
On the Use of Surrogate Species in Conservation Biology

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Abstract: *Conservation biologists have used surrogate species as a shortcut to monitor or solve conservation problems. Indicator species have been used to assess the magnitude of anthropogenic disturbance, to monitor population trends in other species, and to locate areas of high regional biodiversity. Umbrella species have been used to delineate the type of habitat or size of area for protection, and flagship species have been employed to attract public attention. Unfortunately, there has been considerable confusion over these terms, and several have been applied loosely and interchangeably. We attempt to provide some clarification and guidelines for the application of these different terms. For each type of surrogate, we briefly describe the way it has been used in conservation biology and then examine the criteria that managers and researchers use in selecting appropriate surrogate species. By juxtaposing these concepts, it becomes clear that both the goals and selection criteria of different surrogate classes differ substantially, indicating that they should not be conflated. This can be facilitated by first outlining the goals of a conservation study, explicitly stating the criteria involved in selecting a surrogate species, identifying a species according to these criteria, and then performing a pilot study to check whether the choice of species was appropriate before addressing the conservation problem itself. Surrogate species need to be used with greater care if they are to remain useful in conservation biology.*

Uso de Especies Sustituatas en la Conservación Biológica

Resumen: *Biólogos de la conservación han utilizado especies sucedáneas como atajos para monitorear o resolver problemas de conservación. Las especies indicadoras han sido utilizadas para evaluar la magnitud de la perturbación antropogénica, para monitorear tendencias poblacionales en otras especies y para localizar áreas de alta biodiversidad regional. Las especies sombrilla han sido utilizadas para delinear el tipo de hábitat o tamaño de área para protección y las especies bandera han sido empleadas para atraer la atención del público. Desafortunadamente, ha habido una considerable confusión sobre estos términos y muchos han sido aplicados de un amañera vaga e intercambiable. Intentamos proveer algunas aclaraciones y lineamientos para la aplicación de estos diferentes términos. Para cada tipo de sustituto describimos brevemente la forma en que ha sido usado en la conservación biológica y posteriormente examinamos los criterios que los manejadores e investigadores usan en la selección de las especies sustitutas apropiadas. Al yuxtaponer estos conceptos, se hace claro que tanto las metas como los criterios de selección de diferentes clases de sustitutos difieren substancialmente indicando que estos no deberán ser confundidos. Esto puede ser facilitado primero al subrayar las metas de un estudio de conservación, estableciendo explícitamente los criterios involucrados en la selección de la especie sustituta, identificando a las especies utilizando este criterio y posteriormente llevando a cabo un estudio piloto para checar si la especie seleccionada es la apropiada antes de proceder a abordar el problema de conservación en sí. Las especies sucedáneas necesitan ser utilizadas con mayor cuidado si queremos que sigan siendo útiles para la biología de conservación.*

Introduction

Conservation biologists often use one or a small number of species as surrogates to help them tackle conservation problems (Thomas 1972; Cairns et al. 1979; Panwar 1984; Wilcox 1984; Jarvinen 1985; Bibby et al. 1992). Surrogate species are employed to indicate the extent of various types of anthropogenic influence (e.g., Burdick et al. 1989; Stolte & Mangis 1992) or to track population changes of other species; these types of surrogate are by far the best worked examples (D. H. McKenzie et al. 1992). Surrogate species are also used proactively to locate areas of high biodiversity (Ricketts et al. 1999) or to act as “umbrellas” for the requirements of sympatric species (Berger 1997); they thus can help in locating and designing reserves. Finally, surrogate species may be used as flagships in a sociopolitical context for attracting public attention and funding for a larger environmental issue (Dietz et al. 1994). In contrast, a keystone species is an ecological concept that is used to describe a species whose impact on the community or ecosystem is disproportionately large relative to its abundance (Mills et al. 1993; Power et al. 1996). Keystone species are not used as a shortcut to describe patterns and processes in conservation biology and have never been successfully used as surrogate species, although they may be relevant in choosing them (Simberloff 1998).

Conservation biologists employ surrogate species in three main ways. (1) Managers may use a species as a surrogate knowing in advance that it is a sensitive indicator of a particular conservation problem. (2) Managers may use or advocate the use of a species without having determined whether it does act as a proper surrogate for the task at hand. Consequently, the attributes of the species do not always serve the research or conservation goal very well. (3) In more-academic exercises, conservation biologists investigate the ability of a surrogate species to fit a particular research goal. This approach explores the surrogate's suitability rather than examines a particular conservation problem. Unfortunately, in each approach, it is easy to find examples where conservation goals have been poorly defined, where the terms *indicator species*, *umbrella species*, and *flagship species* were applied loosely, and where authors have even substituted different surrogate terms for one another (e.g., U.S. Department of the Interior 1980). For instance, indicators of environmental quality and indicators of population changes in other species have often been conflated, and the terms umbrella species and flagship species have been used interchangeably in promoting the role of a single species in protecting a community. Despite these acknowledged problems with study design and terminology, the use of surrogate species continues to increase in conservation biology.

We attempt to provide guidelines for future workers by drawing attention to different uses of surrogate spe-

cies and systematically examining the criteria that researchers and managers have used in choosing surrogate species successfully. We have drawn on strong studies with clear goals, in which selections of surrogate species have been made with care. For convenience, we have divided criteria used to select surrogates into attributes of measurement, life-history traits, ecological characteristics, attributes of rarity, and sensitivity to environmental change. We conclude by making recommendations for using surrogate terms more appropriately. We do not try to provide a definitive guide to surrogate species or to assess their efficacy from a practical standpoint; instead we attempt to show how they can be used successfully.

