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Letter to the Editor

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Wherefore and Whither the Modeler: Understanding the Population Dynamics of Monarchs Will Require Integrative and Quantitative Techniques

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The editor (LAD) of the recent special feature on Eastern North American monarch butterflies (*Danaus plexippus*, Nymphalidae) and reviewers of these papers (including MLF and colleagues) enjoyed assessing new results, ideas, and hypotheses about this fascinating species. The feature included papers based on carefully collected citizen science data, and generated new ideas and hypotheses that have scientific merit and should not be summarily disregarded unless it is via the standard methods of refuting hypotheses and results in science. Of course, the first step in such a process is a critique that proposes alternative interpretations and a plan for future research. Pleasants et al. (2016) present such a critique, and they raise some very good points, some of which were alluded to by reviewers of the original special feature. The critique by Pleasants et al. (hereafter "feature critique") is a carefully crafted part of a healthy debate, which we would like to further by pointing out some aspects of their position that include too-hasty dismissals of hypotheses and inferences by several of the feature papers. Here, we present a brief criticism of this rebuttal to the monarch special feature summary, and suggest avenues by which we feel monarch studies could profitably move forward.

Before addressing each of the issues presented by the summary critique, it is useful to point out some attributes of the special feature summary by Davis and Dyer (2015; hereafter "feature summary"). The feature summary did not focus only on the three papers examined by the feature critique, rather it pointed to the strengths of all included papers, which combined citizen science data with new hypotheses about the complexities of population dynamics of migratory species. One of the main points of the feature summary was that more modeling and experiments are necessary and that "studies on immature stages, their host chemistry, their potential competitors, and their natural enemies should also contribute to understanding the future ecology and conservation of monarchs." The feature summary also pointed to new hypotheses about monarch population dynamics that are worth testing, and the best way to test these hypotheses will be to use more tools in the ecological toolbox—as argued in the feature summary, "the next steps should be to determine which stages are most critical, . . . and utilize established mathematical approaches to . . . [model] population dynamics." There is no reason to reject new hypotheses outright without utilizing these recommended next steps—any complex ecological phenomenon requires such rigor, especially if it is relevant to applied issues such as conservation of an important natural phenomenon.

It is also worth pointing out that the data generated on both sides of this issue would benefit from novel, mechanistic approaches. Some of the best papers published on monarchs are the careful mechanistic studies that demonstrate the importance of interactions with natural enemies (from Brower 1958 to Petschenka and Agrawal 2015)—these ecological studies rival any other studies on chemical mediation of multitrophic interactions. Thus, it is surprising that the population dynamics studies of monarchs have generally lagged behind the state of the art studies of insect populations (but see Yakabu et al. 2004). It is also surprising how little is known about the effects of natural enemies on population dynamics, despite the excellent research that has been published by the feature critique's authors (e.g., Oberhauser 2012). While the accomplishments of this group and others studying monarchs are to be lauded, especially in light of advances made in restoring milkweed hostplants and new ideas about how to accomplish this (e.g., Cutting and Tallamy 2015), it is time to expand the approaches beyond just counting eggs, caterpillars, or butterflies. The modern ecological toolbox is impressive and can include massive amounts of genomics or metabolomics data, computationally complex simulation models, and voluminous contributions from citizen scientists. These complement the long-used approaches that include observational studies, multiple temporal and spatial scales of manipulative experiments in the field and laboratory, simulation models, analytical models, and statistical models. The best studies combine several or all of these approaches and generate new hypotheses, tractable predictions, and insight into other systems and other research questions. None of the teams or contributors involved in this debate has used all of these approaches, but at least there was some synthesis that generated new hypotheses in the special feature article.

Summary of Criticisms From Pleasants et al.

The feature critique argues that the surveys in the studies for which there were no detectable declines in monarch populations were hindered by several major problems and related methodological and conceptual issues. The major problems identified were: 1) butterfly counts are not as effective as egg counts; 2) the feature summary ignores the evidence that loss of the monarch host plant is the key factor in monarch population declines; 3) counts were completed in nonagricultural habitats. Other minor methodological or conceptual issues are related to these problems and were identified as: 1) surveys were limited to one site per year; 2) surveys were skewed to earlier times in the year before peak egg production; 3) range restrictions of monarchs do not occur because they are excellent fliers. These are all good criticisms and should be taken as relevant caveats to any conclusions from the feature summary. However, to adequately reject a null hypothesis of no decline in summer populations, simple verbal models such as those presented in the critique are not sufficient.

