

LANDSCAPE-SCALE PATTERNS OF BLACK-THROATED SPARROW (*AMPHISPIZA BILINEATA*) ABUNDANCE AND NEST SUCCESS

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Abstract. Analyses of avian demographic patterns across entire, contiguous landscapes are rare, but such analyses are important for understanding population dynamics. We selected the Black-throated Sparrow in the northern Chihuahuan Desert as a model to test patterns of abundance and nest success across a landscape. We integrated abundance, nest density, and nesting success measured on sampling plots with a classified satellite map of the distribution of seven habitat types to analyze spatial and temporal patterns contributing to the population dynamics of this species.

Adult relative abundance ranged from <1 bird/100 ha in pinyon–juniper habitat to 24–39 birds/100 ha in shrubland habitats. Nest density was consistently high in mesquite, moderate to high in creosotebush, and low in black grama grassland; this value exhibited more temporal variability than relative abundance of adults. Nest success rates exhibited a strong habitat effect and ranged from 8% in mesquite to 47% in black grama grassland; overall population nest success was 0.266. In all three years, nest success in mesquite was significantly lower than in all other habitat types ($P < 0.01$). There was no correlation between nest success and adult relative abundance.

While mesquite habitat contained about one-third of all adults in the three years of the study, it contributed as little as 10% of successful nests. In creosotebush, the relative contribution to both adult abundance and successful nests was relatively high. Mesa grassland contained relatively few adults, but up to 44% of successful nests. We discuss how habitat selection theory suggests mechanisms for the observed patterns. Mesquite appears to be a population sink for Black-throated Sparrows and may be an ecological trap. While we do not propose that there is cause for conservation concern for this widespread species, our results underscore the pitfalls associated with using adult abundance as an indicator of habitat quality. The method presented here is applicable for many species and ecosystems and, thus, may be an important tool for conservation and management, as well as a new avenue for scientific investigation of landscape-level population dynamics.

Key words: abundance; *Amphispiza bilineata*; Black-throated Sparrow; Chihuahuan Desert; ecological trap; landscape; nest success; population sink; scale; spatial pattern; temporal pattern.

INTRODUCTION

Understanding the spatial and temporal pattern of species and populations has been a major goal of ecological research since the beginnings of the field (e.g., Grinnell 1917, Cowles 1991). It was recognized early that habitat availability is a key factor in determining avian species presence and abundance (Leopold 1933). A rich theory of habitat selection developed that sought to explain how individuals within a population are distributed in the face of limited habitat resources. For example, the extent to which habitat preferences determine a species' distribution has been the subject of

many studies (e.g., MacArthur et al. 1962, James 1971). Svardson (1949) suggested that increasing density should be associated with increases in the range of habitats occupied by a species, and this thinking was formalized in the models of Brown (1969) and Fretwell and Lucas (1970). Studies on factors that interact with habitat preferences to produce natural distributions have been reviewed in Partridge (1978) and Cody (1985). Recent work has expanded understanding of the implications of habitat selection, including the role of habitat fragmentation in source-sink dynamics of metapopulations (Donovan et al. 1995, Wiens 1996, Schmiegelow et al. 1997).

In recent decades, it has become clear that patterns and processes operating at the landscape scale are a crucial factor in determining species patterning. Landscape ecologists revealed that the spatial pattern of habitat occurrence (e.g., fragmented vs. clumped) is important for area-sensitive species (reviewed in Horn et

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al. 2000). Population ecologists have demonstrated that species distributions can be determined by metapopulation dynamics (Flather and Bevers 2002) or source-sink dynamics (Pulliam 1988).

The current scientific challenge is that hypotheses about habitat selection have rarely been tested at the landscape scale because of a lack of measurements of avian populations and/or avian habitat quality across entire landscapes. The population attributes that are most frequently measured at landscape, regional, and even continental scales are species presence and abundance (e.g., Sauer et al. 2001). While abundance provides important information on population trends, it is a poor estimator of habitat quality and does not permit the testing of habitat selection hypotheses. This is because a species' abundance and its nest success may be negatively correlated (Van Horne 1983), indicating that habitat quality for a species can be poor in a habitat where it is abundant. Such areas may be sink habitats, i.e., areas in which the population is maintained through immigration of individuals from high quality source habitat (Pulliam and Danielson 1991, Brawn and Robinson 1996). Species presence and abundance measurements alone cannot distinguish among population sources and sinks, which is potentially dangerous for species of conservation concern because protection efforts may focus on the wrong areas.

Estimates of reproductive success are the best indicators of relative habitat quality in the breeding range because they provide information about the ability of the habitat to support future offspring; yet obtaining such measurements is logistically difficult and costly, especially at the landscape scale. Methods are lacking that allow obtaining such measurements in an effective manner. Therefore, for most species and most areas, the nature of the relationship of abundance to reproductive success in different habitats and the pattern of habitat quality across space is not known.

Particularly little is known about avian demographic patterns in desert ecosystems at any scale. Climatic events (e.g., rainfall) are stochastic in arid systems, resulting in phenological changes that do not have a predictable onset (Ludwig 1986). The abundance of key resources (e.g., aboveground perennial and annual plant parts, arthropods) are largely determined by these stochastic climatic patterns (Polis 1991), which also affect predator population levels (Rotenberry and Wiens 1989). Due to these factors, avian population levels and demographic rates can undergo great spatial and temporal variation from year to year (Raitt and Pimm 1976, Marr and Raitt 1983). This suggests that patterns of reproductive success in desert ecosystems may differ significantly from those in other ecosystems (e.g., Tomoff 1974), warranting special investigation.

We selected the Black-throated Sparrow (*Amphispiza bilineata*) as a model to investigate the spatial and temporal patterns of abundance and nest success in the northern Chihuahuan Desert (south-central New Mex-

ico, USA), which is the core of its range (Rising and Beadle 1996, Sauer et al. 2001). The Black-throated Sparrow is an ideal species for such an analysis because it occurs in a number of desert habitat types, which facilitates comparisons of nest success across the landscape. Furthermore, this species remains active during the hottest hours of the day (Delasantro 1978, Zimmer 1983; A. M. Pidgeon, *personal observation*) and may be "better adapted to desert life than any other small North American seed-eating bird" (Smyth and Bartholomew 1966). The Black-throated Sparrow is a medium-sized sparrow, and the sexes have similar coloration. It is a summer resident in the northern portion of its range in the west-central states of the United States, and is an all-year resident from New Mexico and Arizona to the southern edge of its range in Hidalgo, Guanajuato, and northern Jalisco, Mexico (Rising and Beadle 1996). Black-throated Sparrows typically select nest shrubs ≤ 0.5 m in height. Suitable nest shrubs are usually isolated from other shrubs (Kozma and Mathews 1997). In some habitat types, shrubs with an understory of the grass bush muhly (*Muhlenbergia porteri*) are selected (Zimmer 1993; A. M. Pidgeon, *personal observation*). During the breeding season, invertebrates are the main food of both adults and young, with desert grasshoppers comprising the majority of the diet during the nestling and fledgling stages (Zimmer 1993).