Indicator Species

Landres et al. (1988) defined “an indicator species [as] an organism whose characteristics (e.g., presence or absence, population density, dispersion, reproductive success) are used as an index of attributes too difficult, inconvenient, or expensive to measure for other species or environmental conditions of interest.” There is a historical dichotomy between indicator species that pinpoint areas of high biodiversity—here termed biodiversity indicators—and those that measure environmental changes (Pearson 1995). Following Landres (Landres et al. 1988; Landres 1992), one can further divide the latter into those that assess changes in habitat (health indicators) and those that serve as a yardstick for changes in populations of other species (population indicators), although in practice these may sometimes be difficult to separate. Indicator species are also used to assess the effects of agricultural practices on habitats. For example, oribatid mite populations have been used to examine the effects of soil disturbance (Franchini & Rockett 1996), and attempts have been made to use populations of some bird species to measure the effects of cattle grazing (Bock & Webb 1984). We do not discuss these types of indicators further, nor have we included environmental variables that might be indices of species richness.

Health Indicator Species

In theory, environmental monitoring might best be achieved by sampling air, water, or soil directly, but, in practice, detection of intermittent pollution sources depends on the time and place of sampling and can be logistically problematic in remote areas. Instead, sublethal hazardous chemicals accumulated within selected tissues of certain species can provide a measure of pollution at a given site over a known time period (e.g., Karlsson et al. 1994). Furthermore, the diversity or abundance of species—often invertebrates—can be used to measure the accumulated concentration of certain pollutants at a

location (e.g., Sarkka 1996). For years, indicator species of this type have been used by environmental toxicologists to assess the effects of pollutants on organisms or on ecosystem processes (e.g., Ott 1978; Cairns et al. 1979; Levin et al. 1989) and to assess environmental conditions such as temperature and pH (Zonnevald 1988). Patton (1987) provides a good definition of a health indicator species: "In biology an indicator is an organism so ultimately associated with particular environmental conditions that its presence indicates the existence of those conditions."

Indicators of environmental health are also used to assess the effects of chemicals on a subsample of organisms in the environment (Karr 1991; Kremen 1992). For example, in describing the "most sensitive species" concept, Cairns (1986) suggested that if standards were set "for toxic materials and other stressors in natural systems, presumably all other species and all other activities at higher levels of biological organization could be protected." Used in this way, health indicators have some of the hallmarks of umbrella species.

More recently, attention has turned to forms of anthropogenic disturbance other than pollution, particularly direct exploitation and extractive use, such as deforestation, fishing (McClenahan et al. 1996), and hunting (Bodmer et al. 1997). For instance, the Spotted Owl (*Strix occidentalis*), specifically its population size and reproductive rate, has been used as a management indicator species (MIS) of the effect of old-growth logging on small mammals and on lower trophic levels in the Pacific Northwest (Dawson et al. 1986). A MIS is defined by the U.S. Forest Service (1984) as any species, groups of species, or species habitat elements selected to focus management attention for the purpose of resource production, population recovery, or maintenance of population viability or ecosystem diversity.

Indicators of environmental health may be successful as a single species or a guild of species (Cook 1976; but see Cairns 1983). In either case, it is important that biologists know a substantial amount about their natural history, particularly the ecological factors affecting their population growth rates, because changes in their population need to be related to specific environmental factors (Pearson & Cassola 1992; but see Kremen 1992). Be-

cause indicators of environmental health are often chosen to reduce the costs of monitoring, they need to be observed, counted, or collected relatively easily (Temple & Wiens 1989; Noss 1990; Pearson & Cassola 1992). For example, it may be helpful if they have accessible breeding sites where they can be monitored (Miller & Davis 1993; Table 1).

Small species are most successful as indicators of environmental health because they are more sensitive to environmental disturbance than are larger species (Siemann et al. 1996). Moreover, small species often have relatively short generation times, an attribute that makes them more sensitive to the effects of pollution or habitat disturbance because juvenile life stages will more often be subjected to environmental insult (Blus et al. 1974). Also, species with high rates of reproduction and the potential for rapid population growth rates may show a quicker response to environmental stresses than slow reproducers, and these are often small species. Species with high metabolic rates—again smaller species—are likely to incorporate environmental pollutants more rapidly than those with low metabolic rates (Walker 1983; Table 2).

If a species is mobile, it will be subjected to different parts or aspects of a polluted environment and will thus provide information on a wider area than if it were restricted to a single site. Amphibians have for this reason been advocated as health indicators (Vitt et al. 1990; Lips 1998). On the other hand, a small home range allows researchers to pinpoint the location of pollution or disturbance with greater accuracy. Whereas indicators of environmental quality might usually be resident species because they are subject to sustained environmental stress, migratory species also can be effective, as in the case of Brown Pelicans (*Pelecanus occidentalis*), which indicated levels of DDT (Anderson et al. 1975). Because species at the end of the food chain accumulate toxic materials rapidly, health indicators may come from particular trophic levels, such as bottom feeders or predators (e.g., Gilman et al. 1979; Mix et al. 1979; Table 3).

Indicators of environmental health are easier to monitor if they have large populations. If they have a wide geographic range, moreover, they can provide an authoritative documentation of habitat disturbance or pop-

Table 1. Measurement attributes of surrogate species.

Type of surrogate	Represents other species	Single or guild of species	Well-known biology	Easily sampled or observed	Accessible breeding site
Health indicator	not necessarily	single or guild	yes	yes	probably
Population indicator	yes	single	yes	yes	possibly
Biodiversity indicator	yes	guild	yes	yes	no
Umbrella species	yes	single*	yes	yes	no
Flagship species	usually	single	not necessarily	no	no

*Usually single.

