Journal of Environmental Management 74 (2005) 79–87

Journal of Environmental Management

www.elsevier.com/locate/jenvman

Cross-taxonomic potential and spatial transferability of an umbrella species index

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Received 13 February 2004; revised 29 July 2004; accepted 26 August 2004

Abstract

Validation that conservation of certain species effectively protects a high proportion of co-occurring species is rare. Our previous work has suggested that an umbrella index based on geographic distribution and life history characteristics would maximize the proportion of conspecifics protected per unit area conserved. Using bird and butterfly data from three mountain ranges in the Great Basin, we examined whether umbrella species also would confer protection to species in different taxonomic groups. Further, we addressed the spatial transferability of umbrella species by considering whether species identified as umbrellas in one mountain range would be effective umbrellas in other mountain ranges. Overall, equal proportions of species would be protected using either cross-taxonomic umbrella species or same-taxon umbrella species. Our data suggested that in a given mountain range, umbrella species identified using data from the same mountain range versus a different mountain range would be equally effective. The ability of one set of umbrella species to confer protection to co-occurring species, however, may vary among taxonomic groups and geographic regions.
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Keywords: Conservation; Great basin; Spatial transferability; Umbrella species

1. Introduction

Ecologists and resource managers are forced to make land-use decisions using limited time, money, and information (Stohlgren et al., 1995; Oliver and Beattie, 1996; Niemi et al., 1997; Simberloff, 1998). Umbrella species, species whose conservation confers a protective umbrella to co-occurring species, are an attractive short-cut under these circumstances. A key advantage of using umbrella species is that it often is easier to survey and monitor a few species in an assemblage than to survey all species. If effective umbrella species can be identified for target ecosystems, then land-use decisions potentially could be made more quickly and efficiently. However, only a few studies have demonstrated that conservation of one or a few species is likely to confer protection to many other species in either the same taxonomic group or different taxonomic groups (Martikainen et al., 1998; Fleishman et al., 2000, 2001b; Suter et al., 2002). The lack of supporting evidence has made the umbrella species concept controversial, and many doubt it is operational (Kerr, 1997; Oliver et al., 1998; Caro and O'Doherty, 1999; Andelman and Fagan, 2000; Rubinoff, 2001). Nonetheless, strong pressure to develop conservation tools for managed landscapes has maintained the conceptual popularity of umbrella species, highlighting the need for further empirical examination.

In theory, selection of umbrella species is prospective, based on the assumption that if the resource requirements of an umbrella species are met, the requirements of many other species also will be satisfied (Fleishman et al., 2001b). In practice, the species usually touted as umbrellas are charismatic vertebrates with legal protection. Instead of using ecological criteria to select umbrella species, biologists usually have been restricted to determining,

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0301-4797/$ - see front matter © 2004 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jenvman.2004.08.010

post hoc, whether other species will benefit from the conservation of listed species.

In an effort to develop a prospective, more quantitative, and objective method for identifying umbrella species, Fleishman et al. (2000) proposed the 'umbrella index'. The umbrella index calculates the potential of each species in a regional biota to serve as a conservation umbrella for other species in that assemblage using three criteria—mean proportion of co-occurring species, occurrence rate, and sensitivity to human land use (Fleishman et al., 2000). Previous work suggested the umbrella index may be useful for prioritizing locations for conservation because it tended to maximize species protection per unit of conserved area (Fleishman et al., 2001b). Here, we use data for birds and butterflies in montane canyons in the Great Basin of western North America to examine whether the index successfully can identify species that might serve as a conservation umbrella for different taxonomic groups. We also assess whether umbrella species identified using the index method are spatially transferable.

2. Methods

2.1. Field methods

We collected data for our analyses in three adjacent mountain ranges in the central Great Basin, the Shoshone

