# An experimental displacement and over 50 years of tag-recoveries show that monarch butterflies are not true navigators 

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#### Abstract

Monarch butterflies (Danaus plexippus) breeding in eastern North America are famous for their annual fall migration to their overwintering grounds in Mexico. However, the mechanisms they use to successfully reach these sites remain poorly understood. Here, we test whether monarchs are true navigators who can determine their location relative to their final destination using both a "compass" and a "map". Using flight simulators, we recorded the orientation of wild-caught monarchs in southwestern Ontario and found that individuals generally flew in a southwest direction toward the wintering grounds. When displaced $2,500 \mathrm{~km}$ to the west, the same individuals continued to fly in a general southwest direction, suggesting that monarchs use a simple vector-navigation strategy (i.e., use a specific compass bearing without compensating for displacement). Using over 5 decades of field data, we also show that the directional concentration and the angular SD of recoveries from tagged monarchs largely conformed to two mathematical models describing the directional distribution of migrants expected under a vector-navigation strategy. A third analysis of tagged recoveries shows that the increasing directionality of migration from north to south is largely because of the presence of geographic barriers that guide individuals toward overwintering sites. Our work suggests that monarchs breeding in eastern North America likely combine simple orientation mechanisms with geographic features that funnel them toward Mexican overwintering sites, a remarkable achievement considering that these butterflies weigh less than a gram and travel thousands of kilometers to a site they have never seen.


mark-recapture | clock-and-compass orientation | numerical model | analytical expectation model | longitudinal displacement

Migration is found in a wide variety of taxa around the globe (1) and the mechanisms animals use to travel such long distances have fascinated biologists for centuries $(2,3)$. True navigators not only know which direction to travel (orientation) but also their geographic location in relation to their goal $(3,4)$. In other words, they are able to detect both latitude and longitude using a bicoordinate navigation system (Fig. 1A). True navigation has been shown in a variety of taxa, including several species of birds (5-7), the eastern newt (Notophthalmus viridescens) (8), the loggerhead sea turtle (Caretta caretta) (9), and the spiny lobster (Panulirus argus) (10). Alternatively, some migrants may use a vector (or clock and compass) navigation strategy ( $4,5,11-16$ ), meaning that they do not possess a map but orient in an inherited direction using just a compass system and a clock or calendar (17, 18). Although migrants using vector navigation may be unable to correct their course en route (Fig. $1 A$ ), a simple compass system may be combined with additional orientation strategies eliciting fixed behaviors in response to specific situations, such as different wind conditions or landscape features. Such additional strategies or "emergency plans" can help animals to narrow in on a specific goal beyond the directedness that would be expected from their fundamental navigation strategy
alone, as has been described for migratory birds in western Europe (19, 20).

Each fall, millions of monarch butterflies (Danaus plexippus) in their first few weeks of life migrate as far as $4,000 \mathrm{~km}$ from their eastern North American breeding grounds to overwintering sites in the Neovolcanic Mountains west of Mexico City (12). Both vector navigation (21) and true navigation (22) have been suggested as strategies used by monarchs to find their overwintering sites. To examine these competing hypotheses, we displaced monarchs from Ontario to Alberta provinces in Canada during fall migration and used flight simulators $(23,24)$ to track their migratory direction. We also used over 5 decades of tagging-recovery data to estimate the directional concentration of monarch butterflies during fall migration, and then compared these results with two mathematical models describing the directional distribution of migrants expected under a simple vector-navigation strategy (16, 25). The simple vector-navigation strategy is very easy to model mathematically, because daily directions are equivalent to randomly picking a migratory direction from a normal-like circular distribution that is independent of the previous days' direction (16). In other words, the vector-navigation strategy is a directed random walk. Following the true-navigation hypothesis, we predicted (i) that individuals displaced during fall migration would shift their flight trajectories to compensate for displacement, and (ii) that recovery data from mark-recaptures would reveal a higher directional concentration than if monarchs used vector navigation (Fig. 1). Finally, we also used tagging-recovery data to examine the role of geographic barriers in influencing the directionality of monarch migration.

