[1978]
Jstor

APPRAISING VARIABILITY IN POPULATION STUDIES[1]

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Abstract: This paper addresses the general question of determining sample size for population studies. Different objectives for population studies are described as a basis for determining the appropriate approach to selecting a sample size. The bases for mathematical models for various methods of population study are discussed, with particular emphasis on the situations in which indices or relative measures of abundance are used. A classification of population census methods is given. Several "variance-laws" for index data are discussed, and an extensive tabulation of data on variability of aquatic and terrestrial indices is presented. Several equations for calculating sample sizes are listed and discussed. References to various published tables and charts for determining sample size follow.

J. WILDL. MANAGE. 42(2):207–238

This paper is addressed mainly to the perennial question of "How large a sample do we need?" Answers to this question depend on a number of factors, and usually require either data from past surveys under similar circumstances, or shrewd guesses as to the magnitude of relevant current parameters of the population. Survey methods inevitably are involved in an answer, and this is now a topic that only can be covered adequately by a textbook. One such text, that of Seber (1973), describes methodology in detail and supplies a comprehensive statistical appraisal of the methods in most instances. Thus Seber's book can be referred to for many purposes, and is cited frequently here. (A detailed review of the book is given by Eberhardt 1975*a*.) Only simple and basic statistical techniques are considered in the present paper. However, no such restriction has been placed on the literature referenced here.

There is a great deal of literature on capture-recapture or mark-and-recapture methods, and almost none on indices or relative measures of abundance. Consequently, some ways to approximate the variability to be expected from indices are described here. Just how one goes about selecting a sample size depends very much on objectives of the study, and usually involves some kind of model for the situation under consideration. For convenience, a classification of methods is included, along with a section giving references to charts and tables useful in ascertaining sample size, as well as some convenient rules of thumb for approximate results. The emphasis here is on estimating population size (or density). Some results appropriate for sampling populations for contaminants appear in Eberhardt (1975*b*), and Eberhardt et al. (1976).

Drs. R. O. Gilbert and J. M. Thomas have contributed extensively to the work reported here, both directly and indirectly. An anonymous reviewer is thanked for a number of stimulating comments.

SAMPLING AND EXPERIMENTAL DESIGN

Both the methods used in a population study and the sample sizes required depend very much on the objectives of the study. Much has been written on the desirability of an explicit statement of objectives and the hazards of starting out with "fuzzy" or overly ambitious goals.

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[1] This paper is based largely on work conducted under United States Energy Research and Development Administration Contract E(45-1)–1830.

[1981]
J Stor

WILDLIFE SCIENCE: GAINING RELIABLE KNOWLEDGE

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Abstract: Two scientific methods called induction and retroduction form the basis for almost all wildlife research. Induction is used to establish reliable associations among sets of facts, whereas retroduction is used to establish research hypotheses about the fact-giving processes driving nature. A 3rd scientific method, the hypothetico-deductive (H-D), is a means for testing research hypotheses, i.e., for gauging their reliability. The H-D method is rarely used in wildlife science. Instead, research hypotheses are proposed, and either made into a law through verbal repetition or lose favor and are forgotten. I develop the thesis that wildlife research should use the H-D method to test research hypotheses, using the threshold-of-security hypothesis for winter mortality for illustration. I show that persistent confusions about the definitions of concepts like carrying capacity, correlation and cause-and-effect, and the reliability of knowledge gained from computer simulation models stem from either inadequate or misused scientific methods.

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Like the Kaibab deer herd, progress in wildlife science may be headed for a crash under the weight of unreliable knowledge. Knowledge, the set of ideas that agree or are consistent with the facts of nature, is discovered through the application of scientific methods. There is no single, all-purpose scientific method; instead, there are several, each suited to a different purpose. When the set of scientific methods is incomplete, or when one method is used for a purpose better fit by another, or when a given method is applied without paying strict attention to the control of extraneous influences, then these errors of misuse cause knowledge to become unreliable.

Unreliable knowledge is the set of false ideas that are mistaken for knowledge. If we let unreliable knowlege in, then others, accepting these false laws, will build new knowledge on a false foundation. At some point an overload will occur, then a crash, then a retracing to the set of knowledge that existed in the past before the drift toward unreliability started. Every field that loses quality control over its primary product must undergo this kind of retracing if it is to survive. Of course, some unreliable knowledge inevitably creeps in—a researcher makes a systematic error here, or fails to do enough replications there. All science is prone to human error, and minor retracing continually occurs. But I think part of wildlife science's knowledge bank has become grossly unreliable owing to the misuse of scientific methods, and major retracing is inevitable.

I read published dissatisfactions on seemingly isolated topics as being symptomatic of past misuses of scientific method, e.g., Chitty's (1967) and Eberhardt's (1970) complaints over the continued confusion between correlation and cause-and-effect, Bergerud's (1974) case against the reliance on induction to generalize laws to the exclusion of testing research hypotheses, Hayne's (1978) dissatisfaction with poor experimental designs, Krebs' (1979) frustration with virtually every aspect of small mammal ecology, Caughley's (1980) claims that most large mammal studies "coalesce into an amorphous mass of nothing much" and that white-tailed deer (*Odocoileus virginianus*) and *Drosophila* are the most studied and least understood of animals, and Eberhardt's (1975) skepticism about the predictive value of computer simulation models of ecological systems.

What are these misuses of scientific method? Of the 3 main scientific methods used in virtually all fields, i.e., (1) induction, (2) retroduction, and (3) hypothetico-deductive (H-D), wildlife science uses the 1st and 2nd methods but almost never the 3rd. Induction and retroduction, by themselves, are inadequate for discovering some kinds of knowledge. Instead of realizing this limitation, wildlife science routinely stretches induction and retroduction beyond their limitations as knowledge-finding tools and unreliable knowledge results.

Let me show how this occurs by explaining each method. The method of induction (Hanson 1965, Harvey 1969) is useful for finding laws of association between classes of facts. For example, if we observed over many trials that the amount of edge vegetation in fields was positively correlated with an index of game abundance, we would be using induction if we declared a law of association. The more trials observed, the more reliability we'd attribute to the law. The method of retroduction (Hanson 1965) is useful for finding research hypotheses about processes that are explanations or reasons for facts. For example, if we observed birds caching seeds more on south slopes than on north slopes (facts), and our best guess for the reason of this behavior (our research hypothesis) was that south slopes tended to be freer of snow than north slopes, we would be using the method of retroduction to generalize a research hypothesis about a process providing a reason for the observed facts of bird behavior. The method of retroduction is the method of circumstantial evidence used in courts of law. Retroduction is not always reliable, because alternative research hypotheses can often be generated from the same set of facts.

The H-D method (Popper 1962, Harvey 1969) complements the method of retroduction. Starting with the research hypothesis, usually obtained by retroduction, predictions are made about other classes of facts that should be true if the research hypothesis is actually true. To the extent that experiment confirms or rejects the predicted facts, the hypothesis is confirmed or rejected. Thus, the H-D method is a way of gauging the reliability of research hypotheses acquired by other means.

Wildlife science's workhorse is the method of induction. I believe it is used in a way that gives reliable knowledge. However, induction has a limitation: it can only give knowledge about possible associations between classes of facts. Although this is undoubtedly useful for decision making (e.g., the correlation between a fish's weight and its length is a money-saving association), it cannot give knowledge about the processes that drive nature. Consequently, you can use induction repeatedly without diminishing the question "Why?" When we ask "Why?" we are asking for an explanation, an abstract process that provides a reason for the facts. If the human mind didn't beg for reliable explanations, the method of induction would suffice. That not being the case, the method of retroduction was invented. It is reliable enough to be used in courts of law but, by itself, it is not reliable enough for science. Science has the most stringent standards of all endeavors. If courts of law followed science's strict standards, suspects identified through retroduction would be set free, and their guilt decided in accordance with whether or not the life of crime predicted for them turned up in future facts. That is, the courts would test a retroductively derived hypothesis using the H-D method.

Because wildlife science hardly uses the H-D method, it is stuck with no way of testing the many research hypotheses generated by retroduction. Herein lies

1859

STATE OF OREGON

DEPT. OF FISHERIES & WILDLIFE
Oregon State University
Corvallis, Oregon 97331

INTEROFFICE MEMO

DEPT.

TELEPHONE

TO: Bob

DATE: 10/5/81

FROM: Jim Hall

SUBJECT:

Enclosed are the reprints you asked for, plus a more recent one.

You can write at
Tom Nickelson
Oregon Dept. of Fish and Wildlife
Research Division
303 Extension Hall
Oregon State Univ
Corvallis, OR 97331

Best regards
Jim Hall

P.S. – I'd like a copy of your monograph when finished

Dick Grand at Albuquerque
7. N. Zesl. -

Hall et al (78)

Murphy, Hall (81)

OFFICE MEMO

TO: Hall & Lantz (69) intensive study **Date**

FROM: Alsea ~~watershed~~ drainage 3 adjacent watersheds studied – fish pop. & physical characteristics studied 7 yrs – then

SUBJECT: 2 watersheds logged timber harvested. – 3rd control –

REMARKS: 1 complete clear-cut

$O_2\downarrow$

2 partial-selective cuts – temp. ↑ – sediment ↑

7 yrs post logging study

coho, little impact cutts ↓ in 5 yrs to 1/3 pre logging stay there

*temp. –

extensive study Cascades

12 watersheds – 6 yrs before 1 yr after

.coho increased 5 decreased 3 (may be nat. var.)

– cutts decline all 4 where good compar. –

most severe in clean-cut w/o buffer.

– 6-10 yrs. after clear-cut – Cascades –

cutts in open area 4 – compare wild a

Propst – chili book
– maps
– AFS abstracts
–

Intensive
Problems 7 yr. before, log, 7 yrs after
Alsea study - 15 yrs

① 1 in 100 yr. flood occurred but! cope w/ - Natural variation

② Two succeeding years after logging below normal rainfall

Extensive
12 Cascade watersheds
1 summer before, 1 summer after logging

OFFICE MEMO

TO: **Date**

FROM:

SUBJECT:

REMARKS:

Discussion

wait Parkinson letter —photos
— — —compare methods —
—test— pizzaro test — no signif. reduct pops
—Dolly - RB - cutts — hybrid [illegible]

Gen. Observations

— ~~Hybrid~~ inflow — ~~[illegible]~~ why? — niche pref — so overlapping, then if environ. dis[illegible]
coastal cutt — RB — lit. confusing variable — but
conclude major strategy avoid hybrid by partitioning
— cutts smaller trib. + headwaters, lower gradient section
w/ backwaters, sloughs, lakes — —
best stream — Gill & Hartman 68
very small (cpr. E. brook trout mature 100-130 mm
seldom exceed 3 years age max 150-200mm size — —
- role of Dolly Varden -

steelhead more var.) life hist. type

— RB: — best known Vancouver life hists as steelhead — resident river or lake Cowichan R. Nesse
not previously as typical resident cutt - life histor, (benefit for cutt genes) —

size
—sea-run
cut
—2 types
timing

— Cutt — sea-run (need shallow water estuary — sloughs) — deep water blocks
(Compton et al) — small stream — resident river (semi mov. trib → river), lake —
— interesting Vancouver Is — ~~lake~~ resident cutts more predaceous than RB or brown
(Cowichan R, (Idyll 42) — lakes — — larger, more abundant — better adapted. (—)
feed young salmon, sticklebacks, sculpins, makes typical predator —
Haig Brown.
Nicholas (78 a b) — no hybrid known from Willamette (but slight introgression would not be recognized) —
Tomasson (78) — Andrusak & Northcote (70)

resident RB — small habitat — larger — Vancouver large habitat — but Crescent L. — small forage
* inter cutts lack this adaptation — replaced by EB

Armstrong (71) age, food, migrates — sea run in Alaska lake [illegible]
Cooper (70) — age, Giger ( ) Sumner ( ) Nilsson (71)
Narver (Gt. Cent. L.) — Ricker (41) — most pred. Cultus L.
Bustard & Narver (75) winter habitat. — Glova & Mason ( )

Johnson, Ringler, Hall

RB/coho
Dolly Varden
typical assoc.
3 spine stickleback
sculpin C. aspera
C. [illegible]

Implications

Hybrid/Introgress identified common in resident stocks — typical
of disturbed environ. when virgin or formerly 2 niches [illegible] — breaks down —
but W. Vancouver virgin — no stocking. —

TAFS clear cut — Chapman — Jim Hall — Warren — Bisson —
Narver, Ringler, Hall — Alsea watershed.
— replace by brookies — no — no real signif. except ex. introgression
— Rm. for improvement — now not used — stream improve. — open canopy
↑ primary production smaller strm (w/o accelerated erosion) — nutrient enrichment
(Au Sable — Odell L. — Binns — N. N. — .25 ppm) — —

— ● Compton · marine phase, isolation

[1986]

sex ratio bias. Furthermore, the bias goes in opposite directions for colour banded males and females, which is hardly to be expected under the age/experience hypothesis. Although she cannot rule out factors associated with possible differential parental abilities to rear sons and daughters, Burley concludes that the most likely cause of the effect is parents adjusting the sex ratios of their broods to produce attractive offspring[9]. This interpretation is based on the assumptions that differences in attractiveness are normally heritable, and that brood reduction is adaptive under normal circumstances.

But what is so special about leg band colour? Burley believes that the answer may lie in the evolutionary history of the species. Band colours preferred by zebra finches were compared with those chosen by the closely-related double bar finch (*Poephila bichenovii*)[10]. Burley found that birds with bands of colours absent from the beak and plumage of conspecifics but similar to those naturally occurring on the other species tended to be less attractive. On the other hand, bands of similar colour to those characteristic of opposite sex conspecifics are more likely to be attractive. Song and courtship behaviour are quite similar among the elstrildrid finches while plumage and beak coloration can vary markedly among species. Perhaps, Burley surmises, some of the preferences she has demonstrated 'reflect strong selection for species identification mechanisms in a group in which colour pattern appears to have played an important role in speciation'[10].

These findings must be considered preliminary. Sample sizes are fairly small, possible confounding factors can sometimes be envisaged, proximate mechanisms are little understood, and the number of extra-pair copulations is unknown. Nevertheless, many of the patterns seem robust and, if they can be demonstrated under more natural conditions, they beg evolutionary interpretation.

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Species Conservation and Systematics: the Dilemma of Subspecies

Oliver A. Ryder

Zoos are gaining recognition as potential *ex situ* conservators of the gene pools of threatened species. The zoo directors, curators, geneticists and population biologists who attempt to pursue the elusive goal of preservation of adaptive genetic variation are now considering the question of which gene pools they should strive to preserve. There are no illusions that zoological parks can conserve but a very small proportion of biotic diversity; charismatic megavertebrates are their stock-in-trade.

Space, or captive habitat as some call it, is limited in zoos. Conway's optimistic estimate[1] suggests that 925 taxa of mammals, birds, and reptiles may be managed with gene pool preservation in mind (see also the article by Ralls and Ballou on page 19 of this issue). Which species should be the focus of concern and which may be neglected? Furthermore, should the focus of *ex situ* conservation effort be directed at populations, subspecies, or species?

The consideration of these issues was the subject of a recent conference of zoo biologists and systematists concerned with the establishment of species' survival programs (SSPs) of the American Association of Zoological Parks and Aquariums (AAZPA). The focus of the meeting, held in July 1985 at the Zoological Society of Philadelphia, was on the subspecies problem. How much space is required for tigers, for example, in zoos is actually a dual problem of how many *individuals* must be held in order to achieve a self-sustaining captive population that only incurs acceptable losses of genetic variation over a sustained period of time (200 years is a current goal) as well as how many of the five extant tiger *subspecies* should be conserved. Thus, the 'subspecies problem' is considerably more than taxonomic esoterica.