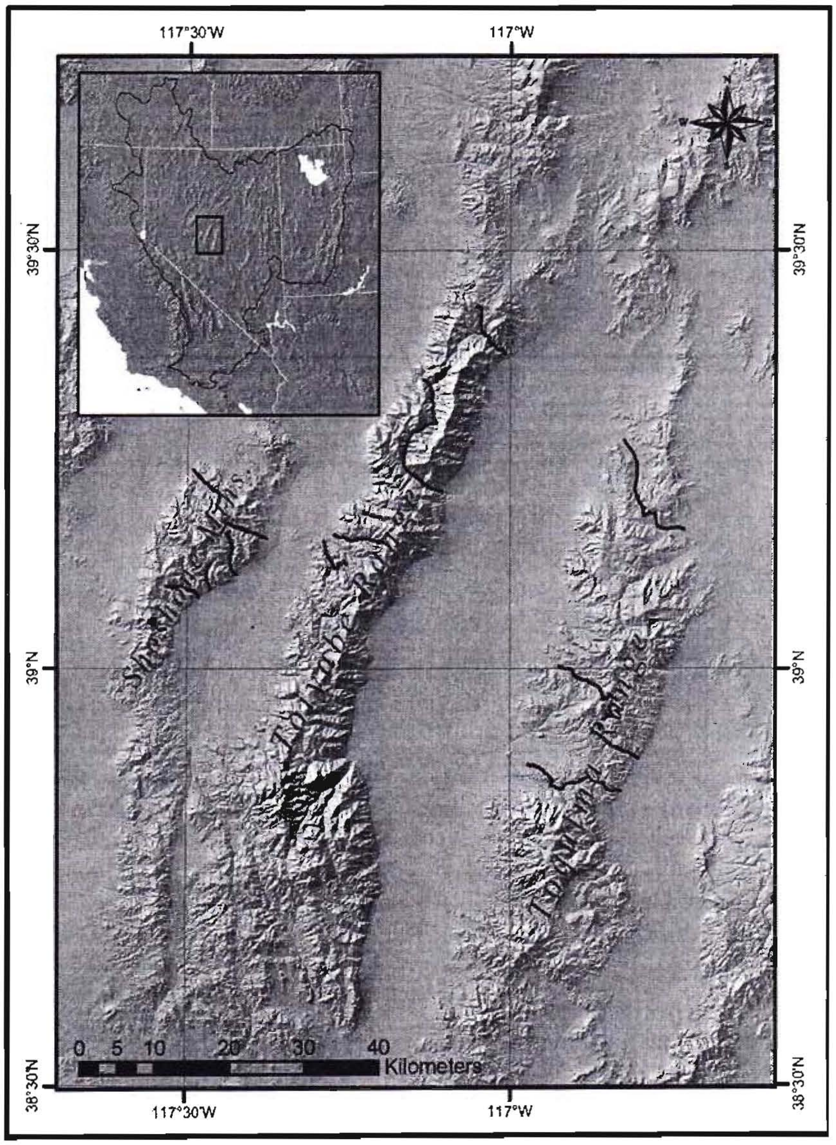

Fig. 1. Location of the Shoshone Mountains and Toiyabe and Toquima ranges (black rectangle, see inset) in the Great Basin (irregular shape with black border, see inset) and of the canyons surveyed in the three mountain ranges. Three pairs of canyons in the Toquima Range and one pair of canyons in the Toiyabe Range connect at the crest of the range.

Mountains (approximate north–south boundaries 39°14′19′–38°57′32′0), Toiyabe Range (approximate north–south boundaries 39°54′00″–38°30′0″), and Toquima Range (approximate north–south boundaries 39°17′50′–38°29′9′) (Lander and Nye counties, Nevada, USA) (Fig. 1). These mountain ranges have similar regional climate, biogeographic past and ancestral biota, and land-use history (Wilcox et al., 1986; Austin and Murphy, 1987; Grayson, 1993; Fleishman et al., 2000).

Our data collection incorporated established techniques that detect species presence reliably and permit assessment of distributional trends across space and time. We provide an abbreviated description here; these methods have been described in considerable detail in previous publications, as well as tested for sampling adequacy (e.g. Fleishman et al., 1998, 2000, 2001a; Mac Nally et al., 2004). We conducted inventories for breeding birds and resident butterflies in five canyons in the Shoshone Mountains, five canyons in the Toiyabe Range, and six canyons in the Toquima Range. These canyons collectively spanned a full gradient of microclimatic conditions and land-cover types in the region.

We divided canyons into multiple contiguous sites from base to crest. Our sampling locations covered an elevational range of 1872–3272 m. Each site was 150 m wide and long enough to span a 100-m change in elevation (Fleishman et al., 1998, 2001a). The mean number of sites per canyon was 5.3 ± 1.3 (SD). Mean site length was 1.4 km; more than two-thirds of the sites were > 1 km long. Inventories were conducted in 28 sites in the Shoshone Mountains, 31 sites in the Toiyabe Range, and 25 sites in the Toquima Range.

We sampled birds during the breeding season (late May through June) using two or three 75-m fixed-radius point counts in each site. Point count locations were at least 200 m apart. Point counts are an effective method of sampling birds in riparian areas in the Great Basin (Dobkin and Rich, 1998). Within a site, points were located in each of the dominant vegetation types (e.g. aspen, willow, piñon-juniper, wet meadow, sagebrush) (Betrus, 2002; Poulson, 2002). Point counts are widely used in studies of birds. Although point counts that do not control for differences in detectability among species or vegetation types (i.e. distance sampling) are of limited value for estimation of abundance, they are reliable for providing data on presence (Buckland et al., 2001).

Each time we visited a point, we recorded all birds actively using terrestrial habitat within the circle. During our inventories, birds displayed a variety of breeding behaviors including frequent song-repetition by males, collection of nest material, nest building, incubation, parental care, and territorial defense. Each point was visited three times during the breeding season. Point counts were conducted only under fair skies and no counts were conducted more than three and one-half hours after dawn. Three surveys are considered sufficient to determine which species of birds are present at point count locations (Siegel et al., 2001); in our work, species accumulation curves for birds at the site and canyon levels generally approached an asymptote before the third round of surveys (Betrus 2002).

We inventoried butterflies using walking transects, a standard, proven method for temperate regions (Pollard and Yates, 1993; Pullin, 1995). Approximately every two weeks throughout the majority of the adult flight season (late May through August), using equal sampling effort per unit area of the site, we recorded the presence of all butterfly species in each site. In temperate regions, it is generally reasonable to interpret that a given butterfly species is absent if the area has been searched repeatedly by experienced observers during the appropriate season and weather conditions (Pullin, 1995). In the Toiyabe Range, for example, we recorded 98% of the theoretical number of species expected under a Michaelis-Menten model (Clench, 1979; Raguso and Llorente-Bousquets, 1990; Soberón and Llorente, 1993; Fleishman et al., 1998). Sites were sufficiently large relative to the home ranges of resident butterflies in the region that the short-term presence of butterfly species in each site was independent (i.e. an individual was not recorded in > 1 site during an inventory round) (Fleishman et al., 1997).

