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Elucidating spatially explicit behavioral landscapes in the Willow Flycatcher

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ABSTRACT

Animal resource selection is a complex, hierarchical decision-making process, yet resource selection studies often focus on the presence and absence of an animal rather than the animal's behavior at resource use locations. In this study, we investigate foraging and vocalization resource selection in a population of Willow Flycatchers, *Empidonax traillii adastus*, using Bayesian spatial generalized linear models. These models produce "behavioral landscapes" in which space use and resource selection is linked through behavior. Radio telemetry locations were collected from 35 adult Willow Flycatchers ($n = 14$ males, $n = 13$ females, and $n = 8$ unknown sex) over the 2003 and 2004 breeding seasons at Fish Creek, Utah. Results from the 2-stage modeling approach showed that habitat type, perch position, and distance from the arithmetic mean of the home range (in males) or nest site (in females) were important factors influencing foraging and vocalization resource selection. Parameter estimates from the individual-level models indicated high intraspecific variation in the use of the various habitat types and perch heights for foraging and vocalization. On the population level, Willow Flycatchers selected riparian habitat over other habitat types for vocalizing but used multiple habitat types for foraging including mountain shrub, young riparian, and upland forest. Mapping of observed and predicted foraging and vocalization resource selection indicated that the behavior often occurred in disparate areas of the home range. This suggests that multiple core areas may exist in the home ranges of individual flycatchers, and demonstrates that the behavioral landscape modeling approach can be applied to identify spatially and behaviorally distinct core areas. The behavioral landscape approach is applicable to a wide range of animal taxa and can be used to improve our understanding of the spatial context of behavior and resource selection.

1. Introduction

A paramount objective of ecology is to understand not only where organisms exist but also to understand why (Krebs, 1978). Space use and resource selection studies are the experimental designs typically invoked to investigate where and why, respectively, an organism exists at a particular moment in time although they are often treated as mutually exclusive research endeavors. In many space use studies estimating the home range, the area an organism uses to fulfill its breeding, foraging, and survival needs (Burt, 1943), is the primary goal. When an animal's daily activity is largely restricted to its home range, we may infer that the home range contains the majority of resources required by an animal for breeding and survival. Hence, the home range serves as the natural spatial boundary within which to examine resource selection although this is rarely if ever done (Marzluff et al., 2004). Unfortunately, despite increasingly sophisticated technology available to study animal resource selection and space use, we remain largely ignorant about the motivations of animals when selecting resources. Inference based on studies of resource selection and space use would greatly improve if resource selection incorporated behavior rather than mere presence (Lima and Zollner, 1996; Marzluff et al., 2001).

Within the home range space use is non-random, and animals typically show a tendency to use certain parts of their home ranges more frequently than other parts (Hayne, 1949). The disparate use of parts of the home range reflects the spatially segregated nature of the resources important to an organism. Areas of intensive use within the home range are known as core areas. Most space use studies focus on delineating a single core area within an individual's home range (Laver and Kelly, 2008) although multiple core areas may exist. If so, across these multiple core areas resource selection may vary as a function of differential behavior indicating that particular core areas are used for unique behavior (e.g. Marzluff et al., 2001; Indermaur et al., 2009).

Resource selection is a complex, hierarchical decision-making process. Most studies of resource selection compare landscape and

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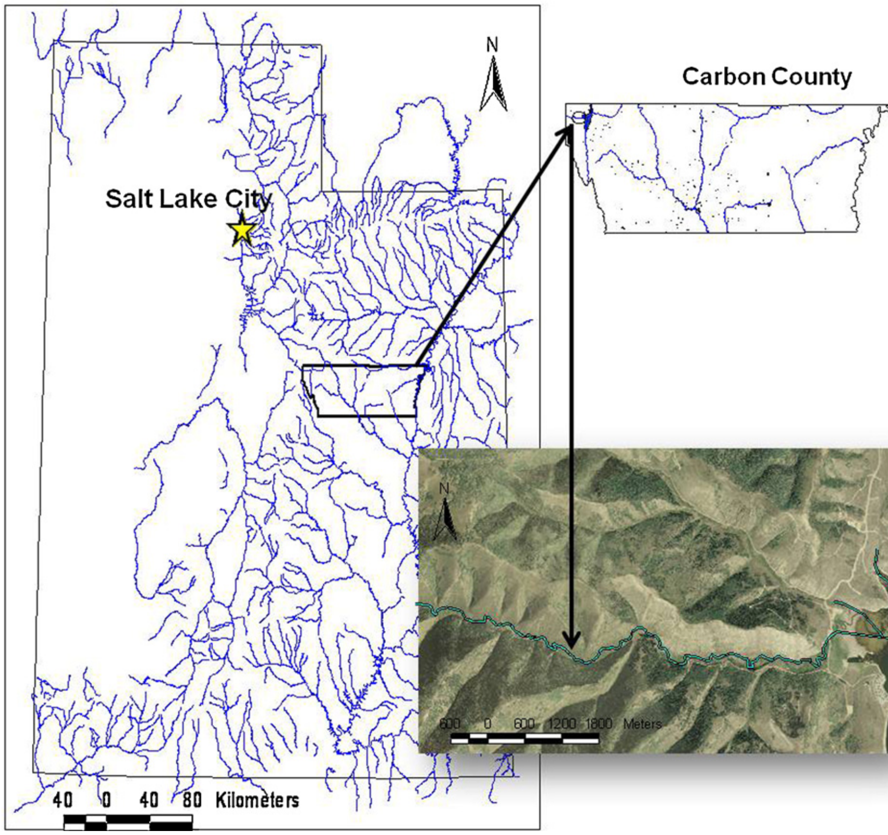

