

WHAT TO PRESERVE? AN APPLICATION OF DIVERSITY THEORY TO CRANE CONSERVATION*

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This paper attempts to demonstrate how “diversity theory” can be applied to the analysis of real-world conservation policies. The specific example chosen to serve as a paradigm concerns preservation priorities among the fifteen species of cranes living wild throughout the world. The example is sufficiently actual to show how diversity theory can be used operationally to frame certain critical conservation questions and to guide us toward answers by providing informative quantitative indicators of what to protect. At the same time the cranes example is rich enough that it illustrates nicely some broad general principles about the economics of diversity preservation.

I. INTRODUCTION

Conservation policy often appears to take place in an analytical vacuum. Frequently, it is not clear what we are supposed to be conserving or what are the relevant trade-offs. The lack of a coherent operational framework seems especially acute when it comes to issues concerning the preservation of biodiversity.

The major unresolved conceptual problem would appear to be about defining an operationally meaningful value of diversity function. If diversity cannot be measured, it is difficult to comprehend how rational decisions are supposed to be made about how best to preserve it.

This paper shows how “diversity theory” can be applied to analyze conservation policy: by using the vehicle of a particular example as a metaphor. The specific example concerns preservation issues among the fifteen species of cranes living wild throughout the world. This example is sufficiently realistic to show how diversity theory can be used operationally to frame certain critical conservation questions and to guide us by providing informative quantitative indicators of what to protect. At the same time the crane paradigm is rich enough that it can be used to illustrate nicely some broad general principles of diversity preservation that go beyond the specific example of cranes.

The paper proceeds as follows. The next section discusses some

*Without implicating them in any errors or conclusions, I would like to thank Scott Swengel and Carey Krajewski for their useful comments on a previous draft of the paper. An editor of this *Journal* made several helpful suggestions on presentation.

general considerations about the purposes and limits of the analysis. This is followed by a presentation of some background information on cranes and crane conservation, along with some relevant data. An attempt is made to pose basic issues in crane conservation in such a way as to motivate the transition to diversity theory. Then diversity theory is introduced and applied to put some structure on the raw data of the problem. Through the intermediary of converting the data into expected present discounted diversity functions, summary statistics relevant for conservation diagnostics are calculated. It is shown how such numbers can be used to analyze policy options for preserving diversity.

Throughout the exercise the paradigmatic aspect of the cranes example is emphasized. My underlying supposition is that general methodological issues and general conclusions about the nature of optimal preservation strategies are best conveyed by a specific "teaching example," like the crane conservation parable chosen to be the centerpiece of this paper. While I believe the example is accurate enough to warrant some faith in a few of the actual conclusions, the main purpose of the exercise is to tell a parable about how, in principle, a conservation problem involving "preservation of diversity" might be analyzed, rather than to draw specific conclusions in this particular case.

II. PURPOSES AND LIMITATIONS OF THE ANALYSIS

The economic problem of how best to preserve diversity (under various resource constraints) is ill defined so long as a value-of-diversity function is not specified. It is this nonclassical aspect of the problem that provides a major source of frustration (and fascination) with trying to make analytical sense out of the idea of maximizing diversity.

In a previous paper published in this *Journal*, "On Diversity" [Weitzman, 1992], I tried to argue that a particular form of diversity function seemed especially appealing on theoretical grounds. Here I want to show how that diversity function might be applied to analyze a specific problem in biodiversity preservation. In so doing, I wish to make clear at the outset some limitations of the analysis.

It seems that increasingly many people believe that there is some inherent value in preserving diversity, even though they cannot exactly define what it is. As economists, either we can walk away from this problem on the grounds that there is ambiguity in

the basic concept, or we can attempt to put some structure on the concept of diversity. This paper takes the constructive route. Using the definition of a diversity function I previously developed on theoretical grounds, I attempt here to apply the apparatus to shed light on the nature of diversity-optimizing policies in a specific example.

This paper is not the first attempt to study the problem of biodiversity preservation. For references to related works, see the relevant citations in Weitzman [1992]. Especially noteworthy is the pioneering study of Solow, Polasky, and Broadus [1993], which seems to be the first paper that introduces an explicit decision-theoretic framework for dealing with biodiversity preservation.

It is important to be clear about what is meant here by "diversity." People frequently cite conservation of diversity as a reason for mounting extraordinary efforts to preserve, say, the whooping crane. What they often really mean is that the whooping crane should be preserved because it is beautiful, or majestic, or inspiring, or because its presence confers some other direct benefit. I would say that these qualities, while important, do not really concern the value of "diversity" per se. Diversity is more a measure of distinctiveness or dissimilarity.

The idea of diversity that this paper uses is essentially a measure of collective dissimilarity. The overall objective in an actual conservation problem might well include direct benefits (such as use value, existence value, and so forth) that are not reflected by my value of diversity function. This paper does not provide a comprehensive analysis of all the relevant factors that might enter into conservation policy. Rather, it concentrates almost exclusively on the pure diversity aspect of the problem.

The paper provides a paradigmatic example of how "diversity theory" can be used to get a useful quantitative handle on the value of diversity under various scenarios. Quantitative information on the value of diversity is an important ingredient in making rational preservation policies, but it is not the only ingredient. Nothing in the theory prevents adding together direct benefits, however appraised, with the value of diversity function to obtain a more comprehensive objective function. It is primarily for pedagogical purposes that I concentrate here exclusively on the diversity function, since this is the more nonclassical and novel aspect of the problem. The other part can always be added on later, with predictable consequences.

There is another conceptual limitation of the paper that needs

to be addressed: namely, the proper unit of analysis. It is not immediately clear in all conservation settings at what level the diversity problem should be attacked. In principle, diversity could be measured at the individual level, the species level, the community level, the ecosystem level, or even some other levels. In this paper I do not attempt to address directly the difficult issue of which conservation unit is the most appropriate for performing diversity analysis. Instead, I limit myself to a particular example defined at the species level. I believe that many of the same issues and themes addressed in this paper will be relevant, with appropriate modifications, for an analysis of diversity policies at any level, but I have not yet worked out the details of any other specific numerical examples.

III. THE PROBLEM OF CRANE CONSERVATION

In several ways, cranes are a near-ideal example for exploring the wildlife conservation problem.¹ Cranes are very large and very beautiful birds. Their graceful majesty, spectacular bugling calls, elaborate dances, and impressive migration flights have inspired awe in people throughout history and have long been reflected in art and literature. So wild cranes are highly visible animals of the attractive, interesting sort that people identify with and care about.

