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THE PLIGHT OF CRANES: A CASE STUDY FOR CONSERVING BIODIVERSITY

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Abstract: Cranes provide an exemplary case for evaluating conservation policy because (1) they are a charismatic group with high public visibility, (2) as migratory vertebrates they provide an umbrella for the protection of aquatic habitats and a wider set of species, (3) they are a widely-distributed avian family, consequently protection efforts have favored international cooperation, (4) genetic and taxonomic relationships have been studied, and (5) populations of at least 7 crane species are threatened, endangered, or otherwise considered at direct risk. We use comparisons among the world's cranes to show how biogeographic, taxonomic, and genetic data bases can be linked for conservation decisions. We show that decisions typically faced by a conservation planner are themselves diverse (e.g., choosing species for captive propagation, or identifying priority habitats for maintaining taxonomic distinctiveness), thereby obviating the utility of any single, all-purpose measure of diversity. Conservation priorities are shown to change with successive informational input regarding phylogenetic relationships, extinction risks, and population trends, and to differ greatly from priorities based on species richness alone.

Key Words: biodiversity, conservation policy, crane systematics, extinction risk, genetic diversity, multidimensional scaling

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With few precedents in the geological record, the Earth's shrinking endowment of and accelerated decline in biodiversity has received extraordinary attention in the last decade (e.g., Norton 1986, Wilson 1988, Reid and Miller 1989). What this "new" focus on biological impoverishment portends for environmental policy is not yet certain, but effective conservation will require bridging the natural and social sciences. Given competing demands for limited financial resources, conservation priorities conceived without regard to all social costs and benefits can lead to a drain of available resources away from the most productive conservation efforts.

Playing triage with the world's biota via policy is highly controversial, even if extinctions are inevitable (Roberts 1988). Conservation choices are difficult and contentious (O'Brien and Mayr 1991), and some form of guided decision-making is necessary if protection efforts are to be implemented in a timely and optimal fashion. Atkinson (1989) has expressed 1 set of criteria: "given two threatened taxa, one a species not closely related to other living species and the other a subspecies of an otherwise widespread and common species, it seems reasonable to give priority to the taxonomically distinct form."

The social sciences also give value to the benefits of biological diversity. Diverse taxa offer diverse market (e.g., food and medicine), aesthetic, or cultural benefits which may not be good substitutes for one another,

while similar species tend to offer more substitutable benefits to mankind. Given uncertainty regarding future events (e.g., global climate change, technological progress) that would affect the benefits of diverse species in very different ways, the preferred strategy is to "hedge one's bets" by maintaining high diversity among biological elements (Broadus and Eiswerth, unpubl. data 1990).

The biodiversity concept is oft-criticized for its metaphorical rather than concise definition, and its multiple connotations. Ray (1988) suggested that the term merely reinforces preexisting biases, and if referring to species diversity alone, it fails to capture inter-taxa diversity at higher phylogenetic categories (e.g., genus, family, or phylum). Similarly, Westman (1990) noted that biodiversity is often used to describe not only species richness, but habitat, ecosystem, and genetic diversity as well. There is a profound need, then, to both explicitly define the kind of diversity being measured (e.g., Vane-Wright et al. 1991), and to link biodiversity's taxonomic, habitat, ecosystem, and genetic elements.

We use biogeographic comparisons, results from recent genetic studies (Ingold et al. 1989, Krajewski 1989), and the current statuses of crane populations to illustrate how conservation decision-making can be improved by successively incorporating greater amounts of scientific information regarding biodiversity. We use crane biology and crane conservation as a simple case study for elucidating how decisions for biodiversity preservation might be better implemented, and we identify the kinds of data necessary to achieve this goal.

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Table 1. Potential choices, faced by a conservation planner or agency, for which information on inter-taxonomic differences can provide a decision criterion.

