Do demographic processes change at extremely low population size in western monarch butterflies?

Collin B. Edwards[1,2*], Cheryl B. Schultz[1], Elizabeth Crone[2,3]

[1] School of Biological Sciences, Washington State University, Vancouver, WA, USA

[2]Department of Biology, Tufts University, 200 College Avenue, Medford, MA, USA

[3]Department of Evolution and Ecology, University of California, Davis, CA, USA

*corresponding author. Correspondence to: Edwards.evoeco@gmail.com

Abstract

Allee effects – the breakdown of biological processes at low population densities – are ecologically important because they can potentially drag already struggling populations to extinction. However, identifying and documenting Allee effects is challenging, especially for natural populations, because it is difficult to know when populations have dropped to critically low densities, and to observe them both above and below this threshold. Here, we compared demographic processes in the western monarch butterfly, *Danaus plexippus,* before and after the population had fallen below the size at which Allee effects were hypothesized to take hold. Comparisons drew on data we collected after a dramatic population crash in 2018, previously published data from other researchers, and community science data. We found no evidence for Allee effects in winter survival, the fraction of females mated in early spring, or eggs laid per day. We did identify a 43% decline in the distance of seasonal range expansion, which could reflect Allee effects in terms of summer population growth rates or density-dependent movement behavior. In addition, overwinter survival of western monarch butterflies has substantially declined since first estimated in 1975 and may be contributing to the long-term population decline. The lack of evidence for Allee effects and the recent rebound in population size provide a more hopeful view for monarch conservation in the future but do not supersede the documented density-independent population decline across the last several decades.

Keywords: *Western monarch butterfly; Danaus plexippus; Allee effects; Depensation; Density Dependence; population viability;*

Introduction

Positive density dependence at low population size – known as Allee effects – can lead to rapid decline and extinction in populations that had previously exhibited only gradual declines or stationary but stochastic fluctuations in population size (Stephens et al. 1999, Courchamp et al. 1999). Allee effects can also limit range expansion and biological invasion, as individuals at range edges and rare long-distance dispersers can experience low local population densities (Taylor and Hastings 2005). When a population falls to sufficiently low density (below it's "Allee threshold"), vital biological processes like mate-finding, group dynamics, and predator satiation can break down (Liermann and Hilborn 2001, Tobin et al. 2007), further reducing population growth rate. The most direct evidence for Allee effects thus comes from signals of density dependence in population growth rates at low densities.

For natural populations, many past studies have tested for positive density dependence at low population sizes by analyzing time series of a single population or comparing growth rates across populations. However, direct evidence of reduced growth rates is hard to obtain in practice (Kramer et al. 2009, but see Budroni et al. 2014, Shuai et al. 2020, Li et al. 2022). To identify Allee effects from time series data, ecologists need sufficient statistical resolution to distinguish Allee effects from year-to-year variability and other determinants of growth rate. Decomposing population growth rates into individual drivers is a considerable task under the best circumstances. When looking for Allee effects, ecologists face two additional challenges. First, Allee effects operate over a range of low population densities in which logistical challenges, measurement error, and sometimes conservation concerns can make it difficult to quantify population change. Second, under the conditions when Allee effects should occur

(small populations), the stochasticity associated with small populations and the Allee effect itself (if present) can accelerate population decline (Liermann and Hilborn 2001). In combination, ecologists have limited ability to identify a signal of Allee effects, and frequently have limited time to do so before the population is extirpated.

An alternative approach to identifying Allee effects is to instead identify positive density dependence in individual biological processes: "component Allee effects" (Stephens et al. 1999). These component Allee effects are distinct from positive density dependence in overall population growth rates (hereafter "demographic Allee effects," following Stephens et al. 1999), and component Allee effects are sometimes compensated for by negative density dependence in other processes. Component Allee effects are often more experimentally tractable to evaluate than demographic Allee effects (Kramer et al. 2009). Studies of component Allee effects measure how some essential process (often fecundity, foraging, or survival) varies between groups of individuals that, either by chance or through manipulation, experience different conspecific densities. These can include studies in artificial settings (Elliott et al. 2017, Ventura et al. 2017, Stringer et al. 2020) or short-term observational studies (McInnes et al. 2017, Ventura et al. 2017, Bayer et al. 2018, Contarini et al. 2009). One limitation of many of these studies is that it is challenging to know whether artificial settings accurately mimic low population sizes in the field, and whether spatial variation in abundance reflects factors other than population sizes. While rare, a few studies test for component Allee effects are based on long-term data, including estimating density dependence in reproduction rates of the crested Ibis (Li et al. 2022) and the dwarf-striped hamster (Shuai et al. 2020) and nest survival for Oystercatchers (Frauendorf et al. 2022).

In recent years, the migratory population of western monarch butterfly (*Danaus plexippus*) has undergone dramatic fluctuations in abundance, creating an opportunity to test for Allee effects. As part of a population viability analysis (Schultz et al. 2017), the authors used expert opinion to estimate that Allee effects would lead to population declines when the population dropped below 30,000 overwintering individuals. After declining at a rate of about 6% / year from the 1980's (millions of butterflies) through mid-2010's (~200-300 thousand butterflies; Schultz et al. 2017), the population experienced a precipitous 85% decline in 2018-2019 to fewer than 30,000 butterflies (Pelton et al. 2019). The population had ~20,000 butterflies in 2019-2020, and fewer than 2,000 butterflies counted in 2020-2021. It then experienced dramatic growth to more than 200,000 butterflies in 2020-2021 and modest growth in 2021-2022, ending 2022 with an overwintering population of approximately a third of a million (Xerces Society Western Monarch Count 2022). Despite the more hopeful current situation, between spring 2018 and fall 2021, there were very real fears that the migratory population of western monarch butterflies might not persist. From an academic perspective, this situation was a rare opportunity to evaluate what happens to a natural population when it drops below a hypothesized Allee threshold. These circumstances are rare, and studies taking this approach are similarly rare (but see Berec et al. 2007). Although it is now known that the migratory population of western monarch butterfly was not destined for extinction after the crash in 2018-2020 as it escaped from low population size, it is informative to find out how demographic processes changed during the low population years.

In this study, we evaluate changes in five processes and parameters that relate broadly to vital rates (survival, reproduction, and movement): (1) winter survival, (2-5) body size, wing

size, matedness, and fecundity of butterflies at the end of winter dormancy, and (6-7) population range size and rate of expansion during summer breeding. Western monarch butterflies are characterized by seasonal multi-generational range expansion, in which the population begins the spring in a series of overwintering sites along the coast of California, expands into summer breeding grounds throughout western North America across several generations, then returns to the overwintering sites again in the fall, where they spend the winter in reproductive diapause (Dingle et al. 2005). Our focus was primarily on overwintering processes (metrics 1-5 in the list above) because of extensive past research on overwintering monarch butterflies in California (see Table 1), with an emphasis on the benefits of aggregation during this time period. For example, Anderson and Brower (1993) hypothesized density dependence in thermoregulation during the winter, suggesting Allee effects on winter survival or body size at the end of winter. Wells et al. (1990) and Wells et al. (1998) hypothesized density dependence in mate-finding for monarchs during the period of mating before aggregations break up in spring, suggesting Allee effects on matedness or fecundity.

During summer breeding, past research on monarch butterflies has tended to emphasize the costs of crowding, i.e., negative density dependence (Fisher & Bradbury 2022, Flockhart et al. 2012, Lindsey et al. 2009, Marini and Zalucki 2017, Yakubu et al. 2004), as opposed to positive density dependence and possible Allee effects. However, it is reasonable to expect that density-dependent mate-finding could be at least as problematic during summer breeding, when populations can be distributed sparsely over large geographic areas, as during mating at the end of overwintering aggregations. Although Allee effects have not specifically been proposed for monarch butterflies during summer range expansion, small populations at

118 geographic range margins are a classic example of potential Allee effects in theoretical models,
119 and it is well known that small population sizes can slow or prevent population expansion (e.g.,
120 Taylor and Hastings 2005, Lewis and Kareiva 1993, Hastings 1996, Morel-Journel et al. 2019). To
121 our knowledge, no prior studies have measured western monarch matedness or female
122 fecundity during summer breeding before the population crash. Therefore, we used
123 community science observations to analyze breeding season range expansion – the rate at
124 which populations expand into summer breeding grounds – as a metric of demographic
125 processes during this time period (Table 1). Rates of geographic range expansion depend on
126 both population growth rates and movement (for a textbook-level introduction see, e.g., Kot
127 2001). Therefore, changes in monarch seasonal range expansion after the population crash
128 could reflect changes in survival, reproduction or movement rates (cf. Crone and Schultz 2022).

129 For each of the seven processes and patterns, we expect that, if component Allee
130 effects are present (and we correctly estimated the Allee threshold), these measures would be
131 lower during and after the 2018 crash than during prior time periods. However, many factors
132 other than population size are also likely to vary through time, especially when comparing
133 metrics from the mid-20th century to the post-crash period. Therefore we divided data into
134 three broad time periods: "historical," before 2000, when there were millions of monarchs;
135 "declining," from 2000-2017 when monarchs were in the hundreds of thousands and slowly
136 declining; and "post-crash," from 2018-2020 when winter counts were below the hypothesized
137 Allee threshold. We note that our eras are based on population sizes, with labels that are
138 generally descriptive rather than prescriptive. For example, we know declines occurred in the
139 late historical era, and the population in the declining era sometimes increased in size in

individual years. In our analyses, differences between the post-crash era and the declining era indicate the presence of Allee effects. Differences between the historic era and post-crash or declining eras indicate possible drivers of long-term declines.

Methods:

Study system

The monarch butterfly (*Danaus pelxippus*) is a broadly distributed species, originating from the Americas, that has colonized many parts of the world, including populations in Europe, Africa, Australia, and numerous Pacific and Caribbean islands (Agrawal 2017). In North America, there are two migratory populations, a larger eastern monarch population that overwinters in Mexico and breeds in North America east of the Rocky Mountains and a smaller western population that overwinters on the California coast (the state of California in the USA and northern Baja California in Mexico) and breeds in North America west of the Rocky Mountains. These two migratory populations are not strongly genetically differentiated, but they are demographically distinct, in the sense that they fluctuate independently (Freedman et al 2021). Although both populations have experienced declines in recent years, the western population is both smaller and is declining at a faster rate, so is at greater risk of extirpation (Semmens et al. 2016, Schultz et al. 2017).