Our general goal was to examine the spatial and temporal pattern of abundance and nest success for a selected avian desert species across an entire landscape. More specifically, we pursued two objectives in our analysis: Our first objective was to assess landscape-scale spatial and temporal variability of (1) relative abundance, (2) total abundance, (3) nest density, and (4) nest success, using a novel GIS-based approach to integrate plot-level measurements with a land cover map. Second, we tested the hypothesis that adult abundance is positively correlated with reproductive success across different habitat types, which would suggest that abundance alone is a sufficient indicator of habitat quality.

METHODS

Study area

We collected field data from 1996 through 1998 on Fort Bliss Military Reserve in the northern portion of the Chihuahuan Desert in south-central New Mexico, USA (Fig. 1). The study area is located in the Tularosa Basin, Otero Mesa, and the foothills of the Sacramento Mountains encompassed within McGregor Range.

The area is relatively undisturbed compared to the surrounding land, which is used primarily for grazing (Fort Bliss Directorate of Environment Conservation Division 1998). For example, black grama (*Bouteloua eriopoda*) grassland, a habitat type that has been replaced by shrubland in most of its former range (Dick-

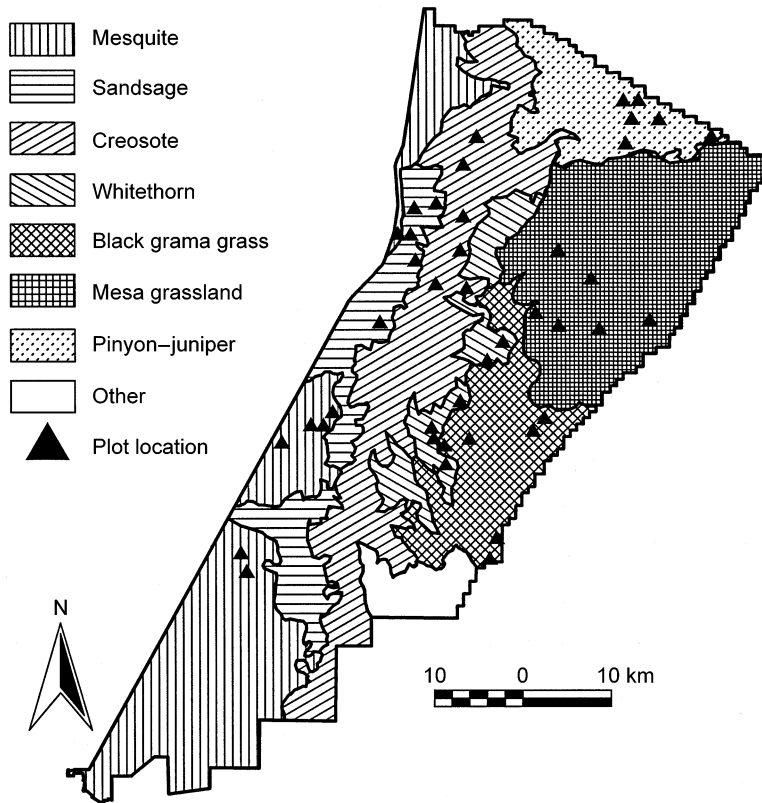


FIG. 1. Location of plots within habitats in the study area, McGregor Range, Fort Bliss, in south-central New Mexico.

Peddie 1993), still occurs in relatively large patches on McGregor Range (Pidgeon et al. 2001).

Habitat types

Previous studies of birds in the Chihuahuan Desert have grouped a wide range of habitats into one type: "desert scrub" (Dixon 1959, Raitt and Pimm 1976, Kozma and Mathews 1997). However, avian species respond to different habitats in this ecosystem with distinct patterns of abundance (Pidgeon et al. 2001), which is why we distinguished among four shrubland habitats (mesquite, sandsage, creosotebush, whitethorn), two grassland habitats (black grama and mesa), and one tree-dominated habitat (pinyon-juniper) in this study (Pidgeon et al. 2001). These seven habitat types represent 240 616 of the 282 500 ha of McGregor Range; the remainder of the study area consists primarily of military housing, intensively used training areas, escarpment, and small patches of other habitat.

Mesquite (*Prosopis glandulosa*) habitat occurs at the lowest elevation (~1200 m) in the center of the Tularosa Basin. The multistemmed mesquite shrub typically occurs in "coppice dune" formations, with dunes averaging $7 \times 5 \times 2$ m. Soils are sandy and well to excessively drained (Derr 1981). Interdunal areas are sparsely vegetated with small shrubs and soap tree yucca (*Yucca elata*). Cover of forbs and grasses is low,

comprising 0.5% and 2.6% of ground cover, respectively.

Sandsage habitat also occurs at low elevation (1200 m) on gently rolling sandy soil. The dominant species, *Artemisia filifolia*, typically occurs as a 1 m tall, dense shrub; subdominants include soap tree yucca (*Yucca elata*), little leaf sumac (*Rhus microphylla*), and mesquite. Forbs averaged 3.5%, and grasses 17%, of ground cover.

Creosotebush-dominated (*Larrea tridentata*) habitat has low shrub species richness and a high component of bare ground. Creosotebush has an open growth form and occurs frequently in stands of uniform height from 0.5 to 1.5 m, occasionally punctuated by small groups of taller yucca or mesquite plants. It occurs on deep well-drained, strongly calcareous and moderately alkaline soils on the lower parts of alluvial fans, fringes of fans, and the valley bottom (Derr 1981) from 1200 to 1600 m. Forbs made up 1.5%, and grasses 22%, of ground cover.

Whitethorn (*Acacia neovernicosa*) habitat occupies mid-elevation sites (1500–1700 m). This open desert shrubland type occupies limestone outcrops intermingled with shallow, well-drained soils (Derr 1981), and includes several species of shrub and cacti as subdominant elements. The most abundant shrub, whitethorn acacia, is a spinescent plant with relatively thin stems

and an open growth form, and reaches 2 m in height. Forbs make up 0.8%, and grasses 14%, of ground cover.

Black grama (*Bouteloua eriopoda*) grasslands intergrade with whitethorn and mesa grassland, and occur at 1500–1800 m elevation. This habitat type includes black grama, scattered shrubs, cane cholla (*Opuntia imbricata*), and *Yucca* sp. It occurs on shallow, well-drained, gravelly alluvium of weathered limestone and carbonate fragments interspersed with small amounts of calcareous eolian sediment (Derr 1981). Average forb cover is 1.6%, and average grass cover is 40%.

