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

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Abstract: Allee effects are processes that become disrupted at low population sizes, causing further declines to eventual extinction. Identifying Allee effects in natural populations is important for both ecological theory and conservation efforts but challenging because populations typically only experience them briefly before collapsing. In 2018, the Western monarch butterfly population fell below the threshold that scientists predicted would trigger Allee effects. Here we show that since 2018, the Western monarch population has expanded more slowly during spring and summer breeding and filled a smaller breeding range. Other aspects of the monarch life cycle (winter survival, fecundity, morphology) have not declined 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 selection for increased dispersal in recent decades. Delayed arrival to parts of the Western monarch breeding range is a novel Allee effect, which could lead to temporal mismatches between monarchs and their and host plants.

Keywords: *Western monarch butterfly; Danaus plexippus; Allee effects; phenology; population viability; surprises*

Introduction

When populations decline to very low densities, individuals can face additional distinct challenges, such as difficulty finding mates, that decrease population growth (Stephens et al. 1999). These challenges can cause even more rapid declines, possibly contributing to an extinction vortex (Gilpin & Soulé 1986*)*. Positive density dependence at low population size – known as Allee effects – can prevent invasions as well as drive extinctions (Courchamp et al. 1999*)*. Documenting and understanding Allee effects is important both for conservation biology and for broader ecological theory. However, there is only a very narrow window of time when Allee effects are observable before a population is extirpated.

Western monarch butterflies have rapidly declined in the past forty years. Overwintering population estimates were millions of butterflies in the 20th century, but the population declined by an average of 6% per year through 2016 (Schultz et al. 2017). In 2017 we predicted that Allee effects would occur if the Western monarch population fell below 30,000 butterflies (Schultz et al. 2017). The following spring there was a massive decline, and the population dipped below that threshold at Thanksgiving 2018 (27,721 butterflies, Xerces Society 2021).

Here, we test for Allee effects in a range of demographic processes. We measured two broad categories of monarch performance following the 2018 crash: traits of overwintering monarch butterflies, and rates of population expansion during the summer breeding season. We compare these measurements to comparable measures of performance from studies done when monarch populations were higher. We categorized time periods 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 hypothesized threshold for Allee effects. 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.

Methods:

Overwintering monarch butterflies: In February 2019, we collected 35 female monarchs near the overwintering site at Pismo Beach State Park. We measured wing length and body size, used the palpitation method to evaluate which had been mated (Van Hook 1997), and measured daily fecundity of caged individuals (see detailed methods in Appendix S1). We analyzed previously published Thanksgiving and New Years Count data to estimate overwinter survival (Xerces Society 2021). We identified studies with comparable demographic measures from before the 2018 crash (overwinter survival: Tuskes & Brower 1978; body mass: Chaplin and Wells 1982, Leong et al. 1995; wing size: Beall 1946, Tuskes and Brower 1978, Leong et al. 1995; fecundity: Leong et al. 1995, 2012). For each performance metric, we either obtained estimates directly or through back-calculation with error propagation (see detailed methods in Appendix S1).

Summer population expansion: To characterize the yearly population expansion into the summer breeding grounds, we used community-science observations of monarchs available through Xerces and iNaturalist (Western Monarch and Milkweed Occurrence database 2018, GBIF.org 2020). These data included monarch observations across western North America from the late 1800s through 2020, but required careful attention to address its ad-hoc and presence-only nature. We used quantile regression (Cade and Noon 2003) to fit distance from overwintering sites through time as a Gaussian curve (Edwards and Crone 2021) (Figure 2B). We used the 0.9 quantile, which represents the boundary between the 10% of monarchs that were most distant and the remaining 90%, as a measure of breeding season range size that is robust to

outliers (we find similar patterns for other quantiles; see Figure S2). From fitted curves for each era, we estimated the maximum (i.e., 90% quantile) distance from overwintering sites (a measure of the size of the breeding range), the day of maximum distance from overwintering sites (a measure of phenology that indicates the shift from population expansion to contraction), and the day the 90% quantile first reached 100 kilometers (a different measure of phenology that indicates how quickly they arrived in summer breeding areas away from the coast).