Decision basis	Decision options
I. Decisions based on allocation of effort (personnel, funding)	<p>A. Habitats</p> <ol style="list-style-type: none"> 1. How is a limited, fixed level of effort for 2 or more habitats allocated when those habitats have disjunct (100% complementary) sets of taxa? 2. How is a limited, fixed level of effort for 2 or more habitats allocated when those habitats have some number of taxa in common? <p>B. Species</p> <ol style="list-style-type: none"> 1. How is a fixed level of effort allocated across 2 or more different species, given some degree of difference between these species (e.g., how are funds allocated for 2 endangered species, each being propagated in zoos)?
II. Decisions based on exclusion of 1 or more species	<p>A. Habitats</p> <ol style="list-style-type: none"> 1. What is the minimal set of reserves or habitats necessary to account for all taxa of interest?^a 2. What is the minimal set of reserves or habitats necessary to accommodate some target threshold (e.g., the majority or 50%) of species as weighted by their distinctiveness? 3. Given funding for a limited number of sites (e.g., 2 tracts for conservation purchase), which sites "capture" the greatest aggregate taxonomic distinctiveness? 4. Given a funding choice between 2 or more sites, which sites contain both the greatest intra- and inter-site distinctiveness? How does distinctiveness compare to the whole (i.e., world) set? <p>B. Species</p> <ol style="list-style-type: none"> 1. Given a mandate to save <i>x</i> species, how do we rank and choose them?
III. Decisions involving time	<ol style="list-style-type: none"> 1. By how much does the aggregate diversity of species in habitats change if and when species are lost via extirpation and extinction, or if species are gained via dispersal, (re)introduction, etc.? How might such changes be evaluated biometrically and economically?

^aThis choice does not require measurement of distinctiveness unless one is considering only taxonomic units that have a degree of distinctiveness above some threshold value (e.g., attention might be focused only on "full" species as opposed to subspecies or races).

Trust, provided the incentive and encouragement for this study. D. H. Thompson, International Crane Foundation (ICF), kindly provided information on recent sizes and trends of crane populations. J. C. Aise pointed out the distinction among numbers of taxa, evolutionary divergence, and the degree of present-day genetic differences. Two anonymous reviewers offered many helpful suggestions for improving the manuscript. Financial support was provided by The Pew Charitable Trusts and the Marine Policy Center of Woods Hole Oceanographic Institution. This is WHOI Contribution 7727.

RATIONALE AND METHODS

Conservation decisions may be initially focused on habitats, on the taxa inhabiting those habitats, or some combination of both. Cranes were chosen as an illustrative taxocene (after Hurlbert 1971:584) for evaluating some of the choices typically faced by conservation planners or agencies (Table 1). In general, vertebrate conservation can serve as an "umbrella" for protecting many other taxa (Scott et al. 1987). Cranes are positioned at upper trophic levels in wetland ecosystems that often encompass relative-

ly large blocks of land. Cranes are migratory, so conservation strategies must protect stopover and wintering sites in addition to breeding areas. The cultural importance of cranes in many societies (Johnsgard 1983) also factored in choosing this family.

Following an approach similar to that used by A. R. Solow (WHOI, unpubl. data 1991), differences among crane species were analyzed graphically with multi-dimensional scaling (MDS) applied to a dissimilarity matrix previously calculated by Krajewski (1989:607). We used the average delta T_m values of the square matrix resulting from his DNA-DNA hybridization study, but MDS can be applied to any dissimilarity matrix resulting from any genetic technique (e.g., mitochondrial DNA, protein electrophoresis). MDS computes coordinates for a set of points (crane species) in 3-dimensional space such that the distances between pairs of points fit as closely as possible to the measured genetic dissimilarities between crane taxa. Two MDS programs, the Guttman/Lingoes and Kruskal procedures, were each run with a Minkowski constant of 2 (Euclidean distance, a specified exponent in a general power metric). Runs consisted of 75 iterations until the goodness-of-fit statistic (stress) was 0.10 or less (Wilkinson 1989). The Kruskal program uses an algorithm based on non-metric optimization after an initial configuration is computed metrically. Point coordinates sum to zero on each dimension. The Guttman/Lingoes program normalizes the extreme values of the configuration to unity and does not plot the configuration with a zero centroid. A monotonic loss function gave non-degenerative solutions for these dissimilarity data after they were subjected to both procedures (see Wilkinson 1989:97).

