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Short communication

Citizen science monitoring demonstrates dramatic declines of monarch butterflies in western North America

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ABSTRACT

Count-based PVA allows researchers to assess patterns of population change through time and to evaluate future persistence. We combined state-space models and citizen science data to evaluate viability of the western population of monarch butterflies over 36 years. A key feature of our analysis was combining irregular sampling from multiple sites to obtain a single estimate of total abundance using state-space models. The average population growth rate was negative, $u = -0.0762$ ($\lambda = 0.927$), average abundance in the 2000s was < 5% of average abundance in the 1980s, and current quasi-extinction risk is 72% within 20 years. Despite wide confidence intervals in some parameter estimates, western monarch monitoring data provide unambiguous evidence for dramatic population declines. To obtain viable populations, managers could target historic abundance and high enough growth rates to avoid near-term extinction.

1. Introduction

From time to time, widespread species decline in abundance so much that they appear to be at risk of extinction. Assessing such declines in the context of historic observations and yearly fluctuations, however, presents a challenge: Are observed declines sufficient to substantially increase extinction risk? Abundance data from long-term monitoring allow us to quantitatively evaluate this question. Count-based population viability analysis (PVA; Dennis et al., 1991; Morris and Doak, 2002; Fieberg and Ellner, 2000) estimates two parameters from monitoring data: a density-independent annual rate of population growth or decline, and year-to-year variation in this population growth rate, i.e., environmental stochasticity. These parameters, combined with current population size, can be used to predict extinction risk (Morris and Doak, 2002) and evaluate the magnitude of changes needed to ensure persistence (e.g., Molano-Flores and Bell, 2012).

Here, we used count-based PVA to evaluate the current status and future prospects of monarch butterflies (*Danaus plexippus plexippus*) in western North America. Like many at-risk species, systematic monitoring of this population began after dramatic declines had already been noticed. Therefore, it has been difficult to assess the status of the western monarch population with respect to historic abundance. We addressed this concern by finding appropriate statistical models to

integrate irregular sampling during the 1980s and 1990s with more systematic monitoring during the past 20 years. Our case study highlights how modern statistical tools can help us make use of long-term monitoring data collected by citizen scientists for status assessment of at-risk species.

Monarchs, well-known for their distinctive migration from their breeding range to overwintering sites in Mexico and coastal California, were once common throughout most of North America. Recently, the viability of eastern monarchs, which overwinter in Mexico, has received considerable attention (Inamine et al., 2016; Pleasants et al., 2016; Semmens et al., 2016). Western monarchs, which breed west of the Rocky Mountains and are considered a distinct population from eastern monarchs, have been largely ignored in the literature and popular press. Most western monarchs overwinter in wooded groves along coastal California, with limited numbers overwintering in Mexico (Morris et al., 2015; Yang et al., 2016). As with eastern monarch declines in Mexico, changes in California overwintering populations may indicate threats occurring in breeding states, or coastal overwintering habitat loss and degradation, and beg the question of population viability.

For several decades, volunteers have been counting overwintering monarchs in coastal California. The data consist of overwintering butterfly counts in individual groves, each of which represents a subset of

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the entire breeding population. The vagaries of the data, e.g., year-to-year fluctuations in population size, added or missing sites across years, and count errors, require sophisticated methods of analysis only recently available to ecologists. State-space models account for noisy data by separating observation error from processes of population growth and environmental stochasticity (DeValpine and Hastings, 2002; Holmes et al., 2012). Here, we used state-space models to estimate the western monarch population growth rate from spatially and temporally erratic sampling data, and show how short-term population fluctuations can have long-term consequences in a species of conservation concern.

2. Materials and methods

2.1. Western monarch wintering sites database

We used overwintering monarch count data from the Xerces Society's Western Monarch Overwintering Sites Database (Xerces Society for Invertebrate Conservation, 2017). This database includes monitoring data from the Western Monarch Thanksgiving Count (WMTC, 1997–present), information from numerous reports, and personal communications (Pelton et al., 2016; see westernmonarchcount.org). For our study, we included records from this database collected using a similar protocol during comparable time periods to the WMTC (November–December). We filtered the full dataset to include only sites monitored at least five years (see Supplement 6). Our analysis includes 186 sites, with counts from 1981–2016 (Fig. 1).