Table 2. Life-history traits of surrogate species.

<i>Type of surrogate</i>	<i>Body size</i>	<i>Generation time</i>	<i>Metabolic rate</i>
Health indicator	small	short	high
Population indicator	irrelevant	short	irrelevant
Biodiversity indicator	irrelevant	irrelevant	irrelevant
Umbrella species	large	long	irrelevant
Flagship species	large	long	irrelevant

ulation trends because their survival and reproduction in one place may be extrapolated across a large geographic area (Pearson 1995). If health indicators are restricted to certain habitats, they will provide specific information about environmental change in that habitat (Table 4).

In general, effective health indicator species need to be acutely sensitive to human disturbance in order to provide an early warning of anthropogenically induced environmental change (Munn 1988; Cairns 1986; Frost et al. 1992). Raptors, for example, are poor indicators of environmental change in Baja California because they rapidly adapt to human-altered habitats (Rodriguez-Estrella et al. 1998). A low level of individual variability in response to environmental change is also important because a subsample of the population will reflect the overall response of the population with some certainty (Frost et al. 1992; Table 5).

Population Indicator Species

Some species have been used as indicators of population trends in other species, such as prey, that may be subject to human disturbance or environmental variation. For example, juvenile mortality in Cape Gannets (*Morus capensis*) has been used as a measure of temperature-dependent changes in the distribution of oceanic fish because young gannets cannot dive deeply enough to find fish in cool waters (Oatley et al. 1992). Surrogates are also used as indicators of the suitability of the habitat for other members of their guild (Verner 1984; Block et al. 1986). Nevertheless, there are considerable difficulties in extrapolating between guild members because the factors that influence their respective populations may differ and are often unknown, because they may show only partial overlap in niche or habitat, and because

there are practical difficulties in identifying the time course over which changes in the population size of one species reflect those in another (Landres 1983; Verner 1984; Szaro 1986; Temple & Wiens 1989; Swanson 1998).

Indicators of population trends in other organisms are usually a single species and may be most successful if the principal factors affecting their population size are well understood (Landres 1983). They need to be monitored relatively easily at least during one stage of their life cycle (Temple & Wiens 1989; Noss 1990; Pearson & Cassola 1992; Table 1).

For a species to be a sensitive indicator of population trends in other species, it should have a rapid rate of reproduction, because changes in population size are difficult to discern in species with long generation times (Table 2).

Population indicators will be most effective if they are resident species and if they occupy particular feeding niches. For example, the best indicator of a prey population may be its specific predator (Elton & Nicholson 1942). Keystone species might be particularly effective in discerning population changes in other species. For example, because the flying fox (*Pteropus samoensis*) pollinates many plants on islands in the South Pacific (Cox et al. 1991), its numbers might indicate plant population viability. On the other hand, the abundance of a keystone species does not necessarily reflect population trends in members of the same guild (Table 3).

Population indicators are easier to monitor if they have large populations themselves. If they have a wide geographic range, their function can be extrapolated across a large geographic area (Pearson 1995). Habitat specificity has relevance for population indicators only if they are being used to monitor population trends in other species based on mutual habitat requirements (Table 4).

A good population indicator must be sensitive to human disturbance in order to provide an early warning of anthropogenically induced environmental change (Cairns 1986; Munn 1988; Frost et al. 1992), and its growth rate should mirror those of other species reacting to anthropogenic disturbance (but see Landres et al. 1988). A low level of individual variability in response to environmental change will reflect the population's overall response (Table 5).

Table 3. Ecological characteristics of surrogate species.

<i>Type of surrogate</i>	<i>Home range size</i>	<i>Resident or migratory</i>	<i>Particular trophic level</i>	<i>Keystone species</i>
Health indicator	medium	resident	yes	not necessarily
Population indicator	irrelevant	resident	possibly	possibly
Biodiversity indicator	irrelevant	either	no	irrelevant
Umbrella species	large	migratory	no	possibly
Flagship species	irrelevant	either	no	not necessarily

Table 4. Attributes of commonness and rarity in surrogate species.

<i>Type of surrogate</i>	<i>Large population size</i>	<i>Wide geographic range</i>	<i>Habitat specialist</i>
Health indicator	probably	yes	probably
Population indicator	probably	yes	not necessarily
Biodiversity indicator	irrelevant	yes	yes
Umbrella species	possibly	probably	yes
Flagship species	no	no and yes	not necessarily

Biodiversity Indicator Species

Areas of high biological diversity are increasingly identified by means of indicator taxa (Humphries et al. 1995; Kerr 1997). Thus, instead of attempting to measure the total number of species or families in an area, conservation biologists use the number of species (or other taxa) in a well-known taxonomic group as a surrogate for the number of species (or other taxa) in sympatric, poorly known taxonomic groups (Beccaloni & Gaston 1994; Dobson et al. 1997). For example, tiger beetle (Coleoptera: Cincindelidae) diversity predicts bird and butterfly diversity at very large scales (Pearson & Cassola 1992; Pearson & Carroll 1998). By this method, large regions of high diversity may be identified and then targeted for protection (N. L. McKenzie et al. 1989; Ryti 1992; Prendergast et al. 1993).

In addition, the number of higher taxonomic groups in a region is used as a surrogate for the number of local species of the same clade, given that a relationship between these different taxonomic levels can be established elsewhere (Gaston 1996). The idea here is that the number of families or genera can be documented more rapidly than the number of species within those families or genera. Positive relationships have been found between higher and lower taxa in many groups (Williams & Gaston 1994; but see Prance 1994).

One or a small number of species may be used to pinpoint the location of biological productivity. For example, Schafer (1989) attempted to compute the future productivity of pine plantations from associations of different types of native vegetation at a site.

