On the dangers of interpopulational transfers of monarch butterflies

In North America there are two migratory populations of the monarch butterfly, Danaus plexippus L. (Nymphalidae). There is an enormous eastern population, which migrates between a summer breeding area east of the Rocky Mountains and overwintering areas in central Mexico, and there is a smaller western population, which breeds west of the Rocky Mountains and migrates to overwinter in numerous sites along the California coast (Figure 1). The degree of natural interchange between the eastern and western populations is unknown; despite nearly 60 years of debate, no quantitative data address this question (Brower in press). We recently became aware of experiments in which adult monarch butterflies captured or reared from eastern populations are being released west of the Rockies, and vice versa. Transfers have been made from Wisconsin to California (number unknown, Anonymous 1992), from California to North Carolina (N=1500, Cherubini 1994), from Nebraska to Oregon (N=300, Anonymous 1994), and from Pennsylvania to Oregon (N=56, Steffy 1994). In articles in The Monarch Newsletter (1994–1995, volume 5, issues 2–4), butterfly specialists are debating the wisdom of this practice. We believe, however, that the situation should be brought to the attention of a broader community of biologists.

We offer three arguments against transferring monarch butterflies between distinct populations: Transferred butterflies can carry infectious and potentially lethal diseases into susceptible populations; transfers may confound our understanding of numerous aspects of the monarch's basic biology; and the hypotheses purportedly being tested with these transfers are unanswerable by this technique.

Disease risk is a potentially disastrous consequence of artificially mixing populations. There is increasing recognition among ecologists that diseases have significant impacts on wild populations and that diseases may cause or exacerbate conservation problems (e.g., Thorne and Williams 1988, Wilson et al. 1994). While most studies have focused on birds and mammals, several insect epidemics are also well documented.

The parasitic mite, Varroa jacobsoni, was first reported in colonies of the European honey bee, Apis mellifera, in the mid-1960s. By 1970 many colonies were being killed by the mites in Japan and eastern Europe, and mite-caused mortality rapidly spread across western Europe, North America, and South America (Beetsma 1992). One factor important in the mite's range expansion has been the export of infected colonies and queens. Some colonies are more resistant to the mites, due to naturally occurring variation in bee development time, nest-cleaning behavior, and grooming behavior (Boecking and Ritter 1994).

In California, a rickettsial bacterium that resembles Wolbachia is spreading through populations of the fruit fly Drosophila simulans (Drosophilidae) at the rate of more than 100 km per year. It takes less than three years for a population to become almost completely infected. Analyses suggest that the rapid spread may be partly attributed to occasional long-distance dispersal of individuals (Turelli and Hoffmann 1991).

These examples could foreshadow the monarch's fate if east-to-west and west-to-east transfers continue. One candidate pathogen is the neogregarine protozoan Ophryocystis elektroscirrhza, which infects both monarch and queen butterflies (Danaus plexippus berenice Cramer; McLaughlin and Myers 1970). The effects of repeated infection of successive generations in the laboratory are cumulative, and after two or three generations the butterflies are so diseased that they fail to develop properly, cannot emerge successfully from their chrysalids, or die shortly after emerging.

Ophryocystis spores are spread in three ways: horizontally by venereal transfer from male to female and vice versa during mating; horizontally by other physical contact between healthy and infected adults (confirmed experimentally in the laboratory with caged butterflies); and vertically by transfer from a female to offspring (spores rub off a female's cuticle onto her eggs or onto the host plant). Infection occurs subsequently when a caterpillar swallows the spores (McLaughlin and Myers 1970). Because dense clusters of adults form during the monarch's fall migration and at the overwintering sites, the transfer of disease from adult to adult is particularly ominous. Butterfly density


S. Altizer, 1994, unpublished data.
in Mexico has been conservatively estimated to be ten million monarchs per hectare.

Leong et al. (1992) determined that *O. elektroscirra* is present to a high degree in coastal California overwintering populations. In the winter of 1990-1991, Leong and colleagues found 53% and 68% of individuals sampled at two sites to be infected. Similarly, Elizabeth Bell at the University of California at Santa Cruz has measured infection rates of 30-60% at Santa Cruz sites. Altizer and colleagues have found that populations from Minnesota, Kansas, and Texas, as well as monarchs from several overwintering sites in Mexico, are infected but to lesser degrees than the western populations. Only three monarchs from

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3E. Bell, 1994, personal communication. University of California, Santa Cruz, CA.