In large part because they are relatively specialized creatures whose habitats have become threatened by development pressures, many crane species are endangered. The combination of being cared about and being endangered has made cranes a high-profile symbol of wildlife conservation. Perhaps for this reason, relative to their scarcity and elusiveness, comparatively good information and data are available on conservation-related aspects of the various crane species.

The crane family (Gruiformes: Gruidae) is commonly accepted as consisting of fifteen extant species. Each species is currently living in the wild, although tenuously in several instances. These fifteen species are listed in Table I, along with some relevant factual information.

The probability of extinction in Table I refers to the probability that the given crane species will become effectively extinct in the

1. For general information about cranes and crane conservation, see Johnsgard [1983], Archibald and Mirande [1986], and Schoff [1991].

TABLE I
CRANE INFORMATION SHEET

Number	Common name	Scientific name	Geographical range	Extinction probability
1	Black crowned	<i>Balearica pavonina</i>	Central Africa	0.19
2	Grey crowned	<i>Balearica regulorum</i>	South-East Africa	0.06
3	Demoiselle	<i>Anthropoides virgo</i>	Central Asia	0.02
4	Blue	<i>Anthropoides paradisea</i>	South Africa	0.10
5	Wattled	<i>Bugeranus carunculatus</i>	South-East Africa	0.23
6	Siberian	<i>Grus leucogeranus</i>	Asia	0.35
7	Sandhill	<i>Grus canadensis</i>	North America	0.01
8	Sarus	<i>Grus antigone</i>	South-East Asia	0.05
9	Brolga	<i>Grus rubicunda</i>	Australia	0.04
10	White-naped	<i>Grus vipio</i>	East Asia	0.21
11	Eurasian	<i>Grus grus</i>	Europe, Asia	0.02
12	Hooded	<i>Grus monachus</i>	East Asia	0.17
13	Whooping	<i>Grus americana</i>	North America	0.35
14	Black-necked	<i>Grus nigricollis</i>	Himalayan Asia	0.16
15	Red-crowned	<i>Grus japonensis</i>	East Asia	0.29

Source. see text.

wild at some time over the next 50 years. Equivalently, one minus the extinction probability represents the probability that the given crane species will have survived as a wildlife species 50 years from now.²

It is important to recognize that the extinction probabilities listed in Table I are just "best guesses" compiled after consulting with several crane experts.³ While ultimately based on estimates of current population size and its likely future trends, the 50-year extinction probabilities are not generated by any sort of consistent underlying demographic methodology or rigorous population model. Actually, there does not seem to be a very wide range of disagreement among knowledgeable crane specialists about the appropriate ordinal rankings from most to least endangered species. (There is more disagreement about the absolute value of survival probabili-

2. As crane species can be induced to breed in captivity, albeit with greatly differing success rates, there does not seem to be such an acute problem concerning the survival of crane species in general. The major problem concerns the existence of crane species in the wild.

3. Specialists who were consulted about crane extinction probabilities include Dr. George Archibald, Professor Carey Krajewski, Ms. Claire Mirande, and Mr. Scott Swengel. I am grateful to them for sharing generously with me their knowledge and insights. But I should make clear that none of these individuals necessarily approves of the numbers I am using, nor the uses to which they are being put in this study, nor, for that matter, the study itself.

ties.) I think that the probability estimates of Table I are sufficiently robust to support the kinds of guarded conclusions I shall draw, but in any event they can serve well enough as elements of the conservation parable I am trying to tell. An important part of any analysis is to indicate its sensitivity to underlying data changes, and I shall comment on this aspect sporadically throughout the paper. Actually, the quantitative requirement of specifying survival functions seems somewhat less problematical for the present example of crane preservation than it does in most other conservation settings, although perhaps this is damning by faint praise.

Cranes are native to every continent except South America (and, of course, Antarctica). The eight crane species of the holarctic northern regions are primarily migratory. The seven crane species of tropical and subtropical regions are nonmigratory. Both types are subject to population pressures. Migratory species must pass through vulnerable bottleneck areas between widely separated breeding and wintering grounds. Their wintering habitat is typically in the southern regions of the northern continents, where provision of sufficient food and cover competes with human development. Nonmigratory species do not have to undergo the rigors of traversing a great geographic range, but some of them are located in third-world areas where there is extreme year-round pressure from rapidly growing numbers of poor people who are preoccupied with many things other than wildlife conservation.

The extinction probabilities of Table I are themselves uncertain for a variety of reasons. While we may have decent current population estimates for some species, we are much less sure about future projections. Even for highly protected species in economically advanced areas, recovery dynamics and vulnerability to natural catastrophes, like infectious diseases, of small concentrated breeding populations are imperfectly understood, while the outcomes of various captive breeding and reintroduction programs are unsure. All crane species depend on the status of wetland and grassland areas, which themselves depend on environmental and man-made changes that are not always easy to foresee but can have significant consequences. We are not exactly sure how to weigh the survival chances of large populations that seem to be declining against the survival chances of small populations that seem to be increasing. Perhaps the greatest uncertainty of all concerns the future economic, political, and social environments in poor third-

world countries and how this factor might play itself out in affecting various conservation scenarios.

The starting data for the survival probabilities of Table I are estimates of current population size. Population numbers alone, however, are not nearly sufficient for determining 50-year mortality probabilities, for reasons that have just been indicated.

For example, the size of the sole existing wild whooping crane flock is about 150, a frightfully low number taken by itself. But that number represents a spectacular recovery from just sixteen individuals in 1941. Furthermore, the whooping crane flock migrates between two well-defined, highly protected areas in Canada and the United States, stable and wealthy countries that have made a strong environmental commitment to preserve and expand the species.

The Siberian crane, on the other hand, has a wild flock size of about 2,500, a low but perhaps not frightful number. However, the Siberian's population has been steadily declining. And the Siberian crane has the longest migratory flight of any species—over 5,000 dangerous miles from its summer breeding grounds in northern Siberia to its wintering grounds in China (India and Iran for the near-extinct western flock). Thus, the Siberian passes through less developed countries, which have a relatively low or unstable level of environmental commitment and where there is much pressure from human encroachment. Additionally, the Siberian is a highly specialized crane, dependent on specific wetland habitats for survival, several of which happen to be threatened. Therefore, although the Siberian is currently much more numerous in the wild than the whooper, they are both ranked equally in Table I as the two "most endangered" crane species over the next 50 years.

