Ecological Uses of Vertebrate Indicator Species: A Critique

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Abstract: Plant and animal species have been used for decades as indicators of air and water quality and agricultural and range conditions. Increasingly, vertebrates are used to assess population trends and habitat quality for other species. In this paper we review the conceptual bases, assumptions, and published guidelines for selection and use of vertebrates as ecological indicators. We conclude that an absence of precise definitions and procedures, confounded criteria used to select species, and discordance with ecological literature severely weaken the effectiveness and credibility of using vertebrates as ecological indicators. In many cases the use of ecological indicator species is inappropriate, but when necessary, the following recommendations will make their use more rigorous: (1) clearly state assessment goals, (2) use indicators only when other assessment options are unavailable, (3) choose indicator species by explicitly defined criteria that are in accord with assessment goals, (4) include all species that fulfill stated selection criteria, (5) know the biology of the indicator in detail, and treat the indicator as a formal estimator in conceptual and statistical models, (6) identify and define sources of subjectivity when selecting, monitoring, and interpreting indicator species, (7) submit assessment design, methods of data collection and

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Resumen: Especies de plantas y animales han sido usados por décadas como indicadores de la calidad de aíre y agua, y de las condiciones de las tierras dedicadas al pastoreo y a la agricultura. Cada vez más, los vertebrados son usuados para evaluar tendencias poblaciónales y la calidad del babitat de otras especies. En este artículo, revisamos las bases conceptuales, las asumciones, y las pautas publicadas para seleción y el uso de vertebrados como indicadores ecologicos. Concluimos que: en ausencia de definiciones y procedimientos precisos, los confundidos criterios usados para la selección de especies y su discordancia con la literatura ecológica, severamente debilita la eficacia y la credibilidad del uso de vertebrados como indicadores ecológicos. En muchos casos, el uso de especies como indicadores ecológicos es inapropiado, pero cuando sea necesario, las siguientes recommendaciones bará tal uso más rigurosos: (1) describir claramente las metas de la avaluación, (2) usar indicadores sólo cuando otras alternativas de avaluación no sean disponible, (3) escoger especies indicadoras a través de criterios explicitamente definidos de acuerdo a las metas de avaluación, (4) incluir todas las especies que cumplen con los criterios de selección, (5) saber la biologa del indicador en detalle, y tratar el indicador como un estimador formal en modelos conceptuales y estadísticos, (6) identificar y definir fuentes de subjetividad cuando se selecciona, monitorea, e interpreta a las especies indicadoras, (7) someter el diseño de la avaluación, los métodos de colección de datos y análsis estadístico, las interpretaciones y las recommendaciones

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statistical analysis, interpretations, and recommendations to peer review, and (8) direct research at developing an overall strategy for monitoring wildlife that accounts for natural variability in population attributes and incorporates concepts from landscape ecology.

para el examen y revisión por colegas, y (8) dirigir la investigación bacia el desarollo de una estrategia comprensiva para monitorear la vida silvestre que motiva una variabilidad natural de atributos poblaciónales e incorpora conceptos sobre ecología del paisaje.

Introduction

Indicator species have been used for decades as a convenient assay of environmental conditions (Thomas 1972; Zonneveld 1983). The National Research Council (1986, p. 81) recommends using indicator species because "only biological monitoring can tell us what [toxic] materials are doing to organisms." Plants and invertebrates have been successfully used to assess air and water quality (Ott 1978; Phillips 1980; Newman & Schreiber 1984; Shubert 1984; Rosenberg et al. 1986), and as indicators of agricultural and range conditions (Clements 1920; Shantz 1938; Stoddart et al. 1975). Vertebrates were first proposed as indicators for temperature or life zones by Merriam (1898) and Hall & Grinnell (1919). Later, Shelford (1963) used plants and animals (including vertebrates) to classify communities. In recent years a dramatic increase has occurred in using vertebrates to indicate the presence and effects of environmental contaminants (Wren 1986), and population trends and habitat suitability for other species (Verner, Morrison, & Ralph 1986). Despite this increased use, the conceptual bases, assumptions, and published guidelines for using ecological indicators have not been adequately examined. In this paper we (1) review traditional and agency definitions of indicator species, (2) evaluate current ecological uses of vertebrate indicators, (3) examine ecological criteria for selecting indicators, (4) discuss practical considerations for using indicators, and (5) when indicators are necessary, offer recommendations for making their use in natural resource management more rigorous.

Definitions

"Indicate" and "index" are derived from the Latin *indicare*, meaning "to point out" or "to show" (Webster 1979). Inhaber (1976, p. 105) states that biological indices "give us information about the state of environmental quality not obtainable in other ways." In contrast, a measure directly quantifies the factor of interest. Thus, an indicator species is 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 (Fig. 1). In effect, the indicator is a

surrogate measure. By definition, indicators may bear no direct or simple cause and effect relationship to the factor or factors of interest.

Agency Definitions

Much of the current use of indicators was initiated by the U.S.D.I. Fish and Wildlife Service (USFWS), and by the U.S.D.A. Forest Service (USFS). The USFWS developed guidelines known as Habitat Evaluation Procedures (HEP) "to document the quality and quantity of available habitat for selected species of wildlife" (USDI 1980b, p. 1-1). These species are referred to as "evaluation species." These widely used procedures were initially derived to assess impacts of water developments on wildlife habitat (Daniel & Lamaire 1974). HEP was subsequently refined and tested (USDI 1976; Flood et al. 1977; Ellis et al. 1979; Baskett et al. 1980). The capacity of a habitat to support the evaluation species is approximated by a Habitat Suitability Index (HSI) derived from

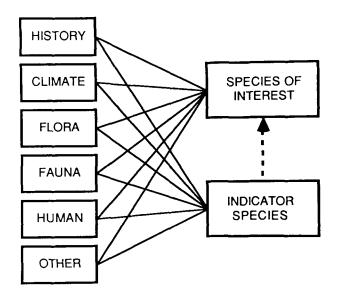


Figure 1. Conceptual model illustrating use of indicator species to infer population trends and babitat suitability for other species of interest. Solid lines show simple cause and effect or direct influence of environmental factors on the indicator species and the species of interest. The dashed line shows inference or extrapolation of population attributes or environmental conditions from the indicator species to the species of interest.

a conceptual or mathematical model (USDI 1980c). Socioeconomic and ecological criteria are used to select evaluation species. Species selected by the first criterion include those that are of high public interest or have high economic value. Species selected by the ecological criterion include those with sensitivity to specific environmental factors, keystone species (i.e., species that exert a major influence on the community), or single species representative of a guild (USDI 1980b).