Good biodiversity indicators necessarily involve the use of several species to estimate the relative number of species in one area compared to another (Gaston 1996). The group should represent diversity within or across taxonomic boundaries within a region (Pearson & Cas-

sola 1992). The extent to which individuals can be identified to the species, generic, or family level will affect the taxonomic level at which analysis can be carried out (Wilcox 1984; Williams & Gaston 1994). Obviously, biodiversity indicators need to be readily surveyed or censused in the field (Wilcox 1984; Table 1).

Biodiversity indicators will be useful only if they have a reasonably wide geographic range (Wilcox 1984). Within this geographic area, they should have high habitat fidelity because their absence (in the face of habitat disturbance) may be a sensitive indicator of the absence of other species (Panzer et al. 1995; Table 4).

Umbrella Species

Where the conservation goal is to protect a habitat or community of species, an umbrella species may be employed as a surrogate to delineate the size of area or type of habitat over which protection should occur. As Wilcox (1984) wrote, "to provide a 'protective umbrella' select a 'target species' such that its minimum area requirement is at least as comprehensive as the rest of the community." Effective protection of a viable population in this area is assumed to protect populations of other sympatric members of the same guild (Berger 1997), biota at lower trophic levels (Launer & Murphy 1994), or appreciable parts of the ecosystem (Foose 1993). Recently, Lambeck (1997) advocated the use of a suite of "focal species," or several umbrella species, each of which is used to define spatial and compositional attributes that must be present in a landscape. Umbrella species differ from biodiversity indicators in that they are used to specify the size and type of habitat to be protected rather than its location (Berger 1997). The use of umbrella species in conservation biology is less devel-

Table 5. Sensitivity to environmental change in surrogate species.

<i>Type of surrogate</i>	<i>Sensitive to human disturbance</i>	<i>Low variability in response</i>	<i>Long persistence time</i>
Health indicator	yes	yes	irrelevant
Population indicator	yes	yes	irrelevant
Biodiversity indicator	irrelevant	irrelevant	irrelevant
Umbrella species	not necessarily	irrelevant	yes
Flagship species	yes	irrelevant	not necessarily

oped than that of indicator species, and we know of no study in which a strong, empirically based argument can be made to support the efficacy of an umbrella species in protecting other species. Nonetheless, many conservation plans implicitly base their conservation philosophy on this concept.

Umbrella species are usually single species (but see Lambeck 1997). It is necessary to know the area and habitat requirements of a species to determine whether it will be an effective umbrella. For example, Berger (1997) determined that the home ranges of black rhinoceros (*Diceros bicornis*) in the Kaokoveld region of Namibia did not change seasonally as did those of other herbivores, making it a poor candidate as an umbrella species despite its large home range (Table 1).

Good umbrella species are likely to be large (Wilcox 1984) because of the allometric relationship between body size and home range size (Gittleman 1986; Brown 1995). Such large species reproduce slowly, but this is not a criterion of an umbrella species (Table 2).

A principal requirement of an umbrella species is that its range is large compared to sympatric species, so that a viable population can encompass the habitat requirements of other similar species (Berger 1997). Thus, migratory species may be particularly effective. For example, the annual range of migratory wildebeest (*Connochaetes taurinus*) was used to delineate the boundaries of the Serengeti and Ngorongoro protected areas in Tanzania (Grzimek & Grzimek 1959). If an umbrella species is a keystone species, the integrity of its population partially guarantees the integrity of other species (Table 3).

Monitoring an umbrella species will be facilitated if its population size is large. An umbrella species will be more useful if it has a large geographic range because the protection it affords other species in one area may be used for similar purposes elsewhere. An umbrella species with specific habitat requirements may be especially beneficial because, other things being equal, it will need a larger area to encompass sufficient fruiting trees or nest sites and thus will overlap the ranges of more species and more individuals within each species (Table 4).

Umbrella species are employed in designing reserves, sometimes in an area little affected by people, so they do not necessarily have to be sensitive to anthropogenic disturbance. Nonetheless, umbrella species that are sensitive to disturbance will be the best suited for pinpointing suitable habitat for other less sensitive species. Umbrella species are only useful if they do not become locally extinct (Table 5).

Flagship Species

Flagship species are used to attract the attention of the public (Western 1987). For example, as Johnsingh & Joshua (1994) wrote, "by focusing on one [flagship] spe-

cies and its conservation needs, large areas of habitat can be managed not only for the species in question but for other less charismatic taxa." Flagship species can garner sympathy for nature at a global level, as in the case of the giant panda (*Ailuropoda melanoleuca*), the emblem for the World Wide Fund for Nature, or at a national level. Indeed, most countries have a national bird or mammal. Flagship species are also an important public relations tool in setting aside areas for protection (e.g., the Cockscomb Jaguar Reserve in Belize [Rabinowitz 1986]). Some flagships are also umbrella species, although flagships need only be popular, not ecologically significant. An umbrella species lacking charisma need not be a flagship species.

Effective flagship species are often restricted to a particular ecosystem, such as Neotropical rainforest, and often are de facto representatives of species in the same community. But global flagships, such as the Arabian oryx (*Oryx leucoryx*) that are used to represent environmental organizations may become relatively divorced from ecological considerations. Flagships are single species by definition (Table 1).

Flagship species are usually large, for example the tiger (*Panthera tigris*) (Dinerstein et al. 1997), mountain tapir (*Tapirus pinchaque*) (Downer 1996), and elephant (*Elephas maximus*) (Johnsingh & Joshua 1994). Nonetheless, the golden lion tamarin (*Leontopithecus rosalia*), a small (<1 kg) primate, has been used as an education tool to great effect in Brazil (Kleiman et al. 1986; Table 2).

