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Herbivorous Fishes: Culture and Use
for Weed Mgt. - Opuszynski & Shireman 1995

SH 167
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1995

- Chapt. 5 grass carp & weed control

* 6 Utilization of phytoplanktivorous fishes
for counteracting eutrophication

- Top-down / bottom up organiz. - macro, phyto, zoo - invertebrates
temp, pH, CO₂, carbonate bicarbonate, ^{sp. shifts}
geomorphology - detritus
- plankton -

(only this page - not back)

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?

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 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 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 indicates 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.

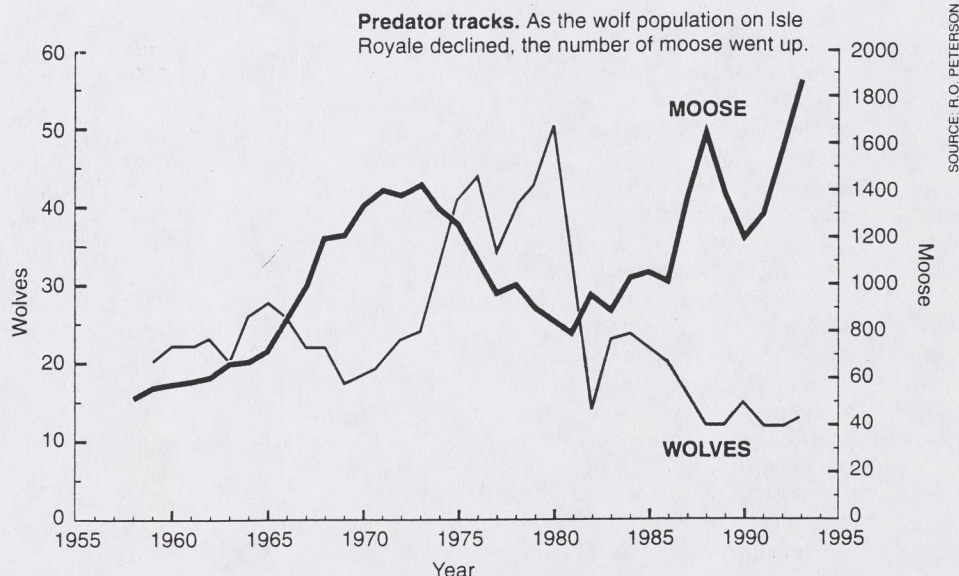
-Christine Mlot

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.



The analysis suggested, Ligon says, that many of dams' harmful effects on river hydrology may come about because they don't permit sediments to pass. As a result, a river will cut into the riverbed, deepening the channel. This can prevent rivers from spilling into their floodplains, thus depriving them of the nutrients they would normally pick up there. Dams that withhold sediments can also simplify riverflows, changing braided rivers into single thread rivers and limiting fish-spawning and rearing grounds as a result. Ligon notes, for example, that dams are gradually changing the McKenzie River in Oregon from a river with many islands to a single thread river, putting the McKenzie's salmon population in jeopardy. When dams are built, Ligon suggests, more attention should be given to keeping sediments moving downstream.

Recent modeling work by stream ecologist Mary Power of the University of California, Berkeley, and civil engineer Gary Parker of the University of Minnesota in Minneapolis and their colleagues also points up the importance of maintaining sediment flows for life in the river. Power's group is collecting data to determine how levees affect a river's hydrology and how that in turn affects feeding relations among species and the abundance of plants, insects, and fish. Preliminary results show, Power says, that riverbeds must be renewed periodically with fresh sediments to provide habitats for weedy plants and the animal species, such as insects, which provide food for fish, that dwell among them.

While a great deal more remains to be learned about the effects of dams or levees on river ecology, the researchers say that even now the work can help guide the management and restoration of large rivers. Such efforts, says Power, "will be critical in maintaining better conditions for biological life within, and human life alongside, the large rivers of our land."

—Anne Simon Moffat

Clearcutting's Soil Effects

When a forest is clearcut, the environmental degradation that occurs above ground is obvious. Less obvious, but equally cataclysmic, is the damage that goes on underground—the loss of fungi, worms, bacteria, and other microbes that can nourish plants or protect them from disease. "Soils can be biologically destroyed, even if they seem physically intact, holding most minerals and topsoil," says Elaine Ingham, a soil microbiologist at Oregon State University in Corvallis who reported the results of her group's analyses of soils from a clearcut forest on the Olympic

Peninsula at the ESA meeting. This loss of subterranean life-forms is important because it can impair efforts to restore forests, although the research is also suggesting ways to improve reforestation.

In their work, Ingham and her colleagues compared the soil populations of a variety of organisms in a large forest area, measuring hundreds of meters on a side, before and after it was clearcut. By 6 to 9 months after the trees were cut, the underground fungal biomass had declined to about one-tenth of what it was before logging started, Ingham says. Also lost were roundworms and some arthropods, such as springtails and mites. Microbial populations were affected as well. One indication of that came about 1 year



Soil despoiler. Cutting all the trees may have just as serious effects below ground as above.

after the clearcut when Ingham and Dennis Knight of the University of Wyoming in Laramie measured a large surge of nitrogen concentrations in groundwater, probably reflecting the death and decay of nitrogen-storing microbes. And the losses of soil organisms only get worse with time: Ingham found that soils were showing a 100-fold decrease in fungal biomass and significant loss of nitrogen 5 years after clearcutting.

Ingham says that these changes reflect the fact that trees provide a source of carbon to subterranean microbes so that when forests are clearcut, some microbes are starved of nutrients. She notes, for example, that smaller gaps in the forest canopy, measuring just tens of meters on a side, did not seem to have such a disastrous effect on soil organisms, presumably because microorganisms moving in from surrounding areas help to keep a healthy underground environment.

Conversely, soil microbes help nourish trees by providing them with water and minerals. Indeed, without a healthy microbial population, reforestation efforts may fare poorly. As many as 75% of Douglas fir seedlings died when they were planted in the clearcut areas studied by Ingham. Reforestation efforts might fare better, Ingham suggests, if they begin within 6 to 9 months of logging. Leaving more mature trees and

keeping large, soil-compacting machinery out of logged areas might also aid reforestation by helping maintain underground biological systems.

—A.S.M.

Pathogens Take Charge

While many in the scientific community are currently concerned with sex as a means of disease transmission, in evolutionary terms sex has been seen as a means of disease avoidance: Sexual reproduction creates the genetic variability that gives rise to disease resistance in a population. "Sex is one way of staying one step ahead of your pathogens," says biologist Leslie Real of Indiana University, who organized the ESA's first symposium on the ecology of disease. Sometimes, however, the pathogen still wins. Indiana University plant population biologist Keith Clay reported on a strategem employed by a fungal pathogen to steer its host plant away from sexual reproduction, simultaneously securing its own future and taking control of the future of the plant.

Poverty grass (*Danthonia*) normally can reproduce in two ways: through wind-pollinated or self-fertilized flowers, as can violets and some other plants. But when a poverty grass plant is infected with the fungus *Atkinsonella hypoxolon*, the fungus engulfs the developing flower at the tip of the plant, mechanically preventing it from opening. This eliminates wind pollination and the possibility of cross-breeding with plants resistant to the fungus; that, in turn, eliminates the production of more individuals that could fight off the fungal onslaught. But the self-fertilizing flowers at the base of the plant still develop and produce seeds—seeds that genetically resemble the fungus-prone parent. The fungus even manages to infect those seeds, condemning the plant and its offspring to infection in perpetuity.

Such associations between systemic fungal parasites and plants are common in nature, according to Clay—choke, another fungal disease of grasses, operates in a similar way. The result, for the plant, is evolutionary stasis. "By suppressing sex and forcing clonal reproduction," he says, "the parasites have been able to subvert the coevolutionary response from their host populations...and [have] taken the driver's seat rather than following behind." And while the parasite's strategy may not be unique, Clay's study is an unusual one, says plant scientist Helen Miller Alexander of the University of Kansas. She calls it a rare look "at the flip side...showing how a pathogen can manipulate its host to stop sexual reproduction."

—C.M.

Christine Mlot is on a Knight Science Journalism Fellowship at MIT.

10/12/95

Uncertainty, Resource Exploitation, and Conservation: Lessons from History¹

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

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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 short-sighted 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 rec-

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ord returns of its most valuable species (5).

2) 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.

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).

3) 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 fu-

ture (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 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 un-

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specified 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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SCIENCE AND THE MANAGEMENT OF NATURAL RESOURCES^{1,2}

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Focus [We are in full agreement with Ludwig et al. (1993) that scientific and technological progress will not, in themselves, lead to sustainable development of resources. One can hardly hope for rational management of resources in a world in which many (if not most) politicians, managers, and economists still believe that resources are either infinite in extent or infinitely substitutable (Ehrlich 1989) and where social dynamics generally lead to overexploitation regardless of beliefs. We agree also with the thrust of their argument that more scientific knowledge is not the main key to sustainable management of our planet's resources.

Social dynamics [We can hardly fault the Ludwig team's (1993) prescriptions either, such as taking action before scientific "consensus" is achieved. After all, social dynamics often prevent action even when there is consensus (which is not necessarily unanimity) among scientists. Consider, for example, the "World Scientists' Warning to Humanity," circulated by the Union of Concerned Scientists in 1992, and signed by a majority of living Nobel laureates in the sciences. It called, among other things, for halting growth of the human population, reducing greenhouse gas emissions, and protecting bio-

diversity. Despite that warning (and many others representing the consensus of environmental scientists in the past), the threats of continued overpopulation, global warming, and extinction are hardly appreciated by the public. That failure can be traced largely to a media penchant for inflating the views of tiny minorities to give the appearance of controversy. A few scientists can always be found who, sometimes because of legitimate scientific concerns, but more often because of political pressures or yearning for public attention, give ammunition to those promoting their private interests at society's expense.

On the other hand, Ludwig et al. (1993) prove their own assertion true, that "the judgement of scientists is often heavily influenced by their training in their respective disciplines." Much of the experience in fisheries is not generalizable to the management of resources most relevant to sustaining human civilization. These include soil, freshwater, forests, atmospheric composition, and some level of biodiversity (see Daily and Ehrlich 1992) for which sustainable use/destruction rates are at least approximately known and for which more research does promise a substantial reduction of uncertainty.

We disagree with the implication of Ludwig et al. [1993:proposition (iii)] that the complexity of bio-

¹ Manuscript received 2 June 1993.

² For reprints of this Forum, see footnote 1, p. 545.

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physical systems is a significant barrier to developing sustainable resource management policy. As Mooney and Sala (1993) point out, achieving sustainability implicitly requires more understanding of a system than does exhausting a resource, but human beings routinely devise policy in the face of enormous complexity. For example, while the complexity of interacting ecological and economic systems is certainly daunting, our interacting ecology and economics group at Stanford has discovered that it comes to rather easy mutual agreement on biophysical aspects of sustainable resource management. (The group despairs when trying to divine how to steer political action in that direction, an issue we treat later.)

Furthermore, it is difficult to see how "trial and error" can lead to optimum management of many types of resources. Trial and error can be very dangerous. Without the scientific research of Mario Molina and Sherwood Rowland (1974), society's trial and error approach to releasing massive quantities and types of chemicals into the atmosphere could have brought down civilization. Decisions informed by sound scientific information will generally be superior to those based on pure guesswork. While science might not be able to calculate the precise *maximum* sustainable flux of a gas into the atmosphere or the *maximum* sustainable harvest rate of a renewable resource, it can help make a safe bet.

Contrary to the impression given by Ludwig et al. (1993), scientists are always confronting uncertainty and need to communicate this much more clearly to decision makers and the general public (e.g., Schneider 1989). It will always be a "human" (i.e., largely political) problem to judge the adequacy of scientific knowledge and to decide how to factor that knowledge into decision making. Science can never provide certainty, but 95% confidence is better than 10% confidence, and 10% confidence is better than no confidence at all. There is, unfortunately, an uninformed scientific culture that attempts to exclude from science any results not carrying an arbitrarily selected high level of statistical "significance," any recommendations based on first principles, or any science that is "descriptive."

The broader and more useful notion of science as systematized knowledge obtained by observation and experiment, rather than as some mystical source of certainty, must be nurtured both within the scientific community and among the public at large. The dominant social paradigm of ecologists is still too much

focused on the high-powered, experimental testing of trivial hypotheses rather than on finding ways to improve understanding of (and generating action to solve) important problems. The Sustainable Biosphere Initiative was an attempt, long overdue, to focus the attention of ecologists on research problems that have more relevance to solving the human predicament. Until there is greater reorientation of and help from the professional community, it is difficult to fault lay

people for their laissez-faire approach to resource over-exploitation and environmental deterioration.

Nonetheless, even with improved focus and knowledge, the basic problem would remain "human": how to make short-term and individual incentives congruent with society's long-term best interest as determined by scientific analysis. This raises a fundamental question: when is such analysis influential in the formulation of social policy to remedy environmental problems? In proposing an answer to the question (G. C. Daily, unpublished manuscript), we distinguish between three separate components of scientific analysis:

- 1) problem perception: widespread recognition of the scope of a problem because it is manifest (phenomenological; e.g., the stratospheric ozone layer has thinned);
- 2) mechanistic understanding: identification of the cause(s) and consequence(s) of a problem (mechanistic; e.g., the emission of chlorofluorocarbons (CFCs) into the atmosphere results in catalytic reactions that destroy ozone);
- 3) strategic assessment: detailed, scientific evaluation of how the problem would evolve under various courses of action/inaction (e.g., short- and long-term total costs/benefits of various strategies to reduce the use of CFCs).

Mechanistic understanding (but not always problem perception) necessarily precedes strategic assessment. For example, thinning of the ozone layer was not manifest until long after Molina and Rowland had identified the probable cause and many of the consequences had been anticipated. Similarly, a human-induced greenhouse warming "signal" has yet to be separated with assurance from climatic "noise."

The great forces that drive environmental policy (at least in the U.S.) appear to us to follow these general patterns. Perception of a problem alone does not tend to generate action. Often, as in the case of coral bleaching, declines in worldwide amphibian and Eastern songbird populations, and Waldsterben, the causes are not immediately clear. Even when the cause is clear, perception often does not lead to quick action. Smog was the subject of jokes for decades (and air pollution disasters with numerous deaths occurred) before effective clean air legislation was enacted.

Mechanistic understanding is rarely, if ever, compelling in itself either, as the ozone example indicates (adequate action was stimulated only after perceiving the "smoking gun" of the Antarctic ozone hole). Non-response to the intertwined critical threats of population growth, global warming, and depletion of biodiversity suggest the same, as we've already noted. Science has clearly outlined both causes and consequences, but relatively few nonscientists appreciate the gravity of these disruptions, and significant action is not being taken. Moreover, even strong, widespread problem perception and a determination of the causes and con-

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sequences may not lead to effective steps toward amelioration. This is amply demonstrated in the rapid degradation of potentially productive land, a problem that currently afflicts nearly 20% of Earth's vegetated land (WRI 1992). But the agricultural situation is little understood and low on the agenda of most educated people and world leaders (Ehrlich et al. 1993).

Only when a special mix of social conditions exists may the combination of perception and mechanistic understanding trigger strategic assessment (usually interdisciplinary) and a significant social response. The social activism of the 1960s, certainly intensified by the Vietnam War, and the environmental movement (given impetus by the publication of Rachel Carson's *Silent Spring* in 1962) set the stage for passage of relatively strong environmental legislation in the U.S.

Not only is the special mix of conditions difficult to generate, but its establishment is difficult to forecast. The conditions seem to include, among other things: a relatively simple solution at hand (involving few parties, little expense, and little or no foreseen short-term change in lifestyle); a clearly perceived high cost associated with inaction; a charismatic, visionary leader; and favorable (short-term) economic conditions. When most of these ingredients are present, and society is deciding to take action, strategic assessment becomes relevant and the availability of the best possible scientific information becomes critical.

Good science is thus important at each stage. It can document and quantify the problem, making it more difficult for countervailing forces to claim it is nonexistent. Good science, and often it alone, can properly pinpoint causes and project consequences. And, collaboration between natural and social scientists can provide decision makers and the general public with

clear evaluations of options, costs, and benefits to guide social action. They can also offer advice on which courses they think best, especially on critical nonscientific issues dealing with how "fail-safe" courses of action should be, and how to deal with zero-infinity problems and thresholds. In that capacity, however, they must shed any mantle of impartiality and simply speak as well-informed citizens, which we believe they have an obligation to do.

ACKNOWLEDGMENTS

We thank Anne H. Ehrlich for helpful comments on the manuscript. The work of G. C. Daily was supported by a Winslow/Heinz Postdoctoral Fellowship.

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GREED, SCALE MISMATCH, AND LEARNING^{1,2}

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Ludwig et al. (1993) make an important criticism of the idea of sustainable exploitation of resources: without an adequate grasp of the human dynamics that drive exploitation, there can be no adequate understanding of how sustainability could be achieved or maintained. Indeed, it is not obvious that a regime of stable use exists under any set of social arrangements, a point underscored by the history cited by Ludwig et al. (1993). History holds other lessons as well, and in

this note I suggest two ways to advance beyond Ludwig et al.'s cautions: first, by considering environmental problems as driven by mismatches of scale between human responsibility and natural interactions; and second, by emphasizing the central roles of learning and conflict as means of correcting human error in the natural world.

Ludwig et al. (1993) cite examples from fisheries, forestry, and irrigated agriculture, demonstrating that technocratic ideas such as maximum sustainable yield may be much more difficult to put into practice than analysts or policy makers have assumed. It may be

¹ Manuscript received 2 June 1993.

² For reprints of this Forum, see footnote 1, p. 545.

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POLICY FORUM

Achieving Sustainable Use of Renewable Resources

A. A. Rosenberg, M. J. Fogarty, M. P. Sissenwine, J. R. Beddington, J. G. Shepherd

Sustainable use is a widely accepted goal for renewable resource management. It "meets the needs of the present without compromising the ability of future generations to meet their own needs" (1). However, natural variability, scientific uncertainty, and conflicting objectives (or values) can cause difficulties in achieving sustainable resource use. In a recent Policy Forum article, Ludwig *et al.* (2) argued that claims of sustainability should not be trusted and that populations are inevitably overexploited (often irreversibly), in part because scientific consensus on resource status cannot be attained. We maintain that the history of fisheries management provides both positive examples of sustainable resource use and lessons for future improvements. Our conclusions have the potential for broader application to other renewable resources. Specifically, we argue that (i) there is a sound theoretical and empirical basis for sustainable use, (ii) overexploitation is not inevitable or necessarily irreversible nor is it generally the result of inadequate scientific advice, and (iii) the tradition of open-access management systems coupled with risk-prone management decisions under uncertainty are the principal obstacles to achieving sustainability. We conclude that sustainable use of renewable resources can be attained.

Theoretical and Empirical Basis for Sustainable Yield

The scientific basis for sustainable use of renewable marine resources evolved during the first half of this century to counter the prevailing view that oceanic resources were inexhaustible (3). Hjort *et al.* (3) defined the "optimum catch" (later called the maximum sustainable yield) as the yield taken under the maximum rate of production. This concept is based on a fundamental

ecological principle—density-dependent population regulation. As the abundance of a density-regulated population is reduced by harvesting, per capita net production increases, until the population cannot compensate for additional mortality. There is extensive documentation of compensatory changes in fecundity, maturation, individual growth, and survival rate for marine populations (4). The production generated through compensation, which is known as "surplus production," can be harvested on a sustainable basis. Because the amount of surplus production depends upon how much the population is reduced by harvesting, there are feasible sustainable yields ranging from zero as population size approaches zero, to some maximum occurring at an intermediate level of population size.

Marine populations typically vary widely under fluctuating environmental conditions, and the implications of variability have received considerable attention in the development of sustainable harvesting strategies (5). In a randomly varying environment, theory predicts a probability distribution of sustainable yields at each level of population abundance. Harvest rates sustainable under one set of environmental conditions may not be sustainable, however, if a directional shift in the environment occurs. Environmental effects and harvesting interact with respect to population production. In the development of a sustainable harvest policy, both environmental conditions and exploitation rates must be taken into account. Directional changes in environmental conditions pose a major challenge to the development of sustainable harvesting policies. Monitoring programs designed to measure population trajectories and selected environmental variables have been implemented in many areas to track these shifts.

Harvesting a sustainable yield does not imply that the catch will be constant, nor is sustainable yield synonymous with maximum sustainable yield (MSY). Ludwig *et al.* incorrectly equated sustainable use in general with the specific difficulties of estimating a single optimal yield which can be harvested every year (6). The dangers of removing a constant catch from a fluctuating resource have long been appreciated (7), and few harvesting regimes of this type

are in place for major fisheries in North America and Europe. The exceptions are cases where precautionary catch quotas are set to facilitate monitoring of fisheries where there is little information on which to base management decisions. The most common fishery management strategy specifies a constant harvest rate. The amount removed through harvesting will therefore vary as population size fluctuates. For example, of 95 regulated fishery resources in the United States, none are managed by constant catch strategies. A strategy of maintaining a constant fishing mortality rate is used for two-thirds of the resources, and "overfishing" is defined by scientific consensus as a rate in excess of sustainability (8). In Europe, fishery managers have also focused on a target harvest rate. The International Council for the Exploration of the Sea annually provides European Community and other managers with options based on a range of alternative harvest rates by consensus of scientists from about 20 countries, for about 100 fishery resources.

Problems and Remedies

Despite the general validity of the concept of sustainability and many examples of sustainable use of fishery resources (9), there are also many instances of overexploitation. In the United States, approximately 45% of 156 populations for which an assessment of resource status is available are currently classified as overutilized; within European waters, 59% of 78 stocks have been classified as overutilized (10). Of these, however, few have been exploited to the point where a viable fishery is no longer possible. Uncertainty in resource status and in the ecological processes that control population dynamics have undoubtedly led to inadequate scientific advice in some cases. However, overexploitation often results from the failure of resource managers to follow scientific advice. For example, postmortem analyses of declines of pelagic fish populations by Saetersdal (11) contrasts the sequence of consensus scientific advice with actual management decisions. Managers consistently allowed higher catch levels than indicated by consensus scientific advice. For haddock on Georges Bank, off the New England coast, a relatively stable domestic fishery was sustained from its inception in the 1930s until the arrival of foreign fishing fleets in the 1960s. When the harvest rate was allowed to increase markedly against scientific advice, the stock declined to a much lower level (12). Stock declines are not necessarily irreversible. Many instances of stock rebuilding following depletion and a subsequent reduction in fishing have been documented (13). Among the most dramatic examples are the broad-scale

recoveries in the North ment of fish world wars.

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recoveries in fish populations documented in the North Atlantic following the curtailment of fishing during the first and second world wars.

Historically, marine fish populations were considered to be too vast to be depleted by harvesting. As a result, the burden of proof that regulation was necessary to sustain renewable resources was placed on resource managers (14). Further, de facto open-access systems in which entry to the fishery was unrestricted were prevalent. In open-access systems, the cost of harvesting is driven up by participants competing to catch a limited supply of the resource. The inevitable result is for the economic value of the resource to be dissipated (15). The solution to this problem is to recognize that property rights must be well defined and that rights imply duties and responsibilities (16). Under open access, no property rights to the resource exist and overexploitation is highly probable.

Substantial progress has been made in addressing factors that have jeopardized sustainable use in the past. Management in most developed countries has evolved toward systems that control access to fishery resources, although the process is far from complete. In addition, New Zealand, Canada, Iceland, Australia, and the United States among other countries have adopted systems that grant individual quotas in some fisheries. These quotas are transferable and eliminate competition among fishers for the resource. These systems can promote more economically viable fisheries (17). Open-access resource use is still a major problem in developing countries, which now account for more than over half of the global fisheries harvest.

Evolving Trends in Scientific Advice

The inherent variability in the dynamics of marine fish stocks, the difficulty and expense of measuring abundance and demographic parameters of widely distributed populations, and the complexity or high dimensionality of ecological systems virtually assure uncertainty in resource status. When confronted with uncertainty, fishery managers have been under enormous pressure to allow continued harvest levels and scientific advice has been discounted (18). Considerable progress has been made, however, in directly confronting uncertainty and in developing probabilistic approaches to providing management advice (19). Risk assessments that explicitly consider variability in resource abundance and productivity have become an integral component of scientific advice to managers. Formal risk assessments are now routinely incorporated

in many stock evaluations in the United States, Canada, Europe, and New Zealand. Resource managers in some areas now often make conservative decisions in the face of uncertainty (10). International management agencies and commissions such as the International Whaling Commission have adopted methods that explicitly account for uncertainty (20). The resulting scientific advice is framed in terms of the probability of certain outcomes under alternative management actions. There are important examples of relatively new fisheries in which access and fishing effort have been controlled from the start and in which scientific advice and management policy have been integrated to achieve sustainable harvesting (21).

The experience in fishery management suggests that the problems in achieving sustainable resource use are challenging but not insurmountable. To meet these challenges we must address fundamental economic biases against sustainability, particularly in open-access management regimes; continue the development and application of methods that directly integrate sources of uncertainty into scientific advice; and learn from past management failures and successes. Sustainable development is achievable if scientific advice based on biological, social, and economic considerations is an integral part of the development of policies for renewable resource use.

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MOVING FORWARD IN THE FACE OF UNCERTAINTY

DEVELOPING ECOLOGICAL RESEARCH THAT IS RELEVANT FOR ACHIEVING SUSTAINABILITY^{1,2}

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In their excellent recent article, Ludwig et al. (1993) accurately identify many of the underlying reasons for nonsustainable resource use. They conclude by enumerating five basic principles of effective management: (1) include human motivation; (2) act before scientific consensus is reached; (3) rely on scientists to recognize problems but not to remedy them; (4) distrust claims of sustainability; and (5) confront uncertainty. I agree, in general and wholeheartedly, with all of these principles. My only quibble is with their assertion, included as an expansion of principle 4, that basic ecological research on the topics identified in the Sustainable Biosphere Initiative (SBI, Lubchenco et al. 1991) is irrelevant to achieving sustainability. A unique feature of the SBI document was that in identifying the research needs for a sustainable biosphere, a group of ecologists pinpointed many areas of research that go well beyond the boundaries of traditional ecology and require a broad, interdisciplinary collaboration. Narrow, traditional ecological research is not relevant by itself, but the broad interdisciplinary research recommended in the SBI can be. But in order for the recommended SBI research to actually be relevant, some additional major changes in how we view science in general, and especially the linkages between science and environmental policy, are going to be needed.

As Ludwig et al. (1993) point out, one of the primary reasons for the problems with current methods of environmental management is the issue of scientific uncertainty, not just its existence, but the radically different expectations and modes of operation that science and policy/management have developed to deal with it. If we are to solve this problem, we must understand and expose these differences and design better methods to incorporate uncertainty into the policy making and management process.

To understand the scope of the problem, it is necessary to differentiate between risk (which is an event with a known probability, sometimes referred to as statistical uncertainty) and true uncertainty (which is an event with an unknown probability, sometimes referred to as indeterminacy). Most important environmental problems suffer from true uncertainty, not merely risk.

Science treats uncertainty as a given, a characteristic of all information that must be honestly acknowledged and communicated. Over the years scientists have developed increasingly sophisticated methods to measure and communicate the uncertainty arising from various causes. It is important to note that the progress of science has, in general, uncovered more uncertainty rather than leading to the absolute precision that the lay public and some policy makers often mistakenly associate with "scientific" results.

The scientific method can only set boundaries on the limits of our knowledge. It can define the edges of the envelope of what is known, but often this envelope is very large and the shape of its interior can be a complete mystery. Science can tell us the range of uncertainty about global warming, the potential impacts of toxic chemicals, or the possible range of fish population dynamics, and maybe something about the relative probabilities of different outcomes, but in most important cases it cannot tell us which of the possible outcomes will occur with any degree of accuracy.

Our current approaches to environmental management and policy making, on the other hand, abhor uncertainty and gravitate to the edges of the scientific envelope. The reasons for this are clear. The goal of policy is making unambiguous, defensible decisions, often codified in the form of laws and regulations. While legislative language is often open to interpretation, regulations are much easier to write and enforce if they are stated in clear, black and white, absolutely certain terms.

As they are currently set up, most environmental regulations, particularly in the United States, demand certainty and when scientists are pressured to supply this nonexistent commodity there is not only frustration and poor communication, but mixed messages in the media as well. Because of uncertainty, environmental issues can often be manipulated by political and economic interest groups. Uncertainty about global warming is perhaps the most visible current example of this effect. In order to rationally use science to make policy we need to deal with the whole envelope of possible futures and all their implications, and not delude ourselves that certainty is possible.

The "precautionary principle" is one way the environmental regulatory community has begun to deal with the problem of true uncertainty. The principle states that rather than await certainty, regulators should

¹ Manuscript received 2 June 1993.
² For reprints of this Forum, see footnote 1, p. 545.

Broad, interdisciplinary research needed

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Risk vs indeterminacy

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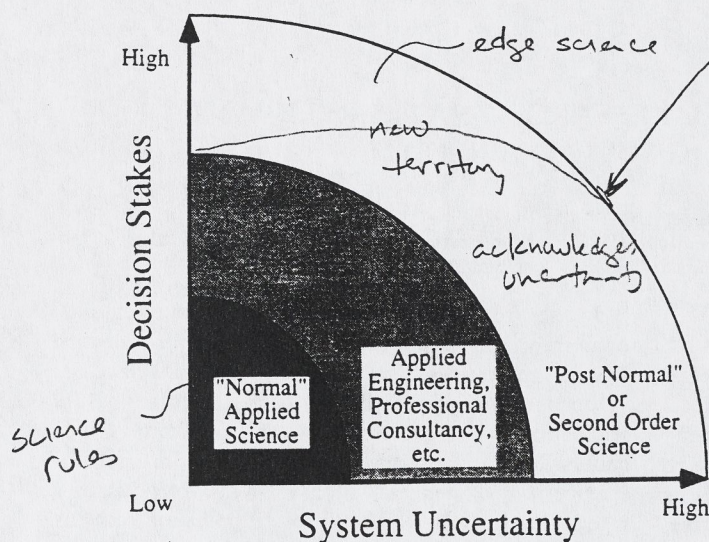


FIG. 1. Three kinds of science (from Funtowicz and Ravetz 1991).

act in anticipation of any potential environmental harm in order to prevent it. The precautionary principle is so frequently invoked in international environmental resolutions that it has come to be seen by some as a basic normative principle of international environmental law (Cameron and Abouchar 1991). But the principle offers no guidance as to what precautionary measures should be taken. It "implies the commitment of resources now to safeguard against the potentially adverse future outcomes of some decision" (Perrings 1991), but does not tell us how much resources or which adverse future outcomes are most important.

This aspect of the "size of the stakes" is a primary determinant of how uncertainty is dealt with in the political arena. The situation can be summarized as shown in Fig. 1, with uncertainty plotted against decision stakes. It is only the area near the origin with low uncertainty and low stakes that is the domain of "normal applied science." Higher uncertainty or higher stakes result in a much more politicized environment. Moderate values of either correspond to "applied engineering" or "professional consultancy" which allows a good measure of judgment and opinion to deal with risk. On the other hand, current methods are not in place to deal with high values of either stakes or uncertainty, which require a new approach, what might be called "post-normal" or "second order science" (Funtowicz and Ravetz 1991). This "new" science is really just the application of the essence of the scientific method to new territory. The scientific method does not, in its basic form, imply anything about the precision of the results achieved. It does imply a forum of open and free inquiry without preconceived answers or agendas aimed at determining the envelope of our knowledge and the magnitude of our ignorance.

Implementing this view of science requires a new approach to environmental protection that acknowledges the existence of true uncertainty rather than ignoring it, and includes mechanisms to safeguard against its potentially harmful effects, while at the same time encouraging development of lower impact technologies and the reduction of uncertainty about impacts. The precautionary principle sets the stage for this approach, but the real challenge is to develop scientific methods to determine the potential costs of uncertainty, and to adjust local incentives so that the appropriate parties pay this cost of uncertainty and have appropriate incentives to reduce its detrimental effects. Without this adjustment, the full costs of environmental damage will continue to be left out of the accounting, and the hidden subsidies from society to those who profit from environmental degradation will continue to provide strong incentives to degrade the environment beyond sustainable levels.

Ecological research (and scientific research in general) in this context, should be focused on defining the edges of the knowledge envelope. This "edge-focused" research should lead to a much more effective use of science as a way to anticipate and head off problems and to link with the policy process.

For example, had this "policy-linked, edge-focused" research been the norm, we could have easily anticipated the greenhouse effect and taken steps to minimize its potential impacts. Arrhenius first described the effect and humans' potential impact on it almost 100 yr ago (Arrhenius 1896), but it remained a scientific curiosity until the 1980s when enough data and models had been assembled to demonstrate that the effect was, in fact, likely to cause global warming. There is still much uncertainty about the magnitude of the warming and especially about its ultimate impacts, but science can do a very good job of anticipating potential problems if we focus the effort on that function, rather than on demonstrating impacts that have already occurred or trying to predict exactly what will happen. To be relevant, ecological research should therefore focus on the edges, as well as the range of uncertainty about these impacts. It should develop better methods to communicate uncertainty and reduce its detrimental impacts, and to link more effectively with other disciplines and the policy process.

How can it do this? Ludwig et al.'s (1993) principles are a good guide. We need to:

- 1) Include human motivation by developing linkages with the social sciences, particularly economics, to develop a comprehensive transdisciplinary synthesis. One effort in this direction has come to be called "ecological economics" (Costanza 1991).

- 2) Act before scientific consensus is reached by focusing on the edges of our knowledge and employing the precautionary principle to guide action (Perrings 1991).

- 3) Rely on ecologists and other scientists to recog-

nize the edges and worst cases, but do not rely on them to remedy the problems themselves. Research needs to be "policy-linked" and "edge-focused."

4) Distrust claims of sustainability and confront uncertainty by shifting the burden of proof from the public to the parties that stand to gain from resources use. One mechanism for doing this is through the use of "environmental assurance bonds" that require resource users to post a bond large enough to cover the worst case damages with the potential for refund if the damages are less (Costanza and Cornwell 1992).

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ACHIEVING SUSTAINABLE DEVELOPMENT THAT IS MINDFUL OF HUMAN IMPERFECTION^{1,2}

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"Uncertainty, resource exploitation, and conservation: lessons from history," by Donald Ludwig, Ray Hilborn, and Carl Walters (1993) is a cry from three people who are convinced that "sustainable development" is an "illusion," and that scientists, especially ecologists, are the principal perpetrators of this illusion. To probe the authors' discomfort more deeply, let us distinguish two kinds of illusions. Might sustainable development be an illusion, call it Type S, rooted in scientific understanding? A perpetual motion machine is a Type S illusion. Or might it be an illusion rooted in human nature, call it Type H? Modern Soviet Man, sacrificing personal welfare for the general good, turned out to be an illusion of Type H.

At the level of fisheries management, the authors implicitly argue that "sustained yield" (a necessary component of sustainable development) is also an illusion. Sustained yield would be an illusion of Type S, if substantial fishing inevitably drives the corresponding fishery to extinction. I infer that the authors believe that sustained yield is an illusion not of Type S but rather of Type H, which would be the case if every human institution invented to manage fishing were to drive the corresponding fishery to extinction. To prove

the authors wrong, that is, to find that sustained yield is not an illusion at all but an attainable achievement, one would have to confirm that the population dynamics of fish are robust and that institutions for the management of fishing can be designed to operate indefinitely within that robustness.

As an outsider, I am surprised by the negative view of the role of ecological science in achieving sustainable outcomes: surely the progress in restricting whaling and poaching has been abetted by population biology.

The distinction between Type S and Type H illusions is crucially important when the argument is generalized to global sustainable development. For the sake of discussion, let us agree that what is to be evaluated are patterns of global economic activity on this planet for at least the next few hundred years. Let us further agree that for a pattern to be judged consistent with sustainable development it must meet two constraints: (1) within a small fraction of the total time under consideration (say, 50 yr out of 500 yr) nearly all of the earth's human beings achieve a lifestyle of considerable vigor and quality, and (2) during the time under consideration the survival of the human population and the populations of nearly all other species sharing this planet is not put in jeopardy as a result of life-threatening changes in the natural environment. If sustainable development so defined is an illusion of Type S, then, in

¹ Manuscript received 7 June 1993.

² For reprints of this Forum, see footnote 1, p. 545.

Predators - Denver Post

Mtn Lion - Coyote - 7.25.

UPN
KAIBAB
deer

2000 lions. 1/wk. 50x; 700,000 deer/yr. > 2x hunting?

- Historical - Utilitarianism - vermin, prod. - bounty!

inductive
reasoning

pred-prey - reduce, control, only crop surplus?!

Elton 1920s-30s - hare/fox lemmings

Wed.
Nov. 18

Errington mink-muskrat - pheasants - winter control

Coevol. - Coadapt. - harmonious? - dysmuscipal

→ pred don't
control prey
for simplification
insects - bio. control
UCB chem. comp.

self interest: - \$ values, base - fox, - hunting license \$

AK Dolly Varden - tails - 20% SO₂, coke, RR

- northern squawfish - 2 miles

Anti-harvest

Chapt. 3 Sp. Problem Concepts

concept
definition

BSC Mayr - reprod. isol. - sympat.

R.S.C. - mating systems - birds display song

P.S.C. - cult. - etc. etc. - books journals

Are sp. real? Yes but, some more real than

- Why "sp." to biodiversity & ESA

"Conserve diversity, not Latin binomials"

ESU.

- Chapt. 6 - Genetics

methods

Quantity sp. ?? - % sequence. G.I. 211-22w.

5% ... H. sapiens + Pan

L. Victoria: - 12,000 yrs.

- MVP PUA

Mol. Clock
71-72 Punct.
w/in - among diversity Equilib.

inbreeding vs. outbreeding depression

Dec.

NAPAP - \$ & time → expensive = resolution of probt

Acid rain 1980 - Reagan - EPA - 570,000,000 - 10yr.

5 for Dec. 7
5 for Dec. 11

slide projector - overhead -

- Fri. 3rd person Sean, Debby, (Lori, Nguyen, Marie (1) & (2))

Mon. Nov. 30 turn back drafts.

besides cite sources Use to display what learned about C.B. - text, lectures, handouts, takehome exam.

- Go over - outline - organization - heading, subheadings - style & substance - factual: basis - citation - readability, clarity - let someone read - understand points?

Penney crop samples

- Wed. Rick Knight re. how C.B. soft professions

- handouts: - Coy wolf: hyperbole - exaggeration - get attention - extinction rate? - based on ^{speculation} assumptions - not fact - ex. Trophal level
but - how many sp.?

- new (1) Nonnative sp. August. Organism -

- balanced view - in perspective of time - "good" valuable sp. - niche - interaction? - comp! - Keystone - modifier - Turbidity -

- Newsletter - 4000 nonnative plants - 2300 animals U.S.

Debbie Nonnative - coevol / adapt. ? "catastrophic" sp. - disruption disturbance

- how analyze - predict ?? if catastrophe - ?

Zebra mussel - Russia - stock - Rutilus roach

do night consensus?

handout (2): self interest - group - special - ^{power} - ^{govt policy}

Sugar subsidies / environmental destruction by subsidy -

- case (7/2) - beet - west - state - Penn. / (Republ.)

- 7 Water Bur. Rec. 1902: ^{160 5000} small / family farm - ^{corporation}

- Grazing? family ranch.

- \$, research solve problem. - Acid rain / -1980

NAPAP ^{5700 mil \$} 60 yr - 10 yrs. - Ann ⁵⁰⁰⁰ Gonsueth ^{with} Borja - EPA

- strategy - delay - fast drag - any costly change -

"further research is necessary" - lack of

--- Oversight - keep on track - Adapt. Mgt. -

Standards of Conservation

ALDO LEOPOLD

The setting of standards to correlate methods and practices has now become a familiar and successful feature of administration on the National Forests. Such standards have proven a simple and effective means of detecting and ironing out the discrepancies in the intensiveness with which similar work is done in separate places, and the relative emphasis given various lines of work.

So far, however, standards have been applied principally to the machinery of administration. What would be the probable result if they were applied to the objectives of administration, as distinguished from the machinery with which those objectives are to be attained?

It is believed such an application of standards would result in certain fundamental and beneficial changes, the nature of which it is the purpose of this paper to discuss.

At the outset, it may be well to give examples of the two classes of standards. When an administrative officer is directed to spend at least 40 days a year on grazing work or to make at least two general inspections per year of each unit of range, there is set up a *machinery standard* (heretofore vaguely called administrative standard, or standard of performance). On the other hand when there is set up as an objective of administration that a certain unit of range should be brought to an .8 density of grama grass capable of carrying 1 head per 20 acres, there is established a *standard of conservation* for that unit.

