The Disconnect Between Summer and Winter Monarch Trends for the Eastern Migratory Population: Possible Links to Differing Drivers

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ABSTRACT The decline of the eastern population of the migratory monarch has become a topic of great concern, but has been based entirely on patterns observed in overwinter colony sizes. Less attention has been paid to population trends during other phases of the migratory cycle. Here, we present an analysis of trends using three monitoring programs, one focused on overwinter colony size and two focused on summer breeding grounds. We discovered an alarming steepening in the decline of winter colony size since 2008. However, population indices from two independent summer monitoring programs were characterized by high year-to-year variability and no statistically detectable trends over time. Despite the mismatch in summer and winter patterns, there is still an association between the yearly fluctuations between these key periods, suggesting a link in population dynamics throughout the year. Further, a suggestion of a downturn near the end of the summer time-series should be carefully tracked into the future. We discuss two possible reasons for this disconnect: 1) higher levels of variance or possibly biased sampling could weaken any statistical signal, and 2) losses during fall migration could potentially contribute to overwinter declines.

KEY WORDS ecology and population dynamics, conservation, Papilionidae

Monarch butterflies (*Danaus plexippus*) are distributed globally, but only in North America does regular, round-trip migration occur. These migrations occur over several generations and adults of each year's final generation return to the same overwinter colony locations year-after-year, despite the fact that returning adults have never been to those colonies (Oberhauser 2004). The spectacular nature of these migrations is one of the factors that have made monarchs the most beloved insect as well as one of the most highly valued species by the American public (Diffendorfer et al. 2014). The Rocky Mountains divide monarchs into relatively distinct eastern and western migratory populations. Here, we focus on the eastern population, which famously has individuals that travel up to 4,500 km to return to a very restricted area of mountain tops in central Mexico, where they overwinter in dense colonies (Oberhauser 2004). A simplified version of the migration of the eastern monarch population is shown in Figure 1.

Over the past several years, concern for the health of the eastern population of the monarch has grown as the overwintering population in Mexico has shown a steady decline (Toone and Hanscom 2003, Brower et al. 2012, Vidal and Rendon-Salinas 2014). However, there has been some controversy about the status of the eastern population, as the decline observed in overwintering populations has not been observed when examining trends during the fall migratory phase (Davis 2012) and trends in other critical steps are relatively unexplored (Ries et al. 2015).

Considering the fact that the migratory cycle of the monarch is so complex, the question arises about the ideal time to assess their yearly population size. As noted, the majority of focus has been on the colony size at the beginning of the overwinter period, after the colonies are fully established but before significant winter mortality begins (Vidal and Rendon-Salinas 2014). This is the easiest time to make a population estimate, as the vast majority of individuals are concentrated in a restricted area (Vidal and Rendon-Salinas 2014). Because overwinter mortality does occur and can be substantial (Brower et al. 2004), the population in Mexico at the end of the winter is also an important point in time, as this represents the actual number of individuals available to seed the next year's population. Another critical point in the cycle is the end of the summer breeding season (Fig. 1, Step 4), when recruitment during the reproductive season promotes growth until the population is at its largest point each year. It is this period of recruitment that determines how resilient the population is and if it is able to bounce back from any previous population losses; yet, because the population is spread throughout much of eastern North America, it is harder to assess its size. Nevertheless,

