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BIODIVERSITY PATTERNS OF SPRING-ASSOCIATED BUTTERFLIES IN A MOJAVE DESERT MOUNTAIN RANGE

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ABSTRACT: We examined whether species richness (number of species), abundance, and species composition (identity) of butterflies at 23 springs in the Spring Mountains, an isolated mountain range in the eastern Mojave Desert (Nevada, USA), had a predictable response to presence of riparian vegetation. The Spring Mountains are the focus of regional conservation planning, and managers are charged with prioritizing its springs for conservation and rehabilitation. We therefore used butterflies to help provide information on faunal responses to potential changes in land cover. Species richness and abundance of butterflies in locations with riparian vegetation consistently was higher than in locations with non-riparian vegetation across several levels of spatial resolution. Similarity of species composition of butterflies decreased as the linear distance between springs increased. Neither local presence of larval hostplants nor vegetation association (riparian or non-riparian) of larval hostplants had a significant effect on occurrence rate or abundance of individual species of butterflies. Nestedness analyses demonstrated that species present in locations with few species of butterflies tended to be subsets of the species present in locations that were richer in species, but that pattern did not appear to be driven by the availability of riparian habitat. The species that were present at the greatest number of springs tended to be geographically widespread taxa that can exploit human and natural disturbances. Our results suggest that reduction in water availability and the extent of riparian vegetation at montane springs in the Mojave Desert is likely to reduce local species richness and abundance of butterflies. The ability of broad categories of vegetation to serve as a predictor of species richness and composition of butterflies, however, may be relatively low.

ADDITIONAL KEY WORDS. conservation, isolation, nestedness, riparian, Spring Mountains.

Springs and spring-fed aquatic systems support a substantial proportion of aquatic and riparian species in the arid western United States (Williams & Koenig 1980, Gubanich & Panik 1986, Myers & Resh 1999). Not only do several hundred endemic species and subspecies of aquatic vertebrates, invertebrates, and plants depend on springs, but springs provide resources for as many as 80% of terrestrial species (Hubbs & Miller 1948, Thomas et al. 1979, Hershler et al. 2002).

Because springs are the only reliable source of water across much of the western United States, human land uses also have tended to concentrate around springs. These uses include diversion of water for domestic and municipal use, livestock grazing, and recreation (Shepard 1993). Moreover, both intentionally and inadvertently, humans have introduced numerous non-native species of animals and plants to springs (Hendrickson & Minckley 1984, Sada & Vinyard 2002), leading to changes in biodiversity patterns and ecological processes (Mills et al. 1993, Kinzig et al. 2001, Soulé et al. 2003). Rates of extinction in the western United States currently are higher for native species that occur at springs and spring-fed aquatic systems than for species associated with any other category of landscape features (Sada & Vinyard 2002). As a result, restoration and rehabilitation of aquatic and riparian areas, often with a focus on vegetation communities, has become a top management priority.

Understanding how native faunal assemblages respond to availability of water and composition of vegetation in spring-fed riparian systems is critical to development of effective, practical strategies for ecological restoration and maintenance. The Clark County Multiple Species Habitat Conservation Plan (MSHCP), issued by the U.S. Fish and Wildlife Service in 2001, illustrates why this information has become so important. Thanks to explosive growth of the Las Vegas metropolitan area, Clark County is the most rapidly urbanizing municipality in the United States. The MSHCP, which covers 79 species, is intended to mitigate the cumulative effects of urbanization while giving participants greater security about future regulatory restrictions. Among the requirements of the 30-year MSHCP is development of a Conservation Management Plan for springs in the permit area. The Spring Mountains, an isolated mountain range in the eastern Mojave Desert, cover about 4000 km^2, contain approximately 300 springs, and are largely public land. They have become a principal focus of these planning efforts.