Successful flagship species are sometimes chosen on the basis of their dwindling population size or endangered status (Dietz et al. 1994). Flagship species may be most effective if they are endemic to one country (Kleiman & Mallinson 1998), although conversely they may also be effective if they are known to many people in a range of nations (Table 4).

Flagship species are frequently chosen post hoc, after a species has suffered from exploitation or habitat destruction; consequently, they may be species that are sensitive to disturbance (Table 5). In sum, there are few strict criteria in choosing flagships, which is one of the main points differentiating them from other surrogate classes.

Conclusions

We constructed tables 1-5 to demonstrate how different classes of surrogates fit different profiles within a fixed set of criteria. They show that, (a) researchers and managers use common features in choosing different classes of surrogate, but that (b) each surrogate has a different selection profile.

(a) Surrogate species usually act as representatives of other species in the community (Table 1). They may be

individual species or, less commonly, a collection of species, usually a guild. (The use of a guild is problematic in that only one species need be tolerant of a perturbation and respond positively for guild abundance to be maintained, even though others respond negatively). For most classes of surrogate, it is helpful if species are well known at either an ecological or a taxonomic level (Pearson & Cassola 1992; but see Kremen 1992). The best surrogate species are those that can be easily monitored, as for example if they have accessible breeding sites.

Body size considerations are often relevant in choosing good surrogates (Table 2). On one hand, small size makes an organism more sensitive to environmental disturbance, whereas on the other, large size is associated with large range size or charisma. Small size is correlated with short generation time, which is a helpful characteristic for health indicators and population indicators, and is also correlated with high metabolic rate, an important attribute for indicators of ecosystem health.

A large area requirement is important in choosing some surrogate species because it enables an organism to experience a greater range of environments or to cover a more representative area (Table 3). Some surrogates occupy particular trophic levels. It has been suggested that certain indicator species should be keystone species (Simberloff 1998). Loss of a keystone species or a reduction in its numbers will have ramifications for the abundance and interactions of other organisms (Gilbert 1980; Noss 1990), but there are many examples of effective surrogate species that are not keystone species.

Some types of surrogate are easier to monitor if they have large populations; they may be of greater use if they have a wide geographic range or specific habitat requirements (Table 4). Most surrogate species need to be sensitive to human disturbance (Table 5).

(b) The second point to emerge is that each class of surrogate has a different selection profile. Our review shows that there is not a single criterion among the 18 we examined for which there is complete agreement across the five classes of surrogates (Tables 1–5). This alone indicates that it is foolhardy to use terms interchangeably because underlying assumptions about them differ so much.

In general, species or guilds that are useful as surrogates for one conservation goal will be unsuitable for another. For example, the Common Loon (*Gavia immer*) has been used by managers as both an indicator of habitat quality and of population changes in other species, but it does neither job well (Strong 1990). Its variable responses to environmental factors and its migratory nature make it a weak indicator of habitat quality, and its slow rate of reproduction makes it insensitive to population changes in smaller bird species. Nevertheless, it may be suitable as a flagship for lacustrine habitats (Esbensen 1990).

Occasionally, however, certain species may be useful for more than one task. For example, the Spotted Owl is a good umbrella species for old-growth forest and animals found within that forest (Franklin 1993), it has acted as a flagship for attracting public attention to logging practices in the Pacific Northwest (Chase 1995) and, more equivocally, it may indicate population trends in other species (Murphy & Noon 1992). More often, however, the opposite is the case, with one species filling multiple roles for which it is unsuited and is a poor surrogate.

Recommendations

As conservation biologists continue to use surrogate species in solving conservation problems, they should define their objectives more clearly. First, we advocate the advance formulation of goals and subgoals before a research study or management plan is carried out. If a number of goals are involved, a single surrogate species is unlikely to satisfy them all (Lambeck 1997). Second, we advocate that criteria on which surrogates are being chosen be specified explicitly and that the species selected meet as many of the criteria (in Tables 1–5) as possible, or represent a reasonable compromise between criteria. The literature currently abounds with cases of surrogate species being implicitly chosen on the basis of charisma, historical precedent, or the ease with which they can be managed (Mealy & Horn 1981; Sidle & Suring 1986), rather than according to objective criteria. Third, we recommend preliminary study of the efficacy of proposed surrogates before the main study is initiated. Choosing a flagship species may be an exception to this rule but demands some knowledge of local or national attitudes (Kellert 1986). If a pilot study reveals the usefulness of the surrogate as a tool for monitoring or delineating an area or for raising money, the main conservation project can proceed.

Careful formulation of research goals, use of appropriate criteria, and judicious choice of surrogate species will eventually overcome the legitimate concerns of using indicator, umbrella, and flagship species as shortcuts in effecting management strategies (Landres 1992; Simberloff 1998). This should enable us to choose surrogates with greater clarity and to employ them more usefully in solving urgent conservation problems.