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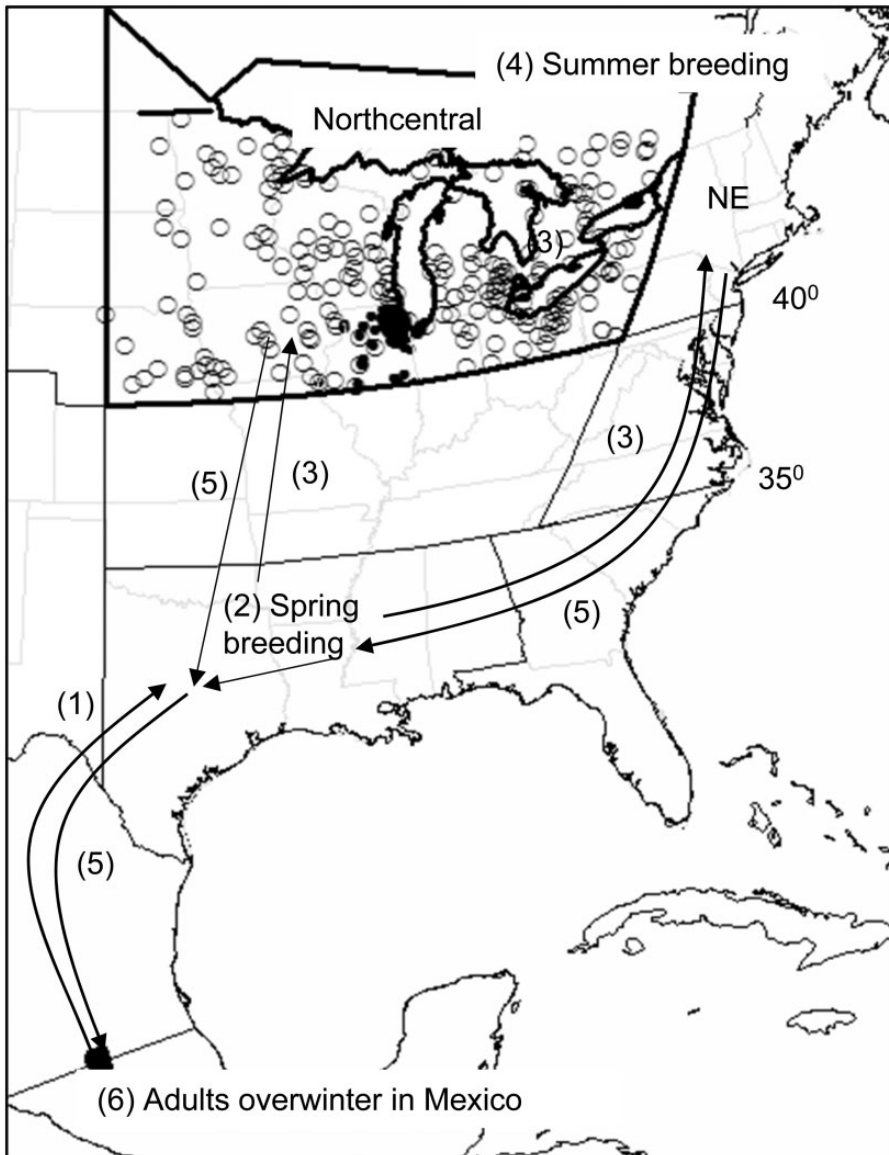
Fig. 1.   A simplified map showing the major steps of the monarch migration: (1) spring migration, (2) spring breeding, (3) summer expansion, (4) majority of summer breeding in the northeast (NE) and north-central regions, (5) southward fall migration, and (6) adults overwintering in Mexico. Our analysis focused on the overwinter colonies (Step 6) and the north-central region during recruitment (Step 4). Data summarizing trends for the northeast region came from two monitoring programs: NABA's count program (survey sites shown with open circles) and Illinois' monitoring network (closed circles).

there are several monitoring programs that can provide yearly indices, yet there has been little exploration of population trends during the breeding season. The only example we are aware of is that of Swengel (1995), which did not report a trend, but noted extreme population fluctuations from year-to-year.

Here, we use the most up-to-date monitoring data to examine three key points for the population each year: the beginning and end of the overwinter period based on colony sizes in Mexico (Fig. 1, Step 6) and the end of the summer recruitment period (Fig. 1, Step 4) in the north-central region when the

population has grown to its yearly maximum size. We focus on trends, year-to-year variability, and how strong the association is in yearly fluctuations between these critical periods. We begin our analysis from the year 1993 because that is the year that regular monitoring began in Mexico (Vidal and Rendon-Salinas 2014). Our goals are to:

1. describe trends in population indices separately for winter (beginning and end) and peak summer periods using the most up-to-date monitoring data currently available (through 2014); and

2. examine similarity and differences in trends, including relationships in year-to-year variability at critical points in the population cycle.

Materials and Methods

We used data from three monitoring programs to examine population trends during the three critical periods that are our focus: peak summer breeding populations, and overwinter colony size (beginning and end). For summer breeding, we focus solely on the north-central region (Fig. 1) because this is where the majority of adults arriving on the overwintering grounds originate from (Wassenaar and Hobson 1998). For this period, we used data from two, independent survey programs, so that we could increase the confidence in our indices of population size. The first summer monitoring program is the North American Butterfly Association's (NABA) Seasonal Count Program and the second is a program run by the Illinois Butterfly Monitoring Network (IBMN). Both are volunteer-based (citizen science) programs that establish set survey sites and use specified protocols to collect abundance data on the entire butterfly community. There is one other long-term adult monitoring program in the north-central region based in Ohio, but data were not available through 2014, so we did not use them for these analyses. Past examinations comparing monarch abundance indices from IBMN, NABA, and Ohio have shown consistent yearly patterns (Ries et al. 2015). For overwintering populations, we use data from monitoring of the overwinter colonies, which has been ongoing continuously since 1993. We describe each of these programs below and how we calculated a yearly index as a proxy for overall population size that could be compared between years and programs.

