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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 suc-

cess 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 (Hötter, 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 re-nesting. 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, λ (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 km² (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 km² 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 multi-stemmed mesquite (*Prosopis glandulosa*) plants growing in

dune formation on sandy soils, with a density of 2 plants/100 m². Mesquite plants average 7 m × 5 m × 2 m tall, and can attain sizes of 20 m × 10 m × 3.5 m tall. Sparse interdunal vegetation consists of forbs (0.5%), grasses (2.6%), bare ground (75%), small shrubs, cholla (*Opuntia* sp.) and soap tree yucca (*Yucca elata*). *Sandsage habitat* (*Artemisia filifolia*), occupying about 30,506 ha, also occurs at the lowest elevations on sandy soils. Sandsage is an approximately 1 m tall, thickly branched shrub, with a density of 16 plants/100 m². Ground cover of forbs (3.5%) and grasses (17%) is significantly higher than in mesquite habitat. *Creosotebush habitat* (*Larrea tridentata*), covering 53,251 ha, spans elevations of 1200–1600 m, and occurs at an average density of 26 plants/100 m², with occasional small groups of yucca or mesquite plants. Cactus is more prevalent in this habitat type than in the previous two, with an average of 38% ground cover. *Whitethorn habitat* (*Acacia neovernicosa*), with a plant density of 25/m², occurs between 1500 and 1700 m in foothills between the valley and mesa habitats, and in this study area encompasses many small arroyos, where rainwater is retained in sediments longer than in surrounding uplands (Atchley et al., 1999), and where shrub species diversity is high. This habitat type covers 16,978 ha. It intergrades with *black grama grassland habitat* (*Bouteloua eriopoda*), which occurs between 1500 and 1800 m and occupies about 12,841 ha. This habitat type is grassland with low shrub density (0.03/m²). At about 1800 m, *mesa grassland habitat*, dominated by blue grama (*B. gracilis*) and covering about 57,033 ha, occurs with other subdominant grasses. Cane cholla (*O. imbricata*), yucca (*Y. torrei*, *elata*, and *baccata*), and several shrubs (e.g., *Ephedra trifurca*, *Flourensia cernua*, *Koeberlinia spinosa*) are scattered throughout mesa grassland habitat. The four shrub dominated habitats differ in their avian communities by at least 30%, and differ from the grass-dominated habitat by at least 40% (Pidgeon et al., 2001). We sampled approximately 1.7% of the area encompassed by these six habitat types.

2.2. Study design

Within each of the six habitats we randomly placed six 108 ha plots (900 × 1200 m) and gridded them at the start of each season with uniquely coded flags every 50 m to facilitate locating of nests. Approximately 50 m of continuous habitat surrounded each plot. We used the interior 54 ha (600 × 900 m) of each plot for nest and habitat measurements, and the full 108 ha for abundance estimates. We measured the density of suitable nest shrubs and the average foliage height diversity (Mills et al., 1991) of each plot once during the study period.

We searched for and monitored nests from early April to mid-August in 1996–1998, except in whitethorn habitat, where plots were searched only in 1997 and 1998. Over this three year period we monitored 430 nests. Each year, observers received training in species detection and nest searching. Nest searching occurred between sunrise and 13:00 (daylight savings time), and included use of behavioral cues, random, and systematic search. In each habitat type three plots were randomly selected for intensive nest-searching efforts, involving 4–6 person/h, 2–3 times/week. Search schedules and maps were maintained to ensure that all sections of intensively searched plots received equal effort each week.

On other plots nest finding was incidental to other activities, and it is likely that at least some nests on these plots were not detected. All nests, on all plots, were monitored every 2–5 days until they either failed or young fledged. Black-throated Sparrows place their nests within 0.5 m of the ground, usually in or at the base of small isolated shrubs. This nest substrate is used consistently among habitats, and monitoring nests does not present logistical challenges. Therefore we believe that our ability to find nests was equal among habitats. Several non-terminal routes to each nest were used to limit depredation due to nest visits. Causes of nest failure were recorded in the field, when they could be determined.

For habitat-year combinations with >5 nests, we estimated average annual clutch size. For habitat-year combinations with at least 10 nests, we calculated nest success (i.e. the percentage of nests in which at least one fledgling is produced; Mayfield, 1975; Hensler and Nichols, 1981) and daily survival rate of nests in the program MICROMORT (Heisey and Fuller, 1985). Number of fledglings per nest, and number of fledglings per successful nest were calculated using data from all plots. Nest density, and fledgling density (the product of nest density and fledglings per successful nest) were calculated using data from the intensively searched plots, and were defined as nests or fledglings, respectively, per ha. We also calculated habitat-specific annual fecundity from the nests that successfully fledged young. We defined fecundity as the number of females produced per adult female (Ricklefs, 1973) and assumed that male and female offspring were produced in equal numbers. Based on this definition fecundity depends on (a) habitat-specific nesting success, (b) the number of fledglings per successful nest averaged over each habitat, (c) the number of re-nesting attempts, and (d) the number of broods produced by those birds that were successful in initial nesting attempts. Because we did not mark birds individually we made two assumptions when determining fecundity, based upon published information; that pairs made an average of 2.5 nesting attempts during the breeding season, and produced up to two broods each season (Johnson et al., 2002). We conservatively held nest success constant for all nesting attempts over the course of each season because without individually marked birds the degree to which nest success declines in this ecosystem is unknown, and the literature is mute on the question. Fledgling density was multiplied by the area of each habitat to estimate the number of fledglings produced annually in each habitat on McGregor Range. Finally, an annual estimate of adult relative abundance (males plus females) was calculated from the average of the highest two point counts of four or five 10 min counts on each 108 ha plot (12 count stations/plot, spaced 300 m apart) conducted between 1 May and 7 June 1996–1998 (Pidgeon et al., 2001).