Results and Discussion

There were no Allee effects in overwinter survival (Fig. 1A), body mass (Fig. 1B), wing length (Fig. 1C), or mating success (Fig. 1D). In contrast, there were strong Allee effects in breeding range. The historic and recent past eras had similar breeding ranges (Fig. 2B, Movie S1), with the 0.9 quantile of the population expanding to up to 1070 and 1003 kilometers from overwintering sites, respectively (Fig. 2F). Starting in 2018, this maximum distance traveled fell by more than 50%, to 491 kilometers. Western monarchs also experienced a shorter breeding season after 2018: summer population expansion stopped almost a week earlier (Fig. 2C). Further, in the current era, monarchs have reached regions within their extant breeding grounds up to two months later (Fig 2D,E).

Shifts in phenology (timing of life history events) are a conspicuous effect of climate change (Parmesan 2007), and can lead to temporal mismatches between interacting species, including insects and their hosts (Forrest 2016). Changes in monarch phenology reported here differ dramatically from typical climate responses; the average phenological shift across 203 species in the Northern hemisphere is 2.8 days/decade (Parmesan 2007), while between recent past and current eras, monarch arrival times were delayed between 3.6 and 60.2 days, depending on distance from overwintering sites. Our findings suggest that later generations of monarchs are

now experiencing very different life stages ("phenophases") of their milkweed hostplants. This shift is especially concerning because monarch caterpillar survival and growth strongly depend on their phenology in relation to host plants and predators (Yang and Cenzer 2020).

Although not Allee effects, there were two notable changes between the historic and current eras: a reduction in overwintering survival (Fig. 1A), and an increase in wing length (Fig. 1C). Reduced winter survival may have contributed to the long-term decline of Western monarchs. This reduction could reflect reduced habitat quality, climate-driven disruption of overwintering behavior, or reduced butterfly conditions in the summer breeding ground (Crone et al. 2019). Larger body size and wing length (measured in February) may indicate biased overwintering survival, with smaller individuals dying at higher rates. Alternately, (Halsch et al 2020) hypothesized that the Central Valley of California (immediately east of many overwintering sites) has been substantially degraded as monarch habitat. If selection favored individuals that flew past the Central Valley, the Western monarch population may have evolved increased wing size, which is associated with long-range movement (Yang et al. 2016).

The Allee effects we found were not the ones we expected (Schultz et al. 2017), highlighting the ways in which dynamics become surprising in small populations. Similarly, while finalizing this manuscript, early reports indicate there will likely be 200,000 or more individuals in the 2021 Thanksgiving count -- far more than in 2020, but far less than the millions of individuals of the late 20th century. Preliminary analyses suggest that the Western monarch breeding range in Summer 2021 was not a return to the fast expansion and larger breeding range of the recent past or historic eras (Fig. 3). Instead, the population increased this year *in spite of* reduced breeding season range. This recent change highlights that we do not know whether reduced colonization of the breeding range is a cause of population declines, or

simply a consequence of unprecedentedly low population sizes. As populations approach extinction, population growth rates of many animal species become more variable among years (Fagan and Holmes 2006). One important lesson from this system is that we should expect surprises in population dynamics as species enter uncharted conditions. It is easy to consider uncharted conditions in terms of the external environment, but it is equally important to recognize the importance of how populations respond to changes in their own abundance, especially to unprecedentedly low population sizes.

Data availability: All custom scripts and data that support the findings of this study will be deposited to Dryad prior to final publication.

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 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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Funding acquisition: CBS, EEC

Investigation: CBS, EEC

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Competing interests: Authors declare they have no competing interests.

Supplemental Information is available for this paper. Correspondences and requests for materials should be addressed to CBE.

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Fig. 1. Comparison across eras for (**A**) winter survival (from Thanksgiving to New Year's Day), (**B**) body mass, (**C**) wing length, (**D**) 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 was below the hypothesized Allee effect threshold. In some cases (B, C, E), no published data was available to for either the historic or recent past eras. Bars represent 84% confidence intervals (nonoverlapping bars represent significant differences) (13). 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.