2.2. Identification of umbrella species

To measure the potential of each species of bird and butterfly to confer protection to other species in either assemblage, we calculated umbrella index values at the site level and at the canyon level. The umbrella index is based on three criteria: proportion of co-occurring species, occurrence rate, and sensitivity to human land use. A more complete rationale for selection of these criteria and detailed calculation methods are presented in Fleishman et al. (2000, 2001b). In brief, mean proportion of co-occurring species is quantified on a scale from 0 (tends to occur with a low proportion of species in the same assemblage) to 1 (tends to occur with a high proportion of species in the same assemblage). Values for occurrence rate are based on the proportion of sampling locations in which the species was present. Occurrence values range from 0 (present in a very high or very low proportion of the sampling locations) to 1.0 (present in exactly half of the sampling locations).

The third criterion in the umbrella index, sensitivity to human land use, is assessed using a metric that incorporates life-history characteristics that influence the vulnerability of a given assemblage to human activities (Fleishman et al., 2000, 2001b). Because taxonomic groups differ in their response to environmental change, and because dominant land uses vary geographically, sensitivity metrics are specific to the assemblage and ecosystem of interest. The goal of these metrics is simply to quantify some of the biology that affects persistence in the face of human disturbance. No one formula is 'correct', and ecologists are likely to differ in their opinion of which life history characteristics are most relevant. Species are assigned integer values (e.g. 1 = low sensitivity, 2 = moderate sensitivity, 3 = high sensitivity) for each chosen life-history

Table 1
Life history criteria used to score sensitivity of birds in the Great Basin to human land use (modified from Hansen and Urban (1992); data from Schoener (1968), Brown (1985), Ehrlich et al. (1988), Martin (1995), Rottenborn (1999), and Warkentin and Reed (1999))

Criterion	Sensitivity score		
	1	2	3
Reproductive effort (eggs/year)	>10	6–10	0–5
Nest form	Cavity	Pendant/globe	Open/cup
Nest height (m)	>3	1–3	0–1
Territory size (ha) or	<4	4–40	>40
Territory density (males/km^2)	>100	15–100	<15
Migratory status	Resident	Short-distance	Neotropical migrant
Riparian dependence	No use	Facultative	Obligate

1, least sensitive; 3, most sensitive.

characteristic. For each species in an assemblage, sensitivity to human land use is calculated by summing the scores for each life-history category and then dividing by the maximum sum for any species in the assemblage. Sensitivity to human land use thus is quantified on a relative scale from 0 (low) to 1 (high). For birds in our study system, sensitivity to human land use was based on six life-history characteristics: reproductive effort, nest form, nest height, territory size or density, migratory status, and riparian dependence (Fleishman et al., 2001b, Table 1). Sensitivity for butterflies was calculated using three life-history characteristics: mobility, larval host-plant specificity, and riparian dependence (Fleishman et al., 2001b, Table 2).

For each species, the umbrella index is calculated as the sum of its scores for mean proportion of co-occurring species, occurrence rate, and sensitivity to human land use. Thus, umbrella index values range from near 0 (low umbrella potential) to 3 (high umbrella potential). We defined umbrella species as those with an umbrella index value greater than one standard deviation above the mean (Fleishman et al., 2000). The latter decision criterion, as with a significance level, is arbitrary. Land managers and researchers employing the index are free to select a different decision criterion they believe to be more appropriate for their application.

We calculated the umbrella index for all species of birds and butterflies at two levels of sampling resolution, sites and canyons, at both the landscape level (i.e. pooled data from all mountain ranges) and separately for each of the three mountain ranges.

The potential effectiveness of conservation strategies can be assessed in several ways. Management of land for the benefit of biodiversity generally involves conserving a subset of locations with relatively high richness of native or endemic species (Scott et al., 1987; Freitag et al., 1997; Myers et al., 2000). Therefore, one measure of effectiveness is the proportion of species in a given assemblage present in the locations that are designated for conservation. Presence is not necessarily correlated with viability; however, throughout this paper, to simplify presentation and discussion, we use the terms 'conservation' and 'protection' to mean either that locations in which umbrella species are present also contain a high proportion of co-occurring species or that land uses in a given location would be compatible with persistence of native biodiversity. We recognize that conservation often requires active management as opposed to benign neglect based on less than perfect information.

An alternative metric of conservation effectiveness, calculated with respect to each species of interest, is the proportion of occupied locations that are conserved. The mean proportion of conserved occurrences for all species in an assemblage can be used to evaluate how effectively a land-use plan might protect species that differ in their baseline occurrence rates. For example, a species that is present in two of ten locations is relatively well protected if both locations (100% of its occurrences) are conserved, regardless of the total proportion of the landscape that is conserved. A species that occurs in eight of the ten locations arguably is not as well protected if only two of the eight locations (25% of its occurrences) are conserved because it may lose 75% of its previously-occupied habitat (Fleishman et al., 2000, 2001b). We assume that, in general, proportion of conserved occurrences is positively correlated with probability of persistence.

