ABSTRACT

REFINING THE UMBRELLA INDEX COMPLEX:

AN APPLICATION TO BIRD AND BUTTERFLY COMMUNITIES

IN MONTANE CANYONS IN THE GREAT BASIN

by Christopher J. Betrus

The purpose of this thesis was to refine and empirically validate the umbrella index, a proposed metric that adds quantitative criteria to the selection of umbrella species. Two versions of the index were evaluated with bird and butterfly occurrence data from montane canyons in three mountain ranges near Austin, Nevada. When conserving all locations with at least one umbrella species, at least 79% of all locations were selected for conservation and protected at least 90% of the species. Subsets of locations with the highest number of umbrella species selected 16 – 21% of the locations for conservation and protected at least 45 and 82% of the bird and butterfly species, respectively. In most situations, cross-taxonomic umbrellas performed similarly to same-taxon umbrellas. Yearly variations in species occurrence influenced umbrellas species and the proportion species protected, indicating that conservation efforts may be more important during years when species exhibit narrower distributions.

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Christopher J. Betrus

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Advisor________________________
(Dr. Robert B. Blair)

Reader_________________________
(Dr. Thomas C. Crist)

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CHAPTER 1: INTRODUCTION TO THESIS

Conservation biologists and land managers seldom have the time or financial resources needed to obtain all of the required knowledge to make informed land-use decisions and therefore are often forced to look for conservation shortcuts (Niemi et al. 1997, Simberloff 1998). These shortcuts include, but are not limited to, the use of flagship, indicator, and umbrella species (Dufrêne and Legendre 1997, Simberloff 1998). The goal of these alternative schemes is to allow conservationists to protect plant and animal communities by focusing conservation efforts on a relatively small number of surrogate species (Berger 1997; Simberloff 1998, 1999; Caro and O'Doherty 1999).

The most common conservation biology term to a non-scientist is "flagship species." Flagships are usually large, charismatic vertebrates that serve as anchors for conservation campaigns (Caro and O'Doherty 1999). The purpose of these alluring species is to attract public attention and support (Western 1987). Financial support raised for the flagship species and its conservation can then be used to protect large areas of habitat. Land managers can subsequently modify lands not only for the flagship species, but also for the less charismatic taxa that live in the conserved areas (Johnsingh and Joshua 1994).

One of the most widely known flagship species is the Florida panther (*Felis concolor coryi*). This exceedingly rare disjunct subspecies of the widely ranging mountain lion has been used in both public and private campaigns with a broad array of conservation objectives (Simberloff 1998). It is an effective flagship because of the unprecedented amount of funds that it has generated for conservation initiatives. As proof to its success in gaining public support, in 2001 over 110,000 people paid an additional $25 to have its picture on their automobile license plate, raising in excess of $2.7 million for conservation efforts. Of these funds, 85% have been invested in the Florida Panther Research and Management Trust Fund while the remaining money is allocated to the Florida Communities Trust Fund (State of Florida DHSMV 2002).

Flagship species are often chosen because their populations are declining in size or they already have endangered species status and a real need for focused conservation efforts (Dietz et al. 1994). Thus, flagship species are often more sensitive to anthropogenic disturbance than are closely related species that are not experiencing declines in population size (Caro and O'Doherty 1999). Therefore, conservation of lands for flagship species should also effectively conserve species with stable population sizes. However, conservation schemes based around flagship species may not be the most effective use of funds. For example, Cox et al. (1994) proposed a conservation plan centered on the Florida black bear (*Ursus americanus floridanus*) that would cost less money and provide protection to more threatened species and subspecies. Flagship species management is also problematic because many ecosystems do not have endangered, charismatic vertebrates to serve as the foundation for a conservation campaign.

The indicator species concept has been used for decades. Initially, it was used as a convenient way to survey environmental conditions, but the concept has since taken on a variety of meanings (Thomas 1972, Caro and O'Doherty 1999). Indicators are species that exhibit distributions, abundances, or population dynamics that can be used to predict the presence of other species in the community or reflect chemical or physical changes within the environment (Karr 1981, Landres et al. 1988, Temple and Wiens 1989, Noss 1990, Kremen 1992, Niemi et al. 1997). *Health* indicators are species that are so closely associated with particular environmental conditions that their presence, diversity, or abundance can be used to indicate the presence of the necessary conditions (Patton 1987). *Population* indicator species are species that are used to indicate population trends in other species (Caro and O'Doherty 1999). Finally, *biodiversity* indicator species are used when scientists want to determine the number of species of poorly studied taxa by surveying the number of species in a well-known taxonomic group (Caro and O'Doherty 1999). Ideally, the presence and fluctuation of populations of indicator species would mirror those of other species in the community (Dufrêne and Legendre 1997, Simberloff 1998). Despite their obvious appeal, only a few species have been identified as reliable and affordable indicators of community composition or environmental degradation (Scott 1998, Anderson 1999, Caro and O'Doherty 1999, Lindenmayer 1999, Ranius 2002). Acquiring further knowledge about species life history and population fluctuations will assist in increasing the number of identified indicator species.

Umbrella species are those that, when conserved, provide protection to sympatrically occurring species (Wilcox 1984). Conserving lands by controlling the amount of development that can occur provides a refuge for many species that cannot find adequate habitat elsewhere. One criterion often used in the selection of umbrella species is the area requirements of individuals. Traditionally, the larger the area requirements, the larger an area the protective umbrella created by their conservation will be and therefore the more effective they will be as an umbrella species (Wilcox 1984, Caro and O'Doherty 1999, Andelman and Fagan 2000). This information on area requirements and umbrella size could then be used to select the size of an area for conservation, although it could not be used to determine its location (Berger 1997).

Umbrella species are of interest for many reasons. If umbrella species can be effectively chosen for a particular ecoregion or taxonomic group then their use can help prioritize and maximize conservation efforts (Fleishman et al. 2001). However, little empirical evidence exists to validate the concept that conservation efforts focused on one or a small set of species will confer a protective umbrella to co-occurring species of the same taxonomic group (Caro and O'Doherty 1999; Andelman and Fagan 2000; but see Fleishman et al. 2000, 2001; Suter et al. 2002). Even fewer data validate the umbrella species concept between taxonomic groups (but see Martikainen et al. 1998). Not surprisingly, several researchers question the effectiveness of protective umbrellas to conserve other species both within and between taxonomic groups (Kerr 1997, Oliver et al. 1998, Rubinoff 2001). Despite the incongruous results obtained by researchers using umbrella species, limits to conservation funding and the immediate need for management guidance keeps the umbrella species concept alive and highlights the need for more empirical tests (Stohlgren et al. 1995, Oliver and Beattie 1996, Longino and Colwell 1997, Niemi et al. 1997, Simberloff 1998, Fleishman et al. 2001).

Perhaps one of the reasons that so few studies have shown the efficacy of umbrella species is the variety of methods used to define and select them. Wilcox (1984) introduced the umbrella species concept and defined an umbrella species as one whose minimum area requirements are at least as comprehensive as the rest of the community. If area requirements for all species in a community are known, this would require selecting the most vagile species as an umbrella. Lambeck (1997) expanded the concept to include a suite of focal species, each of which is used to define spatial and compositional attributes that must be present in a landscape. Berger (1997) presented a slightly different view of umbrella species, noting that they can be used to determine only the size of an area that should be conserved and cannot be used to determine its exact location within a region.

Traditionally, good umbrella species have been thought to have large home ranges and to be sensitive to anthropogenic disturbance (Wilcox 1984, Berger 1997, Andelman and Fagan 2000). Because of the allometric relationship between home-range size and body size, this meant that people viewed large animals as the ultimate umbrella species (Gittleman 1986, Caro and O'Doherty 1999, Andelman and Fagan 2000). The vast areas required by the large, widely roaming species are expected to maintain the minimum area requirements needed for viable populations of more sedentary populations (Fleishman et al. 2001). Umbrella species that are more sensitive to anthropogenic disturbance will provide suitable habitat for species that are equally or less sensitive to human activities (Caro and O'Doherty 1999).

Caro and O'Doherty (1999) highlighted the infancy of the umbrella species concept by acknowledging that umbrella species are less developed than indicator species and that no studies indicated the efficacy of one species to protect conspecifics. Several researchers have shown that the protection of one species can indeed protect conspecifics (Martikainen et al. 1998; Fleishman et al. 2000, 2001; Suter et al. 2002), although several other researchers have documented the lack of success (Kerr 1997, Oliver et al. 1998, Rubinoff 2001).

One similarity between flagship, indicator, and umbrella species management is that historically they have been selected after a species has started to show a decline in population size (Simberloff 1998, Caro and O'Doherty 1999). One reason for this is that ecologists often disagree on what characteristics these surrogate species should exhibit. Thus, scientists are forced to look at endangered species and see if their conservation can gain public support for conservation (flagships), indicate environmental health, trends in other species or biodiversity (indicators), or protect sympatric species (umbrellas).

Prospective selection is difficult for flagships because people are not as eager to give their hard-earned money for a species that is doing just fine in the wild. Indicator species can be selected prospectively if ecologists have a substantial body of knowledge about their natural history and their relationships with other species (Caro and O'Doherty 1999). However, unless population sizes of indicators are large to begin with, the fluctuations they must exhibit as indicators may cause them to become endangered as well (Caro and O'Doherty 1999). Yet the prospective selection of umbrella species is, at least theoretically, feasible. The selection of umbrella species can be accomplished before species start to decline in population size if a wealth of life history information exists and conservation goals are clearly defined *a priori*.

In an attempt to develop a quantitative method for determining the efficiency of individual species to act as umbrellas, Fleishman et al. (2000) proposed the "umbrella index." By using distributional, occurrence, and life history data to determine each of the components, the umbrella index can be used to calculate the potential ability for each species in an area to serve as a conservation umbrella for others of the same taxonomic group (Fleishman et al. 2000). Two of the components, degree of rarity and mean proportion of co-occurring species, are determined from distribution and occurrence data. Although this data still needs to be collected for many communities, it exists for many others. Ultimately, this data is needed to verify the effectiveness of any conservation plan. The final parameter, disturbance sensitivity, is calculated from life history attributes that influence a species' susceptibility to anthropogenic disturbance. Each individual species receives an umbrella index score that is the sum of these three components. Species with umbrella index scores more than one standard deviation above the mean are identified as umbrella species. If the index is normally distributed, this will result in designating approximately 16% of species of the entire species pool as umbrellas. The designation of species receiving umbrella index scores greater than 1 sd above the mean is an arbitrary designation that does not have any necessary biologic validity. Conservation strategies using the umbrella index can focus on conserving locations with at least one umbrella species or on conserving a subset of locations with the greatest number of umbrella species (Fleishman et al. 2000, 2001).

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CHAPTER 2: WHICH METHOD OF CONSERVATION IS BETTER? COMPARING TWO METHODS OF CALCULATING THE UMBRELLA INDEX

ABSTRACT

Conservation biologists must design reserves by selecting locations with the highest conservation priority. Conservation surrogates, such as umbrella species, must often be used with the hopes that the protection of one or a few species will provide protection to many other species. The 'Umbrella Index' is one proposed metric that adds quantitative criteria to the selection of umbrella species. Using sets of data from two taxonomic groups in three mountain ranges, I tested the effectiveness of two proposed methods for calculating the umbrella index. Conserving all locations with at least one umbrella species would result in the protection of a vast majority of locations and species from both assemblages for both methods. The two methods also protected similar proportions of species when conserving subsets of locations with the highest number of umbrella species. When conserving subsets of locations, > 45% of bird species and >82% of butterfly species would receive protection while conserving only about 20% of the habitat. Results indicated that there was no difference in the effectiveness of the two methods of calculating the umbrella index. However, the practicality of the umbrella index may be limited by the proportion of locations selected for conservation when conserving all locations with at least one umbrella species. Future use of the umbrella index should focus on the conservation of a subset of locations with the highest number

of umbrella species because a more reasonable proportion of locations are marked for conservation.

INTRODUCTION

Conservation biologists rarely have the time or depth of knowledge about the flora and fauna of an area to make informed land-management decisions (Stohlgren et al. 1995, Oliver and Beattie 1996, Niemi et al. 1997, Simberloff 1998). As a result, they are often forced to look for short-cuts to conservation. The use of umbrella species, whose conservation provides protection to sympatrically occurring species, is one of the proposed methods to save time and money in conservation efforts (Wilcox 1984, Dufrêne and Legendre 1997, Simberloff 1998). Animals with large home-range sizes have traditionally been selected as umbrella species due to the larger area requirements for individuals (Wilcox 1984, Caro and O'Doherty 1999, Andelman and Fagan 2000). Theoretically, information on area requirements can be used to select the size of an area for conservation, although it cannot be used to determine its location (Berger 1997).

In an attempt to advance the umbrella species concept and determine quantitative criteria for selecting umbrella species, Fleishman et al. (2000) introduced the "umbrella index" concept. The umbrella index measures the degree to which each species within any particular taxonomic group in an area can provide protection to other species that reside in the same area (Fleishman et al. 2000). Three main parameters are used to select the best umbrella species: degree of rarity, sensitivity to human disturbance, and mean percentage of co-occurring species (Fleishman et al. 2000).

Effective umbrellas should be neither extremely rare nor omnipresent. Exceedingly rare species may not be distributed across enough of the landscape to ensure the viability of other species. Omnipresent species are poor umbrellas because it is usually impossible to protect all locations in a region that needs conservation planning. Ideal umbrellas also should be sensitive to human disturbance to ensure that less sensitive species will be relatively unaffected (Blair 1996, Blair and Launer 1997, Fleishman et al. 2000).

Finally, umbrella species should co-occur with a relatively high proportion of species in the same taxonomic group. Protecting species that co-occur with high numbers of other species will help prioritize conservation locations when the protection of species richness is conservation priority (Dufrêne and Legendre 1997, Freitag et al. 1997, Fleishman et al. 2000). Thus, the umbrella index allows researchers to obtain relative scores for how effective each species in a community will be at providing a protective umbrella to co-occurring species. Conservationists can then prioritize locations where high-ranking umbrella species reside as high-priority conservation sites.

Fleishman et al. (2001b) later released a slightly altered method for determining umbrella species. The same three parameters were used, but the rarity calculation was altered. Individual species could receive scores between 0.5 and 3.0 using the old method because two parameters ranged from 0 to 1 and one ranged from 0.5 to 1. The new method of calculation made all three parameters range from 0 to 1, with an ideal umbrella species receiving a summed value of 3. This relatively minor change may, nonetheless, influence the umbrella index scores that individual species receive and ultimately change which species are chosen as umbrella species.

Here, I compare the effectiveness of the original method (introduced in the Ecological Applications journal, henceforth EA) to the more recent method published in the Conservation Biology in Practice (henceforth CBIP) journal on bird and butterfly communities in montane canyons of three mountain ranges in the Great Basin. Individual components of the EA method do not contribute equally to the overall umbrella index score as they do in the CBIP method. Therefore, I predict the CBIP method will select more effective umbrella species than the EA method because all three parameters are measured on the same scale.

METHODS

I conducted this study in the Toquima and Toiyabe Ranges and the Shoshone Mountains, located near the town of Austin, Nevada (Latitude 39.493 °N, Longitude 117.069°W). These are just a few of the more than 200 north-south oriented mountain ranges in the Great Basin (Figure 1). All three of the mountain ranges have numerous canyons incised into the east and west facing slopes. A majority of the canyons are dry except after storms or during periods of snowmelt. Some of the canyons, mostly in the larger Toiyabe Range, have continuous flow while others have seeps or springs that create standing or flowing water in limited portions of canyons. The topography of individual canyons is highly variable.

Bird and butterfly communities were surveyed in six canyons in the Toquima Range, five in the Toiyabe Range, and five in the Shoshone Mountains. Canyons were divided into elevational segments from mouth to crest defined by 100 m change in elevation (Fleishman et al. 1997). Fleishman compiled butterfly species presence data by walking the length of all canyons at a constant pace and recording the presence of all species of butterfly in each segment. Each canyon was surveyed during multiple years between 1996 and 2001 (see Fleishman et al. 1997, 2000, 2001a for details). I assessed bird communities of each segment by performing a series of 75 m fixed-radius point-counts within each segment (Bibby et al. 1992). Three 5-minute point-counts were conducted at each location between 28 May 2001 and 27 June 2001, the peak breeding season for birds in this area. During point-counts, I identified all bird species within 75 m of the point-count location by sight and sound.

Identification of umbrella species

I calculated umbrella index values using both the EA and the CBIP methods to measure the potential of each species of bird and butterfly to serve as an umbrella for other species. Calculations were performed at the segment and canyon level for both birds and butterflies within each of three ranges and for a combined dataset including all three ranges. For segment-level analyses, I used presence-absence data as determined by avian point counts and butterfly transects. Canyon-level presence was established by a species' presence in any of the segments within a specific canyon. Although presence-absence data provides little information on species viability, adequate time and money rarely exist to collect unbiased data about bird and butterfly abundances (Droege et al. 1998, Link and Sauer 1998).

Evaluating the effectiveness of conservation strategies can be done several ways. Management of habitats for the conservation of biodiversity involves protecting locations in a fashion that maintains species richness (Freitag et al. 1997). Species richness is a valid measure of how many species may be conserved by a particular scheme for taxa that are readily sampled; however, richness alone provides no information on how much of a species' range is conserved. An alternative metric to species richness is the proportion of occupied locations (defined as the locations in which a species was detected) conserved for each species that receives protection. The mean proportion of locations conserved for all species in a community can be used to evaluate the degree of protection a conservation scheme provides to species that differ in their baseline occurrences. For example, a species that occurs in two of 10 locations is relatively well protected if both locations (100% of its occurrences) are conserved, regardless of how many total locations are conserved. A species that occurs in eight of the 10 locations is not well protected if only two of these locations are conserved because it has lost 75% of the locations it previously occurred in and would have a proportion of occupied locations conserved value of 2/8 or 0.25 (Fleishman et al. 2000, 2001a).

The EA calculation for degree of rarity (R) is calculated differently from the CBIP method. Using the EA method, each species receives an R-value between 0.5 (the species occurs in either none or all of the locations) and 1.0 (the species occurs in exactly half of the locations). For each species *j*, degree of rarity (R) using the EA method is defined as

$$R_j = 1 - \left| \frac{N_{present}}{N_{total}} - 0.5 \right|$$

where N is the number of locations with the *j*th species present ($N_{present}$) or the total locations considered (N_{total}) (Baz 1991, Fleishman et al. 2000). Degree of rarity values for species were calculated separately in each individual range and for the combined data set.

The CBIP calculation for degree of rarity ranges from 0 (the species occurs in all or none of the locations) to 1.0 (the species occurs in exactly half of the locations). For each species *j*, R is defined as

$$R_j = 1 - 2 \times \left| \frac{N_{present}}{N_{total}} - 0.5 \right|$$

where N is the number of locations with the *j*th species present ($N_{present}$) or the total locations considered (N_{total}) (Baz 1991, Fleishman et al. 2001b).

The other two parameters in the UI are calculated identically under the EA and CBIP methods. Each species receives a mean percentage of co-occurring species (PCS) score between 0 (the species tends to occur with no other species) and 1 (when present, the species occurs with all other species in the community). For each species *j*, PCS is defined as

$$PCS_j = \sum_{i=1}^{l} (S_i - 1)/(S_{\max} - 1)/N_j$$

where *l* is the number of locations in the data set, S_i is the number of species present at each location *i,* S_{max} is the total number of species present in all locations in the data set, and N_j is the number of locations where species *j* occurs (Fleishman et al. 2000). Like R, mean PCS values were calculated separately for each range and the three mountain ranges combined.

The third parameter, disturbance sensitivity (DSI) is a modified form of a sensitivity index proposed by Nelson and Anderson (1994). The DSI for birds was based on six life-history parameters: reproductive effort, nest form, nest height, territory size or density, migratory classification, and primary habitat (Table 1). Each bird species received an integer value score from 1 (low sensitivity) to 3 (high sensitivity) based on existing knowledge about avian life histories. Butterfly DSI values were calculated using three life-history parameters: mobility, larval host-plant specificity, and riparian dependence (Table 2). Each butterfly species received an integer score from 1 (low sensitivity) to 4 (high sensitivity) for each of the three life history traits based on life-history knowledge. DSI scores were standardized by summing the sensitivity scores and then dividing by the maximum calculated value for their taxonomic group. Disturbance sensitivity, thus, is a relative score with the most sensitive species receiving scores of 1 and less sensitive species receiving lower scores. DSI scores were calculated from the combined data sets that included all bird and butterfly species.