The tiger example is by no means unique. Of the 37 taxa that are designated for SSP programs, at least 16 are listed as trinomials. The black rhino of Africa (Fig. 1) has been divided into seven extant subspecies[2]. A recent status review prepared by the African Elephant and Rhino Specialist Group of IUCN suggested that the three northernmost black rhino subspecies have been nearly eliminated[3]. The Somali black rhino (*Diceros bicornis brucii*) is thought to survive with a population of 90 or fewer individuals.

Zoo biologists are now faced with the task of identifying which subspecies actually represent populations possessing genetic attributes significant for present and future generations of the species in question. The folklore of mammalogy is replete with humorous anecdotes such as two subspecies being named from individuals that were littermates. Yet, other taxa that have been considered by some authorities to be conspecific, for example the barking deer or muntjacs of India and China, produce sterile hybrids. Out of a sense of frustration with the limitations of current mammalian taxonomy in determining which named subspecies actually represent significant adaptive variation, those assembled at the Philadelphia conference willingly discarded the concept that all subspecies are equal. Rather, it emerged that zoos ought properly to address the conservation of evolutionarily significant units

Fig. 1. The black rhino, *Diceros bicornis michaeli*, in Amboseli National Park, Kenya. Photo by W.K. Lindsay.

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(ESUs) within species. (No one present really liked the idea of creating a new jargon term. An alternative suggestion was to call such populations 'ESPs', standing for evolutionarily significant populations.)

Identification of ESUs within a species was recognized as a difficult task, requiring the use of natural history information, morphometrics, range and distribution data, as well as protein electrophoresis, cytogenetic analysis, and restriction mapping of nuclear and mitochondrial DNA. The recognition of inevitable uncertainty in the classification of potentially significant populations led to a recommendation that concordance between sets of data derived by differing techniques be a criterion for identifying ESUs. Thus, when geographic distribution data indicate the existence of discrete populations within the range of a species, an estimate of genetic distance, for example, should be made to determine whether the populations have ESU status.

In the past zoos seldom knew the exact location of capture of animals they imported. Data concerning geographic origin of individuals destined to be genetic migrants into captive breeding programs is obviously important, especially where ESUs may be involved, and should be recorded meticulously.

Some ESUs may be in jeopardy of extinction through inbreeding and the inevitable stochastic events that affect small populations. Under what circumstances is the mixing of threatened populations with populations of other related forms justified? The participants at the Philadelphia meeting concluded that mixing was appropriate when the extinction of the small population would jeopardise the higher taxon.

Decisions with important conservation implications increasingly require more understanding of the systematics of populations, subspecies and species than is currently available. Zoo biologists recognize that additional systematic research is needed to ensure that captive management programs can preserve gene pools as they exist in nature. Expertise in diverse areas of vertebrate biology, genetics and ecology is required for zoos to meet these formidable challenges. Although the most current expression of these concerns may now be voiced by zoo biologists, the implications of their concerns reach into other conservation-oriented disciplines such as wildlife management and the management of national parks and nature preserves.

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Cladistics (1990) 6:183–186

REPLICATORS, HIERARCHY, AND THE SPECIES PROBLEM

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Introduction

de Queiroz and Donoghue (Q&D) give (1988) a review of the "conflict" between interbreeding and descent, in relation to different species concepts. Their paper contains many important observations, but their main theme—that there is a fundamental conflict between "wholes" integrated by interbreeding, and monophyletic entities—rests on a misunderstanding. Even if monophyly is a universal concept, it is in a particular case meaningful only in relation to the conceptual singularities in the model concerned. I will illustrate this with an example similar to the one Q&D used. The example may seem absurd to some people, but is chosen to clarify the logical limits.

The cells descending from a zygote (or for that matter from any cell) form a monophyletic entity of *cells* in a model where cells are the cohesive wholes, because the cells once constituted a singularity, a single cohesive whole in this model. A mendelian gene in the zygote can similarly (in the descendant cells), give rise to a "monophyletic group" of genes which at the same time is part of more inclusive monophyletic entities of mendelian genes involving several zygotes. The zygote's genome, acting as a cohesive whole in the process of mitosis, can be said to give rise to a monophyletic group of genomes in the descendant cells. But the collection of mendelian genes in the zygote is not monophyletic as a collection of genes.

In all these cases, the "groups" are monophyletic whether there are 20 descendant cells or just the initial singularity. Hence, if you stretch the concept far enough, you could say that the collection of genes in the zygote is polyphyletic, but it is absurd to say that the genome, as an individual, a singularity with respect to a certain process, is paraphyletic. A "thing" cannot be paraphyletic.

The Model

The singularities in evolutionary models are replicator-continua, replicators being entities that perpetuate their structure through successive generations. In a simple model with a discrete gene pool (the ideal population) through time, we have in principle two levels of replicator continua, the gene continuum (the gene as the ideal unit of recombination, the "‘mendelian" or "dawkinsian" gene) and the gene pool continuum. Genes and populations thus can be regarded as manifestations of information systems to which the same kind of models apply. In the real world replicators are of course a great deal more difficult to circumscribe, because of various kinds of linkage, deme-structure, etc., and, for populations, the temporal resolution (gene flow cannot be atemporally defined; what is "current gene flow"?). Where recombination is lacking, "genes" and gene pools coincide. It is indeed strange that uniparental organisms are often considered as conceptually *more* problematical (for example by Splitter, 1988) in evolutionary models.

Individual organisms are in an evolutionary context only ephemeral compilations of

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THE ILLUSION OF TECHNIQUE AND FISHERIES MANAGEMENT

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I use the term illusion of technique in reference to the common phenomenon whereby the human mind is highly susceptible to indoctrination with a naive belief that chaotic systems of nature can be neatly ordered for predictive purposes if only modern technology, such as a computer simulation model, can be applied to a problem. This phenomenon leads to a naive faith that confuses objectivity, quantification, and sophistication with biological realities. The problem of erroneous predictions concerns the substitution of data for knowledge and the institutionalizing of ignorance under the guise of conflict resolution.

LIMITATIONS OF PREDICTIONS

If a regional farmer's almanac is consulted to observe times of sunrise, sunset, high tide and low tide for any given day, we would have a well-founded belief in the accuracy of these predictions. If this same almanac predicted the weather each day of the year, a year or more in advance, we might chuckle at the expected predictive accuracy of such long range weather forecasts. However, if we loosen the constraints for precision, we would have some confidence in a prediction that claims the maximum and minimum temperatures for any given day in July will be higher than for any given day in January in the Colorado-Wyoming area.

If one can comprehend the reasons why some natural phenomena can be accurately predicted and why some cannot, as illustrated in the above examples, then an understanding of the limitations for accurate predictions made on the basis of environmental or biological models should be apparent -- it concerns patterns of regularity in nature, and our interpretation of these patterns for making predictions.

To obtain consistently accurate predictions based on data from a natural system, the particular system must be stable, isolated (not subjected to external perturbations), and highly regular. Most biological systems do not meet these prerequisites. The law of gravity, the positions and motions of the sun and planets have patterns of regularities that justifies our faith in the accuracy of predictions regarding the times of sunrise, sunset, high tide and low tide. The value of empirical evidence can be demonstrated by considering the fact that accurate predictions are possible from accurate recording and interpretation of the data of regularity, even though the processes causing regularity are unknown. For example, ancient societies could have compiled the essential data on which accurate forecasts of sunrise, sunset, and tides could be made while accepting a theory that the earth is flat, stationary and the center of the universe. For long-range weather forecasts where a multiplicity of unpredictable, short-term influences act to create local conditions, a full understanding of all the processes of weather formation does little to improve long-range predictive accuracy over mythological methodologies such as the degree of fuzz development on caterpillars.

The implication for fisheries management and environmental assessment in general, is that, unless a system is extremely regular and tight cause-and-effect relationships between a proposed action, such as change in flow regime, and the target species can be empirically demonstrated, do not expect predictive accuracy from any model -- the best that can be expected is to demonstrate trends; to be in the ballpark. For example, enrichment of a pond can be expected to result in a trend for increased fish production. The precise amount of increase in a target species such as bass or trout from a known percentage increase in nitrate and phosphate cannot be accurately predicted because of the multiplicity of unknown and unpredictable phenomena that can influence the transfer of energy from primary (or bacterial) production to the target species.

The limitations on predictive accuracy associating nutrient enrichment to fish production was neatly demonstrated by Bill McConnell and students of the Colorado Cooperative Fishery Unit and David Galat in replicated microcosm experiments. Under identical conditions, great variability in fish production was found, but consistent trends were apparent. Higher trophic level species, such as smallmouth bass, always had less production than lower trophic species, such as carp. Thus, a trend associated with trophic level can be predicted, but the actual amount of production cannot be predicted from nutrient levels.

A similar situation applies to other environmental variables as they affect fishes. A computer simulation model that produces precise habitat quantification such as habitat units expressed as weighted useable area (WUA) which display changes in relation to flow changes, has indoctrinated the minds of many naive biologists and administrators who confuse quantification, objectivity and sophistication with biological reality. Such people have assumed that changes in WUA accurately predict changes in fish populations -- they do not; the best that can be hoped for is that trends can be predicted. In recent years, many biologists and administrators have become vaguely aware of this fact, but the appeal for standardization of an assessment method is strong and arguments are developed concerning the relative merits of various methods in relation to negotiability, defensibility, holding up in court, etc. The only way I envision that quantified habitat units lacking valid representation of biological reality can be negotiated and defended is if a game of environmental assessment is created and all of the players agree to play by the rules, which would include treating habitat units as currency similar to play money in the game of Monopoly. If an irreconcilable conflict arose and a case ends up in court, I doubt that the judge and opposing attorneys would agree to the rules of the game.

CONCLUSIONS

What has been said above is only a matter of common sense thinking. Why is common sense so uncommon? The pioneers and leading practitioners of simulation modeling cannot be blamed for our problems with the illusion of technique. People such as MacArthur and Wilson (Island Biogeography) and Hollings (Adaptive Environmental Assessment), who popularized biological and environmental modeling, clearly sounded warnings and cautions concerning the limitations of predictions made from highly simplified and compartmentalized abstracts of nature and emphasized the need to test and continually refine and fine-tune a model. The lure to administrators, however, of a "standard method" for conflict resolution, with or without biological reality, is great and difficult to resist. A negative aspect concerns the expenditure of considerable funds to obtain essentially meaningless data in relation to benefits to a target species when these funds might have been beneficially expended on constructive mitigation or enhancement measures if detailed knowledge of a species life history in a particular environment was used to resolve a conflict. That is, look for ways to reverse the illusion of technique by substituting human knowledge, expertise, and experience for "shotgun"-type of data and "rules".

During 1986 I was involved in an acrimonious legal action in Michigan over no-kill regulations for the Au Sable River. The backers of the no-kill regulation consistently cited a computer simulation model that "proved" a significant increase in larger trout would result from no-kill regulations, despite all empirical evidence to the contrary and a published word of warning from the creator of the model concerning its limitations for predictive accuracy. Highly trained and otherwise disciplined minds can be completely susceptible to the illusion of technique if it furthers their interests and supports a belief.

The Intermountain Region of the U.S. Forest Service published a small booklet entitled: "Macro What?". This booklet tells how analysis of aquatic invertebrates is used "to measure the effects of" such activities as hunting, fishing, camping, and livestock grazing. Are there people in the U.S. Forest Service who really believe that the best way to "measure effects" of hunting and fishing and livestock grazing is by indirectly analyzing the aquatic invertebrates rather than directly "analyzing" the hunters and fishermen or the direct livestock impact on riparian vegetation, bank stability, channel morphology, and fish population? Why not apply the "rule of parsimony" and look for the most simple and direct cause-and-effect relationship of a problem and "analyze" that rather than to instinctively "follow the rules" of a "standard method" when they are not applicable to particular situations?

Evidently, there are indeed such people, as Don Duff told us at our annual meeting, Forest Service administrators, after many years, finally agreed to institute revised grazing management on Silver King Creek, California, to enhance habitat conditions for the federally threatened Paiute cutthroat trout, after they were shown the evidence from aquatic invertebrate analysis. It must be assumed that these same administrators had been previously unconvinced by the direct evidence of cause-and-effect impact of livestock -- the barren, caved-in banks, erosion and actual trout population data -- until they were shown a "scientifically" derived metric of invertebrate diversity which "proved" the negative impact of livestock on the Paiute trout.

The moral of the story is that as long as we have to live and work with problems created by the illusion of technique, we might as well look for ways to use illusion in our favor. I would prefer, however, that in the future, we might have more knowledgeable administrators staffing resource agencies who are capable of exercising reflective judgement and a greater resistance to the illusion of technique -- but as I said, common sense is not common, and I doubt that it can be taught in school.

Colorado State University

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(303) 491-5020
FAX (303) 491 5091

January 15, 1993

Mr. Leo Gomolchak
Trout Unlimited
655 Broadway, Suite 475
Denver, CO 80203

Dear Leo:

Many thanks for the copy of Kochman's letter to T. U. protesting Ray White's articles in Trout magazine. I'll provide some suggestions for a T. U. response.

First, I fully agree with Mr. Kochman's points that we should not mislead, should not be unrealistic, that it is unprofessional to make strong inferences on little basis of evidence, and that we must be aware of the dangers of induction (whereby interpretation from a specific situation is broadly extrapolated to other nonapplicable situations). I also heartily endorse Mr. Kochman's concluding statement regarding ..." engaging in useful debate about how state fishery agencies can best incorporate study results into their fish management decisions, as well as the wishes of the entire angling public."

Mr. Kochman's letter is critiqued solely on the issue of the role of catchable trout in Colorado's fishery program. The critique is made in hope that it may lead to "useful debate" on the role of catchable trout and particularly to point out that such debate must be required before a major commitment of funds is made to increase production of catchable trout. This critique is not pro hatchery vs. anti hatchery but rather rational use of hatcheries vs. overwhelming dominance of catchable trout production in hatchery operations. A basic question in need of open debate is: are more catchable trout desirable for present and future needs in Colorado? If so, are we deriving maximum benefits from catchable programs or is there considerable room for improvement before funds for increased production are committed?

On page two of the letter it is stated that "millions of hours of angling opportunity would not otherwise occur" in the Denver metro area without the stocking of catchable trout. As a professional who does not want to mislead or be unrealistic, Mr. Kochman should be asked to produce the evidence on which such a statement is based.

A DOW report, "Coldwater lakes and reservoirs", Federal Aid Project 7-59 authored by Mary McAfee, 1991, contains pertinent information to address the role of catchable trout for creating "millions of hours" of metro angling. Surveys were made of anglers fishing in several urban or metro ponds and reservoirs in the Denver area and also in Grand Junction, Rifle, Craig, and Georgetown. In response to the question: Would you still fish in city lakes if only species such as sunfishes and catfish were caught (i.e. no stocking of catchables)? The angler response ranged from 88% to 97% "yes" (i.e. they would continue to fish urban-metro waters even if they were not stocked with catchables). Thus, the evidence of DOW surveys on metro lakes contradicts the claim that "millions" of hours of metro angling depend on catchable stocking. This claim is unrealistic, misleading, and an example of making insupportable inferences.

In recent years, after DOW hatcheries were exposed to whirling disease and the waters stocked from these hatcheries were restricted to certain geographical areas, a surplus of catchables was created which resulted in stocking many non-trout waters such as Boyd Lake and Jackson Lake which had not been previously stocked with trout. After these waters were stocked, all angling in them was "attributed" to the stocking of catchable trout. This clever, but dishonest and misleading "attribution" greatly inflated the angler days and angling hours claimed to be supported by catchable trout.

