Population biology of checkerspot butterflies and the preservation of global biodiversity

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Long-term research on Euphydryas populations has yielded much insight into the requirements for conserving invertebrates. It also, however, has shown that too much time is required to obtain such insights species by species to preserve global biodiversity. Instead, quick sampling methods must be devised to take inventories of the biota in prospective reserves, planning use patterns in those reserves, and monitoring the results. Conservation biologist have about a decade to develop and deploy such systems if they are to play a significant role in preventing the loss of more than half of terrestrial biodiversity.

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This paper addresses a series of points that have emerged from the combined work of our research group in two seemingly disparate areas: long-term field and laboratory research on the population biology of butterflies, especially of the checkerspot Euphydryas editha (Nymphalidae: Nymphalinae), and policy research on the preservation of biodiversity and the maintenance of the ecosystem services that depend upon it (Ehrlich and Ehrlich 1981). Here I discuss some of the conclusions I have drawn from more than three decades of work in these two fields. My most important conclusion is distressing. The sort of intensive, species-focused research that I and my colleagues have carried out on Euphydryas appears to have a very limited future in conservation biology. Instead, if a substantial portion of remaining biodiversity is to be conserved, detailed studies of single species must be replaced with "quick and dirty" methods of evaluating entire ecosystems, designing reserves to protect them, and determining whether those reserves are working.

The species approach to biodiversity

In the public mind, the biodiversity crisis is one of loss of species. This view is embodied in the lists of endangered species produced by both governmental bodies and nongovernmental organizations, in the United States' Endangered Species Act, and in the publicity given to species on the brink of extinction such as the black rhino and California condor. This approach is also rooted in the scientific literature, where the tradition of focusing on species diversity as the measure of biodiversity is well entrenched (e.g., MacArthur 1972; but see Hendrickson and Ehrlich 1971).

As useful as a species-based approach to biodiversity has been, it suffers from numerous drawbacks. While it is clear that by far the largest number of animal species live in terrestrial habitats, especially in tropical moist forests (Wilson 1989), it is equally evident that proportionately much greater diversity of phyla and classes is found in the relatively species-poor oceans (May 1989). I'll say no more about this aspect of diversity here, except to point out that from the perspective of biologists, the world would be a much poorer place without...
cephalopods, loricifera, and the like. Whether or not they can provide us with economic benefits or play crucial roles in ecosystems, unusual organisms are fascinating and help us to understand the possible avenues that can be taken by evolution.

The importance of population diversity

Toward the other end of the scale, the importance of population diversity is often overlooked. First of all, the genetic and ecological diversity among populations helps buffer species against extinction. Geographically circumscribed species with little population diversity – especially island species – have proven highly extinction-prone. Population diversity is also extremely important to the ability of species to provide goods and services needed by humanity. Substantial genetic diversity is required, for instance, in potential crop plants and their relatives in order to permit them first to be developed into satisfactory crops and then to keep up in the coevolutionary races they run with their predators and parasites. And if the population of Engelmann spruce trees (Picea engelmannii) in a watershed is destroyed, with it will go the flood-control service of the subalpine ecosystem. It will then be of little comfort to those drowned downstream that the species is in no danger of extinction.

Our work with Euphydryas butterflies has shown clearly the significance of population diversity to problems of conservation (Singer 1971, Gilbert and Singer 1973, Ehrlich et al. 1975, McKechnie et al. 1975, Ehrlich and Murphy 1987, Murphy and Weiss 1991a). Populations of Euphydryas editha, for example, differ from one another in genotypes, phenotypes, phenologies, use of resources, and flight behavior (Singer 1971, 1972, White and Singer 1974, Ehrlich et al. 1975). If this species of herbivorous insect is to be conserved, knowledge of the biology of individual populations will be essential – since phenomena that threaten one population will not necessarily threaten another. This was clearly demonstrated by the varied responses of groups of E. editha populations to the California drought of 1975–77 (Ehrlich et al. 1980). It should also be noted that the sort of population diversity presented by E. editha can be of considerable significance in questions related to delivery of ecosystem services, control of pests, and harvesting of economically important species. It is clear from our work, for instance, that within a single species some populations may have the capacity to be more effective crop pollinators (Murphy 1984) or more dangerous crop pests, and that sustainable yields may vary greatly between populations.