Fourteen crane species were individually ranked according to taxonomic distinctiveness in 3 different procedures. Two phenograms, based on similarity in vocalizations (unison calls: Archibald 1976) and DNA-DNA hybridization (Krajewski 1989: Fig. 6), were subjected to the taxic weighting methods of May (1990) and Van-Wright et al. (1991:238-240). In addition to these cladistic approaches, we ranked cranes by using the average of Krajewski's (1989) square matrix of average delta T_m values to compute a measure of phylogenetic distinctiveness (d_i) among the crane species (Eiswerth and Haney, in press). Based on computational results from each of the 3 procedures, and in order to permit standardized comparisons across methods, ranks were assigned to each of the cranes, the highest ranks going to the most distinct form within the entire set of 14 species.

For cranes weighted by the phylogenetic procedure, we conducted additional exercises by adjusting initial taxonomic weights via addition of weighting terms that incorporated the degree of endangerment: extinction risk

(population size) and survival prognosis (population trends). In previous studies, mathematical models showed that extinction risks depend upon demographic accidents, birth and death schedules, environmental constancy, body size, migratory versus resident status, etc. (e.g., MacArthur and Wilson 1967; Leigh 1981; Lande 1987, 1988; Dennis et al. 1991). However, small populations are generally the most prone to catastrophic extinction (Goodman 1987, Pimm et al. 1988). Assuming that no crane species is completely risk-free, we assigned factorial extinction risks based on the empirical, curvilinear relationship described in Pimm et al. (1988: Fig. 3). On the basis of relative population sizes (D. H. Thompson, ICF, pers. commun.), we assigned an extinction risk for *Grus americana* (<1,000 individuals) = 0.9; for *G. leucogeranus*, *G. japonensis*, *G. nigricollis* (1,000–3,000 individuals) = 0.4; for *Bugeranus*, *G. vipio*, and *G. monachus* (3,000–10,000 individuals) = 0.2; and for all non-threatened or non-endangered taxa with population sizes greater than 10,000 individuals, an extinction risk of 0.1. Factorial terms for survival prognosis were assigned on the basis of current population trends of cranes: 0.7 for taxa with populations believed to be increasing (*G. vipio*, *G. japonensis*, *G. americana*, and *G. monachus*), 1.0 for all non-threatened or non-endangered taxa, 1.1 for taxa with threatened but unknown population trends (*G. leucogeranus*, *G. nigricollis*), and 1.3 for taxa exhibiting declines (*Bugeranus*).

To maintain consistency, we chose terms for both extinction risk and survival prognosis so that higher weights were assigned to the more distinct and threatened species. However, this assignment of weights is still subjective because the factors (phylogenetic distinctiveness, extinction risk, population trend) cannot be measured in comparable units.

Crane distributions obtained from the literature (e.g., Heinzel et al. 1979, Pizzey 1980, Johnsgard 1983) were used to figure continental affiliations: for Asia, 8 taxa (*G. canadensis* was assigned to North America due to its highly restricted range in Asia and because its migration corridor and winter areas are within North America); for Africa, 4 taxa (including *Balearica regulorum* and *B. pavonina*, following Walkinshaw [1964]); for Europe, North America, and Australia, 2 taxa each (Table 2). We also contrasted taxic diversity in the subcontinents of southern Africa and eastern Asia. Three crane taxa (*Balearica regulorum*, *A. paradisea*, *Bugeranus carunculatus*) reside in South Africa and possibly Mozambique, whereas 5 taxa (*A. virgo*, *G. vipio*, *G. monachus*, *G. grus*, *G. japonensis*) reside in southeastern U.S.S.R., Mongolia, and northeastern China (Johnsgard 1983).

We then compared diversity across continents and subcontinents by computing sums of taxonomic distinctiveness

Table 2. Ranks and weights (in parentheses) of 14 crane species according to taxonomic and phylogenetic distinctiveness. Continental affiliations are listed after taxon.

