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THE COLUMBUS HYPOTHESIS: AN EXPLANATION FOR THE DRAMATIC 19TH CENTURY RANGE EXPANSION OF THE MONARCH BUTTERFLY

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ABSTRACT. The dramatic 19th century colonization of Pacific and Atlantic islands by the monarch, *Danaus plexippus plexippus* (Linnaeus), can be well documented. Although the monarch has very recently become established in the Mascarene Islands and gained a toe-hold in Spain, this major range expansion was essentially complete well before 1900. The butterfly has never been recorded reliably from Africa or the Indian subcontinent, and it failed to establish itself west of Wallace's Line in Southeast Asia.

Available records of the North American overwintering colonies of the monarch in California, Florida, and Mexico all postdate the known start of the Pacific and Atlantic expansion. The two phenomena may be linked to the late 18th and 19th century deforestation of North America caused by European colonists, which probably favored a population explosion of this open-ground insect. Before reinforcing selection could lead to the evolution of the highly coordinated migration cycle seen in North America today, the population explosion could have triggered the range expansion. The spectacular monarch roosts of Mexico may be of very recent origin, brought into being, together with the 19th century expansion, as direct consequences of forest destruction in North America by European settlers—the Columbus Hypothesis.

INTRODUCTION

This paper presents an idea, the Columbus Hypothesis, to explain the present global distribution of the monarch butterfly. It suggests that the annual coordinated migration and massed overwintering cycle is a very recent phenomenon and that this, together with the major 19th century range expansion of the monarch in the Atlantic and Pacific, was brought about by the destruction of North America's forests since the arrival of European colonists.

HOW LONG HAVE MIGRATORY MONARCHS BEEN MIGRATING?

The monarch—or the North American variant at least—is a very special butterfly. Its annual migration cycle is the most spectacular (Malcolm, 1987) in the insect world, and it has been described as “a unique biological phenomenon” (Brower, 1985). According to Ward (1987), “the monarch's two-way migration may be unique among the estimated 30 million species of insects on earth.” The monarch is unusual in other ways too—including its mating system (e.g., Boppré, this volume; Schneider, this volume; Van Hook, this volume) and the use of sequestered cardenolides as a potent means of defense (e.g., Rothschild and Marsh, 1978; Brower, 1984; see also Ackery, this volume). The subspecies occurring in North America, *Danaus plexippus plexippus* (Linnaeus), has been studied extensively with respect to its migratory habits (e.g., Brower, 1985; Cockrell et al., this volume; Malcolm et al., this volume) as well as its mimicry by the viceroy *Limenitis archippus* (Cramer) (e.g., Brower, 1958a,b; Ritland and Brower, 1991, this volume).

However, in many parts of Central America and the Caribbean, and the whole of South America, the endemic races of the monarch are not involved in mimicry, nor do they undergo migrations on a scale comparable to those found in North America (Haber, this volume). Although the southern monarch, *Danaus erippus*, is recorded as undergoing seasonal migrations in Argentina (Hayward, 1969), Lamas (pers. comm.) indicates that the autumnal migration of *erippus* is southerly (to mirror the North American monarch it would need to be northerly), and that there is no evidence of a return migration. This lack of spectacular migrations in

the tropical Americas need not surprise us. The whole point of the complex migratory behavior is to permit larval exploitation of the rich, weedy milkweed flora of the United States and Canada—which the monarch can only accomplish during the frost-free months of the northern summer (Young, 1982).

Kitching et al. (this volume; see also Young, 1982) have suggested that the most likely origin of the North American monarch, in the medium term of about 2 myr, is South America, and that it reached the northern continent via the Pliocene Darien Gap connection. If so, then in the shorter term its origin must have been Central America or Mexico (Young, 1982). Eighteen thousand years ago North America was in the maximum grip of the Wisconsinan Glaciation, which brought permafrost south of Chicago and cool boreal forests to Arkansas. Virtually all of the southern United States was forested, right down to the Gulf Coast, including the area now covered by the prairies (Duplessy and Ruddiman, 1984). Even as far back as 40,000 yr B.P., the climatic conditions were almost as harsh, and the vegetation (Delcourt and Delcourt, 1981) would almost certainly have been largely unsuitable for the monarch. As a result, I think we can take an age of about 10,000 yr, at the beginning of the Holocene, post-glacial, or mesolithic periods (Sutcliffe, 1985), as an upper bound for the age of the present North American monarch migration phenomenon. At this time the prairies were beginning to form in the rainshadow to the east of the Rockies (Delcourt and Delcourt, 1981).