2.3. Analyses

2.3.1. Selection of conservation areas

From a practical standpoint, it is impossible to protect the entire distributional range of all but the most highly endangered species (Andelman and Fagan, 2000;

Table 2
Life history criteria used to score sensitivity of butterflies in the Great Basin to human land use (Scott, 1986; Boggs and Jackson, 1991; Fleishman et al., 2001a)

Criterion	Sensitivity score			
	1	2	3	4
Mobility (m)	>100,000	1,000–100,000	100–1,000	<100
Larval hostplant specificity	>1 family	>1 genus in 1 family	>1 species in 1 genus	1 species
Riparian dependence	No use	Facultative, some use of mud puddles	Facultative, frequent use of mud puddles	Obligate

1, least sensitive; 4, most sensitive.

Fleishman et al., 2000). Accordingly, we limited our analyses to portions of the landscape. At the site level, we identified the one site in each canyon with the greatest number of umbrella species. At the canyon level, we identified the one canyon in each mountain range with the greatest number of umbrella species. At either level, this approach would require conserving approximately 19% of the sampled landscape. Then, for each taxonomic group (birds and butterflies), in each mountain range (Shoshone, Toiyabe, Toquima) and across the landscape, we calculated the proportion of species that were present in the 'protected' sites or canyons. For all species that were present in the protected locations, we also calculated the mean proportion of conserved occurrences.

Given that one site per canyon was selected or 'protected', the number of possible permutations of sites that could be protected in each mountain range was $S_i \times S_{i+1} \ldots \times S_n$, where S is the number of sites in canyon i and n is the number of canyons visited in the mountain range. The number of possible permutations of sites was 2520 for the Shoshone Mountains, 8575 for the Toiyabe Range, and 9000 for the Toquima Range. We can attach a level of statistical significance to the effectiveness of the umbrella index by calculating the number of random permutations that would include a higher proportion of species than the permutation selected using the umbrella index. These probabilities can be interpreted in the same manner as 'p-values' obtained from frequentist tests of significance (Bailer and Ruberg, 1996; Manly, 1997). To illustrate, say 90 of 9000 possible permutations included a proportion of species greater than or equal to the proportion of species present in the suite of sites identified using the umbrella index. In the latter case, the probability that a random permutation would protect more species than the umbrella index was 0.01, and we might infer that umbrella index was relatively effective.

2.3.2. *Cross-taxonomic potential*

Using the umbrella index as a tool, we examined whether birds can serve as effective umbrellas for butterflies and vice versa. For each mountain range, we identified the site per canyon and the canyon with the greatest number of umbrella species of birds and of butterflies. We then calculated the proportion of species in either taxonomic group present in those locations and the mean proportion of occurrences conserved. Using McNemar's (1947) Q-test, we compared the proportion of species protected using umbrella species from the same taxonomic group versus cross-taxonomic umbrellas. McNemar's Q is a non-parametric chi-square test used to evaluate differences between dependent proportions and count data (Agresti, 1990). The power of McNemar's Q-test depends on the number and ratio of discordant pairs; power increases as the positive correlation between pairs increases (Wacholder and Weinberg, 1982). Therefore, comparisons in which the proportion of species (or any other variable) in each member of a discordant pair are similar have greater power than comparisons in which these proportions are widely disparate (Wacholder and Weinberg, 1982). This trend occurs because as the correlation between members of a pair decreases, the quotient moves closer to 0.5, and accordingly the power of the test to detect a difference between groups is reduced (Wacholder and Weinberg, 1982). For the sample sizes (number of sites) in our study, power at the alpha$=$0.05 level ranged from approximately 0.084 for pairs of sites with widely different proportions of species to approximately 0.103 for pairs of sites with similar proportions of species (Bennett and Underwood, 1970).

2.3.3. *Spatial transferability*

We tested whether an umbrella index developed using data for one taxonomic group in one mountain range would be effective if implemented for the same taxonomic group in other ranges. In other words, we tested whether umbrella species are transferable in space. For each mountain range, we determined the proportion of species that were present in the site per canyon (and canyon per mountain range) with the greatest number of umbrella species that were identified using data from either the same mountain range or a different mountain range. Using McNemar's (1947) Q test, we compared the proportion of species protected for the six possible mountain-range pairs at both the site level and the canyon level.

3. Results

Across the landscape, we recorded a total of 67 species of breeding birds and 64 species of resident butterflies (Table 3). At the mountain range level, the number of species recorded ranged from 40 to 52 for birds and from 50 to 63 for butterflies. Depending on taxonomic group and spatial resolution, the proportion of species identified as umbrellas ranged from 0.13 to 0.24 (mean 0.18 ± 0.03 SD) (Table 3).

3.1. *Selection of conservation areas*

Conserving either the one site per canyon or the one canyon per mountain range with the greatest number of umbrella species would conserve 0.45–0.68 of the bird assemblage and 0.82–0.92 of the butterfly assemblage (Table 4). The proportion of occurrences conserved fell between 0.32 and 0.44 for birds and between 0.24 and 0.33 for butterflies. Depending on mountain range, the probability that sites identified using the umbrella index would protect more species than a random permutation of sites ranged from 0.59 to 0.80 for birds and from 0.67 to 0.89 for butterflies.

