HABITAT FRAGMENTATION AND THE ABUNDANCES OF VERTEBRATES IN THE FLORIDA SCRUB

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Abstract. Based on presence/absence of species, we proposed previously that large fragments of the Florida sand pine scrub habitat do not possess greater conservation value for vertebrates than do archipelagos of small and medium-sized fragments. We reexamined the values of fragments of different sizes, based this time on abundances of species. We asked whether abundances tend to decrease with decreasing scrub size or are more strongly related to other scrub attribute(s).

We censused vertebrates with trap arrays and by direct observation, and we measured 13 potentially important environmental attributes related to area, isolation, and habitat structure in 16 scrubs distributed along the Lake Wales Ridge of central Florida. We correlated abundance of species with the 13 attributes. We calculated the evenness of relative abundance distributions and grouped scrubs based on the shapes of relative abundance distributions. We determined whether or not members of different groups of scrubs possessed different values for any attribute. Finally, we examined both densities of individuals and dispersions of species among large, medium, and small scrubs.

Abundance was related to many of the attributes. Abundances of 11 of 18 species were correlated positively with area. Percentage of variation explained by area generally was low, and several of the rare species apparently maintain relatively large populations in small scrubs. Abundances of five species were correlated negatively with measures of isolation. Abundances of three species were correlated both positively and negatively with measures of habitat structure. Environmental attributes related to isolation and habitat structure were correlated most strongly with both evenness and groupings of relative abundance distributions. Total density of individuals (i.e., numbers of captures per trap array) could not be shown to differ among scrubs of different sizes. Individually, the species that reached their highest densities in relatively small scrubs often were the ones considered to be rare. Spatial distributions of species tended to become more homogeneous as area decreased, but the strength of this effect varied among species, perhaps accounting, at least in part, for the different relationships between abundance and area among species.

Our results could lead to broad generalizations that seem to be relevant to scrub conservation. For example, because most species are relatively abundant in large scrubs, large scrubs should be selected for reserves over small ones. We suggest, however, that our results actually best serve as a caution about the use of generalizations, based on data from one or a few species, for conservation planning in general. Our results clearly show that the benefits gained for certain species from focusing on the preservation of larger scrub fragments could be offset by harm done to other species, especially rare species. We conclude, therefore, that selection of a system of scrub reserves should be based, in large part, on knowledge of the biologies of as many of the resident organisms as possible. We suggest, however, that any reserve selection procedure for the scrub habitat probably is outmoded, and that ecologists should not even engage in debate about the conservation value of small scrub fragments. When a habitat has declined as precipitously as scrub has, and truly large remaining fragments are, at best, extremely rare, then smaller fragments are likely to be of considerable value, no matter how they compare to larger fragments.

Key words: abundance; Florida scrub; fragmentation; habitat structure; isolation; scrub, Florida; vertebrates.

INTRODUCTION

Can as many species be preserved if conservation efforts focus on smaller habitat fragments rather than on larger ones? The answer for the vertebrates of the critically important sand pine scrub (“scrub”) habitat of peninsular Florida (Eisner et al. 1995, Noss and Peters 1995, Dobson et al. 1997) appears to be “yes” (McCoy and Mushinsky 1994). For the suite of scrubs that we have studied, archipelagoes of small and medium-sized fragments of scrub habitat supported at
least as many vertebrate species as single large fragments. Despite the presence of a strong species–area relationship and substantial nestedness among the vertebrate compositions of these scrubs, no species, not even rare ones, could be shown to have been excluded preferentially from small scrubs (see Doak and Mills 1994). This conclusion fuels the on-going debate about the conservation value of small habitat fragments (e.g., Reznick 1987, Burkey 1989, 1995, 1997, Howe and Davis 1991, McNeill and Fairweather 1993, McCoy and Mushinsky 1994, Shafer 1995, Ghazoul 1996, Guindon 1996, Turner and Corlett 1996, Mushinsky et al. 1997, Schwartz and van Mantgem 1997), and, therefore, it needs additional critical examination.

Our previous conclusion, that larger fragments of the Florida scrub do not necessarily possess greater conservation value for vertebrates than groups of smaller fragments, was based solely on an analysis of the presence/absence of species in scrubs that were treated as replicates within size categories. The values of large and small fragments could have been compared in several other ways, however (McCoy and Mushinsky 1994; see Wilcox and Murphy 1985, Caughley 1994). We could have made the comparison based, for example, on abundances of individual species (e.g., Haila and Hanski 1984, Haila et al. 1987, 1993a, Robinson et al. 1992, Schemske et al. 1994 and references therein) or on autecological characteristics of individual species that contribute to their vagilities and probabilities of local extinction (e.g., Graves and Gotelli 1983, Gotelli and Graves 1990, Cowling and Bond 1991, Pettonen and Hanski 1991, McCoy and Mushinsky 1992a), rather than on presence/absence of species. We address the first of these possibilities here: we ask whether our previous conclusion would need modification if abundances of species were taken into account. Specifically, we determine whether abundances of species tend to decrease with decreasing scrub size and, if they do not, whether the deviations can be related to other scrub attribute(s).

