Umbrellas and flagships: Efficient conservation surrogates or expensive mistakes?

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The use of umbrella and flagship species as surrogates for regional biota whose spatial distributions are poorly known is a popular conservation strategy. Yet many assumptions underlying the choice of surrogate species remain untested. By using biodiversity databases containing spatial incidence data for species of concern for (*i*) the southern California coastal sage scrub habitat, (*ii*) the Columbia Plateau ecoregion, and (*iii*) the continental United States, we evaluate the potential effectiveness of a range of conservation surrogate schemes (e.g., big carnivores, charismatic species, keystone species, wide-ranging species), asking how many species potentially are protected by each scheme and at what cost in each habitat area. For all three databases, we find that none of the surrogate schemes we evaluated performs significantly better than do a comparable number of species randomly selected from the database. Although some surrogate species may have considerable publicity value, based on the databases we analyzed, representing diverse taxa on three different geographic scales, we find that the utility of umbrella and flagship species as surrogates for regional biodiversity may be limited.

For many regions of the world, scientists lack detailed distribution and abundance data for most species of conservation concern. Nevertheless, decisions about which lands to allocate for conservation often cannot be postponed until more data are available, even though additional data might facilitate the identification of more economically efficient reserve networks (1, 2). In such cases, conservationists must seek effective shortcuts to conserve biodiversity. One popular shortcut is to focus conservation planning efforts on a relatively small number of focal or surrogate species (3–5) and assume that if we protect the surrogates we will also do an adequate job of protecting much of the regional biota. Three classes of surrogate species schemes are prevalent: (*i*) flagships (i.e., charismatic species that attract public support); (*ii*) umbrellas (i.e., species requiring such large areas of habitat that their protection might automatically protect other species); and (*iii*) biodiversity indicators (i.e., sets of species or taxa whose presence may indicate areas of high species richness) (5,6).

Although surrogate schemes are often used to set conservation priorities (7, 8), the choice of particular surrogates has largely been *ad hoc* (9), and assumptions underlying those choices usually are implicit, not explicit. Of previous analyses of species richness and co-occurrence patterns (10–16), umbrella taxa (17), and complementarity among taxa (18) at a variety of geographic scales, few (4) have systematically evaluated the effectiveness of typical schemes for identifying surrogate species from a practical standpoint. In this paper, we attempt to clarify the utility and limitations of commonly used flagship, umbrella, and indicator schemes by evaluating patterns of spatial co-occurrence between surrogate species and regional biota in three conservation databases representing different spatial scales and regions of concern.

Background and Methods

Structure of the Conservation Databases. We analyzed three conservation databases containing incidence records of endangered, threatened, rare, and/or "of-concern" species (hereafter simply termed species) for (*i*) the southern California coastal sage scrub community type (Natural Diversity Database, California Department of Fish and Wildlife, Sacramento), an area with many imperiled species, including the California gnatcatcher *Polioptila californica*; (*ii*) the Columbia Plateau (The Nature Conservancy and Natural Heritage network, Arlington, VA), a five-state region in the northwestern United States that was the focus of a recent $50 million federal ecosystem assessment (www.icbemp.gov); and (*iii*) the U.S. Environmental Protection Agency endangered species by county database (19). These databases do not include information on other, more common species residing in the regions. Each database represents a different spatial scale and resolution, and each uses a slightly different operational definition of a "site" or conservation-planning unit. Together, however, these three databases seem representative of the range of data sets with which managers and researchers must contend when attempting to understand species spatial distributions and to make land conservation decisions. For these species and databases, incidence records reflect simply the known presence of species at sites, where "known" is determined through a combination of museum records and field surveys. Table 1 provides summary statistics for each database.