In the USFS, each National Forest must identify "Management Indicator Species" (MIS), as specified in regulations pursuant to the National Forest Management Act of 1976 (Code of Federal Regulations 1985). MIS include (1) recovery species-those identified by state or federal governments as threatened, endangered, or rare, (2) featured species—those of social or economic value, (3) sensitive species—those identified by Regional Foresters as having habitat requirements particularly sensitive to management activities, and (4) ecological indicators-those used to monitor the state of environmental factors, population trends of other species, or habitat conditions. Specific goals, objectives, and standards for MIS appear in each National Forest Plan. In addition, the USFS established the Wildlife Habitat Relationships (WHR) Program, which uses MIS to identify ways to improve wildlife habitat and to predict the consequences to wildlife of a change in habitat (Salwasser et al 1980; Nelson & Salwasser 1982).

Ecological Uses of Vertebrate Indicators

Vertebrate indicators may be divided into three broad classes based on the parameters of the environment that are of interest: presence and effects of environmental contaminants, population trends of other species, and habitat quality for other species or entire communities and ecosystems. Indicators of environmental contaminants have been thoroughly studied (e.g., Phillips 1980; Martin & Coughtrey 1982; Cairns 1986*a*), and we only briefly discuss their use here, focusing our analysis on the latter two uses of indicators.

Indicators of environmental contaminants have a relatively long history and generally require little inference about effects of the contaminant on the indicator, or what is being assessed by the indicator (National Academy of Science 1979). For example, absence of certain lichens indicates SO_2 air pollution (Hawksworth 1976), and the community attributes of benthic macroinvertebrates indicate stream pollution (Hawkes 1979). With vertebrates, distress of canaries indicated bad air quality for miners, and pollutant levels in muscle tissue and population declines of birds were the first indicators of environmental contamination from a variety of chemical pollutants (Morrison 1986). It is primarily with such traditional uses that cause and effect relationships have been established between environmental conditions and response of the indicator (Westman 1985; Morrison 1986). However, the analyses of Roberts & Johnson (1978) and Wren (1986) show that metal pollution levels in vertebrates may result from mobility and transfer potential of the pollutant within the ecosystem, rather than being directly related to pollutant concentration in the environment. These results demonstrate the need for caution and detailed information when using indicators of environmental contaminants.

Indicators of Population Trends

CURRENT USE

The USFWS and USFS use indicators to assess population trends of other species. HEP guidelines state that "The degree to which predicted impacts for these [evaluation] species can be extrapolated to a larger segment of the wildlife community depends on careful species selection," and that these impacts "are extended with some degree of confidence to other guild members" (USDI 1980b, pp. 3-2, 3-3). The Code of Federal Regulations (1985) mandates the USFS to use "population changes [of management indicator species to]... indicate the effects of management activities on other species." Vertebrate indicators are also considered necessary to reduce the time and effort required to develop management strategies or determine minimum area requirements for viable populations (Wilcox 1984; Soulé 1986; Baker & Schonewald-Cox 1986).

EVALUATION

The implicit assumptions in this use of indicators are that they provide a reliable assessment of habitat quality, and that if the habitat is maintained for the indicator, conditions will be suitable for other species (see Fig. 1). Such covariation (or correlation) of species' population trends would most likely occur among members of the same guild. For example, Severinghaus (1981, p. 187) proposed that "Once the impact on any one species in a guild is determined, the impact on every other species in the guild is known." Such extrapolation among guild members is referred to as the "guild-indicator" approach (Verner 1984; Block, Brennan, & Guttierez 1986).

These assumptions fail on conceptual and empirical grounds. Although species in a guild exploit the same class of environmental resources (Root 1967; Jaksic 1981), they are not necessarily alike in other ways they use and respond to the habitat (Landres 1983; Verner 1984). Each species has breeding characteristics, foraging behaviors and diet, and habitat requirements that set it apart from others (e.g., Block, Brennan, & Guttierez 1986). This makes extrapolation from one species to another difficult or impossible. Furthermore, studies of interspecific competition among guild members suggest that the presence of one species may exclude another that is too similar in resource exploitation (Schoener 1983; Martin 1986). Finally, the criteria used to define guilds do not include mechanisms of population regulation. Population density in some species may be limited by habitat, and in others by predation, disease, extreme weather conditions, or unknown factors on migration routes or wintering grounds. Given such complications, it is unlikely that population trends among guild members would change in parallel fashion.

Despite these conceptual problems, it was recently suggested that finer subdivision of guilds might "reduce variability within the guild and allow direct inferences about habitat quality for non-studied species" (Roberts & O'Neil 1985, p. 360), and that "Guilds can be used to select evaluation species to extrapolate information to nonstudied species" (Roberts 1987, p. 473). These suggestions ignore concerns raised by Landres (1983) and Verner (1984) about (1) the reduced generality of the analysis and subsequent decrease in applicability for habitat assessment, (2) unique responses of species to environmental conditions or disturbance, (3) the keystone functions of some species, (4) varying strengths of trophic interactions affecting species' resource-use patterns, and (5) inferences derived from different geographical areas or seasons.

Empirical evidence supports our assertion that population responses cannot be extrapolated from one guild member to another. For example, density estimates of 19 bird species in five guilds were compared in managed and undisturbed mixed-conifer old-growth forests in northeastern Oregon (Mannan et al. 1984). In four of the guilds, population responses of the component species did not exhibit parallel trends and even the direction of the differences was inconsistent. In only one guild (of two species) was there parallel change in abundance. Similar conclusions were reached in a study of yearly change in abundance of birds in ponderosa pine forests in Arizona (Szaro 1986).

Because neither conceptual nor empirical considerations support use of indicators as surrogates for population trends of other species, this approach to wildlife assessment should be avoided. If such use is necessary, it must be justified by research on populations of the species involved, over an extensive area and time.

Indicators of Habitat Quality

CURRENT USE

Various methods (USDI 1980*a,b,c*; Nelson & Salwasser 1982; Capp, Sandfoot, & Lipscomb 1984; Hoover & Willis 1984) are used to assess wildlife habitat quality based on assumptions that the population density of an indi-

cator is an index of habitat quality for that species, that one or more species may indicate habitat suitability for other species, and that species-habitat relationships can be adequately modeled. For example, Powell & Powell (1986) concluded that reduced clutch size and fledgling success in great white herons (Ardea berodias) demonstrated "poor habitat quality" of a shallow estuary in Florida. Mealy & Horn (1981) suggested that management of 414 species of forest vertebrates could be achieved by managing for elk and three species of accipitrine hawks. In these cases, indicator species are used as an early warning of environmental change. Management agencies also use indicators to predict the influence of future impacts on habitat quality for other species through the use of HSI and similar models (USDI 1980b; Nelson & Salwasser 1982).

EVALUATION

Several problems arise when using indicators to assess habitat quality. First, density is a tenuous index of habitat quality if winter habitat, dominance status, reproductive success, predator populations, and seasonal fluctuations in resources and abiotic conditions are not considered (Van Horne 1983; Maurer 1986). Also, difficulties in estimating density may yield spurious results and conclusions, particularly over the short run (see "Practical Considerations When Using Indicators," below).