I would agree that stocking of fingerling rainbow trout in tailwater fisheries where water temperatures are too low for successful natural reproduction is entirely justified - an excellent use of hatchery fish (put-grow rather than put-take). The use of wild Colorado River rainbow trout parents to supply fingerlings to rear in hatcheries is also a commendable and progressive use of hatcheries. The above mentioned DOW coldwater lakes and reservoirs report presented data on the results of fingerling and catchable stocking in Bear Lake and Stillwater Lake. Four strains of fingerlings were used, two highly domesticated and two less domesticated (Eagle Lake rainbow and Snake River cutthroat). Almost all (ratios from 24:1 to 60:1) trout caught two, three, or more years after stocking (i.e. virtually all large or trophy fish in catch) were of the less domesticated strains, especially the Eagle Lake rainbow. This and a long history of other studies over many years clearly have demonstrated that genetically different strains may perform very differently after stocking. To maximize the effectiveness of fingerling put-and-grow stocking many stains, particularly wild or less domesticated stains should be available from hatcheries. Presently, the number of strains reared in DOW hatcheries is severely limited because production of catchable trout utilizes virtually all the total production capacity of hatcheries. This is not an issue of pro vs. anti hatchery but one of emphasis: a change is needed from put-and-take catchable fisheries to put-and-grow fingerling-stocked fisheries by selective use of stains. This is an important issue for "useful debate".

The usefulness of such debate, however, depends on the range and depth of knowledge of the subject matter by the participants. When I read near the bottom of pg. 3..."If wild fish are superior to hatchery fish in pristine habitat, then maybe hatchery fish are superior to wild fish in man-made habitat. We have seen situations where wild fish have greater difficulty surviving than hatchery fish "... serious doubts are raised on the range and depth of knowledge of Mr. Kochman on how natural selection works, differences between natural and artificial selection, principles of evolutionary genetics and evolutionary ecology. It is not useful to simply state that "we have seen situations where wild fish have greater difficulty surviving than hatchery fish" unless specific data and convincing evidence accompanies such a statement. It is frightening for a modern fish manager to believe that "maybe hatchery fish are superior to wild fish in manmade habitat", and since "more than 75% of Colorado's aquatic habitat is manmade", therefore _ _ _ _ _: a very dangerous and a very faulty induction.

The DOW lakes and reservoirs report would be a starting point to gain some knowledge on wild and domestic strains and effects of domestication on trout. In Lake John, two domesticated rainbow trout strains were tested, the "Tasmanian" and the more intensely selected "6F2" strain, a superstar trout for growth in hatcheries. One year after stocking none of the "6F2" trout could be found and after 16 months, both domestic strains had vanished. Simply, the intensity of artificial selection is inversely related to survival after stocking.

The DOW lakes and reservoirs report also contains useful data to evaluate angler use dependency on catchable trout stocking and costs associated with creating increased angler use by stocking. For three years Bear Lake was stocked with 400 catchable trout per surface acre and then with 100 per acre for four years (the lake is also stocked with fingerlings; that is, it is both a put-and-take and a put-and-grow fishery). Angler hours were increased by about 67% when catchable stocking was increased by 300% (100 to 400 per acre). To create each additional angler day with the higher stocking rate about 7 catchable trout had to be stocked, whereas with a stocking of 100 catchables per acre an anglers day required a stocking of only about 1.5 catchable trout.

In Rifle Gap Reservoir with both warm water fishes and trout, 16,500 catchable trout were stocked in 1984 when angler-use was 58,000 hours (April 1 - September 30). In 1987, 61,500 catchables were stocked and angler-use was 61,000 hours during the same time period. Although DOW accounting methods might "attribute" all 61,000 hours in 1987 to catchable trout stocking, a more realistic evaluation shows that by stocking an additional 45,000 catchable trout an additional 3,000 hours were created (dependent on catchable stocking). This figures out to be 15 catchable trout per "dependent" hour - - or in the neighborhood of 50 to 60 catchables per dependent angler day.

These are just a few items for "useful debate" on hatcheries and the role of catchable trout in the state's fishery program. There is no doubt that the use of catchable trout to maximize the effectiveness of creating angler use can be considerably improved, and improvement for more effective use of current catchable production should be clearly demonstrated before any serious thought be given to new hatchery construction. Does anyone in DOW have an understanding of what the costs of additional catchables might be if a new hatchery costing 5, 10, or 15 million dollars is constructed to provide these additional fish?

Colorado presently stocks more catchable trout per licensed angler and spends a greater percentage of license fees to support catchable production than any other state. Is Mr. Kochman committed to maintaining the state's dubious distinction of being number one?

It is also recognized that any Trout Unlimited spokespersons will be strongly biased against catchable trout. They will likely agree with Sagoff (1991) that "put-and-take fisheries is to angling what prostitution is to love". Despite biases, useful debate is possible if all evidence is rationally and impartially evaluated. The time for useful debate should be before visions of new hatcheries dance in our heads.

Sagoff, M. 1991. On making nature safe for biotechnology. Pages 341-365. In L. Ginsburg (ed.), Assessing ecological risks of biotechnology. Butterworth and Heineman, Stoneham, MA.

Sincerely,

Robert Behnke

1994

Nielson Conf, May 21-23 Monterey

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The Illusion of Technique + Fisheries management

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session chairman
Monterrey
May 22-24
define ESU
for ESA

Jennifer L. Nielsen
401 Barker Hall/ AC Wilson Lab
University of California
Berkeley CA 94720

Feb. 13, 1994

Dear Session Chairs,

I send along the updated ESU program outline, publication information from AFS, and a copyright transfer form. I have requested a one-page abstract from your speakers by March 18, 1994 (hard copy and on 3.5" floppy using MSWORD format) for inclusion in the program. You will be copied on all abstracts I receive. This will help us decide on the sequence of speakers in your session. ①

The role of the session chair has evolved slightly due to obligations developing from the executive summary we are trying to get out immediately following the meeting. In the Regulatory Guidelines session 5-6 Federal agencies will be portraying their needs for defining and implementing ESU conservation in aquatic ecosystems. Their brief presentations will be followed by a facilitated open discussion from the floor. Each agency will submit an outline of their administrative, regulatory, and programmatic needs in writing prior to the conference (by May 2), which I will forward to you. ②

executive
synthesis

We request that you work with Dale Burkett (chair for this session) and consider these regulatory needs from the perspective of your session's general theme. You should focus on the conflicts and/or contributions your session's speakers might have with the outline of the current regulatory requirements presented by the agencies. You should address some remarks toward this end in the 15 min introduction you will give at the opening of your session (this need not be your only topic). A brief written statement on you comments concerning the regulatory requirements would be helpful, however, we plan to enlist the help of an independent editor to record and synthesize your (and the other speakers) comments in your session in relationship to the regulatory objectives. You will have a review and comment opportunity before we publish the executive summary.

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Keep in mind that the executive summary (containing your address to regulatory guidelines) is an effort to provide timely food for thought and documentation of scientific concern during the reauthorization arguments for the Endangered Species Act. This was one of the principle objectives first described in my conference outline.

Do you plan to submit a written paper for inclusion in the final book publication? I was hoping an overview (written by the session chair) concerning the application of the theme of your session to Evolutionary Significant Units could be used as a chapter introduction for your session's contributed papers.

wait
till
after

Please, let me know your date of arrival, date of departure and if you will be sharing your room with someone. I need this for the Doubletree Hotel reservations assigned to AFS speakers. I will confirm your room arrangements as soon as you can get this information to me.

Thanks for your help. This looks like a significant conference and I appreciate your contribution.

Sincerely,

Jennifer L. Nielsen

Uncertainty, Resource Exploitation, and Conservation: Lessons from History

Donald Ludwig, Ray Hilborn, Carl Walters

There are currently many plans for sustainable use or sustainable development that are founded upon scientific information and consensus. Such ideas reflect ignorance of the history of resource exploitation and misunderstanding of the possibility of achieving scientific consensus concerning resources and the environment. Although there is considerable variation in detail, there is remarkable consistency in the history of resource exploitation: resources are inevitably overexploited, often to the point of collapse or extinction. We suggest that such consistency is due to the following common features: (i) Wealth or the prospect of wealth generates political and social power that is used to promote unlimited exploitation of resources. (ii) Scientific understanding and consensus is hampered by the lack of controls and replicates, so that each new problem involves learning about a new system. (iii) The complexity of the underlying biological and physical systems precludes a reductionist approach to management. Optimum levels of exploitation must be determined by trial and error. (iv) Large levels of natural variability mask the effects of overexploitation. Initial overexploitation is not detectable until it is severe and often irreversible.

In such circumstances, assigning causes to past events is problematical, future events cannot be predicted, and even well-meaning attempts to exploit responsibly may lead to disastrous consequences. Legislation concerning the environment often requires environmental or economic impact assessment before action is taken. Such impact assessment is supposed to be based upon scientific consensus. For the reasons given above, such consensus is seldom achieved, even after collapse of the resource.

For some years the concept of maximum sustained yield (MSY) guided efforts at fisheries management. There is now widespread agreement that this concept was unfortunate. Larkin (*1*) concluded that fisheries scientists have been unable to control the technique, distribution, and amount of fishing effort. The consequence has been the elimination of some substocks, such as herring, cod, ocean perch, salmon, and lake trout. He concluded that an MSY based upon the analysis of the historic statistics of a fishery is not attainable on a sustained basis. Support for Larkin's view is provided by a number of reviews of the history of fisheries (*2*). Few fisheries exhibit steady abundance (*3*).

It is more appropriate to think of resources as managing humans than the converse: the larger and the more immediate are prospects for gain, the greater the political power that is used to facilitate unlimited exploitation. The classic illustrations are gold rushes. Where large and immediate gains are in prospect, politicians and governments tend to ally themselves with special interest groups in order to facilitate the exploitation. Forests throughout the world have been destroyed by wasteful and shortsighted forestry practices. In many cases, governments eventually subsidize the export of forest products in order to delay the unemployment that results when local timber supplies run out or become uneconomic to harvest and process (*4*). These practices lead to rapid mining of old-growth forests; they imply that timber supplies must inevitably decrease in the future.

Harvesting of irregular or fluctuating resources is subject to a ratchet effect (*3*): during relatively stable periods, harvesting rates tend to stabilize at positions predicted by steady-state bioeconomic theory. Such levels are often excessive. Then a sequence of good years encourages additional investment in vessels or processing capacity. When conditions return to normal or below normal, the industry appeals to the government for help; often substantial investments and many jobs are at stake. The governmental response typically is direct or indirect subsidies. These may be thought of initially as temporary, but their effect is to encourage overharvesting. The ratchet effect is caused by the lack of inhibition on investments during good periods, but strong pressure not to disinvest during poor periods. The long-term outcome is a heavily subsidized industry that overharvests the resource.

The history of harvests of Pacific salmon provides an interesting contrast to the usual bleak picture. Pacific salmon harvests rose rapidly in the first part of this century as markets were developed and technology improved, but most stocks were eventually overexploited, and many were lost as a result of overharvesting, dams, and habitat loss. However, in the past 30 years more fish have been allowed to spawn and high seas interception has been reduced, allowing for better stock management. Oceanographic conditions appear to have been favorable: Alaska has produced record catches of salmon and British Columbia has had record returns of its most valuable species (*5*).

We propose that we shall never attain scientific consensus concerning the systems that are being exploited. There have been a number of spectacular failures to exploit resources sustainably, but to date there is no agreement about the causes of these failures. Radovitch (*6*) reviewed the case of the California sardine and pointed out that early in the history of exploitation scientists from the (then) California Division of Fish and Game issued warnings that the commercial exploitation of the fishery could not increase without limits and recommended that an annual sardine quota be established to keep the population from being overfished. This recommendation was opposed by the fishing industry, which was able to identify scientists who would state that it was virtually impossible to overfish a pelagic species. The debate persists today.

[illegible]

short term

After the collapse of the Pacific sardine, the Peruvian anchoveta was targeted as a source of fish meal for cattle feed. The result was the most spectacular collapse in the history of fisheries exploitation: the yield decreased from a high of 10 million metric tons to near zero in a few years. The stock, the collapse, and the associated oceanographic events have been the subject of extensive study, both before and after the event. There remains no general agreement about the relative importance of El Niño events and continued exploitation as causes of collapse in this fishery (*7*).

The great difficulty in achieving consensus concerning past events and a fortiori in prediction of future events is that controlled and replicated experiments are impossible to perform in large-scale systems. Therefore there is ample scope for differing interpretations. There are great obstacles to any sort of experimental approach to management because experiments involve reduction in yield (at least for the short term) without any guarantee of increased yields in the future (*8*). Even in the case of Pacific salmon stocks that have been extensively monitored for many years, one cannot assert with any confidence that present levels of exploitation are anywhere near optimal because the requisite experiments would

(*Continued on page 36*)

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(*Continued from page 17*)

involve short-term losses for the industry (*9*). The impossibility of estimating the sustained yield without reducing fishing effort can be demonstrated from statistical arguments (*10*). These results suggest that sustainable exploitation cannot be achieved without first overexploiting the resource.

The difficulties that have been experienced in understanding and prediction in fisheries are compounded for the even larger scales involved in understanding and predicting phenomena of major concern, such as global warming and other possible atmospheric changes. Some of the time scales involved are so long that observational studies are unlikely to provide timely indications of required actions or the consequences of failing to take remedial measures.

Scientific certainty and consensus in itself would not prevent overexploitation and destruction of resources. Many practices continue even in cases where there is abundant scientific evidence that they are ultimately destructive. An outstanding example is the use of irrigation in arid lands. Approximately 3000 years ago in Sumer, the once highly productive wheat crop had to be replaced by barley because barley was more salt-resistant. The salty soil was the result of irrigation (*11*). E. W. Hilgard pointed out in 1899 that the consequences of planned irrigation in California would be similar (*12*). His warnings were not heeded (*13*). Thus 3000 years of experience and a good scientific understanding of the phenomena, their causes, and the appropriate prophylactic measures are not sufficient to prevent the misuse and consequent destruction of resources.

Some Principles of Effective Management

Our lack of understanding and inability to predict mandate a much more cautious approach to resource exploitation than is the norm. Here are some suggestions for management.

1) Include human motivation and responses as part of the system to be studied and managed. The shortsightedness and greed of humans underlie difficulties in management of resources, although the difficulties may manifest themselves as biological problems of the stock under exploitation (*2*).

2) Act before scientific consensus is achieved. We do not require any additional scientific studies before taking action to curb human activities that effect global warming, ozone depletion, pollution, and depletion of fossil fuels. Calls for additional research may be mere delaying tactics (*14*).

3) Rely on scientists to recognize problems, but not to remedy them. The judgment of scientists is often heavily influenced by their training in their respective disciplines, but the most important issues involving resources and the environment involve interactions whose understanding must involve many disciplines. Scientists and their judgments are subject to political pressure (*15*).

4) Distrust claims of sustainability. Because past resource exploitation has seldom been sustainable, any new plan that involves claims of sustainability should be suspect. One should inquire how the difficulties that have been encountered in past resource exploitation are to be overcome. The work of the Brundland Commission (*16*) suffers from continual references to sustainability that is to be achieved in an unspecified way. Recently some of the world's leading ecologists have claimed that the key to a sustainable biosphere is research on a long list of standard research topics in ecology (*17*). Such a claim that basic research will (in an unspecified way) lead to sustainable use of resources in the face of a growing human population may lead to a false complacency: instead of addressing the problems of population growth and excessive use of resources, we may avoid such difficult issues by spending money on basic ecological research.

