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Encounters with Pinyon-Juniper Influence Riskier Movements in Greater Sage-Grouse Across the Great Basin☆,☆☆

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ABSTRACT

Fine-scale spatiotemporal studies can better identify relationships between individual survival and habitat fragmentation so that mechanistic interpretations can be made at the population level. Recent advances in Global Positioning System (GPS) technology and statistical models capable of deconstructing high-frequency location data have facilitated interpretation of animal movement within a behaviorally mechanistic framework. Habitat fragmentation due to singleleaf pinyon (*Pinus monophylla*; hereafter pinyon) and Utah juniper (*Juniperus osteosperma*; hereafter juniper) encroachment into sagebrush (*Artemisia* spp.) communities is a commonly implicated perturbation that can adversely influence greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) demographic rates. Using an extensive GPS data set (233 birds and 282,954 locations) across 12 study sites within the Great Basin, we conducted a behavioral change point analysis and constructed Brownian bridge movement models from each behaviorally homogenous section. We found the probability of encountering pinyon-juniper among adults was two and three times greater than that of yearlings and juveniles, respectively. However, the movement rate in response to the probability of encountering pinyon-juniper trees was 1.5 times greater for juveniles. Parameter estimates indicated a 6.1% increase in the probability of encountering pinyon-juniper coupled with a 6.2 km/hour increase in movement speed resulted in a 56%, 42% and 16% increase in risk of daily mortality, for juveniles, yearlings, and adults, respectively. The effect of pinyon-juniper encounters on survival was dependent on movement rate and differed among age class. Under fast speed movements (i.e., flight), mortality risk increased as encountering pinyon-juniper increased across all age classes. In contrast, slower speeds (i.e., average) yielded similar adverse effects for juveniles and yearlings but not for adults. This analytical framework supports a behavioral mechanism that explains reduced survival related to pinyon-juniper within sagebrush environments, whereby encountering pinyon-juniper stimulates riskier movements that likely increase vulnerability to visually acute predators.

Introduction

In the Great Basin of western North America, contemporary encroachment of pinyon (primarily *Pinus monophylla*) and juniper (primarily *Juniperus osteosperma*) (hereafter, "pinyon-juniper") woodland is contributing to the degradation of sagebrush ecosystems and habitat quality for sagebrush obligate species. Greater sage-grouse (*Centrocercus urophasianus;* hereafter, sage-grouse) are one such obligate whose populations have declined concomitantly with the loss and fragmentation of sagebrush ecosystems and now occupy slightly more than half their former range (Schroeder et al., 2004; Miller et al., 2011). This trend has contributed to multiple proposed listings of the species under the Endangered Species Act (CFR, 2015). Pinyon-juniper encroachment, which we define as both expansion and infill, contributes to sagebrush degradation by disproportionately reducing shrub and herbaceous habitat components that provide forage and cover to sage-grouse (Miller et al., 2005, 2011). Subsequent increases in woody biomass can also contribute to larger wildfires that kill sagebrush and propagate invasion of annual grasses such as cheatgrass *(Bromus tectorum)* that fuel more wildfires (Getz and Baker, 2008; Balch et al., 2013; Chambers et al., 2014). It follows that many restoration actions

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focus on thinning or removal of encroaching pinyon-juniper in sagebrush ecosystems, with the intent of enhancing sage-grouse populations by improving habitat quality (Tausch et al., 2009; Davies et al., 2011; Bi-State-Action-Plan, 2012; McIver and Brunson, 2014; Pyke et al., 2015).

Identifying how animals move in relation to habitat features and the demographic consequences of those movements can increase the effectiveness of conservation measures, but it is difficult to quantify these patterns given the inverse relationship between scale of observation and degree of stochasticity (Levin, 1992; Morales et al., 2010). As such, standard measures of animal-habitat interactions (e.g., habitat avoidance or selection) are quantified typically at the population level (Doherty et al., 2008; Freese, 2009; Casazza et al., 2011; Baruch-Mordo et al., 2013; Knick et al., 2013). However, higher-order patterns such as population persistence or distribution stem from individual-based behavioral decisions (e.g., move or stay) made in response to internal and external stimuli (Gurarie et al., 2009), and management strategies that rely on information gathered at larger scales must take into consideration how information is being transferred across scales (Levin, 1992). In the case of sage-grouse, Baruch-Mordo et al. (2013) documented a cessation of lek activity in response to tree cover that exceeded 4%, yet it was unknown whether lek cessation was a product of mortality, emigration, or both. If birds are emigrating to neighboring leks and stabilizing or improving population performance as a result, the negative effects of pinyon-juniper encroachment are likely to be ascribed to reductions in sage-grouse distribution alone. However, if pinyon-juniper encroachment also leads to a reduction in individual survival, the negative effects experienced by the metapopulation could be greater. In a similar analysis, Coates et al. (2017 this-issue) used a temporally higher resolution dataset, which incorporated mortality information (i.e., individual-level data) and found that tree canopy cover of 4% in productive habitat with dispersed trees was associated with a substantial reduction in the annual probability of survival. In other words, by decreasing the scale of observation, Coates et al. (2017 this-issue) identified a likely demographic mechanism for the result observed in the Baruch-Mordo et al. (2013) study. However, the behavioral mechanisms, such as speed and frequency of travel, which might drive lower survival in pinyon-juniper encroached habitats, were not identified. Decreasing the scale of observation to an even finer resolution may help identify these behavioral mechanisms. For example, avoidance patterns observed at coarser scales may reflect faster movements through less desirable habitats. General theories of optimality predict that organisms should spend a greater portion of their time in habitats where resources are plentiful but leave habitats and the resources they provide more quickly when risk of predation is high (Morris and Davidson, 2000). Movement is a temporal function, and therefore it logically extends that less desirable habitats should correlate with faster movements. However, in the case of sage-grouse, increases in movement rate may also increase susceptibility to visually acute predators and could serve as the mechanism driving the demographic consequences documented in Coates et al. (2017 this-issue). Identifying groups of individuals or life stages that demonstrate greater movement rates and, in turn, experience greater risk during encounters with pinyon-juniper encroached habitats could provide managers with a better informed approach to tree-removal strategies. For example, if adult females were to experience the greatest risk of mortality during trips between lek and nest sites, it would be beneficial for managers to focus tree-removal efforts on areas that intersect lek and nest site locations. Such efforts could reduce predator subsidies associated with pinyon-juniper encroachment and reduce movement rates in sage-grouse by decreasing the distance between desirable resources.