But before pursuing this line of argument further, I first wish to illustrate details of the equally spectacular, but far less well-known, monarch phenomenon, the 19th century colonization of the Atlantic and Pacific oceans.

THE MONARCH'S DOUBLE INVASION OF THE OLD WORLD

Prior to about 1840, there is no record of the monarch outside the Americas and Caribbean. A decade later we have reliable records for Bermuda (Jones, 1859; Walker, 1914) and Hawaii (Scudder and Gullick, 1875; Scudder, 1888–1889) and a doubtful account for New Zealand's North Island (Walker, 1914; Gibbs, 1980). By 1860 we have additional records for the Caroline Islands (Scudder and Gullick, 1875; Scudder, 1888–1889) and Marquesas (Walker, 1914) and a doubtful record for New South Wales (Olliff, 1889). During the following 10 yr Australia is confirmed (first at Brisbane, in 1870; Marks, 1963), together with several records for central Pacific islands (Walker, 1914) and Flores and Fayal in the Atlantic Azores group (in 1864; Godman, 1870). As early as 1873, Semper gives an account of its occurrence in the Manado area of northern Sulawesi (where it can evidently still be found, but not elsewhere on that island; Morishita, 1981; R.I.V.-W., pers. obs.), and by 1880 there are

records for New Guinea (BMNH collection), Cape York (BMNH collection), Tasmania (Couchman and Couchman, 1977), South Island of New Zealand (Walker, 1914), France (Baret, 1878), and England (Llewellyn, 1876; Williams, 1942). By 1890 the picture for both the Atlantic and Pacific is consolidated (Walker, 1914), with records for Spain and the Canary Islands, the Solomons and New Caledonia, the Moluccas (MNH collection, Leiden), and even the Straits of Malacca in Malaysia (de Nicéville and Martin, 1896). The next 15 yr sees records for Hong Kong, Taiwan, Java, Borneo, the Philippines, Guam, and a host of other small islands (Walker, 1914; Ackery and Vane-Wright, 1984; BMNH and MNH collections).

By the turn of the century most entomologists were convinced of two things about the monarch: its extraordinary spread (Fig. 1) had been brought about by trade, either directly (Scudder, 1888–1889) or in the wake of the introduction of *Asclepias* (Walker, 1914), and it would continue to advance and eventually encircle the globe (Distant, 1877; Holland, 1893; Walker, 1914). However, during the ensuing 80 yr, practically nothing has happened. The butterfly has become common in the Mascarene Islands in the last 10 yr (J.R. Williams, pers. comm.; Vane-Wright, 1986; Paré, 1987), it has bred for a few years since about 1980 in Spain (Bretherton, 1984; Edwards, 1984, 1988), it has been recorded once from Denmark (Toft, 1980), and it eventually reached the west coast of Australia (Common and Waterhouse, 1972). However, it has never been reported again from the Greater Sunda Islands (Corbet and Pendlebury, 1978), it has failed to colonize the rest of Sulawesi (Morishita, 1981; pers. obs.), it is extinct in the Philippines (pers. obs.; C.G. Treadaway, pers. comm.), and it is probably extinct in mainland China (M. Bascombe, pers. comm.). There has never been a single reliable record for the whole of Africa or the subcontinent of India (Fig. 2).

When you look at the orderly spread reflected by the maps (Figs. 1 and 2), based as they necessarily are on uncoordinated and haphazardly reported sightings, one could speculate that this could have been brought about directly through the introduction of fast trading ships (the Scudder Hypothesis). The paddle steamer *Savannah* crossed the Atlantic from west to east in 1819 and, following the voyage of the *Sirius* from Cork to New York in 18 days in 1837, the Cunard Company introduced a regular Atlantic steamer service in 1840. But in light of this, and the distribution of entomologists, if the monarch was directly transported by shipping, then we would expect records for coasts of Europe or Australia before we received reports from the Azores, Marquesas, or Carolines. The latter information was received not days, or months, but years in advance. And why did the monarch run out of steam by 1905, or even 1880 (see Fig. 1)?—the world's ships certainly hadn't!