NABA's Seasonal Count Program is a volunteer-based (citizen science) program where count circles are established by local coordinators using a system adapted from the Christmas Bird Counts (Swengel 1990). Circles are placed deliberately (not randomly) and are biased toward populated or natural areas. Each circle has a diameter of 15 miles and one to several people explore the circle during a single day and report all individuals of all species observed. Effort is accounted for by multiplying the amount of time spent by the number of parties that searched during the survey (party-hours). Most counts are performed once per year, usually in June or July. The count program was established in 1975 by the Xerces Society and taken over in 1992 by NABA (Swengel 1990). Currently, counts are conducted at about 450 sites each year throughout North America. To calculate our yearly summer index, we calculated the average number of monarchs per party-hour for all counts conducted in the north-central region (Fig. 1) during the period from 19 July–15 August.

The IBMN was established in 1987 and was patterned after the UK Butterfly Monitoring Scheme (Matteson et al. 2012), which follows the basic protocols described by Pollard (Pollard 1977) often called "Pollard walks". The basic protocol is for directors to establish routes and to assign a volunteer to walk those routes regularly over the course of the season. Routes are placed deliberately to capture a variety of habitats, but with an emphasis on natural areas. In Illinois, routes are walked at least six times per year (although more visits are encouraged), with most visits occurring between 1 June and 7 August (with at least four visits before 20 July). Routes vary in length and are walked at a constant pace with all butterflies seen within 6 m in front and to the sides of (not behind) the observer. All butterflies observed are recorded. Currently, about 100 routes are surveyed each year by the IBMN. To calculate our yearly index, we calculated the average number of monarchs per hour observed for all routes (which include some locations in Wisconsin and Indiana) that lie within the north-central region (any route above the 40° latitude band, see Fig. 1) during the period from 19 July to 15 August.

The overwinter colonies were discovered in 1975 (Urquhart and Urquhart 1976) and surveys to measure colony size were sporadic at first (Garcia-Serrano et al. 2004). Starting in 1993, regular monitoring of all known colonies took place each year in the last half of December, where the surface area of each colony was estimated using topographic maps (Garcia-Serrano et al. 2004). Starting in 2004, the World Wildlife Fund took over the monitoring of colonies within the reserve and expanded surveys to include eight monitoring periods rather than just one. Colony size is now estimated for the entire population in half-month periods beginning in December and continuing to the end of March (Vidal and Rendon-Salinas 2014). The area of the colony is currently now measured using GPS technology (Vidal and Rendon-Salinas 2014). Each year, an index of colony size is produced for all eight monitoring periods. Here, we report a post-arrival (beginning-of-winter) index compiled by WWF focused on the period during the second half of December, but depending on the dynamics of the season, sometimes drawing from other periods (Vidal and Rendon-Salinas 2014). For the pre-departure (end-of-winter) period, we used data from the period of the second half of February. These data are only available from 2005 onward.

