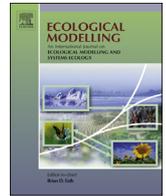




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# Using dynamic population simulations to extend resource selection analyses and prioritize habitats for conservation

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### ABSTRACT

Prioritizing habitats for conservation is a challenging task, particularly for species with fluctuating populations and seasonally dynamic habitat needs. Although the use of resource selection models to identify and prioritize habitat for conservation is increasingly common, their ability to characterize important long-term habitats for dynamic populations are variable. To examine how habitats might be prioritized differently if resource selection was directly and dynamically linked with population fluctuations and movement limitations among seasonal habitats, we constructed a spatially explicit individual-based model for a dramatically fluctuating population requiring temporally varying resources. Using greater sage-grouse (*Centrocercus urophasianus*) in Wyoming as a case study, we used resource selection function maps to guide seasonal movement and habitat selection, but emergent population dynamics and simulated movement limitations modified long-term habitat occupancy. We compared priority habitats in RSF maps to long-term simulated habitat use. We examined the circumstances under which the explicit consideration of movement limitations, in combination with population fluctuations and trends, are likely to alter predictions of important habitats. In doing so, we assessed the future occupancy of protected areas under alternative population and habitat conditions. Habitat prioritizations based on resource selection models alone predicted high use in isolated parcels of habitat and in areas with low connectivity among seasonal habitats. In contrast, results based on more biologically-informed simulations emphasized central and connected areas near high-density populations, sometimes predicted to be low selection value. Dynamic models of habitat use can provide additional biological realism that can extend, and in some cases, contradict habitat use predictions generated from short-term or static resource selection analyses. The explicit inclusion of population dynamics and movement propensities via spatial simulation modeling frameworks may provide an informative means of predicting long-term habitat use, particularly for fluctuating populations with complex seasonal habitat needs. Importantly, our results indicate the possible need to consider habitat selection models as a starting point rather than the common end point for refining and prioritizing habitats for protection for cyclic and highly variable populations.

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## 1. Introduction

In prioritizing and protecting habitats for species of conservation concern, resource managers seek to understand how animals

select and use habitat. To that end, managers often prioritize habitats using analyses that quantify how landscape factors influence patterns of habitat selection. Although this approach has been successful for a number of species, similar conservation actions for declining or highly dynamic populations with complex life histories may not yield the same conservation benefits (Boyce et al., 2016; Osborne and Seddon, 2012). Patterns of habitat use are altered by population size and density, behavior, and movement limitations. These factors, and those that affect the functional access to habitat, are much more difficult to consider in traditional habitat selection analyses. In complex systems, the long-term interacting

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influences of such factors may also shift patterns of habitat use and change which habitats are important for persistence. Despite awareness of these potential challenges, ecologists often lack data and analytical approaches to explore the degree to which important habitats could change as a result of population fluctuations in stable landscapes. An understanding of how important habitats can change with population conditions could indicate how frequently data needs to be collected and the degree to which prioritizations need to be updated to represent a broad range of population conditions. Further, biologically-augmented analyses could indicate the degree to which density dependence and movement constraints can alter expectations of important habitats.

Spatially explicit individual-based modeling can link habitat selection analyses with population conditions, dynamics, individual behavior, and movement decisions to track shifts in population distributions through time. Simulations can examine shifts in habitat use resulting from realistic population conditions by modeling stochastic fluctuations in demography, density-dependent movement, and habitat selection. Here, we use a case study of a wide-ranging galliform species, to compare the consistency of predicted high use habitats among long-term simulation and short-term (statistical) habitat selection analyses.

### 1.1. Assessing important habitats

Species' use of resources can be spatially complex and temporally dynamic, changing stochastically or seasonally (e.g., with fluctuating population sizes, complementary seasonal habitat needs; Dunning et al., 1992), as well directionally through time (e.g., habitat alteration and shifting ecological communities and climates; Travis and Dytham, 2004). Identifying which habitats are the most important to protect for a given species is an important but challenging conservation task, particularly when climates and ecological contexts are changing. This challenge can be even greater for non-equilibrium or fluctuating populations, where changes in abundance and distribution complicate habitat and population assessments.

With the expansion and availability of remotely sensed products, predictive statistical habitat models are increasingly used to identify and assess habitat for species conservation and management (Johnson et al., 2004; McLoughlin et al., 2010; Nielsen et al., 2010). Animal locations and environmental covariates are used to map and assess the probability of animals selecting and using different areas of the landscape (e.g., resource selection functions (RSF); Boyce et al., 2002; Manly et al., 2002). This approach can identify important habitats that may be suitable but currently unoccupied, highlight habitat use outside of previously identified biologically important areas, and provide valuable insights into habitat use and priority areas for protection. Further, recent advancements in resource selection modeling have sought to increase the biological realism and accuracy of predictions by considering resource selection by animals moving through the landscape (e.g., step-selection functions can address habitat accessibility; Thurfjell et al., 2014) as well as movement barriers (Brost et al., 2015), and random walk movement models to weight and estimate selection coefficients (Hooten et al., 2014), among other examples. Although the importance of density-dependent habitat selection is generally recognized as a key factor influencing resource use, density has been explicitly considered only in some RSF models (e.g., Boyce et al., 2002).

Despite their utility, most RSF studies can be logistically challenging and are often conducted within a short time period, representing a small sample of population sizes and conditions. Although this limited sampling window may be appropriate for a stable, non-fluctuating population, RSFs based on short time-series of data may be constrained in their ability to predict habitat selec-

tion over a broader range of population fluctuations and through time periods that are relevant to species conservation initiatives (Boyce and McDonald, 1999). Even in stable landscapes, RSFs based on a few years of data may not fully represent population conditions experienced by fluctuating or cycling populations, those subject to disease outbreaks, or changing interspecific influences. Without explicit consideration of time-varying density-dependent habitat selection, subsequent habitat prioritizations may be prone to errors at different population sizes (McLoughlin et al., 2010). There are also few examples of wildlife RSFs with demonstrated linkages to their direct regulating factors (Aldridge and Boyce, 2007; Boyce et al., 2016; Johnson et al., 2004; Nielsen et al., 2005, 2010), including movement constraints and habitat accessibility. Animal movement, behavior (e.g., site fidelity), and accessibility of habitats are often only represented by RSF analyses in statistical comparisons of used and unused (or available) locations. This allows the prediction of high selection habitats in areas that can be difficult for animals to find or access if movement barriers and restrictions are not explicitly considered by another means (Thurfjell et al., 2014). These considerations can limit the direct use of RSFs for practical management applications such as identifying critical habitat for species of conservation concern (Nielsen et al., 2010).