If not directly introduced to the Pacific and At-

lantic by fast ships, what of the alternative—that the monarch merely used its migratory ability to track the spread of *Asclepias* brought by man's trade (the J.J. Walker Hypothesis; see also Malcolm and Brower, 1987)? If so, we must then ask why it stopped short of Africa and India. One possibility is that the monarch has been inhibited by Old World *Danaus* species capable of out-competing it—or as a result of disease (as suggested by T.J. Walker, in litt.). But there is no species of *Danaus* in Africa or India with which the monarch does not come into contact in the eastern Indo-Australian region (see Ackery and Vane-Wright, 1984, table 31). In Africa, *Danaus chrysippus* is particularly abundant, but so it is in the Canary Islands, where the two species have now coexisted for well over 100 yr. In Mauritius, where the monarch has recently established itself, it has to co-exist with *chrysippus*. In the recent colonization of Spain by both species, the monarch is still present, but *chrysippus* may have already disappeared (Edwards, 1988).

Whereas the monarch's colonization of the Pacific and Atlantic is known to have taken place so recently, and has been such a short-lived phenomenon in terms of rapid advance, the annual migration cycle in North America is usually assumed to be a relatively ancient phenomenon—about 10,000 yr in terms of the picture given above, and it could have occurred even earlier, during previous interglacials. Young (1982) suggests that the presence of both the queen and the monarch in North America represents different responses of these butterflies to a post-Pleistocene invasion of Mexico and Central America by the rich *Asclepias* flora evolved in North America. Kitching et al. (this volume) discuss evidence for the monarch reaching North America during the last 2 myr, since closure of the Darien Gap. Genetic markers, such as the enzyme variations discussed by Kitching et al. (this volume), if studied sufficiently, should eventually enable us to make better estimates of the timing and sequence of various events.

WHITE MONARCHS— NEW MUTANTS OR OLD COLONISTS?

Danaus plexippus plexippus shows little phenotypic variation. One exception is the white or 'nivosus' form, in which the normal bright orange ground-color of the wings is replaced by a faintly pinkish or grayish white. The white monarchs of Oahu, Hawaii, first noted in 1965 (Mitchell, 1966), comprise about 4% of the local monarch population (Clarke and Rothschild, 1980; Stimson and Meyers, 1984), currently rising to even 10% (J. Stimson, pers. comm.).

Form 'nivosus' is a simple autosomal recessive (Stimson and Meyers, 1984), possibly involving the loss of ability to produce the normal orange pigment. According to Stimson and Meyers, 'nivosus' was unknown on Hawaii until 1965 and must therefore be the product of a new mutation. However,

the Rothschild Collection (BMNH) includes a single white monarch labeled 'Hawaii, Palmer'. This specimen, together with "regular" Hawaiian monarchs, was evidently received by Walter Rothschild in the mid-1890s. Thus 'nivosus' has probably persisted on Hawaii since the end of the last century, and the allele responsible may well have been present in the founder population of ca. 1845 (Scudder, 1888–1889).

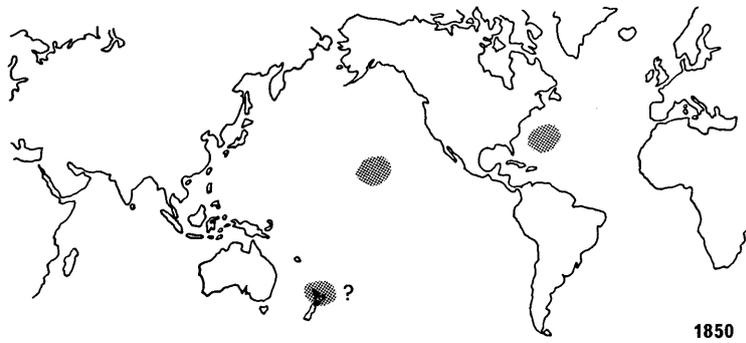
Elsewhere, white monarchs have been reported from Washington, D.C., in 1896 (Clark, 1932); Missouri, 1908 (Gunder, 1927); Pennsylvania, 1921 (Gunder, 1927); the coast of California, ca. 1980 (John Lane, pers. comm., in Vane-Wright, 1987); Brisbane, 1980 (De Baar, 1982); North Island, New Zealand, 1985 (G. Bulow, pers. comm.); and Ambon and Seram (in the Moluccas), 1906–1916 (BMNH collection).