Second, with trivial exceptions, the process of species extinction is actually a complex process of progressive population extinction (Shaffer 1981, Gilpin and Soulé 1986, Murphy et al. 1990, Thomas et al. 1990). If populations are conserved, then species are conserved (but not necessarily vice versa). Our group’s long-term research on checkerspot butterflies (Euphydryas) has provided considerable insight into the causes and consequences of population extinction, and therefore into a wide array of global conservation issues.

The need to conserve plants and invertebrates

Before discussing Euphydryas in more detail, I’d like to emphasize the great need to shift the emphasis in the conservation community from the protection of “charismatic megavegetables” to the protection of smaller or less spectacular organisms. Everyone concerned with conservation wants to see the panda survive, but from the viewpoint of both pandas and people the preservation of more obscure organisms is crucial. Maintaining the diversity of plants is, of course, the key to the entire enterprise of securing the future of the rest of organic diversity and of human society. Without bamboo there would be no pandas; without three kinds of grasses, Zea mays, Oryza sativa, and Triticum spp. (which have been developed into maize, rice, and wheat), there would be no civilization as we know it.

Insects and other terrestrial arthropods are also crucial components of the entire web of life (Gilbert 1980, Wilson 1987). Without insects and their relatives, the living world would be unrecognizable. Loss of the pollination and seed dispersal services performed by insects and the absence of insect herbivory would dramatically alter (and pauperize) plant communities in ways that are difficult to imagine. The absence of insects and mites, which along with the nematodes could comprise more than 95% of species diversity (May 1989), would reverberate through food webs, changing soil faunas and fertility, extinguishing most species of birds and much of the remainder of Earth’s terrestrial vertebrate fauna as well as many freshwater fishes. The loss of ants alone would completely unravel tropical-rainforest ecosystems (in which ants are key herbivores and predators) and cause untold havoc in most other ecosystems (Gilbert 1980, Hölldobler and Wilson 1990).

Insects and other terrestrial arthropods, after all, comprise the vast majority of organic diversity, with the possible addition of the still poorly-known nematodes (May 1989). Indeed, in terms of species diversity, all the rest could almost be considered a side issue. Also, most insects are herbivorous (Erwin 1982); one could therefore view Euphydryas as representing the very core of biodiversity.
Euphydryas and the tactics of conservation

Perhaps the single most important tactical conclusion for conservationists that can be drawn from our long-term research on these butterflies is that the preservation of small invertebrates will require a very different approach from that developed on the basis of megavertebrates. Think of the kinds of issues that pervade the conservation of, say, rhinos, cheetahs, or condors. What is the minimum viable census size that will sustain a population of cheetahs? Are surviving individuals too inbred? How much habitat is required to provide enough territory space for a population of black rhinos? Should ex situ conservation be attempted for California condors? How can deliberate killing of elephants by human beings be prevented?

These are rarely first-order kinds of questions in invertebrate conservation. For example, while establishing a minimum viable population size (MVP) (Souël, 1987) – or, more likely, a minimum viable metapopulation (MVM) (Ehrlich and Murphy 1987) – can be an interesting and useful exercise with invertebrates, normally endangerment is patent long before such a size is even approached. The subspecies Euphydryas editha bayensis in the San Francisco Bay area is clearly imperiled (and has been listed as “threatened” under the U.S. Endangered Species Act). Nevertheless the large reservoir population of the southern Bay area metapopulation (Ehrlich and Murphy 1987) always numbers more than 10^6 adults and often exceeds 10^7 individuals (Murphy and Weiss 1988a).