### 1.2. Simulated habitat use

In this proof of concept, we explore the use of spatially explicit simulation modeling, informed by RSF maps, to predict long-term habitat use that is directly influenced by population dynamics and movement constraints through time. Although conservation practitioners expect landscape change to alter characterizations of priority habitats, the impacts of population fluctuations on long-term habitat selection are often overlooked. The degree to which important habitats (as identified using RSFs) can change through time as a function of population fluctuations, rather than landscape change, is largely unclear. In times of high abundance, populations may spill-over to occupy nearby lower RSF value habitats, as a result of dispersal and habitat availability limitations and site fidelity preferences. These excluded areas could be just below the RSF threshold chosen for habitat protection and offer good, but less frequently used habitat. Conversely, excluded areas could be lower quality habitat that operate as sink habitats that still support near-term population persistence (Heinrichs et al., 2015). Hence, if only higher selection value habitats were protected, population persistence could be compromised by omitting spill-over habitats from formal protection plans. Many RSF models also exclude or simplify habitat accessibility considerations, which may result in the prioritization of areas with limited connectivity and poor long-term occupancy, resulting in ineffective habitat protection and population conservation actions.

To assess how important habitats may deviate through time from those identified RSFs, we simulated population dynamics in a static landscape, with explicit individual movements and habitat selection, in a case study that exemplified: 1) a dramatically fluctuating population, and 2) fragmented habitat with varying degrees of isolation and accessibility. We developed a spatially explicit individual-based model that coupled seasonal input RSF maps with stochastic population dynamics and movement-constrained habitat selection. We simulated individual locations and fates and summarized habitat use through time to produce a biologically-augmented view of important, long-term habitats, and compared these to RSF habitat prioritizations. As high conservation value habitats are often thought of as those that are consistently occupied, areas with higher selection values were deemed of higher conservation value in the RSF map. In the simulated habitat use map, habitat use indicated both the frequency and magnitude of use (i.e., the number of animals using habitats through time). Differences

among RSF and simulation predictions highlighted locations where population processes are strong enough to alter habitat selection through time, indicating changes in the value of habitats that were previously identified as important for species conservation.

In our case study of the Greater sage-grouse (*Centrocercus urophasianus*), we used data from Wyoming, including static seasonal RSF models, seasonal movement distances, nest site fidelities, demographic rates, and West Nile virus outbreaks. Greater sage-grouse (hereafter sage-grouse) are declining across their historical range (Connelly and Braun, 1997; Fedy and Aldridge, 2011; Manier et al., 2013; Schroeder et al., 2004, 1999), although parts of Wyoming are still strongholds for the species (Fig. 1). Key breeding locations (centered on leks – breeding grounds) and associated nesting habitat have been protected as ‘core areas,’ intended to support 74–80% of Wyoming’s nesting females (Wyoming Executive Order No. 2015-4, 2015) by limiting future development and human disturbances. However, the species has seasonally differing habitat requirements and birds often move and select different habitats for summer and winter seasons (Connelly et al., 2011, 2000). Efforts to evaluate the sufficiency of core areas to protect grouse through all seasons and into the future have been limited. Hence, we also assessed the degree to which existing protected areas include summer and winter habitats by simulating seasonal movements and distributions and evaluating the proportion of birds protected within core areas in each season.

## 2. Materials and methods

### 2.1. Overview

To simulate the areas most likely to be used by greater sage-grouse in Wyoming, we incorporated habitat-occurrence (RSF) models into a spatially explicit population model and simulated individual sage-grouse interactions with the landscape. Simulated grouse selected nest sites near leks, moved to and selected summer and winter ranges, and returned to a familiar nest area each year. Stochastic or cyclic variation in survival and reproduction induced variable population densities and West Nile virus outbreaks limited population growth in some areas. We examined the influence that seasonal movements, nest site fidelity, and population variability had on habitat use and overall population outcomes, by simulating grouse dynamics in alternative demographic scenarios (stable, declining, and cyclic population trends) in a static landscape. We recorded habitat use through time and compared these simulated habitat use results to the same areas in the RSF maps.

### 2.2. Resource selection function models

We used RSF models from Fedy et al. (2014) that identified selected sage-grouse habitat for three seasonal periods (nesting, summer, and winter) across the state of Wyoming. The Fedy et al. (2014) modeling approach used the best available data across a large spatial extent, and is more biologically detailed than many traditional RSF models, as the model implicitly considered some movement limitations by constraining ‘available’ locations (to a maximum possible dispersal distance). The model also considered landscape covariates at both landscape and patch scales (i.e., 2 spatial scales of evaluation; patch = 0.045–0.546 km, landscape = 1.55–3.2 km radii moving windows). However, data were limited and habitat selection predictions were based on a limited time series of radio-telemetry observations (1–12; mean 3.7 years, depending on location and season), and spatial sampling did not extend across the complete range of sage-grouse occurrence in the state.

The RSF models predicted the continuous relative probability (0–1) of sage-grouse selection for each 30-m pixel across Wyoming for a given season, based on occurrence records and multi-scale spatial predictors describing vegetation, topography, climate, and development (e.g., agriculture, roads, oil and gas wells). We updated the published seasonal habitat models to reflect the revised species range extent in Wyoming (Wyoming Game and Fish, 2015) and improved the datasets used in the seasonal habitat models in several ways. For instance, the vegetation sagebrush data products originally used by Fedy et al. (2014) masked all elevations above 2377 m (Homer et al., 2012), but leks and sage-grouse habitat occur at elevations as high as 2541 m; therefore, we extended RSF habitat predictions to higher elevations. We also re-calculated the mapped predictions using an improved road layer that more accurately captured the distribution of roads within the state (O'Donnell et al., 2014). The RSF values for non-habitat landscape features such as oil and gas well-pad surfaces, large water bodies, and forested areas were masked (i.e., RSF value set to 0) to induce movement avoidance in the simulation model, and unknown areas (e.g., obscured by clouds in remotely sensed imagery) were given a no-data value. Model covariates did not directly include measures of population density, or associations with protected areas. RSF pixel values were re-scaled (from 0 to 1 to 0–100) and RSF maps (30-m grids) were averaged into hexagonal habitat maps (1-km wide hexagons; 86.6 ha per hexagon, hereafter referred to as a pixel) for use in the spatially explicit population model.

### 2.3. Spatially explicit population model

Seasonal habitat maps were integrated with species life history, behavior, movement, habitat selection, and demographic data within the spatially explicit individual-based modeling platform HexSim (version 3.2; Schumaker, 2015). We created a 3-stage (chick, yearling, adult) model to simulate sage-grouse population dynamics and habitat use. We modeled only females as empirical data for demography, habitat selection and movement, largely represented female conditions and male-only data were unavailable. After initialization at breeding leks, simulated sage-grouse (hereafter, simulated grouse or individuals) experienced an annual cycle of nesting, reproduction, movement to their summer range, possible infection with West Nile virus, movement to their winter range, annual mortality, and dispersal (Fig. 2). During nesting, summer, and winter, individual locations were mapped to assess habitat use and occupancy of protected core areas by simulated birds.

#### 2.3.1. Initialization

Simulations began with adult simulated grouse distributed among active lek locations according to their estimated abundance in 2006 (Wyoming Game and Fish unpublished dataset, fall 2014), which corresponded to the landscape conditions and habitat selection responses evaluated in the Fedy et al. (2014) habitat models. See Table A1 in Appendix A in Supporting Material for lek count estimations and low and high starting population size assumptions.