Although most of the 11 recognized species of *Danaus* (see Kitching et al., this volume) are invariably orange-pigmented, white races do occur in the Austro-Oriental *Danaus melanippus*, and all races of the Wallacean species *Danaus ismare* lack orange wing coloration (see Ackery and Vane-Wright, 1984). Thus, it would not be surprising if 'nivosus' mutants had arisen independently in *plexippus* more than once. However, it is also possible that the disjunct Hawaiian, New Zealand, Australian, and Moluccan white forms have been produced by recombination of a rare but homologous allele, inherited directly from their North American ancestors. Hybridization experiments involving 'nivosus' of different origin could shed some light on this problem. In particular, if double heterozygous Hawaii × non-Hawaii crosses produced only typical F1 monarchs, we could reject the single-origin hypothesis. But if typical 'nivosus' segregated 3:1 in the F1, the American origin hypothesis would receive corroboration—although this would not, of course, reject the multiple-origin possibility.

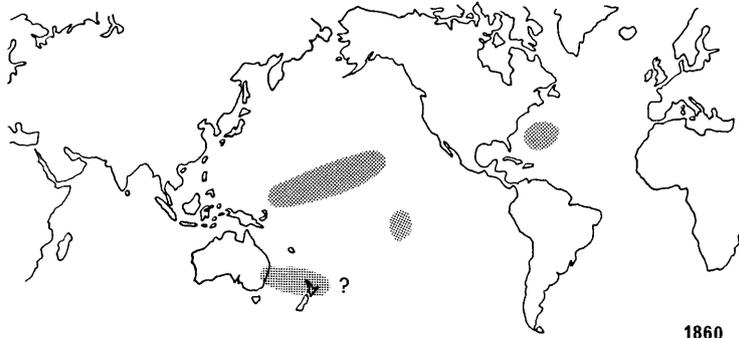
Genetically controlled phenotypic traits such as the 'nivosus' form, the less well-known 'fumosus' trait of the Pacific and North America, and the 'leucogyne' variants of the Caribbean, together with other genetic variations, offer some hope of getting a more detailed picture of the spread of the monarch during the last century. But such phenomena as the white monarchs of Hawaii also remind us of fundamental issues of interpretation in historical biogeography (e.g., Humphries and Parenti, 1986). The need to understand cause and effect and to separate those events that are historically connected from those that have arisen independently are paramount.

EARLY RECORDS OF THE OVERWINTERING COLONIES

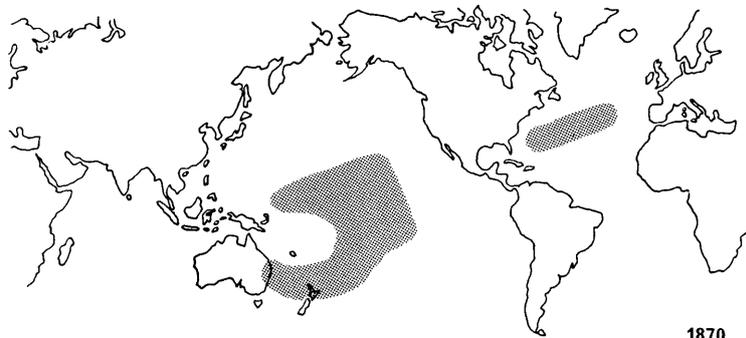
The extraordinary Mexican overwintering sites, although well known to local people at the time of their "discovery" in the mid-1970s, were not reported in the literature until that period (Urquhart,



