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Pinyon and Juniper Encroachment into Sagebrush Ecosystems Impacts Distribution and Survival of Greater Sage-Grouse☆,☆☆

Peter S. Coates [a,*], Brian G. Prochazka [a], Mark A. Ricca [a], K. Ben Gustafson [a], Pilar Ziegler [b], Michael L. Casazza [a]

[a] US Geological Survey, Western Ecological Research Center, Dixon Field Station, Dixon, CA 95620, USA
[b] Bureau of Land Management, Carson City District, Sierra Front Field Office, Carson City, NV 89701, USA

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ABSTRACT

In sagebrush (*Artemisia* spp.) ecosystems, encroachment of pinyon (*Pinus* spp.) and juniper (*Juniperus* spp.; hereafter, "pinyon-juniper") trees has increased dramatically since European settlement. Understanding the impacts of this encroachment on behavioral decisions, distributions, and population dynamics of greater sage-grouse (*Centrocercus urophasianus*) and other sagebrush obligate species could help benefit sagebrush ecosystem management actions. We employed a novel two-stage Bayesian model that linked avoidance across different levels of pinyon-juniper cover to sage-grouse survival. Our analysis relied on extensive telemetry data collected across 6 yr and seven subpopulations within the Bi-State Distinct Population Segment (DPS), on the border of Nevada and California. The first model stage indicated avoidance behavior for all canopy cover classes on average, but individual grouse exhibited a high degree of heterogeneity in avoidance behavior of the lowest cover class (e.g., scattered isolated trees). The second stage modeled survival as a function of estimated avoidance parameters and indicated increased survival rates for individuals that exhibited avoidance of the lowest cover class. A post hoc frailty analysis revealed the greatest increase in hazard (i.e., mortality risk) occurred in areas with scattered isolated trees consisting of relatively high primary plant productivity. Collectively, these results provide clear evidence that local sage-grouse distributions and demographic rates are influenced by pinyon-juniper, especially in habitats with higher primary productivity but relatively low and seemingly benign tree cover. Such areas may function as ecological traps that convey attractive resources but adversely affect population vital rates. To increase sage-grouse survival, our model predictions support reducing actual pinyon-juniper cover as low as 1.5%, which is lower than the published target of 4.0%. These results may represent effects of pinyon-juniper cover in areas with similar ecological conditions to those of the Bi-State DPS, where populations occur at relatively high elevations and pinyon-juniper is abundant and widespread.

Introduction

The degradation, fragmentation, and loss of native shrub-steppe ecosystems, as well as the concurrent decline of wildlife populations that depend on them, are among the most pressing issues facing land managers across western North America (Davies et al., 2011; CFR, 2015a). In sagebrush ecosystems of the Great Basin, distribution and abundance of pinyon (primarily *Pinus monophylla*) and juniper (primarily *Juniperus osteosperma*) woodlands (hereafter, "pinyon-juniper") has increased dramatically (i.e., >150%) since European settlement (Miller et al., 2008) owing to changes in land-use practices (Romme et al., 2009), climate (Miller and Wigand, 1994; Romme et al., 2009), and disturbance regimes (Miller and Rose, 1999). For the purposes of this paper, we define encroachment to include both expansion (establishment of pinyon-juniper into areas previously devoid of trees) and infill (increasing closure of previously sparse pinyon-juniper canopies), as modified from Miller et al. (2013). Although pinyon-juniper is a native component contributing to landscape heterogeneity in the Great Basin and some encroachment may stem from natural recovery of pinyon-juniper woodlands previously cleared by European settlers (Romme et al., 2009), the overall current rate of encroachment is profoundly influencing contemporary sagebrush ecosystem processes (Miller et al., 2005; Davies et al., 2011). Accordingly, a variety of management actions have been directed toward decreasing the rate of pinyon-juniper expansion into sagebrush plant communities (Tausch et al., 2009), and many of these actions are the focus of studies presented in this volume of *Rangeland Ecology & Management.*

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* Correspondence: Peter S. Coates, US Geological Survey, Dixon Field Office, 800 Business Park Drive, Suite D, Dixon, CA 95620, USA. Tel.: +1 530 669 5073.
E-mail address: pcoates@usgs.gov (P.S. Coates).