5) Confront uncertainty. Once we free ourselves from the illusion that science or technology (if lavishly funded) can provide a solution to resource or conservation problems, appropriate action becomes possible. Effective policies are possible under conditions of uncertainty, but they must take uncertainty into account. There is a well-developed theory of decision-making under uncertainty (*18*). In the present context, theoretical niceties are not required. Most principles of decision-making under uncertainty are simply common sense. We must consider a variety of plausible hypotheses about the world; consider a variety of possible strategies; favor actions that are robust to uncertainties; hedge; favor actions that are informative; probe and experiment; monitor results; update assessments and modify policy accordingly; and favor actions that are reversible.

Political leaders at levels ranging from world summits to local communities base their policies upon a misguided view of the dynamics of resource exploitation. Scientists have been active in pointing out environmental degradation and consequent hazards to human life, and possibly to life as we know it on Earth. But by and large the scientific community has helped to perpetuate the illusion of sustainable development through scientific and technological progress. Resource problems are not really environmental problems: They are human problems that we have created at many times and in many places, under a variety of political, social, and economic systems (*19*).

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19. We thank D. Schluter, L. Gass, and L. Rowe for helpful comments. Our research was supported in part by the Natural Sciences and Engineering Research Council of Canada under grants A9239 and A5869 and by a State of Washington Sea Grant.

MEETING BRIEFS

Predators, Prey, and Natural Disasters Attract Ecologists

Some 2200 ecologists turned out for the 78th annual meeting of the Ecological Society of America (ESA), held in Madison, Wisconsin, 31 July to 4 August. Among the offerings: reports on the effect of dams and levees on large river ecology, predator-prey interactions, how parasites might control evolution, and the impact of clearcutting on soil organisms.

Isle Royale: End of an Era?

why not inbreeding F1 – F2

In the hard winter of 1949, a couple of Canadian wolves padded across frozen Lake Superior and hit pay dirt off Ontario's shore: Michigan's Isle Royale, a wild, 45-mile-long island overrun with moose, which had discovered the predator-free haven early in the century. In 1958 wildlife biologist Durward Allen of Purdue University began tracking the changing population numbers, as the wolves tracked the moose in a classical predator-prey pas de deux. Thirty-five years later, Isle Royale is the longest studied system of natural predator-prey dynamics in existence and has been a fount of information on wolf behavior. The notion, for example, that wolves are selective in their predation, taking primarily young and old individuals, grew out of the Isle Royale studies.

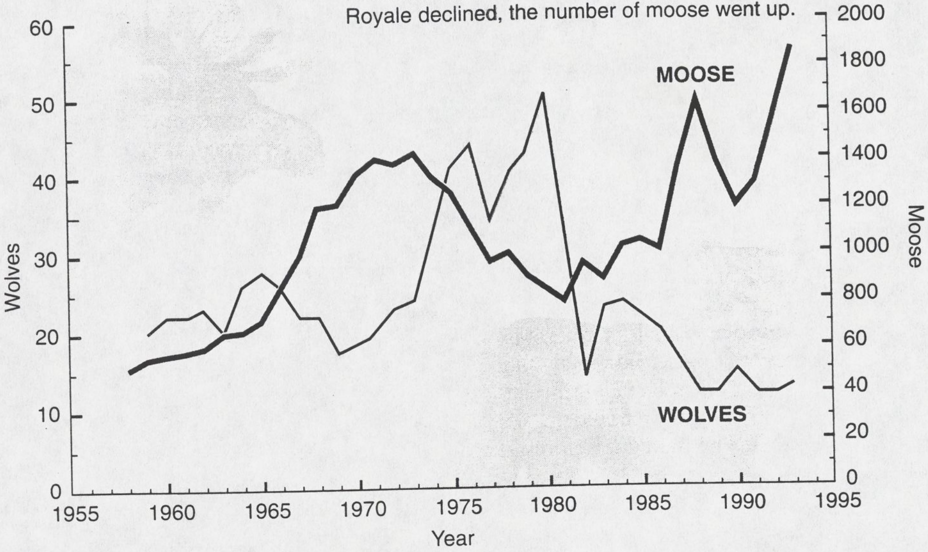
But the time course on this natural experiment may be running out. The wolf population, which at its peak in 1980 numbered 50 animals, took a nosedive in the early 1980s from which it still has not recovered, wildlife ecologist Rolf O. Peterson of Michigan Technological University reported at the ecology meeting. Only four pups have been born in the past 2 years, all to the same female in one wolf pack. The two other packs on the island are down to just a pair of wolves each. The total wolf population is now 13, and, by most accounts, is on its way to extinction. With fewer wolves, the moose population has, predictably, reached a record high of about 1900 this year.

The wolves seem to have been dealt a one-two punch: a narrow genetic base to begin with, followed, in all probability, by an encounter with a deadly canine virus in ① 1981. After the wolves started dying, the animals were captured in 1988 for blood testing to determine what was doing them in. Restriction enzyme analysis of the wolves' mitochondrial DNA turned up a single pattern, indicating the wolves were all descended from a single female, and they had ② only about half the genetic variability of mainland wolves.

Such an isolated and inbred population would have a tough enough time hanging on during the best of times. But antibodies in the blood samples indicated the wolves had also been exposed to parvovirus, a common killer of unvaccinated dogs that emerged in the late 1970s. Though only circumstantial evidence indicts the virus as the killer, the start of the wolves' decline coincides with a 1981 parvovirus outbreak in nearby Houghton, Michigan, and it could have been carried to Isle Royale on the hiking boots of visitors to the U.S. National Park on the island.

Virus or no, the wolves seem to be on their last legs, although not everyone believes they are going extinct. "It's too early to conclude that," says wolf expert L. David Mech of the Fish and Wildlife Service. He points out that the wolves rebounded after other periods of low reproduction in the 1960s, despite their inbreeding. Peterson does concede that the outcome isn't certain, but he's not optimistic. "More likely the population will continue to dwindle with progressively poorer reproductive success until …they run out of one sex," he says. If that happens, the famed predator-prey study could become a study of extinction.

–Christine Mlot



Predator tracks. As the wolf population on Isle Royale declined, the number of moose went up.

SOURCE: R.O. PETERSON

Dams, Levees, and River Health

Civil engineers have long known that constructing dams and levees along major rivers changes their physical characteristics in ways that can have unfortunate results. That lesson was brought home this summer when the mighty Mississippi and some other rivers of the U.S. heartland surged out of their banks in what by all accounts is the flood of the century in North America. The many dams and levees constructed to hold the rivers back apparently contributed to the havoc wreaked by the floods. But while dams' and levees' effects on water flow have long been studied, the impacts of flood control engineering on the biological health of major rivers have barely been explored. One reason: Ecologists have concentrated most of their efforts on smaller rivers and streams because they are much easier to study.

That's now beginning to change as ecologists and other biological researchers are forming equal partnerships with the physical scientists to develop models that describe how the physical alterations brought about by dams or levees in turn affect the biology of large rivers. Judy Meyer, a University of Georgia stream ecologist and president-elect of the ESA, describes this new cooperative effort as "the wave of the future. You need teams of geologists, hydrologists, chemists, and biologists to understand rivers. One researcher can't encompass it all."

A talk given at the ESA meeting by aquatic ecologist Frank Ligon of EA Engineering in Lafayette, California, exemplifies this new approach. With geomorphologist William Dietrich of the University of California, Berkeley, and aquatic scientist William Trush of Humboldt State University in Arcata, California, Ligon measured the rates of the movements of gravel, sand, and cobblestone-sized rocks on both sides of dams on various rivers in California, Georgia, and New Zealand, and related the changes to alterations in the rivers' depth, width, and velocity downstream.

① 2ndary effects of low H. re. resistance
DDT -- insects, Gambusia
dif. from passing on genes for surviv.
- toxins - plants
- need H for selection [illegible]

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The Biology of Rarity: Patterns, Causes and Consequences

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William E. Kunin and Kevin J. Gaston

There is a growing body of evidence suggesting that locally rare and geographically restricted species may have characteristics that differ from those of taxa that are more common. Several studies show that rare taxa have lower levels of self-incompatibility, a tendency toward asexual reproductive pathways, lower overall reproductive effort and poorer dispersal abilities. There are several mechanisms that could be responsible for such differences, but they may in practice be difficult to differentiate. Nonetheless, the documentation of recurrent rare–common differences is of vital importance because it may allow us to compensate partially for the bias of the published literature toward studies of common taxa.

Most of what we know about the biological world stems from the study of common species, but most of the world's species are rare in some sense of the word (Box 1). The primary reasons for this bias are obvious: common species may in some sense be ecologically more 'important' than rare species, and they are certainly much easier to study. But such biases can also be pernicious: if rare and common species are different in important ways, our interactions with rare species may be inappropriately guided by our skewed experience. All of which raises the question: are rare and common species generally different?

Ever since the pioneering work of Deborah Rabinowitz and her co-workers[1–3], there has been a growing literature of research aimed at comparing the properties of species as a function of their population densities and distributions. The purpose of this article is to review a segment of that literature, to examine whether there is any evidence of recurrent rare–common differences, and, if so, what mechanisms might be called upon to explain them.

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Unfortunately, the term 'rare' describes a wide array of spatial and temporal patterns of abundance, from sparsely populated species with wide geographic ranges to point endemics with dense local populations[4,5]. There is little biological reason to group these disparate phenomena under a single word, except by way of convenience. Wherever possible, we will try to differentiate the measures of 'rarity' used by the various studies we cite. In some cases, authors have intentionally restricted their considerations to a particular, well-defined set of cases, such as highly restricted endemics. Many other studies, however, have been based on endangered species lists, which group together local endemics, geographically marginal populations, sparsely populated taxa and other types of rarities. In this article, we use the term 'abundance' to refer to the commonness or rarity of species when no particular measure or pattern is implied.

The literature of rare–common comparisons

In principle, we could look for rare–common differences in any species characteristic. An overall review of all such comparisons, however, would far exceed the limits of this article. Much of the relevant work has been performed with other questions in mind, and so a bit of detective work may be required to discover an abundance comparison. There is a sizable literature, for instance, on the relationship between body size and population density (e.g. Ref. 6), which is as relevant to the study of rarity as it is to the study of body size. If big animals are rare, it is equally true that rare animals are disproportionately likely to be big. The literature on plant defensive chemistry (e.g. Ref. 7) and the island biogeography of parasites on their hosts[8] or of predator functional and numeric responses (e.g. Ref. 9) provide data sets that suggest consistent differences in the biology of rare and common species relative to the species that feed upon them. Possible differences in the competitive abilities of rare and common species have been the focus of a small but interesting literature (e.g. Ref. 3). There is also a number of papers examining the relationship between abundance and niche specialization or habitat requirements (e.g. Ref. 10). Here we focus on a rather narrower question: do rare and common species differ in their reproductive and dispersal characteristics?

In addition to the variety of types of rarity to be considered and the wide variety of effects to be tested, a fairly broad range of analytical techniques have been brought to bear on the subject. Much of the published work consists of pairwise comparisons, studies in which a common species is compared with a closely related rare species. Any such study, viewed in isolation, has little statistical power; any two species, examined closely, are bound to differ in some biologically interesting way. It is only by studying large numbers of species, or by bringing together large numbers of studies, each of which examines a few species, that we can speak of general differences between rare and common species with any confidence. Here we restrict our attention to studies in which at least five species are considered.

Where multiple species are compared, a common strategy is to contrast two groups of species, one deemed by some standard to be 'rare', and the other deemed 'common' (usually by virtue of not fitting the criteria for rarity). Sometimes the sets are nested; rare species are compared to a larger species group of which they are a part. Other researchers have focussed on pairwise contrasts of closely related species, which are then either used as groups or else taken as multiple, paired comparisons. Some studies divide abundance classes more finely, with multiple categories ranging from extremely rare through to extremely common, while still others use a continuous variable (e.g. estimated population size or extent of geographical range) to reflect abundance.

Rare species traits: general patterns

Table 1 lists the findings of 16 studies in which reproductive and/or dispersal characteristics of at least five species are compared as a function of some measure of abundance. Despite a diverse array of study organisms, statistical methods and patterns, several clear generalizations emerge. The reproductive characteristics of rare species tend to be biased away from outcrossing and sexual reproduction. Geographically restricted shrub species and *Paramecium* varieties are disproportionately likely to be autogamous. Both locally peripheral and globally rare mosses tend to be unusually dependent on vegetative reproduction and biased away from spore production. In both darters and mice, reproductive effort is unusually low in geographically restricted species, suggesting a reallocation from sexual reproduction to longevity. Sparsely populated grasses and narrowly distributed oaks have unusually small seeds. Dispersal abilities are unusually restricted in rare species among mosses, beetles and ants. None of these distinctions is absolute; rare and common species generally have broadly overlapping characteristics, and some studies have found no differences whatsoever. Even so, the overall pattern of rare–common differences is striking.

Methodological critique

There are several methodological weaknesses common among such samples of studies. Many of them are statistical fishing expeditions, exploring dozens of possible effects without any correction for the consequences of performing multiple tests on probability estimates (e.g. Bonferonni corrections). Even when specific explanations are proposed, there is often a sense of circularity in the hypothesis testing; it sometimes appears that a knowledge of the study taxa itself suggested the hypotheses that are, in turn, tested on them. In addition, many of the more widely studied traits associated with rarity are themselves highly intercorrelated. For example, reproductive effort and dispersal distances are often correlated, and both are highly correlated with body size in many organisms. All three of these traits seem to be correlated with abundance, and untangling the four-way association may be far from trivial. There have been remarkably few attempts to disentangle such multiple interactions, and this could be a fruitful area for future work.

It is possible that some of the recorded associations are methodological artifacts. For example, the observation that rare plant species have short flowering seasons could easily be explained by the fact that many rarities are found at only a few sites rather than being due to any real differences in the degree of local flowering synchrony. Indeed, potentially artifactual patterns plague the study of rarity[11].

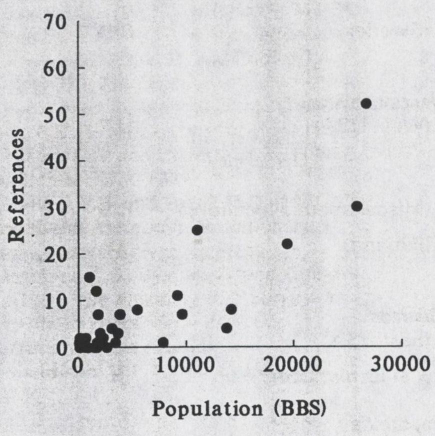
Adaptation and other mechanisms

Perhaps the most controversial aspect of many of these studies is one that often goes unstated, explicitly at least. If rare and common species show consistent differences, it is tempting to view these differences as evolved adaptations to deal with the condition of rarity. Yet the assumption of adaptive evolution as the sole or even the most likely source of pattern formation has come under increasing criticism in recent years (e.g. Ref. 12)

The mechanisms responsible for creating and maintaining rare–common differences may not always be obvious. The set of rare species could become biased by a number of different processes. (1) Not all species are equally likely to become rare, whether because of the rules of community assembly, the laws of trophic pyramids, or the dynamics of local speciation. In other words, certain species characteristics may be the cause rather than the consequence of rarity. (2) Similarly, the primary pathway by which species cease to be rare – extinction – may be biased in its operation, thereby further skewing the list of rarities. (3) Rarity brings with it immediate consequences (in density-dependent behavioural properties, ecological interactions and population genetics) that can influence the perceived properties of rare species. (4) There is the possibility that species may evolve adaptations to the conditions of rarity, provided they remain rare over evolutionarily meaningful lengths of time. Yet most studies implicitly assume that any differences discovered must result from this last process alone.

