EVALUATION OF A MULTIPLE-SPECIES APPROACH TO MONITORING SPECIES AT THE ECOREGIONAL SCALE

Patricia N. Manley,[1,4] William J. Zielinski,[2] Matthew D. Schlesinger,[1] and Sylvia R. Mori[3]

[1]*Pacific Southwest Station, USDA Forest Service, 2121 Second Street, Suite A-101, Davis, California 95616 USA*
[2]*Pacific Southwest Station, USDA Forest Service, 1700 Bayview Drive, Arcata, California 95521 USA*
[3]*Pacific Southwest Station, USDA Forest Service, 800 Buchanan Street, Albany, California 94710 USA*

Abstract. Monitoring is required of land managers and conservation practitioners to assess the success of management actions. ''Shortcuts'' are sought to reduce monitoring costs, most often consisting of the selection of a small number of species that are closely monitored to represent the status of many associated species and environmental correlates. Assumptions associated with such shortcuts have been challenged, yet alternative approaches remain scant. We evaluated an approach that departs significantly from the approach of selecting a few representative species. We explored two primary assertions: (1) that a coordinated multiple-species monitoring effort that collects presence–absence data on a broad range of species is a robust alternative to a few intensive single-species efforts, and (2) that the vertebrate species expected to be detected using this approach are numerous and diverse enough to represent all vertebrate species. We simulated monitoring the vertebrate species pool on an existing sample grid across the 7 million ha of public lands in the Sierra Nevada (USA) ecoregion. Based on the use of eight standard presence–absence protocols, we estimated the number of vertebrate species (excluding fish) with an adequate number of sample points within their range to detect ≥20% relative change in the proportion of points with detections between two points in time. We estimated that adequate detections would be obtained for 76% of the 465 vertebrate species, including 83% of all birds, 76% of all mammals, 65% of all reptiles, and 44% of all amphibians. Detection adequacy varied among life-history and ecological groups, but >50% of the species were adequately detected in every group with the exception of three groups: rare species, endemic species, and species of concern (33%, 24%, and 47% of associated species adequately detected, respectively). A multiple-species monitoring approach represents an effective and feasible alternative to the challenges of large-scale monitoring needs by targeting the most basic of population data for a large number and breadth of species.

Key words: biological diversity; conservation strategies, choosing; inventory; land management; management actions, assessing success of; monitoring; populations; Sierra Nevada (California, USA); species monitoring, multiple-species approach; survey; vertebrate population distributions.

INTRODUCTION

It has been over 25 years since the passage of the Endangered Species Act (1973) and National Forest Management Act (1976).[5] Since that time, scientists and land managers have been challenged with the task of understanding, maintaining, and monitoring biological diversity and ecosystem integrity (Mooney et al. 1995*a, b,* Christensen et al. 1996, DeLeo and Levin 1997, Kinzig et al. 2002). Monitoring to assess the success of management activities in meeting legal, regulatory, and policy objectives is required of land-management agencies. Land managers often look for ''shortcuts'' in the absence of funding to conduct all monitoring that would ideally describe the condition of lands and associated biota to inform management decisions (Tracy and Brussard 1994, Fleishman et al. 2000). In the case of monitoring species diversity, a prominent shortcut is the proposal that the status of a small set of carefully chosen individual species can *represent* the integrity of the entire ecosystem (Thomas 1972, Noss 1990, Frost et al. 1992, Stolte and Mangis 1992, Stohlgren et al. 1995, Oliver and Beattie 1996, Dufrene and Legendre 1997, Lambeck 1997, Longino and Colwell 1997, Niemi et al. 1997, Simberloff 1998). The impetus for such a shortcut comes from the recognition that it is infeasible to monitor all species, and conservation goals and management objectives for biological diversity and ecosystem integrity cannot be met by focusing on one species at a time (Franklin 1993, Wilcove 1993).

Various conceptual approaches have been offered as means to create shortcuts, which can be assigned to two broad groups. The first seeks to identify correlations between the patterns of a target variable and a proxy variable—if two variables are highly correlated,

one can infer the dynamics of one by monitoring the other. Concepts that fit within this first approach include ''umbrella'' species (Wilcox 1984, Fleishman et al. 2000) and ''indicator'' species (Landres et al. 1988, Niemi et al. 1997), as well as tools such as wildlife habitat models (e.g., Mayer and Laudenslayer 1988). The second approach seeks to identify species that play key roles in ecosystem function. Identification of ''keystone'' species (Bond 1995, Power et al. 1996, Simberloff 1998), and ''ecosystem engineers'' (Jones et al. 1994) are examples of this second approach. Then there is the ''flagship'' species concept (Western 1987, Simberloff 1998), which is modestly related to umbrella- and indicator-species concepts, but which is largely based in sociology rather than ecology. Caro and O'Doherty (1999) clarify the use of, and criteria for, many of these contemporary designations, and recent work has provided additional criteria for representatives (e.g., Fleishman et al. 2000). However, all of these approaches assume that the status of a few species or other ecosystem parameters can indicate the abundance or distribution of other species or the condition of an ecosystem, and this assumption has been widely challenged (Verner 1984, Landres et al. 1988, Strong 1990, Niemi et al. 1997, Swanson 1998, Lindenmayer et al. 2002).

Although the notion of monitoring a few select species has appeal from a practical perspective, the absence of complete knowledge of species' ecologies and their functional roles in ecosystems means that indicator approaches should be viewed as hypotheses to test (Caro and O'Doherty 1999, Committee of Scientists 1999). We view this approach as a few-eggs-in-one-basket alternative because agencies typically choose a few indicators whose relationships to ecosystem condition or function are presumed to be known and then invoke expensive programs to track detailed population parameters (e.g., absolute population size, population growth rates, behavior patterns) (e.g., USDA Forest Service 1997*a*), resulting in tremendous financial investment per species. The primary risks of this approach are that: (1) the few chosen species may not represent any other species or show strong relationships with environmental conditions affected by management, (2) species chosen as indicators today may not serve as indicators of current stressors or future threats, and (3) despite huge investments in monitoring individual species, uncertainty and difficulty may thwart attempts to translate population-based results into an appropriate system-based interpretation and response.

Growing threats to biological diversity and ecosystem integrity call for innovative approaches for meeting current conservation challenges. We evaluate a multiple-species approach that targets basic presence–absence data on a large number and breadth of species—essentially a many-eggs-in-many-baskets alternative. By recording the occurrence of species at sample points across an ecoregion, a multiple-species approach simply monitors change in the proportion of sites occupied by individual species. Our logic argues that the larger the proportion of all species represented in a sample, the greater the likelihood that the sample accurately reflects the sum total of all species.

We view the proportion of sample points at which a species is detected as an index of regional occurrence, assuming that it is unlikely that significant population increase or decrease can occur without some change in the proportion of sites where a species is detected. Monitoring the change in regional occurrence of a species is not as informative as direct estimates of abundance for a given species, but this approach deliberately targets a large number and breadth of species at the expense of more detailed population data. Similar approaches to population monitoring based on the extent of a species' occurrence have been proposed using atlas data (e.g., Pearman 1997, Telfer et al. 2002). Although the index of status and change for each species is crude, the areal extent of a population and its size often have a positive relationship (e.g., Nachman 1981, Geissler and Fuller 1986, Bart and Klosiewski 1989, Robbins et al. 1989, Gaston 1994, Syrjala 1996, Thompson et al. 1998).

A multiple-species monitoring approach does not require a priori knowledge about ecological function of individual species; rather these data could *yield* valuable information on spatial and temporal covariance relationships among species and between species and their environment. Examining change in the status of groups of species with different characteristics enables the investigator to develop hypotheses about environmental factors associated with, and perhaps responsible for, changes in species occurrence. Thus, we also evaluated the multiple-species approach by determining how the species predicted to be adequately sampled are distributed among classes of phylogeny, life-history traits, habitat associations, habitat specificity, trophic levels, and rarity.

We asked this basic question: If a set of survey protocols were conducted at an array of monitoring stations across an ecoregion at two points in time, for which vertebrate species would we be able to detect a minimum magnitude of change in occurrence at a minimum level of precision? We estimated how many and which vertebrate species would be adequately sampled using commonly employed detection methods at a given sample of points, based on the probability of detection and the number of points falling within the geographic range of each species. The simulation was intended to explore two primary assertions: (1) that a coordinated multiple-species monitoring effort that collects presence–absence data on a broad range of species is a robust alternative to a few intensive single-species efforts, and (2) that the vertebrate species expected to be detected using this approach are numerous and diverse enough to represent all vertebrate species.
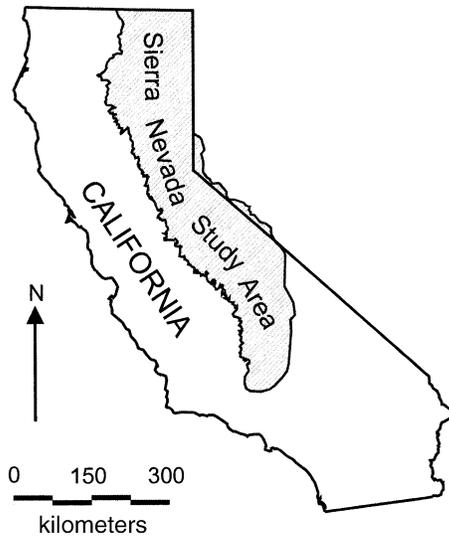
Fig. 1. Location and bounds of the Sierra Nevada study area in California and Nevada, USA.