The western monarch butterfly has a multi-generational life cycle: overwintering individuals emerge from reproductive diapause and travel from the coast of California to lay eggs before they die; many of their offspring also fly substantial distances before laying eggs,

161 and across three to four generations each summer the butterflies spread throughout the
162 western United States and into southern Canada (Dingle et al. 2005). The final generation flies
163 back to overwintering sites on the coast of California in the fall, completing the cycle. Causes of
164 long-term population declines in western monarch butterflies include urban development and
165 degradation of coastal overwintering sites (Pelton et al. 2019), as well as climate change
166 (Stevens and Frey 2010, Espeset et al. 2016, Crone et al. 2019), increased pesticide use (Crone
167 et al. 2019, Halsch et al. 2020), and declines in abundance of its milkweed (*Asclepias* spp.)
168 hostplants (Pelton et al. 2019, Crone and Schultz 2022).

169 Our inference about patterns of abundance in the "eras" defined in our study comes
170 from two sources. The migratory population of western monarchs is monitored annually at
171 wintering grounds using a systematic community science survey, the Western Monarch Count,
172 which includes "Thanksgiving Counts" (in late November and early December, 1997-present)
173 and the "New Year's Counts" (in late December and early January, 2017-present) (Xerces
174 Society Western Monarch Count 2022). Schultz et al. (2017) combined these data with similar
175 counts at wintering grounds to extend this time series to include population estimates from the
176 1980's through 2016. These data provide the general population estimates that define our
177 demographic eras. In addition, Schultz et al. (2021) monitored monarch butterfly breeding
178 abundance and phenology at 12 sites in five western states (Washington, Oregon, California,
179 Idaho and Nevada) from 2017-2019, and 2023-ongoing. These data showed that the
180 population crash in the 2018 Thanksgiving count occurred in early spring of 2018 (Pelton et al.
181 2019). Therefore, we include the summer of 2018 in the "post-crash" era during analyses of
182 breeding season dynamics.

183

184 **Changes in processes and parameters at wintering grounds**

185 *Winter: pre-crash studies*

186 To estimate historic era survival, we used analyses presented by Pelton et al. (2019).
187 This previous analysis used mark-recapture data presented in Tuskes and Brower (1978) to
188 estimate 6-week survival for western monarchs in 1975-1976 near Santa Cruz and at Muir
189 Beach (6 weeks is approximately the time between the Thanksgiving and New Years Counts of
190 the Xerces society). For this paper, we combined the survival estimates for the two locations. In
191 doing so, we corrected one typo in Pelton et al. (2019): the "29% drop" reported for Santa Cruz
192 should instead say "19% drop".

193 For other winter processes and patterns, we identified studies in the historical and
194 declining eras that directly or indirectly report data relating to winter survival, early spring
195 fecundity, early spring matedness, early spring body size, or wing size (Table 1). Although body
196 size and wing size are not direct demographic measures, they were included because they often
197 relate to survival, fecundity and movement ability (for which we had limited or no data).
198 Where possible, we extracted the raw data from published tables and carried out our own
199 analyses as described below. Where this was not possible, we extracted means and standard
200 deviations from published figures using WebPlotDigitizer (Rohatgi 2021). When more than one
201 data set was available for the same era, we combined the estimates, propagating uncertainty
202 using the delta method (Williams et al. 2002), implemented in the R package msm (Jackson
203 2011). The delta method is a flexible mathematical tool for estimating the variance of a derived

204 parameter estimate (e.g., the average of two or more parameter estimates from different
205 studies, each with its own variance).

206 To estimate historical body size, we digitized means and standard errors of body mass
207 data for female western monarchs from Chaplin and Wells (1982) (data from Pismo Beach in
208 February 1972) and Leong et al. (1995) (data from Pismo Beach in February in years 1990-
209 1992). To estimate historical wing size, we digitized data from Beall (1946), Tuskes and Brower
210 (1978), and Leong et al. (1995), who reported estimates for wing length of female western
211 monarchs caught primarily from Ventura and Pacific Grove in Februaries 1938-1939 and 1942,
212 from Muir Beach, Natural Bridges and Santa Barbara in February 1976, and Pismo Beach in
213 Februaries 1990-1992 respectively. Leong et al. (1995) caught 142 females in February of 1990,
214 1991, and 1992 at Pismo Beach and identified mating status using dissections and
215 spermatophore identification; Leong et al. (2012) did the same with 19 females caught in
216 February 2010. We fit these two data sets separately using an intercept-only binomial
217 regression model to estimate the proportion of matedness in the historical and declining eras.
218 Leong et al. (2012) reported estimated means and standard deviations for the lifespan (N=19)
219 and lifetime eggs per female (N=10) for monarchs in February 2010. We calculated mean eggs
220 per day as mean lifetime eggs divided by mean lifespan, using the delta method to propagate
221 error.

222 *Winter: post-crash data & analyses*

223 We used changes in the number of monarch butterflies at overwintering sites to
224 estimate winter survival. Starting in January 2017 (winter 2016-17), the Xerces Society carried

225 out surveys in early January ("New Years Count" data) to complement their Thanksgiving Count
226 surveys (Xerces Society Western Monarch Count 2022). We used binomial regression to
227 estimate winter survival for this period as the ratio of the summed New Year's Count (events)
228 to the Thanksgiving Count (trials) for each year from winter 2016-2017 through winter 2020-
229 2021. We fit these five years of data in a single binomial regression model, with a fixed effect of
230 era ("declining" for the first two winters and "post-crash" for the most recent three) and a
231 random effect of year.

232 We estimated other winter processes and patterns in a post-crash field study. (Due to
233 low population sizes, we were not able to obtain permits to repeat Tuskes' and Browers' mark-
234 recapture study to also measure survival directly.) In February 2019, we collected 35 adult
235 female monarchs near the overwintering site at Pismo Beach State Park. We measured wing
236 length and body size, and estimated means and standard errors using intercept-only regression
237 models. We also used the monarch spermatophore palpation method to evaluate whether
238 butterflies collected had been mated (Van Hook 1999). We treated females with a palpation
239 score of 1 ("rice grain or large pinhead") or higher as having successfully mated, and females
240 with scores of 0 as unmated. Two individuals had an uncertain score and were excluded from
241 further analysis. We used an intercept-only binomial regression model to estimate the
242 proportion of mated individuals. Finally, to estimate daily fecundity, we kept adult female
243 monarchs from Pismo Beach in tents in the greenhouse for two days with access to narrowleaf
244 milkweed plants (*Asclepias fascicularis*), nectar feeders (sponges soaked in Gatorade) and
245 nectar plants (*Lavandula*, *Iberis*, and *Chrysanthemum* sp.) sourced from local garden stores. At
246 the end of two days, we counted all eggs laid by each female during this time and released

247 butterflies back into the site from which they were collected. We analyzed these oviposition
248 data using 0-inflated negative binomial models (using the pscl package in R) (Zeileis et al. 2008,
249 Jackman 2020). 0-inflated models are a statistical technique that separates 0's (in this case,
250 butterflies that were not reproductively active) from a process that might include 0's and higher
251 values (in this case, eggs laid per day for reproductively active butterflies). The model produces
252 two parameters: the proportion of 0's (hereafter, the proportion of non-reproductive
253 butterflies) and the mean of the non-zero distribution (here, the average count of eggs per
254 reproductive butterfly). Unlike Leong et al. (2012), we did not carry out manipulations to break
255 our captured monarchs from reproductive diapause. Therefore, 0's from the 0-inflated negative
256 binomial models likely represent butterflies in reproductive diapause, but could also represent
257 unmated butterflies, and we do not interpret this parameter further.

258 *Winter: comparing eras*

259 To compare differences between eras, we carried out parametric bootstrapping. We
260 generated 1000 replicates of estimated values, generally by drawing randomly from the
261 distribution associated with the combined historical data or from the distribution of the
262 appropriate coefficient estimate from fitted regression models using the bootMer() function of
263 the R package lme4 (Bates et al. 2015). For matedness in the declining era, 100% of individuals
264 were mated, which produces unreasonable estimated distributions using logistic regression. In
265 this case, we sampled directly from the likelihood profile using rejection sampling.

266

267 **Changes in summer population expansion**

Summer: estimating range expansion

We obtained observations of monarchs in California, Oregon, Washington, Nevada, and British Columbia from the late 1800s through January 1, 2023, from iNaturalist (GBIF.org 2020) and the Western Monarch Milkweed Mapper (Western Monarch and Milkweed Occurrence Database 2018); these observations included latitude, longitude, and day of year of observation. Most analyses in this paper are based on data only through December 2020. We carried out additional analyses of 2015-2022 to identify more precisely define the fingerprint of the decline and the 2021 rebound in abundance (GBIF.org 2023).

Because there are resident, non-migratory populations of monarch butterflies in Southern California and southern Nevada, we removed all observations south of the line drawn by connecting the locations (-120.63 latitude, 34.75 longitude) and (-114.02 latitude, 38.49 longitude) (Wells and Wells 1992) (Fig. 2A). We also excluded observations less than 30 kilometers from the coast, as some fraction of individuals have recently begun to remain on the coast or in coastal cities (notably, San Francisco and its environs) year-round (Crone and Schultz 2021). The specific distance cutoff used for exclusion did not affect our conclusions (see "*Summer: sensitivity analysis*" below). We removed duplicate observations (defined as having the same date and latitude and longitude each within 1/1000 degree of each other), and removed obvious outliers based on expert opinion (36 outliers total). For each of the remaining 4489 observations, we calculated the great circle distance ("as the crow flies") to the nearest overwintering sites, using the 185 overwintering sites of Schultz et al. (2017). For this analysis, we used summer 2018 as the start of the post-crash era because the low abundance started in

spring 2018 (Pelton et al. 2019). Analyses of individual years from 2015 to 2022 used the same methods and data sources.

Plots of observations based on day of year and distance from the nearest overwintering sites showed a roughly symmetrical, hump-shaped distribution that could be approximated by a Gaussian curve (e.g., Fig. 2B). Edwards and Crone (2021) show how Gaussian curves can be fit with linear models; we combine this approach with quantile regression to estimate the outer boundary of monarch seasonal range expansion using the quantreg package (Cade and Noon 2003, Koenker 2021). We used the 0.9 quantile to represent the outer boundary of the monarch range; this defines the boundary between the 90% of monarchs nearest the overwintering sites and the most distant 10% on any given day of the year. We chose this method because it captures the expansion of monarchs into their summer breeding range while still being robust to outliers. The specific quantile chosen did not affect our conclusions (see "*Summer: sensitivity analysis*" below). For comparison to analyses of winter data, we aggregated our data into the same historical, declining, and post-crash eras before fitting our models. From fitted curves of the 0.9 quantile for each era, we estimated the maximum distance from overwintering sites as a metric for the summer breeding range size. As metric of the rate of range expansion, we estimated when the 90% quantile first reached 100 kilometers from the nearest overwintering site. One hundred kilometers is approximately the (greater circle) distance from the nearest overwintering site to Sacramento, California's state capital, and was well within the maximum distance traveled in any era. For both metrics (maximum distance and days to 100 km), we estimated confidence intervals using bootstrapping as

implemented in the msm package (Jackson 2011). All calculations were based on day of year (0-366); for readability, we present our results as month and day for a non-leap-year.