Few standardized biological surveys have been conducted at springs in the Spring Mountains. Among invertebrates, several well-known taxonomic groups, including tiger beetles and butterflies, are thought to be associated strongly with changes in land cover (Kremen et al. 1993, New et al. 1995, Carroll & Pearson 1998, Rodrigues et al. 1998). Because invertebrates have relatively short generation times, they may be useful for exploring how expansion or contraction of riparian cover affects native fauna. In this paper, we present the early results from an ongoing study that uses butterflies as a case-study group to infer how changes in water availability and land cover at springs may affect native fauna. As a first step, we have examined patterns of species richness and abundance of butterflies associated with broadly categorized riparian and non-riparian vegetation. We are in the process of collecting detailed data on vegetation composition and structure to increase understanding of potential mechanisms driving the patterns reported here and to help guide regional conservation and restoration efforts.

METHODS

Study system. The Spring Mountains are ca 125 km in length and span an elevational gradient from 1500 m in Las Vegas Valley to 3632 m on Charleston Peak. As elevation increases, annual precipitation increases from less than three cm to more than 55 cm. Summer temperatures may reach 46° C at the lower end of the elevational gradient, decreasing to -9° C at higher elevations during the winter (Hidy & Klieforth 1990).

Most of the springs in the Spring Mountains are small and isolated, and many have been excavated or otherwise developed. Diversion structures, such as spring boxes to collect water and pipes to transport water to nearby troughs or tanks, are common. Numerous non-native species (mostly plants and fishes) have colonized these springs, and many springs are impacted by stochastic environmental phenomena such as fire, avalanche, and flood. Nonetheless, some springs appear to be in good condition and have been minimally affected by either natural or anthropogenic disturbance.

The butterfly fauna of the Spring Mountains is particularly well known and has been subject to intensive sampling for more than four decades (Austin & Austin 1980, Austin 1981).

Field Methods. Between April and August 2003, we conducted surveys of butterflies at 23 springs that collectively span major environmental and land-use gradients in the Spring Mountains. Visits were conducted once per month for a total of five visits per spring. Phenologies of butterflies and plants were similar among springs. Surveys were conducted when weather conditions were most conducive to flight (e.g., mostly sunny, light winds, warm temperatures). Although stronger inferences could be drawn if more than one year of data were available, weather conditions in 2003 were representative–neither particularly dry nor particularly wet. Annual precipitation for 2003 at Red Rock Canyon State Park in the Spring Mountains was 24.2 cm; the mean for the 17-year period of record is 29.4 cm (± 13.6 SD) (Western Regional Climate Center 2004).

Sampling effort was roughly proportional to length of the springbrook (i.e., sampling effort was approximately equal per unit area). We established sampling points at the spring source; 30 m from the source at 0°, 90°, and 270°; and at 100 m intervals downstream from the source along the length of the springbrook. Vegetation at each sampling point was categorized as either riparian or largely non-riparian. Riparian taxa were defined as those that almost always or usually occur in wetlands with permanent water (Reed 1988). Examples of local riparian taxa include *Eleocharis*, *Equisetum*, *Juncus*, and *Muhlenbergia*. Although the existence of non-riparian vegetation at a spring may seem to be a contradiction in terms, many springs are ephemeral, with flow rates that fluctuate seasonally or annually. As a result, plants that do not depend on permanent sources of water (e.g., *Bromus*, *Penstemon*, *Poa*) often become established near the spring source and along the springbrook. As noted above, our vegetation categorizations were intentionally broad; categorizations will be refined and quantified following collection of additional data.

We established a circle with a 10 m radius at the center of each sampling point. During each visit to each spring, using methods that have proven effective in other riparian areas in the Mojave Desert and Great Basin (Fleishman et al. 1999, Mac Nally et al. 2004), an experienced observer identified and recorded all butterflies seen during a 10 min period within the circle. In preliminary "mock" surveys, more than 10 min in a sampling point almost never resulted in the detection of additional species of butterflies. Because sampling effort was approximately equal per unit area of the spring, the risk of sampling error was relatively uniform. Individual butterflies typically did not appear to move among sampling points during each visit to each spring. We calculated species richness (number of species) and abundance (number of individuals) of butterflies over the five-month sampling period for each spring. Where applicable, we also calculated separately species richness and abundance of butterflies associated with riparian and non-riparian vegetation at each spring.