For each species, the umbrella index (UI) is calculated as the sum of its rankings for mean percentage of co-occurring species (PCS), degree of rarity (R), and disturbance sensitivity (DSI). Under the EA method, each species could theoretically receive an UI score from slightly below 1.0 (a very poor umbrella that would protect few other species) to 3.0 (an efficient umbrella that would protect many other species). With the CBIP calculation, each species could receive an umbrella index score from near 0 (a very poor umbrella that would protect few other species) to 3 (an efficient umbrella that would conserve many other species). Potential umbrella species are those that received an UI score greater than 1 sd above the mean. The designation of species receiving umbrella index scores greater than 1 sd above the mean is an arbitrary designation that does not have any necessary biologic validity. For each individual data set, a sensitivity analysis could be used to determine if other cut-offs such as 1.5 or 2 sd above the mean may have more biologic pertinence.

Once umbrella species were selected for a given data set, I used them to select sites for conservation. Two different scenarios were used: the conservation of all locations with at least one umbrella species and the conservation of subsets of locations with umbrella species. Under both of these scenarios, locations selected for conservation are referred to as 'conserved' and species that were surveyed in these conserved locations are referred to as 'protected.'

ANALYSES

Similarity of umbrella species selected by the EA and CBIP methods

I used the Jaccard Index (Magurran 1988) to measure the similarity between umbrella species selected using the EA and CBIP methods in each data set. The Jaccard Index can be used to measure community similarity and was calculated as $C_J = j/(a + b - j)$, where j = the number of umbrella species common to both selection methods, a = the number of species selected as umbrellas using the EA method, and b = the number of species selected as umbrellas using the CBIP method. A data set received a Jaccard score of 0 when no species were shared between the groups and $C_J = 1$ when the same set of species were selected with both methods. I used McNemar's (1947) Q test to compare the sets of species selected by the EA and CBIP methods. McNemar's Q is a non-parametric chi-square test used to evaluate differences between dependent proportions and count data (Agresti 1990). McNemar's Q test analyzes the null hypothesis H_0: Y_{12} pairs are as likely as Y_{21} pairs where Y_{12} and Y_{21} are discordant pairs of dichotomous responses (Figure 2). McNemar's Q test was calculated as $Q = (Y_{12} - Y_{21})^2/(Y_{12} + Y_{21})$. In the context of this analysis, for both the EA and CBIP methods each species in a data set was assigned a label of 1 if it was selected as an umbrella species or 0 if it was not selected as an umbrella species. McNemar's Q test compares the number of species that received different labels by the EA and CBIP methods. To illustrate, for birds in the Toquima Range at the segment level, four species were selected as umbrellas by both the EA and CBIP methods, two species were selected as umbrellas by the EA method and not by the CBIP method, one species was protected by the CBIP method and not by the EA method, and 37 species were not protected by either method (Figure 2). The calculated chi-square value was 0.333 and the associated P-value was 0.5637.

Conservation of all locations with at least one umbrella species

The umbrella index selects multiple umbrella species for each data set. In this scenario, I determined the impact of protecting all locations where one or more of these umbrella species were located. For each data set, I calculated both the proportion of species that would be protected and the proportion of locations that would be designated for protection. I also calculated the mean proportion of occupied locations conserved for all protected species. I used McNemar's (1947) Q test to compare proportions of species and locations protected with the EA and CBIP methods where each species in a data set was assigned a label of 1 if it occurred in any location selected for conservation or 0 if it did not occur in any conserved locations. For example, when conserving a subset of locations for birds in the Toquima Range, 21 species were protected by both the EA and CBIP methods, three species were protected by the EA method and not by the CBIP method, one species was protected by the CBIP method and not by the EA method, and 15 species were not protected by either method. The calculated chi-square value was 1.00 and the associated P-value was 0.3173.

Conservation of subsets of locations with umbrella species

It would be virtually impossible to protect the entire range of all but the most endangered species (Andelman and Fagan 2000, Fleishman et al. 2000). Thus, the effectiveness of the umbrella index may be useful for prioritizing conservation efforts by preserving locations with the highest number of umbrella species. In this scenario, locations with the highest number of umbrella species were conserved. At the segment level, the one segment with the highest number of umbrella species was selected from each canyon within a mountain range. Thus, the number of segments that would be conserved in a range is the same as the number of canyons. At the canyon level, the one canyon per range with the most umbrellas would be conserved. For each data set, I calculated the proportion of species and locations that would be protected. For all species that were present in a conserved location, I calculated the mean proportion of occurrences that would be conserved. I used McNemar's (1947) Q test to compare proportion of species protected with the EA and CBIP methods.

RESULTS

The total number of bird species per range was between 40 and 52, with a total of 67 species surveyed (Table 3). A total of 64 butterfly species were surveyed and the number in each range was between 50 and 63. The proportion of bird species identified as umbrellas using the EA method was between 0.10 and 0.20 (mean ± sd: 0.16 ± 0.04) while proportion of butterfly species selected as umbrellas was between 0.15 and 0.22 (0.18 ± 0.02). The CBIP method identified between 0.13 and 0.23 (0.17 ± 0.03) of the bird species as umbrellas and between 0.13 and 0.24 (0.19 ± 0.03) of the butterfly species as umbrellas.

Similarity of umbrella species selected by the EA and CBIP methods

Umbrella species selected by the two methods had a Jaccard similarity of at least 0.500 for all data sets (Table 4). Butterfly umbrellas selected for the Toiyabe Range had the highest similarity for both scales, whereas avian umbrella species in the Toiyabe Range had the highest similarity at the segment level. The umbrella species selected for the Toquima Range had the lowest values for both butterflies at both the canyon level and segment level and for birds at the segment level. In no data sets was there a statistically significant difference between the species selected as umbrellas by the EA and CBIP methods.

Conservation of all locations with at least one umbrella species

The conservation of all locations with at least one of the identified umbrella species would result in the conservation of a vast majority of the species (EA: birds = 0.95 – 1.00, butterflies = 0.99 – 1.00; CBIP: birds = 0.95 – 1.00, butterflies = 1.00) and locations (EA: birds = 0.91 ± 0.09, butterflies = 0.91 ± 0.07; CBIP: birds = 0.93 ± 0.08, butterflies = 0.94 ± 0.06, Table 5). No significant differences existed in the proportions of species conserved by the EA and CBIP methods. A marginally significant difference existed between the proportions of locations selected for conservation by birds in the Toquima range at the segment level ($P = 0.0833$).

Conservation of subsets of locations with umbrella species

The conservation of subsets of locations with the highest number of umbrella species would protect 0.19 ± 0.02 of the locations regardless of which method is used (Table 6). For the EA method, the proportion of bird species protected fell between 0.45 and 0.68 and the proportion of butterfly species receiving protection was between 0.82 and 0.97. The proportion of bird species receiving protection when utilizing the CBIP method is also between 0.45 and 0.68 and the proportion of butterfly species that would be protected is between 0.82 and 0.92. There were no significant differences in the proportions of bird species that were protected. A marginally significant difference ($P = 0.0833$) existed between the proportions of species that would be protected by the two methods in butterflies in the combined data set. Birds tended to have a higher proportion of their occupied locations conserved than butterflies; however, a greater proportion of butterfly species were usually protected.

DISCUSSION

My results indicate that there is no difference in the proportion of locations, or more importantly, the proportion of species, that would be conserved between the EA and CBIP methods. The conservation of locations with at least one umbrella species will almost always result in the protection of all locations and therefore almost all species. In the Toquima Range at the segment level, where only 0.90 of the species were protected by both methods, the same four bird species were left unprotected. These species were Western Kingbird (*Tyrannus verticalis*), Lark Sparrow (*Chondestes grammacus*), Horned Lark (*Eremophila alpestris*), and Black-billed Magpie (*Pica hudsonia*). All of these species were surveyed in only one location in this range and do not depend on montane canyons for survival. They typically inhabit sagebrush (*Artemisia tridentata* spp.) dominated areas, which are abundant throughout the Great Basin (Ehrlich et al. 1988). Both methods failed to protect American Kestrels (*Falco sparverius*) at the canyon level in the Toquima Range. This species was not surveyed in the Shoshone Range, but was surveyed and conserved using both methods at the canyon and segment level in the

Toiyabe Range. Yellow Warblers (*Dendroica petechia*) were unprotected by both methods in the Shoshone Range at the canyon level; however they were protected at the segment level and in both other ranges using both methods. The only butterfly species to go unprotected in any location was *Satyrium sylvinum* at the canyon level in the Shoshone Mountains using the EA method.

The only time when the two methods selected a marginally different proportion of locations there was no change in the proportion of species receiving protection. The three additional segments protected by the CBIP method did not include any new species. These added segments did, however, provide greater protection to already conserved species as evidenced by the increase in the mean proportion of occupied locations conserved. Increasing the proportion of locations conserved can not only increase the proportion of species receiving protection, but it can also increase the amount of area that protected species can utilize.

Both UI calculation methods select important areas when protecting the subset of locations with the highest number of umbrella species. The power of this comparison is that it holds the proportion of locations constant and allows for the direct comparison between the effectiveness of different methods. The lack of a difference between the proportion of species protected by the EA and CBIP methods indicates that both methods are equally successful at selecting umbrella species. A relatively high proportion of species receive protection by conserving a relatively small proportion of locations. Both methods of calculating the umbrella index are efficient at selecting sites for conservation, which is often a priority for many land mangers (Freitag et al. 1997, Andelman and Fagan 2000).

The only difference between the EA and CBIP methods arises from the calculation of the degree of rarity component. The EA method presents a more simplistic version that is relatively easy to calculate. Species with an intermediate degree of ubiquity (i.e. were surveyed in half of the locations) receive a score of 1. Yet, a species that occurs everywhere or nowhere at all can still receive a score of 0.5 (see Figure 3). This is problematic because the species that score poorly with either of the other parameters receive scores near 0. Thus, a species that does not display median rarity still has a good chance of being selected as an umbrella species because the components are weighted differently. The CBIP method presents a more complex, yet intellectually satisfying method for calculating degree of rarity. Like the EA method, species that are surveyed in half of the locations will receive a score of 1.0. Yet, by multiplying the absolute value of 0.5 minus Q_j by 2, we ensure that nearly ubiquitous or rare species will receive scores near 0.

Regardless of whether the EA or CBIP method is used to select locations, conservation of all locations where there is at least one of the selected umbrella species conserves nearly all of the locations. This is because one goal of the umbrella index is to maximize degree of rarity parameter (Fleishman et al. 2000, 2001a). The selection of multiple species, each of which is present in about half of the surveyed locations, should very quickly have representatives in almost all of the locations. While most conservationists would agree that protecting all of the land would be the best approach to maintaining species diversity, umbrella species are not needed to advise land managers to conserve all of the locations (Andelman and Fagan 2000, Fleishman et al. 2001a). Limiting the number or proportion of species selected as umbrellas could be an effective way to do this. Current methods select about 16% of the species as umbrellas and means that a greater absolute number of umbrella species would be selected in species rich areas than species poor areas.   Limiting this to 10% or even as low as 5% could be effective for areas where lower proportions of locations are needed or available for conservation and can easily be accomplished by selecting species as umbrellas that are 1.28 or 1.645 sd above the mean, respectively.

One component of the umbrella index, disturbance sensitivity, can already be modified to any particular taxonomic group or ecoregion. Modification of the entire umbrella index to particular groups or ecoregions will add to its usefulness. The method that may prove most effective is the intentional weighting of important parameters. Although the differential weighting of components did not influence the results in this study, that does not mean the weighting of components is always unimportant. In particular ecoregions or within particular taxonomic groups, researchers may wish to intentionally weight one parameter of the umbrella index more heavily than the others. For example, some taxonomic groups may be particularly sensitive to anthropogenic disturbance and thus, researchers may want DSI to be more influential than the other parameters. Even within the disturbance sensitivity parameter, some sensitivity criteria may be of greater importance than others.

Despite its performance, there are several limitations to the umbrella index. First and foremost, until a particular species or suite of species is proven to be effective umbrellas for a region, a vast amount of information is needed to calculate the umbrella index. Life history data can be collected relatively easily for most of the criteria, yet particularly time consuming is the collection of the actual field data, required to calculate the degree of rarity and the percentage of co-occurring species. In situations where conservation decisions must be made rapidly, the umbrella index may be of limited utility.

In addition to the large amount of time needed there are other precautions that must be considered before the umbrella index is use for real-world conservation decisions. Locations selected for conservation were designated as ‘conserved’ and it is assumed that this will provide sufficient protection to all of the species that resided in that location so that they are ‘protected’. Species surveyed in particular locations, particularly at the segment level, may use adjacent segments either during the summer months or during other times of the year. Thus, the proportion of species protected in conserved locations may diminish from year to year. Additionally problematic is the idea that if locations selected for conservation were the only conserved locations and the surrounding matrix was altered, we would expect to see changes is species distributions. Finally, even over a relatively short time intervals, changes in species distributions and localized extinctions and colonizations may influence the number of species that would receive protection in conserved locations.

In conclusion, my research has shown that there is no difference in the performance of the two umbrella indices presented in Ecological Applications and Conservation Biology in Practice for birds and butterflies in montane canyons of the Great Basin. Regardless of which method is used, it is important that conservation biologists prospectively select umbrella species by considering life history and distribution characteristics. With foresight, land managers may be able to predict the size of the umbrella and the proportion of other species that will be protected by employing an umbrella species approach.

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Figure 1. Location of the Toquima and Toiyabe Ranges and the Shoshone Mountains (*black rectangle, see inset*) in the Great Basin (*irregular shape with black border, see inset*) and the inventory canyons 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 range's crest.

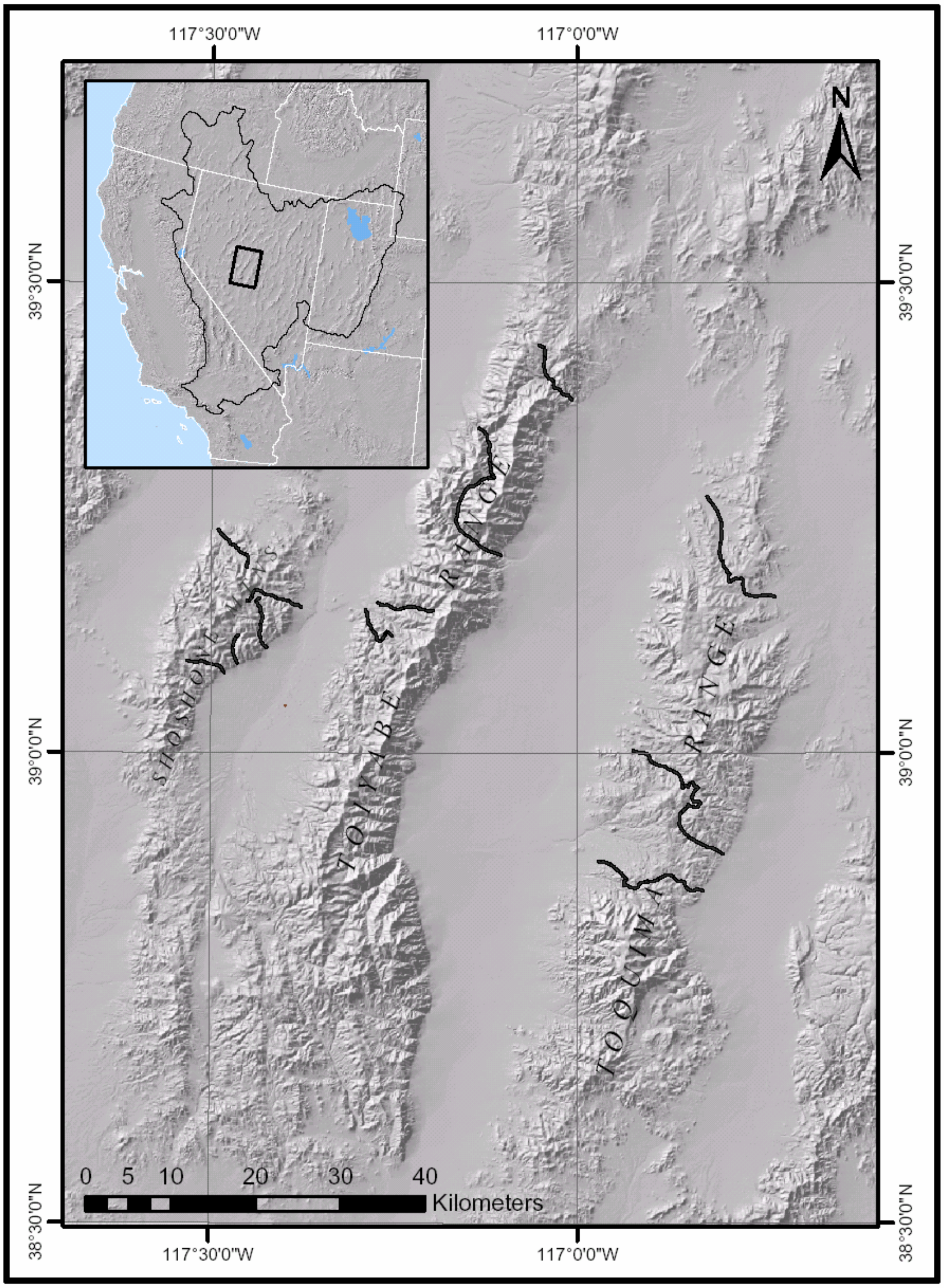

Figure 2. McNemar's (1947) Q test can be used to test the null hypothesis X for matched pair data by comparing the values of discordant pairs (Y_{12} and Y_{21} or 1 and 2, bolded). The general (a) and specific (b) examples illustrate how the data is arrayed to perform the comparison.

a. General example		EA Method		
		Species selected as umbrellas	Species not selected as umbrellas	
CBIP Method	Species selected as umbrellas	Y_{11}	$\mathbf{Y_{12}}$	b
	Species not selected as umbrellas	$\mathbf{Y_{21}}$	Y_{22}	n-b
		a	n-a	n

b. Specific example		EA Method		
		Species selected as umbrellas	Species not selected as umbrellas	
CBIP Method	Species selected as umbrellas	4	**1**	b
	Species not selected as umbrellas	**2**	37	n-b
		a	n-a	n

Figure 3. Weights for calculating degree of rarity scores with the EA and CBIP methods for a theoretical study site with 21 locations. x = EA method, o = CBIP method.

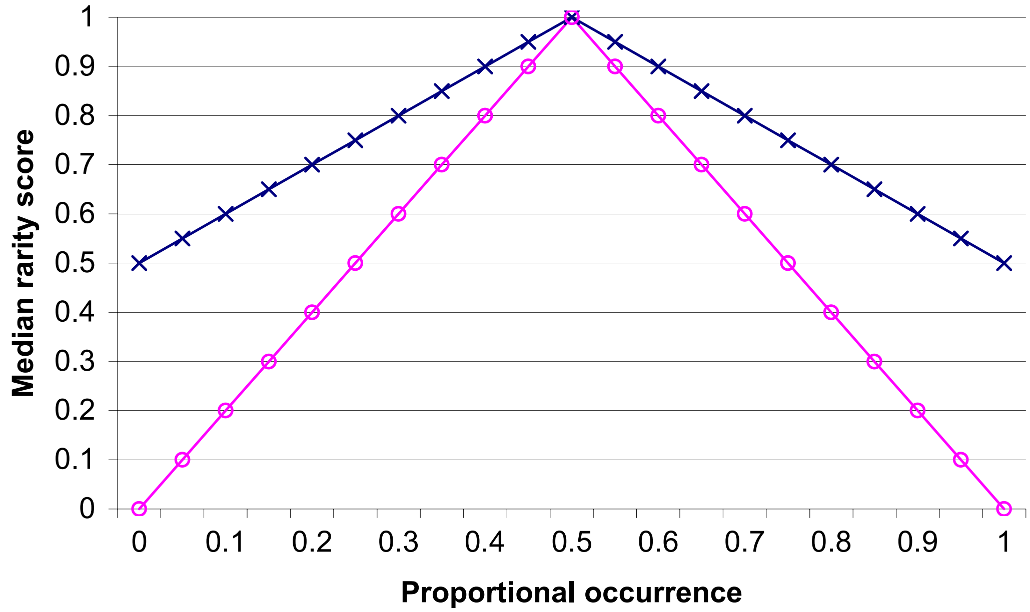

Table 1. Life history criteria used to score sensitivity (1 = least sensitive, 3 = most sensitive) of birds in the Toiyabe and Toquima Ranges and the Shoshone Mountains to human activities (modified from Hansen and Urban 1992; data from Schoener 1968, Brown 1985, Ehrlich et al. 1988, AOU 1992, Martin 1995, Rottenborn 1999, Warkentin and Reed 1999).