2.2. State-space models

We analyzed count data using multivariate autoregressive state-space (MARSS) models implemented in the MARSS package in R (Holmes et al., 2012; R Core Team, 2016; commented R code in Supplement 1). Similar to published PVA for eastern monarchs (Semmens et al., 2016), we assumed that western monarchs comprise a single population with a single rate of overall change in abundance and a single parameter for among-year variation in the population growth

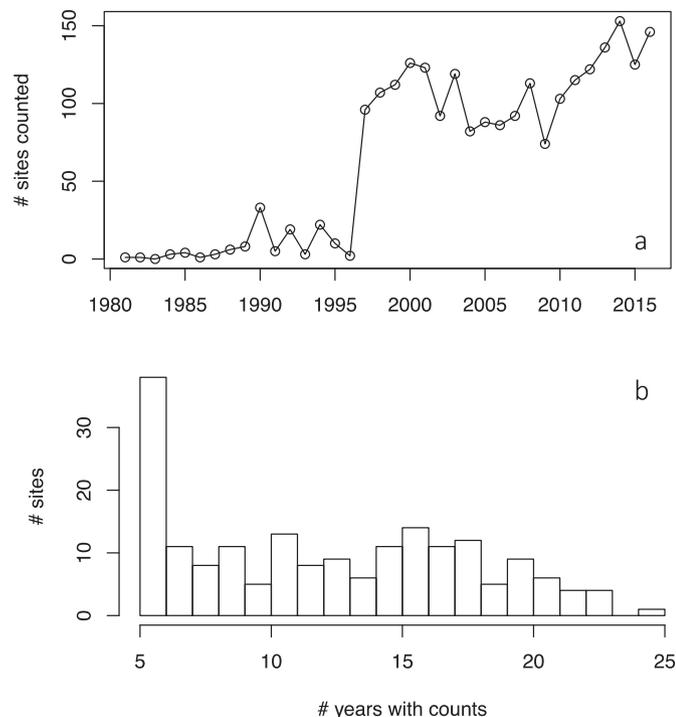


Fig. 1. Number of (a) sites counted per year and (b) frequency of years of data per site for sites used in analyses. All data are from the Western Monarch Overwintering Sites Database.

rate. We also assumed that each site at which monitoring took place in a given year was an independent index of the total abundance in that year (see supporting analyses in Supplements). For each site, the MARSS procedure estimates a parameter for proportionality between the site count and the total population, and an observation error variance parameter unique to each site but stationary through time. These assumptions are expressed using two sets of equations. The first set describes stochastic, density independent, population dynamics:

$$\ln(N_t) = \ln(N_{t-1}) + u + \varepsilon_t$$

$$\varepsilon_t \sim \text{Normal}[0, \sigma_u]$$

where N_t is the regional abundance (total number of western monarchs) in year t , u is the log-scale annual population growth rate, and ε_t is environmental stochasticity (year-to-year variation in population growth rate). Back-transforming this model yields a simple stochastic population growth model, $N_t = \lambda_t N_{t-1}$, where $\lambda_t = \exp(u + \varepsilon_t)$.

The second set of equations describes the relationship between counts at each site and the regional abundance:

$$\begin{bmatrix} \ln(y_{1,t}) \\ \vdots \\ \ln(y_{186,t}) \end{bmatrix} = \ln(N_t) + \begin{bmatrix} a_1 \\ \vdots \\ a_{186} \end{bmatrix} + \begin{bmatrix} v_{1,t} \\ \vdots \\ v_{186,t} \end{bmatrix}$$

$$v_{i,t} \sim \text{Normal}[0, \sigma_{a,i}]$$

where $y_{i,t}$ is the count of butterflies at site i , a_i describes the relationship between the average count at site i and regional abundance (i.e., N_t), and $v_{i,t}$ is the normally-distributed among-year “observation error” with mean 0 and standard deviation $\sigma_{a,i}$. Back-transforming the log-scale relationship makes the count versus abundance strictly proportional: $y_{i,t} = N_t \exp(a_i + v_{i,t})$. In addition, there are different constants of proportionality and observation error parameters for each site, but all sites contribute to inference about the total population.

MARSS models assume that each site contributes to the total abundance, and fit models of y_t to each site based on years when counts were made at that site. In other words, in a year when four sites are counted, we expect the total count to be $\exp(a_1 + a_2 + a_3 + a_4)N_t$. If ten sites are counted, the expected total is $\exp(a_1 + a_2 + a_3 + a_4 + a_5 + a_6 + a_7 + a_8 + a_9 + a_{10})N_t$, etc. Therefore, this model implicitly adjusts for missing data (Holmes et al., 2012; Tolimieri et al., 2017). Because of the scaling factor, the MARSS model gives an index of abundance proportional to total abundance.