Larval hostplants have been identified for virtually all species of butterflies that inhabit the Spring Mountains (G. T. Austin unpublished data). For each species of butterfly that we recorded, we categorized the occurrence and vegetation association of its larval hostplant(s) across the suite of springs we surveyed as present, riparian; present, non-riparian; or absent.

Analyses. We used analysis of variance to test whether species richness and abundance of butterflies varied as a function of vegetation association (riparian versus non-riparian) across all springs. We also used paired t-tests to compare species richness and abundance of butterflies associated with riparian versus non-riparian vegetation at the 18 springs with both types of plant communities.

We calculated similarity (Canberra distances) of species composition (i.e., species identity) of butterflies among all springs, among the riparian component of springs, and among the non-riparian component of springs. We used Mantel tests (Mantel 1967, Douglas & Endler 1982) to evaluate whether similarity of species composition of butterflies decreased as linear distance between springs increased. Canberra distances and Mantel tests were calculated using the R Package (Casgrain & Legendre 2001).

We used analysis of variance to examine whether occurrence rate (i.e., the number of springs at which each species was present) or abundance of butterflies varied as a function of the occurrence or the vegetation association of their larval hostplants in the study system.

To test whether predictability of patterns of species richness and composition varied between riparian and non-riparian vegetation, we used nestedness analyses. Nestedness analyses have greatly expanded our capacity to understand biotic patterns across networks of terrestrial or aquatic islands of resources or habitat (Wright et al. 1998). Nestedness analyses test the degree to which species present in relatively species-poor locations are proper subsets of species present in relatively species-rich locations (Patterson & Atmar 1986, Wright et al. 1998). Nestedness is a property of assemblages, not of individual species, and has been interpreted as a measure of biogeographic order in the distribution of species (Atmar & Patterson 1993).

Numerous studies have demonstrated that nested distributional patterns are common across taxonomic groups and ecosystems. The accuracy of predictions of the sequence in which species will be extirpated from or colonize a set of locations occupied by a nested assemblage is positively correlated with the degree of nestedness. Assemblages can be nested by multiple phenomena, including but not limited to species-specific probabilities of extinction, species-specific probabilities of colonization, and nestedness of resources or habitat types (Darlington 1957, Cook & Quinn 1995, Lomolino 1996).

Nestedness analyses are effective tools for management because they can suggest, albeit via correlation, whether virtually any environmental variable of interest is likely to affect distributional patterns in an array of locations (e.g., Kadmon 1995, Fleishman & Mac Nally 2002). Differential nestedness among groups of species (e.g., functional groups or guilds) that vary in sensitivity to the extent of a particular type of land cover, for example, suggests that the processes affecting the occurrence and extent of that land cover type are driving local extinctions or colonizations (Hecnar & M'Closkey 1997, Fleishman & Murphy 1999, Jonsson & Jonsell 1999). It may not always be possible to establish a causal relationship between environmental variables and species occurrence, but strong correlations can, at minimum, help refine process-based hypotheses that can be tested with more intensive experiments or observations. Nestedness analyses have realistic application because they provide information on patterns and suggest mechanisms affecting not only species richness but also species composition. These data can inform decisions about how to maximize richness of native species across a multiple-use landscape (Margules & Pressey 2000).

To test whether assemblages were nested with respect to vegetation type, we computed the relative nestedness index C (Wright et al. 1990, Wright & Reeves 1992). We estimated statistical significance using Cochran's Q statistic (Wright & Reeves 1992). Values of C vary between 0 and 1.0, approaching 1.0 for perfectly nested matrices. Key advantages of this metric are that it allows for statistical comparison of degree of nestedness among matrices or data sets and is not highly sensitive to matrix size (Wright & Reeves 1992, Bird & Boecklen 1998). We used Z scores (standard-Normal variates) to test whether degree of nestedness was significantly different between assemblages of butterflies associated with riparian versus non-riparian vegetation (Wright & Reeves 1992).

RESULTS

Of the 23 springs in the Spring Mountains that we surveyed, 21 included riparian vegetation and 20 included non-riparian vegetation. Eighteen springs included both riparian and non-riparian vegetation.