Before discussing the possible effects of standards of conservation, it may be well to answer the question of why they need be set. Is it not axiomatic that every resource should be conserved as far as possible? To be sure, but natural resources are a complex affair, and few men agree on what is possible. For example: three administrators were examining a piece of range, having about .5 oak brush and .1 grama grass, with a very few old fire killed Junipers. It developed that one was looking forward to a .5 oak brush and .3 grass objective, another to a .5 oak and .9 grass objective, and the third

to a stand of Juniper and Piñon woodland with a little brush and grass mixed in. Each objective was probably obtainable, but the method of setting about it radically different in each case. How could any man administer this area intelligently without knowing which of the three he was to work toward?

Another example: A certain area was withdrawn for protection of a reclamation project watershed. Previous overgrazing had thinned the grass and begun to let in a little Juniper reproduction, whereas previous to the grazing, Juniper had been kept out by grass fires, as evidenced by charred stumps. One man examining the area wanted to reduce the grazing and restore the grass as watershed cover. Another wanted to increase the grazing to fill out the catch of Juniper reproduction as watershed cover. How could either administer the area intelligently without knowing which kind of cover he was to work toward?

Another example: A certain area on a "watershed" forest was covered with vigorous even aged pine saplings, with a scattering ground cover of nonpalatable *Ceanothus* brush and a few weeds. In the course of an inspection it developed that the ranger had striven for years to stock the area as heavily as possible with cattle, with a view to forcing them to browse the *Ceanothus* and thus reduce the fire hazard. The inspector noticed that this heavy grazing was destroying all the willows in the watercourses, causing heavy silting by tearing out of banks, in spite of the excellent protection of the watershed by the young pines. He wanted to risk the fire hazard and prevent the silting. Here were two men, both anxious to conserve, but with opposite ideas as to what most needed conserving, and hence with opposite plans of administration.

It can be safely said that when it comes to actual work on the ground, the objects of conservation are never axiomatic or obvious, but always complex and usually conflicting. The adjustment of these conflicts not only calls for the highest order of skill, but involves decisions

so weighty in their consequence, and so needful of permanence and correlation, that only the highest authority should make them. And until they are made by competent authority, the local administrators cannot possibly apply their efforts effectively. On the other hand such adjustments when once decided on, constitute standards of conservation, toward which generations of local administrators may work with their eyes open, often devising their own methods or machinery and unifying their efforts toward the attainment of a clearly defined ultimate goal.

To return now to the possible effects of a change of emphasis in standards. It is first necessary to ask: why do we standardize machinery at all?

Some standardization of methods, practices, procedure, customs, forms, and other machinery is so obviously necessary, especially in any big organization, that the point need not be discussed. But is there not a lot of it done for the purpose of regulating, correlating, and stimulating effort toward objectives, when a precise statement of the objective itself would be a more effective means of accomplishing the same purpose? And is not such standardization of machinery apt in time to become merely a subterfuge to cover up the absence of scientific thinking in analyzing the objectives of conservation, willingness to take the responsibility of deciding them, and skill in concisely defining the decisions?

To illustrate: The Forest Service has _____ pages of grazing manual, a large part of which is devoted to setting up a standardized machinery for range conservation. Many thousands of dollars and the efforts of many men are invested each year in the job of keeping this machinery up to date. At this time also the Forest Service, pursuant

to the wishes of the Congressional Committee, is conducting an appraisal of the national forest ranges, which, to speak broadly, will result in the setting up of figures expressing the kind, quality, and quantity of forage now growing on each small unit of range of each forest. To get these figures requires an examination and study of each unit by skilled men. During each examination, why not also set up figures expressing the kind, quality, and quantity of forage which *should* grow on each unit? If this were done, we should have a standard of conservation toward which local administrative effort could be intelligently directed for years to come. And what is more, such effort, having a definite goal, would not need nearly so much prodding in the form of machinery standards. And the time that now goes into establishing and maintaining machinery standards, could be diverted into the technical education of field men to make their efforts constantly more intelligent. "We don't know where we're going, but we're on our way" is a laudable sentiment only up to the point where it becomes scientifically possible to state where we ought to go.

When does it become scientifically possible to state where we ought to go? The big development of recent years in range management knowledge, coupled with the timely opportunity of range appraisal, has already been cited as one example. In forest management, the management plan offers a complete opportunity of expressing standards of conservation; in fact it largely constitutes a standard. Coupled with it would be standards of loss by fire (already broached at Mather Field). In lands management, the standard could be expressed by . . . [the manuscript ends at this point. See the following Comment by J. Baird Callicott. Ed.]

Standards of Conservation: Then and Now

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After serving, improbably, for a year and a half in the post of Secretary of the Albuquerque Chamber of Commerce, Aldo Leopold rejoined the United States Forest Service as Assistant District Forester in Charge of Operations, on August 1, 1919. As the number two man on twenty million acres of national forests in the Southwest he had responsibility for business organization, finance, personnel, roads and trails, public relations, recreation, supplies and equipment, fire control, grazing allotments, and watershed maintenance (Meine 1988). His duties took him on frequent inspection tours. Sometime during 1922 in the course of one such inspection, probably of the Prescott National Forest in Arizona, Leopold recorded his reflections on the ends for which all the activities of the Forest Service and its hierarchy of officers were supposed to be the means.

Published here for the first time, "Standards of Conservation," an unfinished, handwritten essay contains a blank space for a number to be added later and ends in midsentence. It has now been incorporated in *The River of the Mother of God and Other Essays by Aldo Leopold* which Susan L. Flader and I have edited for the University of Wisconsin Press. This new volume, forthcoming in 1991, includes Leopold's unpublished and previously published literary and philosophical papers. It spans nearly half a century—from 1904, when he was a student at Lawrenceville School in New Jersey, to the year before he died near his shack in the sand country of southcentral Wisconsin in 1948.

The River of the Mother of God and Other Essays sheds new light on many of Leopold's life-long concerns—game management, wilderness preservation, resource economics, and conservation biology. It also documents the evolution of his thinking on more abstract topics—land aesthetics, paradigms in ecology and a corresponding general ecological worldview, and, of

course, his land ethic, for which Leopold is most renowned. Among the signal insights afforded by the new collection of his papers is how deeply the severe soil erosion in the Southwest etched itself into Leopold's consciousness. Perhaps his grave concern for soil conservation, so evident in these papers, will give a new, more literal significance to the land ethic.

According to Flader (1990, p. 90),

Leopold's concern about watersheds and erosion stemmed from his earliest days on the Apache Forest in Arizona. . . . By 1922, of 30 mountain valleys he had tallied during his inspections of southwestern forests, 27 were damaged or ruined. The enormity of the problem set Leopold on a quest for causes and solutions that would lead him increasingly to question some of the most basic doctrines of Forest Service management. Forestry at the time began with the premise that . . . fire was the great evil, and grazing was necessary to reduce the fire hazard.

From some of his other essays of the period—"Some Fundamentals of Conservation in the Southwest," "Pioneers and Gullies," and "Grass, Brush, Timber, and Fire in Southern Arizona" (all in the new collection)—we can surmise that Leopold was the man in the several examples he details in "Standards of Conservation" who opted for more grass than brush and trees, because the native grasses, he had concluded, held the soil better than other locally achievable vegetative types. But restoring the grass would imply a radical reduction or even the complete elimination of grazing, to the consternation of cattle and sheep ranchers, and increased risk of fire, to the consternation of lumbermen and Leopold's orthodox colleagues for whom the only good fire was a prevented fire.

The intractable soil erosion problem, more than anything else, convinced Leopold that the advertised mission of the Forest Service—to conserve the forests,

ranges and watersheds under its jurisdiction, a mission Leopold took at face value and to which he was innocently devoted—had been ill-served, in District 3 at any rate, by its fire control via grazing policy. In "Standards of Conservation" Leopold points out that "machinery standards"—by which he means standardizing the allocation of time and effort among various administrative tasks—had been copiously detailed by Service bureaucrats. Leopold finds nothing in principle wrong with that, but it provides him the occasion to propose standards of another sort, the "objectives of administration" which logically ought to precede the wherewithal.

"Scientific thinking in analyzing the objectives of conservation," for which Leopold here pleads, is needed now more than ever. Since 1922 a lot of scientific and philosophical water has flowed under the proverbial conservation bridge. Gifford Pinchot's (1947) turn-of-the-century anthropocentric/utilitarian definition of conservation, "the greatest good of the greatest number for the longest time," is already implicitly rejected here by Leopold.

Attempting to apply that definition reveals its incoherence. Practically speaking, maximizing three values at once—utility, differently stipulated by a multiplicity of human interests, and longevity—may not always be possible. Getting the greatest utility out of the range, in other words, might not be consistent with getting the greatest utility out of the forest. And getting the greatest utility out of either might not be consistent with holding the soil—the long term foundational resource of both the forests and the ranges, to say nothing of the farms. As Leopold here puts it, "when it comes to actual work on the ground, the objects of conservation are never axiomatic or obvious, but always complex and usually conflicting."

More deeply, the subtext of "Standards of Conservation" suggests that Leopold was already starting to question Pinchot's anthropocentric/utilitarian ideal, quite apart from its practicability. He is evidently concerned here more for the integrity of the "resource" itself, than for the interests of its users. He focuses on range management almost exclusively, not forest management, and implicitly advocates restoring the native grass cover—ranching interests be damned; lumber interests, due to increased fire hazard, and take a back seat. When he turns to the basics of conservation, furthermore, he does not prattle about "wise use" but writes instead that "it is axiomatic that every resource should be conserved as far as possible." And later he calls not only for "concisely defining" specific objectives but also for "a clearly defined ultimate goal"—as if Pinchot had not already stated such a goal once and for all.

One can only guess why Leopold never finished this piece. Here is mine: Throughout he has written of grass,

brush, and various species of trees. Then, when in the penultimate paragraph he turns to how the bureaucracy might implement his suggestion for conservation norms, he switches to forage, a patently tendentious term. Perforce. Since the vehicle he has in mind for introducing standards of range conservation is a projected range study conducted at the behest of a Congressional committee, and the committee will have doubtless taken an exclusively utilitarian interest in the conditions of ranges. Leopold may have realized that, despite what he wrote, he was no more interested in the kind, quality, and quantity of forage (as opposed to grass, brush, and trees) which "should grow" on the ranges in his district than in the kind, quality, and quantity of forage "now growing" there. The very term forage implies grazing and grazing was at the root of the erosion problem. In the last paragraph after writing "in forest management, the management plan . . . largely constitutes a standard" of the sort for which he is calling, he may have said to himself, in effect, "who are you kidding" and simply put down his pencil. The paper self-deconstructs, so to speak.

In two years time, Leopold would transfer from the Southwest to the Midwest; and in six, he would leave the Forest Service for good. By 1944, having become a venerated University of Wisconsin professor of wildlife ecology, he would crystallize a new definition of conservation to replace the utilitarian "wise use of natural resources" formula. In another paper, "Conservation: In Whole or In Part?" (also included in the new collection), he states simply that "conservation is a state of health in the land."

Such a definition emphatically shifts the overall philosophy of conservation from an anthropocentric to an ecocentric frame of reference and suggests an approach to specifying standards of conservation, without reference to human utilities. Medicine is able to specify objective norms of human health. 98.6° Fahrenheit body temperature is an example. Might not ecology specify objective criteria of land health?

In "Conservation: In Whole or In Part?" Leopold proposes such a standard. Speaking of the Wisconsin landscape, he writes,

the net trend of the original community was . . . toward more and more diversity of native forms, and more and more complex relations between them. Stability or health was associated with, and perhaps caused by, this diversity and complexity. . . . Both are partly lost, presumably because the original community has been partly lost and greatly altered. Presumably the greater the losses and alterations, the greater the risk of impairments and disorganizations.

It is a tribute to Leopold's scientific sensibilities and intellectual honesty that while he "believed" that the stability of ecosystems was dependent upon their species diversity, as he confesses in *Sand County's* "The

Land Ethic," in "Conservation: In Whole or In Part?" he carefully avoids dogmatically asserting a causal relation between the two—as "perhaps" and the repeated "presumably" amply indicate.

Leopold's general concept of land health as an overall objective of conservation and the retention of native species as a standard or norm of conservation led him to formulate a novel rationale for wilderness preservation. Originally, Leopold (1921) had campaigned for wilderness exclusively on recreational grounds; so much so that he had even defined wilderness in recreational terms: an area "big enough to absorb a two weeks' pack trip." Two decades later, in "Wilderness as a Land Laboratory," Leopold (1941) wrote, "A science of land health needs, first of all, a base-datum of normality, a picture of how healthy land maintains itself as an organism. . . . The most perfect norm is wilderness."

Over the last two decades any simple and straightforward linkage between ecosystem diversity and stability has been called into question (May 1973, Goodman 1975). And William Cronon's (1983) description of the exploitation and management of northeastern North America by its aboriginal human inhabitants has more recently provoked doubts about the serviceability of wilderness as a base-datum of normality for healthy land. The Western hemisphere prior to its discovery by Europeans in 1492 was hardly an area, in the poetic description of the Wilderness Act, "where the earth and its community of life are untrammelled by man, where man himself is a visitor who does not remain." North and South America were fully, if not densely, populated by indigenous *Homo sapiens* who left more than footprints as their signature on the face of the land.

Moreover, as Daniel Botkin (1990) has recently reminded us, change—evolutionary, climatic, successional, cyclical, seasonal, meteorological, and stochastic—is an inherent property of ecosystems. Therefore, we cannot understand the objective of conservation simply to be maintaining and/or restoring the ecological status quo.

Furthermore, we characterize as unnatural, and thus condemn, massive anthropogenic modifications of ecosystems such as clear-cutting, monoculturing, damming, paving, etc. But while such changes are to be sure radical and destructive, they are not "supernatural" or "preternatural," or indeed "unnatural" in any coherent sense of the word. To consider the activities of *Homo sapiens* to be unnatural is to perpetuate the classical man-nature dichotomy with an opposite spin. In the past, nature was the villain and man the hero. Now that man is completing his tragic conquest of nature, we conservationists are inclined to reverse the roles of hero and villain. But in doing so we only perpetuate a false dualism.

If change is natural and anthropogenic changes im-

posed upon ecosystems are as natural as any other, it by no means follows, that any anthropogenic change is as good as any other. If it is clear from Cronon's study that North America was not a wilderness before the arrival of the exotic subspecies *Homo sapiens europi*, it is equally clear that it was "a biota still in perfect aboriginal health" (Leopold 1987). What we require is just what Aldo Leopold began groping for in 1922, the standards of conservation, as he called them, that incorporate both change as a natural property and *Homo sapiens* as a natural component of ecosystems. The task has distinctly philosophical and scientific aspects.

To establish that there can be objective standards of conservation in a dynamic and humanized environment is the philosophical problem. If change is a fundamental fact of nature and anthropogenic changes are as natural as any other, then why isn't any change as good as any other? The key to this conundrum lies in Leopold's concept of land health. Health is at once a descriptive and normative term. Health *sensu stricto* is an objective and specifiable condition of organisms. It is, moreover, a dynamic condition, since organisms, like ecosystems, also change: they grow, mature, age, and eventually die. But it is also a universally valued condition: except in the most extraordinary circumstances, no one would rather be sick than well. It seems, therefore, no less true that, if man is a part of nature, no one would rather live as an integral part of a sick rather than a well biota.

At the interface between science and philosophy is the metaphor itself. To what extent are ecosystems analogous to organisms, and to what extent therefore can we speak intelligibly of land health?

Finally, the purely scientific task, about which I have no competence even to speculate, is the task of specifying the standards of conservation. If such objective standards could be set, independent but not exclusive of human interests, they would provide the ecological parameters for sustainable economies and rescue conservation from its current develop-and-necessarily-destroy or preserve-and-necessarily-lock-up dilemma.

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TABLE 1-1

Chronology of historical events, key conservationists, important books (1607-1849)

YEAR	HISTORICAL EVENTS	KEY CONSERVATIONISTS	IMPORTANT BOOKS
1607	Jamestown settled by the London Company		
1620	Pilgrims land at Plymouth		
1756-1763	French and Indian War		
1776	American Declaration of Independence and Revolution		
1769	Daniel Boone begins exploring the American wilderness	Daniel Boone (1734-1820)	
1789-1797	George Washington (first U.S. president)	George Washington (1732-1799) Patrick Henry (1736-1799) William Bartram (1739-1823)	Bartram's <i>Travels</i> (1791)
1801-1809	Thomas Jefferson (third U.S. president)	Thomas Jefferson (1743-1826)	Thomas Malthus's <i>Essay on the Principle of Population</i> (1798) Alexander von Humboldt's <i>Essays on the Geography of Plants</i> (1807)
1803	Louisiana Purchase; Lewis and Clark Expedition		
1822	Jed Smith joins trapping crew to ascend the Missouri River	Jedediah Strong Smith (1799-1831) Frederick Law Olmsted (1822-1903)	
1830s	First Redemption Act passed	John James Audubon (1785-1851)	Audubon's <i>Birds of America</i> (1826-1838)
1831	First American railroads begin operation	Ralph Waldo Emerson (1803-1882)	Emerson's <i>Nature</i> (1836)
1845	Texas annexed to the United States	Francis Parkman, Jr. (1823-1893)	Parkman's <i>The Oregon Trail</i> (1849)
1849	U.S. Department of the Interior established	Henry David Thoreau (1817-1862)	Thoreau's <i>Walden</i> (1854)

TABLE 1-2
Chronology of historical events, key conservationists, important books (1862-1929)

YEAR	HISTORICAL EVENTS	KEY CONSERVATIONISTS	IMPORTANT BOOKS
1862	Department of Agriculture established;		
1864	First Homestead Act passed Yosemite Valley, California, becomes state park	George Perkins Marsh (1801-1882)	Marsh's <i>Man and Nature; Or, Physical Geography as Modified by Human Action</i> (1864)
1868	John Muir arrives in Cali- fornia		
1869	John Wesley Powell de- scends the Colorado River	John Wesley Powell (1834-1902)	Powell's <i>Report on the Lands of the Arid Regions of the United States</i> (1878)
1872	Creation of Yellowstone National Park;		
1873	Timber Culture Act		
1879	U.S. Geological Survey established		
1881	Division of Forestry created in U.S. Department of Agriculture		
1887	Hatch Act establishes agri- cultural experiment sta- tions		
1891	Yosemite National Park established;		
1892	Forest Reserves Act Sierra Club organized by John Muir	John Muir (1838-1914)	
1898	Gifford Pinchot becomes first Chief Forester	Gifford Pinchot (1865-1946)	
1900	Lacey Act		
1902	Reclamation Act		
1903	Muir's four-day tour with Teddy Roosevelt	Theodore Roosevelt (1859-1919)	
1905	National Audubon Society formed; Teddy Roosevelt creates U.S. Forest Ser- vice with Gifford Pinchot first director		
1906	Antiquities Act		
1907	Teddy Roosevelt doubles for- est area under protection		Pinchot's <i>The Fight for Con- servation</i> (1910)
1908	Teddy Roosevelt and gover- nor's conference on con- servation		
1911	Fur Seal Treaty		Muir's <i>My First Summer in the Sierra</i> (1911); <i>The Yosemite</i> (1912)
1916	National Parks Act; Migratory bird treaty be- tween U.S. and Great Britain;		
1922	National Park Service Act Izaak Walton League orga- nized		
1929	Crash of 1929 leads to Great Depression		

Source: Adapted from Petulla, Joseph. 1977. *American Environmental History*. San Francisco: Boyd and Fraser.

TABLE 1-3

Chronology of historical events, key conservationists, important books (1933-1948)

YEAR	HISTORICAL EVENTS	KEY CONSERVATIONISTS	IMPORTANT BOOKS
1933-1937	Drought and dust storms in the West lead to the "Dust Bowl"; Franklin Roosevelt's "New Deal"; Civilian Conservation Corps (CCC); Tennessee Valley Authority (TVA)	Franklin D. Roosevelt (1882-1945) Robert Marshall (1901-1939)	Marshall's article, "The Problem of the Wilderness," <i>Scientific Monthly</i> (1930) Marshall's <i>Arctic Village</i> , (1933); <i>The People's Forest</i> (1933)
1934	Taylor Grazing Act		
1935	Wilderness Society established		
1938	National Wildlife Federation		
1939-1945	World War II	Aldo Leopold (1886-1948) J. N. ("Ding") Darling (1876-1962)	Leopold's <i>Game Management</i> (1933)
1940	U.S. Fish and Wildlife Service established		
1944	Soil Conservation Society of America founded		
1946	U.S. Bureau of Land Management established; Nature Conservancy established		Pinchot's <i>Breaking New Ground</i> (1947)
1948	International Union for the Conservation of Nature and Natural Resources established		Leopold's <i>A Sand County Almanac</i> (1949)

Source: Adapted from Petulla, Joseph. 1977. *American Environmental History*. San Francisco: Boyd and Fraser.

Chronology of historical events, key conservationists, important books (1952-1969)

YEAR	HISTORICAL EVENTS	KEY CONSERVATIONISTS	IMPORTANT BOOKS
1952	Resources for the Future established	Olaus Murie (1889-1963)	Murie's <i>Field Guide to Animal Tracks</i> (1954)
1956	"Soil bank" agricultural plan enacted; Federal water pollution control passed	Rachel Carson (1907-1963) David Brower (1912-)	Carson's <i>The Edge of the Sea</i> (1955)
1960	National Forest Multiple-use Act passed	Ansel Adams (1902-1984)	Adams's <i>This Is the American Earth</i> (1960)
1961	World Wildlife Fund established	Eliot Porter (1901-)	Porter's <i>In Wilderness is the Preservation of the World</i> (1962); Carson's <i>Silent Spring</i> (1962)
1963	Clean Air Act passed	Stewart L. Udall (1920-)	Udall's <i>The Quiet Crisis</i> (1963)
1964	National wilderness preservation system created under Wilderness Act	Jacques-Yves Cousteau (1910-) Howard Zahniser (1906-1964)	Cousteau's <i>The Living Sea</i> (1963); <i>World without Sun</i> (1964)
1965	Solid Waste Disposal Act passed; Water Quality Act passed		Glacken's <i>Traces on the Rhodian Shore: Nature and Culture in Western Thought</i> (1967)
1969	National Environmental Policy Act (NEPA) passed; Friends of the Earth created by David Brower	Roderick K. Nash (1939-) Paul R. Ehrlich (1932-) Garrett Hardin (1915-)	Nash's <i>Wilderness and the American Mind</i> (1967) Ehrlich's <i>The Population Bomb</i> (1968) Hardin's "Tragedy of the Commons," <i>Science</i> (1968)

Holdren, remain prolific, with the publication of their theoretically sound and encyclopedic works *Eco-science: Population/Resources/Environment* (1977) and *Extinction: The Causes and Consequences of the Disappearance of Species* (1981).

For additional information on these important conservationists consult Zahniser (1984) and Nash (1967) for information on Zahniser. Madsen (1986), Richards (1985), and *U.S. News and World Report* (1985) profile Cousteau. Evory and Metzger (1983) provide information on Ehrlich.

Earth Day and the Energy-Conscious Years (The 1970s)

The controversy stirred by the above writers and by others provided the impetus for Dennis Hayes and other so-called mavericks, dissidents, and cranks, to

organize the first international Earth Day in 1970 (Table 1-5). The event turned out to be a smashing success, with an estimated 20 million people demonstrating their concern for the environment. It was a day of mass rallies, which included the picking up of trash alongside roadways, the cleaning up of debris in rivers, and the conducting of environmental teach-ins. The observance of Earth Day continues today in thousands of cities across the nation and the world.

The 1970s were also the "energy-conscious years" in America. The 1973 Arab oil embargo alerted Americans to how energy dependent we were on outside oil, and "Project Independence" was launched, which included the construction of a controversial pipeline across the Alaskan tundra (1974) and the creation of a separate Department of Energy (1977) to integrate the administration's energy policy.

It was also a time when Barry Commoner, E. F.

TABLE 1-5
Chronology of historical events, key conservationists, important books (1970-1983)

YEAR	HISTORICAL EVENTS	KEY CONSERVATIONISTS	IMPORTANT BOOKS
1970	First Earth Day; Resource Recovery Act passed; Water Quality Control Act passed		
1972	Stockholm Conference on the Human Environment	Barry Commoner (1917-)	Commoner's <i>The Closing Circle</i> (1971) Donella H. Meadow's <i>Limits to Growth</i> (1972)
1973	Arab Oil Embargo alerts na- tion to energy dependence on Middle East	E. F. Schumacher (1911-1977)	Schumacher's <i>Small Is Beau- tiful</i> (1973)
1974	Approval of Alaska Pipeline	Edward Abbey (1927-1989)	Abbey's <i>The Monkey Wrench Gang</i> (1975)
1977	Department of Energy created		Paul Ehrlich, Anne Ehrlich, and John Holdren's <i>Eco- science: Population/Re- sources/Environment</i> (1977)
1980	Woman's Action for Nuclear Disarmament group founded; The Reagan years begin: environmentalists begin to fight back	Helen Caldicott (1939-)	
1982	One million sign anti-Watt petition	Ralph Nader (1934-)	Nader's <i>Who's Poisoning America</i> (1981) Jonathan Schell's <i>The Fate of the Earth</i> (1982)
1983	James Watt resigns as Sec- retary of the Interior (Oc- tober 10)	Lester Brown (1928-)	<i>The State of the World</i> series by Worldwatch Institute first published (1984)
(?)	Earth First! founded	Dave Foreman (?) Mike Roselle (1954-)	Dave Foreman's <i>EcoDe- fense: A Field Guide to Monkey-Wrenching</i> (1985)

Source: Adapted from Petulla, Joseph. 1977. *American Environmental History*. San Francisco: Boyd and Fraser.

The Keystone-Species Concept in Ecology and Conservation

Management and policy must explicitly consider the complexity of interactions in natural systems

L. Scott Mills, Michael E. Soulé, and Daniel F. Doak

Will the extinction of a single species in a community cause the loss of many others? Can we identify a set of species that are so important in determining the ecological functioning of a community that they warrant special conservation efforts? The answer to these questions hinges on the existence of a limited number of species whose loss would precipitate many further extinctions; these species have often been labeled keystone species.

The term *keystone species* has enjoyed an enduring popularity in the ecological literature since its introduction by Robert T. Paine in 1969: Paine (1969) was cited in more than 92 publications from 1970 to 1989; an earlier paper (Paine 1966), which introduced the phenomenon of keystone species in intertidal systems but did not use the term, was cited more than 850 times during the same period.

As used by Paine and other ecologists, there are two hallmarks of keystone species. First, their presence is crucial in maintaining the organization and diversity of their ecological communities. Second, it is implicit that these species are exceptional, relative to the rest of the community, in their importance.

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The term *keystone species* is poorly defined and broadly applied

Given the assumed importance of keystone species, it is not surprising that biologists have advocated that key or keystone species be special targets in the efforts to maximize biodiversity protection (e.g., Burkey 1989, Frankel and Soulé 1981, Soulé and Simberloff 1986, Terborgh 1986) and as species in need of priority protection (e.g., Cox et al. 1991). Management to protect keystone species has been suggested to resolve general policy and land-use dilemmas. For example, it has been proposed that management for individual keystone species should be a focus for the management of whole communities (Rohlf 1991, Woodruff 1989). Further, Carroll (1992) argues that managed keystone species could be used to support populations of other species in reserves that would otherwise be too small to contain viable populations. Conway (1989) suggested that, for restoration, keystone species are necessary to help reestablish and sustain ecosystem structure and stability.

Such policy recommendations imply that a clear operational definition exists for *keystone species*. In contrast, we argue that the term is broadly applied, poorly defined, and nonspe-

cific in meaning. Furthermore, the type of community structure implied by the keystone-species concept is largely undemonstrated in nature, although it has fundamental implications for conservation and food-web theory. These ambiguities and uncertainties motivate this discussion of the implications of the keystone-species concept for ecology and conservation, as well as the dangers inherent in shaping conservation strategies around keystone species.

The varied meanings of the term *keystone species*

The term *keystone species* was originally applied to a predator in the rocky intertidal zone:

[T]he species composition and physical appearance were greatly modified by the activities of a single native species high in the food web. These individual populations are the keystone of the community's structure, and the integrity of the community and its unaltered persistence through time...are determined by their activities and abundances (Paine 1969).

Subsequently, the term has been applied to many species at many trophic levels. For heuristic purposes, we have collapsed the usages of *keystone species* into five types (Table 1). This categorization is not meant to imply mutually exclusive groups or an exhaustive review of the term's application, but rather to show the diversity of keystone effects referred to in the literature.

Keystone predator. Paine (1966, 1969) noted that experimental removal of some rocky intertidal carnivores (such as the starfish *Pisaster*) led to nearly complete dominance of the substrate by one or two sessile species (mussels), resulting in greatly decreased species diversity. In this and other cases, the importance of the keystone predator derived from two requisites (Paine 1969, Pimm 1980): the predator preferentially ate and controlled the density of a primary consumer, and the consumer was capable of excluding (through competition or predation) other species from the community. Essentially, then, the early connotation was that keystone predators are important because they control the densities of important competitor or predator species.

Predators have also been labeled *keystone* when they control the densities of other types of ecologically significant prey species. For example, sea otters (*Enhydra lutris*) have often been referred to as keystone predators (e.g., Duggins 1980, Estes and Palmisano 1974) because they limit density of sea urchins (*Strongylocentrotus* spp.), which in turn eat kelp and other fleshy macroalgae that form the basis of a different community than is present in their absence (VanBlaricom and Estes 1988). Thus, otter removal has community-level influences, by releasing from predation a primary consumer that eats a plant that harbors other organisms.

Other authors have ignored the original requisites for the keystone-predator label and merely require that the species in question has a major effect on community composition. Risch and Carroll (1982) described fire ants (*Solenopsis geminata*) as keystone predators because their absence increases the number of individuals and species of arthropods potentially harmful to agriculture. The ants are generalist species preying on herbivores, which in turn are not highly competitive; hence, neither of the original requisites for keystone predators apply.

Keystone prey. In a theoretical analysis that assumed no competitive interactions between prey species, Holt (1977, 1984) demonstrated that a preferred-prey species that is able to maintain its abundance in the face of pre-

Table 1. Categories of presumed keystones and the effects of their effective removal from a system.

Keystone category	Effect of removal
Predator	Increase in one or several predators/consumers/competitors, which subsequently extirpates several prey/competitor species
Prey	Other species more sensitive to predation may become extinct; predator populations may crash
Plant	Extirpation of dependent animals, potentially including pollinators and seed dispersers
Link	Failure of reproduction and recruitment in certain plants, with potential subsequent losses
Modifier	Loss of structures/materials that affect habitat type and energy flow; disappearance of species dependent on particular successional habitats and resources

dation (via a high reproductive rate) can affect community structure by sustaining the density of a predator, thus reducing the density of other prey. Holt (1977) called such a predator-tolerant prey a *keystone species* "inasmuch as its properties control the density of the predator and restrict the range of parameters open to other prey." As an anecdotal example, Holt describes the contraction of habitat use of arctic hares after the introduction of snowshoe hares on Newfoundland, indicating that the snowshoe hare may have increased lynx populations, which then heavily preyed on the more vulnerable arctic hare. As the term *keystone prey species* was used by Holt, removing the keystone prey species would increase, not decrease, overall species diversity in the community.

However, Noy-Meir (1981) suggested that Holt's model involving a predation-tolerant keystone prey could be modified so that the removal of keystone prey would decrease species diversity. If the predator switches to the keystone prey when numbers of other prey species are low, then sensitive prey that otherwise would have been driven to extinction may coexist in the presence of the predator-tolerant keystone prey. Thus, we again see that the label *keystone* has been applied to species whose removal would either increase or decrease species diversity in their communities.

Keystone mutualists. Some species have been considered to be keystone because they are critical to mutualistic relationships. Gilbert (1980) introduced the term *mobile links* to describe "animals that are significant factors in the persistence of several plant species which, in turn, support otherwise separate food webs." The implication was that mobile links are a kind of keystone species, and mobile links have since been frequently cited as examples of keystone species. In addition to the mobile-link pollinators and seed dispersers described by Gilbert (1980), other examples of this type of keystone species include hummingbird pollinators and mammalian dispersers of mycorrhizal fungi (Wilcox and Murphy 1985).

Keystone hosts. If mobile links, or keystone mutualists, depend critically on ecologically important host plants, then it follows that these hosts also receive the label *keystone*. Included in this group are those plants that support generalist pollinators and those fruit dispersers that are considered critical mobile links (Gilbert 1980). Terborgh (1986) considered palm nuts, figs, and nectar to be keystone resources because they are critical to tropical forest nectar or fruit eaters, including primates, squirrels, rodents, and many birds. Together, these vertebrates account for as much as three-quarters of forest bird and mammal biomass.

Keystone modifiers. The activities of many species greatly affect habitat features without necessarily having direct trophic effects on other species. If the modified habitat affects the survival of many other species, the modifying species has been considered a keystone species. The North American beaver (*Castor canadensis*) was described as a keystone species because its dams alter hydrology, biogeochemistry, and productivity on a wide scale (Naiman et al. 1986). Likewise, the Brazilian termite (*Cornitermes cumulans*) has been called a keystone species because loss of its large, abundant, and uniquely structured mounds would likely precipitate loss of obligate and possibly opportunistic users of the mounds (Redford 1984).

Many species have been called key-

stone herbivores because their foraging causes drastic habitat modification. Based on the observation that large herbivores (more than 1000 kg) can readily convert closed thicket or forest into open grassy savanna, Owen-Smith (1987) posited a keystone-herbivore hypothesis to explain the late Pleistocene extinction of approximately half of the mammalian genera with body masses of 5–1000 kg. This theory posits that the elimination of large herbivores initiated vegetational changes that were deleterious to the fauna.

A keystone-herbivore hypothesis was also advanced to describe red-naped sapsuckers (*Sphyrapicus nuchalis*), which create sap wells in tree bark, thereby providing resources for other herbivores (Ehrlich and Daily 1988). Sea urchins have been called keystone because their grazing prevents the change from a system dominated by encrusting algae to a system dominated by large, fleshy algae (Fletcher 1987, see also VanBlaricom and Estes 1988). Similarly, pocket gophers (*Thomomys bottae*) were described as keystone because they maintain mountain meadow communities by slowing down aspen invasion of the meadows (Cantor and Whitham 1989). After the removal of what they called a "keystone guild" of kangaroo rats (*Dipodomys* spp.), Brown and Heske (1990) documented drastic changes in vegetation type and accompanying changes in the rodent community. Clearly, the distinction between keystone predation and keystone modification becomes fuzzy for those species that modify habitat through predation on plants.

Useful contributions of the keystone-species concept

We have seen that the label *keystone* has been applied to a plethora of species with very different effects—both qualitative and quantitative—on their communities. Given the diversity of the usages of the term *keystone species* in the ecological literature, what are the contributions and liabilities of this concept for ecological and conservation research?

One fundamentally important contribution is the attention these studies have drawn to differing interaction strengths in community food webs.

Table 2. Predicted or observed effect of removing presumed keystones, based on articles in which authors called a species *keystone* and predicted a community composition change upon removal.

Author	Presumed keystone (community type)	Effect of removal
Paine (1966, 1969)	Starfish (rocky intertidal)	Observed reduction of system from 15 to 8 species
Fletcher (1980)	Sea urchins (subtidal)	Observed takeover of large fleshy algae, resulting in loss of approximately one-half of grazers
Terborgh (1986)	Palm nuts, figs, and nectar (tropics)	Predicted loss of one-half to three-quarters of total bird and mammal biomass
Owen-Smith (1987)	Herbivores more than 1000 kg (Pleistocene)	Hypothetical mechanism for loss of approximately half of mammalian genera during late Pleistocene

Robert MacArthur (1972) first advocated close scrutiny of interaction strengths, defining a strong interactor simply as a species whose "removal would produce a dramatic effect." Studies of presumed keystone species have certainly demonstrated the presence of strong interactors in many systems.

To gain some quantitative feel for the extent to which the removal of presumed keystone species may decrease overall species diversity, we reviewed all published studies we could find that refer to a species as a keystone and that predict or describe specific community composition changes occurring on removal of the presumed keystone. Despite the fact that investigators encountered enormous methodological problems and employ different trophic and taxonomic criteria to circumscribe the relevant assemblage, an interesting consistency is revealed (Table 2). Ecologists identify as keystone those species whose removal is expected to result in the disappearance of at least half of the assemblage considered. For reasons we will detail below, however, we hasten to warn against the use of a 50% loss rule as an operational criterion for identifying a species as keystone.

The second important contribution of the keystone paradigm is its implication that only a small minority of species have strong interactions that affect community composition. In other words, reference to a particular species as keystone implies that it is unusual, standing out from the majority of the other species in its effects on community structure or function. If we define the community importance of a given species as the percentage of

other species lost from the community after its removal, we can illustrate this assumption by plotting, for a hypothetical community, the relative community importance of each species (Figure 1). The keystone concept assumes that frequencies of community-importance values are strongly skewed, with only a few species having large effects on the composition or structure of the community (Figure 1a).

In contrast to this assumption, food-web theorists have generally assumed either that species-by-species interaction strengths are drawn from symmetrical distributions (e.g., Figure 1b, normal distributions; Cohen and Newman 1988) or else are uniform (Figure 1c, an implicit assumption of static food webs; see Pimm and Kitching 1988). Although species-by-species interaction strengths are unlikely to directly correspond to community-importance values as defined here, there is likely to be considerable correlation between the two. In particular, it is difficult to imagine a species having a large effect on species diversity (community importance) without having strong interactions with other species. Thus, the keystone concept's implicit assumption about interaction strengths appears to be in conflict with the more explicit, but not necessarily more realistic, food-web models (Lawton 1992).

This apparent dichotomy between food-web theory and the keystone-species concept is certainly worth exploring. The two conceptualizations imply different patterns of community structure and hence require different conservation strategies. If many or most species are of similar importance (Figure 1b,c), any efforts to save

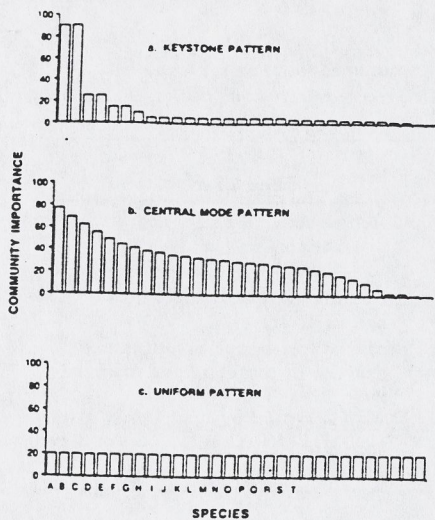


Figure 1. Expected distributions of community importance values (percent of species lost from a community upon removal of a given species) for a hypothetical community based on the keystone-species model (a) and based on food-web theory (b and c). Axes are arbitrarily scaled to demonstrate the general shape of the distributions.

only a few keystones will inevitably fail to protect the rest. Conversely, if only a few species have strong interactions/community effects, then detailed understanding and protection of the few important taxa would be critical to the well-being of the overall community.

What do the data say about this conflict? To date, only one study has addressed the distributions of interaction strengths in part or all of an ecological community. Paine (1992) developed an index of per capita interaction strength and found that only two of seven species of intertidal grazers strongly affect brown algae, which are their major food and also a profound modifier of the local environment. These results indicate "a few strong interactions embedded in a majority of negligible effects" (Paine 1992), supporting an assumption of highly skewed interaction strengths (Figure 1a). Although suggestive, it is premature to generalize this result: Paine looked at only one type of interaction for each species (herbivory of brown algal sporlings) and he looked at only a subset of the grazers within a single community. Indeed, his finding that 29% of the species were strong interactors could be interpreted as indicating that a large fraction of species have strong effects. Clearly, more

studies of this type are needed in many more communities.

Keystones and conservation

What role should the keystone-species concept play in conservation efforts? Currently, implementation of the Endangered Species Act often amounts to emergency-room conservation (Scott et al. 1987), whereby the bulk of conservation resources are spent on single species that are on the brink of extinction. In the absence of comprehensive biodiversity legislation and/or increased funding and support for the Endangered Species Act, it has been suggested that "The Act could serve as an extremely useful tool for preserving keystone species, thus indirectly benefiting the many other life forms in some way dependent upon those species" (Rohlf 1991; see also Burkey 1989, Westman 1990).

We see both technical and philosophical liabilities associated with reliance on keystone species in a conservation context. (See Landres et al. 1988 for a parallel critique regarding labeling certain species "indicator species.") The overriding technical difficulty is one of definition. Before keystone species become the centerpiece for biodiversity protection or habitat restoration, we must be able to say what is and is not a keystone species.

Lacking any a priori definition, the best way to identify keystone species would be perturbation experiments whereby the candidate keystone species are removed and the responses of a predefined assemblage of species are monitored. Such tests would require adequate experimental replication and careful attention to defining the relevant assemblage (MacMahon et al. 1978 give a useful organism-centered definition of community), as well as consideration of time scales over which responses should be measured.