## Results

In flight simulators we successfully tested the orientation of 23 monarchs in both Ontario and Alberta provinces in Canada. As expected, the monarchs oriented toward southwest in Guelph, Ontario [mean direction $=213^{\circ}$, mean directedness $(r)=0.44$, $n=23, P=0.01,95 \%$ confidence interval $\left.(\mathrm{CI})=177^{\circ}-249^{\circ}\right]$ (Fig. 2). The mean direction of the monarchs was in very good agreement with the loxodrome (constant compass course) direction from Ontario to the Mexican overwintering grounds $\left(215^{\circ}\right)$. After being displaced by car 2,500 km westward to Calgary, Alberta (total: 4 d travel time), the same individual monarchs

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Fig. 1. Schematic drawing illustrating the principal differences between a simple vector-navigation (or clock-and-compass) strategy and true navigation. (A) When migratory animals using simple vector navigation (blue arrows) are displaced, they orient in the same mean direction at all locations because they have a compass but no map. True navigators (red arrows) have both compasses and a map and are therefore able to correct back toward the initial migratory route and/or the final goal when they are displaced (adapted from ref. 47). (B) Schematic diagrams showing hypothetical expected distributions of recaptured animals along a migratory route (each dot represents one individual) for vector navigators and true navigators assuming they were marked at the starting point (same as in $A$ ). Because true navigators are able to correct for orientation mistakes, they are predicted to show much less variability in their distribution than animals using a simple vector-navigation strategy.
showed a mean orientation of $244^{\circ}(r=0.44, n=23, P=0.01,95 \%$ $\mathrm{CI}=207^{\circ}-280^{\circ}$ ) (Fig. 2), which was not significantly different from their orientation in Ontario (Mardia-Watson-Wheeler test; $W=$ $0.467, P=0.79$ ). The $95 \%$ CI for the mean direction shown in Calgary included the predisplacement direction toward the Mexican wintering grounds $\left(215^{\circ}\right)$, but differed significantly $(P<0.01)$ from the loxodrome direction $\left(161^{\circ}\right)$ from Calgary to the Mexican overwintering sites (the $99 \%$ CI, $197^{\circ}-292^{\circ}$ did not include $161^{\circ}$ ). The orientation of the displaced individuals in Calgary strongly suggested that monarchs cannot adjust their migratory direction to account for the longitudinal displacement (Fig. 2). Very similar results were observed when all monarchs were included in the analysis regardless of whether an individual was tested at both sites or at just one site (Fig. S1).
Next, we compared the directionality derived from 422 tagged and recaptured monarchs collected between 1952 and 2004 with two models predicting directionality based on vector navigation. To standardize the analysis, all tagging locations were displaced to a mean tagging location and each of the associated recovery locations were displaced by the same direction and distance (Fig. 3 ). To compare these data with predictions from two models, we only used recoveries that were within 800 km of the mean tagging location because no major geographic features, such as oceans or mountains, prevented monarchs from being recaptured within this radius (Fig. 3).
Using a numerical model of the vector-navigation hypothesis already developed and successfully used to describe the distribution of ringing recoveries of migratory birds (25), we predicted how concentrated (measured as the length of the group mean vector, $r$ ) monarch recoveries should be if monarchs used a simple vector-navigation strategy (Fig. $4 A$ and SI Text). We compared these predictions with the $95 \%$ CIs for group mean vector $r$ values derived from the observed monarch recoveries and found that they included the $r$ value predicted by the model in 9 of the 11 distance intervals (Fig. 4A, Fig. S2, and Tables S1 and

S2), with the only exceptions occurring at the closest distances intervals (Fig. 4A).

We also compared the distribution of the monarch tag-recovery data with a mathematical expectation model already developed and successfully used to describe the distribution of ringing recoveries of two species of migratory birds (16). The model makes it possible to predict boundary curves around the ideal direction between the breeding ground and the winter quarters within which one would expect to find a specific percentage of all recoveries if monarchs use the simple vector-navigation strategy (Fig. 4B). The mathematical expectation calculations show that the boundary curves are parabolas. The predicted parabola that should bound approximately $68 \%$ of all recoveries ( $\pm 1 \mathrm{SD}$ ) is shown red in Fig. $4 B$ and was compared with the observed monarch recoveries. We found that $72 \%$ ( 8 of 11 ) of the $95 \%$ CIs for the angular SDs of the actual recoveries overlapped with the model predictions (Fig. 4B), suggesting that the monarchs likely use a vector-navigation strategy. Where the $95 \%$ CIs did not overlap with the predictions, the observed data suggested that individuals were less-well oriented than predicted by vector navigation, which would not be expected if monarchs were true navigators.