Conceptual Basis for Surrogate Species Schemes. For each database, we evaluated the performance of up to 14 alternative schemes for selecting surrogate species. Most of these surrogate schemes have been used or proposed as shortcuts for conserving biodiversity. The remaining schemes seem at least plausible based on general ecological principles. We classified each scheme as flagship (F), umbrella (U), biodiversity indicator (B), or some combination. Only species represented by at least 0.25% of the occurrence records in a database were considered common enough for use as potential surrogates for regional biodiversity. For each database, we used standard reference works on threatened species (e.g., U.S. Fish and Wildlife Service on-line references and The Nature Conservancy vertebrate characterization abstracts), supplemented as needed by personal contacts and knowledge, to determine whether individual species satisfied the criteria for each surrogate scheme. For each database, we then combined all species satisfying the criteria for a scheme into a set of surrogates. As we detail in the next section, membership in these surrogate sets (which ranged in size from 1 to 35 species) depends on ecological traits or anthropogenically assigned features. Consequently, the sets often cross taxonomic boundaries, and thus they provide a different perspective than do analyses that examine distributional overlaps among taxa (12, 14, 18). In

Abbreviations: F, flagship; U, umbrella; B, biodiversity indicator.

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Table 1. Scope, resolution, and size of conservation databases

Database	Spatial extent	Resolution	Sites	Species	Species records	Potential surrogate species
Coastal sage scrub	Part of southern California	25 km^2 grid squares	785	277	3,197	62
Columbia Plateau	Portions of five states	U.S. Geological Society sixth Hydrologic Unit Classification	1,241	211	4,527	83
Environmental Protection Agency by county	U.S. except Hawaii	Counties	2,856	749	10,822	56

Resolution column indicates how ''sites'' in each database were defined. Species definitions are as per the databases; they include species, subspecies, and variants. A species record indicates the known presence of a population of a species at a site. Subwatersheds are defined based on physiography and hydrology, and are used by federal agencies as land management units.

addition, the categories of surrogate species we use are not mutually exclusive. For any database, some species appear in several surrogate schemes. Indeed, we make use of such multiply occurring species to build another set of surrogate species (see *Multicategory tally*). Lists of species identified as potential surrogates for each database and the specific schemes for which each species qualified are provided in the supplementary materials published on the PNAS web site at www.pnas.org.

Surrogate Schemes and Their Rationale. *Big carnivore (U, F).* This set includes large-bodied carnivores requiring large habitat areas (e.g., bears, felids, and raptors). Several large carnivores previously have been proposed as surrogates or flagship species [e.g., *Felis concolor* (7, 8, 20)], and the notion of big carnivores as surrogates motivates several large-scale land conservation projects, including the Wildlands Project (21) and the Yellowstone to Yukon (Y2Y) Project.

Charismatic (F). This set includes species with significant public constituencies (5).

Habitat generalists (B). Included in this set are species with strong dispersal abilities that use a wide range of habitat types, including individual species that use different habitat types during different times of year (8, 22).

Habitat specialists (U). This set encompasses a complementary set of species, each with narrowly defined habitat needs (e.g., sand dunes, caves, or bogs), but as a group encompassing most of the major habitat types in a given planning area (23, 24) and, perhaps, together constituting an effective surrogate scheme (25).

High age at first reproduction (U). This set is made up of species with delayed maturation that may be at additional risk of extinction because of the time lags involved in population recovery after declines in abundance (26), whose protection might provide an umbrella for other species (11). An average age at first reproduction of 4 years was our threshold.

Keystones (U). This set includes species whose impacts on other community members far exceed that expected by consideration of their own biomass or abundance (5, 27, 28). We included only those species suggested as keystones in the peer-reviewed literature, but did not assess the accuracy of such claims.

Long-lived (U). Included in this set are species with the greatest longevity (10 years or more for animals and 5 years or more for plants), whose abundance, at least in some cases, may be indicative of cumulative habitat degradation or destruction (29).

Most data available (U, B). We included in this set well-studied species, or those for which the most natural history and ecological information is known. Such a scheme formed the basis for a statewide conservation planning exercise in Florida (8).

Most expensive to maintain (U). Species whose current protection and future recovery *in situ* would be likely to have significant impacts on regional or national commerce [e.g., fish species that depend on predam flood regimes (30)] and whose protection might benefit other species by requiring radical transformations of the landscape toward ''natural'' conditions are included in this set.

Most threatened (B). In this set are species with unusually small population sizes, even in comparison with other rare species, or those for which formal viability analyses indicate a high likelihood of extinction in the near future. Because such species often receive the majority of conservation attention, it is useful to know the extent to which such attention might also benefit other species.

