The Great Lakes Entomologist

Volume 54
Numbers 1 & 2 - Spring/Summer 2021 *Numbers 1 & 2 - Spring/Summer 2021*

Article 6

November 2021

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Recommended Citation

Douglas, Matthew M. 2021. "Spiraling Flight Behavior May Integrate the Biological Compass Systems of Migratory North American Monarch Butterflies, (Danaus plexippus, L.)," *The Great Lakes Entomologist*, vol 54 (1)
DOI: https://doi.org/10.22543/0090-0222.2395
Available at: https://scholar.valpo.edu/tgle/vol54/iss1/6

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Cover Page Footnote

Thanks to Brandy Van Zalen for her illustration of monarch spiraling flight behavior

Spiraling Flight Behavior May Integrate the Biological Compass Systems of Migratory North American Monarch Butterflies, (*Danaus plexippus* L.)

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Abstract

Here I report a unique spiraling flight and orientation behavior (comprising multiple clockwise and counterclockwise circles coupled by extended figure-8 patterns) observed in free-flying "late" migratory monarchs released under sunny ambient field conditions from a location with an unobstructed view of the sky. Following this spiraling flight, migrants continue to fly at very high altitudes until a final orientation and migratory flight direction is established with vanishing bearings statistically concentrated to the SW/W. These results provide preliminary evidence for the possible calibration and use of an inclination magnetic compass that can be used under all local free-flying field conditions. During this spiraling flight, migrating monarch butterflies are proposed to be measuring the direction and inclination of the continuously varying local magnetic field, in a manner analogous to the figure-8 pattern performed to calibrate digital compasses. This behavioral research focuses on the vital pre-migratory orientation and flight behavior that may provide a key behavioral link explaining how migrating monarch butterflies using a time-compensated sun compass system could also integrate the biophysical input from the polarized UV sensitive dorsal rim area (DRA) and the cellular cryptochrome (CRY) system linked to the proposed inclination-based magnetic compass system residing in the distal end of the antennae.

Keywords: monarch migratory orientation, monarch migratory flight, monarch migratory compass systems, ultraviolet sensitive DRA, CRY, inclination-based magnetic compass system in monarchs, orientation flight dance of monarchs.

The monarch butterfly (*Danaus plexippus* L.) (Lepidoptera: Nymphalidae) and its migratory behavior have been investigated for well over 70 years. Indeed, since 1975, the eastern cohort of the North American monarch butterfly has become known throughout the world for its spectacular annual migration from the provinces of southern Canada and the northern tier states of the United States to fewer than a dozen well-defined overwintering roosts in the montane forests of Michoacan, Mexico (National Geographic 1976). Migrating monarchs in Michigan have an extended migratory period, somewhat variable in timing and success from year to year, but temporally wave-like in occurrence, and most pronounced between 15 August and 15 October (Douglas 2019). Outside of Michigan, individual monarchs also collectively form successive waves of migrating butterflies that leave their natal locations commencing mid- to late August and continuing through the end of October in most years (Brower 1995). Recent research suggests that a "migration window" exists when the Sun Angle at Solar Noon (SASN) is about 57° at the leading edge of the migration and 46° at the trailing edge. Ninety percent of the tagged monarchs (Monarch Watch) recovered in Mexico were from monarchs tagged within this window (Taylor et al. 2019).

Despite the current knowledge concerning the environmental cues and the variety of possible biophysical and physiological receptors involved in inducing the annual migration, the monarch's pre-migratory flight orientation *under field conditions* remain a poorly understood biological phenomenon of seemingly unlimited complexity. One important aspect of monarch migratory behavior that has been ignored under field conditions is a description of any flight orientation behavior that then becomes the directional flight used by migrating butterflies during the late summer and early fall migrations. In the experiment reported here, I show how migratory butterflies orient when released over open water at a central location equidistant from the continuous forested shoreline (so that the shoreline environment could not provide immediate unambiguous visual directional cues). Immediately following release, each butterfly's flight behavior and vanishing bearing were recorded and analyzed.

