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Title: Rapid decline in Western monarch butterflies leads to phenological and geographic Allee effects

One-Sentence Summary: After a population crash, Western monarch butterflies have a smaller breeding range, potentially exacerbating declines.

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Abstract: Allee effects are processes that become disrupted at low population sizes, causing further declines to eventual extinction. In 2018, the Western monarch butterfly population fell below the threshold that scientists predicted would trigger Allee effects. To identify components of Allee effects, we compare monarch performance before and after the 2018 crash. The population has expanded more slowly during spring and summer breeding and filled a smaller breeding range. Other components of the monarch life cycle have not changed after the crash. However, winter survival is much lower and wing sizes of overwintering monarchs are larger now than in the 20th century, suggesting higher mortality and stronger selection than in the past. Western monarchs now face new challenges to recover from low population size, in addition to the original causes of declines.

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Main text: When populations decline to very low densities, individuals can face additional distinct challenges, such as difficulty finding mates, that decrease population growth (*1*). This positive density dependence at low population size – called Allee effects – can drive extinctions and prevent invasions (*2*). Documenting and understanding Allee effects is important both for conservation biology and for broader ecological theory. However, observations of Allee effects in nature are rare; to observe Allee effects in a natural population, the population must already be so small that it is below the density (the "quasi-extinction threshold") when Allee effects occur. As Allee effects lead to further population decline, there is only a very narrow window of time when Allee effects are observable before a population is extirpated (*3*).

Western monarch butterflies have rapidly declined in the past forty years (Fig 1). Overwintering population estimates were millions of butterflies in the 20th century, but the population declined by an average of 6% per year through 2016 (*4*). Causes of these declines include agricultural intensification, loss of breeding and overwintering sites (many of which are not protected) (*5*), and climate (*6*). In 2017 we predicted that Allee effects would occur if the Western monarch population fell below 30,000 overwintering individuals (*4*). The following season there was a massive decline, and the population dipped below that quasi-extinction threshold at Thanksgiving 2018 (27,721 overwintering individuals) (*7*). Since then, as predicted, the population has declined even more dramatically. In Thanksgiving 2020, there were only 1,914 overwintering individuals, and by New Years Day this had fallen to 1,039.

Following the Thanksgiving 2018 crash, we measured demographic processes that could contribute to Allee effects (*8*) (Fig. 1B, Materials and Methods). We compared these measures to previously published estimates, categorizing data into three eras: "historical", before 2000 when there were millions of monarchs; "recent past", from 2000-2017 when monarchs were in the hundreds of thousands; and "current", from 2018-2020 when winter counts were below the

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quasi-extinction threshold (Fig. 1A). Differences between the current era and recent past indicate Allee effects. Differences between the historic era and current or recent past indicate possible drivers of long-term declines.

There were no Allee effects in overwinter survival (Fig. 2A), body mass (Fig. 2B), wing length (Fig. 2C), or mating success (Fig. 2D) (see also Supplementary Text). In contrast, there were strong Allee effects in breeding season range. The historic and recent past eras had similar breeding range dynamics (Fig. 3B), with the 0.9 quantile of the population traveling up to 1070 and 1003 kilometers from overwintering sites, respectively (Fig. 2F). The 0.9 quantile represents the boundary between the 10% of monarchs that are most distant and the remaining 90%, and acts a measure of range expansion that is robust to outliers. Since the population dropped below the quasi-extinction threshold, this maximum distance traveled fell by more than 50%, to 491 kilometers. Western monarch butterflies also experienced a shorter breeding season in the current era, with monarch expansion stopping almost a week earlier (Fig. 3C). Further, since falling below the quasi-extinction threshold, monarchs have reached regions within their extant breeding grounds up to two months later (Fig 3D,E).