Analogous reasoning goes into the construction of the other extinction probabilities. The black crowned and wattled cranes presently have relatively good population numbers, but are declining at an alarming rate because they are located in unstable third-world habitats subject to extreme human encroachment pressure. The brolga crane does not have a notably large population, but it seems relatively secure in most of its current habitat. At the opposite extreme from the whooping or Siberian crane is the sandhill crane, which has a very large population spread over a wide range and seems to be a robust generalist species that adapts relatively well to cohabitation with humans. And so forth.

The picture I wish to convey here is that while the extinction probabilities given in Table I are not rigorously or objectively

derived, they are not arbitrary either. They represent a rough consensus of opinion among crane experts who were consulted, and reflect underlying considerations like what I have described.

To sum up, the extinction probabilities I shall use provide a good working start for analyzing conservation issues from today's perspective, but they should not be viewed as completely accurate or immutable, as some of them will doubtless change over the coming decades.

Having dealt, more or less, with extinction probabilities, there are two other necessary pieces of information that are needed to perform a rational overall analysis of diversity-conservation policies. There is a need to have some sense of the costs of altering the various extinction probabilities. The discussion of this cost aspect will be postponed until later in the paper. The other missing ingredient is the most conceptually difficult of all. It concerns the value of diversity. The stated aim of many conservation-minded groups and individuals is to maintain the maximal amount of diversity. How, then, should diversity be measured so that its correctly defined loss might be minimized?

When a crane species goes extinct in the wild, there is a loss of diversity because the family of wild cranes has been diminished. Intuitively, the magnitude of the diversity loss should be related to how *different* the extinct crane is from the surviving cranes. Other things being equal, there is greater loss of diversity when the extinct crane has no close relations among the survivors than when its nearest relation is comparatively close to it. (In the limit of absolutely identical populations, there is no loss of diversity per se from an individual extinction event.) The problem is to turn this general intuition into an operational formula that measures the diversity of any collection of cranes.

A plausible approach might be to try to construct the diversity function of a set of species out of more fundamental information about the pairwise dissimilarity or distance between any two species of the set. The point is not that such pairwise distance-dissimilarity measures are easy to define or obtain. The point is rather that if dissimilarity cannot be defined for a pair of objects, it is difficult to imagine how diversity, which is intended to be a generalization of the concept of dissimilarity to a collection of many objects, can be defined. If this philosophy is accepted, it throws the problem back in the first instance to an appropriate definition of dissimilarity-distance between species.

Table II presents estimates of genetic distances between all

TABLE II
CRANE DISTANCES

		Species number														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
1	0	86	417	382	392	362	384	372	393	389	336	388	399	364	390	
2	86	0	382	387	408	348	392	368	362	401	355	400	371	351	360	
3	417	382	0	60	113	180	141	149	123	150	110	104	142	156	147	
4	382	387	60	0	138	191	137	173	109	156	111	117	138	117	168	
5	392	408	113	138	0	142	116	143	138	168	115	148	129	121	103	
6	362	348	180	191	142	0	140	107	143	190	121	143	166	144	144	
7	384	392	141	137	116	140	0	136	125	145	114	138	151	176	138	
8	372	368	149	173	143	107	136	0	54	71	112	167	138	146	120	
9	393	362	123	109	138	143	125	54	0	105	111	135	154	181	124	
10	389	401	150	156	168	190	145	71	105	0	145	144	180	166	129	
11	336	355	110	111	115	121	114	112	111	145	0	7	29	53	24	
12	388	400	104	117	148	143	138	167	135	144	7	0	43	63	33	
13	399	371	142	138	129	166	151	138	154	180	29	43	0	72	62	
14	364	351	156	117	121	144	176	146	181	166	53	63	72	0	59	
15	390	360	147	168	103	144	138	120	124	129	24	33	62	59	0	

Units. degrees centigrade multiplied by 100.
Source. see Appendix.

pairs of the fifteen living species of cranes. The derivation of the numbers in this table is explained in the Appendix. For the purposes of the main body of this paper, it suffices to understand that the numbers in Table II are pairwise estimates of the degree of genetic dissimilarity between two species. Essentially, the distances of Table II are roughly proportional to the amount of base-pair mismatch between the underlying DNA of the two species, obtained ultimately from experimental data. Under further assumptions about the relative constancy among crane species of their "molecular clock," the distances of Table II are approximately proportional to the time ago that the two species diverged. Presumably, the measures of genetic differences given in the table are loosely related to some phenetic differences, so that to some crude extent the distances may reflect physical and behavioral differences between crane species as well—but this is a much more controversial sort of proposition.⁴

4. Generally speaking, well-measured genetic distances have proved at least as reliable as phenetic considerations in reconstructing phylogenies. Typically there is good correlation between the two approaches.

Genetic relatedness is not the only possible measure of dissimilarity. In principle, the model of this paper could incorporate physical or behavioral differences, if they could be quantified.⁵ Also, in principle there would be no difficulty including intraspecies diversity, or subspecies diversity, if these measures were empirically known. I am here using genetic distances between species primarily because such numbers have been empirically measured, and only secondarily because genetic distances might be conceptually superior to the alternatives for the purposes of this study.⁶

As I have previously stressed, this paper is focused on the key conceptual element of obtaining estimates of the value of diversity. Other elements that might be involved in preservation decisions, like any direct benefits of species, are temporarily repressed for the pedagogical aim of focusing sharply on the pure diversity aspect.

In the spirit of constructively moving ahead, suppose, for the sake of argument, that the genetic distances of Table II are tentatively accepted as representing the best approximation of pairwise diversity-distances that can be provided.

The next question is how to convert these measures of pairwise dissimilarity-distance between species into an overall measure of the diversity of a set of species. This issue is worthy of serious theoretical study in its own right, but a full treatment transcends the scope of the present paper.⁷ The basic message is that the approach to diversity taken here can be theoretically justified, at least to some degree. The purpose of this paper is to show that the theory is operational enough to actually be useful in analyzing conservation strategies.

Let

$$(1) \quad d(i, j)$$

stand for the dissimilarity-distance between species i and j . (In the present case, $d(i, j)$ would be read out of Table II.)

5. The studies of Archibald [1976] and Wood [1979] are in this direction, although they do not present distance estimates.

6. If we wanted to, we could argue for a long time about whether or not the genetic distances of Table II are the appropriate inputs to use for a diversity measure. But such an argument might easily miss the point. If critics do not like the genetic distances of Table II as measures of pairwise diversity-distance, that is fine, but in fairness they are obliged to propose some better distance measure. We might then proceed from their proposed distances to a diversity function in much the same way that the rest of this paper will proceed. It is not constructive to criticize a set of dissimilarity-distances in the abstract. If you cannot or will not define the diversity of a pair of species, then there is almost no hope of being able to define the diversity of a collection of species. And if you cannot define or measure diversity, then it is very difficult to speak meaningfully about the best way to preserve it.