Fig. 1. Geographical location of the Fish Creek drainage in Carbon County, Utah.

habitat attributes at used locations with attributes at either available or unused locations using popular resource selection function (RSF) modeling approaches such as categorical analysis (Neu et al., 1974), discrete choice models (Cooper and Millspaugh, 1999, 2001), compositional analysis (Aebischer et al., 1993), or logistic regression (Manly et al., 2002). Utilization distribution approaches that measure intensity of space use by behavior have been recommended as a method for conducting behaviorally specific analysis of resource selection (Marzluff et al., 2004; Millspaugh et al., 2006). In this study, we advance this idea and demonstrate how resource selection can be analyzed as a behaviorally and spatially explicit hierarchical process by formulating behavioral resource selection functions with random effects. This approach produces a "behavioral landscape" which we define as a spatially explicit and probabilistically based description or prediction of an animal's behavior within a specified area given a set of environmental or resource variables.

Our models are set in a Bayesian framework to investigate and predict vocalization and foraging behavior in a small passerine bird, the Willow Flycatcher, at individual (home range level) and population-levels. We chose to set our multi-level behavioral RSFs in a Bayesian framework for a number of reasons. First, hierarchical relationships are easily specified in Bayesian models (Wikle, 2003) and given the hierarchical nature of resource selection, the Bayesian framework naturally lends itself to modeling RSFs. Second, as all unknown parameters are treated as random, Bayesian procedures provide a straightforward way to include random effects in generalized linear models (Zeger and Karim, 1991). For example, factors which could be treated as random in an RSF include individual-level information (characteristics of the individual animal such as sex or age-class, or the repeated sampling of observations from a single individual), population-level information (the selection of individuals from a larger population), and site-level information (characteristics of study sites such as annual rain fall or elevation or the selection of a subset of study sites from a larger group of study sites). Third, Bayesian inference is based on interval estimation and not on large-sample theory, and Bayesian inference is less sensitive to the influence of sample sizes than are frequentist significance tests (Ellison, 1996).

The Willow Flycatcher, *Empidonax traillii*, is a small, neotropical migrant that selects riparian habitats for breeding throughout the continental United States. They are territorial and central place foragers (Orians and Pearson, 1979; Stephens and Krebs, 1986). Male flycatchers sing and defend territories from tall perches (McCabe, 1991), and the majority of research on the Willow Flycatcher has focused on male flycatchers due to their easier detectability. An animal's sex can influence its resource selection patterns if, for a specific behavior, the resource requirements associated with that behavior vary as a function of sex during the breeding season. Growing evidence suggests that this is the case for the Willow Flycatcher. For example, during the breeding season, male flycatchers spend the majority of their time singing and defending territories while female flycatchers select nest sites, build nests, and incubate eggs (Sedgwick, 2000; Sogge, 2000). Male and female flycatchers have also been found to differ in their daily patterns of food intake and energy expenditure (Owen et al., 2005) and in the composition of their diets (Drost et al., 2003). Hence, consideration of both sexes is required in a Willow Flycatcher resource selection study aimed at deriving valid population-level inference. Further, Willow Flycatchers are a riparian-habitat obligated species (Sedgwick, 2000), yet circumstantial evidence exists to suggest that they may rely on a diversity of habitat types to meet their resource needs during the breeding season. The degree to which Willow Flycatchers use non-riparian habitats during the breeding season remains largely unknown. By measuring resource selection as a function of specific behavior, we hope to gain an