Materials and Methods

Wild-caught gravid female monarchs captured in the vicinity of Grand Rapids, Michigan (42.96 N, 856.67 W, USA) in August 2015 were allowed to oviposit on mature native *Asclepias syriaca* L. established in a large hexagonal mesh tent (diameter of 5 m and peak dome height of 3 m; mesh of 0.3 cm). The tent was exposed to ambient environmental conditions throughout the study. First instar larvae were removed from the ovipositional plants and reared on fresh milkweed growing within the tent. After pupation, chrysalides were removed and hung on foam supports in the meshed tent. Following eclosion, newly emerged adults fed on nectariferous plants (e.g., cultivars of *Lantana* spp, *Verbena* spp, *Buddleja* spp) as well as at "nectar stations" filled with raw (star thistle) honey and water solution (1:10 ratio), all of which provided adult nutrition, still under ambient conditions within the tent enclosure, until the butterflies were released. In the experimental results reported here, butterflies were released on 7 October 2015 from the middle of a post-glacial kettle lake (Toft (Rome's) Lake, Newaygo County, Michigan, 43° N, 85° W), which comprises approximately 10 hectares of surface water and surrounding wetlands that terminate in a completely forested, undeveloped shoreline.

Prior to release, butterflies were transferred to large cylindrical mesh cages (64 cm high, 40 cm diameter) composed of a translucent white mesh (with mesh openings of .3 cm) and cinch knot tie at the top. They were then transported via a row boat to open water approximately 700 meters from shore in all directions with a clear and unobstructed view of the sky. In all cases, vegetation was reasonably uniform in the background, and immediately unavailable to monarchs after taking flight. Ambient conditions were the following: negligible wind to 4 mps (to avoid butterfly drift), sunny skies (to provide adequate UV exposure to the DRA), ambient temperatures of 25°C (to permit controlled flight) and release time between 1:00 and 2:00 PM (an optimal diurnal migratory window for late migratory monarchs in Michigan (unpublished data)). Monarchs were allowed to exit of their own accord from the narrow opening at the top of the mesh cage created when the cinch knot was loosened. The monarchs readily flew up without provocation and, because of the lake surrounding them and the lack of nectariferous plants at the lakeshore, were compelled to take an orientation. The monarchs were observed until they could no longer be seen with a Nikon 10 × 42, 5.5-degree binocular, at which point the "vanishing bearing" was recorded.

Results

After release, 68 of 71 released monarchs (96 percent) flew rapidly upward using "powered flight" (e.g., Gibo and Pallett 1979); at first in very tight clockwise circles, but then quickly expanding clockwise circles. At this point, many releases made an extended figure-8 as they circled counter-clockwise, and often repeated this scenario a number of times (Fig. 1), until at very high altitudes (greater than 300m), the individuals flew directionally between 180° and 330° with a mean of 247° (SW/W). (Fig. 2). Monarchs released without any nearby physical structure such as trees, such as along the eastern shore of Lake Michigan, will continue to fly directionally until they are completely out of view. Anecdotally, monarchs have been observed flying over Lake Michigan, over tall buildings such as the Empire State Building, as well as by glider pilots at more than 300 meters (Gibo 1981). The remaining 4 percent of released butterflies exhibited more direct flight, elevating quickly after several small circles, and then flying more directly to high elevation without consistent circling. This is in contrast to "summer monarchs" released during June and July, under similar conditions, when only 54 percent of butterflies released exhibited circling behavior (Douglas, unpublished data).

It should be understood that each individual monarch flight orientation is somewhat unique (for example, some first flew counter-clockwise, then clockwise, and some repeated the reversal patterns a number of times prior to maintaining a specific direction). For that reason, the behavior cannot be specifically quantified.