As we had sufficient data to fit separate models to each year for 2015-2022, we repeated our calculations on a yearly basis for this period. Our yearly fits allowed us to examine seasonal range expansion before the 2018-2019 crash, after the crash, and then after the 2020 rebound in abundance.

Summer: sensitivity analysis

To confirm that the results of our range expansion analysis did not depend on specific model-fitting decisions, we repeated the main analysis with each of the following changes: defining the monarch range by the 0.8, 0.7, 0.6, and 0.5 quantiles (instead of the 0.9 quantile used above), or changing the threshold distance from the coast below which we excluded points to 0.1 km, and then 50 km (instead of 30 km used above). Additionally, we observed apparent streaks in the raw data when plotting distance by day of year (Fig. 2B, Fig. S4). The highly overrepresented distances may reflect repeated sampling of populated or popular locations. To ensure these streaks were not driving observed patterns, we generated simulated data sets by randomly subsampling our data such that we never had more than 1 data point in each 1km distance from the overwintering sites for each era. This sampling procedure generated simulated data sets with 1276 observations instead of 4492. We repeated this process 5000 times and carried out our previous analysis on each of these simulated datasets.

Software and key packages

All analyses and figure generation were carried out in the programming language R version 4.2.1 (R Core Team 2022). We used the following key packages: spdata (Bivand et al. 2023), geosphere (Hijmans 2022), maps (Becker et al. 2022), mapdata (Becker and Wilks 2022b), and ggmap (Kahle and Wickham 2013) for our spatial analyses and plots; lme4 (Bates et al. 2015) for regression and mixed models, pscl for zero-inflated regression (Jackman 2020), quantreg for quantile regression (Koenker 2022); msm (Jackson 2011) and boot (Canty and Ripley 2022) for bootstrapping; tidyverse suite (Wickham et al. 2019) for data manipulation; ggplot2 (Wickham 2016), scales (Wickham and Seidel), gridExtra (Auguie 2017), and patchwork (Pederson 2022) for figure-making. For supplementary animations, we used the r "animation" package (Xie et al. 2021) and the software ImageMagick (ImageMagick Studio LLC. 2023).

Results

None of the demographic processes and patterns measured at the wintering grounds showed evidence of component Allee effects. Winter survival was significantly higher in the post-crash era than in the declining era (higher in 97.2% of bootstraps), indicating no Allee effect on this process (Fig 1A). Winter survival was significantly higher in the historical era (75.4%, 95% CI = 71.2% -- 79.0%) than in the declining (53.7%, 95% CI =48.4% -- 58.9%) or post-crash eras (60.4%, 95% CI = 56.2% -- 64.6%) (higher in 100% of bootstraps in both cases). Body mass was slightly higher in the post-crash era (0.48 grams, 95% CI = 0.48 – 0.508) than in the historical era (0.47 grams, 95% CI = 0.461 – 0.478), but this difference was not statistically significant (higher in 83.5% of bootstraps), and was in the opposite direction of an Allee effect

(Fig 1B). Wing length was greater in the post-crash (52.4 mm, 95% CI = 51.4-- 53.4) than historical era (51.2 mm, 95% CI = 50.8 – 51.6) (higher in 98.1% of bootstraps) (Fig. 1C). The fraction of females mated was highest in the declining era (100%, 95% CI = 90.3% -- 100%), followed by the post-crash era (88%, 95% CI = 74% -- 96%) and then the historical era (70%, 95% CI = 63% -- 78%) (Fig. 1D). The fraction of females mated was significantly higher in the post-crash and declining eras than the historical era (higher in 97.8% and 100% of bootstraps, respectively), while the difference between declining and post-crash eras was not significant, indicating there was no support for a component Allee effect (declining era had higher matedness in 87.7% of bootstraps). Egg production was higher in the declining era (12.8 eggs per day, 95% CI = 3.3 – 22.4) than in the post-crash era (5.5 eggs per day, 95% CI = 2.7 – 11.2), but this difference was not statistically significant (declining era was higher in 90.2% of bootstrapped replicates) (Fig. 1E).

There was strong evidence for positive density dependence in monarch summer breeding range size and the rate of range expansion. The historic and declining eras had similar summer breeding ranges, with the 0.9 quantile of the population expanding to up to 1103 km (95% bootstrapped CI = 1037 –1202) and 1001.98 km (95% bootstrapped CI = 1002 – 1051) from overwintering sites, respectively (Fig. 1F, Fig. 2B, Movie S1). This 9% decline in distance from the historic to the declining eras was statistically significant (historic era distances were greater than declining era distances in 98.5% of bootstrapped replicates). In the post-crash era, the maximum distance traveled fell by a further 43% to 587 kilometers, suggesting density-dependent range expansion (95% bootstrapped CI = 518 – 657 km; less than historical and declining eras in 100% of bootstraps). Models fit separately to each year of 2015-2022 show a

clear relationship between breeding range size and population size, with the distance of range expansion falling in 2018 at the time of the population crash, then increasing somewhat during and after the 2020 bounce (Fig. 2C).

The rate of range expansion showed similar patterns (Fig. 1G): Monarch populations reached 100 km from the coast at a slightly earlier date in the historic (March 28, 95% bootstrapped CI: March 26-April 1) and declining (March 31, 95% CI: March 29 – April 1) eras (declining era later than historic in 87.4% of bootstraps). In the post-crash era, the date at which they reached 100 km from the coast was more than a week later than in the historic era (April 7, 95% CI: April 4-12; later than historical and declining eras in 100% and 99.9% of bootstraps).

When repeating our analyses using different quantiles and different distances for excluding coastal sightings, individual estimates changed, but the same qualitative patterns remained (Supplemental Fig. S2, S3). Similarly, randomly subsampling our data to remove streakiness changed specific estimates but produced qualitatively similar results to our analysis of the complete data set (Supplemental Fig. S4).

Discussion:

We found no evidence for component Allee effects in demographic processes or patterns for monarch butterflies during winter. Matedness and fecundity were lower in the post-crash era than in the declining era, but these differences were not statistically significant; overwintering survival was significantly higher in the post-crash era than in the declining era.

395 We expected to find evidence for mate limitation, as this is one of the best-documented
396 component Allee effects in other species (Kramer et al. 2009, Gascoigne et al. 2009) and has
397 been specifically identified as a potential issue for overwintering monarch butterflies (Wells et
398 al. 1990, Wells and Wells 1992). Similarly, overwintering aggregation has long been proposed as
399 a method for temperature regulation to improve survival (Allee 1927), and has also been
400 hypothesized as a benefit of monarch aggregation during overwintering (Anderson and Brower
401 (1993), although Chaplin and Wells (1982) found that overwintering monarchs were generally
402 at air temperature regardless of their level of aggregation, and Wells and Wells (1992) outline
403 further indirect evidence that winter aggregations do not mitigate temperature-related
404 mortality.

405 Certainly, one possibility is that our historical data were too sparsely distributed in space
406 and time (see Table 1) to provide a robust comparison with our estimates from 2019. An ideal
407 but unrealistic experimental design would be to measure vital rates at multiple sites before and
408 after the population crash; this study design is unrealistic because we could not have predicted
409 this population crash and also because there were too few butterflies at most sites to conduct
410 research after the crash. A similar concern is that we did not know the correct threshold
411 population size for demographic Allee effects; our study design was based on a published Allee
412 threshold (Schultz et al. 2017), but the exact threshold value was largely a guess based on
413 expert opinion. Furthermore, in other systems, threshold population sizes for demographic
414 Allee effects are known to vary spatially and temporally (Tobin et al. 2007, Walter et al. 2020),
415 so our estimated Allee effect threshold may have been correct on average, but fortunately in
416 this instance the population avoided demographic Allee effects. Nonetheless, in spite of these

417 caveats, our study was a rare opportunity to repeat past demographic studies after a sudden
418 85% drop in population size.

419 An alternative "null" explanation for lack of component Allee effects during
420 overwintering is that the individual site surveyed did not reach low enough densities, even in
421 this unprecedented population crash. Our survey and both past studies of matedness (Leong et
422 al. (1995) and Leong et al. (2012)) were all carried out at Pismo Beach, in part because it is a
423 reliable overwintering site with high densities of monarchs. Pismo Beach experienced a
424 substantial reduction in overwintering numbers between the surveys in the declining era,
425 where the average count was ~25,000 individuals (range: 12,284-38,438), and our post-crash
426 experiments, when 3,092 individuals were reported in Fall 2018 (Xerces Society Western
427 Monarch Count 2022). However, in the fall of 2018, Pismo Beach had the most reported
428 individuals of all overwintering sites. In contrast, 47% of monitored sites with at least one
429 monarch present had fewer than ten individuals reported, and a third of monarchs reported
430 were in sites with less than 600 individuals. It is possible that we would have detected
431 component Allee effects at some of the less densely populated sites, although there were so
432 few monarchs there that experiments would not have been feasible. It is also possible that we
433 might have detected component Allee effects in the winter of 2020-2021, when the
434 overwintering population crashed again to an all-time low Thanksgiving Count of fewer than
435 2000 monarchs counted across all sites. However, at that point, there were essentially no
436 overwintering sites with enough monarch butterflies to conduct rigorous experiments; in 2020
437 Pismo Beach had a Thanksgiving count of 199 butterflies, and only one site had a higher count
438 (550 at Natural Bridges). Thus, our study is an unusual opportunity to test hypothesized

439 component Allee effects, but also emphasizes the challenges of doing so (cf. Liermann and
440 Hilborn 1997, 2001).

