Journal of the Lepidopterists' Society
55(4), 2001, 162–168

MONARCH BUTTERFLY (*DANAUS PLEXIPPUS* L., NYMPHALIDAE) FALL MIGRATION: FLIGHT BEHAVIOR AND DIRECTION IN RELATION TO CELESTIAL AND PHYSIOGRAPHIC CUES

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ABSTRACT. To learn more about the specific routes that monarch butterflies take from their breeding grounds in the northern United States and Canada to overwintering areas in the Transvolcanic Belt of central Mexico, and to investigate the guidance mechanism by which they locate these small overwintering sites, vanishing azimuths were taken during different times of day and at different locations in Texas and Mexico. Monarchs were shown to employ either a time compensating sun/sky compass or to follow other non-solar cues over open terrain. Upon reaching the Sierra Madre Oriental of eastern Mexico, monarchs change their course and follow these ranges. The implications of this course change for orientation and the use of the Sierra Madre Oriental as a focusing mechanism to insure that the maximum numbers of butterflies reach the Mexican overwintering sites are discussed.

Additional key words: orientation, Sierra Madre Oriental, Texas, Mexico.

Among invertebrates, the monarch butterfly, *Danaus plexippus* L. is the best known and most extensive migrant (Baker 1980). Long term mark and recapture records carried out by Urquhart have disclosed the extent and the general direction of the migration (Urquhart 1960, 1965, 1966). The final destination of the eastern population of monarchs was learned in 1974 (Urquhart 1976). Unlike most migrants, whose movements are into broad habitats favorable for winter foraging, monarchs fly to specific sites of very limited extent in Mexico's Transvolcanic Belt, where they aggregate by the tens of millions (Calvert & Brower 1986). The fidelity of monarchs to these circumscribed sites that are a few hectares or less in extent taxes the imagination and must require precise navigational skills.

Several studies have addressed navigational aspects of the monarch migration. Monarchs intentionally displaced longitudinally from their fall range and released did not compensate for the displacement (Urquhart 1965) as do species that home (Baker 1978). Studying monarch migrants in cages under various conditions of visibility and lighting, Kanz (1977) found orientation to the sun, but little evidence of compensation for time of day. On the basis of these findings, he hypothesized that, if the butterflies flew towards the sun between 1000 h and 1400 h, they would eventually end up at their overwintering destination. In contrast to Kanz's findings, Schmidt-Koenig (1985), recording flight vanishing azimuths of migrating monarchs in the eastern United States, found them to be highly directional and little affected by overcast conditions. He concluded that they use a magnetoclinic system for orientation similar to that used by birds (Kiepenheuer 1984). More recent studies revealed that monarchs use a sun/sky compass that is best discerned by body orientation, not direction of travel (Perez et al. 1997), and that the solar agent by which they orient is likely plane polarized light (Hyatt 1993).

Due to the physiographic constraints to migration afforded by the Gulf of Mexico and the Rocky Mountain and their extension into Mexico, the Sierra Madre Oriental, the monarchs' flight path at the latitude of the southern tip of Texas is approximately 8% of the width it was when they started from their breeding grounds in the north. This flight-path compression results in enormous numbers of monarchs traveling through the mountainous areas in the Mexican states of Coahuila and Nuevo Leon and further south. Almost everyone who lives in this flyway is aware of the migratory phenomenon. Many can give the exact date(s) when they pass through, when, as one campesino put it, "the sky was pure butterfly". Further south, closer to the overwintering grounds in Michoacan and the state of Mexico, the Mazahua Indians have a special word in their language for "the butterfly that passes in October and November" (Muro 1975). In spite of the high profile of the monarch migration, little is known about the breadth and duration of the migration or the orientation mechanisms of the butterflies. Here I report observations of behavior and flight azimuths of migrating and non-migrating monarchs and document for the first time a change in course that occurs during the migration to the Mexican overwintering sites.

MATERIALS AND METHODS

To establish flight directions of migrating monarchs, vanishing azimuths were taken with a Suunto sighting compass in the plains of Texas, and in the mountains (Sierra Madre Oriental) of Mexico during the falls of 1977 and 1978. To avoid parallax problems, only butterflies that flew directly over head were sighted. For comparison, vanishing azimuths of non-migrating individuals were taken in fields near Amherst, Massachusetts during the summer of 1978. Vanishing azimuths

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taken during the summer months are referred to as summer monarchs; those taken during the fall are referred to as fall monarchs.

