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MONARCH BUTTERFLY ORIENTATION: MISSING PIECES OF A MAGNIFICENT PUZZLE

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Summary

From late August to early September, millions of adult monarch butterflies of the eastern North American population cease reproducing, become highly gregarious and begin migrating southwards. By mid-October, they migrate through central Texas into Mexico where they follow the Sierra Madre Oriental across the Tropic of Cancer. They then shift direction westwards towards the Transverse Neovolcanic Belt of mountains where they overwinter without breeding. A rapid exodus northwards occurs at the spring equinox, and by early April both sexes reach the Gulf Coast states where the females lay eggs on the resurgent spring milkweed (*Asclepias*) flora and die. Adults of the new generation continue the migration to the northernmost breeding range, arriving by early June. Two or more short-lived breeding generations are produced over the summer, spread eastwards across the Appalachian Mountains and, by September, the autumn migration is again under way. This paper presents a new hypothesis that the orientation of adult monarchs undergoes a continual clockwise shifting throughout the 3–5 generations, rotating by 360˚ in the course of the year. This hypothesis is consistent with the timing of arrivals and the relative abundances of the successive generations of monarchs throughout eastern North America, with the directions of movement of their spring, summer and autumn generations, and with the timing of their arrival at the overwintering area in central Mexico.

Key words: *Danaus plexippus*, migration, annual cyclic orientation hypothesis, North America, successive generations, insect movements.

Introduction

Two migratory populations of the monarch butterfly (*Danaus plexippus* L., Nymphalidae, Lepidoptera) occur in North America (see Figs 1, 2). One population breeds west of the Rocky Mountains, and in the autumn the butterflies migrate southwestwards to overwinter at low-altitude, forested sites along the Pacific Coast of California. A much larger population breeds east of the Rocky Mountains and migrates in the autumn up to 3600 km during about 75 days (approximately 50 km per day) to overwinter in high-altitude forests in Central Mexico (for a review, see Brower, 1995). In both populations, the autumn migrants use the same highly localized overwintering areas year after year. This fidelity is remarkable, because the individuals that move south in the autumn are 3–5 generations away from their ancestors that occupied the sites in the previous winter. It has become generally accepted (Williams, 1930; Urquhart, 1960, 1987; Johnson, 1969; Baker, 1978; Brower, 1985*a*, 1995) that the annual cycle involves an inherited behavior pattern in which migration is (1) activated in the autumn and spring, (2) repressed during the winter and summer, and (3) switches in orientation by 180˚ between autumn and spring.

This paper concentrates on the eastern population, because directional data on both the autumn and spring migrants in California are incomplete and controversial (Wenner and Harris, 1993; for a review, see Brower, 1995). The findings of the past two decades are summarized with respect to (1) the overwintering locations of the butterflies in Mexico, (2) the spring remigration to the Gulf Coast states, and (3) the next generation which continues the migration northwards to Canada. The extensive data now available provide new insights on the butterfly's changing orientation during its annual cycle. I propose a new, testable hypothesis that is consistent with old and new knowledge about the monarch's phenology and distribution in North America.

The overwintering area of the eastern population

Determination of the terminus of the autumn migration of the eastern population of the monarch has a tortuous history that began in 1857 (for a review, see Brower, 1995). Riley (1878) established that the Great Plains populations undergo bird-like southward migrations in the autumn, and anecdotal reports collated by Williams (1930, 1938) indicated that the direction of the autumn migration is principally southerly and southwesterly. Urquhart (1941) developed a tagging system involving several thousand collaborators that confirmed the general southwesterly orientation of the autumn migrants (Urquhart, 1960, 1987; Urquhart and Urquhart, 1978, 1979*b*). But even with this extensive program, the question of where the vast numbers of autumn migrants overwintered remained a mystery.

Thaxter (1880, expanded in Moffat, 1902) had seen monarchs clustering on trees near the Gulf of Mexico in northern Florida in the winter of 1873. Over the ensuing years, clusters in pine trees were sporadically reported in the Gulf Coast states during the autumn migration period. By analogy with the well-known overwintering colonies along the Pacific Coast – especially at Pacific Grove on the Monterey Peninsula – it was assumed that the Gulf Coast states were the overwintering area of the eastern population. Because of the sporadic nature of the reports, Williams (1938) speculated that some of these eastern migrants must continue into Mexico. Brower (1961) discovered extensive spring breeding in central Florida and questioned whether overwintering occurs at all, while Urquhart (1949, 1965, 1973) suggested that some of the autumn migrants may fly westwards through New Mexico and Arizona, ultimately to join the butterflies overwintering in California.

On 2 January 1975, two of the Urquharts' research associates, K. and C. Brugger, discovered that the eastern North American population overwinters south of the Tropic of Cancer in the mountains of central Mexico (Urquhart, 1976; Urquhart and Urquhart, 1976). Millions of individuals in reproductive diapause were found densely aggregated on Oyamel fir trees [*Abies religiosa* (H. B. K. Schl. & Cham.), Pinaceae] on Sierra Pelon. This 3500 m high mountain is located about 120 km west of Mexico City in the Transverse Neovolcanic Belt of mountains that crosses Mexico from the Pacific to the Atlantic Oceans (not the Sierra Madre Oriental, as originally stated by the Urquharts). The Oyamel forest is a Pleistocene relictual ecosystem that is now limited to 13 of the highest mountain areas of Mexico and is similar in many ecological aspects to the Boreal forests of Canada (Snook, 1993). Subsequent research by Calvert and Brower (1986) and de la Maza and Calvert (1993) uncovered a total of about 30 overwintering colonies on nine separate mountain massifs, all between 70 and 170 km west of Mexico City. The five major overwintering mountain massifs are limited to a precariously small area of about 800 km^2 (for a review, see Brower, 1995).