#### 2.3.2. Initial lek – nest movement

After placement at a lek, simulated female grouse followed movement rules in search of a nest. Individuals searching for a nest traveled an average of 3 km (0–11 km), approximating observed lek – nest Euclidean adult movement distances (Kaiser, 2006; mean 3.2, 0.1–12.7 km). Simulated grouse then explored over a 2-km radius to identify a nest site with a high nesting RSF value. The highest scoring pixel was selected (containing <48 simulated grouse), with a preference to select an unoccupied pixel if available. To ensure that all individuals that were able to find a nesting location (as typically observed), simulated grouse were allowed to return to the lek and take multiple forays until a nest was established within

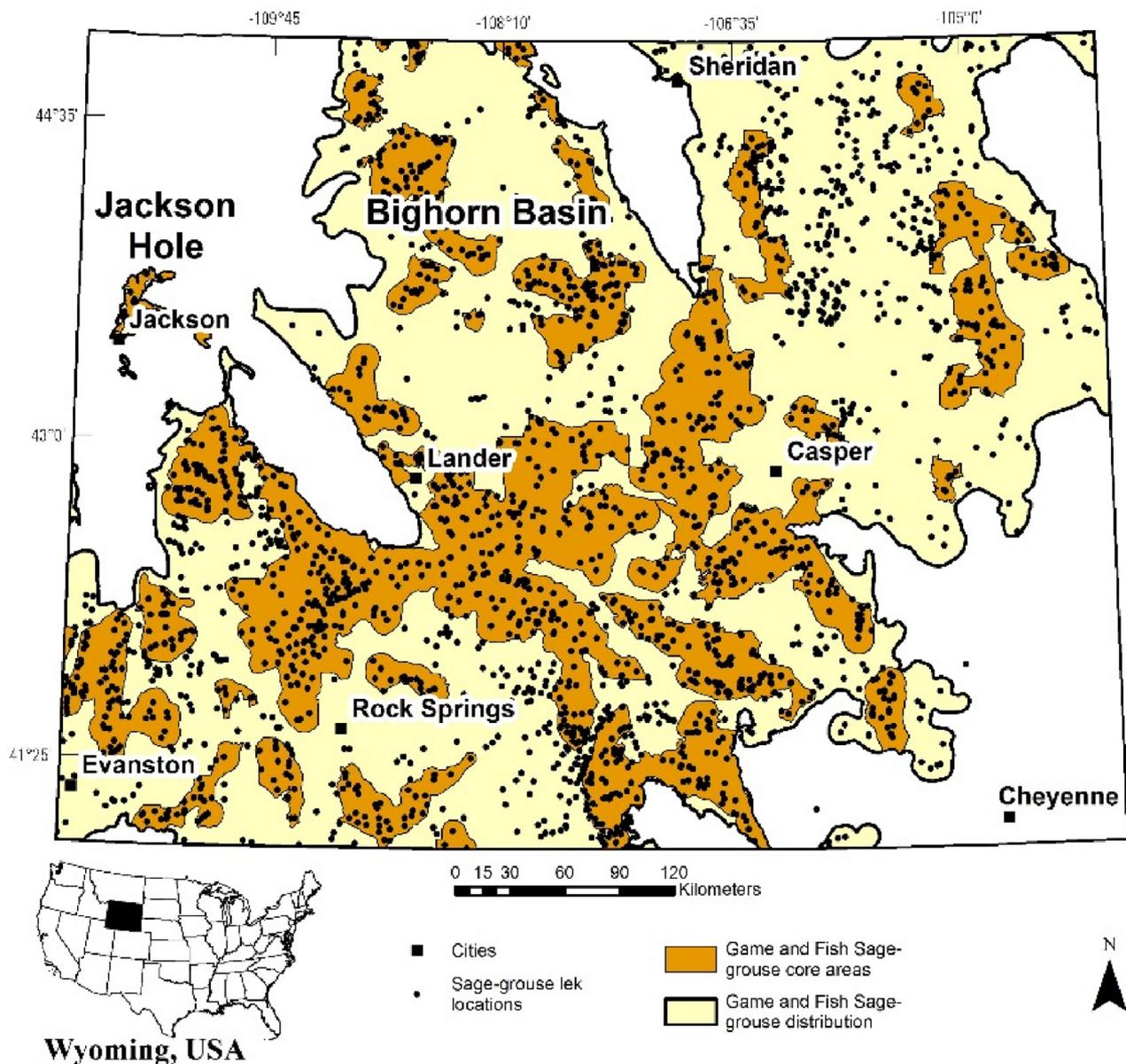


Fig. 1. Greater sage-grouse distribution, lek locations, and protected core areas in Wyoming.

9 km of a lek (93% of nests occur within 8.5 km of a lek in south-western Wyoming; Holloran and Anderson, 2005). We recorded female nesting locations, allowing subsequent return (nest-site fidelity) and to map simulated nesting habitat use. Regardless of season, individuals moved with forward momentum and paths (auto-correlation and choice of direction) were influenced by the RSF map scores. Simulated grouse were increasingly attracted to higher RSF scores (with a strength that increased with RSF score), corresponding to higher probabilities of habitat selection. Conversely, individuals avoided hexagons with scores below the seasonal RSF habitat optimization thresholds (selected at the lower confidence interval value). The thresholding procedure aimed to maximize capture of grouse “use” locations while minimizing the area required to do so (see Fedy et al., 2014 for details). Areas above the RSF thresholds were used by simulated grouse to establish their ranges. Simulated grouse moved through areas below the seasonal habitat thresholds and would occasionally cross intervening gaps separating habitat areas.

Simulated grouse that nested in close proximity to other areas were subject to density-dependent mortality. This negative feedback maintained the observed densities of nesting individuals at levels approximating literature values, and allowed the population to fluctuate around its historical (1990–2014) mean population size (see Appendix A for details).

### 2.3.3. Reproduction and chick survival

Although sage-grouse demographic rates vary spatially, data limitations necessitated that we parametrized our model using a single set of values across the study area for each demographic variable. Nesting adults ( $\geq 2$  yrs.) and first-year breeders (hereafter yearlings) were randomly assigned probabilities of producing a successful nest on their first, second, and third nesting attempts. Population nest success probabilities were drawn annually with replacement from the following normal distributions (mean/SD) that included initiation rates for each nest attempt from Taylor et al. (2012): Yearling 1st – 0.34/0.13, Yearling 2nd – 0.08/0.13; Adult 1st – 0.42/0.12, Adult 2nd – 0.23/0.14, Adult 3rd – 0.06/0.13). Individ-