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Literature Cited

- Anderson, D. W., J. R. Jehl, R. W. Risebrough, L. A. Woods Jr., L. R. DeWeese, and W. G. Edgecomb. 1975. Brown Pelicans: improved reproduction off the southern California coast. *Science* **190**:806-808.
- Beccaloni, G. W., and K. J. Gaston. 1994. Predicting the species richness of Neotropical forest butterflies: Ithomiinae (*Lepidoptera: Nymphalidae*) as indicators. *Biological Conservation* **71**:77-85.
- Berger, J. 1997. Population constraints associated with the use of black rhinos as an umbrella species for desert herbivores. *Conservation Biology* **11**:69-78.
- Bibby, C. J., N. J. Collar, M. J. Crosey, M. F. Heath, C. Imboden, T. H. Johnson, A. J. Long, A. J. Stattersfield, and S. J. Thirgood. 1992. Putting biodiversity on the map: priority areas for global conservation. International Council for Bird Preservation, Cambridge, United Kingdom.
- Block, W. M., L. A. Brennan, and R. J. Guterrez. 1986. The use of guilds and guild indicator species for assessing habitat suitability. Pages 109-113 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationship of terrestrial vertebrates*. University of Wisconsin Press, Madison.
- Blus, L. J., B. S. Neely Jr., A. A. Belisle, and R. M. Prouty. 1974. Organochloride residues in Brown Pelican eggs: relation to reproductive success. *Environmental Pollution* **7**:81-91.
- Bock, C. E., and B. Webb. 1984. Birds as grazing indicator species in southeastern Arizona. *Journal of Wildlife Management* **48**:1045-1049.
- Bodmer, R. E., J. E. Eisenberg, and K. H. Redford. 1997. Hunting and the likelihood of extinction of Amazonian mammals. *Conservation Biology* **11**:460-466.
- Brown, J. 1995. *Macroecology*. University of Chicago Press, Chicago.
- Burdick, D. M., D. Cushman, R. Hamilton, and J. G. Gosseink. 1989. Faunal changes and bottomland hardwood forest loss in the Tensas watershed, Louisiana. *Conservation Biology* **3**:282-289.
- Cairns, J. 1983. Are single species toxicity tests alone adequate for estimating environmental hazard? *Hydrobiologia* **100**:47-57.
- Cairns, J., G. P. Patil, and W. E. Waters. 1979. Environmental biomonitoring, assessment, prediction, and management: certain case studies and related quantitative issues. International Cooperative Publishing House, Fairland, Maryland.
- Cairns, J., Jr. 1986. The myth of the most sensitive species. *BioScience* **36**:670-672.
- Chase, A. 1995. In a dark wood: the fight over forests and the rising tyranny of ecology. Houghton Mifflin, New York.
- Cook, S. E. K. 1976. Quest for an index of community structure sensitive to water pollution. *Environmental Pollution* **11**:269-288.
- Cox, P. A., T. Elmquist, E. D. Pierson, and W. E. Rainey. 1991. Flying foxes as strong interactors in the south Pacific island ecosystems: a conservation hypothesis. *Conservation Biology* **5**:448-454.
- Dawson, W. R., J. D. Ligon, J. R. Murphy, J. P. Myers, D. Simberloff, and J. Verner. 1986. Report of the scientific advisory panel on the Spotted Owl. *The Condor* **89**:205-229.
- Dietz, J. M., A. L. Dietz, and E. Y. Nagagata. 1994. The effective use of flagship species for conservation of biodiversity: the example of lion tamarins in Brazil. Pages 32-49 in P. J. S. Olney, G. M. Mace, and A. T. C. Feistner, editors. *Creative conservation: interactive management of wild and captive animals*. Chapman and Hall, London.
- Dinerstein, E., E. Wikramayake, J. Robinson, V. Karanth, A. Rabinowitz, D. Olson, T. Mathew, P. Hedao, M. Connor, G. Hemley, and D. Bolze. 1997. A framework for identifying high priority areas and actions for the conservation of tigers in the wild. *World Wildlife Fund*, Washington, D.C.
- Dobson, A. P., J. P. Rodriguez, W. M. Roberts, and D. S. Wilcove. 1997. Geographic distribution of endangered species in the United States. *Science* **275**:550-553.
- Downer, G. C. 1996. The mountain tapir, endangered "flagship" species of the high Andes. *Oryx* **30**:45-58.
- Elton, C., and M. Nicholson. 1942. The 10 year cycle in numbers of the lynx in Canada. *Journal of American Ecology* **11**:215-244.
- Esbensen, B. J. 1990. *Great northern diver: the loon*. Little Brown, Boston.
- Foose, T. J. 1993. Global management of rhinos. Pages 32-47 in O. A. Ryder, editor. *Rhinoceros biology and conservation*. San Diego Zoological Society, San Diego.
- Franchini, P., and C. L. Rockett. 1996. Oribatid mites as "indicator" species for estimating the environmental impact of conventional and conservation tillage practices. *Pedobiologia* **40**:217-225.
- Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes. *Ecological Applications* **3**:202-205.
- Frost, T. M., S. R. Carpenter, and T. K. Kratz. 1992. Choosing ecological indicators: effect of taxonomic aggression on sensitivity to stress and natural variability. Pages 215-228 in D. H. McKenzie, D. E. Hyatt, and V. J. McDonald, editors. *Ecological indicators*. Volumes 1 and 2. Elsevier Science Publishers, New York.
- Gaston, K. J. 1996. Species richness: measure and measurement. Pages 77-113 in K. J. Gaston, editor. *Biodiversity: a biology of numbers and difference*. Blackwell Science, Oxford, United Kingdom.
- Gilbert, L. E. 1980. Food web organization and the conservation of Neotropical diversity. Pages 11-34 in M. E. Soulé and B. A. Wilcox, editors. *Conservation biology: an evolutionary-ecological perspective*. Sinauer Associates, Sunderland, Massachusetts.
- Gilman, A. P., D. P. Peakall, D. J. Hallett, G. A. Fox, and R. J. Norstrom. 1979. Herring Gulls (*Larus argentatus*) as monitors of contamination in the Great Lakes. Pages 280-289 in S. W. Nielsen, G. Migaki, and D. G. Scarpelli, chairs. *Animals as monitors of environmental pollutants*. National Academy of Sciences, Washington, D.C.
- Gittleman, J. L. 1986. Carnivore life history patterns: allometric, phylogenetic and ecological associations. *American Naturalist* **127**:744-771.
- Grzimek, B., and M. Grzimek. 1959. *Serengeti shall not die*. Ullstein, A. G., Berlin, Germany.
- Humphries, C. J., P. H. Williams, and R. I. Vane-Wright. 1995. Measuring biodiversity value for conservation. *Annual Review of Ecology and Systematics* **26**:93-111.
- Jarvinen, O. 1985. Conservation indices in land use planning: dim prospects for a panacea. *Ornis Fennica* **62**:101-106.
- Johnsingh, A. J. T., and J. Joshua. 1994. Conserving Rajaji and Corbett National Parks: the elephant as a flagship species. *Oryx* **28**:135-140.
- Karlsson, G. P., G. Sellden, L. Skarby, and H. Pleijel. 1994. Clover as an indicator plant for phytotoxic ozone concentrations: visible injury in relation to species, leaf age and exposure dynamics. *Agriculture Ecosystems and Environment* **59**:55-62.
- Karr, J. R. 1991. Biological integrity: a long-neglected aspect of water resource management. *Ecological Applications* **4**:244-250.
- Kellert, S. R. 1986. Social and perceptual factors in the preservation of animal species. Pages 50-73 in B. G. Norton, editor. *The preservation of species: the value of biological diversity*. Princeton University Press, Princeton, New Jersey.
- Kerr, J. T. 1997. Species richness, endemism, and the choice of areas for conservation. *Conservation Biology* **11**:1094-1100.
- Kleiman, D. G., and J. J. C. Mallinson. 1998. Recovery and management committees for lion tamarins: partnerships in conservation planning and implementation. *Conservation Biology* **12**:27-38.
- Kleiman, D. G., B. B. Beck, J. M. Dietz, L. A. Dietz, J. D. Ballou, and A. F. Coimbra-Filho. 1986. Conservation program for the golden lion tamarin: captive research and management, ecological studies, educational strategies and reintroduction. Pages 959-979 in E. Benirschke, editor. *Primates: the road to self-sustaining populations*. Springer-Verlag, New York.
- Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* **2**: 203-217.
- Lambeck, R. J. 1997. Focal species: a multi-species umbrella for nature conservation. *Conservation Biology* **11**:849-857.
- Landres, P. B. 1983. Use of the guild concept in environmental impact assessment. *Environmental Management* **7**:393-398.