Identifying variation in sage-grouse movement behavior resulting from encounters with pinyon-juniper trees in sagebrush landscapes and their direct linkages to fitness has also been hampered by technological and analytical limitations. Previous studies have utilized relatively coarse spatiotemporal datasets such as traditional VHF telemetry data to quantify avoidance patterns of pinyon-juniper by sage-grouse (Doherty et al., 2008; Freese, 2009; Casazza et al., 2011, Coates et al. 2017 this-issue) or lek counts (Baruch-Mordo et al., 2013) and presence/absence of leks (Knick et al., 2013) to quantify effects of pinyon-juniper on integrated demographic processes. From the technological standpoint, recent advances in Global Positioning Systems (GPSs) small enough to place on small-game-size animals have increased the temporal accuracy of location data by reducing the length of time between sampling intervals and removing "the human-monitoring element" by transmitting data via satellite or cellular network. From the analytical standpoint, these large volumes of GPS-derived data led to the adoption of more advanced space-use estimators capable of dealing with serial autocorrelation and complex data error structures (Horne et al., 2007; Gurarie et al., 2009; Fischer et al., 2013). Yet these techniques often need to be adapted and modified in novel ways to address specific management questions and improve understanding of complex systems (Ovaskainen, 2004; Horne et al., 2008; Hebblewhite and Haydon, 2010; Morales et al., 2010).

Movement is a continuous process observed at discrete intervals. Therefore, relating movement processes to land-cover characteristics requires probabilistic space-use estimators. Brownian bridge movement models (BBMMs) have garnered considerable attention for their ability to estimate utilization distributions (UDs) along autocorrelated movement paths. However, before calculating BBMMs it is imperative that the data used to inform the model originate from a uniform movement process or that the UD estimated along a bridge reflect the heterogeneity across relocations (Kranstauber et al., 2012). This becomes problematic when working with temporally long datasets, as it is well known that mobile organisms are capable of displaying a variety of motility patterns and thus introduce heterogeneity to relocation datasets. Constructing a BBMM from data depicting ≥ 2 movement processes without the use of a dynamic BBMM (Kranstauber et al., 2012) would result in an "averaged" value of the Brownian motion variance (BMV), a measure of animal mobility (Horne et al., 2007), and in turn an underestimation of the UD during periods of rapid movement and an overestimation during periods of slower movement. If the end goal is to extract habitat data on the basis of an encounter probability, the previously described scenarios would result in the false exclusion and inclusion, respectively, of habitat features.

To better link changes in behavior to environmental stimuli, and subsequent demographic consequences of those changes in behavior, movement paths with underlying heterogeneous behavior should first be segregated statistically into homogenous sections that allow construction of more accurate and behaviorally specific BBMMs. State-space modeling is a popular approach to this issue, which allows for separation of a process model (e.g., movement behaviors) from an observation model (i.e., observation error) but also requires the number and type of behavioral states to be known a priori (Jonsen et al., 2005; Royer et al., 2005; Patterson et al., 2008). Gurarie et al. (2009) provided an alternative likelihood-based method for identifying changes in animal movement called behavioral change point analysis (BCPA) that does not require a priori knowledge of the number and types of behavioral states that an organism can transition into or out of, and is robust enough to deal with observation error, multidimensionality, and autocorrelation. Using the BCPA to identify shifts in the underlying movement process and constructing UDs from BBMMs that are informed by behaviorally homogenous location data provide a meaningful space use metric within a movement context. Hierarchical models that predict movement patterns in relation to encounters with external stimuli (e.g., habitat characteristics extracted to the UDs within a geographic information system) can then be developed. Once established, consequences to fitness can be modeled directly by relating when an animal dies to how its behavior changed when encountering different levels of habitat-related external stimuli (Gurarie et al., 2009; Halstead et al., 2012).

Kranstauber et al. (2012) developed a streamlined approach to computing dynamic Brownian bridges by combining a BCPA and BBMM into