Mesa grassland is found on Otero Mesa (1800 m elevation), a 473 000-ha, flat tableland extending to the east of the study area, and occurs on fine sandy loam (Derr 1981). The community is dominated by blue grama (*Bouteloua gracilis*), which occurs in combination with other grasses, including black grama (*B. eriopoda*), hairy grama (*B. hirsuta*), threeawn grass (*Aristida* sp.), tobosa grass (*Hilaria mutica*), New Mexico needlegrass (*Stipa neomexicana*), and others. Soap tree yucca (*Y. elata*), banana yucca (*Y. baccata*), and cane cholla (*O. imbricata*) provide vertical structure in this habitat type.

Pinyon–juniper habitat is dominated by small-statured pinyon pine (*Pinus edulis*), and juniper (*Juniperus deppeana* and *J. monosperma*), and the subdominant shrubs mountain mahogany (*Cercocarpus montanus*) and oceanspray (*Ceanothus gregii*). The structure of this habitat type ranges from savanna, with individual trees and shrubs scattered in grass, to woodland, with closed canopy. It occurs primarily on calcareous gravelly loam slopes (Derr 1981) in the foothills of the Sacramento Mountains (1800–2400 m).

Field methods

Plot selection.—Within each of the seven habitat classes we randomly placed six 1200 × 900 m plots (108 ha each) with a surrounding buffer of at least 50 m of continuous habitat. The initial visual classification of shrubland plots into habitat types was later corroborated by ordination and cluster analysis of vegetation data that reclassified only one of the 24 plots from sandsage to mesquite (Pidgeon et al. 2001). To facilitate estimating distance during point counts and in locating nests, plots were gridded at 50-m intervals with flags labeled with alphanumeric codes in March each year before the nesting season began.

Bird abundance surveys.—We surveyed abundance of breeding Black-throated Sparrows in each plot at 12 sampling stations located 300 m apart in a 3 × 4 rectangular pattern between 1 May and 7 June, from 1996 through 1998, using 10-min point counts (Martin et al. 1997; nest initiation peaked between 19 May and 31 May each year). All Black-throated Sparrows heard or observed ≤150 m from each point were recorded. Surveys were conducted on mornings with low wind (<12 km/h) and no rain, beginning within 0.25 h of sunrise and ending within 3.5 h after sunrise.

Nest monitoring.—We estimated nesting success by monitoring nests from April to mid-August from 1996 through 1998, except in whitethorn habitat, where plots were searched only in 1997 and 1998. In each habitat type, we randomly selected three plots in which to focus intensive nest-searching efforts that consisted of 4–6 person-hours, 2–3 times/wk. We included only nests found in the interior 54 ha (900 × 600 m) of each plot (the plot minus 150 m of perimeter on each side), to be as sure as possible that the nesting attempt was influenced by processes within homogeneous habitat, and not confounded by edge effects. While total search effort on each plot varied slightly from week to week, search effort was distributed evenly among plots over the entire nesting season. At plots that were not searched intensively, nest finding was incidental to other activities.

Each year, 12 to 15 observers received training in nest searching, bird vocalizations, and behavioral cues. Nest searching occurred between sunrise and 1300 hours (daylight savings time), and included use of behavioral cues, random, and systematic search. Search maps of the plots were maintained to ensure that all sections of intensively searched plots received equal effort. All nests were monitored every 2–5 d until they either failed or young fledged. Several nonterminal 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 the majority of depredation events, it was not possible to identify the predator.

We recorded data on nests only after egg laying commenced. In the absence of eggs, we could not reliably distinguish the age of a nest, i.e., whether it was constructed in the current or previous nesting season.

Data analysis

Adult abundance.—Landscape-level population dynamics depend on several factors, including the abundance of adults and nests. Our relative adult abundance estimates (number of adults per 100 ha) are based on field measurement made on all 42 plots. From the 4–5 sampling times during each breeding season on each plot, the average of the highest two counts was used for further analysis. Relative abundance was estimated for each habitat annually (Pidgeon et al. 2001). Because goals of the study focused on differences between habitats, we averaged relative abundance over the six plots in each habitat and calculated its standard deviation. Significance of differences among habitats in the relative abundance of adults was tested using the Kruskal–Wallis test.

The product of relative adult abundance and the area of each habitat type can provide estimates of total adult abundance in each habitat type, as well as the relative contribution of each habitat to the total population across the landscape. Area estimates for the seven habitat types were derived from land cover classification

of McGregor Range based on Landsat Thematic Mapper (TM) satellite imagery (30-m resolution, minimum mapping unit 0.5 ha; Mehlhop et al. 1996; Fig. 1).

The land cover data was also used to scale up the plot-level data to the landscape level, thereby deriving maps of the spatial patterns of relative abundance. We estimated relative abundance for each 600×600 m cell of a regular grid (i.e., 20×20 pixels of the TM image) across the entire study area. Relative extent of each habitat, R_h , in a given 600×600 m analysis cell, is the proportion of 30×30 m pixels of habitat h . This estimate is only based on those 30×30 m pixels that were classified as one of the seven habitat types we sampled. Relative abundance in a given habitat-year combination is given by $A_{h,i}$. The relative abundance for each 600×600 m analysis cell in a given year i was calculated as the average of all $A_{h,i}$ for those habitats present in the cell, weighted by R_h . Habitats where no Black-throated Sparrows were detected on point counts were included in this weighting, because it is as important to know what constitutes non-habitat as what constitutes habitat. Therefore, the abundance estimate was calculated weighting by all (of the seven sampled) habitats present in a 600×600 m cell, irrespective of whether birds were detected in a given habitat in a given year.

Nest density.—Nest density was estimated due to its importance in population dynamics. Of two areas that function as a population source, the one with the higher nest density will have a stronger effect on overall population trends. As in the calculation of adult abundance, the weighted average density for a 600×600 m cell was calculated based on all habitats. These estimates are based on nests found in the intensively searched plots only. We do not assume that our search efforts were 100% successful and some nests were probably missed. However, search effort was equal among habitat types, and we do assume that our sampling efforts captured the general spatial pattern.

Nest success.—In order to calculate nest success rates, we pooled nests from all plots for each habitat. We estimated nest success, with confidence intervals, using the Mayfield method (Mayfield 1961, 1975), as modified by Hensler and Nichols (1981) in the program MICROMORT (Heisey and Fuller 1985). For this estimate, we divided the nesting cycle into three stages: egg laying, incubation, and nestling. Nest success was estimated from daily survival rates in each stage, based on number of nest failures and number of nest exposure days. We calculated stage survival rates by raising the daily survival rate to the power of the average length of the stage. The nest success rate, i.e., the percentage of nests that were successful, was calculated by multiplying the three stage rates. An individual nest was considered successful if it fledged one or more young.