Second, numerous problems are associated with indices that combine several variables into a single index (Jarvinen 1985; Gotmark, Ahlund, & Eriksson 1986), as when using indicator species to assess habitat quality. For example, the contribution of each component of the index is obscured, and as demonstrated with diversity indices (Faaborg 1980; Samson & Knopf 1982; Christensen & Peet 1984), different combinations of component scores can give identical index values. Similarly, Westman (1985) and Schroeder (1987) identified several conceptual and mathematical problems in HSI models. Even so, such models are considered the most expedient methods for evaluating impacts of habitat change on wildlife populations (Salwasser 1986; Verner 1986). Despite problems, these indices continue to be used by resource management agencies, at least over the short term, because of legal mandates (Kirby 1984).

Third, without adequate research, it is difficult or impossible to judge the efficacy of an indicator as an index of habitat quality for other species. Habitat "quality" probably includes species composition and structure of the vegetation, wildlife taxa and their reproductive rates, interactions among the biota, as well as abiotic and stochastic factors. Given the extreme complexity of natural systems, the probability is small (even with adequate research) that a single species could serve as an index of the structure and functioning of a community

or ecosystem (Ward 1978; Cairns 1986b). Schroeder (1987) suggested that a lack of quantitive studies clearly linking indicators with specific community attributes precludes using them at the habitat or community level. Olendorff, Motroni, & Call (1980) reached a similar conclusion regarding raptorial birds. In addition, managing an area for an indicator may preserve only those environmental conditions needed by that species, ignoring ecological processes and resources needed by other species (Kushlan 1979). We agree with Baker & Schonewald-Cox (1986, p. 74) that "Incorrectly assuming that other species are receiving protection as a result of the protection of [an indicator] can result in the inadvertent loss of those other species." We conclude that using one or more vertebrates to indicate habitat quality for other species should not be undertaken until research confirms the validity of this approach.

Fourth, a distinction exists between using indicators to assess past or current environmental conditions and predicting future conditions from HSI or similar models. The influences of factors outside the species-habitat relationship (e.g., weather, disease, anthropogenic disturbance), plus the problems discussed above, decrease the accuracy of predictions. Also, circularity arises when using indicators to predict habitat conditions, because the initial choice of the indicator depended on those habitat conditions (Emlen 1973). For these reasons, model validation (Marcot, Raphael, & Berry 1983) and examination of extrinsic factors must be incorporated into the process of using indicators for predicting habitat quality, if this approach is used.

Ecological Criteria for Selecting Indicators

Ecological criteria are important whenever a proposed action might affect the population structure, geographic distribution, or genetic constitution of a species, or might alter the structure or functioning of a community or ecosystem process. Two different approaches may be used to address ecological criteria. A species-based approach would be used when a particular species or group of species is of concern. In this approach, data on such attributes as population density, dispersion, reproductive output, and food and habitat requirements are needed. Community-based approaches are used when the quality or integrity of a habitat or community is of concern, with data collected on attributes of community structure, and on processes such as nutrient cycling, primary and secondary production, and the factors regulating these processes. Because the types of data needed under each approach are different and, generally, cannot be substituted for one another, it is essential to determine whether either approach alone, or both, meet assessment goals. The criteria currently used to select indicators for ecological assessments are examined below.

Sensitivity

Effective indicators are sensitive to the environmental contaminants or habitat attributes of concern. Two assumptions are implicit in this criterion. First, sensitivity should be related to habitat attributes by cause and effect, not merely correlation. Otherwise, the influence of habitat change on population attributes of the indicator (e.g., density or dispersion) may not be separable from influences of other regulating factors (e.g., extreme weather, predation, disease, or interspecific competition). For example, in the first draft of one National Forest's management plan, the raccoon (Procyon lotor) was proposed as an indicator of riparian habitat. However, because the raccoon thrives on human discards and is flexible in habitat use, it is a poor choice as an indicator of the quality of this habitat and for species dependent on pristine riparian conditions. Second, management agencies are necessarily restricted to selecting indicators that are sensitive to habitat attributes that the agency can control (Sidle & Suring 1986).

In contrast, an increase in abundance of insensitive or tolerant species may provide information on habitat conditions (Westman 1985). Although this approach is successfully used (e.g., Karr 1981), caution is necessary because the density of such species may increase for reasons unrelated to the environmental conditions being managed. For example, European starlings (*Sturnus vulgaris*) increased in density and broadened their distribution because of their aggressiveness in displacing other cavity-nesting birds, not because of a change in environmental conditions (Troetschler 1976). Therefore, the abundance of such species should not be used as the only indicator of a change in habitat attributes.

Variability of Response

An effective indicator must exhibit low levels of variability in response to the environmental factors of interest. Alternatively, the contribution from each significant source of variation must be identified. Variability may result from differences within individuals, over time, with the influence of such factors as hunger, reproductive or dominance status, or differences in age and acclimatization to environmental conditions (Morse 1974; MacMahon et al. 1981). Among individuals, differences may result from genetic and nongenetic (e.g., experience or learning) differences and inter-deme genetic differences (Grant & Grant 1983).

Specialist Versus Generalist

Species vary in the range of resources or habitats used, each species falling somewhere along a specialistgeneralist continuum. Odum (1971) first identified this criterion for selecting indicators, suggesting that specialists are better indicators because they are more sensitive to habitat changes. Use of specialists is also advocated on the assumption that meeting their needs will provide for generalists as well (USDI 1980*b*; Graul & Miller 1984).

Although managing for specialists may provide conditions in which some other species find suitable habitat, it may not provide for all. For example, some species need a combination of habitat types in certain proportions and spatial arrays (Forman & Godron 1981; Pickett & White 1985). In addition, specialists may be less abundant than generalists, leading to problematic sampling and higher costs. Therefore, we suggest that if indicators are used, they exhibit a demonstrated relationship to habitat attributes of interest, and not be selected solely on the basis of whether they are specialists or generalists.

Size

Odum (1971) and Ward (1978) suggested that species of large size are better indicators than smaller species, because larger species exhibit slower turnover rates and are therefore more stable. Odum (1971, p. 139) states that "Large species usually make better indicators than small species because ... a larger and more stable biomass or standing crop can be supported with a given energy flow. The turnover rate of small organisms may be so great (here today, gone tomorrow) that the particular species present at any one moment may not be very instructive as an ecological indicator." Similarly, Ward (1978, pp. 28-29) states that "small species with rapid turnover rates usually are not suitable as indicator species, since they are not often stable in their presence in an environment. Larger organisms are usually more stable when they are present in an environment; their generation time is longer, and their turnover rate is smaller." Turnover rate can be interpreted as population turnover (i.e., generation time) or species turnover (i.e., change in species composition at a given location). We examine both types of turnover because proponents of this criterion give little explanation of its usage.