2.3. Model checks and evaluation

Visually, annual estimates of monarch abundance did not meet our expectations for stereotypical stochastic exponential decline (see Results and Fig. 2a); specifically, there seemed to be a change in the growth rate over time. To evaluate whether growth rates were stationary over time, we converted log-scale annual abundance estimates to log-scale annual population growth rates, i.e.,

$$\hat{u}_t = \ln(\hat{N}_t) - \ln(\hat{N}_{t-1})$$

where \hat{u}_t and \hat{N}_t are the estimated annual growth rate and regional abundance in year t . We used the MARSSparamCIs function to estimate the standard error associated with \hat{N}_t and converted this to standard error of \hat{u}_t using the delta method implemented via the msm package in R (Jackson, 2011).

We used Generalized Additive Models (GAMs, Zuur, 2012), estimated with generalized cross-validation as implemented in the mgcv package in R (Wood, 2011), to evaluate trends in annual population growth rate, and squared deviations of \hat{u}_t from the average \hat{u}_t (i.e., variance of \hat{u}_t ; cf. Fagan and Holmes, 2006). If population growth were consistent with the simple exponential model, we would expect non-significant smoothed terms for the mean and variance of \hat{u}_t in relation to time. We also evaluated stationarity of the mean and variance in

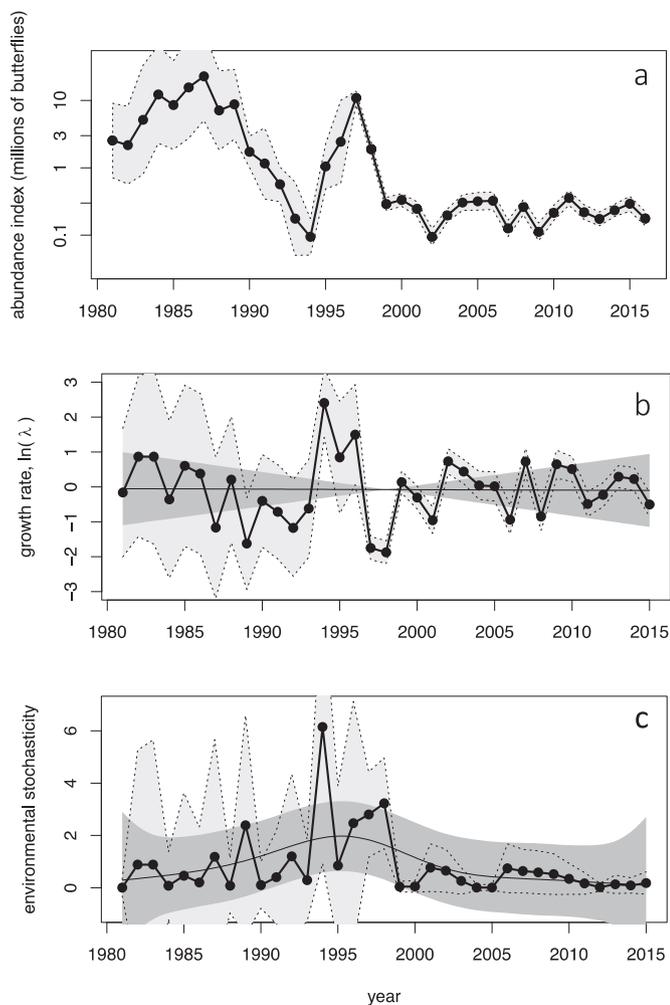


Fig. 2. Western monarch butterfly 1981–2015 estimates for (a) overwintering abundance in coastal California, (b) population growth rate, $\ln(\lambda)$, population growth rate and (c) environmental stochasticity (i.e., squared deviations of annual growth rates from average growth rate). Light gray envelopes are 95% confidence intervals for estimates in each year (a, b & c); dark gray envelopes are confidence intervals for GAM smoothers (b & c).

growth rate using a breakpoint analysis (Supplement 3), autocorrelations followed by Ljung-Box tests (Supplement 4), and a level change test (Supplement 2). Conclusions were consistent across tests, so we only present the GAMs, which are the most flexible, in the main manuscript text.