7. See Weitzman [1992] for a full theoretical treatment.

Let Q be any subset of species. (In the present case, think of Q as any subcollection of surviving cranes at some indefinite future time, the rest of the crane species having become extinct in the wild.) Let j be any species not belonging to Q . (In the example, j is a species of crane that became extinct as wildlife.)

Let $d(j, Q)$ be defined as the distance from species j to set Q :

$$(2) \quad d(j, Q) \equiv \min_{i \in Q} d(j, i).$$

(In words, $d(j, Q)$ is the distance between the extinct crane species j and its closest relative among the set of surviving crane species Q .)

The definition of diversity will be recursive.

For any set S , the diversity function $V(S)$ is defined to be the solution of the recursion:

$$(3) \quad V(S) = \max_{i \in S} \{V(S \setminus i) + d(i, S \setminus i)\},$$

where $S \setminus i$ stands for the set S without the element i .

The dynamic programming equation (3) is the theoretical centerpiece of the present paper. The diversity of a set is the maximum, over all members of the set, of the distance of that member from its closest relative in the set plus the diversity of the set without that member. This is not the place to discuss why (3) might be a "good" definition of diversity, as this issue has been addressed in much detail elsewhere.⁸ Suffice it here to note that a rather rich theory of diversity can be built around equation (3); in this applied paper we shall draw on just a few specific features of the theory.

The solution of (3) is unique once the initial conditions,

$$(4) \quad V(i) \equiv d_0,$$

are specified for all species i and any large d_0 . (In the present example, d_0 can be specified as the common genetic distance from each crane species back to the nearest outgroup relative of the crane family, the limpkin *Aramus*. From Krajewski's work, $d_0 = 680$ is an appropriate value to use in this case.)

IV. THE MAXIMUM LIKELIHOOD EVOLUTIONARY TREE OF CRANES

Now it is a basic result of diversity theory (called the fundamental representation theorem) that the solution of (3) generates a

8. See Weitzman [1992] for a full theoretical treatment.

genealogical tree that can be interpreted as a "maximum likelihood" evolutionary tree in some sense.⁹ This taxonomic tree, which is derived from the data of Table II and represents the "most likely" evolutionary branching pattern that gave rise to the fifteen existing crane species, is depicted in Figure I.

A detailed treatment of the statistical interpretation of evolutionary trees is beyond the scope of this paper.¹⁰ However, the main features of genealogical relations are important in interpreting the application of diversity theory to preservation issues, and so I shall summarize here the story being told by the Figure I depiction of the crane data. The maximum likelihood tree of crane evolution depicted in Figure I indicates several relational features among the crane species that will be useful to bear in mind when interpreting the conservation diagnostics to be introduced later.

The diagram indicates clearly that the two crowned-crane species represent a separate lineage that branched off from the remaining crane species a long time ago. *Balearica pavonina* and *Balearica regulorum* are relatively close to each other but are relatively extremely distant from any of the other thirteen living crane species. This visual interpretation of the maximum likelihood evolutionary tree can be supported at an extremely high level of statistical confidence.

The next statement of taxonomic structure, in which we can have a quite high degree of confidence, is that the two *Anthropoides* species, *virgo* and *paradisea*, are each other's closest living relations among the crane species.

The genealogical tree seems to be showing that the five holarctic species numbered 11 through 15 are relatively tightly clustered together as a clade. This conclusion can be held at a respectable, if not extraordinarily high, confidence level. The five species of what might be called the "americana group"—*G. grus*, *G. monachus*, *G. americana*, *G. nigricollis*, and *G. japonensis*—are all very close to each other and of moderate distance from their next closest crane relations.¹¹

A somewhat weaker structural statement, which has about a three out of four chance of holding in a maximum likelihood

9. See Weitzman [1992] for an exposition of this "maximum likelihood interpretation."

10. See Weitzman [1991] for a treatment of the connection between diversity theory and "maximum likelihood evolutionary trees" (as I am defining them), including an application to the crane data of this paper. The probabilistic statements in the text are summaries from that paper.

11. The term "americana group" was used by Archibald [1976].

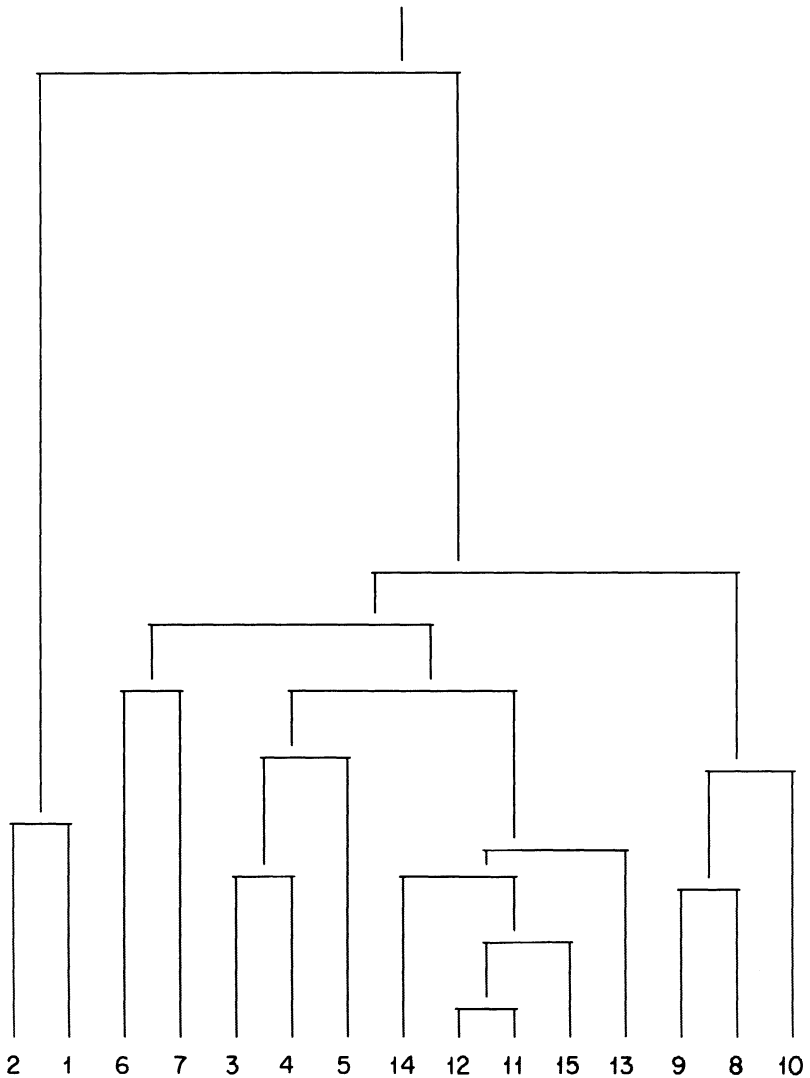


FIGURE I
The Maximum Likelihood Tree Representation

taxonomy, is that the sarus (*G. antigone*) and brolga (*G. rubicunda*) cranes are sister species. Finally, there is a greater than even chance that the trio of *Grus* species *antigone*, *rubicunda*, and *vipio* can be grouped together in a clade.