The large numbers of migrants in the Mexican Sierra Madre Oriental presented a problem. Sometimes hundreds, even thousands passed by each minute, all going in the same direction. Taking individual azimuths did not convey the magnitude of the phenomenon. In instances where many hundreds were passing by, all in the same direction, the count was stopped at 100. The total number counted in migration in the Sierra Madre Oriental using this limit was 3099. However, for statistical computations, each observation, no matter how many individuals were flying in the same direction, was treated as one observation. This number is reported in the tables. Also noted were the location and time of the day and, when appropriate, the sun's azimuth, the wind direction and magnitude, and the facing direction or heading of monarchs being blown by the wind. The facing direction is the direction towards which the body of the butterfly is oriented, as opposed to the direction it is traveling. Wind speeds were estimated by the author in mph and converted to kmph. When available, smoke, flags, or other blowing objects were used to improve the accuracy of the estimation.

Orthodromic (great circle) directions were computed using a program derived by Paul Donn. The sun's azimuths were computed for various latitudes and longitudes using a Hewlett-Packard # Nav-07A program. Loxodromic (map) directions and mountain range azimuths were obtained from Instituto Nacional de Estadistica Geografia e Informatica topographic maps Ciudad de Mexico and Monterrey, 1:1,000,000 scale (Anon. 1982, 1984). Orthodromic directions from the approximate center of the cluster of open plains observations at Austin, Texas (97.7°W, 30.3°N) to the western boundary of the overwintering zone (100.8°W, 19.7°N) were computed using the Donn program. Loxodromic directions were measured from the map. These directions were obtained for the cluster of mountain observations from Avila y Urbina, Tamaulipas (99.6°W, 23.7°N), the approximate geographic center of the mountain group, to the eastern boundary of the overwintering zone (99.9°W, 19.1°N).

All mean flight azimuths were corrected for magnetic declination and averaged vectorially. A circular statistics program (Watson's U^2 test) was applied to distinguish differences between the mountain and open plain distributions. Standard statistical tests, such as Student's t and Fisher PLSD, were used to compare deviations from expected directions. Mean angles derived vectorially differed from arithmetic means by only 1.7° and 3.7° for butterflies flying over open plains and in mountains, respectively. These differences are small enough so that the arithmetic means and standard deviations are very close approximations of mean angles and angular deviations. Therefore standard, non-circular statistical comparisons may be applied (Batschelet 1972). Vanishing azimuths and the associated circular statistics were computed using a circular graphics program Vector Rose 3.0 written by P. Zippi (1997).

For comparison, the loxodromic (map) azimuths are also given. They are more familiar and easier to understand that orthodromic (great circle) azimuths. I do not wish to imply that monarchs use to orient map azimuths that are the result of projections of spherical surfaces onto flat ones.

RESULTS

Observations of summer versus fall behavior. Monarchs observed during mid-summer were occupied mainly with feeding and oviposition. Occasionally courtship investigations and chases also occurred. Flight normally was confined to the first 3 m above the ground except during courtship chases, where the pair might fly up to 15 m before descending. In their search for nectar, mid-summer monarchs cruised over or among prospective plants in ziz-zag or circular paths. Flight in any one direction was short, usually less than 2 m, and flight direction was random (Fig. 2). The mean flight azimuth for 101 mid-summer monarchs was not significantly different from zero (Rayleigh test, $z = 0.87$, $p > 0.4$; Batschelet 1972).

In contrast, fall monarchs flying over the plains of Texas and in the Sierra Madre Oriental exhibited highly directional flight (Figs. 3 and 4). Mean flight azimuths computed for these two groups were 239.0° and 174.6° for open plain and mountainous terrain, respectively (Rayleigh test, Batschelet 1972; $z = 40.4$, $p < 0.001$ for open plains; $z = 158.2$, $p < 0.001$ for mountainous terrain).