Bender et al. (1984) evaluated mathematical approaches for evaluating the consequences of the inevitable omission of certain species in perturbation experiments and the impact of lumping together the interactions of related groups of organisms (e.g., combining data for related ant species to measure the effect of removing a granivorous rodent). Extraordinary difficulties await researchers attempting such experiments (see Bender et

al. 1984, Carpenter et al. 1985). The problem of objectively defining which species are keystone makes it likely that subjectively chosen subsets of species will be so labeled, whereas other species of similar importance will be ignored.

Even if keystone species could readily and reliably be identified for a given location at a given time, several philosophical dangers arise. First, the term is burdened with historical connotations that, as shown earlier, mean different things to different people. The lack of a clear operational definition hinders any political or legal implementation. Second, the term *keystone species* is misleading because it indicates the existence of a species-specific property of an organism, when in actuality the keystone role is particular to a defined environmental setting, the current species associations, and the responses of other species (Gautier-Hion and Michaloud 1989, Jackson and Kaufmann 1987, Levey 1988, Palumbi and Freed 1988). Thus, it is exceptionally difficult to confidently define a priori which local populations (not to mention species) are keystone (Elner and Vadas 1990, Foster and Schiel 1988). Another problem is that removal of combinations of nonkeystone species could have effects as large as removal of a keystone.

Finally, a conservation criterion that favors the maintenance of keystone species—and with them the majority of species in a community—may fail to protect other species of interest to conservationists or the public at large. For example, spotted owls, wolverines, grizzly bears, and California condors may have little role in the maintenance of species richness in their respective habitats, yet the protection of these charismatic species has been advanced because their fates are thought to indicate the integrity or health of their habitats, or because the viability of many such species requires large areas; these areas may ensure, in turn, sufficient habitat heterogeneity and space for large numbers of other species, some of which may have specialized requirements.

In sum, both the complexity of ecological interactions and ignorance of them militates against the application of the keystone-species concept for practical management recommen-

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dations. Despite its heuristic value, we see more harm than good in the formalization of the term in laws and policy guidelines that have rigid practical implications.

Conclusions

The lack of data addressing both the range of interaction strengths within communities and the generality of trends across communities leads us to suggest that neither the science of ecology nor the protection of biodiversity is advanced by continuing to label certain species as keystone. Instead, we advocate the study of interaction strengths and subsequent application of the results into management plans and policy decisions. Emphasizing strengths of interactions instead of a keystone/nonkeystone dualism is more than a semantic improvement; it recognizes the complexity, as well as the temporal and spatial variability, of interactions.

Although Paine's 1992 study is compelling in its demonstration of the existence of just a few strong interactors for the rocky intertidal zone, no data address whether other systems have similarly distributed interaction strengths. Paine's tantalizing results should inspire theoreticians to explore the implications of assemblages structured with many weakly interacting species and only a few strong interactors. At the same time, further empirical studies could assess, at the level of both short- and long-term effects (Carpenter and Kitchell 1988), the generality of skewed interaction strengths and trophic cascades (e.g., Carpenter et al. 1985, Paine 1980, Power 1990) or mesopredator release in the absence of a larger predator (Soulé et al. 1988).

If they abandon the keystone-species concept and the rigid structure it imposes on species interactions, investigators are less likely to assume that interactions or their strengths and distributions are constant in space and time. The concept has been useful in demonstrating that under certain conditions some species have particularly strong interactions, and we recognize that in recommending the abandonment of a popular and evocative concept there is a danger of making it more difficult for biologists to communicate with policy makers, manag-

ers, and the public. We think, however, that the inconvenience caused by the dropping of the label *keystone species* will, in the long run, be compensated by the development of management and policy guidelines that more explicitly accounts for the complexity of interactions in natural systems.

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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 poly-

morphisms 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 histocompatibility 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 invariable 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-km² home ranges,

and thereby pinpointed the timing of births and location of lairs. Soon after a female had given birth, Laurenson entered lairs to count and weigh the cubs while the mother was known to be away hunting. Regular monitoring of the family showed that cubs suffered from extremely high mortality in the first weeks of life such that only 36 out of 125 cubs (29%) emerged from the lair at 2 months of age. By the time cubs reached independence over a year later, only 5% had survived. Other long-term studies of large and medium-sized felids have yet to document mortality in the lair, but comparative mortality estimates between emergence and independence average 50% as 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 calici 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 demo-

graphic 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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Office Hours:

(1 hr immediately after classes? And others?)

Those are my formal hours. I enjoy teaching and helping students and ask you to please make an appointment with me or my secretary if you have questions that were not covered in class and recitations.. Lunch time is the best time to catch me in the office. I try to maintain an active schedule of working with persons off of campus (½ my job), thus planning to visit during office hours is best for all.

University catalogue description:

Effective public relations and public information programs applicable to natural resource professionals.

My course description and philosophy about public relations in natural resources:

Welcome to the people-side of natural resources management. The scientists and managers of natural resources have positive impacts only when society allows them to operate. People out there, our publics, are becoming more knowledgeable about how the environment works and they have strong emotions about how their natural resources are managed. They tell us what should be done and often how to do the work; it does not matter if they are right or wrong, they have gained power and they have become leaders. As friends or foes, these publics are right wing, left wing, and middle roaders who live in local neighborhoods and the nation's capital. They work in your organization and they have organized against you.

The proliferation of leaders associated with natural resources means that scientists, managers, and especially CSU graduates must also lead. Public Relations in Natural Resources means learning and using communications principles in your organizations and externally that enable individuals and their institutions to understand the climate of beliefs about natural resources and to effect proper resolution of differences to maintain and enhance the integrity of natural resources for generations to come.

You need to develop skills with communications, organization, and doing work to be leaders in thought and action in your chosen field of study, your avocation, and in your life. Some of you will become motivated by our class activities and relationships and some will be stimulated by others in your life, but all of you must make the eventual commitment to become the best that you can be: to be a professionals.

This could be the most valuable course in your career, because it is about dealing with people. People at home and at work are your allies or your barriers. In this course you can learn about working with people, improving yourself, and having proper relations with the publics that you serve. I want to change or reinforce your behaviors about dealing with people. I'll be asking you to include the most important principle of public relations into your behaviors: include the wants, needs and inputs of people into your decisions about natural resource management and in life.

My goals for you:

I want you to be leaders and natural resources stewards at all the various employment levels of governmental and nongovernmental organizations in which you will work. If you do not become natural resources professionals, then I want you to be good citizens and stewards of the land. Leaders must be able to follow, communicate, listen, organize, think, act, react, and evaluate in a circular process that never ends. You must understand and respect differences and have empathy for the needs of others. You must learn to speak, write, and work with other persons. You must be reliable, punctual, and persistent: always do your share. Successful public relations includes having a vision, knowing how to plan, being effective at putting plans into action, knowing if you are successful, and knowing when to quit. You must care and know enough about history to understand that good ideas take time to reach maturity and that you should not quit too soon. My goal is for you to be professionals!

Objectives for you:

Students shall be able to do the following:

Discuss the importance of public relations to their work objectives.

Identify internal and external publics with which they will work.

Diagram how ideas are adopted or rejected and discuss barriers to communications..

Draw and explain a communications model.

Prepare and use visual aids.

List steps in organizing presentations, committees, conferences, and projects.

Write a fact sheet, news article, or memorandum using inverted pyramid style.

Prepare a brochure.

Design an exhibit.

Write a personal public relations plan, strategy, credo, etc.

Practice facilitation techniques.

Participate in conflict resolution.

Discuss public involvement procedures.

Keep a journal of public relations activities.

Complete a workbook about principles of public relations.

Participate in a service learning project with local organizations that involves structured learning about public relations

Reflect about the service learning experience through discussions with peers.

Work on a team project.

Learn how to prepare, implement and evaluate objectives. Working with clear objectives is an important principle of public relations.

The role of service learning in your education:

The beginning of our service learning plan places you with a natural resources organization to see and hear what they say about their public relations needs. You will learn about areas of study and personal attributes that can help you to become effective leaders of public relations processes. As the class progresses, you will work with the organization and represent them on discussions about a joint class project.

Class project:

Your final evaluation will be based on a public relations and communication plan for a joint class project. Input to the plan should be by discussions with class groups. The project can be real, as identified through the "Service Learning Gatherings" of natural resources agency personnel in the area, or a hypothetical project will be given. Your report will be graded upon completeness, creativity, likelihood of accomplishment, prudent consideration of time and budgets, etc. You will be expected to identify components of the plan and to fill in appropriate activities, details etc. based upon what you learned in and out of class. If no other project is more appropriate, you will develop a public relations and communications plan for a "Goose Festival" to be held in Fort Collins. Details about the festival shall be developed by you with the help of your small groups and entire class.

My Teaching Philosophy:

I work from the philosophy that my job is to help **you to learn**, not for me to focus all attention on **what I will teach**. It is your responsibility to learn. This course is a mixture of learning methods: I will facilitate lectures, discussions, and demonstrations; guest experts will add variety and special expertise to the class; and we will always strive to involve you to a maximum extent in the learning process even though class size is large. Filling in workbooks, keeping notes in journals and active discussions in recitation sessions are designed to make learning more student-centered. Learning is not complete by memorizing facts sufficient to get good grades on tests. I want you to remember information by using many of your senses through active engagement in the learning process. I expect reading assignments, notes in journals, and sections of the workbook to be completed before coming to class and I will occasionally make spot checks. Our discussions and your questions will be much more thoughtful when you are prepared. Being prepared, is an important principle of public relations.

Teachers can merely facilitate learning to happen by their expertise, enthusiasm, coaching, and the motivational climates they create. Learning involves a change in your behavior caused by new knowledge, skills, and attitudes, or a combination of each. I will provide a varied climate of learning opportunities designed to meet your unique learning styles. You will hear me lecture using a variety of visual aids and I will expect you to talk, show, and do work on your own. You will discuss, read, take notes, keep journals, fill in work books, take tests, learn by doing service, and work on projects. I will teach from an assumption based on an educational development scheme developed by Baxter Magolda in 1992 suggesting that most freshmen are absolute learners (68%) believing that right and wrong answers exist for all areas of knowledge while

juniors (83%) and seniors (80%) were in the stage of transitional knowing where certain and uncertain categories of knowledge can be separated. One year after graduation, 57% of the former students in the study had reached the stage of independent knowing when knowledge is open to many interpretations. Students use more individual ways to deal with knowledge. Twelve percent, were at the stage of contextual knowing where individuals create their own perspectives by judging evidence in a context. We will teach and learn from each of these stages, but to be leaders, you will eventually have to use your own judgement and make decisions within the context of the moment using the bags of knowledge, skills, and attitudes that you have accumulated. Good public relations reflects thinking that is thoughtful, knowledgeable, diverse, adaptable, and clear.

Attendance and Tardiness Policies:

I know that students can learn on their own without instructors being present exemplified by the 4 correspondence courses which I developed and teach via CSU Continuing Education. Students read, view video tapes, work on assignments, and take tests designed to help them learn on their own and to integrate what they learned into real life situations. For this course however, class time is useful for discussions, to add new information not covered in readings, to make announcements, to clarify assignments, and perhaps most importantly to provide an atmosphere of learning amongst your peers which motivates and stimulates you to learn synergistically. Class participation (quantity and quality) is part of the grading system; if you are not in attendance you cannot be evaluated. Being late is rude and disruptive to students and to me. I will never expect to answer questions for students during office visits who miss classes. Absences and tardiness will not gain you favorable public relations internally in this class or externally in jobs or in life.

Class Atmosphere:

Discussions and activities in class used to develop your own public relations styles will expose you to risks and criticism from peers and instructors. I want you to take those risks. It is the your responsibility to have honest and supportable inputs. It is all of our responsibility to respect each other and understand diverse views and actions. There can be no guarantee that all opinions and actions will be accepted however. Respect and kindness are important principles of public relations. Disruptive behavior is grounds for dismissal.

Texts:

1. Public Relations and Communications for Natural Resource Managers. 1986. Fazio, James R. and Douglas L. Gilbert. Kendall/Hunt.

This is a classic text used as the standard. It provides the foundation for students of natural resources to see how communications and people management fits into all of their jobs as managers of land, vegetation, and wildlife.

2. Environmental Leadership developing effective skills and styles. 1993. Berry, Joyce K. And John C. Gordon (eds.). Island Press. 286pp.

Authors from various private and public fields of natural resources provide essays with useful thoughts about attributes of leaders, how leadership fits into organizations, and suggestions for developing your personal leadership qualities.

3. The Communications Handbook 2nd edition. Patricia Calvert. Maupin House.
A source book for working on most communications needs. This guide will be a useful reference for specific tools used to improve your communications tasks.

4. Group Decision-making Techniques for Natural Resource Management Applications. 1992. Beth A. K. Coughlan and Carl L. Armour. USDI Fish and Wildlife Service. 55pp.
Working with groups of persons for internal public relations or with external publics requires use of facilitation and evaluation techniques. This publication contains numerous methods that are used for conducting meetings.

Course Outline and Reading Assignments (more planning, detail, and specific scheduling):

Dates	Topics	Text # and Pages
	Introduction, organization, definitions, principles, assignments, and history of public relations in natural resources	
	Perspectives of natural resources agency personnel about public relations	
	Leadership needs, traits, and role of professionals	
	Principles of how people learn and act: considerations for leadership, communications, group processes, social action, sequence of adoption, rejection and diffusion, and related public relations	
	Internal Publics: who they are and the need for good communications and relations within organizations first	
	External Publics: who they are, what they say, and how to work with them	
	Communications: planning, organization, writing, facilitation roles and procedures, meetings, conferences, internal media, radio, TV, newspapers, magazines, public appearances, Extension education and field demonstrations	

Visual aids preparation and use

Public involvement and citizen participation

Conflict resolution

The final plan and steps in between: planning today
for the future

Recitation Sessions: (schedule and describe)

Reflections about service learning activities (using various meeting formats and information sharing techniques)

Group processes (with changing meeting formats and techniques over time) will be used toward problem solving

Planning discussions for final project (small group interations)

Help sessions generally

Grading Policy: (review and describe)

Journal (summary of notes, service learning reflections, and group experiences	10 %
Workbook answering questions about concepts and using techniques of communications from readings and classroom activities	50 %
Exam #1	10 %
Exam #2	10 %
Final: Public Relations Plan for real or hypothetical project	<u>20 %</u>
	100 %

— handout questions to answer —

① seminar, week before

② class, 'surprise' (take attendance)
pop quiz

— small group discussion — ~~teacher~~ — questions —
25 min question —

③ — Each student turn in question (5) work out cond.

list/copies ³⁰⁰ ~~signif. paper~~ (brown bag)
presuit = discussion book

C.B. > Co. genetics

go over with
read reprint

Make copies of these
papers (1 copy each) - can be
back/back (some already are) -
for Fall seminar FW 561AV

DK

1.11

Names: _____, _____, _____

Instructions: Please read the information for each situation and answer that question before looking at the next situation/info./question.

(1) You are a Peace Corps Volunteer helping villagers in Tropicana to raise tilapia in small ponds. Tilapia are prolific omnivores, eating invertebrates, plankton and aquatic plants; spawn at 1+ yrs; and seldom exceed 400 g (1 lb).

Q1: The goal for this tilapia fishery should be: 1st ANS:____ (ANS:____)
 (A) Food for the villagers,
 (B) Sport fishing to attract tourist income for the villagers, or
 (C) Sell the fish in Swelter City, 90 km away, for village income.

-- [STOP] -----

(2) The village has no electricity nor refrigeration; fish would spoil during the half-day trip on the primitive road to Swelter City. No tourist would make the trip to catch hand-sized fish in a "mud-hole pond". Villagers eat a protein-deficient, subsistence diet. (Reconsider answer to Q1, above?)
 Simple earthen dams, hand-built in small drainages by villagers, create small ponds that are stocked with tilapia, easily caught in a nearby river. Tilapia grow rapidly and reproduce year-round in the stable, optimum habitat. In 2-3 years, every pond is crowded with small tilapia, none exceeding 200 g.

Q2: You should advise the villagers to: 1st ANS:____ (ANS:____)
 (A) Stock fewer fish in each pond,
 (B) Harvest fish whenever they reach "hand size" (0.2 kg) in a pond, or
 (C) Introduce a predator fish to thin tilapia so some grow much larger.

-- [STOP] -----

(3) Stocking fewer fish may delay the goal of maximum biomass for harvest. Villagers don't want to share their tilapia crop, not even with an edible competitor; that would "lose" 70% of a pond's productivity during transfer to a higher level, from tilapia to predator. Villagers eat chopped fish in soups, stews and with rice; small fish by standards of a western angler are as useful as "trophy-tilapia" in Tropicana. (Reconsider answer Q2, above?)

Q3: You'll advise villagers to harvest tilapia by: 1st ANS:____ (ANS:____)
 (A) Use seine nets to capture fish as needed,
 (B) Use hook and line to provide some sport as well as food, or
 (C) Break the dam, drain the pond and pick up all the fish. Later, restore the dam and restock the pond for the next fish crop.

-- [STOP] -----

(4) Cooperative labor is needed to build ponds, and all villagers can share in the harvest of a pond. Similar to a fallow crop field, resting a pond can break disease and pest life cycles and restore fertility. Seines are useful for interim harvest, but they are expensive and difficult to maintain. The villagers have no concept of sport fishing. (Reconsider answer Q3, above?)

Q4: In the future, you would most like to see your villagers: ANS:____
 (A) Maintain their present level of simple, effective management,
 (B) Train people in adjacent villages to raise tilapia for food,
 (C) Get government assistance to develop improved transportation and refrigeration ("Mosquito Coast"?) thereby enabling villagers to market fish in Swelter City and pursue a higher standard of living.

SUMMARY: A FOOD-FISH POND IS SIMILAR TO A CORNFIELD (berry patch? orchard?)

10/19/95

Gee

What Is a Species?

BY STEPHEN JAY GOULD

I HAD VISITED EVERY STATE BUT IDAHO. A FEW MONTHS AGO, I finally got my opportunity to complete the roster of 50 by driving east from Spokane, Washington, into western Idaho. As I crossed the state line, I made the same feeble attempt at humor that so many of us try in similar situations: "Gee, it doesn't look a bit different from easternmost Washington." ■ We make such comments because we

feel the discomfort of discord between our mental needs and the world's reality. Much of nature (including terrestrial real estate) is continuous, but both our mental and political structures require divisions and categories. We need to break large and continuous items into manageable units.

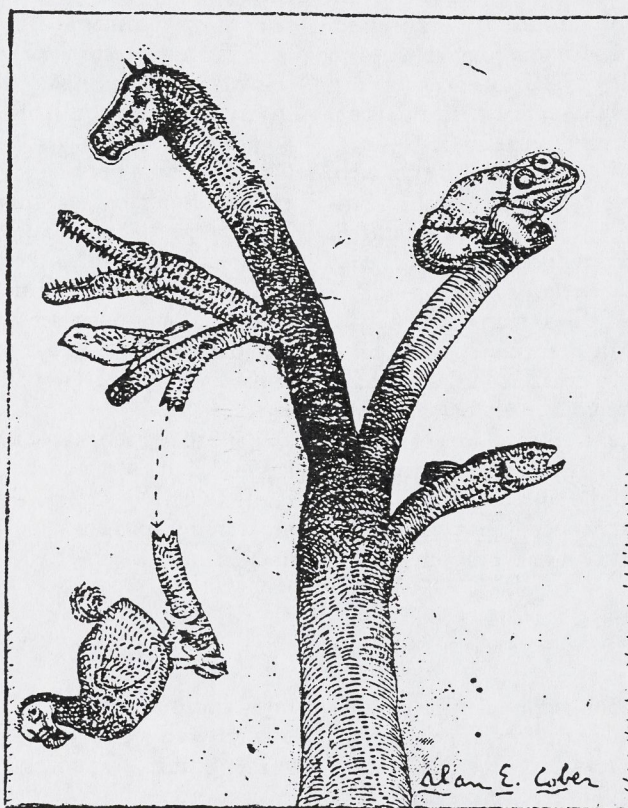
Many people feel the same way about species as I do about Idaho—but this feeling is wrong. Many people suppose that species must be arbitrary divisions of an evolutionary continuum in the same way that state boundaries are conventional divisions of unbroken land. Moreover, this is not merely an abstract issue of scientific theory but a pressing concern of political reality. The Endangered Species Act, for example, sets policy (with substantial teeth) for the preservation of species. But if species are only arbitrary divisions in nature's continuity, then what are we trying to preserve and how shall we define it? I write this article to argue that such a reading of evolutionary theory is wrong and that species are almost always objective entities in nature.

Let us start with something uncontroversial: the bugs in your backyard. If you go out to make a complete collection of all the kinds of insects living in this small discrete space, you will col-

lect easily definable "packages," not intergrading continua. You might find a kind of bee, three kinds of ants, a butterfly or two, several beetles, and a cicada. You have simply validated the commonsense notion known to all: in any small space during any given mo-

in some spaces

ment, the animals we see belong to separate and definable groups—and we call these groups species. In the eighteenth century this commonsense observation was translated, improperly as we now know, into the creationist taxonomy of Linnaeus. The great Swedish naturalist regarded species as God's created entities, and he gathered them together into genera, genera into orders, and orders into classes, to form the taxonomic hierarchy that we all learned in high school (several more categories, families and phyla, for example, have been added since Linnaeus's time). The creationist version reached its apogee in the writings of America's greatest nineteenth-century naturalist (and last truly scientific creationist), Louis Agassiz. Agassiz argued that species are incarnations of separate ideas in God's mind, and that higher categories (genera, orders, and so forth) are therefore maps of the interrelationships among divine thoughts. Therefore, taxonomy is the most important of all sciences because it gives us direct insight



It's becoming a vital political issue. How should we define what we are trying to preserve?

into the structure of God's mind.

Darwin changed this reverie forever by proving that species are related by the physical connection of genealogical descent. But this immensely satisfying resolution for the great puzzle of nature's order engendered a subsidiary problem that Darwin never fully resolved: If all life is interconnected as a genealogical continuum, then what reality can species have? Are they not just arbitrary divisions

*

of evolving lineages? And if so, how can the bugs in my backyard be ordered in separate units? In fact, the two greatest evolutionists of the nineteenth century, Lamarck and Darwin, both questioned the reality of species on the basis of their evolutionary convictions. Lamarck wrote, "In vain do naturalists consume their time in describing new species"; while Darwin lamented: "we

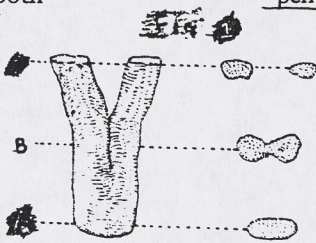
shall have to treat species as . . . merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species" (from the *Origin of Species*).

But when we examine the technical writings of both Lamarck and Darwin, our sense of paradox is heightened. Darwin produced four long volumes on the taxonomy of barnacles, using conventional species for his divisions. Lamarck spent seven years (1815-1822) publishing his generation's standard, multivolume compendium on the diversity of animal life—*Histoire naturelle des animaux sans vertèbres*, or *Natural History of Invertebrate Animals*—all divided into species, many of which he named for the first time himself. How can these two great evolutionists have denied a concept in theory and then used it so centrally and extensively in practice? To ask the question more generally: If the species is still a useful and necessary concept, how can we define and justify it as evolutionists?

Figure 2. The time of ambiguity at the origin of the new species (B) from a parental line (A) is relatively short.

The solution to this question requires a preamble and two steps. For the preamble, let us acknowledge that the conceptual problem arises when we extend the "bugs in my backyard" example into time and space. A momentary slice of any continuum looks tolerably discrete; a slice of salami or a cross section of a tree trunk freezes a complexly changing structure into an apparently stable entity. Modern horses are discrete and separate from all other existing species, but how can we call the horse (*Equus caballus*) a real and definable entity if we can trace an unbroken genealogical series back through

time to a dog-size creature with several toes on each foot? Where did this "dawn horse," or "eohippus," stop and the next stage begin; at what moment did the penultimate stage become *Equus caballus*? I now come to the two steps of an answer.



First, if each evolu-

Figure 1. Species go through a period of ambiguity while a new branch is forming (B), and then become clearly separate (C).

tionary line were like a long salami, then species would not be real and definable in time and space. But in almost all cases large-scale evolution is a story of branching, not of transformation in a single line—bushes, not ladders, in my usual formulation. A branch on a bush is an objective division. One species rarely turns into another by total transformation over its entire geographic range. Rather, a small population becomes geographically isolated from the rest of the species—and this fragment changes to become a new species while the bulk of the parental population does not alter. "Dawn horse" is a misnomer because rhinoceroses evolved from the same parental lineage. The lineage split at an objective branching point into two lines that became (after further events of splitting) the great modern groups of horses (eight species, including asses and zebras) and rhinos (a sadly depleted group of formerly successful species).

Failure to recognize that evolution is a bush and not a ladder leads to one of the most common vernacular misconcep-



tions about human biology. People often challenge me: "If humans evolved from apes, why are apes still around?" To anyone who understands the principle of bushes, there simply is no problem: the human lineage emerged as a branch, while the rest of the trunk continued as apes (and branched several more times to yield modern chimps, gorillas, and so on). But if you think that evolution is a ladder or a salami, then an emergence of humans from apes should mean the elimination of apes by transformation.

how does he know this?

Second, you might grasp the principle of bushes and branching but still say, Yes, the ultimate products of a branch become objectively separate, but early on while the branch is forming, no clear division can be made, and the precursor of the two species that will emerge blend indefinitely (figure 1). And if ev-

olution is gradual and continuous, and most of a species' duration is spent in the state of incipient formation, then species will not be objectively definable during most of their geologic lifetimes.

Fair enough as an argument, but the premise is wrong. New species do (and must) have this period of initial ambiguity. But species emerge relatively quickly, compared with their period of later stability, and then live for long periods—often millions of years—with minimal change (figure 2). Now, suppose that on average (and this is probably a fair estimate), species spend 10 percent of their geologic lifetimes in this initial state of imperfect separation. Then, on average, about one species in a hundred will encounter problems in definition, while the other 99 will be discrete and objectively separate—cross-sections of branches showing no confluence with others (C, figure 1). Thus the principle of bushes, and the speed of branching, resolve the supposed paradox: continuous evolution can and does yield a world in which the vast majority of species are separate from all others and clearly definable at any moment in time. Species are nature's objective packages.

I have given a historical definition of species—as unique and separate branches on nature's bush. We also need a functional definition, if only because historical evidence (in the form of a complete fossil record) is usually unavailable. The standard criterion, in use at least since the day of the great French naturalist Georges Cuvier (a contemporary of Linnaeus), invokes the capacity for interbreeding. Members of a species can breed with others in the same species but not with individuals belonging to different species.

This functional criterion is a consequence of the historical definition: distinct

separateness of a branch emerges only with the attainment of sufficient evolutionary distance to preclude interbreeding, for otherwise the branch is not an irrevocably separate entity and can amalgamate with the parental population. Exceptions exist, but the reproductive criterion generally works well and gives rise to the standard one-liner for a textbook definition of a species: "a population of actually or potentially reproducing organisms sharing a common gene pool."

MUCH OF THE ORDINARY ACTIVITY of evolutionary biologists is devoted to learning whether or not the groups they study are separate species by this criterion of "reproductive isolation." Such separateness can be based on a variety of factors, collectively termed "isolating mechanisms": for example, genetic programs so different that an embryo cannot form even if egg and sperm unite; behaviors that lead members of one species to shun individuals from other populations; even something so mundane as breeding at different times of the year, or in different parts of the habitat—say, for example, on apple trees rather than on plum trees—so that contact can never take place. (We exclude simple geographic separation—living on different continents, for example—because an isolating mechanism must work when actively challenged by a potential for interbreeding through spatial contact. I do not belong to a separate species from my brethren in Brazil just because I have never been there. Similarly, reproductive isolation must be assessed by ordinary behavior in a state of nature. Some truly separate species can be induced to interbreed in zoos and laboratories. The fact that zoos can make tiglons—tiger-lion hybrids—does not challenge the separate status of the two populations as species in nature.)

Modern humans (species *Homo sapiens*) fit these criteria admirably. We are now spread all over the world in great numbers, but we began as a little twig in Africa (the historical criterion). We may look quite different from one another in a few superficially striking aspects of size, skin color, and hair form, but there is astonishingly little overall genetic difference among our so-called races. Above all (the functional criterion), we can all interbreed with one another (and do so with avidity, always, and all over the world), but not with any member of another species (movies about flies notwithstanding). We are often reminded, quite correctly, that we are very similar in overall genetic program to our nearest cousin, the chimpanzee—but no one would mistake a single individual of either species, and we do not hybridize (again, various science fictions notwithstanding).

I do not say that these criteria are free from exceptions; nature is nothing if not a domain of exceptions, where an example against any clean generality can always be found. Some distinct populations of plants, for example, can and frequently do interbreed with others that ought to be separate species by all other standards. (This is why the classification of certain groups—the rhododendrons, for example—is such a mess.) But the criteria work in the vast majority of cases, including humans. Species are not arbitrary units, constructed for human convenience, in dividing continua. Species are the real and objective items of nature's morphology. They are "out there" in the world as historically distinct and functionally separate populations "with their own historical role and tendency" (as the other textbook one-liner proclaims).

Species are unique in the Linnaean hierarchy as the only category with such objectivity. All higher units—genera, families, phyla, et cetera—are human conventions in the following important respect. The evolutionary tree itself is objective; the branches (species) emerge, grow, and form clusters by subsequent branching. The clusters (figure 3) are clearly discernible. But the status of the two populations as species in nature.)

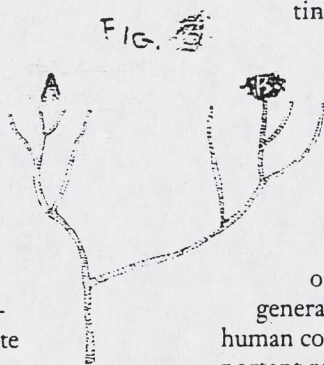


Figure 3. Branches are objective species. But the clusters they form (A and B) are classified partly according to human conventions.

we award to these so-called higher taxa (clusters of branches with a single root of common evolutionary ancestry) is partly a matter of human decision. Clusters A and B in the figure are groups of species with a common parent. Each

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branch in each cluster is an objective species. But what are the clusters themselves? Are they two genera or two families? Our decision on this question is partly a matter of human preference constrained by the rules of logic and the facts of nature. (For example, we cannot take one species from cluster A and one from cluster B and put them together as a single genus—for this would violate the rule that all members of a higher taxon must share a common ancestor without excluding other species that are more closely related to the common ancestor. We cannot put domestic cats and dogs in one family while classifying lions and wolves in another.)

The taxonomic hierarchy recognizes only one unit below species—the subspecies. Like higher taxa, subspecies are also partly objective but partly based on human decision. Subspecies are defined as distinctive subpopulations that live in a definite geographic subsection of the entire range of the species. I cannot, for example, pluck out all tall members of a species, or all red individuals, wherever they occur over the full geographic range, and establish them as subspecies. A subspecies must

be a distinct geographic subpopulation—not yet evolved far enough to become a separate species in its own right but different enough from other subpopulations (in terms of anatomy, genetic structure, physiology, or behavior) that a taxonomist chooses to memorialize the distinction with a name. Yet subspecies cannot be irrevocably unique natural populations (like full species) for two reasons: First, the decision to name them rests with human taxonomists, and isn't solely dictated by nature. Second, they are, by definition, still capable of interbreeding with other subpopulations of the species and are, therefore, impermanent and subject to reamalgamation.

THIS DIFFERENCE BETWEEN SPECIES and subspecies becomes important in practice because our Endangered Species Act currently mandates the protection of subspecies as well. I do not dispute the act's intention or its teeth, for many subspecies do manifest distinctly evolved properties of great value and wonder (even if these properties do not render them reproductively isolated from other populations of the species). We would not, after all, condone the genocide of all Caucasian human beings because members of other races would still exist; human races, if formally recognized at all, are subspecies based on our original geographic separations. But since subspecies do not have the same objective status as species (and since not all distinct local populations bear separate names), argument over what does and does not merit protection is inevitable. Most of the major ecological wrangles of recent years—rows over the Mount Graham red squirrel or the Northern spotted owl—involve subspecies, not species.

These taxonomic issues were once abstract, however important. They are now immediate and vital—and all educated people must understand them in the midst of our current crisis in biodiversity and extinction. I therefore close with two observations.

By grasping the objective status of species as real units in nature (and by understanding why they are not arbitrary divisions for human convenience), we may better comprehend the moral rationale for their preservation. You can expunge an arbitrary idea by rearranging your conceptual world. But when a species dies, an item of natural unique-

ness is gone forever. Each species is a remarkably complex product of evolution—a branch on a tree that is billions of years old. All the king's horses and men faced an easy problem compared with what we would encounter if we tried to reconstitute a lost species. Reassembling Humpty-Dumpty is just an exceedingly complex jigsaw puzzle, for the pieces lie at the base of the wall. There are no pieces left when the last dodo dies.

But all species eventually die in the fullness of geologic time, so why should we worry? In the words of Tennyson (who died exactly 100 years ago, so the fact is no secret):

From scarp'd cliff and quarried stone
She cries, "A thousand types are gone:
I care for nothing. All shall go."
(From *In Memoriam.*)

The argument is true, but the time scale is wrong for our ethical concerns. We live our lives within geologic instants, and we should make our moral decisions at this proper scale—not at the micro-moment of thoughtless exploitation for personal profit and public harm; but not at Earth's time scale of billions of years either (a grand irrelevancy for our species' potential tenure of thousands or, at most, a few million years).

We do not let children succumb to easily curable infections just because we know that all people must die eventually. Neither should we condone our current massive wipeout of species because all eventually become extinct. The mass extinctions of our geologic past may have cleared space and created new evolutionary opportunity—but it takes up to 10 million years to reestablish an interesting new world, and what can such an interval mean to us? Mass extinctions may have geologically distant benefits, but life in the midst of such an event is maximally unpleasant—and that, friends, is where we now reside, I fear.

Species are living, breathing items of nature. We lose a bit of our collective soul when we drive species (and their entire lineages with them), prematurely and in large numbers, to oblivion. Tennyson, paraphrasing Goethe, hoped that we could transcend such errors when he wrote, in the same poem:

I held it truth, with him who sings
To one clear harp in divers tones
That men may rise on stepping-stones
Of their dead selves to higher things. ☐

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Very interesting

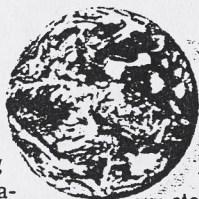
When Rigor Meets Reality

Ecological experiments have become quite good at isolating causes and effects. But there's a debate brewing over whether these results reveal anything about the natural world

When ecologist Andrew Blaustein linked vanishing amphibians to disappearing ozone last year, he made a splash in the popular press. Alarming field studies showing big drops in frog and salamander populations all over the world have had scientists scrambling for explanations. One controversial idea was that a thinner ozone layer—produced by global atmospheric changes—was the culprit. And Blaustein and his colleagues at Oregon State University had what looked like dramatic experimental data suggesting the amphibians are suffering from higher levels of ultraviolet radiation—a result of thinner ozone. The scientists had placed UV filters over some frog and salamander eggs and left other eggs uncovered. Survival rates in the uncovered eggs were markedly lower. And media attention suddenly became higher. *The New York Times* editorialized that “the Oregon team has provided suggestive evidence that wildlife is affected by the thinning ozone layer. Those vanishing frogs are telling us something.”

But some of Blaustein's colleagues aren't sure what that something is. “The study was very poorly grounded in long-term, quantitative field data,” says Joseph Bernardo, an ecologist at the University of Texas. The Oregon team failed to investigate whether UV levels had actually risen over the last 10 years—the period in which, according to Blaustein, amphibians have become more difficult to find—nor did they test other possible explanations for frog egg mortality, Bernardo says. For instance, a fungus known to be spreading through some frog populations in the Northwest could have killed enough of the eggs to provide a more mundane solution to the mystery of the attenuated amphibians.

Although Blaustein insists that “we've been doing natural history on these animals since 1979,” and “we studied UV because we can't find any other reason why they are dy-



Ecologists use many tactics in their attempts to understand how organisms relate to one another and to their surroundings. In the News section of this special issue on ecology, our lead story deals with one of those tactics, experimentation, and an emerging debate over how ecologists design these tests of the natural world. This is followed by stories on how small organisms have large influences, two hugely ambitious conservation plans, and the value of a biological survey in Hawaii.

Articles, beginning on page 324, start with an exploration of the value of large- and small-scale manipulations of ecosystems. Other topics discussed include strategies for assessing climate-driven effects on ecosystems, world biodiversity, the impact of human population growth, land restoration programs, public opinion on the environment, and the effects of environmental discontinuities and synergisms.

ing,” Bernardo is not impressed. The “inferential chain to what's going on in nature” is weak in this work, he says.

And there are too many such experiments being done, he and others charge. For 3 decades, ecologists have been replacing assumptions about natural systems with testable theories and rigorous statistical analyses, says William Resetarits, an ecologist for the Illinois Natural History Survey. While this effort has been key to the field's progress, Resetarits says it's gone a bit too far, and experiments often reduce nature to oversimplified caricatures that have little to do with the real world. “Experiments can do something for ecology that no other approach can do: establish cause and effect. But they don't tell you what questions to ask, or

whether you are testing your questions appropriately,” Resetarits says.

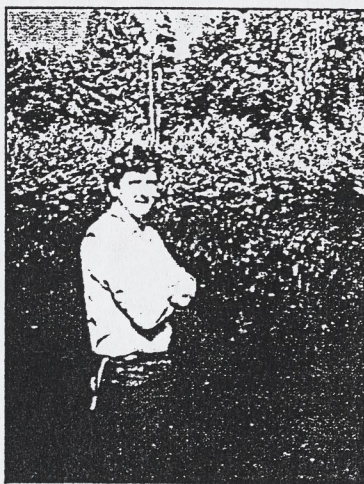
Now, says Bernardo, “there is a little bit of a backlash from people like me, younger folks

who are fed up with that kind of artificiality.” And at the annual meeting of the American Society of Zoologists in St. Louis in January, in a 2-day symposium called “The State of Experimental Ecology,” these new experimentalists held an organizational rally of sorts. They argued that only by combining careful experimental design with long periods spent observing ecosystems and their inhabitants—what field researchers call “muddy-boots biology”—can ecologists come up with truly meaningful results. “We wanted to provide a framework for the next paradigm in experimental ecology,” says Resetarits.

Ecology's evolution

This budding revisionist movement is a reaction to what, 30 years ago, was a revisionist trend of its own: controlled lab and field manipulations. Now comprising at least 60% of the studies published in ecology's three major journals, according to a 1994 survey, such research was rare throughout most of the discipline's history, says Robert Holt, a community ecologist at the University of Kansas Museum of Natural History. “People would observe patterns in nature consistent with their theories, then conclude that this proved the theories right,” Holt says. Beginning in the 1960s, however, “ecology went through a very critical phase where it was realized that in order to actually nail down that a particular process is taking place, you have to go out and kick the system.”

Trailblazing investigations published by ecologists Joseph Connell in 1961 and Robert Paine in 1966 did much to convince their colleagues of the power of experiment. By removing, enclosing, or transplanting small populations of the barnacle *Balanus balanoides* along the intertidal zone of the rocky Scottish coastline, Connell proved that the distribution of another barnacle species, *Chthamalus stellatus*, was regulated mainly by competition with *Balanus*. Paine, by contrast, was able to show that the removal of a “keystone” carnivore, the starfish *Pisaster ochraceus*, from patches of Washington shoreline allowed its favorite prey, the mussel *Mytilus californianus*, to edge out most other local invertebrates, drastically altering local species diversity (see p. 316). Although ecologists had long suspected the importance of mechanisms like competition and predation in shaping species distribution, never before had these

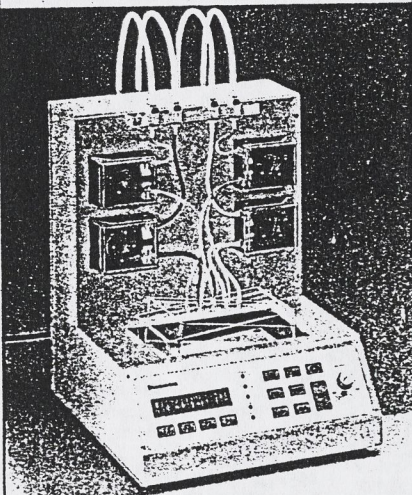


UNIVERSITY OF BRITISH COLUMBIA

Natural design? Experiments to test evolutionary theories, such as ecologist Dolph Schluter's artificial fish pond (above), have some wondering if the tests are too artificial.