Although there is an assumption that these population indices are robust estimates of population size and are comparable from year-to-year, this can be difficult to support directly without mark–recapture data or other more sophisticated monitoring methods (Haddad et al. 2008). Therefore, for this study, we are looking for a trend in the indices and whether those trends are similar between programs as a preliminary step to understand what mechanisms may be causing observed patterns. Patterns in indices are likely to be a combination of biological reality and biases in sampling schemes and we do not attempt to tease those apart here. NABA and IBMN have been shown to produce very similar year-to-year patterns (Ries et al. 2015), and that remains true with the data used for these analyses (Fig. 2). Each index has its strengths and weaknesses; NABA covers the entire north-central region, whereas
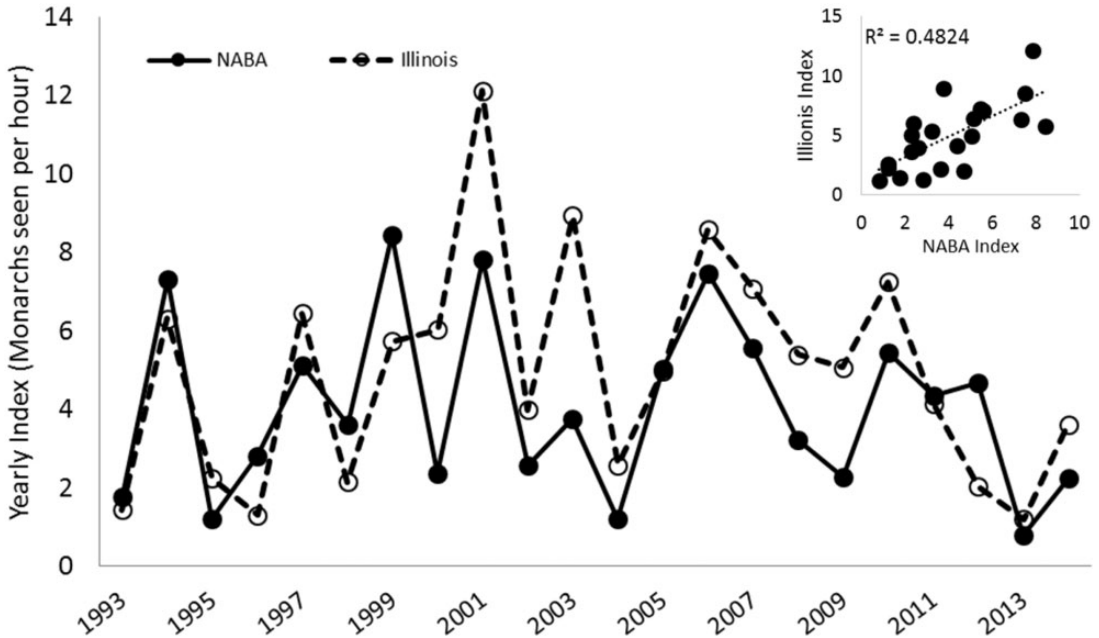
Fig. 2. Yearly indices for NABA and IBMN data from 1993 through 2014 in the north-central regions (see Fig. 1) between July 19 and August 15. The two indices are highly correlated (inset, **$P < 0.001$).

IBMN covers just a small portion, but IBMN has a much more intensive survey protocol. Because there was no reason to prefer one index over the other or a reasonable rationale to combine them, we ran all summer analyses separately using both indices.

To test whether there are any trends in population indices, we regressed indices on time (year $1993 =$ year 1) and tested for a significant slope parameter. We calculated slopes using ordinary linear regressions for the three focal periods (pre-departure at the wintering grounds, peak summer indices, and post-arrival back at the wintering grounds). In addition to ordinary linear regressions, we also determined if there were any significant break-points in the pattern by using piecewise linear regression. This technique determines if there is any significant change in slope and could be used to detect asymptotes or changes in population trajectory, either positive or negative (Toms and Lesperance 2003).

To determine if there is a predictive relationship between critical population periods, we used ordinary linear regression to determine if variability in pre-departure colony size in Mexico is a predictor of peak summer indices in the north-central region and, subsequently, whether those peak summer indices are then predictive of post-arrival colony size at the beginning of winter. If significant trends were discovered through the previous analysis, we performed the regression using residuals to detrend the data. Because only a positive association is expected, we used one-tailed tests for determining statistical significance of parameter estimates.

For any analyses including summer breeding, we weighted the regression using the number of surveys conducted each season. There were always the same

number of colony surveys during winter, so no weighting factor was used. We used Shapiro's test to determine if residuals were normally distributed and also examined residuals for evidence of heteroscedasticity; if found, response values were ln-transformed and then retested to determine if they met statistical assumptions (Quinn and McGeoug 2002). Outliers were discarded if they exhibited high leverage (Cook's D score >1) as per Cook and Weisberg (1982). Multiple tests for the same trends or associations were corrected separately for multiple comparisons using the Holm method (Holms 1979). For all regressions, we set an *a priori* alpha value of 0.05, but we considered trends ($P < 0.10$), especially when there was consistency between multiple comparisons. All analyses were done in R v.3.1.2 (R Core Team 2014). Piecewise regressions were calculated using the R-package "segmented" (Muggeo 2014).