Stage-Specific Population Dynamics

For all six criticisms above, it is preferable to utilize a combination of experiments and simulation or analytical models that would provide more information about the particulars of stage-specific, temporally and spatially explicit, or dispersal-dependent population dynamics of monarchs. Thus, for the first major criticism, that it is preferable to count eggs, it is actually preferable to have good quantitative data on all stages—and this should certainly be accomplished before rejecting a null hypothesis of no change in populations over long periods of time. Such an approach would allow one to understand the impacts of perturbations (such as herbicidal depletion of host plants) on each stage of monarch development. Without such approaches, it is difficult to conclude that counts of eggs are more relevant to long-term population dynamics than counts at any other stages (e.g., for forest pests, such as gypsy moths, this is well studied, Elkington and Liebhold 1990). The illustrative statement from the feature critique that counts of eggs are "equivalent to having watched the patch for adult butterflies every day for an entire week and is therefore far more comprehensive than adult surveys that record only part of a single day at each location" makes several assumptions about relationships between egg and adult stages that may or may not fit predictions from appropriate models or experiments that can reveal the actual relationships between egg densities and adult abundances at specific times.

Loss of Host Plant Versus Other Density-Dependent Effects

The second major criticism is the idea that the feature summary ignores "the evidence that the key driver of population decline is the massive loss of milkweeds." This imprecise language yields a variety of interpretations, but the use of the word "key" implies that some authors have completed key factor analysis or (preferably) a comprehensive alternative (Royama 1996), when in fact the monarch population effects of host plant decline versus other mortality factors have never been carefully quantified and compared, using any modern techniques in quantitative population biology. As Pleasants and Oberhauser (2012) acknowledge, "there are many factors that can affect survivorship from egg to L5 that have nothing to do with milkweed availability, such as predation and weather." It is very clear that there is a strong causal relationship between host plant availability and population dynamics of most Lepidoptera, but the feature critique confuses "key driver" with "a significant determinant" of the monarch population decline. One cannot conclude that any one factor is a key driver in population decline unless careful population studies, including life tables and models, have been completed. For example, a careful study on a not-so glamorous species of Lepidoptera, *Ochrogaster lunifer* Herrich-Schäffer (Lepidoptera: Thaumetopoeidae), shows that it is not regulated by resource availability alone but by natural enemies plus resource patches (Floater and Zalucki 1999).

To be clear, hypothesizing that there is an unknown mortality factor does not discount known mortality factors, and in the case of the special feature, the putative existence of unknown mortality factors provides interesting hypotheses to test that could refine our knowledge of what affects monarch populations across their migratory range. The special feature summary never suggested that milkweed recovery efforts should be abandoned or that less effort should be put into them. There are plenty of enhancements to the existing conservation efforts that could benefit from experimental or modeling approaches—for example, experiments demonstrate that simple garden planting approaches could be a very effective conservation tool for increasing monarch host plants (Cutting and Tallamy 2015).

Counts in Agricultural Versus Other Habitats

The third major point in the feature critique is that the counts are made in a variety of nonagricultural habitats despite the fact that agricultural fields accounted for much of the monarch egg production in the late 1990s. The feature critique authors argue that counts in nonagricultural habitats would have increased because of the increasing proportion of the population occupying nonagricultural habitats. This assumption is used to support the argument that the Eastern North America population of monarchs is declining because of a lack of increase of adults in nonagricultural habitats. The idea that declines in an insect population in one area will lead to increases in adjacent habitat certainly has theoretical merit, but can not be taken for granted, and certainly needs to be grounded in data for any particular system. What evidence is there that this happens for butterflies generally and for monarchs specifically? Such evidence must come from combining existing observations, experimental data, and modeling.

As an illustrative example of how one might use parameter estimates from citizen science data to address the hypothesis presented by the summary critique, we utilized a very simple, discrete time, Ricker equation model, with two generations. The first is the "overwintering" generation which breeds in the spring, and the second is the "summer" generation, which splits between two habitats (e.g., agricultural versus other habitats). The split between the two habitats can change over time, such that in the early years it might be 50:50 (or 85:15), and then over time more individuals move to the alternative habitat. There is also a general and linear decline in the population that is applied between the first and second generations, before they split into the two habitats for the second generation. This is a simple and qualitative investigation of the suggestion that a shift from agriculture to other habitats due to loss of host plants would make it difficult to measure a decline because the proportion of adults is increasing in the alternative habitats.