We observed a total of 55 species of butterflies at plots, at springs, and along springbrooks (Figure 1). All of the species were recorded in association with riparian vegetation; 37 species were recorded in association with non-riparian vegetation. Many of the 18 species that we recorded only in association with riparian vegetation are known to occur in non-riparian vegetation elsewhere in their distributional ranges, including within the Spring Mountains. No species was recorded in association with

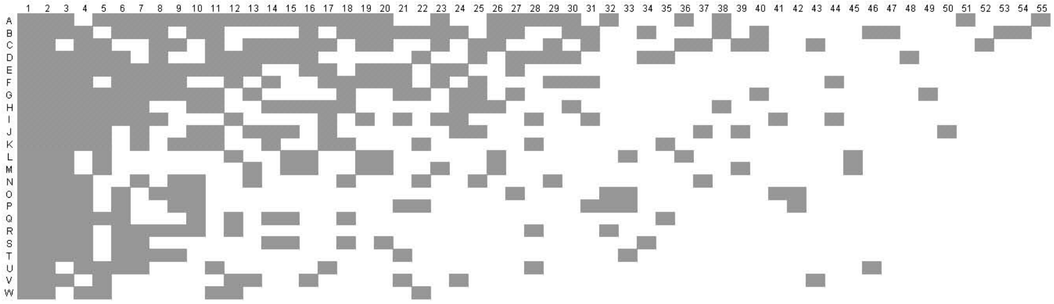

FIG. 1. Species of butterflies present at 23 springs in the Spring Mountains. Springs are listed in decreasing order of species richness; species are listed in decreasing order of number of springs occupied. * indicates butterflies found only in association with riparian vegetation in this study (may occur in non-riparian vegetation elsewhere). Springs: A, Sawmill Spring; B, Willow Creek; C, Switchback Spring; D, Pine Creek; E, Cold Creek; F, La Madre Spring; G, Ash Creek; H, Lost Creek; I, Mountain Springs; J, Ice Box Canyon; K, Oak Creek; L, Bonanza-f; M, Bonanza-u; N, Calico Spring; O, Mud Spring 1; P, Mud Spring 2; Q, First Creek; R, Red Spring; S, Willow Spring; T, Wheeler Spring; U, White Rock Spring; V, Willow Seep; W, Calico Tanks. Butterflies: 1, *Leptotes marina*; 2, *Vanessa cardui*; 3, *Pontia protodice*; 4, *Danaus gilippus*; 5, *Anthocharis sara*; 6, *Hemiargus isola*; 7, *Eurema nicippe*; 8, *Colias eurytheme*; 9, *Junonia coenia*; 10, *Nathalis iole*; 11, *Pontia sisymbrii*; 12, *Danaus plexippus*; 13, *Vanessa annabella*; 14, *Adelpha bredowii*; 15, *Celastrina ladon*; 16, *Erynnis brizo*; 17, *Incisalia fotis*; 18, *Pyrgus communis**; 19, *Cercyonis sthenele*; 20, *Limenitis weidemeyerii*; 21, *Papilio polyxenes*; 22, *Chlosyne acastus neumoegeni*; 23, *Colias cesonia*; 24, *Nymphalis antiopa**; 25, *Papilio indra*; 26, *Nymphalis californica*; 27, *Pontia beckerii*; 28, *Strymon melinus*; 29, *Erynnis meridianus**; 30, *Heliopetes ericetorum**; 31, *Megathymus yuccae*; 32, *Brephidium exile*; 33, *Hemiargus ceraunus*; 34, *Atlides halesus*; 35, *Euchloe hyantis**; 36, *Hesperia comma**; 37, *Icaricia acmon**; 38, *Pieris rapae**; 39, *Speyeria carolae*; 40, *Vanessa virginiensis**; 41, *Apodemia mormo*; 42, *Apodemia palmerii*; 43, *Euphilotes ancilla**; 44, *Mitoura siva**; 45, *Polygonia zephyrus*; 46, *Vanessa atalanta*; 47, *Chosyne acastus robusta**; 48, *Chlosyne californica**; 49, *Copaeodes aurantiaca**; 50, *Erynnis funeralis**; 51, *Everes amyntula*; 52, *Loranthomitoura spinetorum**; 53, *Nymphalis milberti**; 54, *Polygonia satyrus*; 55, *Satyrium behrii*

non-riparian vegetation only. Species richness of butterflies at the spring level ranged from 7 to 30 (16.2 ± 6.2, mean ± SD). Species richness of butterflies in riparian vegetation fell between 6 and 30 (15.6 ± 6.5), and species richness in non-riparian vegetation ranged from 1 to 14 (8.2 ± 3.2).