Table 3
Number of species, number of umbrella species, and proportion of species selected as umbrellas (in parentheses) in each mountain range and across the landscape (pooled data from all mountain ranges)

	Spatial level	Species	Umbrellas
Birds			
Shoshone	Site	44	6 (0.14)
	Canyon	44	10 (0.23)
Toiyabe	Site	52	9 (0.17)
	Canyon	52	9 (0.17)
Toquima	Site	40	6 (0.15)
	Canyon	40	5 (0.13)
Landscape	Site	67	11 (0.16)
	Canyon	67	12 (0.18)
Butterflies			
Shoshone	Site	50	9 (0.18)
	Canyon	50	12 (0.24)
Toiyabe	Site	63	11 (0.17)
	Canyon	63	13 (0.20)
Toquima	Site	52	11 (0.21)
	Canyon	52	7 (0.13)
Landscape	Site	64	12 (0.19)
	Canyon	64	12 (0.19)

3.2. Cross-taxonomic potential

With only two exceptions, the proportion of species protected using cross-taxonomic umbrellas did not differ significantly from the proportion of species protected using umbrellas from the same taxonomic group (Table 5). In the Toquima Range at the site level, a significantly higher proportion of butterfly species was protected using butterflies as umbrellas than by using birds; the difference between the proportion of butterfly species protected using butterflies versus birds as umbrella species at the canyon level in the Shoshone Mountains was marginally significant. The mean proportion of occurrences protected using cross-taxonomic umbrellas did not differ significantly from the mean proportion of occurrences protected using umbrellas from the same taxonomic group (Table 5). Although the power of our statistical tests was relatively low (see Section 2), we note that the greatest difference among proportions that was not identified as statistically significant was 0.11, and most differences were much smaller (Table 5).

Table 4
Proportion of species and occurrences (i.e. occupied locations) that would be protected by conserving the one site per canyon or one canyon per mountain range (approximately 19% of the area sampled) with the greatest number of umbrella species

	Spatial level	Proportion protected	
		Species	Occurrences
Birds			
Shoshone	Site	0.68	0.40
	Canyon	0.64	0.37
Toiyabe	Site	0.54	0.32
	Canyon	0.54	0.38
Toquima	Site	0.55	0.44
	Canyon	0.45	0.43
Landscape	Site	0.64	0.34
	Canyon	0.60	0.35
Butterflies			
Shoshone	Site	0.82	0.31
	Canyon	0.88	0.33
Toiyabe	Site	0.89	0.24
	Canyon	0.89	0.24
Toquima	Site	0.83	0.33
	Canyon	0.88	0.30
Landscape	Site	0.92	0.24
	Canyon	0.89	0.25

Table 5
Proportion of species and occurrences (i.e. occupied locations) that would be protected by conserving the one site per canyon or one canyon per mountain range with the greatest number of same-taxon (U_{same}) or cross-taxon (U_{cross}) umbrella species

	Spatial level	Proportion protected			
		Species		Occurrences	
		U_{same}	U_{cross}	U_{same}	U_{cross}
Birds					
Toquima	Site	0.55	0.53	0.44	0.38
	Canyon	0.45	0.53	0.43	0.49
Toiyabe	Site	0.54	0.54	0.32	0.43
	Canyon	0.54	0.54	0.38	0.39
Shoshone	Site	0.68	0.68	0.40	0.38
	Canyon	0.64	0.64	0.37	0.36
Landscape	Site	0.64	0.67	0.34	0.37
	Canyon	0.60	0.60	0.35	0.33
Butterflies					
Toquima	Site	0.83	0.83	0.33	0.32
	Canyon	0.88**	0.56**	0.30	0.26
Toiyabe	Site	0.89	0.89	0.24	0.21
	Canyon	0.89	0.89	0.24	0.26
Shoshone	Site	0.82	0.78	0.31	0.25
	Canyon	0.88*	0.76*	0.33	0.27
Landscape	Site	0.92	0.95	0.24	0.22
	Canyon	0.89	0.89	0.25	0.19

P-values reflect whether a significantly different proportion of species or occurrences was protected using same-taxon versus cross-taxon umbrellas. *, $0.05 < P \leq 0.10$; **, $P \leq 0.05$.

3.3. Spatial transferability

The spatial transferability of umbrella species identified using the umbrella index appeared to be relatively high. In only one case did umbrella species identified using data from a different mountain range protect a significantly lower proportion of species than umbrella species identified using data from the same mountain range (Table 6). Again, we acknowledge low statistical power; the greatest difference among proportions that was not identified as statistically significant was 0.16, and most differences were much smaller (Table 6).

4. Discussion

Using presence/absence data and the umbrella index, conservation practitioners can estimate the proportion of an assemblage that will be represented if a certain proportion of

Table 6
Spatial transferability of the umbrella index

Source of data	Spatial level	Proportion protected		
		Shoshone	Toiyabe	Toquima
Birds				
Shoshone	Site	[0.68]	0.64	0.66
	Canyon	[0.64]	0.64	0.45*
Toiyabe	Site	0.54	[0.54]	0.54
	Canyon	0.62	[0.54]	0.46
Toquima	Site	0.58	0.60	[0.55]
	Canyon	0.48	0.48	[0.45]
Butterflies				
Shoshone	Site	[0.82]	0.80	0.84
	Canyon	[0.88]	0.88	0.80
Toiyabe	Site	0.89	[0.89]	0.95
	Canyon	0.87	[0.89]	0.89
Toquima	Site	0.88	0.88	[0.83]
	Canyon	0.88	0.88	[0.88]