Migratory flight behavior. Fall monarchs also differed from summer monarchs in their use of rising air currents to avoid powered flight. During the fall, the arrival and departure of migrating monarchs generally is associated with the arrival of cold air masses (see also Gibo 1987). Monarchs often ride the rising layers of warm air preceding these fronts and also take advantage of northerly winds that may blow for days in association with such fronts. On calm days or when winds were favorable, e.g., from a northerly direction, migrants were found flying at elevations from one me-

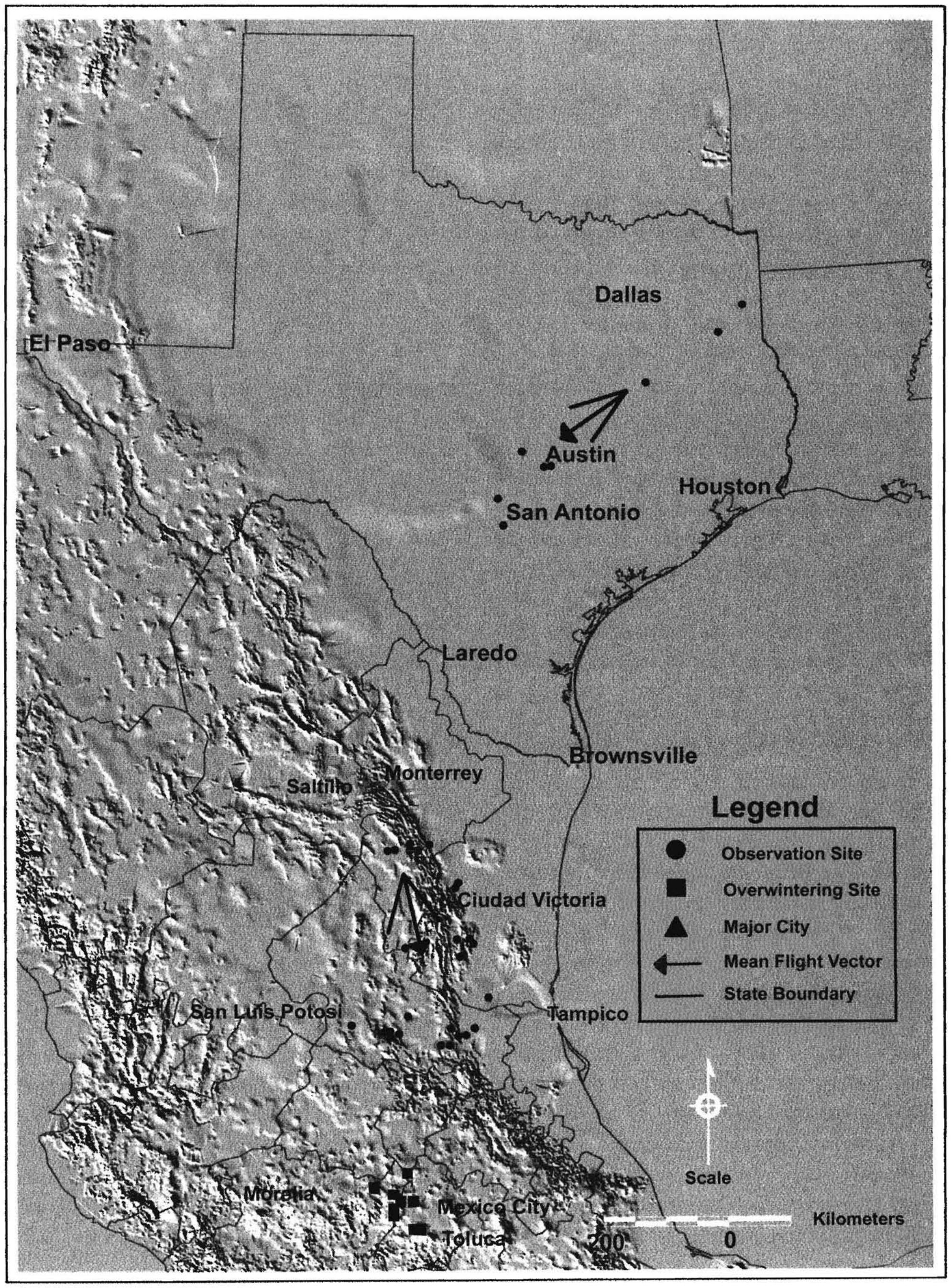

FIG. 1. Average flight vectors and confidence intervals for open plains and mountainous terrain in Texas and Mexico respectively. Without a course correction, monarchs flying over open plains would fly too far west to attain the overwintering sites. Monarchs flying in the mountains would miss all but the easternmost sites.

ter to the limits of binocular vision (ca. 300 m). When opposed by southerly winds, they could be found in riparian areas sheltered from the wind in loose gregarious roosts.

