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Geographic variation in fitness and foraging habitat quality in an endangered bird

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ABSTRACT

Models are important tools for conservation, but the usefulness of any given model for decision-making depends on its accuracy and precision. Few models designed for conservation purposes are validated with real-world data, and such models are even less likely to be revisited and improved with post-implementation results. We test the performance of a model frequently used and heavily relied-upon for the management of the endangered red-cockaded woodpecker (*Picoides borealis*). The RCW Foraging Matrix Application incorporates spatially-explicit forest stand data and woodpecker territory locations to produce quantitative assessments of foraging habitat quality. Model parameters were based on expert opinion and research performed on several key populations at a time when range-wide habitat quality was relatively poor. Since the model's inception, many red-cockaded woodpecker populations have been monitored intensely in restored habitat, providing an opportunity to evaluate model performance range-wide. We assessed the relationship of habitat quality, as measured by the RCW Matrix Application, to group size and fledgling production from populations across the species range in the southeastern United States. We also evaluated foraging habitat quality directly by relating woodpecker fitness components to foraging habitat metrics through regression tree analyses. Results showed that some, but not all, of the habitat metrics included in the RCW Matrix Application were consistently related to fitness components range-wide, but threshold values for these habitat metrics identified by regression tree analyses were site-specific rather than universal. Our findings indicate opportunities for improving on "one-size-fits-all" range-wide models with analyses of additional locally-relevant foraging habitat metrics.

1. Introduction

Models are important tools for endangered species management and conservation (Beissinger et al., 2006). Models can also allow conservationists and managers to explore the consequences of understandings of biological systems. Examples include the use of population viability analysis to assess species vulnerability to extinction (Brook et al., 2000), bioclimatic niche models to predict range shifts under future climate change (Carroll, 2010), and spatially-explicit habitat models to evaluate population responses to changes in landscape conditions or management policies (Liu et al., 1995; McFarland et al., 2012). As increases in computing power continue to improve model realism, there will likely be increased reliance on models for policy and decision-making.

The usefulness of any particular model for decision-making depends on its accuracy and precision, and on the needs of conservationists. Ecological models are, by definition, simplified representations of natural systems, and most rely on field data for both parameterization and validation. However, few models built for conservation purposes are ever validated with real-world data (Collier et al., 2012; McCarthy et al., 2000; O'Connor and Wagner, 2004; Schiegg et al., 2005). Even rarer are cases in which such models are revisited and improved with real-world data (Mitchell et al., 2001; Schiegg et al., 2005). Yet, unrealistic models derived from limited data can lead to unreliable estimates and poor management decisions (Beissinger and Westphal, 1998).

Model validation involves comparing model predictions to actual population performance, which can be conducted in several ways. One method for assessing how well a model generalizes across time is to develop a model based on a particular population and then test predictions with that same population's performance

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during a different time period (Brook et al., 2000). A model's ability to generalize across space can be evaluated by parameterizing a model with data from one region and testing how well the model predicts conditions in another region (Carroll et al., 1999; McCarthy et al., 2000; Schiegg et al., 2005). Finally, certain types of models may only be amenable to having secondary model predictions validated with field data (McCarthy et al., 2001).

The red-cockaded woodpecker (*Picoides borealis*) is an endangered species that has received considerable conservation investment, including the development of ecological and conservation-oriented models to facilitate management decision-making. We here test the performance of a model frequently used to assess red-cockaded woodpecker foraging habitat quality. In doing so, we incorporate aspects of model validation described above, including a comparison of model predictions and observed outcomes, a comparison between time periods, and an assessment of model performance across space involving multiple populations. We additionally evaluate how the model might be improved through localized assessments of fitness components (group size and fledgling production) and variation in foraging habitat quality.

1.1. Red-cockaded woodpeckers

The red-cockaded woodpecker is an endangered species endemic to the pine forests of the southeastern United States. Once perhaps the most common woodpecker in the region, today less than 1% of the bird's pre-colonial population size is thought to remain (Conner et al., 2001). Though widely scattered and highly fragmented, remnant populations occur throughout most of the species' historic range (Fig. 1). Three major factors contributed to drastic population declines over the past 500 years. First, loss of habitat through intense logging and land conversion reduced the species' preferred longleaf pine (*Pinus palustris*) forest habitat to only 3% of its original extent (Frost, 1993). Second, loss of old pines contributed further to habitat degradation, as red-cockaded woodpeckers are cooperative breeders that excavate roosting and nesting sites in live mature pines (Jackson et al., 1979). The abundance of such cavities has been shown to be a driver of population processes (Walters et al., 1992). Third, fire suppression across the region allowed the development of dense hardwood midstories that shaded out the diverse ground cover that historically characterized these pine systems (Peet and Allard, 1993), reducing foraging habitat quality.

