

MULTISCALE HABITAT ASSOCIATIONS OF THE SAGE SPARROW: IMPLICATIONS FOR CONSERVATION BIOLOGY

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Abstract. General patterns of habitat association of common shrubsteppe passerine birds, as indicated by correlations of population abundance with plot-level habitat variables, are well known. We demonstrated that for Sage Sparrows (*Amphispiza belli*) these population correlations were consistent with the behavior of individual birds as they selected patches of shrubs on which to forage. Furthermore, individuals appeared to track local-scale variation in habitat variables that changed annually. Despite these linkages, the ability of plot-level correlations to predict abundances across sites or years was weak. We also examined landscape-level correlates of species distributions. For Sage Sparrows, presence and persistence at a sampling point were related to landscape attributes such as shrubland fragment size and configuration. We concluded that failure of plot-level correlations to predict changes in abundance at broader scales stemmed both from failure to include landscape-level attributes and from failure to consider an intrinsic decoupling of population density from local habitat details. We discuss the implications of these results for conservation studies.

ASOCIACIONES DE HÁBITAT MULTIESCALA DEL GORRIÓN DE ARTEMISIA: IMPLICACIONES PARA LA BIOLOGÍA CONSERVACIONISTA

Sinopsis. Son bien conocidos los esquemas generales de asociación de hábitat de aves paseriformes comunes en las estepas arbustivas. Estos fueron indicados a través de las correlaciones de abundancia de población con variables de hábitat a nivel de parcela. Demostramos que para los Gorriónes de Artemisia (*Amphispiza belli*), estas correlaciones de población fueron concordantes con el comportamiento de aves individuales cuando escogían parcelas de arbustos donde forrajear. Además, las aves individuales parecían adoptar cambios anuales en las variables de hábitat a nivel local. A pesar de estas conexiones, la habilidad de predecir abundancias entre sitios o años usando correlaciones a nivel de parcela fue leve. Examinamos también los correlativos de distribución de especies a nivel de paisaje. Para los Gorriónes de Artemisia, se relacionaron su presencia y persistencia en un sitio de muestreo a características de paisaje tales como tamaño y configuración del fragmento de matorral. Inferimos que la deficiencia de las correlaciones a nivel de parcela para predecir los cambios en abundancia en escalas amplias, radicaba en la falta de inclusión de atributos a nivel de paisaje y en no considerar una separación intrínseca entre la densidad de población y los detalles del hábitat local. Analizamos las implicaciones de estos resultados para los estudios conservacionistas.

Key Words: *Amphispiza belli*; *Artemisia tridentata*; bird-habitat relationships; Great Basin; individual behavior; landscape; sagebrush; Sage Sparrow; shrubsteppe.

Research into the relationships between the abundance of vertebrates and certain features of their habitat, both physical and biotic, has been a cornerstone of modern ecology (Rotenberry 1981). Once such relationships are established, they can be applied both to theoretical and practical questions. Many theoretical models that seek to explain adaptive variation in animal behavior include as one of their essential elements the relationship between the number of individuals in a habitat and various aspects of environmental “quality,” quality presumably relating to the fitness of the individual within that habitat. Such information is of increasing importance to wildlife managers concerned with preserving adequate numbers of individuals or species in an environment increasingly disrupted and fragmented by humans. Indeed, the conservation value of identifying animal-habitat relationships cannot be underestimated. In the case of songbirds, their populations are usually managed by manipulating features of their habitat rather than

by directly manipulating numbers. If we can identify habitat attributes that directly or indirectly influence bird-population numbers—through the provision of food, shelter, nest sites, or protection from predators—then we can attempt to alter these attributes to achieve a desired conservation goal.

The use of information about bird-habitat relationships rests on certain assumptions, however, and it is an empirical examination of those assumptions that we examine here. This review is not exhaustive but instead relies heavily on our own research on Great Basin shrubsteppe birds, conducted over a span of almost 20 yr.

Because of the hierarchical nature of the processes involved (e.g., Allen and Starr 1982), we discuss three levels of investigation in our research. Presumably, the process of habitat selection that results in associations between a species and its habitat is an evolutionarily derived mechanism that ensures that individuals seek out and remain in the particular habitats to which

they are adapted. Thus, we expect successful individuals to reflect a phenotype that has been molded by and remains suitable for the habitat in which we find them. Expression of this phenotype may be morphological or behavioral or, more likely, both. We further expect that the patterns of habitat selection by individuals are reflected in habitat occupancy by populations. It is this emergent property of individual behavior that we assume is responsible for producing correlations between bird densities and habitat variables, and it provides the rationalization for interpreting these bird-habitat correlations in an adaptationist framework.