	Sensitivity score		
Parameter	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 distance	resident	short-distant	neotropical
Riparian dependence	no-use	facultative	obligate

Table 2. Life history criteria used to score sensitivity (1 = least sensitive, 4 = most sensitive) of butterflies in Toiyabe and Toquima Ranges and the Shoshone Mountains to human activities (Scott 1986, Boggs and Jackson 1991, Fleishman et al. 2001a).

	Sensitivity score			
Parameter	1	2	3	4
Vagility (m)	> 100,000	1,000 - 100,000	100 - 1,000	< 100
Larval host plant specificity	> 1 family	> 1 genus in 1 family	> 1 species in 1 genus in 1 family	1 species
Riparian dependence	no use	facultative, with individuals occasionally seen at puddles	facultative, with individuals frequently at puddles	obligate

Table 3. Number of species, umbrella species calculated by the two methods, and survey locations in each dataset.

Data set	Scale	Species	Umbrella method EA	Umbrella method CBIP	Locations
BIRDS					
Toquima Range	segment	40	6 (0.15)	6 (0.15)	28
	canyon	40	4 (0.10)	5 (0.13)	6
Toiyabe Range	segment	52	10 (0.19)	9 (0.17)	31
	canyon	52	8 (0.15)	9 (0.17)	5
Shoshone Mountains	segment	44	5 (0.11)	6 (0.14)	25
	canyon	44	9 (0.20)	10 (0.23)	5
All ranges combined	segment	67	10 (0.15)	11 (0.16)	84
	canyon	67	13 (0.19)	12 (0.18)	16
BUTTERFLIES					
Toquima Range	segment	52	8 (0.15)	11 (0.21)	28
	canyon	52	10 (0.19)	7 (0.13)	6
Toiyabe Range	segment	63	11 (0.17)	11 (0.17)	31
	canyon	63	11 (0.17)	13 (0.20)	5
Shoshone Mountains	segment	50	9 (0.18)	9 (0.18)	25
	canyon	50	10 (0.20)	12 (0.24)	5
All ranges combined	segment	64	14 (0.22)	12 (0.19)	84
	canyon	64	11 (0.17)	12 (0.19)	16

Notes: Proportions of total species are given in parentheses. EA = Ecological Applications method. CBIP = Conservation Biology in Practice method. Locations indicates the number of segments or canyons in a data set.

Table 4. Jaccard similarities between species selected as umbrellas by the EA and CBIP methods.

Data set	Scale	Jaccard similarity
BIRDS		
Toquima Range	segment	0.500
	canyon	0.800
Toiyabe Range	segment	0.900
	canyon	0.545
Shoshone Mountains	segment	0.571
	canyon	0.583
All ranges combined	segment	0.750
	canyon	0.923
BUTTERFLIES		
Toquima Range	segment	0.583
	canyon	0.545
Toiyabe Range	segment	0.692
	canyon	0.846
Shoshone Mountains	segment	0.636
	canyon	0.692
All ranges combined	segment	0.625
	canyon	0.769

Table 5. Consequences of protecting all locations with at least one umbrella species for each data set using the Ecological Applications and Conservation Biology in Practice umbrella indices.

Data set	Scale	Proportion Protected: Species		Locations		Occupied Locations	
		EA	CBIP	EA	CBIP	EA	CBIP
BIRDS							
Toquima Range	segment	0.90	0.90	0.79*	0.89*	0.87 ± 0.19	0.96 ± 0.12
	canyon	0.98	0.98	0.83	0.83	0.95 ± 0.11	0.95 ± 0.11
Toiyabe Range	segment	1.00	1.00	1.00	1.00	1.00 ± 0.00	1.00 ± 0.00
	canyon	1.00	1.00	1.00	1.00	1.00 ± 0.00	1.00 ± 0.00
Shoshone Mountains	segment	1.00	1.00	0.92	1.00	0.95 ± 0.10	1.00 ± 0.00
	canyon	0.98	0.98	0.80	0.80	0.92 ± 0.12	0.92 ± 0.00
All ranges combined	segment	0.99	0.99	0.99	0.99	0.99 ± 0.07	0.99 ± 0.07
	canyon	1.00	1.00	0.94	0.94	0.98 ± 0.05	0.98 ± 0.05
BUTTERFLIES							
Toquima Range	segment	1.00	1.00	0.86	0.89	0.95 ± 0.09	0.99 ± 0.03
	canyon	1.00	1.00	0.83	0.83	0.93 ± 0.11	0.93 ± 0.11
Toiyabe Range	segment	1.00	1.00	0.94	0.97	0.97 ± 0.06	0.99 ± 0.02
	canyon	1.00	1.00	1.00	1.00	1.00 ± 0.00	1.00 ± 0.00
Shoshone Mountains	segment	1.00	1.00	0.92	0.92	0.97 ± 0.05	0.97 ± 0.05
	canyon	0.98	1.00	0.80	1.00	0.89 ± 0.12	1.00 ± 0.00
All ranges combined	segment	1.00	1.00	0.98	0.98	1.00 ± 0.01	1.00 ± 0.01
	canyon	1.00	1.00	0.94	0.94	0.98 ± 0.04	0.98 ± 0.04

Notes: EA = Ecological Applications method. CBIP = Conservation Biology in Practice method. Occupied Locations = mean proportion of occupied locations conserved for all protected species ± standard deviation. * = 0.05< P-value < 0.10; ** = P < 0.05.

Table 6. Consequences of protecting subsets of locations for each dataset using the Ecological Applications and Conservation Biology in Practice umbrella indices.

Data set	Scale	Proportion Protected: Species EA	Species CBIP	Locations All	Occupied Locations EA	Occupied Locations CBIP
BIRDS						
Toquima Range	segment	0.63	0.55	0.21	0.52 ± 0.30	0.44 ± 0.23
	canyon	0.45	0.45	0.17	0.43 ± 0.30	0.43 ± 0.30
Toiyabe Range	segment	0.54	0.54	0.16	0.32 ± 0.22	0.32 ± 0.22
	canyon	0.54	0.54	0.20	0.38 ± 0.28	0.38 ± 0.28
Shoshone Mountains	segment	0.68	0.68	0.20	0.38 ± 0.24	0.40 ± 0.27
	canyon	0.64	0.64	0.20	0.52 ± 0.35	0.37 ± 0.21
All ranges combined	segment	0.60	0.64	0.19	0.34 ± 0.18	0.34 ± 0.18
	canyon	0.60	0.60	0.19	0.35 ± 0.18	0.35 ± 0.21
BUTTERFLIES						
Toquima Range	segment	0.87	0.83	0.21	0.32 ± 0.13	0.33 ± 0.14
	canyon	0.88	0.88	0.17	0.30 ± 0.17	0.30 ± 0.17
Toiyabe Range	segment	0.89	0.89	0.16	0.24 ± 0.09	0.24 ± 0.09
	canyon	0.89	0.89	0.20	0.24 ± 0.13	0.24 ± 0.13
Shoshone Mountains	segment	0.82	0.82	0.20	0.31 ± 0.17	0.31 ± 0.17
	canyon	0.88	0.88	0.20	0.33 ± 0.23	0.33 ± 0.23
All ranges combined	segment	0.95	0.92	0.19	0.24 ± 0.06	0.24 ± 0.04
	canyon	0.97*	0.89*	0.19	0.25 ± 0.13	0.25 ± 0.12

Notes: For segment level, the one segment in each canyon that had the most umbrella species was conserved. For canyon level, the one canyon per range with the most umbrella species was conserved. Occupied Locations = mean proportion of occupied locations conserved for all protected species ± standard deviation. * = 0.05 < P-value < 0.10; ** = P < 0.05.

CHAPTER 3: EMPIRICAL VALIDATION OF THE UMBRELLA INDEX: A CASE STUDY WITH BIRDS AND BUTTERFLIES IN MONTANE CANYONS OF THE GREAT BASIN

ABSTRACT

Empirical validation that conserving lands for selected umbrella species protects many co-occurring species is unusual. Using bird and butterfly data sets from montane canyons in three mountain ranges of the Great Basin, I tested the effectiveness of the umbrella index, which can be used to determine the ability for each species in a community to provide protection to co-occurring species. I also examined whether umbrella species selected for one range would be effective umbrellas in other mountain ranges. Finally, I evaluated whether the umbrella index could identify effective cross-taxonomic umbrellas. Conserving all locations with at least one umbrella would result in the protection of a vast majority of species and locations. Conserving a subset of locations with the most umbrella species usually protected a majority of species from each assemblage in only a portion of the landscape. Umbrella species from one range provided similar levels of protection as umbrellas developed for another range. Cross-taxonomic umbrellas tended to provide similar levels of protection as same-taxon umbrellas. Although the umbrella index can be used to select species that provide high levels of protection to sympatric species, further empirical validation is needed to support widespread use of the index.

INTRODUCTION

Conservation biologists are often forced to make land-use decisions without the time or funds necessary to collect all of the pertinent data for many species (Stohlgren et al. 1995, Oliver and Beattie 1996, Longino and Colwell 1997, Simberloff 1998). Umbrella species, species whose conservation provides protection to sympatrically occurring species, offer an attractive shortcut when time or funds are limited. If effective umbrella species can be identified for particular ecoregions, then land managers could quickly and efficiently make conservation decisions. Two obvious advantages are that it is easier to monitor a single species than all species and individual species are more likely to be protected by law than are groups of species or ecosystems (Martin 1995a, Simberloff 1998). However, only a few empirical studies have demonstrated that one or a few species can confer protection to many other closely related species (Martikainen et al. 1998; Fleishman et al. 2000, 2001a; Suter et al. 2002). Even fewer data validate the effectiveness of umbrella species between different taxonomic groups (Fleishman et al. 2001a, but see Martikainen et al. 1998). The lack of supporting evidence has made the umbrella species concept controversial and many doubt the ability of one species to serve as a protector for many other species, both within and between taxonomic groups (Kerr 1997, Oliver et al. 1998, Caro and O'Doherty 1999, Andelman and Fagan 2000, Rubinoff 2001). Yet, the limited funds for conservation and the alacrity with which many conservation decisions must be made, keeps the concept of umbrella species alive and highlights the need for further empirical tests (Stohlgren et al. 1995, Oliver and Beattie

1996, Longino and Colwell 1997, Niemi et al. 1997, Simberloff 1998, Fleishman et al. 2000, 2001a).

Perhaps one of the reasons that so few tests have documented the effectiveness of umbrella species is that there is little consistency in how they are defined or how well they should perform. Wilcox (1984) introduced the umbrella species concept and defined an umbrella species as one whose minimum area requirements are at least as comprehensive as the rest of the community. Another common criterion used in the selection of umbrella species is sensitivity to human disturbance, especially landscape fragmentation (Fleishman et al. 2001a). Berger (1997) furthered the umbrella species notion, by noting that they can be used to determine only the size of an area that should be protected and not its location. Lambeck (1997) expanded the concept to include a suite of focal species, each of which is used to define spatial and compositional attributes that must be present in a landscape.

Regardless of the method used to select umbrella species, their selection is meant to be prospective, based on the assumption that the ecological requirements held by the umbrella species include those of many other species (Fleishman et al. 2001a). However, in practice, animals with legal protection are usually designated as umbrella species (Rubinoff 2001). An overwhelming number of these are vertebrates because a majority of animals with legal protection are vertebrates (U.S. Fish and Wildlife Service 2000). Little thought has been given as to whether species from other taxonomic groups may have more extensive area requirements and therefore go unprotected (Rubinoff 2001). Instead of selecting umbrella species based on their ecological requirements, conservation biologists retrospectively try to determine if other species will be protected by the conservation of land for legally protected species. Thus, it is only hoped that conservation of lands for umbrella species will also conserve other species.

However, if conservation biologists can determine a method of prospectively selecting efficient umbrella species, then their utility would be increased if the umbrella species were from a large ecoregion. This would allow the umbrella species approach to be used to designate lands for conservation at many locations within the ecoregion. Thus, conservation strategies developed for a subset of a geographic region could be implemented at other locations where conservation efforts are needed if umbrella species are proven to be effective.

In an attempt to develop a quantitative method for determining the efficiency of individual species to act as umbrellas, Fleishman et al. (2000) proposed the "umbrella index." By using three criteria, the umbrella index can calculate the potential ability for each species in an area to serve as a conservation umbrella for sympatric species (Fleishman et al. 2000). The criteria are mean percentage of co-occurring species, degree of rarity, and sensitivity to human disturbance.

Here, I test whether the umbrella index can successfully identify effective umbrella species from two different taxonomic groups with multiple independent sets of data and a combined data set from montane canyons in central Nevada. To further assess the performance of the index, I test whether cross-taxonomic umbrellas are effective surrogates for conservation by evaluating the success of an index developed for one range to select lands for conservation in a neighboring range. I hypothesize that the same-taxon umbrellas will conserve a greater proportion of species than cross-taxonomic umbrellas. I also hypothesize that the umbrella index developed for a particular mountain range will protect a greater proportion of species than umbrella species selected for neighboring ranges.

METHODS

This study was conducted in the Toquima and Toiyabe Ranges and the Shoshone Mountains (Figure 1). These are just a few of the more than 200 north-south oriented mountain ranges in the Great Basin and are located near the town of Austin, Nevada (Latitude 39.493 °N, Longitude 117.069°W). The Toiyabe Range, the largest of the three, is 200 km long and reaches its apex of 3,595 m in the Arc Dome Wilderness area. The Toquima Range is 150 km long with a majority (~90%) of its crest lying at about 2,700 m. Near the center of the range is a 13 km segment named Mount Jefferson, which towers above the remainder of the range with three peaks above 3,300 m (Grayson 1993). The smallest of the three, the Shoshone Mountains are only 70 km long and reach their high point of 3,143 m near the north end of the range at North Shoshone Peak. Wide valleys separate the three mountain ranges. The Toquima and Toiyabe Ranges are separated by Big Smoky Valley, which averages approximately 1,700 m in elevation and ranges from 9 to 21 km in width. The Toiyabe Range and the Shoshone Mountains are separated by the Reese River Valley, which averages about 1,950 m in elevation and is approximately 10 km wide.

All three of these mountain ranges have numerous canyons incised into the east and west facing slopes. A majority of these canyons are dry, except after storms or during periods of snowmelt. Some of the canyons, mostly in the larger Toiyabe Range, have continuous flow, while others have seeps or springs that create standing or flowing water in limited portions of canyons. The topography of individual canyons is highly variable.

The dominant vegetation of these ranges is highly dependent upon the elevation and the amount of available water (Grayson 1993). The valleys between ranges and the lower elevations of the ranges are dominated by sagebrush (*Artemisia tridentata* spp.). Sagebrush is replaced by pinyon-juniper (*Pinus monophylla*, *Juniperus osteosperma*) woodlands then mountain mahogany (*Cercocarpus ledifolius*) then dwarf sagebrush (*Artemisia tridentata vaseyana*) and wildflowers with increasing elevation (Tueller and Eckert 1987). Limber pine (*Pinus flexilis*) can be found in some areas at the timberline. The highest summits in the Toquima and Toiyabe Ranges have a relatively depauperate alpine flora (Trimble 1989, Grayson 1993). Quaking aspen (*Populus tremuloides*) and willow (*Salix spp*.) grow on exposed slopes with seeps and flourish in canyons with a continuous flow of water. Canyons that have surface water, either ephemerally or permanently, often also have willow, rose (*Rose woodsii*), nettle (*Urtica dioica*), and an understory composed of many species of grasses and forbs.

Study canyons and segments

I selected six canyons in the Toquima Range, five in the Toiyabe Range, and five in the Shoshone Mountains based on the existence of butterfly data sets and the feasibility of conducting avian surveys throughout the length of the canyon. Characteristics such as amount of available water, vegetation, and exposed rock in the selected canyons were highly variable.

Each study canyon was divided into elevational segments from its mouth to its crest defined by a 100 m change in elevation. The average number of segments per canyon was 5.25 $\pm$ 1.34 sd. I surveyed a total of 84 elevational segments, 25 in the Toquima Range, 31 in the Toiyabe Range, and 28 in the Shoshone Mountains. Canyon segments had a median length of 1413.5 m and inter-quartile range of 944. I measured elevation with a pocket altimeter then verified it with a differentially corrected Global Positioning System (GPS) to within 5 m accuracy (Fleishman et al. 1998).

Butterfly communities

Fleishman et al. (1997, 1998, 2000, 2001a) compiled species presence data for all segments in each of the 16 study canyons. Each canyon was surveyed during multiple years between 1996 and 2001. To compensate for differences in flight phenology among species and locations, Fleishman inventoried each canyon approximately every 2 weeks throughout most of the flight season (May - August) (Fleishman et al. 1997, 1999). Each visit consisted of walking the length of the canyon at a constant pace and recording the presence of all species of butterflies in each segment. Butterfly communities are frequently surveyed by walking transects and this method is particularly effective for determining species presence (Shapiro 1975, Pollard 1977, Swengel 1990, Kremen 1992, Pollard and Yates 1993, Harding et al. 1995). When butterflies could not be identified in flight, individuals were caught and identified on site or later in the lab. Voucher specimens were deposited at the University of Nevada, Reno and the Nevada State Museum and Historical Society, Las Vegas (Fleishman et al. 1999). The nomenclature for butterflies in this manuscript follows that proposed by Austin (1998).

Bird communities

I determined the avian species richness of each segment by conducting 75 m fixed-radius point-counts (Bibby et al. 1992) at two or three locations within each elevational segment. I selected the point-count locations by driving or walking the length of each segment and choosing locations that were representative of each major habitat type within the segment. This approach was used, rather than selecting random locations in each segment, because the goal of surveys was to determine the component species of each segment for a well-known taxonomic group with species that exhibit relatively high degrees of habitat specificity. Thus, sampling random locations would not have resulted in an accurate assessment of all species that occurred within a segment. Each segment included at least two point-count locations even if there was only one major habitat type. Segments included three point-count locations when there were three different habitats within the segment. I recorded all birds using habitat within 75 m of the point-count location and thus locations had to be at least 150 m apart. I conducted three 5-minute point-counts at each location: the first between 28 May 2001 and 08 June 2001, the second between 09 June 2001 and 17 June 2001, and the last between 18 June 2001 and 27 June 2001. I conducted point-counts only under fair skies. I did counts so that each point received at least one count within 2 hours of dawn and at least one count between 2 and 3 1/2 hours after dawn. Point-counts are an effective method of surveying avian communities in Great Basin canyons and riparian habitats (Dobkin and Rich 1998).

The purpose of point-counts was to establish species presence in segments without performing time consuming transects along the length of each segment. Thus, sampling two or three point-counts per segment (at least one in each major habitat type) was necessary to maximize the number of segments that could be surveyed while still accurately representing the species in a segment because habitat variables such as tree species, size and water availability have great influence on avian species richness and abundance (Poulson 2002). To determine if bird species richness was influenced by the number of point-counts in a segment, I calculated the mean number of bird species surveyed in segments with 2 and 3 point-counts. To determine if species richness was a function of the number of point-count performed in a segment, I calculated the number of bird species detected per unit time for each study segment.