Proportion of species that would be protected by conserving the one segment per canyon or one canyon per mountain range with the greatest number of umbrella species selected using data from either the same mountain range (in brackets) or a different mountain range. In only one case did umbrella species selected using data from another mountain range protect a significantly lower proportion of species than umbrella species selected using data from the same mountain range (*, $P \leq 0.05$).

the landscape is protected. Our work suggests that using the umbrella index to identify conservation areas encompassing approximately 19% of the sampled landscape would confer protection to 45–66% of the regional assemblage of birds and 80–95% of the regional assemblage of butterflies. We do not pass judgment on whether these proportions are 'good enough'—the answer inevitably will depend on context and the eye of the beholder. We do note, however, that these proportions are considerably higher than those that would be reflected in a random set of locations of roughly equal area. Previous work suggested that although a similar proportion of taxa would be protected by using either a set of species identified with the umbrella index or a randomly-selected set of species, the latter set of species would require a larger proportion of the landscape to be designated for conservation to achieve a given level of species protection (Fleishman et al., 2001b). In other words, application of the umbrella index appeared to maximize species protection per unit of conserved area. In addition, we emphasize our belief that it is preferable to employ a suite of umbrella species rather than a single species in conservation planning because stochastic and deterministic environmental changes affect the distribution of many organisms, often asynchronously (Lambeck, 1997; Fleishman et al., 2000).

The ability of one taxonomic group to confer protection to another taxonomic group rarely has been testing using field data. Several studies have found low correlation in species richness among taxonomic groups at scales associated with local management (Prendergast et al., 1993; Chase et al., 1998; Rubinoff, 2001), although evidence on correlation in species richness among taxonomic groups at scales associated with ecoregional assessment is more equivocal (Olson and Dinerstein, 1998; Ricketts et al., 1999; Stein et al., 2000). Correlations between species richness of different taxonomic groups often increase as the spatial grain and extent of sampling increase (e.g. Swengel and Swengel, 1999).

Earlier workers suggested that large-bodied vertebrates with extensive home ranges and high sensitivity to human disturbance had the greatest potential to serve as umbrella species (Wilcox, 1984; Gittleman, 1986; Berger, 1997; Caro and O'Doherty, 1999; Andelman and Fagan, 2000). The area needed to conserve species with large home ranges generally is expected to exceed the minimum area requirements for viable populations of more sedentary species and to include the food and other resources required by the latter species. However, protection of the entire geographic range of megavertebrates rarely is realistic. Accordingly, we believe that species with intermediate rates of occurrence are more likely to be effective umbrella species in managed landscapes than widely dispersed generalists—provided the former species also tend to co-occur with a high proportion of co-occurring species and are sensitive to human land use. Our work lends tentative support to the argument that objectively selected umbrella species in one taxonomic group can confer protection to other taxonomic groups, especially butterflies and birds. The potential cross-taxonomic effectiveness of umbrella species almost certainly will be greater among groups that are highly resource-limited (e.g. water is the most limited resource in arid ecosystems, Huxman et al., 2004) and use broadly similar resources. Resource limitation and similarity of resource use, of course, may differ geographically.

The spatial transferability of umbrella species seems promising. It may be possible to save time and money by developing an umbrella index using data from one portion of an ecosystem and implementing the index throughout a landscape provided biogeography and human land-use history across the landscape are relatively similar.

Is the potential of birds to serve as umbrella species lower than the potential of butterflies? On the one hand, when we selected umbrella species using data from the same taxonomic group, the proportion of birds protected was much lower than the proportion of butterflies. On the other hand, in neither taxonomic group was the proportion of protected species reduced by using cross-taxonomic umbrella species. In other words, birds appeared to protect a higher proportion of a different assemblage than of their own assemblage. This counterintuitive result likely reflects that beta diversity of birds (i.e. between-habitat diversity or dissimilarity of species composition) tends to be greater than beta diversity of butterflies at all levels of sampling resolution in this system (Mac Nally et al., 2004). Although breeding birds in our study system have larger home ranges than resident butterflies, birds may have more specialized resource requirements related to vegetation structure and composition than adult butterflies (Mac Nally et al., 2004).

Although the umbrella index appears to be a promising method for identifying umbrella species, the merits of the umbrella species concept may deserve more critical inspection. First, as we noted earlier, merely restricting human land-uses in conservation areas may not be sufficient to protect native species; maintenance of species and ecological processes may require active human intervention. Second, if species richness and composition vary considerably over time in response to stochastic or deterministic environmental change, the proportion of species present in conserved locations may decrease. Using umbrella species to prioritize locations for conservation also does not account for potentially negative impacts of activities in the locations not selected for conservation (D. Spring, personal communication). Finally, identification of umbrella species usually is based on presence/absence data. For practical reasons, 'counts' or simply detections of species often are emphasized throughout the process of ecological assessment and monitoring. Inexperienced observers may have insufficient knowledge or time to collect unbiased data on abundance or population dynamics (Link and Sauer, 1998), and predicting occurrence patterns using relatively simple models is logistically more feasible than collecting detailed demographic data (see Scott et al., 2002). It is widely recognized, however, that presence/absence data have limited utility for inferences about long-term viability.

5. Conclusions

Few methods exist for a priori, quantitative selection of umbrella species and other types of focal species. This study and others have demonstrated that a transparent, quantitative umbrella index can be adapted for different taxonomic groups and ecosystems to maximize the proportion of species protected per unit of conserved area (Fleishman et al., 2000, 2001b). The effectiveness of species identified using the index does not appear to decay appreciably among taxonomic groups or across the landscape. The future utility of umbrella species concepts and methods ultimately depends on the demand for conservation short-cuts and the degree to which the effectiveness of such short-cuts can be validated.