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**Figure 1.** Migration routes of the monarch butterfly in North America. a. The western population breeds west of the Rocky Mountains during the spring and summer and migrates to numerous overwintering sites, mainly along the California coast, from north of San Francisco to south of Los Angeles. The vastly larger eastern population breeds east of the Rocky Mountains and migrates to winter at a few spectacular overwintering sites in the Transverse Neovolcanic Belt, south of the Tropic of Cancer in central Mexico. The magnitude of a fall migration across the Gulf of Mexico is uncertain. b. Overwintering individuals of the western population migrate in early spring into the Coast Ranges, the Central Valley, and the Sierra Nevada where they lay their eggs on the resurgent milkweed flora and produce the first spring generation. Monarchs that overwintered in Mexico remigrate at the end of March and early April to the Gulf Coast states and produce a new spring generation on the southern milkweeds. This new generation then flies northwards to southern Canada and breeds in an area of approximately 2.2 million km$^2$. After three or four spring and summer generations, the monarchs enter reproductive diapause and migrate to their respective overwintering sites. Spring migration across the Gulf of Mexico is also open to question. (From Brower in press, used with permission of the Lepidopterists' Society.)
At this time, it is not possible to rule out infection by *Ophryocystis elektroscirrhosa* while rearing monarchs attest to its highly infectious, debilitating, and ultimately lethal nature.

Although the pathogen is present on both sides of the Rocky Mountains, an insidious possibility is that several neogregarine species or distinct strains may occur in different populations of monarch butterflies. If so, the impact of strains introduced through butterfly transfers could be more severe than the impact within the original host populations. We should take warning from the harsh effects of new strains of previously encountered pathogens, such as influenza, in human populations.

The numbers of monarch butterflies at California overwintering sites in the winter of 1994–1995 were the lowest on record. At the Pismo State Beach colony, for example, Sakai (1995) estimated the population at 15,000, one-tenth its usual number. At this time, it is not possible to rule out infection by *Ophryocystis elektroscirrhosa* as one cause of the butterflies’ scarcity.

Transfers could destroy the possibility of understanding numerous aspects of the basic biology of the monarch. Although the monarch butterfly is one of the best studied nonpest insects (Malcolm and Zalucki 1993), we know little about the biological differences between the eastern and western populations. Deliberate transfers are likely to result in reciprocal gene flow and decrease any existing differentiation between the populations. Analysis of monarch mitochondrial DNA revealed almost no polymorphism either within or between samples from Mexico, California, and the West Indies (Brower and Boyce 1991). Using electrophoresis, however, Eanes and Koehn (1978) found substantial allozyme variation in eastern samples. Comparable electrophoretic data for western monarchs are not available.

Possible differences between the eastern and western populations include, but are not limited to, the following:

- The eastern population migrates to a handful of sites in a tiny region of Mexico to overwinter, while the western population overwinters in more than 200 sites stretching along much of the California coast. The problems of orientation and navigation faced by migrants in the two populations are different. For example, in both populations many migrants encounter large bodies of water (the Great Lakes, Atlantic Ocean, and Gulf of Mexico in the east, and the Pacific Ocean in the west). Because the orientations of these coastlines relative to the overwintering destinations differ, eastern and western migrants may demonstrate different directional responses to large bodies of water.
- The macro and microclimates of the high-altitude overwintering sites in Mexico are vastly different from those in the coastal overwintering sites in California. The two populations probably have different responses to cold temperatures, including biochemical, physiological, and/or behavioral adaptations. We know, for example, that monarchs migrating to Mexico build up much larger lipid reserves than those migrating to overwintering sites in California (Brower 1985, Tuskes and Brower 1978).
- The timing of the spring migrations, and sexual behavior at the overwintering sites, differ in the east and west. In California, almost all overwintering female butterflies mate at the sites between December and March, while in Mexico fewer of the butterflies mate before departing (Brower 1985, Herman et al. 1989).
- The milkweed flora differs east and west of the Rockies. Milkweeds vary in, for example, their cardenolide chemistry, phenologies, and life forms, and we do not know the extent of coevolution between populations of the monarch and these two floras.