Fig. 2. (**A**) Raw observation data 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 of the distance from observations to the nearest overwintering site (a measure of expansion into the summer breeding range) show substantial reduction in the current era, even after correcting for changes in abundance. (**C**) Comparisons across eras of day of the maximum distance (i.e. 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; 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; in E, gray region shows 95% CI.

Fig. 3 High numbers of monarch observations allow us to the past seven years individually. (A-C) Breeding range measures analogous to Fig. 2F, Fig. 3C-D. Bars show 84% CI. (A) and (C) show clear differences between eras that reflect the patterns reported in the main text, although monarchs had particularly late phenology in 2019. 2021 estimates were fit using observations through October 27, 2021, and were not part of the main analyses. These preliminary estimates show that despite higher counts in Thanksgiving 2021, the spatial Allee effect still occurred during the preceding summer.

Figure 1

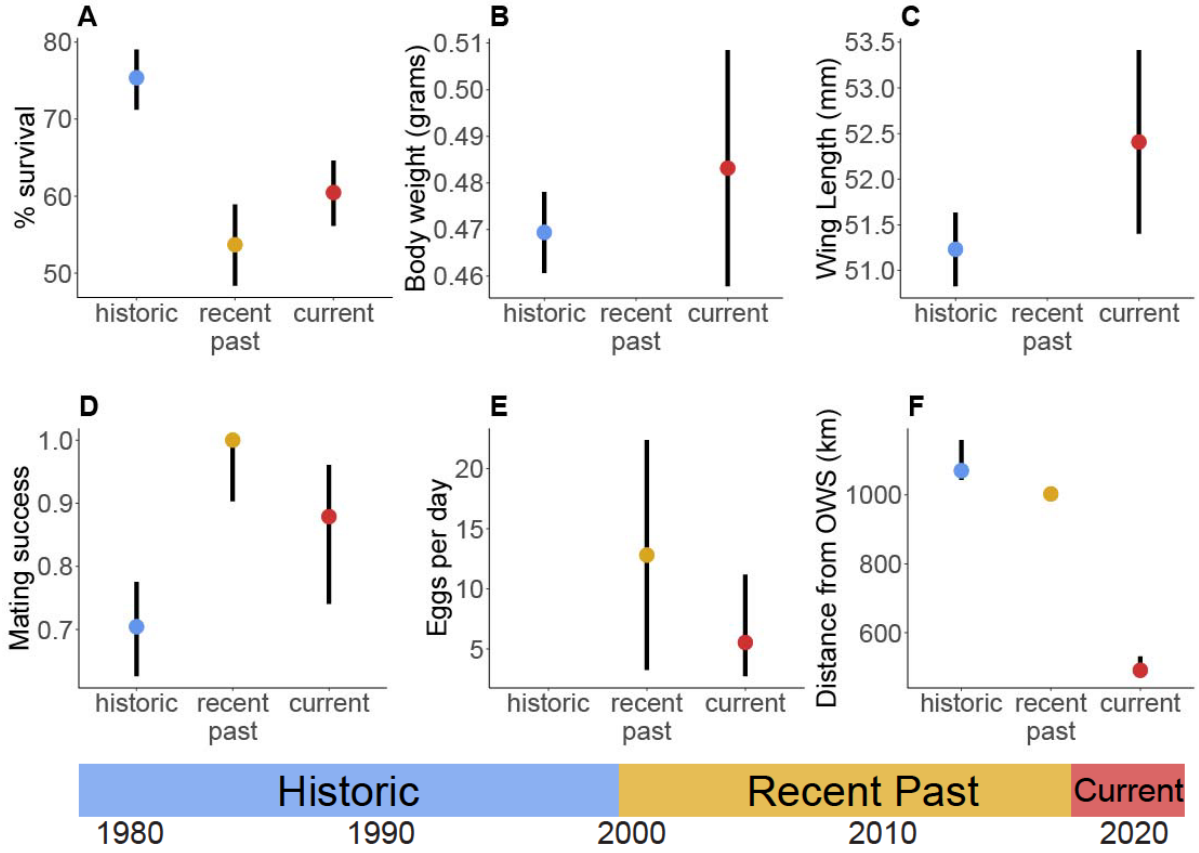

A
% survival
80
70
60
50
historic
recent past
current
B
Body weight (grams)
0.51
0.50
0.49
0.48
0.47
0.46
historic
recent past
current
C
Wing Length (mm)
53.5
53.0
52.5
52.0
51.5
51.0
historic
recent past
current
D
Mating success
1.0
0.9
0.8
0.7
historic
recent past
current
E
Eggs per day
20
15
10
5
historic
recent past
current
F
Distance from OWS (km)
1000
800
600
historic
recent past
current
Historic
Recent Past
Current
1980
1990
2000
2010
2020

Figure 2

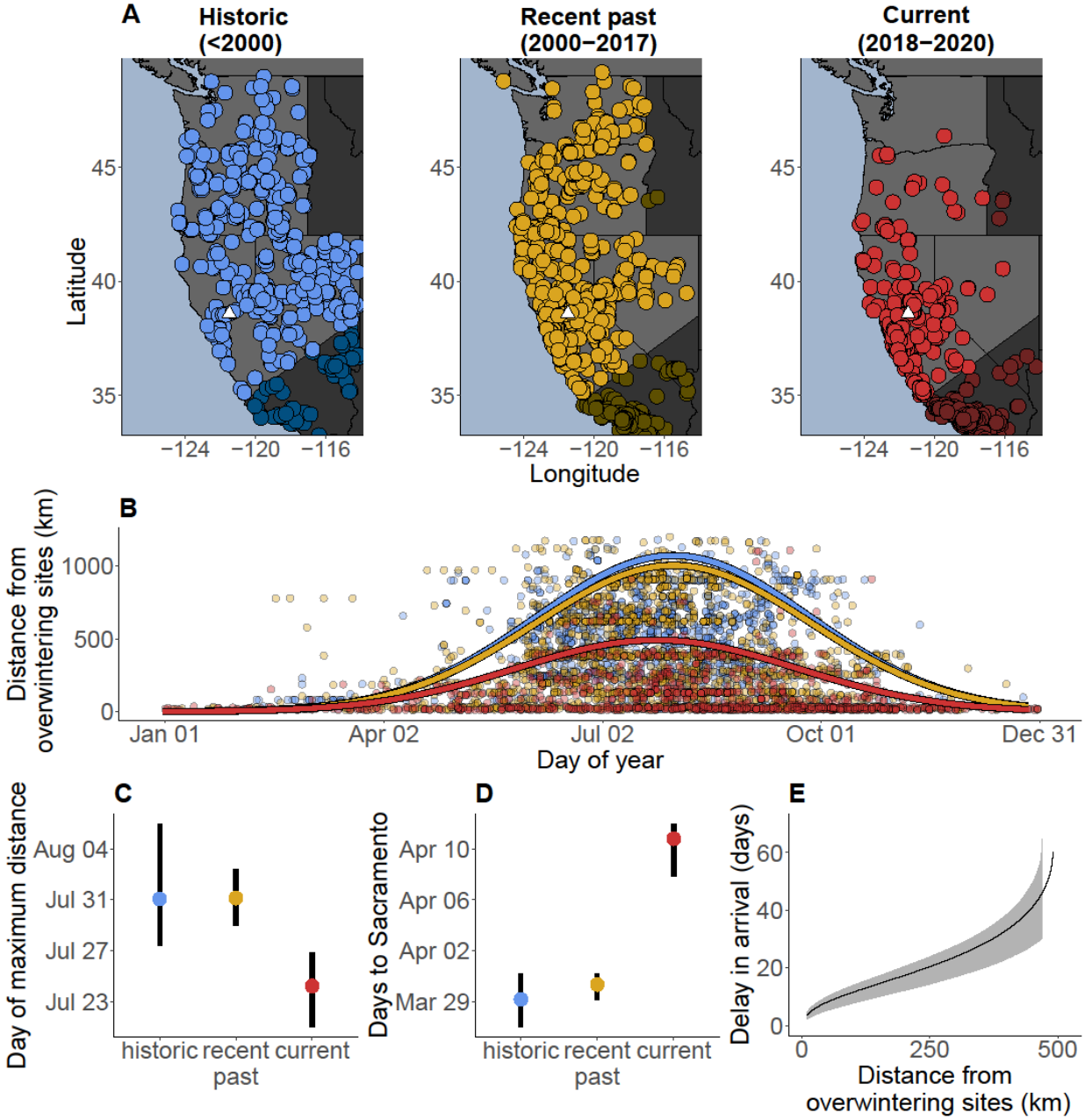
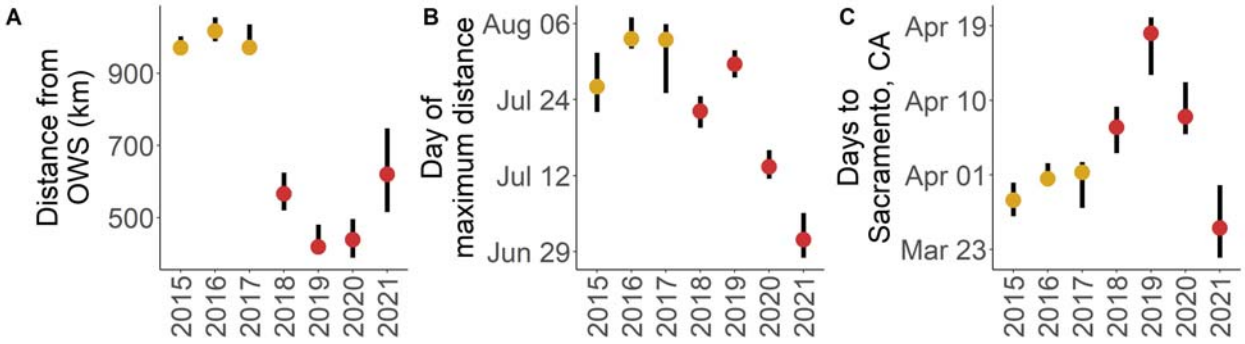