Convection thermaling was common. When winds were calm or blowing from the north, monarchs rose on thermals, and then glided. During the course of the glide they lost altitude. At some point they ceased gliding, and began again to circle in thermals to gain altitude. Often monarchs were seen in thermals with hawks and vultures. In mountainous area, monarchs often used orographic lift, riding on winds pushed up by the mountain ranges. The greatest concentrations of low flying migrants were nearly always encountered

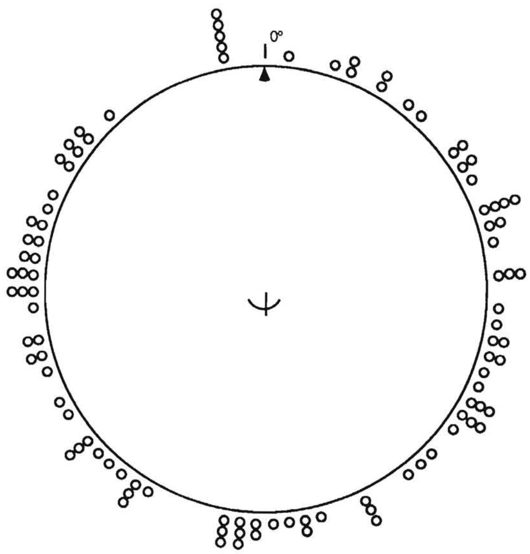

FIG. 2. Flight azimuths of monarchs during mid-summer near Amherst, MA, indicate no directional tendency. (mean vector = 180.3°; angular deviation = 124.9°; n = 101; r = 0.09; p = ns).

on the east face of ranges of the Sierra Madre Oriental riding prevailing easterly winds (Mosiño-Aleman 1974).

Monarchs adapt to changing wind speeds and high velocity winds, but did not always appear to be in full control. A group of ca. 40 monarchs flying between 30 and 40 m altitude in nearly calm air, immediately dropped vertically to 1–3 m when headwinds suddenly increased (see also Gibo & Pallett 1979). Monarchs appear to have difficulty flying in high velocity winds. On one occasion near Monterrey, Mexico, a large concentration of migrants (>500 passing through a

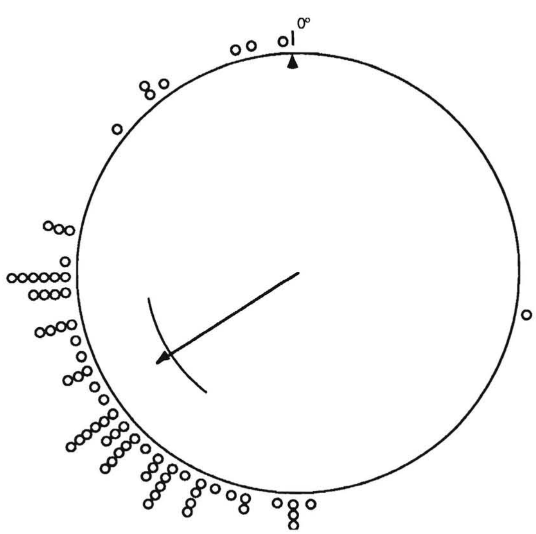

FIG. 3. Flight azimuths of fall monarchs in the plains of Texas showing that flight is highly directional towards the SSW (mean vector = 239.0°; angular deviation = 42.5°; n = 70; r = 0.76; p < 0.001).