Species	Continental affiliation	Cladistic weighting				Phylogenetic weighting plus endangerment		
		Vane-Wright et al. method		May method		Phylogenetic weighting	Phylogenetic weighting and extinction risk	Phylogenetic weighting, extinction risk, and population trend
		Archibald 1976	Krajewski 1989	Archibald 1976	Krajewski 1989			
<i>Balearica regulorum</i> ^a	Africa	1(5.00)	1(5.00)	1(6.00)	1(7.00)	1(3.74)	5(0.37)	6(0.37)
<i>Anthropoides paradisea</i>	Africa	3(1.25)	13(1.00)	3(1.50)	8(1.17)	6(1.47)	10(0.15)	10(0.15)
<i>A. virgo</i>	Asia, Europe	3(1.25)	13(1.00)	3(1.50)	8(1.17)	7(1.43)	13(0.14)	12(0.14)
<i>Bugeranus carunculatus</i> ^b	Africa	3(1.25)	4(1.25)	3(1.50)	4(1.40)	4(1.54)	6(0.31)	4(0.40)
<i>Grus leucogeranus</i> ^b	Asia	3(1.25)	2(2.50)	3(1.50)	2(3.50)	2(1.70)	2(0.68)	2(0.75)
<i>G. rubicunda</i>	Australia	13(1.00)	4(1.25)	8(1.09)	5(1.27)	8(1.40)	12(0.14)	12(0.14)
<i>G. antigone</i>	Asia, Australia	13(1.00)	4(1.25)	8(1.09)	5(1.27)	5(1.49)	10(0.15)	10(0.15)
<i>G. vipio</i> ^b	Asia	3(1.25)	4(1.25)	7(1.33)	5(1.27)	11(1.30)	7(0.26)	7(0.18)
<i>G. canadensis</i>	North America	2(1.67)	3(1.66)	2(1.71)	3(1.75)	3(1.55)	9(0.16)	9(0.16)
<i>G. americana</i> ^b	North America	3(1.25)	4(1.25)	10(1.00)	13(1.00)	13(1.28)	1(1.15)	1(0.81)
<i>G. japonensis</i> ^b	Asia	3(1.25)	4(1.25)	10(1.00)	8(1.17)	10(1.36)	4(0.54)	5(0.38)
<i>G. monachus</i> ^b	Asia	3(1.25)	4(1.25)	10(1.00)	13(1.00)	11(1.30)	7(0.26)	7(0.18)
<i>G. nigricollis</i> ^b	Asia	3(1.25)	4(1.25)	10(1.00)	8(1.17)	9(1.37)	3(0.55)	3(0.61)
<i>G. grus</i>	Europe, Asia	3(1.25)	4(1.25)	10(1.00)	8(1.17)	14(1.05)	14(0.11)	14(0.11)

^a *Balearica pavonina* not included in Krajewski (1989).

^b Endangered or threatened taxa.

ness values. Continents were first ranked by species richness, then by phylogenetic distinctiveness (d_i), and finally by phylogenetic distinctiveness as weighted by both extinction risk and survival prognosis. For weights derived from the phylogenetic method, the continental or subcontinental endowment of taxonomic distinctiveness for area k is given by:

$$G_k = \frac{n_k}{\sum_1^k d_i^k}$$

where d_i^k is the phylogenetic distinctiveness of species i residing in area k . This measure is useful because it is derived by weighting each continent's endowment by distinctiveness of the taxa present, and provides an alternative to n_k alone, the species richness of continent or subcontinent k .