Discussion

With these data of flight behavior and vanishing orientation in mind, it is possible to create a reasonable hypothesis concerning their significance in the much larger picture of monarch butterfly migration. We know that all life on Earth has evolved against a backdrop of environmental cues that entrain an organism's biological rhythms to the external biophysical cues around it. These biophysical cues, or "zeitgebers" include latitude and longitude, the azimuthal change and passage of the sun across the sky (sun path/day arc); the type of radiation (such as infrared and polarized ultraviolet light) that

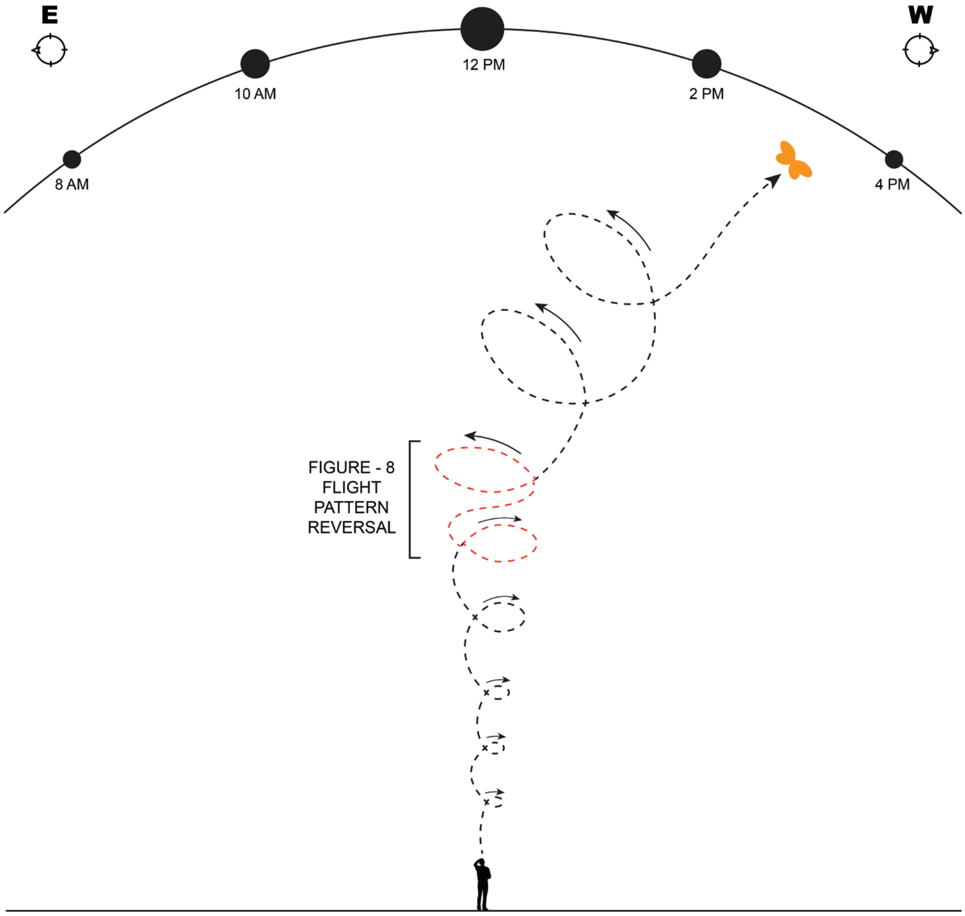

Figure 1: Depiction of Spiraling Pre-Migratory Flight Behavior Under Field Conditions (video available online at https://www.youtube.com/watch?v=IcRmcI9v7b4). SASN estimated to be about 45 degrees N.

Toft (Rome's) Lake: October 7; Clear skies, 25° C, variable winds less than 4mps, butterflies released from central location over the lake and vanishing directions noted: Ninety-six percent of butterflies exhibited circling counterclockwise and clockwise prior to powered directional flight until visibly out of sight, at which point the vanishing direction was taken. Releases took place between 1:00 and 2:00 pm, with SASN elevation at approximately 45 degrees.

can be sensed and measured; the strength, declination, inclination, and regional and temporal variation of the magnetic field; the prevailing winds of land and the currents of oceans; gravity, and the rotation of the earth, its inclination, and its annual passage around the sun. This list is not exhaustive. Navigation in many organisms, whether diurnally or nocturnally local, or truly migratory, is dependent on the reception and interpretation of these biophysical cues and their variation over time and location.