The butterflies are adapted to this high-altitude forest ecosystem which allows a lowering of their metabolic rates and activities from mid-November to mid-March. Though generally quiescent in dense clusters on the boughs and trunks of the firs, large numbers of butterflies occasionally fly to drink water from nearby streams and dewy fields, while others, overheated by direct exposure to the sun, fly and glide in the cold air above the canopy, thereby reducing their body temperature (Masters *et al.* 1988). The frequency of mating increases as winter proceeds. The great beauty of the butterflies in these Mexico enclaves is described and illustrated in several popular articles, including Urquhart (1976) and Brower (1977, 1985*b*, 1986, 1987, 1988). Unfortunately, because of progressive deforestation at the overwintering sites, the migration of the eastern population of the monarch butterfly has become an endangered biological phenomenon (Brower and Malcolm, 1991; Malcolm and Zalucki, 1993).

Orientation of the autumn migrants

Williams' (1930, 1938) original literature collations, together with the Urquharts' data (Urquhart, 1960, 1965, 1966; Urquhart and Urquhart, 1976, 1978, 1979*a*,*b*,*c*), as summarized in Baker (1978, 1984), have led to the general agreement that the autumn migrants follow a southwesterly direction in most areas, with a subset moving southeasterly out of the north towards the east coast, probably resulting in part from west wind drift. Schmidt-Koenig's (1979, 1985, 1993) studies of the vanishing bearings of autumn migrants from northern New York to the Blue Ridge Mountains have confirmed the southwesterly orientation, as have the studies of Gibo (1986) in Ontario. Gibo's data, as well as Walton and Brower's data (1996) from New Jersey, are consistent with the eastern drift hypothesis. Gibo's (1986) and Schmidt-Koenig's (1993) data suggest, however, that the butterflies compensate for wind displacement by changing their headings.

Data gathered by the Urquharts' tagging progam have generally been reported with insufficient detail to analyze quantitatively or to correlate with weather patterns, and have frequently been presented in generalized maps without updating (compare Urquhart, 1960, Plate XII, with Urquhart, 1987, Plate 9). More generally, recapture data have severe limitations for the study of orientation because individual routes traveled, stops, detours and wind drift between the points of release and recapture can only be inferred (Roer, 1967; Papi, 1992). The method is also inefficient: the frequency of recaptures more than 100 km from the release points is less than 1/1000 (Brower *et al.* 1995). We await the day when technological advances will make it possible to track individual monarchs continuously.

Notwithstanding these limitations, the Urquharts' data suggest the following flight directions of the autumn migrants (summarized in Fig. 1). From the Great Lakes region, the butterflies fly southwestwards to south-southwestwards into Texas. East of the Appalachians, they migrate southwestwards along the Atlantic Coast. Urquhart and Urquhart (1979*c*) argue that this coastal migration is 'aberrant', but extensive evidence indicates that it is a normal part of the autumn migration (Brower, 1995; Walton and Brower, 1996). Although numerous migrants follow the Atlantic coast, shift to a south-southeasterly course through the Florida Peninsula, and possibly turn west across Cuba to an uncertain fate, Urquhart and Urquhart (1979*b*) hold that the majority continue on their southwesterly course, cutting over land across Georgia to the Gulf Coast. Urquhart and others (for a review, see Brower, 1995) hold that they largely avoid flying over the Gulf of Mexico, instead turning west and following the Gulf Coast into Texas, there turning south to join the main migration into Mexico. The Urquharts assume that the relatively few monarchs produced in the western Great Plains migrate south-southeastwards into Texas (Urquhart and Urquhart, 1978, 1979*b*).

Summing up the findings described above, our current understanding of the orientation of monarch butterflies during their 90 day autumn migration to Mexico is based on two major assumptions: (1) individuals of the entire eastern migratory population aim towards localized overwintering areas in Mexico; and (2) the flight direction of the migrants varies from southeast to west in different parts of the range and at different times.

The role of weather and winds during the autumn migration

As far as is known, monarchs interrupt their autumnal migratory flights as dusk approaches. They fly and glide down into trees where they form temporary overnight clusters that break up the next morning when the sun's rays fall on the clusters. Whether migration is resumed, or the butterflies enter a nectar-searching period, appears to depend on the weather and the direction and speed of the prevailing winds. If the wind is from the south, the butterflies may accumulate in 'staging areas' for several days (Schmidt-Koenig, 1985). Gibo and Pallett (1979) found that autumn migrants in southern Canada avoid strong headwinds from the south, southwest and west either by utilizing powered, flapping flight and staying within 1 m of the ground or by interrupting their flight. In contrast, when weather and wind directions are favorable (wind from the north to east), the butterflies glide upwards on rising air currents, i.e. they give up most of their flapping flight and soar upwards. Binocular observations indicated soaring to the limits of vision (300–500 m), whereas altitudes observed by glider pilots ranged from 490 to 1250 m above the ground (Gibo, 1981).