To compare nest success rates in each habitat-year combination, we tested for differences using the program CONTRAST, which applies a chi-square test to

multiple rate estimates with associated variances and covariances (Sauer and Williams 1989). Although CONTRAST is commonly used for testing daily survival rates, the method is appropriate for all rate estimates with associated variances and covariances (Sauer and Williams 1989). We tested for differences only when there were at least 10 nests in a group. An alpha value of 0.05 was used as the threshold of significance.

The product of nest density, nest success, and area of each habitat provides an estimate of the total number of successful nests in each habitat, as well as the relative contribution of each habitat to the total number of successful nests across the landscape. We estimated this relative contribution, which can be an important indicator of the importance of a given habitat for overall population viability.

Modeling nest success at the landscape level.—The analysis of spatial patterns of avian nest success utilized plot data on nest success rates, nest abundance, and integrated it with habitat availability estimates based on land cover data. Plot-level data was scaled up to the landscape level following the method used for relative adult abundance, with one important difference: We included only those habitat types in which nests were found, because we assume that the nest success rate in a given cell is not affected by the abundance of non-habitat in an analysis cell as long as suitable habitat is found.

The nest success rate in a given habitat-year combination, $S_{h,i}$, is the proportion of nests that, once initiated, produce at least one fledgling. We estimated $S_{h,i}$ for each habitat-year combination based on the pooled data from all plots within a given habitat. The proportion of successful nests S for each 600×600 m analysis cell in a given year i was calculated as the average of all $S_{h,i}$ for those habitats present, in the cell, weighted by R_h .

We estimated the annual contribution of each habitat to successful nests by weighing nest success in each habitat by the area of that habitat, for each year. The grand mean nest success, \bar{S} , is the average nest success rate across all habitats and years. For mapping and comparison purposes, nest success rates were grouped into four classes based on the grand mean nest success rate \bar{S} (i.e., 0.266; Fig. 2a). The lowest class encompasses all cases where $0 \leq S < 0.5(\bar{S})$ (i.e., $S < 0.14$). The second class contains cells where $0.5(\bar{S}) < S < \bar{S}$ (i.e., $0.13 < S < 0.28$); the third contains cells where $\bar{S} < S < 1.5(\bar{S})$ (i.e., $0.27 < S < 0.41$); and the highest class contains those cells where $S \geq 1.5(\bar{S})$ (i.e., $S \geq 0.41$).

Reliability estimates of nest success rate.—The high variability in the number of nests found among years and habitats required incorporating confidence estimates into the analysis. To avoid confusion of this estimate with confidence intervals, we use the term *reliability estimates*. The reliability of a nest success rate

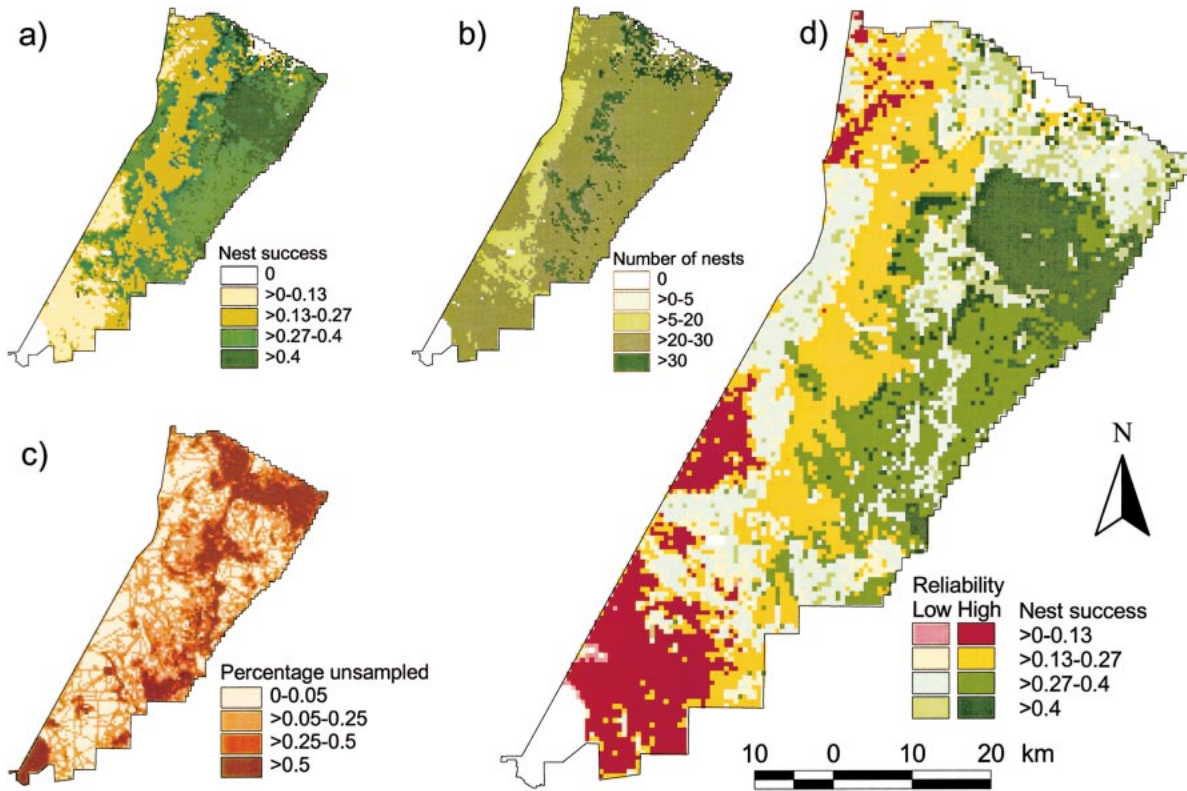


FIG. 2. Three sources of information determine the nest success rate with reliability estimates. The example shows Black-throated Sparrow nest success in 1998, within McGregor Range, Fort Bliss, New Mexico: (a) nest success rate estimates, (b) number of nests used to estimate nest success in each habitat type, (c) location of sampled and unsampled habitat types, and (d) the combined map of nest success with reliability estimates.

estimated for a given 600×600 m cell depends on two factors: the number of nests found in a given habitat and year, and the percentage of 30×30 m pixels within the analysis cell that were classified into one of the seven habitat types for which plot-level nest success data were available. The estimated number of nests, n , in each 600×600 m cell of the satellite classification was calculated as the average of the $N_{h,i}$ number of nests found in each of the habitats in a given year weighted by R_h (Fig. 2b). Only cells with $n \geq 20$ are classified as having highly reliable nest success rate estimates. If less than five nests occurred in a given habitat, nest success rate was not calculated.