It is also clear that the associations between a species and habitat variables recorded on any particular plot of ground can be influenced by the nature of the surrounding landscape (O'Neill et al. 1988). In most cases, these landscape-level effects are manifest through processes related to habitat fragmentation and its effects on population dynamics (e.g., Rolstad 1991, Perneluzi et al. 1993). Increasingly, however, it is recognized that it is often the structure of an entire landscape mosaic that may be important to birds, not just the size and shape of individual fragments (e.g., Bolger et al. 1991, 1996; Pearson 1993; Knick and Rotenberry 1995). Thus, it is reasonable to expect an interaction between local- and landscape-level attributes in determining observed bird-habitat relationships.

A second major assumption is that the ecological associations we observe are stable and consistent through time and space—that patterns detected at one time and place can be generalized to other times and places. It is often assumed that natural selection for some sort of optimal habitat response is strong and continuous, and thus that populations are generally at or near equilibrium with respect to the resources with which any set of habitat variables is associated (e.g., Cody 1981, 1985).

We know that environments vary through time, however, and this can be especially true in arid regions. For example, one can easily document substantial fluctuation in the physical environment in the form of annual variation in precipitation. In arid lands these fluctuations can in turn drive enormous annual changes in primary and secondary productivity, and the difference between a dry and a wet year can be substantial (Noy-Meir 1973, Rotenberry and Wiens 1980, Cody 1981, Fuentes and Campusano 1985). This annual variation can influence the reproductive success of bird species in these ecosystems (Rotenberry and Wiens 1989, 1991). Likewise, abundance of bird species may also fluctuate substantially, both from year to year as well as from site to site within years (Wiens and Roten-

berry 1981a, Knick and Rotenberry 1995). Of primary interest is whether these changes in bird abundance are associated with changes in habitat. In other words, are population numbers coupled to environmental variation, and do fluctuations in animal numbers represent a "tracking" of changes in habitat?

Clearly, this is an important question for both scientists and conservationists to consider: are individuals and populations consistent and predictable in their habitat associations through time and space? Do populations track environmental variation in a consistent fashion at the spatial and temporal scales over which habitat relationships are traditionally determined? There may be a variety of reasons why species abundances might not be associated with changes in habitat or its associated resources (see below). If so, population densities may become "decoupled" from habitat parameters that might otherwise influence changes in local population sizes. If this is the case, what are the implications for populations, and how do we go about studying them? Our studies of birds in shrubsteppe habitats of the northern Great Basin can shed some light on these issues.

STUDY AREA AND SPECIES

Our research was conducted in arid shrubsteppe habitat of western North America, primarily in the northern Great Basin and Snake River Plains. This shrubsteppe is dominated by sagebrush (*Artemisia* [primarily big sagebrush (*A. tridentata*)]), saltbush (*Atriplex*), rabbitbrush (*Chrysothamnus* [particularly gray rabbitbrush (*C. nauseosus*) and green rabbitbrush (*C. viscidiflora*)]), and greasewood (*Sarcobatus*) among the shrubs and by bluegrass (*Poa*), wheatgrass (*Agropyron*), fescue (*Vulpia* [= *Festuca*]), and brome (*Bromus*) among the grasses.

In this paper we restrict our analyses to habitat relationships of the Sage Sparrow (Emberizidae: *Ampelisca belli nevadensis*), a common and widespread inhabitant of shrubsteppe. In the Great Basin this species is found mainly in association with sagebrush. Individuals weigh about 20 g and, where present, densities range from about 15 to 180 individuals per square kilometer (Wiens and Rotenberry 1981a). This subspecies is migratory, wintering in arid shrublands from central Nevada through northern Mexico (Martin and Carlson 1998).

PLOT-LEVEL ASSOCIATIONS

The most common method of establishing bird-habitat correlations is to census a series of representative plots or transects, usually ranging in area from 5 to 50 ha (Wiens and Rotenberry 1981b, Rotenberry 1982). A variety of habitat variables, both physical and biotic, are scored on the same plots or transects. Habitat relationships then are estimated using correlations between species abundance and environmental variables,

frequently employing a variety of bivariate and/or multivariate approaches (Wiens and Rotenberry 1981b).