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The 1994 paper by Blaustein *et al.* did include the statement that "There is no known single cause for the amphibian declines, but their widespread distribution suggests involvement of global agents—increased UV-B radiation, for example." David Reznick, when interviewed by me, noted several alternatives to the view that a global UV increase was responsible. It was not clear in our discussion that his statement, "These global patterns don't lend themselves to a single easy explanation," was derived from Blaustein's own writings. I regret the error, and apologize for the misunderstanding.—Wade Roush

Dioxin and Advisory Board

We take strong exception to Richard Stone's summary of the U.S. Environmental Protection Agency (EPA) Science Advisory Board (SAB) meeting and the accompanying headline, ("Panel slams EPA's dioxin analysis," 26 May, p. 1124), as members of the panel in question. At the conclusion of the meeting, one of us (D.O.) characterized the panel's recommendations as "in no way a repudiation," but rather a judgment that two of the nine chapters

(parts of chapter eight and chapter nine the health assessment document need "clarification and ripening." No one of the 39-member panel disagreed publicly with that judgment, and there were several dissenting opinions on the record.

As noted by Stone, we did commend the agency for considering dioxins and related compounds as a class, and many of us were highly supportive of the work reflected in the first seven chapters of the health assessment document. In particular, we do agree with Stone's assertion that "Our board members say EPA also ignored the fact that fail to support its conclusion that dioxin is harmful to human health." The board member Stone cites in this context, Michael Gough, a microbial geneticist at the Office of Technology Assessment of the U.S. Congress, and we disagree with him and think he is not representative of the group. Moreover, his long-held views on this subject are well known.

Finally, we point out that the one point on the agenda in the 2-day meeting from an organization not representing the industry also commended the EPA for its work to date. We think it is likely that when the EPA redrafts the health assessment document for the molecule TCDF, it will maintain the scientific core of the

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ral world, but to attack Blaustein for not having followed this principle is absurd. The declines in amphibian populations that have recently been observed in many parts of the world are disturbing to many biologists, and increased UV radiation resulting from ozone depletion is an obvious candidate as a cause of at least some of these declines. Blaustein's experiments were a simple, well-designed, and carefully carried out test of this hypothesis, and they yielded strong and persuasive results in its support; they should be judged on their merits as experiments, and it is for the biological community to evaluate their wider significance. They do not solve the mystery of the declines, and Blaustein has never claimed that they do; they do, however, open up important new areas of investigation. Blaustein's decision to study the effects of UV radiation on amphibian eggs may have been a largely intuitive one, but where would science be if researchers ignored their intuition?

Tim Halliday*

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*Director, Declining Amphibian Populations Task Force,
Species Survival Commission, World Conservation Union

Who would have anticipated 10 years ago that collecting long-term data on UV might be important now? The point of Blaustein's research is that UV exposure *does* affect amphibian egg survival and that changes in UV radiation *have the potential* to contribute to declines in some populations.

Most ecologists recognize that the two approaches to studying ecology are not in opposition, but are complementary. Long-term field experiments of the type advocated by Bernardo and Resetarits have the advantage of retaining some of the complexity of natural systems. Disadvantages include (i) a lack of control of factors that may affect the population under study; (ii) little replication of results; and, in many cases, (iii) little power to prove or disprove inferences about causality. Laboratory or controlled field experiments have the advantage of larger numbers of replicate studies, greater statistical power, and more power to reveal causality. The primary sacrifice made in the latter approach is the elimination of possibly relevant factors.

I agree with Bernardo and Resetarits on the general point that it is critical to articulate biological hypotheses and to collect precise experimental or observational data that distinguish among alternative causes,

although I suspect that most ecologists would agree that this should be standard operating procedure.

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Response: Some of the experiments discussed in my news article—studies by Andrew Blaustein and colleagues and by Dolph Schluter—had generated discussion and debate among ecologists well before I wrote about them. The article reflected that debate. It also allowed the scientists to refute the critiques; for instance, Blaustein's initial point in his letter, that he had 15 years of data on his study population, is also made by him in the news article.

The criticisms of Blaustein's work conveyed in the news story focused on a specific paper [A. R. Blaustein *et al.*, *Proc. Nat. Acad. Sci. U.S.A.* 91, 1791 (1994)]. That paper did not include the qualification that a pathogenic fungus might be another source of egg mortality, nor did it contain any reference to the 1991 paper in *Biological Conservation* that Blaustein cites in his letter above. Nevertheless, the news article should have acknowledged that Blaustein himself had raised the fungal hypothesis elsewhere.

Yeah right, where's the rest of it?

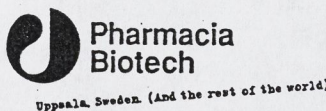
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is mistakenly attributed to David Reznick, apparently because Reznick paraphrased one of my papers (5) on amphibian declines to Roush (6). It is unfortunate that Bernardo and Resetarits appear not to have read our papers carefully and have criticized us for what some of the popular press has said about our work.

Instead of being poorly grounded in long-term field data, as Bernardo alleges, we believe that our work demonstrates how long-term observations point the direction toward relevant, realistic experiments.

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6. D. Reznick, personal communication.

I wish to express my concern over the quote attributed to me in the article by Roush. The quote (which gives the incorrect im-

pression that I am critical of Blaustein's work) was actually derived from Blaustein's own writings (1). Blaustein is at the forefront of the worldwide investigations into all the potential causes of amphibian decline, including UV radiation. In view of his clear statement of likely multiple causes of the amphibian decline, I interpreted Blaustein's experiment as a test of the plausibility of UV radiation as one of those possible causes. The fact that the experiment was performed without the benefit of prior long-term data indicating an increase in UV radiation should not be a concern because, in a rapidly changing world, it is impossible to foresee what the important changes might be. Rather than criticize the work for not being motivated by such data, I instead view it as contributing to the motivation for collecting such data in the future.

More generally, it is ironic that Roush featured criticism of two such fine papers. Both Dolph Schluter (2) and Blaustein were working on systems for which there are abundant ecological data. Both took these prior observations into account when designing and executing their experiments. Both studies represent novel approaches to a problem and produced interesting results that should be of interest to a general, critical audience such as *Science's* reader-

ship. Both studies incorporated complexities that merit some open debate, so it is not unreasonable that one of them has been discussed in *Science's* Technical Comments section (3); however, the tone of Roush's news article in no way represents the subtleties of this kind of work or the costs and benefits of alternative experimental approaches to a problem, such as the role of density or the use of hybrids in Schluter's work. In my opinion, Schluter made the right decisions. For all of these reasons, I feel that Roush's article presents an inaccurate, destructive view of the scientific process.

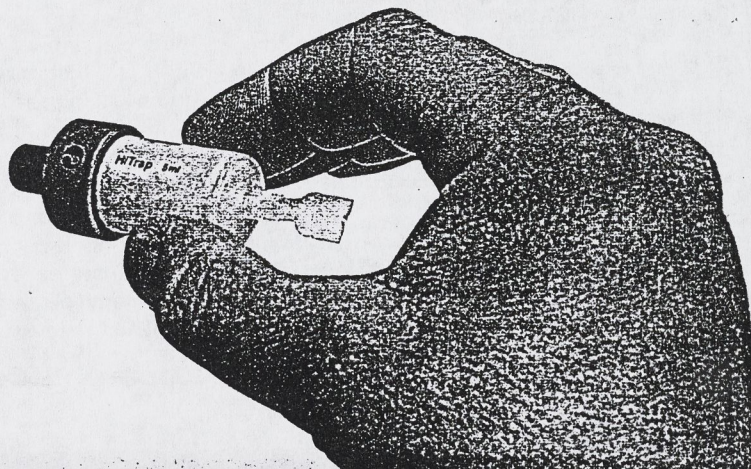
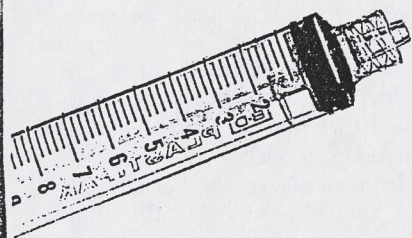
David Reznick
Department of Biology,
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Riverside, CA 92521, USA

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I am appalled and dismayed by the views attributed to Bernardo and Resetarits in the article by Roush. Experiments in ecology, as in all branches of biology, must be well grounded in an understanding of the natu-

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LETTERS

Western toad at high noon?

Field experiments show that ultraviolet (UV) light can damage amphibian eggs. Field observations show a decline in many populations of frogs and toads, such as this threatened toad *Bufo boreas*.

But to what degree is solar radiation a factor in the decline? The latter, more complex, question is of a global scale. Many letters praising the UV light experiments of Andrew Blaustein and his colleagues were received in response to the 21 July special section "Frontiers in Biology: Ecology." How the media, including *Science*, report on such experimental findings, and what kind of studies should be done next, are more problematic for these writers.



WILLIAM LEONARD

Ecological Research

Our recent work showing that ultraviolet (UV) radiation can contribute to amphibian egg mortality is criticized by Joseph Bernardo and William Resetarits in a news article for, as Bernardo says, being "very poorly grounded in long-term, quantitative field data" ("When rigor meets reality," by Wade Roush, in a special section: *Frontiers in Biology: Ecology*; 21 July, p. 313). These criticisms are unfounded. We have collected and published data (including yearly egg mortality estimates) on the ecology of northwestern amphibians for 15 years. Moreover, we have about 40 years of background data on northwestern amphibians from Robert Storm and his numerous students.

With this natural history basis, we became concerned in the mid-1980s when we observed unprecedented mortality of amphibian eggs in the Cascade Range. After systematically analyzing pond water for pollutants, acidification, and many other factors, we found only one factor associated with egg mortality—a pathogenic fungus (1). Bernardo ignores relevant issues when he presents the fungus as an alternative to UV for high egg mortality without acknowledging that I proposed this explanation (1). We also noted that dying eggs were laid in shallow, open water, an observation consistent with the view that mortality is related to UV radiation. Thus, after 8 years of observing dying eggs, conducting preliminary experiments, and after ruling out many potential mortality factors, we designed field experiments to test the hy-

pothesis that amphibian embryos are sensitive to ambient UV-B radiation.

Eggs of several species were placed in enclosures in a randomized block design at natural oviposition sites. This design allows experimental and control treatments to be conducted simultaneously, side by side, after randomly assigning enclosures to positions along the shore. Each block had three treatments (not just filtered and unfiltered treatments, as stated by Roush): enclosures (i) open to natural sunlight including UV-B, (ii) covered with a UV-B blocking filter, or (iii) covered with a filter that transmitted UV-B (a control for placing a filter over eggs). Each block was replicated four times. To ensure that our results were not unique to a specific site, each species was tested at two sites. Experiments were conducted in both 1993 and 1994. Our published papers (1, 2), those in press, and those in review suggest that in certain species both UV radiation and the fungus contribute to egg mortality, and that is all we have stated in our papers. We do not know how continued egg mortality will affect amphibians at the population level. But we do know that our experiments had the potential to invalidate the view that UV radiation contributes to egg mortality. We have not claimed that UV radiation is the single worldwide cause of amphibian population declines, as is implied in the news article. We have repeatedly stated that habitat destruction is the main cause for the declines (3–5); that they do not lend themselves to single explanations is a point that we have made in several papers (3–5). However, this statement



lenged them in a recent Technical Comment (*Science*, 19 May, p. 1065). The experiment's fatal flaw, they say, was that Schluter failed to control for the possibility that plain overcrowding in the treated halves of the two ponds—rather than the specific presence of the top-feeders—gave the bottom-feeding generalists a growth advantage over their competitors. One simple way to establish such a control, says Resetarits, would have been to add an equal number of generalists to the untreated halves of the ponds, thus keeping the sticklebacks' densities in the two halves equal.

In addition, the critics point out, Schluter artificially increased the frequency of extreme characteristics among the generalist sticklebacks by using hybrid fish with genes from both top- and bottom-feeding species. As a result the generalists were swimming in a far richer gene pool, so to speak, than could be drawn on by individuals in a natural lake.

Schluter responds that extreme phenotypes are so rare in nature that his experiment could not have been done within a reasonable research budget without priming the genetic pump. "If you wanted to [test character displacement] with purely natural variation in those same traits, you would need a much larger sample size and a greater number of ponds," says Schluter. "It's doable in principle, but in practice it would be very daunting."

He acknowledges that his experiment did not strictly rule out density as a contributor to morphological changes. He says he chose the design described in the *Science* paper over the alternative Resetarits outlines because the alternative design would not have yielded any information about selection pressures.

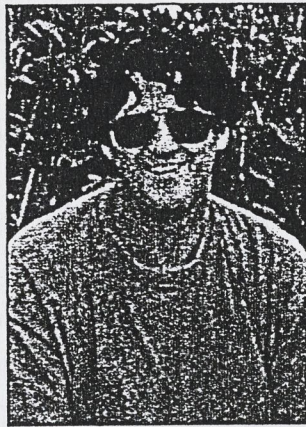
In this, Schluter has allies. "I strongly respect the call for ecological realism in the design and conduct of field experiments. But Bernardo and his colleagues have argued the hard line a little too strongly," says Peter Grant, an evolutionary ecologist at Princeton University. "Not only does the stickleback experiment demonstrate a phenotype-specific effect of a competitor on individual growth rates of another—in a manner expected from the hypothesis of character displacement—but it is solidly grounded in 30 years' worth of knowledge of the animals in nature."

Bernardo, however, says the gospel of good experimental design can never be reinforced too strongly, as "there are still plenty of young [ecologists] doing mindless, stupid experiments." Too many researchers, Bernardo and Resetarits say, fail to identify explicitly the biological questions they are trying to address or to translate these ques-

tions into a set of precise, statistical tests that unambiguously distinguish between alternative hypotheses. In addition, they say, too many ecologists let their interpretations stray beyond the theory being tested or the natural system under investigation.

Such experiments carry risks that go beyond ecology, says Dunham. "When you overgeneralize your results—particularly when there is a need for applied ecological principles in conservation and biodiversity protection—then you run the risk of having bad science accepted by resource managers, with potentially disastrous results," he says.

The remedy, says Bernardo, is to "allow more complexity and multiple causality to enter into our designs." The revisionists point to ongoing field studies by James H. Brown, an ecologist at the University of New Mexico, as an example of experimental ecology done right. On two dozen quarter-hectare plots in the Chihuahuan desert of southeastern Arizona (a hectare is 2.47 acres), Brown and colleagues have spent the last 18 years manipulating one factor after another in an attempt to explain predator-prey relationships and species composition among seed-eating rodents, ants, and seed-producing plants (*Science*, 10 February, p. 880). At times Brown has fenced out certain ant spe-



Hard questions. Ecologists Joseph Bernardo (left) and William Resetarits (right) have challenged some of their colleagues' methods. Says Bernardo: "There are still plenty of young [ecologists] doing mindless, stupid experiments."

cies to study the effects of decreased competition; at other times he has fenced out certain rodent species to study resulting changes in grass cover and cascading effects on other species. Says Bernardo: "The experiments have been tedious, costly, and difficult, but very realistic."

The limits of description

Many researchers believe, however, that Bernardo and his fellow critics are setting unrealistic standards. They argue that complex problems like the ecological effects of global environmental change will never be untangled without help from the most reductionist of

experiments: computer simulations and lab-based ecosystems. John Lawton, an ecologist at the U.K.'s Imperial College, has used a terrarium-like enclosure called the Ecotron to measure plant productivity and carbon dioxide uptake as functions of species diversity. He advocates such "controlled environment facilities" as "halfway houses between the simplicity of mathematical models and the full complexity of the field" (see p. 316 and Article by Lawton on p. 328). Adds Rutgers' Morin, "There are some ecologists who put down [lab experiments] because we have abstracted things so much. Our response is that if you don't start with a simple system, you won't understand what's going on anyway."

Other ecologists say critics like Dunham, Bernardo, and Resetarits sometimes make too much of the occasional flaws in published experiments. "It's possible to do anything badly," says Nelson Hairston, an emeritus ecologist at the University of North Carolina, Chapel Hill, and author of the 1989 volume *Ecological Experiments*.

But many ecologists not in the thick of the debate, such as Minnesota's Tilman, say participants in the St. Louis symposium are prescribing a necessary antidote to the excesses of experimentalism. Continuing generational change will reinforce this message, he believes. "Twenty or 30 years ago, most ecologists were either theorists or experimentalists or natural historians. But as younger generations are drawn in, an increasing number of individuals are acquiring skills in all three disciplines." Tilman says this has fostered "a trend in the whole field ... toward the realization that ecology will advance most rapidly through a balanced combination."

That advance won't be easy, notes Gary Polis, a community ecologist at Vanderbilt University in Tennessee. Understanding the natural variability in conditions at most field sites and detecting subtle, infrequent, or hidden ecological processes takes studies much longer than the usual timescale of ecological experiments. Restoring natural history to ecological experiments will also mean broadening their spatial scales, Polis says, because many natural processes like mobility, dispersal, and species interactions can create patterns visible only from a macroperspective.

All that will take money, and although funding is scarcer than ever, many ecologists think it's worth the effort to try. "I think we're at a very early, embryological stage in the ontogeny of ecology," says Polis. "There are lots of really neat questions out there for the picking. It's just a question of recognizing them." And asking them in the proper manner.

—Wade Roush

forces been so explicitly demonstrated.

These and similar experiments spawned "an incredible maturation and intellectual momentum" in ecology, says David Tilman, director of the University of Minnesota's Cedar Creek Long Term Ecological Research area. "In the intervening 3 decades, ecology has gone from not even considering the possibility of being able to predict patterns in nature to having an understanding of some broad general principles," Tilman says. Contemporary ecologists conduct experimental manipulations in nearly every accessible habitat and on every practical scale, from Rutgers University ecologist Peter Morin's laboratory investigations of food webs among bottled algae and bacteria to Tilman's own studies of changing species diversity within dozens of square-meter plots, each seeded with up to 54 local plant species, on the Minnesota prairie.

And ecology journals, full of differential equations and multiple regression analyses, are growing more and more difficult to distinguish from their counterparts in "hard" sciences like geophysics or applied mathematics. "The push toward experimentation beginning in the 1960s was the result of 'physics envy,'" says Resetarits. "We wanted to be a hard science."

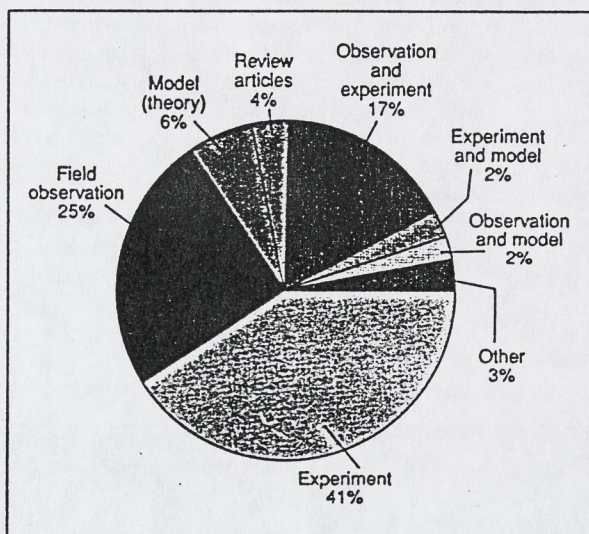
A disconnect with nature

But this effort to transform ecology into an experimental science has had a downside, say critics. "Now that we've infused people with the need for rigor, we've perhaps drawn them a bit too far from the roots of ecology," says Resetarits. Authors can have difficulty persuading journal editors to include tables of field observations germane to their experiments, he says. And unlike Connell's and Paine's pioneering field experiments, which were based on prolonged observation of local population dynamics, Bernardo argues that many experiments conducted by today's ecologists evidence no such intimacy with nature. "The problem is that ecologists threw out the proverbial baby with the bath water," Holt says.

One instance of this estrangement, Bernardo and other critics say, was the Oregon team's work on amphibians and UV radiation. Blaustein and co-workers found that frog and salamander eggs inside UV-protected enclosures had a much greater chance of developing into tadpoles than those in unfiltered enclosures. They also discovered that eggs from a frog species with high natural levels of photolyase, an enzyme that repairs UV damage to DNA, survived better in all the enclosures than did those with lower photolyase levels. Human activity, they concluded, may be depleting Earth's ozone layer faster than many amphibian spe-

cies can evolve new defense mechanisms against UV radiation [*Proceedings of the National Academy of Sciences* 91, 1791 (1994)].

Bernardo, however, dismisses Blaustein's study as a "science fair experiment" whose central variable, UV radiation, was chosen with no strong grounding in local field conditions. "Has UV influence over those lakes changed over the same period that frog egg mortality has changed? He has no data," Bernardo states. "Suppose Blaustein had decided to manipulate temperature instead of UV—then the story he's weaving in the press would have been that global warming is



Hard science. Experiments have taken on a dominant role in ecology, indicated by this breakdown of observational techniques used in studies published in the journals *Ecology*, *Oecologia*, and *Oikos*, from 1987 to 1991.

causing [the amphibian decline]."

David Reznick, an ecologist at the University of California, Riverside, adds that some amphibian populations—such as one Central American tree frog species that inhabits dense foliage—are declining even though they live beneath UV radiation's reach, indicating that some other mechanism must be at work. Says Reznick, "These global patterns don't lend themselves to a single easy explanation."

Blaustein agrees with this last point, saying "UV is definitely not a universal explanation for amphibian declines," and adds that new experiments are already under way to test for a possible synergism between UV radiation and a fungal disease now spreading quickly through amphibian populations in the Oregon Cascades. But while he admits there are no data showing that UV incidence has increased at the team's field sites, he notes "there are absolutely no long-term data on UV anywhere, let alone in our area ... so that can be a criticism of any UV study." Further, he says his team searched hard for other environmental changes that might be harming amphibians, such as acid rain,

heavy metals and other pollutants, and habitat destruction, but found nothing. "What we've seen in about 15 different field sites is that the eggs that are dying are right out in the open," where they are most exposed to solar UV, Blaustein says.

Bruce Menge, a community ecologist also at Oregon State University, calls the lack of long-term UV data to back up Blaustein's findings irrelevant. "If we followed [Bernardo's] arguments, we wouldn't do much of anything relevant to these pressing problems" like ozone thinning, Menge says. Blaustein is "an outstanding naturalist" who "doesn't go out and do experiments without having a natural-history basis to do them," Menge adds.

Designing reality

Whatever the truth of the amphibian puzzle, being disconnected from nature isn't the only factor that can throw off an ecological experiment, the revisionists say. Many studies are also undermined by basic flaws in their design. It's on these grounds that Bernardo, Resetarits, and University of Pennsylvania ecologist Arthur Dunham have attacked an influential study of "character displacement" published in *Science* last year. Character displacement is the theory that competition for an ecological niche can force species that initially have similar characteristics to evolve in slightly different directions—in effect to keep out of one another's way. In the study, Dolph Schluter, an ecologist at the University of British Columbia in Vancouver, filled both halves of each of two divided artificial ponds with "generalist" three-spine stickleback fish (*Gasterosteus aculeatus* complex) that feed both high and low in the water columns of their native glacial lake (*Science*, 4 November 1994, p. 798). To one half of the pond, he added a second stickleback species that feeds exclusively on plankton near the water's surface.

After 3 months, Schluter began recording the generalists' growth. Fish in the untreated halves of the two ponds grew normally. But in the presence of the top-feeders, he found the quickest growing generalists were those whose mouths and gill shapes most resembled those of a third, bottom-feeding type of stickleback. Schluter's conclusion: Natural selection was starting to favor the generalists with more bottom-feeding capabilities. If the trend had been allowed to continue through subsequent generations, the initial generalist characteristics would have been displaced because they are heritable.

Says Resetarits, "It's a sexy result, and it's gotten a lot of play, but it's a very bad experiment." Resetarits was so skeptical of the results that he, Bernardo, and Dunham checked

HOMAGE TO SANTA ROSALIA
or
WHY ARE THERE SO MANY KINDS OF ANIMALS?*

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When you did me the honor of asking me to fill your presidential chair, I accepted perhaps without duly considering the duties of the president of a society, founded largely to further the study of evolution, at the close of the year that marks the centenary of Darwin and Wallace's initial presentation of the theory of natural selection. It seemed to me that most of the significant aspects of modern evolutionary theory have come either from geneticists, or from those heroic museum workers who suffering through years of neglect, were able to establish about 20 years ago what has come to be called the "new systematics." You had, however, chosen an ecologist as your president and one of that school at times supposed to study the environment without any relation to the organism.

A few months later I happened to be in Sicily. An early interest in zoogeography and in aquatic insects led me to attempt to collect near Palermo, certain species of water-bugs, of the genus *Corixa*, described a century ago by Fieber and supposed to occur in the region, but never fully reinvestigated. It is hard to find suitable localities in so highly cultivated a landscape as the Concha d'Oro. Fortunately, I was driven up Monte Pellegrino, the hill that rises to the west of the city, to admire the view. A little below the summit, a church with a simple baroque facade stands in front of a cave in the limestone of the hill. Here in the 16th century a stalactite encrusted skeleton associated with a cross and twelve beads was discovered. Of this skeleton nothing is certainly known save that it is that of Santa Rosalia, a saint of whom little is reliably reported save that she seems to have lived in the 12th century, that her skeleton was found in this cave, and that she has been the chief patroness of Palermo ever since. Other limestone caverns on Monte Pellegrino had yielded bones of extinct pleistocene *Equus*, and on the walls of one of the rock shelters at the bottom of the hill there are beautiful Gravettian engravings. Moreover, a small relic of the saint that I saw in the treasury of the Cathedral of Monreale has a venerable and

*Address of the President, American Society of Naturalists, delivered at the annual meeting, Washington, D. C., December 30, 1958.

petrified appearance, as might be expected. Nothing in her history being known to the contrary, perhaps for the moment we may take Santa Rosalia as the patroness of evolutionary studies, for just below the sanctuary, fed no doubt by the water that percolates through the limestone cracks of the mountain, and which formed the sacred cave, lies a small artificial pond, and when I could get to the pond a few weeks later, I got from it a hint of what I was looking for.

Vast numbers of Corixidae were living in the water. At first I was rather disappointed because every specimen of the larger of the two species present was a female, and so lacking in most critical diagnostic features, while both sexes of the second slightly smaller species were present in about equal number. Examination of the material at leisure, and of the relevant literature, has convinced me that the two species are the common European *C. punctata* and *C. affinis*, and that the peculiar Mediterranean species are illusionary. The larger *C. punctata* was clearly at the end of its breeding season, the smaller *C. affinis* was probably just beginning to breed. This is the sort of observation that any naturalist can and does make all the time. It was not until I asked myself why the larger species should breed first, and then the more general question as to why there should be two and not 20 or 200 species of the genus in the pond, that ideas suitable to present to you began to emerge. These ideas finally prompted the very general question as to why there are such an enormous number of animal species.

There are at the present time supposed to be (Muller and Campbell, 1954; Hyman, 1955) about one million described species of animals. Of these about three-quarters are insects, of which a quite disproportionately large number are members of a single order, the Coleoptera.¹ The marine fauna although it has at its disposal a much greater area than has the terrestrial, lacks this astonishing diversity (Thorson, 1958). If the insects are excluded, it would seem to be more diverse. The proper answer to my initial question would be to develop a theory at least predicting an order of magnitude for the number of species of 10^6 rather than 10^8 or 10^4 . This I certainly cannot do. At most it is merely possible to point out some of the factors which would have to be considered if such a theory was ever to be constructed.

Before developing my ideas I should like to say that I subscribe to the view that the process of natural selection, coupled with isolation and later mutual invasion of ranges leads to the evolution of sympatric species, which at equilibrium occupy distinct niches, according to the Volterra-Gause principle. The empirical reasons for adopting this view and the correlative view that the boundaries of realized niches are set by competition are mainly indirect. So far as niches may be defined in terms of food, the subject has been carefully considered by Lack (1954). In general all the indirect evi-

¹There is a story, possibly apocryphal, of the distinguished British biologist, J. B. S. Haldane, who found himself in the company of a group of theologians. On being asked what one could conclude as to the nature of the Creator from a study of his creation, Haldane is said to have answered, "An inordinate fondness for beetles."

dence is in accord with the view, which has the advantage of confirming theoretical expectation. Most of the opinions that have been held to the contrary appear to be due to misunderstandings and to loose formulation of the problem (Hutchinson, 1958).

In any study of evolutionary ecology, food relations appear as one of the most important aspects of the system of animate nature. There is quite obviously much more to living communities than the raw dictum "eat or be eaten," but in order to understand the higher intricacies of any ecological system, it is most easy to start from this crudely simple point of view.

FOOD CHAINS

Animal ecologists frequently think in terms of food chains, of the form *individuals of species S_1 are eaten by those of S_2 , of S_2 by S_3 , of S_3 by S_4 , etc.* In such a food chain S_1 will ordinarily be some holophytic organism or material derived from such organisms. The simplest case is that in which we have a true *predator chain* in Odum's (1953) convenient terminology, in which the lowest link is a green plant, the next a herbivorous animal, the next a primary carnivore, the next a secondary carnivore, etc. A specially important type of predator chain may be designated Eltonian, because in recent years C. S. Elton (1927) has emphasized its widespread significance, in which the predator at each level is larger and rarer than its prey. This phenomenon was recognized much earlier, notably by A. R. Wallace in his contribution to the 1858 communication to the Linnean Society of London.

In such a system we can make a theoretical guess of the order of magnitude of the diversity that a single food chain can introduce into a community. If we assume that in general 20 per cent of the energy passing through one link can enter the next link in the chain, which is overgenerous (cf. Lindeman, 1942; Slobodkin in an unpublished study finds 13 per cent as a reasonable upper limit) and if we suppose that each predator has twice the mass, (or 1.26 the linear dimensions) of its prey, which is a very low estimate of the size difference between links, the fifth animal link will have a population of one ten thousandth (10^{-4}) of the first, and the fiftieth animal link, if there was one, a population of 10^{-49} the size of the first. Five animal links are certainly possible, a few fairly clear cut cases having been in fact recorded. If, however, we wanted 50 links, starting with a protozoan or rotifer feeding on algae with a density of 10^6 cells per ml, we should need a volume of 10^{26} cubic kilometers to accommodate on an average one specimen of the ultimate predator, and this is vastly greater than the volume of the world ocean. Clearly the Eltonian food-chain of itself cannot give any great diversity, and the same is almost certainly true of the other types of food chain, based on detritus feeding or on parasitism.

Natural selection

Before proceeding to a further consideration of diversity, it is, however, desirable to consider the kinds of selective force that may operate on a food chain, for this may limit the possible diversity.

It is reasonably certain that natural selection will tend to maintain the efficiency of transfer from one level to another at a maximum. Any increase in the predatory efficiency of the n^{th} link of a simple food chain will however always increase the possibility of the extermination of the $(n-1)^{\text{th}}$ link. If this occurs either the species constituting the n^{th} link must adapt itself to eating the $(n-2)^{\text{th}}$ link or itself become extinct. This process will in fact tend to shortening of food chains. A lengthening can presumably occur most simply by the development of a new terminal carnivore link, as its niche is by definition previously empty. In most cases this is not likely to be easy. The evolution of the whale-bone whales, which at least in the case of *Balaenoptera borealis*, can feed largely on copepods and so rank on occasions as primary carnivores (Bigelow, 1926), presumably constitutes the most dramatic example of the shortening of a food chain. Mechanical considerations would have prevented the evolution of a larger rarer predator, until man developed essentially non-Eltonian methods of hunting whales.

Effect of size

A second important limitation of the length of a food chain is due to the fact that ordinarily animals change their size during free life. If the terminal member of a chain were a fish that grew from say one cm to 150 cms in the course of an ordinary life, this size change would set a limit by competition to the possible number of otherwise conceivable links in the 1-150 cm range. At least in fishes this type of process (metaphoetesis) may involve the smaller specimens belonging to links below the larger and the chain length is thus lengthened, though under strong limitations, by cannibalism.

We may next enquire into what determines the number of food chains in a community. In part the answer is clear, though if we cease to be zoologists and become biologists, the answer begs the question. Within certain limits, the number of kinds of primary producers is certainly involved, because many herbivorous animals are somewhat eclectic in their tastes and many more limited by their size or by such structural adaptations for feeding that they have been able to develop.

Effects of terrestrial plants

The extraordinary diversity of the terrestrial fauna, which is much greater than that of the marine fauna, is clearly due largely to the diversity provided by terrestrial plants. This diversity is actually two-fold. Firstly, since terrestrial plants compete for light, they have tended to evolve into structures growing into a gaseous medium of negligible buoyancy. This has led to the formation of specialized supporting, photosynthetic, and reproductive structures which inevitably differ in chemical and physical properties. The ancient Danes and Irish are supposed to have eaten elm-bark, and sometimes sawdust, in periods of stress, has been hydrolyzed to produce edible carbohydrate; but usually man, the most omnivorous of all animals, has avoided

almost all parts of trees except fruits as sources of food, though various individual species of animals can deal with practically every tissue of many arboreal species. A major source of terrestrial diversity was thus introduced by the evolution of almost 200,000 species of flowering plants, and the three quarters of a million insects supposedly known today are in part a product of that diversity. But of itself merely providing five or ten kinds of food of different consistencies and compositions does not get us much further than the five or ten links of an Eltonian pyramid. On the whole the problem still remains, but in the new form: why are there so many kinds of plants? As a zoologist I do not want to attack that question directly, I want to stick with animals, but also to get the answer. Since, however, the plants are part of the general system of communities, any sufficiently abstract properties of such communities are likely to be relevant to plants as well as to herbivores and carnivores. It is, therefore, by being somewhat abstract, though with concrete zoological details as examples, that I intend to proceed.

INTERRELATIONS OF FOOD CHAINS

Biological communities do not consist of independent food chains, but of food webs, of such a kind that an individual at any level (corresponding to a link in a single chain) can use some but not all of the food provided by species in the levels below it.

It has long been realized that the presence of two species at any level, either of which can be eaten by a predator at a level above, but which may differ in palatability, ease of capture or seasonal and local abundance, may provide alternative foods for the predator. The predator, therefore, will neither become extinct itself nor exterminate its usual prey, when for any reason, not dependent on prey-predator relationships, the usual prey happens to be abnormally scarce. This aspect of complicated food webs has been stressed by many ecologists, of whom the Chicago school as represented by Allee, Emerson, Park, Park and Schmidt (1949), Odum (1953) and Elton (1958), may in particular be mentioned. Recently MacArthur (1955) using an ingenious but simple application of information theory has generalized the points of view of earlier workers by providing a formal proof of the increase in stability of a community as the number of links in its food web increases.

MacArthur concludes that in the evolution of a natural community two partly antagonistic processes are occurring. More efficient species will replace less efficient species, but more stable communities will outlast less stable communities. In the process of community formation, the entry of a new species may involve one of three possibilities. It may completely displace an old species. This of itself does not necessarily change the stability, though it may do so if the new species inherently has a more stable population (cf. Slobodkin, 1956) than the old. Secondly, it may occupy an unfilled niche, which may, by providing new partially independent links, increase stability. Thirdly, it may partition a niche with a pre-existing species. Elton (1958) in a fascinating work largely devoted to the fate of species accidentally or purposefully introduced by man, concludes that in very

diverse communities such introductions are difficult. Early in the history of a community we may suppose many niches will be empty and invasion will proceed easily; as the community becomes more diversified, the process will be progressively more difficult. Sometimes an extremely successful invader may oust a species but add little or nothing to stability, at other times the invader by some specialization will be able to compete successfully for the marginal parts of a niche. In all cases it is probable that invasion is most likely when one or more species happen to be fluctuating and are underrepresented at a given moment. As the communities build up, these opportunities will get progressively rarer. In this way a complex community containing some highly specialized species is constructed asymptotically.

Modern ecological theory therefore appears to answer our initial question at least partially by saying that there is a great diversity of organisms because communities of many diversified organisms are better able to persist than are communities of fewer less diversified organisms. Even though the entry of an invader which takes over part of a niche will lead to the reduction in the *average* population of the species originally present, it will also lead to an increase in stability reducing the risk of the original population being at times underrepresented to a dangerous degree. In this way loss of some niche space may be compensated by reduction in the amplitude of fluctuations in a way that can be advantageous to both species. The process however appears likely to be asymptotic and we have now to consider what sets the asymptote, or in simpler words why are there not more different kinds of animals?

LIMITATION OF DIVERSITY

It is first obvious that the processes of evolution of communities must be under various sorts of external control, and that in some cases such control limits the possible diversity. Several investigators, notably Odum (1953) and MacArthur (1955), have pointed out that the more or less cyclical oscillations observed in arctic and boreal fauna may be due in part to the communities not being sufficiently complex to damp out oscillations. It is certain that the fauna of any such region is qualitatively poorer than that of warm temperate and tropical areas of comparable effective precipitation. It is probably considered to be intuitively obvious that this should be so, but on analysis the obviousness tends to disappear. If we can have one or two species of a large family adapted to the rigors of Arctic existence, why can we not have more? It is reasonable to suppose that the total biomass may be involved. If the fundamental productivity of an area is limited by a short growing season to such a degree that the total biomass is less than under more favorable conditions, then the rarer species in a community may be so rare that they do not exist. It is also probable that certain absolute limitations on growth-forms of plants, such as those that make the development of forest impossible above a certain latitude, may in so acting, severely limit the number of niches. Dr. Robert MacArthur points out that the development of high tropical rain forest increases the bird fauna more than that of mam-

mals, and Thorson (1957) likewise has shown that the so-called infauna show no increase of species toward the tropics while the marine epifauna becomes more diversified. The importance of this aspect of the plant or animal substratum, which depends largely on the length of the growing season and other aspects of productivity is related to that of the environmental mosaic discussed later.

We may also inquire, but at present cannot obtain any likely answer, whether the arctic fauna is not itself too young to have achieved its maximum diversity. Finally, the continual occurrence of catastrophes, as Wynne-Edwards (1952) has emphasized, may keep the arctic terrestrial community in a state of perennial though stunted youth.

Closely related to the problems of environmental rigor and stability, is the question of the absolute size of the habitat that can be colonized. Over much of western Europe there are three common species of small voles, namely *Microtus arvalis*, *M. agrestis* and *Clethrionomys glareolus*. These are sympatric but with somewhat different ecological preferences.

In the smaller islands off Britain and in the English channel, there is only one case of two species co-occurring on an island, namely *M. agrestis* and *Clethrionomys* on the island of Mull in the Inner Hebrides (Barrett-Hamilton and Hinton, 1911-1921). On the Orkneys the single species is *M. orcadensis*, which in morphology and cytology is a well-differentiated ally of *M. arvalis*; a comparable animal (*M. sarnius*) occurs on Guernsey. On most of the Scottish Islands only subspecies of *M. agrestis* occur, but on Mull and Raasay, on the Welsh island of Skomer, as well as on Jersey, races of *Clethrionomys* of somewhat uncertain status are found. No voles have reached Ireland, presumably for paleogeographic reasons, but they are also absent from a number of small islands, notably Alderney and Sark. The last named island must have been as well placed as Guernsey to receive *Microtus arvalis*. Still stranger is the fact that although it could not have got to the Orkneys without entering the mainland of Britain, no vole of the *arvalis* type now occurs in the latter country. Cases of this sort may be perhaps explained by the lack of favorable refuges in randomly distributed very unfavorable seasons or under special kinds of competition. This explanation is very reasonable as an explanation of the lack of *Microtus* on Sark, where it may have had difficulty in competing with *Rattus rattus* in a small area. It would be stretching one's credulity to suppose that the area of Great Britain is too small to permit the existence of two sympatric species of *Microtus*, but no other explanation seems to have been proposed.

It is a matter of considerable interest that Lack (1942) studying the populations of birds on some of these small British islands concluded that such populations are often unstable, and that the few species present often occupied larger niches than on the mainland in the presence of competitors. Such faunas provide examples of communities held at an early stage in development because there is not enough space for the evolution of a fuller and more stable community.

NICHE REQUIREMENTS

The various evolutionary tendencies, notably metaphoresis, which operate on single food chains must operate equally on the food-web, but we also have a new, if comparable, problem as to how much difference between two species at the same level is needed to prevent them from occupying the same niche. Where metric characters are involved we can gain some insight into this extremely important problem by the study of what Brown and Wilson (1956) have called *character displacement* or the divergence shown when two partly allopatric species of comparable niche requirements become sympatric in part of their range.