Most valuable real estate (B). This set is made up of species known to inhabit the most valuable parcels of land within the region encompassed by a given database (e.g., shoreline habitats). It recently was suggested (19) that a large proportion of the endangered species in the U.S. could be protected within a small proportion of the nation's land area. However, the areas identified also represented some of the most expensive real estate in the country.

Most widespread (U). Included in this set are species with extensive spatial distributions; in our case, those species occurring in at least 5% of the sites in a given database.

Riparian (B). This set encompasses species requiring riparian, aquatic, or wetland habitats for a major portion of their life cycles or during a set period of the year. Riparian habitats are known to have high species richness; therefore, species that depend on riparian habitats might make efficient surrogates.

Multicategory tally (F, U, B). Those species that met the criteria for several surrogate schemes within a database are included in this set. Because an effective surrogate set might comprise species with combinations of traits not reflected in the individual schemes, we included those species that met the criteria for three or more schemes for the coastal sage scrub and Columbia Plateau databases and five or more schemes for the U.S. Environmental Protection Agency database.

Approach and Methodology for Evaluating Effectiveness of Surrogate Schemes. In most large-scale applications of umbrella, flagship, or indicator schemes, one would likely have little information on the spatial distribution of other species. Lacking such detailed data, one would not necessarily be able to optimize the selection of sites so as to protect the same number of species in the fewest number of sites (1, 31). The databases we used contain incidence data only, and lack information on the boundaries or sizes of local populations. Such data, in general, are critical to current techniques for evaluating the extinction likelihood of populations (32–34). As such, our analysis can evaluate the potential effectiveness of surrogate schemes at the level of species coverage only. With these data, we can compare the distributions of surrogate species among sites with the distributions of other threatened species (which we call ''background'' species) to identify what species might be ''protected'' if we conserved the surrogates. However, we cannot discriminate among large, small, viable, or extinction-prone populations. Thus, our comparisons among schemes involve currencies of the number of species protected, the number of representations (i.e., populations) of a species protected, and the number of sites required to achieve that protection.

We first tallied the number of species represented within a hypothetical network of reserves if we could protect all sites in which at least one member of a surrogate set was found. Thus, this analysis assesses the maximal coverage that each surrogate scheme could provide. Next, to evaluate the utility of different surrogate schemes, we compared their performance to that of sets of randomly selected species. Because the number of species in the different surrogate schemes varied widely (Fig. 1), we constructed, for each database, 15 random sets of species, 5 sets each consisting of 5, 10, or 20 species. Only those species that met our initial 0.25% occurrence criterion in each database were included in random species sets. We then calculated mean and standard error in performance for these random sets, against which we evaluated the performance of potential surrogate schemes.

For the best performing schemes in each database, we asked a more refined series of questions. Namely, how many species would be protected and how many sites would be required if, rather than protecting all sites where at least one surrogate occurred, we instead aimed to conserve only a subset of the sites containing surrogate species? That is, because it is unrealistic to assume that all sites containing any surrogate species, no matter how charismatic, would ever be protected, we asked how well would we do if we only protected each surrogate species at 1, 3, 5, or 10 sites? Here we used an iterative heuristic algorithm (PA2) (35) to select a complementary set of sites including the specified number of representations of each surrogate species. The algorithm first selects the site with the highest richness of surrogate species, then sequentially adds complementary (i.e., nonduplicative) sites, according to their richness of surrogates, until the target number of sites for each surrogate has been reached. The distribution of background species does not affect this algorithmic site selection process. Instead, after the algorithm has found the minimal set of sites that provides the specified number of occurrences of each surrogate species, we reexamined the database to determine the number of background species that happened to co-occur with surrogate species on the selected sites. Background species that occurred on at least one selected site were considered minimally protected. Our overall site selection approach thus mimicked real-world situations in which a conservation planner might know the distribution of surrogate species, but would likely lack detailed knowledge of the incidence patterns of other species in the region.

Results

Conserving All Occurrences of Surrogate Species. Conserving all occurrences of each member of a surrogate species set protected between 9.5% and 98.5% of all species, depending on the particular scheme and database (Fig. 1). The habitat costs (i.e., the number of sites) required for these levels of protection varied between 4.8% and 91.5% of sites, again depending on the particular scheme and database.