By constructing and simulating a sampling scenario with specified effort and precision, we evaluated the ability of the approach to provide sufficient data on vertebrate species to confirm these assertions.

MATERIALS AND METHODS

Study system

We based our evaluation on the geographic area encompassing the Sierra Nevada and Southern Cascade ranges in California, USA (Fig. 1), identified by the Sierra Nevada Ecosystem Project (1996) as the extent of the greater Sierra Nevada ecoregion. The area serves as an illustrative case study for three primary reasons: (1) it is a distinct ecoregion, being a mountain range juxtaposed to desert, valley, and Great Basin ecosystems; (2) it has high biological diversity (Ricketts et al. 1999), and (3) concerns are mounting for the fate of its biological diversity as affected by a combination of past and present land-use practices, increasing pressure from a growing human population in California, and rising recreational use (Duane 1996, Sierra Nevada Ecosystem Project 1996, USDA 2001). The Sierra Nevada ecoregion covers over 12×10^6 ha with ~60% consisting of public lands, and 465 species of vertebrates (excluding fish) have some or all of their geographic range within the bounds of the analysis area (USDA Forest Service 2001).

Vertebrate species were selected for the simulation because the breadth of standardized and tested survey techniques for vertebrates made it more feasible to estimate their effectiveness at detecting species. Further, the availability of life-history information on each species made it possible to assess the information conveyed by species predicted to be adequately detected. We selected a set of eight standardized, commonly employed, nonlethal, multiple-species detection methods to be applied at sample locations to maximize the number of vertebrate species that would be detected (Table 1). The assumed effort expended in each protocol (e.g., number of traps, number of visits, area searched) followed generally prescribed levels for maximizing detectability with reasonable effort (Table 1).

Simulated sample design

We used a systematic grid of points based on the national Forest Inventory and Analysis (FIA) program

TABLE 1. Protocols selected to simulate detection rates for vertebrates in the Sierra Nevada, California, USA, using the multiple-species monitoring approach.

Protocol†	Effort	Reference	Target taxa
Point counts	7 stations, 10-min counts, 3 visits	Ralph et al. (1993, 1995)	233 birds and 3 mammals
Broadcast calling (nocturnal)	2 visits	Fuller and Mosher (1981)	13 nocturnal birds, including owls
Live trapping (Sherman-long traps)	100 traps, 4 nights	Jones et al. (1996)	67 mammals, all of them small terrestrial species
Live-trapping (Tomahawk traps)	50 traps, 4 nights	Jones et al. (1996)	14 mammals, all of them small to mid-sized terrestrial species
Track stations with cameras	6 stations, 16 days	Zielinski and Kucera (1995)	17 mammals, all mid-sized carnivores
Area searches for vertebrates and their sign	10-ha area, 2 visits	Crump and Scott (1994), Wemmer et al. (1996)	12 terrestrial amphibians, 50 terrestrial reptiles, and 12 mammals, including large rodents and all ungulates
Mist netting and acoustic surveys	3 net sites, 6 visits	Jones et al. (1996)	17 mammals, all bats
Aquatic visual encounter surveys	2 visits	Crump and Scott (1994), Fellers and Freel (1995)	20 amphibians, 5 reptiles, and 2 mammals, all primarily aquatic

† These eight standardized protocols are commonly employed, nonlethal, multiple-species detection methods.

(Roesch and Reams 1999) to represent the location and density of monitoring sites. The National Forest Management Planning Act of 1976 authorized and promoted a nationwide survey and analysis of all renewable natural resources (Frayer and Furnival 1999); one result was the establishment of the FIA program. The current design consists of sample points located in a systematic hexagonal grid (centers of each hexagon spaced 5.4 km apart) across all ownerships in the United States, and vegetation structure and composition are scheduled to be described at each point once every 10 years (Roesch and Reams 1999). We selected the FIA grid as the basis of our evaluation because it promised a temporally and spatially reliable source of vegetation data across land ownerships, and thus constituted an attractive system on which to build species-monitoring schemes. Further, the density of the grid was low enough to assume independence between points for species with all but the largest home ranges (Zeiner et al. 1988, 1990a, b). We created a mock hexagonal grid using the spacing parameters of the actual FIA grid and, based on the location of the center point of each hexagon, we estimated that ~2760 FIA grid points occurred on Federal lands in the ecoregion. These points were treated as the set of potential monitoring sites.

Through a series of steps described below, we estimated the number of species that had at least the minimum number of sample points within their range sufficient to detect a given magnitude of change between two points in time (i.e., detection of decrease *or* increase; two-tailed test) at a set level of precision. We tested the null hypothesis that a change of a given magnitude or greater occurring between two sample periods could not be detected, vs. the alternative that the specified change could be detected. We chose to base the evaluation on the comparison of two points in time vs. alternative scenarios (e.g., trend analysis based on multiple sample periods) because such a comparison represents the most modest monitoring objective. For the purposes of this evaluation, we chose a relative change of ≥20% in the proportion of sites with observations of a species as a minimum effect size, δ, given that a change of this magnitude would certainly signal cause for concern for most species and could represent a great risk to viability for species already of concern.

Probability of presence and detection

We estimated the number of sites at which we expected to detect each species during the first sample period by evaluating the probability of observing at least one individual at a given location within its range. The proportion of monitoring sites at which a species is observed, the probability of observation during a sample period t (P_t), is a function of the species' (1) probability of presence (p_p), and (2) probability of detection if present (p_d). The relationship between the three probabilities is as follows:

$$P_t = p_p \times p_d. \tag{1}$$

The probability of presence, p_p, for each species was estimated based on the proportion of the species' range in the study area that was comprised of suitable habitat. Maps of the approximate extent of the range of each species in the Sierra Nevada were obtained from the California wildlife habitat relationships (CWHR) Program (CDFG 2000), and then range boundaries were updated using expert opinion. We used definitions of suitable habitat obtained from the CWHR database and habitat maps for the Sierra Nevada were obtained from interpreted satellite imagery (USDA Forest Service 1997b). Habitat types in the CWHR Program are defined by a combination of vegetation series, seral stage, and canopy-cover values. We overlaid the habitat maps onto the estimated species' ranges to calculate the proportion of the area within each species' range comprised of suitable habitat (Fig. 2). Species were assigned one of three levels of p_p: those with <30% of their range comprised of suitable habitat types were assigned a low p_p (modeled as $p_p = 0.10$), those with 30–70% of their range comprised of suitable habitat types were assigned a moderate p_p (modeled as $p_p = 0.5$), and those with >70% of their range comprise of suitable habitat types were assigned a high p_p (modeled as $p_p = 0.80$).

We created three levels of p_p instead of evaluating it as a continuous variable because our estimates were crude and the information available did not justify attempts at greater resolution. Our calculation of the proportion of the range occupied by each species is likely to overestimate the probability of presence in that it implicitly assumes suitable habitat is occupied. The potential optimism of our estimates was largely mitigated by assigning a probability-of-presence interval to each species as opposed to using the specific calculated values. Further, we evaluated the effects of potentially inflated p_p on the outcome of our evaluation.

We then assigned one of three levels of probability of detection given presence, p_d (high, moderate, and low, modeled as 0.8, 0.5, and 0.1, respectively), based on characteristics such as visibility and ease of identification using the typical survey methods. Assigned values were based on published literature and the professional experience of multiple taxonomic experts and local researchers. For example, if we designated a species as having a moderate p_d, our assumption was that employing the detection methods over a reasonable area and for a reasonable duration where the species is present would result in detecting at least one individual of that species 50% of the time. Our determinations were routinely conservative (i.e., when in doubt, we assigned lower p_d values), resulting in a potential bias toward an overestimate of requisite minimum sample sizes.