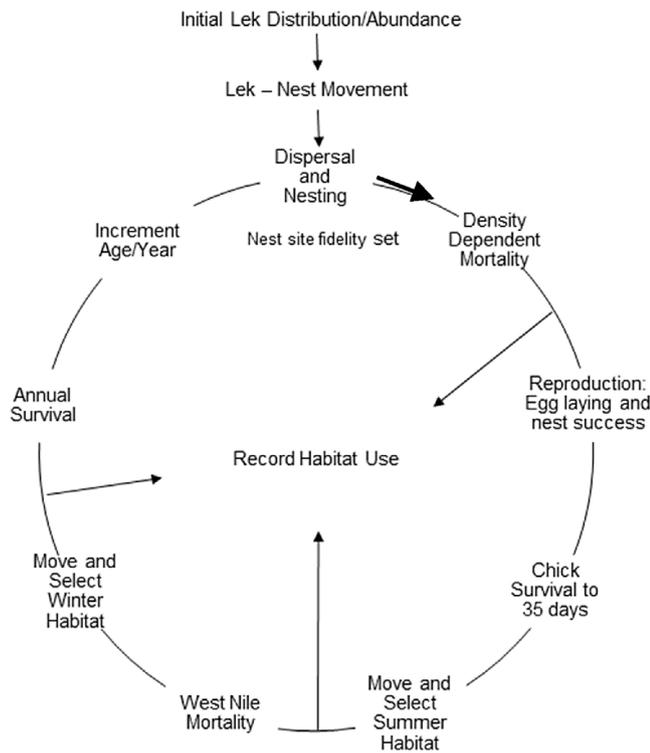


Fig. 2. Simulated annual cycle of events for greater sage-grouse in Wyoming.

uals that had probabilistically successful nests were then assigned a clutch size of female eggs, based on their stage and which nest attempt was successful, drawn annually from normal distributions (mean/SD) from Taylor et al. (2012): Yearling 1st – 3.48/0.60, Yearling 2nd – 2.84/1.32; Adult 1st – 3.77/0.49, Adult 2nd – 3.03/0.99, Adult 3rd – 2.57/0.99. Rates include egg hatching probabilities and assumed a balanced sex ratio (Atamian and Sedinger, 2010). Each year, the likelihood of chicks (<1 year old) surviving to 35 days was drawn from a normal distribution with a mean of 0.41 and SD = 0.07 (Taylor et al., 2012), and applied to all chicks in the population. To approximate the magnitude of observed inter-annual population variation, nest success and survival (chick and annual) were assumed to be correlated within a given year. Hence, a year with high nest success would also have high chick, yearling, and adult survival.

### 2.3.4. Movement to summer habitat

Following nesting, all simulated grouse dispersed to summer habitat. Using a lognormal distribution of path lengths, individuals relocated an average Euclidean distance of 8.4 km (0–57 km), approximating the lognormal distribution of observed movement distances in Wyoming (mean 8.1 km, 0–58 km; Fedy et al., 2012). After moving, individuals explored a 2-km radius (as described for nesting) to select a pixel around which to base their summer range. To compensate for a lack of summer movement memory, simulated individuals iteratively dispersed from their nest until they found a suitable summer range. Individuals from older stages (i.e., adults) had site selection priority over younger stages.

### 2.3.5. West Nile virus infection and mortality

Outbreaks of West Nile virus (WNV) affect greater sage-grouse, especially in the northeast portion of Wyoming, and can limit the abundance and persistence of populations (Naugle et al., 2005, 2004). We used a spatially-explicit degree-day surface describing the predicted risk of West Nile virus transmission (degree-day model; Schrag et al., 2011) to identify simulated grouse at risk of

WNV infection. At-risk individuals drew a probability of infection from a stretched beta distribution (mean = 0.07, SD = 0.05, 0.005–1) and infected individuals were subject to a 0.04 survival rate (Walker and Naugle, 2011; as in Walker et al., 2007).

### 2.3.6. Movement to winter habitat and annual survival

Simulated grouse left their summer ranges in search of a suitable wintering site, using the winter habitat map to inform movement paths and site selection (as previously described). On average, grouse moved 16.4 km (0–127 km) from their summer locations (using a lognormal distribution of path lengths), approximating observed movement distances and distribution of movement distances from telemetry studies across Wyoming (mean = 17 km, 1–83 km; Fedy et al., 2012). Individuals dispersed iteratively from their summer range until they located a suitable winter site, and explored a 2-km radius (as described for nesting) to select a pixel around which to base their winter range.

Annual survival rates were drawn from a normal distribution (mean/SD) and applied to individuals based on their stage (from Taylor et al., 2012): juvenile (>35 days) – 0.75/0.27; yearling – 0.65/0.14; adult – 0.58/0.13. Surviving individuals transitioned to the next stage class, and prepared to return to their previous nest or natal site.

### 2.3.7. Return to nest and long-distance dispersal

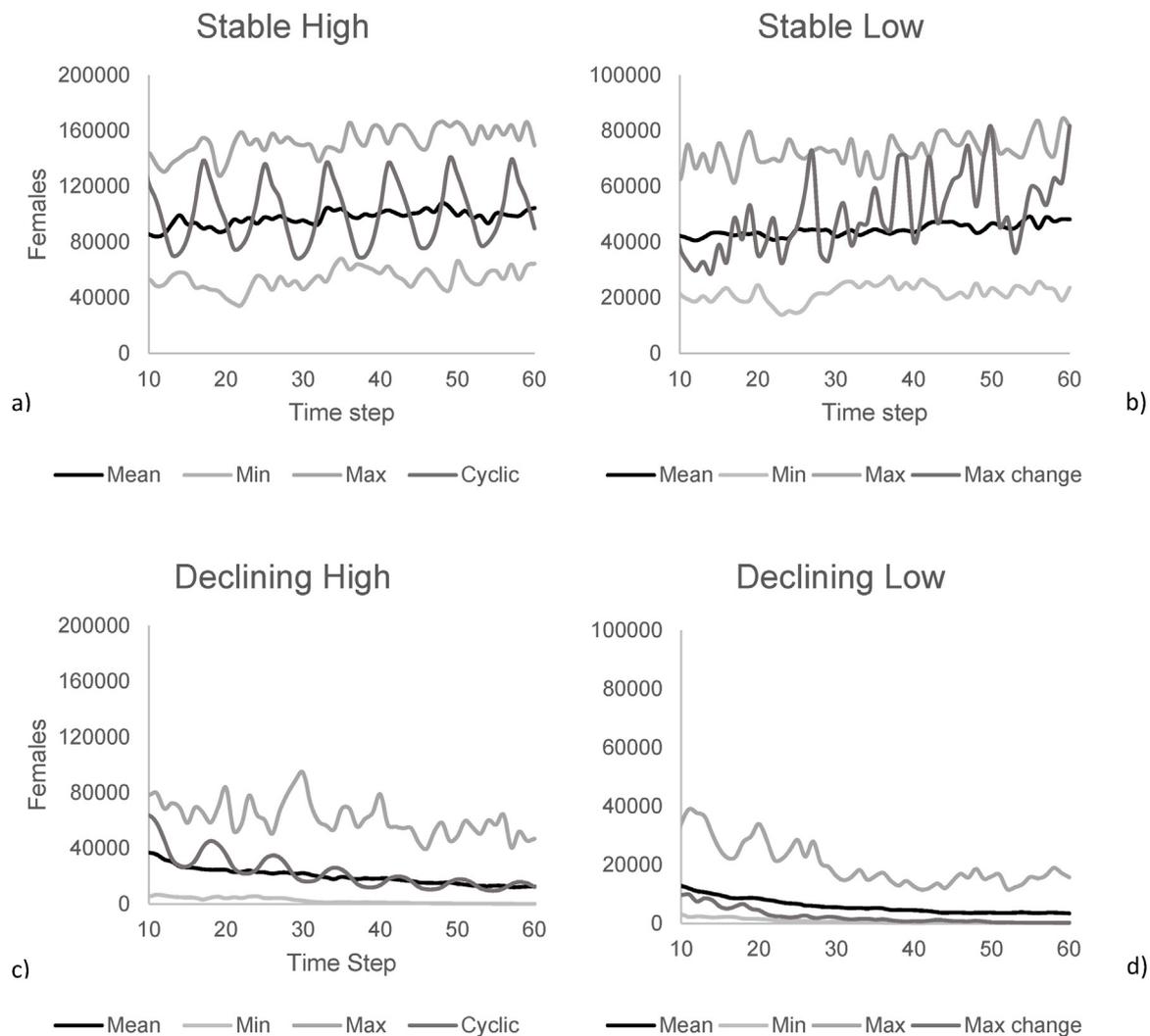
Adults returned to their previous nesting area and attempted to re-nest within a 2-km radius of their previous nest site. Yearlings returned to their natal nest, and the majority (82%) explored a 5-km radius to select a nest site. The remaining ~18% embarked on a longer dispersal (5–12 km, drawn from a uniform distribution) from their natal nest before selecting a nest, approximating sage-grouse natal dispersal frequency and distance estimates from western Wyoming (Thompson, 2012).

