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Contrasting measures of fitness to classify habitat quality for the black-throated sparrow (*Amphispiza bilineata*)

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ABSTRACT

Habitat quality is an important consideration when identifying source and sink habitat and setting priority areas for avian conservation. The problem is that different measures may lead to different conclusions about habitat quality, and may also vary in the resources required to estimate them. Individual level measures, such as nest success, and fecundity, will often identify different high quality habitats than population level measures, such as abundance or the number of fledglings produced per unit area. We tested measures of fitness in the Black-throated Sparrow both at the individual and at the population level for six habitats in the northern Chihuahuan Desert, to explore their value as indicators of habitat quality. We compared clutch size, number of nestlings per nest, number of fledglings per successful nest, nest density, nest success, daily nest survival rate, season-long fecundity, number of fledglings produced per 100 ha, and adult abundance, in each habitat type. We also modeled source–sink dynamics to estimate the scale at which they operate, to infer survival rates, and to ascertain the relative source potential of each habitat. We found that fecundity is the best indicator of individual level habitat quality but a poor indicator of population level habitat quality. Nest success (or fecundity, if resources are available to adequately estimate it) plus nest density provide the most robust indicator of population level habitat quality, which is the level at which priority habitats for conservation should be identified. Mesa grassland and black grama grassland functioned as source habitats most consistently, and mesquite was consistently a sink but also probably a reservoir of individuals available to occupy other habitats.

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1. Introduction

Habitat quality is an important factor in avian population dynamics (Simons et al., 2000) and a crucial consideration when setting conservation priorities (MacNally and Horrocks, 2000). The problem is that the best breeding habitat for a given pair of nesting birds may not be the same as the most important breeding habitat for an entire population. For example, in two habitats where clutch size and nesting success are similar, habitat quality at the individual breeding pair level (hereafter referred to as the individual level) is similar. However, if one of these two habitats has a much higher nest density than the other, then it will produce a greater number of next year's breeding individuals, and it may be of higher importance for the population as a whole. Thus different demographic parameters are useful for answering different questions about habitat quality. The question for conservation is to disentangle the relationship among different

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methods, and to identify the most robust and cost effective parameters for answering a given question.

Conservationists are faced with tradeoffs in measuring the value of habitat for a population in a given ecosystem, given finite resources. Tradeoffs include, for example, decisions to conduct in-depth analyses in one habitat versus less detailed surveys in multiple habitats, gathering data that is geographically narrow but long-term, or the reverse. Tradeoffs also occur in deciding how to measure breeding habitat quality. The classic example for this is Van Horne's, 1983 revelation that abundance and reproductive success are not necessarily correlated. High abundance of adult birds in a given habitat may suggest that it is of high quality, but low nest success may indicate otherwise. Empirical measures used to assess differences in habitat quality abound in the literature, including relative abundance (Holmes and Sherry, 2001), density (Maurer, 1986), morphometric attributes (e.g., tarsus length, body weight, Dias et al., 1994), movement data (Winker et al., 1995), concentrations of corticosterone (Marra and Holberton, 1998), and nesting phenology (Fretwell, 1970).

Early measures of fitness centered on clutch size (e.g., Lack, 1954). Studies conducted over long time spans have measured annual production of fledglings (Hötker, 1989; Orians and Beletsky, 1989), together with adult survival (Hochachka et al., 1989) to estimate lifetime reproductive success. More recent measures and models have used nest success (i.e., the probability that a nest will produce at least one fledgling) or daily survival rate of the nest as measures of habitat quality (e.g., Donovan et al., 1995, Moorman et al., 2002; Shochat et al., 2005). When nest success is high, a habitat patch or type that is saturated is assumed to support a source population for the broader regional population (Pulliam, 1988). While in many cases adult density is a reliable indicator of habitat quality (Bock and Jones, 2004), unless the relationship between density and reproductive success is known for a set of habitats, the best assessment of habitat quality includes some measures of fitness that predict the reproductive success of individuals in one habitat relative to other habitats (Van Horne, 1983; Vickery et al., 1992).