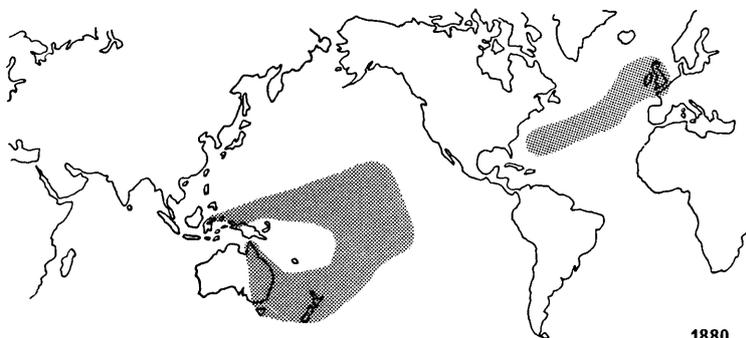
1850



1860



1870



1880

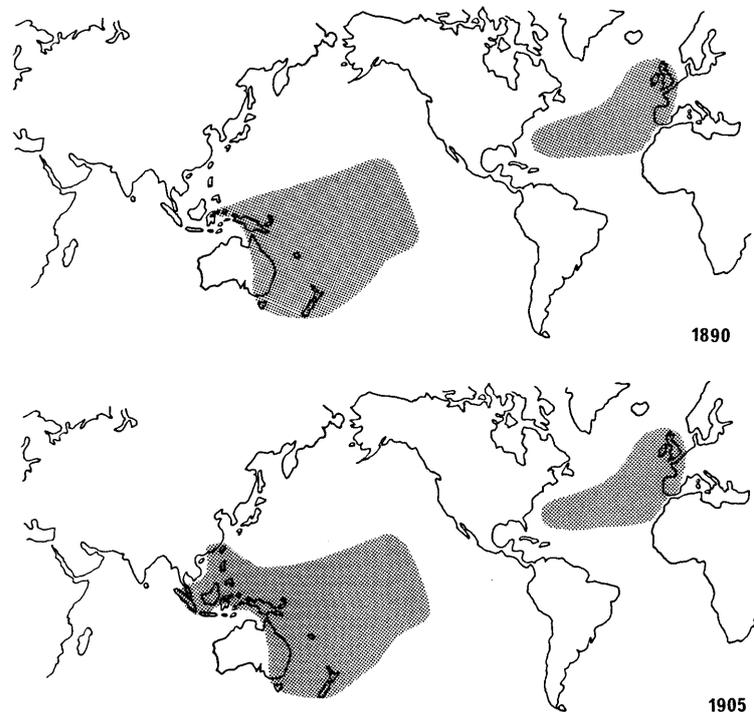


Figure 1. Cumulative maps of the recorded distribution of *D. p. plexippus* outside the Americas, up to 1850, and in 1860, 1870, 1880, 1890, and 1905. Based mainly on information in Walker (1914); see also text.

1976; Brower, 1977). The first published observations of massed overwintering colonies in Florida (at Apalachicola) and at Pacific Grove in California that I have been able to trace are those by Thaxter (1880) and Bush (1881), respectively (also see Lane, this volume). Bush states emphatically that “A lady resident informed me that for the twelve years she had lived there the appearance [of the massed monarchs on the pine trees] had been the same,” thus documenting the phenomenon in California back to about 1869.

Lucia Shepardson, in her charming yet curious booklet published in 1914, states that “The earliest authentic information as to this annual migration [at Pacific Grove] dates back fifty years [1864], when the monarchs were seen upon the pines just as they are to-day.” (This reference probably relates to Bush, but I am not certain.) She goes on, “Previous to that, no mention has been found of this interesting phenomenon The early Spanish chronicles and traditions make no mention of it, although Monterey, a scant three miles distant, was gay with life when the last century came in . . . even David Douglas, the world-famed botanist, and the keenest-eyed of all the strangers who came here, is silent regarding it.” Douglas, who died a sudden and tragic death in 1834, visited Monterey from December 1830 to August 1832 (Harvey, 1947). During this time he discovered the Monterey pine (*Pinus radiata* Don; *Pinus insignis* Douglas), noted by Shep-

ardson as *the* tree to which the Pacific Grove monarchs flocked.