I have collected together a number of cases of mammals and birds which appear to exhibit the phenomenon (table 1). These cases involve metric characters related to the trophic apparatus, the length of the culmen in birds and of the skull in mammals appearing to provide appropriate measures. Where the species co-occur, the ratio of the larger to the small form varies from 1.1 to 1.4, the mean ratio being 1.28 or roughly 1.3. This latter figure may tentatively be used as an indication of the kind of difference necessary to permit two species to co-occur in different niches but at the same level of a food-web. In the case of the aquatic insects with which I began my address, we have over most of Europe three very closely allied species of *Corixa*, the largest *punctata*, being about 116 per cent longer than the middle sized species *macrocephala*, and 146 per cent longer than the small species *affinis*. In northwestern Europe there is a fourth species, *C. dentipes*, as large as *C. punctata* and very similar in appearance. A single observation (Brown, 1948) suggests that this is what I have elsewhere (Hutchinson, 1951) termed a fugitive species, maintaining itself in the face of competition mainly on account of greater mobility. According to Macan (1954) while both *affinis* and *macrocephala* may occur with *punctata* they never are found with each other, so that all three species never occur together. In the eastern part of the range, *macrocephala* drops out, and *punctata* appears to have a discontinuous distribution, being recorded as far east as Simla, but not in southern Persia or Kashmir, where *affinis* occurs. In these eastern localities, where it occurs by itself, *affinis* is larger and darker than in the west, and superficially looks like *macrocephala* (Hutchinson, 1940).

This case is very interesting because it looks as though character displacement is occurring, but that the size differences between the three species are just not great enough to allow them all to co-occur. Other characters than size are in fact clearly involved in the separation, *macrocephala* preferring deeper water than *affinis* and the latter being more tolerant of brackish conditions. It is also interesting because it calls attention to a marked difference that must occur between hemimetabolous insects with annual life cycles involving relatively long growth periods, and birds or mammals in which the period of growth in length is short and of a very special nature compared with the total life span. In the latter, niche separation may be possible merely through genetic size differences, while in a pair of ani-

TABLE 1

Mean character displacement in measurable trophic structures in mammals (skull) and birds (culmen); data for *Mustela* from Miller (1912); *Apodemus* from Cranbrook (1957); *Sitta* from Brown and Wilson (1956) after Vaurie; Galapagos finches from Lack (1947)

	Locality and measurement when sympatric	Locality and measurement when allopatric	Ratio when sympatric
<i>Mustela nivalis</i>	Britain; skull ♂ 39.3 ♀ 33.6 mm.	(<i>boccamela</i>) S. France, Italy ♂ 42.9 ♀ 34.7 mm.	♂ 100:128 ♀ 100:134
<i>M. erminea</i>	Britain; " ♂ 50.4 ♀ 45.0	(<i>iberica</i>) Spain, Portugal ♂ 40.4 ♀ 36.0 (<i>hibernica</i>) Ireland ♂ 46.0 ♀ 41.9	
<i>Apodemus sylvaticus</i>	Britain; " 24.8	unnamed races on Channel Islands 25.6-26.7	100:109
<i>A. flavicollis</i>	Britain; " 27.0		
<i>Sitta tephronota</i>	Iran; culmen 29.0	races east of overlap 25.5	100:124
<i>S. neumayer</i>	Iran; " 23.5	races west of overlap 26.0	
<i>Geospiza fortis</i>	Indefatigable Isl.; culmen 12.0	Daphne Isl. 10.5	100:143
<i>G. fuliginosa</i>	Indefatigable Isl.; " 8.4	Crossman Isl. 9.3	
<i>Camarhynchus parvulus</i>	James Isl.; " 7.0	N. Albemarle Isl. 7.0	James 100:140:180 100:129
<i>C. psittacula</i>	Indefatigable Isl.; " 7.5 S. Albemarle Isl.; " 7.3 James Isl.; " 9.8 Indefatigable Isl.; " 9.6	Chatham Isl. 8.0 Abington Isl. 10.1 Bindloe Isl. 10.5	
<i>C. pallidus</i>	S. Albemarle Isl.; " 8.5 James Isl.; " 12.6 Indefatigable Isl.; " 12.1 S. Albemarle Isl.; " 11.2	N. Albemarle Isl. 11.7 Chatham Isl. 10.8	S. Albemarle 100:116:153 100:132
			Mean ratio 100:128

mals like *C. punctata* and *C. affinis* we need not only a size difference but a seasonal one in reproduction; this is likely to be a rather complicated matter. For the larger of two species always to be larger, it must never breed later than the smaller one. I do not doubt that this is what was happening in the pond on Monte Pellegrino, but have no idea how the difference is achieved.

I want to emphasize the complexity of the adaptation necessary on the part of two species inhabiting adjacent niches in a given biotope, as it probably underlies a phenomenon which to some has appeared rather puzzling. MacArthur (1957) has shown that in a sufficiently large bird fauna, in a uniform undisturbed habitat, areas occupied by the different species appear to correspond to the random non-overlapping fractionation of a plane or volume. Kohn (1959) has found the same thing for the cone-shells (*Conus*) on the Hawaiian reefs. This type of arrangement almost certainly implies such individual and unpredictable complexities in the determination of the niche boundaries, and so of the actual areas colonized, that in any overall view, the process would appear random. It is fairly obvious that in different types of community the divisibility of niches will differ and so the degree of diversity that can be achieved. The fine details of the process have not been adequately investigated, though many data must already exist that could be organized to throw light on the problem.

MOSAIC NATURE OF THE ENVIRONMENT

A final aspect of the limitation of possible diversity, and one that perhaps is of greatest importance, concerns what may be called the mosaic nature of the environment. Except perhaps in open water when only uniform quasi-horizontal surfaces are considered, every area colonized by organisms has some local diversity. The significance of such local diversity depends very largely on the size of the organisms under consideration. In another paper MacArthur and I (Hutchinson and MacArthur, 1959) have attempted a theoretical formulation of this property of living communities and have pointed out that even if we consider only the herbivorous level or only one of the carnivorous levels, there are likely, above a certain lower limit of size, to be more species of small or medium sized organisms than of large organisms. It is difficult to go much beyond crude qualitative impressions in testing this hypothesis, but we find that for mammal faunas, which contain such diverse organisms that they may well be regarded as models of whole faunas, there is a definite hint of the kind of theoretical distribution that we deduce. In qualitative terms the phenomenon can be exemplified by any of the larger species of ungulates which may require a number of different kinds of terrain within their home ranges, any one of which types of terrain might be the habitat of some small species. Most of the genera or even subfamilies of very large terrestrial animals contain only one or two sympatric species. In this connection I cannot refrain from pointing out the immense scientific importance of obtaining a really full insight into the ecology of the large mammals of Africa while they can still be studied under natural conditions. It is

indeed quite possible that the results of studies on these wonderful animals would in long-range though purely practical terms pay for the establishment of greater reservations and National Parks than at present exist.

In the passerine birds the occurrence of five or six closely related sympatric species is a commonplace. In the mammal fauna of western Europe no genus appears to contain more than four strictly sympatric species. In Britain this number is not reached even by *Mustela* with three species, on the adjacent parts of the continent there may be three sympatric shrews of the genus *Crocidura* and in parts of Holland three of *Microtus*. In the same general region there are genera of insects containing hundreds of species, as in *Athela* in the Coleoptera and *Dasyhelea* in the Diptera Nematocera. The same phenomenon will be encountered whenever any well-studied fauna is considered. Irrespective of their position in a food chain, small size, by permitting animals to become specialized to the conditions offered by small diversified elements of the environmental mosaic, clearly makes possible a degree of diversity quite unknown among groups of larger organisms.

We may, therefore, conclude that the reason why there are so many species of animals is at least partly because a complex trophic organization of a community is more stable than a simple one, but that limits are set by the tendency of food chains to shorten or become blurred, by unfavorable physical factors, by space, by the fineness of possible subdivision of niches, and by those characters of the environmental mosaic which permit a greater diversity of small than of large allied species.

CONCLUDING DISCUSSION

In conclusion I should like to point out three very general aspects of the sort of process I have described. One speculative approach to evolutionary theory arises from some of these conclusions. Just as adaptative evolution by natural selection is less easy in a small population of a species than in a larger one, because the total pool of genetic variability is inevitably less, so it is probable that a group containing many diversified species will be able to seize new evolutionary opportunities more easily than an undiversified group. There will be some limits to this process. Where large size permits the development of a brain capable of much new learnt behavior, the greater plasticity acquired by the individual species will offset the disadvantage of the small number of allied species characteristic of groups of large animals. Early during evolution the main process from the standpoint of community structure was the filling of all the niche space potentially available for producer and decomposer organisms and for herbivorous animals. As the latter, and still more as carnivorous animals began to appear, the persistence of more stable communities would imply splitting of niches previously occupied by single species as the communities became more diverse. As this process continued one would expect the overall rate of evolution to have increased, as the increasing diversity increased the probability of the existence of species preadapted to new and unusual niches. It is reasonable to suppose that strong predation among macroscopic metazoa

did not begin until the late Precambrian, and that the appearance of powerful predators led to the appearance of fossilizable skeletons. This seems the only reasonable hypothesis, of those so far advanced, to account for the relatively sudden appearance of several fossilizable groups in the Lower Cambrian. The process of diversification would, according to this argument, be somewhat autocatakinetic even without the increased stability that it would produce; with the increase in stability it would be still more a self inducing process, but one, as we have seen, with an upper limit. Part of this upper limit is set by the impossibility of having many sympatric allied species of large animals. These however are the animals that can pass from primarily innate to highly modifiable behavior. From an evolutionary point of view, once they have appeared, there is perhaps less need for diversity, though from other points of view, as Elton (1958) has stressed in dealing with human activities, the stability provided by diversity can be valuable even to the most adaptable of all large animals. We may perhaps therefore see in the process of evolution an increase in diversity at an increasing rate till the early Paleozoic, by which time the familiar types of community structure were established. There followed then a long period in which various large and finally large-brained species became dominant, and then a period in which man has been reducing diversity by a rapidly increasing tendency to cause extinction of supposedly unwanted species, often in an indiscriminate manner. Finally we may hope for a limited reversal of this process when man becomes aware of the value of diversity no less in an economic than in an esthetic and scientific sense.

A second and much more metaphysical general point is perhaps worth a moment's discussion. The evolution of biological communities, though each species appears to fend for itself alone, produces integrated aggregates which increase in stability. There is nothing mysterious about this; it follows from mathematical theory and appears to be confirmed to some extent empirically. It is however a phenomenon which also finds analogies in other fields in which a more complex type of behavior, that we intuitively regard as higher, emerges as the result of the interaction of less complex types of behavior, that we call lower. The emergence of love as an antidote to aggression, as Lorenz pictures the process, or the development of cooperation from various forms of more or less inevitable group behavior that Allee (1931) has stressed are examples of this from the more complex types of biological systems.

In the ordinary sense of explanation in science, such phenomena are explicable. The types of holistic philosophy which import *ad hoc* mysteries into science whenever such a situation is met are obviously unnecessary. Yet perhaps we may wonder whether the empirical fact that it is the nature of things for this type of explicable emergence to occur is not something that itself requires an explanation. Many objections can be raised to such a view; a friendly organization of biologists could not occur in a universe in which cooperative behavior was impossible and without your cooperation I could not raise the problem. The question may in fact appear to certain

types of philosophers not to be a real one, though I suspect such philosophers in their desire to demonstrate how often people talk nonsense, may sometimes show less ingenuity than would be desirable in finding some sense in such questions. Even if the answer to such a question were positive, it might not get us very far; to an existentialist, life would have merely provided yet one more problem; students of Whitehead might be made happier, though on the whole the obscurities of that great writer do not seem to generate unhappiness; the religious philosophers would welcome a positive answer but note that it told them nothing that they did not know before; Marxists might merely say, "I told you so." In spite of this I suspect that the question is worth raising, and that it could be phrased so as to provide some sort of real dichotomy between alternatives; I therefore raise it knowing that I cannot, and suspecting that at present others cannot, provide an intellectually satisfying answer.

My third general point is less metaphysical, but not without interest. If I am right that it is easier to have a greater diversity of small than of large organisms, then the evolutionary process in small organisms will differ somewhat from that of large ones. Wherever we have a great array of allied sympatric species there must be an emphasis on very accurate interspecific mating barriers which is unnecessary where virtually no sympatric allies occur. We ourselves are large animals in this sense; it would seem very unlikely that the peculiar lability that seems to exist in man, in which even the direction of normal sexual behavior must be learnt, could have developed to quite the existing extent if species recognition, involving closely related sympatric congeners, had been necessary. Elsewhere (Hutchinson, 1959) I have attempted to show that the difficulties that *Homo sapiens* has to face in this regard may imply various unsuspected processes in human evolutionary selection. But perhaps Santa Rosalia would find at this point that we are speculating too freely, so for the moment, while under her patronage, I will say no more.

ACKNOWLEDGMENTS

Dr. A. Minganti of the University of Palermo enabled me to collect on Monte Pellegrino. Professor B. M. Knox of the Department of Classics of Yale University gave me a rare and elegant word from the Greek to express the blurring of a food chain. Dr. L. B. Slobodkin of the University of Michigan and Dr. R. H. MacArthur of the University of Pennsylvania provided me with their customary kinds of intellectual stimulation. To all these friends I am most grateful.

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Anthropogenic Disturbance and Biodiversity in Rivers: Influence of Impoundments on Mid-order Rivers

ABSTRACT

According to the Serial Discontinuity Concept (Ward and Stanford 1983), biodiversity is reduced below impoundments on mid-order rivers, primarily as a result of an altered thermal regime. Studies on 2 rivers, the Grand in Ontario, Canada and the Blue in Colorado, support this hypothesis. In a concomitant study on the Blue River, 6 sampling sites were set up in a geometric progression starting at 0.25 km and ending at 11.0 km below the impoundment. This study documented the recovery of the lotic zoobenthos (especially insects) as the thermal regime returned to near pre-impoundment conditions. Though no single factor controls diversity, temperature certainly plays a major role.

OUTLINE

- I. Introduction
- II. Biodiversity and the Serial Discontinuity Concept
- III. Influence of an impoundment on biodiversity of lotic zoobenthos and fish in a Canadian river.
- IV. Influence of an impoundment on biodiversity of lotic zoobenthos in a high elevation Colorado river.

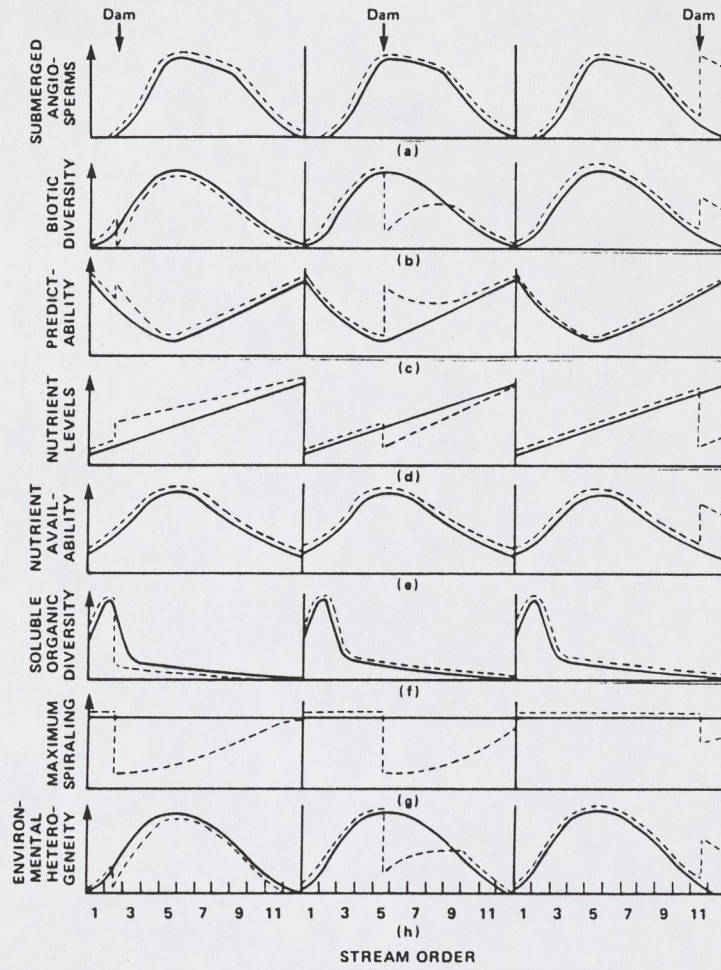


Figure 2. Relative changes in additional parameters (see Fig. 1 legend).

Ward, J. V. and J. A. Stanford. 1983.

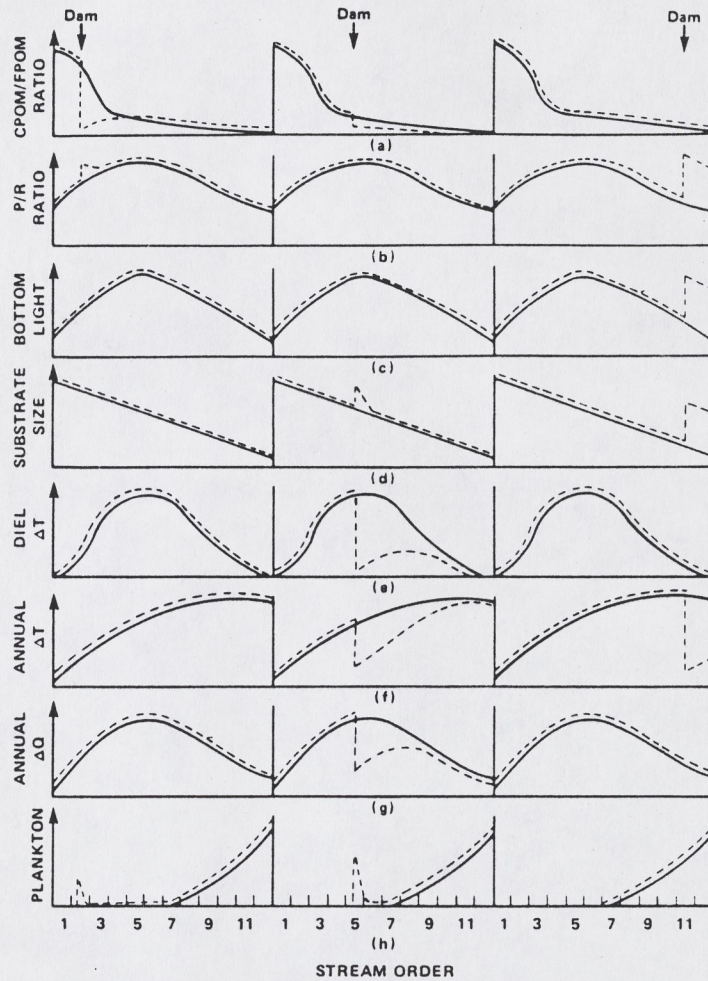


Figure 1. Relative changes in various parameters as a function of stream order, based on our interpretation of natural stream continua theory (solid lines) and postulated effects (dashed lines) of damming headwaters (left column), middle reaches (center column), and lower reaches (right column) of a river system. See text for further explanation.

Ward, J. V. and J. A. Stanford. 1983.

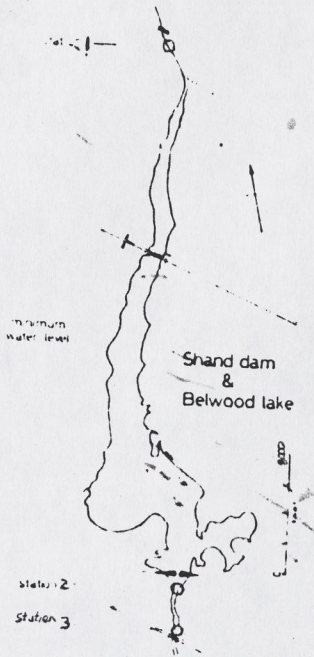


FIG. 1. Study area, Shand Dam and Belwood Lake on the Grand River, Ont., showing the three sampling stations.

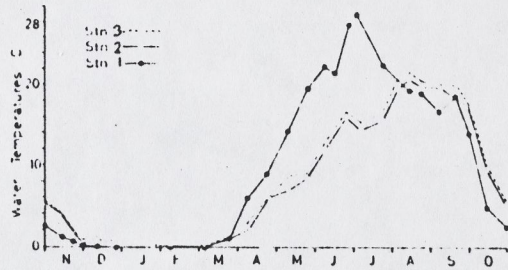


FIG. 2. Temperature regime (noon water temperatures) 1 mile downstream (station 3), immediately downstream (station 2), and $\frac{1}{2}$ mile upstream (station 1) of the impoundment, November 1965-November 1966.

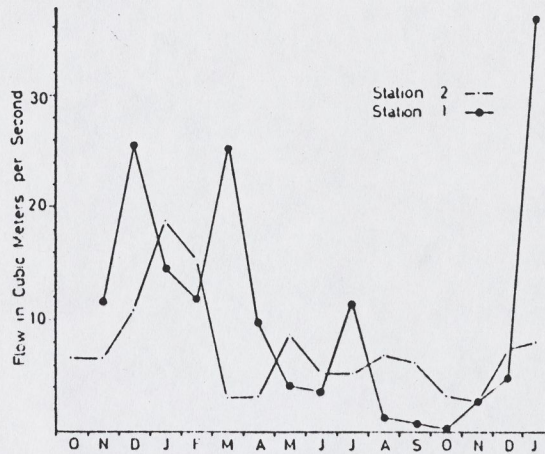


FIG. 3. Flow of water above and below the Shand Dam, October 1965-January 1967.

Spence, J. A. and H. B. N. Hynes. 1971a.

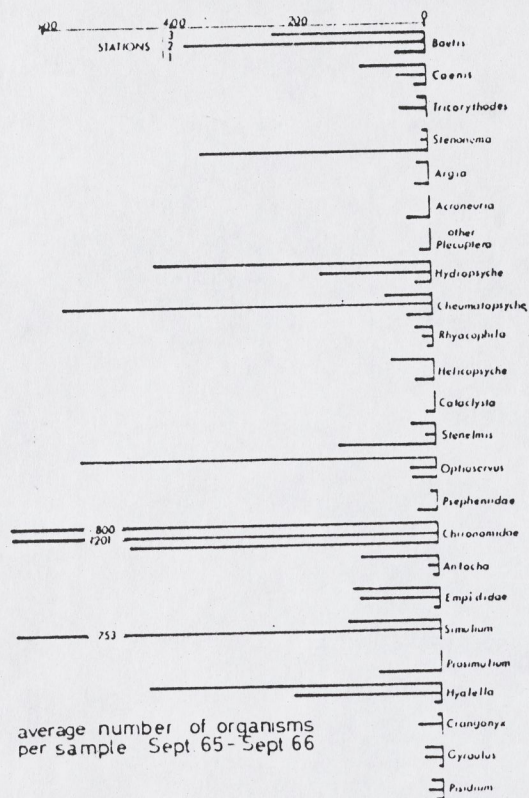


FIG. 5. Average number of organisms per sample at stations 3, 2, and 1 for the 24 main taxonomic groups.

Spence, J. A. and H. B. N. Hynes. 1971a.

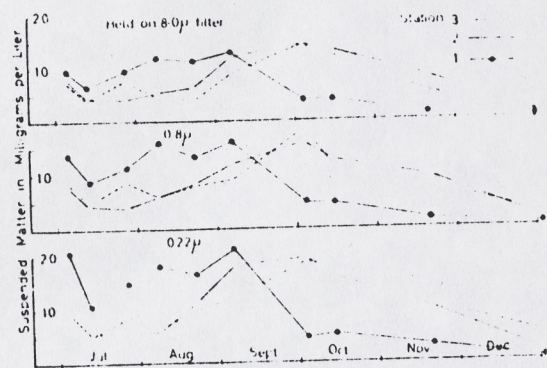


FIG. 4. Suspended matter fractions retained by membrane filters of pore size 8.0, 0.8, and 0.22 μ .

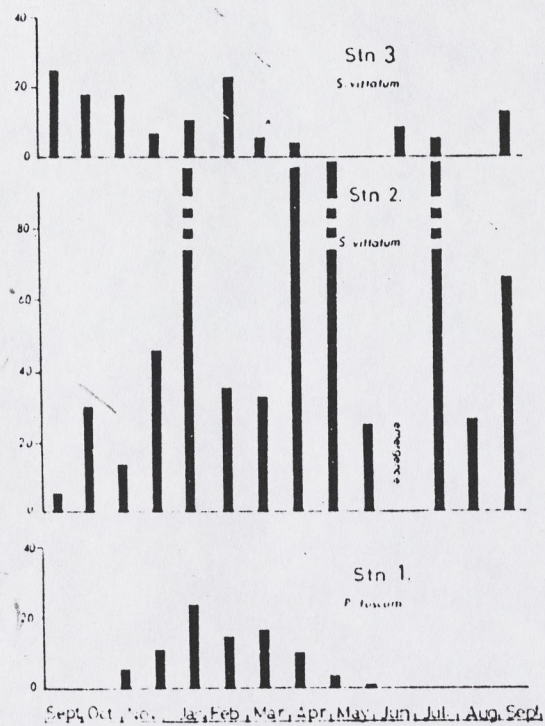


FIG. 6. Numbers of simuliid larvae per sample, September 1965 September 1966, at stations 3, 2, and 1.

Spence, J. A. and H. B. N. Hynes. 1971a.

TABLE 3. Differences in the trichopteran fauna upstream and downstream of the dam.

Family and species	Station		
	3	2	1
Rhyacophilidae			
<i>Rhyacophila fuscula</i> Walker	+	+	+
<i>Agapetus</i> sp.	-	-	+
<i>Glossosoma</i> sp.	-	-	!
Philopotamidae			
<i>Chimarra atterrima</i> Hagen	+	+	+
<i>Chimarra obscura</i> Walker	-	-	+
Hydropsychidae			
<i>Hydropsyche bifida</i> Banks	+	+	-
<i>H. slosonae</i> Banks	+	+	+
<i>H. betteni</i> Ross	-	-	+
<i>H. recurvata</i> Banks	-	-	+
<i>Cheumatopsyche minuscula</i> Banks	+	+	+
Hydroptilidae			
<i>Agraylea multipunctata</i> Curtis	+	+	+
<i>Myatichia ayama</i> Mosely	-	-	+
<i>Ochrotrichia</i> sp.	-	-	+
Phygadeiidae			
<i>Pilostomus</i> sp.	+	+	-
Limnephilidae			
<i>Limnephilus consocius</i> Walker	+	-	+
<i>Neophylax autumnus</i> Vohries	-	-	+
<i>Pycnopsyche lepida</i> Hagen	-	-	!
<i>Pycnopsyche</i> sp.	-	-	-
Leptoceridae			
<i>Leptocella candida</i> Hagen	+	+	-
<i>Athripsodes tarsipunctatus</i> Vohries	+	+	-
<i>Athripsodes</i> sp.	-	-	+
<i>Ocoetis avata</i> Banks	-	-	+
<i>O. inconspicua</i> Walker	-	-	+
Brachycentridae			
<i>Micrasema</i> sp.	+	+	-
<i>Brachycentrus americanus</i> Banks	-	+	-
Helicopsychidae			
<i>Helicopsyche borealis</i> Hagen	+	-	+
Total of 26 species	10	9	20

TABLE 2. Differences in the ephemeropteran fauna upstream and downstream of the dam.

Species	Station		
	3	2	1
<i>Baetis rusticans</i> McDunnough	+	+	-
<i>B. levitans</i> McDunnough	+	+	+
<i>B. pygmaeus</i> Hagen	+	+	!
<i>B. vagans</i> McDunnough	+	+	+
<i>B. herodes</i> Burks	-	-	+
<i>Caenis</i> sp.	+	+	+
<i>Tricorythodes</i> sp.	+	+	!
<i>Ephemerella bicolor</i> Clemens	+	+	+
<i>E. deficiens</i> Morgan	-	-	+
<i>E. needhami</i> McDunnough	-	-	+
<i>Pseudocloeon</i> sp.	-	-	!
<i>Heterocloeon</i> sp.	-	-	+
<i>Paraleptophlebia mollis</i> Eaton	-	-	+
<i>Centroptilum</i> sp.	-	-	+
<i>Stenonema tripunctatum</i> Banks	+	+	+
<i>S. bipunctatum</i> McDunnough	-	-	!
<i>S. femoratum</i> Say	-	-	+
<i>S. canadense</i> Walker	-	-	+
<i>S. neopotellum</i> McDunnough	-	-	+
<i>S. fuscum</i> Clemens	-	-	+
<i>S. heterotarsale</i> McDunnough	-	-	+
<i>S. rubomaculatum</i> Clemens	-	-	!
Total of 23 species	8	8	19

TABLE 4. Differences in the dipteran fauna upstream and downstream of the dam.

Family and species	Station		
	3	2	1
Tipulidae			
<i>Antocha</i> sp.	+	+	+
<i>Tipula</i> spp.	+	+	-
<i>Pedicia</i>	-	-	+
<i>Dicranota</i>	+	-	-
Empididae			
<i>Hemerodromia</i> sp.	+	!	!
Other species	+	+	!
Ceratopogonidae			
	+	!	!
Simuliidae			
<i>Simulium vittatum</i> Zetterstedt	+	!	-
<i>Prosimulium fuscum</i> Syme and Davis	-	-	+
<i>P. mixtum</i> Syme and Davis	-	-	+
Tanypodinae			
<i>Procladius</i> sp.	+	+	+
<i>Thienemannimyia</i> sp.	-	-	+
Diametinae			
cf. <i>Pagastia</i> sp.	+	-	+
Orthoclaudiinae			
<i>Adactylocladius</i> sp.	-	+	-
<i>Cricotopus</i> sp.	!	+	-
<i>Eukiefferiella</i> spp.	+	+	+
<i>Orthocladus</i> sp. A	+	-	+
sp. B	-	-	+
sp. C	-	-	+
<i>O. (Euorthocladus)</i> sp.	+	+	!
<i>Paraericotopus</i> sp.	+	!	-
<i>Trissocladus</i> sp.	+	-	+
Chironomini			
<i>Dicrotendipes</i>	+	+	+
<i>Glyptotendipes (Phytotendipes)</i>	-	+	-
<i>Microtendipes</i>	-	-	+
<i>Stictochironomus</i>	+	-	+
Tanytarsini			
<i>Tanytarsus sensu strictu</i> spp.	+	+	+

TABLE 5. Differences in the crustacean and molluscan fauna.

Family	Station		
	3	2	1
Crustacea			
<i>Hyalella azteca</i> Saussure	+	+	!
<i>Crangonyx gracilis</i> Smith	+	+	-
<i>Cambarus bartonii</i> Fabricius	+	-	+
<i>Orconectes virilis</i> Hagen	+	+	!
Total of four species	4	3	3
Mollusca			
<i>Sphaerium simile</i> Say	-	-	+
<i>S. striatum</i> Lamarck	-	-	+
<i>Pisidium</i> sp.	+	!	!
<i>Alasmidonta calceolus</i> Lea	-	-	!
<i>Ferrissia rivularis</i> Say	!	!	-
<i>Physa</i> sp.	!	+	+
<i>Fossaria</i> sp.	+	-	-
<i>Valvata tricarinata</i> Say	+	+	-
<i>Helisoma anceps</i> Minke	!	!	+
<i>Gyraulus parvus</i> Say	+	+	!
Total of 10 species	7	6	7

Spence, J. A. and H. B. N. Hynes, 1971a.

TABLE 1. Fish species taken downstream of the Shand Dam and above its impoundment, Belwood Lake.

	Down-stream	Up-stream
Catostomidae		
<i>Catostomus commersonii</i>		
Lacépède	+	+
Cyprinidae		
<i>Semotilus atromaculatus</i>		
Mitchill	Common	+
<i>Chrosomus eos</i> Cope	+	+
<i>Pimephales notatus</i> Rafinesque	-	+
<i>Notropis cornutus</i> Mitchill	+	Common
<i>N. spilopterus</i> Cope	-	+
<i>Hybopsis biguttata</i> Kirtland	-	Common
<i>H. micropogon</i> Cope	-	+
<i>Rhinichthys atratulus</i> Herman	+	+
<i>R. cataractae</i> Valenciennes	-	+
Centrarchidae		
<i>Ambloplites rupestris</i> Rafinesque	+	+
Percidae		
<i>Perca flavescens</i> Mitchill	Common	+
Cottidae		
<i>Cottus bairdi</i> Girard	Common	+

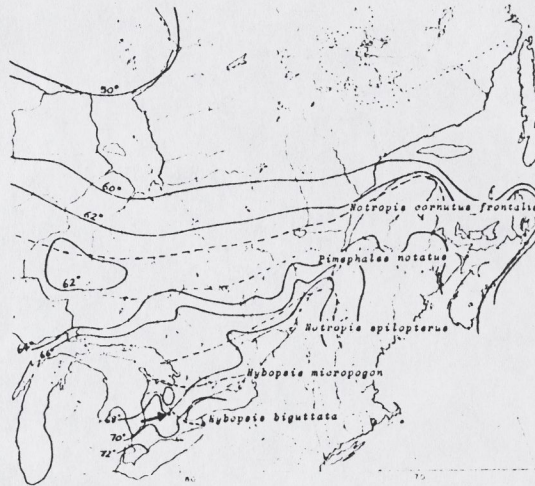


FIG. 1. July isotherms across eastern Canada (solid lines) and approximate northern limits of distribution in eastern Canada of five species of cyprinid fishes (broken lines). The data for the July isotherms were taken from Brown et al. (1968) and Chapman and Thomas (1968).

Spence, J. A. and H. B. N. Hynes. 1971b.

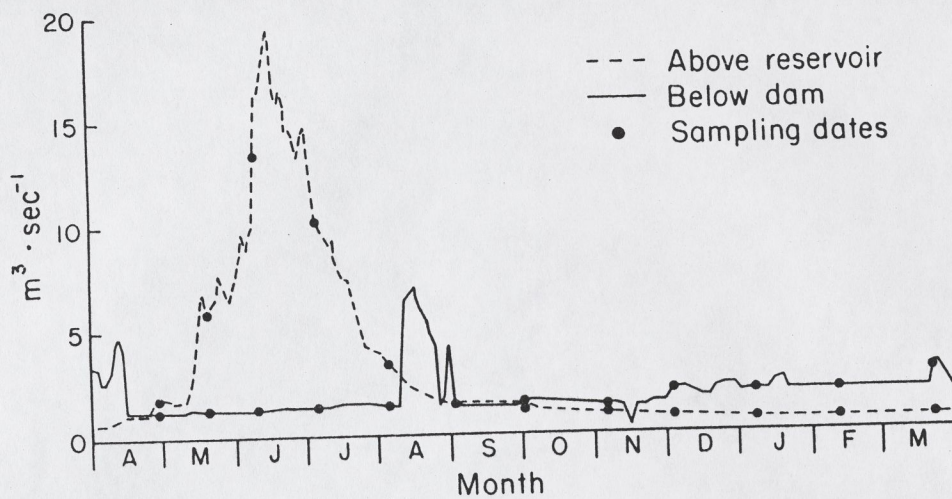


Fig. 1. Flow regime of the Blue River, Colorado, during the year of the study.

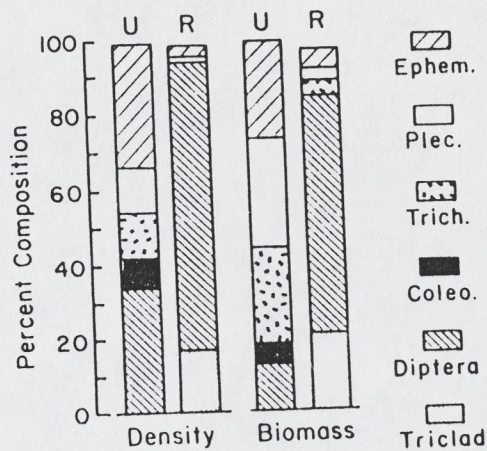


Fig. 2. Relative contributions of major taxa to total zoobenthos at unregulated (U) and regulated (R) sites on the Blue River, Colorado. Values less than 1% are not indicated.

Ward, J. V. and N. J. Voelz. 1988.

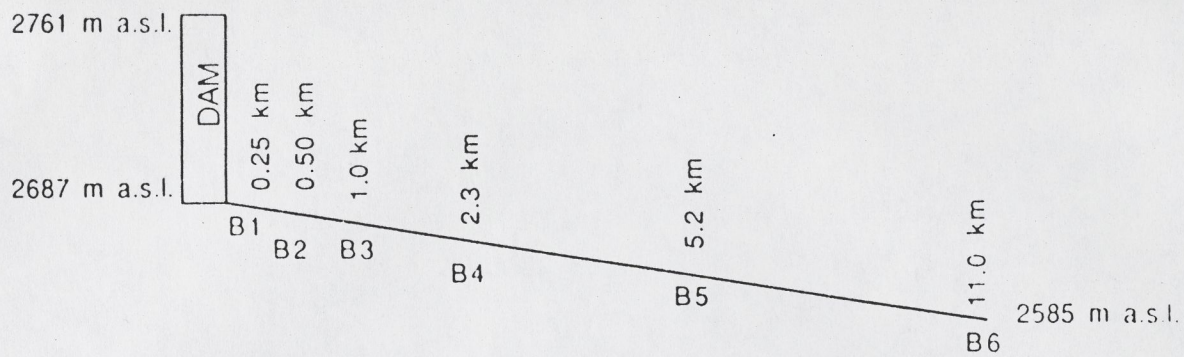


Figure 1. Location of study area (black square) on the western slope of the Rocky Mountains (top). Locations of sampling sites (B1-B6) are shown diagrammatically (bottom)

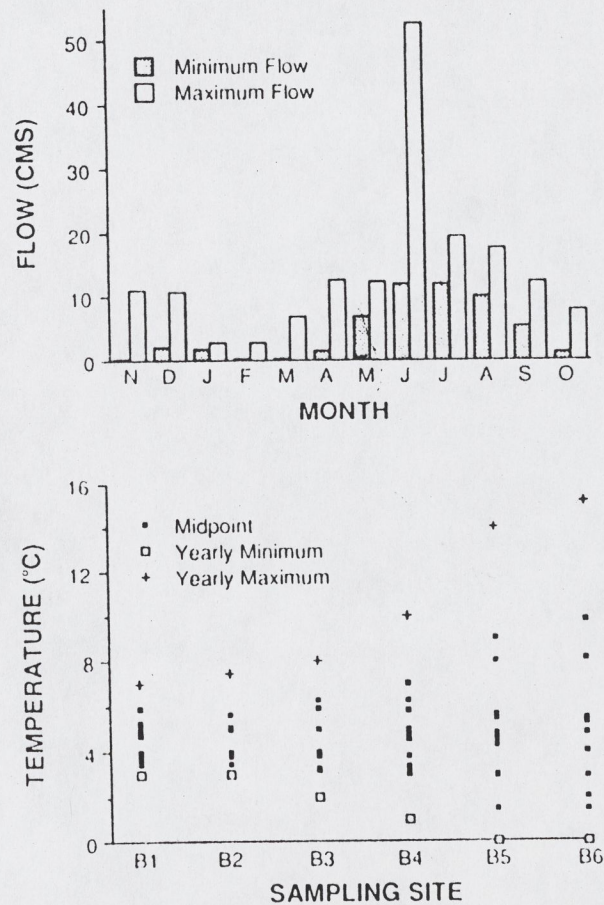


Figure 2. Flow and temperature data for the study period. Midpoint refers to the average of the maximum-minimum temperatures for each month. Temperature data for July 1985 are excluded (see text)

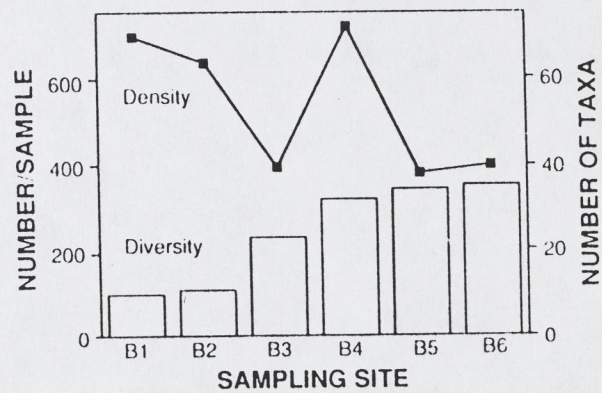


Figure 4. Annual average number of zoobenthos per sample (line) and total number of taxa (bars) at each sampling site. Number of taxa (mostly species) excludes rare species (i.e. those that occurred in <2 months). Chironomids were not identified further than family.

Voelz, N. J. and J. V. Ward. 1989.