As an example, we surveyed 14 "original" sites scattered throughout the northern Great Basin of southeastern Oregon and northern Nevada and selected to represent an array of common shrubsteppe habitats (Wiens and Rotenberry 1981a). At each site we censused birds and measured habitat features for 3 successive years. Birds were surveyed along 600-m Emlen-type transects (Emlen 1977). Percent coverage of each shrub species was determined from 10 100-m transects arrayed perpendicular to the bird transects and then reduced to independent axes using principal components analysis. We derived relationships of Sage Sparrows to habitat variables using both bivariate and multiple correlations. Although we also measured a variety of other habitat attributes, we discuss below only those variables associated with shrub coverage because they yielded the strongest patterns with widespread shrubsteppe bird species (Wiens and Rotenberry 1981a).

Sage Sparrow abundance was highly correlated with sagebrush coverage ($r = 0.61$, $df = 40$, $P < 0.001$; Wiens and Rotenberry 1981a). Additionally, substantial variation in the distribution of Sage Sparrows was statistically explained by a multiple regression of abundance on shrub-species components ($R^2 = 0.70$, $N = 42$, $P < 0.001$; Rotenberry 1986). The pattern of significance of regression coefficients again implicated sagebrush as the dominant covariate. A similar association was shown by Dobler (1994) using a different approach. Examining 55 10-ha transects scattered throughout southeastern Washington, Dobler noted that transects with Sage Sparrows had significantly higher coverage of sagebrush than those without. Taken together, these observations, based on plot-level analyses, lead to the conclusion that Sage Sparrow population levels in shrubsteppe habitat are strongly associated with sagebrush coverage.

INDIVIDUAL-LEVEL ASSOCIATIONS

The strength of population-level patterns in Sage Sparrows led us to investigate the behavior of individual birds, to see if individuals acted in a manner consistent with those patterns (Wiens 1985, Rotenberry and Wiens 1998). We assumed that population-level correlations reflected the aggregate response of individuals to habitat variation. We observed individual birds in a study area and quantified their behavior throughout a range of habitat variations, which we also quantified. We changed methods of measuring habitat variables to reflect the fact that we changed the scale of our focus from 600-m transects to the

TABLE 1. PATCH SELECTION BY SAGE SPARROWS

Patch component	Selection
I: size	large***
II: % sage vs. % green rabbitbrush	sage***
III: shape	compact, densely foliated***
IV: % sage vs. % gray rabbitbrush	sage**

Note: Patch components are independent axes of variation in patch attributes determined from principal components analysis of 900 randomly selected patches. Selection denotes direction and significance of difference between randomly selected and bird-selected ($N = 181$) patches. See Rotenberry and Wiens 1998 for details.

** $P < 0.01$, *** $P < 0.001$.

few square meters in the vicinity of an individual bird. Here we emphasized the attributes of individual or small clusters of shrubs ("patches"), most of which were less than 2 m in canopy diameter. As before, we concentrated on both floristic and physiognomic variables. We then asked if birds used these patches in a non-random fashion.

For each of 3 yr, we randomly selected 300 patches in an 800- × 300-m sampling area to characterize the structure and composition of patches available to foraging birds. A patch was defined as a more or less contiguous association of living and/or standing dead shrub material, distinctly set off from neighboring patches and usually consisting of one or a few closely imbricated shrubs. We measured variables relating to the size, shape, and shrub-species composition of each patch. During mornings, we followed individual Sage Sparrows and marked the patches in which they foraged. During afternoons, we returned to the plot and measured the same physical and compositional attributes of bird-selected patches that we had measured on randomly selected patches.

We summarized independent patterns of covariation of attributes of randomly selected patches using principal components analysis. We scored bird-selected patches on those components and then compared those average scores to the random ones using one-way analysis of variance (ANOVA) and multiple analysis of variance (MANOVA).