Because of the different zeitgebers available, multiple modes of orientation are possible, depending on the group of organisms. In support of this statement, Barrie (2019) points out that "Much of the confusion that surrounds bird navigation, probably arises from the fact that birds (like many other animals) use a range of different navigational mechanisms and make their choice among them, according to the precise circumstances in which they find themselves. They may well have some way of assessing the quality of information available from each source, before "deciding" which system is likely to be the most reliable, and they probably use different navigational tools at different stages in their journeys."

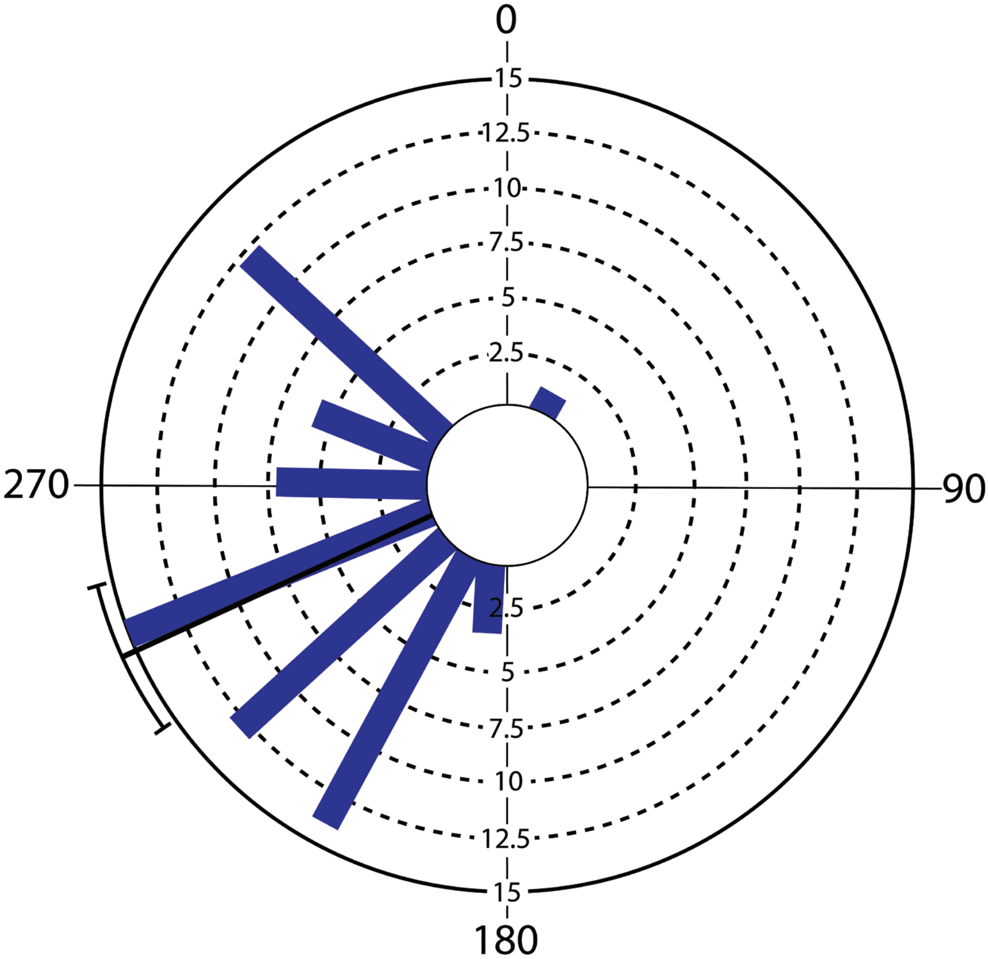

Figure 2: Vanishing Orientations (N = 71); mean vector (u) = 247 (SW/W); length mean vector ® = .79; circular variance = .214; circular std. dev. = 39.7; Raleigh test error function = 1E-12.