Precision parameters and sampling adequacy

Minimum sample size requirements were influenced by the following factors: (1) the proportion of moni-
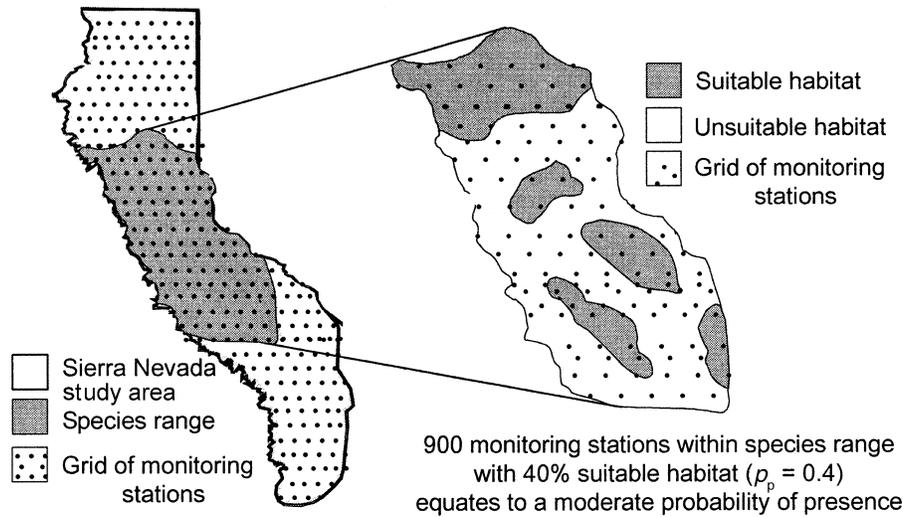
FIG. 2. Example calculation of number of monitoring stations within a species' range and probability of presence (p_p), the proportion of the range occupied by suitable habitat.

toring stations estimated to have observations during the first sample period (P_1), (2) the effect size (δ), (3) the prescribed error rates (α and β), and (4) the direction of change desired to detect (one- or two-tailed) (Sokal and Rohlf 1995). The relationship between the proportion of points with detections before (P_1) and after (P_2) given a decline of a given effect size (δ) is as follows:

$$P_2 = P_1 \times (1 - \delta). \qquad (2)$$

Thus, if $P_1 = 0.25$, then a $\geq$20% relative decrease in P_1 equates to a P_2 of $\leq$0.20.

We selected $\alpha \leq 0.2$, or 80% confidence ($[1 - \alpha] \times 100 =$ percentage confidence), as an acceptable Type I error rate; the likelihood of incorrectly rejecting the null hypothesis. The Type II error rate, the likelihood of incorrectly accepting the null hypothesis, was set at 0.20, or statistical power of 80% (power $= [1 - \beta] \times 100$). A two-tailed test was selected because it offers the greatest flexibility in data analysis and provides a more rigorous test of the detection adequacy. The minimum number of samples (N^*) necessary to detect change between two sample periods for a given species was estimated using the normal approximation (Fleiss 1981), and is given by the following inequality:

$$N^* > \frac{(z_\alpha \times \sigma_0 + z_\beta \times \sigma_a)^2}{(\delta \times P_1)^2} \qquad (3)$$

where z_α and z_β represent the two-tailed critical values from a normal distribution, and σ_0 and σ_a represent standard deviations of the difference between P_1 and P_2 under the null and alternative hypothesis, respectively (Fleiss 1981). We assumed that the site correlation between sample periods was high (0.90) but not perfect (1.0) because although all the same sites were being remeasured, some errors in relocation during the

second sample period could occur (Hoel et al. 1971a). We calculated variance based on a binomial distribution, and then calculated minimum sample sizes based on the assumption that the observed P_t was approximately normally distributed (Hoel et al. 1971a, b). Variance associated with binomial distributions is greatest at the midpoint (0.50) and tapers toward 0 and 1 from the midpoint (Zar 1984). Given that we used a two-tailed test, variance and associated sample size requirements were asymmetrical, with the larger value associated with increases when $P_1 < 0.5$ and declines when $P_1 > 0.5$. We always selected the larger of the two sample-size estimates to increase the rigor of our evaluation.

We calculated the minimum sample size requirement, N^*, for each species, and then compared it to the number of FIA monitoring sites within that species' range. If N^* for a given species was less than the number of monitoring stations in its range, we concluded that the multiple-species monitoring approach would be adequate to detect change in that species. The end result of the analysis was a list of species for which implementing the approach across the Sierra Nevada would be adequate to detect a $\geq$20% change in the proportion of sites with detections between two sample periods. We refer to this list of species as the set of "adequately detected species."

Evaluation of adequately detected species

The multiple-species monitoring approach was evaluated in terms of the two basic assertions put forth in the introduction: (1) multiple-species monitoring can provide data for assessing population status of a large number of species at an ecoregional scale, and (2) the suite of species observed using the approach may serve to represent species diversity and environmental influ-

ences. We assessed the representativeness of the adequately detected set by evaluating their membership in a variety of taxonomic, life-history, and ecological groups. The proportion of each group for which the sampling effort would be adequate to detect change in P_t was calculated and summarized.

Taxonomic and life-history groupings included phylogeny, trophic level, home-range size, body mass, and habitat affiliation, as derived from a variety of sources (Licht 1965, Kaufman and Gibbons 1975, Burt and Grossenheider 1976, Lewke 1979, Parmenter 1981, Dunning 1984, Kline 1985, Ehrlich et al. 1988, Zeiner et al. 1988, 1990*b*, Whittier and Crews 1990, Meienberger et al. 1993, Talbot and Feder 1993, Holland 1994; G. Fellers, *unpublished data*; H. Welsh and A. Lind, *unpublished data*; L. Diller, *unpublished data*). Taxonomic diversity serves as a coarse proxy for genetic diversity in large-scale assessments, given that genetic diversity is greater among than within taxonomic groups. We assessed the representation of species within vertebrate orders and classes. Trophic levels have various responses to environmental changes and perturbations as a result of different resource needs and vulnerabilities (Noss et al. 1996, Polis and Winemiller 1996, Terborgh et al. 1999), and we recognized four distinct trophic levels: carnivore, omnivore, herbivore, and scavenger. Home-range size has been linked to vulnerability to population decline (Terborgh 1974). Body mass and home range tend to be positively related (Harestad and Bunnell 1979), but not consistently among taxonomic groups. In an analysis of monitoring data, trends by home-range size and body-mass categories would be most informative if calculated within taxonomic groups. However, for the purposes of evaluating representation we simplified the analysis by looking across taxonomic groups. Four home-range size categories were established: small (<0.1 ha), medium (0.1–39.9 ha), large (40–500 ha), and extensive (≥500 ha). Three categories of body mass were established: small (<0.75 kg), medium (0.75–2.0 kg), and large (>2.0 kg). Habitat affiliation was represented by three primary categories: terrestrial, semi-aquatic, and aquatic. Species were considered aquatic if their entire life cycle required being in or on water (e.g., Pied-billed Grebe [*Podilymbus podiceps*], river otter [*Lutra canadensis*]). Species were considered semi-aquatic if one part of their life cycle required water or if at least a portion of their prey base consisted of aquatic species (e.g., Belted Kingfisher [*Ceryle alcyon*], beaver [*Castor canadensis*], western toad [*Bufo boreas*]). The remaining species were considered terrestrial.

Ecological groupings included habitat specificity, rarity, endemism, exotics, and species of concern, and were derived from State Natural Heritage Program data bases (Zeiner et al. 1988, 1990*a*, *b*, CDFG 2000). Habitat specialists are often at greater risk of extirpation than habitat generalists (e.g., Rabinowitz 1981, Kattan 1992, MacNally and Bennett 1997). Three categories

TABLE 2. Estimated vertebrate detectability in the Sierra Nevada, California, USA, study area: (a) the number of vertebrate species present assigned each combination of probability of presence and detection levels, and (b) the number of monitoring stations required within a species' geographic range for each combination of parameters.

Probability of presence‡	Probability of detection†			Total
	Low	Moderate	High	
a) Number of species				
Low	25	52	131	208
Moderate	23	72	123	218
High	9	12	18	39
Total	57	136	272	465
b) Number of monitoring stations required within geographic range				
Low	2352	450	272	···
Moderate	450	70	34	···
High	272	34	12	···

† Probability of detection (p_d): low = 0.10, moderate = 0.50, high = 0.80.
‡ Probability of presence (p_p): low = 0.10, moderate = 0.50, high = 0.80.

of relative habitat specificity (low, moderate, and high) were derived by calculating the proportion of all habitat types (i.e., vegetation type, seral stage, and canopy-cover class combinations) occurring in the Sierra Nevada (Mayer and Laudenslayer 1988, CDFG 2000) that were used by each species. Species were considered rare if their geographic ranges occupied <5% of the Sierra Nevada or had population size of ≤100 individuals. Population size was estimated by soliciting information from specialists most familiar with the status of each species. Experts were asked to place each species in one of five log-scale intervals of population size ranging from potentially extirpated to >10 000 individuals. We also evaluated Sierra Nevada and California endemics because endemic species contribute significantly to local biological diversity in that they occur nowhere else (Meffe and Carroll 1997). Exotic species, particularly aggressive invasives, can have severe impacts on the biological integrity of an ecosystem (Soulé 1990, Graber 1996, Cox 1999). The identification and conservation of species that are sensitive or vulnerable, and thus of concern, is a common component of landscape conservation efforts (e.g., Noss and Cooperrider 1994). Species of concern were defined as those with one of more of the following designations: Federally Threatened or Endangered, Forest Service sensitive, and California State Threatened or Endangered.