- Landres, P. B. 1992. Ecological indicators: panacea or liability? Pages 1295-1318 in D. H. McKenzie, D. E. Hyatt, and V. J. McDonald, editors. Ecological indicators. Volumes 1 and 2. Elsevier Science Publishers, New York.
- Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. *Conservation Biology* 2: 316-327.
- Launer, A. E., and D. D. Murphy. 1994. Umbrella species and the conservation of habitat fragments: a case of a threatened butterfly and a vanishing grassland ecosystem. *Biological Conservation* 69: 145-153.
- Levin, S. A., M. A. Harwell, J. R. Kelly, and K. D. Kimball. 1989. Ecotoxicology problems and approaches. Pages 3-8 in S. A. Levin, editor. Ecotoxicology: problems and approaches. Springer Verlag, New York.
- Lips, K. R. 1998. Decline of a tropical montane amphibian fauna. *Conservation Biology* 12:106-117.
- McClenahan, T. R., A. T. Kamukuru, N. A. Muthiga, M. G. Yebio, and D. Obura. 1996. Effect of sea urchin reductions on algae, coral and fish populations. *Conservation Biology* 10:136-154.
- McKenzie, D. H., D. E. Hyatt, and V. J. McDonald. 1992. Ecological indicators. Volumes 1 and 2. Elsevier Science Publishers, New York.
- McKenzie, N. L., L. Belbin, C. R. Margules, and G. J. Keighery. 1989. Selecting representative reserve systems in remote areas: a case study in the Nullarbor region, Australia. *Biological Conservation* 50: 239-261.
- Mealy, S. P., and J. R. Horn. 1981. Integrating wildlife habitat objectives into the forest plan. *Transactions of the North American Wildlife and National Resources Conference* 46:488-500.
- Miller, G. D., and L. S. Davis. 1993. Foraging flexibility of Adie Penguins *Pygoscelis adeline*: consequences for an indicator species. *Biological Conservation* 63:223-230.
- Mills, L. S., M. E. Soulé, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. *BioScience* 43:219-224.
- Mix, M. C., S. R. Trenholm, and K. I. King. 1979. Benzo[a]pyrene body burdens and the prevalence of proliferative disorders in mussels (*Mytilus edulis*) in Oregon. Pages 52-64 in S. W. Nielsen, G. Migaki, and D. G. Scarpelli, chairs. Animals as monitors of environmental pollutants. National Academy of Sciences, Washington, D.C.
- Munn, R. E. 1988. The design of integrated monitoring systems to provide early indications of environmental/ecological changes. *Environmental Monitoring and Assessment* 11:203-217.
- Murphy, D. D., and B. R. Noon. 1992. Integrating scientific methods and habitat conservation planning: reserve design for Northern Spotted Owls. *Ecological Applications* 2:3-17.
- Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4:355-364.
- Oatley, T. B., L. G. Underhill, and G. J. B. Ross. 1992. Recovery rate of juvenile Cape Gannets: a potential indicator of marine conditions. *Colonial Waterbirds* 15:140-143.
- Ott, W. R. 1978. Environmental indices: theory and practice. Ann Arbor Science, Ann Arbor, Michigan.
- Panzer, R., D. Stillwaugh, R. Gnaedinger, and G. Derkovitz. 1995. Prevalence of remnant dependence among the prairie and savanna inhabiting insects of the Chicago region. *Natural Areas Journal* 15: 101-116.
- Panwar, H. S. 1984. What to do when you've succeeded: Project Tiger, ten years later. Pages 183-189 in A. Jeffrey, editor. National parks, conservation and development: the role of protected areas in sustaining society. Smithsonian Institution Press, Washington, D.C.
- Patton, D. R. 1987. Is the use of "management indicator species" feasible? *Western Journal of Applied Forestry* 2:33-34.
- Pearson, D. 1995. Selecting indicator taxa for the quantitative assessment of biodiversity. *Philosophical Transactions of the Royal Society of London B* 345:75-79.
- Pearson, D. L., and S. S. Carroll. 1998. Global patterns of species richness: spatial models for conservation planning using bioindicator and precipitation data. *Conservation Biology* 12:809-821.
- Pearson, D. L., and F. Cassola. 1992. World-wide species richness patterns of tiger beetles (Coleoptera:Cicindelidae): indicator taxon for biodiversity and conservation studies. *Conservation Biology* 6: 376-391.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenko, and R. T. Paine. 1996. Challenges in the quest for keystones. *BioScience* 46:609-620.