Given that our results provided evidence that monarchs only use simple compass mechanisms to migrate and are not true navigators, we then used tagging-recovery data to examine the influence of geographic features on monarch migration. As expected, as distance from the tagging site increased, the mean orientation shifted


Fig. 2. Circular plots depicting the individual and group mean orientations of monarch butterflies in Guelph, Ontario and in Calgary, Alberta in Canada. In Ontario, before displacement, the mean orientation was very close to the constant compass course direction (215 $)$ to the Mexican overwintering sites. The orientation following displacement to Calgary was not significantly different from the same butterflies' orientation in Ontario, and the 95\% and $99 \% \mathrm{Cls}$ for their mean orientation includes $215^{\circ}$ but not the $161^{\circ}$ direction from Calgary to their Mexican overwintering sites. Each dot at the circle periphery indicates the mean orientation of an individual monarch tested at the given site. The black arrow indicates the direction and length of the group mean vector at the given site. The lines flanking the group mean vectors define the $95 \%$ Cls. The dashed circles indicates the length of the group mean vector required for significance at the $5 \%$ and $1 \%$ level, respectively, according to the Rayleigh test. The large red arrows indicate the direction to the Mexican overwintering sites. (Inset) Monarch butterfly, image courtesy of H.M.


Fig. 3. Spatial distribution of monarch butterfly recoveries within eastern North America depicted relative to the mean tagging location. The black squares indicate where the tagged monarchs were recovered after they had migrated at least 20 km . All tagging sites were displaced to have origin at the small red square at the south end of Lake Erie, and each recovery location was then displaced the equivalent distance and direction. The black circles show radii of $500,1,000,1,500,2,000$, and $2,500 \mathrm{~km}$ around the average tagging location and the red circle indicates a migration radius of 800 km used for the model comparisons. The red square in Mexico is the position of the overwintering sites. Note that the apparent recoveries over the Atlantic Ocean and the Great Lakes stem from the displacement of tagging sites to the average tagging location and the equivalent displacement of recovery site. The red dashed line toward the north indicates where human population density drops to less than one person per square kilometer (48) and, thus, recoveries are unlikely. The map used is for illustrative purposes only and is a Lambert Conformal Conic Projection. The directions on the map are not directly comparable to the directions of the recoveries which are drawn in an $x$ - $/ y$-coordinate system where $0^{\circ}, 90^{\circ}, 180^{\circ}, 270^{\circ}$ indicates north, east, south, and west, respectively. The distances shown on the map, however, are in close agreement with the true recovery distances.
from south to southwest and the directedness (rvalue) of recoveries increased (SI Text, Fig. S2, and Table S1). To test whether the observed shift in orientation westward could be explained by geographic restrictions, we first examined the recovery distributions at 100-199 km, 300-399 km, and 500-699 km, but also excluded recoveries at each of these intervals that would have been highly unlikely at either $1,000-, 1,500-$, or $2000-\mathrm{km}$ distances because of geographic restrictions (Fig. 5). For all three distance intervals, the mean orientation shifted significantly westwards and the directional concentration of the recoveries increased significantly when these recovery data were excluded ( $95 \%$ CIs of the distributions with $1,500-$ or $2,000-\mathrm{km}$ recovery restrictions applied do not overlap with the original distributions) (Fig. 5 and Table S3). Importantly, the directional distributions after the geographic restrictions were imposed closely matched the actual directional distributions derived from monarch recoveries for distance intervals at $900-1,099 \mathrm{~km}$, $1,300-1,700 \mathrm{~km}$, and $1,800-2,200 \mathrm{~km}$ (Fig. 5 and Table S3), providing evidence that the change in orientation direction and part of the increase in directionality further away from the tagging site was because of the presence of geographic barriers.

## Discussion

The results of monarchs flown in flight simulators before and after a $2,500-\mathrm{km}$ westward displacement suggests that they are unable to correct for displacements and are, therefore, not true navigators.

The lack of true navigational abilities is further supported by our analyses of recapture data from free-flying tagged individuals. Recaptured monarchs showed a distribution that was in agreement with a simple vector-navigation strategy, and there was no evidence suggesting that free-flying monarchs were more concentrated in their distribution than expected from a vectornavigation strategy. If they had used true navigation, corrective orientation should have led to a much more directed distribution than that predicted by the vector-navigation models. Taken together, these results provide clear experimental and analytical evidence that monarch butterflies are not true navigators.