Across ecological systems, shifts in phenology are one of the most conspicuous effects of climate change (*9*). These shifts can lead to temporal mismatches between interacting species, including insects and their hosts or nectar sources (*10*). The shift in monarch phenology reported here differs dramatically from typical climate responses; the average phenological shift across 203 species in the Northern hemisphere is 2.8 days per decade (*9*), while between recent past and current eras, monarch breeding range phenology delayed between 3.6 and 60.2 days depending on distance from overwintering sites. Given the general shift of plant leaf out occurring earlier in recent years in response to climate change (*11*), our findings suggest that later generations of monarch butterflies are now experiencing very different life stages ("phenophases") of both their

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milkweed hostplants and their nectar sources. This shift is especially concerning because monarch caterpillar survival and growth depend strongly on their phenology in relation to host plants and predators (*12*).

Although not Allee effects, there were two notable changes between the historic and current eras: a reduction in overwintering survival (Fig. 2A), and an increase in body size and particularly wing length (Fig. 2B and C). Reduced winter survival may have contributed to the long-term decline of the Western monarch butterfly. This could reflect reduced overwintering habitat quality or climate-change disruption of overwintering behavior (*13*), or factors reducing butterfly conditions in the summer breeding ground (*6*). Larger body size and wing length (measured in February) may indicate biased overwintering survival, with smaller individuals dying at high rates through the winter. Alternately, monarchs may have experienced strong selection for higher movement capabilities across the last few decades. (*14*) hypothesized that the Central Valley of California (immediately east of many overwintering sites) has been substantially degraded as a monarch habitat, and detected pesticides on all milkweeds sampled there. If selection favored individuals that flew past the Central Valley, populations may have evolved increased wing size, which is associated with long-range movement in monarchs (*15*).

Our results emphasize the frightening potential of Allee effects. Once populations become small, new problems arise. In this case, the crash of the migratory monarch population led to changes in breeding season range that differ dramatically from either the history or recent eras. This Allee effect led to massive phenological shifts in parts of the butterfly's range. To recover Western monarch butterflies, conservation efforts must now address both the original causes of declines and the current consequences of Allee effects.

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Acknowledgments:

Leone Brown, Norah Warchola, and Chelsea Thomas assisted with the field surveys and extraction of previously published results; Emma Pelton and Stephanie McKnight provided guidance and insight in working with Xerces data. California State Parks, California Department of Fish and Game and USFWS were all important in securing permits to work with monarch butterflies at Pismo Beach State Park. California State Parks generously provided use of their greenhouse to conduct studies on reproductive biology of female monarchs at Pismo Beach, including Danielle Bronson, Stephanie Little and Ronnie Glick. Cheryl Powers, a docent volunteering at the Pismo Beach site, generously opened her home to us to support lodging needs by staff throughout February 2019, and Shore Cliff Hotel donated additional lodging during the peak activity period. We are grateful to Marm Kilpatrick and Sarina Jepsen for discussions during planning and interpretation of data.

Funding:

Funding for this work was contributed by CREOi (Conservation Research Education and Opportunities International), WSU Vancouver Fund for Ecology and Conservation of Northwest Butterflies and Their Habitats as well as private donors to WSU and UC Santa Cruz, and the National Science Foundation DEB 1920834.

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Formal Analysis: CBE

Funding acquisition: CBS, EEC

Investigation: CBS, EEC

Methodology: CBE, EEC

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Software: CBE

Supervision: CBS, EEC

Visualization: CBE

Writing – original draft: CBE

Writing – review & editing: CBE, CBS, EEC

Competing interests: Authors declare they have no competing interests.

Data and materials availability: All data and code will be available on the data repository Dryad.