The relative abundance of 30×30 m pixels in habitat for which no nest success data were available, R_0 , is the proportion of cells that are not classified as one of the seven major habitat types, out of all pixels present in the cell (Fig. 2c). Only cells with $R_0 < 0.5$ are considered as having highly reliable nest success estimates (Fig. 2c). Thus, for a nest success rate to be assigned high reliability, $>50\%$ of the habitat in a 600×600 m cell must have been a habitat type that was sampled as part of our study, and at least 20 nests must have made up the estimate of nest success rate (Fig. 2d).

RESULTS

Relative abundance of Black-throated Sparrows was consistently lowest in pinyon-juniper habitat and highest in mesquite. In the two grassland habitat types, relative abundance was only about half of what it was in the four shrub habitats (Table 1). Interannual variation was significant ($P < 0.05$) in two habitat types (sandsage and whitethorn) and near significant ($P = 0.058$) in mesquite. Standard deviations of relative abundance estimates were in almost all cases higher for grassland habitats compared with shrub habitats (Table 1). Based on relative abundance and habitat area, we estimate that the total population of adult Black-throated Sparrows ranged from $\sim 110\,000$ to $137\,000$ individuals each year, the majority of which occurred in mesquite, sandsage, and creosote habitats (Table 2).

Nest density exhibited more temporal variability than adult abundance (Table 3). Overall, highest nest densities occurred in 1997, when they were up to 4.7 times higher than the lowest densities, which were observed in 1996. In all three years, the rank of nest density among habitats remained essentially unchanged, and was always among the highest in mesquite. The total estimated number of nests, based on

TABLE 1. Relative abundance (number observed per 100 ha) of adult Black-throated Sparrows (with 1 SD in parentheses) by year within habitat type, 1996–1998, McGregor Range, Fort Bliss, New Mexico.

Habitat type	1996	1997	1998	P †
Mesquite	32.9 (4.8) ^a	38.8 (9.6) ^a	28.3 (7.5) ^{ab}	0.0578
Sandsage	33.2 (5.0) ^a	36.9 (10.4) ^a	21.3 (9.0) ^{bc}	0.0328
Creosote	26.3 (5.0) ^b	32.2 (3.3) ^a	31.0 (8.7) ^a	0.2423
Whitethorn	25.8 (6.7) ^b	35.3 (8.2) ^a	24.2 (5.1) ^{abc}	0.0251
Black grama	14.4 (7.0) ^c	15.7 (9.8) ^b	15.9 (10.8) ^c	0.9535
Mesa grassland	12.4 (9.2) ^c	14.7 (10.3) ^b	15.2 (8.1) ^c	0.8565
Pinyon–juniper	0.23 (0.6) ^d	0.3 (0.6) ^c	0.1 (0.2) ^d	0.0695

Note: Within each year, values with different letters are significantly different ($P < 0.0001$).
† P values represent differences in abundance between years in each habitat.

density of the nests found and habitat area, also exhibited strong interannual variation (Table 2). Mesquite habitat had the largest number of nests; it contained 48% of the total number of nests in the overall low year 1996, and 36% in the high year 1997.

Nest success estimates were based on a total of 430 Black-throated Sparrow nests detected and monitored. There was a value of 0.266 for overall population nest success (average of all habitats weighted by habitat area).

The relative contribution of each habitat to both total adult population and total number of successful nests (i.e., the product of nest density, nest success, and area of each habitat type) reveals some interesting differences among these two population measures. While mesquite contained about one-third of all adults in each year, it contributed as little as 10% (in 1998) of the successful nests to the population. Creosotebush is the only habitat with both high relative contribution to adult numbers as well as successful nests (both values ranked second highest in all three years). Mesa grassland, on the other hand, never contained >16% of the adults, but up to 44% of the successful nests. Combined, creosote and mesa grassland contained ~66% of all successful nests in each of the three years, highlighting their importance for overall population demographics.

Nest success rates exhibited a strong habitat effect; nest success ranged from 8% in mesquite in 1996 to 47% in black grama grassland in 1997 (Table 3). In all three years, nest success in mesquite was significantly lower than nest success in the other habitat types (χ^2 test; $P = 0.0088$, <0.0001 , and 0.001 in 1996, 1997, and 1998, respectively). In mesquite and whitethorn, nest success values varied by only 4% among years, while in other habitats values varied by 17% to 20% (Table 3). Nest success rates in creosotebush (0.39, 0.22, 0.19 for 1996, 1997, and 1998, respectively) were similar to rates in creosote bush found in other studies (Delesantro 1978:0.25; Kozma and Mathews 1997: 0.29; Zimmer 1993:0.61, 0.65, 0.70).

The integration of plot-level data, pooled by habitat, with the land cover classification allows comparisons of the spatial pattern of relative abundance, nest density, and nest success rates across habitats and years, thus, capturing both spatial and temporal patterns (Fig. 3). In mapping nest success, highly reliable estimates could be derived over approximately one-third of the study area in 1996, three-quarters in 1997, and two-thirds in 1998 (Fig. 3). Nest success estimates of low reliability resulted from low nest numbers for a particular year–habitat combination (e.g., Fig. 2b, d). Areas dominated by unsampled habitat also resulted in nest success estimates of low reliability, as can be seen

TABLE 2. Estimated total abundance of adult Black-throated Sparrows, the relative contribution of each habitat type of total abundance by year within habitat type, 1996–1998, and the area of each habitat type; McGregor Range, Fort Bliss, New Mexico.

Habitat type	Area of habitat type (ha)	Total estimated abundance based on relative abundance of adults observed			Total estimated number of nests based on density of nests found		
		1996	1997	1998	1996	1997	1998
Mesquite	60 817	40 060	47 145	34 429	6750	15 471	6750
Sandsage	30 506	20 224	22 484	12 993	848	3386	1412
Creosote	53 251	28 026	34 268	33 036	3941	11 822	6896
Whitethorn	16 978	8750	12 000	8228	...†	1676	1990
Black grama	12 841	3686	4023	4083	317	871	871
Mesa grassland	57 033	14 174	16 814	17 342	2110	9850	7032
Pinyon–juniper	9249	43	57	14	0	0	0
Total	240 676	114 963	136 792	110 125	13 967	43 076	24 952

† No intensive nest searching was conducted in whitethorn habitat in 1996.