POPULATION TURNOVER

We assume the reasoning behind the use of population turnover is that individuals of smaller species are exposed to contaminants or altered environmental conditions for shorter periods of time because of their shorter generation times (Begon & Mortimer 1986). This increases variability in the smaller species' responses. Also, smaller species generally exhibit higher reproductive potential and may exhibit rapid evolutionary change (Peters 1983). Over several generations this could reduce the sensitivity of the species and, therefore, its usefulness as an indicator. Size is thus inversely related to long-term variability in the response of the species, so larger species would be preferred as indicators.

We question this assertion and suggest caution in applying this criterion. First, the scale of disturbance relative to the indicator and species of interest needs to be determined. For example, smaller species may exploit microhabitats unaffected by altered macroenvironmental conditions, reducing the variability of their response. Or, larger species may range over several habitats, making them poor indicators of smaller-scale disturbance. Second, because small species reach maximum population biomass per unit area faster than large species, "The examination of community response at a fixed period after perturbation is inappropriate because small organisms may have overcome any effect of perturbation long before larger species approach equilibrium" (Peters 1983, p. 139). Thus, to track short- and long-term responses to environmental perturbation, it may be important to monitor both small and large species.

SPECIES TURNOVER

The other interpretation of turnover rate implies that small species exhibit greater variability in space and time (i.e., here today, gone tomorrow) than larger species. Fugitive or pioneer species provide the only support we could find for the assertion that small species exhibit high turnover rates. These species are generally smaller, exploit newly disturbed areas (e.g., early successional stages), reproduce quickly, and then disperse. However, many species of similar size do not exhibit this fugitive life-history strategy and remain in an area (e.g., a late successional stage) for long periods of time.

Thus, large species are not necessarily preferable to smaller species under either interpretation of turnover rate; size *per se* is a poor selection criterion. Indeed, both small and large species may be necessary for environmental assessments to document population effects over both short and long time scales.

Residency Status

We agree with Szaro & Balda (1982) and Bock & Webb (1984) that indicators of on-site environmental conditions should be permanent residents. Migrants are subject to a variety of sources of mortality on their wintering grounds and during migration. A measured decline in their abundance may be unrelated to habitat conditions on the breeding grounds. However, assessment objectives may specifically include monitoring of migrants that breed on managed lands, or of environmental conditions in areas used by migrants during the winter.

Area Requirement

If a single species is used as an indicator of habitat quality or of a community, it is commonly assumed that the

species should require a large area for its territory or home range. Ideally, the indicator would have greater area requirements than any other species in the community, because the larger the area required the more likely it is to include the spectrum of resources needed by other organisms dependent on that particular habitat. Typically, such species would be high trophic-level mammalian or avian carnivores, called "umbrella species" (Wilcox 1984). However, such a species may more easily adjust to changes in environmental conditions by shifting its use of resources within its home range, integrating adverse and beneficial effects, and thus be a poor indicator. (Also see "Indicators of Habitat Quality" above for other problems when using indicator species to assess habitat quality.) Area per se is a tenuous criterion unless research confirms that a species with a large home range can serve as an indicator of habitat quality or of an entire community in that particular location (Ward 1978; Graul & Miller 1984; Murphy & Wilcox 1986).

Practical Considerations When Using Indicators

Several problems may arise in the practical process of applying indicator species to management needs. First, selection criteria are often confounded. That is, species chosen to fill the needs of one criterion are then used to satisfy another. For example, HEP guidelines state that "Species of high public interest should be included because in many cases such species do serve as ecological indicators" (USDI 1980b, p. 3-3), and in some National Forests, elk (Cervus elaphus), a species with high socioeconomic value, was proposed as an indicator of habitat suitability for other species (Mealy & Horn 1981). Socioeconomic and political criteria, based on cultural mores and legal mandates, are not appropriate for selecting ecological indicators. Game species, such as elk, are especially problematic as ecological indicators because their population density and distribution are affected by hunters and direct control actions to meet socioeconomic and political objectives, and "probably indicate little beyond their own numbers" (Thomas 1982, p. 41).

In addition, HEP assessment suggests that "selection [of indicators] can be arbitrary or according to some ranking scheme" (USDI 1980*b*, p. 3-10). "Arbitrary" criteria may introduce bias. For example, HEP guidelines suggest that "availability of habitat data" be used as part of the ranking scheme (USDI 1980*b*, p. 3-10). Using quantity of information as a selection criterion reduces time and cost, but may negate the relevance of the indicator for habitat assessment. For example, little habitat information may exist for a sensitive indicator, but much information may be available for an insensitive one. The less sensitive species might be chosen as the indicator for this reason, although the more sensitive one may be a better indicator of change in habitat conditions.

The choice of criteria used to select evaluation species and MIS is critical for meeting stated project goals. Confounded criteria reduce the effectiveness and credibility of using indicators for ecological purposes. We recognize that species chosen for socioeconomic or political reasons do have legitimate roles in the management plans of agencies (Holbrook 1974; Hoover 1984; Sidle & Suring 1986), but such species need to be distinguished from species used for ecological reasons. Indicators should not be used in multiple roles without research verifying the appropriateness of the species for each criterion.

Second, the number of indicator species used in habitat assessment or monitoring plans is important from scientific and budgetary perspectives. In HEP the use of guilds is proposed as an aid in identifying whether the number of indicators "is too large" (USDI 1980b). HEP guidelines recommend that the "combined number of guilds [be] approximately four to five times the desired number of evaluation species" (USDI 1980b, p. 3-10). Although using guilds may aid in identifying indicators, this suggestion is problematic for several reasons. No methods are given to determine if the number of indicators is "too large," meaning that time and funding constraints, not the accuracy and validity of the ecological assessment, will determine the number of guilds studied. Altering guild designations to fit a "desired" number of indicators suggests a priori selection of species that is not based on an objective analysis of the data. Even if there are "too many" indicators, no guidelines are given to eliminate guilds, allowing arbitrary decisions. Thus, no clear guidelines exist for choosing the number of indicators, although in a study on the number of indicators used in HEP, Fry et al. (1986) recommended that the maximum possible number of species be used to increase precision of the assessment.

Third, several statistical problems are associated with sampling populations, especially deriving density estimates that are the basis for many wildlife-habitat models (Eberhardt 1976; Thomas, McKenzie, & Eberhardt 1981; Van Horne 1983; Verner 1985; Best & Stauffer 1986). In a species with a low population density, sampling problems are particularly severe and may preclude accurate assessment, despite the species being considered a good indicator for other reasons. Long term research on each species is also needed to assess natural variation in population attributes unrelated to environmental change, which may confound interpretation of a species' response to habitat change.

Associated with these statistical problems is the fact that costs of monitoring population trends to show significant changes can be prohibitively high. Presumably, cost effectiveness is one of the major reasons behind agency use of indicators because "of a very practical problem: too many needs, too few funds" (Jarvinen 1985, p. 102). However, Verner (1986) showed that to detect a 10% change between years (with 95% confidence) in population numbers of the pileated wood-pecker (*Dryocopus pileatus*) sampled at random locations, total costs would exceed one million dollars per year. Although costs can be reduced by using indicators that are abundant, conspicuous, and easily recognized (Szaro & Balda 1982; Sidle & Suring 1986), Verner's analysis dispels the cost effectiveness notion of indicator species.