441 The most striking change between the declining and post-crash era was the nearly 50%
442 reduction in the maximum distance of the seasonal range expansion. Demographic Allee effects
443 slow the rate of geographic spread in mathematical and simulation models (Lewis and Kareiva
444 1993, Veit and Lewis 1996, Wang and Kot 2001, Morel-Journel et al. 2019), suggesting that the
445 reduced rate of range expansion in western monarch butterflies could reflect lower survival or
446 fecundity during breeding in the post-crash era. Past studies of monarch butterflies during the
447 breeding season have shown either negative (Flockhart et al. 2012, Lindsey et al. 2009, Marini
448 and Zalucki 2017) or no (Fisher & Bradbury 2022) density dependence. However, these studies
449 were all done in the eastern monarch butterfly population, where monarch butterfly densities
450 are typically much higher than in the West. Studies that experimentally manipulated densities
451 also did not include very low densities, e.g., 1-10 larvae per 3.8L container (Lindsey et al. 2009)
452 or 1-2 larvae per 4 milkweed (host plant) stems (Fisher & Bradbury 2022). In contrast, typical
453 western monarch densities were one larva per ~10-100 milkweed stems in 2017 (prior to the
454 crash) and one larva per ~1,000-10,000 stems in 2018 (after the crash) (Pelton et al. 2019).
455 These past studies of density dependence also focused on competition at the life stages from
456 oviposition through larval pupation. To our knowledge, no one has tested for density-
457 dependent mate limitation in monarch butterflies during summer breeding, even though mate
458 limitation was a leading reason why ecologists had proposed component Allee effects in
459 overwintering aggregations (Wells et al. 1990, Wells and Wells 1992). Spongy moths, an

460 invasive lepidopteran species, experience demographic Allee effects at their range edge due to
461 mate-finding failures (Tobin et al. 2007, Contarini et al. 2009).

462 A second mechanism for reduced seasonal range expansion is density-dependent
463 dispersal. Reduced dispersal at lower population sizes has been reported for several other
464 butterfly species (Nowicki and Vrabec 2011, Bonelli et al. 2013, Kuussaari et al. 2016). In most
465 cases, density dependent dispersal is framed as a way of avoiding crowded conditions. For the
466 western monarch, an additional mechanism for positive density-dependent dispersal is a
467 reduction in multiple matings of overwintering monarchs when the population is small (Wells
468 and Wells 1992). Male monarch butterflies transfer a large nutrient-rich spermatophore during
469 mating, and multiple matings can provide female butterflies with substantially increased
470 energy, in turn increasing their dispersal capabilities (Wells et al. 1992, Wells and Wells 1992).

471 In contrast with the notion of reduced movement, monarch butterflies in our 2019 post-
472 crash data set had larger wing sizes than samples from the historic era (Fig. 1C). We observed a
473 1.2 millimeter increase in size in the post-crash era, which is approximately equal to the
474 difference observed between migratory and non-migratory individuals (Altizer and Davis 2010).
475 Across monarch populations, larger wing sizes are associated with increased capability of
476 movement: the eastern monarch butterflies, which migrate farther, have larger wings than
477 western monarch butterflies or monarch butterflies from nonmigratory populations (Altizer and
478 Davis 2010). Similarly, within the western monarch population, larger wings in overwintering
479 individuals are associated with the isotopic fingerprints of more distant summer breeding
480 grounds (Yang et al. 2016). Larger wing sizes could also be interpreted as a sign of more
481 stressful conditions and higher mortality during Fall migration (Altizer et al. 2015), which could

482 potentially translate to slower inland movement and/or lower fecundity during the first
483 generation of monarch breeding in Spring. It is possible that small changes in the rate of range
484 expansion during early generations could lead to mismatched timing of monarch butterflies and
485 host plants, with knock-on consequences of reduced larval survival (cf. Yang and Cenzer 2020).

486 If reduced seasonal range expansion is a component Allee effect, it seems likely that
487 other parts of the life cycle showed compensatory responses, so this effect did not lead to
488 population declines. The western monarch population grew dramatically from Fall 2020 to Fall
489 2021, in spite of a continued reduction in the breeding range during the summer of 2021.
490 Similarly, in Fall 2021 and 2022, the western monarch Thanksgiving count was similar to counts
491 in the declining era, but the breeding range was significantly smaller in summer 2021 and
492 summer 2022 than in the declining era, even though it was significantly larger than in the post-
493 crash era. It is not uncommon for positive density dependence in one life cycle stage to be
494 counterbalanced by demographic or behavioral changes at other life cycle stages (Levitan 1991,
495 Shuai et al. 2020, Stephens et al. 1999). Some past studies of eastern monarch butterflies have
496 suggested an opposite pattern of demographic compensation to our results for western
497 monarchs: faster declines in winter than summer in the east (Inamine et al. 2016, Crossley et al.
498 2022), and faster recovery of winter population counts than breeding range size in our data.
499 The difference in findings may arise in part because the summer counts used in Inamine et al.
500 (2016) and Crossley et al. (2022) represent only a portion of the eastern monarch breeding
501 range, and are likely biased toward higher-quality habitat (Pleasants et al. 2017). Additionally,
502 Crossley et al (2022) compared trends in winter monarch counts for the eastern population to
503 trends in summer monarch butterflies for all of North America, including western and non-

504 migratory populations, so divergent trends might reflect different dynamics of these groups.
505 Nonetheless, these studies all point to the general importance of considering Allee effects
506 throughout a species' life cycle, which includes understanding migratory species throughout
507 their full annual life cycle.

508 In general, our results suggest that the western monarch butterfly population is
509 remarkably resilient to fluctuations in abundance. This resilience may not be surprising, since
510 insect populations often vary by orders of magnitude among years (Fox et al. 2019, Didham et
511 al. 2020). However, this positive conclusion is moderated by at least three cautionary caveats:
512 The first of these is that overwinter survival was much higher in the historic era than the
513 declining and post-crash eras. This difference could be due to differences in methodology
514 (mark recapture analyses in the historic era and inference from population counts in more
515 recent years; see *Methods*). However, the western monarch population has declined
516 substantially since the mid-20th century and is about an order of magnitude smaller than in the
517 1980's, even after the recent upswing in numbers. We emphasize the importance of
518 conserving and restoring wintering groves, as well as summer breeding habitat (Pelton et al.
519 2019).

520 A second caveat is that, although the differences were not statistically significant, the
521 estimated proportion of mated females and eggs laid per day fell in the post-crash era,
522 consistent with component Allee effects. If these nonsignificant effects were real, females in
523 the spring of the post-crash era would have laid less than half as many eggs on average as those
524 in the declining era (% mated × eggs/day: declining era = 12.8; post-crash era = 4.9). This is
525 within the range of other estimated component Allee effects on fecundity. In island foxes, the

526 proportion of breeding females varied from approximately 60% at high-density sites to
527 approximately 20% at low-density sites (Berec et al. 2007), the pregnancy rate of striped
528 hamsters varied between approximately 35% and 10% from high to low density years (Shuai et
529 al. 2020), and in two small reintroduced populations of Crested Ibis, the larger population
530 averaged 65% larger clutch sizes and 58% higher breeding success (Li et al. 2022).

531 The third caveat is that, although the migratory population of the western monarch did
532 not decline to extinction, we do not know how or why it increased from the Fall of 2020 to the
533 Fall of 2021. The drivers of western monarch population dynamics are complex, interrelated,
534 and ecologists are still seeking to understand them (Yang 2023). It might be that the western
535 monarch population was suffering from severe component Allee effects in 2019 and 2020 but
536 the detrimental consequences were counterbalanced by unusually good conditions or a "series
537 of fortunate events" (see Greenberg 2022). There are many non-exclusive alternative
538 explanations, including the potential that the population was rescued by migration from the
539 east (there is at least some mixing between the populations) (Billings 2019). The lack of
540 evidence for component Allee effects for the western monarch does not guarantee that the
541 population will always recover from low abundance but does imply low population sizes are not
542 a guarantee of extinction.

543

544

545

References

Agrawal, A. 2017. Monarchs and milkweed: A migrating butterfly, a poisonous plant, and their remarkable story of coevolution. - Princeton University Press

Allee, W. C. 1927. Animal Aggregations. – The Quarterly review of biology 2:367–398.

Altizer, S., and Davis, A. K. 2010. Populations of Monarch butterflies with different migratory behaviors show divergence in wing morphology. – Evolution 64: 1018–1028.

Altizer, S., Hobson, K.A., Davis, A.K., De Roode, J.C. and Wassenaar, L.I. 2015. Do healthy monarchs migrate farther? Tracking natal origins of parasitized vs. uninfected monarch butterflies overwintering in Mexico. – PloS one 10: e0141371.

Anderson, J. B., and Brower, L. P. 1993. Cold-hardiness in the annual cycle of the monarch butterfly. – Biology and Conservation of the Monarch Butterfly 157-164

Auguie, B. 2017. gridExtra: Miscellaneous Functions for “Grid” Graphics. -- <https://cran.r-project.org/package=gridExtra>

Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. – Journal of Statistical Software, 67: 1-48.

Bayer, S. R., Wahle, R. A., Brady, D. C., Jumars, P. A., Stokesbury, K. D. E., and Carey, J. D. 2018. Fertilization success in scallop aggregations: reconciling model predictions and field measurements of density effects. – Ecosphere 9: e02359.

Beall, G. 1946. Seasonal variation in sex proportion and wing length in the migrant butterfly, Danaus Plexippus l. (Lep. Danaidae). – Transactions of the Royal Entomological Society of London 97: 337–353.

Becker R.A. and Wilks, A.R. 2022. mapdata: Extra Map Databases. --<https://CRAN.R-project.org/package=mapdata>.

Becker R.A., Wilks, A.R., Brownrigg, R., Minka, T.P. 2022b. maps: Draw Geographical Maps. --<https://CRAN.R-project.org/package=maps>.

Berec, L., Gascoigne, J., and Courchamp, F. 2007. Double Allee effects and extinction in the island fox. – Conservation 21: 1082-1091.

Bivand, R., Nowosad, J., and Lovelace, R. 2023. spData: Datasets for Spatial Analysis. --<https://CRAN.R-project.org/package=spData>.

Bonelli, S., Vrabec, V., Witek, M., Barbero, F., Patricelli, D., and Nowicki, P. 2013. Selection on dispersal in isolated butterfly metapopulations. – Population Ecology 55: 469–478.

Budroni, M. A., Farris, E., Zirulia, A., Pisanu, S., Filigheddu, R., and Rustici, M. 2014. Evidence for age-structured depensation effect in fragmented plant populations: The case of the Mediterranean endemic Anchusa sardoa (Boraginaceae). – Ecological Complexity 20: 142–150.

Cade, B. S., and Noon, B. R. 2003. A gentle introduction to quantile regression for ecologists. – Frontiers in ecology and the environment 1: 412–420.

Canty, A. and Ripley, B. 2022. boot: Bootstrap R (S-Plus) Functions. --<https://CRAN.R-project.org/package=boot >.

Chaplin, S. B., and Wells, P. H. 1982. Energy reserves and metabolic expenditures of monarch butterflies overwintering in southern California. – Ecological entomology 7: 249–256.

