Reply to Oberhauser et al.: The experimental evidence clearly shows that monarch butterflies are almost certainly not true navigators

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Oberhauser et al. (1) raise several concerns related to our recent PNAS paper (2), all of which we address here. To test for true navigation, one can use translocation experiments (3) and modeling (4). Truly navigating animals know where they are relative to their goal and thus can correct their orientation if they drift "off-course." A proper test of true navigation requires distant displacements, because the correction angles would be too small to be reliably detected using short displacements (2, 3, 5). Furthermore, per definition, one must move animals away from their migratory path (ref. 3 and others) to test for true navigation. Therefore, our displacement location was highly appropriate for testing true navigation. Reciprocal translocations are not necessary (ref. 3 and many others), and because monarchs do not occur regularly in Calgary, this was not possible.

As for the timing of our experiments: Mouritsen and Frost (5) successfully clock-shifted the light/dark cycle of one group of monarchs 6 h forward and another group 6 h backward over 5 d and observed the predicted shifts in compass orientation. Thus, our timing was not based solely on avian species. Furthermore, any putative map cues should not take days to detect. Thus, 4 d for a 2-h shift is perfectly adequate and, as stated in our report (2), a nonshifted clock would result in southward shifted orientation, the opposite of what we observed.

It is postulated that we only tested whether the recovery data conformed to the vector navigation strategy without testing the true navigation strategy. This claim is wrong. The prediction for true navigation is that significantly more than 68% of butterflies should be recovered within the predicted parabolic distribution (figure 1 combined with figure 4*B* in ref. 2). This situation was not the case and, therefore, we rejected the true navigation hypothesis.

Recoveries of monarchs tagged in the west indeed show a more southerly distribution than monarchs tagged in the east. However, as we address in our report, recovery likelihood limitations unavoidably lead to artifacts in the recovery distributions beyond some distance. If readers imagine the distance circles in figure 3 of ref. 2 moved to the eastern monarch's western range, because monarchs don't cross the Rockies, there can be no recoveries beyond ∼800–1,000 km toward the west. This fact alone will result in a more southerly mean recovery direction of western than eastern populations. However, this is not evidence "that the monarchs were actually flying in different directions," but rather suggests that previous authors have not properly considered the effects of recovery biases. Considerable evidence supports that insects, including monarchs, migrate primarily on days with favorable tail winds (6) (i.e., from the northeast).

Finally, we take exception to the claim that vector navigation is our "preferred hypothesis." Our study was clearly laid out to test two competing hypotheses and each test made predictions that could have supported either vector navigation or true navigation. The substantial scientific evidence presented in our paper, as well as parsimony, support the vector navigation hypothesis. The much more complex true navigation hypothesis should not be invoked when less-complex systems can account for the data. The data presented in our report (2) indeed make true navigation in monarchs highly unlikely.

1 Oberhauser KS, et al. (2013) Are monarch butterflies true navigators? The jury is still out. *Proc Natl Acad Sci USA*, 10.1073/pnas.1308369110.

2 Mouritsen H, et al. (2013) An experimental displacement and over 50 years of tag-recoveries show that monarch butterflies are not true navigators. *Proc Natl Acad Sci USA* 110(18): 7348–7353.

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5 Mouritsen H, Frost BJ (2002) Virtual migration in tethered flying monarch butterflies reveals their orientation mechanisms. *Proc Natl Acad Sci USA* 99(15):10162–10166.

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Are monarch butterflies true navigators? The jury is still out

Mouritsen et al. (1) used a flight-simulator experiment and recapture data to examine two hypotheses: whether monarchs use true navigation or a vector-navigation strategy. In the flight-simulator experiment, flight directions of wild-captured, migratory butterflies were assessed near their capture location, and then ∼2,500 km west. The authors' finding that monarchs flew southwest in both locations does not rule out true navigation because: (*i*) the experiment did not include reciprocal translocations and therefore lacked controls; (*ii*) experimental monarchs were moved to a location that an Ontario monarch would never traverse and where monarchs are only rarely found, and thus tell us little about monarchs following a normal migratory trajectory; and (*iii*) the experiment did not adequately allow for acclimation of a circadian clock or potential cognitive map to Alberta. Physiological—not chronological—time applies to insects, and the claim that animals "adjust their inner clock" by "approximately 1 time-zone hour per day" (1) is based solely on avian studies.

Mouritsen et al. (1) tested their conclusion from the displacement experiment using recapture data. Curiously, the authors only determined whether the data conformed to the vector-navigation strategy without testing a true-navigation strategy. Rejecting hypotheses that do not explain the data is as important as corroborating preferred hypotheses.

Tagging locations were displaced to a "mean tagging location," making analysis of a true-navigation strategy impossible, and ignoring the possibility that monarchs originating in different locations experience different conditions that might affect their long-distance flight ability. It is possible that some of the scatter in figure 4*B* of ref. 1 is explained by location; indeed, the fact that the data were more scattered than predicted by the vector model could be taken as support for an alternative hypothesis.

Mouritsen et al. (1) suggest that geography and wind funnel monarchs using southwest-vector navigation into southern Texas. The geography component of this suggestion might apply to monarchs flying from the mean location in this study or farther east. However, most monarchs originate farther to the west in the United States Corn Belt (2). There is no evidence that butterflies from this region move toward the Rockies (3), as suggested by Mouritsen et al.'s (1) model. The suggestion that "monarch autumn migration is supported by dominant northeasterly winds that push the butterflies in westerly directions" makes little sense. Indeed, figure S3 of ref. 1 shows dominant southwest, south, or southeast winds throughout most of the migrating range.

The single-minded focus on the vector-navigation hypothesis is illustrated by the authors' explanation of a previous finding (4) that monarchs in the western and eastern part of their breeding range fly south and southwest, respectively, as expected from a true-navigation strategy. Mouritsen et al. (1) state that this "apparent significantly different mean orientation" could be the result of a bias in recovery distributions, rejecting the more parsimonious explanation that the monarchs were actually flying in different directions.

We do not know whether monarchs have a true map sense or not, and the question of how they navigate from their northern breeding grounds to a relatively small wintering area remains unanswered. The results presented by Mouritsen et al. (1) do not rule out true navigation.

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