Fourth, several problems arise when an indicator from one area is assumed to be appropriate for use in another area. Although geographically separated habitats may appear similar, subtle differences in vegetation structure or life form of dominant or subdominant plant species (James & Wamer 1982), floral composition (Rotenberry 1985), habitat and resource patchiness (Forman & Godron 1981), or natural disturbance regimes (Pickett & Thompson 1978) may influence an indicator's density or role in the community. Investigators typically assume that quantified habitat variables are related to parameters to which the animal responds. In studies examining the application of HSI and other habitat-relationship models of birds and mammals in a wide variety of habitats, large deviations from model assumptions were documented (Bart, Petit, & Linscombe 1984; Dedon, Laymon, & Barrett 1986; Laymon & Barrett 1986; Maurer 1986; Raphael & Marcot 1986; Stauffer & Best 1986). Such discrepancies suggest that unquantified or indiscernible differences in habitat attributes had marked effects on species' responses.

Within an indicator's range, demes from different geographic areas may possess genetic differences resulting in ecotypic or subspecific differentiation. Such differences could cause a species to respond differently in similar habitats, making a model developed in one area unreliable in another.

Zoogeographic distributions of species may result in similar habitats exhibiting different faunal composition or species richness. A different species milieu may have a large impact on both positive (e.g., mutualism) and negative (e.g., predation or competition) interactions among species. These interactions are significant when quantifying and interpreting species' responses to the environment and their roles in a community.

Thus, differences in habitat attributes, genotype, and species milieu may produce variation in phenotype, physiology, or behavior within species. Mayr (1970, p. 147) comments that such variation is "largely ignored by ecologists, most of whom discuss the ecological requirements of a species in a strictly typological manner" and that this variation is "of considerable practical importance, for instance, in wildlife management." Because each population of a species is embedded in a particular environmental context, the response of an indicator in one area should not be extrapolated to another without verifying the indicator's response in each area.

Conclusions and Recommendations

Using indicators to directly assess environmental contaminants seems justified. However, we feel that current techniques of directly measuring contaminants may often be more accurate and cost effective than this traditional use. Using indicators to assess population trends and habitat suitability for other species is inappropriate without confirmatory research, and current regulations and mandates requiring this use are scientifically problematic and financially infeasible. We realize, despite our analysis, that ecological indicators will continue to be used because the tradition is firmly established, current regulation mandates their use, and they are considered cost effective, at least in the short term. Until alternative approaches to environmental assessment and wildlife monitoring are developed, we offer the following recommendations to make the use of ecological indicators more rigorous.

1. Clearly state assessment goals, including criteria used to determine when those goals have been achieved.

2. Use indicators only when appropriate and necessary. In our literature review we found no clear guidelines to determine when an indicator is needed. For "species management" (i.e., management of species mandated under socioeconomic and political criteria) the use of indicators is not appropriate, because direct measurement of requisite resources and species' populations is needed to evaluate management actions. Likewise, for "resource management" (i.e., management of specific resources or habitats), direct measurement is usually feasible (e.g., timber resources or specific components of wildlife habitat [Thomas et al. 1986]), cost effective, and averts the need for inference from the response of an indicator. In general, indicators should be used only when direct measurement is impossible. We agree with Beanlands & Duinker (1983, p. 69) that "When all else fails, biologists ... may resort to the use of indicators as a means of obtaining some measurement of stress on a natural system. This would normally be a fall-back position ... when the possibilities for studying the valued ecosystem components, either directly or indirectly, are limited."

3. Choose indicator species by criteria that are unambiguously and explicitly defined, and in accord with assessment goals. In the current practice of using indicators, selection criteria are often confounded. To avoid this problem, agencies should state the reasons for choosing the criteria (and their underlying assumptions) used in each assessment. Further, the rigorous and unconfounded processes used to choose indicators should be stated. These steps would help ensure that interpretations of results do not exceed the bounds of inference established by the selection process.

4. To meet assessment goals, include all species that fulfill stated selection criteria. Substituting one indicator for another, or one criterion for another (e.g., based on the amount of information or because of funding), abates the credibility and precision of the analysis. Typically, all sets of criteria (socioeconomic, political, ecological) are needed to meet assessment goals. Including indicators from each criterion will involve compromise in the management plan to accommodate the needs of the various indicators, and each additional indicator adds to assessment costs. Such compromise is preferable to plans made under confounded criteria that may ignore the collective needs of an entire set of species (Herricks & Schaeffer 1985).

5. Know the biology of the indicator in detail. This may entail research to determine cause and effect relationships. Because assessments and resulting recommendations depend on species-specific data, all assumptions about food and habitat requirements and life history need to be verified. To facilitate this process, a conceptual and statistical model could be developed for each use of an indicator species. The indicator could then be treated as a statistical estimator (as, for example, in a path regression analysis), determining the accuracy and precision of the indicator's ability to indicate. We emphasize that indicators in one habitat, area, or season may not be adequate for use in other habitats, areas, or seasons.

6. Identify and define sources of subjectivity in selecting, monitoring, and interpreting indicator species. All assessments and technical decisions entail unavoidable value judgments which, if treated formally, could be discussed and the merits of each determined (Susskind & Dunlap 1985).

7. Submit assessment design, methods of data collection, and statistical analyses to external peer review. Interpretations, conclusions, and recommendations of management plans could also be reviewed at specified intervals and at completion of monitoring. Currently, only a small fraction of assessment and monitoring programs are reviewed. For example, of 172 rare-plant monitoring programs conducted by state, federal, and private organizations, only 13 programs (8%) were externally reviewed (Palmer 1987). Although cumbersome, peer review would increase assessment quality and effectiveness (Beanlands & Duinker 1983; Palmer 1987) and, over the long term, may reduce the time and cost of management plans and actions.

8. Direct research toward developing an overall strategy for monitoring wildlife that accounts for natural variability in population attributes and that incorporates concepts from landscape ecology (Risser, Karr, & Forman 1984; Forman & Godron 1986; Noss & Harris 1986; Urban, O'Neil, & Shugart 1987). Accepting *status quo* indices (e.g., carrying capacity, diversity, or indicator species), with their attendant limitations, may preclude agencies from adequately assessing the ecological integrity of natural systems and recommending effective management actions.

A potential strategy for environmental assessment and monitoring wildlife is a species-habitat approach (Thomas 1979) that includes risk analysis. Risk analysis formalizes the process of making decisions under uncertainty (Salwasser et al. 1983; Salwasser, Mealey, & Johnson 1984; Maguire 1986; Marcot 1986; Verner 1986; Patton 1987) and entails assessing threats to continued existence of habitats (including edges, corridors, and mosaics) and species (i.e., population viability). Despite immediate need for better assessment and monitoring strategies, they are still in embryonic form awaiting further research and development.