Increased understanding of red-cockaded woodpecker ecology, greater emphasis on prescribed fire, and development of new management strategies such as construction of artificial nest and roost cavities have helped populations to increase (Walters, 1991; Walters et al., 1992). Further studies in certain restored habitats indicated the impact of foraging habitat quality on productivity. Larger group sizes, which generally indicated higher-quality territories (Conner et al., 2001), and greater fledging production, were related to habitat features that included greater herbaceous groundcover, higher densities of large pines, and a reduced hardwood midstory (Hardesty et al., 1997; James et al., 1997, 2001; Walters et al., 2002). These findings were used to develop a new Red-Cockaded Woodpecker Recovery Plan (USFWS, 2003) that included two sets of guidelines for managing foraging habitat: the recovery standard and the standard for managed stability. The recovery standard was recommended for use by federal agencies and state properties to facilitate recovery and increase population sizes. The standard for managed stability, on the other hand, was not designed to increase population size, but to be used when landowners could not manage to the recovery standard. Standards were based on pine and hardwood tree size and density, and extent and composition of ground cover (USFWS, 2003).

In 2004, the U.S. Fish and Wildlife Service (USFWS), in collaboration with Environmental Systems Research Institute, Inc. (Redlands, CA), Fort Bragg, and the U.S. Army Environmental Center, developed the RCW Foraging Matrix Application to evaluate conditions based on the foraging habitat criteria in the Recovery Plan to produce habitat quality scores (later updated by Intergraph Corporation). Based on the Recovery Plan's criteria for good-quality foraging habitat, and expert opinion used to weight foraging habitat metrics, the RCW Matrix Application incorporates spatially-explicit forest stand data and territory locations to produce quantitative assessments of stand-level and territory-level foraging habitat quality (Tables A1, A2 – Appendix A). These evaluations can be used to assess the impacts of projects that may cause the loss

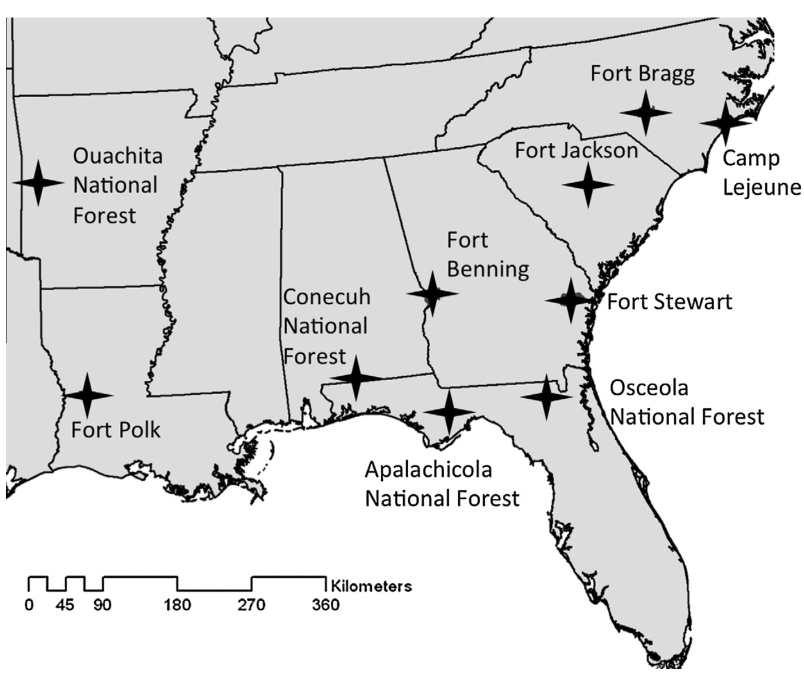

Fig. 1. Sampling locations for an analysis of fitness and foraging habitat quality in the red-cockaded woodpecker.