Contarini, M., Onufrieva, K. S., Thorpe, K. W., Raffa, K. F., and Tobin, P. C. 2009. Mate-finding failure as an important cause of Allee effects along the leading edge of an invading insect population. – Entomologia experimentalis et applicata 133: 307–314.

Courchamp, F., Clutton-Brock, T., and Grenfell, B. 1999. Inverse density dependence and the Allee effect. – Trends in ecology & evolution 14: 405–410.

Crone, E. E., Pelton, E. M., Brown, L. M., Thomas, C. C., and Schultz, C. B. 2019. Why are monarch butterflies declining in the West? Understanding the importance of multiple correlated drivers. – Ecological applications 29: e01975

Crone, E. E., and Schultz, C. B. 2021. Resilience or Catastrophe? A possible state change for monarch butterflies in western North America. – Ecology letters 24: 1533–1538.

Crone, E.E. and Schultz, C.B. 2022. Host plant limitation of butterflies in highly fragmented landscapes. – Theoretical Ecology 15: 165-175.

Crossley, M. S., Meehan, T. D., Moran, M. D., Glassberg, J., Snyder, W. E., and Davis, A. K. 2022. Opposing global change drivers counterbalance trends in breeding North American monarch butterflies. – Global change biology 28: 4726-4735.

Kahle, D. and Wickham, H. 2013. ggmap: Spatial Visualization with ggplot2. – The R Journal, 5: 144-161.

Didham, R. K., Basset, Y., Collins, C. M., Leather, S. R., Littlewood, N.A., Menz, M.H.M., Müller, J., et al. 2020. Interpreting insect declines: seven challenges and a way forward. – Insect conservation and diversity 13: 103–114.

607 Dingle, H., Zalucki, M. P., Rochester, W. A., and Armijo-Prewitt, T. 2005. Distribution of the
608 monarch butterfly, Danaus plexippus (L.) (Lepidoptera: Nymphalidae), in western North
609 America. – Biological journal of the Linnean Society. 85: 491–500.
610 Edwards, C. B., and Crone, E. E. 2021. Estimating abundance and phenology from transect count
611 data with GLMs. – Oikos 130: 1335-135.
612 Elliott, K. H., Betini, G. S., and Norris, D. R. 2017. Fear creates an Allee effect: experimental
613 evidence from seasonal populations. – Proceedings of the Royal Society B: Biological
614 sciences 284: 20170878.
615 Espeset, A.E., Harrison, J.G., Shapiro, A.M., Nice, C.C., Thorne, J.H., Waetjen, D.P., Fordyce, J.A.
616 and Forister, M.L. 2016. Understanding a migratory species in a changing world: climatic
617 effects and demographic declines in the western monarch revealed by four decades of
618 intensive monitoring. – Oecologia 181: 819-830.
619 Fisher, K.E. and Bradbury, S.P. 2022. Plant abandonment behavior and fitness of monarch
620 larvae (Danaus plexippus) is not influenced by an intraspecific competitor. – Journal of
621 Insect Conservation 26: 851–856.
622 Flockhart, D.T.T., Martin, T.G., and Norris, D. R. 2012. Experimental examination of intraspecific
623 density-dependent competition during the breeding period in monarch butterflies
624 (Danaus plexippus). –PloS one e45080.
625 Fox, R., Harrower, C. A., Bell, J. R., Shortall, C. R., Middlebrook, I., and Wilson, R. J. 2019. Insect
626 population trends and the IUCN Red List process. – Journal of insect conservation 23:
627 269–278.

Frauendorf, M., Allen, A. M., Jongejans, E., Ens, B. J., Teunissen, W., Kampichler, C., van Turnhout, C. A. M., et al. 2022. Love thy neighbour?—Spatial variation in density dependence of nest survival in relation to predator community. -- Diversity and Distributions 28: 624–635.

Freedman, M.G., de Roode, J.C., Forister, M.L., Kronforst, M.R., Pierce, A.A., Schultz, C.B., Taylor, O.R. and Crone, E.E., 2021. Are eastern and western monarch butterflies distinct populations? A review of evidence for ecological, phenotypic, and genetic differentiation and implications for conservation. -- Conservation Science and Practice 3: e432.

Gascoigne, J., Berec, L., Gregory, S., and Courchamp, F. 2009. Dangerously few liaisons: a review of mate-finding Allee effects. -- Population Ecology 51: 355–372.

GBIF.org (10 January 2023) GBIF Occurrence Download <https://doi.org/10.15468/dl.3zunfj>

GBIF.org (17 December 2020) GBIF Occurrence Download <https://doi.org/10.15468/dl.aq6d3w>

Greenberg, A. 2022. "Western monarch populations grew over 100-fold in 2021. Why?". https://www.pbs.org/wgbh/nova/article/western-monarch-population-growth-2021/

Halsch, C. A., Code, A., Hoyle, S. M., Fordyce, J. A., Baert, N., and Forister, M. L. 2020. Pesticide Contamination of Milkweeds Across the Agricultural, Urban, and Open Spaces of Low-Elevation Northern California. -- Frontiers in Ecology and Evolution 8: 162.

Hastings, A. 1996. Models of spatial spread: A synthesis. -- Biological conservation 78: 143–148.

Iler, A. M., CaraDonna, P. J., Forrest, J.R.K., and Post, E. 2021. Demographic Consequences of Phenological Shifts in Response to Climate Change. – Annual Review of Ecology, Evolution, and Systematics 52: 221-245

ImageMagick Studio LLC. 2023. ImageMagick. Available from <https://imagemagick.org>

Inamine, H., Ellner, S.P., J. P. Springer, and Agrawal, A. A. 2016. Linking the continental migratory cycle of the monarch butterfly to understand its population decline. -- Oikos 125: 1081–1091.

Jackman, S. 2020. pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory. --<https://CRAN.R-project.org/package=pscl>.

Jackson, C. 2011. Multi-State Models for Panel Data: The msm Package for R. *Journal of Statistical Software*, Articles 38: 1–28.

Koenker, R. 2021. quantreg: Quantile Regression. --<https://CRAN.R-project.org/package=quantreg>.

Kot, M. 2001. Elements of mathematical ecology. -- Cambridge University Press.

Kramer, A. M., Dennis, B., Liebhold, A. M., and Drake, J. M. 2009. The evidence for Allee effects. -- Population Ecology 51: 341–354.

Kuussaari, M., Rytteri, S., Heikkinen, R. K., Heliölä, J., and von Bagh, P. 2016. Weather explains high annual variation in butterfly dispersal. -- Proceedings of the Royal Society B: Biological sciences 283: 20160413

Leong, K. H. L., Yoshimura, M. A., and Williams, C. 2012. Adaptive Significance of Previously Mated Monarch Butterfly Females (Danaus plexippus (Linneaus)) Overwintering at a California Winter Site. -- The Journal of the Lepidopterists' Society 66: 205–210.

Leong, K. L. H., O'Brien, E., Lowerisen, K., and Colleran, M. 1995. Mating Activity and Status of Overwintering Monarch Butterflies (Lepidoptera: Danaidae) in Central California. -- Annals of the Entomological Society of America 88: 45–50.

Levitan, D. R. 1991. Influence of Body Size and Population Density on Fertilization Success and Reproductive Output in a Free-Spawning Invertebrate. -- The Biological bulletin 181: 261–268.

Lewis, M. A., and Kareiva, P. 1993. Allee Dynamics and the Spread of Invading Organisms. -- Theoretical population biology 43: 141–158.

Li, M., Dong, R., Tuohetahong, Y., Li, X., Zhang, H., Ye, X., and Yu, X. 2022. Impact of Allee effects on the establishment of reintroduction populations of endangered species: The case of the Crested Ibis. -- Global Ecology and Conservation 35: e02103.

Liermann, M. and Hilborn, R., 1997. Depensation in fish stocks: a hierarchic Bayesian meta-analysis. -- Canadian Journal of Fisheries and Aquatic Sciences, 54: 1976-1984.

Liermann, M. and Hilborn, R. 2001. Depensation: evidence, models and implications. -- Fish and fisheries 2: 33–58.

Lindsey, E., Mehta, M., Dhulipala, V., Oberhauser, K., Altizer, S. 2009. Crowding and disease: effects of host density on response to infection in a butterfly–parasite interaction. -- Ecological Entomology 5: 551-61.

Marini, L., and Zalucki, M. P. 2017. Density-dependence in the declining population of the monarch butterfly. -- Scientific reports 7: 13957.

McInnes, A. M., McGeorge, C., Ginsberg, S., Pichegru, L., and Pistorius, P. A. 2017. Group foraging increases foraging efficiency in a piscivorous diver, the African penguin. -- Royal Society Open Science 4: 170918.

Morel-Journel, T., Assa, C. R., Mailleret, L., and Vercken, E. 2019. Its all about connections: hubs and invasion in habitat networks. -- Ecology letters 22: 313–321.

Nowicki, P., and Vrabec, V. 2011. Evidence for positive density-dependent emigration in butterfly metapopulations. -- Oecologia 167: 657–665.

Payton, M. E., Greenstone, M. H., and Schenker, N. 2003. Overlapping confidence intervals or standard error intervals: what do they mean in terms of statistical significance? -- Journal of Insect Science 3: 34.

Pedersen, T. L. 2022. patchwork: The Composer of Plots. --<https://CRAN.R-project.org/package=patchwork>.

Pelton, E. M., Schultz, C. B., Jepsen, S. J., Black, S. H., and Crone, E. E. 2019. Western Monarch Population Plummets: Status, Probable Causes, and Recommended Conservation Actions. -- Frontiers in Ecology and Evolution 7: 258.

Pleasants, J. M., Zalucki, M. P., Oberhauser, K. S., Brower, L. P., Taylor, O. R., and Thogmartin, W. E. 2017. Interpreting surveys to estimate the size of the monarch butterfly population: Pitfalls and prospects. -- PloS one 12: e0181245.

Rohatgi, A. 2021. Webplotdigitizer: Version 4.5.

Schultz, C. B., Brown, L. M., Pelton, E., and Crone, E. E. 2017. Citizen science monitoring demonstrates dramatic declines of monarch butterflies in western North America. -- Biological conservation 214: 343–346.

Schultz, C. B., McKnight, S., Pelton, E., Jepsen, S., Thomas, C. and Crone, E. 2021. Conservation and Management of Western Monarchs on DoD Lands: Implications of Breeding phenology. -- Report to the DoD Legacy Natural Resources Program, Project NR 19-001. Vancouver, WA.

