Long-term Trends in the Number of Monarch Butterflies (Lepidoptera: Nymphalidae) Counted on Fall Migration at Long Point, Ontario, Canada (1995–2014)

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ABSTRACT In Canada, the monarch butterfly, *Danaus plexippus* (L.), is designated a species of "special concern." During their southward journey each year, hundreds of thousands of monarchs funnel through Long Point, Lake Erie in Canada. Standardized daily counts of migrating monarchs have been conducted at two sites on Long Point for 20 consecutive years (1995–2014). Using a Bayesian framework, we estimated long-term trends in the number of migrants passing through Long Point. Over the 20-yr period, credible intervals for trends estimated at each site overlapped, with an estimated decline of $5.11\%\mathrm{yr}^{-1}$ across sites. However, trajectories differed between sites. At the more inland site, a more constant $7.78\%\mathrm{yr}^{-1}$ decline was detected, but at the tip of the peninsula, counts increased by $10.04\%\mathrm{yr}^{-1}$ from 1995–2005, followed by a decline of $11.9\%\mathrm{yr}^{-1}$ from 2004–2014. This resulted in an estimated 20-yr decline of $2.74\%\mathrm{yr}^{-1}$ at this site. Lower and less variable counts since 2010 appear to be driving the apparent long-term population declines. Relative to the tip site, counts from the more inland site are less likely to be biased by large accumulations of monarchs blown off-course during headwinds or stopping over to replenish fuel supplies. Trends from the more inland site also show strong correspondence with declines in egg production and milkweed abundance in the upper Midwest, which suggests that the number of individuals counted on migration is evidence of a potentially broader-scale condition. Additional years of data should be collected to determine whether the apparent decline will continue.

KEY WORDS monarch butterfly, *Danaus plexippus*, migration, population monitoring, population trend

Counts of migrating individuals are a commonly used method to assess status and broad-scale population trends for migratory animals (Francis and Hussell 1998, Dunn 2005, Walton et al. 2005, Gibbs et al. 2006, Farmer et al. 2007, Findlay et al. 2011, Davis 2012). Standardized daily counts of migrating monarch butterflies, *Danaus plexippus* (L.), have been collected since 1995 at two sites at Long Point, Ontario (Fig. 1), and provide the only long-term dataset available to assess monarch status in Canada. In late August to mid-October each year, tens of thousands of monarchs funnel through Long Point as they migrate south to their overwintering grounds in Mexico. The number of individuals detected each year is assumed to be a reflection of fluctuations in the underlying catchment population (i.e., the breeding population representing the geographic origin of detected individuals).

In Ontario, the breeding distribution of the monarch butterfly is determined largely by the distribution of the various species of its larval host plant, milkweed (*Asclepia sp.*; Schappert 1996). Although the historical amount of milkweed, and therefore the distribution of monarchs, increased across Ontario with the development of the road network and an increase in abandoned agricultural fields, the current amount of monarch host and nectaring plants has the potential to be reduced or lost through continued urban development, the regeneration of trees and shrubs in abandoned fields (Crolla and Lafontaine 1996), as well as by the use of herbicides and (at least until 2014) the control of milkweed as a noxious weed under Ontario's Weed Control Act. On a broader spatial scale, low numbers of monarchs returning to the Mexican overwintering grounds each year are thought to be the result of high storm-caused mortality at the overwintering sites, wet and cold weather during the spring and summer breeding seasons in the United States and Canada, and the loss of milkweed host plants in intensive agricultural systems (Brower 1995, Brower et al. 2012, Pleasants and Oberhauser 2013).

The use of migration counts to estimate trends in population size relies on the assumption that detection remains consistent over time (Dunn 2005, Crewe et al. 2015). In reality, the proportion of the migratory population of monarch butterflies that is detected by migration counts can vary annually and daily with factors including sampling effort, observer skill, and local weather conditions. Low temperatures can impact flight ability (Brower 1995); thus, counts often increase