Indeed, a population of 10^7 E. editha may exist on a few dozen hectares when environmental conditions are optimal. In contrast, it is possible that there have never been 10^5 grizzly bears at one time in the coterminous United States. Few, if any, vertebrates would be considered endangered with populations of 10^6 adults. But then few vertebrate populations (and no populations of large vertebrates) typically go through 2–5 fold annual size fluctuations, as E. editha does often (Ehrlich et al. 1975, Murphy and Weiss 1988a). For most vertebrates, again unlike E. editha, population extinctions are not a normal part of their population dynamics (Ehrlich et al. 1975, 1980).

Endangered invertebrate populations do not ordinarilypersist with only a handful of individuals over many generations (Murphy et al. 1990). Inbreeding depression, therefore, has not often been a serious concern. The standard that populations should be maintained at several hundred individuals or more over many generations to avoid inbreeding (Lande and Barrowclough 1987) is rarely violated. Small demographic units in E. editha metapopulations appear to receive immigrants frequently enough to prevent genetic difficulties (Murphy et al. 1990), and that may be typical of insect species. Furthermore, even in Euphydryas populations that appear vulnerable to inbreeding effects, those effects have not yet been detected. A transplanted colony of E. gillettii (Holdren and Ehrlich 1981) has persisted with an N_e apparently less than 50 individuals for thirteen generations; it may eventually provide important information on inbreeding resistance or susceptibility in Euphydryas.

Terrestrial invertebrates normally do not have large home ranges or territories. Individuals of some traplining species in tropical forests, such as Euglossine bees and heliconine butterflies (Ehrlich and Gilbert 1973), may require many hectares of habitat to support them because of the dispersion of their food resources. But areal requirements measured in square kilometers, seen in organisms such as California condors, grizzly bears, and Sumatran rhinos (Hutchinson and Ripley 1954) have rarely been ascertained in insects, and individuals of even medium-size butterflies often are quite site tenacious and largely confine their activities to a few hectares (Daily et al. 1991).

Indeed for Euphydryas, and many (if not most) other insect herbivores, the detailed quality of the habitat is much more important than its extent. Relatively restricted areas of the most suitable environment can support reservoir populations that supply the long-distance dispersers that maintain a species’ metapopulation in a large area. Given enough space, grizzly bears, with their great mobility and catholic diets, can find food. Furthermore, they are able to persist in a wide range of climates, from arctic tundra to semi-desert. Almost all “generalist” insects, however, are specialists when compared to vertebrates. If the appropriate oviposition plant or plants for a population of a Euphydryas species disappears from a reserve, the butterfly will not persist, no matter how large the reserve. Furthermore, the density of the food plant usually must be high enough to permit larvae to move to a new plant when one has been devoured (few host plants are large enough to support the dozens of larvae from an egg mass from hatch to diapause) (Singer 1972). Grizzly bears can move tens of kilometers in search of food, larvae at most tens of meters.

Also unlike most vertebrates, Euphydryas are heavily dependent on appropriate microclimates for their survival. In the most intensively studied populations, those of E. gillettii bayensis, the eggs are laid in March and April, and the newly hatched larvae immediately find themselves in a race with the senescence of their food plants (Singer 1972). If they fail to reach the instar that can diapause through the dry summer months before the plants senesce, they will not survive. Whether or not the larvae can win the race depends on a complex phase relationship between the phenology of the host plant and the insect populations (Singer and Ehrlich 1979). That relationship, in turn, depends heavily on the interactions between topography of the habitat and its macroclimate that create diverse thermal microenviro-