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Habitat selection theory generally predicts that animals will occupy areas that optimize their fitness (i.e., survival and reproduction; Rosenzweig, 1981; Morris, 1989), and identifying mechanisms that link selection of environmental features with fitness is a lynchpin for implementing management actions that improve habitat suitability (Van Horne, 1983; Aldridge and Boyce, 2007; Casazza et al., 2011). Yet individuals do not always make decisions that maximize their fitness as they move through their environment, perhaps owing to variability in how they perceive environmental cues (Matthiopoulos et al., 2015) or respond to intraspecific competition for limited resources (Fretwell and Lucas, 1970). Moreover, maladaptive selection can lead to the formation of ecological traps, which can be defined as environments that provide attractive cues that yield lower survival and/or reproduction output, thereby decoupling an individual's perception of the habitat's fitness-harming traits (Robertson and Hutto, 2006). Directly linking an organism's fitness to its decisions becomes even more daunting and complex when these sources of variation are coupled with logistical difficulties in obtaining sufficient data on movement processes, environmental features, and fitness repercussions in a time-dependent fashion for multiple individuals of a species that occupy remote and vast landscapes (Morales et al., 2010).

Greater sage-grouse (*Centrocercus urophasianus,* hereafter sage-grouse) require large continuous areas of sagebrush-dominated ecosystems for population persistence (Knick et al., 2013), and this species is considered an indicator species for the health of sagebrush ecosystems because they require distinct ecological states to fulfill their diverse life history requirements at large spatial scales (Rowland et al., 2006; Hanser and Knick, 2011). Populations of sage-grouse have declined concomitantly with the loss and fragmentation of sagebrush ecosystems that now occupy slightly more than half of their former range (Schroeder et al., 2004; Miller et al., 2011). In large parts of the Great Basin, encroachment of pinyon-juniper has been identified as a primary threat to sage-grouse populations (CFR, 2015a) by contributing to fragmentation of continuous expanses of sagebrush and accelerating a positive feedback between wildfire and invasive annual grass (the other primary threat in the Great Basin) that often eliminates and replaces sagebrush (Brooks et al., 2004; Balch et al., 2013; Chambers et al., 2014a).

Several studies have documented strong avoidance of pinyon-juniper by sage-grouse at multiple spatial scales and across different grouse life history stages (Doherty et al., 2008; Atamian et al., 2010; Casazza et al., 2011; Knick et al., 2013) even at relatively low density (e.g., <4% canopy cover; Baruch-Mordo et al., 2013). Importantly, avoidance of pinyon-juniper by sage-grouse can have population-level consequences to brood survival (Casazza et al., 2011) and lek persistence (Baruch-Mordo et al., 2013), and can lead to genetic isolation (Oyler-McCance et al., 2005; Oyler-McCance et al., 2014). Different levels of pinyon-juniper cover (e.g., sagebrush dominant to pinyon-juniper woodland) may vary in their effects on sage-grouse behavior and population dynamics. For example, important resources to sage-grouse such as food and concealment cover decrease disproportionately as the percent of pinyon-juniper overstory increases (Bates et al., 2005; Miller et al., 2005; Miller et al., 2011). Additional tall vertical structures (such as trees) that provide perching and nesting habitat in an otherwise flat landscape can increase risk of avian predation (Coates et al., 2014a; Howe et al., 2014), which sage-grouse may perceive as a threat that changes with the density of trees on the landscape.