2.4. Population viability metrics

We used maximum likelihood estimates (MLEs) of u and σ_u (estimated via the MARSS() function) to calculate the probability of persistence. We based calculations on current (2000–2016) and historic (1981–1989) average abundance. We approximated extinction risk using diffusion approximation (Dennis et al., 1991) and code modified from Morris and Doak (2002) in the popbio package in R (Stubben and Milligan, 2007) to calculate quasi-extinction risk, i.e., the probability a population reaches a threshold below which it is likely doomed to extinction. We used an extinction threshold of 30,000 butterflies based on expert opinion about densities needed to thermoregulate and support mating during winter (Wells and Wells, 1992; Wells et al., 1998), assuming butterflies are distributed across several sites. Because this estimate is based on expert opinion, we explored a lower ($n = 20,000$ butterflies) and a higher ($n = 40,000$ butterflies) threshold. We also calculated quasi-extinction risk using a lower estimate of variance obtained by analyzing a dataset including sites with > 20 counts

(Supplement 6).

3. Results

3.1. State-space models

Based on the MARSS model, the average log-scale population growth rate, u , for western monarchs is -0.076 (SE = 0.182), equivalent to a discrete-time annual growth rate of $\lambda = 0.927$ (95% CI = 0.668, 1.345). The estimated among-year variance of log-scale growth rates, σ_u^2 , is 1.077 (SE = 0.279). Annual abundance estimates were high in the 1980s, fluctuating in the 1990s, and low in the 2000s (Fig. 2a). The standard error of estimates (Fig. 2a–c) is higher in earlier years due to less regular monitoring (Fig. 1b). Average abundance from 2000–2016 was 3.5% of that from 1981–1989; 95% confidence limits of this ratio (estimated using the delta method) are 2.4%–6.7%. If we scale this estimate using recent maximum counts of $\sim 300,000$ butterflies (e.g., 293,435 counted in 2015, 293,040 in 2016), we estimate that there were at least 4,500,000 butterflies in the 1980s (Fig. 2a).

3.2. Model checks

Population growth rate was constant during the study period (GAM of u versus time: $F = 0.009$, $P = 0.925$, smoother df = 1.0; Fig. 2b; see also Supplements 2, 3 and 4). However, there was a trend for higher environmental stochasticity during the 1990s than the 1980's or 2000's (GAM of (residual u)² versus time: $F = 2.307$, $P = 0.070$, smoother df = 5.4; Fig. 2c; see also Supplements 2 & 4). The average squared deviation in the 1980s and 2000s was 0.5, and in the 1990s was 1.6.

3.3. Population viability metrics

Using point estimates of $u = -0.076$ and $\sigma_u^2 = 1.077$, and the approximate count of in the most recent surveys (300,000 butterflies), the western monarch has a quasi-extinction probability of 0.717 within 20 years and 0.862 within 50 years (range with lower/higher extinction threshold = 0.665/0.754 in 20 years and 0.834/0.881 in 50 years). Assuming the average variance in the 1980s and 2000s, $\sigma_u^2 = 0.500$, and the approximate count of in the most recent survey (300,000 butterflies), the western monarch has a quasi-extinction probability of 0.631 within 20 years and 0.842 within 50 years. If the population were not declining ($u = 0$) at its current size and variance, quasi-extinction risk would be 0.467 in 20 years and 0.654 in 50 years. A population of 300,000 monarchs with $\sigma_u^2 = 0.500$ would need an annual growth rate of $u = 0.300$ ($\lambda = 1.34$) to achieve 0.05 probability of quasi-extinction within 20 years (and $u = 0.240$, assuming $\sigma_u^2 = 0.38$ as estimated from the time series with higher count threshold, Supplement 6). For a larger population (4,500,000 monarchs, similar to the 1980s) with $u = -0.076$ and $\sigma_u^2 = 0.50$, the probability of quasi-extinction in 20 years is 0.224 (and 0.179 assuming $\sigma_u^2 = 0.380$). If a population of 4,500,000 butterflies were not declining ($u = 0.000$, $\sigma_u^2 = 0.500$), it would have a 0.113 probability of quasi-extinction within 20 years (and 0.069 assuming $u = 0.000$, $\sigma_u^2 = 0.380$). With $u = 0.000$ and $\sigma_u^2 = 0.500$, ≥ 10 million butterflies would be needed for ≤ 0.05 quasi-extinction risk within 20 years.