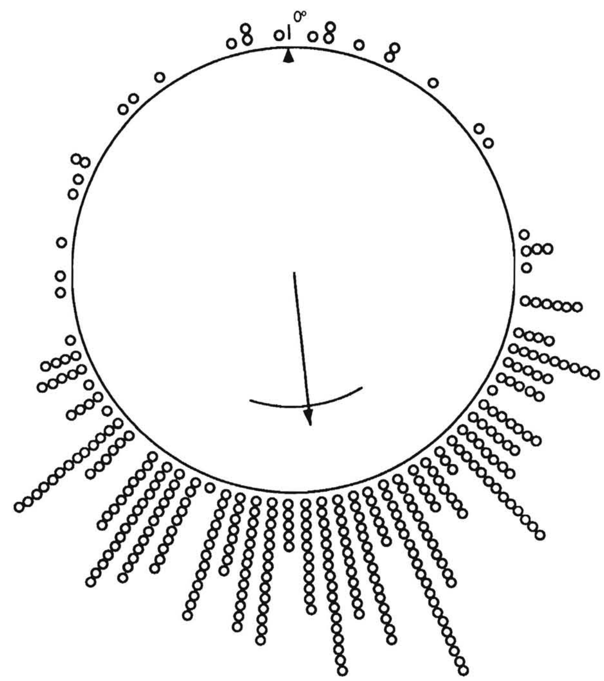

FIG. 4. Flight azimuths of fall monarchs in mountainous areas of Mexico showing that flight is highly directional, but now towards the SSE (mean vector = 174.6°; angular deviation=49.4°; n = 333; r = 0.84; p < 0.001).

plane perpendicular to their flight path per minute) was found flying in the lee of a ridge, the windward face of which was receiving winds in excess of 30 kmph. On another occasion near Brownsville. Texas, monarchs were seen tumbling in the air apparently out of control in high velocity north winds gusting to 50 kmph.

Migration over open plains. Over open plains, in Texas, the mean of 70 vanishing azimuths was 239.0° (vector length = 0.76; Fig. 1, Table 1). Surprisingly, the 99% confidence interval of 15° included neither the orthodromic nor the loxodromic direction to the western edge of the Mexican overwintering zone located 1300 km SSW ca. 30 km west of Cd. Hidalgo in the state of Michoacan. If monarchs flying over open terrain continued on this course, they would fly too far to the west and miss the entire distribution of known overwintering sites.

Migration within the mountains. Within the Sierra Madre Oriental, the mean vanishing azimuth for 333 sightings shifted significantly eastward from 239.0° to 174.6° (99% confidence interval = 9°; vector length = 0.69). The 99% confidence interval barely includes the orthrodromic direction to the eastern boundary of the overwintering area (Table 1). Thus butterflies flying over open terrain fly in a direction that will take them too far to the west to strike any part

TABLE 1. Comparison of mean flight azimuths with directions to the overwintering areas for various locations in the United States and Mexico.

Migratory status/ location	N	Mean flight azimuth	99% conf. interval	Orthrodromic	Loxodromic	Vector length	Prob.[1]
Non-migratory/Amherst, MA	101	209.3°	—	—	—	0.09	>0.4
Migratory/Open plains,Texas	70	239.0°	224–254°	195.4°[2]	195.5°[2]	0.76	<0.001
Migratory/Sierra Madre, Mexico [4]	333	174.6°	166–176°	182.9°[3]	184°[3]	0.69	<0.001
Migratory/Eastern US [4]	477	220.0°	216–224°	223°	228°	0.88	<0.001

[1] Rayleigh test for uniformity from Batschelet 1972. If p > 0.05, the distribution of observations is random.
[2] From Austin, TX (97.7°W, 30.3°N) to the western extreme overwintering site at Mil Cumbres (19.7°N, 100.8°W).
[3] From the approximate center of mountain observations at Avila y Urbina (99.6°W, 23.7°N) to the the eastern extreme overwintering site at Palomas (99.9°W, 19.1°N).
[4] Data from Schmidt-Koenig 1979.

of the overwintering zone, while those flying in the Sierra Madre Oriental will fly too far to the east to strike all but its eastern-most fringe. The distribution of azimuths observed in the mountains differed significantly from the distribution over open terrain (Watson's U^2 test: $U^2 = 2.10$, n = 333, m = 82, p < 0.001).

Diel flight periods. Most overnight monarch roosts broke up within 15 minutes after the rays of the morning sun struck them. Unless the sun's radiation was blocked by topography or vegetation, this occurred between 0745 and 0830 h (CST). At roost breakup, initially most butterflies flew at least a short distance towards the sun before alighting to bask or beginning to ride morning thermals upwards. Occasionally morning thermaling commenced as early as 0715 h. Migratory flight usually ceased from mid- to late afternoon when monarchs descended to take nectar, to form nighttime roosts, or both. But directional flight was observed as late as 1745–1800 h. After 1800 h, most monarchs were either searching for or forming roosts. Rarely, a monarch was seen in directional flight until nearly dark (ca. 1900 h in central Mexico at latitude 24°N). Monarchs flew at the same azimuth during all times of the day over open plains (Table 2; ANOVA F = 0.96, n = 70, p < 0.39). In mountainous terrain, they flew at the same azimuth until 1400 h and slightly more westerly after 1400 h (F = 8.51, n = 333, p = 0.0002).