RESULTS

General patterns of detectability

Of the 465 vertebrate species evaluated, only 8% were assigned a high probability of presence (p_p; Table 2a), and 58% were assigned a high probability of detection (p_d). The higher p_p or p_d, the greater the likelihood that a species was adequately detected (Table
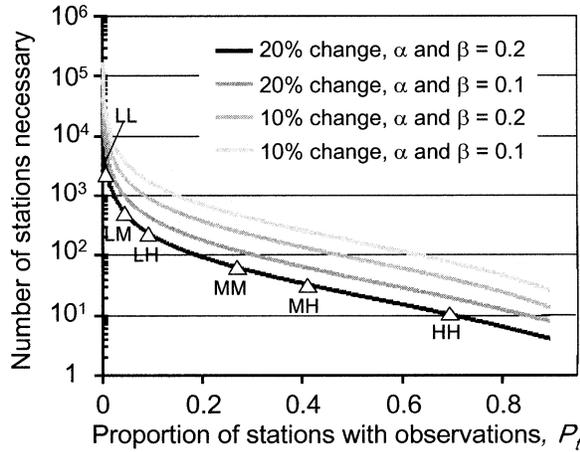
FIG. 3. The relationship between the proportion of points in a species range with observations at the first time period (P_1) and the number of monitoring stations required to detect the species, displayed using a logarithmic scale. Four combinations of effect size (δ, percentage change) and precision (prescribed error rates α and β) are reported. Along the line representing the effect size and precision parameters evaluated in this paper (20% change in the proportion of sites with observations of a species) we note the sample size requirements for each of six pairwise combinations of low (L), moderate (M), and high (H) probabilities of presence (p_p) and of detection (p_d). Correlation between sites sampled in each period was set at 0.90.

2a). An average of 93% of all species with p_d and p_p ≥ 0.5 were adequately detected. Detection adequacy declined to an average of around 50% when either p_d or p_p was low.

The general relationship between P_t (the probability of observation), and minimum sample-size was such that sample-size requirements increased as a power function as P_t linearly decreased from 1 to 0 (Fig. 3). Based on the values selected for our evaluation, detecting a 20% relative change in P_t with Type I and Type II error rates of 20% required 12 monitoring stations when p_d and p_p were both high, 70 monitoring stations when p_d and p_p were both moderate, and over 2300 monitoring stations when p_d and p_p were both low (Table 2b).

When we evaluated species in the Sierra Nevada (USA) based our desired level of precision, we predicted that 76% ($n = 355$ species) of the 465 vertebrate species would be adequately detected (Fig. 4a). Of the 110 species not adequately detected, 27 species had small ranges encompassing fewer than 13 points, which was the minimum number of points required to be adequately detected when presence and detection were at their highest (i.e., p_p and $p_d = 0.80$). Detection of the remaining 83 species was limited primarily by low p_p or p_d. At the assigned levels of p_p or p_d, only 10 of these species would be adequately detected to discern a $\leq 20\%$ change in the proportion of points with detections with the addition of ≤ 50 more points within their range; the remaining 73 species would require

even more points to be adequately detected, ranging from 50 to >2000 additional points (Fig. 4b).

Each of the statistical parameters of the evaluation had substantial effects on the number of species estimated to be adequately detected. We compared our selected effect size of 20% to that of 10%, and our selected error rate of 20% to that of 10% and 5%. For a given effect size, reductions in error rate resulted in 27 to 52 fewer species being adequately detected (Fig. 5). However, reductions in effect size had the greatest influence on the number of adequately detected species. At a given error rate, changing the effect size from 20% to 10% resulted in an average of 115 fewer species being adequately detected, and 32 fewer species were adequately detected when effect size was 10% and error rates were at their highest (20%) than when effect size was 20% and error rates were at their lowest (5%) (Fig. 5). Altering the assigned values of probability of presence and detection to reflect potential design changes did not have a substantial effect on species detections. Given the potential overestimate of probability of presence, we looked at the effect of reducing probability of presence to a maximum of 0.50, which resulted in only three fewer species being adequately detected. We also evaluated the potential gains associated with increasing probability of detection to 0.5 for species with
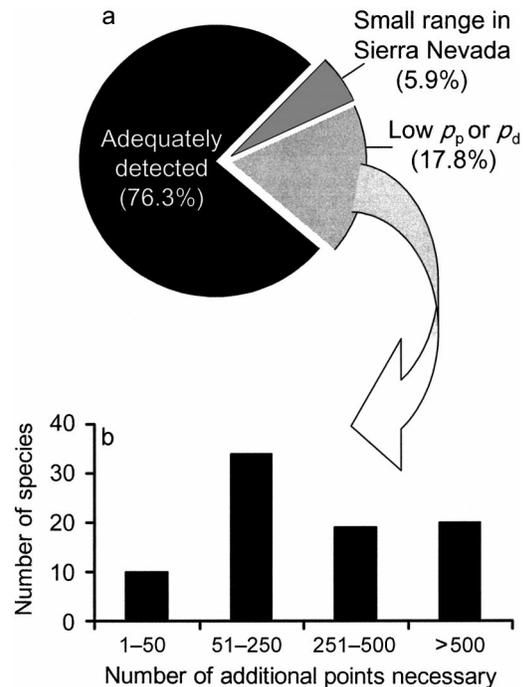

FIG. 4. Summary of predicted detection adequacy for vertebrate species in the Sierra Nevada (USA) based on the multiple-species monitoring approach: (a) proportion of species predicted to be adequately detected based on detecting $\geq 20\%$ relative change between two points in time with 80% confidence and power; (b) the number of additional points necessary to adequately detect species with low probability of presence (p_p) or of detection (p_d).
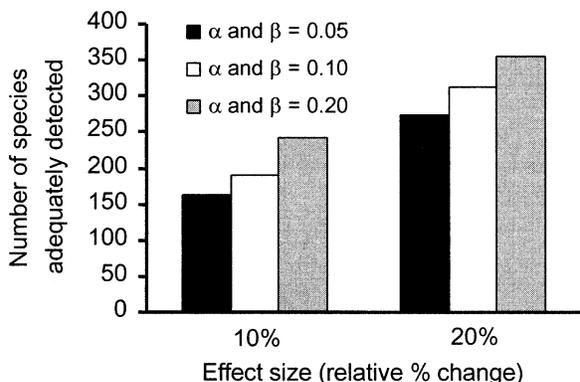
FIG. 5. Predicted number of vertebrate species adequately detected at two effect sizes and three levels of error rates α and β based on the comparison of two points in time using the multiple-species monitoring approach.

low detectability, which resulted in only 14 more species being adequately detected.

Representation

The multiple-species monitoring approach was predicted to adequately detect $\geq 20\%$ change with 20% error for the majority of species in three of the four vertebrate classes: 83% ($n = 205$ species) of birds, 76% ($n = 100$ species) of mammals, 65% ($n = 36$ species) of reptiles, and 44% ($n = 14$ species) of amphibians (Table 3). Also, all but one order of vertebrates (Perissodactyla) was represented by one or more species based on expected detections (Table 3). Particularly well represented ($\geq 85\%$ of all taxa) among birds and mammals were the avian orders Charadriiformes, Falconiformes, Strigiformes, Caprimulgiformes, Coraciiformes, and Piciformes, and the mammalian orders Chiroptera, Lagomorpha, and Marsupalia. Orders with few species were less well represented ($\leq 67\%$), namely the avian orders Gruiformes, Pelecaniformes, Cuculiformes, Galliformes, and Ciconiiformes and the mammalian orders Insectivora and Perissodactyla (Table 3).

TABLE 3. Predicted adequacy of the multiple-species monitoring approach in detecting $\geq 20\%$ relative change (with 80% confidence and power) in the occurrence of vertebrate species by taxonomic class and order in the Sierra Nevada, California, USA.