Because monarchs use a time-compensated sun compass that relies on an accurate circadian clock $(23,26)$, it is possible that the clock shift associated with the longitudinal displacement influenced orientation. However, individuals were continually exposed to natural light conditions during the 4 d between experiments in Ontario and Alberta, which should have allowed them to recalibrate their sun compass based on local conditions (for details, see Materials and Methods). Starlings (Sturnus vulgaris) and homing pigeons (Columba livia) have been shown to recalibrate their circadian rhythms in 3-6 d following a 6-h time shift $(27,28)$ and there is also evidence that monarchs are capable of this


Fig. 4. Comparison between observed monarch butterfly tagging recoveries and predictions from two models. (A) Comparison between the directional concentration ( $r$ ) obtained from recoveries of monarch butterflies within the first 800 km of migration (black dots) and $r$ values predicted by the numerical model (25) if migrants use a simple vector-navigation strategy (red line). The error bars show the $95 \% \mathrm{Cl}$ for each $r$ value. The bars indicate the number of recoveries in each distance interval. (B) Comparison of the distribution of tagging recoveries of migrating monarch butterflies with the predictions from the analytical expectation model based on the simple vector-navigation strategy (16). The tagging recoveries (small black dots) between 50 and 800 km from the tagging site are plotted as if each tagging site coincided with the origin of the Cartesian coordinate system. The model predicts that the red parabola should bound $\pm 1$ SD ( $68 \%$ ) of all recoveries, if monarchs use a simple vector-navigation strategy. Fifty-six percent of all recoveries fall within the red parabola. The blue dots indicate the deviation from the mean migratory direction within which $68 \%$ ( $\pm 1 \mathrm{SD}$ ) of the tagging recoveries are found at 11 different distance intervals $<800 \mathrm{~km}$. The black curved lines indicate the $95 \% \mathrm{Cls}$ for $\pm 1$ angular SD of the tagged monarch recoveries (for details see text).

low, however, recoveries within the $50-$ to $99-\mathrm{km}$ distance interval (the equivalent to the first migratory step in the model) (Fig. 4A) included butterflies that had traveled one to four migratory steps.
Both the numerical and analytical models suggest that monarch butterflies use a vector-navigation strategy. If there is any deviation from the vector-navigation strategy, it looks as if monarchs may even be less-well oriented than predicted if they use a vector-navigation strategy (Fig. 4). This result may appear surprising because vector navigation is the simplest conceivable strategy leading to the least concentrated distribution given the monarchs' known compass orientation capabilities (23, 24, 26). What we may see here are the effects of additional complicating factors. It could be that we overestimated the basic ability of monarchs to fly in their migratory direction $r_{\text {step }}(S I T e x t)$. However, this overestimation is unlikely because the directional concentration of $r=0.312$ found in monarchs recovered after 1 d (and used in the predictive modeling) is very low (equivalent to an angular SD of $\pm 87^{\circ}$, which is correspondingly very high). Given that insect migrants are known to be strongly influenced by prevailing winds $(29,30)$, another possibility is that monarchs may experience major changes in the large-scale wind system during their migration, and their mean flight direction could be altered systematically because of wind drift (SI Text and Fig. S3). Variation in the genetically encoded migratory direction between individuals $(31,32)$ could also have contributed to the lower than expected concentration. However, regardless of these possible effects, our results reject the true-navigation hypothesis.
We also show that geographic restrictions (Fig. 5, Fig. S2, and Tables S1 and S3) rather than corrections made en-route, as suggested by Rogg et al. (22), are likely to be responsible for the westward shift in orientation and contribute to the decrease in orientation scatter with increasing flight distance. Because geographic features prevent monarch recoveries in the east and southeast (Atlantic Ocean), in the south (Gulf of Mexico), and in the west (Rocky Mountains), recovery distributions at large distances from the tagging locations are biased toward the southwest (Fig. 5). The same bias may also explain the apparent significantly different mean orientation of monarchs originating in the western (southerly mean direction) and eastern (southwesterly mean direction) part of the breeding range, respectively (33).