After the above statements, it is difficult to have significant

confidence in any further taxonomic structure. In particular, we do not know with any reasonable degree of assurance the correct placement within the non-crowned crane subfamily of the three crane "mystery species": the wattled (*Bugeranus carunculatus*), the Siberian (*Grus leucogeranus*), and the sandhill (*Grus canadensis*). The maximum likelihood tree of Figure I by definition places all of the cranes in a maximum likelihood configuration, but further statistical probing reveals that the placement of species 5, 6, 7 is particularly sensitive to relatively small errors in the data.¹² This may present a problem for the taxonomist, but it is not a particular problem for the analytical preservationist. Whatever the evolutionary history of these three enigmatic species, they are quite distant, and therefore different, from their nearest crane relatives. (Indeed, this is part of the reason why species 5, 6, 7 are difficult to place exactly in an evolutionary tree: we know they branched off on their own some time ago, but we are unsure *from what* they branched off.)

The visualization of crane relationships depicted in the maximum likelihood evolutionary tree, along with the above description of what we are entitled to infer about the stability of certain subgroup relations, will prove useful in what follows. Essentially, the diversity function defined by the recursive equation (3) can be geometrically represented as the total branch length of the corresponding tree that the equation generates.¹³ As a very rough approximation, when a species goes extinct, the diversity lost is its corresponding branch length, and to some degree, depending on the accuracy of the underlying approximation, this formula can be repeated over multiple extinctions. Properly interpreted, the maximum likelihood tree conveys an enormous amount of intuitively useful information relevant to the preservation of diversity: in the form of a simple two-dimensional picture that is easily comprehended by most people.

V. EXPECTED CRANE DIVERSITY

Having defined diversity, we are now in a position to define expected present discounted diversity, and then, in the next section, to analyze what it depends upon.

12. See Weitzman [1991] for the details.

13. Again, this is a deep theoretical result that is developed fully in Weitzman [1992].

Each crane species has a probability of going extinct in the wild over the next 50 years that is given in Table I. The distance-dissimilarity relations between crane species are given in Table II. Now the two pieces of information will be combined.

We need to assume some mortality function for each crane species. The easiest and most natural assumption is that the survival functions are independently exponentially distributed with mortality parameters fixed by the 50-year extinction probabilities given in Table I. This makes all calculations relatively straightforward because it is easy for a computer program to handle polynomials and geometric series. But, as I hope is clear, the methodology is general and could readily handle more complicated scenarios if anyone had a good reason to specify them.

Let

$$(5) \quad P_i$$

represent the probability that species i goes extinct as wildlife over a 50-year period given that it existed at the beginning of the period. For $i = 1, 2, \dots, 15$, the extinction probabilities $\{P_i\}$ are given in Table I.

If i, j , and k are three currently existing species, the probability that i and j will have survived while k has gone extinct after t periods (meaning in this example $50t$ years from now) is

$$(6) \quad (1 - P_i)^t(1 - P_j)^t(1 - (1 - P_k)^t).$$

Using a relationship like (6), for each of the 2^{15} possible survival-extinction patterns among the fifteen species of cranes, we can calculate the probability of any particular survival-extinction pattern occurring t periods hence for any positive integer t . And, for each collection of existing species, we can calculate from equation (3) the diversity of the collection. Once we specify a discount rate, it is a routine brute force calculation for the computer to calculate an *expected present discounted diversity function*. If $P(Q,t)$ is the survival probability of collection $Q \subseteq S$ existing in period t (meaning collection $S \setminus Q$ has gone extinct by period t), and α is the one-period discount factor, then expected present discounted diversity is

$$(7) \quad EV \equiv \sum_i \sum_Q P(Q,t) V(Q) \alpha^t.$$

In this problem, expected present discounted diversity is a function of the extinction probabilities, the matrix of dissimilarity-distances, and the discount rate.

For a base-case scenario I chose an annual discount rate of 2.5 percent. Having tried several alternatives, I can testify that there is no substantial difference in the story to be told when annual discount rates vary in a range from 1 percent to 5 percent, although, of course, some of the relevant policy numbers are changed. Later I shall indicate what is the main effect, even if it is of second order in this range, of changing the rate at which the future is discounted.

Now the basic ingredients are in place to perform some diagnostic mental exercises in the conservation of crane diversity.

VI. DIVERSITY PRESERVATION DIAGNOSTICS

Table III contains some numbers that are useful in obtaining an overall perspective on the worldwide crane preservation problem.

Given the framework of this paper, we have seen how expected present discounted diversity functions can be calculated. Then it is but a small step to compute (finite difference) partial derivatives of the diversity function with respect to (slight) differences in the

TABLE III
CONSERVATION DIAGNOSTICS

Species number i	Probability of extinction $P(i)$	Marginal diversity $-\frac{dV}{dP(i)}$	Elasticity of diversity $-\left(\frac{dV}{dP}\right)(i) * \left(\frac{P(i)}{V}\right)$
1	0.19	8.7	11.3
2	0.06	14.1	5.8
3	0.02	7.0	0.9
4	0.10	4.8	3.3
5	0.23	7.8	12.3
6	0.35	10.3	24.6
7	0.01	11.1	0.8
8	0.05	4.7	1.6
9	0.04	6.5	1.8
10	0.21	9.2	13.1
11	0.02	1.3	0.2
12	0.17	1.4	1.6
13	0.35	4.5	10.7
14	0.16	5.8	6.3
15	0.29	2.9	5.7
		100.	100.

underlying probabilities of species extinction. This is done for all fifteen crane species and presented in two ways in Table III.

The column titled marginal diversity reports the partial derivative of expected present discounted diversity with respect to extinction probabilities for each crane species, normalized to add up to 100. These numbers represent the marginal rates of substitution among extinction probabilities along an isodiversity surface. They tell us the relative payoff, in terms of expected discounted diversity, of improving the survival probabilities of the various crane species.