We realize that short-term ("snap-shot") estimates of abundances of species need not reflect long-term viabilities. Prior to the mid-1940s, very little development of the scrub habitat had occurred and, therefore, the habitat was minimally fragmented. For the suite of scrubs that we have studied, the rate of area reduction of a fragment since either the mid-1940s or the mid-1960s is strongly negatively correlated with its current area (McCoy and Mushinsky 1994). These observations suggest that current relationships between area of fragments and abundances of species substantially reflect the changes occurring as a result of fragmentation of the scrub habitat over the past 40–60 yr. How well these current relationships reflect future changes is, of course, unknown, but the fact that the future potentially is a very short one for the scrub habitat may well render the issue of long-term viability moot (e.g., Kautz 1993).

METHODS

Study sites

Our study sites were 16 scrubs distributed along a 70-km segment of the southern Lake Wales Ridge of Florida, USA, from ~5 km south of Frostproof (Polk County) to ~22 km south of Lake Placid (Highlands County). Three of the scrubs (HEN, ARC, AB3) were large (~200 hectares), four (AB1, HH1, AB2, JOS) were medium (25–50 hectares), and nine (CHU, HH2, JUN, EGL, LAK, BAR, COL, DUF, CUT) were small (10 hectares or less). Our choice of study sites reflects the fact that most remaining fragments of scrub are rarely even as large as a few hundred hectares (USFWS 1993). Detailed descriptions of the study sites have been presented previously (McCoy and Mushinsky 1994). General information on the scrub (sand pine/rosemary/scrub oak) habitat and its complement of vertebrates can be found in Christman (1988), Fernald (1989), Richardson (1989), and Myers (1990). The characteristic vertebrates of the scrub habitat (i.e., species that regularly include it, if available, within their home ranges), include eight amphibians, 30 reptiles, 19 mammals, and 39 birds (Christman 1988).

We measured 13 potentially important environmental attributes of each scrub (McCoy and Mushinsky 1994; also see Adler and Wilson 1985, Freemark and Merriam 1986, Rolstad 1991, Bolger et al. 1997). Complete tabulations of data for these attributes are in McCoy and Mushinsky (1994) and Mushinsky and McCoy (1995). Three attributes are related to size: current area, area reduction since the mid-1940s, and area reduction since the mid-1960s. We evaluated area reduction over time with a temporal series of aerial photographs of each scrub. Aerial photographs of Highlands County taken in the 1940s, 1960s, and 1980s were made available to us by Archbold Biological Station, and aerial photographs of Polk County, taken in the same decades, were made available to us by the Florida Department of Transportation and the Polk County Property Appraiser. Photographs of the scrubs were traced, and the tracings were digitized with SIGMASCAN software. We calculated the area of each scrub from tracings and plotted the areas against time to obtain each scrub’s rate of decline in area. We minimized the effects of distortion in the aerial photographs by using distances between landmarks, measured on the ground, to scale the estimates of scrub area. Seven attributes are related to isolation: distance to the nearest other scrub, distance to the nearest larger scrub, presence/absence of potential “corridor” habitats (habitats with sandy substrate) between scrubs, number of habitats surrounding scrubs (habitats that we recognized were scrub, other upland, low pine flatwoods, wetland, citrus, and disturbed; see Humphrey et al. 1985, Myers and Ewel 1990), percentage of surrounding disturbed land, presence/absence of surrounding undisturbed upland, and distance to the nearest permanent water. The final three attri-
...density and area (see related to area, without scaling up from one or a few individuals. Using cumulative catches, we could determine if abundance, rather than density, was directly related to area, without scaling up from one or a few samples. Later, we also address the relationship between density and area (see Methods: Calculating within-scrub density and dispersion).