2.3. Data analysis

2.3.1. Differences in measures of fitness among habitats

We tested for differences among habitats each year in the following measures of fitness for each habitat year combination to explore their value as indicators of habitat quality: 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 relative abundance (males plus females). To estimate season-long fecundity, we multiplied the number of females produced per successful nest (assuming a 1:1 sex ration) by the habitat-specific nest success rate to find the number of females produced in the first nesting attempt. We assumed all failed nesters made a second attempt, and that 1/2 of those failing in their second attempt made a third nesting attempt. We summed the female fledglings resulting from the two or three nesting attempts of each adult female.

We tested for differences among habitats each year in all of these measures using ANOVAs in a generalized linear model framework, with the protected least-squares differences (LSD) method. The level of significance was set at $\alpha = 0.05$. Difference among years was calculated with the same method. To understand the similarity of response of the fitness variables to each other and to key vegetation characteristics (nest shrub density and foliage height diversity, Pidgeon et al., 2001), we calculated Pearson correlation coefficients.

2.3.2. Population dynamics analysis

To ascertain the relative source potential of each habitat in our study area and the scale of source–sink dynamics for the Black-throated Sparrow in this part of its range, we conducted exploratory analyses of population dynamics within habitats using three approaches. In the first approach we examined the relationship between adult and juvenile survival rates and λ over the range of habitat-year-specific fecundity rates observed in our study. We found no published survival rates for Black-throated Sparrows. We surveyed the literature and found 28 studies reporting on 16 species of resident or short distance migrant Embizerid sparrows. Mean adult annual survival rates were between 0.35 and 0.66 (overall mean = 0.52; Karr et al., 1990; Arcese et al., 1992; Martin and Li, 1992; DeSante et al., 1995; Martin, 1995; Perkins and Vickery, 2001; Sandercock and Jaramillo, 2002). For our analysis we selected four adult survival rates, S_A (0.4, 0.5, 0.6, 0.7), that approximated this range. For each S_A we determined the corresponding juvenile survival rate, S_J , required to set $\lambda = 1$ over the range of fecundity levels observed in our six habitats. Our calculations of S_J were based on the following relationship, adapted from Ricklefs (1973):

$$S_J = 1 - S_A / (\text{fecundity}). \quad (1)$$

In the second approach to exploring population dynamics, we assumed that the Black-throated Sparrows within each habitat on McGregor Range constitute a closed population. While this assumption is almost assuredly false, as birds rarely stay in one habitat year round, it is of theoretical value as a way to estimate how differences in fecundity and survival rates among habitats contribute to population dynamics across the landscape. We calculated λ for each habitat in each pair of consecutive years using the discrete form of the exponential growth equation (Gotelli, 1995) as follows:

$$\lambda = N_{t+1} / N_t, \quad (2)$$

where N_t is the population size at year t . Incorporating annual estimates of adults per 100 ha in each habitat from a related study (Pidgeon et al., 2003), we rearranged the following equation:

$$N_{t+1} = (N_{A(t)} * S_A) + (N_{J(t)} * S_J) \quad (3)$$

and solved for the adult and juvenile survival rates that resulted in the observed λ values.

We conducted the analysis twice, first using a more relaxed assumption of juvenile survival, $S_J = 0.5 * S_A$, and second using a more conservative assumption, $S_J = 0.25 * S_A$. To determine a biologically realistic range of S_J for Black-throated Sparrows, we searched for empirical estimates of S_J for passerine species, and found three: A resident population of Song Sparrows (*Melospiza melodia*; Emberizidae) had an S_J of 0.36 (Arcese et al., 1992); The cavity nesting long distance migrant Collared Flycatcher (*Ficedula albicollis*; Tyrannidae), had an S_J of 0.15–0.28 (Doncaster et al., 1997), and a population of Swainson's Thrush (*Catharus ustulatus*; Turdidae) in California had an S_J of 0.25 (Gardali et al., 2003). Ricklefs (1973) estimated that average S_J for resident temperate passerine species is ~25% of S_A . Greenberg (1980) noted that S_J/S_A is lower for residents and short-distance migrants than for long-distance migrants. Population models of migrant passerines frequently parameterized S_J as 50% of S_A (Temple and Cary, 1988; Flaspohler et al., 2001; Howe et al., 1991; Donovan et al. 1995). Empirical evidence from the post-fledging, pre-independence period for several passerine species suggests that juvenile survival may be lower (e.g., post-fledging survival rate of Lark Bunting (*Calamospiza melanocorys*; Emberizidae) 0.37, Yackel Adams et al., 2001; Yellow-eyed Junco (*Junco phaenotus*; Emberizidae) 0.32, Sullivan, 1989; Wood Thrush (*Hylocichla mustelina*; Turdidae) 0.42, Anders et al., 1997). Because of the wide range of published estimates we felt a comparison of the two S_J rates was warranted. We conducted a sensitivity analysis to determine whether S_A or S_J during year t have a stronger influence on population levels in year N_{t+1} .