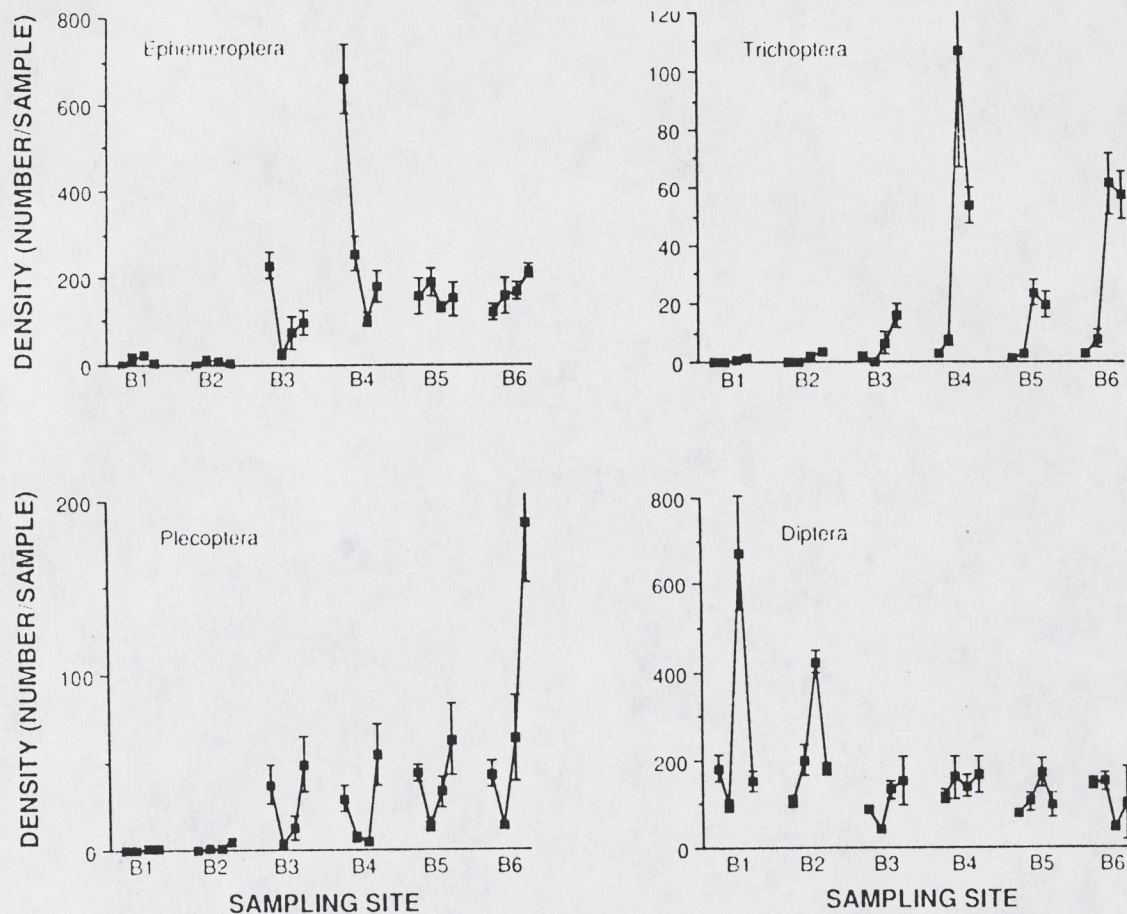


Figure 5. Seasonal mean numbers (± 1 SE) per sample of the major insect orders ($n = 12$, winter and spring; $n = 8$, spring at site B6; $n = 8$, summer and fall). The four squares at each site represent winter, spring, summer, and fall, respectively.

Voelz, N. J. and J. V. Ward. 1989.

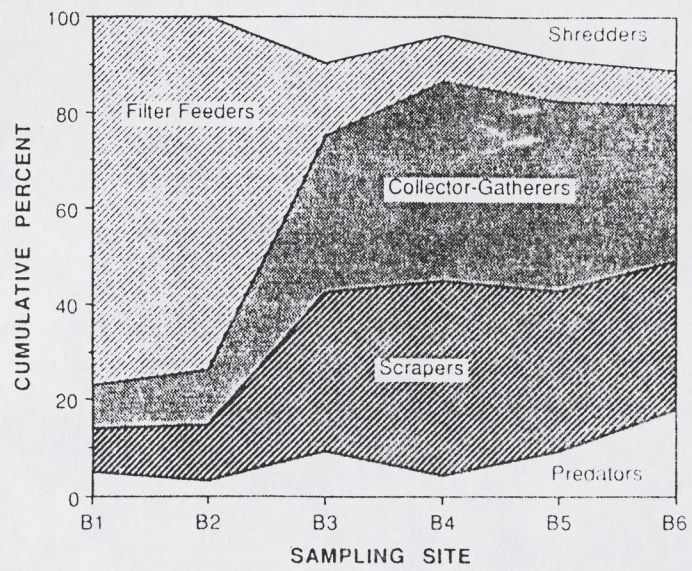


Figure 3. Relative contributions of macroinvertebrate functional feeding groups (*sensu* Merritt and Cummins, 1984) along the regulated Blue River longitudinal gradient

Voelz, N. J. and J. V. Ward. 1990.

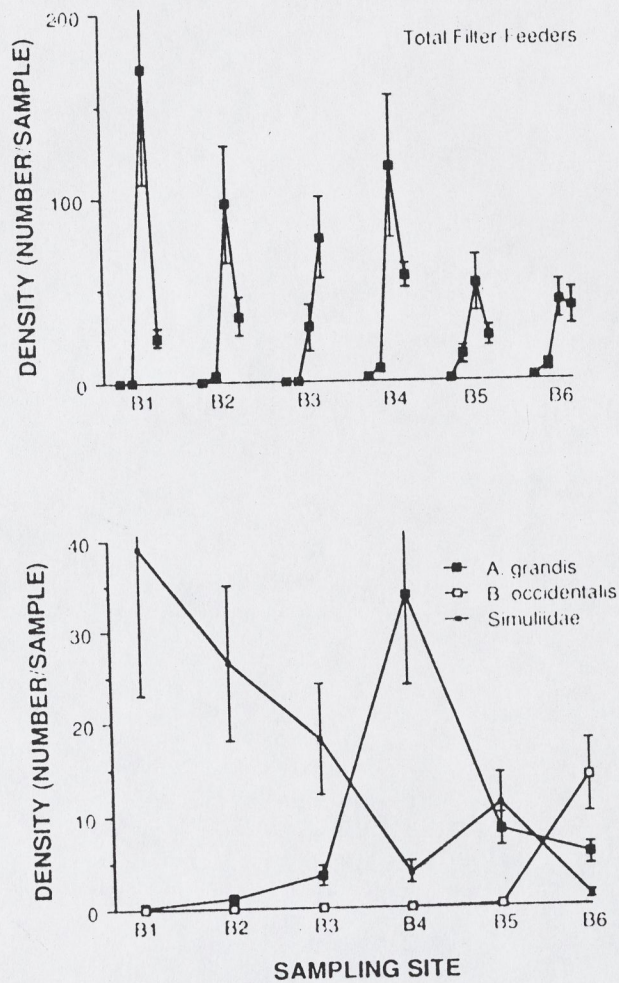


Figure 7. Top graph shows seasonal mean number (± 1 SE) per sample of total filter-feeders ($n = 12$, winter and spring; $n = 8$, spring at site B6; $n = 8$, summer and fall). The four squares for each site represent values for winter, spring, summer, and fall, respectively. Bottom graph depicts the annual mean number of organisms per sample (± 1 SE) for the filter-feeders *Arctopsyche grandis*, a hydropsychid caddisfly; *Brachycentrus occidentalis*, a brachycentrid caddisfly; and Simuliidae, black flies ($n = 40$; $n = 36$ at site B6)

Voelz, N. J. and J. V. Ward. 1989.

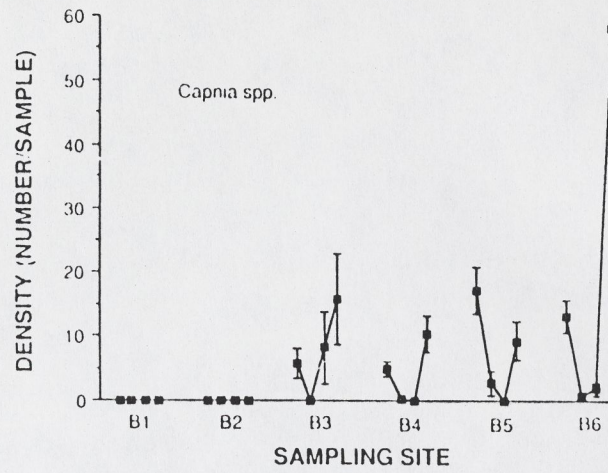


Figure 6. Seasonal mean numbers (± 1 SE) per sample of nymphs of the stoneflies *Capnia* spp. ($n = 12$, winter and spring; $n = 8$, spring at site B6; $n = 8$, summer and fall). The four squares at each site represent values for winter, spring, summer, and fall, respectively.

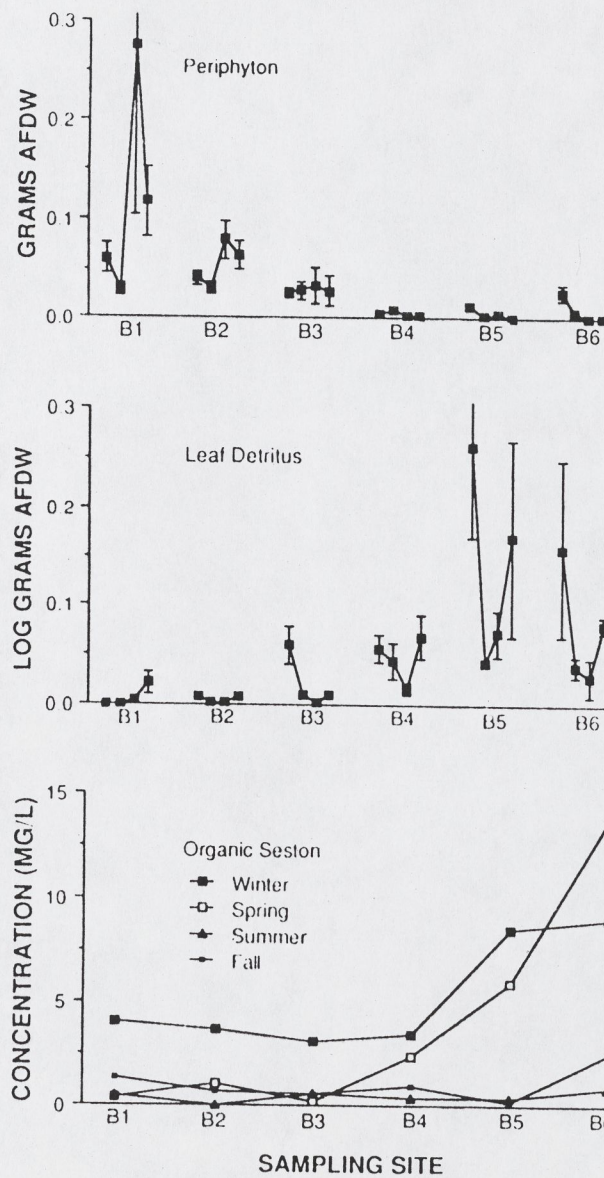


Figure 3. Food resource gradients. Periphyton ($n = 9$, winter and spring; $n = 6$, spring at site B6; $n = 6$, summer and fall) and leaf detritus ($n = 3$) are represented as seasonal means ± 1 SE. The four squares for periphyton and leaf detritus at each site represent values for winter, spring, summer, and fall, respectively. Values from single seasonal samples are shown for organic seston.

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SANTA ROSALIA RECONSIDERED: SIZE RATIOS AND COMPETITION

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"When Prof. Buckland, the eminent osteologist and geologist, discovered that the relics of St. Rosalia at Palermo, which had for ages cured diseases and warded off epidemics, were the bones of a goat, this fact caused not the slightest diminution in their miraculous power."

A. D. White, 1896, p. 29

Hutchinson's (1959) seminal paper, "Homage to Santa Rosalia or Why are there so many kinds of animals?" raised many issues that have subsequently dominated evolutionary ecology. One answer Hutchinson proposed to his question was that two species in the same trophic level can coexist if the ratio of sizes of their trophic apparatus is sufficiently large, since this would allow them to avoid competitive exclusion. For birds and mammals Hutchinson suggested a critical size ratio of 1.3. Two species whose sizes (or whose skulls' or culmens' sizes) differ by a factor less than 1.3 would not be able to occur sympatrically and syntopically: "This latter figure may tentatively be used as an indication of the kind of difference necessary to permit two species to co-occur . . ." He arrived at this ratio inductively, by examining a few sets of birds and mammals, and he interpreted his results as examples of competitively induced character displacement (Brown and Wilson, 1956). In the 20 years since Hutchinson's suggestion, interest in the importance of size differences for coexistence has led to two related ideas, codified in textbooks (e.g., Ricklefs, 1973; Pianka, 1978) and cited very frequently:

- 1) There is a minimum size ratio compatible with coexistence of ecologically similar species (Hutchinson, 1959; Schoener, 1965, 1970; MacArthur, 1971; McNab, 1971; Diamond, 1972, 1973; MacArthur et al., 1972; Price, 1972, 1975; Barbour, 1973; Brown, 1973; Enders, 1974, 1975, 1976; Fen-

chel, 1975; Hespeneide, 1975; Robison, 1975; Inouye, 1977, 1978; Uetz, 1977; May, 1978; Pearson and Mury, 1979; Edwards and Emberton, 1980).

- 2) Three or more ecologically similar coexisting species tend to have constant size ratios between species adjacent in a size-ranking, though the constant factor may vary from site to site (Holmes and Pitelka, 1968; MacArthur, 1971, 1972; McNab, 1971; Diamond, 1972, 1973, 1975; Brown, 1973, 1975; Schoener, 1974; Pulliam, 1975; Inouye, 1977, 1978; May, 1978; Smith, 1978; Terborgh et al., 1978; Krzysik, 1979; Oksanen et al., 1979).

Further, both patterns are attributed to the workings of interspecific competition.

These two patterns—minimum and constant size ratios, respectively—are so widely heralded that they have even filtered into the lay press: Gould (1979), in an homage to "Homage to Santa Rosalia," views these ratios as extremely important and even states the proper null hypothesis—"I do not think it is an accident"—without proposing a test. Horn and May (1977) have extended the notion of constant ratios to ensembles of musical instruments, sets of skillets, and bicycle wheels, again without statistical tests.

Here we present tests for whether species' sizes really are reasonably viewed as non-random and not independent, and apply them to appropriate literature data. We also examine statistically several related claims about patterns of size ratios and the relationship of these patterns to interspecific competition.

Tests for Constancy of Ratios

Our tests are based on whether one or more points on a line segment can be reasonably construed as having been uni-

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form-randomly and independently thrown down between the endpoints. That is, we assume that the largest and smallest animals in a series respectively represent the maximum and minimum sizes that this type of animal can have in a region, for physiological, anatomical, historical, or whatever reasons, and ask whether the logarithms of the intermediate species' sizes may be viewed as independently and randomly drawn from a uniform distribution between the extremes. Asking whether size ratios are constant is equivalent to asking whether the logarithms of sizes are equidistant on a line, since $\log(a/b) = \log a - \log b$. That is, if the ratios $a/b, b/c, c/d, \dots$ were equal, $\log a - \log b = \log b - \log c = \log c - \log d = \dots$. One could reasonably argue that the true possible size range is not that spanned by the observed maximum and minimum, but rather a larger range. Except where physiological or anatomical research indicates otherwise, this argument may be true. But if so, the results that we detail below are likely biased in the direction of constancy. A set of points that is significantly overdispersed (constant ratios) along a line segment (a, z) could actually be random or even significantly clumped along an extended segment (A, Z) , where $A < a$ and/or $Z > z$. So apparent constancy of ratios could be illusory, but the opposite illusion would not as likely occur, at least by means of falsely narrow limits.

Barton and David (1956) provide a simple, powerful test for whether points along a line, scaled either arithmetically or logarithmically, are unlikely to be the result of independent, uniform-random placement. If there are $n - 1$ interior points, producing n segments, for $n + 1$ species total, let g_i be the length of the i th smallest segment, and $G_{rs} = g_r/g_s \leq 1$ be the ratio of the r th smallest segment to the s th smallest, where $r < s$. If a is any number, they show that

$$\begin{aligned} Pr(G_{rs} < a) &= a^n C_s {}^s C_{r+1} r(r+1) \sum_{i=0}^{r-1} \sum_{j=0}^{s-r-1} (-1)^{i+j} \\ &\cdot (r-1) C_i (s-r-1) C_j \end{aligned}$$

$$\cdot [(n-s+j+1)\{s-r+i-j\}a + (n-s+j+1)]^{-1} \quad (1)$$

This equation reduces to compact form for three cases: (i) the ratio of the r th smallest segment to the largest, $Pr(G_{rn} < a)$; (ii) the ratio of the smallest segment to the r th smallest, $Pr(G_{1r} < a)$; and (iii) the ratio of the smallest to the largest segment, $Pr(G_{1n} < a)$. We have used the following three ratios as test statistics, where H_0 is the null hypothesis that the ratios of sizes are random, and H_1 is the alternative hypothesis that they are regularly spaced (constant): $G_{1n}, G_{2n}, G_{1(n-1)}$. Our rationale was that one might not want to reject or accept an hypothesis simply because one size ratio was remarkably large or small. For example, it may be that two species' sizes are very similar, generating a small g_1 and small G_{1n} , but all other size ratios are very similar. Or one size ratio may be very large, generating a large g_n and small G_{1n} , but all other ratios are similar. Of course we could have used any other G_{rs} , but we felt these three were as good as any, and also are defined whenever the number of species exceeds three. Barton and David also give the distributions for $D_{rs} = g_s - g_r$, and we could have used these as well. Smart (1976) used $D_{(n-1)m}$ to test whether species-abundance curves are distributed according to the broken-stick model. This is but another version of the same problem, since one is again asking if several points on a line can reasonably be viewed as independently and uniformly distributed.

One kind of data for which the claim of constant size ratios has been made, including Hutchinson's original examples, consists of species trios, so that we are examining a logarithmically scaled line with a single break and wish to know if the break can reasonably be construed as randomly located, according to a uniform distribution. As test statistics here, by analogy to Barton and David's statistics, we use G_{12} , the ratio of the smaller to the larger segment. If the largest point is L , the smallest point is S , and the intermediate point is M , let $b = \min[(L -$

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$M), (M - S)], c = \max[(L - M), (M - S)],$ and $a = b/c$. It can easily be shown that

$$Pr(G_{12} < a) = \frac{2b}{b + c} = (\frac{1}{2} + 1/2a)^{-1}. \quad (2)$$

We still require a test when the precision of data measurement or reporting is sufficiently low to produce ties, for when two sizes are equal, their ratio is 1, and the log of their ratio = $g_1 = 0$, so that $Pr(G_{1m} < \text{observed}) = 0$ for any m . One should, of course, view such a tie as damaging to an hypothesis of ratio constancy, but one would not, for a large set of data, wish to rest one's assessment of H_0 vs. H_1 on one pair of sizes. Further, presumably no two sizes would be exactly equal if measurement were precise enough, so $Pr(G_{1m} < \text{observed})$ would never really be nil. We have replaced G_{1n} and $G_{1(n-1)}$ with $G_{(n-1)n}$ and $G_{(n-2)n}$ when $g_1 = 0$. When $g_2 = 0$ as well, we omitted G_{2n} . We note in passing that Poole and Rathcke (1979) suggest as test statistic for whether a set of points may be viewed as independently and uniform-randomly distributed on a line the sample variance of the sizes of the g_i 's. Their test may be used even when several $g_i = 0$, but with several sets of data we found that this test is markedly less sensitive to non-randomness than are the Barton-David tests, so we have used the latter.

Tests for Minima

We have now described our test for *constancy* of size ratios in a set of three or more species. Our test for the significance of an observed *minimum* size ratio parallels the Barton-David test for constancy of size ratios. Since any set of numbers has a minimum, the observation in a given set of data of a particular minimum size ratio cannot be adduced as evidence that competitive exclusion has precluded species that would have produced smaller ratios. For, if measurements are precise enough, presumably no two species' sizes are completely identical, so any set of data consisting of one or more species pairs will always show a ratio exceeding unity.

The strongest evidence for a necessary minimum size ratio would require experimental introductions. But even without these, we suggest two possible ways to generate a falsifiable hypothesis about minima. First, one might ask of a set of n observed ratios (or a set of differences of logarithms of $n + 1$ sizes) produced by $n + 1$ size-ranked species whether the minimum, g_1 , is less than could reasonably have been expected if the points had been randomly strewn on a line. Barton and David show that the expected size of the minimum segment when a unit line is broken into n segments is

$$E(g_1) = 1/n^2, \quad (3)$$

while its variance is

$$\text{var}(g_1) = (n - 1)/n^4(n + 1). \quad (4)$$

Irwin (1955) proves that the probability that the minimum segment is smaller than any given number a is

$$\begin{aligned} Pr(g_1 < a) &= 1 - (1 - na)^{n-1} \\ &\quad \text{for } a \leq 1/n \\ &= 1 \quad \text{for } a > 1/n. \end{aligned} \quad (5)$$

It is equation (5), the exact test, that we use to test for whether an observed minimum ratio is larger than chance alone would likely have produced. In other words, we ask if sizes independently and uniform-randomly distributed on a log-scaled line would likely have produced a minimum segment as large as that observed.

Second, one might ask of a group of pairs of species, each pair in a different site, whether the observed minimum size ratio for all pairs is less than one would have expected if the logarithms of each pair's sizes were simply two points independently and uniform-randomly thrown on a line. Of course the endpoints of the line—maximum and minimum possible sizes—would have to be known to render this question a falsifiable hypothesis. One might view this problem in two ways: (a) If the species' sizes were fixed, the maximum and minimum sizes at any site would be the maximum and minimum sizes, re-

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spectively, in the species pool. (b) If, on the other hand, the species' sizes were evolutionarily plastic in response to pressure exerted from sympatric species (e.g., Brown and Wilson's [1956] model of character displacement), the maximum and minimum sizes would be those permissible on physiological and developmental grounds.

Were (a) the model chosen, the proper test of an observed minimum for a set of species pairs would be to see how it fit into the distribution of minima if species pairs were randomly drawn with replacement from the pool and assigned to sites (e.g., Strong et al., 1979). Since we are assuming throughout that character displacement is possible and are asking whether evolution has molded the joint distribution of species' sizes in any particular way, we instead choose model (b). Here the appropriate test of an observed minimum for a set of species pairs is given by Pielou and Arnason (1966), i.a., who note that for a unit line on which two points are randomly placed, the distribution function of the distance x between them is $2x - x^2$. Thus, for any specified a between 0 and 1, $Pr(x < a) = 2a - a^2$. This in turn means that if we log-scale the endpoints of a line segment, then scale the segment to unity by multiplying it by a factor b , the null (random) probability that an observed ratio a would have been exceeded is $Pr(x > a) = 1 - 2ab + a^2b^2$. The null probability that all n ratios would exceed a is then $(1 - 2ab + a^2b^2)^n$.

RESULTS

Table 1 lists the literature claims of necessary minimum ratios and/or constant ratios for which sufficient data appear to be available to test the claim statistically. In fact, it is likely that some of these studies are not amenable to statistical analysis since several bodies of data were used to examine an hypothesis but only those sustaining it were reported, although, unlike other examples cited below, the literature descriptions do not permit us to know this for sure. For instance, Hutchinson's original study (Table 1.8) describes three trios of species; were these "dredged" (Selvin

and Stuart, 1966) from a survey of many groups of species? Similarly, MacArthur's kingfishers (Table 1.13), MacArthur et al.'s flycatchers (Table 1.14), and Storer's hawks (Table 1.17) cited by MacArthur (1972) may all be examples claimed to manifest constant ratios dredged from a survey of unreported data that did not appear to manifest the trend. And Brown (1975) cites seven examples (Table 1.6, 1.7, 1.16, 1.17, 1.20, 1.21, 1.26) that he believes show constant size ratios; these were likely not the only data sets he examined.

But even if we include these questionable cases, the most striking fact about Table 1 and its statistical summary in Table 2 is how few of the examples support the contentions of ratio constancy and extraordinarily large minima at traditional levels of statistical significance. Of 21 claims of ratio constancy, only four (Table 2.7, 2.15, 2.17, 2.19) are unequivocally sustained at the .05 level for all data. For another three (Table 2.6, 2.11, 2.27), for a large fraction (but not a majority) of the individual cases one would reject the independent, random hypothesis in favor of one of constancy. One example (Table 2.22) shows that all data cited as showing ratio constancy actually manifest ratio clumping (too many small ratios)! If we raise our level for rejecting H_0 (independent, uniform-random size dispersion on a log-scaled line) in favor of H_1 (constant ratios) from .05 to .30, we find that of the 21 claims 11 are generally sustained (though several still with a number of cases not showing the claimed trend), while for two claims (Table 2.10, 2.22) the data show exactly the opposite trend—too many small ratios. For Brown's seven examples noted above, only three (including his own desert rodents) clearly manifest a tendency toward constant size ratios.

Eighteen authors claimed some data set(s) demonstrated that a particular minimum size ratio is required for species to coexist, but for only one (Table 2.31) is the independent, uniform-random hypothesis rejected for all data at the .05 level in favor of the alternative, a large minimum. For two studies (Table 2.29,

TABLE 1. Studies that have been adduced as manifesting either minimum size ratios (M) or constancy of ratios (C). "Probability" is null probability of a result as extreme as that observed. Bracketed results represent the same data set.

Study	Taxon	Statistic	Probability	
1. McNab, 1971 C, M	Bats	$G_{13} = .544$	} { .078 .127 .276 .134	
		$G_{23} = .855$		
		$G_{12} = .636$		
		Min = .211		
2. McNab, 1971 C, M. Data of Phillips, 1968	Bats	$G_{12} = .295$.544	
	Vella Lavella	$G_{12} = .145$.747	
	San Cristobal	$G_{12} = .157$.728	
	Shortland	$G_{12} = .218$.642	
	Florida	$G_{12} = .403$.466	
	Malaita	$G_{13} = .483$	} { .110 .250	
	Kolombangara	$G_{23} = .750$		
		$G_{12} = .644$	} { .356 .123	
		Min = .216		
	Fauro	$G_{14} = .727$	} { .003 .043 .004 .001	
		$G_{24} = .741$		
		$G_{13} = .897$		
		Min = .222		
		Santa Ysabel	$G_{14} = .134$	} { .391 .631 .470 .386
			$G_{24} = .215$	
			$G_{13} = .217$	
			Min = .068	
		Choiseul	$G_{16} = .130$	} { .194 .129 .211 .205
			$G_{26} = .318$	
			$G_{15} = .201$	
		Min = .045		
	Bougainville	$G_{16} = .215$	} { .072 .129 .023 .050	
		$G_{26} = .318$		
		$G_{15} = .457$		
		Min = .075		
	Guadalcanal	$G_{17} = .308$	} { .011 .030 .020 .026	
		$G_{27} = .388$		
		$G_{16} = .379$		
		Min = .065		
3. McNab, 1971 C, M. Data of Goodwin and Greenhall, 1971	Bats	$G_{15} = .173$	} { .189 .480 .157 .158	
	fruit-eaters	$G_{25} = .199$		
		$G_{14} = .325$		
		Min = .074		
		insect-eaters	$G_{14} = .030$	} { .805 .349 .880
			$G_{24} = .376$	
		$G_{13} = .038$		
		Min = .014	.845	
4. Fleming et al., 1972 ¹	Bats	$G_{1,27} = 0$	} { 1 .597 .810	
	La Pacifica	$G_{26,27} = .755$		
		$G_{25,27} = .494$		
		Sherman	$G_{1,30} = 0$	} { 1 .391 .376
			$G_{29,30} = .856$	
			$G_{28,30} = .722$	
		Rodman	$G_{1,27} = 0$	} { 1 .241 .337
			$G_{26,27} = .912$	
			$G_{25,27} = .732$	

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TABLE 1. *Continued.*

Study	Taxon	Statistic	Probability	
5. Brown, 1973 ² <i>C, M</i>	Desert rodents 1	$G_{17} = .093$	} { .229 .116 .382 .299	
		$G_{27} = .263$		
		$G_{16} = .096$		
		Min = .026		
	2	$G_{15} = .258$	} { .086 .197 .229 .166	
		$G_{25} = .353$		
		$G_{14} = .263$		
		Min = .072		
	3	$G_{14} = .376$	} { .074 .135 .139 .086	
		$G_{24} = .757$		
		$G_{13} = .506$		
		Min = .140		
	4	$G_{14} = .472$	} { .036 .132 .081 .037	
		$G_{24} = .579$		
		$G_{13} = .605$		
		Min = .167		
	5	$G_{16} = .221$	} { .067 .191 .125 .058	
		$G_{26} = .270$		
$G_{15} = .266$				
Min = .072				
6	$G_{16} = .263$	} { .041 .090 .125 .058		
	$G_{26} = .360$			
	$G_{15} = .266$			
	Min = .072			
7	$G_{16} = .245$	} { .050 .090 .083 .074		
	$G_{26} = .360$			
	$G_{15} = .316$			
	Min = .068			
8	$G_{12} = .667$	} { .200 .046		
	$G_{12} = .913$			
14	$G_{12} = .942$	} { .030 .144		
	$G_{12} = .748$			
15	16	$G_{13} = .180$	} { .454 .049 .738 .556	
		$G_{23} = .942$		
		$G_{12} = .191$		
		Min = .085		
17	18	$G_{14} = .096$	} { .507 .342 .708 .595	
		$G_{24} = .381$		
		$G_{13} = .102$		
		Min = .040		
18	19	$G_{16} = .112$	} { .241 .015 .343 .359	
		$G_{26} = .541$		
		$G_{15} = .139$		
		Min = .031		
6. Brown, 1975 <i>C, M</i>	Desert rodents Great Basin	$G_{14} = .374$	} { .075 .136 .139 .087	
		$G_{24} = .573$		
		$G_{13} = .506$		
		Min = .139		
	Sonoran	20	$G_{15} = .360$	} { .033 .131 .029 .020
			$G_{25} = .416$	
			$G_{14} = .563$	
			Min = .125	

TABLE 1. *Continued.*

Study	Taxon	Statistic	Probability	
7. Brown, 1975 C. Data of Rosenzweig, 1966	Mammals	$G_{1,14} = 0$	} { 1 .092 .002 .034	
		$G_{2,14} = .106$		
		$G_{13,14} = .999$		
		$G_{12,14} = .899$		
8. Hutchinson, 1959. <i>M</i>	Finches			
	James	$G_{12} = .745$.146	
	Indefatigable	$G_{12} = .977$.023	
	S. Albemarle	$G_{12} = .540$.299	
9. Schoener, 1974 ³ Data of Schoener, 1965	Birds			
	<i>Eriola</i> , N. Mackenzie	$G_{14} = .198$	} { .254 .005 .467	
		$G_{24} = .904$		
		$G_{13} = .219$		
		<i>Trogon</i> , lowlands, W. Costa Rica	$G_{14} = .067$	} { .620 .058 .774
			$G_{24} = .703$	
			$G_{13} = .076$	
		<i>Trogon</i> , Panama	$G_{14} = 0$	} { 1 .781 .917
			$G_{24} = .144$	
			$G_{34} = .215$	
		<i>Thryothorus</i> , Pacific lowlands, C.R.	$G_{14} = 0$	} { 1 .330 .592
			$G_{24} = .390$	
			$G_{34} = .506$	
		<i>Dicaeum</i> , Bohol	$G_{14} = 0$	} { 1 .938 .468
			$G_{24} = .064$	
			$G_{34} = .605$	
		<i>Dendroica</i> , Maine	$G_{14} = 0$	} { 1 1 .984
			$G_{24} = 0$	
			$G_{34} = .105$	
		<i>Aimophila</i> , highlands, Oaxaca	$G_{14} = 0$	} { 1 .918 .938
		$G_{24} = .076$		
		$G_{34} = .187$		
	<i>Tangara</i> , central Costa Rica	$G_{15} = 0$	} { 1 .110 .020 0	
		$G_{25} = .441$		
		$G_{35} = .853$		
		$G_{45} = 1$		
	<i>Tangara</i> , central Costa Rica	$G_{15} = 0$	} { 1 .623 .620 .739	
		$G_{25} = .147$		
		$G_{35} = .294$		
		$G_{45} = .441$		
10. May, 1978 C, M. Data of Cody, 1974	Birds			
	Wyoming Willows	$G_{1,11} = .066$	} { .145 .385 .002 .021	
		$G_{2,11} = .072$		
		$G_{1,10} = .305$		
		Min = .029		
		Wyoming Sagebrush	$G_{14} = .036$	} { .771 .880 .840 .779
			$G_{24} = .096$	
			$G_{13} = .052$	
			Min = .020	
		Colorado Saltbush	$G_{14} = .202$	} { .247 .587 .453 .277
			$G_{24} = .237$	
			$G_{13} = .227$	
			Min = .087	
		Mohave Desert	$G_{1,11} = .024$	} { .476 .065 .279 .449
			$G_{2,11} = .164$	
			$G_{1,10} = .062$	
		Min = .007		

TABLE 1. *Continued.*

Study	Taxon	Statistic	Probability
	California	$G_{1,16} = 0$	1
	Chaparral	$G_{15,16} = .848$.341
		$G_{14,16} = .302$.951
		Min = 0	1
	Lower Sonoran Desert	$G_{1,15} = .026$.302
		$G_{2,15} = .032$.569
		$G_{1,14} = .052$.185
		Min = .007	.212
	Arizona	$G_{1,13} = .003$.887
	Mesquite	$G_{2,13} = .013$.905
		$G_{1,12} = .003$.921
		Min = .001	.855
	Arizona Pine-Oak	$G_{1,19} = 0$	1
		$G_{2,19} = .010$.858
		$G_{18,19} = .879$.292
		$G_{17,19} = .709$.320
		Min = 0	1
	Coastal Scrub, Chile	$G_{14} = .096$.507
		$G_{24} = .175$.715
		$G_{13} = .300$.343
		Min = .060	.439
	Matorral, Chile	$G_{1,18} = 0$	1
		$G_{2,18} = .033$.435
		$G_{17,18} = .812$.430
		$G_{16,18} = .512$.694
		Min = 0	1
	Chilean	$G_{1,15} = 0$	1
	Savannah	$G_{2,15} = .017$.807
		$G_{14,15} = .697$.616
		$G_{13,15} = .571$.534
		Min = 0	1
11. Terborgh et al., 1978 C, M	Birds		
	Guadeloupe nectivores	$G_{12} = .747$.145
	Guadeloupe gleaners	$G_{12} = .636$.222
	Terre de Bas fruit- and seed-eaters	$G_{13} = .324$.239
		$G_{23} = .436$.576
		$G_{12} = .742$.188
		Min = .184	.201
	Desirade fruit- and seed-eaters	$G_{15} = .498$.008
		$G_{25} = .742$.008
		$G_{14} = .553$.031
		Min = .123	.022
	Guadeloupe fruit- and seed-eaters	$G_{18} = .130$.090
		$G_{28} = .315$.033
		$G_{17} = .145$.165
		Min = .029	.153
12. Pulliam, 1975 C. Data of Pulliam and Mills, 1975	Sparrows	$G_{17} = .047$.463
		$G_{27} = .047$.828
		$G_{16} = .106$.345
13. MacArthur, 1971 C, M	Kingfishers	$G_{14} = .320$.110
		$G_{24} = .671$.074
		$G_{13} = .333$.300
		Min = .108	.183
14. MacArthur et al., 1972 C, M	Flycatchers all four species	$G_{13} = .350$.212
		$G_{23} = .730$.249
		$G_{12} = .480$.419
		Min = .168	.245

TABLE 1. *Continued.*

Study	Taxon	Statistic	Probability
	omitting largest species	$G_{12} = .730$.156
15. Holmes and Pitelka, 1968 C	Sandpipers	$G_{13} = .896$ $G_{23} = .896$ $G_{12} = 1$	$\left. \begin{array}{l} .003 \\ .090 \\ 0 \end{array} \right\}$
16. Brown, 1975 C. Data of Pulliam and Enders, 1971	Finches	$G_{14} = .126$ $G_{24} = .177$ $G_{13} = .360$	$\left. \begin{array}{l} .413 \\ .711 \\ .269 \end{array} \right\}$
17. MacArthur, 1972; Brown, 1975 C. Data of Storer, 1966	Hawks males females	$G_{12} = .932$ $G_{12} = 1$.033 0
18. Schoener, 1970 ⁴	Anoles 3-species associations	$G_{12} = .742$ $G_{12} = .707$ $G_{12} = .041$ $G_{12} = .692$ $G_{12} = .839$ $G_{12} = .096$ $G_{12} = .480$ $G_{12} = .508$ $G_{12} = .085$.148 .171 .921 .182 .088 .825 .351 .326 .842
	4-species associations	$G_{13} = .009$ $G_{23} = .398$ $G_{12} = .024$ $G_{13} = .324$ $G_{23} = .591$ $G_{12} = .548$ $G_{13} = .040$ $G_{23} = .251$ $G_{12} = .160$ $G_{13} = .286$ $G_{23} = .883$ $G_{12} = .324$ $G_{13} = .086$ $G_{23} = .239$ $G_{12} = .358$ $G_{13} = .086$ $G_{23} = .212$ $G_{12} = .403$	$\left. \begin{array}{l} .960 \\ .621 \\ .964 \\ .239 \\ .396 \\ .355 \\ .837 \\ .799 \\ .778 \\ .284 \\ .102 \\ .582 \\ .683 \\ .813 \\ .545 \\ .683 \\ .844 \\ .497 \end{array} \right\}$
19. Krzysik, 1979 C	Salamanders snout-vent length head width	$G_{16} = .144$ $G_{26} = .767$ $G_{15} = .144$ $G_{16} = .359$ $G_{26} = .498$ $G_{15} = .489$	$\left. \begin{array}{l} .164 \\ .001 \\ .330 \\ .013 \\ .024 \\ .017 \end{array} \right\}$
20. Barbour, 1973 M Brown, 1975 C. Data of Barbour, 1973	Fish	$G_{12} = .133$ $G_{13} = .319$ $G_{23} = .950$ $G_{12} = .330$ Min = .140 $G_{17} = .080$ $G_{27} = .300$ $G_{16} = .100$ Min = .023	$\left. \begin{array}{l} .611 \\ .244 \\ .042 \\ .575 \\ .336 \\ .278 \\ .078 \\ .367 \\ .349 \end{array} \right\}$

TABLE 1. *Continued.*

Study	Taxon	Statistic	Probability		
21. Brown, 1975 C. Data of Roughgarden, 1974	Reef fish groupers largest	$G_{1,15} = .011$	} { .593		
		$G_{2,15} = .066$		} { .223	
		$G_{1,14} = .016$		} { .587	
	mean	$G_{1,15} = .034$	} { .214		
		$G_{2,15} = .076$		} { .167	
		$G_{1,14} = .035$		} { .317	
	parrotfish and surgeonfish largest	$G_{1,12} = 0$	} { 1		
		$G_{2,12} = .121$		} { .115	
		$G_{11,12} = .941$		} { .123	
		$G_{10,12} = .587$		} { .441	
		mean		$G_{1,12} = .005$	} { .836
				$G_{2,12} = .111$	
22. Smith, 1978 ⁵ C	Reef fish Tekite reef 1	$G_{1,51} = 0$	} { 1		
		$G_{50,51} = .687$		} { .786	
		$G_{49,51} = .648$		} { .637	
	same species, several collections	$G_{1,50} = 0$	} { 1		
		$G_{49,50} = .696$		} { .771	
		$G_{48,50} = .684$		} { .553	
	as above, minus last 4 points	$G_{1,46} = 0$	} { 1		
		$G_{45,46} = .696$		} { .763	
		$G_{44,46} = .623$		} { .672	
	23. Price, 1972 M	Parasitic wasps	$G_{14} = .274$	} { .151	
			$G_{24} = .471$		} { .230
			$G_{13} = .288$		} { .359
Min = .102			} { .207		
24. Price, 1975 M. Data of Heatwole and Davis, 1965	Parasitic wasps	$G_{12} = .584$	} { .262		
25. Pearson and Mury, 1979 ⁶	Tiger beetles pond edge	$G_{1,11} = .009$	} { .752		
		$G_{2,11} = .009$		} { .966	
		$G_{1,10} = .056$		} { .314	
		Min = .006		} { .519	
	grassland	$G_{15} = .039$	} { .673		
		$G_{25} = .217$		} { .437	
		$G_{14} = .052$		} { .754	
		Min = .017		} { .694	
	26. Brown, 1975 C. Data of Evans, 1970	Wasps <i>Tachysphex</i>	$G_{14} = .172$	} { .302	
			$G_{24} = .455$		} { .248
			$G_{13} = .297$		} { .347
		<i>Philanthus</i>	$G_{13} = .538$	} { .081	
$G_{23} = .706$			} { .273		
$G_{12} = .763$			} { .172		
27. Inouye, 1977 ⁷ C, M		Bees Gothic	$G_{12} = .892$	} { .057	
			$G_{12} = .954$		} { .024
	Virginia Basin	$G_{12} = .912$	} { .046		
		$G_{12} = .607$		} { .245	
	Firth of Clyde	$G_{12} = .456$	} { .347		
		$G_{12} = .632$		} { .225	

TABLE 1. *Continued.*

Study	Taxon	Statistic	Probability	
28. Uetz, 1977 M	Wandering spiders	$G_{14} = .258$	} { .169	
		$G_{24} = .435$.271
	large spiders	$G_{13} = .327$	} { .308	
		Min = .104		.200
		$G_{12} = .782$.123
29. Enders, 1974 M. Data of Locket and Millidge, 1953	crab spiders	$G_{17} = 0$	} { 1	
		$G_{27} = .060$.757
	Orb-weaving spiders	$G_{67} = .424$	} { .836	
		$G_{57} = .347$.688
		$G_{17} = 0$		1
30. Enders, 1974 M. Data of Menge, 1866	Orb-weaving spiders	$G_{27} = .133$	} { .412	
		$G_{67} = .782$.347
		$G_{57} = .685$	} { .161	
31. Robison, 1975 ⁸ M	Trilobites	$G_{12} = .909$	} { .048	
		$G_{14} = .149$.353
		$G_{24} = .294$.481
		$G_{13} = .235$.439
		Min = .072		.361
	Site C	$G_{12} = .072$	} { .030	
		$G_{14} = .153$.344
		$G_{24} = .267$.530
		$G_{13} = .320$.317
		Min = .081		.309
	Site E	$G_{12} = .906$	} { .049	
		$G_{14} = .130$.402
		$G_{24} = .437$.269
		$G_{13} = .175$.547
		Min = .056		.467
Site F		} { .317		
			.309	
			.317	
			.530	
			.344	
Site G		} { .309		
			.317	
			.530	
			.344	
			.309	

¹ No detectable minimum; many small ratios. Poole-Rathcke test sustains claim for La Pacifica and Sherman.