Results

The indices produced from each monitoring period are presented, along with the number of surveys used to calculate summer indices, in Table 1. No analyses indicated any points with significant leverage, so no outliers were omitted. Estimated parameters and statistical tests for all regressions are shown in Table 2. Winter colony sizes were ln-transformed to meet assumptions. Colony sizes showed a significant decline based on beginning-of-winter colony sizes. A decline was also observed for the end of winter, but was not significant (Fig. 3a). However, end-of-winter colony estimates have only been made since 2005. The shorter time for which these data are available might have

been insufficient for detecting a pattern. The piecewise regression detected a significant change in slope for beginning-of-winter censuses at around year 16 (2008), suggesting a recent, sharper downturn in populations (Fig. 3a). However, the procedure failed for the end-of-winter, possibly owing to the shorter time-series.

There was no linear pattern with respect to year for either NABA or IBMN peak summer survey data (Fig. 3b). A significant shift in trend was detected at year 9 (2001) for IBMN, but this was associated with a single high population point in 2001 for the IBMN series (and the breakpoint disappeared after that high point was removed). For NABA, there was a significant breakpoint with a downturn estimated at year 19 (2011). This error estimate overlapped with the end of

the series, but also with the 2008 downturn noted in the overwinter data (Table 2). Currently, the evidence is equivocal for a recent downturn in summer populations; however, we will track these trends carefully into the future.

We found a trend for associations between end-of-winter colony sizes and subsequent summer peak values (Fig. 4a). As there was a significant trend in beginning-of-winter colony size (Fig. 3a), we used residuals in the test of association to remove any impact of a trend, especially as this trend was absent in the full series of summer numbers (Fig. 3b). Here, there was a significant relationship between summer peaks and subsequent arrival colony size in Mexico for both NABA and IBMN data (Fig. 4b).

Discussion

Population trends during the breeding season have not received much attention, despite the fact that population sizes at the end of the summer are the maximum point reached during a typical yearly cycle (Ries et al. 2015). Monarch populations arriving in Texas each spring are always much smaller than the ones heading back to Mexico the previous fall, suggesting that spring and summer recruitment is the key to monarch resilience. Further, these peak breeding numbers represent a critical point in their population cycle, although a much more difficult one to assess in terms of their population sizes (Vidal and Rendon-Salinas 2014). While the decline of the winter population is well-known (Toone and Hanscom 2003, Brower et al. 2012, Vidal and Rendon-Salinas 2014), this study is the first to show evidence for a quickening pace of decline (Fig. 3a). However, this study is also the first to show a disconnect with summer breeding populations; summer indices show no obvious pattern over the years (Fig. 3b). The pattern of high variability, but no trends, was first presented by Swengel (1995) and is updated here (Fig. 3b) overlapping a period associated with rapid declines in the winter population (Fig. 3a). Interestingly, explorations of trends of fall roosting sites at Cape May and Peninsula Point also indicated patterns at odds with the dominant story about declines (Davis 2012). Hereafter, we explore the extent and potential causes of this disconnect between summer and winter trends.

Table 1. Yearly indices from WWF, NABA, and IBMN monitoring programs for 1993 through 2014

Year	No.	Winter-end WWF	Summer-peak NABA (# surveys)	Summer-peak IBMN (#surveys)	Winter-start WWF
1993	1		1.76 (14)	1.44 (42)	6
1994	2		7.32 (12)	6.31 (50)	7.75
1995	3		1.22 (16)	2.24 (36)	12.5
1996	4		2.8 (17)	1.3 (44)	18
1997	5		5.11 (24)	6.44 (66)	5.75
1998	6		3.62 (13)	2.15 (46)	5.5
1999	7		8.44 (14)	5.74 (83)	9
2000	8		2.35 (22)	6.03 (86)	4
2001	9		7.83 (19)	12.12 (134)	9.25
2002	10		2.58 (25)	3.98 (145)	7.5
2003	11		3.75 (24)	8.94 (203)	11
2004	12		1.2 (18)	2.58 (211)	2.19
2005	13	1.62	5.03 (17)	4.96 (217)	5.92
2006	14	6.28	7.47 (18)	8.58 (199)	6.67
2007	15	3.51	5.55 (20)	7.08 (190)	4.61
2008	16	0.89	3.22 (23)	5.39 (202)	5.06
2009	17	3.4	2.28 (28)	5.06 (216)	1.92
2010	18	0.77	5.43 (17)	7.25 (149)	4.02
2011	19	2.95	4.36 (15)	4.15 (133)	2.89
2012	20	1.19	4.68 (13)	2.03 (107)	1.19
2013	21	0.89	0.79 (21)	1.19 (149)	0.67
2014	22	0.98	2.25 (22)	3.62 (150)	1.13