The third approach to analyzing population dynamics also involved estimating survival rates, this time under the assumption that McGregor Range in its entirety constituted a closed population, because we had no a priori reason to assume adult survival rates are related to the habitat in which individuals nest. We focused this analysis on 1997–1998, because results of the second approach suggested that in that pair of years it would have been possible for source sink dynamics to operate at the scale of McGregor Range. We determined the adult and juvenile survival rate (one rate each for all habitats) that would result in the observed changes between 1997 (adults plus fledglings) and the 1998 breeding population. The 1997 population consisted of the estimated number of adults in each habitat (adults/ha * number of ha) plus the estimated number of fledglings produced in each habitat (Table 1), summed over all habitats. The 1998 population consisted of the number of adults in each habitat, summed over all habitats. In this analysis we estimated the net source and sink potential of each habitat, once under a liberal assumption of juvenile survival ($S_J = 0.5 * S_A$), and once under a conservative assumption of juvenile survival ($S_J = 0.25 * S_A$).

Table 1 – Mean (and standard deviation) of demographic values for the Black-throated Sparrow in six habitats in the northern Chihuahuan Desert, 1996–1998

	Sandsage	Mesquite	Creosote	Whitethorn	Black Grama grassland	Mesa grassland
<i>Clutch size</i>						
1996	2.2(0.8)	2.5(0.7)	2.6(0.6)	–	2.8(0.7)	2.8(0.4)
1997	2.9(0.6)ab ^a	2.7(0.9)ab	2.9(0.7)ab	2.6(0.7)b	2.8(0.7)ab	3.1(0.8)a
1998	3.0(0.5)b	3.4(0.6)a	3.0(0.4)b	2.8(0.6)b	2.9(0.7)b	2.8(0.5)b
Mean [n]	2.8[28]ab	2.8[117]ab	2.9[73]ab	2.7[61]b	2.9[48]ab	3.0[53]a
<i>N. nestlings/nest</i>						
1996	0.8(0.8)	0.5(0.9)	0.8(1.2)	–	1.6(1.5)	1.5(1.5)
1997	0.9(1.2)	0.5(1.0)	0.9(1.3)	1.0(1.2)	1.1(1.2)	0.8(1.3)
1998	1.1(1.3)ab	0.65(1.3)b	0.5(0.9)b	1.7(1.2)a	0.9(1.3)ab	1.7(1.3)a
Mean [n]	0.1[29]abc	0.5[117]c	0.8[77]abc	1.3[62]a	1.1[48]ab	1.3[53]a
<i>N. fledge/successful nest</i>						
1996	1.3(0.6)b	2.3(0.7)ab	2.2(1.1)ab	–	2.8(0.8)a	3.0(0)a
1997	2.3(0.5)	2.3(0.8)	2.6(0.7)	2.3(0.8)	2.2(0.9)	2.6(0.9)
1998	2.3(0.9)	2.2(1.6)	2.2(0.4)	2.3(0.8)	2.3(1.0)	2.6(0.4)
Mean [n]	2.1[13]b	2.3[27]ab	2.4[24]ab	2.3[37]ab	2.3[23]ab	2.7[25]a
<i>Average season-long fecundity^b</i>						
1996	0.6	0.6	1.7	–	2.5	2.0
1997	1.6	0.4	1.2	1.7	1.6	1.3
1998	1.8ab	0.4b	0.9b	1.9ab	1.2b	2.1a
Mean	1.3a	0.5b	1.3ab	1.8a	1.8a	1.8a
<i>Nests/100 ha^c</i>						
1996	2.8(1.3)b	11.1(7.5)a	7.4(5.6)ab	–	2.5(2.8)b	3.7(3.2)ab
1997	11.1(5.2)	25.4(8.3)	22.2(14.9)	9.9(4.6)	6.8(8.7)	17.3(4.3)
1998	4.6(1.3)	11.1(5.4)	13.0(5.3)	11.7(9.5)	6.8(5.3)	12.3(8.3)
Mean	6.2b	15.8a	14.2a	7.4b	5.3b	11.1ab
<i>Nest success rate</i>						
1996	0.23(0.2)b ^d	0.12(0.01)c	0.39(0.13)a	–	0.47(0.2)a	0.34(0.2)a
1997	0.35(0.15)a	0.08(0.03)c	0.22(0.03)b	0.38(0.09)a	0.37(0.1)a	0.23(0.09)b
1998	0.40(0.18)a	0.09(0.04)c	0.19(0.08)b	0.42(0.09)a	0.27(0.1)b	0.40(0.09)a
Mean [n]	0.32[30]b	0.11[136]d	0.25[80]c	0.38[70]a	0.29[54]b	0.30[59]b
<i>Daily survival rate</i>						
1996 ^c	0.94(0.03)	0.92(0.01)	0.96(0.01)	–	0.97(0.01)	0.96(0.02)
1997	0.96(0.02)a ^d	0.90(0.01)b	0.96(0.01)a	0.96(0.00)a	0.96(0.01)a	0.94(0.01)a
1998	0.96(0.02)a	0.90(0.02)c	0.93(0.02)b	0.96(0.01)a	0.95(0.02)a	0.96(0.01)a
Mean	0.95a	0.90c	0.93b	0.96a	0.96a	0.95a
<i>Fledglings per 100 ha</i>						
1996	3.5b	13.2a	24.5a	–	12.3a	14.0a
1997	36.0b	20.8c	53.4a	33.7b	23.1c	38.5ab
1998	16.2ab	9.6b	22.8ab	43.8ab	16.9ab	50.8a
Mean	18.6b	14.5b	33.6a	38.8a	17.4b	34.4a
<i>Total fledglings produced</i>						
1996	1076	8014	13,056	–	1582	8016
1997	10,977	12,631	28,415	5729	5729	21,928
1998	4952	5834	12,150	7437	2167	28,969
Mean	5668	8826	17,874	7437	2237	19,637
<i>Adults/100 ha (males plus females)^e</i>						
1996	33.2(5.0)a	32.9(4.8)a	26.3(4.9)ab	25.8(6.7)b	14.4(7.0)c	12.4(9.2)c
1997	36.9(10.4)a	38.8(9.6)a	32.2(3.3)a	35.3(8.2)a	15.7(9.7)b	14.7(10.3)b
1998	21.3(9.0)bc	28.3(7.4)ab	31.0(8.7)a	24.2(5.0)abc	15.9(10.7)c	15.2(8.0)c
Mean	30.4(10.4)a	33.3(8.4)a	29.8(6.3)a	28.4(8.1)a	15.3(8.7)b	14.1(8.7)b
<i>Nest shrub density (per ha) foliage height diversity</i>						
	0.15(0.10)b	0.06(0.05)c	0.23(0.13)a	0.21(0.13)a	0.02(0.03)d	0.02(0.04)d
	1.1(0.34)a	1.1(0.34)a	1.2(0.30)a	1.2(0.29)a	0.5(0.24)b	0.5(0.24)b