For management purposes, continuous encroachment of pinyon-juniper is often categorized into three transitional phases (i.e., Phase I, II, and III) indicating the dominant vegetation influencing ecological processes (Miller et al., 2005; Miller et al., 2013). For plant community structure, Phase I is characterized by relatively low pinyon-juniper canopy cover and overall dominance of sagebrush and associated perennial grasses. During Phase II, herbaceous sagebrush understory begins to thin significantly and become codominant with pinyon-juniper, while Phase III is characterized by dominance of pinyon-juniper and little to no herbaceous sagebrush understory. For sage-grouse, these transitional phases may elicit different demographic and behavioral responses that have important implications for management of pinyon-juniper and the mechanisms underlying degradation of sage-grouse habitat suitability.

A deeper understanding of relationships between evolved environmental cues that influence sage-grouse behavioral choices (e.g., to avoid or select an area) and the demographic consequences (e.g., mortality) of those choices could benefit conservation actions for sage-grouse populations. In the case of restoring sagebrush ecosystems by removing recently established pinyon-juniper trees, identifying these complex patterns and processes in relation to transitional phase is especially important because specific management actions designed to improve habitat suitability (e.g., removal of all trees in lower-density stands vs. thinning of higher-density stands) may elicit different behavioral responses from sage-grouse, which in turn might yield unique consequences for sage-grouse fitness components and management efficacy. Furthermore, quantifying thresholds within phases where management actions achieve desired goals (e.g., maintain or increase fitness) is paramount for effective conservation planning (Baruch-Mordo et al., 2013). Identifying linkages between ecological mechanisms driving both the "how" and "why" (e.g., selection and fitness) is an integral, yet largely unknown, part of the conservation planning process.

Typical quantitative approaches for linking sage-grouse habitat selection with fitness consequences use available habitat as a covariate in traditional survival (Aldridge and Boyce, 2007; Aldridge and Boyce, 2008; Casazza et al., 2011) or regression-type analyses (Baruch-Mordo et al., 2013). These approaches treat survival probability as a function of habitat in a time-independent or static manner and often link overall estimates of resource selection at the individual level to demographic performance at the population level without explicit consideration of the frequency or timing of encounters with landscape features (such as pinyon-juniper among different phases). Time-dependent analyses, in contrast, can be more computationally complex, yet they can more clearly establish a linkage between how individual sage-grouse respond behaviorally and demographically to specific encounters of pinyon-juniper among different phases. Studies that integrate both time-dependent and independent analyses can better identify mechanisms driving selection and survival.

Herein, we employ a novel two-stage Bayesian modeling approach to link estimated probability of avoidance of different pinyon-juniper cover classes with concomitant changes in annual probability of survival, while accounting for confounding factors and uncertainty in parameter estimation. Most importantly, this Bayesian approach incorporates the range of behavioral heterogeneity among individual sage-grouse, which allows for uncertainty in behavioral choices and their consequences for fitness. To provide target values for conifer removal to reach survivability, we then carried out a post hoc analysis that estimated survival directly as a function of time-dependent use of pinyon-juniper cover under conditions with varying levels of primary plant productivity. We focus on sage-grouse within the Bi-State Distinct Population Segment (Bi-State DPS) along the central border of California and Nevada, which has been recently ruled unwarranted for protection under the Endangered Species Act. Pinyon-juniper encroachment has been identified as the primary threat to the Bi-State DPS (CFR, 2015b), and the listing decision was informed in large part by planned implementation of large-scale treatments (thinning or removal) of encroaching pinyon-juniper across thousands of acres of habitat (Bi-State Action Plan, 2012).

Study Area

The Bi-State DPS comprises 18 325 km^2 split along the border of Nevada and California at the interface of the Sierra Nevada Mountains to the west and the Great Basin to the east (Fig. 1A; lat 119°11′1.94″N, long 38°6′30.80″W). We collected sage-grouse data from seven subpopulations: Bodie Hills (BH), Long Valley (LV), Parker Meadows (PM), Pine Nut Mountains (PN), Mount Grant (MG), Desert Creek/Fales (DF), and White Mountains (WM), which comprise three distinct subregions: northern (consisted of PN), central (consisted of BH, LV, PM,