Identification of umbrella species

To measure the potential of each species of bird and butterfly to serve as an umbrella for other species, I calculated umbrella index values at the segment and canyon level. The calculation of the umbrella index is based on three criteria: percentage of co-occurring species, degree of rarity, and sensitivity to human disturbance. A detailed explanation for these particular criteria can be found in Fleishman et al. (2000). I did calculations at the canyon and segment level for both birds and butterflies in all three ranges and for the combined dataset including all three ranges. For segment level analysis, I used presence-absence data as determined by avian point-counts and butterfly transects. Canyon-level presence was established by a species' presence in any of the segments within a specific canyon. Although presence-absence data provides little information on species viability, adequate time and money rarely exist to collect unbiased data about bird and butterfly abundances (Droege et al. 1998, Link and Sauer 1998).

The effectiveness of conservation strategies can be determined in several ways. Management of habitats for the conservation of biodiversity involves protecting locations in a fashion that maintains species richness (Freitag et al. 1997). Species richness is an accurate measure of how many species may be conserved by a conservation scheme; however, richness alone provides no information on how much of a species' range is conserved or its long-term viability. An alternative metric to species richness is the proportion of occupied locations (defined as the locations in which a species was detected) conserved for each species that receives protection. The mean proportion of occupied locations conserved for all species in a community can be used to evaluate the degree of protection a conservation scheme provides to species that differ in their baseline occurrences. For example, a species that occurs in two of 10 locations is relatively well protected if both locations (100% of its occurrences) are conserved, regardless of how many total locations are conserved. A species that occurs in eight of the 10 locations is not well protected if only two of these locations are conserved because it has lost 75% of the locations it previously occupied and would have a proportion of occupied locations conserved value of 2/8 or 0.25 (Fleishman et al. 2000, 2001a). All other things being equal, the higher the mean proportion of occupied locations conserved for a data set, the higher the probability of persistence for component species. Here, I compare the proportions of species, locations, and mean proportion of occupied locations conserved for different data sets and taxonomic groups (birds or butterflies).

A species' umbrella index score is calculated as the sum of three individual criteria. Each species receives a mean percentage of co-occurring species (PCS) value between 0 (the species occurs with no other species) and 1 (the species occurs with all other species). For each species *j*, PCS is defined as

$$PCS_j = \sum_{i=1}^{l} (S_i - 1)/(S_{\max} - 1)/Nj$$

where *l* is the number of locations in the data set, S_i is the number of species present at each location *i,* S_{max} is the total number of species present in all locations in the data set, and N_j is the number of locations where species *j* occurs (Fleishman et al. 2000). I calculated scores separately for each dataset and then for combined datasets.

The calculation for degree of rarity (R) is based on the extent of a species' distribution with the study area. Each species receives an R value from 0 (the species occurs in almost all or none of the locations) to 1.0 (the species occurs in exactly half of the locations). For each species *j*, degree of rarity is defined as

$$R_j = 1 - 2 \times \left| \frac{N_{present}}{N_{total}} - 0.5 \right|$$

where N is the number of locations with the *j*th species present ($N_{present}$) or the total locations considered (N_{total}) (Baz 1991, Fleishman et al. 2001a). I calculated these values for each individual data set and for the combined data set.

The third parameter -- disturbance sensitivity (DSI) -- is sensitivity to human disturbance. This parameter is a modified form of a sensitivity index proposed by Nelson and Anderson (1994). Variations among species in their life-history traits can influence the degree of anthropogenic influences they can tolerate. The DSI for birds was based on six life-history parameters: reproductive effort, nest form, nest height, territory size or density, migratory classification, and primary habitat (Table 1). I assigned each species an integer value score from 1 (low sensitivity) to 3 (high sensitivity) based on existing knowledge about avian life histories. Butterfly DSI values were calculated using three life-history parameters: mobility, larval host-plant specificity, and riparian dependence (Table 2). Each butterfly species received an integer score from 1 (low sensitivity) to 4 (high sensitivity) for each of the three life history traits based on life-history knowledge (Murphy and Wilcox 1986, Fleishman et al. 1997, 1998). DSI scores were standardized by summing the sensitivity scores and then dividing by the maximum calculated value for their taxonomic group. Disturbance sensitivity, thus, is a relative score with the most sensitive species receiving scores of 1 and less sensitive species receiving lower scores. DSI scores were calculated from the combined data sets that included all bird and butterfly species.

For each species the umbrella index (UI) is calculated as the sum of its scores for mean percentage of co-occurring species (PCS), degree of rarity (R), and disturbance sensitivity (DSI). Thus, each species could theoretically receive an umbrella index score from near 0 (a very poor umbrella that would protect few other species) to 3 (an efficient umbrella that would protect many other species). I defined potential umbrella species as those who received a UI score greater than 1 sd above the mean.

Once umbrella species were selected for a given data set, I used them to select sites for conservation. Two different scenarios were used: the conservation of all locations with at least one umbrella species and the conservation of subsets of locations with the highest number of umbrella species. Under both of these scenarios, locations selected for conservation are referred to as 'conserved' and species that reside in these conserved locations are referred to as 'protected.'

ANALYSES

Conservation of all locations with at least one umbrella species

The umbrella index selects multiple umbrella species for each data set. In this scenario, I determined the impact of protecting all locations where one or more of these umbrella species were located. For each data set, I calculated both the proportion of species that would be protected and the proportion of locations that would be designated for protection. For all species that were protected, I also calculated the mean proportion of occupied locations that were conserved.

Conservation of subsets of locations with umbrella species

It is usually economically and practically impossible to protect the entire range of all but the most endangered species (Andelman and Fagan 2000, Fleishman et al. 2000). Thus, the umbrella index may be useful for prioritizing areas for conservation by selecting the locations with the highest number of umbrella species. In this scenario, locations with the highest number of umbrella species were selected. At the segment level, the one segment with the highest number of umbrella species was selected from each canyon within a mountain range. Thus, the number of segments that would be conserved in a range is the same as the number of canyons. At the canyon level, the one canyon per range with the most umbrellas would be conserved. For each data set, I calculated the proportion of species and locations that would be protected. For all species that were protected, I also calculated the mean proportion of occupied locations conserved.

There are a limited number of possible segment permutations that can be selected. Since only one segment is selected per canyon, the number of possible permutations for each mountain range can be calculated as Perm = $seg_i * seg_{i+1} ... * seg_n$ where seg is the number of segments in canyon i and n is the total number of canyons in a mountain range. The number of possible segment permutations for the Toquima Range was 9000, for the Toiyabe Range the number was 8575, and for the Shoshone Mountains 2520. For any mountain range, the combination of segments selected by the umbrella index is just one of the total possible permutations. The utility of this is that it allows researchers to attach a level of statistical significance to the proportion of species protected by the umbrella index by using a permutation-based test. We can assign statistical significance by calculating the proportion of permutations that protect a greater proportion of species than the actual combination of segments selected by the umbrella index. For instance, if 90 out of 9000 permutations protect a proportion of species that is greater than or equal to number of species protected by the umbrella index, then the probability of protecting more species than the umbrella index (by chance) is 0.01. The probabilities obtained from permutation tests that have large numbers of possible combinations can be interpreted in the same was as "p-values" that are obtained from traditional significance tests (Bailer and Ruberg 1996, Manly 1997).

Conservation of locations with highest species richness vs. umbrella species

I compared the performance of sets of species selected using the umbrella index to conservation of the most species-rich locations. Since the 'conserving all locations with at least one umbrella' scenario results in the conservation of more than one segment per canyon or more than one canyon per range, it was omitted from this analysis. However, I did compare the effects of conserving locations with the highest number of umbrella species to the locations with the highest species richness because the proportion of locations conserved could be held constant. To do this, I calculated the proportion of species and the mean proportion of occupied locations conserved under both conservation strategies. I used McNemar's (1947) Q test to compare proportion of species protected when conserving locations with the most umbrella species to the proportion of species protected when conserving locations with the highest species richness. McNemar's Q is a non-parametric chi-square test used to evaluate differences between dependent proportions and count data (Agresti 1990). McNemar's Q test analyzes the null hypothesis H_0: Y_{12} pairs are as likely as Y_{21} pairs where Y_{12} and Y_{21} are discordant pairs of dichotomous responses (Figure 2). McNemar's Q test was calculated as $Q = (Y_{12} - Y_{21})^2/(Y_{12} + Y_{21})$. For both the umbrella index and locations with highest richness scenarios, each species in a data set was assigned a label of 1 if it occurred in any location selected for conservation or 0 if it did not occur in any conserved locations. For example, when conserving a subset of segments for birds in the Toquima Range, 21 species were protected by both the umbrella index and species rich scenarios, one species was protected by the umbrella index and not by species rich locations, four species were protected by the species richness scenario and not by the umbrella index, and 14 species were not protected by either scenario. The calculated chi-square value was 1.800 and the associated P-value was 0.1797.

Cross-taxonomic implications of the umbrella index

I examined whether birds and butterflies can serve as effective umbrellas for one another. For each data set, I determined the locations that would be conserved by protecting the location with the greatest number of umbrella species from a particular taxonomic group. I then calculated the proportion of species and the mean proportion of occupied locations conserved for both taxonomic groups. Using McNemar's (1947) Q test, I compared the proportion of species receiving protection from umbrella species of the same taxonomic group to the proportion of species receiving protection from cross-taxonomic umbrellas.

Among mountain range potential of the umbrella index

I tested whether the umbrella index developed for a particular taxonomic group in a particular mountain range would be effective if it was implemented in other ranges. In other words, I used species selected as umbrellas for each individual range as umbrella species in the other ranges. I determined the proportion of species and locations that would be protected if a subset of the locations with the highest number of umbrella species were conserved. Using McNemar's (1947) Q test, I compared the proportion of species protected for all possible mountain-range pairs.

General rules for conserving locations with at least one umbrella species

In previous studies, conserving locations where there was at least one umbrella species has resulted in the conservation of almost all lands (Fleishman et al. 2000, 2001a). Since conservation of all lands is usually impossible, land managers may need to preserve a portion of the landscape. In addition to being able to select locations with the highest number of umbrella species, I address this question by conserving all locations with the highest scoring umbrella species. In this scenario, I analyze the change in the proportion of species and locations that are protected when conserving locations with at least one umbrella for an increasing number of umbrella species.

RESULTS

A total of 67 bird and 64 butterfly species were recorded during surveys (Table 3). The number of bird species per mountain range was between 40 and 52 and the number of butterfly species in each range was between 50 and 63. All data are expressed as mean ± sd. The proportion of species identified as umbrellas ranged from 0.13 to 0.24 (0.18 ± 0.03).

Bird species richness was higher in the 13 segments that had three point-counts (16 ± 2.86) performed in them at three locations than the 71 segments that had only two point-counts (7.82 ± 2.89) ($P < 0.001$). Segments with three point-counts received a total of 45 minutes of surveys while segments with two point-counts received 30 minutes of surveys. Segments with 3 point-counts averaged one species per 0.356 minutes while segments with two point-counts averaged one species per 0.260 minutes.

Conservation of all locations with at least one umbrella species

The conservation of all locations with at least one of the identified umbrella species would result in the conservation of a vast majority of the species (birds = 0.98 ± 0.03, butterflies = 1.00 ± 0.00) and locations (birds = 0.93 ± 0.08, butterflies = 0.94 ± 0.06, Table 4).

Conservation of subsets of locations with umbrella species

The conservation of subsets of locations with the highest number of umbrella species would protect 0.19 ± 0.02 of the locations at the segment level and 0.19 ± 0.01 at the canyon level for both taxonomic groups (Table 5). The proportion of bird species receiving protection is between 0.45 and 0.68 (0.58 ± 0.07) and the proportion of butterfly species that would be protected is between 0.82 and 0.92 (0.88 ± 0.04).

For all three mountain ranges and for both taxonomic groups, selecting a subset of locations with the highest number of umbrella species protected a higher proportion of species than a majority of all possible segment permutations. The permutation-based p-values for the proportion of bird species protected by the umbrella index compared to all possible permutations was 0.41 for the Toquima Range, 0.26 for the Toiyabe Range, and 0.20 for the Shoshone Mountains (Figure 3). For butterflies, the permutation-based p-value was 0.16 for the Toquima Range, 0.11 for the Toiyabe Range, and 0.33 for the Shoshone Mountains (Figure 4).

Conservation of locations with highest species richness vs. umbrella species

The proportion of bird species receiving protection when the subset of locations with the highest species richness were conserved tended to be higher than when the subset selected by the umbrella index were conserved; however, in no data set was the difference statistically significant ($P = 0.1797$ to 1.00). A higher proportion of occupied locations tended to be conserved when selecting locations with the highest species richness. For butterflies, the difference in the proportion of species protected between the two scenarios was even smaller than for birds. The locations selected by the umbrella index protected an identical proportion of species as would be protected by conserving locations with the highest species richness in 4 of 8 data sets. In the other data sets, conserving the most species rich locations conserved more butterfly species than locations selected by the umbrella index; but in no data set was this difference statistically significant (P = 0.1573 to 1.00).

Cross-taxonomic implications of the umbrella index

In the Toquima Range at the segment level, the proportion of bird species receiving protection was higher when conservation locations were selected using bird umbrellas rather than butterfly umbrellas (Table 6). However, this was only a slight difference and was not statistically significant (P = 0.7389). In the Toquima Range at the canyon level and in the combined ranges at the segment level, butterfly umbrella species protected more bird species than did bird umbrellas, but these differences were not statistically significant (P = 0.5127 and 0.5637, respectively). There was a statistically significant difference (P = 0.0002) between the proportions of butterflies protected in the Toquima Range at the segment level. A marginally significant difference (P = 0.0578) existed between the proportions of butterfly species protected in the Shoshone Mountains at the canyon level. In the Shoshone Mountains at the segment level slightly more butterflies were protected by butterfly umbrellas than by bird umbrellas, however the difference was not statistically significant (P = 0.4795). A greater proportion of butterflies were protected in the combined data set at the segment level by bird umbrellas than by butterfly umbrellas; however, it was only a slight difference and was not statistically significant ($P = 0.3173$).

Between mountain range potential of the umbrella index

Umbrella species selected for one mountain range performed quite well in other mountain ranges. The proportion of species protected by umbrellas for different mountain ranges was between 0.45 and 0.66 for birds and 0.80 and 0.95 for butterflies (Table 7). On only one occasion (birds in the Shoshone Mountains at the canyon level) did the umbrella species selected for another range protect a significantly lower proportion of species than umbrella species selected for that data set ($P = 0.0455$).

General rules for conserving locations with at least one umbrella species

When using only the highest scoring umbrella species, all scenarios protected approximately 50% of the locations, but higher proportions of butterflies tended to be protected than birds (Figure 5). Nearly all bird and butterfly species and locations were protected when conserving locations that had at least one of the five highest scoring umbrellas. Within a taxonomic group, the proportion of species protected tended to depend more on the number of umbrella species than the scale of conservation efforts. Thus, conserving locations with at least one of any number of umbrella species for a particular taxonomic group would protect similar proportions of species at the segment and canyon level.

DISCUSSION

By collecting distribution data and using the umbrella index, land managers can ask either of two questions: 1) I want to protect X proportion of the species, what proportion of the landscape do I need to conserve? or 2) What proportion of the species will I protect if I conserve Y proportion of the locations? With accurate information about species distributions and occurrences, umbrella species selected with the umbrella index can be used to answer both of these questions in two different ways. First, locations with at least one umbrella species can be conserved. Second, a subset of locations with the greatest number of umbrella species can be conserved.

Within a taxonomic group, conserving all locations with at least one umbrella species would protect a vast majority of the assemblage. Previous studies using the umbrella index have had similar results (Fleishman et al. 2000, 2001a). A vast majority of individuals from other taxonomic groups would probably also receive protection, although this would only necessarily occur because almost all of the locations are marked for conservation. Obviously, neither an umbrella index nor umbrella species are needed to tell us that if we conserve almost all of the land that we will protect most of the species. Decades of research on the species-area relationship have revealed that an increase in area is accompanied by an increase in the number of species (Arrhenius 1921, Preston 1962, Johnson 1975).

Most locations are designated for conservation when conserving all locations because of how the umbrella index selects umbrella species. For each data set, all species receiving an umbrella index score more than 1 sd above the mean are selected as umbrellas. In a normally distributed population, this would mean that approximately 16% of the species pool would be identified as umbrellas. The distribution of umbrella index scores tends to be slightly skewed to the right so slightly more than 16% tend to be selected as umbrella species. Although each one of these umbrella species likely received a relatively high score for each parameter in the index, the degree of rarity has the greatest influence on the number of locations chosen for conservation. Species with high degree of rarity scores exhibited median rarity and were surveyed in about half of the locations. In most communities, regardless of whether individuals are randomly distributed or aggregated around particular resources, conserving all locations that have any of several species that display median rarity (the species selected as umbrella species), would result in the conservation of most locations.

Several possible alternatives address how to select a smaller proportion of the region for conservation. Selecting a smaller portion of the species pool to serve as umbrellas is a logical choice. A single umbrella species should occur in about half of the locations because it needed to have near median rarity to be selected as an umbrella. In other situations, it may be feasible to conserve more than half of the locations in an area. On these occasions, land managers may want to start with only the highest scoring umbrella species and then analyze the influence of adding progressively more umbrella species. Obviously, when conserving locations with any umbrella species, we would expect the addition of more species to conserve additional locations and thus, more species. The only time more species would not be protected with the addition of more umbrella species is when the additional umbrellas occur only in locations that were already conserved because of the presence of a higher scoring umbrella.

Data from this study indicate that the outcome of increasing the number of umbrellas depends more on the taxonomic group of interest than on the scale of conservation efforts (see Figure 5). When using the same number of umbrella species, a higher proportion of butterflies than birds are usually protected. More butterfly species than bird species were surveyed in each segment and canyon. Thus, the conservation of a similar number of locations should protect a greater proportion of butterflies than birds. The comparison between scales (segment and canyon) within either taxonomic group reveals that similar proportions of species will be conserved with an equal number of umbrella species. Thus, when conserving all locations with at least one umbrella species, conservation plans centered around birds or butterflies will protect similar proportions of their own taxonomic group if similar numbers of umbrella species are used.

When less than 50% of a region can be marked for conservation, locations with the highest numbers of umbrella species may be a useful approach. The permutation-based tests for each mountain range revealed that the umbrella index performed well compared to all possible permutations of segments and may be an efficient way of selecting a subset of locations for conservation. Since only one canyon is conserved per range at the canyon level, the best canyon to conserve would automatically be the one with the highest species richness. At the segment level (and in all ranges combined at the canyon level), however, multiple locations are conserved per data set. If an assemblage of species within a taxonomic group exhibit nested species subsets, with species in depauperate locations always present in the most speciose areas as well, the best combination of locations would again be the ones with the highest species richness. With species that do not show a nested distribution, the combination of locations selected to protect the highest proportion of conspecifics may not be the most speciose locations. Interestingly, Fleishman et al. (2002) found that in this study area, butterflies exhibit a more highly nested distribution than birds.

The umbrella index tends to select species with high rates of co-occurrence as umbrella species. In communities with highly-nested species, like butterflies, speciose locations would contain virtually all species and conservation of these locations would be effective at protecting species richness. For species with a low degree of nestedness, such as birds, conserving species rich locations may not necessarily protect a majority of species because all species do not co-occur with one another. In these situations, conserving locations with a high number of umbrellas may not result in the protection of a majority of the species. To prioritize portions of the landscape for conservation, land managers may want to select species-rich locations or utilize iterative approaches that protect species that do not receive protection in other conserved locations (Freitag et al. 1997, Kerr 1997).