Sage Sparrows did indeed use habitat nonrandomly (Table 1; Rotenberry and Wiens 1998), and the pattern of patch use by individuals was generally consistent with the population patterns noted before: individuals used sagebrush much more often than either green or gray rabbitbrush, were associated with larger shrubs, and were seen much more frequently in compact and densely, rather than sparsely, foliated shrubs. Furthermore, because we conducted this study

over a 3-yr period during which precipitation (and hence patch attributes) varied considerably, we documented that patterns of use by birds changed in concert with variation in the patch variables we measured. For Sage Sparrows, the average scores on patch components not only varied significantly among years (MANOVA: $F = 11.11$; $df = 4, 1076$; $P < 0.001$), but these scores were also significantly correlated with changes in random patch components ($r = 0.93$, $df = 6$, $P < 0.001$). In other words, not only did individual birds use features of the habitat non-randomly, they also tracked changes in those features from one year to the next.

PROJECTING BIRD-HABITAT RELATIONSHIPS THROUGH SPACE AND TIME

Results from the individually based studies, when combined with the strong patterns of correlations noted at the plot level, led us to expect that we would see variation in avian population numbers that closely matched temporal and spatial variation in habitat parameters. We expected that populations would be consistent in their expression of the detailed habitat associations described by the various correlations and that we could take those correlations, combine them with values of habitat variables at any given site or time, and accurately predict bird numbers.

To assess temporal consistency, we continued to census birds and measure habitat variables on a representative subset of five of our original sample sites for 4 yr or longer (Rotenberry 1986). We then ran the new habitat measurements through the previously derived multiple regression model (see above; Rotenberry 1986) to generate predicted bird abundances. We compared predicted with observed abundances; if the correlation was high, we inferred consistency in the expression of the details of habitat relationships through time.

For Sage Sparrows, the correlation between predicted and observed abundances was essentially nonexistent ($r = -0.07$, $df = 18$, $P > 0.75$; Rotenberry 1986). What was previously the best-fitting model (Sage Sparrow abundance and shrub-species principal components), with an R^2 of 70%, now explained less than 1% of the variation in Sage Sparrow abundances. This poor fit was not the result of some peculiarity of the sites selected for continued sampling, as a cross-validation correlation between predicted and observed abundances during the initial sampling period was 0.80 ($df = 13$).

To assess the degree of spatial consistency in habitat association, we selected four additional shrubsteppe sites that were sampled during the original time period but were not included in the

original analysis. Two of these were located in the same general area as the original sites, and two were located in similar habitat but about 500 km north in southeastern Washington (Rotenberry 1986). As before, we applied the original multiple regression model to the habitat measurements for the new sites to generate expected bird abundances which could then be compared to observed abundances. Because the sample size was small, however, correlation coefficients were too weak to detect a good relationship; instead, we used a t-test (each value predicted from the regression analysis had an associated standard error). If observed abundances were close to predicted abundances, a t-test would not be significant; if the t-test was significant, there would be a serious discrepancy between observed and predicted abundances.

Results from these tests were inconsistent. The model predicted accurately for Sage Sparrows at both of the distant sites (i.e., the probability that the observed abundance at a site was sampled from the population estimated by the multiple regression was > 0.05) but failed at both of the near sites (the same probability was < 0.05 ; Rotenberry 1986).

Finally, we wanted to know what happens when we intentionally modify the environment in a quasi-experimental design: do Sage Sparrows respond in ways that are consistent with their previous habitat responses and thus are predictable from the original correlations? We were afforded an excellent opportunity to address this question by assessing the effects of a large-scale habitat manipulation "experiment" conducted by the Oregon State Land Board. One of our original plots (Guano Valley) was included in an approximately 75-km² area that was sprayed with a broad-spectrum herbicide in an attempt to eradicate sagebrush. The area was subsequently chained and reseeded with non-native grasses (mainly crested wheatgrass [*Agropyron desertorum*]) to make it more suitable for cattle-grazing. The herbicide treatment came at the end of our initial 3-yr monitoring period, so we continued to visit the site to survey habitat and birds for an additional 3 yr postspray (Wiens and Rotenberry 1985). The treatment had an immediate effect: sagebrush coverage was much reduced and there was a substantial change in the structure of the habitat (Wiens and Rotenberry 1985). Even after 4 yr the site had not recovered; sagebrush coverage remained low, whereas green rabbitbrush and grasses had increased considerably, filling in much of the previously bare areas between shrubs.