We trapped scrub vertebrates for 2 yr: 1989 and 1990. Trapping effort was apportioned among three “thermal” seasons, of 4 mo each, to accommodate known differences in the activities of scrub vertebrates. These three seasons, winter (November, December, January, and February), spring/fall (March, April, September, and October), and summer (May, June, July, and August), were each divided into two 2-mo sampling periods. When open, traps were checked for captured animals daily. During the first two sampling periods of 1989, we trapped eight scrubs (two large, two medium, and four small) for 10 d each. During the remainder of 1989, we sampled all four medium and eight small scrubs and two of the three large scrubs in each sampling period. We discontinued trapping the large scrub at Lake Arbuckle (AB3) at the end of 1989, because continued sampling there was unlikely to yield new species, and we added an additional small scrub (Duffer’s = DUF) in its place. In 1990, we instituted a more comprehensive trapping regime. We shortened the duration of trapping in each sampling period, from 10 to 7 d, a reduction that our first year’s data indicated to be insignificant. We trapped approximately half of the scrubs for 7 d, and the remainder for the following 7 d in each sampling period. Because they are incomplete, we shall not use the 1989 capture data to make comparisons among scrubs, but we shall use them for post hoc corroboration and for other suitable purposes.

We have complete data from 1990 for 15 of the 16 scrubs: the large scrub AB3 was not trapped in 1990. For all of the three medium (AB1, AB2, JOS) and two small (LAK, COL) scrubs that we trapped for the full 24 mo, frequencies of capture among species were very similar between years ($r_s > 0.69$, $P < 0.05$, $n = 11–22$).

The capture data were used to estimate abundances of vertebrate species trapped in our suite of scrubs over the 2-yr sampling period. To use capture (or “count”) data directly, one must assume that the sampling fraction (i.e., number of individuals sampled per number of individuals available to be sampled) is identical among locations and over time (Nichols 1992). To avoid having to make this assumption, one can use recaptures of marked individuals instead (see White et al. 1982). We had marked individuals of 22 species of amphibians, reptiles, and mammals, and so, potentially, we could have estimated abundances from marked recaptures for all of them. Amphibians and reptiles had been given unique numbers by toe clipping (amphibians, lizards) or caudal scale clipping (snakes), and mammals had been fitted with uniquely numbered ear tags. We realized early on, however, that not very many of the 22 species were going to be captured and/or recaptured in sufficient numbers to produce reliable estimates. We also realized, therefore, that it would be necessary to use count data, and we determined that they could provide valid estimates of abundances (see Results: Vertebrate abundances).

The abundances of two important characteristic scrub species could not be captured in our trap arrays. We estimated abundance of Gophers polyphemus (gopher tortoise) from the number of burrows. We walked a total of 264 transects, each 300 meters long and seven
meters wide, in the 16 scrubs, searching for burrows. We recorded the number of “active,” “inactive,” and “abandoned” burrows encountered on each transect, and then converted our counts of burrows to estimates of numbers of individuals, using the method of McCoy and Mushinsky (1992b). We estimated abundance of *Aphelocoma coerulescens* (Florida Scrub Jay) by observing the activities of this conspicuously territorial bird (Woolfenden and Fitzpatrick 1984) on several visits.

Relating vertebrate abundances to scrub attributes

We used a subset of the 28 vertebrate species captured/counted in 1990 in the analyses. The subset included the 18 species that were represented by >40 individuals each. These species were *Bufo querccius* (oak toad), *Bufo terrestris* (southern toad), *Gastrophyne carolinensis* (narrow-mouth toad), *Gopherus polyphemus* (gopher tortoise), *Anolis carolinensis* (green anole), *Chenomedusus seileneatus* (six-lined racerunner), *Eumeces egregius* (mole skink), *Eumeces ineceptatus* (southeastern five-lined skink), *Neoseps reynoldsi* (sand skink), *Sceloporus woodi* (Florida scrub lizard), *Cemophora coccinea* (Florida scarlet snake), *Coluber constrictor* (southern black racer), *Masticophis flagellum* (eastern coachwhip), *Tantilla recta* (crowned snake), *Aphelocoma coerulescens* (Florida Scrub Jay), *Cryptotis parva* (least shrew), *Peromyscus polionotus* (oldfield mouse), and *Podomys floridanus* (Florida mouse). The ten excluded species were represented by fewer than 25 individuals each. These species were *Eleutherodactylus planirostris* (greenhouse frog), *Rana capito* (gopher frog), *Scaphiopus holbrooki* (eastern spadefoot toad), *Ophisaurus ventralis* (eastern glass lizard), *Rhineura floridana* (Florida worm lizard), *Blarina carolinensis* (southern short-tailed shrew), *Ochotomys nuttalli* (golden mouse), *Peromyscus gossypinus* (cotton mouse), *Reithrodon tomis humilis* (eastern harvest mouse), and *Sorex longirostris* (southeastern shrew). For species with low abundances, such as these ten, it seems reasonable to use presence/absence data (see McCoy and Mushinsky 1994). Only one rare (sensu McCoy and Mushinsky 1992a) vertebrate, *R. capito*, was not included among the 18 species that we selected.