The ability for one taxonomic group to provide protection to another taxonomic group has received little empirical validation (Kerr 1997, Oliver et al. 1998, Simberloff 1998, Caro and O’Doherty 1999, Andelman and Fagan 2000, Fleishman et al. 2001a, Rubinoff 2001, but see Martikainen et al. 1998). Species traditionally thought of as good umbrellas have large home-ranges and are sensitive to anthropogenic disturbance (Wilcox 1984, Berger 1997, Andelman and Fagan 2000). Because of the allometric relationship between home range size and body size, this meant that people viewed large vertebrates that were sensitive to human disturbance as the ultimate umbrella species (Gittleman 1986, Caro and O'Doherty 1999, Andelman and Fagan 2000). The vast areas required by large, widely roaming species are expected to maintain the minimum area requirements needed for viable populations of more sedentary populations (Fleishman et al. 2001a). However, numerous studies have demonstrated that invertebrates maintain a finer spatial relationship with their habitat and require different reserve designs than vertebrates (Murphy and Wilcox 1986). Therefore, conservation of vertebrates does not automatically provide protection to invertebrates.

Rubinoff (2001) showed that California Gnatcatchers (*Polioptila californica*), a bird used as an umbrella species for California coastal sage scrub habitats, utilize smaller habitat patches than some Lepidopteran species. Thus, conservation of locations that only meet the minimum size requirements for California Gnatcatchers would not provide adequate protection to all butterfly species. Yet, there is still hope for the umbrella species concept. No quantitative criteria were used to select California Gnatcatchers as umbrella species. Instead, they were chosen because they are an endangered vertebrate species in a vanishing ecosystem (Rubinoff 2001). Perhaps a more effective umbrella species, both for conspecifics and for other taxonomic groups, could be determined if objective and quantifiable criteria are the basis for selecting umbrella species.

This study lends tentative support to the argument that umbrella species in one taxonomic group can provide protection to other taxonomic groups. However, the methods used to select lands for conservation in this study were quite different from other studies of umbrella species. Here, umbrella species were used to select segments and canyons for conservation, rather than selecting the size of an area for conservation. Segments themselves were relatively large (1.5 ± 0.87 km) and canyons were composed of at least 3 segments. Thus, only species with extremely large home ranges would not receive protection with this scheme. Situations such as these, where one taxonomic group seems to provide protection to others, may only occur when relatively large pieces of land can be conserved, such as in the Great Basin where land management decisions are often developed for individual mountain ranges. Since this study was performed in three adjacent ranges, the extent to which selected species can be used as umbrella species for montane canyons throughout the Great Basin is unknown. Large differences in topography, water availability, vegetative structure, and bird and butterfly communities exist among segments and canyons in the mountain ranges surveyed in this study and larger differences probably arise in more distant mountain ranges of the Great Basin.

The ability for umbrella species from one mountain range to protect species in other ranges seems promising. If an umbrella index could be developed for one mountain range and implemented in several, it could save much needed time and money. However, the limitation to this is that entire species lists are still needed from all ranges in which the index is to be implemented. If species lists already exist, or if communities are surveyed in these ranges, then a new index could be calculated for each range.

Despite its performance in this study, there are several limitations to the umbrella index. First and foremost, until a particular species or suite of species is proven to be effective umbrellas for a region, a vast amount of information is needed to calculate the umbrella index. Life history data can be collected relatively easily for most of the criteria, yet particularly time consuming is the collection of the actual field data, required to calculate the degree of rarity and the percentage of co-occurring species. In situations where conservation decisions must be made rapidly, the umbrella index may be of limited utility.

The differences in lengths and the number of point-count locations per segment in this study were initially cause for concern. Butterflies are extremely sensitive to changes in elevation and data were collected along an elevational gradient to determine the extent of this pattern in the Great Basin. Since segments differed in length, and butterfly surveys were performed by walking the length of each segment at a constant pace, long segments were surveyed for longer periods of time than short segments. However, in the Toquima Range and Shoshone Mountains the sampling length was not correlated with butterfly species richness (Fleishman et al. 2001b). Since birds were surveyed by point-counts in each major habitat type within a canyon, the length of a segment would not bias species richness estimates as much as the number of point-count locations per segment. Since the number of bird species detected per unit time was higher in segments that received point-counts at three locations than in segments that received two point-counts, we know that the increased species richness in segments with more point-count (and a greater variety of habitats) was due to increased habitat diversity and not an increase in survey time.

In addition to the large amount of time needed there are other precautions that must be considered before the umbrella index is used for real-world conservation decisions. Locations selected for conservation were designated as ‘conserved’ and it is assumed that this will provide sufficient protection to all of the species that resided in that location so that they are ‘protected’. Thus, complete species lists for all locations are needed to accurately assess the proportion of species will be protected. Species surveyed in particular locations, particularly at the segment level, may use adjacent segments either during the summer months or during other times of the year. Thus, the proportion of species protected in conserved locations may diminish from year to year. Additionally problematic is the idea that if locations selected for conservation were the only conserved locations and the surrounding matrix was altered, we would expect to see changes is species distributions. Even over a relatively short time intervals, changes in species distributions and localized extinctions and colonizations may influence the number of species that would receive protection in conserved locations. Another potential short-coming of the umbrella index is that a single representative of a species in a particular location has the same influence as numerous recordings of a species. Since the umbrella index assigns each species a potential umbrella value based occurrence rather than abundance data, long-term viability of populations may be difficult to assess with the current version of the index. Future improvements to the index should focus on incorporating species and location specific abundances into the degree of rarity component of the umbrella index.

The utility of the umbrella index is difficult to measure because so few other methods exist for the quantitative selection of umbrellas. Since it is unlikely that any one species can encompass the needs of all other species, especially among different taxonomic groups, a multi-species umbrella approach may be more appropriate than a single-species umbrella. This study and others (Fleishman et al. 2000, 2001) have demonstrated that the umbrella index can be adapted for different taxonomic groups to protect a majority of species when only a small portion of the habitat can be conserved. The future of umbrella species in general, and more specifically in the umbrella index, depends on the demand for conservation shortcuts and the degree to which their effectiveness can be validated.

CONCLUSIONS

The umbrella index can be used to select species that will confer protection to sympatric species. Effectiveness of umbrella species can be measured as the proportion of species receiving protection. The effectiveness of umbrella species in this study depended on the taxonomic group of interest and method in which umbrella species were utilized. A greater proportion of butterfly species than bird species tended to receive protection because individual segments had more butterfly than bird species. Conserving all locations with any umbrella species is not practical because it selects almost all of the locations within a landscape for conservation. A more realistic method would be to select all locations where only one or a few of the highest scoring umbrella species are surveyed. More pragmatic proportions of the landscape can also be selected when conserving a subset of locations with the highest number of umbrella species. Conserving these locations typically provided protection to a majority of species in a small portion of the landscape. The ability of umbrella species selected in one range to provide protection to a majority of species when implemented in another range seems promising. Umbrella species from one range provided similar levels of protection as umbrellas developed for other ranges. Cross-taxonomic umbrellas also tended to provide similar levels of protection as same-taxon umbrellas. Although the umbrella index can be used to select species that provide high levels of protection to sympatric species, further empirical validation is needed to support widespread use of the index.

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Figure 1. Location of the Toquima and Toiyabe Ranges and the Shoshone Mountains (*black rectangle, see inset*) in the Great Basin (*irregular shape with black border, see inset*) and the inventory canyons 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 range's crest.

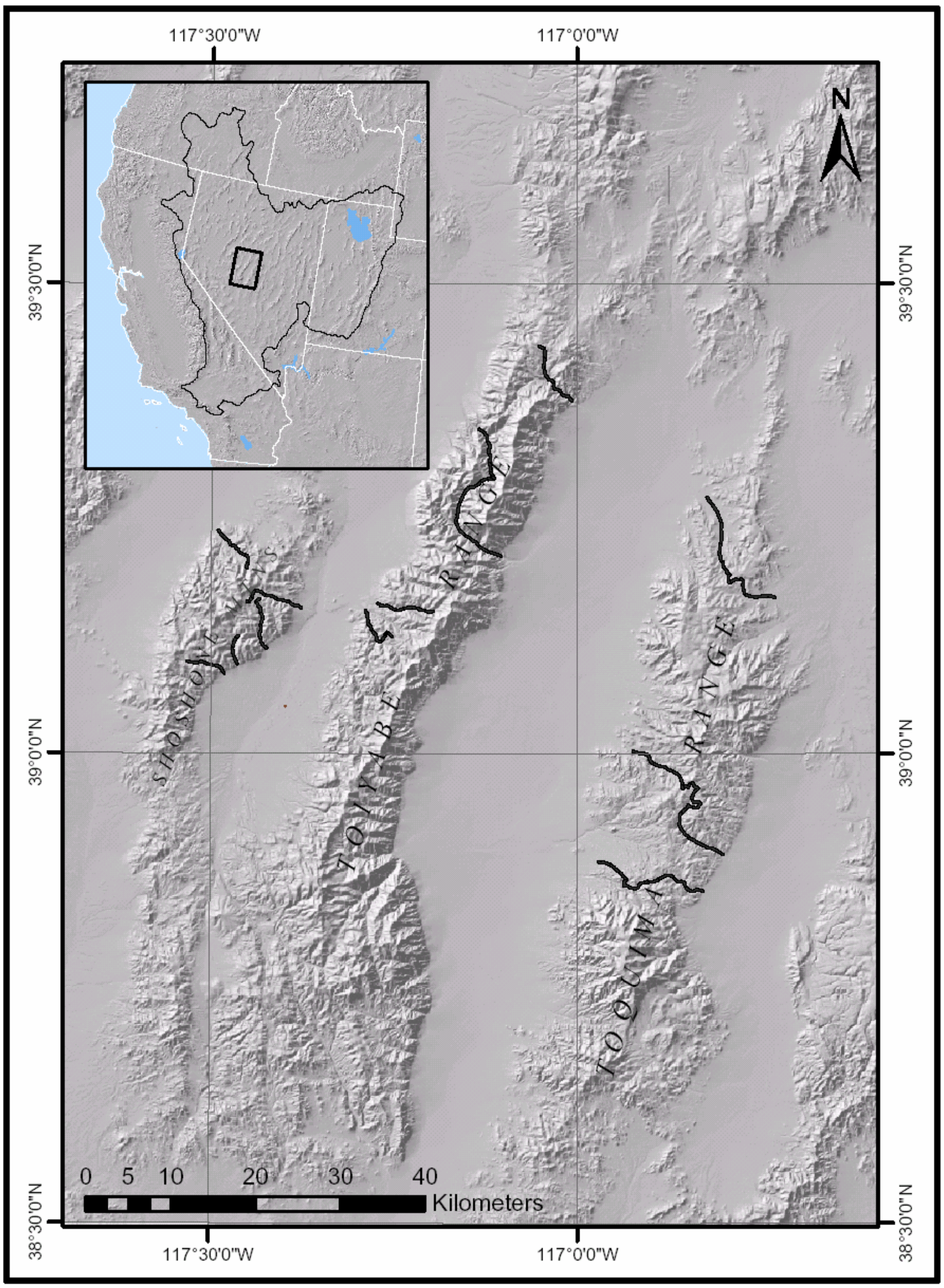

Figure 2. McNemar's (1947) Q test can be used to test the null hypothesis X for matched pair data by comparing the values of discordant pairs (Y_{12} and Y_{21} or 1 and 2, bolded). The general (a) and specific (b) examples illustrate how the data is arrayed to perform the comparison.

a. General example		Protect locations with highest richness		
		Species selected as umbrellas	Species not selected as umbrellas	
Protect locations selected by umbrella index	Species selected as umbrellas	Y_{11}	$\mathbf{Y_{12}}$	b
	Species not selected as umbrellas	$\mathbf{Y_{21}}$	Y_{22}	n-b
		a	n-a	n

b. Specific example		Protect locations with highest richness		
		Species selected as umbrellas	Species not selected as umbrellas	
Protect locations selected by umbrella index	Species selected as umbrellas	21	**1**	b
	Species not selected as umbrellas	**4**	14	n-b
		a	n-a	n

Figure 3. Histograms of the proportion of bird species protected by all possible segment permutations. Dashed line indicates the proportion of species protected by the segment combination selected by the umbrela index. A = Toquima Range, B = Toiyabe Range, C= Shoshone Mountains.

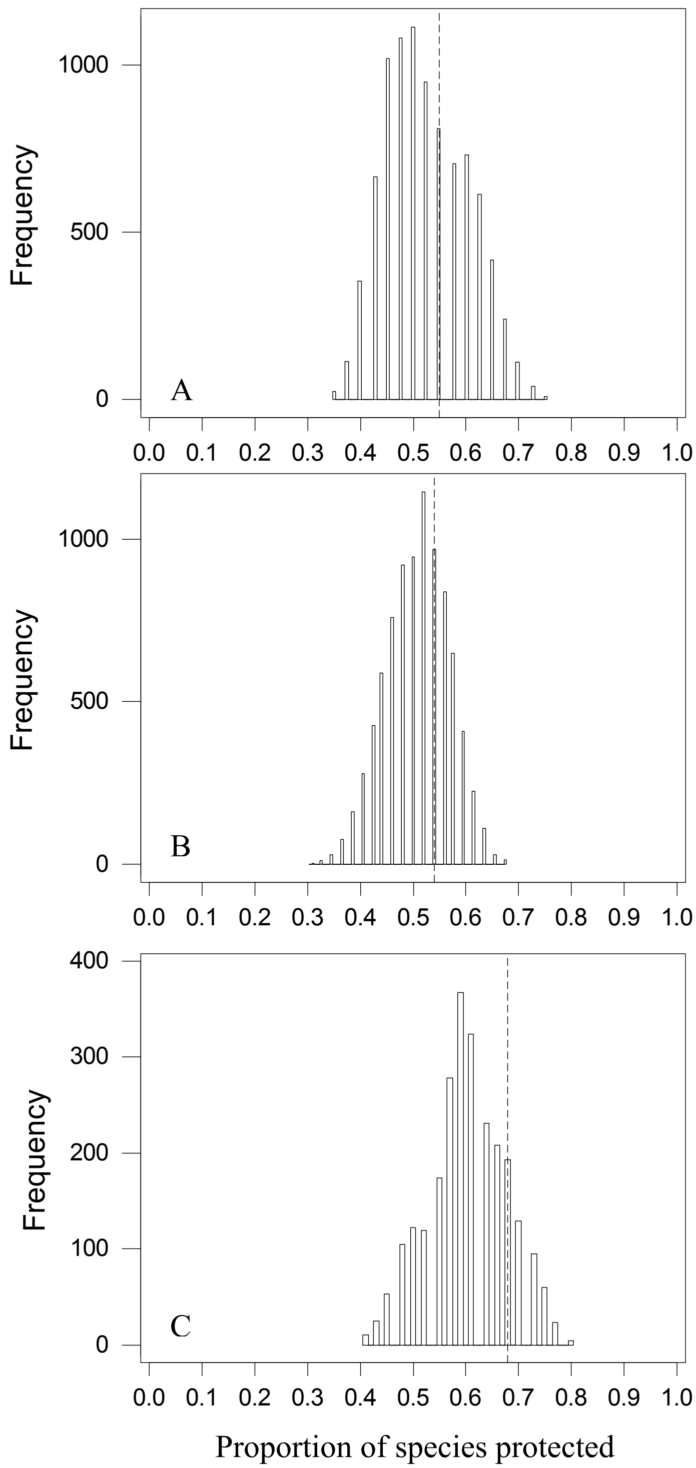

Figure 4. Histograms of the proportion of butterfly species protected by all possible segment permutations. Dashed line indicates the proportion of species protected by the segment combination selected by the umbrela index. A = Toquima Range, B = Toiyabe Range, C= Shoshone Mountains.

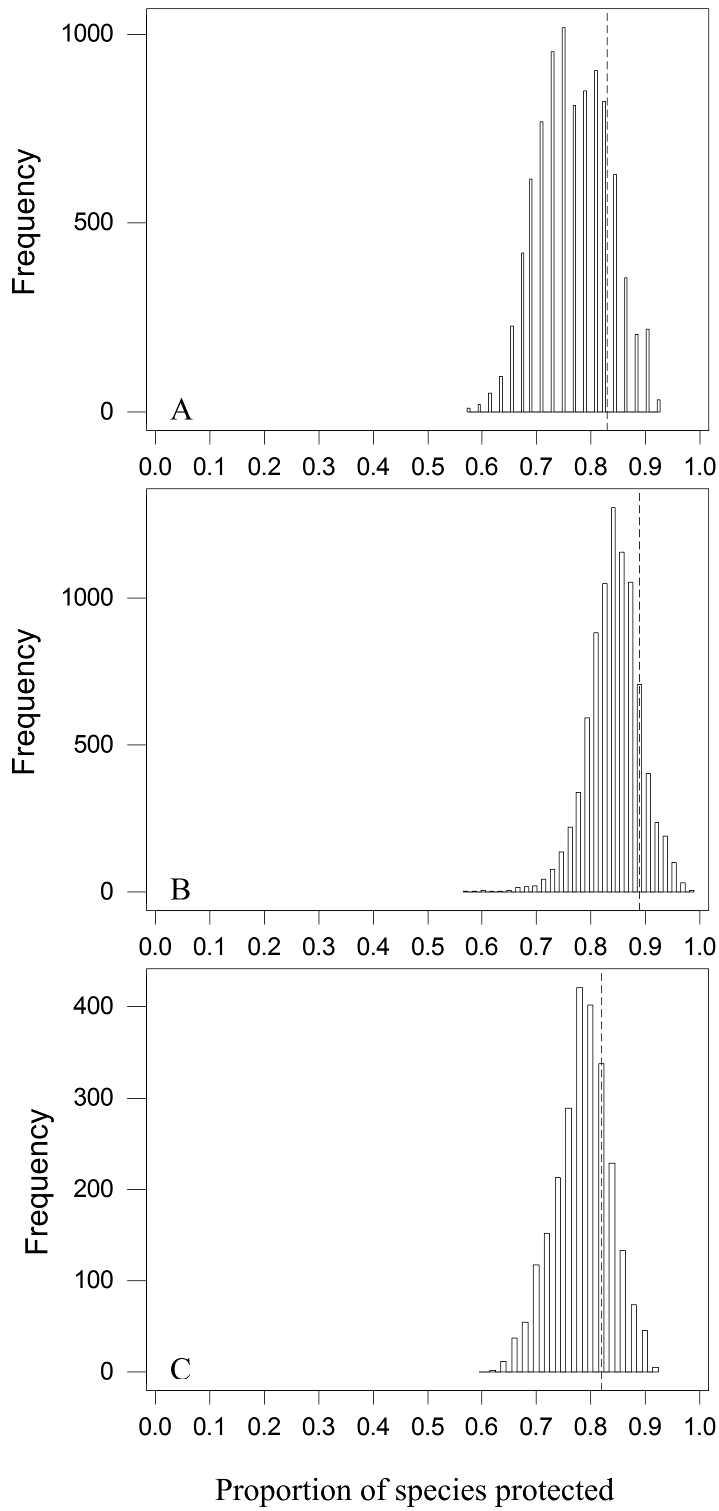

Figure 5. Proportion of species and locations that would be protected when conserving all locations with at least one umbrella species. x = locations, o = species. Mean ± sd. A) birds at the segment level, B) birds at the canyon level, C) butterflies at the segment level, D) birds at the canyon level.