For the coastal sage scrub database, 7 of the 11 different surrogate schemes evaluated would have protected more than 50% of the species in the database if one conserved all sites where surrogate species were found (Fig. 1*A*). Surrogate schemes consisting of 9 widespread species and 19 riparian species afforded protection to over 90% of the species in the database at a "cost" of roughly 50% of the sites. However, surrogate schemes developed from sets of 10 or 20 randomly selected species performed as well or better (as measured by the ratio of percentage of species protected to percentage of sites required), encompassing on average 75–80% of the species in the database at a cost of <30% of the sites. Surrogate schemes oriented around the 1 or 2 species for which the most data were

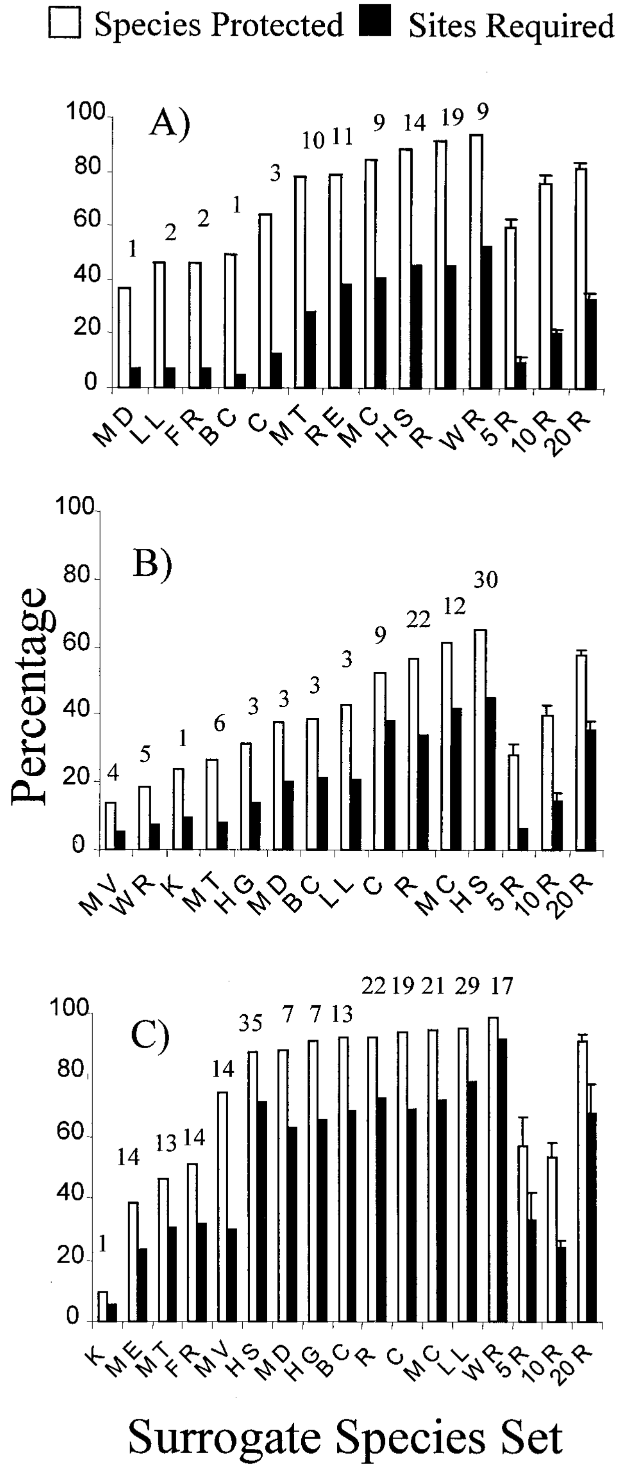

Fig. 1. Percentage of all species of concern protected and percentage of sites required by different surrogate schemes for each of three biodiversity databases when all occurrences of each surrogate species are protected. (*A*) California coastal sage scrub database; (*B*) Columbia Plateau ecoregion; and (*C*) Environmental Protection Agency U.S. by county database. Background species are protected if at least one occurrence is included in the selected suite of sites. Surrogate set abbreviations: BC, big carnivore; C, charismatic; FR, high age at first reproduction; HG, habitat generalists; HS, habitat specialists; K, keystones; LL, long-lived; MC, multicategory tally; MD, most data available; ME, most expensive to maintain; MT, most threatened; R, riparian; RE, most valuable real estate; WR, most widespread; 5R, 5 random species; 10R, 10 random species; and 20R, 20 random species. For sets 5R, 10R, and 20R, we present means (±SE) of five sets. Numbers of surrogate species in each set are listed above each column.