A
Historic (<2000)
Recent past (2000−2017)
Current (2018−2020)
Latitude
45
40
35
−124
−120
−116
Longitude
B
Distance from overwintering sites (km)
1000
500
0
Jan 01
Apr 02
Jul 02
Oct 01
Dec 31
Day of year
C
Day of maximum distance
Aug 04
Jul 31
Jul 27
Jul 23
historic
recent past
current
D
Days to Sacramento
Apr 10
Apr 06
Apr 02
Mar 29
historic
recent past
current
E
Delay in arrival (days)
60
40
20
0
0
250
500
Distance from overwintering sites (km)

Figure 3


A
Distance from OWS (km)
900
700
500
2015
2016
2017
2018
2019
2020
2021
B
Day of maximum distance
Aug 06
Jul 24
Jul 12
Jun 29
2015
2016
2017
2018
2019
2020
2021
C
Days to Sacramento, CA
Apr 19
Apr 10
Apr 01
Mar 23
2015
2016
2017
2018
2019
2020
2021

Movie S1: Western monarch butterfly yearly range expansion reaches half the distance and takes up to two months longer since the population fell below the hypothesized Allee effect threshold. Top: plots of raw data observations separated by era (Historic = 20th century, Recent past = 2000-2017, Current = 2018-2020). Colored circles represent observations in the last 7 days; smaller white diamonds act as placeholders to identify locations of earlier observations. Note the exclusion of AZ and southern regions of CA and NV to avoid resident populations. Only points at least 10 kilometers from overwintering sites are plotted. Bottom: the same observations plotted by day of year and distance from the nearest overwintering sites; curves show Gaussian curves fit to the 0.9 quantile of observations for each era, representing the yearly expansion into the summer breeding range.