Using this approach, it is clear that one would always estimate a negative slope (fewer individuals observed over time), regardless of where the sampling is focused (Fig. 1). This is most clear for the first two scenarios presented in Fig. 1, which include no change in the distribution of individuals across habitats (left column) and a simple linear shift away from one habitat (middle column). The situation is slightly more complex when the shift away from one habitat is exponential (right column), but even there the overall decline can be detected in the recipient habitat, albeit more weakly (histogram in lower right of Fig. 1). This modest effort does not represent a test of the hypotheses presented by the summary critique, but it does suggest

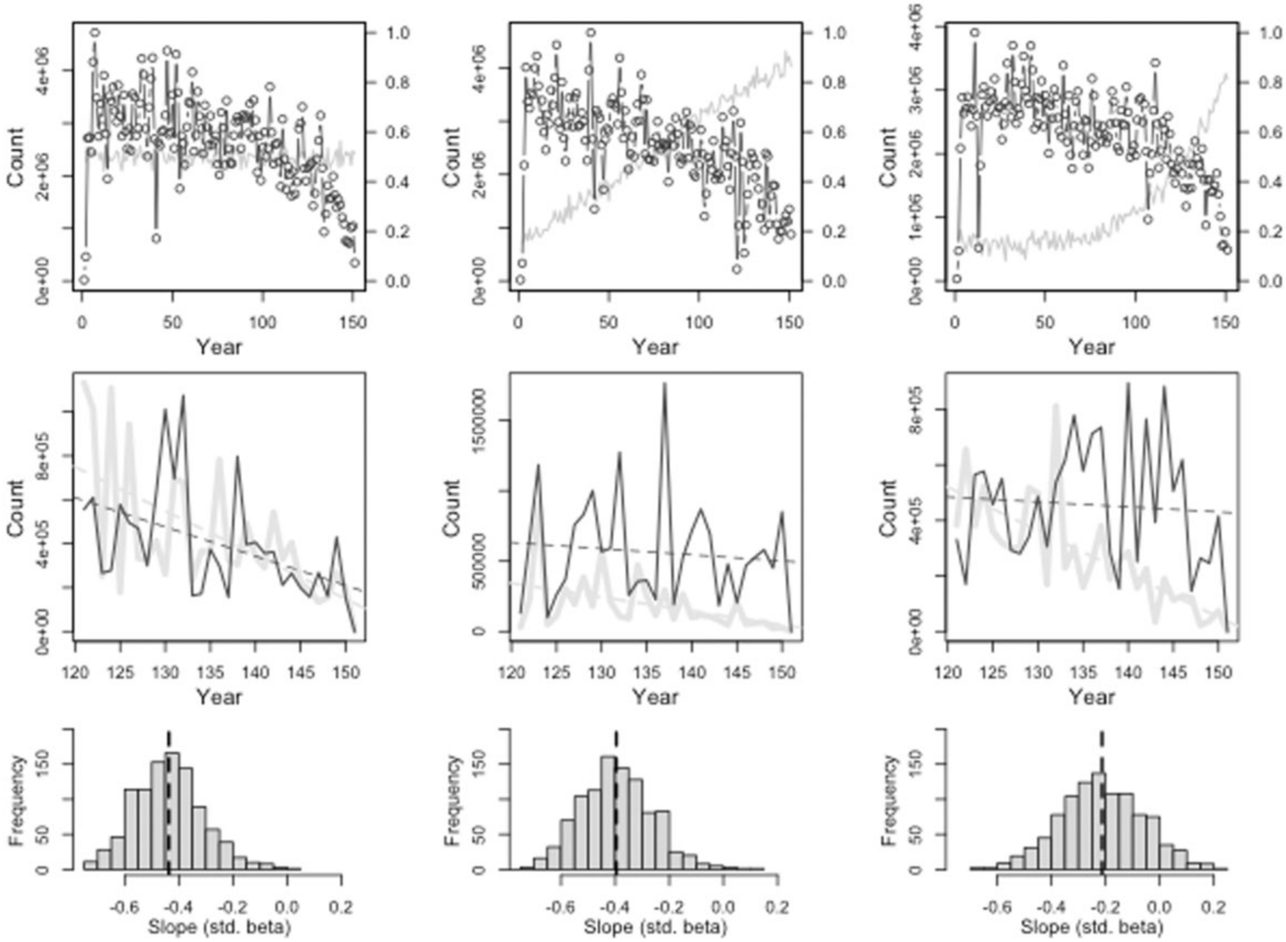

Fig. 1. Results from a discrete time, Ricker equation model with two generations. **Left column**: simulations from a population for which second generation production is evenly divided between two habitats. **Middle column**: simulations in which the fraction of the second generation in native habitat increases steadily over time. **Right column**: simulations in which the fraction in the native habitat increases abruptly in later years. For all columns, the graphs in the **top row** show the total count of individuals (across both generations) per year as the open circles connected by lines (corresponding to the left vertical axes) from example simulations; the light gray line in each graph is the fraction of production (of the second generation) in native habitat (corresponding to the right vertical axes). The **middle row** graphs show details from the last 30 years of example simulations: the light gray, thick lines, and matching dotted lines are counts of individuals in agricultural habitat; the dark, thin lines and matching dotted lines are counts in native habitat (dotted lines are from simple linear regressions across 30 years). The graphs in the **bottom rows** are histograms from 1,000 replicate simulations, showing the frequency of slopes, of counts in native habitat versus years, for the last 30 years (as shown in the examples in the middle row). Note that slopes are in units of standardized beta coefficients. The distributions of slopes tend to be negative because most simulations for all three scenarios (left, middle, and right columns) recovered a negative relationship between counts (in native habitat) and years. Vertical dotted lines on histograms mark the means of the distributions.

that certain assumptions should be more closely evaluated. And, although this model is indeed overly simple, it makes another point: the rate at which individuals shift between the two habitat classes over time matters a great deal (compare the middle and right columns), and without a knowledge of that rate we should tread cautiously when evaluating trends reported from any location. We have used a generic framework to investigate an idea, without tailoring specifics to the monarch butterfly. Researchers that have studied monarchs for decades could certainly generate a more realistic model that would be a direct test of hypotheses that have been raised.

Conclusions