## 2.4. Scenarios

To assess different scenarios of habitat use, we evaluated several population alternatives (see Table A2 in Appendix A): 1) We simulated stable population dynamics (using the above described parameters) wherein the population fluctuated about a historical mean; 2) In a declining population scenario, an additional survival penalty was applied such that the population decreased through time with an average growth rate ( $\lambda$ ) of approximately 0.97 (0.63–1.04, Edmunds et al., *In Prep.*; Manier et al., 2013; WAFWA, 2008) over 60 years; 3) We compared habitat use among high and low starting population sizes; 4) We also implemented predictable population fluctuations to visually assess a common range of cyclical variation against stochastic variation in demographic rates (See Appendix A for details). Each scenario was run for 60 time steps and replicated 50 times (see Appendix A for details), with the exception of cyclic scenarios for which 10 replicates were conducted as population trajectories were deterministic. Population sizes and variability were recorded through time and summarized among replicates.

## 2.5. Verifying the range of population fluctuations

The input parameters resulted in simulated female grouse abundance fluctuating widely among years and replicates in all scenarios, with larger population size fluctuations in the Stable population scenarios (Fig. 3a) than in the Declining population scenarios (Fig. 3b). In Declining population scenarios, annual decreases (averaging 3%) reduced populations to less than a tenth of the initial number of individuals (on average) by time step 60 (Fig. 3c, d). Considerable random stochastic variation in population sizes was observed in both High and Low population scenarios, with variable



**Fig. 3.** Variability in Wyoming greater sage-grouse population size under alternative population scenarios a) Stable and Cyclic High populations b) Stable Low populations displaying the single replicate with the greatest change in overall population size c) Declining High and Cyclic population sizes d) Declining Low population showing the single replicate with the greatest overall (max) change in population size through time. Min and max lines represent the lowest and highest population sizes in each time step (respectively) across all replicates. Cyclic scenarios depict the mean of 10 replicates.

annual population growth rates and divergent overall trajectories among simulation replicates. See [Appendix A](#) for additional details.

## 2.6. Spatial analysis and outputs

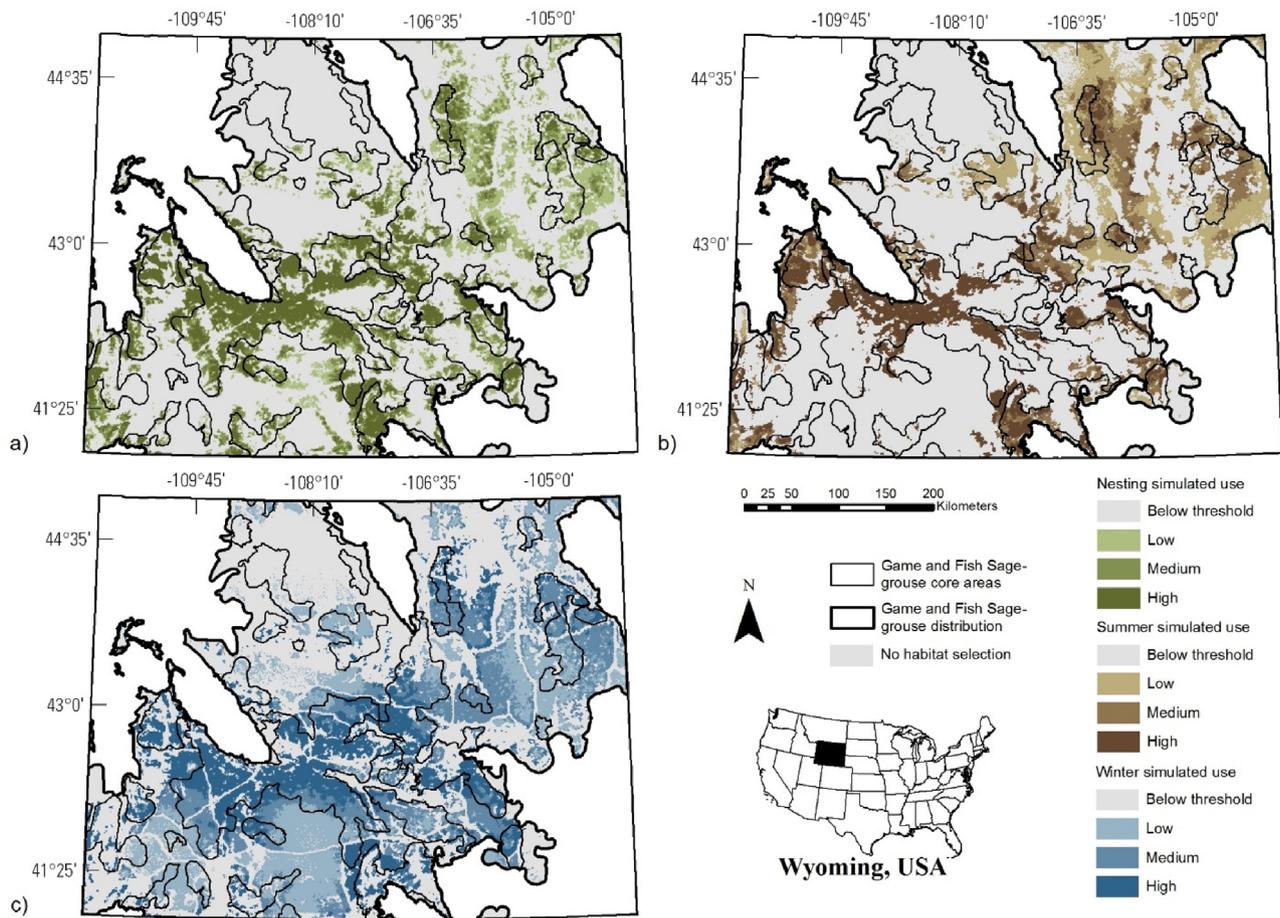
Individual locations (i.e., occupied 1-km pixels) were mapped during nesting, summer, and winter seasons. The cumulative use of each habitat pixel was summed over 60 years and averaged over 10 replicates to create maps of simulated habitat use (hereafter 'simulated use') for each season. These simulated use maps depicted areas where simulated grouse consistently occupied habitats, and were visualized by binning habitat use scores above identified habitat thresholds into low, medium and high quantiles. We then compared simulated use maps to RSF maps to highlight areas of agreement and disagreement among approaches. To facilitate comparisons with RSF maps of different scales, maps were standardized by dividing each pixel by the calculated mean pixel value of the map (excluding zero-valued pixels for occupancy maps and pixels below habitat thresholds for RSF maps; 12, 14, 8 for nesting, summer, and winter seasons, respectively). The RSF maps were subtracted from simulated use maps, and differences between maps were visualized by categorizing the data based on pixel deviations from the mean difference (up to  $\pm 2.5$  standard deviations). Lastly, to quantify the