Taxonomic group	No. of vertebrate species			Proportion adequately detected
	Adequately detected	Not adequately detected	Total	
Amphibians (Amphibia)	14	18	32	0.44
Frogs and toads (Anura)	8	7	15	0.53
Salamanders (Caudata)	6	11	17	0.35
Birds (Aves)	205	41	246	0.83
Birds of prey (Falconiformes)	14	0	14	1.00
Cranes and rails (Gruiformes)	2	2	4	0.50
Cuckoos and allies (Cuculiformes)	1	1	2	0.50
Fowl-like birds (Galliformes)	6	3	9	0.67
Goatsuckers and allies (Caprimulgiformes)	3	0	3	1.00
Herons and allies (Ciconiiformes)	6	4	10	0.60
Kingfishers (Coraciiformes)	1	0	1	1.00
Owls (Strigiformes)	10	1	11	0.91
Pelicans and cormorants (Pelecaniformes)	1	1	2	0.50
Perching birds (Passeriformes)	108	20	128	0.84
Pigeons (Columbiformes)	3	1	4	0.75
Shorebirds and gulls (Charadriiformes)	13	1	14	0.93
Swifts and hummingbirds (Apodiformes)	8	2	10	0.80
Waterfowl (Anseriformes)	15	3	18	0.83
Woodpeckers (Piciformes)	11	2	13	0.85
Mammals (Mammalia)	100	32	132	0.76
Bats (Chiroptera)	15	2	17	0.88
Carnivores (Carnivora)	14	5	19	0.74
Even-toed ungulates (Artiodactyla)	4	1	5	0.80
Insectivores (Insectivora)	8	4	12	0.67
Marsupials (Marsupalia)	1	0	1	1.00
Odd-toed ungulates (Perissodactyla)	0	2	2	0.00
Rabbits and hares (Lagomorpha)	7	1	8	0.88
Rodents (Rodentia)	51	17	68	0.75
Reptiles (Reptilia)	36	19	55	0.65
Lizards (Squamata: Sauria)	16	7	23	0.70
Snakes (Squamata: Serpentes)	19	10	29	0.66
Turtles (Testudines)	1	2	3	0.33
Total	355	110	465	0.76

A wide variety of life-history characteristics appeared to be well represented by the species adequately detected (Table 4). All four primary trophic groups were represented equally well, although the approach was variously effective in representing dietary subgroups of carnivores and herbivores (ranging from 50 to 82% of species adequately detected). The multiple-species approach was predicted to adequately detect a greater proportion of species with moderate, large, or extensive home ranges (73–84%) compared to species with small home-ranges (62%). Unlike home range size, body mass did not appear to have any bearing on sampling efficiency, given that similar proportions of species were adequately detected in each body-mass category. Terrestrial, semi-aquatic, and aquatic species were about equally represented, with 64–79% of all species being adequately detected in each category.

Some greater discrepancies in representation were observed among ecological groupings (Table 4). Most common species (90%) and almost all habitat generalists (98%) were adequately detected, whereas 68% of habitat specialists and only 33% of rare species were adequately detected. Over 70% of the rare species were considered rare based on the small size of their ranges, therefore there were few monitoring points within their ranges. Exotics, endemics, and species of concern were underrepresented relative to most of the other species groups, with 53%, 24%, and 47% predicted to be adequately detected, respectively (Table 4).

Discussion

Overall performance

Our evaluation revealed that a multiple-species monitoring approach has the potential to accomplish many monitoring objectives widely shared among land-management agencies. Evaluation results indicated that this approach can yield data on changes in occurrence for a large number and breadth of species. The relatively equitable representation of most ecological traits also indicates that this monitoring approach can provide a robust characterization of the sum total of all vertebrate species. Although growing threats to biological diversity highlight the need for ecoregional-scale monitoring systems, examples of cross-taxonomic-group monitoring systems are rare. A few large-scale monitoring schemes have been designed for individual taxonomic groups (e.g., Breeding Bird Survey for birds [Bystrak 1981, Droege 1990], North American Amphibian Monitoring Program for amphibians [Weir and Mossman, *in press*]), but sampling designs tailored to one taxonomic group may have limited utility for other taxonomic groups. For example, road-based surveys such as the Breeding Bird Survey have the potential to provide biased results for local areas because their placement is nonrandom and some taxa are affected by the presence and impacts of roads (e.g., Mumme et al. 2000, Robitaille and Aubry 2000). A primary strength of the multiple-species monitoring approach is its cross-taxonomic construct, which relies on a systematic or random sampling approach that is not biased toward a single taxonomic group.

We believe that the assigned values for probability of presence and detection provided a reliable portrayal of the benefits associated with this monitoring approach. Although we assumed that suitable habitat was occupied, the majority of species were assigned the lowest probability of presence ($p_p = 0.10$), and even if only 50% of all suitable habitat were occupied by each species, our results indicate detections would remain adequate for a substantial number of species ($n \approx 170$ species). Probability of detection, on the other hand, was based only on the primary method of detection even when additional sampling methods targeting other species would likely increase detection rates. Also, presence at each sample point is accomplished by a single detection, making detection of species that occur at moderate to high densities relatively certain. Overall, the multi-species monitoring approach obtained an adequate number of detections for the majority of vertebrate species, and in many cases the number of monitoring points was two and three times the number needed. Admittedly, desired levels of precision are likely to be more ambitious (i.e., smaller effect sizes and greater confidence and power) for some individual species of interest. Our results indicate that even with more ambitious objectives, a substantial number of species would be adequately detected, certainly more than are currently considered feasible by most land managers.

Calculating change between two points in time may not satisfy information needs for some species where more detailed information on trends over time are desired. Given equivalent effect size and error rates, detecting trends generally requires a greater minimum sample size than comparing two points in time (Copas 1988). The parameters we used to evaluate this approach were intended to reflect a sampling effort that would meet the needs of a decade-long monitoring program with moderate assurance that changes in population status would be detected.

The cost and logistics associated with implementing a multiple-species monitoring approach are not trivial. However, preliminary field tests conducted in the Sierra Nevada ecoregion (P. Manley, *unpublished data*) suggest that implementation is not only feasible, but reasonably cost efficient. For example, the combination of point counts, small-mammal trapping, and area searches could be considered a core suite of detection methods for a multiple-species monitoring effort, given the large number and range of species they detect. In the Sierra Nevada, these three protocols were the primary detection method for 80% of the vertebrate species (Table 1). Based on the protocol specifications outlined in this paper and then used in our field test, it cost a total of approximately $2800 per site to conduct

TABLE 4. Predicted adequacy of the multiple-species monitoring approach in detecting ≥20% relative change (with 80% confidence and power) in the occurrence of vertebrate species by species group in the Sierra Nevada, California, USA.

	No. of vertebrate species			Proportion adequately detected
Species group	Adequately detected	Not adequately detected	Total	
Trophic level and diet				
Carnivore	199	62	261	0.76
Vertivore	52	13	65	0.80
Piscivore	9	2	11	0.82
Invertivore	76	30	106	0.72
Insectivore	62	14	76	0.82
Scavenger	2	0	2	1.00
Omnivore	74	23	94	0.76
Herbivore	80	25	105	0.76
Grazer/browser	46	12	58	0.79
Frugivore	1	1	2	0.50
Granivore	28	10	38	0.74
Nectar-eater	5	2	7	0.71
Home range				
Small	53	30	83	0.62
Medium	214	54	268	0.80
Large	56	11	67	0.84
Extensive	32	12	44	0.73
Body mass				
Small	303	95	398	0.76
Medium	25	7	32	0.78
Large	27	8	35	0.77
Habitat type				
Terrestrial	297	86	383	0.78
Semi-aquatic	47	21	68	0.69
Aquatic	11	3	14	0.79
Habitat specificity				
Highly specific	227	108	335	0.68
Moderately specific	88	2	90	0.98
Generalist	40	0	40	1.00
Rarity				
Rare	38	76	114	0.33
Common	317	34	341	0.90
Endemics and exotics				
Sierra Nevada endemic	3	6	9	0.33
California endemic	2	10	12	0.17
Sierra Nevada exotic	10	9	19	0.53
Species of concern	18	20	38	0.47

point counts ($800), small-mammal trapping ($1500), and area searches ($500), including data collection, entry, and analysis. As a point of reference, current costs for the full suite of vegetation data targeted by the national Forest Inventory and Analysis (FIA) program are approximately $2500 per site (B. Rhoads, *personal communication*). Further, the monitoring program for the California Spotted Owl in the Sierra Nevada alone is currently funded at approximately $1 million per year (J. Robinson and S. Thompson, *personal communication*). This same level of funding would enable multiple-species data collection at approximately 13% of the points in the Sierra Nevada, which exceeds the FIA program's 10% annual sample target (Schreuder et al. 2000). Thus, using existing monitoring efforts as a benchmark, the cost of a multiple-species monitoring approach at the ecoregional scale is within the fiscal and institutional capacity of land-management agencies.