If monarchs are not true navigators, how do they successfully complete this spectacular long-distance migration? One hypothesis, supported by our geographic restriction analysis, is that the geography of North America funnels migratory monarchs into southern Texas if they, in addition to their compass system, also use two simple additional orientation strategies. One such strategy may be to follow large mountain ranges in the direction most compatible with the monarchs' inherited migratory directions. Such behavior was observed by Calvert (21) within the Sierra Madre Oriental, where monarchs change their flight orientation to follow the direction of the intermountain valleys. Another additional strategy could be to follow coast lines upon reaching a large water body, as long as this is roughly compatible with the inherited migratory direction. Several authors (e.g., refs. 12 and 33-37) have observed this behavior. In addition, monarchs may wait for favorable wind conditions before they cross the water, as has been observed in other insects (30). By combining these additional strategies, monarchs from the whole breeding range could be funneled into southern Texas even if they use a quite simple and rather imprecise orientation strategy (21) (Figs. 3 and 5). This "funnel" would lead to an increase in directional concentration over distance from the tagging origin that is not an effect of either decreased likelihood of recovery or of true navigation; in effect, these barriers are providing the same "geographic restriction" as was done in our analysis, by preventing monarchs from flying in certain migratory orientations along the way. Finally, monarch autumn migration is supported by dominant northeasterly winds
that push the butterflies in westerly directions toward the Rocky Mountains and the Sierra Madre Oriental (Fig. S3).

The data, models, and analyses presented here are able to explain how monarchs find their way during the first two phases of their migration: (i) a "long-distance orientation phase" based on their time-compensated sun compass $(23,24,26)$ and a simple vector-navigation strategy, and (ii) a "narrowing-in phase" based on large-scale topographic features. However, our results do not explain the last "pinpointing-the-goal phase" where monarchs find the specific locations of the wintering sites. One intriguing possibility is that they use olfactory cues closer to their destination (35). Olfactory cues are used for navigation in other migratory animals, such as seabirds (38), green turtles (39), and homing pigeons (40), and recent sequencing of the monarch genome (41) has revealed monarch-specific expansions of olfactory receptors that could be associated with migration. Future analyses of the genome in conjunction with additional experimental tests related to geographic funneling and olfaction are needed to understand the last steps of this incredible migration.

## Materials and Methods

Field Experiment. Monarchs were captured in successional old fields in southern Ontario (Port Stanley: $42^{\circ} 39^{\prime} 50^{\prime \prime} \mathrm{N}, 81^{\circ} 10^{\prime} 12^{\prime \prime} \mathrm{W}, n=19$; the Long Point area: $42^{\circ} 46^{\prime} 08^{\prime \prime} \mathrm{N}, 80^{\circ} 32^{\prime} 48^{\prime \prime} \mathrm{W}$; $42^{\circ} 34^{\prime} 45^{\prime \prime} \mathrm{N}, 80^{\circ} 44^{\prime} 08^{\prime \prime} \mathrm{W}$; $42^{\circ} 32^{\prime}$ $54^{\prime \prime} \mathrm{N}, 80^{\circ} 02^{\prime} 57^{\prime \prime} \mathrm{W}, n=53$; Brantford: $\left.43^{\circ} 07^{\prime} 11^{\prime \prime} \mathrm{N}, 80^{\circ} 15^{\prime} 35^{\prime \prime} \mathrm{W}, n=4\right)$ between September 17 and September 25, 2011. At the time of capture, none of the monarchs displayed mating behavior and all were flying in a southwesterly direction, suggesting individuals were on migration. Captured monarchs were marked on the hind wing with a unique letter and number using a fine-tipped permanent marker and then housed in mesh insect houses, exposed to natural light, and fed a 1:4 mixture of sugar/honey and water.

To record migratory orientation, individuals were tethered with a tungsten rod, fastened to their backs with a 1:1 mixture of bee's wax and violin rosin, inside one of three cylindrical flight simulators $(23,24)$. These flight simulators consist of white, translucent plastic cylinders, which provided the monarchs with an approximately $120^{\circ}$ visual field of the sky but prevented them from seeing landmarks outside the barrel. The tests were conducted during the middle of the day when the sun was visible from inside the simulator $(23,24)$. The tungsten rod was connected to an optical encoder that sent timesequenced data on an individual's compass orientation at a rate of five samples per second to a laptop computer. Monarchs were able to fly in any orientation but could not move back and forth or up and down during flight.