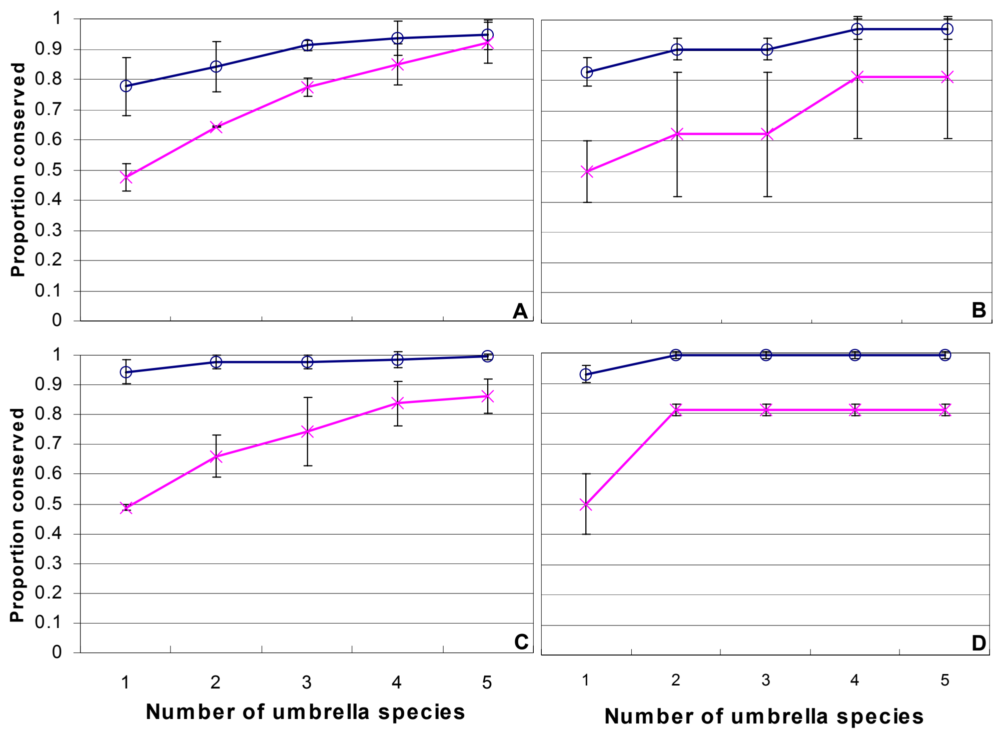

Table 1. Life history criteria used to score sensitivity (1 = least sensitive, 3 = most sensitive) of birds in the Toiyabe and Toquima Ranges and the Shoshone Mountains to human activities (modified from Hansen and Urban 1992; data from Schoener 1968, Brown 1985, Ehrlich et al. 1988, AOU 1992, Martin 1995b, Rottenborn 1999, Warkentin and Reed 1999).

	Sensitivity score		
Parameter	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 distance	resident	short-distant	neotropical
Riparian dependence	no-use	facultative	obligate

Table 2. Life history criteria used to score sensitivity (1 = least sensitive, 4 = most sensitive) of butterflies in Toiyabe and Toquima Ranges and the Shoshone Mountains to human activities (Scott 1986, Boggs and Jackson 1991, Fleishman et al. 2001).

	Sensitivity score			
Parameter	1	2	3	4
Vagility (m)	> 100,000	1,000 - 100,000	100 - 1,000	< 100
Larval host plant specificity	> 1 family	> 1 genus in 1 family	> 1 species in 1 genus in 1 family	1 species
Riparian dependence	no use	facultative, with individuals occasionally seen at puddles	facultative, with individuals frequently at puddles	obligate

Table 3. Number of species, umbrella species, and survey locations in each dataset.

Data set	Scale	Species	Umbrellas	Locations
BIRDS				
Toquima Range	segment	40	6 (0.15)	28
	canyon	40	5 (0.13)	6
Toiyabe Range	segment	52	9 (0.17)	31
	canyon	52	9 (0.17)	5
Shoshone Mountains	segment	44	6 (0.14)	25
	canyon	44	10 (0.23)	5
All ranges combined	segment	67	11 (0.16)	84
	canyon	67	12 (0.18)	16
BUTTERFLIES				
Toquima Range	segment	52	11 (0.21)	28
	canyon	52	7 (0.13)	6
Toiyabe Range	segment	63	11 (0.17)	31
	canyon	63	13 (0.20)	5
Shoshone Mountains	segment	50	9 (0.18)	25
	canyon	50	12 (0.24)	5
All ranges combined	segment	64	12 (0.19)	84
	canyon	64	12 (0.19)	16

Notes: Proportions of total species are given in parentheses. Locations indicates the number of segments or canyons in a data set.

Table 4. Consequences of protecting all locations with at least one umbrella species for each dataset.

		Proportion Protected		
Data set	Scale	Species	Locations	Occupied Locations
BIRDS				
Toquima Range	segment	0.90	0.89	0.96 ± 0.12
	canyon	0.98	0.83	0.95 ± 0.11
Toiyabe Range	segment	1.00	1.00	1.00 ± 0.00
	canyon	1.00	1.00	1.00 ± 0.00
Shoshone Mountains	segment	1.00	1.00	1.00 ± 0.00
	canyon	0.98	0.80	0.92 ± 0.00
All ranges combined	segment	0.99	0.99	0.99 ± 0.07
	canyon	1.00	0.94	0.98 ± 0.05
BUTTERFLIES				
Toquima Range	segment	1.00	0.89	0.99 ± 0.03
	canyon	1.00	0.83	0.93 ± 0.11
Toiyabe Range	segment	1.00	0.97	0.99 ± 0.02
	canyon	1.00	1.00	1.00 ± 0.00
Shoshone Mountains	segment	1.00	0.92	0.97 ± 0.05
	canyon	1.00	1.00	1.00 ± 0.00
All ranges combined	segment	1.00	0.98	1.00 ± 0.01
	canyon	1.00	0.94	0.98 ± 0.04

Notes: Occupied Locations = mean proportion of occupied locations conserved for all protected species ± standard deviation.

Table 5. Consequences of protecting subsets of locations for each dataset.

Data set	Scale	Proportion Protected				
		Species		Locations	Occupied Locations	
		UI	Rich	All	UI	Rich
BIRDS						
Toquima Range	segment	0.55	0.63	0.21	0.44 ± 0.23	0.54 ± 0.28
	canyon	0.45	0.53	0.17	0.43 ± 0.30	0.49 ± 0.35
Toiyabe Range	segment	0.54	0.60	0.16	0.32 ± 0.22	0.42 ± 0.31
	canyon	0.54	0.62	0.20	0.38 ± 0.28	0.43 ± 0.32
Shoshone Mountains	segment	0.68	0.73	0.20	0.40 ± 0.27	0.44 ± 0.27
	canyon	0.64	0.64	0.20	0.37 ± 0.21	0.37 ± 0.21
All ranges combined	segment	0.64	0.69	0.19	0.34 ± 0.18	0.39 ± 0.22
	canyon	0.60	0.67	0.19	0.35 ± 0.21	0.38 ± 0.26
BUTTERFLIES						
Toquima Range	segment	0.83	0.90	0.21	0.33 ± 0.14	0.35 ± 0.19
	canyon	0.88	0.88	0.17	0.30 ± 0.17	0.30 ± 0.17
Toiyabe Range	segment	0.89	0.89	0.16	0.24 ± 0.09	0.24 ± 0.09
	canyon	0.89	0.89	0.20	0.24 ± 0.13	0.24 ± 0.13
Shoshone Mountains	segment	0.82	0.84	0.20	0.31 ± 0.17	0.32 ± 0.18
	canyon	0.88	0.88	0.20	0.33 ± 0.23	0.33 ± 0.23
All ranges combined	segment	0.92	0.94	0.19	0.24 ± 0.04	0.25 ± 0.06
	canyon	0.89	0.95	0.19	0.25 ± 0.12	0.23 ± 0.13

Notes: UI = Umbrella Index. Rich = Protection of locations with the highest species richness. Occupied Locations = mean proportion of occupied locations conserved for all protected species ± standard deviation. For segment level, the one segment in each canyon that had the most umbrella species was conserved. For canyon level, the one canyon per range with the most umbrella species was conserved. Hence, the proportion of locations conserved by both methods is identical. No differences are statistically significant.

Table 6. Proportion of species and occupied locations that would be protected if locations for conservation were determined by protecting the one with the greatest number of same-taxon umbrella species or cross-taxonomic umbrella species.

Data set	Scale	Proportion Protected: Species		Occupied Locations	
		U_{same}	U_{cross}	U_{same}	U_{cross}
BIRDS					
Toquima Range	segment	0.55	0.53	0.44 ± 0.23	0.38 ± 0.25
	canyon	0.45	0.53	0.43 ± 0.30	0.49 ± 0.35
Toiyabe Range	segment	0.54	0.54	0.32 ± 0.22	0.43 ± 0.35
	canyon	0.54	0.54	0.38 ± 0.28	0.39 ± 0.32
Shoshone Mountains	segment	0.68	0.68	0.40 ± 0.27	0.38 ± 0.25
	canyon	0.64	0.64	0.37 ± 0.21	0.36 ± 0.23
All ranges combined	segment	0.64	0.67	0.34 ± 0.18	0.37 ± 0.26
	canyon	0.60	0.60	0.35 ± 0.21	0.33 ± 0.26
BUTTERFLIES					
Toquima Range	segment	0.83	0.83	0.33 ± 0.14	0.32 ± 0.15
	canyon	0.88**	0.56**	0.30 ± 0.17	0.26 ± 0.17
Toiyabe Range	segment	0.89	0.89	0.24 ± 0.09	0.21 ± 0.08
	canyon	0.89	0.89	0.24 ± 0.13	0.26 ± 0.16
Shoshone Mountains	segment	0.82	0.78	0.31 ± 0.17	0.25 ± 0.11
	canyon	0.88*	0.76*	0.33 ± 0.23	0.27 ± 0.15
All ranges combined	segment	0.92	0.95	0.24 ± 0.04	0.22 ± 0.09
	canyon	0.89	0.89	0.25 ± 0.12	0.19 ± 0.09

Notes: U_{same} = same-taxon umbrella species, U_{cross} = cross-taxonomic umbrella species. Occupied Locations = mean proportion of occupied locations conserved for all protected species ± standard deviation. For segment level, the one segment in each canyon that had the most umbrella species was conserved. For canyon level, the one canyon per range with the most umbrella species was conserved. The proportion of locations conserved for each data set is identical to Table 5.
* = 0.05 < P-value < 0.10; ** = P < 0.05.

Table 7. Proportion of species and locations in a given data set that would be protected if a subset of locations with the most umbrella species from another ranged were conserved.

Data set	Scale	Proportion Protected: Species			Proportion Protected: Locations
		TQ	TY	SH	All methods
BIRDS					
Toquima Range	segment	**0.55**	0.60	0.58	**0.21**
	canyon	**0.45**	0.48	0.48	**0.17**
Toiyabe Range	segment	0.54	**0.54**	0.54	0.16
	canyon	0.46	**0.54**	0.62	0.20
Shoshone Mountains	segment	0.66	0.64	**0.68**	0.20
	canyon	0.45**	0.64	**0.64****	0.20
BUTTERFLIES					
Toquima Range	segment	**0.83**	0.88	0.88	**0.21**
	canyon	**0.88**	0.88	0.88	**0.17**
Toiyabe Range	segment	0.95	**0.89**	0.89	0.16
	canyon	0.89	**0.89**	0.87	0.20
Shoshone Mountains	segment	0.84	0.80	**0.82**	0.20
	canyon	0.80	0.88	**0.88**	0.20

Notes: TQ = Toquima Range, TY = Toiyabe Range, SH = Shoshone Range. Bolded proportions indicate that the species assemblage from that range was used to determine the proportions. Comparisons should be made between the bolded proportion and the other proportions in that row. For segment level, one segment in each canyon that had the most umbrella species was conserved. For canyon level, the one canyon per range with the most umbrella species was conserved. Hence, the proportion of locations conserved by using any set of species as umbrellas was identical. * = 0.05 < P-value < 0.10; ** = P < 0.05.

CHAPTER 4: DOES YEARLY VARIATION IN SPECIES COMPOSITION INFLUENCE THE EFFICIENCY OF THE UMBRELLA INDEX ?

ABSTRACT

The efficiency of conservation efforts based on data collected at one point in time may not adequately represent the true impacts of a conservation plan. Protected areas need to serve as refugia that sustain populations of species over time. Thus, the effectiveness of conserving lands is best determined by evaluating the effectiveness over many years. This study examined the influence of turnover on the effectiveness of selecting lands for conservation using the umbrella index. Results indicated that over a relatively short (1-year) period, species turnover and changes in distributions could dramatically influence the effectiveness of protecting a portion of the landscape. Conservation efforts need to include analyses that assess whether reserve networks will adequately incorporate these fluctuations by incorporating them into the reserve design and evaluation procedures. Future studies should incorporate a larger time scale to determine if yearly fluctuations under or over estimate the amount of change that happens during multiple years.

INTRODUCTION

The conservation of biological diversity requires that locations selected for conservation provide protection to component species over the long term. The continued protection of individual species can only be accomplished if reserves are designed to encompass variations in home range size, weather, species distributions, and species turnover (Russell et al. 1995, Oliver et al. 1998, Krasinska et al. 2000, Rodrigues et al. 2000). The persistence of reserve features has traditionally been incorporated into reserve design by focusing attention on target species, such as endangered species, that were thought to be more sensitive to change (Thomas 1991, Madsen et al. 1998). However, non-target species may go unprotected if they are not also taken into account during the reserve design process (Kerr 1997).

Long term survival of individual species in reserve areas may be impacted by the assemblage fidelity and species turnover of different taxonomic groups. Assemblage fidelity, or the degree to which assemblages from different phylogenetic groups co-occur in space and time, varies among taxonomic groups (Oliver et al. 1998). When managing for multiple taxonomic groups, conservation efforts focused on assemblages that show high fidelity would be expected to be effective for both taxonomic groups. Conservation schemes would not be expected to be effective for multiple taxonomic groups if they do not exhibit high assemblage fidelity. Species turnover (β diversity) also varies among taxonomic groups (Oliver et al. 1998) and successful conservation efforts must account for changes in species occurrence through the years.

Individual species persistence probabilities and community turnover have traditionally been incorporated into quantitative reserve design by utilizing abundance data (Araújo and Williams 2000). One might expect that abundance and persistence would be related; the greater the density of individuals of a particular species in an area, the greater the probability of long-term persistence for that species (Araújo and Williams

2000). However, recent research on source-sink population dynamics has shown that this intuitive relationship doesn't always hold true. Additionally problematic with abundance data is that it is difficult to obtain. The amount of time required to determine the number of pairs of each species of breeding bird is at least three and can be up to seven times that of presence-absence data (Gregory et al. 1994)

Conservation decisions must often be made without the needed time, money, or distribution and abundance data (Oliver and Beattie 1996, Niemi et al. 1997, Simberloff 1998, Andelman and Fagan 2000). Thus, important aspects such as species turnover, assemblage fidelity, and species permanence are based on rapidly assessed presence-absence data or are not incorporated into conservation plans (Rodrigues et al. 2000). Umbrella species -- species whose conservation provides protection to sympatrically occurring species -- are just one shortcut that conservation biologists employ to make decisions with limited information. The utilization of the umbrella species approach has become widespread for the conservation of threatened habitats yet their use is controversial and their effectiveness seldom validated (Simberloff 1998, Andelman and Fagan 2000, but see Martikainen et al. 1998, Fleishman et al. 2000, 2001, Suter et al. 2002).

In an attempt to advance the umbrella species notion and determine quantitative criteria for selecting umbrella species, Fleishman et al. (2000) introduced the "umbrella index" concept. The umbrella index measures the ability of each species in an area to serve as an umbrella for other species that reside in the same area (Fleishman et al. 2000). This method can be used to select umbrella species from any particular taxonomic group (Fleishman et al. 2000). Life history and distributional data for each species are used to calculate rarity, sensitivity to human disturbance, and mean percentage of co-occurring species, the three parameters used in the model (Fleishman et al. 2000). Effective umbrellas should be neither extremely rare nor omnipresent because exceedingly rare species may not be distributed across enough of the landscape to ensure the viability of other species. Ideal umbrella species should also be sensitive to human disturbance so that sympatric species that are less sensitive to similar types of anthropogenic disturbance will also be protected in the protection offered by using the umbrella species for management (Blair 1996, Blair and Launer 1997, Fleishman et al. 2000). Finally, umbrella species should co-occur with a relatively high proportion of species in the same taxonomic group. Since species are rarely protected throughout their entire range, protection of locations with the highest richness should be a priority of conservation (Dufrêne and Legendre 1997, Freitag et al. 1997, Fleishman et al. 2000).

Modeling the effectiveness of umbrella species from one year to the next is important to determine the utility of the umbrella index. For the long-term persistence of species in protected areas, initially selected locations must adequately protect species in subsequent years. Yearly variations in species' distributions must be small enough that conservation of a specific location will be within the area used by particular species every year. If yearly variations in species' distributions are large, conserved locations may protect a certain suite of species in one year, but protect an entirely different group, or even worse, no species whatsoever, in following years.

Yearly variations in species' distributions are dependent upon the degree to which individuals return and reoccupy nest sites and locations that they held or occupied during previous breeding season. Avian breeding site fidelity is known to be highly variable and is dependent on a variety of factors including, but not limited to, an individual's or species' habitat specificity, previous reproductive success, sex, and age of the returning individual (Gauthreaux 1982, Newton and Marquiss 1982, Shields 1984, Gratto et al. 1985, Poulson 2002). Natal site fidelity, or the return of young birds to the locations where they were born, may also contribute to changes in species distributions.

In this study, I explore the efficiency of the umbrella index, as measured by the proportion of species conserved, between two years of breeding bird data from montane canyons in the Great Basin. I hypothesize that since many species of breeding birds exhibit high levels of habitat specificity and natal and breeding site fidelity, that conservation of locations in one year will protect a similar proportion of species in subsequent years.

METHODS

This study was conducted in montane canyons of the Toquima and Toiyabe Ranges and the Shoshone Mountains. These are just a few of the more than 200 north-south oriented mountain ranges in the Great Basin and are located near the town of Austin, Nevada (Latitude 39.493 °N, Longitude 117.069°W). All three of these mountain ranges have numerous canyons incised into the east and west facing slopes. Some of the canyons have continuous flow, others have seeps or springs that create standing or flowing water in portions of canyons, while others are dry almost year-round. The topography of individual canyons is highly variable.

The elevation and amount of available water determines the dominant vegetation of these ranges (Grayson 1993). The inter-mountain valleys and lower elevations in all of the ranges are dominated by sagebrush (*Artemisia tridentata* spp.). Sagebrush is replaced by pinyon-juniper (*Pinus monophylla*, *Juniperus osteosperma*) woodlands then mountain mahogany (*Cercocarpus ledifolius*) then dwarf sagebrush (*Artemisia tridentata vaseyana*) with increasing elevation. The highest summits in the Toquima and Toiyabe Ranges have a relatively depauperate alpine flora (Trimble 1989, Grayson 1993). Permanently or ephemerally moist areas have quaking aspen (*Populus tremuloides*), water birch (*Betula occidentalis*), willow (*Salix spp*.), rose (*Rose woodsii*), nettle (*Urtica dioica*), and an understory composed of many species of grasses and forbs.

Study segments and canyons

I selected six canyons in the Toquima Range, five in the Toiyabe Range, and five in the Shoshone Mountains based on the feasibility of conducting avian surveys throughout the length of the canyon. The characteristics of the selected canyons were highly variable.

Each study canyon was divided into 100 m vertical elevation segments from its mouth to its crest. The average number of segments per canyon was 5.25 ± 1.34 sd. I surveyed a total of 84 elevational segments, 25 in the Toquima Range, 31 in the Toiyabe Range, and 28 in the Shoshone Mountains. Canyon segments had a median length of 1413.5 m and inter-quartile range of 944. I measured elevation with a pocket altimeter and then verified it with a differentially corrected Global Positioning System (GPS) to within 5 m accuracy (Fleishman et al. 1998).

Avian communities

I determined the avian species richness of segments from presence-absence data collected in each of two years by conducting a series of fixed-radius point-counts at two or three locations per segment (Bibby et al. 1992). I selected the point-count locations by driving or walking the length of each segment and choosing locations representative of each major habitat type within the segment. This approach was used, rather than selecting random locations in each segment, because the goal of surveys was to determine the component species of each segment for a well-known taxonomic group with species that exhibit relatively high degrees of habitat specificity. Thus, sampling random locations would not have resulted in an accurate assessment of all species within a segment. Each segment received at least two point-count locations even if there was only one major habitat type. I recorded all birds using habitat within 75 m of the point-count location and thus, locations had to be at least 150 m apart. I conducted three 5-minute counts at each location in both the 2001 and the 2002 breeding seasons. I visited each point at least once within 2 hours of dawn and at least once between 2 and 3 1/2 hours after dawn only under fair skies. Fixed-radius point-counts are an effective method of surveying avian communities in Great Basin canyons and riparian habitats (Dobkin and Rich 1998). To determine if bird species richness was influenced by the number of point-counts in a segment, I calculated the mean number of bird species surveyed in segments with 2 and 3 point-counts. To determine if species richness was a function of the number of point-count performed in a segment, I calculated the number of bird species detected per unit time for each study segment.