Enhancement options

One of the primary challenges in designing a multiple-species monitoring approach is to maximize the number and range of species adequately detected. The multiple-species approach was predicted to be successful in detecting occupancy change for over three quarters of all vertebrate species. The variety of life-history and ecological groups evaluated in our analysis was generally well represented. However, a monitoring effort that omits 24% of all species, or the majority of

rare species, may be unacceptable in some situations. In these circumstances, a multiple-species monitoring approach can be augmented to improve detections for target species or species groups. Augmentations can target one or more factors that affect probability of observation: probability of presence, probability of detection, and the number of monitoring stations within the range of a species. For example, probability of detection may be improved by increasing effort per protocol (effort per visit and number of visits) and adding protocols. In addition, the number of monitoring points (i.e., grid density) can be increased within a species' range or throughout a region. However, such field-based augmentations may not always be effective at improving detection rates for species with low densities or limited geographic ranges in the region. In these cases, either independent, species-specific monitoring programs will need to be developed or imbalances in representation among species groups can be dealt with using statistical techniques (e.g., Efron 1983, Chambers and Hastie 1993).

A central design parameter, and also a limitation, of the multiple-species monitoring approach is the reliance on presence–absence data. Recent literature reflects a growing appreciation for the contribution of presence–absence data in addressing large-scale population-trend questions (e.g., Scott et al. 2002). In addition to providing trends in the proportion of sites occupied by species, presence–absence data may be analyzed in innovative ways to extract additional information about populations, such as comparing the proportional occupancy of ''sink'' vs. ''source'' habitats as an index of change in abundance (Krohn 1992, Bowers 1996). However, clearly binomial occurrence data do not provide precise estimates of abundance. In some cases, multiple-species detection methods readily provide abundance estimates without additional field effort. For example, relative abundance estimates can be derived from point-count data without additional field effort, and density estimates can be acquired by distance sampling (Buckland et al. 2001). However, estimates of abundance or density as monitoring metrics could require a greater sample size (Whittemore and Gong 1991, Thompson 2002) than indicated by binomial data.

Another potential limitation is that the multiple-species monitoring approach is retrospective in nature (NRC 1995). It is an inductive approach that is valuable for describing conditions and detecting undesirable changes, but it is not designed to determine the causes of changes nor is it tailored to monitor specific changes that are expected. The alternative approach, predictive monitoring, seeks to detect indications of undesirable effects before they have a chance to become serious (NRC 1995). It focuses on detecting changes expected to result from actions or activities, referred to as ''stressors'' or ''affectors'' (Noon et al. 1999, Manley et al. 2000). Predictive monitoring assumes a cause–

effect relationship between affectors and expected changes, and is an efficient monitoring approach where there is a high level of confidence about cause–effect relationships. Its weakness is that assumptions about cause–effect relationships may be inaccurate, effects may have multiple causes, and ecological vulnerabilities may be unknown, resulting in a failure to detect critical changes. In practice, retrospective and predictive monitoring are complementary and any large-scale monitoring system would benefit from a combination of both.

Collateral applications

Multiple-species monitoring data have an array of potential applications to conservation and management. First, such an omnibus approach can provide data on correlative relationships between species and environmental conditions, which in turn can be used to build habitat-relationship models (e.g., Morrison et al. 1998, Carroll et al. 1999, Scott et al. 2002). Habitat models are useful tools for conservation and land-management planning in that they can be used to estimate the amount and location of suitable habitat for multiple species, assess the potential effects of various management or conservation scenarios, and identify biological diversity hot spots and conservation priorities (e.g., Scott et al. 1987, 1993, 2002, Noon et al. 1997). Indeed, the development of reliable habitat models is a critical need of land-management agencies that are mandated to monitor habitat conditions for species of concern (Verner et al. 1986, Stauffer 2002, Van Horne 2002).

Second, monitoring data could be used to test existing or potential indicator species by validating relationships between candidate indicators and the species or conditions they are assumed to represent. Typically, land managers select indicator species that are intended to serve multiple objectives, such as species of concern that are also closely associated with some habitat type of interest. However, the process of validation (Committee of Scientists 1999), let alone monitoring, is rarely accomplished (e.g., GAO 1997). Validation processes are commonly envisioned as detailed and costly efforts directed at individual species (e.g., Lint et al. 1999). A multiple-species monitoring approach offers the alternative of generating correlative data to evaluate several proposed or existing indicator species. For example, validation of umbrella species (Berger 1997, Caro and O'Doherty 1999) could be accomplished by correlating habitat associations and population trends of candidate umbrella species with those of species in the community being represented (e.g., Fleishman et al. 2000), as well as overall trends in the characteristics of the represented community itself (e.g., vegetation structure and composition, species composition and diversity).

Data provided by a multiple-species monitoring approach could also be used to empirically derive indi-

cator species a posteriori, unfettered by preconceived notions of features that presage a strong indicator. This approach to selecting indicators could rely on some form of classical ordination (e.g., Hill 1979, Lebreton et al. 1991, Dufréne and Legendre 1997) and would reflect an adaptive form of monitoring. Through the course of monitoring, the emphasis of monitoring could shift as information-rich indicators are discovered and integrated into the design of a monitoring program.

Finally, assessing patterns of change across species and species groups could serve to validate ecosystem-based conservation strategies. For example, a coarse-filter conservation approach that maintains a representative set of ecological communities is assumed to sustain all the components and processes that make the ecosystem function (Wilcove 1993, Noss and Cooperrider 1994). Change data for a broad array of species could serve to provide early evidence of the success or failure of coarse-filter conservation efforts.

Conclusions

Our approach represents a ''bet-hedging'' strategy that targets basic population data for a large number and great breadth of species. Clearly, multiple-species monitoring can be considered a promising complementary approach to those that focus on individual species of interest, including species of concern and indicator species. More notably it summons a shift in thinking about options for obtaining information about biological diversity and system function by monitoring the status of many species. Any effort that relies solely on a small set of indicator species will be subject to skepticism given the history of misuse, overuse, and poor performance of the indicator concept. However as Simberloff (1998:248) stated regarding the objectives of indicator species approaches, ''The *reductio ad absurdum* of this confusion of goals is the proposition (Noss 1990) that we should monitor virtually everything as indicators—a large group of species, dominance-diversity curves, canopy height diversity, percent cover . . . etc. . . . . Of course the absence of resources to do all this measurement was the *raison d'etre* for indicator species in the first place!'' The multiple-species monitoring approach represents a middle ground in this argument and is a feasible solution to this management conundrum because it targets the most basic of population data for a breadth of species at a feasible cost. It thus becomes practical to consider monitoring many species. The range of benefits to be gained from a multiple-species monitoring approach, as depicted in this simulation exercise, needs to be corroborated through field testing. However, rapid declines in biological diversity should compel us to welcome novel approaches, move quickly to empirically test ones that have promise, and then refine and implement those that prove effective.

Literature Cited

Bart, J., and S. P. Klosiewski. 1989. Use of presence–absence to measure changes in avian density. Journal of Wildlife Management **53**:847–852.

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

Bond, W. J. 1995. Keystone species. Pages 237–253 *in* E. D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Springer-Verlag, New York, New York, USA.

Bowers, M. A. 1996. Species as indicators of large-scale environmental change: a computer simulation model of population decline. Ecoscience **3**:502–511.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laacke, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, London, UK.

Burt, W. H., and R. P. Grossenheider. 1976. Peterson field guide to western mammals. Houghton Mifflin, Boston, Massachusetts, USA.

Bystrak, D. 1981. The North American breeding bird survey. Pages 34–41 *in* C. J. Ralph and J. M. Scott, editors. Estimating numbers of terrestrial birds. Studies in Avian Biology 6. Allen Press, Lawrence, Kansas, USA.

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

Carroll, C., W. J. Zielinski, and R. Noss. 1999. Using presence–absence data to build and test spatial models for the fisher in the Klamath Region, U.S.A. Conservation Biology **13**:1344–1359.

CDFG [California Department of Fish and Game]. 2000. California wildlife habitat relationships program database, version 7.0. California Department of Fish and Game, Sacramento, California, USA.

Chambers, J. M., and T. J. Hastie. 1993. Statistical models. Chapman and Hall, New York, New York, USA.

Christensen, N. L., et al. 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. Ecological Applications **6**:665–691.

Committee of Scientists. 1999. Sustaining the people's lands: recommendations for stewardship of the National Forests and Grasslands into the next century. USDA Forest Service, Washington, D.C., USA.

Copas, J. B. 1988. Binary regression models for contaminated data. Journal of Royal Statistical Society, Series B **50**:335–226.

Cox, G. W. 1999. Alien species in North America and Hawaii: impacts on natural systems. Island Press, Washington, D.C., USA.

Crump, M. L., and N. J. Scott, Jr. 1994. Visual encounter surveys. Pages 84–92 *in* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, editors. Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press, Washington, D.C., USA.