Flight simulators were first set up in an open field in Guelph, Ontario (43 ${ }^{\circ}$ $31^{\prime} 44.7^{\prime \prime} \mathrm{N}, 80^{\circ} 14^{\prime} 03.8^{\prime \prime} \mathrm{W}$ ). To ensure that individuals were not attracted to visible landmarks that could bias their orientation, the simulators were set up in an area such that no trees or buildings were visible when the individual was inside the cylinder (23). Each monarch $(n=76)$ was flown inside the simulator for 15 min , up to five times per day, for a total of 8 d between September 20 and October 6, 2011. We did not conduct experiments on overcast days, as monarchs do not orient properly under heavy cloud cover (23). The monarchs and flight simulators were then transported to Calgary, Alberta ( $51^{\circ} 04^{\prime} 34.4^{\prime \prime} \mathrm{N}, 114^{\circ} 08^{\prime} 41.5^{\prime \prime} \mathrm{W}$ ) by car and all measurements were repeated on a subset of these individuals $(n=43)$ between October 11 and October 14, 2011. During the journey from Guelph to Calgary, which took 4 d , monarchs were kept under natural light conditions. We arrived in Calgary on the afternoon of April 10 and began the flight-simulator experiments in the afternoon of April 11, providing the monarchs enough time to recalibrate their compass. Most animals are known to adjust their inner clock to a new time-zone by approximately 1 time-zone hour per day (27, 28). Our transportation approximately $35^{\circ}$ west is equivalent to 2.3 time-zones, which the monarchs should thus easily have adapted to before they were retested.

For each 15-min flight, we calculated vector length ( $r$ ) using Oriana 4 statistical software (Kovach Computing Services). Vector length indicates the concentration of the data around the mean direction (range: $0-1$ ), with higher values indicating a higher concentration around the mean direction (42). Flights were not included if $r<0.2$, or if a graphic representation of the data did not suggest a unimodal distribution (Fig. S4). Because the flight simulators were aligned to magnetic North using a magnetic compass, we had to correct for magnetic declination by subtracting $10^{\circ}$ from each Ontario flight and adding $16^{\circ}$ for each Alberta flight.

Using second-order statistics, the mean orientation over two-to-five flights (mean $=3.5$ flights per individual; SD $=0.7$ ) was calculated for each individual at each location. We compared orientation between Ontario and

Alberta by the Mardia-Watson-Wheeler test and compared the orientation at both locations with the direction to the Mexican wintering grounds by considering the $95 \%$ and $99 \%$ Cls.

Tagging-Recovery Data. We compiled monarch recovery data collected between 1952 and 2004 from the following sources: Urquhart (43), Urquhart and Urquhart (44), Taylor (45), and Monarch Watch searchable tag-recovery database 2002-2004 (www.monarchwatch.org/tagmig/recoveries.htm). We limited our analyses to autumn monarchs tagged and recovered between $31^{\circ}$ and $50^{\circ}$ latitude and $70^{\circ}$ and $100^{\circ}$ longitude because these recoveries are less likely to be strongly effected by funneling effects. Butterflies that were recovered less than 50 km away ( 20 km away for 1-d recoveries) from the tagging location were excluded from the mathematical analyses to ensure that only migratory, nonforaging movements were analyzed ( $n=422$ ). Recoveries of artificially displaced monarchs were excluded from all analyses.

For each recovery, we calculated the loxodrome direction and distance between the tagging and the recovery site. Loxodrome routes are described by constant compass courses and are therefore in accordance with vector navigation. For graphic representation and modeling purposes, tagging sites were displaced to have their origin at the center of mass for all tagging locations, and recovery locations were displaced an equivalent distance in the same direction and distance. The average tagging location coincided with the southern tip of Lake Erie, $41^{\circ} 77^{\prime}$ latitude, $-82^{\circ} 63^{\prime}$ longitude. The recoveries were then plotted on a map of North America relative to this location. For comparison with the model predictions, we also grouped the recoveries in 15 distance intervals: $50-99 \mathrm{~km}, 100-149 \mathrm{~km}, \ldots, 350-399 \mathrm{~km}, 400-499 \mathrm{~km}$, $500-599 \mathrm{~km}, \ldots, 800-899 \mathrm{~km}, 900-1099 \mathrm{~km}, 1,100-1,499 \mathrm{~km}$, and 1,500$2,199 \mathrm{~km}$. For each of these distance intervals, we calculated the mean direction and the directional concentration of the recoveries: that is, the length of the mean vector ( $r_{n}$ values) (Table S2).