RESULTS AND DISCUSSION

Without additional structure imposed by hierarchical representations and branching diagrams, MDS portrays the relative differences within the entire crane clade (Fig. 1). As in virtually every other systematic scheme (e.g., Archi-

bald 1976, Wood 1979, Krajewski 1989), the MDS plots show *Balearica* to be highly distinct from all other cranes (Fig. 1: cluster A). Both the Kruskal and Guttman/Lingoes procedures placed *Bugeranus carunculatus* well apart from remaining cranes, separated *Anthropoides* from other taxa, and identified a cluster of 5 closely related *Grus* species (*grus*, *monachus*, *americana*, *nigricollis*, and *japonensis*; cluster C in Fig. 1). This cluster was termed "Species Group *Grus*" by Krajewski (1989). However, the Kruskal procedure (plot 1 in Fig. 1) best illustrates the distinctiveness of *G. leucogeranus* (Krajewski 1989), placing it near *Bugeranus* as did Archibald (1976). The Guttman/Lingoes procedure supports systematic views that favor proximity of *Anthropoides* and *Bugeranus*, placing both within *Grus* (Ingold et al. 1989), that identify *G. canadensis* as a distinct clade (leftmost taxon in cluster E: plot 2 in Fig. 1), and that cluster "Species Group *Antigone*" (*G. vipio*, *G. antigone*, and *G. rubicunda*; Krajewski 1989).

Values for species weighting of cranes depended on the topological resolution of evolutionary tree diagrams, the weighting method used (counting nodes or branches), and whether a cladistic or phylogenetic procedure was employed (Table 2). Fewer ties in ranks, and better agreement with systematic representations, are apparent when

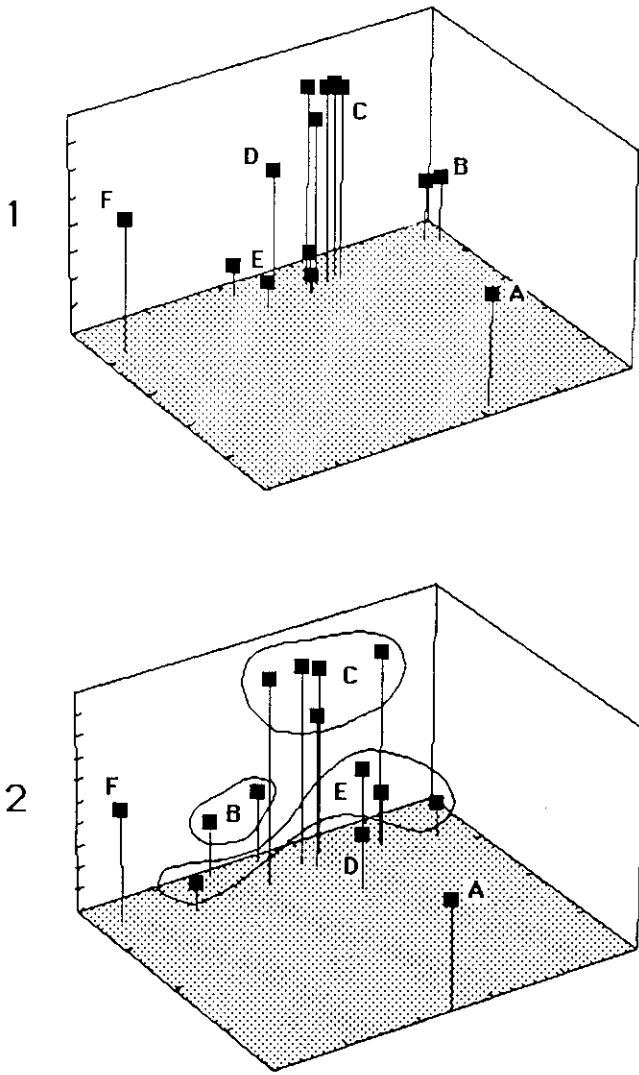


Fig. 1. Phylogenetic similarities of the world's cranes (based on Krajewski 1989) depicted with multidimensional scaling. Plot 1, with a stress value of 0.03081 for final configuration, was derived from minimizing Kruskal stress in 3 dimensions. Plot 2, with a stress value of 0.07448 for final configuration, was derived from minimizing Guttman/Lingoes coefficient of alienation in 3 dimensions. Groups of crane species are designated as follows: A = *Balearica*; B = *Anthropoides virgo*, *A. paradisea*; C = *Grus grus*, *G. monachus*, *G. americana*, *G. nigricollis*, *G. japonensis*; D = *G. leucogeranus*; E = *G. canadensis*, *G. vipio*, *G. antigone*, *G. rubicunda*; F = *Buggeranus carunculatus*.