How well did Sage Sparrows respond to this manipulation given their previous habitat relationships? Not well at all, at least in terms of

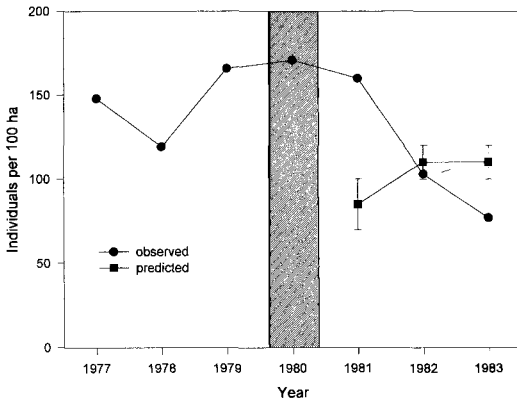


FIGURE 1. Observed abundance of Sage Sparrows before and after major habitat modification (herbicide, chaining, reseeding) at Guano Valley, Oregon. Predicted values (± 1 SE) from multiple regression of Sage Sparrow abundance on shrub-species components ($R^2 = 0.70$, $N = 42$, $P < 0.001$; Rotenberry 1986). Hatched area denotes year in which treatment was applied.

consistency with predictions from the previously derived multiple regression model (Fig. 1). Despite the fact that the observed value for 1982 fell within the 95% confidence limits of the predicted abundance, there was a poor fit between the two, and trends between predicted and observed abundances were in opposite directions.

We conclude, therefore, that although we can develop models of relatively high statistical significance that account for a high proportion of variation in Sage Sparrow abundance, the habitat associations they describe are insufficient to project Sage Sparrow abundance accurately through time or space, either as a result of natural changes or of environmental modification.

INTERACTION BETWEEN LOCAL- AND LANDSCAPE-LEVEL ATTRIBUTES

More recently we have examined the relationship between landscape-level attributes and their potential influence on shrubsteppe bird abundances, particularly how variation in the landscape context of sampling points may appear to alter patterns of association between bird abundance and local-level habitat variables (Knick and Rotenberry 1995). These studies are based on 183 sample points scattered over approximately 200,000 ha in the Snake River Birds of Prey National Conservation Area in southwestern Idaho. In addition to counting birds (5-min unlimited-radius point counts), at each point (plus 213 additional random points) we measured local vegetation characteristics (percent cover of individual shrub species and some

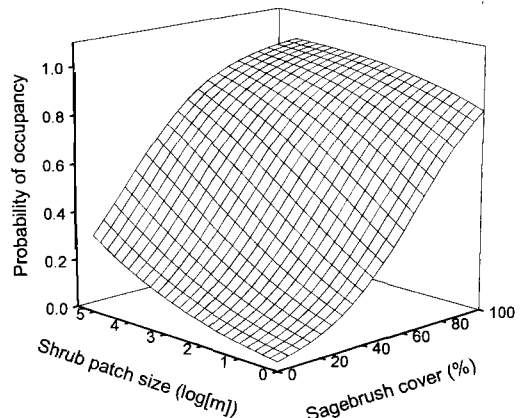


FIGURE 2. Relationship between probability of occupancy and sagebrush cover and shrub patch size for Sage Sparrows. The surface was developed by varying patch size and sagebrush cover and setting spatial similarity and shadscale coverage to systemwide values, using a logistic regression of sparrow presence/absence on local and landscape habitat variables (Knick and Rotenberry 1995).

grass/shrub cover types) on transects scattered throughout a 4-ha area. We determined landscape characteristics for a 1-km radius around each sampling point from a detailed habitat classification map derived from satellite imagery (Knick et al. 1997). Variables obtained from this large-scale (>300 ha) analysis included average size of shrubland or grassland patches, proportion of landscape in shrubland or grassland, and spatial similarity (related to fractal dimension; Palmer 1988). We used logistic regression of Sage Sparrow presence/absence to develop a habitat-selection model based on both local and landscape variables (e.g., Manly et al. 1993).

The probability of the presence of Sage Sparrows at a sampling point increased with increasing spatial similarity of sites (i.e., decreased habitat heterogeneity over the landscape scale), increasing shrubland patch size, and increasing local coverage of sagebrush and shadscale (*Atriplex confertifolia*; Fig. 2). Standardized estimates of regression coefficients implied that landscape features were more important in predicting presence than was coverage of individual shrub species, and that sagebrush was more important than shadscale (Knick and Rotenberry 1995). Furthermore, it was clear that landscape features interacted with local habitat variables to alter the expression of probability of occurrence. For example, the form of the relationship between percent cover of sagebrush and probability of occupancy by Sage Sparrows, although always positive (hence consistent with both plot-