Box 1. Representation of rarity in the literature

Most biologists would guess that rare species were underrepresented in the published literature, but the point can be easily established by using a computerized reference database. The figure shows the number of publications listed in the Compact Cambridge Biological Index for 1982–1990 on North American sparrows and grosbeaks.



Each species is listed by its abundance as measured by the 1977 breeding bird survey[19]. A list of species for which this survey was judged appropriate was provided by Dr G. Butcher at the Cornell Laboratory of Ornithology, Ithaca, NY, USA, and only those species (30 in all) are shown. More studies have been published in recent years on the single commonest species than on the rarest 60% of the species combined.

As an example of how these different processes could be responsible for similar patterns, take the case of plant breeding systems. As we mentioned earlier, several studies have shown greater levels of self-compatibility in rare plant species. It is easy to make an adaptationist argument that sparsely populated plants should evolve self-compatibility as a response to the low pollination rates often associated with rarity [mechanism (4)]. But it is at least equally plausible that one or more of the other processes listed could contribute to the pattern.

For example, (1) self-compatible lineages may be more prone to producing rare species, either owing to the fitness consequences of inbreeding or because of a higher propensity to speciate in such taxa (owing to the greater probability of population establishment after a rare long-distance dispersal event[13], resulting in isolated and genetically bottlenecked populations that

Table 1. Published rare–common comparisons

Organism (and location)	Type of rarity[a]	Spatial scale[b]	Type of comparison[c]	Number of species[d]	Rarity effect	Source
Mosses						
(East Canada)	E	l/r	2	20r, 17c	Fewer spore producing, more gemmae and vegetative reproduction (less sexual, lower dispersal)	20
(UK)	S	r g	2	177r, 515c 76r	More likely to be monoecious Less likely to have sporophytes	21
(Sweden)	S/D	l/r	4	18	Produce diaspores less frequently (poorer dispersal)	22
Vascular plants						
(West USA)	U/F	r	3	569r, 12823t (5 datasets)	Fewer wind pollinated, more bilateral flowers	23
(Miscellaneous locations)	R/S	g	1	11 genera	No difference in breeding systems	24
(Finland)	U	r	1,2	83r, 64c	Shorter flowering seasons, no difference in dispersal, etc.	25
Quercus						
(East USA)	R	g	4	28	Smaller acorns	26
(California, USA)	R	g	4	11	Same, if island species excluded	
Psychotria						
(Central America)	R	g	4	66	Less heterostyly (probably more self-compatible)	27
Grasses						
(USA)	D	g	4	7	Smaller diaspores, no difference in dispersal distance; better competitors in mixtures	1,2,3
Paramecium						
(North America, Europe)	R	g	4	16	More often autogamous	28
Ciliates						
(Canada)	S/F	l	4	11	Fast population growth for their size	29
Carabids						
Brachinus (North America)	R/S	g	4	62	More brachypterous or apterous species (poor dispersal)	30
Nebria (North America)	R	g	4	49	More brachypterous species	31
Ants						
(Miscellaneous locations)	H	g	1	14r, 14c	More polygynous, less dispersal	32
Fish						
darters (North America)	R	g	4	28	Lower reproductive effort, smaller clutches of larger eggs	33
Mice						
Peromyscus (North and Central America)	R	g	4	46	Lower reproductive effort, smaller litters; greater size, greater longevity	34

[a] Types of rarity: R, range extent ('extent of occurrence' *sensu* Ref. 35); S, sites or grid squares inhabited ('area of occupancy' *sensu* Ref. 35); H, habitat or niche restriction; E, Edge-of-range rarity; F, frequency in censused area; D, density of population where found (dense versus sparse); U, unspecified or mixed categories (e.g. endangered species lists).

[b] Spatial scale: l, local (in area of study); r, regional (e.g. state or national); g, global.

[c] Types of comparisons: 1, multiple rare and common pairs; 2, rare group versus common group; 3, rare subset versus whole set (nested); 4, continuous (e.g. regression).

[d] Species number: (if group comparison) r, rare; c common; t, total species.

could develop into rare, endemic daughter species[14]). Similarly, (2) the reproductive difficulties associated with rarity[15] could result in the extinction of sparse populations of self-incompatible species, whereas similarly distributed self-compatible plants might persist as viable populations (cf. Ref. 16). Alternatively, (3) the high levels of inbreeding and genetic drift typical of small population sizes can themselves cause the breakdown of certain incompatibility systems (e.g. Ref. 17), resulting in an increase in self-compatibility even in the absence of any direct selective pressures. Thus, any one, or some combination, of the four categories of mechanisms mentioned above could potentially contribute to the apparent association between breeding systems and abundance.

Yet, when rare–common differences are discovered, many authors automatically ascribe them to evolutionary adaptations, as if that were the only, or the most probable, source of pattern. This tendency is unfortunate – it not only involves a fairly risky leap to possibly unwarranted conclusions, but it could also overshadow the true importance of such data sets. As the tools of comparative analysis for evolutionary hypotheses have become more refined[18], there is the risk that important patterns of rare–common differences will be passed over because they do not prove to be *evolved* patterns, and thus tend to disappear in the newer phylogeny-based tests. Indeed, these new techniques may serve an important role in differentiating between the various possible mechanisms that could be responsible for rare–common differences. Differences due to selective recruitment or extinction of rarities in certain lineages [mechanisms (1) and (2)] should show up in simple interspecific comparisons but fail some of the newer, phylogenetic tests, whereas differences due to either of the latter two mechanisms should pass both tests. Other recent comparative methods make it possible to test such questions more explicitly[19]. The question of whether particular species characteristics are a cause or a consequence of species abundance may soon be answerable.

Where next?

We began this article by demonstrating just how little was known about most rare species, and we should probably end it by suggesting that more research be done on them (as undoubtedly it should). But given the vast number of rare species and the scale of our ignorance, it is unlikely that this knowledge deficit will be made up in any reasonable amount of time. In the interim, conservation decisions must be made – decisions which cannot always be held up awaiting better data. It is in this context that comparative studies of rare and common species can be most useful. If, as seems likely, rare species often have different properties from the commoner species we know the most about, documenting such patterns will allow us to make better informed guesses. If we know nothing else about most rare species, we know at least that they are rare. That, in itself, may tell us a great deal.

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BIODIVERSITY AND THE CULTURE OF ECOLOGY

The image of the Great Chain of Being epitomizes the moral and religious attention people within the Western tradition have long paid to the diversity of life. From Plato's theory of perfect Forms to the quest of many recent ecologists to find order and balance in nature, philosophers, poets, painters, and scientists have attempted to describe the living world in ways that answer to religious and moral expectations. Ecologists in this century—like theologians and poets in previous centuries—have argued that the diversity of living things results not from mere contingency or chaos but serves larger purposes, instantiates universal principles and ideas, or expresses an intelligible order or a meaningful plan.

In the 11th Century, the French theologian Abelard, following Plato's *Timaeus* (30c), defined one aspect of the Chain-of-Being theme, namely that a sufficient reason explains the existence of every kind of organism. "Whatever is generated is generated by some necessary cause, for nothing comes into being except there be some due cause and reason for it" (cited in Lovejoy 1936). Along with the idea of sufficient reason, the principles of plenitude, continuity, and gradation determined the order of creatures from the least to the greatest in a vast Chain of Being.

These principles have analogies in the ecological theory of recent decades. Plenitude—the principle that the richness and diversity of creation is so great because it expresses the fullness of God's perfection—is found in various versions of the diversity–stability hypotheses, for example, in G. E. Hutchinson's (1959) speculation that there are so many species "at least partly because a complex trophic organization of a community is more stable than a simple one." The themes of gradual continuity and gradation likewise echo in hierarchy theory, the theories of trophic levels, food chains and webs, in the concept of orderly succession, and in other concepts that characterized ecology earlier this century.

Fundamental to the idea of the Great Chain of Being was a belief that God creates nothing in vain. Accordingly, we are obliged to care as

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much for the least creature in nature as for the greatest. The popular analogy associated with Paul Ehrlich that likens species to rivets in the wing of an airplane echoes the well-known passage in Alexander Pope's *Essay on Man*:

> Vast chain of being! which from God began,
> Natures aethereal, human, angel, man,
> Beast, bird, fish, insect, what no eye can see . . .
> Where, one step broken, the great scale destroyed
> From Nature's chain whatever link you strike,
> Tenth, or ten thousandth, breaks the chain alike.

Commenting upon the centrality of the Chain of Being metaphor, historian A. O. Lovejoy (1936) observed that according to this tradition, the diversity of nature corresponds to law-like principles that establish its order; the "universe was at least not a many-ringed circus." Lovejoy notes, however, that in the eighteenth century, a controversy arose pitting philosophers like Spinoza and Leibniz, who believed that the principle of sufficient reason necessitated a such a hierarchical order in the variety of nature, against those who followed the British philosopher Samuel Clarke in arguing that only God's essence implied existence, and that contingency pervaded the created world. In 1712, a British poet put that thesis as follows:

> Might not other animals arise
> Of different figure and of diff'rent size?
> In the wide womb of possibility
> Lie many things which ne'er actual may be:
> And more productions of a various kind
> Will cause no contradiction in the mind . . .
> These shifting scenes, these quick rotations show
> Things from necessity could never flow,
> But must to mind and choice precarious beings owe
> (cited in Lovejoy 1936)

A controversy that rages between those who believe that nature must exhibit a "balance" or "order" and those who argue that it is all chaos and contingency—a many-ringed circus—characterizes ecological debates today as it did cosmological debates in earlier centuries. As we shall see, these two positions—one emphasizing continuity and order in nature, the other emphasizing change—suggest grounds for valuing biodiversity, but they present quite different reasons that biodiversity should be preserved.

The Great Chain of Being Today

Earlier this century, ecologists such as Paul Sears and Frederic Clements, remaining firmly within Great Chain of Being tradition, approached ecology as the study of harmony, continuity, gradation, and equilibrium. Clements, as historian Donald Worster (1977) observes, contended that nature's course "is not an aimless wandering to and fro but a steady flow toward stability that can be exactly plotted by the scientist." Following Clements, Gaian theorists recast the Great Chain of Being in modern terms, representing the earth as a vast superorganism, possessing as much internal order as the organisms that make up its functioning parts.

E. P. Odum (1969), an ecologist who seems among those most indebted to Great Chain of Being analogies, restated the 18th Century principle of plenitude as "the strategy of ecosystem development" which is "directed toward achieving as large and diverse an organic structure as is possible within the limits set by the available energy input and the prevailing conditions of existence." This "strategy" is supposed to lead ecosystems in law-like ways through orderly successive changes to species composition to achieve a state of mature homeostasis in which the stability and diversity of the system are the greatest it can achieve under given conditions. In such a system, just as in the Chain of Being, every possible creature finds its place. In Odum's version of plenitude, this happens, for example, when weedy generalists (*r*-selected species) become replaced by a greater variety of specialized (*K*-selected) plants and animals able to exploit all the niches available to them.

Environmentalists drew many arguments for protecting species from two fundamental ideas: first, that plants and animals, through a hierarchy of relationships, are interconnected and interdependent; and, second, that nature progresses in predictable ways to greater diversity and stability. The hypothesis that the diversity and complexity of ecosystems support their stability, for example, contributed to the enactment of the Endangered Species Act in the United States. The hypothesis first advanced by Odum that salt marshes "outwell" nutrients to feed coastal fisheries served as a powerful argument for preserving those wetlands. The theory of forest succession to a climax state in which biomass remains constant helped people to appreciate the importance of rain forests. One could multiply these examples. The recreation of Great Chain of Being cosmography in post World War II community ecology provided concepts and theories crucial to the efforts environmentalists made to protect biodiversity and to preserve ecological systems.

Yet this traditional way of regarding nature, however helpful as it may be to the goals of environmental protection, cannot in itself suffice to sustain an argument for preserving biodiversity. Just as in the eighteenth century, so today many scholars advance a different approach that emphasizes the historical, the unique, and the contingent in nature. In our effort to appreciate and preserve biodiversity, we must look to this tradition as well—one that eschews theoretical generalizations and attends instead to the careful observation and description of historically contingent objects and events.

The Limits of Community Ecology

The problem with the tradition that runs from Sears and Clements to Odum is not that it fails to capture the concepts of balance, order, harmony, plenitude, and sufficient reason associated with Chain of Being cosmology, for this it does well. The problem is that this school of ecology, by secularizing a traditional vision of nature—by clothing it as science rather than as theology—demystified it. This led to two kinds of difficulties. First, the central theories that linked stability and diversity, that called for an orderly succession of communities, and that arranged creatures in trophic levels and webs opened themselves to empirical and theoretical refutations. In a kind of war between the generations, the students of Odum and of many other founders of community ecology set out to test and in the process debunked theories of forest succession (see Drury and Nisbet 1973, Connell and Slayter 1977), the "stability-- diversity" hypothesis (Goodman 1975), the "outwelling hypothesis" (Nixon 1980), and other tenets basic to the discipline.

Second and more relevant to our purposes, biologists who emphasized ecosystem-level properties and processes, such as productivity, energy flow, respiration, trophic webs, nutrient cycling, and efficiency, showed less and less interest in the minute particularities of individual organisms. These ecologists remained committed to a vision of science that insisted on a priori grounds on the centrality of testing by prediction the robustness of abstract and general mathematical theories (Sagoff 1988). According to one historian, community ecologists came to emulate "the language of systems scientists" and began to work on models at the intersection of biology and engineering (Patten 1971).

In the context of these developments in ecology, especially the branch that became known as "systems ecology," both scientists and policy makers found it easier to think of living creatures as resources to be manipulated than as—in John Muir's expression—"conductors of divinity" (Wolfe 1979). To be sure, both community and systems ecology retained faith with the central thesis of the Great Chain of Being that nature exemplifies a timeless and intelligible order rather than sheer historical contingency. By secularizing this religious intuition, however, ecosystem science replaced a priesthood of theologians with one of mathematical modelers and engineers.

It is not surprising that many environmental engineers and other experts found even in ecological theories that took up Great Chain of Being themes grounds not to venerate but to manipulate nature or, as Donald Worster notes, to manage the earth for improved efficiency. "'Governing' of all nature was the dream of these ecosystem technocrats" (Worster 1993, see also Taylor 1988). Experts have used the theory of forest succession, for example, to argue that rain forests, being "climax" or "mature" ecosystems must be in equilibrium and thus cannot add to global oxygen budgets (Whitmore 1980). More generally,

> human beings are more able to use ecosystems at young successional stages, which tend to be more productive. Accordingly, a general characteristic of human development is that we tend to maximize productivity by creating and maintaining ecosystems at such stages (Robinson 1993).

As this passage suggests, ecological science, which many of us pursue because of our love of nature, may fuel a technology intended to manipulate or transform nature. For example, in a well known article, ecologist Dan Janzen views with horror the possibility that agriculturally desirable organisms may be adapted by genetic

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The prospect that genetic engineering may turn rain forests to agricultural use, which dismays Janzen, appeals to others as a professional challenge. Frank Forcella (1984), writing in the ESA *Bulletin*, called upon his colleagues to embrace the "biotechnologist" credo "to engineer and produce plants, animals, and microbes that better suit the presumed needs and aspirations of the human population." He continued:

> Ecologists are the people most fit to develop the conceptual directions of biotechnology. We are the ones who should have the best idea as to what successful plants and animals should look like and how they should behave... Armed with such expertise, are we going to continue investing nearly all our talents in Natural History? . . . Or should we take the forefront in biotechnology, and provide the rationale for choosing species, traits, and processes to be engineered? I suspect this latter approach will be more profitable for the world at large as well as for ourselves.