Comparison of mean flight azimuths to the sun's azimuth and to the direction of the mountain ranges. Azimuths of monarchs flying over open terrain and in the mountains both differed significantly from the sun's azimuth (ANOVA, F = 8.4, n = 57 p < 0.0007 and F = 38.6, n = 313, p < 0.0001 respectively; Table 1). To test Kanz's hypothesis that monarchs fly towards the sun between 1000 and 1400 h, deviations of monarch flight azimuths from the sun's azimuth were calculated for 3 diel time periods: <1000 h, between 1000 and 1400 h, and >1400 h. The flight azimuth of most groups remained significantly different from the sun's azimuth (Table 2). As would be expected, the open terrain group flew closest to the sun after 1400 h, and the mountain group flew in the direction of the sun between 1000 and 1400 h.

The direction of individual ranges composing the Sierra Madre Oriental often deviated from the general axis of the ranges (163°) as measured from the two Instituto Nacional de Estadistica Geografia e Informatica topographic maps that covered the region. In general, the northern ranges run more easterly than the southern ones. Monarchs flying in the intermontane valleys of the Sierra Madre Oriental flew an average of 11.6° to the west of the general direction of the ranges as indicated on the map (Table 1).

TABLE 2. Flight azimuths and deviations from potential cues for various time periods.

	Location							
	Open terrain				Mountains			
Time period	N	Mean azimuth	Dev.[2] sun	Prob.[3]	N	Mean azimuth	Dev.[2] sun	Prob.[3]
<1000 h	2	247.5 a[1]	−147.5	—	42	161.7[a]	−53.8	0.0001
1000–1400 h	9	221.7 a	−68.1	0.01	117	167.6[a]	+3.2	NS
>1400 h	59	243 4 a	−22.1	0.001	174	189.6[b]	+34.0	0.0001

[1] Different letters in columns indicate that the means differ significantly among times at 0.05 (Fisher PLSD test).
[2] Deviation from the sun. A negative deviation means that the butterfly is flying to the west of the sun or the axis of the Sierra Madre Oriental.
[3] Probability (Students t-test) that the butterfly azimuths are different from the sun's azimuth. In the first case (<1000 h over open plains) there were insufficient data to make a statistical determination.

DISCUSSION

Without physiographic markers such as mountains or shore lines, monarch butterflies in Texas and Mexico maintained a strongly directed course to the SSW (Table 1). Monarchs migrating in the eastern United States followed a similar course (Schmidt-Koenig 1979), although my measurements in Texas indicated that group flew slightly more westerly than the eastern group (Table 1). By the time the migrants reach south-central Texas, both the loxodromic and orthdromic directions to the overwintering areas are directly south. Yet, over open plains the monarchs continue to fly SSW which, if continued, would take them far to the west of the overwintering zone. When they reach the ranges of the Sierra Madre Oriental, they change their course to the SSE. If they continued in this direction, they would pass to the east of the major overwintering area centered around Angangueo, Michoacan (19.6°N; 100.3°W).

Assuming that monarchs cannot home, and correct the consequences of a miss, migrants flying in from the north must strike the Transvolcanic Belt somewhere within a 1.1° (115 km; 99.9°W–101.0°W) corridor to find the overwintering sites. The dimension and extent of this narrow corridor is based on the locations of the known overwintering sites (Urquhart 1976, Calvert & Brower 1986) and on extensive searching for additional sites by the Mexican Forestry Department (J. de la Maza, pers. com.) and others (de la Maza & Calvert 1992). Small aggregations were located as far west as the states of Jalisco and Colima and as far south as the Sierra de Juarez in eastern Oaxaca, but none of these compared in size to the major overwintering colonies located from the west face of the Nevado de Toluca, state of Mexico (99.9°W) to Mil Cumbres, state of Michoacan (101.0°W).

Monarch migrants' failure to follow orthodromic or loxodromic directions to the overwintering area suggests a complex guidance senario. In the absence of physiographic cues, they must use a genetically programmed sun/sky, magnetic, or other based guidance system that takes them to the SSW. A course correction is necessary to avoid missing the overwintering sites by flying too far to the west. The ranges of the Sierra Madre Oriental apparently provide cues for this course correction. The monarchs follow these ranges to the SSE. But this correction is too great and, if continued, would take them too far east. Either another course correction to the SSW takes place in the relatively rangeless plains and mountains of the states of Hidalgo, Queretaro and southern San Luis Potosí, or perhaps the constant pressure of prevailing easterly winds (Mosiño-Aleman 1974) eventually displaces them the proper distance to reach their objective.