The use of tailwinds has long been debated (Johnson, 1969, 1971). Walker and Riordan (1981, p. 440) concluded that 'whatever proves the case about use of strong winds as fast transport in a predetermined direction, there are no data, for any butterfly, supporting the hypothesis that upper air or synoptic-scale wind systems regularly determine its direction of migration'. However, recent observations of monarchs' adeptness at soaring and exploiting tailwinds are beginning to erode this conclusion.

Gibo and Pallett (1979) determined that, by taking advantage of strong tailwinds, monarchs can achieve ground speeds in excess of 50 km h^{-1}. Other reports of autumn migrants flying 'rapidly' (velocities undetermined) at relatively high altitudes on strong tailwinds are given by Schmidt-Koenig (1985) and Dennis (1993). I believe that the importance of tailwinds in transporting monarchs has been underestimated in the literature, and I have made two relevant observations which support this contention, one during an autumn migration, the other during a spring migration. On 9 October 1994, a strong northern cold front passed through central Texas. For 7 h of overcast and then partly sunny weather, W. H. Calvert and I made sample counts along an 80 km southwesterly transect

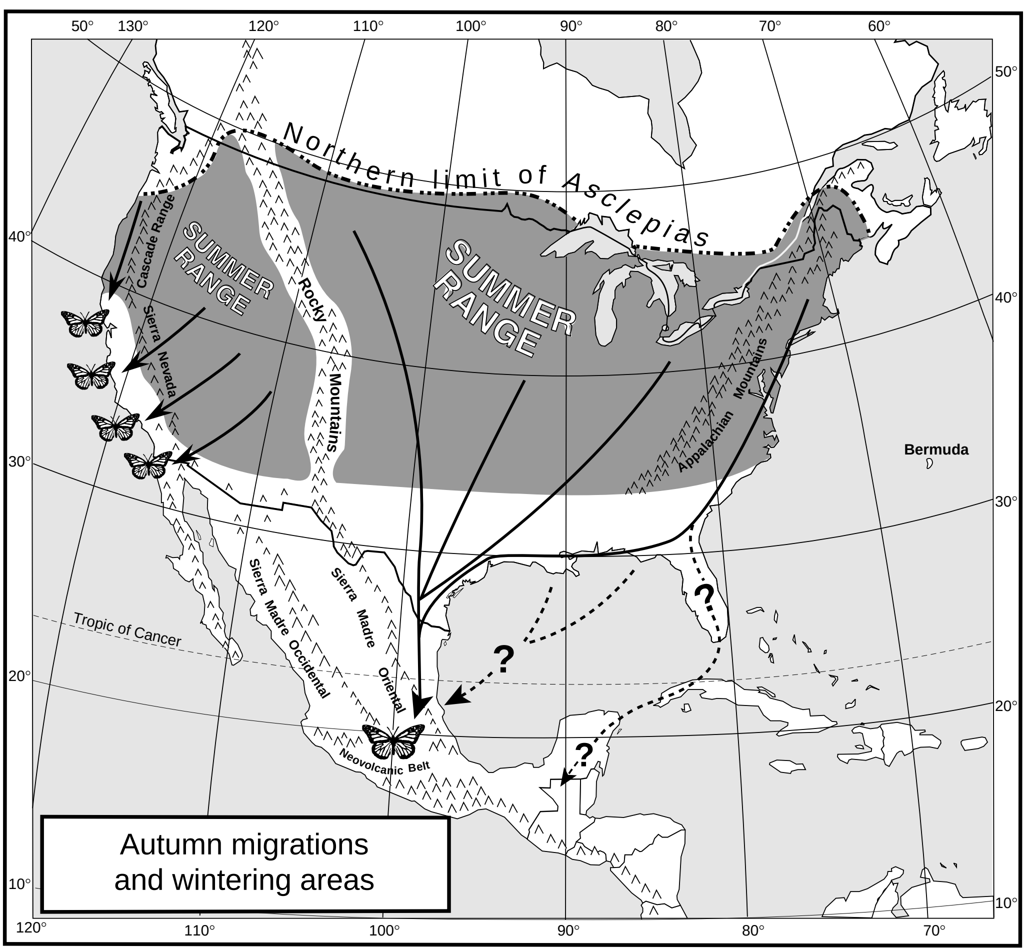

Fig. 1. Two migratory populations of the monarch butterfly occur in North America. The *western population* breeds west of the Rocky Mountains during the spring and summer and migrates to numerous overwintering sites, mainly along the California Coast. The second, much larger, *eastern population* breeds over several generations east of the Rocky Mountains and in the autumn migrates southwards to overwintering sites in the high peaks of the Transverse Neovolcanic Belt, south of the Tropic of Cancer in central Mexico. The autumn migration has been assumed to occur only in a southwesterly direction with some wind drift eastwards, but probably involves a gradual shifting from south to west as proposed in Fig. 4. Migration across the Gulf of Mexico and through Florida and Cuba to Guatemala remains hypothetical. (Reproduced from Brower, 1995, with permission of the Lepidopterists' Society.)

from Kerrville to Garner State Park. Our binocular observations to an altitude of about 300 m suggested that more than 100 million monarchs migrated southwards over Texas on that day (L. P. Brower, W. H. Calvert, L. S. Fink and T. Dennis, in preparation). On 14 May 1985, I was collecting spring remigrants in a clover field in southeastern Kansas. By noon, the sky had become overcast and I saw dozens of adults flying about 20 m high on a moderate tailwind from the south-southeast (170 ˚). A more subtle indication that winds may be important in transporting monarchs on their autumn migration is the near-pristine condition of the butterflies clustering at their overwintering sites in Mexico. Some of these butterflies have travelled for more than 3600 km between late August and early December (Brower, 1995). Had they engaged largely in powered flight, their wings should have shown heavy wear, but they did not (Brower, 1985*a*). It seems very likely that soaring, in combination with the ability to exploit tailwinds, increases ground speed, conserves lipid reserves and reduces wing wear during migration.