Monarchs, their unique migratory patterns, and their associated communities of host plants, natural enemies, and competitors are global treasures worthy of strong conservation efforts. These efforts should be accompanied by rigorous ecological methods that yield effective predictions. What are the specific predictions for future monarch populations given different conservation scenarios? What are the goals of ecological research on monarchs? For example, it would be useful to predict how much any population parameter for monarchs would change in response to a unit change of host plant availability. How much milkweed is necessary to change overwintering densities with significant and relevant effect sizes? More important, with respect to the new hypotheses presented in the recent special feature, how would one predict the effects of monarch declines in agricultural habitats to affect observations in other natural or managed communities? Similarly, what predictions can we make about the effects of increasing parasitism rates due to neoclassical biological control? Without these sorts of predictions, one cannot summarily dismiss alternative hypotheses—it is alternative hypotheses and their tests that can either shift or strengthen an existing paradigm.

In sum, the criticisms provided by Pleasants et al. (2015) are important caveats to the inference that there is no decline in eastern North American monarch populations. Nevertheless, the original conclusions of the feature summary are still supported by the publications: 1) Despite clear declines in the Mexican overwintering numbers, reports from the eastern breeding grounds do not reflect that trend, and no thorough population studies have either explained the lack of connection between the two stages or made quantitative predictions into the future. 2) Host plant availability is important, but we do not yet know to what extent it is limiting, and other factors that contribute to population dynamics should be examined. 3) Citizen Science data are very useful and it is encouraging to see such data used by many different monarch research groups. However, these data should be combined with multiple approaches to understanding population biology and must yield predictions supported by quantitative data and modeling. Ensuring the persistence and abundance of the host plant makes good sense in the light of basic insect biology, but does the available evidence warrant a myopic conservation focus on host plants when other factors in a complex life cycle remain to be studied? What about maintaining diverse communities that include a more diverse mix of natural enemies and other indirect mutualists? Even though our knowledge of monarch movements at a continental scale is advanced and hard-won from decades of field work, we clearly have more to learn about fine-scale movements between habitats and perhaps also about perils the adults face on the longest flights. Finally, it is interesting to note that the western monarch migration is relatively understudied by comparison. For a major migratory insect species, the monarch is unusual in having two prominent migrations, and we can hope that future studies will take advantage of this natural replication for all manner of studies that will put the monarch at the forefront of both basic and applied ecology.

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