Acknowledgements

We gratefully acknowledge G.T. Austin, A.J. Bailer, T.O. Crist, J.P. Fay, M.R. Hughes, D.D. Murphy, L.P. Bulluck, and E.E. Porter for help during various phases of this project. Thanks to M.A. Betrus for assistance with data collection and to the Humboldt-Toiyabe National Forest for logistic support in the field. Support for this research was provided by the Nevada Biodiversity Research and Conservation Initiative, by Miami University, and by the Joint Fire Sciences Program via the Rocky Mountain Research Station, Forest Service, US Department of Agriculture.

References

Agresti, A., 1990. Categorical Data Analysis. Wiley, New York.

Andelman, S.J., Fagan, W.F., 2000. Umbrellas and flagships: efficient conservation surrogates, or expensive mistakes? Proceedings of the National Academy of Sciences 97, 5954–5959.

Austin, G.T., Murphy, D.D., 1987. Zoogeography of Great Basin butterflies: patterns of distribution and differentiation. Great Basin Naturalist 47, 186–201.

Bailer, A.J., Ruberg, S.J., 1996. Randomization tests for assessing the equality of area under curves for studies using destructive sampling. Journal of Applied Toxicology 16, 391–395.

Bennett, B.M., Underwood, R.E., 1970. On McNemar's test for the 2×2 table and its power function. Biometrics 26, 339–343.

Berger, J., 1997. Population constraints associated with the use of black rhinos as an umbrella species for desert herbivores. Conservation Biology 11, 69–78.

Betrus, C.J., 2002. Refining the umbrella index complex: an application to bird and butterfly communities in montane canyons in the Great Basin. MS thesis, Miami University, Oxford, OH.

Boggs, C.L., Jackson, L.A., 1991. Mud puddling by butterflies is not a simple matter. Ecological Entomology 16, 123–127.

Brown, E.R. (Ed.), 1985. Management of fish and wildlife habitats in forests of western Oregon and Washington. USDA Forest Service R6-F and WL-192, Portland, OR.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, New York.

Caro, T., O'Doherty, G., 1999. On the use of surrogate species in conservation biology. Conservation Biology 13, 805–814.

Chase, M.K., Rotenberry, J.T., Misenhelter, M.D., 1998. Is the California Gnatcatcher an indicator of bird-species richness in coastal sage scrub? Western Birds 29, 468–474.

Clench, H.K., 1979. How to make regional lists of butterflies: some thoughts. Journal of the Lepidopterists' Society 33, 216–231.

Dobkin, D.S., Rich, A.C., 1998. Comparison of line-transect, spot-map, and point-count surveys for birds in riparian habitats of the Great Basin. Journal of Field Ornithology 69, 430–443.

Ehrlich, P.R., Dobkin, D.S., Wheye, D., 1998. The Birder's Handbook. Simon and Schuster, New York.

Fleishman, E., Austin, G.T., Murphy, D.D., 1997. Natural history and biogeography of the butterflies of the Toiyabe Range Nevada (Lepidoptera: Hesperioidea and Papilionoidea). Holarctic Lepidoptera 4, 1–18.

Fleishman, E., Austin, G.T., Weiss, A.D., 1998. An empirical test of Rapport's rule: elevational gradients in montane butterfly communities. Ecology 79, 2482–2493.

Fleishman, E., Murphy, D.D., Brussard, P.F., 2000. A new method for selection of umbrella species for conservation planning. Ecological Applications 10, 569–579.

Fleishman, E., Austin, G.T., Murphy, D.D., 2001a. Biogeography of Great Basin butterflies: revisiting patterns, paradigms, and climate change scenarios. Biological Journal of the Linnaean Society 74, 501–515.

Fleishman, E., Blair, R.B., Murphy, D.D., 2001b. Empirical validation of a method for umbrella species selection. Ecological Applications 11, 1489–1501.

Freitag, S., van Jaarsveld, A.S., Biggs, H.C., 1997. Ranking priority biodiversity areas: an iterative conservation value-based approach. Biological Conservation 82, 263–272.

Gittleman, J.L., 1986. Carnivore life history patterns: allometric, phylogenetic and ecological associations. American Naturalist 127, 744–771.

Grayson, D.K., 1993. The Desert's Past: A Natural Prehistory of the Great Basin. Smithsonian Institution Press, Washington, DC.

Hansen, A.J., Urban, D.L., 1992. Avian response to landscape pattern: the role of species' life histories. Landscape Ecology 7, 163–180.

Huxman, T.E., Smith, M.D., Fay, P.A., Knapp, A.K., Shaw, M.R., Loik, M.E., Smith, S.D., Tissue, D.T., Zak, J.C., Weltzin, J.F., Pockman, W.T., Sala, O.E., Haddad, B.M., Harte, J., Koch, G.W., Schwinning, S., Small, E.E., Williams, D.G., 2004. Convergence across biomes to a common rain-use efficiency. Nature 429, 651–654.

Kerr, J.T., 1997. Species richness, endemism, and the choice of areas for conservation. Conservation Biology 11, 1094–1100.

Lambeck, R.J., 1997. Focal species: a multi-species umbrella for nature conservation. Conservation Biology 11, 849–856.