We related abundances of the selected species in our suite of scrubs to the 13 environmental attributes. We identified relationships with two methods. The first method correlated the estimates of abundance with the various attributes and the second correlated the estimates of abundance with the relative positions of scrubs ordered by habitat structure, both using Spearman’s rank correlation analysis. The second method allowed the attributes related to habitat structure to be considered simultaneously. We used Principal Coordinates Analysis (SYN-TAX IV program PRINCOOR [Podani 1990]) to order the scrubs. The first coordinate, which explained 89.9% of the variation, ordered the scrubs...
bers of species in less-rich scrubs that are very similar to one-another, but they are nearer the numbers of species actually observed. The Kolmogorov-Smirnov test could not distinguish between 19 of the 120 pairs of relative abundance distributions, for \( P \leq 0.05 \). Among these 19, were five pairs (out of a possible ten) involving the large and medium scrubs AB1, AB2, AB3, ARC, and HH1. With the exception of ARC, these scrubs form the same group as one of those identified by rarefaction analysis. The relative abundance distributions at HEN and JOS are different from one another, and from the other large and medium scrubs. The observed number of coincidences, three pairs of scrubs, of accurate predictions of numbers of species by rarefaction analysis and determination of similarity of relative abundance distributions by the Kolmogorov-Smirnov test was not likely to have occurred by chance (joint hypergeometric probability = 0.015). Two groups of large and medium scrubs resulted, therefore, from the RA-KS method: (1) AB1, AB2, AB3, HH1 and (2) HEN, JOS.

The second method (dissimilarity method) was based on differences between actual and expected relative abundances (cf. Haila and Hanski 1984). Dissimilarities between pairs of scrubs were calculated by assigning a value of 1 for each match (i.e., when observed number of individuals of a species minus expected number was either positive, negative, or zero for both scrubs), one-half for each partial match (i.e., when observed number of individuals of a species minus expected number was either positive or negative for one scrub and zero for the other), and zero otherwise, and then summing the values for all species. We then grouped scrubs with simple polar ordination, based on dissimilarities. We calculated expected abundances by identifying the scrub with the largest estimated abundance, and then scaling abundances in all other scrubs relative to it, based on their numbers of trap arrays (Fig. 1). For example, if a species was captured most often at AB3 (17 arrays), then we would expect 10/17th’s as many individuals to be captured at ARC (10 arrays), over the same time period, all else being equal. Three groups resulted from the dissimilarity method: (1) the medium scrub JOS and the small scrubs COL, EGL, JUN, and LAK, which were associated closely with the large scrub HEN; (2) the medium scrubs AB1 and AB2 and the small scrubs BAR, CHU, and HH2, which were associated closely with the large scrub ARC; and (3) the small scrubs CUT and DUF, which were the two smallest scrubs. The medium scrub HH1 was intermediate between groups 1 and 2.

Similar groups of scrubs, based on relative abundance distributions of resident vertebrate species, were defined both by using the RA-KS and dissimilarity methods. The two methods allowed unambiguous placement of 14 of the scrubs into groups: (1) COL, EGL, HEN, JOS, JUN, LAK; (2) AB1, AB2, AB3, BAR, CHU, HH2; and (3) CUT, DUF. They were equivocal, however, in placement of the other two scrubs, ARC and HH1. We related the groups of scrubs identified by the two methods to the environmental attributes by determining whether or not members of different groups also possessed different values for any of the attributes, with the Wilcoxon rank sum test.

Calculating within-scrub density and dispersion

Interpretation of the distributions of species hinges, at least in part, on the densities and dispersions of individuals. For example, the theory surrounding species-area relationships assumes that density of individuals across species is constant over the range of areas examined (Coleman 1981), and because we know that such constancy often is not the case (see Nilsson 1986 and references therein, Møller 1987), the theory likely is simplistic. Previously, we documented differences in both density and dispersion of individuals related to both habitat area and isolation for G. polyphemus (Mushinsky and McCoy 1994, Mushinsky et al. 1997; also see Schoenewald-Cox and Buechner 1991, Schoenewald-Cox et al. 1991), and we suspected that the same might be true for many scrub vertebrates. Indeed, if the abundance of a particular species is not positively related to scrub area, then its density actually must be higher in some smaller scrubs than in some larger ones. In such cases (‘‘density compensation’’; see Williamson 1981, Schoener 1986) the line fit to actual abundances would possess a shallower slope than the line fitted to expected abundances (Fig. 1). To document differences in density, we tabulated the number of individuals captured per array, and then compared the numbers among scrubs of different sizes with the Wilcoxon rank sum test. To document differences in dispersion, we compared the identities of species captured by each pair of arrays within a scrub in the same year and by each array between years (except for AB3, which was sampled for only 1 yr) with the Jaccard Index.