As for examples of circular displays of orientation in insects, Baird et al. (2012) and Dacke et al. (2013) determined that dung beetles perform a circular dance on top of their dung ball while observing polarized light patterns in the sky above it. This orientation procedure is vital to the successful movement of the dung ball in a straight line, thereby minimizing effort and maximizing the deposition of the dung ball away from competitors. It is hypothesized that the dorsal rim area (DRA), detects polarized light from the moon to accomplish this amazing straight-line orientation (see Stalleicken et al. (2006) for a physiological characterization of the DRA in monarch butterflies). Benvenuti et al. (1994) established that the red admiral, *Vanessa atalanta* (L.) performs regular multigenerational bidirectional migrations from Africa to Europe, presumably flying along straight paths at average speeds of 14 km/h. Observations of the red admiral in Michigan, using similar experimental design reported here, suggests that they also are capable of using spiraling flight when released over open water. In contrast, other butterfly species such as the Aphrodite fritillary (*Speyeria aphrodite* (Fabricius)), the cabbage white (*Pieris rapae* (Linnaeus)); the silver-spotted skipper (*Epargyreus clarus* (Cramer)), the giant swallowtail (*Papilio cresphontes* Cramer), and the red-spotted purple (*Limenitis arthemis astyanax* (Fabricius)) exhibit only directional powered flight from their origin of release, often just above the water. This suggests that these latter-mentioned species do not have the compassing capabilities exhibited by monarch butterflies.

Late summer and mid-fall migrating butterflies from the eastern cohort of the North American monarch have a number of mechanisms they can use alone or in combination (depending on the environmental zeitgebers available) to orient themselves and navigate their journey to the overwintering roosts of Mexico. (These roosts may be over 4,000 km away from their natal locations; monarchs from the most northern areas complete this flight in about 75 days traveling a rough average of 50 kms per day, according to multiyear data from Monarch Watch.) For example, migratory monarchs may use a time-compensated sun compass (Perez et al. 1997), polarized light (Reppert et al. 2004, Stalleicken et al. 2005), antennal circadian clocks that coordinate the sun compass orientation (Merlin et al. 2009), the integration of skylight cues via the sun compass (Heinze and Reppert 2011), a magnetic compass measuring the intensity of the local magnetic field as well as the inclination (Guerra et al. 2014). A basic understanding of the neurobiology of monarch butterfly migration has been established by Reppert et al. (2016), although Mouritsen et al. (2013) have suggested that monarch butterflies are not true navigators, and that their displacement from their natal origins a thousand miles west did not affect their ability to orient and choose a consistent flight direction that can be measured directly by their vanishing bearings. In addition, Guilford and Taylor (2014), suggest that a solar heading (of migrating monarchs) need not require time compensation at all. They conclude, ". . . that clock shift experiments alone are neither necessary nor sufficient to identify the occurrence of all conceivable use of solar information in animal orientation, so that a predictable response to clock shift should not be regarded as an acid test of the use of solar information in navigation."

It seems certain, at least, that monarchs have a time-compensated sun compass and can measure the seasonal position, azimuth, and height of the sun in the sky; respond to the e-vector produced by the polarization of ultraviolet light; likely use geomagnetic strength and inclination cues as well as "channelizing" geographic barriers such as mountains and oceans. Alone or in combination, migrating monarchs are able to locate fewer than a dozen overwintering roosts at 3,000 m in the oyamel and false white pine forests of the Transvolcanic Mountains of central Mexico in the states of Michoacan and Mexico.

Recent anatomical, neural, and genetic research suggests that sunlight is perceived by the retina and records the azimuthal angle of the light. Light polarization is detected by the specialized cells of the dorsal rim area (e.g., Barta et al. 2004, Labhart et al. 2009) and is interpreted by the central complex of the brain, where single neurons "combine the azimuthal location of the sun and the e-vector angle" of the polarized light (Reppert 2004). Although the central complex processes the neural input from the sun and its polarized ultraviolet light, the distal tip of the antennae contains the receptive sensilla that control the circadian clock (Merlin et al. 2009). This circadian clock relies on a transcriptional-translational auto-regulatory negative feedback loop that drives rhythms in the mRNA and protein levels of core circadian clock components, which involves two cryptochrome proteins, CRY 1 and CRY 2. CRY 1 apparently functions as a blue light photoreceptor that "sets" the circadian clock whereas CRY 2 is similar to the mammalian CRY in that it functions as one of the major repressors in the feedback loop (Reppert et al. 2016). In effect, cryptochromes may define a circadian clock mechanism in monarch butterflies that may itself underlie sun compass navigation (Kyriacou 2009). This would not be unexpected as Gegear et al. (2008) determined that cryptochromes mediate light-dependent magnetosensitivy in *Drosophila.*