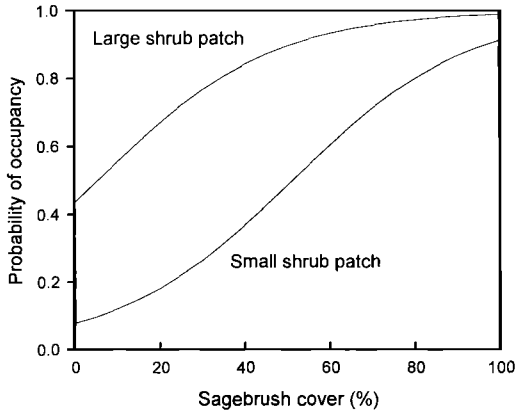


FIGURE 3. Relationship between probability of occupancy by Sage Sparrows and local sagebrush cover for large (10^5 m²) and small (10^2 m²) average shrub patch sizes in a landscape. These curves are slices through the surface in Fig. 2.

and individual-level results), changed shape as a function of shrub patch size (Fig. 3). Thus, differences in the structure of landscapes in which local plots are embedded may produce differences in apparent bird-habitat relationships derived from those local plots.

As we sampled a subset of 66 point counts for 4 consecutive years, we were also able to assess habitat correlates of temporal persistence. We classified points into three categories based on Sage Sparrow occurrence rates: unoccupied (never present), marginal (present 1–2 yr), or occupied (present 3–4 yr). We then contrasted sites with different occupancy rates using canonical discriminant analysis applied to the set of local and landscape habitat variables.

There were significant differences among habitat attributes associated with temporal persistence (MANOVA: $F = 4.97$; $df = 2, 63$; $P < 0.001$), and the first canonical axis (the only one statistically significant at $P < 0.05$) explained 63% of the variation in occupancy rates (Fig. 4). Persistence increased with increasing local cover of sagebrush and shadscale, increasing proportion of the landscape in shrubland and the minimum size of shrubland patches, and decreasing local cover of Russian thistle (*Salsola iberica* [= *kali*]), a species associated with severe habitat disturbance. As before, landscape variables were as important as local variables in determining habitat associations.

SUMMARY AND CONCLUSIONS

Although the behavior of individual Sage Sparrows was generally consistent with bird-habitat associations derived from plot-based cor-

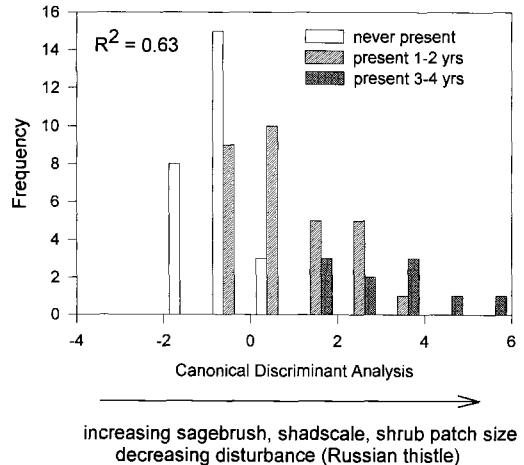


FIGURE 4. Histogram of canonical scores for sites where Sage Sparrows were observed in 0, 1–2, or 3–4 yr at 66 sites surveyed in 3 consecutive years. Interpretation of canonical discriminant axis is based on correlations of original variables with canonical scores.

relations of population abundances, those population-level relationships did not match habitat variation projected through space or time, or via habitat manipulation. From these observations and subsequent analyses, we draw two general conclusions.

First, although there appears to be a basic component to habitat association in Sage Sparrows (i.e., they are rarely found in areas in the Great Basin lacking sagebrush), once this coarse habitat preference is expressed, fluctuations in density become largely decoupled from the details of habitat variation, both among sites and years. Thus, although there exist individual behavioral responses that are generally appropriate to environmental variation, these do not translate readily into strong patterns linking variations in population density with variation in habitat. Such linkages may be eroded because this species is migratory; it breeds in the Great Basin, where we study it, but winters in the southwestern United States and northern Mexico, up to 2,000 km farther south (Martin and Carlson 1998). We and others (e.g., Pulliam and Parker 1979, Rotenberry and Wiens 1980, Wiens and Rotenberry 1981b, Dunning and Brown 1982, Dunning 1986) have proposed that sizes of shrubsteppe passerine populations are most likely regulated during winter. We assume that most mortality for postfledging and adult shrubsteppe birds occurs during migration and in winter, as is the case for many migrant passerines (e.g., Sherry and Holmes 1995). Thus, a breeding territory may become empty (and hence influence