Whether autumn migrants cross the Gulf of Mexico (a minimum distance of about 1000 km) is linked to the question of whether the butterflies use high-speed tailwinds. The accumulated evidence suggests that they do not fly at night and become waterlogged within minutes if they alight on water surfaces (Brower, 1995).

Weather records of successive fronts passing across eastern Mexico and the southern United States (Wolf *et al.* 1986; Taylor and Reling, 1986), the existence of fast-moving low-level jet streams at night (Showers *et al.* 1993) and coordinated ground and airborne radar observations (Drake, 1985; Pair *et al.* 1987; Wolf *et al.* 1990) strongly suggest that numerous insect species can be transported by winds at rates of 50–70 $\mathrm{km\,h^{-1}}$ for several hundred kilometers. Radar technology, allowing the determination of the rates, numbers and directions of movements of specific insects, could shed light on monarch migration. Questions to be addressed include the distance, direction and speed of monarchs flying with weather fronts, as well as the extent to which they avoid flying with, or correct for, winds that would carry them in wrong directions. It is possible that monarchs migrating during the autumn along the Atlantic Coast take advantage of prevailing westerly winds in northern latitudes, and then prevailing easterly winds in southern latitudes. This strategy appears to be utilized by broad-winged hawks (*Buteo platypterus* Vieillot, Accipitridae), which have frequently been seen with monarch butterflies while migrating southwards in the eastern United States (Kerlinger *et al.* 1985, as discussed in Walton and Brower, 1996).

Orientation mechanisms

The observations summarized in this paper provide evidence that adult monarch butterflies orient in specific directions, compensate for wind drift, maintain direction while flying under overcast skies, stop at appropriate overwintering destinations (Schmidt-Koenig, 1985, 1993; Gibo, 1986; Papi, 1992) and, as will be shown below, change their orientation systematically during the course of the year. Moreover, as has been determined for numerous migratory bird species (Berthold, 1990), the orientation mechanism(s) underlying the monarch's migratory performance is innate, rather than a consequence of a learning process. This conclusion is based on the fact that the individuals that migrate southwards for several thousand kilometers to the overwintering sites are 3–5 generations distant from butterflies that flew there the previous year.

How monarchs maintain their migratory course is unknown. Kanz (1977) demonstrated experimentally that they can orient towards the sun's changing azimuth during clear days, but found no evidence for polarized light orientation. He hypothesized that the butterflies may limit their flight each day to a few hours, heading towards the sun in the autumn and away from it in the spring, which would account for the general migratory directions observed. Monarchs, however, fly on overcast days as well (Schmidt-Koenig, 1993; my observations in Texas and Kansas, see previous section), and they can often be observed in flight throughout the day (Brower, 1995).

No one has shown that monarchs have time compensation, an inherited map template similar to the one postulated for the savannah sparrow [(*Passerculus sandwichensis* (Gmelin), Emberizidae)] (Able, 1980; Able and Able, 1996) or a receptor mechanism (Papi, 1992; Wehner, 1992) that can read planetary gradients, such as the changing angle of magnetic dip, which, in conjunction with a second directional reference, may guide individuals to a predetermined point (Kiepenheuer, 1983; see also Wiltschko and Wiltschko, 1996). However, MacFadden and Jones (1985) and Jungreis (1987) experimentally determined that monarchs do contain magnetic particles, probably magnetite, which appear to be synthesized in the thorax during metamorphosis of the chrysalid to the adult. Monasterio *et al.* (1984) cited evidence that magnetic readings near the center of the main overwintering areas in Mexico are 100 times higher than normal and suggested that the butterflies may be drawn into the overwintering areas by sensing the strong fields. The observation that some moths have the ability to sense magnetic fields (Baker and Mather, 1982) makes it worthwhile to pursue this possibility in the monarch.

Spring remigration from Mexico to the Gulf Coast states

The *modus operandi* of the spring remigration has long been debated. Edwards (1878) proposed a successive brood hypothesis, arguing that survivors from the unknown overwintering areas oviposit in the southern United States, and that the resulting new spring generation recolonizes the northern range. In contrast, Scudder (1881) maintained that overwintered butterflies remigrate and oviposit across the entire breeding range, effectively re-establishing the first spring generation in a single sweep from Texas to Canada.

We tested these alternative hypotheses using a chemical microassay that allows determination of the amounts and patterns of the cardenolide chemicals that monarch larvae sequester from milkweeds (Brower *et al.* 1982; Brower, 1984; Seiber *et al.* 1986; Malcolm *et al.* 1993). Our assay exploited the fact that different species of milkweed have different geographic ranges and also contain specific arrays of cardenolides that can be visualized by thin layer chromatography. After establishing a cardenolide ‘fingerprint’ library of monarchs raised on major milkweeds species, we determined the geographic origin of individual monarchs caught during the autumn, at the overwintering sites in Mexico, during the spring remigration to the Gulf Coast and from the northern range in late spring.

