Ecological Modelling 359 (2017) 449–459

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

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

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ARTICLE INFO

Article history:
Received 9 February 2017
Received in revised form 16 May 2017
Accepted 17 May 2017
Available online 26 June 2017

Keywords:
Greater sage-grouse
Habitat prioritization
Habitat selection model
Individual-based model
Protected areas
Resource selection function

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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http://dx.doi.org/10.1016/j.ecolmodel.2017.05.017
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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 selection 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

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