Results

Vertebrate abundances

Data on numbers of individuals were available for 28 species in 1990. We recaptured marked individuals of four species in 1990. The number of marked recaptures exceeded 10 individuals for only two species of lizards, however, the widespread *Cnemidophorus sexlineatus* (26 recaptures of 23 individuals in eight scrubs) and the precinctive *Sceloporus woodi* (108 recaptures of 93 individuals in 10 scrubs). We recaptured marked individuals of seven species in 1989. The number of marked recaptures exceeded 10 individuals for only the same two species, *C. sexlineatus* (18 recaptures of 17 individuals in 11 scrubs) and *S. woodi* (65 recaptures of 56 individuals in eight scrubs). We computed recapture fractions (i.e., number of recaptured individuals/number of captured individuals) for these
two species, and found that, in general, the computed recapture fractions were remarkably similar among scrubs for both of them. Most recapture fractions fell within the range 0.10–0.18; the binomial test indicated that only one of the 28 fractions could be shown to fall outside this range, for \( P \leq 0.05 \). The 1989 data mirrored the 1990 data well, although a tendency existed for the sampling fractions to be uniformly smaller in 1989. We concluded that we could reliably use count data (i.e., captures) as an estimate of abundance for these two species, and, because we were interested in estimates of relative, not absolute, abundances, that our conclusion also would hold for the species for which we had no recaptures, or too few, to calculate meaningful recapture fractions. Subsequent detailed studies of the relationship between count data and known abundances of a species that is very different in lifestyle than either \( C. sexlineatus \) or \( S. woodi \), the secretive sand-swimming lizard \( Neoseps reynoldsi \) (McCoy et al. 1999), indicate that the latter conclusion is a reasonable one.

**Relationships between vertebrate abundances and scrub attributes**

Two correlations illustrate the connection between abundances of vertebrate species and their distributions among scrubs (McCoy and Mushinsky 1994). Cumulative abundance of a species in all scrubs combined is related strongly to number of scrubs occupied (\( r_s = 0.85, P < 0.05 \)) (see Brown 1984, Hanski 1991, Wright 1991) and species that are relatively abundant in large scrubs tend to be present in more medium and small scrubs than species that are not relatively abundant in large scrubs (\( r_s = 0.88, P < 0.05 \)) (see Diamond 1984, Soulé et al. 1988, Bolger et al. 1997). These correlations indicate, as one might expect, that a given species tends to be more vulnerable to within-fragment ex-
tinction if it has relatively low abundances than if it has relatively high abundances.

We documented several correlations between abundance and the environmental attributes. Abundance was correlated positively with area for eleven species. Abundance also was correlated with number of surrounding habitats (positive correlations for nine species), percentage of surrounding disturbed land (negative correlations for seven species), and area reduction since the mid-1940s (negative correlations for seven species). All of the latter three attributes are correlated strongly with area, however. Four of the attributes related to isolation, distance to the nearest other scrub, distance to the nearest larger scrub, distance to the nearest permanent water, and presence/absence of potential corridor habitats, are not correlated strongly with scrub area, but only seven correlations with abundance (for five species) were found for these four attributes combined. All of the correlations were in the expected direction, however; estimated abundance declined with distance and with absence of potential corridor habitat. The only attribute related to habitat structure that was commonly correlated with abundance was relative representation of rosemary (positive correlations for nine species). Relative representation of rosemary is correlated strongly with area, however. We note that both a positive correlation with the relative abundance of rosemary (which we used as an index of “open-canopied” scrub) and a negative correlation with the relative abundance of oaks (which we used as an index of “closed-canopied” scrub) were observed for three species: two lizards (C. sexlineatus and S. woodi), and a tortoise (G. polyphemus). All three species are known from independent evidence (Jackson 1973, Mushinsky 1985, Enge et al. 1986, Mushinsky and Gibson 1991, McCoy and Mushinsky 1992c, Mushinsky and McCoy 1994) to require open areas. Habitat structure, therefore, is important to these species, as well as other scrub vertebrates (see Campbell and Christman 1982, Greenberg et al. 1994), but additional sampling will be necessary to separate its effects from those of area. No strong correlations between abundance and order of scrubs based on habitat structure, as determined by principle coordinates analysis, were found that were not expected from the univariate analyses.