The multiplicity of known and likely differences imply that suites of adaptations under genetic control could differ substantially in the two populations. It is conceivable that transfers could result in considerable genetic disequilibrium and force massive selective reorganization and genetic deaths in both populations.

In addition, human-caused gene flow could make it impossible to estimate the degree of natural interchange of monarch butterflies across the Rocky Mountains (Brower in press, Malcolm and Zalucki 1993). Transfers could also muddle our ability to understand the monarch’s nineteenth-century transpacific dispersal, including the pattern of island-hopping and the colonizations of Australia and New Zealand (Vane-Wright 1993).

Deliberate transfers of individuals between donor and recipient populations with subtle genetic differences have resulted in conservation and management problems in several taxa. For example, on small oceanic islands off of New Zealand’s North Island, small relict populations of the tuatara (*Sphenodon*), large iguana-like animals, are the only survivors of an order of reptiles that flourished during the Triassic, 200 million years ago. Recent allozyme analyses have indicated that several islands support genetically distinct populations and even different species. Attempts to conserve the diminishing populations by legislation ignored known taxonomic differences and transferred animals among the islands. Ignoring these differences has unfortunately resulted in the loss of several well-differentiated populations and possibly even one species (Daugherty et al. 1990).

The hypotheses purportedly being tested by the transfer experiments have never been clearly articulated, are not being posed in rigorously testable form, and, even if reformulated, are unlikely to be answerable with available methodology. Urquhart and Urquhart (1972, 1974, review in Urquhart 1987) organized reciprocal transfers of thousands of monarchs between eastern and western populations in order to answer the following question: Would monarch butterflies continue to travel southward or southwestward dur-
ing the fall migration if they were transferred from one part of North America to another? Recaptures of released, tagged individuals indicated that at least some did still travel south, but there was no gain of any further knowledge of the monarch's biology. The number of monarchs transferred by the Urquharts and their collaborators has never been published.

Two purposes have been stated for the current round of butterfly transfers: "to determine how California monarchs behave east of the continental divide" (Cherubini 1994), and to determine if the direction of migration is "innate...or determined directly by the butterflies from stimuli perceived in the external environment of the release location itself" (Cherubini 1995). The first question has already been answered by the Urquharts' transfers. Monarchs captured at Muir Beach, California, and released in North Dakota flew south and were recaptured in Nebraska and Kansas (Urquhart and Urquhart 1974). The second question, unraveling the influences of genetic and environmental factors on monarch orientation and navigation, is more complex. It is not clear how our understanding is to be advanced by haphazard transfers, which lack a carefully designed protocol and are unrelated to any laboratory experiments.

The potential to gain new insights about migration from monarch tagging, beyond those already obtained by the Urquharts and their associates, is limited because of the extremely low rate at which tagged butterflies are recaptured far from their release sites (Table 1). The proportion of butterflies recaptured more than 100 km from their point of release generally does not exceed 2 in 1000. Even with a recent claim of 10% return rates (Cherubini 1995), the numbers are still low. Thus, to obtain a statistically valid test of alternative hypotheses, transfers of thousands of butterflies would be required, exacerbating the biological and disease problems we have addressed.

An unknown number of transfers are also being conducted by schools. Some monarch rearers, including commercial suppliers, mail various life-history stages to teachers for their students to rear, tag, and release. While we do not know the extent of these mailings, we are concerned that unless this practice is discouraged, it will increase.