Summer indices are calculated based on number of hours surveyed per hours searched by each "party" (in the case of IBMN, there is always one observer in one party, but for NABA, there can be several observers among multiple parties). For NABA and IBMN, the number of surveys that each index is based on is included in the table. For WWF, the same number of colonies is measured each year in hectares. End-of-winter surveys by WWF did not begin until 2005.
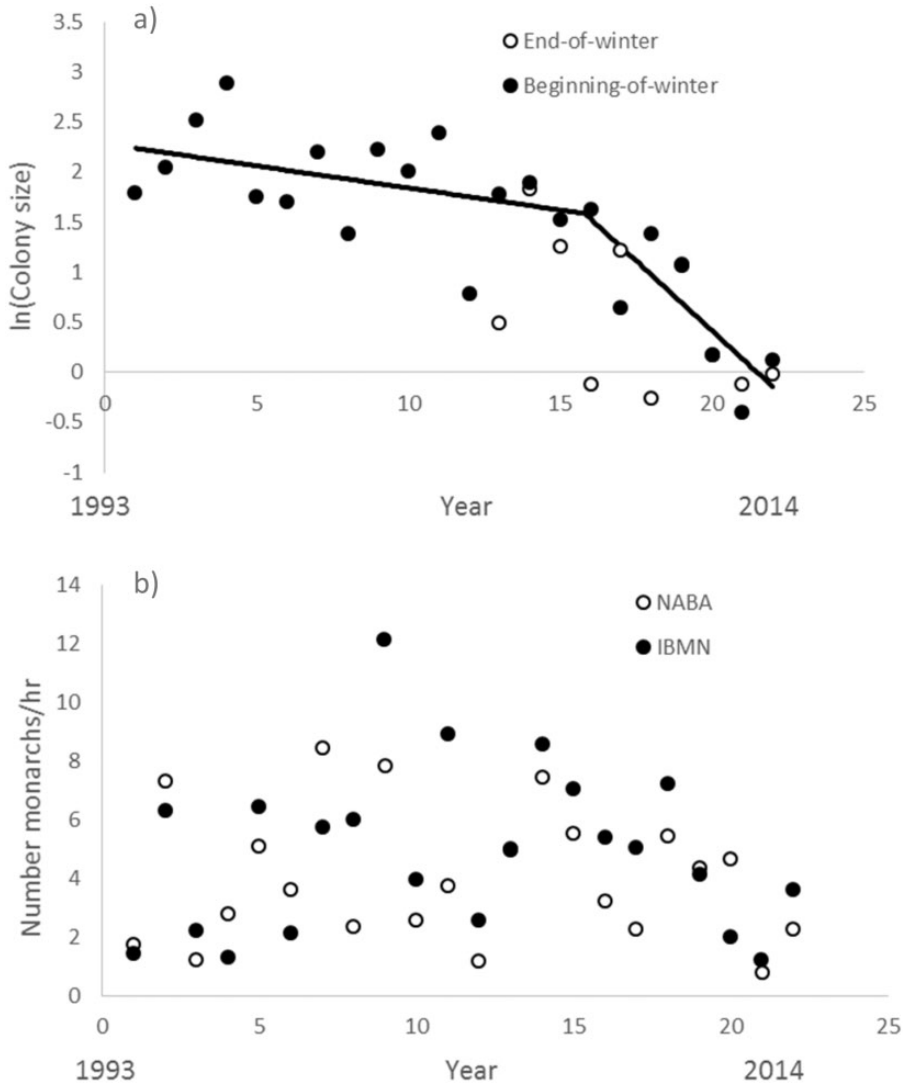
Table 2. Regression results for trends and associations between overwinter colony size (separated into beginning-of-winter and end-of-winter) and peak breeding populations in the north-central region (see Fig. 1) using data from NABA and IBMN

Explanatory variable	Response variable	n (yrs)	Int	Slope	R^2	Adj P	Break point	Fig
Year	ln(Beginning-of-winter colony sizes)	22	2.65	−0.10	0.56	<0.0001	15.7 ± 1.84	3
Year	ln(End-of-winter colony sizes)	10	2.83	−0.13	0.20	0.11	Failed	3
Year	NABA Peak summer	22	4.48	−0.05	−0.03	1.0	19.3 ± 3.03	4
Year	IBMN Peak summer	22	6.87	−0.11	−0.01	1.0	8.83 ± 2.57	4
ln(End-of-winter colony sizes)	NABA Peak summer	10	3.14	1.32	0.14	0.09	NA	5
ln(End-of-winter colony sizes)	IBMN Peak summer	10	4.19	1.63	0.22	0.09	NA	5
NABA Peak summer	resid(ln(Beginning-of-winter colony sizes))	22	−0.43	0.11	0.17	0.02	NA	5
IBMN Peak summer	resid(ln(Beginning-of-winter colony sizes))	22	−0.66	0.14	0.44	<0.0001	NA	5