proportion of simulated grouse occupying core areas through time, the number of grouse occupying each core were tallied and compared to the number outside cores using the 2014 and 2015 core areas maps ([Wyoming Executive Order No. 2015-4, 2015](#)).

## 3. Results

### 3.1. Habitat use in a large, dynamic, stable population

Habitat-population simulations run with a high starting population size and a stable population trajectory resulted in the majority of simulated grouse choosing habitats within protected core areas ([Fig. 4a–c](#)). We expected high occupancy of core areas during nesting as core habitats were designed to encompass habitat adjacent to leks. An average of 69% of birds nested and summered in core areas (excluding areas connecting cores and winter concentration areas which accounted for up to 1.5% and <1% of the population respectively) at the start of the scenario, and 58–59% at time step 60. The long-term simulated use of nesting habitat generally resembled the habitat predictions generated by the resource selection function ([Fig. 5a](#)), although there were notable differences. The nesting RSF map scores predicted some outlying and fragmented areas to have higher probabilities of sage-grouse occurrence than were observed



**Fig. 4.** Predicted simulated habitat use of greater sage-grouse in Wyoming during a) nesting, b) summer, and c) winter seasons in the stable high population scenario, displaying cumulative usage over 60 time steps, averaged over 10 replicates. Low, medium, and high values for each season were determined by binning landscape pixels at identified habitat thresholds into 3 quantiles. Areas that were below the minimum habitat threshold are shown in gray.

in simulations (Fig. 5a – purple). Conversely, simulated use indicated that accessible areas and centrally located habitats were used more often than indicated by habitat selection values (Fig. 5a – green).

Comparisons for summer and winter seasons yielded more notable differences (Fig. 5). Peripheral and isolated areas (e.g., summer habitat in Jackson Hole; Fig. 5b – purple) were used less than expected. Conversely, central, easily accessible areas, and edges near nesting sites with little proximate summer habitat were used more than indicated by habitat selection scores (Fig. 5b – green). Simulated winter habitat use was less than expected by habitat selection values primarily in the SW portion of the state (Fig. 5c – purple) and in the Bighorn basin (NW), where the state-wide habitat selection surface under-predicts known summer habitat. Few simulated grouse were nearby during summer and able to move into these winter areas. In these regions, the ability to predict habitat use, and occupancy of cores, was restricted due to input habitat (RSF model) limitations. Occupancy of cores during the winter was lower with more birds travelling to areas outside of protected areas (63% of simulated grouse occupied cores at the start of simulations, declining to 56% by time step 60).

### 3.2. Habitat use in a dynamic, declining population

When a smaller population was parameterized to exhibit a declining trend, the spatial pattern of simulated use changed and differences among RSF and simulated use intensified (e.g., Fig. 6). Lower population densities allowed a larger fraction of the simu-

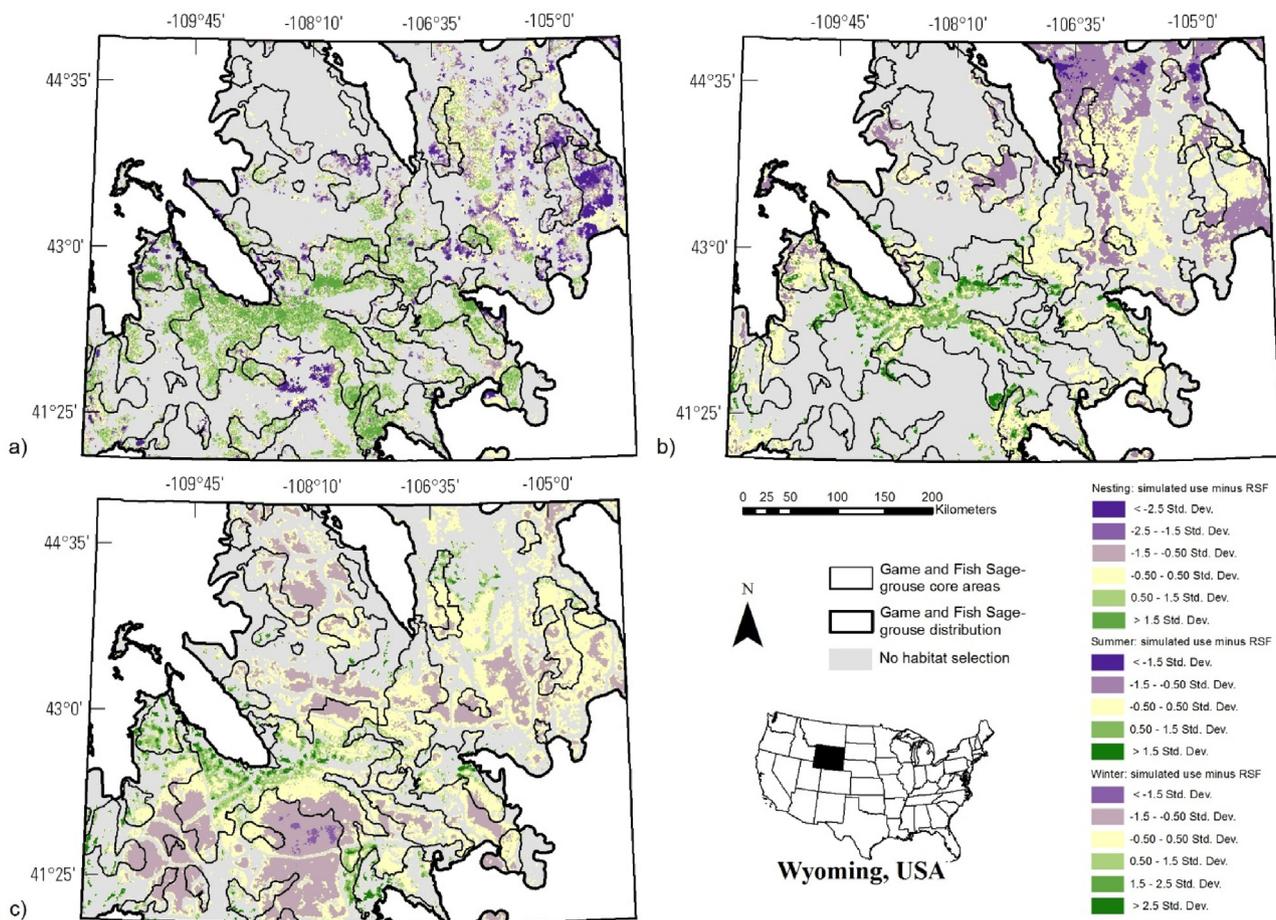
lated grouse to occupy habitat within protected areas, with 68% residing there during nesting and summer at the start of simulations, and increasing through time to 77% as the population dwindled in size. More birds were found in cores during the winter, with 62% of simulated grouse using core areas during winter at the start of simulations but 71% occurring within cores at the end of the simulations. Even during nesting, more distant and isolated areas outside of protected areas were used less through time than predicted by the RSF (Fig. 6).