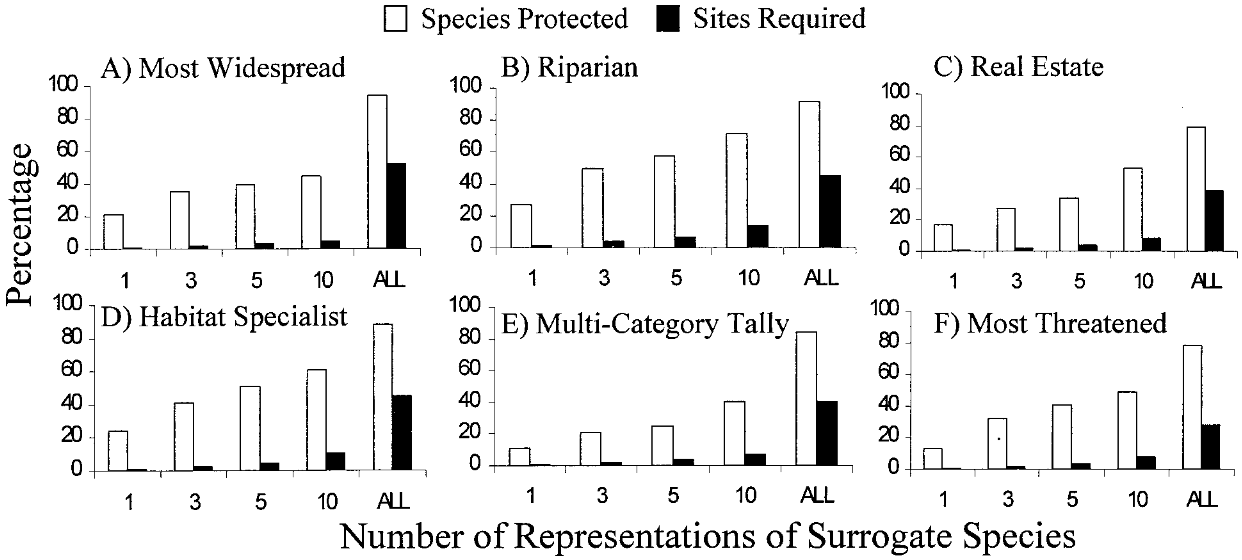

Fig. 2. Percentage of species protected and percentage of sites required if 1, 3, 5, 10, or all populations of surrogate species are protected for top-performing surrogate sets using the California coastal sage scrub database. ''ALL'' results are from Fig. 1. Sites were chosen by using the PA2 algorithm (35), which minimizes the cost in sites while still satisfying the representation criteria (1, 3, 5, or 10 occurrences) for surrogate species.

available, that had a high age at first reproduction, were long-lived, or were large carnivores, protected fewer than 50% of the species in the database, but were relatively inexpensive in terms of the number of sites required (Fig. 1*A*).

For the Columbia Plateau database, the habitat specialist scheme (30 species) and the multicategory tally scheme (12 species) protected the most species (both >60%) when all occurrences of each surrogate species were protected (Fig. 1*B*). In contrast, surrogate schemes based on the most valuable land parcels (four species) and the five most widespread species protected the fewest total species (both <20%). However, as was true for the coastal sage scrub, none of the 12 surrogate schemes evaluated for the Columbia Plateau performed substantially better (in terms of either coverage or efficiency) than did schemes consisting of a comparable number of randomly selected species (Fig. 1*B*).