Supplementary Materials

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Materials and Methods

Supplementary Text

Figs. S1 to S6

Table S1

Movie S1

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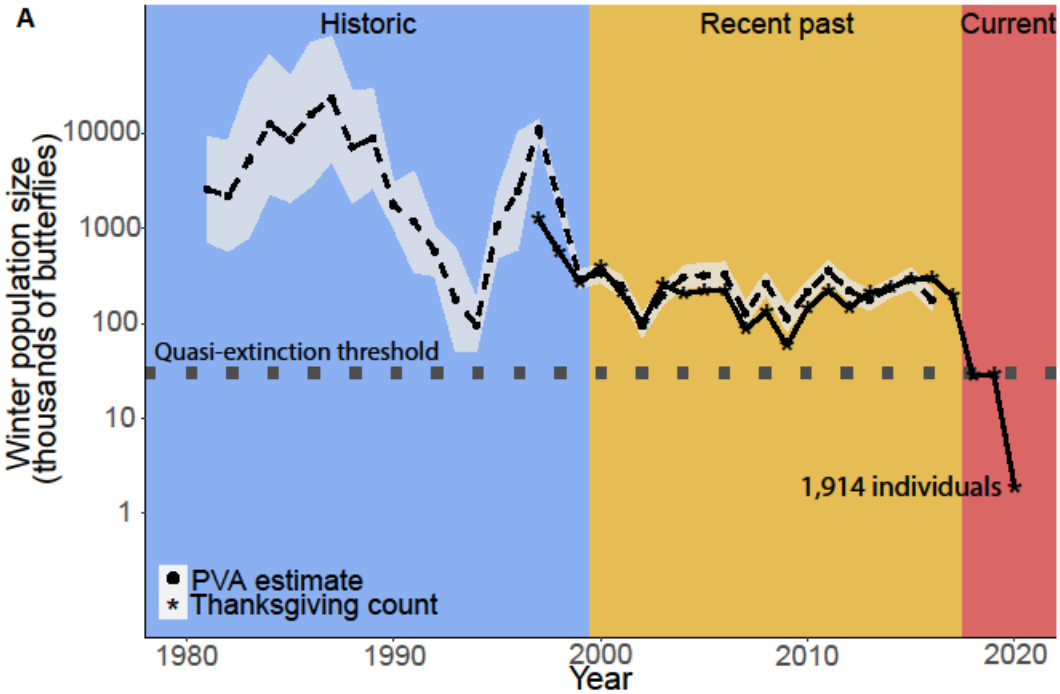
A



B

Hypothesized component Allee effect	Examples	Monarch performance metric tested	Allee effect
Reduced mating success	(*16*)	% mated	*none*
		eggs per day	*none*
Reduced group facilitation	(*17*)	winter survival	*none*
		body mass	*none*
		wing length	*none*
Density dependent movement	(*3, 18*)	maximum range	~50% reduced breeding season range
		phenology	Massive delays scaling with distance from overwintering sites

Fig. 1. Western monarch populations have collapsed, and Allee effects may disrupt their life cycle and breeding season range. (**A**) Monarch populations have fallen dramatically from the 1900s to today; in winter 2017/2018 populations fell below the quasi-extinction threshold (dotted line). Estimated population abundances using MARSS state-space model (dashed) and Xerces Thanksgiving counts (solid); note log scale. Plot colored by eras used in analyses (**B**) Allee effects may disrupt aspects of the life cycle and breeding season range of Western monarchs now that their population size is below the quasi-extinction threshold. Allee effects

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occurred for expansion into breeding season range but not for mating or survival; the population expanded half as far and arrived up to two months later.