- Prance, G. T. 1994. A comparison of the efficiency of higher taxa and species numbers in the assessment of biodiversity in the Neotropics. *Philosophical Transactions of the Royal Society of London B* 345:89-99.
- Prendergast, J. R., R. M. Quinn, J. H. Lawton, B. C. Eversham, and D. W. Gibbons. 1993. Rare species, the coincidence of diversity hot-spots and conservation strategies. *Nature* 365:335-337.
- Rabinowitz, A. 1986. Jaguar: one man's struggle to establish the world's first jaguar preserve. Arbor House, New York.
- Ricketts, T. H., E. Dinerstein, D. M. Olson, and C. Loucks. 1999. Who's where in North America. *BioScience* 49:369-381.
- Rodriguez-Estrella, R., J. A. Donazar, and F. Hiraldo. 1998. Raptors as indicators of environmental change in the scrub habitat of Baja California Sur, Mexico. *Conservation Biology* 12:921-925.
- Ryti, R. 1992. Effect of focal taxon on the selection of nature reserves. *Ecological Applications* 2:404-410.
- Sarkka, J. 1996. Meiofauna of the profundal zone of the northern part of Lake Ladoga as an indicator of pollution. *Hydrobiologia* 322: 29-38.
- Schafer, G. N. 1989. Site indicator species for predicting productivity of pine plantations in the southern Cape. *South African Forestry Journal* 148:7-17.
- Sidle, W. B., and L. H. Suring. 1986. Management indicator species for the national forest lands in Alaska. Technical publication R10-TP-2. U.S. Forest Service, Juneau, Alaska.
- Siemann, E., D. Tilman, and J. Haarstad. 1996. Insect species diversity, abundance and body size relationships. *Nature* 380:704-706.
- Simberloff, D. 1998. Flagships, umbrellas and keystones: is single-species management passé in the landscape era? *Biological Conservation* 83:247-257.
- Stolte, K. W., and D. R. Mangis. 1992. Identification and use of plant species as ecological indicators of air pollution stress in Nat'l Park Units. Pages 373-392 in D. H. McKenzie, D. E. Hyatt and V. J. McDonald, editors. Ecological Indicators vols 1 and 2, International Symposium, Fort Lauderdale, Florida USA. Elsevier Science Publishers Ltd., New York.
- Strong, P. I. V. 1990. The suitability of the Common Loon as an indicator species. *Wildlife Society Bulletin* 18:257-261.
- Swanson, B. J. 1998. Autocorrelated rates of change in animal populations and their relationships to precipitation. *Conservation Biology* 12:801-808.
- Szaro, R. C. 1986. Guild management: an evaluation of avian guilds as a predictive tool. *Environmental Management* 10:681-688.
- Temple, S. A., and J. A. Wiens. 1989. Bird populations and environmental changes: can birds be bio-indicators? *American Birds* 43: 260-270.
- Thomas, W. A. 1972. Indicators of environmental quality. Plenum Press, New York.
- U.S. Department of the Interior. 1980. Habitat evaluation procedures. Ecological services manual 102. U.S. Fish and Wildlife Service, Division of Ecological Services, Washington, D.C.
- U.S. Forest Service. 1984. Wildlife, fish and sensitive plant habitat management. Title 2600. Amendment 48. U.S. Forest Service, Washington, D.C.
- Verner, J. 1984. The guild concept applied to management of bird populations. *Environmental Management* 8:1-14.
- Vitt, L. J., J. P. Caldwell, H. M. Wilbur, and D. C. Smith. 1990. Amphibians as harbingers of decay. *BioScience* 40:48.
- Walker, C. H. 1983. Pesticides and birds: mechanisms of selective toxicity. *Agriculture, Ecosystems and Environment* 9:211-226.

Western, D. 1987. Africa's elephants and rhinos: flagships in crisis. *Trends in Ecology* 2:343-346.

Wilcox, B. A. 1984. In situ conservation of genetic resources: determinants of minimum area requirements. Pages 639-647 in J. A. McNeely and K. R. Miller, editors. *National parks: conservation and development*. Smithsonian Institution Press, Washington, D.C.

Williams, P. H., and K. J. Gaston. 1994. Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? *Biological Conservation* 67:211-217.

Zonneveld, I. S. 1988. Environmental indication. Pages 491-498 in A. W. Kuchler and I. S. Zonneveld, editors. *Vegetation mapping*. Kluwer Academic Press, Dordrecht, The Netherlands.