the first 5 columns in the table are inspected from left to right. Resolution of taxonomic distinctiveness of cranes generally improved as more conveyed or encoded information was available for use in the weighting method. For example, the lowest resolution among crane taxa occurred with Archibald's (1976) phenogram and Vane-Wright et al.'s (1991) weighting procedure. Krajewski's (1989)

phenogram for cranes is more fully resolved than Archibald's, and May's (1990) procedure for counting nodes instead of branches from topologies gives fewer ties in assigning taxonomic ranks (see discussion in Vane-Wright et al. 1991:241). The best resolution, however, occurred with the phylogenetic weighting procedure. Only 1 tie occurred with this method (Table 2: column 5).

Rankings of crane taxa changed as progressively more information was used to prioritize each species (Table 2). When phylogenetic weighting, extinction risk, and population trend were combined, the 8 highest-ranked taxa included all 7 endangered or threatened species (column 7 in Table 2). The highly endangered whooping crane (*G. americana*) was ranked first, in spite of low distinctiveness and a steadily increasing population. Its placement at the top of the ranking was driven mainly by the value used for degree of endangerment (extremely low population size). The Siberian crane (*G. leucogeranus*) ranked second. This crane is both taxonomically distinct and highly endangered due to small population size and an uncertain population trend. The black-necked crane (*G. nigricollis*) ranked third. Although not particularly distinct in a taxonomic sense (column 5 in Table 2), its population is quite small (1,500–3,000; D. H. Thompson, ICF, pers. commun.) and current trends in population stability are unknown. The wattled crane (*Buggeranus carunculatus*) ranked fourth, driven by high distinctiveness and a population currently believed to be declining (D. H. Thompson, ICF, pers. commun.), albeit total numbers are still larger than in many endangered *Grus*. The Japanese crane (*G. japonensis*) ranked fifth. Placement higher in the rankings for this crane was precluded mainly by low distinctiveness and an increasing population. Occurrence of *Balearica* as the sixth-ranked form was driven mainly by its phylogenetic distinctiveness. The hooded (*G. monachus*) and white-naped (*G. vipio*) cranes tied for seventh rank. Both species breed in the same general area (Siberia, China, Korea, Japan), have similar population sizes, and have populations currently believed to be stable or increasing.

Comparisons of crane species richness to phylogenetic endowment and endowment weighted by endangerment highlights another oversight that could arise in conservation efforts. The most species-rich areas are not necessarily the most taxonomically diverse (Table 3). For example, eastern Asia has more crane species than southern Africa, but southern Africa's collection of cranes is more distinct (phylogenetic endowment of 6.76 vs. 6.44). Similarly, even though Asia has twice the number of crane species as Africa, the phylogenetic endowment of the continents is quite similar (11.00 vs. 10.50). As with weighting individual taxa (Table 2), incorporating progressively more information broke ties and produced a different final ranking of

Table 3. Geographic diversity of cranes. Ranks and computed values for toxic endowment (in parentheses) are listed by continents or subcontinents.

	Species richness	Phylogenetic endowment	
		Of taxonomic distinctiveness	Weighted by endangerment
Continent			
Asia	1 (8)	1 (11.00)	1 (2.50)
Africa ^a	2 (4)	2 (10.50)	2 (1.29)
North America	3 (2)	4 (2.83)	3 (0.97)
Europe	3 (2)	5 (2.48)	5 (0.25)
Australia	3 (2)	3 (2.89)	4 (0.29)
Subcontinent			
eastern Asia	1 (5)	2 (6.44)	1 (0.99)
southern Africa	2 (3)	1 (6.76)	2 (0.92)

^a *Balearica pavonina* was included using the distinctiveness value of *B. regulorum*.

geographic priorities for crane conservation (Table 3). According to results of our weighting procedure, Asia would receive the highest priority ranking, followed successively by Africa, North America, Australia, and Europe.