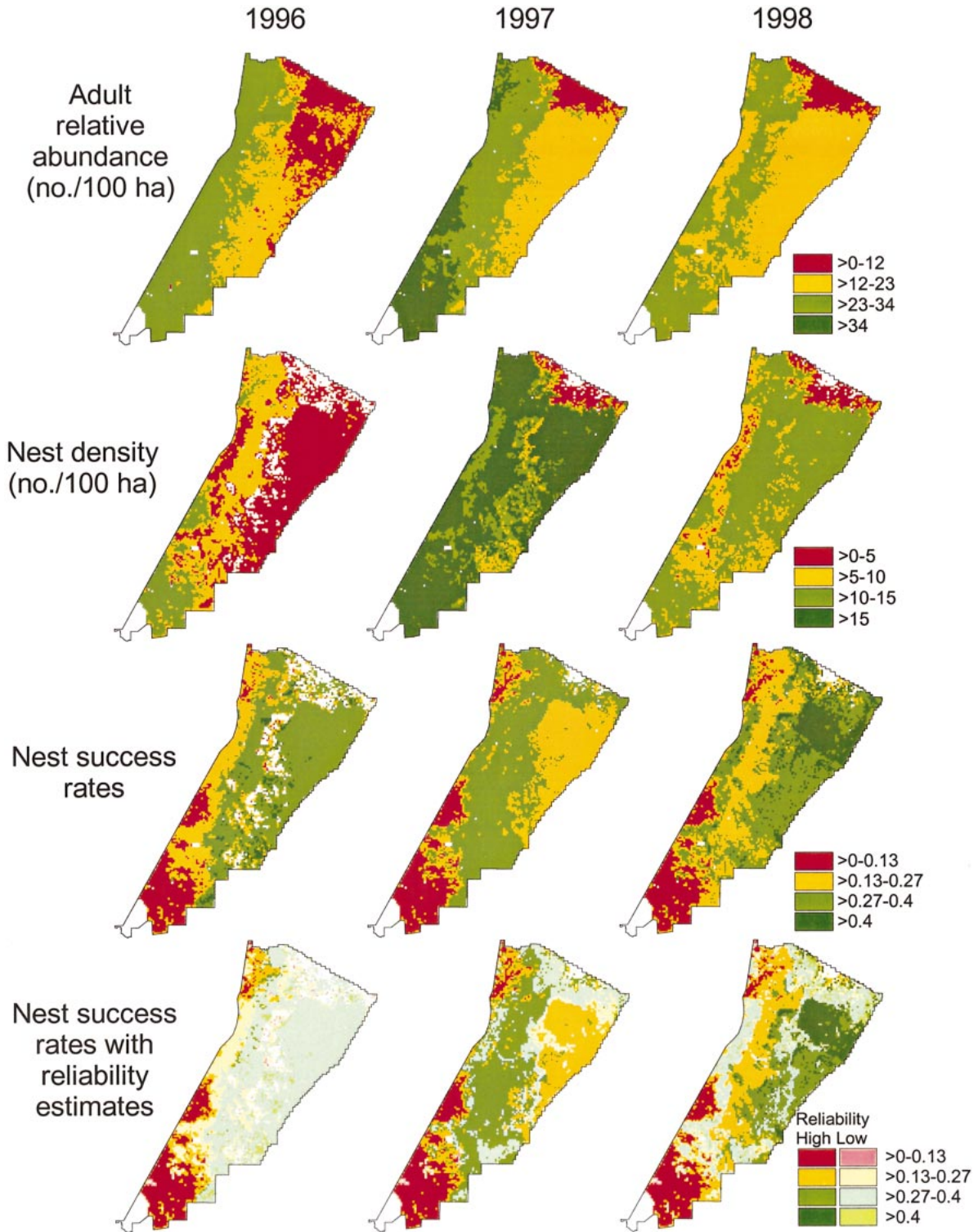


FIG. 3. Spatial pattern of the relative abundance of adults, index of nest density, and nest success estimates for Black-throated Sparrow, 1996–1998, within McGregor Range, Fort Bliss, New Mexico.

TABLE 3. Nest success rates, nest sample size (n), number of exposure days, and index of nest density for Black-throated Sparrow, 1996–1998, McGregor Range, Fort Bliss, New Mexico.

Habitat type	Year	Nest success [†]	No. nests	Exposure days	Index of nest density [‡]
Mesquite	1996	0.12	38	306	11.1
	1997	0.08	72	522	25.4
	1998	0.09	26	214	11.1
Sandsage	1996	0.23	6	50	2.8
	1997	0.35	15	141	11.1
	1998	0.40	9	108	4.6
Creosotebush	1996	0.39	17	186	7.4
	1997	0.22	39	363	22.2
	1998	0.19	24	260	13.0
Whitethorn acacia	1996	...§	1	12	...
	1997	0.38	32	405	9.9
	1998	0.42	38	391	11.7
Black grama grassland	1996	0.47	11	130	2.5
	1997	0.37	20	223	6.8
	1998	0.27	23	261	6.8
Mesa grassland	1996	0.34	6	69	3.7
	1997	0.23	28	270	17.3
	1998	0.40	25	268	12.3
Years and habitats pooled		0.27	430	4177	

Note: No nests were found in pinyon–juniper habitat.

[†] Nest success was calculated for categories containing five or more nests.

[‡] The index of nest density (nests per 100 ha) was calculated from intensively searched plots.

[§] Whitethorn acacia habitat was not intensively searched for nests in 1996.

where an escarpment bisects the study area approximately into east and west halves (Fig. 2c, d). In all three years, nest success estimates in areas dominated by mesquite are highly reliable, because of both a high number of nests and high proportions of the 600 × 600 m analysis cell composed of sampled habitat (Fig. 3). In creosotebush, whitethorn, black grama, and mesa grassland, highly reliable estimates were obtained in two of the three years. Nest success estimates in sandsage are of low reliability in all three years due to low numbers of nests found.

DISCUSSION

The objectives of our study were (1) to assess spatial and temporal variability in abundance, nest density, and nest success of Black-throated Sparrows across an entire landscape, and (2) to test the hypothesis that abundance is positively correlated with nest success, which would suggest that abundance estimates alone are sufficient for measuring habitat quality. Our data reveal strong temporal and spatial patterns in adult abundance and nest success rates. Progressing from relative abundance of adults, to nest density, and finally to nest success rates, both the complexity of spatial patterns and the annual variability increases (Fig. 3). Abundance and nest success are not positively correlated (Fig. 4); mesquite is consistently the habitat with the highest relative and total abundance, as well as nest

density, but lowest nest success rates (Tables 1–3, Fig. 3).

The rank of adult relative abundance among habitats was largely consistent among years. Nest density exhibited more variability among habitats and years, possibly reflecting the greater resource demands of nesting birds, which are not met every year in each habitat. Despite the higher variability, nest density patterns followed adult density patterns closely. The stable pattern in which the population was partitioned among habitats each year suggests that the mechanism governing settlement patterns is not subject to the vagaries of environmental stochasticity, but has to do with more stable habitat elements. For example, the consistently low nest density in black grama is most likely the result of the low density of suitable nesting shrubs (0.02 shrubs/m² in black grama vs. 0.16/m² in desert shrubland; Pidgeon et al. 2001).