Link, W.A., Sauer, J.R., 1998. Estimating population change from count data: application to the North American breeding bird survey. Ecological Applications 8, 258–268.

Mac Nally, R., Fleishman, E., Bulluck, L.P., Betrus, C.J., 2004. Comparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies. Journal of Biogeography 31, 917–929.

Manly, B.F.J., 1997. Randomization, Bootstrap, and Monte Carlo Methods in Biology. Chapman and Hall, New York.

Martikainen, P., Kaila, L., Haila, Y., 1998. Threatened beetles in White-backed Woodpecker habitats. Conservation Biology 12, 293–301.

Martin, T.E., 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65, 101–127.

McNemar, Q., 1947. Note on the sampling error of the difference between correlated proportions or percentages. Psychometrika 13, 153–157.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Niemi, G.J., Hanowski, J.M., Lima, A.R., Nichols, T., Weiland, N., 1997. A critical analysis of the use of indicator species in management. Journal of Wildlife Management 61, 1240–1252.

Oliver, I., Beattie, A.J., 1996. Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. Ecological Applications 6, 594–607.

Oliver, I., Beattie, A.J., York, A., 1998. Spatial fidelity of plant, vertebrate, and invertebrate assemblages in multiple-use forest in eastern Australia. Conservation Biology 12, 822–835.

Olson, D.M., Dinerstein, E., 1998. The global 200: a representation approach to conserving the earth's most biologically valuable ecoregions. Conservation Biology 12, 502–515.

Pollard, E., Yates, T.J., 1993. Monitoring Butterflies for Ecology and Conservation. Chapman and Hall, London.

Poulson, B.O., 2002. Avian richness and abundance in temperate Danish forests: tree variables important to birds and their conservation. Biodiversity and Conservation 11, 1551–1566.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C., Gibbons, D.W., 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. Nature 365, 335–337.

Pullin, A.S. (Ed.), 1995. Ecology and Conservation of Butterflies. Chapman and Hall, London.

Raguso, R.A., Llorente-Bousquets, J., 1990. The butterflies (Lepidoptera) of the Tuxlas Mts., Veracruz, Mexico, revisited: species-richness and habitat disturbance. Journal of Research on the Lepidoptera 29, 105–133.

Ricketts, T.H., Dinerstein, E., Olson, D.M., Loucks, C., 1999. Who's where in North America? Patterns of species richness and the utility of indicator taxa for conservation. BioScience 49, 369–381.

Rottenborn, S.C., 1999. Predicting the impacts of urbanization on riparian bird communities. Biological Conservation 88, 289–299.

Rubinoff, D., 2001. Evaluating the California Gnatcatcher as an umbrella species for conservation of southern California Coastal Sage Scrub. Conservation Biology 15, 1374–1383.

Schoener, T.W., 1968. Sizes of feeding territories among birds. Ecology 49, 123–141.

Scott, J.A., 1986. The Butterflies of North America. Stanford University Press, Stanford, CA.

Scott, J.M., Csuti, B., Jacobi, J.D., Estes, J.E., 1987. Species richness. BioScience 37, 782–788.

Scott, J.M., Heglund, P.J., Morrison, M., Raphael, M., Haufler, J., 2002. in: Wall, B. (Ed.), Predicting Species Occurrences: Issues of Scale and Accuracy. Island Press, Washington, DC.

Siegel, R.B., Desante, D.F., Nott, M.P., 2001. Using point counts to establish conservation priorities: how many visits are optimal?. Journal of Field Ornithology 72, 228–235.

Simberloff, D., 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era?. Biological Conservation 83, 247–257.

Soberón, J., Llorente, J., 1993. The use of species accumulation functions for the prediction of species richness. Conservation Biology 7, 480–488.

Stohlgren, T.J., Quinn, J.F., Ruggiero, M., Waggoner, G.S., 1995. Status of biotic inventories in U.S. National Parks. Biological Conservation 71, 97–106.

Stein, B.A., Kutner, L.S., Adams, J.S. (Eds.), 2000. Precious Heritage: The Status of Biodiversity in the United States. Oxford University Press, Oxford, UK.

Suter, W., Graf, R.F., Hess, R., 2002. Capercaillie (*Tetrau urogallus*) and avian biodiversity: testing the umbrella-species concept. Conservation Biology 16, 778–788.

Swengel, S.R., Swengel, A.B., 1999. Correlations in abundance of grassland songbirds and prairie butterflies. Biological Conservation 90, 1–11.

Wacholder, S., Weinberg, C.R., 1982. Paired versus two-sample design for a clinical trial of treatments with dichotomous outcome: power considerations. Biometrics 38, 801–812.

Warkentin, I.G., Reed, J.M., 1999. Effects of habitat type and degradation on avian species richness in Great Basin riparian habitats. Great Basin Naturalist 59, 205–212.

Wilcox, B.A., 1984. In situ conservation of genetic resources: determinants of minimum area requirements, in: McNeely, J.A., Miller, K.R. (Eds.), National Parks: Conservation and Development, 1984. Smithsonian Institution Press, Washington, DC, pp. 639–647.

Wilcox, B.A., Murphy, D.D., Ehrlich, P.R., Austin, G.T., 1986. Insular biogeography of the mantane butterfly faunas in the Great Basin: comparison with birds and mammals. Oecologia 69, 188–194.