In general, RSF and simulated use maps were most similar when nesting habitat was restricted to areas nearby leks and strong site fidelities returned most birds to familiar locations, and when the population size was stable. The two approaches were most dissimilar when populations were in decline and when simulated grouse had to move large distances to access summer and overwintering habitats.

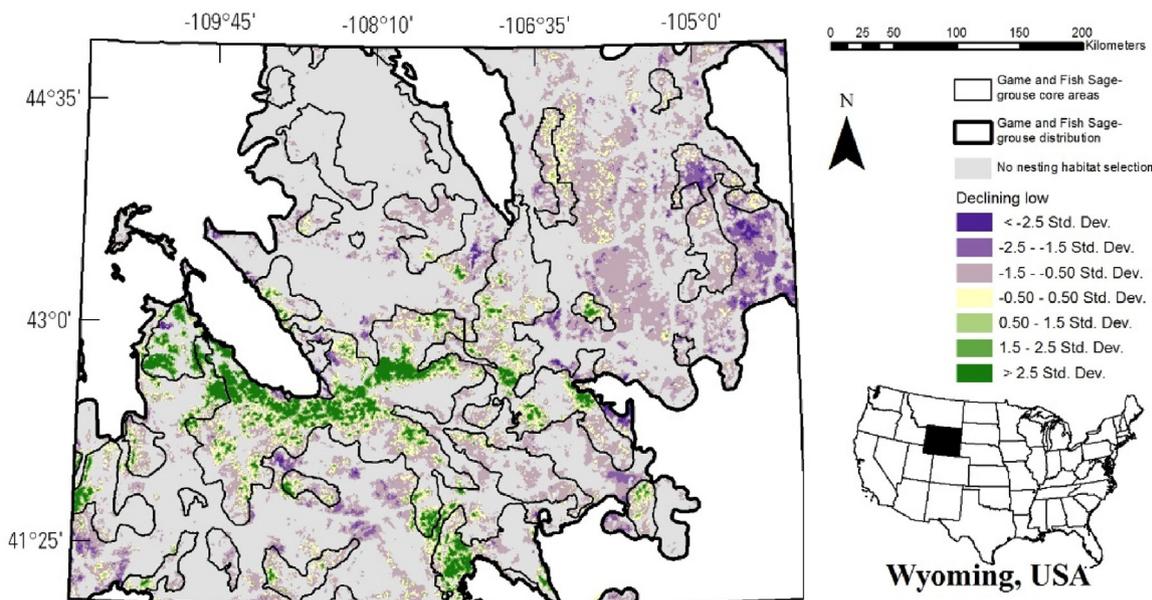
## 4. Discussion

### 4.1. Movement and habitat accessibility

Connectivity is an important element of functioning landscapes (Taylor et al., 1993) and in our analyses, geographic accessibility within and among seasonal habitats created differences between RSF and simulated use. Isolated areas (e.g., Jackson Hole, WY) and other peripherally located areas were not easily found by yearling dispersers as they lacked prior knowledge of the landscape, which reduced simulated use relative to selection values.



**Fig. 5.** Differences among habitat selection (RSF) and simulated greater sage-grouse habitat use maps for a) nesting, b) summer, and c) winter seasons in the Stable population scenario. Yellow indicates areas of little predicted difference between simulated use and habitat selection characterizations for sage-grouse in Wyoming. Green describes areas of greater simulated use than expected by habitat selection scores, and purple indicates simulated use less than expected by RSF scores. Differences among standardized RSF and simulated use maps were expressed as deviations from mean differences, with negative standard deviation values indicating areas where simulated use is less than the mean difference among maps.



**Fig. 6.** Differences among nesting habitat selection (RSF) and simulated greater sage-grouse habitat use maps for Declining Low scenario. Yellow indicates areas of little predicted difference between simulated use and habitat selection characterizations for sage-grouse in Wyoming. Green describes areas of greater simulated use than expected by habitat selection scores, and purple indicates simulated use less than expected by RSF scores. Differences among standardized RSF and simulated use maps were expressed as deviations from mean differences, with negative standard deviation values indicating areas where simulated use is less than the mean difference among maps.

Conversely, central or easy to find habitats received more use relative to their selection values. This may result in part from simulated grouse selecting habitat within more realistically constrained distances. These distances reflected empirical propensities or limitations of movement from their previous location (i.e., lognormal decay of movement distances as is common in many species; Fedya et al., 2012), rather than assuming that all individuals are able to access areas within the maximal inter-seasonal movement distances, as used in this case to constrain availability points in the RSF model. Although it is possible to simulate more complex movement, wherein individual or movement-types are represented by unique movement histories, we lacked data to account for within-individual patterns of movement through time. As this could be an additional source of difference among simulated and RSF predictions, future simulation approaches could investigate the impact of this generalization.

Seasonal interactions can also operate to influence dynamics at the individual and population levels, with locations used during one season influencing outcomes in the following season (Norris and Marra, 2007). Although inter-seasonal habitat selection patterns are captured to some degree in use locations, RSF extrapolations beyond known use areas often do not consider accessibility from individual prior locations (Thurfjell et al., 2014). In our simulation approach, seasonal habitat use depended on the distribution of birds in the previous season and their ability to access the next season's habitats. Hence, simulated grouse were more likely to use areas where resources for all seasons coincided or were easy to find (e.g., brood rearing habitat proximate to nesting habitat). Simulated birds were not always able to use some areas that were predicted to have high habitat selection values if successive seasonal habitats were not within plausible or common movement distances, or if the locations were difficult to find (not connected). Our simulations highlight the importance of connectivity of habitats across life stages (seasons), and could be used to identify areas of limited connectivity, where restoration could improve access to habitats for all life stages.

#### 4.2. Fluctuating population densities

Although some resource selection function approaches explicitly account for changes in population densities (e.g., using a time series of density data), many RSF approaches rely on the implicit clustering of 'use' locations to represent population density during data collection (Boyce et al., 2002; Hooten et al., 2013; McLoughlin et al., 2010). Previous studies have indicated that if animal densities are not explicitly modeled in RSFs, habitat predictions through space and time can lead to errors in prioritization of habitat resources under different population conditions (Boyce et al., 2016; McLoughlin et al., 2010). Our results support that the explicit consideration of time-varying population densities and responding habitat selection could lead to meaningful differences in habitats identified as important for conservation for some species.