To summarize: Poets and theologians who described the Great Chain of Being understood the principles of sufficient reason, plenitude, continuity, and gradation in terms of religious beliefs and moral values. Ecological concepts developed earlier this century and in popular vogue today adhere closely to these same principles—optimization is the current version of sufficient reason; diversity of plenitude; succession of continuity; and hierarchy of gradation. Yet, when these concepts occur in scientific theories, they may be shorn of their religious and moral significance. They may then be open to empirical and theoretical refutation. They may also support arguments that back efforts not necessarily to protect nature for its own sake but to manipulate it to meet our consumer demands.

At that point, we may wonder how much we wish the ecological and biological sciences—including genetic engineering—to succeed. Knowledge is power—but it can be the power to control or the power to protect—the power to bend nature to our purposes or to appreciate nature for its own ends.

The Study of Minute Particulars

We have noted that during the eighteenth century, a group of philosophers argued against Great Chain of Being principles to assert the contingency of creation; they harkened back to Aristotle's view that "it is possible for that which has a potency not to realize it" (*Metaphysics* XI 1071b 13). These writers held that the proper appreciation or reflection upon creation does not lose itself in grand theory—the quest for general mathematical laws and principles—but finds enough to admire and appreciate in nature's tiniest details. This approach sees "the world in a grain of sand/ And a heaven in a wild flower," as William Blake wrote in "Auguries of Innocence." It builds knowledge up from the study of minute particulars rather than seeking to deduce it from timeless a priori truths.

Ecologists who supported this approach early this century included taxonomists such as Henry Gleason, who opposed the a priori attribution of balance, equilibrium, succession, and other "systems" properties to nature. He argued that nature is more like a Heraclitean flux than like a Chain of Being. In "The Individualistic Concept of the Plant Association," Gleason (1926) wrote that each species of plant "is a law unto itself."

During the almost 70 years since Gleason wrote, ecologists have emphasized the search for universal theories, mathematical principles, and general properties over the historical study of individual organisms. This may be the reason that ecosystem modelers and theory-builders vastly outnumber trained taxonomists today. Nevertheless, some ecologists are now turning away from system-level analogies with engineering and other mathematical sciences toward "rich descriptions" of individual organisms in their habitats (Slobodkin et al. 1980).

"Whenever we seek to find consistency" in nature, an ecologist has recently written, "we discover change" (Botkin 1990)—thus echoing Gleason's remark that each species is a law unto itself. This biologist compares nature not to a three-ring circus, but to several musical compositions played in the same hall at once, each intruding on the pace and rhythms of the others. Appreciation then comes down to the intense and patient observation of details, not speculation about overarching harmonies. This kind of patient observation and rich or "thick" interpretative description characterizes the study of natural history in contrast to theoretical ecology.

The empirical work of natural history, including taxonomy, has been ignored, even ridiculed, paleontologist S. J. Gould has written, because it does not indulge in the high-priori mathematical modeling thought to characterize "hard" science. Yet our knowledge of species depends entirely on "the historical sciences, treating immensely complex and non-repeatable events (and therefore eschewing prediction while seeking explanation for what has happened) and using the methods of observation and comparison" (Gould 1984).

The essence of historical explanation, Gould (1989) writes, is contingency: A historical explanation does not rest on direct deductions from laws of nature, but on an unpredictable sequence of antecedent states, where any major change in any step of the sequence would have altered the final result. This final result is therefore dependent, or contingent, upon everything that came before—the unerasable and determining signature of history.

Gould (1989) observes that historical narratives that explain the minute particulars of plants and animals at specific times and places "are endlessly fascinating in themselves, in many ways more intriguing to the human psyche than the inexorable consequences of nature's laws." Biologist E. O. Wilson (1992) elegantly takes up this theme in arguing that every kind of organism, large and small—the flower in the crannied wall—"*is* a miracle," but one that makes sense—is explicable—in the context of a rich historical narrative. "Every kind of organism has reached this moment in time by threading one needle after another, throwing up brilliant artifices to survive and reproduce against nearly impossible odds." To study these artifices—to appreciate the toil each species endures to prevail in the vast labor of evolution—is to be moved to more than scientific understanding. As Darwin understood, this understanding fills our minds with reverence and awe.

The Uses of Diversity

The naturalists who built in the 18th and 19th centuries the great museum collections of species would be surprised at the direction ecological science has taken in our century away from natural history and toward mathematical modeling and general theory-building. These naturalists were rather "wanderers and wonderers" who could be fascinated equally by starfish and stars; they studied the living world for the love of it, not to gain power over it. For these scientists, the infinite variety of nature—as Shakespeare said of Cleopatra—did not cloy the appetite it fed, but where it most satisfied it made most hungry. E. O. Wilson has described this orgy of intellectual satisfaction as *biophilia*, which is a love or affiliation with all of the aspects of the living world.

This attitude toward the living world will not necessarily help us to exploit its resources efficiently; it may not even offer us instrumental or prudential arguments for protecting biodiversity. Naturalists do not necessarily insist, for example, that the moths or mites they study serve as rivets holding Spaceship Earth together; nor need they be concerned with the possible medicinal uses of these species. Rather, simply by describing these organisms and the toil of their coming to be, these naturalists show us how deeply these creatures reward our curiosity and inspire our sense that they have a rightful place upon the earth.

Even if natural historians appeal to ethical and aesthetic rather than to economic and instrumental values, they may nevertheless point to two important uses of biodiversity. First, the particular flora and fauna indigenous to a locality constitute along with details of landscape the fundamental characteristics that identify that place. Thus, insofar as a sense of place is important to human beings—insofar as it is important to people themselves to be native to a place—then it is crucial to maintain an affiliation with its native and indigenous species. Many of us worry that the global reach of markets brings with it a kind of cultural homogeneity—that global unity threatens a kind of global uniformity. Only by resisting the leveling effects of the marketplace can we maintain the integrity of communities—and in this context, ecological and human communities will stand or fall together.

Second, the world's endangered and threatened species include many migratory animals as well as other species whose range is international. The protection of these species—and the seas, forests, and other environments that sustain them—thus becomes an international responsibility. In setting up international institutions and regimes, as well as in entering and implementing arrangements like the Biodiversity Convention, nations learn to work together to maintain what the ancients called *res publica*, which is to say, a public place or thing (in ancient times, typically a monument or town square) which every group honors for its his-

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torical meaning or intrinsic value, not necessarily for its economic utility. Thus the concept of *res publica* is to be distinguished from that of a commons, for people create the former because of a shared sense of moral or cultural community; they police the latter to rationalize their competition over resources they would otherwise waste.

Consider, first, the importance of a sense or spirit of place in decisions local communities make in favor of protecting indigenous plants and animals. The concept of place helps us to understand what we deplore about the human subversion of nature and fear about the destruction of the environment. Many of our moral and aesthetic sentiments about nature are rooted in the sense of loss of places we keep in shared memory and cherish with instinctive and collective loyalty. This sense of loss underlies our concern about the decline of diversity and an attendant loss of security—the security one has when one relies on characteristic aspects of places one knows well.

Thus, a principal reason we set about to protect the habitats of native and indigenous species while caring less about the survival of exotic (including engineered) organisms has to do with our commitment to continuity of places—continuity that requires a sense of community with the past, with each other, and with nature. The preservation of biodiversity is the first step we must take in becoming ourselves native to a place.

What may worry us most in the disappearance of species is the prospect, then, of becoming ourselves strangers to the earth, of never quite settling into it, of losing touch with the places that help constitute the identity of our communities, of therefore being at home nowhere. For the sake of our own identities we must maintain the identities of the places where we live—and this entails maintaining its flora and fauna as well as larger landscapes. The motive for saving ecosystems may most fundamentally lie in our need to feel at home where we live—to attach ourselves to what becomes safe and secure because it retains its aesthetic and cultural characteristics in the midst of change.

In this context, the creation of shared places—*rei publicae*—becomes the most serious work of international relations. The point of this work is to allow groups that may compete over resources, ideology, nationality, and other goals to embrace and act upon values they share. In the Biodiversity Convention, in the Mediterranean Action Plan, in regions that govern the North Sea, the Baltic, and other international waters, in rules regulating trade in endangered species, and in other environmental regimes, we find nations that may be at odds over other issues joining together in a common purpose that is ethical, perhaps religious, at its core. It is this act of making peace not only with the rest of creation but also with each other—learning to put aside differences to act on common commitments—that may be the most important outcome of the preservation of biodiversity.

Conclusion

The American ecologist Robert MacArthur in his book *Geographical Ecology* argued that what is important about diversity is not the history of individual species—the sort of thing that interests naturalists—but the principles and patterns that explain diversity from the point of view of an a-historical mathematical and predictive science. "Hence, we use our naturalist's judgment," MacArthur (1972) wrote, "to pick groups large enough for history to have played a minimal role but small enough so that patterns remain clearer." He wondered: "Will the explanation of these facts degenerate into a tedious set of case histories, or is there some common pattern running through them all?"

We have discussed two ways of thinking about nature. The first is that of MacArthur; community and systems ecologists following him invoked concepts such as complexity, equilibrium, stability, orderly succession, and hierarchy that echo the principles of plenitude, gradation, continuity, and sufficient reason found in Great Chain of Being cosmology. Ultimately, these principles go back to Plato who considered ideal forms to be the appropriate objects of knowledge and believed that actual beings and events at best offer only vague clues or hints about those forms. On the other hand, we described a complementary tradition in ecology, going back to Aristotle, that insist upon what MacArthur calls "tedious case histories." This approach appreciates the individuality and contingency of particular things and claims these as the proper objects of knowledge.

Ecologists this century such as MacArthur sought to identify Platonic or intelligible forms in nature; these ecologists worked in the tradition of Great Chain of Being cosmology. While they took up concepts that have clear theological origins, however, they demystified them in order to give them scientific legitimacy. These concepts therefore lost their religious connotations—their affiliation with and affection for nature—and became central to an effort to predict phenomena in order better to control nature for our efficient use.

In contrast, natural historians took up techniques of observation, taxonomy, and classification, as well as thick description and historical explanation associated not with religion or cosmology but with empirical science ever since Aristotle. These naturalists, however, turned this task into a nearly religious mission, teaching their readers to appreciate and care about the plants and animals they so lovingly described. Naturalists such as S. J. Gould and E. O. Wilson stand firmly within an Aristotelian tradition of empiricism, yet they turn this tradition into a spiritual quest. This is the reverse of ecologists who followed the path of Platonic rationalism and who transformed, however inadvertently, an essentially religious cosmology into a basis for environmental engineering.

Thus, the recent history of ecology presents a paradoxical face. One group of ecologists—followers of MacArthur—took up essentially religious ideas from Great Chain of Being cosmology but divested these concepts of all their spiritual connotations to convert them to the uses of "hard" predictive and universal science. The other group took up the rather dispassionate concepts of systematics and taxonomy, which had constituted the core of biological science since Aristotle, and have endowed these concepts with an almost religious significance.

Each of these approaches gives us strong reasons to value biodiversity. The first tradition, which seeks to predict natural events on the basis of mathematical patterns and principles, helps us to understand the economic and instrumental role biodiversity plays in sustaining ecosystems. This approach warns us against the extinction of species on prudential grounds—for example, because one never knows when one might have a use for some chemical compound they may contain. And even biotechnologists need the raw material that they may recombine to form new genetic worlds for us to conquer and use.

The second approach, which focuses our moral attention on case histories, teaches us to appreciate the wonder of nature and to attach ourselves culturally and aesthetically to the places nature has given us to live. In this context, we are most loathe to surrender even a single species, even if it could be shown not to be economically or instrumentally useful. To those who make this moral commitment to the rest of Creation, even the gesture of identifying and naming a species is a morally important act. Every parent with a new baby—or every child with a new pet—understands that the process of naming is central to the process of taking possession and assuming responsibility. The prospect of the extinction of millions of species, some of which we have not even named, must fill us with remorse that is moral, not just prudential. We say good-bye to what is not yet ours; we are relinquishing what we have not yet possessed.

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A PARADIGM FOR ENVIRONMENTAL MANAGEMENT DECISION-MAKING

The academic community plays a number of important roles in supporting those of us who are day-to-day practitioners of environmental management. One of these is to provide sound scientific bases for management actions. ESA is to be congratulated for filling this role with the journal *Ecological Applications*. Study of the first volumes shows just how effective this series is at defining the parameters of applied ecology.

Another crucial contribution from academia is ongoing idea generation. To manage the environment in protective, cost-effective fashion, we need innovative, useful ideas for interpreting findings and projecting risks and benefits. Ecology as a whole is just awakening to a key analytical idea: that natural systems in general, and perhaps ecosystems most particularly, operate through "fuzzy," rather than "crisp," processes.

Ecosystems have long been studied as examples of von Bertalanffy-type dynamic control systems (von Bertalanffy 1968). This approach has been heuristically useful (for example, Gist and Crossley 1975, Odum 1986, Elliott et al. 1988), but has proven to be less effective for management. In practice, it is often difficult to reproduce experimental findings at the ecosystem scale. Projected outcomes frequently fail to validate, rendering the uncertainty of management decisions very high, and weakening cost–benefit comparisons.

The problem in linking specific experimental findings to large-scale management may be that von Bertalanffy systems are a limiting case of a more general class of constructs: Zadeh (fuzzy) systems (Zadeh 1965). Fuzzy systems are de-

ON THE RELATION OF SYNECOLOGY AND NATURAL HISTORY TO THE WONDER OF LIFE.

A REPLY TO SAGOFF

The vocation of practicing ecologists is, for the most part, a labor of love. The struggles and frustrations inherent in a career in ecology probably would not be tolerated if ecologists did not feel strongly about their chosen subject matter. In this regard, I find that I agree wholeheartedly with the general tenor of the sentiments expressed in an engaging article by Mark Sagoff (1993) regarding the need to preserve biodiversity. These sentiments are essentially embodied in the following proposition:

> "For the sake of our own identities we must maintain the identities of the places where we live--and this entails maintaining its flora and fauna as well as larger landscapes. The motive for saving ecosystems may most fundamentally lie in our need to feel at home where we live--to attach ourselves to what becomes safe and secure because it retains its aesthetic and cultural characteristics in the midst of change." (Sagoff 1993:379)

Unfortunately, the relationship described by Sagoff (1993) between 'the culture of ecology' and non-economic justifications for preserving biodiversity is unnecessarily oversimplified. The article distinguishes two approaches to ecology: (1) the theoretical study of communities and ecosystems (synecology), and (2) the natural history of organisms and species (autecology). The former approach is traced to 'clear theological origins' as symbolized by the "Great Chain of Being" metaphor of Lovejoy (1936). However, the subdiscipline of synecology, as epitomized by the works of Robert MacArthur, 'demystified' this metaphor in order to confer scientific legitimacy, and in the process synecology was reduced to *technology*. Consequently, synecology is unable to provide a basis for the proper appreciation of the wonder of nature. On the other hand, the 'rich descriptions' afforded by natural history, as exemplified by the works of Edward O. Wilson and Stephen Jay Gould, provide such a basis for a proper appreciation of the wonder of nature by focussing our moral attention on case histories. "This approach sees 'the world in a grain of sand/ And a heaven in a wild flower,' as William Blake wrote in 'Auguries of Innocence.'" (Sagoff 1993:377)

Scientists (including ecologists) tend to be a hard-nosed lot, among whom the percentage of atheists seems to be fairly high. Nevertheless, the capacity to appreciate the wonder of nature (even among theoretical community and ecosystem ecologists) is at least as widespread. More importantly, it is unclear why the scientific study of the dynamics of communities and ecosystems should destroy any sense of the wonder of nature--or even crush religious feelings. (In Boulder, Colorado, at least one Church of Gaia sponsors weekly drum-beating sessions!)