For the national endangered species by county database, 9 of the 14 surrogate schemes examined would have covered at least 87% of the species in the database, and 4 schemes (charismatic, multicategory tally, long-lived, and most widespread) covered at least 94% of the species (Fig. 1*C*). However, the high levels of species coverage attained by the top nine schemes were expensive, in all cases requiring at least 70% of the sites in the database to protect those species. Surrogate schemes focused on keystone species, species requiring the most expensive maintenance, and species most threatened with extinction performed worst on this database, protecting <50% of the background species. Randomly selected sets of 20 species again performed similarly to individually defined surrogate schemes involving comparable numbers of species. However, random surrogate schemes based on 5 or 10 species sets fared worse than did roughly comparable 7-species surrogate schemes structured around habitat generalists or species for which the most data were available (Fig. 1*C*).

Conserving Only a Specified Number of Occurrences of Surrogate Species. Somewhat different patterns emerged when only a few, rather than all, occurrences of each surrogate species were protected. Of otherwise well performing schemes, only a few would conserve sizable fractions of the biota in the database when our goal was to protect only a handful of occurrences for each surrogate species (Fig. 2). For example, for three schemes (habitat specialist, most widespread, and riparian), protecting a single occurrence of each surrogate species in the scheme protected >20% of the species in the database at a cost of <2% of the sites (Fig. 2 *A*, *B*, and *D*). When targeting 10 occurrences of each surrogate species, three schemes (habitat specialist, riparian, and most expensive real estate) provided minimal protection to at least 50% of the species in roughly 10% of the sites. However, when enforcing more stringent requirements for protection of background species (≥3 occurrences), none of these schemes protected >26% of the background species.

For the Columbia Plateau database, the riparian and habitat specialist schemes protected more species for a given number of surrogate representations than did the charismatic and multicategory tally schemes, even though all four schemes fared comparably well when we protected all occurrences of each surrogate species (Fig. 3). When conserving 10 sites for each surrogate, the riparian and multicategory schemes provided minimal protection to roughly 50% of species at a cost of about 10% of the sites (Fig. 3 *B* and *C*). Again, however, even these otherwise successful schemes failed to protect multiple representations of the background species, protecting ≥3 occurrences for only 22% of the background species.

For the national database, protecting only a few sites for each member of a surrogate scheme protected far fewer species than did protecting all occurrences (Fig. 4). For example, protecting 10 sites for each member of the big carnivore scheme protected only 10% of the species in the database (Fig. 4*D*). For only one scheme (long-lived species), did protecting 10 sites for each surrogate species protect >25% of the species in the database (Fig. 4*F*). None of these schemes protected ≥3 occurrences for >5% of background species.

Discussion

Despite the popularity of surrogate species, based on the databases we examined, we find little evidence to support the claim that umbrella, flagship, or biodiversity indicator schemes have special biological utility as conservation surrogates for protecting regional biota. Specifically, for the California coastal sage scrub, the Columbia Plateau, and the U.S. endangered species by county databases, surrogate species schemes did not perform substantially better than did randomly selected sets of a com-

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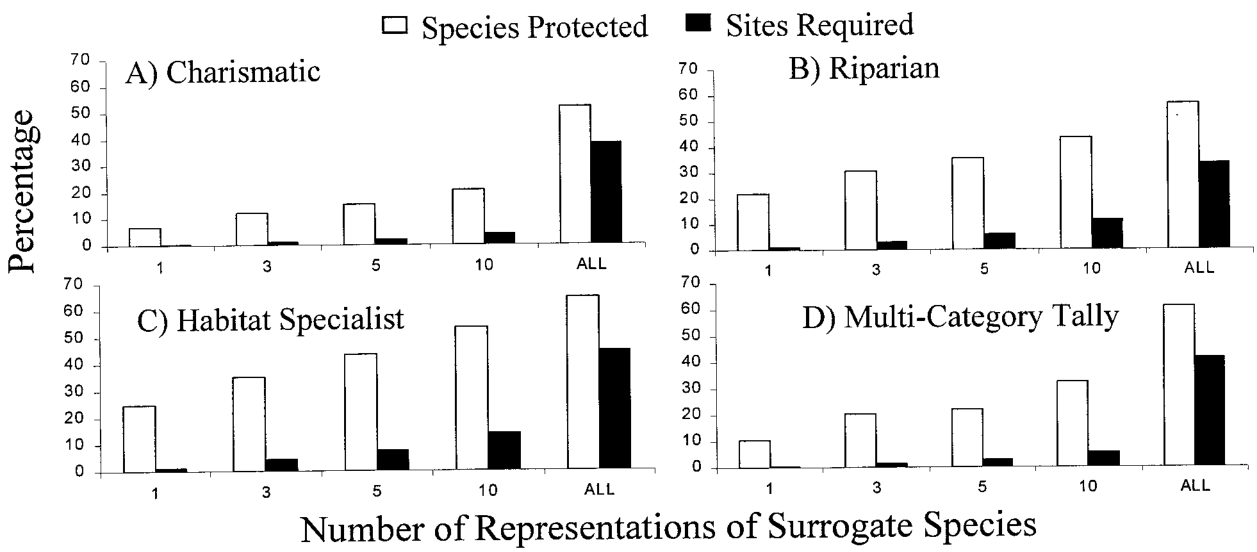