Edwards was correct: 6-month-old individuals return from Mexico to the Gulf Coast states, lay their eggs on the resurgent spring milkweeds from Texas to Florida, and die. The first spring generation is produced largely in Texas and Louisiana (Riley, 1993; Lynch and Martin, 1993; Cockrell *et al.* 1993; Malcolm *et al.* 1993), with fewer individuals produced in central and northern Florida (Malcolm *et al.* 1987, 1993). No quantitative data exist for the intervening states of Mississippi and Alabama. These offspring – the *first* generation – then continue the migration northwards to the Great Lakes region and southern Canada (Fig. 2). The complete spring recolonization thus involves both the overwintered survivors of the previous autumn generation *and* their first-generation offspring. Although this successive brood recolonization prevails, *a few* overwintered individuals do migrate at least as far north as Maryland and Kansas (T. Wells, in Riley, 1871; Fales, 1984; Brower, 1985*a*).

Summing up the findings described above, two major points derive from the successive brood recolonization: (1) the 6-month-old butterflies that migrate to Mexico in the autumn reverse the direction of their orientation between November and March, and (2) since the southward migration of the autumn migrants *and* the northward migration of the subsequent new spring generation butterflies are to destinations where none of the individuals has ever been, *both* migrations are inherited behavioral patterns.

It seems likely that these abilities are evolutionarily labile in terms of both migratory distance and direction. This notion is supported by the observation that the timing and direction of the monarch’s migration in Australia are reversed by 6 months and 180 ° (James, 1993). What is remarkable about this is that

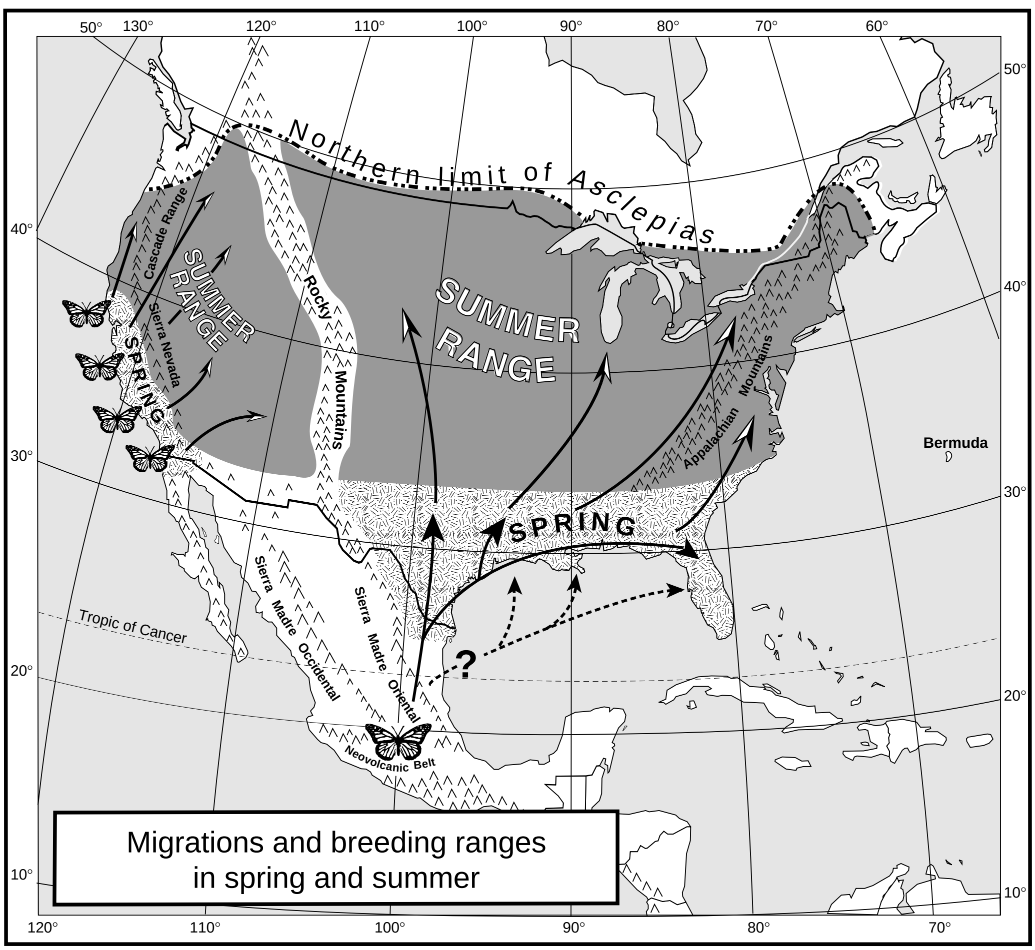

Fig. 2. Spring remigrations of the monarch butterfly in North America. Western monarchs leave the coastal overwintering areas in early spring and re-establish their summer breeding range as shown. Monarchs that overwintered in Mexico remigrate at the end of March to the Gulf Coast states, where they oviposit on southern milkweeds (*Asclepias*) and produce the first new spring generation of adults by the end of April to early May. The butterflies produced in Texas and Louisiana migrate northeastwards across the midwestern states to southern Canada, laying eggs along the way and establishing a large second generation in the western and central Great Lakes region. The far fewer monarchs produced in northern Florida migrate northeastwards along the coastal plain and appear to contribute minimally to the second generation. The midwestern component of the second generation monarchs is produced in June and appears to continue the migration eastwards over the Appalachians. Two or three more summer generations (depending on temperature) follow in the midwest and east of the Appalachians, with the last generation entering reproductive diapause and migrating southwards in the autumn. Spring remigrations over the Gulf of Mexico and through Cuba to Florida remain hypothetical. (Reproduced from Brower, 1995, with permission of the Lepidopterists’ Society.)

monarchs were not known to occur in Australia until 1870. The most likely explanation of their trans-equatorial range expansion is that humans spread milkweeds across the Pacific Ocean and monarchs followed by hitch-hiking on ships (Brower, 1995). In addition, the distances and directions of monarch migrations in North America must have changed frequently during the interglacial and glacial episodes of the Pleistocene.

