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## REPLY TO WEPPRICH AND RIES ET AL.: Alternative methods do not provide support for the contribution of GM crops to monarch declines

J. H. Boyle<sup>a</sup>, H. J. Dalgleish<sup>a</sup>, and J. R. Puzey<sup>a,1</sup>

We are pleased to see Wepprich (1) and Ries et al. (2) engaging with the museum records data presented in our original study (3). One of the strengths of digitized specimen data is that its portability allows precisely this kind of reanalysis.

The main point of our original study was that genetically modified (GM) crops were unlikely to be an important factor in monarch declines because milkweed and monarchs began their declines decades before the introduction of GM crops (3). Both Wepprich (1) and Ries et al. (2) propose alternative methodologies for using museum data to calculate monarch butterfly abundance over time, and both suggest that the currently available data are insufficient to estimate the true monarch abundance trends over the past century. If Wepprich (1) and Ries et al. (2) are correct that monarch abundance over the 20th century is still unknown (we discuss the specifics of their proposals below), this does not change our primary conclusion. Farming of GM crops has been proposed to impact monarch populations by the effect of GM-associated herbicides on the monarch's milkweed host plants (e.g., refs. 4-7). However, the decades-long declines we show across milkweed species, both on and off agricultural fields, do not support this hypothesis, and these declines in milkweeds are not questioned by either Wepprich (1) or Ries et al. (2). Milkweed trends are likely more robust than monarch trends for 2 reasons: First, there are about 30 times more milkweed specimen records than there are monarch records. Second, the question of what taxonomic group comprises an appropriate comparison group appears to be less fraught in plants, probably because botanists show less taxon specificity in collection methods than do entomologists. As long as milkweed declines begin decades before GM crops, this is strong evidence against the milkweed-limitation hypothesis driven by GM crops, regardless of when monarch declines began.

Turning to the specifics of their approaches, both Wepprich (1) and Ries et al. (2) argue that it is inappropriate to use the number of Lepidoptera specimens to estimate monarch collection effort. They note that Lepidoptera includes both butterflies and moths, 2 sets of organisms with very different life histories. We find this argument plausible, and the effect shown by Wepprich (1) is an important consideration for future studies using these kinds of data. In theory, many comparison groups are possible: smaller ones (e.g., a sister species, or members of the same genus) include species that are most similar to the focal species, sharing similar trait- and taxon-specific collection biases; but using a small number of species will produce more variable estimates of collection effort. Using larger comparison groups (class, phylum, etc.) will reduce this variance but will necessarily include less similar organisms. The proper comparison group is thus a tradeoff, and it is not possible to determine a "correct" or "appropriate" comparison group a priori. When possible, a good comparison group may be determined a posteriori by comparing abundance trends derived from specimen records data to those derived from data with better-understood biases, such as systematic monitoring. This has not been rigorously done for monarchs, for which systematic monitoring data are limited. It is worth noting that our approachnormalizing monarch records against Lepidopteracaptures the late 20th-century decline seen in, for example, surveys of abundance at the Mexican overwintering grounds (6, 8), while the approaches preferred by Wepprich (1) and Ries et al. (2) do not.

Ries et al. (2) further note that strong geographic biases exist in monarch museum records, and they propose limiting the monarch dataset to those specimens collected in particular regions and times of year that correlate well with monarch abundance at their overwintering grounds in recent years (9). We believe that this is an approach that may also prove useful in other species when their demography is well understood. We caution, however, that the well-parameterized models used in refs. 2 and 9 may not necessarily be useful across the 20th century.

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<sup>&</sup>lt;sup>a</sup>Department of Biology, College of William and Mary, Williamsburg, VA 23187

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<sup>&</sup>lt;sup>1</sup>To whom correspondence may be addressed. Email: jrpuzey@wm.edu.

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We agree with the conclusions of Wepprich (1) and Ries et al. (2) that monarch trends are sensitive to the methodology used to account for collection bias. In light of this, the monarch trend presented in our original study (3) may or may not represent the true trend in monarch abundance over the 20th century. While midcentury declines in milkweed are, by themselves, enough to provide evidence against the GM-crops hypothesis for monarch declines, having a good understanding of monarch trends over

this period would be very useful in determining what the major causes of monarch decline actually are. We therefore share the hope expressed by both Wepprich (1) and Ries et al. (2) that this trend will clarify as more museum records are digitized and methodological best practices for these data are determined. It is these conversations that will promote the latter, and so we are grateful to Wepprich (1) and Ries et al. (2) for engaging with our study.

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