If we knew the relative costs of specific projects that might improve survival probabilities of the different crane species by various amounts, we would be well on our way to having an operational framework for selecting the most effective diversity-improving investment strategy from a global perspective. A "project" in this context is a conservation action that improves the survival probabilities by some amount of one or possibly several sympatric species, but at a certain cost. An optimal strategy might select projects to maximize present discounted expected diversity subject to something like a budget constraint. I shall not push the analysis too hard in this direction for lack of any firm cost data on survival-probability-improving projects, but it should be pretty clear how one would proceed along this path to its logical conclusion.

Some revealing insights emerge from even a casual study of relative marginal diversities.

The extremely endangered whooping crane does not have a particularly high marginal diversity in the overall scheme of things because it belongs to the closely related cluster of *americana* cranes (species 11 through 15). Even if the whooping crane ceased to exist, there is a very low probability that all of the members of this tight-knit clade will become extinct in the near future, especially, but not only, because the Eurasian crane has such a high survival probability. The same comments apply with even greater force to the highly endangered red-crowned crane.

Some members of the *americana* group (species 11 through 15) are identified with the rich, highly developed countries that constitute part of their natural range: the whooping crane with the United States and Canada, the Eurasian crane with Scandinavia, the red-crowned and hooded cranes to some extent with Japan. Such high-income environmentally-conscious countries have naturally expended relatively significant resources on preserving "their"

cranes.¹⁴ This is arguably as it should be. But, the analysis of this paper is tending to show, from a worldwide perspective of preserving overall crane biodiversity, the *americana* group is not the major problem area.

The second highest marginal diversity belongs to the most secure species of all: the sandhill crane. There is a greater payoff in expected diversity to raising the survival probability of the sandhill crane from 0.99 to 0.995 than there is to raising the survival probability by 0.005 of any other species except the grey crowned crane. (Of course, it may well be more difficult or costly to lower the extinction probability of the sandhill crane from 0.01 to 0.005 than it is to lower the extinction probability of the whooping crane from 0.35 to 0.345—more on this later.) The reason why the secure sandhill crane has such a high marginal diversity is that the marginal diversity of a species is more dependent on the distance of that species from its closest secure relative than on its degree of endangerment per se. The sandhill crane has no close relatives, whereas the whooper has several. Therefore, an extra amount of tiny survival probability is more effectively placed on the sandhill than the whooper, if that choice is available, even though the sandhill is the least, and the whooper the most, endangered species. Actually, this effect is even stronger than the above example suggests—as the following comparison shows.

The two African crowned cranes have almost identical distances from each of the other thirteen crane species. The grey crowned and black crowned cranes are almost perfectly symmetrical in their relation to other crane species. The only significant difference is that the central-African black crowned crane is, according to the probability numbers presented here, more than three times as endangered as the southern-African grey crowned crane. (This is primarily because the black crowned is located in drought-sensitive, poverty-stricken areas of the African Sahel, subject to explosive human population growth and civil unrest.) Yet, seemingly paradoxically, the black crowned crane has significantly *lower* marginal diversity than the grey crowned crane. If 0.01 of survival probability could be taken away from the relatively endangered black crowned, so that its extinction probability went up to 0.20, and given to the relatively safe grey crowned crane, so that its extinction probability went down to 0.05, then expected

14. The whooping crane is a well-known inspiring example. See Doughty [1989] for a readable account of this story.

diversity would be *increased*. How can this seemingly paradoxical result be rationalized, and what does it mean for conservation policy?

I shall give an answer in terms of a two-period model, but the effect generalizes, and is actually strengthened, for a multiperiod horizon.

From the numbers in Table I, the probability of both crowned cranes surviving in the wild is $(0.81)(0.94) = 0.7614$, while the probability of both crowned cranes becoming extinct in the wild is $(0.19)(0.06) = 0.0114$. After the hypothetical transfer of 0.01 of survival probability from *pavonina* to *regulorum*, the probability of both crowned cranes surviving is $(0.80)(0.95) = 0.76$, while the probability of both cranes going extinct is $(0.20)(0.05) = 0.01$. The net effect of the thought experiment is to decrease the probability of both crowned cranes surviving by 0.0014 and to decrease the probability that both crowned cranes become extinct by the same 0.0014.

Now it would, of course, be good for diversity to have both crowned cranes survive. But it would be a significant disaster for biodiversity if both crowned cranes went extinct, because a whole lineage would then have been extinguished. Therefore, other things being equal, the analytical preservationist favors making the safe species safer at the expense of making the endangered species more endangered, because a whole line may therefore be made safer—if a one-to-one trade-off of survival probabilities is possible.

Continuing the seeming paradox, other things being equal the strength of this effect is greater when there is a longer time horizon or a lower discount rate. The reason is that, to be realistic, the relatively endangered species is not expected to be around as long as the relatively safe species. Therefore, features like long time horizons or low discount rates that weigh the present less heavily relative to the future will only strengthen the above-described optimal conservation policy of making the safe species safer at the expense of letting the endangered species become more endangered.

The policy outlined above, which is optimal *if* the structure of preservation costs is such that there is a one-to-one trade-off between survival probabilities, is completely opposite to what might be construed as current conservation strategy, including the conservation strategy of the U. S. government as embodied in such laws as the Endangered Species Act. To the extent that there is a coherent biodiversity conservation policy, it seems to involve

waiting until a species is on the brink of extinction and then paying no attention, or at least very little attention, to the underlying cost trade-offs involved in protecting that species—sometimes seemingly at almost any cost. If the message of the above example rings true, it may already be too late when a species is considered endangered. It may be much more economical to spend scarce biodiversity conservation dollars to prevent threatened species from becoming endangered in the first place than to expend relatively large resources on expensive high-visibility efforts to prevent already highly endangered species from going over the edge. Of course, this analysis takes a coldly technocratic view of biodiversity. It could well be that in certain instances there may be important benefits, like raising consciousness or feeling good, that are not factored into the analysis.

The issues underlying the “crowned-crane paradox” are likely to be complicated in practice, and the outcomes depend very specifically on how much it costs to reduce extinction probabilities of various species. But there is at least the germ of an argument that current biodiversity conservation strategy, to the extent that there exists one, may be fundamentally flawed in the sense that it is not at all close to minimizing the expected loss of diversity. At the very least, I think the message that comes out of this example is that relative costs of changing survival probabilities are important ingredients of any rational policy and that it makes sense to look hard at indicators like expected diversity gain per conservation dollar. An efficient diversity conservation strategy would always move toward equalizing marginal diversity per dollar’s worth of extinction-probability change, but we seem to be a long way from a world where such conditions hold on the margin.