Within each row, means with different letters are significantly different at $p \leq 0.05$ unless followed by †, which indicates $p \leq 0.1$.

a Results are from analysis of variance protected least squares difference method.

b The product of # female fledglings/nest * nest success rate, assuming 2.5 nesting attempts/female, and a maximum of two successful nests per female. For example, in sandsage in 1996, 0.67 female fledglings/nest * 23% of nests successful in the first attempt, producing 15.3 fledglings. The remainder (77%) re-nested, and 23% of these second attempts were successful, resulting in 11.8 fledglings. Of the remainder, 1/2 of the adult

(Continued on next page)

Table 1 – continued

females made a third nesting attempt, of which 23% were again successful, resulting in 9.4 additional fledglings. Thus, the first successful nesting attempt for all adult females resulted in $15.3 + 11.8 + 9.4 = 36.5$ female progeny. Of those adults that were successful in their first nesting attempt, 23% were successful in a second attempt, and of those that failed in a first attempt but were successful in their second attempt, 23% were successful in producing another nest of fledglings. These mid- and late-season nesting attempts produced an additional 15.3, and 11.8 female, fledglings, respectively. Summed across the season, the total is 63.6 per 100 females, resulting in a fecundity rate of 0.6 females per female in sandsage in 1996.

c Data on nest density and nest success are from Pidgeon et al. (2003).

d Results are from the χ^2 test in the program Contrast (Sauer and Williams, 1989).

e Data on adult density was first published in Pidgeon et al. (2001).

3. Results

3.1. Indicators of habitat quality

3.1.1. Three year averages of fitness

Different measures of fitness resulted in different rankings of habitat quality. Averaged across years, one or both grassland habitat types supported the highest clutch size, number of nestlings per nest and per successful nest, and season-long fecundity. However, adult abundance, was lowest in the grasslands, and highest in the shrublands (Table 1). Sandsage supported the lowest number of nestlings per successful nest, and nest density was lowest in both sandsage and black grama grassland. Highest nest density but lowest nest success and lowest daily nest survival rate occurred in mesquite, followed by creosotebush habitat (Table 1). The mean annual number of fledglings contributed by each habitat ranged from 2,237 in black grama to 19,637 in mesa grassland (Table 1). Mesquite, with greatest extent (60,817 ha), produced one-third the mean annual number of fledglings produced in mesa grassland (57,033 ha).

3.1.2. Annual variation in measures of fitness

We monitored 430 nests and found that clutch size, nest success, daily nest survival rate and fledgling density varied in rank among years (Table 1). Average number of fledglings per nest ranged from 0.5 to 1.7, and average number of fledglings per successful nest ranged from 1.3 to 3.0. Season-long fecundity ranged from 0.4 to 2.5 females produced per female, and was consistently among the lowest in mesquite and among the highest in the grassland habitats (Table 1). Nest density was consistently among the highest in mesquite, although the difference was significant only in 1996. Nest success and daily nest survival rate in all three years were lowest in mesquite and in two years nest success was lower in creosotebush than in sandsage and whitethorn (Table 1). Fledgling density ranged from 3.5/100 ha in sandsage and mesquite to >50/100 ha in creosotebush and mesa grassland.

In an effort to identify the most reliable but least resource-intensive way to identify breeding habitat quality, we evaluated the similarity of several fitness measures to each other, and their response to key vegetation variables on an annual basis (Table 2). Nest density and fecundity were not consistently correlated. Adult relative abundance was strongly negatively correlated with nest success, number of fledglings per successful nest, and fecundity. Daily survival rate of nests was strongly correlated with nest suc-

cess. Nest shrub density was positively correlated with adult relative abundance and fledgling density, but negatively correlated with the number of fledglings per successful nest (Table 2). Foliage height diversity was strongly negatively correlated with fecundity, and number of fledglings per successful nest, and positively correlated with adult relative abundance and nest shrub density.