As an integral part of their migratory machinery, migrating monarchs can also detect the magnetic field of the earth (Zhu et al. 2008). This would likely involve measuring its intensity as well as the inclination—both of which are available but often ambiguous because the inclination signal, for example, can easily be swamped by the daily and the local variations of the magnetic field. Magnetic sensors have not been found, and they could occur anywhere or everywhere on the body because the earth's magnetic field easily penetrates living tissue, which means that the presence of magnetite is not necessarily an indicator that an organism possesses the ability to "see" the magnetic field. If so many different zeitgebers are available, and so many mechanisms of detection for orientating and maintaining migratory flight are available, how do the monarch butterflies integrate them to commence and maintain migratory orientation?

In 1974, during a graduate ecology class at the University of Kansas, Dr. Orley (Chip) Taylor (founder of Monarch Watch) exposed his students to the strange spiraling flight pattern of some migratory monarchs when release over a semi-open field (1976 personal notes, University of Kansas). At the time we assumed, as had Kanz (1977) and others, that this flight pattern was a defensive strategy in which escaping butterflies flew toward the sun to escape predation. Lincoln Brower also observed this flight pattern (personal communication, 2001), as has Gibo (1986) who attributed it to gliding and altitudinal gain by circling during migration, when they can fly well over 1 km above the ground. And interestingly, released butterflies not exhibiting directional flight (e.g., those "spiraling upwards on thermal currents") were excluded from analyses by Perez et al. (1997). According to Jonathan Weiner, even Fred Urquhart pondered his observations of spiraling flight: "They form a ring, or circle, and follow each other around and around, like children on a carrousel, drifting in the wind. Caged monarchs, when released, often fly straight up and form this magic circle." Why, Urquhart does not speculate—perhaps it is an exercise in orientation." (Weiner 1983). In effect, early reports of "spiraling behavior" were discounted or explained in terms of other possible phenomena.

It should be noted, however, that a specific flight behavior may serve more than one function, just as with the colors of butterfly wings, which serve multiple functions (e.g., thermoregulation, cryptic coloration, warning coloration, and mate attraction). In this case, the unusual and stereotypical flight orientation of migratory monarch butterflies upon release could provide a reliable means of integrating *all* of the potential mechanisms used by migrating monarch butterflies both for orientation and maintaining a preferred SE-SW flight toward the overwintering roosts in Mexico. This flight pattern cannot be an escape pattern because the final orientation direction during migration, regardless of when or where the butterflies are released, is consistently between SE and SW (Douglas, unpublished data). In addition, released migratory butterflies do not fly toward the sun; their final vanishing direction is established within a few minutes of flight and is consistent and independent of the time of when they were released. Finally, this flight is *active powered flight* comprising reversals and figure-8's—hardly an efficient way to locate thermal updrafts. At first it is invariably a rapid upward "explosive" flight (usually less than 30 seconds in duration) and comprises constant and vigorous powered spiraling flight until a specific orientation and direction is achieved, at which point, often thousands of feet above ground, the butterflies continue to intermittently use a mix of power flight and gliding, usually in a linear direction, as long as wind direction and strength remain stable. The upward spiraling flight pattern exposes the migratory butterflies to the polarized light patterns of the sun, and the circling and reversals could conceivably measure the constantly changing local magnetic field of the earth at the release location.