The northward migration of the spring generation produced along the Gulf Coast

Prior to the discovery of the overwintering sites in Mexico, the direction of the spring migration was inferred from very limited evidence dating back to the 19th century. Subsequent observations led Urquhart (1960, 1966) to conclude that spring migrants from the southern United States move in a generally northeasterly direction, crossing Michigan to the northeast shore of Lake Superior, without reaching further eastwards into the Ontario peninsular region. Tagging at the overwintering sites in Mexico led to seven recaptures of spring remigrants in the United States, supporting the northeasterly direction of the earlier spring remigration (Urquhart and Urquhart, 1979*a*). Urquhart and Urquhart (1978, 1979*c*) also speculated that a northeasterly orientation of the new generation spring migrants results in a paucity of monarchs in the northwestern Great Plains.

New data on the spring recolonization

During May and June of 1985–1987, my colleagues and I engaged in a major effort to collect monarch butterflies during the spring. We searched agricultural and natural meadows with binoculars for the presence of monarchs and intensively netted all adults that we could find before moving on. The data allowed us to compare relative abundances of monarchs through time over much of their range. Censuses of milkweed plants for eggs, larvae and chrysalids provided confirmatory evidence of adult abundances. The results are summarised here; some of them have been published in Cockrell *et al.* (1993). The transects and the numbers of adults collected or seen at the various sites over the three years are indicated in Fig. 3.

1985

Between 26 May and 20 June, we conducted a 2600 km east–west transect of the northern tier of states from the

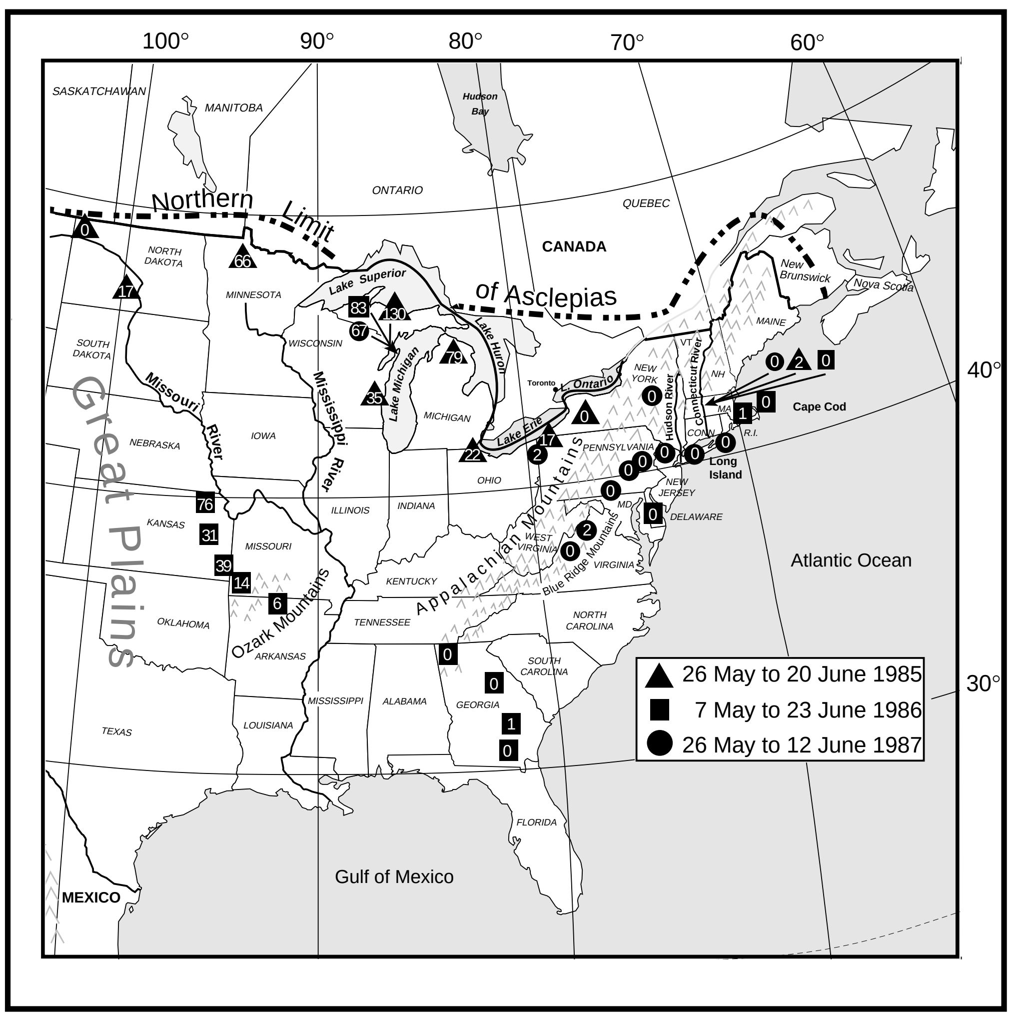

Fig. 3. Locations of the spring and early summer collecting transects made in 1985–1987. The numbers of adult monarchs caught or seen at the various sampling sites are indicated. See text for details.