3.2. Population dynamics at different scales

In the first analysis of population dynamics, conducted over the range of fecundity rates observed in our study, every habitat except mesquite was a source in most years under the liberal estimate of juvenile survival, $S_j = 0.5(S_A)$, and an assumed adult survival rate of 70% (Fig. 1a). When adult survival rate was reduced to 60%, five habitats functioned as sources in at least in some years. However, under an adult survival rate of 50% and juvenile survival rate of 25%, mesquite, creosotebush and sandsage habitats were population sinks in all three years, and in both whitethorn and mesa grassland population dynamics were close to the source–sink boundary in one year, leaving only black grama grassland as a clear source (Fig. 1b), albeit in one year only. Under the conservative estimate of juvenile survival ($S_j = 0.25(S_A)$) no habitats were a source when adult survival was assumed to be 50%, and at an adult survival rate of 40% no habitats remained as a source at either juvenile survival rate. Notably, under all adult survival rates examined, using both juvenile survival rate scenarios, mesquite appears to be a population sink.

In the second, exploratory, approach to analyzing the McGregor Range population dynamics, we assumed each habitat was a closed system over the three years of our study. There was an increase in relative adult abundance between the 1996 and 1997 breeding seasons in all habitats, resulting in λ values >1 in all habitats (Table 3). The unlikely consequence was that the S_A required to achieve these λ values was 0.9–1 in all habitats, and even more unlikely, the S_j was 1 in shrub-dominated habitats. This suggests there was substantial immigration from outside of McGregor Range. However the change in adult relative abundance between 1997 and 1998 resulted in more plausible λ values, as well as S_A and S_j values that are in line with findings for other resident passerine species (Table 3).

Under the assumption of closed habitats for 1997–1998, λ values ranged from 0.58 in sandsage (Table 3), where adult relative abundance decreased from 37 to 21 adults/ha (Table 1), to 1.01 in black grama grassland and 1.03 in mesa grassland, where adult relative abundance values reflected virtually no

Table 2 – Correlation matrix of key fitness and habitat measures calculated on an annual basis

	Successful fledglings per nest			Fecundity			Nest density			Nest success			Daily nest survival			Fledgling density			Adult relative abundance			Nest shrub density			
	1996	1997	1998	1996	1997	1998	1996	1997	1998	1996	1997	1998	1996	1997	1998	1996	1997	1998	1996	1997	1998	1996	1997	1998	
Fecundity	0.65 ^a																								
Nest	NS	0.63 ^a	0.66 ^a																						
Nest success	NS	0.34 ^a	0.41 ^a	0.20 ^c																					
Daily nest survival	NS	0.51 ^a	0.49 ^a	0.98 ^a	-0.71 ^a	NS																			
Fledgling density	NS	0.53 ^a	0.49 ^a	0.98 ^a	0.96 ^a	0.98 ^a	-0.78 ^a																		
Adult relative abundance	NS	0.66 ^a	0.52 ^a	0.62 ^a	0.92 ^a	0.97 ^a	0.59 ^b	-0.28 ^b	NS																
Nest shrub density	NS	-0.68 ^a	-0.70 ^a	-0.58 ^a	-0.73 ^a	0.76 ^a	0.94 ^a	0.55 ^a	0.70 ^a	0.75 ^a	0.98 ^a	0.98 ^a	0.53 ^a	0.66 ^a	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Foliage height diversity	NS	-0.30 ^a	-0.53 ^a	NS	NS	NS	NS	0.48 ^a	0.26 ^b	0.21 ^c	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		-0.54 ^b	-0.62 ^a	-0.37 ^a	-0.74 ^a	-0.21 ^c	0.49 ^c	0.26 ^b	NS	-0.67 ^a	-0.30 ^b	-0.37 ^a	-0.73 ^a	-0.37 ^a	0.81 ^a	0.58 ^b	0.94 ^a	0.90 ^a	0.77 ^a	0.61 ^a	0.85 ^a	0.59 ^a	0.69 ^a	0.86 ^a	

a Indicates $p \leq 0.01$.
 b Indicates $p \leq 0.05$.
 c Indicates $p \leq 0.10$, and NS indicates non-significant relationships.

change in abundance among years. To conform with the observed λ values under the assumption $S_j = 0.5(S_A)$, the required adult survival ranged from 0.35 in sandsage to 0.60 in mesa grassland. Under the assumption $S_j = 0.25(S_A)$, the observed λ values were achieved when adult survival ranged from 0.44 in sandsage to 0.76 in mesa grassland while juvenile survival ranged from 0.11 to 0.19. Sensitivity analysis of population levels to adult versus juvenile survival showed there was a stronger response to changes in adult survival rates than to juvenile survival rates. Each incremental increase of 10% survival rate for adults resulted in 17 more individuals/100 ha, while the same increase in juvenile survival rate resulted in eight more individuals/hundred ha.

Lastly, under the assumption of a closed range population for 1997–1998, with an assumed $S_j = 0.5(S_A)$, an adult survival rate of 0.49 resulted in the observed population changes among the habitats, without the need for immigration or emigration (Fig. 2). Under the stricter assumption of juvenile survival, $S_j = 0.25(S_A)$, an adult survival rate of 0.62 achieved similar results (Fig. 2).

4. Discussion

4.1. Indicators of habitat quality

Our findings confirm the dilemma that different measures of avian demographics result in different ranking of habitat quality. A conservationist charged with protecting Black-throated Sparrows in our study area would prioritize different areas depending on whether the criterion was relative adult abundance, nest success, or the number of fledglings produced per unit area. This highlights the need to disentangle the relationships among different measures of habitat quality.

The best measure of individual level habitat quality is a metric that provides the most complete information about breeding success, and is most cost-effective. Were there no constraints on resources, season-long fecundity would be the best measure of habitat quality for individual breeding pairs, as it takes into account nest success, number of fledglings per nest, and number of times a pair successfully nested in a season. However given the constraints under which most field work is conducted, it is useful to understand the performance and limitations of other measures as indicators of habitat quality, both for individuals and for populations.