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Literature Cited

Baker, R. J., and C. M. Shonewald-Cox. 1986. Management strategies for improving population viability. Pages 73–87 *in* B. A. Wilcox, P. F. Brussard, and B. G. Marcot, editors. The Management of Viable Populations: Theory, Applications and Case Studies. Center for Conservation Biology, Stanford University, Palo Alto, California.

Bart, J., D. R. Petit, and G. Linscombe. 1984. Field evaluation of two models developed following the Habitat Evaluation Procedures. Transactions of the North American Wildlife and Natural Resources Conference **49**:489–499.

Baskett, T. S., D. A. Darrow, D. L. Hallett, M. J. Armbruster, J. A. Ellis, B. F. Sparrowe, and P. A. Korte. 1980. A Handbook for Terrestrial Habitat Evaluation in Central Missouri. U.S.D.I. Fish and Wildlife Service, Resource Publication 133, Washington, D.C.

Beanlands, G. E., and P. N. Duinker. 1983. An Ecological Framework for Environmental Impact Assessment in Canada.

Institute for Resource and Environmental Studies, Dalhousie University, Nova Scotia, Canada.

Begon, M., and M. Mortimer. 1986. Population Ecology: A Unified Study of Animals and Plants. 2nd ed. Sinauer Associates, Sunderland, Massachusetts.

Best, L. B., and D. F. Stauffer. 1986. Factors confounding evaluation of bird-habitat relationships. Pages 209–216 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Madison, Wisconsin.

Block, W. M., L. A. Brennan, and R. J. Gutierrez. 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, Wisconsin.

Bock, C. E., and B. Webb. 1984. Birds as grazing indicator species in southeastern Arizona. Journal of Wildlife Management 48:1045–1049.

Cairns, J., Jr., editor. 1986a. Community Toxicity Testing. ASTM Publications, Philadelphia, Pennsylvania.

Cairns, J., Jr. 1986b. The myth of the most sensitive species. BioScience **36:**670–672.

Capp, J. C., W. W. Sandfoot, and J. F. Lipscomb. 1984. Managing forested lands for wildlife: Roaring Creek Management Area, Roosevelt National Park. Pages 323–346 *in* R. L. Hoover and D. L. Willis, editors. Managing Forested Lands for Wildlife. Colorado Division of Wildlife and U.S.D.A. Forest Service, Rocky Mountain Region, Denver, Colorado.

Christensen, N. L., and R. K. Peet. 1984. Measures of natural diversity. Pages 43–58 *in* J. L. Cooley and J. H. Cooley, editors. Natural Diversity in Forest Ecosystems. Institute of Ecology, University of Georgia, Athens, Georgia.

Clements, F.E. 1920. Plant Indicators. Carnegie Institute of Washington, Publication No. 290, Washington, D.C.

Code of Federal Regulations. 1985. 36 CFR Chapter II 219.19:64.

Daniel, C., and R. Lamaire. 1974. Evaluating effects of water resource developments on wildlife habitat. Wildlife Society Bulletin 2:114–118.

Dedon, M. F., S. A. Laymon, and R. H. Barrett. 1986. Evaluating models of wildlife-habitat relationships of birds in black oak and mixed-conifer habitats. Pages 115–119 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Madison, Wisconsin.

Eberhardt, L. L. 1976. Quantitative ecology and impact assessment. Journal of Environmental Management 4:27–70.

Ellis, J. A., J. N. Burroughs, M. J. Armbruster, D. L. Hallett, P. A. Korte, and T. S. Baskett. 1979. Appraising four field methods of terrestrial habitat evaluation. Transactions of the North American Wildlife and Natural Resources Conference 44:369–379.

Emlen, J. M. 1973. Ecology: An Evolutionary Approach. Addison-Wesley, Reading, Massachusetts.

Faaborg, J. 1980. Potential uses and abuses of diversity concepts in wildlife management. Transactions of the Missouri Academy of Science 14:41–49.

Flood, B. S., M. E. Sangster, R. D. Sparrowe, and T. S. Baskett. 1977. A Handbook for Habitat Evaluation. U.S.D.I. Fish and Wildlife Service, Resource Publication 132, Washington, D.C.

Forman, R. T. T., and M. Godron. 1981. Patches and structural components for a landscape ecology. BioScience **31**:733–739.

Forman, R. T. T., and M. Godron. 1986. Landscape Ecology. John Wiley & Sons, New York, New York.

Fry, M. E., R. J. Risser, H. A. Stubbs, and J. P. Leighton. 1986. Species selection for habitat-evaluation procedures. Pages 105–108 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Madison, Wisconsin.

Gotmark, F., M. Ahlund, and M. O. G. Eriksson. 1986. Are indices reliable for assessing conservation value of natural areas? An avian case study. Biological Conservation **38**:55–73.

Grant, B. R., and P. R. Grant. 1983. Fission and fusion in a population of Darwin's finches: An example of the value of studying individuals in ecology. Oikos 41:530–547.

Graul, W. D., and G. C. Miller. 1984. Strengthening ecosystem management approaches. Wildlife Society Bulletin 12:282–288.

Hall, H. H., and J. Grinnell. 1919. Life-zone indicators in California. Proceedings of the California Academy of Science 9:37–67.

Hawkes, H. A. 1979. Invertebrates as indicators of river water quality. Pages 2:1–2:45 *in* A. James and L. Evison, editors. Biological Indicators of Water Quality. John Wiley & Sons, New York, New York.

Hawksworth, D. L. 1976. Lichens as Air Pollution Monitors. Arnold Publishers, London, England.

Herricks, E. E., and D. J. Schaeffer. 1985. Can we optimize biomonitoring? Environmental Management 9:487–492.

Holbrook, H. L. 1974. A system for wildlife habitat management on southern National Forests. Wildlife Society Bulletin 2:119–123.

Hoover, R. L. 1984. Ecological principles of forest wildlife management. Pages 5–41 *in* R. L. Hoover and D. L. Willis, editors. Managing Forested Lands for Wildlife. Colorado Division of Wildlife and U.S.D.A. Forest Service, Rocky Mountain Region, Denver, Colorado.

Hoover, R. L., and D. L. Willis, editors. 1984. Managing Forested Lands for Wildlife. Colorado Division of Wildlife and U.S.D.A. Forest Service, Rocky Mountain Region, Denver, Colorado. Inhaber, H. 1976. Environmental Indices. John Wiley & Sons, New York, New York.

Jaksic, F. M. 1981. Abuse and misuse of the term "guild" in ecological studies. Oikos 37:397-400.

James, F. C., and N. O. Wamer. 1982. Relationships between temperate forest bird communities and vegetation structure. Ecology **63**:159–171.

Jarvinen, O. 1985. Conservation indices in land use planning: Dim prospects for a panacea. Ornis Fennica **62**:101–106.

Karr, J. R. 1981. Assessment of biotic integrity using fish communities. Fisheries 6:21–27.

