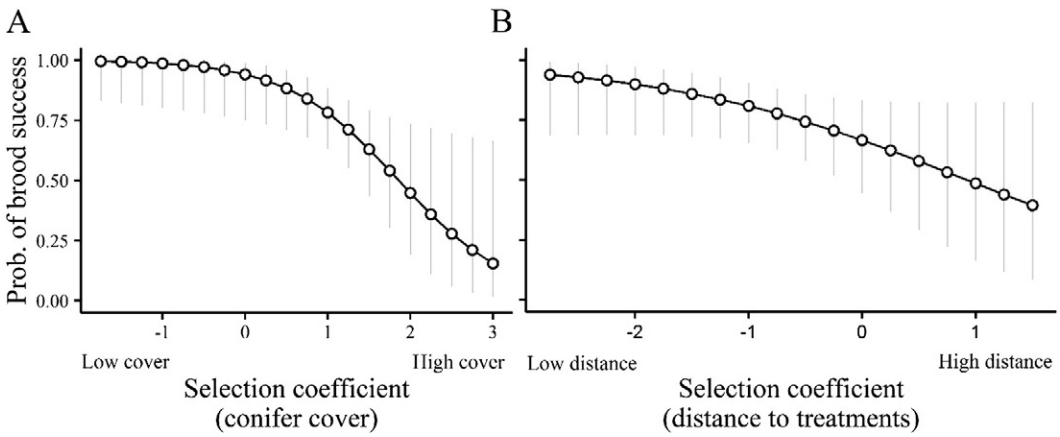

Figure 3. Probability of greater sage-grouse *(Centrocercus urophasianus)* brood success plotted against selection coefficient estimates of the average female of conifer canopy cover (**A**) and distance to conifer removal area (**B**) in Park Valley, Utah from 2012 to 2015. Probability of brood success decreased by 77.2% for each unit increase in canopy cover (95% CI = −2.74, −0.22) and decreased by 52.6% for each unit increase in distance from conifer removal area (95% CI = −1.60, 0.11).

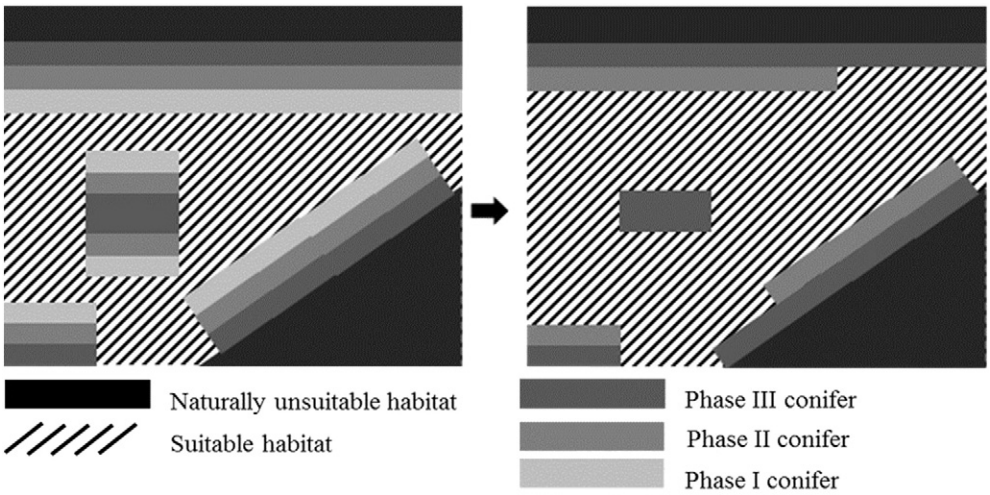

Figure 4. This figure demonstrates how the mechanical removal of Phase I and II conifer (*Pinus* spp. and *Juniperus* spp.) encroachment (Miller et al., 2005) can immediately create suitable greater sage-grouse (*Centrocercus urophasianus;* sage-grouse) breeding habitat. In areas bounded by naturally unsuitable habitat, the landscape-level projects that remove Phase I and II conifer encroachment can dramatically increase the suitable habitat available for sage-grouse.

had a positive effect on individual female nest and brood success rates. In our study area, > 8 100 ha of conifers have been removed using various mechanical methods, generally on the periphery of existing sagebrush habitat. However, more information is needed regarding female sage-grouse selection and fitness relative to methods and scale of conifer canopy removal projects and the effect of this management strategy on population stability. Lastly, we recommend the incorporation of animal-mounted GPS technology to increase the sample size of sage-grouse site selections. The use of this technology could also better detect female sage-grouse behavioral responses to different conifer canopy removal methods at a finer temporal scale.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.rama.2016.09.002.

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