In effect, spiraling flight may be a behavioral means of exposing migratory monarchs to all of the zeitgebers they need to migrate in approximately the right direction toward the overwintering roosts, regardless of the environmental conditions (e.g., as long as ambient temperatures allow flight, monarchs will migrate when skies are sunny, partly cloudy, and completely overcast; even during light rain (Floyd Preston, University of Kansas; personal observations), when thermals are very weak or absent. As migratory monarchs approach large open expanses of water, such as Lake Michigan, they may continue powered flight directionally over the lake, or perform spiraling formations, singly or in small groups, on sunny and partly cloudy days when thermals may form along the lakeshore. However, monarchs may also fly over Lake Michigan with robust directionality on completely overcast days—when thermals are rare, weak, or unpredictable. Thus, these initial spiraling flights are likely not due to modes of escape, or necessarily to sun location, nor to riding the thermals because there is virtually no temperature variation at their level of flight over the numerous large lakes and wetlands in Michigan during completely overcast days that could provide thermal uplift. However, there is always a constant but temporally variable magnetic field that can provide information, despite the possible lack of a distinct polarized light pattern due to its absorbance by the atmosphere. It makes more sense that these migratory monarchs, forced to orient over open water with few visible landmarks such as trees or buildings, are flying in tight circles and figure-8 patterns in an attempt to calibrate the magnetoreception mechanism—analogous to the figure-8 pattern some digital compasses require for calibration.

In summary, these results may provide preliminary evidence for the possible calibration and use of a monarch inclination magnetic compass that can be used under all local free-flying field conditions in which migrating monarch butterflies are proposed to be measuring the direction and inclination of the local magnetic field, in a manner analogous to the figure-8 pattern performed to calibrate digital compasses. This behavioral research reported here is but a single study of those conducted over variable environmental conditions over many years, which focuses on the vital pre-migratory orientation and flight behavior. This "orientation flight dance" may provide a key behavioral link explaining how migrating monarch butterflies using a time-compensated sun compass system could also integrate the biophysical input from the polarized UV sensitive dorsal rim area (DRA) and the cellular cryptochrome (CRY) system linked to the proposed inclination-based magnetic compass system residing in the distal end of the antennae. The orientation- and pre-migratory- "orientation flight dance" performed by migratory monarchs may calibrate and integrate the time-compensated sun compass, the plane-polarized light detection system in the DRA, as well as the magnetic compass of migratory monarchs.

Acknowledgment

Thanks to Brandy Van Zalen for her illustration of monarch spiraling flight behavior.

Literature Cited

Barrie, D. 2019. *In* Super Navigators: Exploring the wonders of how animals find their way. The Experiment, NY.

Baird, E., Byrne, M.J., Smolka, J., Warrant, E.J. and M. Dacke. 2012 The dung beetle dance: An orientation behavior? PLos ONE. Available from https://doi.org/10.1371/journal.pone.0030211.

Barta, A., and G. Horvath. 2004. Why is it advantageous for animals to detect celestial polarization in the ultraviolet? Skylight polarization under clouds and canopies is strongest in the UV. Journal of Theoretical Biology 226: 429–437.

Benvenuti, S., P. Dall'Antonia, and P.L Ioale. 1994. Migration pattern of the red admiral, *Vanessa atalanta* L. (Lepidoptera, Nymphalidae), in Italy. Italian Journal of Zoology 61(3): 343–351.

Brower, L.P. 1995. Understanding and misunderstanding the migration of the monarch butterfly (Nymphalidae) in North America: 1857–1995. Journal of the Lepidopterists Society 49: 304–385 (1995).

Brower, L.P. 2001. Department of Biology, Sweet Briar College; Personal communication. (TGLE unable to verify).

Dacke, M., Baird, E., Byrne, M., Scholtz, C.H., and E.J. Warrant. 2013. Dung beetles use the Milky Way for orientation. Current Biology 23(4): 298–300.

Douglas, M.M. 2019. Use of Spotted Knapweed/ Star Thistle (Asterales: Asteraceae) as the Primary Source of Nectar by early Migrating Monarch Butterflies (Lepidoptera: Nymphalidae) from Beaver Island, Michigan. The Great Lakes Entomologist 51(3–4): 35–41.

Gegear, R.J., Casselman, A., Waddell, S., and S.M. Reppert. 2008. Cryptochrome mediates light-dependent magnetosensitivity in *Drosophila.* Nature 454: 1014–1018. Doi: 10.1038/nature07183.

Gibo D.L. 1981. Altitudes attained by migrating *Danaus p. plexippus* (Lepidoptera: Danaidae), as reported by glider pilots. Canadian Journal of Zoology 59: 571–572.