There are few, if any, accounts of the autumnal clustering and migratory behavior of the monarch before the 1860s, when the then burgeoning North American literature suddenly starts to report observations by the dozen—together with argument and speculation as to their meaning. If we accept Shepardson’s account literally, the earliest historical record of massed overwintering appears to have been made at about the same time, in 1864 (but see Lane, this volume). Douglas, the indefatigable fir tree collector, appears to have made no mention of the phenomenon in 1830–1832, despite spending two winters at Monterey. As outlined above, range expansion by the monarch into the Pacific and Atlantic is known to have started exactly midway between these dates. Are the two phenomena linked historically? If so, which is the cause and which the effect?

THE COLUMBUS HYPOTHESIS

The monarch is an open-country, frost-intolerant insect (Anderson and Brower, this volume) that exploits the rich North American asclepiad flora by means of the annual remigration cycle (Young, 1982). In the tropical Americas, from Nicaragua southward, the monarch is also largely restricted to open areas but only makes more limited local

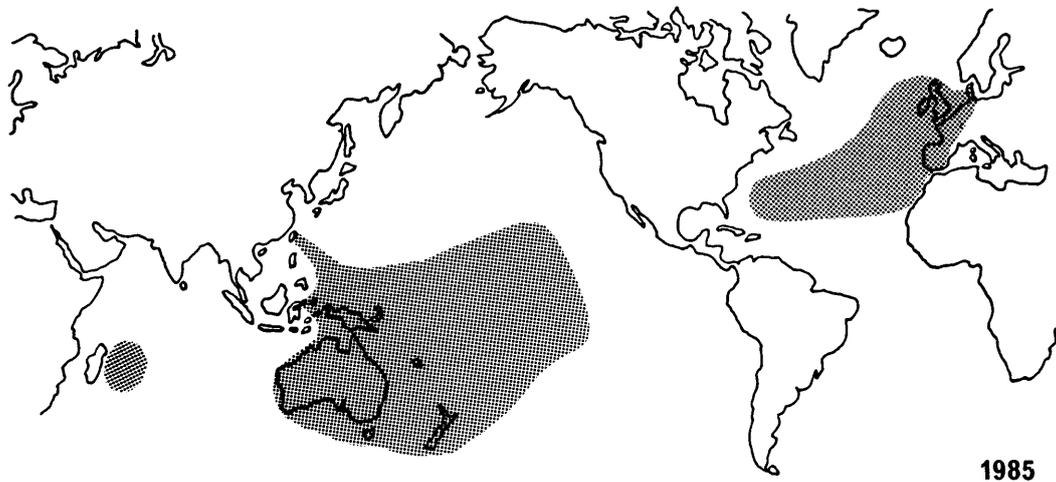


Figure 2. Current (1985) known range of *D. p. plexippus* outside the Americas. [Note: Apart from the east coast region of Spain (Edwards, 1988) monarchs are not known to breed in the British Isles or continental Europe, but they still occur as more or less occasional vagrants on western coasts (e.g. Bretherton and Chalmers-Hunt, 1982).]

migrations (such as the east–west, dry–wet season movements observed in Costa Rica: Haber, this volume; note also Young, 1982). Before Europeans destroyed extensive areas of woodlands and forest, the weedy, disturbed-ground asclepiads of North America must have been much less common than they are now. Before this, in the natural prairies, monarchs may have behaved much as they now do in Australia or New Zealand, or as *D. erippus* appears to do in the Argentinian pampas (Williams, 1942; Hayward, 1969).

Could the deforestation of North America, which started in earnest about 200 yr ago (Delcourt and Delcourt, 1981), have led to a 19th century population explosion of milkweed plants and, in turn, of the native monarch, from which the overspill colonized the Atlantic and Pacific? Is it possible that in succeeding autumns, millions of monarchs flew east and west as well as south, until the locally adaptive, southerly, massed and orderly, “out-and-back” annual migrations and overwintering roosts rapidly evolved through reinforcing selection? Did the anticipated global colonization run out of steam simply because, by about 1880, nearly all North American monarchs had been programmed in this way to fly south in autumn (those that weren’t simply never came back)? Do the monarchs of Australia and New Zealand (Common and Waterhouse, 1972; Wise, 1980; Gibbs, 1980) fail to show this precise north–south behavior pattern because they are derived from an ancestral population in which it had not fully evolved?