We also documented several correlations between shape of relative abundance distribution and the attributes. Evenness was correlated strongly with percentage of the ground covered with living vegetation in summer ($r_s = 0.56, P < 0.05$), and moderately with some of the attributes related to isolation, the strongest being distance to nearest larger scrub ($r_s = 0.42, P = 0.10$). Recall that we also used two methods to group scrubs by relative abundance distributions, yielding: (1) COL, EGL, HEN, JOS, JUN, LAK; (2) AB1, AB2, AB3, BAR, CHU, HH2; and (3) CUT, DUF. The Wilcoxon rank sum test showed that area clearly could distinguish members of group 3 from members of the other two groups ($W = 15, P < 0.05, m = 2, n = 6$). Distance to nearest larger scrub could distinguish between members of groups 1 and 2 strongly ($W = 52.5, P < 0.05, m = 6, n = 6$): members of group 1 tended to be relatively far from larger scrubs, and members of group 2 tended to be relatively near them. Relative representation of scrub oaks also could distinguish between members of groups 1 and 2 strongly ($W = 50, P < 0.05, m = 6, n = 6$): members of group 1 tended to have relatively low abundances of scrub oaks, and members of group 2 tended to have relatively high abundances. Attributes related to isolation and habitat structure thus were good predictors of group membership, as they also were of evenness.

**Within-scrub density and dispersion of species**

Densities of individuals across all species, as measured by captures in single trap arrays, were indistinguishable ($W, P = 0.28–0.89$) in small (number of arrays = 9), medium ($n = 13$), and large ($n = 22$) scrubs (Fig. 2). Densities of individuals within species differed markedly among scrubs of different size, however. The species that displayed a positive correlation between abundance and area often reached their highest densities in relatively large scrubs, and the species that did not display a positive correlation between abundance and area often reached their highest densities in

**Fig. 2.** Densities of individuals across species in scrubs of different sizes. Open boxes are medians, aggregated by scrub.
Fig. 3. Rarity (sensu McCoy and Mushinsky 1992a) of each species plotted against the scrub size in which its density was highest. Closed boxes are species that displayed a strong positive correlation between abundance and scrub area; open boxes are species that did not. Species below the horizontal line ($n = 5$) were considered rare, while species above the line ($n = 11$) were not; species to the left of the vertical line ($n = 8$) were considered to reach their highest densities in relatively large scrubs, while species to the right of the line ($n = 8$) were considered to reach their highest densities in relatively small scrubs.

Relatively small scrubs, much as one would expect ($G$ test, $G = 13, P < 0.05$) (Fig. 3). Prominent among the species that reached their highest densities in relatively small scrubs were species that could be considered rare (sensu McCoy and Mushinsky 1992a), which one would not necessarily expect ($G = 8, P < 0.05$) (Fig. 3). Single arrays in both medium ($W = 72, P = 0.04$, $m = 9, n = 13$) and large ($W = 104, P = 0.09$, $m = 9, n = 22$) scrubs tended to capture more species than arrays in small scrubs, but numbers of species captured by single arrays in medium and large scrubs were indistinguishable ($W = 267, P = 0.27$, $m = 13, n = 22$) (Fig. 4).

Dispersions of individuals were not similar among scrubs. Within years, pairs of arrays in the large scrub ARC and the medium scrubs tended to capture more similar sets of species than did pairs of arrays in the large scrubs AB3 and HEN. Distributions of Jaccard Index values among arrays in ARC and the medium scrubs (MS) are distinct from the distributions in AB3 (Kolmogorov-Smirnov test; $D = 0.41, P < 0.05, n = 45$ (ARC); $D = 0.38, P < 0.05, n = 16$ (MS)) and HEN ($D = 0.46, P < 0.05, n = 45$ (ARC); $D = 0.38, P < 0.05, n = 16$ (MS)). Likewise, arrays within ARC, the medium scrubs, and the small scrubs tended to capture more similar sets of species between years than did arrays within HEN. Distributions of Jaccard Index values between years in ARC, the medium scrubs, and the small scrubs (SS) (excluding DUF, which was sampled for only 1 yr) are distinct from the distributions in HEN ($D = 0.51, P < 0.05, n = 10$ (ARC); $D = 0.60, P < 0.05, n = 12$ (MS); $D = 0.87, P < 0.05, n = 8$ (SS)). The simple interpretation of these results is that as scrub size decreases, and number of species decreases concomitantly (McCoy and Mushinsky 1994), spatial distributions of species also tend to become more homogeneous (see Mushinsky et al. 1997).

Changes in density and dispersion with scrub area comprise a “spatial scale effect” that is important in drawing conclusions about the effects of fragmentation (see Addicott et al. 1987, Morris 1987, Wiens 1989, McCoy and Bell 1991, Doak et al. 1992, Bell et al. 1993, Haila et al. 1993b). (A “temporal scale effect,” in which a system is studied after certain species already have been lost from the system, also is important in drawing conclusions about the effects of fragmentation [e.g., Matthiae and Stearns 1981], but we shall not deal with it here.) The spatial scale effect that we have identified provides a potential reason for why ARC is more like the medium and small scrubs than the other large scrubs in species’ similarity both among arrays and within arrays between years. Unlike AB3 and HEN, which are comprised of essentially contiguous scrub habitat, ARC is comprised of numerous
pieces of scrub habitat in close geographical proximity, with similar vegetational composition and structure, and surrounded by similar suites of other habitats (see Abrahamson et al. 1984, Fahrig and Merriam 1994). The greater internal division of ARC may cause it to behave more like an archipelago of small scrubs than a single large scrub, and thus differentiate it from the other large scrubs in terms of species’ abundance.