² Other dunes had two species each.

³ Schoener (1974) suggests that some data show constant ratios, other data show ratios increasing with size. See text.

⁴ Claim is that ratios increase with size, and is sustained. See text.

⁵ Largest specimens of each species used. All 3 sets clumped by Poole-Rathcke test.

⁶ Claim is that grassland species exhibit a clear minimum, pond edge species do not.

⁷ First value for queens, second for workers; nectar robbers omitted.

⁸ Claim is that data from C, E, and F manifest large minimum, data from G do not; where 2 sets of values, first is for all species, second omits those with fewer than about 10% of all individuals.

2.30) the result is significant at the .05 level in exactly the opposite direction: too small an observed minimum for the sizes to be uniform-random and independent on a log-scaled line. Another six studies (Table 2.2, 2.5, 2.6, 2.8, 2.11, 2.27) have a large number (but often not a majority) of their cases manifesting the claimed high minimum, while one study (Table 2.10) shows many cases manifesting exactly the opposite tendency. If the rejection criterion is raised from .05 to .30, 13 studies generally (but usually with exceptional cases) support the contention of high minima, while three (Table 2.10, 2.29, 2.30) support the opposite contention. Finally, in three studies claiming necessary mini-

num ratios (and four other studies claiming constancy) sizes of at least one species pair were listed as identical, producing a ratio of 1.00. That this did not deter the claim of a necessary minimum ratio is discussed below. We also note that Fleming et al. (1972) were correct to suggest that their data showed too many small ratios to be compatible with a claim of either necessary minimum ratios or ratio constancy (Table 2.4).

Schoener (1965) presents size data for 61 trios of birds and 23 quartets, yielding pairs and trios of size ratios, respectively. Although he did not claim ratio constancy for all these data (Schoener, 1974), the set is so large that we examined it to see if the

TABLE 2. Statistical summary of data in Table 1. For a case to be denoted significant, half or more of the relevant statistics must be significant at the appropriate level. Entry in left of column is for significance in claimed direction; in right is for significance in opposite direction.

Claim C	Significance		Claim M	Significance		Cases with 0 ratios	Other claim	Significance		Claim sustained
	At .05	At .30		At .05	At .30			At .05	At .30	
1. Yes	0/1	1/1	Yes	0/1	1/1					
2. Yes	2/11	5/11	Yes	3/11	5/11					
		2/11			2/11					
3. Yes	0/2	1/2	Yes	0/2	1/2					
		1/2			1/2					
4. No			No				Too many small ratios	1/3	2/3	Yes
5. Yes	2/14	12/14	Yes	3/14	11/14					
6. Yes	1/2	2/2	Yes	1/2	2/2					
7. Yes	1/1	1/1	No			1				
8. No			Yes	1/3	3/3					
9.			No			7	Some constant, some increase with size			
10. Yes	0/11	2/11	Yes	1/11	3/11	4				
		4/11		4/11	6/11					
11. Yes	1/5	5/5	Yes	1/5	5/5					
12. Yes	0/1	1/1	No							
13. Yes	0/1	1/1	Yes	0/1	1/1					
14. Yes	0/1	1/1	Yes	0/1	1/1					
15. Yes	1/1	1/1	No							
16. Yes	0/1	0/1	No							
17. Yes	1/1	1/1	No							
18. No			No				Increase with size	1/1	1/1	Yes
19. Yes	1/1	1/1	No							
20. Yes	0/3	1/3	Yes	0/3	0/3					
21. Yes	0/2	0/2	No			1				
22. Yes	0/2	0/2	No			2				
	2/2	2/2								
23. No			Yes	0/1	1/1					
24. No			Yes	0/1	1/1					
25. Yes*	0/1	0/1	No				i no, ii yes	0/1	0/1	No
26. Yes	0/2	1/2	No							
27. Yes	1/3	3/3	Yes	1/3	3/3					
28. No			Yes	0/2	2/2					
29. No			Yes	0/1	0/1	1				
				1/1	1/1					
30. No			Yes	0/1	0/1	1				
				1/1	1/1					
31. No			Yes*	3/3* or 1/3	3/3* or 1/3		Manifested in 3 of 4 cases			Yes*

* If omit some species.

pattern was manifest. These data in tabular form suggest no pattern: some G_{ij} 's are large, others small; most are not statistically significant. A graph of the 61 trio data (Fig. 1) indicates a tendency toward regular spacing, however. We plot the fraction of the 61 trios on the ordinate vs. the probability level of the observed G_{12} (based on the null hypothesis of randomness) on the abscissa, and find a higher fraction of the cases at any probability

level than chance alone would have dictated if the null hypothesis were true. For example, for 36% of the species trios, one would have expected a more extreme result (greater G_{12} , or more equal size ratios) only 20% of the time. For 64% of the species trios one would have predicted a more extreme result (greater G_{12}) only 50% of the time. For 90% of the trios one would have predicted a more extreme result only 80% of the time. For the species

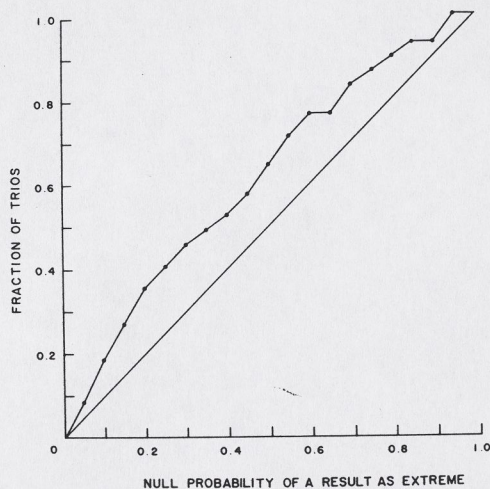


FIG. 1. Fraction of 61 bird trios (Schoener, 1965) vs. probability level of observed G_{12} (see text). Straight line is 45° .

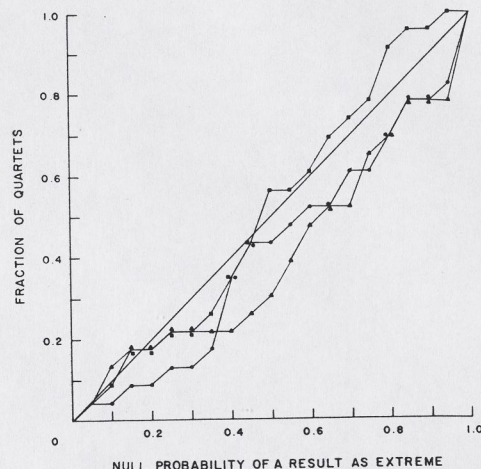


FIG. 2. Fraction of 23 bird quartets (Schoener, 1965) vs. probability of observed G_{13} (\blacktriangle), G_{23} (\blacksquare), and G_{12} (\bullet). Straight line is 45° .

quartets (Fig. 2) none of the test statistics (G_{13} , G_{23} , G_{12}) manifest this tendency; if anything, the trend is the opposite.

We may summarize this survey of hypotheses of ratio constancy and necessary minimum ratios in suites of three or more species as not generally sustained at traditional significance levels against an alternative of one particular model of independence of species' sizes. Some individual claims are supported, most are not, and for a few the data actually show exactly the opposite trend to that claimed. If the significance level is raised to 30%, more than half the studies' data are consistent with the contentions they generated, but rarely unequivocally. And there is good reason to believe that the data have been selected or dredged in a way that would inflate the likelihood of observing ratio constancy and large minimum ratios, a point to which we return in the Discussion.

Williams (1972), expanding on work by Schoener (1970), and Barbour (1973) have advanced the falsifiable claim that species pairs in several sites have unusually high minimum ratios. The claim is testable since they have either enumerated the species in the pool available for coloniza-

tion of two-species islands or have characterized the pool sufficiently that a null hypothesis can be framed. Schoener and Williams noted for seven West Indian islands, each of which has only two anole species of the *bimaculatus* subgroup, that size ratios always exceed 1.4. For three other islands each with only two species from the *roquet* subgroup, the ratios all exceed 1.5. That is, sizes on a log-scaled line are always at least .336 apart for the *bimaculatus* subgroup, and .405 apart for the *roquet* subgroup. Similarly, Barbour has observed that, in four lakes with two fish species each, size ratios all exceed 1.833 (the difference of logs always exceeds .606). In both studies the species pool is specified: for the fish, the maximum species in the pool is 298 mm long, the minimum 48 mm. Williams (1972) suggests that, for a variety of reasons, the smallest possible anole snout-vent length is 38 mm, the largest 191 mm.

Both studies interpret the large size ratios as caused by interspecific competition. A test of the hypothesis that the size ratios are greater than random placement of points on a log-scaled line would have produced depends on whether (1) the original contention was that all ratios would

exceed some amount specified *before* the data were examined, or (2) the contention was simply that the particular values of observed ratios are extraordinarily large. For Barbour's study, (2) clearly obtains; he specifies no specific ratio of interest before his examination, and simply observes post facto that the ratios are remarkably large. The appropriate statistical test, then, is Fisher's method for combining independent probabilities, where the test statistic is $-2 \sum \ln p_i$ (with p_i the probability of the i th result); this is distributed as χ^2 with $2n$ d.f. for n independent cases. Each p_i is assessed by the Pielou-Arnason test (1966) and we find, for Barbour's four lakes, $-2 \sum \ln p_i = 11.049$ (8 d.f.), $Pr = .199$.

For Williams' and Schoener's anoles it is not clear whether a prior hypothesis was examined. Schoener (1970) observed that all snout-vent length ratios equalled or exceeded Hutchinson's (1959) ratios. If this were an hypothesis stated before data were scanned, for the *roquet* islands the null probability (by the Pielou-Arnason test) that the colonists on any *one* island would have produced a ratio greater than 1.5 is .561, so the null probability that all three islands would have such a large ratio is $(.561)^3 = .176$. For the seven *bimaculatus* islands the single-island probability of a size ratio exceeding 1.4 is .627, and for all seven islands to exceed this ratio the null probability is $(.627)^7 = .038$. If, on the other hand, the ratios were simply taken as a set of independent observations originally made in the absence of an hypothesis, for the *bimaculatus* islands $-2 \sum \ln p_i = 12.875$ (14 d.f.), $Pr = .536$, and for the *roquet* islands $-2 \sum \ln p_i = 3.4341$ (6 d.f.), $Pr = .631$. In sum, the fish data are consistent with the random colonization hypothesis, while the anole data are inconsistent with it only if the data are construed as testing a prior hypothesis.

Related Claims About Size Ratios

A number of authors have adduced size data to support an hypothesis of competition, but have claimed that the observed

trend that supports the hypothesis is not constancy of size ratios, but rather a particular kind of inconstancy. Notable are models by Schoener (1965, 1970, 1974; Schoener and Gorman, 1968), Oksanen et al. (1979), and Croker (1967).

Schoener (1965, 1970, 1974) suggests that species' sizes must be more different when food is rare and that in such situations contiguous size ratios must increase, not remain constant, as one goes up the size scale. An example would be if larger species used larger food and larger food were rarer. Schoener's observation (1970) that for seven of nine three-species islands in the West Indies the size ratio of the largest two species exceeds that of the smallest is compelling; there is a clearly non-random size pattern. For each trio one may set up the null hypothesis that the logarithm of the intermediate species' size is randomly drawn from a uniform distribution between the logarithms of the two extreme sizes, and ask whether the data falsify the hypothesis. The G_{12} statistics (Table 1.18) do not, but they say nothing about *which* size ratio is larger. One might ask for each trio what the null probability is that the ratio of the largest species will exceed that of the smallest species. In other words, if L = largest, M = intermediate, and S = smallest, we wish to know for what fraction of the segment $[S, L]$ is $L/M > M/S$, or $M < \sqrt{SL}$. This fraction is $(\sqrt{SL} - S)/(L - S)$. These null probabilities for the nine islands are, respectively, .343, .438, .351, .340, .331, .458, .355, .352, and .381. If

we now compute for each of the $\binom{9}{7} = 36$ combinations of seven islands the null probability that that particular septet of islands, and no others, will have the size ratio of the larger species greater than that of the smaller species, and sum these 36 terms, we find that the null probability of having exactly seven islands with this characteristic (the observed result) is only .010. Similarly, the probability of a result at least as extreme (that is, seven *or more* islands with the size ratio of the larger two

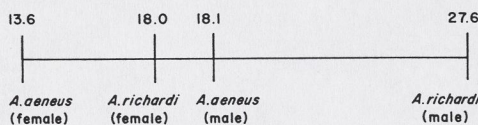


FIG. 3. Observed mean sizes of largest third of *Anolis aeneus* and *A. richardi* on Grenada (Schoener and Gorman, 1968).

species exceeding that of the smaller two) is only .012. So the random null hypothesis is rejected.

Schoener and Gorman (1968) advance a related argument about intraspecific size ratios. On Grenada, *Anolis richardi* and *A. aeneus* are both sexually dimorphic, and the ratio of head widths between sexes for the larger species, *richardi*, exceeds that for the smaller, *aeneus* (Schoener and Gorman, 1968). They observe that this difference is compatible with Schoener's 1965 model that large species must space themselves further apart on a size axis since large food is rarer. To test this claim that more pronounced sexual dimorphism in a larger lizard (1.53 ratio of head sizes) than in a sympatric smaller one (1.331 ratio of head sizes) is likely not the result of chance, we arranged the sizes on a line as in Figure 3. Schoener (pers. comm.) suggests using mean sizes of the largest third of all specimens examined, and provided the appropriate corrected data (Fig. 3). The claim is that the size ratio for the larger species, r_δ/r_φ , exceeds that for the smaller, a_δ/a_φ . What must be tested is whether the observed excess could not be attributed to random uniform dispersion of the interior points (r_φ and a_δ) along the line between the two extremes. Represent the observed differences between the two ratios as

$$D = \frac{r_\delta}{r_\varphi} - \frac{a_\delta}{a_\varphi} \quad (6)$$

Then for randomly placed points y_1 and y_2 between the extremes, where y_1 would represent female *richardi* and y_2 male *aeneus*, we wish to know the probability Pr that

$$r_\delta/y_1 - y_2/a_\varphi > D = .202. \quad (7)$$

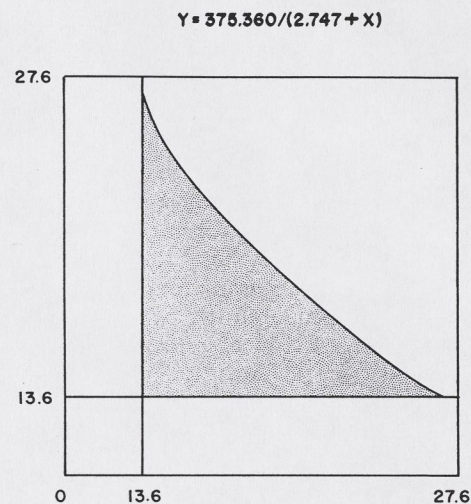


FIG. 4. Stippled area represents fraction of randomly sized male *A. aeneus* and female *A. richardi* that would produce difference of size ratios greater than that observed. Small square represents all possible pairs of sizes (see text).

When we insert observed values of r_δ and a_φ , rearrange terms, and recall that y_1 and y_2 must be interior points, (7) becomes

$$y_1 < \frac{375.360}{2.747 + y_2}, \quad 13.6 \leq y_1, y_2 \leq 27.6. \quad (8)$$

Figure 4 demonstrates that to find the probability that y_1 and y_2 randomly drawn between the extremes will satisfy inequality (8), we must first determine what values of y_2 are permissible in the equation.

$$y_1 = \frac{375.360}{2.747 + y_2}. \quad (9)$$

Since $y_2 > 24.853$ produces $y_1 < 13.6$,

$$Pr = \left[\int_{13.6}^{24.853} \left(\frac{375.360}{2.747 + y_2} \right) dy_2 - (13.6 \times (24.853 - 13.6)) \right] / (27.6 - 13.6)^2 = .223. \quad (10)$$

If 22% of the time chance alone would have generated at least as large a differ-

TABLE 3. Ground-feeding birds of Finnish boreal peatlands. Data from Oksanen et al., 1979.

Species	Weight (g)	Ratio
<i>Grus grus</i>	5,000	13.889
<i>Numenius phaeopus</i>	360	2.000
<i>Tringa nebularia</i>	180	1.895
<i>Gallinago gallinago</i>	95	1.397
<i>Lymnocyptes minimus</i>	68	1.133
<i>Tringa glareola</i>	60	

TABLE 4. Barton-David and Irwin statistics for data of Table 3. Associated probabilities are for values at least as large as those observed. *Grus* omitted.

$G_{14} = .180, Pr = .286$
$G_{24} = .482, Pr = .218$
$G_{13} = .195, Pr = .509$
Min = .070, Pr = .373

ence between degrees of dimorphism in the large vs. the small species, it is unnecessary to seek the cause for this dimorphism in competition. If the sizes are log-scaled instead of arithmetic as above, 32% of the time uniform-random placement of the two intermediate sizes would have generated a difference at least as large as that observed.

Crocker (1967), examining five species of intertidal amphipods, calculates the ten pairwise size ratios and finds that ratios are slightly higher for co-occurring pairs than for others, slightly lower for pairs showing strong habitat isolation and/or highest densities in separate habitats than for others. He feels that these patterns indicate the kind of size difference necessary for coexistence at the same trophic level. The classifications are not exclusive, since some pairs that strongly co-occur also show strong habitat isolation and/or have highest densities in separate habitats. If we test the ranks of the ten size ratios by the Wilcoxon test, we find that for pairs that *only* strongly co-occur vs. other pairs, $W = 7$ ($Pr = .4$), while for *all* pairs that strongly co-occur vs. other pairs, $W = 27$ ($Pr = .176$). So the hypothesis that size ratios are *not* different for strongly co-occurring pairs than for other pairs is not falsified.

Oksanen et al. (1979) believe that in open habitats shorebirds and waterfowl exhibit constant size ratios among the smaller members of a community but that the largest species are so much larger than the others that they generate "gaps" in the size ratio sequence. These gaps they attribute to interspecific aggression, rendered "economically" advantageous by the open

habitat. Without arguing the merits of their explanation, we note that they performed no statistical tests of their hypothesis against alternatives. Such tests suggest that the data do not require their explanation. Their Table 2, reproduced here as Table 3, is said to "approximate a Hutchinsonian series [constant size ratios]" except for the crane *Grus grus*. If one omits this crane and focusses on the remaining five species, one computes the Barton-David and Irwin statistics shown in Table 4; these data are consistent with the independent, uniform-random hypothesis. As for the "exceptional" ratio, 13.889, Darling (1953) has proven that for $n - 1$ points on a line, if β is the largest segment, the probability of finding a still larger one had the $n - 1$ points been independently and uniform-randomly distributed is

$$Pr(g_n > \beta) = 1 - \sum_{0 \leq j < 1/\beta} \binom{n}{j} \cdot (-1)^j (1 - \beta_j)^{n-1}.$$

For the data in Table 3, this probability is .135, so we would still not reject the random, independent model. The other data that Oksanen et al. adduce to support their model are sizes of four dabbling waterfowl in Finnish boreal peatlands. Again, if one omits the largest (which is 8.182 times as large as the next species), the remaining three species do not form particularly constant ratios: $G_{12} = .445, Pr = .384$. For the extreme ratio of 8.182, the probability of one even larger is .438. So again, the entire data set does not require either of the authors' explanations for it.

When we move to other claims that are in principle falsifiable (but have never

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been tested), we find the same ambiguity and lack of pattern that surfaced from the survey of claimed constancy of ratios or high minimum ratios. For example, Uetz (1977) observes that both size ratios in a ranked trio of wandering spiders—1.34 and 1.26—fall in the range observed by Hutchinson (1959) and argues that this supports both the generality of Hutchinson's pattern and the importance of interspecific competition in determining sizes of coexisting species. Hutchinson's observed ratio range was [1.09, 1.43], while Uetz's three spiders fall in the size range [3.50, 5.90]. If we assume that the endpoints of the size range are fixed, and ask over what fraction of this range would an intermediate point produce two ratios in Hutchinson's range, we find the fraction to be $([3.815, 5.005] \cap [4.126, 5.413]) / [3.50, 5.90] = .366$. If the size line is log-scaled, the fraction of the range over which an intermediate point would produce a permissible intermediate point is .371. So the null hypothesis of uniform random placement of either sizes or their logarithms is not rejected. Many other papers that cite the similarity of some observed ratios to Hutchinson's ratios could be tested similarly.

Barbour (1973) finds in a small lake that two species colonized from a large lake with four species, the missing two species are the intermediate ones in a size ranking, and attributes this to competitive exclusion. However, if we state as a null hypothesis that the two species in the small lake are randomly drawn from the four in the large lake, we find there are $\binom{4}{2} = 6$ possible draws, of which one is the observed set. Since this draw would have occurred .167 of the time we would not have rejected the null hypothesis from these data alone, although several small lakes (or even two) displaying a similar pattern would certainly have suggested rejection.

DISCUSSION

We have shown that when they are subjected to statistical analysis, some claims

that size ratios are non-random in some way (usually in the direction of regularity or overdispersion) are sustained, others rejected. At the 5% level, seven of 21 claims of ratio constancy and seven of 18 claims of large minima are generally sustained. For the majority of claims, had the null hypothesis been one of random distribution of ratios between two extreme size limits (or a similar one appropriate for some particular claim), it would not have been rejected. This does not, of course, imply that the null hypothesis is usually true. In addition to other points that we raise further on, this particular null hypothesis may have a high type II error rate. And in general one can at best disprove, not prove, an hypothesis. But at least it is clear that the "1.3 rule" is not even a pattern in nature, much less a rule. Maiorana's (1978) explanation for why size ratios tend to be constant and why the constant factor is ca. 1.28 is premature. We have seen that size ratios do *not* in general tend to be constant, nor is the factor separating species' sizes usually ca. 1.28. In fact, it has not been shown empirically that *any* particular minimum size ratio is required for coexistence of species in the same trophic level. It is demonstrably not true that "for related species to coexist within a habitat on an island, they must differ by size to some degree" (Faaborg, 1977). Several entries of Table 1 show sympatric, syntopic, related species of virtually identical size.

Of course exceptions to the "1.3 rule" or the "1.x rule" have been noted before. We have already mentioned Fleming et al. (1972). Johnson (1966) and Hesperheide (1966, 1971) pointed out for various birds that it is simplistic to think morphological sizes are the predominant index of feeding differences, while Root (1967) suggested for one bird guild that beak size and prey size are not highly correlated and showed that species' bill size ratios were generally smaller than the 1.14 that, following Schoener (1965), he took as required for competitive exclusion to be avoided by size difference alone. Wiens and Rotenberry (1980) found little regularity in

grassland and shrubsteppe bird size ratios and felt that what size "gaps" were apparent were unlikely to have resulted from competition. Wilson (1975) also questioned the assumption that body size is an adequate index of the food niche, and the implication that character displacement based on food size will be apparent for most taxa. We would guess that for every worker like Fleming or Root, who unsuccessfully sought minimum and/or constant ratios and duly reported their absence, several workers who failed to find them did not bother to report even the search, instead concentrating on other aspects of their material. The tendency to publish positive but not negative results is well enough known for us not to belabor it here, except to note that it renders hypotheses based on literature surveys difficult or impossible to test statistically (Selvin and Stuart, 1966).

Why then does the rule continue to be cited as a rule, in spite of known exceptions? In what sense is it a rule? We suggest that at least part of the problem has been failure to state a null hypothesis clearly and to attempt rigorously to falsify it. One ought always to be able to state a specific conceivable observation that would cause an hypothesis to be rejected. For example, May (1978) cites Cody's (1974) 11 bird communities as "conform[ing] to the 1.3 ratio." However, if one takes as a null hypothesis that observed minima are no larger than would be expected if the sizes of species in each community were randomly and independently arranged between the smallest and largest sizes, one finds (Table 1.10) that the observed ratios do not falsify the hypothesis in ten communities. Further, of the 130 ratios that Cody lists, 120 are less than 1.3. If this constitutes conformance to the notion that a difference of 1.3 is necessary for species to co-occur, one might ask what set of data could conceivably be viewed as not conforming. Similarly, Smith (1978) claims that for two sets of coral reef fish data, adjacent species in a size-ranking differ by 5-12%, and interprets this constancy as resulting from

competition. Yet for one data set only 29.4% of the ratios fall in this range, for the other set only 32% fall in this range, and for both sets of data (Table 1.22) the sizes tend toward statistical clumping (too many small ratios) rather than regularity as Smith contends. Again one might ask what conceivable set of data would have been construed as *not* conforming to a pattern of constant size ratios.

Even when rules about size ratios *are* stated as hypotheses, they are generally embedded in a hierarchical hypothesis, and though that part of the hierarchical hypothesis consisting of the rule can be stated so as to be testable (as we have demonstrated above), the hierarchical hypothesis itself is not falsifiable by the sorts of data usually presented, only by experiment. The hierarchical hypothesis is, of course, that of Hutchinson (1959): that species' sizes differ by a minimum amount *because* of competition. An exception to a posited minimum size difference need not damn this hypothesis, so long as the exceptional group of species differ in some other way. But since some other way (or ways) can generally be found in which any group of species differ substantially, one always finds the competition part of the null hypothesis confirmed. In short, we have a version of Gause's Law or the Competitive Exclusion Principle, that supremely unfalsifiable hypothesis (Slobodkin, 1961) that, because of competition, no two species occupy the same niche, "niche" being defined by as many dimensions as are necessary to have no two species identical or even similar.

Enders (1974) finds that some *Araneus* species do not differ by the requisite 28% that he claims is sufficient to prevent competitive exclusion. This is not problematic since these spiders differ in habitat. The species that *do* differ in size by 28% do so because of competition. Price (1972) suggests that a 10% difference in ovipositor length is required for coexistence of members of a parasitoid guild. That an introduced species has survived and insinuated itself in the size ranking so as to produce two ratios of 1.05 does not damage the

hypothesis that the size differences are caused by competition; spatial factors "separate" the too close species and allow them to coexist. Horn and May (1977) feel that part of Uetz's (1977) ten spiders conform to the 1.3 ratio (we assume they mean the ratios 1.34, 1.26, and 1.28; the first two we discussed above). Those five species that do not, and that instead produce ratios of 1.05, 1.02, 1.06, and 1.03, do not cause concern: "these spiders further subdivide their habitat by flourishing at different times of the year." Even body size and seasonal activity do not greatly separate some of Southwood's 28 carabid beetles (1978), but addition of diel rhythms teases apart the few remaining similar pairs of species, so that the competition hypothesis need not be discarded. Wilson's (1975) "Adequacy of body size as a niche difference," discussed above, deduced that one would *expect* the minimum ratio rule to be violated frequently *because of competition*; his models are based on exploitation competition.

Against this formidable array of explanations for exceptions to the size rules it would be extremely difficult to gather data that could in principle impugn the hierarchical hypothesis of size-differences-caused-by-competition. One might seek negative correlations between interspecific ratios and interspecific differences measured along a priori independent niche axes, such as seasonal activity, but to our knowledge this has never been rigorously and systematically done; Croker's (1967) is an attempt in this direction. In principle the more limited hypotheses of ratio constancy or minima *are* falsifiable (and we feel we have made a fair start here towards falsifying them), but the hierarchical hypothesis bids fair to be a "panchreston" (Hardin, 1956), a concept that, by explaining everything, explains nothing. As adduced to date, it exemplifies the unfalsifiable hypothesis that Popper (1963) views as the bugbear of true science. It is not alone in this respect; absence of a falsifiable null hypothesis is very common in ecology, especially community ecology (Strong, 1980).

It is worth observing that the studies whose data we *have* tested here comprise but part of the literature claiming either minimum or constant size ratios. Many such studies do not permit a test of a null hypothesis, since only data are given that support the claim (Selvin and Stuart, 1966). For example, Diamond (1973) states, "Among congeners *sorting by size* in New Guinea, the ratio between the weights of the larger bird and the smaller bird is on the average 1.90; it is never less than 1.33 . . ." (our italics); and Diamond (1972) tabulates "Weights of congeners which sort out by size" for 31 pairs of birds. But one would have to know the sizes of all species, not just a few pairs, to know if the observed minimum size ratio were really larger than one would have expected if the birds' sizes were independent of one another, or if there is anything striking about the fact that 31 pairs (of how many?) differ in size by a factor greater than 1.33.

Similarly, Diamond's (1973) depiction of eight species in two genera of fruit pigeons, with weights differing by a nearly constant factor, cannot test an hypothesis that sizes are not independent since these are the only data given. By the Barton-David test these birds *do* produce ratios that are extraordinarily constant: observed $G_{17} = .537$, $Pr < .001$. But what about the *other* groups of eight species? There are 513 breeding birds in New Guinea (Diamond, 1973), so there are $\binom{513}{8} = 1.13 \times 10^{17}$ octets. How many octets comprise just two genera cannot be determined without species lists, but surely there are very many. So the observation that *one* octet produces constant ratios need not falsify an hypothesis that all birds' sizes are independent.

Cody (1975) similarly notes for birds of Mediterranean-like sites that some species differ in size, others do not but differ in other ways, and claims that these differences are necessary for coexistence. No one would deny that any pair of species differs in some way, nor is it surprising that if species do not differ in size they differ in other ways. But without all data

one cannot ask whether more size differences are large than chance alone would have predicted, or whether observed minima are surprisingly large.

We emphasize that we are *not* claiming that competition does not exist. We do not even claim that competition is not responsible for some (maybe even most) observed size differences. In particular, we do not claim that our null hypothesis of independent, uniform-random dispersion of sizes on a log-scaled line is correct, only that it is at least as consistent with observations as hypotheses of constant or large minimum size ratios are in the majority of cases. We also note that an hypothesis of random, independent sizes is probably not falsifiable, since if the *uniform* random distribution is falsified, one can easily attempt to fit a plethora of other distributions, and an infinity of parameter values. For example, we have also tried to fit the data of Table 1 to a uniform distribution on an arithmetic, not logarithmic, scale. Some sections fit better, some worse, and again no overall pattern is discernible. For the hypothesis of large minimum ratios, the uniform distribution on a log-scaled line is exceptionally unlikely to cause rejection given a set of observed values. Two values randomly drawn from the uniform distribution have an expected difference greater than two values drawn from any other we can think of; therefore a large minimum log of a ratio (difference of two logs) is less surprising if drawn from a uniform distribution than from any other. But we have yet to find either data or theory that convincingly suggest that the a priori distribution of sizes in a small, coexisting group of species sharing a given trophic level conforms to any other distribution, so we have used the uniform because of its simple and natural biological interpretation.

But if we do not claim that our hypothesis of random independent size dispersion is correct, we *do* claim that most putative support for the contention that an array of sizes is determined by competition is flawed, and suggest a different approach: (1) First, verify statistically that some suite

of sizes is non-random, using a clearly stated null hypothesis and appropriate test. (2) Use the resulting statistical evidence to generate *falsifiable* mechanistic hypotheses (including, if this seems reasonable, competition) for observed size differences and, if appropriate, other biological phenomena. (3) Attempt to *falsify*, not to confirm, the hypotheses generated in (2), preferably by experimental manipulation. (4) Keep in mind that an hypothesis that two species differ in some unspecified way is trivially true, so that an hypothesis that competition causes two species to differ in an unspecified way cannot be disproven.

We would be remiss were we not to point out a further difficulty with the interpretation of some observed set of size ratios. Different studies, even within the same taxon, have focussed on different variables to represent size. For example, Diamond (1972) gave weight ratios for birds, while Hutchinson (1959) described culmen length ratios, and Grant (1968) looked at both bill length and wing length ratios. There is no a priori reason why one particular variable is better than another in this respect, except where independent evidence establishes that one better reflects the ecology (usually feeding ecology) of the animals in question. But choice of the variable *is* important, for two reasons.

First, by the tests we have described above, it frequently happens that a set of species manifesting constant size ratios for one size variable do not manifest constancy with a different size variable. In fact, two different size variables need not even *order* species identically.

Second, Mosimann and James (1979) have shown that size and shape usually covary and that in a population at most one size variable can be statistically independent of shape (though in a sample several size variables can be nearly independent of shape). The usual assumption in studies of closely related species is that morphological divergence results from selection on size, and that change in shape is just a passive, correlated response (Lande, 1979). The literature claiming

either minimum or constant size differences takes exactly this tack, and no study attempts to isolate a size variable that is independent of shape. Yet there is no a priori reason to assume that selection in a particular group has acted on size and not shape, and it is certainly conceivable that size differences observed in a group are actually epiphenomena of selection for shape, or partially epiphenomena. Furthermore, unless a size variable is known to be statistically independent of shape, observed constant size ratios in a suite of species could conceivably be explained as an artifact of some set of shape relationships. The published data did not usually permit us to attempt to find a size variable independent of shape, nor were data given that would allow us to copy Lande's (1979) attempt to determine which of two correlated variables natural selection has primarily acted on. We have not dealt with this problem further, but we note that the above two caveats should render any conclusions about minimum or constant size ratios tentative.

Finally, we observe that perceived patterns in size ratios between successive molts in arthropods, such as Dyar's Law (1890) and Prizbram's Law (1931) claiming constant ratios, have never been examined statistically; the Barton-David test would be a good beginning. And statistically, the problem of the distribution of morphological sizes is identical to other venerable ecological-evolutionary problems, such as the distribution of flowering times for a plant community (Poole and Rathcke, 1979) and some formulations of species-abundance or niche-width relations (e.g., Pielou and Arnason, 1966; DeVita, 1979). Perhaps the statistical methods outlined here can therefore be more generally useful.

SUMMARY

Hutchinson's (1959) claim that there is a minimum size ratio between adjacent species in a size-ranking and the related contention that size ratios tend to be constant between adjacent species pairs in a suite of three or more species have often

been repeated and interpreted as resulting from interspecific competition, but never subjected to statistical analysis. Many data sets for which these claims have been made cannot be tested since they are incomplete, but we have attempted to examine the other sets by tests based on those of Barton and David (1956). Our null hypothesis was generally that the logarithms of species sizes did not differ from an independent set of points uniform-randomly distributed on a line segment between the logs of the largest and smallest observed sizes, and the alternative was constant ratios or unusually high minimum ratios. At the .05 level few of the data sets falsified the null hypothesis, though at the .30 level one would reject the null in favor of the alternative hypothesis about half the time (though rarely without ambiguity). Related claims about size ratios are a mixed bag; some are consistent statistically with the data on which they are based, others are not.

In no sense is the "1.3 rule" of size ratios a rule of nature; even published results tend to support it weakly at best, and negative results are probably much less frequently reported. Its continued popularity is likely due to its inclusion in a larger tacit hypothesis that sizes differ *and* this is caused by competition. Since one can usually find other differences between similarly sized species, failures of the rule or its variants in specific instances are not generally taken to falsify the larger hypothesis. We do *not* claim that sizes are not partly determined by competition, nor that our hypothesis of independent, random sizes is correct. But we do feel that the evidence presented to date that sizes are competitively determined is weak, and that in particular the "1.3 rule" was probably always a red herring and has certainly outlived its usefulness to evolutionary ecologists.

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SKEPTICISM TOWARDS SANTA ROSALIA, OR WHY ARE THERE SO FEW KINDS OF ANIMALS?¹

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In a classic paper, Hutchinson (1959) set the tone for much of the ecological work done during the past 20 years by suggesting that ecologists try to explain the numbers of species of animals. Hutchinson's approach was ecological, explaining diversity by explaining how the species could coexist. There can be little question that competitive exclusion sets an upper limit on species diversity, but it is not obvious that this upper limit will be achieved. There may be additional constraints on the process of speciation, constraints set by genetics rather than ecology. It has been usual for evolutionists to reject the possibility of sympatric speciation, and this amounts to asserting the existence of such genetic constraints. Even if the ecological opportunity for coexistence is present, under the conventional view lack of geographic isolation can prevent speciation. The attempt by Rosenzweig (1975) to give a comprehensive explanation of continental species diversity takes as its starting point the assumption that geographic isolation is a necessary prerequisite to species formation.

A number of workers have made and analyzed detailed population genetic models of sympatric or parapatric speciation, in particular Maynard Smith (1966), Dickinson and Antonovics (1973), and Caisse and Antonovics (1978). Balkau and Feldman (1973) made a model of migration modification which can also be regarded as a model of parapatric speciation. The upshot of these models is that it is not difficult for sympatric speciation to occur. While these authors have largely been concerned with showing that sym-

patric speciation is possible, one might come away from some of these papers with the disturbing impression that it is all but inevitable.

If this were the case, one would expect to find nearly infinite numbers of species, a different species on every bush. More precisely, if there were no genetic constraints on speciation, an "island-biogeography" model of speciation could be constructed, resembling that of Rosenzweig but with no requirement for geographical isolation in order to get speciation. There would be a balance between speciation and the extinction of small species. Without having such a model in hand, it is my impression that the number of species in nature is far smaller, and their size far larger, than such a model would predict.

This raises the question of whether there is any genetic constraint on speciation. If there is, we would wish to know in population genetic terms what forces were opposing speciation. This paper presents a simple model of speciation, in an attempt to search for and characterize evolutionary factors acting against speciation. Such a force is found, and in fact can also be seen to have been acting in at least three of the earlier population genetic models. The picture of speciation which emerges here involves a new distinction between two kinds of speciation, one which cuts across the usual allopatric-sympatric spectrum. The distinction made is between speciation in which the reproductive isolating mechanisms come into existence by the substitution of different alleles in the two nascent species, and speciation in which the same alleles are substituted in both species. This distinction seems to be an important one.

Caisse and Antonovics (1978) have dis-

¹ Dedicated to Sewall Wright, in celebration of his 90th birthday.

cussed many of these same issues, and reached conclusions completely consistent with those of this paper. The present model differs from theirs in detail, and may help round out our picture of the genetics of speciation. It must be emphasized that the model presented here is not intended as a realistic genetic model of the speciation process. Rather, it is the simplest model I can find which exhibits many of the genetic effects which will be found in more complex, more realistic models of speciation. The purpose of this paper is to clarify the nature of the genetic forces involved in speciation, and to get some sense of the direction in which they act and their relative strengths.

THE MODEL

We consider an infinite haploid population with discrete generations. Haploidy is considered primarily to avoid mathematical and computational complications: we shall see below that qualitatively identical results are obtained with a diploid model whenever the two cases are compared. We suppose that there are three loci: A, B, and C, each with two alleles. Loci B and C are under natural selection, and locus A controls a cue for assortative mating. We start by considering the case of sympatric speciation. Our model resembles that of Maynard Smith (1966). The population consists of two subpopulations, within each of which there is separate density-dependent regulation of population size, according to the model of Levene (1953).

Each generation the organisms are distributed randomly into the two subpopulations. Selection (which it is convenient to think of as involving differential viability) takes place within each subpopulation. Each subpopulation regulates its density separately, and the survivors of selection and of density regulation emerge into a single mating pool containing individuals from both subpopulations. We take the two subpopulations to have adult populations of equal size (after density regulation), so that they contribute equally to the mating pool.

Natural selection acts at loci B and C according to the following fitness scheme:

Genotype	Subpopulation	
	I	II
BC	$(1 + s)^2$	1
Bc	$1 + s$	$1 + s$
bC	$1 + s$	$1 + s$
bc	1	$(1 + s)^2$

In population I alleles B and C are at an advantage, and in population II alleles b and c are at an advantage. The selection coefficients have all been taken to be s for simplicity. Fitnesses at different loci are assumed to combine multiplicatively. Initially we shall assume that the three loci are unlinked.