In habitats with a single exposure (say a gentle south-facing slope) sequences of years may occur with weather that makes the plant-Euphydryas phenologies incompatible in the single available topoclimate, and the population will be driven to extinction. But if the habitat contains a variety of exposures, it will possess areas with at least some favorable topoclimates under nearly all weather conditions conceivable in the macroclimate, and the population will probably persist even if the area of habitat is relatively small. The California drought of 1975–77 caused numerous extinctions of component populations of the Santa Clara County E. e. bayensis metapopulation because of the very early senescence of the host plants (Singer and Ehrlich 1979, Ehrlich et al. 1980, Ehrlich and Murphy 1987, Harrison et al. 1988). Larvae simply had too little time to grow to the size at which they can enter diapause. The heavy rains that accompanied the 1982–83 El Niño also resulted in large population declines, in this case because a paucity of winter sunshine delayed adult flight (and oviposition) longer than it delayed host plant senescence, again shortening the time available for larval growth (Dobkin et al. 1987).

Environmental-quality factors, especially those connected with weather (Ehrlich et al. 1972) and human-caused disturbance of habitats, also seem to govern the persistence of other temperate-zone butterfly populations (see summaries in Ehrlich 1984 and Murphy et al. 1990). I suspect the extinction dynamics of many other invertebrate groups are similarly controlled by the combined effects of habitat fragmentation and environmental extremes (drought, deluge, wildfire, etc.) in temperate areas, while other factors such as demographic stochasticity and overexploitation are much more important for vertebrates.

Almost nothing, unfortunately, is known about the factors influencing population persistence of invertebrates in tropical ecosystems, although it is those systems that are most endangered. Certainly host-plant relationships are critical for butterflies (Ehrlich 1984) and other herbivorous insects, and for at least some butterflies, adult pollen sources are crucial as well (Ehrlich and Gilbert 1973). Herbivores in general are probably more specialized in the tropics; thus the massive destruction of tropical forest vegetation now occurring (Myers 1989) is certainly leading to losses of populations and species of invertebrates unprecedented at least since the last ice age and possibly in the 65 million years since the extinctions at the K-T boundary. A special problem in the tropics is the conversion of low elevation habitat with warm exposures to agriculture and other forms of development. This removes an array of niches with particular insolation, temperature, and precipitation regimes along with the biota associated with them (Murphy and Weiss 1991a, b).

Overall, the best tactic for conservation may be to establish the extent of reserves with an eye on the home ranges and resource needs of charismatic megavertebrates, the areal requirements of “big things that run the world” (Terborgh 1988), but to locate the reserves with attention to habitat diversity required by the “little things that run the world” (Wilson 1987).

Euphydryas and strategies for conservation

I believe that the most important conclusion from our group’s work on Euphydryas is strategic rather than tactical. Our research has made it crystal clear that the sorts of detailed ecological and evolutionary information that one would ideally like to have before recommending conservation programs for invertebrate species will almost never be available. Research on the Euphydryas system has provided a great many tactical lessons about single-species conservation for invertebrates—that is, how to accomplish the preservation of a given species. It has shown the importance of identifying demographic units, of differentiating migration from gene flow, of recognizing subtle key habitat quality factors such as slope and exposure, and so on (Ehrlich and Murphy 1987).

But those tactical successes have shown us how to win battles while losing the war. More than three decades of research by dozens of investigators has been required to gain a reasonable understanding of the population biology of Euphydryas editha, to provide some notion of the geographic scale upon which conservation planning must proceed and the phenomena that must be addressed, and to be able to make sound recommendations for the conservation of the best-known metapopulations. That work has shown that lessons learned working on one suite of populations of E. editha are not necessarily applicable to co-occurring close relatives such as E. chalcedona (Brown and Ehrlich 1980, Murphy et al. 1986) or to distant populations of E. editha itself (Ehrlich et al. 1975, 1980). The amount of effort that would be required to advance understanding of the biology of just the 600 or so species of butterflies that live in North America to the level of E. editha today is mind-boggling; it might be done in a decade with thousands of investigators working at it—if those investigators could be trained instantly.