**Discussion**

How do our results concerning abundances and within-site variation of scrub vertebrates affect our previous conclusion that groups of smaller fragments of the Florida scrub possess at least comparable conservation value for vertebrates as single larger fragments? The answer to this question is not straightforward. On the one hand, abundances of ~60% of the species tended to be higher in larger scrubs. On the other hand, abundances of ~40% of the species did not tend to be higher in larger scrubs, and, even for those species for which abundances did tend to be higher in larger scrubs, percentages of variation explained by scrub size ranged only from 21% to 83% (median = 45%). Furthermore, some scrubs simply were more “valuable” than others for a variety of species, regardless of their sizes (see McCoy 1983). In particular, several of the rare species apparently maintain relatively large populations in certain small scrubs. These differences in value among scrubs of similar sizes may be related, at least in part, to differences in isolation and habitat structure. For example, abundances of some, but not all, species tended to be lower in more isolated scrubs, and shapes of relative abundance distributions of some, but not all, species were related to habitat structure. A further complication in answering the question just posed is the spatial scale effect that we identified. The density and dispersion of many species is not independent of scrub area, and the actual size range of scrubs over which this effect occurs varies among species. The variation among species could account, at least in part, for the different relationships between abundance and scrub area observed among species.

Although our results support the broad generalization that abundances of resident species tend to decrease with decreasing scrub size, we do not think this generalization should form a basis for scrub conservation planning. We suggest that our results actually are best viewed as a caution about the use of limited ecological data as a basis for conservation planning. Our results clearly show that the benefits gained for certain species from focusing on the preservation of larger scrub fragments could be offset by harms done to other species. Automatically relinquishing smaller scrub fragments would not appear to be prudent for the simultaneous conservation of a variety of scrub vertebrates. When the conservation of several species is attempted simultaneously, it appears that a strategy derived from analysis of one, or even several, species may be inappropriate for others (e.g., Marsh and Pearson 1997), or may even be illogical (e.g., Yahner 1992). Preserving a system of scrub reserves, chosen not solely on the basis of size, but on a variety of important features, is the proper action to take. We shall return to this point.

Our caution carries over to the use of metapopulation ideas in conservation planning. The apparent role of size reduction and isolation in reducing abundances, at least of some species, of scrub vertebrates suggests that a metapopulation or refuge model (e.g., De Vries and Den Boer 1990, Thomas and Jones 1993, Gulve 1994, Hanski 1994, Hanski et al. 1994) might be appropriate for understanding the responses of these vertebrates. Our results seem to confirm the possibility that population size influences vulnerability to local extinction (see Fahrig and Merriam 1985, Hanski 1994, Burkey 1997; but also see Schoener and Spiller [1992] on the role of population size variability, and Mangel and Tier [1994] on the role of catastrophes). The relationship between metapopulation or refuge models and habitat fragmentation is not well-explored (Caughley 1994), however, and we are reticent to suggest that a metapopulation or refuge model be employed for the remaining scrub fragments (see Quintana-Ascencio and Menges 1996), for two reasons.