Fig. 3. Percentage of species protected and percentage of sites required if 1, 3, 5, 10, or all populations of surrogate species are protected for top-performing surrogate sets using the Columbia Plateau database. "ALL" results are from Fig. 1; sites were chosen as in Fig. 2.

parable number of species. As others have suggested (4, 5), regardless of their publicity value or other appeal, for surrogate species concepts to be useful biologically, several assumptions must be met. At a minimum, surrogate species must spatially co-occur with a large proportion of other species in the area of interest, and, ideally, surrogates also should have a high probability of persistence. Overall, our analysis suggests that the surrogate species schemes frequently advocated as a means to protect regional biota fail to meet the requirements of the first assumption. For large-scale, regional conservation planning efforts, data to evaluate the second assumption are seldom available.

In a few cases, we found surrogate schemes that provided better conservation coverage than did random sets of threatened species. For example, protecting 10 occurrences of each member of a set of 19 riparian surrogate species in the Coastal sage scrub system would provide minimal protection to 71% of the background species in just 14% of the sites (Fig. 2*B*). Yet, in many such instances, the most effective surrogate schemes do not necessarily involve the species sets most frequently proposed in practice. For example, in the Columbia Plateau region, conserving 3 occurrences of each member of the habitat specialist scheme would protect almost twice as many background species as would protecting 10 occurrences of each member of the charismatic scheme for essentially the same cost in sites (Fig. 3 *A* and *C*). In the few cases where surrogate schemes provided truly effective coverage for background species, complementarity in surrogate species distributions among sites seems to be a key component underlying their effectiveness. However, complementarity approaches failed to provide added coverage in a recent analysis of South African biodiversity patterns (18).