However, using nest success alone as an indicator of source populations may not reveal the true value of a habitat patch for a given breeding pair in cases of low numbers of fledglings per nest, poor juvenile survival (McCoy et al., 1999) or low rates of renesting. A fitness measure that incorporates several components of breeding season performance, such as season-long fecundity (i.e. the number of female nestlings produced per female over the entire season; Ricklefs, 1973; Donovan et al., 1995) is well suited to assess habitat quality at the individual level, but may not capture population level habitat quality. Assessing the relative value of habitats for maintaining the population of a region requires information about the success of breeding pairs as well as the density of reproductive effort (i.e. density of nests or density of fledglings per unit area). By incorporating season-long fecundity, along with adult and juvenile survival, it is possible to calculate the finite rate of population increase, lambda (λ; McCoy et al., 1999). Estimates of λ for different habitats in a landscape can reveal source–sink dynamics. Both source potential and regional importance of a habitat type are consequential considerations for conservationists.

Evidence from field studies suggests many avian species in North America exhibit source–sink dynamics (Pulliam, 1988; Dias, 1996; Graves, 1997; Purcell and Verner, 1998; Murphy, 2001; Perkins et al., 2003). Where populations are structured as sources and sinks, the population dynamics may operate at different spatial scales in different regions depending on the pattern and size of suitable habitat patches. For example, the northern forests of the Great Lakes states may act as a source population for forest species nesting in the agriculturally fragmented areas of southern Minnesota, Wisconsin, and Michigan and northern Illinois and Indiana (Temple and Cary, 1988; Brawn and Robinson, 1996). A similar scale of source–sink dynamics is evident in the case of the Black-throated Blue Warbler (*Dendroica caerulescens*) for which high relative abundance and a greater proportion of older males occur in probable source habitat along the axis of the Appalachian Mountains than in probable sink habitat in peripheral areas (Graves, 1997). On the other hand, the Kirtland's Warbler (*Dendroica kirtlandii*) may exhibit source–sink dynamics on the much narrower geographic scale of a few hundred km^2 (Probst et al., 2003), due to its ecosystem specificity. Finally, it is possible that source–sink dynamics may also operate at different spatial scales in different years, if resource density or environmental conditions fluctuate among years. Understanding the scale at which source–sink dynamics operate is important for conservationists for two reasons. First and foremost, attempts to sustain bird populations in sink habitats are futile unless source populations are protected as well. The second reason is that it is possible to infer hard-to-measure demographic attributes, such as survival rates, when the scale at which population dynamics operate is known.

The goal of this study was to contrast different measures of habitat quality, both at the individual and at the population level, and examine the scale of source–sink dynamics. Our model species, the Black-throated Sparrow (*Amphispiza bilineata*), exhibits source–sink dynamics in the northern Chihuahuan Desert (Pidgeon et al., 2003), and nests in a range of desert habitat types. Our objectives were: (1) to compare and contrast different measures of fitness and key habitat elements as indicators of habitat quality; and (2) model population dynamics among habitats in order to estimate the scale of source–sink dynamics and understand the relative value of each habitat to the overall population.

2. Methods

2.1. Study area

We conducted our study on the McGregor Range of Fort Bliss Military Reserve, a 2825 km^2 landscape in the northern Chihuahuan Desert of New Mexico. The study area encompasses three major ecosystems: shrubland, grassland, and woodland. Black-throated Sparrows nest in six major habitats found in the shrubland and grassland ecosystems, spanning an elevation range from 1200 to 1800 m (above sea level), but do not nest in woodland. These six major habitats are named according to the dominant plant species. *Mesquite habitat*, which covers about 60,817 ha (Pidgeon et al., 2003), occurs at the lowest elevation and is dominated by multistemmed mesquite (*Prosopis glandulosa*) plants growing in