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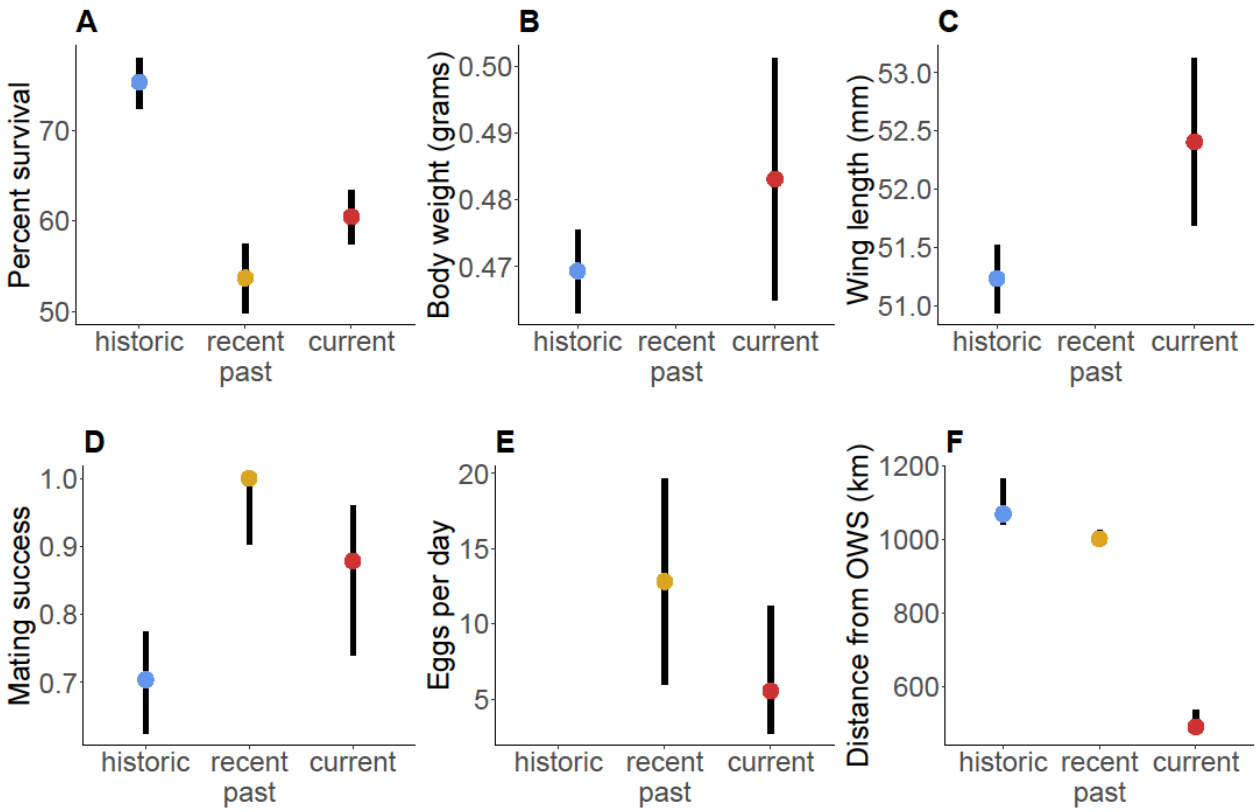

Fig. 2. Allee effects detected only for breeding season range. Comparison across eras for (**A**) wintering survival (estimated for 6-week timespan), (**B**) body mass, (**C**) wing length, (**D**) mating success as measured by proportion of females mated, (**E**) fecundity, and (**F**) breeding season range as measured by maximum distance from overwintering sites. Points correspond to estimated values before 2000 ("historic"), from 2001-2017 ("recent past"), and from 2018-2020 ("current") when the population has been below the quasi-extinction threshold. In some cases (B, C, E), there were no published data available to compare with one of either the historic or recent past eras. Bars represent 84% confidence intervals (nonoverlapping bars represent significant differences) (*19*). Allee effects imply a decrease in performance for very small populations; for the Western monarch butterfly, this means a change from the recent past to the current era. Only breeding season range (F) shows signs of an Allee effect.