The explanatory and response variable are shown separately, and whether data were transformed for analysis (ln) and whether residuals (resid) were used for the comparisons. For each comparison, we show the number of years in the analysis, intercept, slope, adjusted R^2, and P-values (adjusted using the Holm's method to account for multiple comparisons within each type). Results from a piecewise linear regression show estimated breakpoints (year 1 = 1993).

Fig. 3. Trends for overwinter data (a) and peak summer data (b). Only the beginning-of-winter series showed a significant trend and is illustrated here including the significant breakpoint from a piecewise linear regression. Parameter estimates and statistical test results are in Table 2.

Despite a mismatch between summer and winter trends (compare Fig. 3a with 3b), there is still an association between year-to-year fluctuations for the summer compared with the winter trends (Fig. 4). The relationship between summer and winter indices shows persistent low-to-moderate strengths of association (R^2 values between 0.17 and 0.44, Table 2). Nevertheless, we see a consistent relationship between summer and winter numbers in both directions, despite the mismatch in temporal trends, suggesting that the size of the population at each step has an influence on population sizes at subsequent stages. This also suggests that the substantial yearly fluctuations that have been consistently observed for monarchs (Swengel 1995) are being detected in a consistent manner between three independent monitoring programs.

One of the biggest questions raised by this analysis is whether population sizes during the summer are really not experiencing a downward trend as has been consistently reported for winter colony sizes (Toone and Hanscom 2003, Brower et al. 2012, Vidal and Rendon-Salinas 2014, Fig. 3a). Previous research suggests that loss of milkweed habitat is a major contributor to the decline of the monarch (Pleasants and Oberhauser 2013) and that if milkweed loss is taken into account, then potential recruitment closely tracks the decline observed (Pleasants 2015). While these surveys did not pick up a decline, it is possible that biases in the placement of transects could be missing declines in largely agricultural regions where much of the past recruitment is thought to have occurred (Pleasants and Oberhauser 2013) or that significant year-to-year
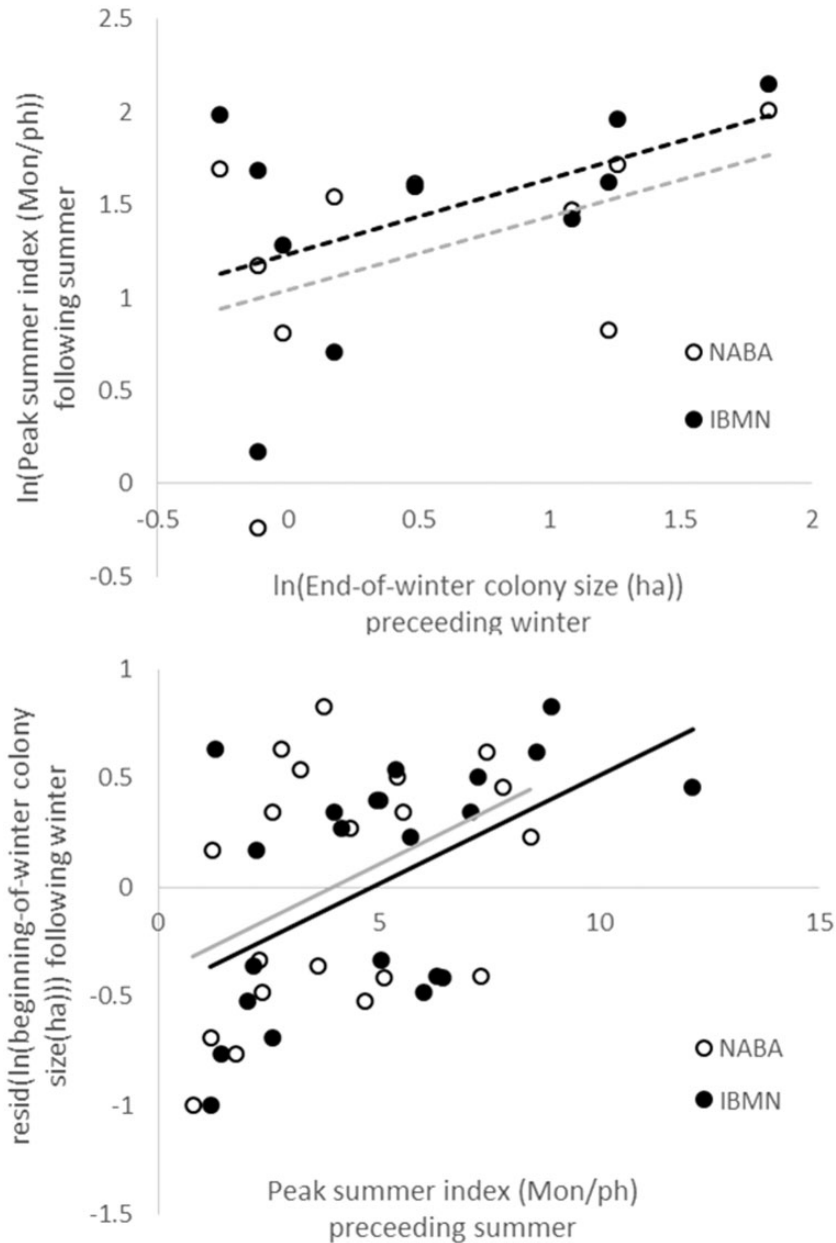
Fig. 4. Associations between year-to-year variability in population indices between two key periods in the monarch migration cycle: winter colony size and peak breeding periods. Results show relationship between end-of-winter colony size and following peak summer populations (a) and peak summer populations and following beginning-of-winter (b). Comparisons are done for both NABA and IBMN data for peak summer populations. Solid lines indicate significant slopes (black for IBMN, gray for NABA) based on ordinary linear regression, while dotted lines indicate trends ($P < 0.10$). Parameter estimates and statistical test results are in Table 2.