Adult relative abundance was a poor indicator of population level habitat quality, as it was negatively correlated with fecundity and nest success. Nest density and fledgling density were strongly correlated, but nest density alone was also not a good indicator of population level habitat quality because it was negatively correlated with nest success and exhibited a weak relationship with fecundity. Where fecundity was high, it was due to a combination of high nest success and a high number of fledglings per nest.

Fecundity alone was a good indicator of individual level habitat quality, but a poor indicator of the ability of habitat to maintain a regional population. For instance in 1996 fecundity was greatest in black grama grassland, yet the contribution of this habitat to the population of McGregor Range was minimal due to low nest density and the small areal extent of this habitat type. While nest success and

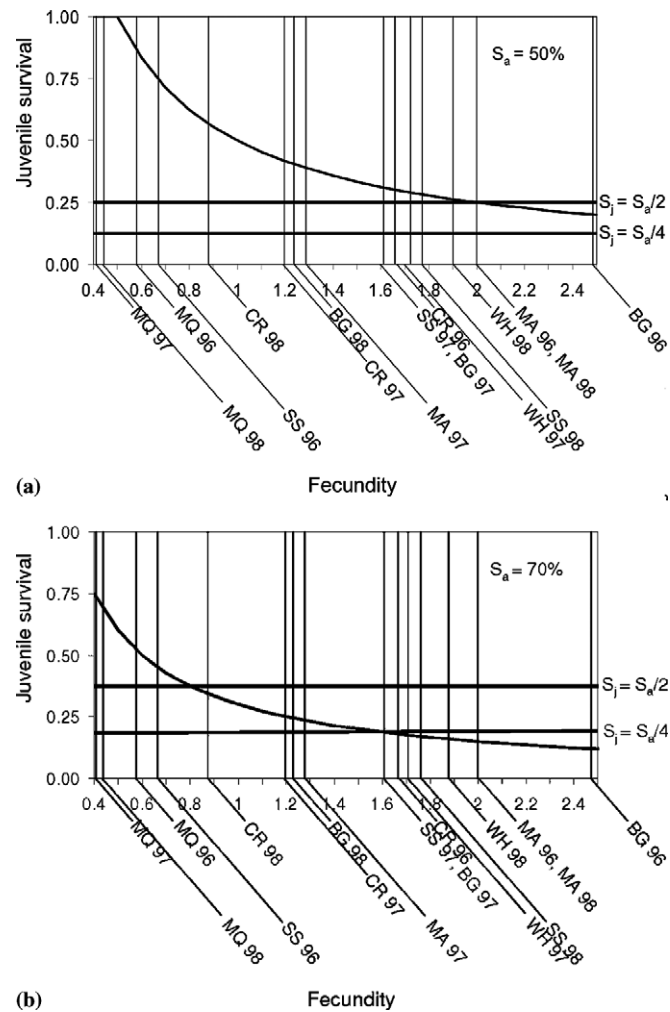


Fig. 1 – Curve depicting the relationship between lambda, adult survival (S_A) and juvenile survival (S_J) over the range of fecundity levels observed for Black-throated Sparrows in six habitats in south central New Mexico, 1996–1998 when the probability of adult survival is (a) 0.50 and (b) 0.70. Fecundity rates observed in each habitat-year combination are indicated along the x-axis by their abbreviation and year for mesquite (MQ), sandsage (SS), creosotebush (CR), whitethorn (WH), black grama grassland (BG), and mesa grassland (MA). Lower horizontal line indicates rate of juvenile survival when $S_J = 0.25(S_A)$ and upper horizontal line indicates juvenile survival when $S_J = 0.5(S_A)$. The point at which curve and horizontal lines cross is the point at which births and deaths are balanced. Populations to the right of this point are considered a source, while populations to the left of this point are considered a sink.

Table 3 – Values of lambda, λ , and survival rates of adults, S_A , and juveniles, S_J , of the Black-throated Sparrow, calculated in a theoretical exercise in which each habitat was assumed to be a closed population

	λ^a		Survival rates required to achieve 1997–1998 λ values			
	1996–1997	1997–1998	$S_J = 0.5 * S_A$		$S_J = 0.25 * S_A$	
			Adult	Juv.	Adult	Juv.
Mesquite	1.18	0.73	0.44	0.22	0.55	0.14
Sandsage	1.11	0.58	0.35	0.18	0.44	0.11
Creosote	1.22	0.96	0.54	0.26	0.69	0.17
Whitethorn	–	0.69	0.42	0.21	0.52	0.13
Black grama	1.09	1.01	0.47	0.24	0.64	0.16
Mesa grassland	1.19	1.03	0.60	0.30	0.76	0.19

Relative adult abundance during the breeding season on McGregor Range of Ft. Bliss, New Mexico, 1996–1998, was the basis of λ values. Fecundity values observed in each habitat during the 1997 breeding season, as well as the λ values, were the basis of survival rate calculations.
 $a \lambda = N_{t+1}/N_t$.