Semmens, B. X., Semmens, D. J., Thogmartin, W. E., Wiederholt, R., López-Hoffman, L., Diffendorfer, J. E., Pleasants, J. M., et al. 2016. Quasi-extinction risk and population targets for the Eastern, migratory population of monarch butterflies (Danaus plexippus). -- Scientific reports 6: 23265.

Shuai, L.-Y., Wang, L.-Q., Yang, Y.-P., and Zhang, F.-S. 2020. Effects of density dependence and climatic factors on population dynamics of Cricetulus barabensis: a 25-year field study. -- Journal of mammalogy 101: 507–514.

Stephens, P. A., Sutherland, W. J., and Freckleton, R. P. 1999. What is the Allee effect? -- Oikos 185–190.

Stevens, S.R., Frey, D.F. 2010. Host plant pattern and variation in climate predict the location of natal grounds for migratory monarch butterflies in western North America. -- Journal of Insect Conservation 14: 731-44.

Stringer, L. D., Sullivan, N. J., White, R., Jiménez-Pérez, A., Furlong, J., Kean, J. M., Beggs, J. R., et al. 2020. Mazes to Study the Effects of Spatial Complexity, Predation and Population Density on Mate Finding. -- Insects 11: 256

Taylor, C. M., and Hastings, A. 2005. Allee effects in biological invasions. -- Ecology letters 8: 895–908.

Tobin, P. C., Whitmire, S. L., Johnson, D. M., Bjørnstad, O. N., and Liebhold, A. M. 2007. Invasion speed is affected by geographical variation in the strength of Allee effects. -- Ecology letters 10: 36–43.

Tuskes, P. M., and Brower, L. P. 1978. Overwintering ecology of the monarch butterfly, Danaus plexippus L., in California. -- Ecological entomology 3: 141–153.

Van Hook, T. 1999. The use of bursa copulatrix dissection and abdominal palpation to assess female monarch butterfly mating status. -- 1997 North American conference on the monarch butterfly. Commission for Environmental Cooperation.

Veit, R. R., and Lewis, M. A. 1996. Dispersal, Population Growth, and the Allee Effect: Dynamics of the House Finch Invasion of Eastern North America. -- The American naturalist 148: 255–274.

Ventura, L., Smith, D. R., and Lubin, Y. 2017. Crowding leads to fitness benefits and reduced dispersal in a colonial spider. -- Behavioral ecology 28: 1384–1392.

Walter, J. A., Grayson, K. L., Blackburn, L. M., Tobin, P. C., and Johnson, D. M. 2020. Spatiotemporal variability in Allee effects of invading gypsy moth populations. -- Biological invasions 22: 189–193.

Wang, M., and Kot, M. 2001. Speeds of invasion in a model with strong or weak Allee effects. -- Mathematical biosciences 171: 83–97.

Wells, H., Strauss, E. G., Rutter, M. A., and Wells, P. H. 1998. Mate location, population growth and species extinction. -- Biological conservation 86: 317–324.

Wells, H., Wells, P. H., and Cook, P. 1990. The importance of overwinter aggregation for reproductive success of monarch butterflies (Danaus plexippus L.). -- Journal of theoretical biology 147: 115–131.

Western Monarch and Milkweed Occurrence Database. 2018. Data accessed from the Western Monarch Milkweed Mapper, a project by the Xerces Society, U.S. Fish and Wildlife Service, Idaho Department of Fish and Game, and Washington Department of Fish and Wildlife. Available: www.monarchmilkweedmapper.org. Accessed: 4/14/2023

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. -- <https://CRAN.R-project.org/package=ggplot>.

Wickham, H., and Seidel, D. 2022. scales: Scale Functions for Visualization. --<https://CRAN.R-project.org/package=scales>.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., et al. 2019. Welcome to the tidyverse. -- Journal of open source software 4: 1686.

Williams, B. K., Nichols, J. D., and Conroy, M. J. 2002. Analysis and Management of Animal Populations. -- Academic Press.

Xerces Society Western Monarch Count. 2022. Western Monarch Thanksgiving Count and New Year's Count Data, 1997-2021. Available at www.westernmonarchcount.org.

Yakubu, A.-A., Sáenz, R., Stein, J. , and Jones, L. E. 2004. Monarch butterfly spatially discrete advection model. -- Mathematical biosciences 190: 183–202.

Yang, L. H. 2023. Complexity, humility, and action: a current perspective on monarchs in Western North America. -- Current opinion in insect science 59: 101078.

Yang, L. H., and Cenzer, M. L. 2020. Seasonal windows of opportunity in milkweed-monarch interactions. -- Ecology 101: e02880.

Yang, L. H., Ostrovsky, D., Rogers, M. C., and Welker, J. M. 2016. Intra-population variation in the natal origins and wing morphology of overwintering western monarch butterflies Danaus plexippus. -- Ecography 39: 998–1007.

Zeileis, A., Kleiber, C., and Jackman, S. 2008. Regression Models for Count Data in R. -- Journal of statistical software 27: 1–25.

Table 1. Sources of data for comparing demographic processes and patterns. Subscripts indicate geographic locations of data coverage

Process / pattern	Data sources for different eras		
	Historic	Declining	Post-crash
1. Winter survival	Tuskes & Brower 1978[1,2]	Western Monarch Count[9]	Western Monarch Count[9]
2. End-of winter body mass	Chaplin & Wells 1982[5]; Leong et al. 1995[4]		2019 data (this study)[4]
3. End-of-winter wing size	Beall 1946[6,7,8]; Tuskes & Brower 1978[1,2,3]; Leong et al. 1995[4]		2019 data (this study)[4]
4. End-of-winter matedness	Leong et al. 1995[4]	Leong et al. 2012[4]	2019 data (this study)[4]
5. End-of-winter fecundity		Leong et al. 2012[4]	2019 data (this study)[4]
6. Summer range size		Western Monarch Milkweed Mapper[9]	Western Monarch Milkweed Mapper[9]
7. Rate of summer range expansion		Western Monarch Milkweed Mapper[9]	Western Monarch Milkweed Mapper[9]

[1]Muir Beach (37.86°N, 122.41°W); [2]Natural Bridges (37.95°N , 122.06°W); [3]Santa Barbara (34.41°N, 119.87°W); [4]Pismo Beach (35.07°N , 120.37°W); [5]Rancho dos Pueblos (Goleta) (34.44°N, 119.96°W); [6]Ventura (34.28°N, 119.29°W); [7]Pacific Grove (36.62° N, 121.92°W); [8]also includes some samples from Bolinas, El Cerrito, San Francisco, San Jose, Owens Valley and San Diego; [9]range-wide data for western monarch butterflies

780

Figure. 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, (**F**) summer breeding season range as measured by maximum distance from overwintering sites, and (**G**) the day the 0.9 quantile of seasonal range expansion reaches 100 km from overwintering sites (OWS). Points correspond to estimated values before 2000 ("historic"), from 2001-2017 ("declining"), and from 2018-2020 ("post-crash") when the population was below the hypothesized Allee effect threshold. Bars represent 84% confidence intervals (non-overlapping bars correspond to significant 2-tailed T tests; Payton et al. 2003).

Figure. 2. (**A**) Fewer monarchs were observed in OR and WA in the post-crash era (shaded CA and NV regions were excluded to avoid resident populations). White triangles show Sacramento, CA, a representative location 100 km from the overwintering sites. (**B**) Fitted curves of the 0.9 quantile of the distance from observations to the nearest overwintering site show substantial reduction and an earlier peak in the post-crash era, and are robust to differences in abundance. (**C**) High numbers of monarch observations allow us to fit the past eight years individually, calculated as in Fig. 1F. The dramatic decline in maximum distance from overwintering sites (OWS) exactly corresponds to the crash in early 2018; the bounce in 2020-2021 corresponds to a partial recovery of the maximum distance.