If we were only confronted with loci B and C, the outcome would be fairly simple. A globally stable polymorphism will be maintained at both loci, and it will involve gene frequencies of 0.5 for all alleles, as well as coupling linkage disequilibrium (gametic phase disequilibrium), with an excess of BC and bc genomes. The larger the selection coefficient s , the stronger this disequilibrium will be. When s is infinite, only genotypes BC and bc will exist after selection, and each will exist in only one of these two subpopulations.

In effect, the natural selection creates a partial postzygotic isolation between the two types, as expressed in the nonrandom association between B and C. We now add to the model the locus A, which embodies a prezygotic isolating mechanism, assortative mating. We assume that in the mating pool, which is formed from the survivors of selection and density regulation, the frequencies of different mating types are as follows:

	A	a
A	$p^2(1 - d) + pd$	$p(1 - p)(1 - d)$
a	$p(1 - p)(1 - d)$	$(1 - p)^2(1 - d) + (1 - p)d$

This is the simplest possible type of assortative mating. A fraction d of the individuals mate with their own type, and a fraction $1 - d$ mates at random. If the

A locus were the only locus segregating, this type of assortative mating would not result in any change of gene frequency at that locus. Some mechanisms leading to this type of assortative mating are briefly explored in Appendix 1.

We have not yet specified how the assortative mating affects loci B and C. The assumption will be that the genotypes at these loci are carried along passively in the assortative mating. For example, the probability that a mating is $ABC \times AbC$ will simply be the overall probability of an $A \times A$ mating, times the product of the fraction of all A genomes which are also BC, and the fraction of all A genomes which are also bC.

POSSIBLE OUTCOMES

We now have a model involving postzygotic partial isolation, plus a potential partial prezygotic isolating mechanism. There are two parameters, s and d . We know that a two-locus polymorphism will be maintained at the B and C loci. If there were initially linkage equilibrium (gametic phase equilibrium) between locus A and loci B and C, then it is relatively easy to see what will happen. The natural selection at the latter two loci will have no effect on locus A, which will maintain its initial gene frequency. There will of course be nonrandom mating at locus A, but this in turn will have no implications for loci B and C as long as this linkage equilibrium continues to hold.

It is only when there is initial linkage disequilibrium that we see interaction between the assortative mating and the natural selection. Linkage disequilibrium is particularly critical to this model. We interpret the disequilibrium between loci B and C to be partial postzygotic isolation between two entities, BC and bc, the intermediate forms Bc and bC being less frequent. We are interested in whether the prezygotic isolating mechanism A becomes nonrandomly associated with the genes B and C which demarcate the two entities. We interpret such an association as progress in the direction of speciation.

Of course, the disequilibria between A and loci B and C involve three parameters: the pairwise disequilibria between A and B and between A and C, as well as a third-order disequilibrium parameter which measures whether the disequilibrium between B and C is the same among A genomes as among a. In the numerical iterations, disequilibrium between A and the other loci has been monitored by following the pairwise linkage disequilibrium between loci A and C. In most of the cases run, the symmetries of the initial population composition were such that the disequilibrium between A and B would remain the same as between A and C. In many of these runs, the third-order disequilibrium would be forced to remain zero by these symmetries. The disequilibrium between B and C was followed separately as an indication of the effectiveness of postzygotic isolation. If BC individuals tend to be A as well, and bc to be a, then this association serves to prevent the mating of BC with bc. This in turn reduces the rate of production of the maladapted Bc and bC types. That these are in fact maladapted is seen by an average fitness calculation. The average fitness of BC or bc is

$$1 + s + s^2/2,$$

whereas the average fitness of Bc or bC is $1 + s$, which will always be smaller.

Thus the association of isolating mechanisms increases mean fitness. This in itself does not guarantee that the association will be brought about, and we are particularly interested in cases in which it will not. The reader who is skeptical of whether this association between isolating mechanisms really constitutes a step in the direction of speciation is invited to contemplate the case in which $d = 1$. Then if only ABC and abc were present, they would be completely isolated species. Note of course that the labelling of the alleles at the A locus is arbitrary: we would be equally interested in an association involving an excess of aBC and Abc types.

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NUMERICAL RESULTS

The model just described has eight haploid genotypes, so that it is described by seven variables. A formal description of the model in algebraic terms will be found in Appendix 2. While some special cases can be treated analytically, this is quite tedious. A computer program has been written to iterate genotype frequencies, using the language PASCAL on an 8080 (SOL-20) microcomputer. This iteration is entirely deterministic. A variety of different cases have been run. They involve a large range of values of s and of d . Initial gene frequencies at the three loci and initial values of linkage disequilibrium have been less thoroughly explored.

In all cases it has been found that B and C reach equilibrium gene frequencies of one-half, and that there is an excess of BC and bc coupling genomes at equilibrium. When initial linkage disequilibria between A and the B-C complex are introduced, these disequilibria may or may not disappear. Which happens has never proven to be dependent on the sizes of the initial disequilibria. In the case of disequilibrium between A and C (or between A and B), if linkage disequilibrium is destined to become established, it seems to do so even if the initial disequilibrium is very slight. There is, of course, a dependence of the sign of the final disequilibrium on the sign of the initial disequilibrium, but no dependence of the magnitude of the ultimate disequilibrium.

Under the assumption that these observations constitute a general pattern, we can investigate which values of s and d allow the establishment of linkage disequilibrium. Figure 1 shows the division of the (s, d) plane into these two regions. Above the curve is the region in which disequilibrium between A and B-C can become established. As we approach the top of the region ($d = 1$) we find more and more complete disequilibrium. As we approach the curve from above, the disequilibrium between A and B (and also that between A and C) becomes less. Be-

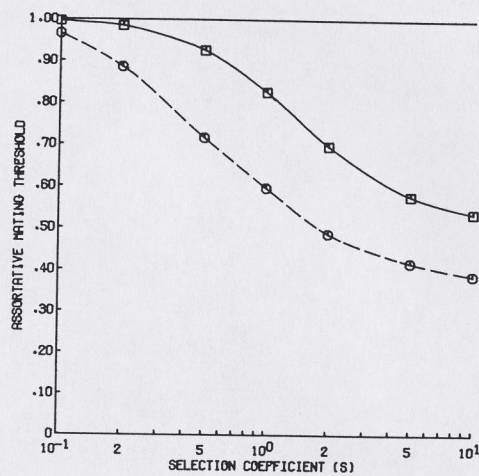


FIG. 1. The minimum amount of assortative mating (d) required to get stable association between the locus A and loci B and C, plotted for various selection coefficients in a haploid model. The squares (interpolated by the solid curve) are for $m = 0.5$, the circles (interpolated by the dashed curve) are for $m = 0.1$.

low the curve no disequilibrium will persist.

The immediate conclusion which we can draw from these results is that it is possible to construct a sympatric speciation model which sometimes does not speciate. (As we shall see, this property was also possessed by some earlier models.) Speciation in this case requires sufficiently strong selection and an isolating mechanism of sufficient potential strength. There is a complex tradeoff between the two. Note that the selection required in order that progress be made toward speciation is very strong, the major dip in the curve in Figure 1 being in the vicinity of $s = 1$.

We are interested in this model, not as a particularly realistic model of speciation but as a means of investigating the direction in which various evolutionary forces are operating. In order to look into this, it is necessary to alter various aspects of the model. The first alteration will involve the amount of gene flow between the two subpopulations.

TABLE 1. Threshold values of the amount of assortative mating in various cases involving different amounts of migration and linkage. The threshold value of d lies between the two values given in the appropriate column. SMR and SRM refer to the two orderings of events (Selection, Migration, and Recombination) in the life cycle.

s	r_{12}	r_{23}	m	d	
				SMR	SRM
1.0	.5	.5	.5	.82-.83	.81-.82
1.0	.5	.5	.1	.59-.60	.57-.58
1.0	.5	.5	.01	.51-.55	.53-.54
1.0	.1	.5	.1	.28-.29	.27-.28
1.0	.5	.1	.1	.86-.87	.86-.87

Restricting Migration

The dashed curve on Figure 1 shows the result when we restrict migration between the two subpopulations at the point in the life cycle following selection and density regulation. Instead of having individuals from both subpopulations contributed to a common mating pool, we make a conventional migration model. Each generation, there is exchange of individuals between the two subpopulations. Following this migration, a fraction m of each subpopulation will consist of new arrivals from the other subpopulation. Mating and recombination follow this migration. The case of a single mating pool will be seen to be the same as that in which $m = 0.5$.

The dashed curve is for the case of $m = 0.1$, which is in effect a case of parapatric speciation rather than sympatric speciation. In every case which has been investigated, restriction of migration eases the conditions for speciation. Whereas with $m = 0.5$ one could not get progress toward speciation unless d exceeded 0.5, no matter how strong the selection, this restriction on d is relaxed when m is small, and when $m = 0.1$ very strong selection can lead to speciation even with a fairly small value of d .

This pattern is quite consistent with conventional theory, which asserts the difficulty of sympatric speciation, but considers allopatry as a situation favorable to speciation. In the present model the sym-

patry-allopatry spectrum is represented by the value of m . Sympatry corresponds to $m = 0.5$, which implies complete random mating and random distribution of offspring among habitats, and allopatry requires that m be zero.

When $m < 0.5$, BC is the most frequent genotype in subpopulation I, and bc the most frequent genotype in subpopulation II. If there is a linkage disequilibrium of these loci with A, this is reflected in a higher frequency of one allele (say A) in subpopulation I, and a higher frequency of the other in subpopulation II. In effect, there are clines in all three loci. Slatkin (1975) has noted that when two loci have clines in the same region, there will be linkage disequilibrium between the two loci, and it will tend to steepen both clines and increase the adaptation of individuals to their environment. The cline in the A locus is favored in the present context because it reinforces this disequilibrium.

Recombination Fractions

Table 1 shows the results of changing the recombination fractions between the loci. The implicit genetic map is A-B-C. The recombination fraction between A and B is given by r_{12} , and between B and C by r_{23} . The cases in the Table are for partially restricted migration ($m = 0.1$), although the same patterns are seen when $m = 0.5$. For different recombination fractions the Table shows the lower limit of d which gives speciation (the actual lower limit is between the two values given in the table). When r_{12} is reduced, speciation becomes easier to envisage. When r_{23} is reduced, conditions for speciation become more restrictive. This same pattern has been seen in all cases examined.

EVOLUTIONARY FORCES AND SPECIATION

We are now in position to make a preliminary interpretation of the direction in which different evolutionary forces are working. In this model, natural selection produces linkage disequilibrium between B and C. With this disequilibrium established, natural selection will act so as to

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increase the magnitude of any disequilibrium between A and the B-C complex.

That natural selection will have such an effect in this case can be seen from a heuristic example. Suppose that linkage disequilibrium between A and the B-C complex were nearly complete, selection very strong, and assortative mating nearly complete. If almost all individuals were either ABC or abc, an Abc individual would tend to mate with an ABC. This union would give rise to some ABc and AbC gametes, but as a result of the near absence of Bc and bC individuals, there would be no corresponding production of bc from matings of Bc and bC individuals. This destruction of bc genotypes by recombination occurs among Abc individuals, which are nonrandomly likely to mate with ABC. By contrast, abc individuals will tend to mate with other abc individuals, and the bc genotype will be preserved in their offspring. There is a corresponding preservation of ABC and elimination of aBC.

The result is a reduction of the frequency of A among bc individuals, and of a among BC individuals. This reinforces the linkage disequilibrium. Note that the effect involves selection against bC and Bc as well as recombination between loci B and C.

Another way of intuiting this result is to realize that there are in effect two parts of the population, one consisting of the A individuals and the other of the a's. In the A pool the genotypes are mostly BC, with a few bc's, and in the a pool the reverse is true. When there is selection against Bc and bC and in favor of BC and bc, recombination within each of these nearly isolated mating pools will result in a reduced frequency of whichever of the two types (BC and bc) is in the minority. This will reinforce the disequilibrium by raising the frequencies of ABC and of abc and lowering the frequencies of Abc and of aBC.

With an understanding of the part played by recombination between loci B and C in this process, it becomes apparent why reduction of this recombination makes speciation more difficult. In both

of the above intuitive arguments, recombination between B and C plays a crucial role in the selection against (say) A alleles in bc genomes, and against a alleles in BC genomes. If the recombination between B and C is eliminated, there is no selection creating disequilibrium between A and these loci.

An understanding of the role of recombination between A and the other loci is even more important. It tends to break down the association between the prezygotic and postzygotic isolating mechanisms, so that it is always eroding the degree of progress toward speciation. In this light it should be clear why restricting recombination between A and B makes speciation easier. There is a continual conflict between selection, which increases the association between isolating mechanisms, and recombination, which reduces it. Restricting this recombination can only improve chances for speciation.

We have now identified the evolutionary force responsible for favoring speciation—natural selection—and the force opposing it—recombination. However it should be kept in mind that the recombination between B and C is favorable for the recruitment of the prezygotic isolating mechanism A/a into the scheme of reproductive isolation. We can describe the pattern in teleological terms: the assortative mating is associated with the substantive adaptations at loci B and C "in order to" prevent the formation of maladapted bC and Bc genotypes. It should be noted that although the recombination between B and C is favorable for the maintenance of disequilibrium between A and the B-C complex, this is achieved at the cost of having less disequilibrium between B and C (and hence less effective postzygotic isolation) in the first place.

VARIATIONS ON THE MODEL

Now that we have a general picture of the forces at work, we can make some further changes in the model to see how they alter this pattern. In particular, we want to know how dependent the results are on the ordering of events in the life cycle, on

diploidy, and on the type of interaction between loci B and C.

Timing of Migration

In our model, the order of events in a single generation has been Selection-Migration-Recombination. Without violating the haploid model, it would be possible to have recombination (and hence mating) precede migration. In Table 1, the column labelled SMR shows the standard ordering of events which we have discussed, and the column labelled SRM shows this alternative ordering. The patterns are the same in both columns, although the value of d needed to prevent disappearance of the linkage disequilibrium is somewhat smaller with the SRM ordering than with the SMR ordering. This result is typical of the effect of changing from SMR to SRM ordering, in all haploid cases. In some diploid cases speciation was more difficult with SRM than with SMR, as will be mentioned below, but in no case have the other qualitative patterns been much altered by the order of events.

Interaction Between Loci

The heuristic rationale presented above for the patterns seen involved a lower fitness for Bc and bC , averaged over both subpopulations, than for BC and bc . This in turn depends on the multiplicative combination of fitnesses at the two loci. If the fitness of BC in subpopulation I is instead $1 + 2s$, there is no difference in average fitness of different genotypes, if one averages arithmetically over both subpopulations. Would locus A be recruited into the nascent speciation in this case?

To check this, a version of the computer program was constructed in which the fitness of BC in subpopulation I (and correspondingly of bc in subpopulation II) was taken to be

$$1 + 2s + ks^2$$

and runs were made for different values of k with $m = 0.5$. When $k = 1$, the fitnesses combine multiplicatively, and when $k = 0$ they combine additively. A striking pattern immediately emerged. If

$k \leq 0$, it becomes impossible to find any value of d for which locus A is recruited into the nascent speciation. As k is raised above zero, association of A with B-C becomes possible, but only if d is very near 1. The larger k is taken to be, the more parameter combinations there are in which one gets association of A with B-C.

This would make it seem that association of the prezygotic and postzygotic isolating mechanisms depends on the rather subtle distinction between additive and multiplicative combination of fitnesses. However, when m is reduced this is not the case. With $m = 0.1$, progress toward speciation was possible even with negative values of k as extreme as -0.5 .

Thus the lower mean fitness of types Bc and bC is necessary for speciation only in the case of the Levene Model, where $m = 0.5$, while in parapatric situations conditions for speciation seem to be less restrictive. Although only a few cases have been studied numerically, the condition for there to be any values of d enabling progress toward speciation seems likely to be that migration and selection lead to positive disequilibrium within each subpopulation between B and C. It is interesting in this context that when $k = 0$ in a Levene Model, there will be no disequilibrium within each subpopulation between B and C. This phenomenon was found by Gillespie and Langley (1976) in two-locus Levene Models with fitnesses varying randomly in time and combining additively between loci. It seems to result from an exact cancellation between the positive linkage disequilibrium which results from mixture of individuals from the different populations (Wahlund, 1928), and the negative disequilibrium which results from directional selection within populations with additive fitnesses (Felsenstein, 1965).

Interestingly, the value $k = 0$ is also the boundary of the set of k values which allow the two-locus polymorphism for loci B and C to be stable. We then have a pleasing correspondence between the conditions for polymorphism in the postzygotic loci and the conditions for a prezygotic mechanism to become associated

with them. To see whether this correspondence might be general, a few additional runs were done for $m = 0.1$. Based on this limited information, it seems that the correspondence may be general. Those values of k which allow progress towards speciation when there is a sufficiently high value of d also seem to be precisely those which allow the two-locus polymorphism at loci B and C to persist.

If loci B and C do not interact and control separate phenotypes, and if these phenotypes affect viability, then the natural assumption for the way their viabilities combine is to assume that they are multiplicative ($k = 1$). If the loci are physiologically related (as when they contribute to the same phenotype), or if they affect fertility, multiplicative combination is less plausible as a null hypothesis.

Initial Gene Frequencies

The picture that has been presented here is not sensitive to different initial gene frequencies (or gamete frequencies) at loci B and C. They will rapidly move to their equilibrium gene and gamete frequencies, and since the association between A and B-C is insensitive to the initial amount of disequilibrium between them (except in regard to its sign), any increase or decrease of this disequilibrium which occurs as a byproduct of these initial changes of frequency at loci B and C will have only a transitory effect.

It is a bit less obvious whether the outcome is sensitive to the initial gene frequency at the A locus. In the absence of disequilibrium between A and the other loci, there is no selection changing gene frequencies at locus A. When disequilibrium between these loci does exist, it is possible in principle that it results in effective selection to change gene frequencies at the A locus.

Computer iterations to check this starting with one allele rare at the A locus showed a pleasing pattern: if the values of s and d were such as to result in progress toward speciation, and if there was initial disequilibrium between loci A and B-C, then selection at the latter loci resulted in

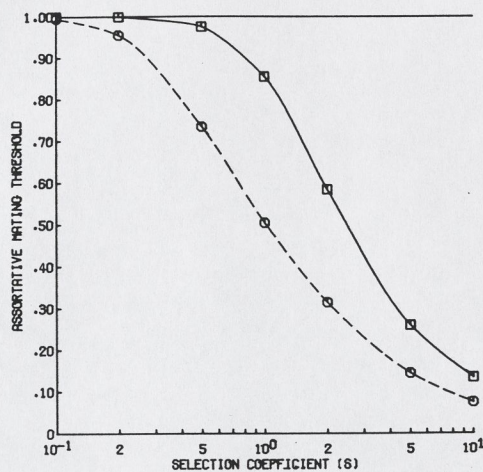


FIG. 2. The minimum amount of assortative mating (d) required to get stable association between the locus A and loci B and C, plotted for various selection coefficients in a diploid model. The squares (interpolated by the solid curve) are for $m = 0.5$, the circles (interpolated by the dashed curve) for $m = 0.1$.

changes in gene frequency at the A locus, so that A proceeded to a gene frequency of one-half. Thus if selection is able to be effective in the face of recombination between A and the other loci, it will not only result in association between the isolating mechanisms, but will also act to actively maintain polymorphism for a prezygotic mechanism such as the one we are studying.

Little time was spent investigating cases in which the associations between A and B-C would disappear. Since the effective selection at locus A results from the disequilibrium with the other loci, we would expect in those cases that as the disequilibrium disappeared, gene frequency change at the A locus would gradually cease, and it might end up not having changed much from the initial gene frequencies.

Modifiers of Assortative Mating

When the assortative mating locus is in association with the selected loci, speciation has not yet been fully achieved unless $d = 1$. We can only count this linkage disequilibrium as progress toward speciation

TABLE 2. *Threshold values of the amount of assortative mating necessary to allow progress toward speciation in some diploid cases. The threshold value of d lies between the two values given in the appropriate column. SMR and SRM refer to the two orderings of events in the life cycle.*

s	r_{12}	r_{23}	m	d	
				SMR	SRM
1.0	.5	.5	.5	.86-.87	.66-.67
1.0	.5	.5	.1	.50-.51	.46-.47
1.0	.5	.5	.01	.44-.45	.44-.45
1.0	.1	.5	.1	.28-.29	.25-.26
1.0	.5	.1	.1	.55-.56	.53-.54

if further events are capable of carrying the population to complete reproductive isolation. One way in which this might happen is by the substitution of modifiers which increase the strength of assortative mating.

To see whether this could happen, a program was written in which a fourth locus, D, was added whose alleles modified the strength of assortative mating. $D \times D$ matings were assumed to involve assortative mating with $d = d_1$, $D' \times D'$ to have $d = d_2$, and $D \times D'$ to have $d = (d_1 + d_2)/2$. The object was to see whether an allele, D' , which increased the strength of assortative mating, would increase in a situation in which linkage disequilibria are established between A and B-C. Of course, there are many other ways modification of assortative mating could be modelled. This scheme was chosen because it places no direct selection on the modifier, and in hopes that the result will prove to be insensitive to the specific modification scheme.

Only a few runs of this program could be made, as the presence of the fourth locus greatly increased the number of computations. In those runs, the allele which increased d was observed to increase, albeit very slowly. In our model, the natural selection on locus A is a consequence of its linkage disequilibrium with B and C. The natural selection on the modifier locus D is a consequence of its disequilibrium with A, and hence indirectly its disequilibrium with B-C, and is therefore very

weak. When there is no disequilibrium established between A and B-C, we expect no selection on the modifier alleles D and D' .

Diploidy

All of the above models have been haploid. To see whether this simplification has a qualitative effect on the results, a diploid model was investigated. In this diploid model, fitnesses were taken to be multiplicative both between and within loci. The fitnesses were thus:

Genotypes	Fitness in subpopulation	
	I	II
BBCC	$(1 + s)^4$	1
BbCC, BBcC	$(1 + s)^3$	$1 + s$
BBcc, BbCc, bbCC	$(1 + s)^2$	$(1 + s)^2$
Bbcc, bbCc	$1 + s$	$(1 + s)^3$
bbcc	1	$(1 + s)^4$

The assortative mating scheme used was also analogous to the haploid case. Locus A was assumed to code for the probability that the individual would enter the first of the two mating pools. The probability that the individual joined pool 1 was taken to be:

AA	Aa	aa
$(1 + d)/2$	$1/2$	$(1 - d)/2$

It was assumed that each individual entered one of the two mating pools. Within each mating pool mating was at random, and the number of offspring expected from each mating was taken to be equal, aside from effects of loci B and C. As in the haploid case, the loci B and C were assumed to play a passive role in the mating process, the probability of two genotypes mating depending only on their genotype at the A locus. Some further algebraic details concerning this simple system of assortative mating are given in Appendix 1.

In spite of the fact that the haploid case is not a special case of the diploid case, the two models give qualitatively similar results. Figure 2 and Table 2 show the minimum values of d which will enable

permanent association between locus A and loci B and C for some diploid cases. As can be seen, the qualitative patterns are the same as in the haploid case, giving us some confidence that we are not being seriously misled by concentrating our attention on haploid models. One exception to this is the effect of tightening linkage between B and C, which does not seem to cause as much restriction in the conditions for speciation as it does in the haploid case. When we discuss the work of Dickinson and Antonovics (1973) below, we will see that this effect is significant.

TWO KINDS OF SPECIATION

The picture of speciation which has emerged from considering the present models involves two opposing forces, selection and recombination, with movement towards speciation only being possible when selection is strong enough that its effect is not overwhelmed by recombination. We may contrast this picture with the situation in the model by Balkau and Feldman (1973). They imagined two populations and two loci. At one locus there were two alleles, each well-adapted to one of the populations, so that a cline was set up. At the other locus, a modifier locus, an allele was introduced which had the effect of reducing the migration rate of its bearers. They showed that this modifier allele would always increase when rare, irrespective of the recombination fraction between the two loci.

Their model was intended to model selection pressures for modification of migration, but we could just as well regard it as a model of speciation. If the process of modification were to continue, the outcome would be two allopatric reproductively isolated populations. Note that in their model, there is neither a threshold amount of selection necessary to allow speciation, nor any effect of linkage of the modifier locus to the selected locus.

The key to the different behavior of Balkau and Feldman's model is that speciation in their model proceeds by substituting the same allele in both populations. If the modifier locus has the same fre-

quency in both populations, then recombination between individuals from the two populations has no tendency to destroy reproductive isolation. Selection is then unopposed by recombination, and can be effective even when weak. By contrast, in the model presented in this paper speciation proceeds by substituting different alleles in the two nascent species. This means that selection is at risk of being overwhelmed by recombination, and that speciation can proceed only when there is sufficiently strong selection at loci B and C, or sufficiently weak gene flow between the two nascent species.

We may tentatively call these two classes of models of speciation "one-allele" and "two-allele" models. The critical distinction between them is whether reproductive isolation is strengthened by substituting the same or different alleles in the two nascent species. Of course, there is nothing to prevent both kinds of processes from going on at the same time, but at different sets of loci. This distinction cuts across the traditional sympatric-parapatric-allopatric spectrum. Both the present model and the Balkau-Feldman model can be formulated with initial random mating between the two populations, or with little gene flow between them. Thus neither is intrinsically sympatric or intrinsically allopatric.

A distinction similar to this one has been made by Endler (1977), who distinguishes between "Type I" and "Type II" modifiers. In the parapatric cases which Endler considers, these are modifiers which increase fitnesses of locally-adapted genotypes in both regions of a cline (Type I) or which increase fitnesses of the genotypes adapted to one region but decrease fitnesses of genotypes adapted to the other (Type II). Endler does not discuss the effect of recombination between genotypes from the two regions on the fate of these two kinds of modifiers. In fact, they are incidental to his model of parapatric speciation, a one-allele model in which a modifier of the amount of assortative mating spreads in both nascent species.

The sympatric speciation models of

Maynard Smith (1966) include both one-allele and two-allele models. Maynard Smith's basic model framework has a Levene Model with two subpopulations, and one locus, A, whose two alleles are adapted to the two subpopulations with the following fitness scheme:

Subpopulation	Genotype		
	AA	Aa	aa
I	$1 + K$	$1 + K$	1
II	1	1	$1 + k$

Maynard Smith notes that a modifier causing "habitat selection," which in his context means a tendency to remain in the subpopulation where the animal was born, will spread in both subpopulations, and cause speciation. This is in effect a one-allele speciation model very similar to that of Balkau and Feldman, although Maynard Smith did not attempt a full mathematical analysis to confirm his intuition. Another of Maynard Smith's models involves a modifier of the amount of assortative mating. This is also a one-allele model.

Yet another of his models involves a second locus, B, which codes for two phenotypes according to which there is assortative mating. Except for his assumption that there is complete dominance at that locus, it has exactly the same properties as the assortative mating locus A in the present model. His model is of the two-allele type, and we should expect to see the same sort of threshold effect as in the present model. Maynard Smith does not discuss this matter, but presents a numerical example involving complete assortative mating, strong selection, and some restriction of migration between the subpopulations. In that case speciation occurs, and it is implicit in Maynard Smith's discussion that there are parameter combinations for which speciation would not occur. He was more concerned with showing that there were sympatric models for which speciation would occur.

Dickinson and Antonovics (1973) made a more extensive study of a model which

was quite similar to this model of Maynard Smith's. They found that strong selection, strong assortative mating, and restricted migration all favored the establishment of an association between the assortative mating gene and the selected locus. Their results are thus completely consonant with the picture presented above. They found that "any tendency toward isolation could be swamped if the level of gene flow increased," although they did not present information on the exact parameter combinations for which this swamping occurred.

Their work complements the present model in that the phenomenon which speciation prevents is not recombination between two loci in a situation of coadaptation, but formation of heterozygotes between two alleles adapted to different environments. It is therefore questionable whether a counterpart to their model could be made to work in haploids. In fact, if we eliminate segregation at one of the selected loci in our diploid model, it would come to resemble their model. A few runs have been made on the diploid model with segregation at loci A and B only. Interestingly enough, speciation turns out to be possible in our diploid model even when there is segregation only at one locus (or what is nearly equivalent, when there is complete linkage between loci B and C). This apparently results from the fact that the formation of ill-adapted heterozygotes is avoided by the occurrence of assortative mating.

Caisse and Antonovics (1978) presented a model involving parapatric speciation, with one locus (A) having a selection-migration cline, and another (B) for which assortative mating occurs. They find many of the same patterns, including parameter combinations for which the B locus did not show a cline of its own. They find that tightening the linkage between the A and B loci makes speciation happen more readily. They explicitly raise the question of why speciation does not always occur, and conclude that "the conditions leading to isolation are far more

stringent than those permitting genetic divergence." It is not known whether a haploid version of their model would show the same behaviors as their diploid model. Since the "purpose" of the assortative mating in their model is to prevent formation of ill-adapted heterozygotes, I suspect that it would not.

Predictions

From the picture presented here, a few predictions can be made as to how the patterns of speciation seen in nature should relate to the distinction between one- and two-allele speciation models. We have found that increased migration between the subpopulations is an unfavorable condition for speciation in a two-allele model. In a one-allele model we would expect it to make little difference. Thus there should be a correlation between the sympatry-allopatry spectrum and the distinction between one- and two-allele speciation. Allopatry is a situation favorable to either, but in sympatric situations, two-allele cases should be rarer. Thus we expect that after speciation there will be less genetic differentiation with respect to the genes involved in isolating mechanisms in cases of sympatric speciation than in cases of allopatric (or near-allopatric) speciation.

In a case of sympatry, speciation would be nearly impossible unless it were based on genetic variation which could lead to one-allele reproductive isolation. I find it easier to imagine genetic variation of the two-allele sort than of the one-allele sort. If there were a shortage of genetic variation of the one-allele sort, then recombination between the loci involved in pre- and postzygotic mechanisms could form an effective block to speciation. On the other hand, if genetic variation of both sorts is readily available, then there will be no block to speciation. If evolution is never limited by a shortage of any particular type of genetic variation, then the block to speciation presented here will never be relevant.

There may also be implications for the linkage relations between genes affecting

the isolating mechanism and the genes which affect adaptation to the different environments. We have seen that this linkage has no influence in Balkau and Feldman's one-allele model. In the two-allele models it makes speciation easier. We may therefore find that there has been some tendency for two-allele reproductive isolating mechanisms to have arisen at loci linked to loci which affect the substantive adaptations. This need not be the result of linkage modification, but could simply result from the fact that unlinked loci coding for two-allele isolating mechanisms failed to become involved in a successful speciation. This may not be a large effect.

One test for the occurrence of two-allele isolation suggests itself. In a speciation carried out wholly by one-allele isolating mechanisms, laboratory crosses of the two species, if possible at all, should result in no breakdown of the prezygotic isolation, although the postzygotic mechanisms which involve differentiation between the two species will become randomized. To the extent that prezygotic isolation is based on two-allele mechanisms, it will be broken down by crossing. Of course, care must be taken to observe the behavior or phenotype which leads to isolation, not merely the isolation itself. Otherwise we might conclude that a hybrid had lost the isolation when it was in reality still engaging in a behavior such as stringent mate selection, but was selecting other hybrids as mates.

LIMITATIONS OF THE MODEL

There are a number of directions in which it would be desirable to expand this model. One would involve making the genetic determination of both sets of traits, the adaptations as well as the reproductive isolation, polygenic. It is not clear a priori whether the results found here are sensitive to the number of loci assumed involved in the traits, although some effects, such as the breakdown of isolation by crossing, must also occur in polygenic cases. Extension of the model to examine effects of unequal subpopulation sizes is also called for, in part to examine situa-

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tions where a new species arises in a peripheral population.

A more important extension would involve making a model of postzygotic isolation. The B and C loci in our model may be thought of as constituting a postzygotic mechanism causing partial reproductive isolation—after all, Bc and bC gametes are being eliminated by the selection. But one could also imagine a modifier locus which had an allele which intensified postzygotic isolation by decreasing the fitness of Bc and bC, or by increasing the fitness of BC and bc. If the same allele at that locus increased the fitnesses of both BC and bc, this would be a one-allele isolating mechanism, while if one allele increased the fitness of BC and the other increased the fitness of bc, this would be a two-allele case.

The papers of Bazykin (1965, 1969) and Slatkin (1975) present phenomena relevant to the construction of models of postzygotic isolation in clines. It is less than obvious how to construct a simple canonical model of postzygotic isolation. One could imagine evolution bringing into play more loci like B and C, or modifiers which increase the fitness of BC and bc, or modifiers which decrease the fitness of Bc and bC. All of these would behave differently.

An additional direction for future work is suggested by the effects of gene interaction studied above. When the mean fitnesses of BC and bc, averaged across the two subpopulations, did not exceed the fitnesses of Bc and bC, then sympatric speciation became impossible no matter how strong the assortative mating. In this case the generalists Bc and bC do not have lower average fitness than the specialists. This suggests that we may be able to relate these fitness patterns to measurements of niche overlap between the forms adapted to the two subpopulations, and that when this overlap is too great, speciation will not occur.

Only when we can bring genetic and ecological constraints on speciation into a common framework will we begin to have a satisfactory overview of the speciation

process. Only then will geneticists be able to join ecologists in paying homage to Santa Rosalia.

SUMMARY

A model of speciation has been constructed involving two loci under natural selection in two subpopulations, with different alleles adapted to the different subpopulations. Progress toward speciation in this model consists of association of a third locus, at which there is assortative mating, with the original two loci. Cases can be found in which speciation cannot occur. The evolutionary force acting against speciation turns out to be recombination, which acts to randomize the association between the prezygotic isolating mechanism (assortative mating) and the adaptations to the two environments. This model suggests that there is an important distinction between two kinds of speciation. One involves speciation by substitution of the same alleles in the two nascent species, the other by substitution of different alleles. Only in the latter case does recombination act as a force retarding or blocking speciation.

ACKNOWLEDGMENTS

I am grateful to Monty Slatkin, Takeo Maruyama, Alan Templeton, Janis Antonovics, Freddy Christiansen, and Marcy Uyenoyama for helpful suggestions and discussions. Apologies are due G. Evelyn Hutchinson for misuse of the title of his classic paper. This work was funded by Task Agreement No. DE-AT06-76EV71005 under contract No. DE-AM06-76RLO2225 between the United States Department of Energy and the University of Washington.

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APPENDIX 1. Further comments on the models of assortative mating.

The assortative mating scheme in the haploid model was specified by stating that a fraction d of the population mated with individuals of the same genotype at the A locus, and $1 - d$ mated at random. Another mechanism which would lead to the same mating type frequencies would be the following: The A locus controls the division of the mating pool into two mating groups (according to space, time, or phenotype). Type A has probability $(1 + x)/2$ of entering mating group 1, and probability $(1 - x)/2$ of entering mating group 2. For allele a the probabilities are the reverse, $(1 - x)/2$ and $(1 + x)/2$. Within each of the two mating groups mating is at random. In this model it is specified that the likelihood of an individual reproducing is not affected by its genotype at the A locus or by the mating group it is in. It is not hard to show that the resulting mating type frequencies are then as previously given, with

$$d = \frac{x^2[1 - (p - q)^2]}{1 - x^2(p - q)^2} \quad (\text{A1-1})$$

where p and q are respectively the frequencies of alleles A and a .

In the case of the diploid model, we use a very

similar model of assortative mating. Every individual joins one of the two mating pools, and the probabilities of joining pool 1 are $(1 + d)/2$, $1/2$, and $(1 - d)/2$ for the three genotypes AA , Aa , and aa . This form of assortative mating differs from the haploid case in that when $d = 1$ some heterozygotes will still be formed, while in the haploid case all matings would then be $A \times A$ or $a \times a$. However, if $d = 1$ the frequency of heterozygotes at the A locus will gradually decline to zero through time. In a single population without effects of other loci, this scheme of assortative mating will reach equilibrium with gene frequency unchanged from its initial value. When the initial gene frequency is p , the final genotype frequencies of AA , Aa , and aa will be P , $2p - 2P$, and $1 - 2p + P$, where P is the smaller of the two solutions to the quadratic equation

$$\begin{aligned} -d^2P^2 + P[1 - 8d^2p^2 + 12d^2p - 4d^2] \\ - p^2 = 0 \end{aligned} \quad (\text{A1-2})$$

which for $p = 0.5$ becomes

$$-1/4 + P - d^2P^2 = 0. \quad (\text{A1-3})$$

Note that the frequency of AA individuals in the diploid case is not the same as the frequency of $A \times A$ matings in the haploid case, so that we cannot directly compare haploid and diploid cases with the same value of d .

It must be emphasized that the division of a population into mating groups has no necessary relation to the question of allopatry. The offspring of these matings are in the same ecological population, in that they compete perfectly with each other. The mating groups might simply be those individuals who mate in the morning and those who mate in the afternoon.

APPENDIX 2. A more formal statement of the haploid model.

Let $x_{ijk,u}^{(t)}$ be the frequency of genotype ijk in subpopulation u in generation t , where i, j , and k are indices which take on the values 0 for (respectively) alleles a, b , and c , and the values 1 for A, B , and C . The fitnesses of these genotypes are given by the values $w_{ijk,u}$. After selection, the genotype frequencies are given by

$$y_{ijk,u}^{(t)} = x_{ijk,u}^{(t)} w_{ijk,u} / w_u^{(t)} \quad (\text{A2-1})$$

where $w_u^{(t)}$ is the mean fitness of subpopulation u in generation t . Migration takes place according to a conventional island model:

$$z_{ijk,u}^{(t)} = \sum_{v=1}^2 m_{uv} y_{ijk,v}^{(t)} \quad (\text{A2-2})$$

where m_{uv} is $1 - m$ if $u = v$ and m otherwise, in the two-population case. Mating now takes place in each subpopulation. If $M_{ijk, fgh,u}^{(t)}$ is the frequency of matings between genotypes ijk and fgh , under the present scheme of assortative mating this is given by

$$M_{ijk, fgh, u}^{(t)} = (1 - d)z_{ijk, u}^{(t)}z_{fgh, u}^{(t)} + dz_{ijk, u}^{(t)}z_{fgh, u}^{(t)}\delta_{if}/z_{i, \dots, u}^{(t)} \quad (A2-3)$$

where δ is the Kronecker delta function which is 1 if $i = f$ and 0 otherwise. Here $z_{i, \dots, u}^{(t)}$ is the overall frequency of allele i in subpopulation u in generation t , after selection.

Recombination then occurs in each subpopulation. To avoid tedium, it will not be described here,

except to say that it follows the autosomal Mendelian rules with no interference, with recombination fractions r_{12} and r_{23} , and with the resulting gametes being denoted by $x_{ijk, u}^{(t+1)}$.

This Appendix has described the haploid model with the SMR ordering of life cycle events. The other ordering and the diploid model can be formalized in a similar fashion.

EVOLUTION SOCIETY NEWS

Society Election

The results of the 1980 election of officers are as follows:

President elect	OTTO SOLBRIG
Vice President I	WYATT W. ANDERSON
Vice President II	LINDA MAXON
Vice President III	A. H. D. BROWN
Councilor I	MICHAEL ROSENZWEIG
Councilor II	MARY F. WILLSON

New Associate Editors

The associate editors for 1981–1983 are as follows:

DR. JOSEPH FELSENSTEIN, University of Washington
 DR. SUBBODH JAIN, University of California, Davis
 DR. ROBERT RICKLEFS, University of Pennsylvania

DR. STEVAN ARNOLD, University of Chicago, will fill Dr. Futuyma's 1981–1982 term as associate editor.

SPECIES

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The fundamental tenet of the molecular clock hypothesis is that evolution of homologous proteins is a random process; that the interval separating two species from common ancestors is proportional to the degree of protein dissimilarity between them. In general, the difference in the number of independent substitutions recorded in a relatively insubstantial interval is a determinant of protein dissimilarity. In neglecting implicit inter-species differences, the postulation of a constant rate presuppases protein evolution rates to be uniform despite outstanding differences. The neutral explanation of regularity, the neutral mutation drift theory (Kimura, 1968 and Jukes, 1969), lies in its prediction that the rate of amino acid replacement is proportional to the nucleotide mutation rate and that the latter to be constant. The equilibrium between mutational replacement by drift and natural selection, realized, however, the species number remain indefinitely extended interval in evaluating empirical data. The central thesis, that the number of replacements are indifferent to natural selection, is complicated by ordinary circumstances in the natural world—stochastic variability (see, e.g., Haig-Smith, 1972; Nei et al., 1977). Perhaps in part the validity of the neutral theory (or more properly, the explanation) is problematic in debate.

But does the molecular clock depend upon validation