Gibo, D.L. 1986. Flight Strategies of Migrating Monarch Butterflies (*Danaus plexippus* L.) in Southern Ontario. In: Danthanarayana W. (eds) Insect Flight, pp 172–184. Proceedings in Life Sciences. Springer, Berlin, Heidelberg. Available from https://doi.org/10.1007/978-3-642-71155-8_12.

Gibo D.L and M.J. Pallett. 1979. Soaring flight of monarch butterflies *Danaus plexippus* (Lepidoptera: Danaidae) during the late summer migration in southern Ontario. Canadian Journal of Zoology 57: 1393–1401.

Guerra, P.A., Gegear, R.J., Reppert, S.M. 2014. A magnetic compass aids monarch butterfly migration. Nature Communications 5:4164. Available from https://doi.org/10.1038/ncomms5164

Guilford, T. and G. K. Taylor. 2014. The sun compass revisited. Animal Behaviour 97: 135–143.

Heinze, S., and S.M. Reppert. 2011. Sun compass integration of skylight cues in migratory monarch butterflies. Neuron 69: (345–358).

Kanz J.E. 1977. The orientation of migrant and non-migrant monarch butterflies, *Danaus plexippus* (L.). Psyche 84(2): 120–141.

Kyriacou, C.P. 2009. Clocks, cryptochromes and monarch migrations. Journal of Biology 8: #55. Available from https://doi.org/10.1186/jbiol153.

Labhart, T., Baumann, F., and G.D. Bernard. 2009. Specialized ommatidia of the polarization-sensitive dorsal rim area in the eye of monarch butterflies have non-functional reflecting tapeta. Cell and Tissue Research 338: #391. Available from https://doi.org/10.1007/s00441-009-0886-7.

Merlin, C., Gegear, R.J., Reppert, S.M. 2009. Antennal circadian clocks coordinate sun compass orientation in migratory monarch butterflies. Science. 325: 1700–1704.

Mouritsen, H., Derbyshire, R., Stalleicken, J., Mouritsen, O., Frost, B.J., and D.R. Norris. 2013. An experimental displacement and over 50 years of tag-recoveries show that monarch butterflies are not true navigators. Proceedings of the National Academy of Sciences 110 (18): 7348–53.

National Geographic. 1976. Discovering the monarch's Mexican haven. 150 (2): 161–174.

Perez, S.M., O.R. Taylor, R. Jander. 1997. A sun compass in monarch butterflies. Nature 387: 29.

Preston, F. University of Kansas; unpublished correspondence. (TGLE unable to verify).

Reppert, S.M., Zhu, H., and R. White. 2004. Polarized light helps monarch butterflies navigate. Current Biology 14: 155–158.

Reppert, S.M., P.A. Guerra, and C. Merlin. 2016. Neurobiology of Monarch Butterfly Migration. Annual Review of Entomology 61: 25–42.

Stalleicken, J., Mukhida, M., Labhart, T., Wehner, R., Frost, B., and H. Mouritsen. 2005. Do monarch butterflies use polarized skylight for migratory orientation? Journal of Experimental Biology 208: 2399–2408.

Stalleicken, J., Labhart, T., and H. Mouritsen. 2006. Physiological characterization of the compound eye in monarch butterflies with focus on the dorsal rim area. Journal of Comparative Physiology 192 (3): 321–31.

Taylor, O.R. Lovett, J.P, Gibo, D.L., Weiser, E.L., Thogmartin, W.E., Semmens, D.J., Diffendorfer, J.E., Pleasants, J.M., Pecoraro, S.D., and R. Grundel. 2019. Is the timing, pace, and success of the monarch migration associated with sun angle? Frontiers in Ecology and Evolution 7: 442 Available from https://doi.org/10.3389/fevo.2019.00442

Weiner, J. 1983. Field Notes, A Flight of Butterflies. The Sciences 23: 57–58.

Zhu, H., Sauman, I., Yuan, Q., Casselman, A., Emery-Le, M., Emery P., and S.M. Reppert, 2008. Cryptochromes define a novel circadian clock mechanism in monarch butterflies that may underlie sun compass navigation. PLos Biol. 6, e4. Available from https://doi.org/10.1371/journal.pbio.0060004