We recorded a total of 4357 individual butterflies. Abundances of butterflies at the spring level ranged from 40 to 456 (189.0 ± 125.0, mean ± SD). Abundances of butterflies in riparian vegetation fell between 13 and 383 (154.4 ± 115.0), and abundances in non-riparian vegetation ranged from 3 to 136 (55.2 ± 35.2).

Across all springs, species richness of butterflies was significantly higher in riparian vegetation than in non-riparian vegetation ($F_{1,39} = 21.1$, $P < 0.001$). Within spring sites that had both riparian and non-riparian vegetation, the effect of vegetation category was significant as well ($t = 4.119$, $df = 17$, $P < 0.001$). Mean abundance of butterflies in riparian vegetation was significantly higher than in non-riparian vegetation, both across all sites ($F_{1,39} = 13.7$, $P < 0.001$) and within the 18 spring sites that contained both categories of vegetation ($t = 3.788$, $df = 17$, $P < 0.01$).

At the level of individual sampling points, species richness and abundance of butterflies also were significantly higher in locations with riparian vegetation than in locations with non-riparian vegetation (species richness: $F_{1,145} = 40.43$, $P < 0.001$; abundance: $F_{1,145} = 41.52$, $P < 0.001$). Thus, although vegetation in a higher proportion of the sampling points (sampled area) was categorized as riparian (0.55) than as non-riparian (0.45), this difference did not appear to explain the discrepancy in species richness and abundance of butterflies between riparian and non-riparian vegetation.

Similarity of species composition of butterflies decreased as the linear distance between springs increased (Table 1). Neither local presence of larval hostplants nor vegetation association of larval hostplants had a statistically significant effect on occurrence rate or abundance of individual species of butterflies.

The distributional pattern of butterflies at all springs, at riparian portions of springs, and at non-riparian portions of springs was significantly nested (Table 2); therefore, the butterfly faunas at relatively depauperate springs were statistically proper subsets of the species present at relatively species-rich springs. Relative nestedness of assemblages associated with riparian versus non-riparian vegetation was not significantly

TABLE 1. Correlations between distance between springs and similarity of species composition of butterflies at all springs, the riparian component of springs, and the non-riparian component of springs. Values are Mantel r statistics. For all values, $P \leq 0.001$.

	Mantel's r	P
All springs	0.27	0.01
Riparian vegetation	0.14	0.06
Non-riparian	0.30	0.003

TABLE 2. Size and values of the relative nestedness index C for matrices that included all springs, the riparian component of springs, and the non-riparian component of springs. Degrees of freedom are (number of species - 1). All P-values < 0.0001.

	Sites	Species	*C*
All springs	23	55	0.366
Riparian	21	55	0.367
Non-riparian	20	37	0.352

different, suggesting that vegetation type as categorized in this study to date does not have an important influence on the ability to predict the order of butterfly colonizations or extirpations (i.e., the order of species associated with riparian vegetation is no more or less predictable than the order of species associated with non-riparian vegetation).

DISCUSSION

Our results suggest that reductions in water availability and the extent of riparian vegetation at montane springs in the Mojave Desert are likely to reduce local species richness and abundance of butterflies. Across several levels of spatial resolution, species richness and abundance of butterflies consistently were higher in riparian vegetation than in non-riparian vegetation. This is not surprising given the importance of water, especially in xeric systems, for sustaining larval hostplants, adult nectar sources, and moist soil from which some species of butterflies draw water and nutrients (Nelson & Andersen 1999, Mac Nally et al. 2004). In semi-arid and arid environments, butterflies, like many other terrestrial taxa, rely heavily on resources provided by springs, spring-fed riparian systems, and other isolated wetlands (Shapiro 1984, Austin 1985, Murphy & Wilcox 1986, Schlicht & Orwig 1998). In addition, the structurally complex vegetation often characteristic of riparian areas creates refugia for many species of butterflies that cannot tolerate relatively hot or dry microclimates (Galiano et al. 1985).