CONSERVATION AND MANAGEMENT IMPLICATIONS

Each of the weighting schemes we used for characterizing biodiversity (Table 2) has attached to it biological or computational uncertainty. This uncertainty can originate from at least 3 sources. One is computational errors within the taxonomic weighting term. Genetic distance statistics, for example, are dependent upon the specific measure used (i.e., $T_{50}H$, delta-mode, or delta T_m), reciprocity and symmetry of metric distances, the outgroup chosen for reference, and experimental error and other "signal to noise" problems inherent to DNA hybridization data (see Sibley and Ahlquist 1983, Sheldon 1987, Krajewski 1989). It is also virtually certain that better estimates for extinction risk and survival prognosis (Table 2: columns 6–7) could be obtained with additional information. If population trends can be analyzed with time-series data (e.g., whooping crane), then much better estimates of the statistical properties necessary for forecasting recovery of endangered species can be obtained (Dennis et al. 1991). The degree of fragmentation within crane populations could affect relative extinction risks; for a given population size, populations concentrated into 1 or a few subpopulations might be more subject to a single demographic or

environmental catastrophe. Also, genetic consequences of fragmentation may be substantial (e.g., Rabb 1991), leading to insufficient diversity for future founder populations. A second source of uncertainty concerns the assignment of weights to the various terms used in decision-making. For example, should taxonomic distinctiveness and current population size be given equal weight, or is one considered more important than the other? Finally, adding more terms to the analysis would likely reduce uncertainty and improve the effectiveness of the decision-making process. The costs and difficulties of captive propagation could be added to phylogenetic distinctiveness, extinction risk, and survival prognosis in order to establish broader decision criteria for cranes.

Conservation practices, and in many circumstances biological research itself, often have failed to capture and numerically evaluate the aggregate importance of living systems in ways that would be most useful for informed policy decisions (Vane-Wright et al. 1991). As May (1990) noted, the "calculus of biodiversity" has yet to be fully developed. Our exercise in comparing crane species richness to phylogenetic distinctiveness illustrates how biodiversity, expressed conventionally as species richness per unit area, may not be a sufficient criterion for such policy actions as allocating funding (Eiswerth and Haney, in press), ranking endangered species for protection (Table 2), or identifying specific areas with the greatest taxonomic distinctiveness (Table 3). Conservation priorities for cranes, which incorporated number of taxa, their distinctiveness, and degree of endangerment, provided results that are intuitively consistent with ongoing protection efforts for this group.

Part of the concern for biological impoverishment stems from the inevitable loss of genetic diversity, a non-renewable resource (Ehrlich 1988). Failure to ascertain genetic relationships also results in confusion and misdirected judgements in the task of conserving endangered taxa (see Avise 1989, Daugherty et al. 1990, O'Brien and Mayr 1991). A focus on genetic diversity, particularly genomic measures of taxonomic distinctiveness such as DNA-DNA hybridization, can augment the conservation of biodiversity. Explicit incorporation of genetic information also serves to bridge the taxonomic and genetic components ascribed to diversity (Westman 1990).

Because metric measures of taxonomic distinctiveness, like those we used for cranes, are not limited solely to the species level of taxonomy, they could theoretically account for diversity across all taxonomic levels, including the generic, familial, and ordinal. There is, in fact, no need to assign categorical statuses if metric measures are used. We believe measures that assign high-resolution, weighted values to individual taxa offer practical improvements over

diversity measures derived solely from hierarchical classifications. Diversity measures based on topologies of evolutionary trees may give the undesirable value of zero for a set containing only 1 species (e.g., Altschul and Lipman 1990), thus precluding any basis for decisions between 2 sets of 1 species each. Given the common occurrence of incompletely resolved phenograms and resultant ties (Table 2: columns 1–4), such measures may not provide decision criteria if conservation choices are to be made across even several species (cf. Table 2: column 5, May 1990, Vane-Wright et al. 1991). Because they can be used in a broader array of circumstances (e.g., see Table 1), metric measures can be used singly or collectively to compare more realistic representations of biodiversity endowment across habitats, geographic areas, and other management units.

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