In this regard, it must be remarked that the portraits of MacArthur, Wilson and Gould painted by Sagoff distort their true attitudes towards nature. Robert MacArthur was no flinty-eyed biotechnocrat. In Wilson's own words:

> "He was not a mathematician of the first class--very few scientists are ... --but he joined superior talent in that field with an extraordinary creative drive, decent ambition, and a love of the natural world, birds, and science, in that order." (Wilson 1984:68)

The collaboration between MacArthur and Wilson that led to the publication of *The Theory of Island Biogeography* (MacArthur and Wilson 1967) was undertaken not "in order better to control nature for our efficient use" (Sagoff 1993:380), but for the sheer love of discovery (Wilson 1984:67–74). Moreover, island biogeography provides the theoretical mainstay of conservation biology not only to preserve potentially useful chemical compounds, but also to preserve the wonder of nature embodied in every single species that Sagoff is so loathe to surrender.

Much pleasure can be derived from the pursuit of antiquarian natural history for its own sake, but that is not the whole story. According to Gould (1989:281):

> "The historical scientist focuses on detailed particulars--one funny thing after another--because *their coordination and comparison* permits us, by consilience of induction, to explain the past ..." (emphasis added)

Similarly, Wilson (1992:5) describes his personal thoughts before an impending storm over the Amazon:

> "I sorted the memories this way and that in hope of stumbling on some pattern not obedient to abstract theory of textbooks. I would have been happy with *any* pattern. The best of science doesn't consist of mathematical models and experiments, as textbooks make it seem. Those come later. It springs fresh from a more primitive mode of thought, wherein the hunter's mind weaves ideas from old facts and fresh metaphors and the scrambled crazy images of things recently seen."

Thus we see that theory *per se* does not capture the wonder of nature. Theory is, however, a reflection--is indeed a product of--the wonder of nature to be found in the patterns that cut across rich descriptions of minute particulars. Consequently, Sagoff's distinction between synecology and natural history in relation to the proper appreciation of the wonder of nature (in the transcendental sense of Emerson and Thoreau, see Norton 1991) seems arbitrary.

Sir J. Arthur Thomson, Late Professor of Natural History at the University of Aberdeen, in an essay entitled "The Wonder of Life", remarked on the sentiment expressed in the phrase 'the world in a grain of sand/ And a heaven in a wild flower':

> "We must not, however, exaggerate a truth into a fallacy by pretending that all things are equally impressive. For the intensity of the appeal depends on our personal susceptibility *and on our knowledge of what we are looking at*, as well as on objective qualities. To most of us a diamond is more impressive than a dewdrop, and an eagle than a midge." (Thomson 1936:311, emphasis added)

So it is with communities and ecosystems. Synecology has not 'demystified' nature. Quite the opposite: every advance leads further to the ultimate mystery as described by Thomson (1936:316):

> "We think of the [rich descriptions of natural history]; but the big fact is that the World of Life is shot through and through, and up and down, with a quality which affords the highest product of evolution one of his finest joys, and surely gives him glimpses of some harmony lying deep in the heart of things, especially in those

that live. We are wise to recall Emerson's profound saying: 'I do not so much wonder at a snowflake, a shell, a summer landscape, or the glory of the stars; but at the necessity of beauty under which the universe lies'."

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Ecological and Genetic Factors in Conservation: A Cautionary Tale

T. M. Caro and M. Karen Laurenson

During the last decade, genetic problems potentially faced by small populations have constituted a central topic in conservation biology (*1*). Genetic theory predicts that inbreeding between members of small populations will reveal deleterious recessive alleles, which may be manifested in lowered fecundity, high infant mortality, and reduced growth rates that could eventually drive a population to extinction (*2*). In addition, loss of heterozygosity may reduce a population's ability to respond to future environmental change, such that the probability of extinction is increased or, at best, opportunities for evolution are limited (*3*). Consequently, genetic considerations play a central role in identifying risks to wild and captive populations (*4*).

The effects of inbreeding and loss of genetic diversity on the persistence of populations in the real world are, however, increasingly questionable (*5*). Although inbreeding results in demonstrable costs in captive (*6*) and wild situations (*7*), it has yet to be shown that inbreeding depression has caused any wild population to decline (*8*). Similarly, although loss of heterozygosity has detrimental impact on individual fitness, no population has gone extinct as a result. In the absence of such empirical data, circumstantial evidence is often marshalled to support the importance of genetic factors driving wild populations to extinction [for example, (*9*)]. One key example used in such arguments has been the cheetah because it is depauperate in genetic variation (*10*) and has poor survival prospects in the wild (*11*).

Specifically, a genetic survey of 55 cheetahs from southern Africa demonstrated a complete absence of genetic variation at each of 47 allozyme loci (*10*). Two-dimensional gel electrophoresis of 155 proteins from six animals revealed a percentage polymorphism of 3.2% and average heterozygosity of 0.013, both far lower than other Felidae sampled (*12*) and lower than other mammalian populations, which averaged 14.7% polymorphisms and 0.036 heterozygosity (*13*). Subsequent work in East Africa, mostly in the Serengeti ecosystem, Tanzania, detected only two allozyme polymorphisms in an electrophoretic survey of the products of 49 genetic loci (*14*). Additional evidence of depauperate variation came from 14 reciprocal skin grafts performed between pairs of unrelated cheetahs (*15*). Eleven grafts were accepted and three showed slow rejection, in marked contrast to skin of domestic cats, which was rejected by cheetahs within 2 weeks of the operation. These results suggested that the major histocompatability complex (MHC), a highly polymorphic group of tightly linked loci in vertebrates that is responsible for cell-mediated rejection of allogenic skin grafts, was unusually invariate in cheetahs.

As homozygous loci may expose deleterious recessives, O'Brien *et al.* (*15*) suggested that juvenile mortality should be high in cheetahs and cited elevated rates of juvenile mortality in captivity in comparison with other exotics [but see (*16*)]. They also reasoned that species-wide homozygosity would make populations and the species more susceptible to extinction from pathogens: If one member was unable to mount an effective immune response to a pathogen, the whole population would be similarly vulnerable. Examining a case study of disease sweeping through a successful felid breeding colony of 42 cheetahs in Oregon, O'Brien *et al.* noted that 43% [or 60%, (*17*)] died from coronavirus-associated diseases, including feline infectious peritonitis, while none of the lions developed symptoms. Rightly, the authors noted that such mortality was consistent with but was not necessarily the consequence of genetic uniformity, and in their subsequent papers were properly cautious in linking their genetic findings to the conservation problems faced by cheetahs such as low population density compared to other carnivores (*18*) and poor breeding performance in captivity (*19*). Nevertheless, a considerable secondary conservation and evolutionary literature, as well as the popular press, has uncritically assumed that lack of genetic variation is the cause of the cheetah's plight in the wild and in captivity [for example, (*20*)]. Now, in light of new evidence that has emerged from a long-term study of cheetah reproduction in the wild, we reexamined the potential consequences of genetic homozygosity for this species.

Laurenson (*21*) radio-collared female cheetahs in the Serengeti, relocated them regularly in their 800-km^2 home ranges, and thereby pinpointed the timing of birt and location of lairs. Soon after a fema had given birth, Laurenson entered lairs count and weigh the cubs while the moth was known to be away hunting. Regul monitoring of the family showed that cul suffered from extremely high mortality the first weeks of life such that only 36 o of 125 cubs (29%) emerged from the lair 2 months of age. By the time cubs reache independence over a year later, only 5 had survived. Other long-term studies large and medium-sized felids have yet t document mortality in the lair, but comparative mortality estimates between emergence and independence average 50% a opposed to 80% for cheetahs (*22*).

Direct observation of lairs and circumstantial evidence surrounding cub disappearances in many instances enabled the causes of mortality to be determined. Predation was by far the most important cause (35.5 out of 48.5 cubs; one litter size was unknown but estimated as 3.5, the mean size); four cubs were abandoned by their mothers when prey was scarce, seven died of fire and exposure, and two may have been inviable. Lions were responsible for all of the observed instances of predation in the lair and, with spotted hyenas, were responsible for most of the predation in this and parallel studies conducted in the same ecosystem (*23*). Stringent checks ruled out the possibility that mortality was influenced by visits to the lair or intensive observation schedules (*24*). Elsewhere in sub-Saharan Africa, large carnivores may also be important in depressing cheetah populations. Analysis suggests that across protected areas cheetah densities are low where lion densities are high and vice versa once the effects of prey biomass in the range 15 to 60 kg have been removed (*25*). Predation on young cubs is therefore a strong candidate for explaining why cheetahs have low population densities in comparison with lions and spotted hyenas in many areas of Africa.

These findings suggest that genetics may have been overemphasized in relation to the plight of cheetahs. First, only two of the observed cub deaths in the lair could have been attributable to genetic defects. Second, neonatal mortality in the first days of life before cubs were examined was probably low because observed litter sizes were similar to those reported at birth in captivity. Third, elevated juvenile mortality in utero in this species seems improbable because mothers reproduced extremely rapidly following the loss of an unweaned litter. Fourth, the high numbers of females breeding and rapid rates of litter production imply that neither the reproductive anatomy or physiology of either sex is functionally compromised as a result of genetic monomorphism (*26*). Finally,

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wild cheetahs tested seropositive to a number of infectious agents or microparasites including feline coronavirus (32% to 62%), herpesvirus (44%), feline immunodeficiency virus (22%), and toxoplasmosis (69%) (*17, 27*), and captive cheetahs produced antibodies after vaccination with modified live feline panleukopenia, herpes, and calci viruses (*28*). Similarly, only 60% (that is, not nearly all) of captive cheetahs succumbed to feline infectious peritonitis in Oregon. All of these studies demonstrate a variability in individuals' responses to pathogens and show that some cheetahs' immune systems can recognize and mount an immune response to a range of agents. While lack of variation at the MHC leaves a species potentially vulnerable to disease, as yet there is no evidence that a disease has circumnavigated the immune defenses of all cheetahs. With hindsight, it is easy to understand why exciting genetic results were invoked to explain low population density of cheetahs, but predation on cubs is clearly more important in natural populations.

What of cheetahs' poor reproductive performance in captivity—can genetic problems account for their poor breeding success? The key problem preventing the North American cheetah population from being self-sustaining is failure of females to conceive (*19*). However, a physiological survey of 68 captive females shows almost no anatomical or physiological impairment of reproductive function (*26*). Instead, marked differences in the success of institutions in breeding cheetahs suggests that husbandry practice may be crucial, and difficulties in detecting estrus, and perhaps inappropriate social conditions may act as impediments to mating (*29*). Juvenile mortality is of lesser import in preventing the captive population from increasing (*19*). Moreover, in response to a partially open-ended questionnaire, zoos ascribed much of their juvenile mortality to poor husbandry (10 of 37 mentions), maternal neglect (10 cases), and cannibalism (5), all unconnected to homozygosity. Congenital defects (5), disease (4), and stillbirths (3) played a lesser role (*30*). Disease and juvenile mortality are secondary to other factors in preventing the captive population from expanding.

Genetic considerations are clearly important in the management of captive populations but may only be relevant to free-living populations in limited circumstances because they impact populations on a slower time scale than environmental or demographic problems (*8, 31*). Indeed, there is widespread agreement that the environmental consequences of human disturbance present the greatest challenge to most populations in the wild (*32*), and these usually occur at a far swifter rate than inbreeding. Rapid declines in populations due to poaching [for example, rhinoceroses and elephants (*33*)], habitat fragmentation [primates, birds, and bees (*34*)], decimation by exotics [birds (*35*)], and pollution [crayfish (*36*)] attest to this. Among populations less subject to anthropogenic influence, such as those of the checkerspot butterfly, extinctions still result from environmental rather than genetic causes (*37*). Even in natural or reintroduced populations exhibiting reduced genetic variation, population growth and persistence may be little affected (*38*). Species that have undergone a demographic bottleneck such as the California sea otter or Great Indian rhinoceros (*39*) do not necessarily show reduced genetic variation, and in those that do, the number of deleterious recessives will depend on how fast the bottleneck occurred because they will have been purged not fixed if decline was slow.

In practical terms, the cheetah case history highlights the necessity of carrying out detailed ecological studies of endangered species in order to determine environmental causes of population decline (*40*). Studies collecting ecological data require a longer time to complete than those collecting genetic samples and are labor intensive but may be the key to understanding and hence preventing population extinctions.

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IMPOUNDMENTS AND THEIR EFFECTS ON AQUATIC RESOURCES [1]

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The need for adequate and controllable water supplies for purpose of irrigation, municipal supply, power, and flood control has long been recognized. Man has engaged in the control of flowing water since history began. Among his early recorded efforts were reservoirs for municipal water supplies for ancient Jerusalem and irrigation for Egypt as long ago as 2,000 B.C. (Martin and Hanson, 1966).

The construction of dams and reservoirs over the last 30-40 years has been described as one of the most striking world-wide, man-made phenomena since ancient pyramid building (BSFW, USDI, 1961). There are now some 9.1 million acres of reservoirs, larger than 500 acres, in the United States at mean annual pool level, which provide better than one-third of the acreage of fresh water available for public fishing (Jenkins, in press). This exceeds the acreage of natural lakes by 400,000 acres excluding Alaska and the Great Lakes (Stroud, 1967).

The need for adequately defining the effects of impoundments on aquatic resources has been recognized only relatively recently. Recognition of impoundment significance and codification of impoundment ecology has made some impressive strides over the last decade or two. Nevertheless, lack of definitive data on the effects of impoundments on aquatic resources continues to represent a keenly felt deficiency in many areas of fish management.

In this panel discussion, I propose to emphasize some limited observations that primarily relate to Colorado, Wyoming and Utah. Construction of reservoirs in all parts of the world is proceeding so rapidly and the effort in studying them is so varied that any attempted summary would be superficial at best.

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ATTITUDES, PERSPECTIVE, AND REALITY

We hear a lot these days about the purest delights of streams--almost as if reservoirs were immoral. Such comparisons are as spacious as worm versus fly fishermen. What's needed is to differentiate what works, or works best in a given situation. Nature has only one criteria of success, what works.

Reservoirs, streams, regulations, and even special baits all have their place in fisheries management. If the term trade-off is indeed idsquieting, it should not be overlooked that beavers have been building dams and altering streams for thousands of years; as a result, habitats change, some plants and animals are destroyed and new plants and animals capable of coping with the disrupted environment appear (Jenkins, 1964).

No one will argue that construction of many dams astride anadromous fish spawning rivers has not been followed by sharp declines in those resources. No one will argue that some dam projects should not have been built. No one will argue that remaining high quality stream fisheries should be vigorously protected ever more. But, it also follows that water storage has contributed materially to economic development. Here in the West, the successful agricultural economy depends largely upon storage of a part of the annual water supply for use during the growing season. Our municipal and industrial centers have been made possible only by means of adequate water supplies. Fisheries biologists cannot afford emphasizing the negative end of the pendulum, while dismissing lightly the forces responsible for reservoir building programs.

Reality clearly shows that reservoirs are here to stay, cannot be ignored, and offer great potential benefits in terms of sport fishing. The 1970 National Survey of Fishing and Hunting (BSFW, USDI, 1972) indicates just under 600 million angler-days occurred in fresh water, not counting kids under 12 years old. Nationally about 28% of this fishing effort was distributed to reservoirs, 13% to small artificial ponds (under 10 acres), 27% to natural lakes, and 32% to streams. Here in the mountain states, almost twice the national average, 47% compared to 28%, was spent fishing reservoirs. Angler use of small artificial ponds and natural lakes was about one-fourth and one-half, respectively, of the national average whereas angler use of streams was only three percentage points higher than the collective norm of the U.S.