Figure 1

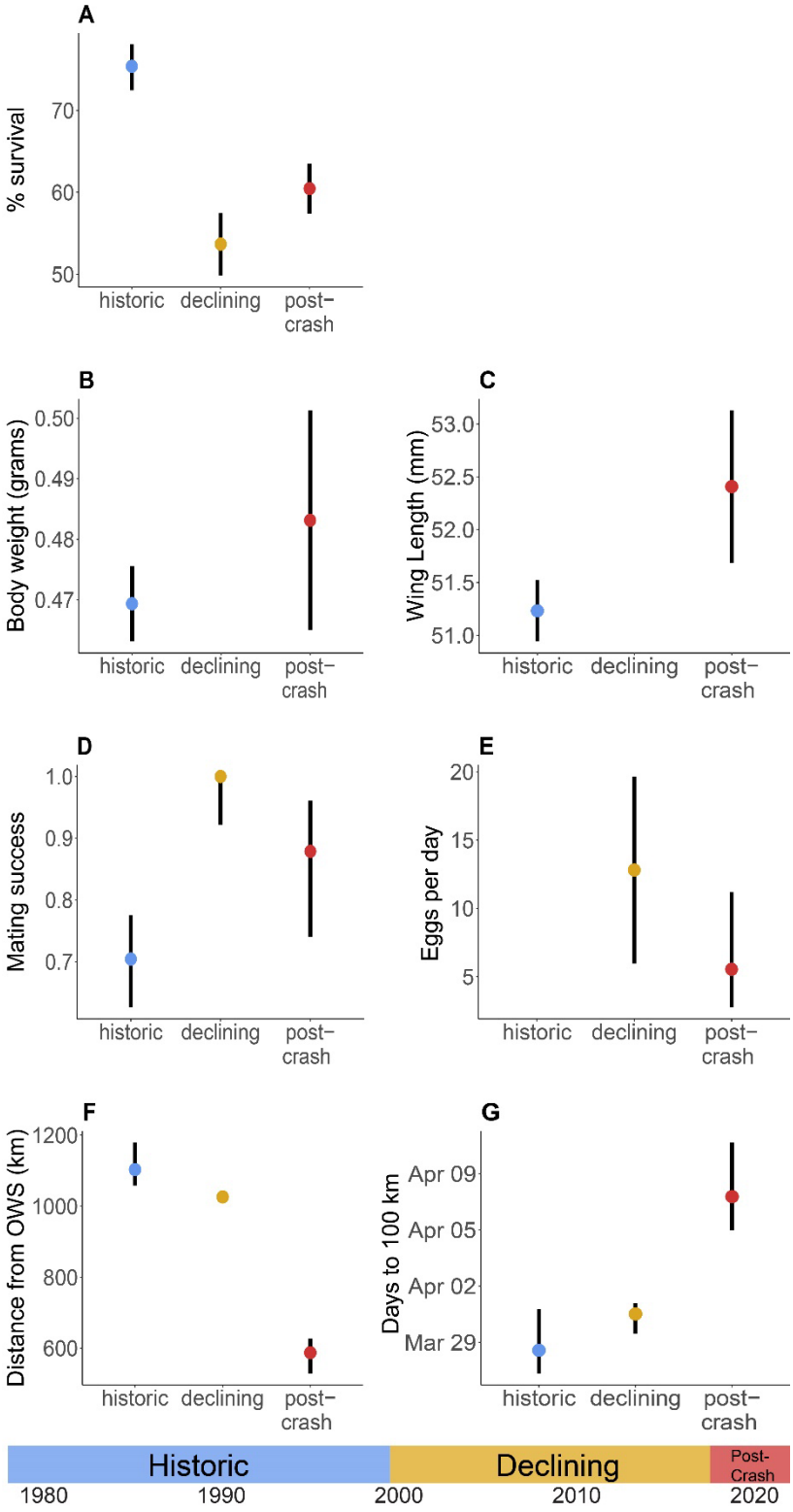
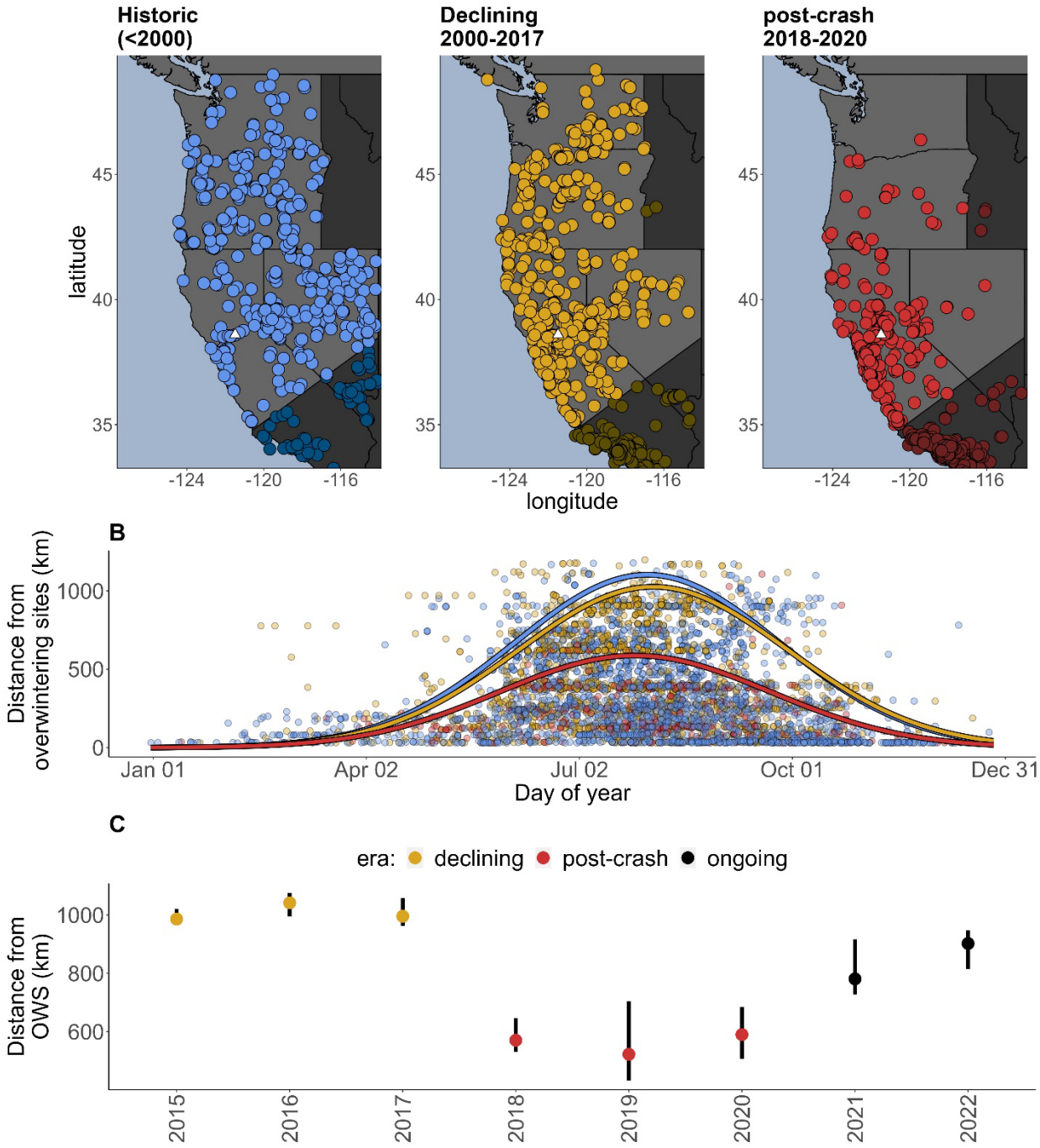
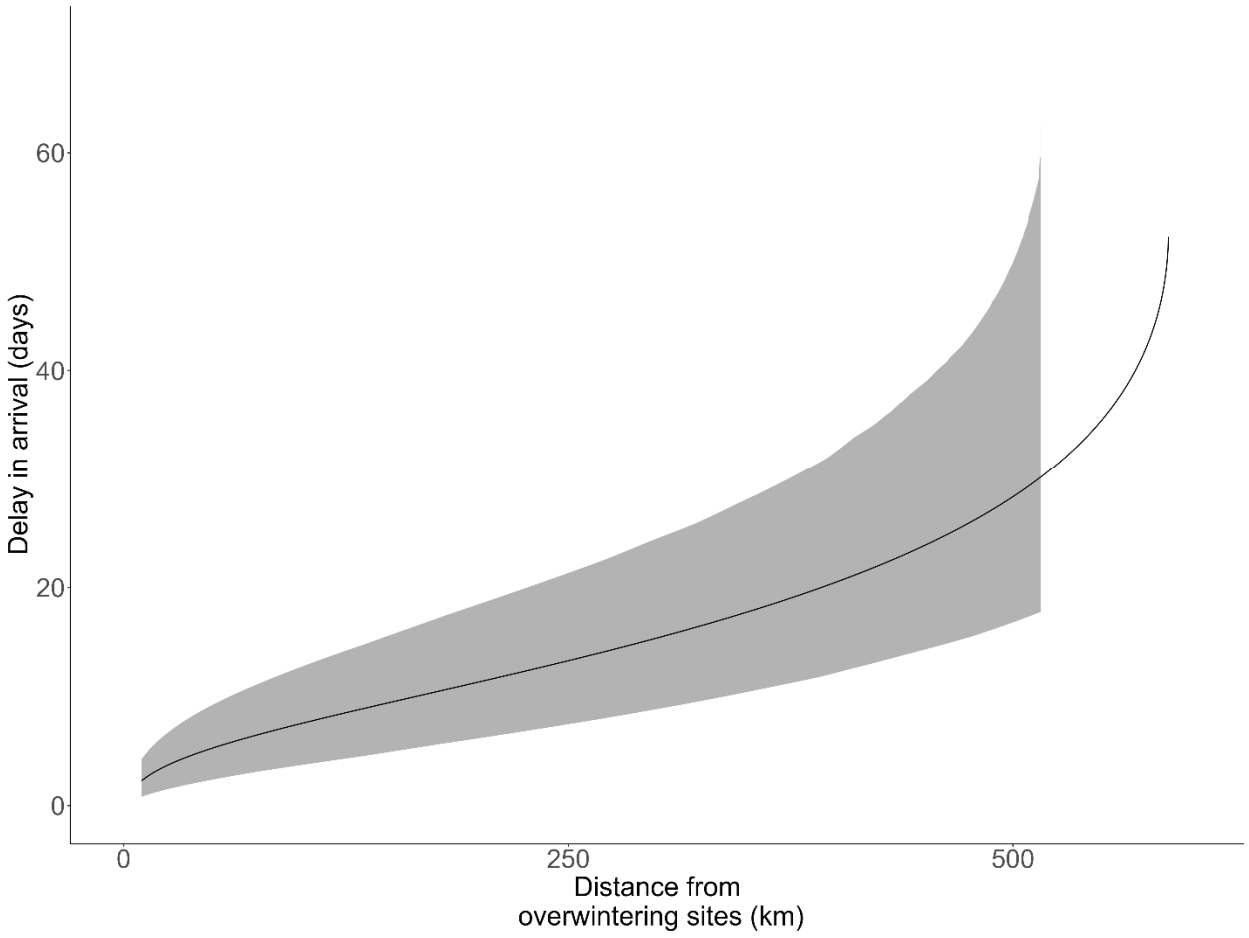

A
% survival
70
60
50
historic
declining
post–crash
B
Body weight (grams)
0.50
0.49
0.48
0.47
C
Wing Length (mm)
53.0
52.5
52.0
51.5
51.0
D
Mating success
1.0
0.9
0.8
0.7
E
Eggs per day
20
15
10
5
F
Distance from OWS (km)
1200
1000
800
600
G
Days to 100 km
Apr 09
Apr 05
Apr 02
Mar 29
Historic
Declining
Post-Crash
1980
1990
2000
2010
2020

Figure 2

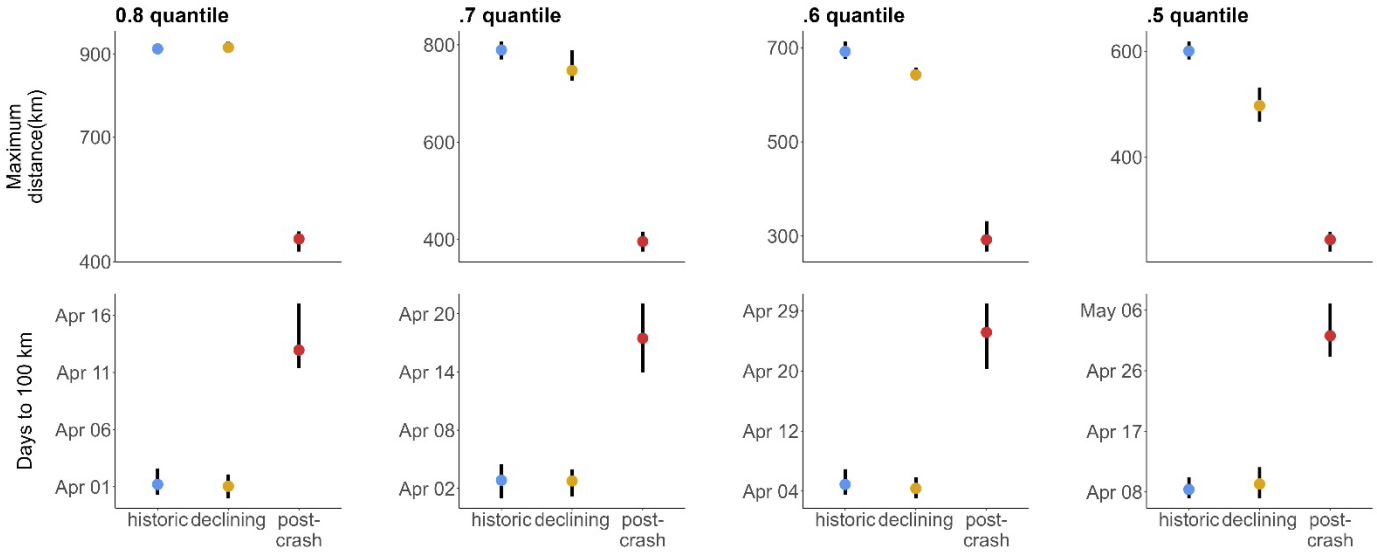

Historic
(<2000)
Declining
2000-2017
post-crash
2018-2020
latitude
45
40
35
-124
-120
-116
longitude
B
Distance from
overwintering sites (km)
1000
500
0
Jan 01
Apr 02
Jul 02
Oct 01
Dec 31
Day of year
C
era: declining post-crash ongoing
Distance from
OWS (km)
1000
800
600
2015
2016
2017
2018
2019
2020
2021
2022