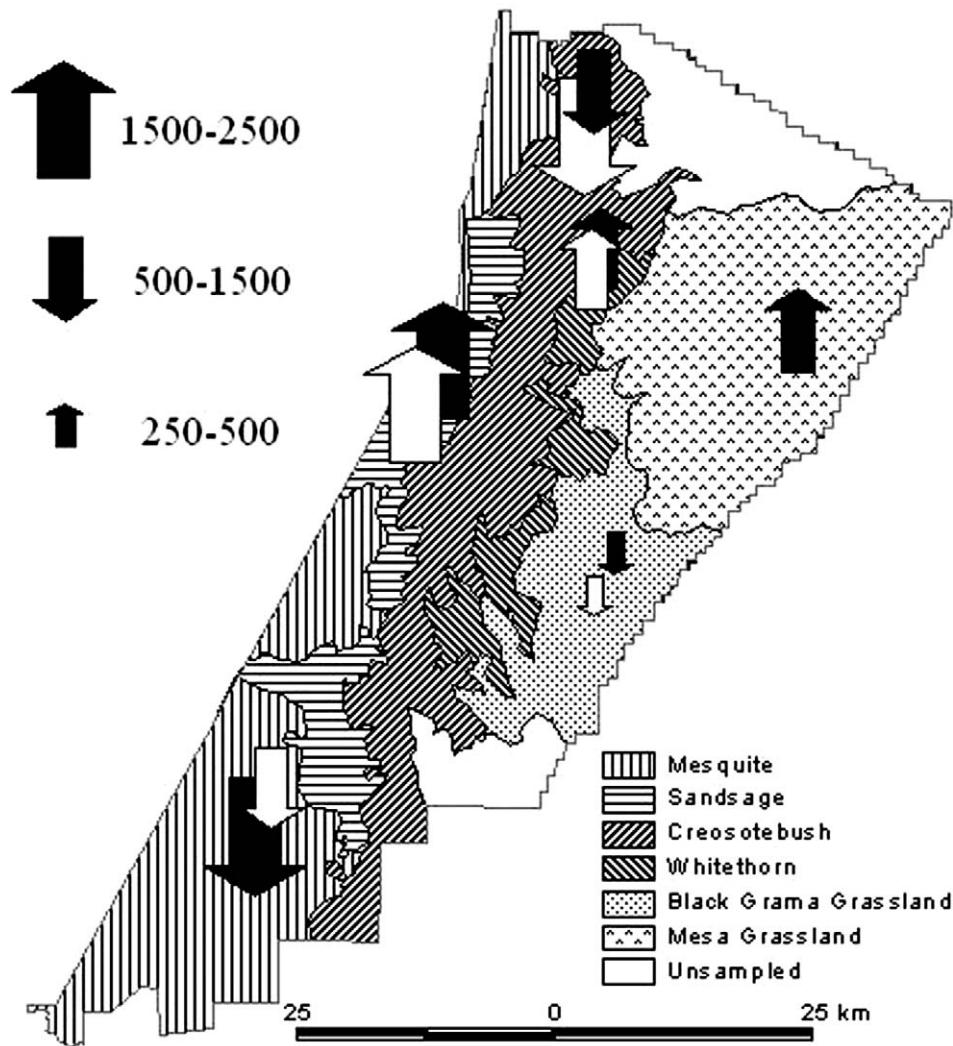


Fig. 2 – Population dynamics of Black-throated Sparrows among six habitats on McGregor Range, Fort Bliss, NM, during 1997–1998, under the assumption of no immigration or emigration from McGregor Range. Black arrows indicate source (up) or sink (down) status when $S_j = 0.5(S_A)$. White arrows indicate source (up) or sink (down) status when $S_j = 0.25(S_A)$.

daily nest survival rate were useful in assessing individual level habitat quality, they did not reflect differences among habitats in the number of fledglings contributed to the population (nests are considered successful if one or more fledglings are produced). Combining fecundity and nest density with areal extent of habitat provided the best indicator of the contribution of different habitats to maintaining the regional population, as exemplified by Mesa grassland, which stands out as an important habitat for Black-throated Sparrows. Creosotebush ranked second in number of fledglings produced due to high nest density, average fecundity, and the broad areal extent of the habitat. Surprisingly, mesquite ranked third in number of fledglings produced due to high nest density and high areal extent, despite extremely poor nest success and fecundity. The interactions elucidated here suggest that in considerations of breeding habitat quality for maintaining a regional population, information about nest success, nest density, and number of fledglings per nest are all important, as is the areal extent of each habitat.

4.2. Population analyses

There are many steps along the continuum from source to sink (e.g., McCoy et al., 1999). Habitats within McGregor Range vary in the degree to which there is a net surplus or deficit in fledglings produced (i.e. their source or sink status) among years. This is due to interactions between nest success, nest density, number of fledglings produced in successful nests, and survival of adults and juveniles. We found that no habitat is likely to be a consistent source over the entire range of observed fecundity levels. In fact, even under the most liberal survival rates examined, mesquite habitat still functioned as a sink. If actual juvenile survival is closer to 25% than 50% of adult survival, then it is likely that infrequent years of high adult survival, plus high season-long fecundity in the grassland habitats and whitethorn, sustain the regional population in the area of McGregor Range over broader time horizons.

The two grassland habitats together cover approximately 29% of McGregor Range. They appear to be the most important habitats for this species as they function as sources most

consistently in the many scenarios we explored. Even so, adult survival must be high relative to established survival rates of Embizerid sparrows for a net surplus to occur. Mesquite habitat covers approximately 25% of McGregor Range, and despite the sink status of populations breeding in this habitat in most years, the extent of mesquite habitat and the density of adults and nests found therein makes it important at minimum as a reservoir from which individuals may disperse into better habitat (Murphy, 2001).