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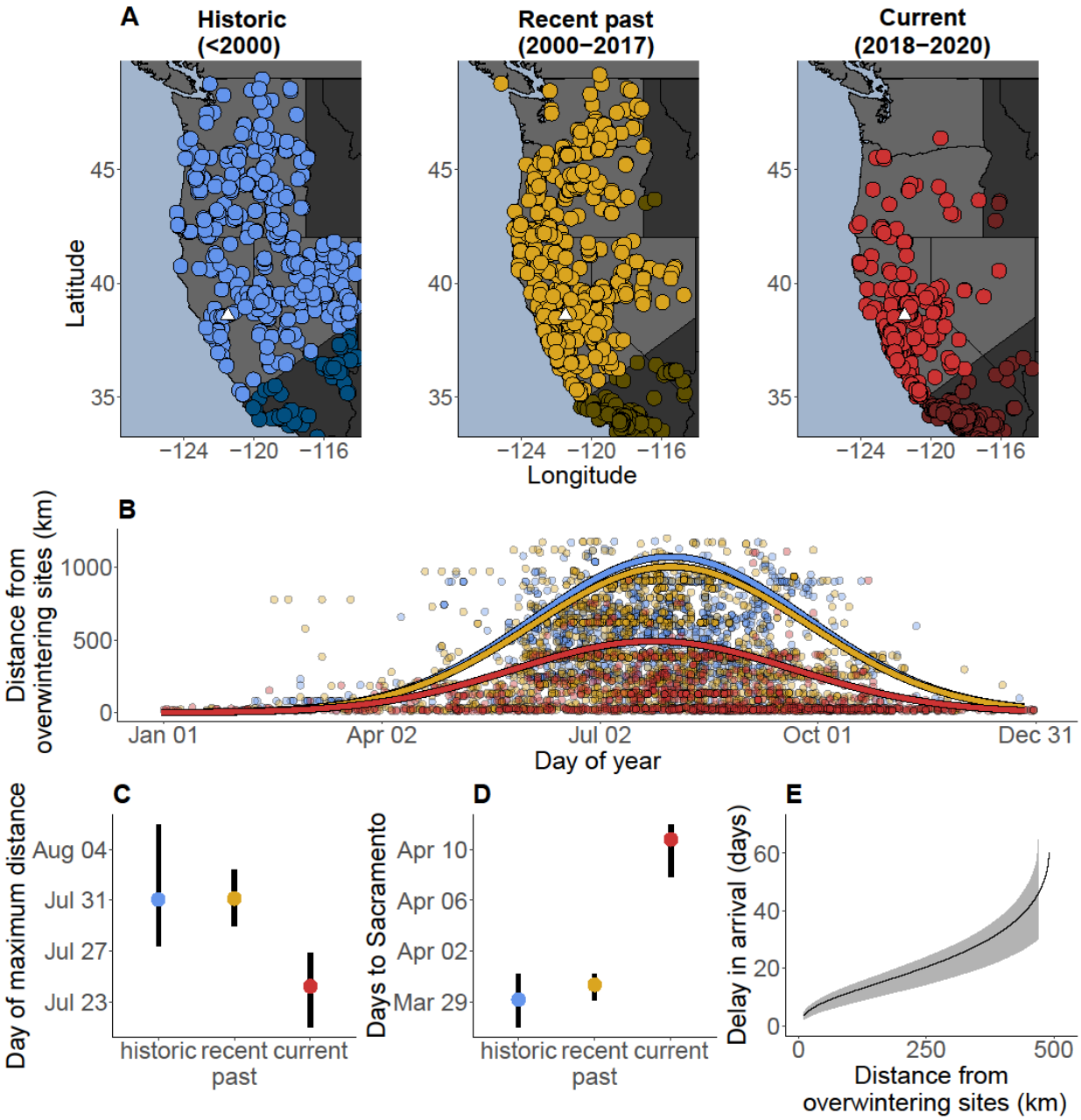

Fig. 3. Breeding season range expansion has shifted dramatically since the monarch population fell below the quasi-extinction threshold. (**A**) observations from iNaturalist (*20*) and the Western Monarch Milkweed Mapper (21) through August 1 show fewer observations in OR and WA in the current era. Shaded southern CA and NV excluded to avoid resident populations. White triangles show Sacramento, CA (see D). (**B**) Fitted curves of the 0.9 quantile

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of the distance from observations to the nearest overwintering site (a measure of expansion into the summer breeding range) show similar patterns between historic era and recent past, but substantial changes in the current era. (**C**) Comparisons across eras of day of the maximum distance (ie day of peak in (B)) show monarchs now leave their summer breeding range sooner. (**D**) Days for the 0.9 quantile to reach 100 km from the nearest overwintering site, corresponding to the time monarchs would first reach Sacramento, CA; arrival day is much later in current era than in recent past or historical era. (**E**) Phenology in the current era is delayed compared to the recent past, with more delay further from overwintering sites. Black line: difference in arrival of 0.9 quantile in current era compared to recent past. In C&D, bars show 84% confidence intervals calculated via bootstrapping; in E, gray region shows 95% CI.