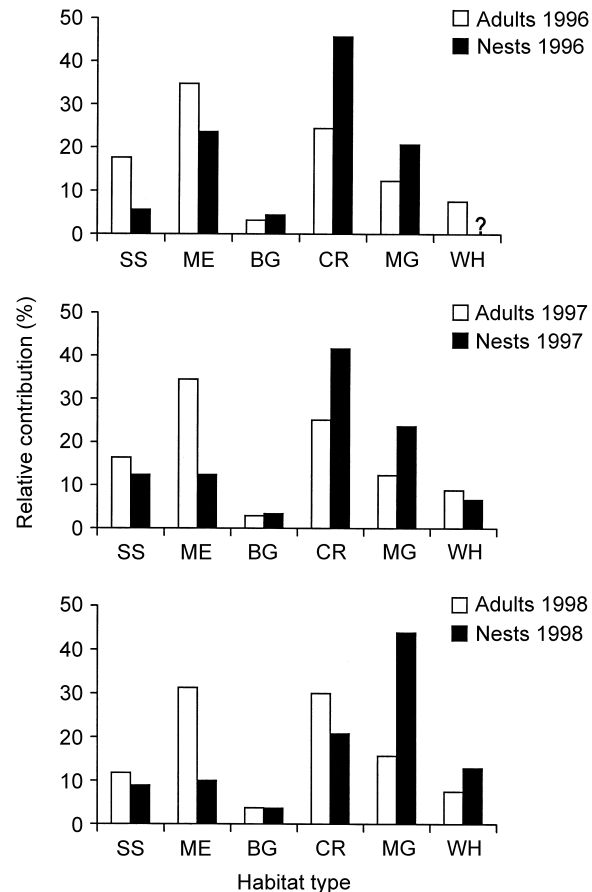


FIG. 4. Relative contribution (percentage) of different habitats to adult population and to successful nests. Pinyon–juniper habitat is not depicted because it contributed <1% to either estimate in any of the three years. In whitethorn habitat, no plots were intensively searched for nests in 1996. Abbreviations are: SS, Sandsage; ME, Mesquite; BG, Black grama grassland; CR, Creosotebush; MG, Mesa grassland; WH, Whitethorn.

Nest success showed both high interannual variation as well as spatial patterns that are markedly different from those for adult abundance and nest density. This is likely a reflection of the stochastic variation in environmental conditions typical for desert environments. In each of the three years, nest success rates were lowest or among the lowest in mesquite, where highest adult relative abundance occurred, while nest success rates were among the highest in the grassland habitats, where lowest relative abundance occurred. In creosotebush and whitethorn habitat, both nest success and adult relative abundance were moderately high.

These patterns raise two sets of questions: First, what are the proximate mechanism(s) for high adult abundance and poor nesting success in mesquite, and second, how does habitat selection operate in the case of Black-throated Sparrows in this desert landscape? Why do about one-third of the adults, and one-quarter to one-half of all nests (depending on the year), occur in a habitat where the likelihood for successful nesting is only about 10%, while each year other habitats within the same landscape present a 40% chance of successfully raising young?

Neither the literature nor our study provide definite causes for the low nest success rate in mesquite. However, we hypothesize that the proximate causal mechanism for poor nesting success has to do with trade-offs faced by breeding adult birds. Higher ambient temperatures in mesquite caused by the physiognomy of the habitat (the bare sand reflects incoming infrared radiation more than does grass-covered habitat; mesquite dunes break the wind and reflect radiation sideways toward nests) may pose two possible mechanisms for higher nest failure rates. Adults may have faced a trade-off between the competing needs of foraging and maintaining optimal egg and nestling temperature through shading (Reid et al. 2002). In addition to positioning nests within the shrub nonrandomly so as to enhance natural shading from the afternoon sun, females spend time shading nests at midday (Delesantro 1978). They have also been noted to forage throughout the day (Smyth and Bartholomew 1966; A. M. Pidgeon, *personal observation*). In the extreme environment of mesquite dunes, adults may be unable to meet the competing needs of effectively shading nests and foraging, resulting in nestling morbidity from either starvation or heat exposure. Alternatively, longer nest attendance by adults for shading may have stimulated more nestling activity and noise, resulting in greater detectability of nests by predators. Regardless of the proximate mechanism for consistent poor nest success in mesquite, the question remains: If nest success is so poor in mesquite, why is abundance so high?

Habitat selection theory suggests at least two possible explanations for the high relative abundance of adult birds in mesquite. First, adults may actively choose areas high in mesquite density. Lack (1933) postulated that birds recognize conspicuous features of

appropriate ecosystems and use these features as cues to select a place to live. Black-throated Sparrows do not commonly select mesquite shrubs as nest sites (Kozma and Mathews 1997; A. M. Pidgeon, *personal observation*); however, selection of this habitat during the breeding season by adult Black-throated Sparrows may be a response to a habitat cue, such as the presence of large dense shrubs, which are significantly more abundant in mesquite habitat than in other habitats in the study area (Pidgeon et al. 2001). Mesquite shrubs offer a secure refuge from many predators, and they are probably choice foraging areas when in bloom, being rich sources of insects.

Building on Lack's hypothesis, we suggest that recent landscape changes in the desert southwest could be the reason why Black-throated Sparrows cue in on mesquite habitat despite extremely low nest success rates. Mesquite habitat has expanded greatly in extent at the expense of grasslands since the 1880s, when European settlers arrived (e.g., Buffington and Herbel 1965, Archer et al. 1998, Pidgeon et al. 2001). Prior to that time, it occurred on the margins between mesas and valleys (Bartlett 1854 and Parry 1895, both cited in Buffington and Herbel 1965), as well as in riparian areas. The tree form of mesquite, rather than the coppice dune form, was probably more predominant, as suggested by references to mesquite trees (Wizlizenus 1848, cited in Buffington and Herbel 1965), but also existed in its "scrubby" form (Bartlett 1854, cited in Buffington and Herbel 1965). Increased grazing combined with drought (Connin et al. 1997), altered fire regimes (Brown and Archer 1989), and increased levels of atmospheric carbon dioxide (Fredrickson et al. 1998) have facilitated the transition from a grass-dominated state to a state dominated by mesquite coppice dunes (Archer 1989, Laycock 1991). This land cover conversion occurred very recently in evolutionary history, and Black-throated Sparrows may be poorly adapted to the mesquite dune formations that were at most a minor part of the landscape until the early 20th century (Buffington and Herbel 1965, van Devender and Spaulding 1979). In the pre-European settlement landscape, nesting near the occasional mesquite shrub occurring near a riparian area may have been advantageous for Black-throated Sparrows, as it provided cover and probably a food source during the period of nestling provisioning. But if indeed nesting among mesquite was an advantage in the past, it has become a disadvantage in the present, at least in years similar to those we sampled.