Identification of umbrella species

To measure the potential of each species of bird to serve as an umbrella species, I calculated umbrella index values for individual species at both the segment and canyon level. I used three main criteria to calculate the umbrella index: percentage of co-occurring species, degree of rarity, and sensitivity to human disturbance. A detailed explanation for these particular criteria can be found in Fleishman et al. (2000).

Mean percentage of co-occurring species (PCS) is a measure of the average species richness of locations in which particular species occur. Each species receives a mean PCS value between 0 (the species occurs in areas with no other species) and 1 (the species occurs in areas with many other species). For each species *j*, PCS is defined as

$$PCS_j = \sum_{i=1}^{l} (S_i - 1)/(S_{\max} - 1)/ Nj$$

where *l* is the number of locations in the data set, S_i is the number of species present at each location *i,* S_{max} is the total number of species present in all locations in the data set, and N_j is the number of locations where species *j* occurs (Fleishman et al. 2000).

The second parameter is the degree of rarity, which assumes that conservation of areas where species are neither rare nor ubiquitous is superior to conserving areas where rare or ubiquitous species are found (i.e. it does no good to conserve either very few sites or every possible site). Each individual species can receive a score from 0 (the species occurs in almost all or none of the locations) to 1.0 (the species occurs in exactly half of the locations). For each species *j*, degree of rarity is defined as

$$R_j = 1 - 2 \times \left| \frac{N_{present}}{N_{total}} - 0.5 \right|$$

where N is the number of locations with the *j*th species present ($N_{present}$) or the total locations considered (N_{total}) (Baz 1991, Fleishman et al. 2001).

The third parameter used to calculate the umbrella index is the Disturbance Sensitivity Index (DSI) which accounts for sensitivity to human disturbance. This variable is a modified form of a sensitivity index proposed by Nelson and Anderson (1994) that can combine multiple vulnerability scores into a single metric. Variations among species in their life-history traits can influence the degree of anthropogenic influences they can tolerate. The DSI for birds in montane canyons was based on six life-history factors: reproductive effort, nest form, nest height, territory size or density, migratory classification, and primary habitat (Table 1). For each individual factor, a species received an integer value score from 1 (low sensitivity) to 3 (high sensitivity) based on existing knowledge about avian life histories. The value for all life history factors were summed for each individual species and then divided by the maximum total value of all species, thus normalizing the numbers used as DSI scores. Disturbance sensitivity, thus, is a relative score with species obtaining scores from 0 (low sensitivity) to 1 (high sensitivity). DSI scores were calculated separately for each year, using every species that was surveyed in any of the ranges during that breeding season.

All species receive an umbrella index (UI) score that is calculated as the sum of its scores for mean percentage of co-occurring species (PCS), degree of rarity (R), and disturbance sensitivity (DSI). Thus, each species could theoretically receive an umbrella index score from 0 (a very poor umbrella that would protect few other species) to 3 (an efficient umbrella that would conserve many other species). I defined potential umbrella species as those who received a UI score greater than 1 sd above the mean.

The effectiveness of conservation strategies can be determined in several ways. Management of habitats for the conservation of biodiversity involves protecting locations in a fashion that maintains species richness (Freitag et al. 1997). Species richness is an accurate measure of how many species may be conserved by a conservation scheme; however, richness alone provides no information on how much of a species' range is conserved or its long-term viability.

After umbrella species were selected for each data set, I used them under two different scenarios to select locations for conservation. First, all locations with at least one umbrella species were conserved. Second, a subset of locations with umbrella species was conserved. Under both of these scenarios, locations selected for conservation are referred to as 'conserved' and species that reside in these conserved locations are referred to as 'protected.'

ANALYSES

Conservation of all locations with at least one umbrella species

The umbrella index selects multiple umbrella species for each data set. To determine how effective the umbrella index would be when developed in either year, I used the data collected in 2001 and 2002 to determine the impact of protecting all locations with at least one umbrella species. I calculated both the proportions of species that would be protected and the proportions of locations that would be conserved if the umbrella index were developed separately for each year. Additionally, I calculated the proportion of species that were observed in both years in a specific mountain range (shared species) that would receive protection. I used McNemar's (1947) Q test to compare the proportions of shared species protected in 2001 to the proportions of shared species receiving protection in 2002. McNemar's Q is a non-parametric chi-square test used to evaluate differences between dependent proportions and count data (Agresti 1990). McNemar's Q test analyzes the null hypothesis H_0: Y_{12} pairs are as likely as Y_{21} pairs where Y_{12} and Y_{21} are discordant pairs of dichotomous responses (Figure 1). McNemar's Q test was calculated as $Q = (Y_{12} - Y_{21})^2/(Y_{12} + Y_{21})$. For each year, shared species were assigned a label of 1 if it occurred in any location selected for conservation or 0 if it did not occur in any conserved locations. For example, when conserving a subset of segments in the Shoshone Mountains, 22 of the shared species were protected during both years, nine species were protected in 2001 but not in 2002, seven species were protected in 2002 but not in 2001, and two species did not receive protection in either year. The calculated chi-square value was 0.25 and the associated P-value was 0.6171.

Conservation of subsets of locations with umbrella species

It would be virtually impossible to protect the entire range of all but the most endangered species (Andelman and Fagan 2000, Fleishman et al. 2000). Thus, the effectiveness of the umbrella index may be useful for prioritizing areas for conservation by conserving the locations with the highest number of umbrella species. Consequently, I determined the number of umbrella species for each location in a dataset, and selected a subset of locations which contained the most umbrella species. For the segment level analysis, the one segment with the most umbrella species in each canyon of a range would be conserved. Thus, the number of segments marked for conservation is equal to the number of canyons in a mountain range, regardless of the year being analyzed. At the canyon level, I marked the one canyon with the highest number of umbrella species for conservation. For the combined dataset, I marked the one canyon from each of the three mountain ranges with the most umbrella species. Using umbrella species selected in 2001 and 2002, I calculated the proportion of species that would be protected and the proportion of locations that would be designated for protection. For all protected species, I calculated the mean proportion of their distributions protected. I also determined the proportion of species that were observed in both years that would receive protection. For all species that were surveyed in a range during both survey years, I used McNemar's test to compare the proportion receiving protection in 2001 to the proportion receiving protection in 2002.

There are a limited number of possible segment permutations that can be selected. Since only one segment is selected per canyon, the number of possible permutations for each mountain range can be calculated as Perm = $seg_i * seg_{i+1} ... * seg_n$ where seg is the number of segments in canyon i and n is the total number of canyons in a mountain range. The number of possible segment permutations for the Toquima Range is 9000, for the Toiyabe Range the number is 8575, and for the Shoshone Mountains 2520. For any mountain range, the combination of segments selected by the umbrella index is just one of the total possible permutations. The utility of this is that it allows researchers to attach a level of statistical significance to the proportion of species protected by the umbrella index by using a permutation-based test. By determining the proportion of species protected by each possible permutation of segments, we can assign statistical significance by calculating the proportion of permutations that protect a greater proportion of species than the actual combination of segments selected by the umbrella index. For instance, if 90 out of 9000 permutations protect a proportion of species that is greater than or equal to number of species protected by the umbrella index, then the probability of protecting more species than the umbrella index (by chance) is 0.01. The probabilities obtained from permutation tests that have large numbers of possible combinations can be interpreted in the same was as “p-values” that are obtained from traditional significance tests (Bailer and Ruberg 1996, Manly 1997).

Protecting birds in 2002 by conserving locations with at least one umbrella in 2001

To test the idea that locations conserved for umbrella species in one year will provide protection to species in subsequent years, I determined the proportion of species in the 2002 that would be protected by conserving areas in 2001. Consequently, I calculated the umbrella index for the birds surveyed in 2001. All locations with at least one umbrella species were then marked for conservation. Next, I determined the proportion of shared species that would be protected in each of the years. I used McNemar's (1947) Q test to compare the proportion of shared species that were conserved by protecting all locations with at least one umbrella species in 2001 to the proportion of shared species that would be protected in 2002 by protecting the same locations.

Protecting birds in 2002 by conserving a subset of locations in 2001

To further test the idea that protecting lands in one year can provide protection to species in subsequent years, I determined the influence of conserving a subset of locations in 2001 on the proportions of species protected in the following year. As detailed above, I selected subset of locations for conservation using the distribution data of birds in 2001. Next, using only species that were surveyed in a particular range during both years, I determined the proportion that would be protected in each of the years. I used McNemar's (1947) test to compare the proportion of shared species that were protected by conserving a subset of locations with the most umbrella species in 2001 to the proportion of species that would be protected in 2002 by protecting the same locations.

RESULTS

One more bird species was recorded during 2001 than during 2002 and a total of 76 species were recorded during the two years (Table 2). The number of bird species per segment was higher in 2002 than in 2001 (mean ± sd: 2001 = 8.91 ± 4.26, 2002 = 13.18 ± 4.26; t = 5.872, P = < 0.0001) (Table 3). The number of bird species per canyon in 2001 was higher than in 2002 (mean ± sd: 2001 = 21.25 ± 5.97, 2002 = 39.44 ± 7.16; t = 3.5414, P = 0.0014). The number of bird species per range was between 40 and 52 in 2001 and between 45 and 56 in 2002. The proportion of species recorded during both years (shared species) exhibited the same trends as separate data sets with the Toquima Range having the lowest species richness and the Toiyabe Range the highest richness. The proportion of species identified as umbrella species ranged from 0.13 to 0.23 (0.17 ± 0.03) in 2001 and from 0.14 to 0.21 (0.18 ± 0.02) in 2002. The exact same study canyons and segments were used during both years of the study.

Bird species richness was higher in the 13 segments that had three point-counts (16 ± 2.86) performed in them at three locations than the 71 segments that had only two point-counts (7.82 ± 2.89) (P < 0.001). Segments with three point-counts received a total of 45 minutes of surveys while segments with two point-counts received 30 minutes of surveys. Segments with 3 point-counts averaged one species per 0.356 minutes while segments with two point-counts averaged one species per 0.260 minutes.

Conservation of all locations with at least one umbrella species

When developing the umbrella index separately for each year, the conservation of all locations that had any of the selected umbrella species would result in the protection of a vast majority of the species (2001, 0.90 - 1.00; 2002, 0.95 - 1.00) and locations (2001, 0.93 ± 0.08; 2002, 0.95 ± 0.07) (Table 4). A vast majority of the shared species would also receive protection during both years (2001, 0.91 - 1.00; 2002, 0.98 - 1.00). In only one location was there a difference between the proportions of shared species conserved by umbrellas selected in 2001 to umbrellas selected in 2002. In the Toquima Range at the segment level a marginally significant difference ($P = 0.0833$) existed between the shared species conserved in 2001 and 2002.

Conservation of subsets of locations with umbrella species

The conservation of subsets of locations with the highest number of umbrella species would protect 0.19 ± 0.02 of the locations (Table 5). The proportion of bird species receiving protection by the umbrella index developed in 2001 was between 0.45 and 0.68 (0.58 ± 0.07). The proportion of species protected by the umbrella index developed in 2002 was between 0.51 and 0.88 (0.70 ± 0.13). The umbrella index developed for birds in 2002 protected a significantly higher proportion of shared species in two of the data sets. A significant difference existed between the proportions of shared species protected. Umbrella species in 2002 protected a statistically higher proportion of species in the Toiyabe Range at the canyon level ($P = 0.0209$) and in the combined data set at the canyon level ($P = 0.0124$).

For all three mountain ranges in 2001 and for two of the mountain ranges in 2002, selecting a subset of locations with the highest number of umbrella species protected a higher proportion of species than a majority of all possible segment permutations. The permutation-based p-values for the proportion of shared bird species protected by umbrella species in 2001 compared to all possible permutations was 0.41 for the Toquima Range, 0.26 for the Toiyabe Range, and 0.20 for the Shoshone Mountains (Figure 2). For 2002 data sets, the permutation-based p-value was 0.98 for the Toquima Range, 0.10 for the Toiyabe Range, and 0.32 for the Shoshone Mountains (Figure 3).

Protecting birds in 2002 by conserving locations with at least one umbrella in 2001

The conservation of all locations with at least one umbrella species in 2001 would result in the protection of a vast majority of bird species in 2002 (0.99 ± 0.03) (Table 6). Similar proportions of shared species also received protection (0.98 ± 0.03). No statistically significant differences existed between the proportion of shared species that would be protected in 2001 and 2002.

Protecting birds in 2002 by conserving a subset of locations in 2001

Conserving a subset of locations with the most umbrellas in 2001 tended to protect higher proportions of species in 2002 than in 2001 (Table 7). The proportion of species receiving protection in 2001 was between 0.45 and 0.68 (0.58 ± 0.07) and in 2002 was between 0.42 and 0.82 (0.69 ± 0.13). The proportion of shared species receiving protection in 2001 was between 0.46 and 0.73 (0.64 ± 0.10) and in 2002 was between 0.51 and 0.85 (0.71 ± 0.11). In two data sets a significant difference existed between the proportion of shared species conserved in 2001 and 2002. A marginally greater ($P = 0.0833$) proportion of shared species were protected in 2002 than in 2001 in the combined data set at the canyon level. A statistically significant ($P = 0.0209$) difference existed between the proportion of shared species protected in 2001 and 2002 in the Toiyabe Range at the canyon level.

DISCUSSION

Yearly variations in species distributions and occurrences can have dramatic influences on the effectiveness of conservations efforts. Changes in distribution may appear as localized extinctions or colonization when reserves are not designed to accommodate yearly fluctuations (Rodrigues et al. 2000). In this study, the proportion of species that would receive protection when a subset of locations was conserved varied significantly between years. Although similar numbers of species were seen during the two years, individual species exhibited wider distributions in 2002 than in 2001. Thus conservation effectiveness, viewed as the proportion of species receiving protection, would have been greater in 2002 than in 2001.

Variations in distribution from one year to the next may be relatively small, but cumulative effects of localized colonizations and extinctions over many years may be more dramatic (Russell et al. 1995). Observed turnover of birds on oceanic islands has been shown to increase through time so that 1-year turnover underestimates the turnover of a decade or a century (Russell et al. 1995). If more than one year elapses between surveys, some colonizations and extinctions may go undetected, necessitating the use of the term apparent turnover (Margules et al. 1994). This can happen if particular species colonize and then go extinct or disappear and then recolonize locations between surveys (Diamond and May 1977). Thus, censuses separated by many years may find little or no species turnover regardless of cumulative turnover rates (Russell et al. 1995)

Most reserves are designed to maintain species richness over the long term. Yearly turnover may cause the number of species that receive protection in a conserved area to vary from year to year, although yearly changes may cancel out over many years. In this study, an increased proportion of shared species received protection in the second year. These changes may be accounted for by demographic stochasticity or prevailing weather patterns. At their best, reserves may hold the number of species that receive protection constant. More realistically, the number of species receiving protection on reserves will decline over time. Some studies have found that reserves may lose as much as 8% of their avifauna over a ten-year period (Rodrigues et al. 2000).

The proportion of species protected by conserving a subset of locations with the greatest number of umbrella species tended to be higher in 2002 than in 2001. Yet, this does not necessarily mean that the umbrella index developed for 2001 did a poor job at selecting locations for conservation. In fact, the permutation-based tests for each mountain range revealed that the umbrella index performed well compared to all possible permutations of segments for all ranges in 2001 but only two of the three ranges in 2002.

The extremely poor performance of umbrella species in the Toquima Range in 2002 is somewhat enigmatic. Although more bird species were detected per segment in 2002 than in 2001, that does not necessarily mean that a higher proportion of species will be protected by conserving that location. Since five more species were detected in the Toquima Range in 2002 than in 2001, protecting the exact same number of species would have resulted in a decrease in the proportion of species protected. However, this does not explain why a vast amount of the possible permutations protected a higher proportion of species than the segment combination selected by the umbrella index.

The higher levels of species richness in a majority of segments and canyons in 2002 can account for the increased proportion of *shared* species that were protected in 2002 when conserving locations with the greatest number of umbrella species in 2001. If the same locations were conserved in both years, we would expect more species to be protected when locations have higher levels of richness. As a result, umbrella species selected in 2001 did an excellent job of protecting birds in 2002.

But will locations with the highest number of umbrella species always do an excellent job of protecting species in subsequent years? Probably not. The best that reserve systems can hope to do is maintain richness, yet species occasionally go locally extinct, decreasing the efficiency of the reserve (Rodrigues et al. 2000). If locations in 2001 had higher levels of species richness than the same locations in 2002, we would have observed a decrease in the proportion of species protected at the canyon level. At the segment level, where combinations of locations are conserved, we would not necessarily see a decrease in the proportion of species conserved, although we would again expect it. The proportion of species conserved could stay the same with a decrease in richness if different species disappeared from different conserved locations, but all species continued to be protected with a portion of their original range. However, such protection is more likely to be the exception rather than the rule. Typically, a decrease in richness across a region would result in a decrease in the number of species that would receive protection. Changes in abundance of individual avian species show similar patterns to changes in occurrence. Short-term temporal variation in abundances can be caused by a variety of factors including migratory status, successional changes in habitat, and severe weather events such as drought (Blake et al. 1994).

When protecting a subset of locations in 2001 and determining the proportion of shared species in 2001 and 2002 that would receive protection, significant differences existed at the canyon level in the Toiyabe Range and in the combined data set. It appears that the variation of species distributions between years in the Toiyabe Range may be driving the observed differences in the combined data set. Canyons within the Toiyabe Range averaged the highest richness of any range during both years of the study and would therefore contribute heavily to the combined data set at the same scale. The species richness of canyons in the Shoshone Mountains increased slightly more than canyons in the Toiyabe Range (9.4 to 9.0, respectively). However, the proportion of shared species (surveyed in a range during both years) that showed a turnover may not have exhibited these same trends and also contribute greatly to changes in the combined data set.

CONCLUSIONS

The efficiency of any conservation scenario should not be based solely on the proportion of species that are conserved in any one year. Protected areas need to serve as refugia for many species for long periods of time. Thus, the effectiveness of conserving lands is best determined by evaluating the effectiveness of over many years. This study examined the influence of turnover on the effectiveness of selecting lands for conservation using the umbrella index. Results indicated that over a relatively short (1-year) period, species turnover and changes in distributions could dramatically influence the effectiveness of a protecting a portion of the landscape. Future studies should incorporate a larger time scale to determine if yearly fluctuation under or over estimate the amount of change that happens during multiple years.

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Figure 1. McNemar's (1947) Q test can be used to test the null hypothesis X for matched pair data by comparing the values of discordant pairs (Y_{12} and Y_{21} or 1 and 2, bolded). The general (a) and specific (b) examples illustrate how the data is arrayed to perform the comparison.

a. General example		Shared species protected in 2001		
		Species selected as umbrellas	Species not selected as umbrellas	
Shared species protected in 2002	Species selected as umbrellas	Y_{11}	$\mathbf{Y_{12}}$	b
	Species not selected as umbrellas	$\mathbf{Y_{21}}$	Y_{22}	n-b
		a	n-a	n

b. Specific example		Shared species protected in 2001		
		Species selected as umbrellas	Species not selected as umbrellas	
Shared species protected in 2002	Species selected as umbrellas	22	**7**	b
	Species not selected as umbrellas	**9**	2	n-b
		a	n-a	n

Figure 2. Histograms of the proportion of bird species in 2001 protected by all possible segment permutations. Dashed line indicates the proportion of species protected by the segment combination selected by the umbrela index. A = Toquima Range, B = Toiyabe Range, C= Shoshone Mountains.