And yet the fate of a substantial portion of Earth’s terrestrial fauna, invertebrates as well as vertebrates, will be determined in the next decade or two (Vitousek et al. 1986, Myers 1989, Wilson 1989, Ehrlich and Wilson 1991). Conceivably, 10 to 25 million species could go extinct, and with them could go much of the ability of Earth’s ecosystems to supply humanity with essential services (Ehrlich and Ehrlich 1981, 1990). The destruction of tropical forests, for example, is already greatly adding to the atmospheric build-up of greenhouse gases.
gases, worsening a problem with the potential to bring down civilization.

In short, there is not remotely the time, the personnel, nor the financial support available to study the biology of most of the populations that must be preserved if the majority of Earth’s biological diversity is to be saved — and along with it the crucial functioning of ecosystems. Indeed, it has long been evident that even a rough catalogue of species diversity is unlikely to be completed before most of that diversity is gone (Ehrlich 1964). In some cases, conservation biologists will be able to use their growing understanding of population viability analysis (PVA) in aid of the preservation of target populations and species. But most populations and species almost certainly will go extinct before they are even discovered, let alone investigated. The sort of intensive short-term effort that has recently been expended on understanding the conservation biology of the northern spotted owl (Strix occidentalis caurina) in the United States (Thomas et al. 1990) could serve as a model for research on the conservation biology of vertebrates, as the work on Euphydryas can for invertebrates. But together these techniques are likely to be applied to less than 1/10,000 of all species, and less than 1/1,000,000 of all genetically distinct populations or subspecies. A new strategy is required for the overall goal of saving ecosystems, not species one at a time.

A new approach for conservation biology

So conservation biologists must take another approach, even as they continue honing their PVA skills for those rare occasions when they can be put to good use. They must develop cookbook responses for the preservation of endangered species to serve in the absence of extensive autecological data. They must learn to do rapid and rough inventories of the biodiversity in entire ecosystems, plan the preservation and management of those ecosystems, and develop techniques for monitoring success in preserving the biota of those systems. This inevitably means using samples, both systematic and geographic, to represent the entire taxonomic range of organisms and the entire extent of the ecosystems. Such rough sampling is bound to lead to some serious errors that could result in the loss of some populations and species, but this circumstance must now be accepted. Without such “quick and dirty” inventory, planning, and monitoring procedures, future losses will inevitably be far greater. It has, after all, been a decade since publication of the landmark report “Research Priorities in Tropical Biology” (NRC 1980). That report urged, among other things, establishment of crash programs of sampling tropical diversity and greatly increased support for systematics. But little has been done on the former, and the status of systematics has, if anything, deteriorated.

One of the first tasks of the conservation community is to decide on taxonomic groups to be used as indicators in inventorying and monitoring, and settle on appropriate techniques to be used. I would suggest that the major effort go into three already-well-known groups: vascular plants, birds, and large butterflies (Papilionidae, Pieridae, Nymphalidae). The plants, forming the base of most food chains and the basic food resource for almost all animals, are an obvious choice. Indeed, with an effort funded to the level of the cost of two useless B-2 bombers ($1300 million), the task of more or less completing a global survey of plants could be completed. Botanists, plant collections, and botanical gardens are crucial to the future of humanity, and botanical resources need rapid expansion and deployment to accomplish the task of understanding and protecting Earth’s flora. It is an indication of misplaced priorities within the scientific community that relatively unimportant exercises such as the sequencing of the human genome can take priority over the assessment and preservation of Earth’s irreplaceable botanical wealth.

In theory, plants alone, because of their fundamental roles in ecosystems, could form the basis of most inventorying/planning/monitoring activity. But the problems of identifying plants in the field (especially in the tropics) can be substantial. Subtle changes in tree florals will often be signalled by shifts in recruitment (adult trees may persist for a century or more in habitats no longer able to support a viable population), and saplings can be especially hard to identify. The shortage of skilled botanical taxonomists and field workers therefore makes supplementation with animal groups desirable.