estimates of population density) not because of its intrinsic character but because its previous owner perished 1,500 km to the south. If breeding-bird densities are not near saturation, as seems to be the case in our system (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981a, Wiens 1985), then otherwise suitable territories may remain unfilled for several years. The superposition of strong site tenacity for returning breeders, even in the face of substantial habitat alteration (Wiens and Rotenberry 1985, Wiens et al. 1986), further exacerbates this decoupling.

Our second conclusion is that landscape-level features are as important as local-level features in determining patterns of local occupancy and abundance, as well as temporal persistence, of Sage Sparrows and other shrubland species (Knick and Rotenberry 1995, 1999). Perhaps more importantly, differences in the structure of landscapes in which local study plots are embedded may produce differences in apparent bird-habitat relationships derived from local plots. This may account not only for the inability to project plot-level relationships through time and space (because relevant habitat [landscape] variables have been omitted in deriving those relationships) but also for discrepancies in relationships observed between different studies (e.g., Wiens and Rotenberry 1981a, Petersen and Best 1987) or in the same study over a large geographical area (e.g., Collins 1983).

The foregoing observations carry important implications for how we study bird populations in a conservation context. Many birds breeding in temperate North America are migratory and thus manifest many of the same traits as Sage Sparrows. Because most bird species in North America migrate, studies of these species concern "open" ecological systems. Conditions far beyond the local plot's boundaries influence these birds on their breeding grounds. Instead of finding breeding populations in equilibrium at carrying capacity, we might expect to find a pattern of habitat occupancy not well explained in terms of local biotic conditions. The conservation and management implications are clear: attempts to frame management policies based on assessing the effects of various treatments (e.g., herbicide application in our case), or any other scheme that alters habitat structure and composition, will require much more than a single before-and-after survey to determine those effects. Because systems such as shrubsteppe may be variable even when unaltered, it will take more than a single survey to determine the "normal" state of such systems prior to treatment (Wiens 1981). Clearly, natural-resource management programs will require a long-term perspective. Constraints imposed by the immediate need for

management decisions prompted by political considerations may favor short-term studies or experiments as being better than none at all. In any system characterized by any of the attributes we have discussed, however, short-term studies may yield incomplete and even misleading results. Thus, we strongly support the caveat brought forth by Petersen and Best (1999): inadequate study design and duration can lead to inaccurate conclusions and misdirected conservation efforts.

Although our principal argument is for the necessity of considering landscape-level influences on habitat associations, we do not mean to imply that research focused on individual breeding birds should be secondary. Although individually based patterns of habitat associations may be too variable to predict bird abundances effectively, they are nonetheless key to understanding how organisms are adapted and how they interrelate with other species. On the breeding ground we can still study foraging behavior, mate selection, predator avoidance, reproductive success, and a host of other features that contribute to the fitness of individuals and populations. Although populations of these individuals may not be in equilibrium with respect to habitat and its resources, this does not mean natural selection has stopped shaping other adaptations of these species. Perhaps most importantly, it is at the local level that we are most likely to determine the biological mechanisms that produce landscape-level associations (e.g., nest predation, nest parasitization; Johnson and Temple 1990).

FUTURE DIRECTIONS

The analyses presented above suggest three major avenues for future research. The first is to test the ability of the large-scale logistic regression and discriminant models to predict occurrences of Sage Sparrows through time and space. Although we are optimistic that the present models accurately capture the appropriate level at which habitat associations are most likely to be repeatable (Rotenberry 1986), we were previously optimistic about the abilities of the plot-level relationships to be projected as well. Our second goal is to document more carefully the apparent geographical variation in local habitat associations. We propose to do this by examining a variety of data sets containing vegetation and bird-abundance data collected by several different investigators throughout the Intermountain West. Finally, we are undertaking a study to examine potential mechanisms acting at the level of the individual that ultimately may be responsible for both plot- and landscape-level patterns in abundance. Our initial focus is on

reproductive success as a function of local and landscape habitat features. We believe that by combining these three lines of investigation, we may approach a better understanding of the relationships among individual behavior, habitat selection, and population dynamics in Sage Sparrows.

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