Financial and logistic obstacles make it impossible to inventory terrestrial and aquatic taxonomic groups at each spring in the Spring Mountains. Accordingly, land managers would like to develop a method to predict measures of biodiversity as functions of readily categorized attributes such as land cover. Although species richness and abundance of butterflies appears to benefit from maintenance of riparian vegetation, our results indicate that the ability of broad categories of vegetation to serve as a predictor of species richness and composition of butterflies may be relatively low. In our study system, for example, neither local presence of larval hostplants nor vegetation association of larval hostplants was an effective predictor of occurrence rate (proportion of locations in which the species was present) or abundance of individual species of butterflies. We suspect that observation at least in part reflects a relatively high degree of polyphagy among the butterfly species encountered in this study, which may serve to reduce effective differences in the suitability of springs that differ substantially in the composition of their vegetation. Nonetheless, species present in relatively depauperate locations tended to be subsets of the species present in locations that are richer in species, but the degree of order in species composition (i.e., the predictability of local extirpations and colonizations) did not appear to be affected by whether riparian habitat was available.

We recognize that conclusions drawn from one year of data on butterfly occurrence and abundance may not be definitive. We also acknowledge that the estimates of resource quantity and quality presented here are relatively coarse; we currently are collecting data on more-detailed measures of vegetation structure and composition that may have greater ability to predict the order of butterfly colonizations or extirpations. Nonetheless, absence of a tight link between occurrence of butterflies and occurrence of larval hostplants is not uncommon (Holl 1996, Waltz & Covington 2004). Although adults that are facultative or obligate nectarivores may be drawn to the high concentrations of flowering plants that can be characteristic of riparian areas, considerable proportions of the distributions of primary larval hostplants in arid environments, as well as entire distributions of potential alternative hosts, may occur beyond riparian boundaries (Galiano et al. 1985).

To some extent, the apparent inability of vegetation type to serve as an effective predictor of biodiversity patterns of butterflies may reflect the tremendous variation in abiotic and biotic attributes of springs in the Spring Mountains, including but not limited to area and morphology of the spring head and springbrook; water volume, chemistry, and seasonal variability; and history of disturbance from all sources (Wettstein & Shmid 1999). We have observed similarly weak relationships between species richness and composition of aquatic invertebrates in the Spring Mountains and gradients in disturbance intensity and major environmental variables (Sada et al. 2005). The isolation of an individual spring also appears to play a important role in determining its butterfly species composition; springs that are closer together tend to have more similar assemblages of butterflies than springs that are further apart.

One of several useful considerations in establishing location-specific priorities for conservation and rehabilitation is presence of ubiquitous or "weedy" species-in any taxonomic group-that are characteristic of biotic homogenization or are able to exploit specific natural and human disturbances as opposed to species characteristic of less disturbed locations (Noss 1990, Lockwood & McKinney 2001, McKinney 2002). In our study system, individual species of butterflies were present in one to 23 springs, with a median occurrence rate of six springs (6.8 ± 5.6, mean ± SD). The two species of butterflies present at all 23 springs surveyed, *Leptotes marina* and *Vanessa cardui*, are highly vagile as adult individuals, are geographically widespread, and often occur in locations subject to relatively intensive human land uses (Scott 1986). The third and fourth most prevalent species among the springs we surveyed, *Pontia protodice* and *Danaus gilippus*, likewise are fairly opportunistic. Our results, therefore, reinforce the principle that protection of locations that currently support a large number of species, while desirable and necessary for protection of biodiversity, may not be sufficient to meet all conservation goals. Even in a significantly nested system, some species that are absent from relatively species-rich locations are present in locations with equal or lower species richness. Establishment of conservation priorities and strategies requires not only information on species richness and abundance but also complementary measures of ecological condition and function (Kinzig et al. 2002).

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