I am not suggesting that migration and clustering is limited to North American monarchs. Such behavior is of course widespread not only in the monarch as a whole, but also in many other danaines as well (see for example review in Ackery and Vane-Wright, 1984; and recent detailed work of Scheer-

meyer, 1987; Wang and Emmel, 1991; Kitching and Scheermeyer, this volume; Scheermeyer, this volume). What I do want to suggest is that the *spectacular annual migration cycles*, found only in the populations of North American monarchs, have evolved in their present form as a result of the cataclysmic ecological changes wrought by European colonists—the Columbus Hypothesis. According to Dasmann (1965), for example, extensive coastal lumber extraction in northern California started in 1851, shortly after the Gold Rush, and by “1870 most of the redwoods in the immediate vicinity of Humboldt Bay were cut, and the hills behind Eureka and its sister town of Arcata were left deforested.” More generally for North America, Williams (1989) states that “300 million acres of forest land had been cleared by the beginning of the twentieth century.” It is perhaps ironic to contemplate the idea that the Mexican winter roosts, which, together with the Californian sites, were among the first “Threatened Phenomena” to be designated in the history of international conservation (Wells et al., 1983), are less than 200 yr old—and a product of man’s destruction!

The only monarch populations to have had their migration and dormancy cycles extensively studied are those of the United States and Australia. They exhibit a number of differences (Herman, 1981, this volume; James and Hales, 1983; James, 1984, this volume). Recently it has been suggested that in the Australian monarchs, over the last 115 yr, “both diapause-mediated dormancy and migration behavior have been altered” (Tauber et al., 1986: 243). Altered in relation to what? An equal possibility is that the “standard” North American populations have changed. As in the case of the white monarchs, the Australian populations may have merely retained characteristics of their early Victorian an-

cestors—able to make local migrations between breeding and overwintering sites, but not necessarily capable of the extreme coordinated behavior seen in North America. The universal need to distinguish primitive from specialized traits (Hennig, 1966), just as with the white monarchs of the Pacific, means that comparative physiologists and ecologists dealing with historical events can no more safely ignore Hennig's principles than can other systematists.

FEW ANSWERS, MORE QUESTIONS

I am well aware that these suggestions raise far more questions than they resolve. In general, it is certain that some form of migration occurred in North American monarch populations, before the arrival of Europeans, to take advantage of the naturally occurring prairie milkweeds. Did deforestation merely cause quantitative enhancement of this phenomenon, or has there been some qualitative change in behavior as well? The fact that monarchs, particularly in the southern parts of North America, operate a sort of "mixed strategy" (Malcolm, 1987), with some individuals joining the mass migrations south while others remain to form more or less continuously breeding colonies, may throw some light on this problem.

More particular questions include, amongst others: What is the earliest record of massed overwintering in California? If indeed it is only 1864 or 1869, is this significant, or does it merely reflect the late European settlement of western North America? (The Spanish established Monterey as the capital of California in 1770, the Mexicans took over in 1821, and it was seized by Americans in 1846 and ceded to the United States in 1848.) Can anyone make an estimate of the progress of North American deforestation up to about 1880 (see Williams, 1989), and its likely impact on native milkweed plants? Does the continuing arrival of monarchs along the western coasts of Europe, notably in peak years such as 1933 (Williams, 1958) and 1981 (Bretherton and Chalmers-Hunt, 1982), tell against the Columbus Hypothesis—or have many of these latter-day wanderers only strayed from closer established colonies, such as those on the Canary Islands?

In addition to answers to such questions, we require a thorough investigation of the monarch's genetics, particularly its molecular variation. Before speculation outruns the supply of essential facts, we really need a worldwide survey of this beautiful—and still mysterious—insect. We also need to devise critical tests or experiments, in the hope of eliminating the Columbus Hypothesis—or its rivals.

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