At a high level of abstraction, a conservation “project” is an investment in preserving or improving a natural habitat that raises the survival probabilities of some diversity-increasing elements. (In Nature Conservancy terminology the “elements” of a site are rare species or ecological communities.) Conceptually, society wants to fund the preservation of sites that contribute a lot to diversity relative to their opportunity costs. The logical next step in the exercise of this paper is to plug in costs of reducing extinction probabilities for each crane species, and then to examine where is the greatest potential gain in expected biodiversity for a given budget constraint. Computationally, this step is easy to take because the analytical apparatus has already been developed and is in place. But at this stage the requisite data on costs of reducing

extinction probabilities are just not there except as crude back-of-the-envelope calculations. It should be a high priority of environmental research to develop formally such cost figures. Still, even without having formal estimates of the costs of specific conservation projects that would reduce extinction probabilities for the various crane species, it is possible to get some sense of overall worldwide biodiversity priorities.

The counterintuitive crowned-crane paradox hinges crucially on the assumption that a small unit of survival probability could be transferred from one African crowned crane to the other at a one-to-one transformation rate. But, from the law of diminishing returns, it might make more sense to believe that it is generally cheaper to reduce by 0.01 a high probability of extinction than it is to reduce by 0.01 a low probability of extinction.

In the final column of Table III is calculated the elasticity of diversity (or the conservation potential) of each crane species. This elasticity measures the percentage change in expected present discounted diversity per percentage change in extinction probability, normalized to sum to 100. Another name for this indicator might be "conservation potential" because it measures the increase in expected present discounted diversity that would come from making a species completely safe.

The elasticity of diversity has a certain intuitive appeal, and it is exactly the right measure to look at *if* the costs of reducing species extinction probabilities are proportional to the extinction probabilities themselves. My sense is that conservation potential is the single most useful species-alert indicator in the absence of specific knowledge about preservation cost trade-offs.

In a class by itself in terms of its conservation potential is the Siberian crane. The reason the Siberian may be an especially worthy candidate for extraordinary conservation efforts is that it combines a very high probability of extinction with the absence of any close relations among the other crane species. For any given fractional decrease in extinction probability, the Siberian yields almost twice the increase in expected present discounted diversity above the next most critical crane species ranked by this indicator.

After the Siberian, the next four high-alert crane species seem to cluster rather closely together in terms of their conservation potential. These four, all in double digits, are far ahead of the next grouping's diversity elasticities. They are, in order, the white-naped, wattled, black crowned, and whooping cranes. To belong to the very high conservation priority "group of five," defined as

having distinctively large elasticities of diversity, a crane species must possess some combination of a big probability of extinction, or the lack of a close relative, or in the case of the Siberian, both. Some fairly highly endangered species that have very close safe relatives, like the red-crowned crane, do not score particularly high by this criterion. Neither do species, like the sandhill, that possess very high marginal diversities because they lack close crane relations, but are in virtually no danger of extinction. While these kinds of conclusions are only as good as the numbers standing behind them, I think the general picture they are painting is moderately robust to possible errors in the underlying data.

While it may appear easy to offer after-the-fact explanations of the conservation diagnostic indicators of Table III, the reality is that they are the product of an extremely complicated combinatorial interaction of risk and relatedness factors that would be impossible to determine without the help of a modern computer.¹⁵

Note that the crowned-crane paradox disappears when the trade-offs between changes in extinction probabilities are proportional to the extinction probabilities, instead of being one-to-one. This points up yet again the crucial importance (to doing a correct analysis) of making the right assumptions about the relative costs of reducing extinction probabilities. In future work I hope to return to the example of crane conservation: to push this paradigm all the way through to its logical conclusion by applying the relevant information on preservation costs. Even so, I hope the example as it now stands demonstrates how a judicious application of diversity theory can usefully guide and inform conservation strategies.

VII. CONCLUDING REMARKS

The example of this paper should show clearly that in order to do a thorough analysis of the best way to preserve biodiversity, one needs to have a decent picture of the relationships of species to each other, the relevant survival probability distribution functions, and the costs of improving species survival. Without a sense of the magnitudes of the appropriate species distances, extinction probabilities, and extinction probability reduction costs, society is un-

15. This is an appropriate place to acknowledge my indebtedness to my research assistant Michael Sarel. Before working with him, I had no idea that diversity theory could be pushed this far in practical applications because I thought the computational and programming requirements would be so severe. Mr. Sarel made it all seem easy.

likely to do a good job of obtaining the maximum diversity out of the limited conservation resources that it is willing to spend on the problem.

While the model presented in this paper may appear to be overly simplistic in some ways, it can be readily extended in several directions. For example, complex interactions between species within an ecosystem (like predator-prey relations at an extreme) could be modeled by appropriately specifying the joint probability distribution of the relevant extinction patterns. Indeed, the issue of which entire sites should be purchased for preservation (what might be called the "Nature Conservancy approach") will involve many of the same aspects of diversity theory presented here.¹⁶

The good news, which I hope this paper demonstrates, is that an operational analytical framework is available that, given the right information, really can help to guide actual conservation policy in a diversity-improving direction. Although the specific application of this paper was to the example of crane preservation, it should be clear that many of the same basic themes apply to a broad class of biodiversity conservation problems.

APPENDIX: DERIVATION OF CRANE DISTANCES

This appendix gives a succinct description of how the genetic distances of Table II were derived.

The underlying data come from DNA-DNA hybridization experiments. Since this subject constitutes a fairly intricate set of procedures, there is space here for only the barest sketch of experimental methodology.¹⁷ Basically, DNA hybridization is a serious scientific technique that has been used to measure overall

16. Without going into full details, the Nature Conservancy approach to ranking the biodiversity potential of sites appears to complement nicely the approach of this paper. In Nature Conservancy methodology, the underlying "mapping units" or "elements" (species or communities) are ranked by how rare they are as measured by numbers of site occurrences: from G1 = critically important (5 or fewer occurrences) to G5 = demonstrably secure (over 100 occurrences). Then individual sites containing an element are graded by the likelihood that the element would survive on that preserved site: from A = highly likely to D = very unlikely. These two factors are then combined by prescribed guidelines to yield an overall biodiversity ranking of sites: from B1 = outstanding significance (e.g., presence of an A-ranked G1 element) to B4 = moderate significance (e.g., presence of a C-ranked G3 element). Under a number of simplifying assumptions, the Nature Conservancy biodiversity rank of a site can be interpreted as a rough approximation of the expected increase in biodiversity if the site were preserved.