Conclusions and recommendations

Monarch rearing and tagging have become popular educational projects throughout the United States. We are not opposing local tagging and releasing of captured monarch butterflies or of reared butterflies that are first-generation offspring of locally captured wild adults. Concerns about the spread of Ophryocystis lead us to caution against using lab stocks as sources of adults for releases and to urge anyone rearing monarchs to become familiar with the symptoms of this disease (McLaughlin and Myers 1970). There may be circumstances where the potential to enhance our knowledge or to gain other benefits outweighs the intrinsic risk of transferring organisms between populations. In the case of the monarch butterfly, however, we believe the costs—in terms of risks to monarch health and survival and confusion of future research—outweigh any of the currently posed benefits. Thus,

Table 1. Examples of the low frequencies of tagged monarch butterflies recaptured at least 100 km from their release sites.

<table>
<thead>
<tr>
<th>Monarch release sites</th>
<th>Release dates</th>
<th>Number released</th>
<th>Number recaptured</th>
<th>Recaptures per 1000</th>
</tr>
</thead>
<tbody>
<tr>
<td>Presqu'ile Park, Ontario*</td>
<td>Fall 1992–1994</td>
<td>7400</td>
<td>12</td>
<td>1.6</td>
</tr>
<tr>
<td>Cape May, New Jersey†</td>
<td>Fall 1992–1994</td>
<td>1776</td>
<td>1</td>
<td>0.6</td>
</tr>
<tr>
<td>Southern Maryland‡</td>
<td>Fall 1989–1994</td>
<td>823</td>
<td>1</td>
<td>1.2</td>
</tr>
<tr>
<td>Eastern United States§</td>
<td>Fall 1992–1994</td>
<td>21,239</td>
<td>21</td>
<td>1.0</td>
</tr>
<tr>
<td>St. Marks National Wildlife Refuge, Florida‖</td>
<td>Fall 1988–1992</td>
<td>8491</td>
<td>5</td>
<td>0.6</td>
</tr>
<tr>
<td>Overwintering sites, California¶</td>
<td>Winter 1986–1987</td>
<td>50,771</td>
<td>35</td>
<td>0.7</td>
</tr>
<tr>
<td>Oregon (transfers from Nebraska)¶</td>
<td>Fall 1994</td>
<td>300</td>
<td>3</td>
<td>10.0</td>
</tr>
</tbody>
</table>

†Richard K. Walton, 1995, unpublished data. Cape May Bird Observatory, Cape May Point, NJ.
‡John F. Fales, 1995, unpublished data. Research scientist (retired), Huntingtown, MD.
§Orley Taylor, 1995, unpublished data. Department of Entomology, University of Kansas, Lawrence, KS.

Overwintering monarch butterflies make dense clusters on fir trees (Abies religiosa) in Mexico. Photo: L. P. Brower.
our collective position is that it is
highly inadvisable to transfer trans
release living monarch butterflies in
any life-history stages between popu-
lations that are naturally separated
from each other. Transfers across the
Rocky Mountains should defini-
tely be discontinued.

Additionally, so that the infor-
mation is available to future re-
searchers, we request that those per-
sons who have already made
transfers publish documentation of
the points of origin and release of
the butterflies, the dates of collect-
ions (or earings) and releases, and
the numbers, stages, and sexes of all
individual monarchs released. Pos-
sible places to publish these data in-
clude The Monarch Newsletter
and the News of the Lepidopterists’
Society.7

The problems we have described
are not unique to monarch but-
tterflies. Spread of disease, disrup-
tion of local adaptations, and the mudd-
ing of biogeographic and genetic patterns are risks to be consid-
ered before transferring any organisms between distant populations. While
conservation biologists and many
other scientists have become cau-
tious about mixing populations, the
monarch’s situation reminds us that
the general public and commercial
ventures are also conducting trans-
fers. The widespread marketing across the United States of wild-
flower seeds grown by a few nurser-
ies is a potential case in point. Regu-
lations and permit requirements
prevent nonscientists from trans-
porting most vertebrates, but many
plants and invertebrates are not so
regulated.

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