DeLeo, G. A., and S. Levin. 1997. The multifaceted aspects of ecosystem integrity. Conservation Ecology **1**:3.

Droege, S. 1990. The North American breeding bird survey. Pages 1–4 *in* J. R. Sauer and S. Droege, editors. Survey designs and statistical methods for the estimation of avian population trends. U.S. Fish and Wildlife Service Biological Report **90**.

Duane, T. P. 1996. Recreation in the Sierra. Pages 557–609 *in* Sierra Nevada ecosystem project: final report to Congress. Volume II. Wildland Resources Center Report Number 37. University of California, Davis, California, USA.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs **67**:345–366.

Dunning, J. B. 1984. Body weights of 686 species of North American birds. Western Bird Banding Association Monographs **1**:1–38.

Efron, B. 1983. The jackknife, the bootstrap, and other resampling plans. CBMS-NSF Regional Conference Series on Applied Mathematics 19003. Society for Industrial and Applied Mathematics, Philadelphia, Pennsylvania, USA.

Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The birder's handbook: a field guide to the natural history of North American birds. Simon and Schuster, New York, New York, USA.

Fellers, G. M., and K. L. Freel. 1995. A standardized protocol for surveying aquatic amphibians. Technical Report NPS/WRUC/NRTR-95-01. U.S. Department of Interior, National Park Service, Western Region, San Francisco, California, USA.

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

Fleiss, J. L. 1981. Statistical methods for rates and proportions. Second edition. John Wiley and Sons, New York, New York, USA.

Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? Ecological Applications **3**:202–205.

Frayer, W. E., and G. M. Furnival. 1999. Forest survey sampling designs: a history. Journal of Forestry **97**:4–8.

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. Proceedings of an international symposium. Volumes 1 and 2. Elsevier Science Publishers, New York, New York, USA.

Fuller, M. R., and J. A. Mosher. 1981. Methods of detecting and counting raptors: a review. Pages 235–246 *in* C. J. Ralph and J. M. Scott, editors. Estimating numbers of terrestrial birds. Studies in Avian Biology 6. Allen Press, Lawrence, Kansas, USA.

GAO [U.S. General Accounting Office]. 1997. Forest Service decision-making. GAO/RCED 97-71. U.S. Government Printing Office, Washington, D.C., USA.

Gaston, K. J. 1994. Rarity. Population and community biology series 13. Chapman and Hall, London, UK.

Geissler, P. H., and M. R. Fuller. 1986. Estimation of the proportion of an area occupied by an animal species. Pages 533–538 *in* Proceedings of the section on survey research methods. American Statistical Association, Alexandria, Virginia, USA.

Graber, D. M. 1996. Status of terrestrial vertebrates. Pages 709–734 *in* Sierra Nevada ecosystem project: final report to Congress. Volume II. Wildland Resources Center Report Number 37. University of California, Davis, California, USA.

Harestad, A. S., and F. L. Bunnell. 1979. Home range and body weight—a reevaluation. Ecology **60**:389–402.

Hill, M. O. 1979. TWINSPAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Department of Ecology and Evolutionary Biology, Cornell University, New York, New York, USA.

Hoel, G. H., S. C. Port, and C. J. Stone. 1971a. Introduction to statistical theory. Houghton Mifflin, Boston, Massachusetts, USA.

Hoel, G. H., S. C. Port, and C. J. Stone. 1971b. Introduction to probability theory. Houghton Mifflin, Boston, Massachusetts, USA.

Holland, D. C. 1994. The western pond turtle: habitat and history. U.S. Department of Energy, Bonneville Power Administration, Portland, Oregon, USA.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos **69**:373–386.

Jones, J., W. J. McShea, M. J. Conroy, and T. H. Kunz. 1996. Capturing mammals. Pages 115–155 *in* D. E. Wilson, F. R. Cole, J. D. Nichols, R. Rudran, and M. S. Foster, editors. Measuring and monitoring biological diversity: standard methods for mammals. Smithsonian Institution Press, Washington, D.C., USA.

Kattan, G. H. 1992. Rarity and vulnerability: the birds of the Cordillera Central of Colombia. Conservation Biology **6**:64–70.

Kaufman, G. A., and J. W. Gibbons. 1975. Weight–length relationships in thirteen species of snakes in the southeastern United States. Herpetologica **31**:31–37.

Kinzig, A. P., S. A. Pacala, and D. Tilman, editors. 2002. The functional consequences of biodiversity. Monographs in Population Biology 33. Princeton University Press, Princeton, New Jersey, USA.

Kline, L. W. 1985. Calcitonin-induced body mass loss in the lizard *Sauromalus obesus*. Canadian Journal of Zoology **63**:2780–2782.

Krohn, W. 1992. Sequence of habitat occupancy and abandonment: potential standards for testing habitat models. Wildlife Society Bulletin **20**:441–444.

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

Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. Conservation Biology **2**:316–328.

Lebreton, J. D., R. Sabatier, G. Banco, and A. M. Bacou. 1991. Principal component and correspondence analyses with respect to instrumental variables: an overview of their role in studies of structure–activity and species–environment relationships. Pages 85–114 *in* J. Devillers and W. Karcher, editors. Applied multivariate analysis in SAR and environmental studies (Eurocourses, Volume 2). Kluwer Academic Publishers, Dordrecht, The Netherlands.

Lewke, R. E. 1979. Neck-biting and other aspects of reproductive biology of the Yuma kingsnake. Herpetologica **35**:154–157.

Licht, P. 1965. Heart rates in lizards. Physiological Zoology **38**:129–137.

Lindenmayer, D. B., A. D. Manning, P. L. Smith, H. P. Possingham, J. Fischer, I. Oliver, and M. A. McCarthy. 2002. The focal-species approach and landscape restoration: a critique. Conservation Biology **16**:338–345.

Lint, J., B. Noon, R. Anthony, E. Forsman, M. Raphael, M. Callopy, and E. Starkey. 1999. Northern Spotted Owl effectiveness monitoring plan for the Northwest Forest Plan. General Technical Report PNW-GTR-440. USDA Forest Service, Pacific Northwest Station, Portland, Oregon, USA.

Longino, J. T., and R. K. Colwell. 1997. Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. Ecological Applications **7**:1263–1277.

MacNally, R., and A. F. Bennett. 1997. Species-specific predictions of the impact of habitat fragmentation: local extinction of birds in the box–ironbark forests of central Victoria, Australia. Biological Conservation **82**:147–155.

Manley, P. N., W. J. Zielinski, C. M. Stuart, J. J. Keane, A. J. Lind, C. Brown, B. L. Plymale, and C. O. Napper. 2000. Monitoring ecosystems in the Sierra Nevada: the conceptual model foundation. Journal of Environmental Monitoring and Assessment **64**:139–152.

Mayer, K. E., and W. F. Laudenslayer, Jr. 1988. A guide to wildlife habitats of California. California Department of Fish and Game, Rancho Cordova, California, USA.

Meffe, G. K., and C. R. Carroll. 1997. Principles of conservation biology. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Meienberger, C., I. R. Wallis, and K. A. Nagy. 1993. Digestibility in the desert tortoise (*Xerobates agassizii*). Physiological Zoology **66**:847–862.

Mooney, H. A., J. Lubchenco, R. Dirzo, and O. E. Sala. 1995*a*. Biodiversity and ecosystem functioning: basic principles. Pages 275–325 *in* V. H. Heywood and R. T. Watson, editors. Global biodiversity assessment. Cambridge University Press, New York, New York, USA.

Mooney, H. A., J. Lubchenco, R. Dirzo, and O. E. Sala. 1995*b*. Biodiversity and ecosystem functioning: ecosystem analyses. Pages 327–452 *in* V. H. Heywood and R. T. Watson, editors. Global biodiversity assessment. Cambridge University Press, New York, New York, USA.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1998. Wildlife habitat relationships: concepts and applications. Second edition. University of Wisconsin Press, Madison, Wisconsin, USA.

Mumme, R. L., S. J. Schoech, G. E. Woolfenden, and J. W. Fitzpatrick. 2000. Life and death in the fast lane: demographic consequences of road mortality in the Florida Scrub-jay. Conservation Biology **14**:501–512.

Nachman, G. 1981. A mathematical model of the functional relationship between density and spatial distribution of a population. Journal of Animal Ecology **50**:453–460.

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

Noon, B. R., K. McKelvey, and D. D. Murphy. 1997. Developing an analytical context for multispecies conservation planning. Pages 29–42 *in* S. T. A. Pickett, R. S. Ostfeld, M. Shachak, and G. E. Likens, editors. The ecological basis of conservation—heterogeneity, ecosystems, and biodiversity. Chapman and Hall, New York, New York, USA.