Connecticut River Valley in central Massachusetts, across the Great Lakes, to the western border of North Dakota. We found only two adults in the Connecticut River Valley, none along the southern shore of Lake Ontario, 17 along the southeastern shore of Lake Erie, 22 near the southwestern shore of Lake Erie, 79 near the southern border of Lake Huron (on the Michigan Thumb), 35 near the western shore of Lake Michigan, 130 near the shore of northwestern Lake Michigan (on the Door Peninsula), 66 in north central Minnesota, 17 along the Missouri River in North Dakota, and none in the northwestern corner of North Dakota.

1986

Between 7 and 19 May, we conducted a 1700 km survey from central Georgia northwestwards through the Ozark Mountains to northeastern Kansas. We found a few late immatures and one adult monarch in Georgia; we caught 6 fresh adults in the Ozarks, 14 in southwestern Missouri and 39 in southeastern Kansas; further north in Kansas we captured 31 and then 76 adults, most of which were very fresh. Two censuses in Door County (8 and 23 June) on northern Lake Michigan captured 30 and 53 adults. Two censuses east of the Appalachians, one in the Connecticut River Valley (30–31 May), the other on Cape Cod (27–29 May), southeast of Boston, produced one fresh adult and 18 young immatures. Finally, on 6 June in Delaware we found 12 eggs and no adults.

1987

From 26 May to 12 June 1987, we conducted a 750 km census along the eastern border of the Blue Ridge and Shenandoah Mountains, and then northeastwards along the eastern border of the Appalachian Mountains, to central New York. We next searched the north shore of Long Island, New York, and again searched the Connecticut River Valley. On this entire census, we saw one (possibly two) adult monarchs. We again crossed the Appalachians to the south shore of Lake Erie to obtain a sample comparable to the 1985 sample; two adults were seen. Returning to Door County on northern Lake Michigan on 12 June, we captured 67 adults.

Spring versus *summer abundance in New England*

The two adults seen over 1985–1987 in the May and early June censuses in the Connecticut River Valley of Massachusetts pale in comparison with the numbers seen in the same area in July and August: L. Brower and Walford (in Walford, 1980) caught 109 monarchs from 21 July to 3 August 1979 and 121 from 4 to 17 August 1979. One possible explanation for the huge difference from spring to summer in this area is that 1979 might have been a year when monarchs were excessively common. This, however, was not the case: the Xerces Society ‘Fourth of July’ summer monarch butterfly counts made at nine localities east of the Rockies in 1979 (0.8 butterflies per census hour) were slightly below average ($0.9\,h^{-1}$) for the 1979–1988 decade. In contrast, the Xerces counts made at 14–28 sites for 1985–1987, the years when we made our spring censuses, were the three largest in the decade (Swengel, 1990).

Bearing of the 1985–1987 census data on the orientation of the spring migration

From the above data, we see that, during the late spring and early summer, very few monarchs were found east of the Appalachian mountains in the eastern United States. West of the Appalachians, their numbers were much higher in the midwestern states, along the Great Lakes and across Minnesota, but then petered out further westwards in North Dakota. While few monarchs reach the Connecticut River Valley in the spring, by mid-July they are found there in large numbers.

The consistency of the 1985–1987 censuses in showing few monarchs east of the Appalachians and larger numbers in the midwest during the late spring strongly supports our findings based on cardenolide fingerprinting (Malcolm *et al.* 1993). The combined data sets almost certainly indicate that the orientation of the adults of the new generation produced in Texas and Louisiana is north to northeasterly through the southern midwestern states towards the western and central Great Lakes region. The new spring adults produced in central and northern Florida also migrate northeastwards, along the Atlantic Coastal Plain (Fales, 1984; Malcolm *et al.* 1993). While recolonization of the midwest by these first-generation spring migrants is extensive, the census data indicate that few succeed in recolonizing the area east of the Appalachians.

Range expansion by monarchs of the summer generations

The data of Cockrell *et al.* (1993) and Malcolm *et al.* (1993) and the 1985–1987 censuses established that the first spring generation produced along the Gulf Coast states has a migratory phase that carries them into the Great Lakes region by early June. These data are consistent with the 19th century idea that the spring remigrants lay eggs as they migrate northwards, thereby establishing populations along their route through the central plains and midwestern states. An important question is whether the adult offspring of the next summer generation(s) disperse randomly or whether they continue to exhibit directional migration.

Urquhart (1960, 1966) contended that monarchs are rare further east in Canada until mid-summer. As shown in release and recapture diagrams (Urquhart, 1966) and a map (Urquhart, 1960, facing p. 297), Urquhart’s data suggested that, compared with the northeasterly direction of the spring migrants (which we now know are the *first* new generation produced along the Gulf Coast states), monarchs of the next generation in southern Canada during June and July begin to show an easterly movement. Our spring and summer census data, demonstrating that monarchs are abundant in the northern midwestern states in June but rare in the more eastern regions until July, are in agreement. Thus, adults of the June generation produced in the central and northern midwestern states must continue the migration in an easterly direction.