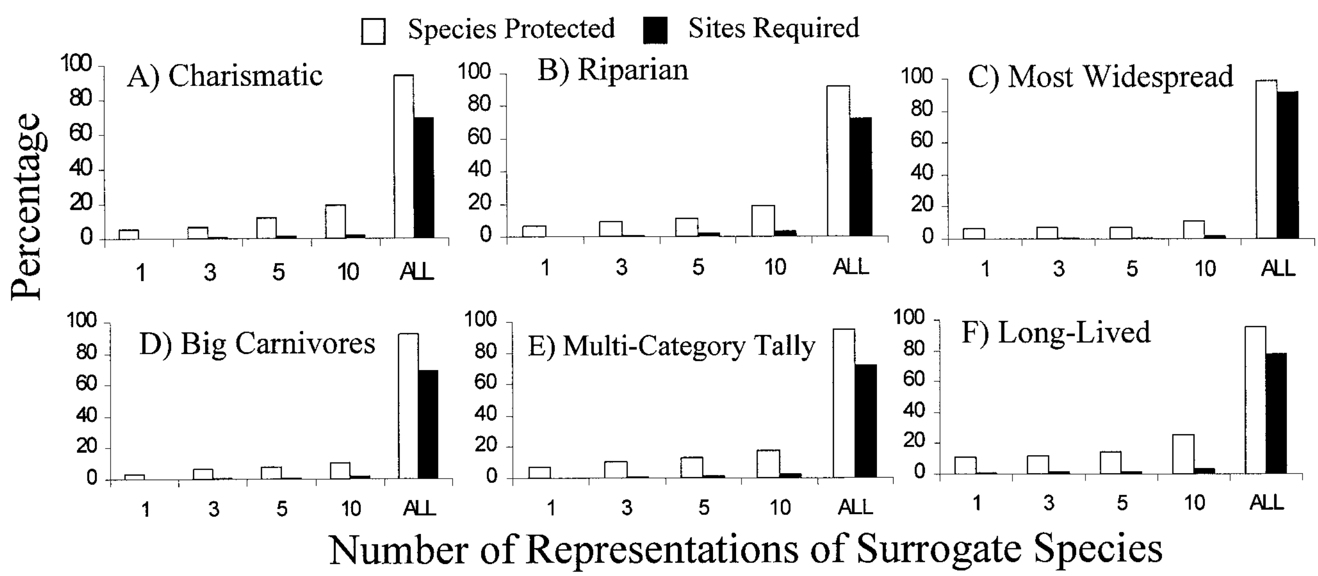

Fig. 4. Percentage of species protected and percentage of sites required if 1, 3, 5, 10, or all populations of surrogate species are protected for top-performing surrogate sets using the national Environmental Protection Agency endangered species by county database. "ALL" results are from Fig. 1; sites were chosen as in Fig. 2.

Although protecting all occurrences of each member of a set of surrogate species often can shelter high percentages of a region's threatened biota, such protection typically comes with unrealistically high costs in sites (Fig. 1). When we instead focused on more achievable goals of protecting one or several occurrences of each surrogate species, the fraction of background species protected declined sharply (Figs. 2–4). This finding suggests that extensive reliance on surrogate species may be a poor allocation of scarce conservation resources.

However, it is important to recognize limitations of our analyses. For example, surrogate species had to be drawn from databases of candidates that included only species of concern. Although such species are in fact often suggested as potential surrogates (4), the current databases preclude investigations of whether inclusion of more common species meeting the same biological criteria into surrogate schemes would yield different results. In addition, and as mentioned before, our approach tallies species occurrences without distinguishing among large, small, viable, or extinction-prone populations. Although not considered here (and difficult to obtain), biodiversity databases outlining patterns of concordance between occupancy and abundance would help overcome some of the limitations of our approach.

Recent investigations of Ugandan biodiversity (36) evaluated how well sets of sites chosen by using distributional information for particular taxa (e.g., woody plants, large moths, butterflies, birds, or small mammals) represented diversity in other taxa. With a threshold allocation of 20% of the existing forest estate to potential reserves, selecting sites based on butterflies or birds was found to be just as effective at representing all groups as was selecting sites by using data on all taxa. However, these analyses also indicated that a random selection of sites performed nearly as well as sets of sites identified by using focal taxa (36).

The relative effectiveness of random suites of surrogate species in these databases has an important implication for conservation efforts. It suggests that using distributional data for a random assortment of species to plan reserve systems may be as effective or more effective at conserving a region's biota than by using data on more conventional flagship, umbrella, or indicator species. Intuitively, this makes sense based on basic sampling theory. In contrast, the relatively poor performance of some carefully chosen surrogate schemes is more disconcerting. It suggests that, in many cases, our understanding of the patterns of overlap and lack of overlap in species distributions is inadequate to identify effective surrogate schemes.

In practice, comprehensive databases, such as the one for Ugandan forests (based on nearly 100 person-years of systematic survey effort costing >$1 million) will rarely be available to conservation planning efforts. Without further systematic evaluations of similarly comprehensive biodiversity data sets in both temperate and tropical regions, we suspect that the efficacy of even the most carefully selected surrogate schemes might prove inadequate and inefficient. Moreover, we emphasize that scientists and resource managers appear most interested in using conservation surrogates precisely because the systems they are trying to manage and protect are insufficiently known. Hence, the fact that one might be able to develop a cost-efficient surrogate scheme that provided broad coverage of background species in a system that one knew extremely well is not in itself a particularly useful result. Instead, the key question is, "How well do plausible surrogate schemes work in situations where the background biota are poorly known?" This issue is what we have evaluated here by examining the success of surrogate schemes only after the fact. We urge caution in adopting umbrellas or flagships as conservation surrogates until their usefulness as predictors of biological diversity and its persistence has been more fully investigated. We believe the answers will rarely be obvious or consistent among systems.

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