17. More detailed descriptions can be found in Krajewski [1989], Li and Grauer [1991], Hillis and Moritz [1990], and the references cited in these works.

genetic differences between species, primarily in order to assess evolutionary relationships.

The DNA molecule is a long double-stranded helix. Each strand is made up of permutations of four fundamental units called nucleotides, denoted G, A, T, C, that are attached to a sugar-phosphate backbone. The base-pair nucleotides (G-C) and (A-T) line up with each other across complementary DNA strands and are held together by (relatively weak) hydrogen bonds. Roughly speaking, the genetic distance between two species is proportional to the fraction of differences in their DNA nucleotide positions, or, equivalently, the fraction of base-pair mismatches that would occur if each of their single strands were combined into an artificial "hybrid" double helix. Two complementary DNA strands from the same species would have their base pairs lined up (almost) perfectly, and hence would have (almost) zero genetic distance from each other.

The experimental procedure involves the creation of artificial DNA hybrids between two species. First, "natural" double-stranded DNA is disassociated into single stranded DNA by heating in an appropriate solvent. The single DNA strand from one species, called the "tracer," is radioactively labeled. Then it is "hybridized" with the nonradioactive complementary strand from the other species (called the "driver") by slowly cooling the mixture of two DNA strands until they recombine into an artificial "hybrid" DNA molecule. Next, the hybrid DNA is slowly heated, causing it to come apart gradually as the base-pair hydrogen bonds are broken. The thermal stability of the hybrid DNA is measured by the temperature at which 50 percent of the duplex molecule is disassociated into single strands, as determined by radioactivity counts on the tracer.

The more closely related are the species to each other, the lower is the fraction of base pair mismatch between their complementary single strands, and the higher is the thermal stability of the hybrid. A standard measure of genetic distance between two species is the difference between the thermal stability of the heteroduplex hybrid DNA of the two different species and the thermal stability of the homoduplex hybrid DNA of one species from the same experimental set with itself. The difference between median melting temperatures of homoduplex and heteroduplex DNA hybrids, called " ΔT_m " has been shown empirically to be approximately linearly related to the fraction of base-pair mismatches. However, the experimental error on any trial is signifi-

cant, so that many replicate observations must be made from the same pair of species.

The raw data for Table II come from an impressively crafted study by Krajewski [1989].¹⁸ Basically, Krajewski used an experimental DNA-DNA hybridization method to generate over 1,100 pairwise comparisons among fourteen species of the family Gruidae (cranes). The fourteen species that Krajewski measured are those listed in Table I as species 2 through 15. Later I shall discuss the special treatment of species 1.

The starting point is the more than 1100 ΔT_m values reported for each experimental result in Krajewski's appendix. With minimal modification,¹⁹ these serve as the raw data for estimating a symmetric genetic distance matrix.

The following regression was used to estimate the matrix of symmetric genetic distances:

$$(8) \quad \Delta_{ij}^k = D_{ij} + C_i + \epsilon_{ij}^k,$$

where

i = tracer species

j = driver species

k = cell observation

Δ_{ij}^k = Delta T_m value observed for (i, j, k)

D_{ij} = "true" Delta T_m genetic distance, constrained to be symmetric

C_i = any systematic tracer effect, possibly from tracer degradation

ϵ_{ij}^k = "everything else" sampling error, assumed normal i.i.d.

I shall not attempt here to defend vigorously this particular estimation procedure as the best possible way of processing the primary data. Basically, this is a more appropriate aggregation procedure than taking a raw average of experimental species distances, but the final results are not terribly different. The "tracer effect" specification seems reasonable as a first approximation since it is known that the process of radioactive labeling can cause part of the tracer DNA to deteriorate idiosyncratically, and it

18. I am grateful to Krajewski for helping me many times by courteously providing answers to naive questions from an outsider. Nevertheless, he bears no responsibility or blame for how I have used his raw data, or for the substance or tone of this paper, which are exclusively my own doing.

19. A few minor typographical errors in the reported matrix were kindly corrected for me by Krajewski. Also, where he trimmed means in three instances (out of more than 1100) by eliminating the outliers, I thought it better statistical procedure to trim outlier values by including them at the reduced level of the next highest values in the relevant set. None of these slight modifications should make much difference to the outcomes.

is empirically useful in correcting Krajewski's *vipio* data, which are clearly yielding too-low tracer distances generally.

The D_{ij} estimates from regression (8) are reported as the distances from species 2 through 15 in Table II.²⁰ The units of Table II are degrees centigrade, multiplied by 100.

Species 1 (*Balearica pavonina*) was treated as follows. The coverage of crane species in Krajewski's [1989] study was comprehensive except for *Balearica pavonina*, for which only sporadic distance measurements were made. (The basic reason Krajewski measured only sporadically the distance between *Balearica pavonina* and the remaining fourteen cranes is because it was well-known that the two *Balearica* species form an ancient line that diverged long ago from all the other crane species, and therefore no interesting taxonomic insights were likely to come out of isolated *pavonina* distances.)

The distances involving *Balearica pavonina* in Table II were obtained as follows. The distance between *B. pavonina* and *B. regulorum* is the average of the two distances reported by Krajewski in his appendix. From Table II the mean distance of *B. regulorum* from all thirteen other crane species except *B. pavonina* is 376. The synthetic distance between *Balearica pavonina* and each of the remaining thirteen species was made equal to the arithmetic average of 376 with the Table II distance between *B. regulorum* and that species—whenever no *pavonina* distances were reported by Krajewski, which is the majority of cases. When *pavonina* distances to another species were reported (usually one value, at most two), the distance recorded in Table II is the three-way average of (1) the mean reported value (corrected by the regression adjustment); the *regulorum* distance to the species; (3) the mean of all *regulorum* distances, namely 376. The fact that the two *Balearica* cranes have by construction been made almost equally distant from all other crane species (because only an insignificant number of *pavonina* distances were calibrated by Krajewski) generates an interesting insight, which in the text is called the "crowned-crane paradox."²¹

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20. A full accounting of the regression results is reported in Weitzman [1991].

21. Having tried other reasonable methods of constructing synthetic *B. pavonina* distances, I can report that there is no substantial difference on the basic results of the paper. Perhaps the simplest method would have been to equate all *pavonina* distances to the corresponding *regulorum* distances. But I thought it might be more interesting to have some variation between the crowned cranes, as there would be if the *B. pavonina* distances had been real instead of synthetic.

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