A new hypothesis: monarch butterfly orientation changes continuously through all generations of the annual migratory cycle

This reasoning has led me to propose a new hypothesis for monarch butterfly orientation: all generations of monarch butterflies are migratory and their orientation shifts clockwise at a rate of 1° per day throughout the year (Fig. 4). Increasing daylength towards the spring equinox, together with warmer weather, triggers the migration due north out of the overwintering areas into central Texas. I assume that there is some degree of scattering in each successive geographic displacement. Winds sweeping northeasterly up along the Mexican Gulf Coast may disperse some of the butterflies eastwards across the Gulf Coast states, accounting for their established arrival in Louisiana and north central Florida by late March and early April. Most, however, probably end up in Texas and western Louisiana. By early May, adults of the *first spring generation* would be hatching, and these now orient northeastwards and fly to the Great Lakes, laying eggs along the way, as the data indicate. Their eggs would result in the *second spring generation* of adults, hatching around 21 June, as the field data also indicate. The second-generation adults would now migrate due east, also laying their eggs along the way. Some overlapping of generations undoubtedly occurs, because of different rates of development due to temperature differences along the migratory route to the Great Lakes. The *third generation* of adults produced in July would migrate southeastwards across the Appalachians to the Atlantic coastal plain. From mid-August onwards, butterflies of the *fourth generation* (and, depending on temperature, possibly the *fifth generation*) will respond to shortening daylength and cooler temperatures by shutting down oocyte and sperm production, becoming highly gregarious and commencing the autumn migration (review in Brower, 1985*a*). By 21 September, according to my hypothesis, the monarchs would be moving due south, changing gradually to a southwesterly orientation as the autumn progresses. By November, as they fly through Mexico, their heading would shift westwards, carrying them into the overwintering area where their mean arrival time is from 15 November to early December (Brower, 1985*a*; Calvert and Brower, 1986). Once there, they form tight winter clusters and lose all migratory tendency for about 90 days. However, my hypothesis maintains that their orientation clock continues to shift by 1° per day while they overwinter, so that by the time the cycle is complete at the new spring equinox, they are primed to migrate due northwards (Fig. 4).

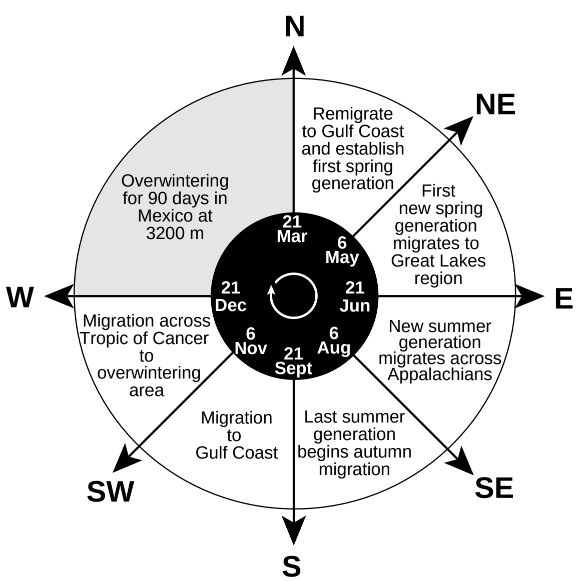

Fig. 4. The new rotational orientation hypothesis presented in this paper holds that all generations of monarch butterflies are migratory and that their orientation shifts clockwise at a rate of 1° per day throughout the year. The number of generations produced in each annual cycle varies from three to five and is temperature-dependent. The spring equinox apparently triggers the northward remigration from Mexico. As time proceeds, the hypothesis holds that the orientation of subsequent generations shifts as shown, with some degree of scattering in each successive geographic displacement. Once the last generation has reached the overwintering sites, their migratory activity is repressed by the cold weather and short daylength, but their orientation clock is assumed to continue running. By the time the cycle is complete at the new spring equinox, the overwintered butterflies are primed to migrate due northwards.

Conclusions and suggested further research

The synthesis of our fingerprinting studies, the field data given in this paper, together with the Urquharts' studies and Gibo's (1986) and Schmidt-Koenig's (1993) orientation observations, are consistent with my rotational orientation hypothesis. While supporting data are incomplete, the hypothesis is amenable to testing experimentally. Butterflies reared under daylength and temperature conditions simulating the summer solstice period should orient eastwards, while those reared under autumn equinox conditions should orient southwards, etc.

I present this new hypothesis as a challenge to stimulate new research on monarch butterfly orientation. Less complex orientation mechanisms, in fact, may operate. Perhaps monarchs simply switch from a northeasterly orientation in the spring to a southwesterly orientation in the autumn. If the single rule of not flying across large bodies of water were added to this model, potential losses over the Atlantic Ocean and Gulf of Mexico could be cut substantially. Totally random flight out of the Mexico overwintering area in the spring is also possible, implying large losses. Another possibility is that, once they arrive in the United States, the spring migrants fly into any river valley they encounter. Following the dendritic drainage patterns would then lead to their wide dispersion.

A major difficulty in proposing and in testing orientation hypotheses for the monarch butterfly is the inadequacy of our knowledge of the butterfly's arrival times and abundances in much of eastern North America between March and September. Despite Urquhart's extensive tagging program (1987), and despite excellent research into diverse aspects of the butterfly's biology (Malcolm and Zalucki, 1993), basic natural history information is still needed.

We are thus left with the tantalizing situation that the orientation mechanism(s) of the monarch butterfly migration remains unknown. This seems true to date for butterflies in general (Walker and Littell, 1994).

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