The alpha taxonomy of the roughly 9000 bird species is largely complete, and in most areas of the world there are ornithologists and bird watchers capable of identifying most species and training others to do so as well. Birds are indicators of vegetational structure and, in some situations, of the presence or abundance of certain floral components (e.g., many fruiting trees in tropical forests), and migratory species carry information on the condition of distant habitats. A great deal of work on monitoring techniques has already been done, but more will be required to standardize and simplify them so that they will be readily used by relatively inexperienced people.

Butterflies are also well known taxonomically, and people without extensive biological training can quickly learn to identify the larger ones. Butterflies are more tightly linked to the taxonomic diversity of the plant community than are birds, and should provide a rather sensitive indicator of the state of that community. They are also very sensitive to pesticides, a major factor in the overall toxification of the planet, and, as our work on Euphydryas has shown, are responsive to a variety of other subtle aspects of habitat quality. Appropriate transect, malaise trapping, and baiting techniques have
been worked out for butterflies and should be easily modifiable and standardized for monitoring.

In tropical areas, monitoring the health of ecosystems by sampling the bird and butterfly faunas may prove simpler than attempting to monitor the flora at all. The selection of aquatic organisms to monitor will also be required, with frogs perhaps being the easiest. Frogs also are suffering mysterious declines in many areas of the world and should therefore be watched closely and be the subjects of investigations to determine the cause or causes. Monitoring of stream nutrients and silt loads could also provide a sensitive indicator for evaluating ecosystem health (O’Neill et al. 1977); the techniques for doing so are well developed, and sample analysis could be successfully done in tropical countries. Our group is currently setting up a test inventorying/monitoring system adjacent to La Amistad National Park on the Costa Rica – Panama border with the collaboration of Latin American biologists. We plan to evaluate various ideas and techniques and establish joint programs for training of para-ecologists to employ successful techniques elsewhere in the neotropics.

Simple, accurate, repeatable inventory and monitoring programs of coastal and marine systems need also be developed. There is some evidence that shorebirds (waders) (Myers et al. 1987) and pelagic birds (Boersma 1986) might prove to be useful indicator organisms for oil pollution. Indeed, shorebirds and migratory land birds are already providing civilization with a generalized warning about the state of Earth’s environment (Terborgh 1989, Ehrlich 1990). There is some movement toward developing such programs, but more effort (and funding) is clearly needed.

While developing techniques for sampling biodiversity must have high priority, so must decisions on allocating effort to the understanding of Earth’s diverse ecosystems. A balance of effort clearly must be achieved between establishing inventory/planning/monitoring systems for established or prospective reserves, quick surveys of future extinction hotspots to capture some idea of the diversity about to be lost (and thus provide stimulus for the establishment of reserves), and in-depth studies that will provide a picture of the basic structure of diversity. The latter could range from lists of species of all organisms in habitat plots of tropical forests (May 1989) to efforts to catalogue the biota of an entire nation (as now being attempted by INBIO in Costa Rica). I will not deal with the issue of the geographic allocation of effort in depth now, but only emphasize that sensible decisions on where to study can only be made after those on how to study have been made – and point out that every day the options of where to study get fewer. It is hardly possible to exaggerate the urgency with which these issues should be addressed (NRC 1980, Ehrlich and Ehrlich 1981, Ehrlich and Wilson 1991).

Conclusions
In sum, we have learned a great deal of value to conservation in more than three decades of intensive work with the *Euphydryas* system and other butterflies (Ehrlich and Murphy 1987). But the most important lesson is that Earth’s biota cannot now be saved by the sort of laborious dissection of the biology of populations that we have engaged in. Rather, it is critical that conservation biologists build on what is already understood about well-known organisms to develop tools that can be used to save biodiversity quickly and en masse. And it is also critical that they be active politically to press for the resources required to allow them to apply their tools before it is too late.

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