Source–sink dynamics may operate at the scale of multiple states covering hundreds of thousands of km², as suggested by Brawn and Robinson (1996) for neotropical migrants in the upper Midwest, and by Graves (1997) for Black-throated Blue Warblers (*Dendroica caerulescens*) in the Appalachians and northeastern US. In these situations population dynamics operate at a scale that is an order of magnitude larger than the scale of McGregor Range, which encompasses approximately 2825 km² (Pidgion et al., 2001). Population dynamics of the Collared Flycatcher on the island Gotland Sweden (3027 km²) operate at approximately the same scale as those on McGregor Range (Doncaster et al., 1997).

Source–sink dynamics may operate at different scales in different years. If we know the scale of these population interactions, i.e. the scale at which sources and sinks balance, we can infer survival rates. For example for the 1996–1997 pair of years, population dynamics appear to have operated at a scale broader than that of McGregor Range and we did not pursue the closed population exercises for this pair of years. The survival rates required for maintenance of the Black-throated Sparrow sub-population within each habitat from 1996 to 1997 are so high under the assumption of no migration into McGregor Range (Table 3) that we infer there was substantial immigration from outside the study area during or before the 1997 breeding season.

In the second pair of years, 1997–1998, the adult survival rates required to attain λ values resulting in the observed estimates of relative abundance estimates under the rule $S_j = 0.5 * S_A$ are more plausible and fall within the range of those reported for other Embizeridae species. For example, the required survival rate to achieve observed levels of adults in sandsage in 1998 was only 0.35. This is why, in the Range-wide exercise, sandsage was a source habitat under both juvenile survival rules, as was whitethorn. In mesa grassland, despite the high survival rates required to meet the observed value of λ (Table 3) this habitat still functioned as a source under the liberal juvenile survival rule (Fig. 2). Several long-term studies with individually marked birds have shown that individuals contribute unevenly to future generations (e.g., Dhondt, 1989). This underscores the important effect that differential survival among individuals nesting in different habitats (Payne, 1989) and among individuals within habitats (Hochachka et al., 1989) can have on lifetime reproductive success and on population viability.

Changes in source–sink dynamics may occur over longer time horizons than those examined here, as species adapt to a changing environment. A population is maladapted to a given habitat if the individuals dominating it have lower average fitness than individuals in other habitats (Dias, 1996). Black-throated Sparrows seem to be relatively well adapted to the spatial and temporal pattern of resource availability

in grasslands and whitethorn, and poorly adapted to conditions in mesquite. In creosotebush and sandsage the relationships are less clear. Evidence suggests that the amount of time since the initiation of human disturbance impacts on habitat is related inversely with the degree to which birds occupy the places best suited for their reproduction within the modified habitat (Bock and Jones, 2004). Following this logic, it is quite possible that, given a long enough period of exposure to the highly modified mesquite habitat, Black-throated Sparrows will evolve through natural selection to accurately assess the relative value of this habitat.

4.3. Management and conservation considerations

In an ideal world, a manager would have data on the whole suite of demographic measures available before assessing habitat quality and prioritizing conservation action. However, these measures are costly to obtain and conservationists are faced with tradeoffs when deciding how to measure avian habitat quality. The cost of obtaining various demographic measures of breeding habitat quality depends on the field skills needed, the number of visits to an area that are required, the time on task required during each visit, and ease of access to the site of interest. At the low-cost end, estimates of relative adult abundance typically require 2–4 visits to each count station per season, and approximately 10 min at each station per visit to sample an area of between 0.008 km² (for a 50 m fixed radius point count) and 0.07 km² (for a 150 m radius point count), depending on the structure and vegetation volume of the habitat (Ralph et al., 1993). In the middle of the cost range, estimates of clutch size require finding nests, and inspecting them once during the incubation phase of the nesting cycle. Estimating the daily survival rate or nest success (i.e. the probability of a nest producing ≥ 1 fledgling) requires visiting nests regularly until the nesting attempt is complete, while estimating number of fledglings per nest and fledgling density requires vigilance in monitoring the nest at fledging time, and large sample sizes, due to high predation rates during the nestling phase of the nest cycle (Martin et al., 2000). Continuing toward the high end of the cost spectrum, estimating nest density requires thorough and frequent searching of a discrete area for the duration of the nesting season. Estimating adult survival is also quite resource-intensive, and requires several years of data (DeSante et al., 1995) while juvenile survival is the most resource-intensive estimate to obtain, requiring data on survival during two periods, (1) prior to independence, and (2) from independence until the following spring, when most passerine species are considered adults. Due to the wide range in cost, it pays to carefully select focal demographic parameter(s) when estimating breeding habitat quality.

Fecundity is the best indicator of individual level habitat quality, however it may not be possible to spend enough time and resources on field sampling to obtain an adequate estimate of this fitness measure. Components of fecundity include nest success, number of fledglings per successful nest, and the number of nesting attempts made by a female during a breeding season. We found a strong positive relationship between fecundity and nest success, and suggest nest success as an adequate measure of individual level habitat quality. Gi-

ven the large number of studies using nest success as a measure of habitat quality, this is a satisfying recommendation. The best indicator of population level habitat quality includes a measure of fitness and a measure of density of the reproductive effort. In the absence of data on adult and juvenile survival, consideration of nest success and nest density together provide the most robust estimate.

In general, management decisions should be based on measures of habitat quality at the population level, not at the individual level. Commonly used indicators of habitat quality, such as daily survival rate and nest success, can misrepresent population level dynamics in areas where nest sites are limited. Such areas may characterize the best habitat for an individual pair of birds, but may not be the habitat where conservation efforts have the biggest impact on population viability.

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