An alternative hypothesis for the observed discrepancy between abundance and nest success is the ideal dominance distribution model put forth by Fretwell and Lucas (1970). Territoriality of behaviorally dominant birds in the preferred habitats may exclude others from those habitats, forcing them into lower quality habitat. Abundance patterns may be due to low density of critical breeding resources (e.g., suitable nesting sites or

suitable dispersion of food patches) in habitat where nest success is higher. Under the ideal dominance distribution, we would expect to see, on average, that individuals in the best habitats have the highest reproductive success (Petit and Petit 1996). Using this criterion, the highest quality habitats for Black-throated Sparrows are creosotebush, black grama grassland, whitethorn, and mesa grassland.

The data collected in this study does not permit testing whether Lack's (1933) model or Fretwell and Lucas' (1970) model best explains the observed patterns. We lack information on individual age and fitness, and did not monitor phenology of habitat occupancy (under the ideal dominance model it is assumed that the most preferred habitat is occupied first [Fretwell and Lucas 1970, Finch 1991, Petit and Petit 1996]). Regardless of which model is the correct one, some clear conservation concerns emerge from our study, especially when viewed in the larger context of recent landscape changes in the desert southwest. If habitat trends continue their current trajectory, we can assume that, at least at lower elevations, there will be more mesquite and creosotebush on the landscape and less grassland.

If we accept Lack's hypothesis explaining the patterns of adult abundance, we can conclude that mesquite habitat, in its current predominant coppice dune form on the landscape, is an ecological trap. That is, there are elements within the habitat that entice Black-throated Sparrows to settle and nest in large numbers, but the habitat does not ultimately support reproductive success as well as other available habitats (Gates and Gysel 1978). Regardless of its possible role as an ecological trap, mesquite likely functions as a population sink (*sensu* Pulliam and Danielson 1991). Nest success rates in mesquite during the three years of our study were not adequate to replace adult death rates.

If we instead assume that the ideal dominance model best explains the patterns found, then the replacement of grassland habitats by mesquite is cause for conservation concern, because high nest success in grasslands suggests that these are preferred habitat. Of less concern is the expansion of creosotebush at the expense of grassland (Buffington and Herbel 1965), because Black-throated Sparrow's abundance and reproductive success are both moderately high in creosotebush.

However, despite the negative impacts of recent landscape changes, we do not want to give the impression that Black-throated Sparrow populations in our study area are in immediate danger or in need of concerted management efforts. We selected the Black-throated Sparrow as the focal species for this study because it is widespread, which provided us with the opportunity to compare abundance and nest success rates across all habitats of an entire landscape. However, our results suggest that investigation may be warranted into the demographics of species that are exhibiting serious population declines and for which mesquite habitat may be a critical detriment if it functions

as an ecological trap and/or a population sink as it does for Black-throated Sparrows. Our observation that Crissal Thrashers (*Toxostoma crissale*) and Pyrrhuloxias (*Cardinalis sinuatus*) had high abundance in mesquite (Pidgeon et al. 2001) suggests these two species as candidates for further investigation.

In general, adult abundance is widely used as an indicator of habitat quality (e.g., Morrison et al. 1992), but this index has been criticized because it may convey misleading information about relative habitat quality (Van Horne 1983). The relative abundance and nest success patterns of Black-throated Sparrows in mesquite are a prime example of the validity of this criticism. In our study area, if estimates of habitat quality had been based on adult abundance alone, mesquite would have been ranked as high quality despite the very poor nest success rates. Black grama, with very low adult abundance, would have been ranked as low quality habitat despite the high nest success rates that consistently occur there. Therefore, estimates of habitat quality based on adult abundance alone would misrepresent the value of these habitat types to breeding Black-throated Sparrows.

It must be noted that, while mesquite is poor habitat for supporting successful reproduction, it may be adequate to meet the maintenance needs of adults. In this sense, it may function as a refugium or holding area of sorts during the nesting season, a habitat in which less competitive, probably younger birds can gain experience, and from which potential replacements can quickly disperse to occupy territorial vacancies in higher-quality habitat (Murphy 2001).

Limitations and strengths of the method

This study utilized a novel approach of integrating plot-level data on avian demographics with a land cover map to estimate spatial patterns of abundance and nest success. This method could potentially be used for any species and/or landscape, which makes it important to understand its limitations and strengths. Our approach scaled nest success from the plot level to the landscape level in a linear fashion. We believe that the strong differences in nest success among habitats justified this approach. However, we realize that other factors may influence landscape patterns that are not accounted for at the plot level. First, landscape pattern, such as the size of habitat patches, has significant effects on nest success in other species (Hoover et al. 1995). Second, habitat edges are often zones of particularly high predation levels, yet are not recognized at the level of our plots (Gates and Gysel 1978). Additional nest monitoring across habitat edges is necessary to determine the importance of edge-related phenomena. Unfortunately, many landscape-level metrics rely on well-defined edges like those found at forest-nonforest borders. In our region of the Chihuahuan Desert, patch boundaries tend to be less well defined than in forested ecosystems, either because the vegetation is structurally similar (e.g., be-

tween crosotebush and whitethorn) or because there is a broad ecotone between habitat types (e.g., between sandsage and mesquite, or whitethorn and black grama). Consequently, such landscape-level metrics in this ecosystem may not provide as much useful information relative to forested environments.

Among the strengths of the method outlined in this paper are that it provides a method for estimating the relative contribution of habitat types to the overall population. The method furnishes spatially explicit information about trends in reproductive success and can be applied to data sets collected in many biomes. The use of the overall mean as the basis of mapping also facilitates inter-species comparisons that are a logical next step toward the goal of understanding spatial patterns of breeding habitat quality for the entire avian community. The use of reliability estimates contributes further to such comparisons and may prevent false conclusions. The emerging availability of large data sets on both avian reproductive success and land cover (e.g., The Breeding Biology Research and Monitoring Database, Martin et al. 1997; and the National Landcover Data Set, Vogelmann et al. 2001) make inter-species comparisons over broad areas increasingly possible. We believe that this spatially explicit approach enhances our ability to account for scale-specific parameters that otherwise might go undetected.

The conservation implications of understanding the spatial and temporal variability of a population are significant. Nesting success is a crucial factor driving avian population dynamics and is known to vary widely among habitats (e.g., Petit and Petit 1996, Vierling 1999). Multiyear landscape-scale studies result in a clearer understanding of variability that is inherent in population dynamics. Resource management based on knowledge of a sensitive demographic parameter such as nesting success at the landscape scale, has greater prospects of success than management based on more local data and less sensitive parameters such as abundance. Conservation actions based on abundance data alone may be worse than no action at all, as the misleading evidence may indicate management or preservation activities that degrade high quality habitat, and maintain or expand habitat that is inadequate to support nesting success levels necessary to maintain a population.

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