The differences between RSF and simulated use (stable high population scenario) resulted in part from active density-dependent habitat selection in the simulation model (e.g., Fig. 5a). In simulations, animals were directed by RSF maps but their ultimate choice of location depended on population density and nearby habitat availability. In the declining low population size scenario, differences among RSF and simulated use predictions were magnified as the dwindling population occupied less of the landscape. Simulated grouse intensified their use of some components of the habitat (e.g., core areas; Fig. 6a), with more transient use of others (i.e., non-core). In stable and high population size conditions, habitats in and adjacent to high-density populations were used more than expected by their RSF scores. Fluctuating population sizes resulted in increased occupancy of proximate, lesser-used

habitat during times of high abundance (e.g., areas next to core areas). This suggests that areas with lower habitat selection can be important in sustaining the overflow of sage-grouse during times of periodic high density. Even sink habitats can be integral to stalling or avoiding population declines and extinction (Heinrichs et al., 2015). Our results emphasize the need to quantify the contributions of unprotected and lower RSF value areas to bolstering and connecting protected populations. In dynamic populations, the removal or degradation of lesser-used habitats could limit long-term population growth and stability, particularly if they also connect higher quality or seasonal habitats. Habitat prioritizations for dynamic populations should consider protecting not only highly-used and high quality habitats, but also the proximate lesser-used and lower quality connecting habitats.

#### 4.3. Habitat prioritization implications

In comparing predicted habitat use between RSF and simulated long-term occupancy maps, we assessed the degree to which the inclusion of biological realism can yield alternative conservation conclusions. Not surprisingly, our results indicated that approaches to prioritizing habitat that implicitly versus explicitly consider movement, connectivity, and population fluctuations and trends, can produce different characterizations of important long-term habitat. Our case study results indicate that species with dramatically fluctuating populations, declining population trends, and complex seasonal movements, are likely to benefit from analyses that extend RSF predictions to capture dynamic population and movement processes. Yet species with stable population sizes and distributions, and highly mobile animals with fewer movement constraints, may not require these efforts and equivalent habitat prioritizations may result from RSF-based analyses. The magnitude of differences among RSF and simulated habitat use predictions is expected to be influenced primarily by the type of species and system, but also by the types and structures of models being compared. The degree to which the explicit consideration of population dynamics, movement limitations, and habitat accessibility influence results is likely to depend on the magnitude and timing of population fluctuations and the functional connectivity and movement ability of animals. The types of RSFs and individual-based models, including input data and model structures also influence habitat prioritization comparisons. For example, movement routines in the individual-based model provide distance-based movement constraints that preclude access to some areas deemed suitable by the RSF. However, movement routines are often generalized representations of the wide range of complex movements observed among individuals of a population. Hence, the degree of realism in movement routines is also likely to influence RSF-simulated habitat use comparisons. Future research could evaluate how habitat prioritizations change as a result of even greater biological realism, as well as evaluate the most important factors driving the need for biologically nuanced assessments of important habitats.

#### 4.4. Simulation approach

Spatially explicit individual-based models, as used here, provide a means of explicitly linking habitat with individual and population outcomes, and can aid in evaluating priority or protected areas (e.g., contributions of non-core areas for sage-grouse). In the absence of new data to update or improve RSF models through time, simulation approaches can be helpful in gauging the degree to which habitat prioritizations could change under different population and habitat scenarios. In doing so, simulation could also inform the future need for intensive habitat and occurrence data collection to update RSF models.

Although simulation modeling approaches can add biological realism, their strengths lie in relative rather than absolute predictions. Ideally, our results and this general concept would be validated in future studies with rigorous historical data. Even though many systems (including our case study) lack validation data, future studies with such data could aid in more broadly evaluating the species, systems, and conditions under which biologically-augmented simulations substantively augment RSF habitat prioritizations. Although beyond the scope of this analysis, future research could also use spatially explicit individual-based models to predict the population consequences of changes in the future habitat suitability, connectivity, and demography of climate-sensitive species (e.g., pika; Galbreath et al., 2009). Analyses that combine and explore alternative climate, habitat, and demographic scenarios may be helpful in prioritizing habitats for both contemporary and future conditions.

Habitat prioritizations for sage-grouse in Wyoming can be strengthened by the addition of male-specific habitat needs and spatially varying demographic rates (e.g., Aldridge and Boyce, 2007). Future simulation models could also make use of sex-specific site fidelities in summer and winter habitats, and learned behaviors that result in the occupancy of areas that are difficult to find and access. Although fine-scale predictions may be possible with the integration of spatially stratified or spatially explicit demographic rates (e.g., Kirol et al., 2015; Schumaker et al., 2014) and use of region-specific habitat selection layers (i.e., Northeast, Central, Southwest; Fedy et al., 2014), our predictions are best interpreted regionally (i.e., planning area or field office units) rather than locally (i.e., pixel by pixel). The comparison of RSF and simulated use predictions also illustrates the ability of the simulation model to compensate for RSF over-predictions in habitat, but the inability to compensate for RSF under-predictions in habitat. In the summer (Fig. 5b), simulated grouse used the Northeast portion of the state less than expected by habitat selection values, corresponding with the noted observation that the habitat selection models somewhat over-predict the amount of habitat in this region (Fedy et al., 2014). Conversely, simulated winter habitat use was less than expected by lek count data in some SW portion of the state, resulting from challenges in data availability and predictive power of the winter RSF map (Fedy et al., 2014).

#### 4.5. Summary and conclusions

Results from habitat selection models have formed the foundation of many species conservation actions, and will continue to provide a valuable tool for characterizing habitat needs for species of conservation concern. Yet data restrictions and nuances in RSF model construction can limit management inferences, particularly in changing environments and fluctuating populations (Brost et al., 2015; McLoughlin et al., 2010; Rubin et al., 2002). We developed a simulation analog of a biologically-augmented RSF that takes advantage of traditional RSFs, but with added population dynamics and movement mechanisms that RSFs are often unable to directly incorporate (Thurjell et al., 2014). Our results indicate that RSF-based habitat prioritizations for fluctuating, non-equilibrium populations (e.g., declining or increasing; Boyce et al., 2016), those with spatially and temporally differing habitat needs (as for sage-grouse), or influenced by lag effects of past population or landscape changes (Morris, 1999), may not fully indicate the degree to which habitats are consistently important to wildlife. This case study analysis also echoes the conclusions of other studies, and indicates that in similar systems, protecting habitats purely on the basis of a snapshot of habitat selection may be misleading (Osborne and Seddon, 2012; Van Horne, 1983) for dynamic species like sage-grouse. In these circumstances, the use of more biologically-informed RSF approaches and/or the use of

RSF-based simulation modeling may help in producing more realistic and longer-term habitat prioritizations. Explicitly considering the influences of movement propensities, habitat accessibility, and population dynamics on habitat use may be particularly valuable in identifying important habitats for sage-grouse conservation, refining best management practices, and predicting animal responses to future development and habitat change.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2017.05.017>.

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