One reason that we are resistant to employing a metapopulation or refuge model is that although the assumptions and conditions of the model may hold for some species, they may not hold for all species (see Collins and Glenn 1997). We suspect that because of the extremely heterogeneous nature of the scrub habitat (see Myers 1990), many scrub vertebrates have dealt successfully with habitat fragmentation throughout much of their evolutionary histories (see Jackson 1973, Campbell and Christman 1982), and can, on the one hand, resist extinction at what seem to the observer to be very low population sizes and, on the other hand, disperse between habitat fragments that seem to the observer to be isolated from each other (see Harrison 1989, 1991). We suspect that some vertebrates may not even find many of the remaining scrub fragments particularly isolated, and immigration of individuals or even recolonization counters extinction (see McCoy and Mushinsky 1994). If many scrubs are not particularly isolated for these species, then other explanations for our results suggest themselves (see, for example, Gotelli and Simberloff 1987). Information on the extinction rates, dispersal capabilities, and colonization potentials of scrub vertebrates is needed to determine just how small and isolated a particular scrub fragment really is. In other words, we need to know if a particular fragment is “pathologically small” and/or “pathologically isolated,” for each species (see Shrad-er-Frechette and McCoy 1993). Such information is notoriously difficult to obtain (e.g., Dennis et al. 1991, Taylor 1991, Foley 1994, Nunney and Elam 1994, Harrison et al. 1995).
Another reason that we are resistant to employing a metapopulation or refuge model is that the fragmentation that scrub species currently face probably is of a quite different kind and degree than the fragmentation they have faced in the past. Species that may once have conformed to a metapopulation or refuge model cannot now conform, because of the greatly modified landscape that faces them (see May 1991). Even birds, which would seem to be affected much less by increasing isolation of fragments than other vertebrates (see Möller 1987, Rolstad 1991, McCoy and Mushinsky 1994), can succumb to drastic changes in habitat structure at the landscape and regional levels (see Diamond 1984, McCollin 1993). One possible consequence of the different kind and degree of fragmentation that scrub species currently face is that some of the species that have relatively high abundances in relatively small scrub may not be flourishing there. In drastically modified habitats, high abundances need not indicate good quality habitat; rather, they could indicate that the individuals simply have nowhere else to go (Mushinsky et al. 1997, McCoy et al. 1999). Demographic analyses of individual species are needed to spot these situations.

If our caution about the use of limited ecological data as a basis for conservation planning is important, then it suggests that selection of a system of scrub reserves should be based, in large part, on knowledge of the biologies of as many of the resident organisms that one wishes to conserve as possible. Such knowledge, in turn, can be gained from a set of relatively small-scale intensive studies (see Wright 1990, Hobbs et al. 1993, Hanski 1994, Short and Hestbeck 1995, Taper et al. 1995). Choosing scrub reserves in this way would lead to preservation of “a rather dense matrix of sites from the southern through the northern limit of scrub” (Simberloff 1993, p. 183; also see USFWS 1993). Several methods are available for selecting a system of reserves that best satisfies a particular conservation goal, an approach which is preferable to selecting reserves one-by-one on the basis of decreasing relevance to the goal (see McCoy 1983; Smith and Thebarge 1986, 1987, Lomolino 1994, Kiester et al. 1996). Such an approach, if applied correctly, potentially could promote conservation of all scrub vertebrates simultaneously, but applying it to the scrub habitat is a complex undertaking (E. D. McCoy and K. S. Shrader-Frechette, unpublished manuscript).

Selection of a system of scrub reserves is also is likely to consider the costs of acquisition (see USFWS 1993) and maintenance, however. The costs of maintenance include periodic burning to prevent the pyrogenic scrub habitat from disappearing (see McCoy and Mushinsky 1992c, Simberloff 1993), periodic intervention to ensure the well-being of individuals on the conserved scrubs (see Mushinsky et al. 1997), and complementary management of the surrounding landscape (see Mushinsky and McCoy 1994). Without prescribed burning and other critical management interventions, virtually all of the remaining scrub fragments are likely to be gone within the next 30 yr. It is at least conceivable that the costs of acquiring and maintaining an ecologically desirable, but rather large, set of scrubs could outweigh the perceived benefits, and tip the scale in favor of acquiring and maintaining a few select scrubs here-and-there. Unfortunately, real-world conservation often forces choices that are not necessarily the best ones from an ecological perspective.

How can ecologists begin to tip the scales in favor of ecologically, rather than economically based conservation of the scrub habitat? Abandoning the arcane debate about the conservation value of small habitat fragments entirely would be a good first step. The ecological debate about the conservation value of small habitat fragments seems to be based on the choice bound up in the SLOSS (“single large or several small”) idea, which presupposes that some truly large areas actually exist. A different idea, which can be called ‘SLATS’ (‘several little, all too small’), probably is more relevant to the conservation value of small scrub fragments, as well as small fragments of many other kinds of habitat. Conservation value is not an absolute; rather, it is a function of rarity. When a habitat has declined as precipitously as scrub has, and truly large remaining fragments are, at best, extremely rare, then smaller fragments are likely to be of considerable value, no matter how they compare to larger fragments. It would seem eminently reasonable, as well as ecologically sound, to argue that, because so few scrub fragments of any sort remain, all of them should be preserved. Appreciating the complimentary nature of conservation and restoration is another important step (see Jackson 1992). Scrub and other severely fragmented and degraded habitats may not provide enough habitat quantity and/or quality to be of much value to resident species, no matter how well the remaining fragments are managed. Increasing the number of scrub fragments or increasing the sizes of existing fragments, by reclaiming lands that have been cleared of scrub, is an underappreciated way to retain at least some of the conservation value of the scrub habitat (E. D. McCoy, H. R. Mushinsky, and R. A. Kluson, unpublished manuscript).

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