The Sierra Madre Oriental and Rocky Mountains may also be a focusing mechanism. Monarchs traveling across the continental United States from breeding areas scattered across the mid-west and eastern seaboard would be expected to proceed along a broad front. Reports to the National Monarch Watch (unpubl. archived reports to Dplex-L@raven.cc.ukans.edu) indicate that they migrate through a wide area of the mid-western states. Some years even western Kansas and New Mexico are traversed. Traveling SSW along such broad fronts, they would strike the Rocky Mountains and Sierra Madre Oriental at many places in Texas, northeastern Mexico, and possibly as far north as New Mexico or Colorado. Once encountered, turning to follow these ranges would insure that they eventually joined with other migrants proceeding in the same direction. This focusing mechanism could result in monarchs that were born a thousand miles apart traveling within the same intermontane valley in the Sierra Madre Oriental.

Yet another advantage may be afforded migrant monarchs once they enter the intermontane valleys and ridges of the Sierra Madre Oriental. By following mountain crests, they enter into extensive areas of rising air currents (orographic lift) caused when prevailing easterly winds (Mosiño-Aleman 1974) are pushed up by the mountain ranges. By soaring on the windward slopes of these intermontane valleys, monarchs may be able to travel long distances with little powered flight and thereby conserve energy.

Gibo and Pallett (1979) estimated that if soaring requires only a basal level of metabolism, a butterfly with an initial supply of 140 mg of fat could soar as long as 44 days without replenishment. Thermaling and gliding may be especially important during the segment of the migratory pathway between central Texas and the Sierra Madre Oriental. Nectar resources in the desert and chaparral regions of north-central Mexico and southwestern Texas are sporadic, and their abundance depends upon unpredictable rainfall. Preliminary evidence indicates that monarchs lose approximately 12 mg or about 2% of their wet weight in crossing this ca. 300 km area (Calvert unpubl.).

Riding rising currents generated by mountain ridges may be even more important for migrant lipid conservation further south within the Sierra Madre Oriental where a pronounced rain shadow is evident. The driest area through which monarchs migrated by the thousands was Tula in the Chihuahuan Desert region of the state of Tamaulipas. Many monarchs that cross the first major range through the Novilla Canyon near Ciudad

Victoria must traverse a ca. 200-km dry desert region from Jaumave to Ciudad del Maize where more mesic conditions are found.

Although there are some unexplained small variations in flight direction during the three diel periods (Table 2), clearly monarchs do not fly towards the sun as proposed by Kanz (1977), nor is their flight restricted to mid-day between 1000 and 1400 h. Directed migratory flight was observed before 0800 h and after 1800 h. Flying towards the sun would not be sufficient to get them from breeding to overwintering grounds since such flight would, over the course of a day, take them due south. This would be inappropriate for longitudes east of 99°W longitude where much of the breeding area is located.

ACKNOWLEDGMENTS

I am indebted to many people for help in collecting the data. These include Willow Zuchowski, Philip Russell, Gary Mathews, David Palmer, Melinda Linquist, and Mary Margaret Quadlander. During the majority of the research, a film crew from Nippon TV, Japan under the direction of I. Yamaguchi helped collect data and lent an international flavor to the expedition. Paul Donn wrote the program to compute the orthodromic (great circle) directions to the overwintering sites. The concepts in this paper benefited greatly from campfire-side conversations with Martin Hyatt and Hugh McIsaac. Lincoln P. Brower and Raymond Neck made many helpful suggestions to improve the manuscript, as did Deane Bowers and two anonymous reviewers. Changiang Lui of Texas Parks and Wildlife's GIS Laboratory compiled Fig. 1 partly based on information supplied by Miguel Pavon of the Texas Water Development Board. This research was conducted as an adjunct to research supported by U.S. National Science Foundation grant DEB 78-10658-A01 to Amherst College and DEB 80-40388 to the University of Florida with Lincoln P. Brower as principal investigator.

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Received for publication 8 November 1999; revised and accepted 3 November 2001.