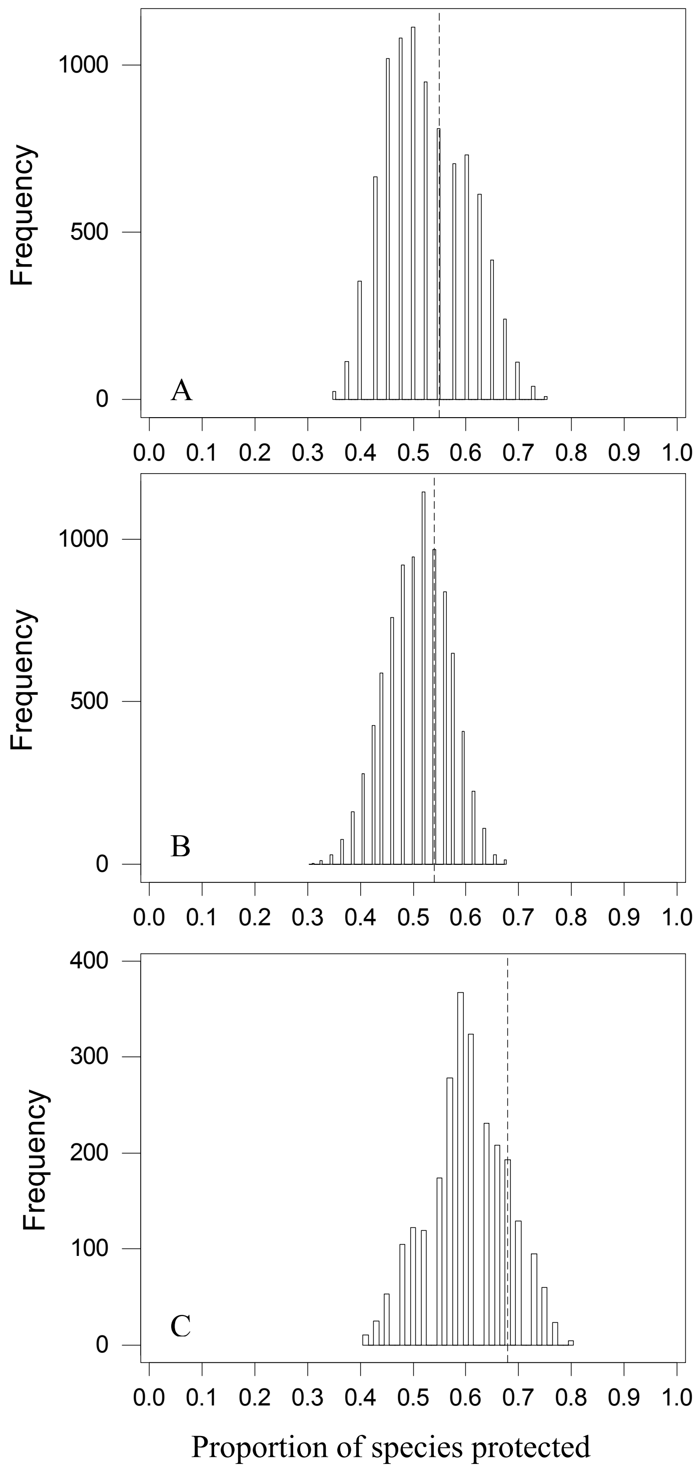

Figure 3. Histograms of the proportion of bird species in 2002 protected by all possible segment permutations. Dashed line indicates the proportion of species protected by the segment combination selected by the umbrela index. A = Toquima Range, B = Toiyabe Range, C= Shoshone Mountains.

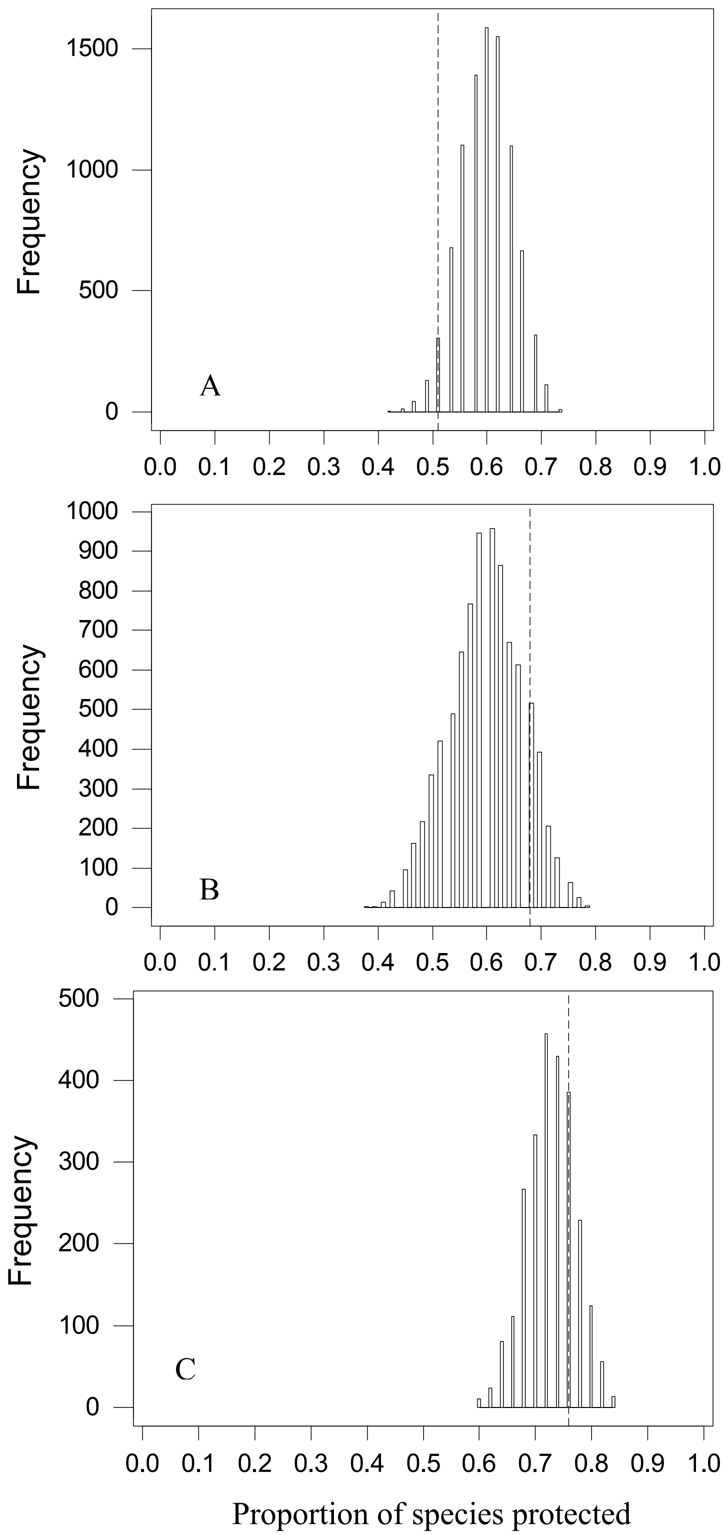

Table 1. Life history criteria used to score sensitivity (1 = least sensitive, 3 = most sensitive) of birds in the Toiyabe and Toquima Ranges and the Shoshone Mountains to human activities (modified from Hansen and Urban 1992; data from Schoener 1968, Brown 1985, Ehrlich et al. 1988, AOU 1992, Martin 1995, Rottenborn 1999, Warkentin and Reed 1999).

	Sensitivity score		
Parameter	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) <u>or</u>	< 4	4 - 40	> 40
territory density (males/km^2)	> 100	15 - 100	< 15
Migratory distance	resident	short-distant	neotropical
Riparian dependence	no-use	facultative	obligate

Table 2. Number of species, umbrella species, and survey locations in each dataset.

Data set	Scale	Species richness			Umbrella species		**Locations**
		2001	2002	Shared	2001	2002	
Toquima Range	segment	40	45	35	6 (0.15)	9 (0.2)	28
	canyon	40	45	35	5 (0.13)	8 (0.18)	6
Toiyabe Range	segment	52	56	42	9 (0.17)	9 (0.16)	31
	canyon	52	56	42	9 (0.17)	12 (0.21)	5
Shoshone Mountains	segment	44	50	40	6 (0.14)	8 (0.16)	25
	canyon	44	50	40	10 (0.23)	7 (0.14)	5
All ranges combined	segment	67	66	56	11 (0.16)	11 (0.17)	84
	canyon	67	66	56	12 (0.18)	13 (0.20)	16

Notes: Proportions of total species are given in parentheses. Locations indicates the number of segments or canyons in a data set.

Table 3. The number of species surveyed per segment and canyon in 2001 and 2002.

Toquima	2001	2002	Toiyabe	2001	2002	Shoshone	2001	2002
Segment level								
ME01	6	10	BC01	11	16	BA01	10	10
ME02	7	10	BC02	10	17	BA02	7	11
ME03	12	8	BC03	9	13	BA03	10	15
ME04	6	12	BC04	10	13	BA04	11	14
MW01	4	3	BC05	7	15	BA05	4	6
MW02	6	10	BC06	3	16	BA06	4	10
MW03	6	13	BC07	3	6	BE01	7	18
MW04	7	14	BI01	14	13	BE02	8	17
MW05	6	12	BI02	8	15	BE03	8	13
NE01	5	8	BI03	16	26	RI01	10	16
NE02	5	10	BI04	17	21	RI02	9	11
NE03	5	13	BI05	8	12	RI03	16	15
NE04	7	10	BI06	4	6	RI04	9	17
NE05	4	10	BI07	2	6	RI05	8	15
NW01	8	8	KI01	9	8	SH01	15	21
NW02	10	11	KI02	8	9	SH02	18	26
NW03	9	9	KI03	12	16	SH03	22	20
NW04	8	7	KI04	10	17	SH04	12	24
NW05	12	11	KI05	9	13	UN01	8	14
NW06	6	11	KI06	11	13	UN02	9	14
PE01	14	10	KI07	6	8	UN03	6	11
PE02	8	12	SJ01	16	23	UN04	11	24
PE03	9	11	SJ02	18	24	UN05	3	7
PW01	3	7	SJ03	4	11	UN06	3	6
PW02	7	16	SJ04	6	9	UN07	4	10
PW03	11	13	SJ05	3	4			
PW04	9	15	WS01	15	22			
PW05	7	13	WS02	14	18			
			WS03	17	20			
			WS04	13	18			
Canyon level			WS05	17	17			
ME	16	21	BC	21	31	BA	21	28
MW	13	24	BI	28	43	BE	15	24
NE	11	20	KI	23	29	RI	28	34
NW	21	23	SJ	26	39	SH	28	38
PE	18	20	WS	32	33	UN	20	35
PW	19	29						

Notes: Letters refer to canyon name, numbers refer to elevational segment. Toquima Range: ME (Moore's East), MW (Moore's West), NE (Northumberland East), NW (Northumberland West), PE (Pete's East), PW (Pete's West). Toiyabe Range: BC (Big), BI (Birch), KI (Kingston), SJ (San Juan), WS (Washington). Shoshone Range: BA (Barrett), BE (Becker), RI (Riley), SH (Shoonover), UN (Underdown).

Table 4. Consequences of protecting all locations with at least one umbrella species.

Data set	Scale	Proportion Protected					
		All species		Shared Species		Locations	
		2001	2002	2001	2002	2001	2002
Toquima Range	segment	0.90	1.00	0.91*	1.00*	0.89	1.00
	canyon	0.98	1.00	1.00	1.00	0.83	1.00
Toiyabe Range	segment	1.00	0.96	1.00	1.00	1.00	0.90
	canyon	1.00	0.95	1.00	0.98	1.00	0.80
Shoshone Mountains	segment	1.00	0.98	1.00	0.98	1.00	0.92
	canyon	0.98	1.00	0.98	1.00	0.80	1.00
All ranges combined	segment	0.99	1.00	1.00	1.00	0.99	1.00
	canyon	1.00	1.00	1.00	1.00	0.94	1.00

Notes: All species indicates separate data sets with all species included; shared species is a proportion calculated only for species that were observed in a data set in both years; 2001 = proportion of species protected in 2001; 2002 = proportion of species protected in 2002; * = 0.05 < P-value < 0.10; ** = P < 0.05.

Table 5. Consequences of protecting subsets of locations.

Data set	Scale	Proportion Protected: All species		Shared species		Locations
		2001	2002	2001	2002	
Toquima Range	segment	0.55	0.51	0.57	0.57	0.21
	canyon	0.45	0.53	0.46	0.57	0.17
Toiyabe Range	segment	0.54	0.68	0.62	0.74	0.16
	canyon	0.54	0.77	0.64**	0.83**	0.20
Shoshone Mountains	segment	0.68	0.76	0.73	0.78	0.20
	canyon	0.64	0.76	0.70	0.83	0.20
All ranges combined	segment	0.64	0.74	0.71	0.80	0.19
	canyon	0.60	0.88	0.75**	0.93**	0.19

Notes: All species indicates separate data sets with all species included; shared species is a proportion calculated only for species that were observed in a data set in both years; 2001 = proportion of species protected in 2001; 2002 = proportion of species protected in 2002; * = 0.05 < P-value < 0.10; ** = P < 0.05.

Table 6. Proportion of bird species that would be protected during the 2001 and 2002 breeding seasons if all locations with umbrella species in 2001 were conserved.

		Proportion Protected				
Data set	Scale	All species		Shared species		Locations
		2001	2002	2001	2002	
Toquima Range	segment	0.90	0.91	0.91	0.91	0.89
	canyon	0.98	1.00	1.00	1.00	0.83
Toiyabe Range	segment	1.00	1.00	1.00	1.00	1.00
	canyon	1.00	1.00	1.00	1.00	1.00
Shoshone Mountains	segment	1.00	1.00	1.00	1.00	1.00
	canyon	0.98	1.00	0.98	1.00	0.80
All ranges combined	segment	0.99	0.97	0.98	0.96	0.99
	canyon	1.00	1.00	1.00	1.00	0.94

Notes: All species indicates separate data sets with all species included; shared species is a proportion calculated only for species that were observed in a data set in both years; 2001 = proportion of species protected in 2001; 2002 = proportion of species protected in 2002; * = 0.05 < P-value < 0.10; ** = P < 0.05.

Table 7. Proportion of bird species that would be protected during the 2001 and 2002 breeding seasons if the subset of locations for conservation were the locations with the most umbrella species in 2001.

Data set	Scale	**Proportion Protected** *All species*		Shared species		Locations
		2001	2002	2001	2002	
Toquima Range	segment	0.55	0.64	0.60	0.69	0.21
	canyon	0.45	0.42	0.46	0.51	0.17
Toiyabe Range	segment	0.54	0.61	0.62	0.71	0.16
	canyon	0.54	0.77	0.64**	0.83**	0.20
Shoshone Mountains	segment	0.68	0.82	0.73	0.85	0.20
	canyon	0.64	0.68	0.70	0.73	0.20
All ranges combined	segment	0.64	0.76	0.73	0.77	0.19
	canyon	0.60	0.80	0.73*	0.84*	0.19

Notes: All species indicates separate data sets with all species included; shared species is a proportion calculated only for species that were observed in a data set in both years; 2001 = proportion of species protected in 2001; 2002 = proportion of species protected in 2002; * = 0.05 < P-value < 0.10; ** = P < 0.05.

CHAPTER 5: CONCLUSION TO THESIS

This study had three primary objectives. First, I compared the effectiveness of two different methods of calculating the umbrella index. Second, I empirically validated the efficiency of the more intellectually satisfying umbrella index method with bird and butterfly occurrence data sets in montane canyons of three Great Basin mountain ranges. Finally, I evaluated whether changes in species occurrences between years would influence the effectiveness of conservation decisions based on the implementation of the umbrella index.

In comparing the two methods of calculating the umbrella index I determined that they protected similar proportions of birds and butterflies when analyzed in either of two ways. The conservation of all locations with at least one of the selected umbrella species would almost always result in the protection of all lands and all species. Conserving locations that had the highest concentrations of umbrella species would conserve less species than the previous scenario. However, a majority of species would still be protected in a fraction of the landscape. Both umbrella index calculation methods showed these results.

Empirical validation of the umbrella index included several different analyses. I determined the proportions of species and locations that would be protected under two conservation scenarios. First, all locations with at least one umbrella species were conserved. Second, a subset of locations with the most umbrella species were conserved. I also determined the proportion of cross-taxonomic species that would be protected by this second conservation scenario. Finally, I determined the proportion of species would be protected if umbrella species selected for one range were implemented as umbrellas in other ranges. Results indicated that a greater proportion of butterfly species than bird species would receive protection in any of the above conservation scenarios. Additionally, cross-taxonomic and among-range umbrellas protected almost as many species as same-taxon and same-range umbrellas.

During a relatively short time interval, changes in species distribution and localized extinctions and colonizations had sometimes dramatic influences on the performance of locations selected by the umbrella index. Umbrella species selected with the umbrella index based on bird distributions in 2001 protected equal or greater proportions of shared species in 2002 than in 2001. These differences can be accounted for by the increase in the number of bird species surveyed in most segments and canyons.

The umbrella index has several advantages over other umbrella species management schemes. First, and foremost, it incorporates objective, quantitative criteria into the process of selecting umbrella species for particular regions (Fleishman et al. 2000). Generally, umbrella species are selected as umbrellas because they are protected by the U.S. Endangered Species Act and their conservation is federally mandated (Rubinoff 2001). Without the incorporation of life history characteristics and knowledge about the extent of geographic distribution being incorporated into umbrella species selection, their protection tells us little about how well quantitatively selected umbrella species could perform. Lambeck (1997) suggested another method of incorporating quantitative criteria and life history attributes into umbrella species selection. The utilization of multiple umbrella species, each of which are the most susceptible to a particular threat, can assist with designing reserves that meet the minimum acceptable requirements for all species (Lambeck 1997). Although this focal species approach has been utilized with some success (Watson et al. 2001, Brooker 2002), some conservation biologists are critical of its use because of the impractically large amount of information that is needed and its failure to consider multiple taxonomic groups (Zacharias and Roff 2001, Lindenmayer et al. 2002).

Another advantage of the umbrella index is that it specifies which lands to conserve. Traditional umbrella species can be used to determine the minimum area requirements needed for conservation efforts, however they cannot determine their placement (Berger 1997). The placement of reserves may have a large influence on the long-term persistence of component species, especially in ecoregions that have a wide variety of habitats such as montane canyons in the Basin.

Despite these advantages, there are several limitations to the umbrella index. Like Lambeck's (1997) multiple umbrella approach, a vast amount of information is needed to calculate the umbrella index. Life history data can be collected relatively easily for most of the criteria. Even more time consuming is the collection of the actual field data. Two parameters of the umbrella index (degree of rarity and percentage of co-occurring species) are calculated from field collected data. Currently, these data need to be collected for all locations in which land managers wish to use the umbrella index. If it can be validated that the top-scoring umbrella species from one area can be used as umbrellas in neighboring areas, surveys would only need to determine the presence-absence of these species.

Like many other conservation schemes, the umbrella index only uses distribution data collected at one point in time. Yearly variations in distribution and abundance may or may not influence the efficiency of conservation efforts over large amounts of time. However, little is known about the impacts of localized colonizations and extinctions in nature reserves. Theoretical calculation of these effects is further confounded by the influences that the surrounding matrix to species richness within conserved areas. For example, in this study, segments and canyons had higher species richness during the second year of the study. Yet, the habitat surrounding "conserved" locations was not modified or developed in any way. If these adjacent habitats had been developed, then richness levels would probably have declined between years. The current umbrella index would benefit from the incorporation of a species-specific long term survival component that would limit the chance effects of species occupancy in any particular location.

Within-year variation of communities is another reason that surveying at one point in time is problematic. Species from many taxonomic groups, including birds and butterflies, have different habitat requirements at different times of the year. The conservation of only individual segments within a canyon would be detrimental to species such as Greater Sage-Grouse (*Centrocercus urophasianus*), Mountain Chickadees (*Poecile gambeli*), and Northern Flickers (*Colaptes auratus*) that exhibit yearly altitudinal migrations. The conservation of habitat for species such as Red Crossbills (Loxia curvirostra) and Gray-crowned Rosy-Finches (*Leucosticte tephrocotis*) that only winter in the area is not even incorporated into the current model. Unconsidered factors such as these must be integrated into reserve design and the umbrella index if reserves are to serve as refugia for long periods of time. Even then, no single surrogate species or conservation shortcut will be able to resolve all conservation problems.

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