Kirby, P. C. 1984. Natural diversity requirements in environmental legislation affecting National Forest planning (except the National Forest Management Act). Pages 11–20 *in* J. L. Cooley and J. H. Cooley, editors. Natural Diversity in Forest Ecosystems. Institute of Ecology, University of Georgia, Athens, Georgia.

Kushlan, J. A. 1979. Design and management of continental wildlife reserves: Lessons from the Everglades. Biological Conservation **15**:281–290.

Landres, P. B. 1983. Use of the guild concept in environmental impact assessment. Environmental Management 7:393–398.

Laymon, S. A., and R. H. Barrett. 1986. Developing and testing habitat-capability models: Pitfalls and recommendations. Pages 87–91 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Madison, Wisconsin.

MacMahon, J. A., D. J. Schimpf, D. C. Anderson, K. G. Smith, and R. L. Bayn. 1981. An organism-centered approach to some community and ecosystem concepts. Journal of Theoretical Biology 88:287–307.

Maguire, L. A. 1986. Using decision analysis to manage endangered species populations. Journal of Environmental Management **22**:345–360.

Mannan, R. W., M. L. Morrison, and E. C. Meslow. 1984. The use of guilds in forest bird management. Wildlife Society Bulletin **12**:426–430.

Marcot, B. G. 1986. Concepts of risk analysis as applied to viable population assessment and planning. Pages 1-13 in B. A. Wilcox, P. F. Brussard, and B. G. Marcot, editors. The Management of Viable Populations: Theory, Applications, and Case Studies. Center for Conservation Biology, Stanford, California.

Marcot, B. G., M. G. Raphael, and K. H. Berry. 1983. Monitoring wildlife habitats and validation of wildlife-habitat relationships models. Transactions of the North American Wildlife and Natural Resources Conference **48**:315–329.

Martin, M. H., and P. J. Coughtrey. 1982. Biological Monitoring of Heavy Metal Pollution. Applied Science Publishers, London, England.

Martin, T. E. 1986. Competition in breeding birds: On the importance of considering processes at the level of the individ-

ual. Pages 181–210 in R. F. Johnston, editor. Current Ornithology. Volume 4. Plenum Press, New York, New York.

Maurer, B.A. 1986. Predicting habitat quality for grassland birds using density-habitat correlation. Journal of Wildlife Management **50:**556–566.

Mayr, E. 1970. Populations, Species, and Evolution. Belknap Press, Cambridge, Massachusetts.

Mealy, S. P., and J. R. Horn. 1981. Integrating wildlife habitat objectives into the forest plan. Transactions of the North American Wildlife and Natural Resources Conference **46**:488– 500.

Merriam, C. H. 1898. Life Zones and Crop Zones of the United States. U.S.D.A., Division of Biological Survey, Bulletin 10.

Morrison, M. L. 1986. Bird populations as indicators of environmental change. Pages 429–451 *in* R. F. Johnston, editor. Current Ornithology. Volume 3. Plenum Press, New York, New York.

Morse, D. H. 1974. Niche breadth as a function of social dominance. American Naturalist **108**:818–830.

Murphy, D. D., and B. A. Wilcox. 1986. Butterfly diversity in natural habitat fragments: A test of the validity of vertebratebased management. Pages 287–292 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Madison, Wisconsin.

National Academy of Science. 1979. Animals as Monitors of Environmental Pollutants. National Academy Press, Washington, D.C.

National Research Council. 1986. Ecological Knowledge and Environmental Problem-solving. National Academy Press, Washington, D.C.

Nelson, R. D., and H. Salwasser. 1982. The Forest Service Wildlife and Fish Habitat Relationship Program. Transactions of the North American Wildlife and Natural Resources Conference 47:174–183.

Newman, J. R., and R. K. Schreiber. 1984. Animals as indicators of ecosystem responses to air emissions. Environmental Management 8:309–324.

Noss, R. F., and L. D. Harris. 1986. Nodes, networks, and MUM's: Preserving diversity at all scales. Environmental Management 10:299–309.

Odum, E. P. 1971. Fundamentals of Ecology. 3rd edition. W.B. Saunders, Philadelphia, Pennsylvania.

Olendorff, R. R., R. S. Motroni, and M. W. Call. 1980. Raptor management—the state of the art in 1980. Pages 468–523 *in* Management of Western Forests and Grasslands for Nongame Birds. USDA Forest Service General Technical Report INT-86.

Ott, W. R. 1978. Environmental Indices: Theory and Practice. Ann Arbor Science, Ann Arbor, Michigan.

Palmer, M. E. 1987. A critical look at rare plant monitoring in the United States. Biological Conservation **39**:113–127.

Patton, D. R. 1987. Is the use of "Management Indicator Species" feasible? Western Journal of Applied Forestry 2:33–34.

Peters, R. H. 1983. The Ecological Implications of Body Size. Cambridge University Press, New York, New York.

Phillips, D. J. H. 1980. Quantitative Aquatic Biological Indicators. Applied Science Publishers, London, England.

Pickett, S. T. A., and J. N. Thompson. 1978. Patch dynamics and the design of nature reserves. Biological Conservation 13:27–37.

Pickett, S. T. A., and P. S. White. 1985. Patch dynamics—a synthesis. Pages 371–384 *in* S. T. A. Pickett and P. S. White, editors. Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York, New York.

Powell, G. V. N., and A. H. Powell. 1986. Reproduction by great white herons *Ardea berodias* in Florida Bay as an indicator of habitat quality. Biological Conservation **36**:101–113.

Raphael, M. G., and B. G. Marcot. 1986. Validation of a wildlifehabitat-relationships model: Vertebrates in a douglas-fir sere. Pages 129–138 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Madison, Wisconsin.

Risser, P. G., J. R. Karr, and R. T. T. Forman. 1984. Landscape Ecology: Directions and Approaches. Illinois Natural History Survey Special Publication 2, Champaign, Illinois.

Roberts, R. D., and M. S. Johnson. 1978. Dispersal of heavy metals from abandoned mines and their transfer through terrestrial food chains. Environmental Pollution 16:293–309.

Roberts, T. H. 1987. Construction of guilds for habitat assessment. Environmental Management **11**:473–477.

Roberts, T. H., and L. J. O'Neil. 1985. Species selection for habitat assessments. Transactions of the North American Wildlife and Natural Resources Conference **50**:352–362.

Root, R. B. 1967. The niche exploitation pattern of the bluegray gnatcatcher. Ecological Monographs **37**:317–350.

Rosenberg, D. M., H. V. Danks, and D. M. Lehmkuhl. 1986. Importance of insects in environmental impact assessment. Environmental Management **10**:773–783.

Rotenberry, J. T. 1985. The role of habitat in avian community composition: Physiognomy or floristics? Oecologia **67**:213–217.

Salwasser, H. 1986. Modeling habitat relationships of terrestrial vertebrates—the manager's viewpoint. Pages 419–424 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Madison, Wisconsin.