People troubled by man's dam building and concomitant landscape scarring assume that biological consequences must be all bad. Such sentiments not only prejudice thought and action in naturalist circles, but delay concerted study of the fishery management opportunities presented by impoundments (Jenkins, 1964).

Estimated 1970 angler harvest in U.S. reservoirs (9.1 million acres) was 198 million pounds or 21.8 pounds per surface acre (Jenkins, 1971). Potential of these reservoirs to provide increased fishing opportunity is illustrated in that a mere one pound increase in yield per acre would eclipse the total poundage of all fishes propagated and distributed from national fish hatcheries for the fiscal year 1973 (BSFW, USDI, 1973).

Such unused production, along with the construction of new reservoirs and the realization of minor miracles wrought through research and development, has long been projected as absorbing much of the vast future increases in fishing (BSFW, USDI, 1962). The now twelve year old report "Sport fishing - today and tomorrow," depicted the mountain states in 1960 as being in the most favorable position, compared to the eight other regions in the country, in supplying fishing opportunity based on acres of fresh water habitat per inhabitant, with first rank position continuing through to the end of the century.

Specifically, Montana, Idaho, Nevada, and Wyoming were projected to continue to provide exceptional fishing opportunities through the remainder of the century. Construction of new waters in Utah were expected to maintain the per capita acreage near the 1960 ratio. New Mexico and Arizona were projected as being hard pressed to provide comparable fishing for future generations after 1976 because of the lack of opportunity to develop new waters after that date. New reservoirs in Colorado were expected to satisfy increased future demands, but a decline in the number of acres of water per person was estimated.

I have no way of specifically knowing how well these projections are on course, but various observations and deductions suggest they are in the ball park. I do know that the fisheries value of many impoundment projects in the late 1950's and early 1960's were grossly underestimated or entirely overlooked. Examples of such bonuses are Starvation and Willard Bay Reservoirs in Utah, and the outstanding trout tailwater fisheries developed below Flaming Gorge Reservoir in Utah, Navajo Reservoir in New Mexico, and Fontenelle Reservoir in Wyoming. In each of these large river sections affected there virtually had been no fisheries at all prior to impoundment due to poor water quality.

Eiserman (1974) recently described the situation in Wyoming, "Probably the most significant and exciting development in trout fisheries management...is the development of new fishing waters and the restoration of streams too polluted by either silt or industrial wastes to support trout. ...In 1890, ..., there were 49,000 surface acres of natural lakes... Today there are an additional 207,240 surface acres...constructed, for the most part, in non or low-producing trout streams." General observations suggest that Utah has similarily benefitted as predicted in the "Sport fishing - today and tomorrow" report. Colorado's prophecy of benefits and problems is a reality (State of Colorado, Div. Wildl., 1974, p. 84).

Overall, one can only conclude that in the mountain states containing about 6% of the nation's fishermen, experiencing a little over 4% of the national fishing effort (BSFW, USDI, 1972), but containing about 15% ofl the nation's reservoir (Martin and Hanson, 1966), that the effects of impoundment on aquatic resources has been generally favorable.

CHALLENGES, OPPORTUNITIES AND NEEDS

Introduction or periodic stocking of striped bass, walleye, rainbow trout and other exotics, command center stage in the reservoir management scene in the mountain states as it does nationally. Unlike the rest of the country, however, the area has a preponderance of excellent rainbow trout fisheries sustained by stocking fry or fingerlings.

Flaming Gorge Reservoir (42,000 S.A.) in Utah and Wyoming is such a fisheries. Three periods have characterized the fisheries since filling began in 1962. Typically in the initial period, stocking was heavy (213-575/S.A.), the harvest rate high (1.2 trout/hour), and the actual catch rate even higher, but not recorded, as fishermen easily caught and released multitudes of smaller fish in selecting one-half pound trout for take home. Adding to the euphoria was the fact that these trout were readily caught from the shore even during the summer months. Over the next six year period, 1966-71, fewer trout were stocked (56-143/S.A.), trout could no longer readily be caught from the shore in summer, the rate of harvest trended downward (0.78-0.41 fish/hour), and angler use went into a slide beginning in 1967. However, the average size of trout caught doubled to one pound fish.

The decline was reversed in the 1970's, apparently by increasing the size of trout stocked from about three to five inches. Estimated angler days in 1973 were 328,543 compared to the heyday peak of 306,000. Harvest of 646,900 trout in 1973 was three-fourths the peak harvest of 808,265 trout in 1966. Annual yield fluctuated only within the hearty norms of 18.2 to 26.1 pounds per surface acre over the first decade of use.

Wiltzius (1974) has documented the ups-and-downs of a similar fisheries for Blue Mesa, Colorado's largest reservoir (10,000 S.A.), particularly the advantages of stocking large (4.5 inches) rainbow trout fingerlings once rough fish have attained high population densities. The question must be asked if this isn't but one more temporary management expedient after having watched the glow fade from so many promising innovations and reservoir fisheries? It is highly questionable whether the successional changes noted for Flaming Gorge correspond to the trophic evolution described by Baranov (1961) for Russian reservoirs--trophic upsurge, trophic depression, followed by gradual raising of the trophic level and eventual, relative stability. Brevity of existence argues against anything approaching ecological equilibrium.

Regardless of all else, we can safely assume that stocking will continue to play a dominant role in the management of such reservoirs. Barring a minor miracle, however, we are not going to replicate the stocking of 30,000 pounds of fingerlings to put upward of one-half million pounds of trout in angler creels as occurred initially in Flaming Gorge.

Rainbow trout have proven a very functional fish in such management. It is easily raised in hatcheries, adapts to a fairly wide range of environmental conditions, grows rapidly to a size of 11-12 inches on a predominant diet of zooplankton, representing the principle trophic pathway in fluctuating reservoirs, is relatively easy to catch, and is both a good fighting and eating fish. Disadvantages most often cited include inflexibility in shifting over to a diet of fish when the need for food items larger than zooplankton becomes essential for further growth, relatively short life-span, and, in general, lack of reproduction. These latter qualities can also be viewed as advantages, depending on the management objective, in that they provide the options of limiting predation on newly stocked fingerlings and controlling growth, by regulating population density.

Despite the inherent attributes of the currently used strain(s) of rainbow trout, it does not fill all of the dictates of the cold water habitats that exist, varying from river-like to natural lake, with wide variations in water quality. Principle ecological distinction between some reservoirs and natural lakes are higher water exchanges, greater water level fluctuations, or both. Extreme flushing rates and water level fluctuations characterize the irrigation reservoirs of the mountain states.

At first glance there would not seem to be anywhere near the choice of options in selecting cold water fish species, compared to the more numerable warm water fish species, in satisfying a particular management need. The rather rigid ecological requirements and low angling potential of lake trout are well known. The adjunct, co-dominant potential of kokanee salmon in particular fisheries would seem to have been fairly well delineated (Seeley and McCammon, 1966, Wiltzius, 1974). Coho salmon have only been successful in inland waters in the Great Lakes (Avery, 1973; Wiltzius, op, cit.). Whitefishes are currently largely unacceptable to the public. The generally recognized trout species have been studied rather exhaustively, and while this is not a complete listing, does tend to accent another reason why rainbow trout command center stage.

There are options, however, deserving of scrutiny at least to the level afforded the kokanee salmon. These involve the native cutthroats and any variant forms of the original rainbow trout. Until recently it was believed that most, but not all, of the native forms of these closely related species were extinct or generally unrecognizable now because of cross-breeding in hatcheries and widespread transplanting. Astute studies on the taxonomic relationships of the genus <u>Salmo</u> by Dr. Behnke, Colorado State University, and others has resolved some of the muddled status of these forms and allowed for identification of remanent pure populations in some cases (Behnke, 1969; Behnke, personal communication). Behnke (1968) has long stressed that evolution by natural selection has produced some highly adapted genotypes for specific environmental conditions.

The immense importance attached to the recognition and possible ultimate utilization of these specialized genotypes in fish management programs is illustrated in the history of Salmo-clarki henshawi in Pyramid Lake, Nevada (Behnke, 1974). A unique faunal complex coexisting in Pyramid Lake over 50,000 to 100,000 years evolved specialized adaptive features in behavior and physiology so as to maximize efficiency of energy conversion of a super concentration of nutrients (5,500 ppm T.D.S.). The end result was a highly productive fisheries, featuring the largest trout (62 pounds) native to western North America. Behnke (op. cit.) estimates a minimal harvest of one million pounds of Lahontan cutthroat trout annually during the late nineteenth and early twentieth century. Elimination of spawning grounds by intensive diversion of water from the Truckee River, beginning in 1920, culminated in the extinction of the original Lahontan genotype in 1938-39, and the productive fisheries as well. Although the Lahontan cutthroat is not extinct and various sources of Salmo clarki henshawi are propagated and stocked into Pyramid Lake today, these hybrids are only a good counterfeit of the original, attaining a maximum size (19 lbs. 9 oz.) of less than the average weight of the last spawning run in 1938.

Purported behavioral and physiological differences among rainbow trout forms include migratory, non-migratory, fish eating, etc. Although these attributes are frequently alluded to, they have rarely been adequately demonstrated due to crossbreeding and inability to identify slight genetic changes producing major behavioral and physiological differences. Recent developments in identifying the particular enzyme make-up of trout, as determined by starch gel electrophoretic patterns, would appear to represent a major breakthrough in identifying slight genetic differences between forms. Equally important, the genetically determined enzyme make-up of a particular trout form represents a cold blooded animal's response to a given set of environmental conditions, unlike a warm blooded animal which is capable of regulating its body temperature, p.H., etc. Thus, it would appear that we are on the verge of a new era in getting a handle on ecological variable trout forms adaptive to particular management needs (personal communication, Dr. Clair Stalnaker, Utah State University).

Although much work has been devoted to selective breeding of trout, invariably this effort has been directed to increasing growth and egg production in hatcheries. Many people have questioned whether the necessary qualities for wild existence haven't been merely traded-off for desired hatchery qualities in such breeding. There is perhaps no possible way to completely duplicate all the attributes that might be desired in a single trout species. However, at this juncture in time, there definitely is a need for conclusively demonstrating whether there are behavioral and physiological differences in the various rainbow and cutthroat forms associated with differences in enzyme make-up. If this proves out, as indicated in preliminary studies (Huzyk and Tsuyuki, 1974; Stillings, 1974), then these forms exhibiting ecological and behavioral differences should be rigorously field tested, emulating the studies of Sekulich (1974) and Trojnar (1972) on Snake River cutthroat, so as to know how they might fit into the management scheme in maximizing angling opportunity.

At the other end of the trophic level--the forage base--there is also a pressing need for improving and identifying management options as illustrated by threadfin shad.

The desirability of the threadfin shad as a manageable forage fish has inspired widespread introductions outside of its original range. Advantages of the species include its small maximum size, prolonged spawning period and short life span. Its susceptibility to winter-kill in areas where the mean January air temperature is less than 40° F. is a mixed blessing (Jenkins, 1973). Utah introduced threadfin shad into Flaming Gorge Reservoir two years ago. Insofar as known only one threadfin shad, recovered from a brown trout stomach, is known to have over-wintered.

The reasons for and postulated benefits resulting from establishing threadfin in such habitat are so utopian that they deserve examination. First, they would increase the forage base, which would be efficiently cycled into trout production, particularly during winter when dying threadfin shad gradually spiraling surface-ward are inciting prey even for normally plankton feeding rainbow trout. Second, based on the apparent suppression of gizzard shad populations by introduced threadfin in southern reservoirs, there is the likelihood that they might do the same to Utah chub populations, the principle rough fish having similar food habits.

Barring natural acclimatization of introductory stockings, there are three other possible solutions to threadfin management in such cold habitat--annual introduction of seed stock on a large scale, warming of a portion of the reservoir for over-wintering of breeding stock, and acclimatization of the species to colder water temperatures through some kind of a selective breeding program, possibly emulating Russian acclimatization work on mosquito fish and other exotics (Stroganov, 1962; Prevolnev, 1970). Admittedly, these do not appear to represent very practical solutions, but the point is we don't really know.

And the same is true in properly identifying management options relative to a host of other opportunistic animals--mysid, crayfish, cladoceran, landlocked alewives, smelt--that do or could dominate the food chains of reservoirs. Until such time as we learn enough about such organisms on an ecosystem basis and are capable of effectively manipulating them for a desired effect, comparable to the technology of agriculture, the ultimate potential of reservoirs will go untapped.

INPUT, FEEDBACK AND PROGRESS

Opportunities for effective management are greater in man-controlled reservoirs and rivers than in nature-controlled lakes and rivers, but to acquire the wisdom necessary for such management will require the coordinated efforts of many disciplines. Fry (1967) upon returning from an over-view of Russian reservoir research described the two greatest deficiencies in the U. S. effort as the relative lack of continuing intensive studies on particular reservoirs and the fact that many investigations wind up as processed reports, which can scarcely be considered part of the scientific literature.

Although there has been progress in correcting these deficiencies, noteably by the under-funded National Reservoir Research Program and a few of the states, the interrelated problem remains. Colorado, Utah, and Wyoming have major and diversified efforts underway to understand the limnology and fisheries of selected reservoirs and tailwaters. Very few of their findings from a decade or more of work have been published, however. It appears, in fact, that many valuable findings are "buried" so deep, due to personnel turn-over and inertia in facing up to the rigors of publication, that implication of those findings will never be available to the sponsoring agencies, let alone nationally and internationally as they should be.

Bill Wiltzius, Colorado's highly qualified project leader on Gunnison River impoundments and tailwaters illustrates the foregoing. Continuity of experience on one ecosystem, a high degree of innate curiosity, and total dedication to the job has produced at least one of the world-wide authorities on tetracycline and fluorescent granule marking of salmonids and an inland authority on purse seins and kokanee salmon. Voluminous though his recordation of findings have been (mimeographed and typed), they do not include one legitimate publication in the strict sense. The essentiality of publication to research and management, and the myraid of excuses for not publishing is an old story, but there is one aspect of the process--feedback--that is continually ignored.

Feedback is a term that is part and parcel of the new computer technology. In technical terms it can be described as the automatic furnishings of information on a machine's output to a control device, so that errors can be corrected. Thus a feedback system is self-correcting. Readily accessible research findings evaluated by others provide the feedback necessary for progressive management. Without feedback there can be no progression of thought or coordinated effort in problem solving.

The short-circuiting effects of the lack of feedback in reservoir research can be illustrated by the following. In 1972 the National Reservoir Research Program assisted the Division of River Basins, B.S.F.W., in predicting the impact of the proposed Bureau of Reclamation enlargement of Strawberry Reservoir, Utah (5,850 to 12,160 S.A.) (Jenkins, 1972). Predictions of fish standing crop and sport fish harvest were based on correlation and multiple regression analysis of data from reservoirs throughout the U. S. and from comparative information on Strawberry Reservoir available in processed D-J reports pertinent to conditions prevailing prior to reclamation for rough fish in the early 1960's. Not surprisingly the projected predictions of harvest and use proved entirely erroneous compared to the field results of this extremely successful trout management in the years since. What is surprising is that no one at the federal or state level bothered to provide the necessary corrective feedback to the National Reservoir Research Program. Certainly the ever increasing predictive capability of reservoir forecasting pioneered by the national program would have benefitted, as well as all the agencies involved in the planning for this eventual enlargement.

People are like computers in that their awareness is directly proportional to the informational input and the amount and kinds of feedback received. This is a very important concept in that program progress or growth is pretty much a matter of growth-development of project leaders.

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