Noon, B. R., T. A. Spies, and M. G. Raphael. 1999. Conceptual basis for designing an effectiveness monitoring program. Pages 21–48 *in* B. S. Mulder, B. R. Noon, T. A. Spies, M. G. Raphael, C. J. Palmer, A. R. Olsen, G. H. Reeves, and H. H. Welsh, Jr., editors. The strategy and design of the effectiveness program for the Northwest Forest Plan. General Technical Report PNW-GTR-437. USDA Forest Service, Pacific Northwest Station, Portland, Oregon, USA.

Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conservation Biology **4**:355–364.

Noss, R. F., and A. Y. Cooperrider. 1994. Saving nature's legacy: protecting and restoring biodiversity. Island Press, Covelo, California, USA.

Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology **10**:949–963.

NRC [U.S. National Research Council]. 1995. Review of EPA's environmental monitoring and assessment program: overall evaluation. National Academy Press, Washington, D.C., USA.

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

Parmenter, R. R. 1981. Digestive turnover rates in freshwater turtles: the influence of temperature and body size. Comparative Biochemistry and Physiology **70**:235–238.

Pearman, D. 1997. Presidential address, 1996. Towards a definition of rare and scarce plants. Watsonia **21**:231–251.

Polis, G. A., and K. O. Winemiller, editors. 1996. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. BioScience **46**:609–620.

Rabinowitz, D. 1981. Seven forms of rarity. Pages 205–217 *in* H. Synge, editor. The biological aspects of rare plant conservation. John Wiley and Sons, New York, New York, USA.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. General Technical Report PSW-GTR-144. USDA Forest Service, Pacific Southwest Station, Albany, California, USA.

Ralph, C. J., J. R. Sauer, and S. Droege, editors. 1995. Monitoring bird populations by point counts. General Technical Report PSW-GTR-149. USDA Forest Service, Pacific Southwest Station, Albany, California, USA.

Ricketts, T. H., E. Dinerstein, D. M. Olson, C. J. Loucks, W. Eichbaum, D. DellaSala, K. Kavanagh, P. Hedao, P. T. Hurley, K. M. Carney, R. Abell, and S. Walters. 1999. Terrestrial ecoregions of North America: a conservation assessment. Island Press, Washington, D.C., USA.

Robbins, C. S., S. Droege, and J. R. Sauer. 1989. Monitoring bird populations with Breeding Bird Survey and atlas data. Annales Zoologici Fennici **26**:297–304.

Robitaille, J. F., and K. Aubry. 2000. Occurrence and activity of American martens, *Martes americana,* in relation to roads and other routes. Acta Theriologica **45**:137–143.

Roesch, F. A., and G. A. Reams. 1999. Analytical alternatives for an annual inventory system. Journal of Forestry **97**:33–37.

Schreuder, H. T., J. S. Lin, and J. Teply. 2000. Annual design-based estimation for the annualized inventories of Forest Inventory and Analysis: sample size determination. General Technical Report RMRS-GTR-66. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Scott, J. M., B. Cusuti, J. D. Jacobi, and F. E. Estes. 1987. Species richness, a geographic approach to protecting future biological diversity. BioScience **37**:782–788.

Scott, J. M., F. Davis, B. Csuti, R. Noss, B. Butterfield, C. Groves, H. Anderson, S. Caicco, F. F'Erchia, T. C. Edwards, Jr., J. Ulliman, and R. G. Wright. 1993. GAP analysis: a geographic approach to protection of biological diversity. Wildlife Monographs **123**:1–41.

Scott, J. M., P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. 2002. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, D.C., USA.

Sierra Nevada Ecosystem Project. 1996. Status of the Sierra Nevada. Sierra Nevada Ecosystem Project: final report to Congress. Volume I. Wildland Resources Center Report Number 37. University of California, Davis, California, USA.

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

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. Third edition. W. H. Freeman and Company, New York, New York, USA.

Soulé, M. E. 1990. The onslaught of alien species, and other challenges in the coming decades. Conservation Biology **4**:233–239.

Stauffer, D. 2002. Linking populations and habitats: Where have we been? Where are we going? Pages 53–62 *in* J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, D.C., USA.

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

Stolte, K. W., and D. R. Mangis. 1992. Identification and use of plant species as ecological indicators of air pollution stress in National Park Units. Pages 373–393 *in* D. H. McKenzie, D. E. Hyatt, and V. J. McDonald, editors. Ecological indicators. Proceedings of an international symposium. Volumes 1 and 2. Elsevier Science Publishers, New York, New York, USA.

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.

Syrjala, S. E. 1996. A statistical test for a difference between the spatial distributions of two populations. Ecology **77**: 75–80.

Talbot, C. R., and M. E. Feder. 1993. Relationships among cutaneous surface area, cutaneous mass, and body mass in frogs: a reappraisal. Physiological Zoology **65**:1135–1147.

Telfer, M. G., C. D. Preston, and P. Rothery. 2002. A general method for measuring relative change in range size from biological atlas data. Biological Conservation **107**:99–109.

Terborgh, J. 1974. Preservation of natural diversity: the problem of extinction prone species. BioScience **24**:715–722.

Terborgh, J., J. A. Estes, P. Paquet, K. Ralls, D. Boyd-Heger, B. J. Miller, and R. F. Noss. 1999. The role of top carnivores in regulating terrestrial ecosystems. Pages 39–64 *in* M. E. Soulé and J. Terborgh, editors. Continental conservation: scientific foundations of regional reserve networks. Island Press, Washington, D.C., USA.

Thomas, W. A., editor. 1972. Indicators of environmental quality. Plenum Press, New York, New York, USA.

Thompson, S. K. 2002. Sampling. John Wiley and Sons, New York, New York, USA.

Thompson, W. L., C. Gowan, and G. C. White. 1998. Monitoring vertebrate populations. Academic Press, New York, New York, USA.

Tracy, C. R., and P. F. Brussard. 1994. Preserving biodiversity: species in landscapes. Ecological Applications **42**: 205–207.

USDA Forest Service. 1997a. Tongass land management plan revision. USDA Forest Service, Petersburg, Alaska, USA.

USDA Forest Service. 1997b. Existing vegetation. USDA Forest Service Remote Sensing Laboratory, Pacific Southwest Region, Rancho Cordova, California, USA.

USDA Forest Service. 2001. Sierra Nevada forest plan amendment, Final environmental impact statement. USDA Forest Service, Pacific Southwest Region, Vallejo, California, USA.

Van Horne, B. 2002. Approaches to habitat modeling: the tensions between pattern and process and between specificity and generality. Pages 63–72 *in* J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, D.C., USA.

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

Verner, J., M. J. Morrison, and C. J. Ralph, editors. 1986. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, Wisconsin, USA.

Weir, L. A., and M. J. Mossman. *In press*. The protocol and history of the amphibian calling survey of the North American Amphibian Monitoring Program (NAAMP). Pages 565–584 *in* M. J. Lannoo, editor. Status and conservation of U.S. amphibians. Volume 1. Conservation essays. University of California Press, Berkeley, California, USA.

Wemmer, C., T. H. Kunz, G. Lundie-Jenkins, and W. J. McShea. 1996. Mammalian sign. Pages 157–176 *in* D. E. Wilson, F. R. Cole, J. D. Nichols, R. Rudran, and M. S. Foster, editors. Measuring and monitoring biological diversity: standard methods for mammals. Smithsonian Institution Press, Washington, D.C., USA.

Western, D. 1987. Africa's elephants and rhinos: flagships in crisis. Tree **2**:343–346.

Whittemore, A. S., and G. Gong. 1991. Poisson regression with misclassified counts: application to cervical cancer mortality rates. Applied Statistics **40**:81–93.

Whittier, J. M., and D. Crews. 1990. Body mass and reproduction in female red-sided garter snakes (*Thamnophis sirtalis parietalis*). Herpetologica **46**:219–226.

Wilcove, D. 1993. Getting ahead of the extinction curve. Ecological Applications **3**:218–220.

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., USA.

Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Zeiner, D. C., W. F. Laudenslayer, Jr., and K. E. Mayer, editors. 1988. California's wildlife. Volume I. Amphibians and reptiles. California Department of Fish and Game, Sacramento, California, USA.

Zeiner, D. C., W. F. Laudenslayer, Jr., K. E. Mayer, and M. White, editors. 1990a. California's wildlife. Volume II. Birds. California Department of Fish and Game, Sacramento, California, USA.

Zeiner, D. C., W. F. Laudenslayer, Jr., K. E. Mayer, and M. White, editors. 1990b. California's wildlife. Volume III. Mammals. California Department of Fish and Game, Sacramento, California, USA.

Zielinski, W. J., and T. E. Kucera, editors. 1995. American marten, fisher, lynx, and wolverine: survey methods for their detection. General Technical Report PSW-GTR-17. USDA Forest Service, Pacific Southwest Station, Albany, California, USA.