Salwasser, H., J. C. Capp, H. Black, and J. F. Hurley. 1980. The California Wildlife Habitat Relationships Program: An overview. Pages 369–378 *in* Management of Western Forests and Grasslands for Nongame Birds. U.S.D.A. Forest Service General Technical Report INT-86.

Salwasser, H., C. K. Hamilton, W. B. Krohn, J. F. Lipscomb, and C. H. Thomas. 1983. Monitoring wildlife and fish: Mandates and their implications. Transactions of the North American Wildlife and Natural Resources Conference **48**:297–307.

Salwasser, H., S. P. Mealey, and K. Johnson. 1984. Wildlife population viability: A question of risk. Transactions of the North American Wildlife and Natural Resources Conference **49**:421–439.

Samson, F. B., and F. L. Knopf. 1982. In search of a diversity ethic for wildlife management. Transactions of the North American Wildlife and Natural Resources Conference 47:421–431.

Schoener, T. W. 1983. Field experiments on interspecific competition. American Naturalist **122**:240–285.

Schroeder, R. L. 1987. Community Models for Wildlife Impact Assessment: A review of Concepts and Approaches. USDI Fish and Wildlife Service, Biological Report 87(2).

Severinghaus, W. D. 1981. Guild theory development as a mechanism for assessing environmental impact. Environmental Management **5:**187–190.

Shantz, H. L. 1938. Plants as soil indicators. Pages 835–860 in Soils and Man, U.S.D.A., Yearbook of Agriculture.

Shelford, V. E. 1963. The Ecology of North America. University of Illinois Press, Urbana, Illinois.

Shubert, L. E., editor. 1984. Algae as Ecological Indicators. Academic Press, New York, New York.

Sidle, W. B., and L. H. Suring. 1986. Management Indicator Species for the National Forest Lands in Alaska. U.S.D.A. Forest Service, Alaska Region, Technical Publication R10-TP-2, Juneau, Alaska.

Soulé, M. E. 1986. Introduction. Pages 1–10 *in* M. E. Soulé, editor. Viable Populations for Conservation. Cambridge University Press, Cambridge, England.

Stauffer, D. F., and L. B. Best. 1986. Effects of habitat type and sample size on habitat suitability index models. Pages 71–77 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Madison, Wisconsin.

Stoddart, L. A., A. R. Smith, and T. W. Box. 1975. Range Management. McGraw-Hill, New York, New York.

Susskind, L. E., and L. Dunlap. 1981. The importance of nonobjective judgments in environmental impact assessments. Environmental Impact Assessment Review 2:335–366.

Szaro, R. C. 1986. Guild management: An evaluation of avian guilds as a predictive tool. Environmental Management 10:681-688.

Szaro, R. C., and R. P. Balda. 1982. Selection and Monitoring of Avian Indicator Species: An Example from a Ponderosa Pine Forest in the Southwest. U.S.D.A. Forest Service General Technical Report RM-89. Thomas, J. M., D. H. McKenzie, and L. L. Eberhardt. 1981. Some limitations of biological monitoring. Environment International 5:3–10.

Thomas, J. W., editor. 1979. Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington. U.S.D.A. Forest Service, Agricultural Handbook 553.

Thomas, J. W. 1982. Needs for and approaches to wildlife habitat assessment. Transactions of the North American Wildlife and Natural Resources Conference 47:35–46.

Thomas, J. W., D. A. Leckenby, L. J. Erickson, S. R. Thomas, D. L. Isaacson, and R. Murray. 1986. Wildlife habitat by design: National Forests in the Blue Mountains of Oregon and Washington. Transactions of the North American Wildlife and Natural Resources Conference **51**:203–214.

Thomas, W. A. 1972. Indicators of environmental quality: An overview. Pages 1-5 *in* W. A. Thomas, editor. Indicators of Environmental Quality. Plenum Press, New York, New York.

Troetschler, R. G. 1976. Acorn woodpecker breeding strategy as affected by starling nest-hole competition. Condor **78:151**–165.

Urban, D. L., R. V. O'Neil, and H. H. Shugart. 1987. Landscape ecology. BioScience 37:119-127.

USDI. 1976. Habitat Evaluation Procedures. Division of Ecological Services, U.S.D.I. Fish and Wildlife Service, Washington, D.C.

USDI. 1980*a*. Habitat as a Basis for Environmental Assessment. Ecological Services Manual Number 101. Division of Ecological Services, U.S.D.I. Fish and Wildlife Service, Washington, D.C.

USDI. 1980b. Habitat Evaluation Procedures (HEP). Ecological Services Manual Number 102. Division of Ecological Services, U.S.D.I. Fish and Wildlife Service, Washington, D.C.

USDI. 1980c. Standards for the Development of Habitat Suitability Index Models. Ecological Services Manual Number 103. Division of Ecological Services, U.S.D.I. Fish and Wildlife Service, Washington, D.C. Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Verner, J. 1983. An integrated system for monitoring wildlife on the Sierra National Forest. Transactions of the North American Wildlife and Natural Resources Conference **48**:355–366.

Verner, J. 1984. The guild concept applied to management of bird populations. Environmental Management 8:1–14.

Verner, J. 1985. Assessment of counting techniques. Pages 247–302 in R. F. Johnston, editor. Current Ornithology. Volume 2. Plenum Press, New York, New York.

Verner, J. 1986. Future trends in management of nongame wildlife: A researcher's viewpoint. Pages 149–171 *in* J. B. Hale, L. B. Best, and R. L. Clawson, editors. Management of Nongame Wildlife in the Midwest: A Developing Art. Proceedings of the 47th Midwest Fish and Wildlife Conference, Grand Rapids, Michigan.

Verner, J., M. L. Morrison, and C. J. Ralph, editors. 1986. Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Madison, Wisconsin.

Ward, D.V. 1978. Biological Environmental Impact Studies: Theory and Methods. Academic Press, New York, New York.

Webster, N. 1979. Webster's New Universal Unabridged Dictionary. Simon and Schuster, New York, New York.

Westman, W. E. 1985. Ecology, Impact Assessment, and Environmental Planning. John Wiley & Sons, New York, New York.

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: The Role of Protected Areas in Sustaining Society. Smithsonian Institution Press, Washington, D.C.

Wren, C. D. 1986. Mammals as biological monitors of environmental metal levels. Environmental Monitoring and Assessment 6:127–144.

Zonneveld, I.S. 1983. Principles of bio-indication. Environmental Monitoring and Assessment 3:207-217.



Special Section: Edge Effects and Fragmented Landscapes

The following Comment and the three Contributed Papers that follow it comprise a special section of this issue of *Conservation Biology* on the subject of edge effects and fragmented landscapes. The Contributed Papers are based on talks given at a symposium that was part of the annual Meeting of the Society for Conservation Biology at Bozeman, Montana, in June, 1987. Dr. Larry D. Harris, of the University of Florida, was Chairman of the symposium.