For the mean directions and $r$ values to be reliable measures of the natural directional distribution of migrants, recaptures should be equally likely in all directions. It can be seen in Fig. 3 that this is generally the case within the first $\sim 800 \mathrm{~km}$ of monarch migration, as no major geographic feature prevents monarch recaptures (red circle in Fig. 3). Beyond 800 km , recovery likelihoods decrease because of geographic barriers (e.g., the Atlantic Ocean). This decrease is the case if monarchs actually fly out over the ocean (without being recovered), if they correct their course based on a map sense, or if they change their direction and follow the coast line $(36,37)$. Because of these problems, we restricted the comparison between predicted and naturally occurring directional concentrations ( $r_{n}$ values) or angular SDs ( $\sigma_{\theta}$ ) to the distance intervals $<800 \mathrm{~km}$, where the $r$ values from the recoveries should reflect the true directional concentration of wild migrants.

To evaluate the uncertainty in the $r$ values derived from the tagging recoveries, we estimated the $95 \%$ Cls for $r$ in each distance interval using the bootstrap technique: the data were resampled with replacement in each given distance interval randomly 50,000 times. After sorting the resulting $r$ values in ascending order, the $r$ values at position $1,250(0.025 \times 50,000)$ and $48,751(0.975 \times 50,000+1)$ of the 50,000 iterations indicated the lower and upper limit of the $95 \% \mathrm{Cl}(25,46)$ for that distance interval (Table S1).

Numerical Model. To compare the predicted $r_{n}$ values for monarchs using vector navigation directly with the $r$ values found for each distance interval from tagging recoveries, we plotted the predicted $r_{n}$ values after $n$ migratory steps (Table S2) as a function of the mean distance traveled (see SI Text for generation of predicted $r_{n}$ values). Therefore, we calculated the net movement in the mean migratory direction during one migratory step as described by Mouritsen (25) assuming that monarchs fly, on average, $75 \mathrm{~km} / \mathrm{d}$ (Fig. 4A and SI Text). In Fig. 4A, we then plotted the $r$ values and $95 \% \mathrm{Cls}$ for the $r$ values found from the tagging recoveries in each distance interval as a function of distance (Table S1).

Analytical Expectation Model. In addition to this numeric approach, we also compared the monarch recovery data with the predictions of an analytical expectation model describing the directional distribution of migratory animals using a vector-navigation strategy (16). Mouritsen and Mouritsen (16) show that there is an extremely good agreement between the predictions from the analytical expectation model and the distribution of ringing recoveries of two free-flying migratory birds: European Robins, Erithacus rubecula, and Pied Flycatchers, Ficedula hypoleuca. The mathematical expectation model for monarchs is based on the same assumptions and done in the same way as it was done for migratory birds in Mouritsen and Mouritsen (16) except for the necessary parameter adjustment; that is, migratory step length is set to 75 km and the basic ability of the monarchs to fly in their migratory direction is described by an angular SD of $\sigma_{\theta}=1.525$ (SI Text) (16). The parameter $\sigma_{\theta}$ is
derived from $r_{\text {step }}=0.3124$ (value for 1 migratory step in Table S2) using the formula $\sigma_{\theta}=\sqrt{-2 \ln r}$ (42).

The theoretical expectation model predicts boundary curves around the ideal direction between the breeding ground and the winter quarters within which one would expect to find a specific percentage of all recoveries. The mathematical expectation calculations show that the boundary curves are parabolas. The predicted parabola that should bound $\sim 68 \%$ of all recoveries ( $\pm 1 \mathrm{SD}$ ) is shown red in Fig. 4B. To compare the expectation model predictions with the distribution of tag recoveries of free-flying monarchs, we plotted the tagging recoveries as if all tagging sites coincided with the origin of a Cartesian coordinate system in which the $y$ axis points into the mean migratory direction of all recoveries ( $\alpha=183^{\circ}$ ). Thus, in this coordinate system, the $y$ axis denotes the net migratory distance toward, and the $x$ axis denotes the perpendicular spread away from the mean migratory direction. We then used the recovery data to estimate the curve, which actually includes $68 \%$ of our tagging recoveries of wild migrating monarchs. This estimate was done by first transforming the $r$ values for each distance interval into an angular SD $\sigma_{\theta}$. Then, we converted the location of the mean vector $+\sigma_{\theta}$ and $-\sigma_{\theta}$ into $x$ and $y$ coordinates (for details, see ref. 16). The resulting points were connected by means of linear interpolation.

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Finally, the $95 \%$ Cls for $r$ in each distance interval were converted to $\sigma_{\theta}$ values and then to $x / y$ coordinates and plotted in the same graph to test if the predicted parabolic curve was significantly different from the actual recovery distribution.

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