4. Discussion

Our analysis informs status assessment and recovery goals for the western monarch butterfly. The population has declined over the past 36 years and MLE parameters predict high risk of extinction: ~ 50 –75% within 20 years and ~ 65 –85% within 50 years. This level of risk exceeds estimates for the eastern population. Semmens et al. (2016) estimated an annual growth rate of $u = -0.06$ and $\sigma^2 = 0.24$ for eastern monarchs, and a 62% risk of reaching a quasi-extinction threshold of 0.25 Ha of overwintering habitat (~ 9 million individuals) from trends

in breeding and overwintering habitat. Flockhart et al. (2015) estimated an annual growth rate of $u = -0.033$ and a 3–4% chance of reaching an extinction threshold of 1000 eastern monarchs (~0.0025 Ha of overwintering habitat). Like our analysis, both Semmens et al. and Flockhart et al. report uncertainty in their point estimates of u and a confidence intervals which include $u = 0$. To ensure persistence of western monarchs, we recommend reaching and maintaining the lower confidence interval of our estimate of abundance from the 1980s (~4.5 million overwintering butterflies) at a minimum, i.e., high enough for likely persistence if $u = 0$ and variance is similar to historic levels. We also recommend aiming for a near-term growth rate of $u = 0.3$ ($\lambda = 1.34$), i.e., high enough to minimize extinction risk during recovery. The lower extinction threshold and lower estimate of minimum viable population size for western monarchs, compared to the eastern population, is consistent with the fact that the monarch population at overwintering sites has consistently been smaller in the west than the east, through at least the past half-century (Pelton et al., 2016; Pleasants et al., 2016).

Western monarch monitoring data provide unambiguous evidence for dramatic population declines. However, there are two possible explanations for this decline: negative ($u < 0$) population growth rate, or steady state population ($u \approx 0$, which is included in the confidence interval) with high variance. The importance of environmental stochasticity in determining extinction risk is well known to theoretical ecologists (Fagan et al., 2001; Inchausti and Halley, 2003; Fagan and Holmes, 2006), but not always appreciated in conservation decision-making. Both possibilities indicate the need for a near-term increase in population growth rates, although the magnitude of near-term extinction risk differs between $u = -0.07$ (the MLE) and $u = 0$. Given the high variation in annual population growth rates, it will be difficult to distinguish these two possibilities from monitoring data at overwintering sites. We encourage development of life cycle models based on field-estimated vital rates as a powerful tool for both assessing population status and effects of management (see Morris and Doak, 2002 for general discussion and Schultz and Crone, 1998 and Brown et al., 2017 for application to at-risk butterflies). Although monarchs have been extensively studied in many ways, some key vital rates are poorly understood, even for the well-studied eastern population (Flockhart et al., 2015; Oberhauser et al., 2017).

In closing, a strength of our analysis is the use of citizen science data to obtain a long time-series of abundance estimates. These data unambiguously show dramatic declines in abundance. Although there was some evidence that environmental stochasticity is lower now than in the 1990s, there is no evidence that the average population growth rate has changed. There is also no evidence that observation error changed from the early to later periods (Supplement 2), perhaps in part due to selection of historic data collected with comparable methods to current volunteer surveys (see Tolimieri et al., 2017 for a contrasting example in rockfish). The oldest data were usable because we had a statistical method to account for irregular sampling through space and time (Holmes et al., 2012). Conservation biologists are increasingly asked to assess how long-term trends in environmental conditions affect plant and animal populations, and citizen science data are an important resource for evaluating these trends (Silvertown, 2009). This case study emphasizes the importance of developing statistical methods for robust inference from existing data, as declines of formerly widespread species may take conservation biologists by surprise.

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Appendix A. Supplementary data

Supporting material include (S1) R code for main analysis, (S2) test if variance in observation error is constant over time, (S3) test if breakpoint model for population growth rate is better than model with a single constant growth rate, (S4) test for stationarity of mean and variance using autocorrelation tests and ADF test for a random walk vs stationarity in time series, (S5) R code for S2, S3 and S4, (S6) Additional analyses with smaller subsets of the data as well as tests of covariance between sites, and (S7) R code for S6. Supplementary data associated with this article can be found in the online version, at <http://dx.doi.org/10.1016/j.biocon.2017.08.019>.

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