Movie S1: Western monarch butterfly seasonal range expansion reaches half the distance and takes up to 1.5 months longer since the population fell below the hypothesized Allee effect threshold. Top: plots of raw data observations separated by era (Historic = 20th century, Declining = 2000-2017, Post-crash = 2018-2020). Colored circles represent observations in the last 7 days; smaller white diamonds act as placeholders to identify locations of earlier observations. Darker gray regions were excluded from analysis, including southern regions of CA and NV to avoid non-migratory 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.

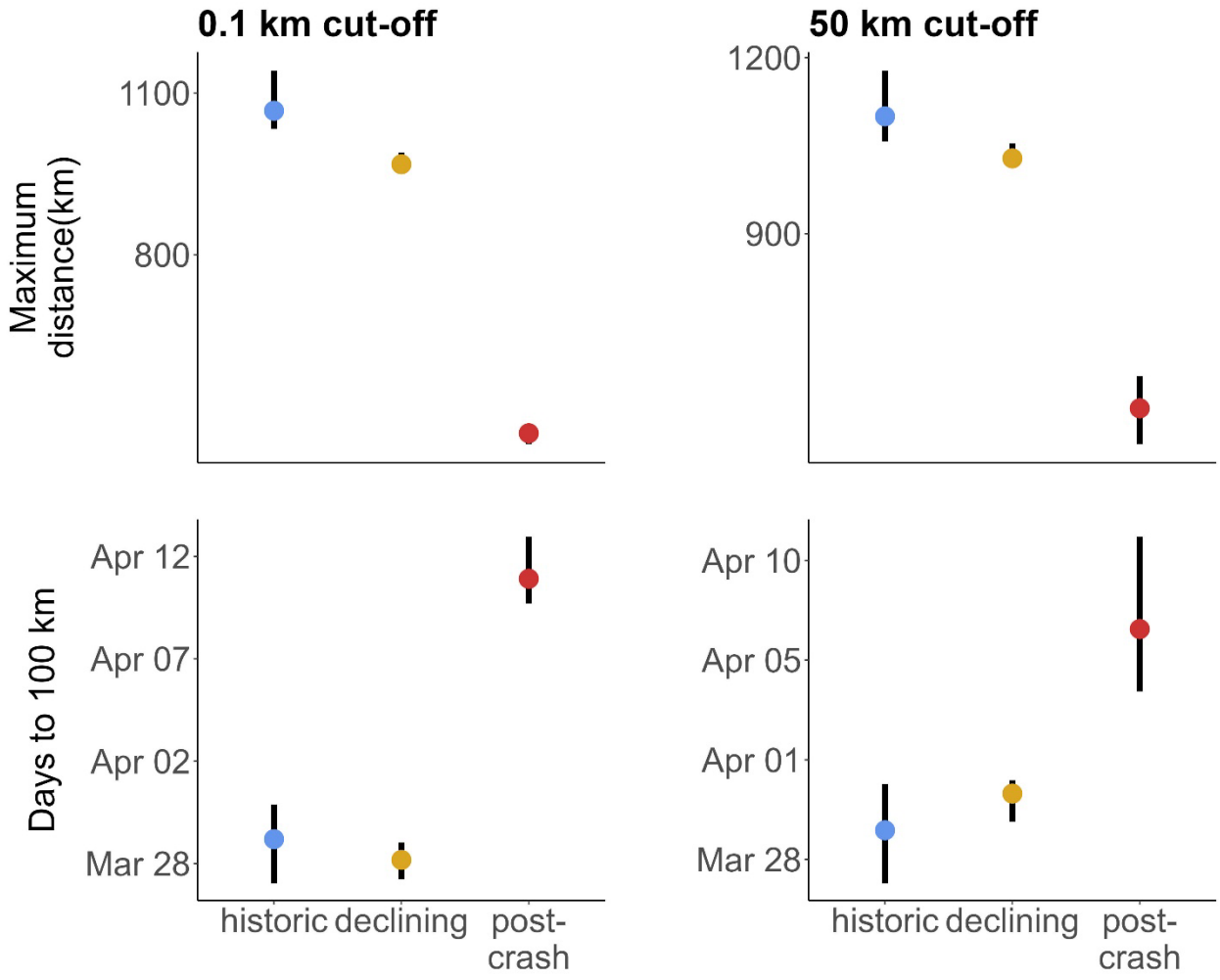
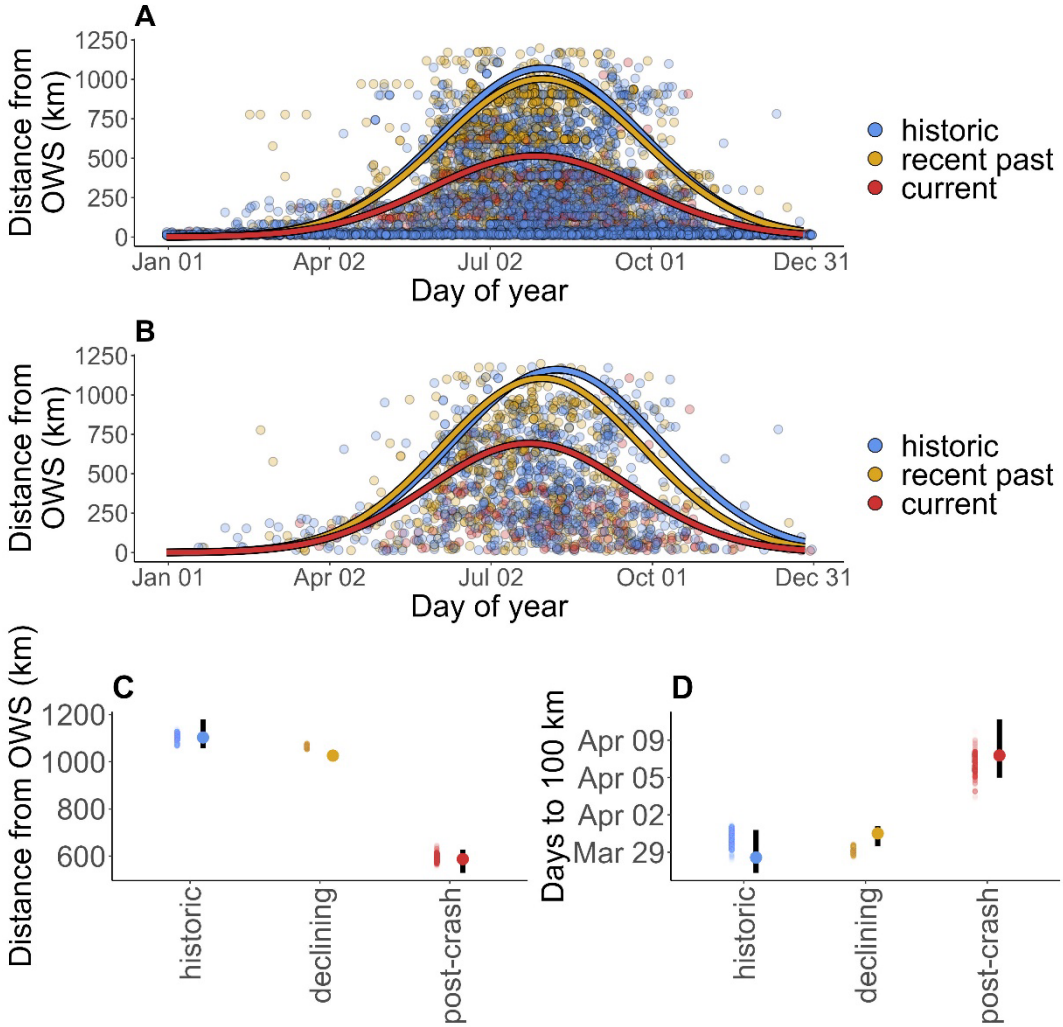
Supplemental Figure S1: Difference in the days to 0.9 quantile between the declining and post-crash eras as a function of distance. Western monarch phenology was delayed in the post-crash era, and for regions sufficiently far from overwintering sites, the 0.9 quantile of seasonal range expansion arrived more than a month later in the post-crash era. Black line shows estimated distance, gray area shows bootstrapped 95% confidence envelope.



Supplemental Figure S2: Qualitative patterns of seasonal range expansion are insensitive to changes in the quantile choice. We repeat our analyses and replicate Fig. 1F and 2C using 0.8 to 0.5 quantiles (as compared to 0.9 in the main text).



Supplemental Figure S3: Qualitative patterns of seasonal range expansion are insensitive to choice of threshold distance for excluding observations near the overwintering sites. We repeat our in the quantile choice. We repeat our analyses and replicate Fig. 1F and 2C for 50 km or 0.1 km threshold distances (as compared to 30 km in the main text).



Supplemental Figure S4: (A) Data showed apparent horizontal "streaks" of multiple data points at the same distance from overwintering sites, potentially representing individual locations with frequent sampling. To ensure dynamics of these locations were not biasing our results, we simulated data by randomly sampling only one observation per era per kilometer of distance from the overwintering site (i.e., "data thinning"). (B) Example of this simulated data. C-D: range and phenology metrics calculated from 5000 simulated datasets (cloud of points, left) qualitatively reflected the estimates from the full data set (point and bars, right, same as Fig. 1F-G).