variability is making it difficult to detect a trend. Importantly, the significant breakpoints from the piecewise linear regression suggest there may be a downward trend later in the data (Table 2), but these were difficult to interpret because the IBMN result was driven by a single high year and the NABA result overlapped with the end of the series. It is thus possible that a

recent decline is occurring, but currently difficult to detect statistically.

While the high correlation between independent surveys (Fig. 2) and a clear association between summer and winter fluctuations (Fig. 4) suggests that the dynamics reported are based on biological dynamics, there still could be bias in the indices clouding a

decline in summer populations. Future work should carefully examine the bias in placement for summer surveys, both in national (NABA) and local (e.g., Ohio and Illinois) programs. To strengthen evidence that monarch losses are owing to loss of milkweed, we would expect surveys done in areas more dominated with cropland to show declines, whereas surveys in other areas would not.

Another possibility that could underlie declines seen in winter populations is an increasing probability over time that monarchs are not successfully completing their fall migration to Mexico from their summer breeding grounds. Recent research suggests that some monarchs may be breaking diapause to lay eggs on newly available exotic milkweeds in the southern United States (Batalden and Oberhauser 2015), although it is not clear if this is common enough to have any impact on the size of the arriving colonies. This dynamic could remove some individuals from the population and has also been shown to increase disease, which could be further stressing migrating populations (Satterwait et al., *in press*). Of course, the hypothesis that monarchs are failing to migrate successfully does not exclude the possibility that they are also experiencing declines owing to loss of breeding habitat. It may be possible to tease apart some of these dynamics by examining mechanistic patterns by drawing on a larger set of data, including land-cover, climate, larval development, and disease. However, to truly tease apart these or other potential drivers, it may be necessary to include additional experimental, observational, or modeling approaches to add to the data that citizen scientists are currently collecting.

The results presented here show the power of citizen science to capture large-scale and long-term dynamics. In recent years, several new monitoring programs have been initiated (Ries and Oberhauser, 2015), and these will increase our power to be able to grapple with these complex dynamics. Although the analyses we presented here used data sets with the longest time-series, some of the mechanistic hypotheses that could be generated (included differential relative abundances in areas with differing amounts of crops) could leverage data from the many monitoring programs that have been established more recently. This includes monitoring networks in Ohio, Iowa, and Michigan. Further, programs like the Monarch Larvae Monitoring Project and Monarch Health, which engage volunteers to look at patterns in monarch development and disease, could help us tease apart some of the physiological dynamics that could be underlying observed declines. The patterns presented here can serve as a basis for exploring diverse mechanistic drivers to the complex dynamics observed for this iconic insect and help us determine the best approaches to halt their alarming decline.

Acknowledgments

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