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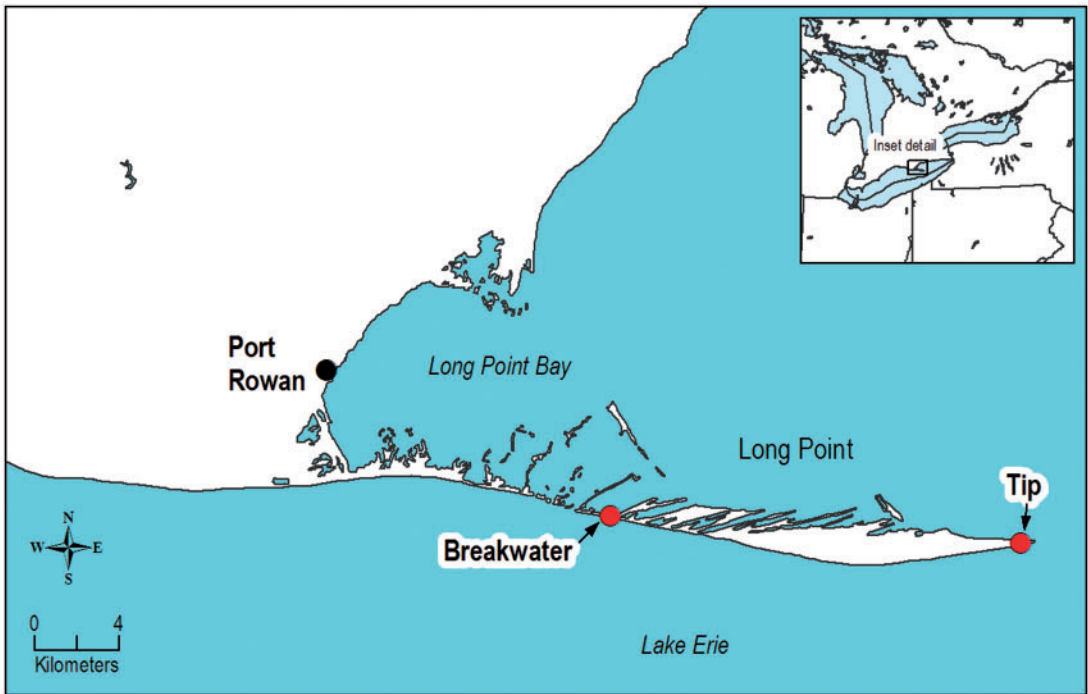
Fig. 1. Location of the Tip and Breakwater count sites along the Long Point peninsula in Lake Erie, Ontario, Canada.

with temperature (Meitner et al. 2004). Strong or unfavourable headwinds can also result in higher counts (Gibo and Pallett 1979, Davis and Garland 2002), as monarchs are more likely to stay close to the ground or not migrate (Gibo and Pallett 1979). Importantly, because of the west to east orientation of the Long Point peninsula on the north shore of Lake Erie, Long Point acts as a bottleneck during west headwinds, such that monarchs blown off their overall southwesterly migratory course (Gibo and Pallett 1979, Brower 1995) will accumulate in large numbers at the tip of the peninsula until migratory conditions improve. Accumulations of monarchs can result in the detection of a larger than average proportion of the daily migratory population and, when individuals remain on site for extended periods, the re-counting of individuals during successive counts. Counts at a second count site ("Breakwater") that is located closer to the base of the peninsula are typically much lower than counts at the tip of the peninsula, and are less likely to be influenced by large accumulations of monarchs during headwinds.

Although detection probability will vary with the above factors, random variation in factors that influence detection will not bias estimates of long-term population change (Crewe et al. 2015). However, a systematic change in detection will bias trends (Hochachka and Fiedler 2008, Kéry et al. 2009, Crewe et al. 2015). On a broad spatial scale, a change in breeding distribution, for example, can lead to false inferences about population trends (Paprocki et al. 2014). At the scale of a migration count site, a systematic change in the stopover behaviour of migrating animals as a result of habitat or

climate change (Schaub et al. 2004, Calvert et al. 2009), can also bias population trends (Hochachka and Fiedler 2008, Crewe et al. 2015). Mark–recapture methods have been used to estimate and account for systematic changes in detection using counts of marked migrants (Hochachka and Fiedler 2008). Conversely, because monarchs counted on migration at Long Point are not marked, detection cannot be estimated directly from the data. As a result, we are unable to determine whether broad-scale systematic changes in factors that influence detection have occurred. However, the geographic proximity of the two count areas at Long Point provides an opportunity to test whether site-specific biases in detection might be occurring. Because both sites are assumed to monitor the same population of migrating monarch butterflies, they should detect similar rates of long-term population change. Yet differences in habitat and geographic orientation between the two monitoring sites might lead to site-specific temporal variation in detection probability, and therefore site-specific rates of population change. Correspondence of estimated rates of population change among nearby sites can provide support that site-specific biases in detection probability are not confounding trend estimates.

In this paper, we used 20 consecutive years (1995–2014) of standardized daily migration counts collected at the two sites at Long Point, Ontario, to estimate trends in the number of migrating monarch butterflies detected across three time periods: an overall 20-yr trend, and 10-yr trends using the first and last 11 yr of data. Further, we used model selection to test whether

a difference in the detected population trend between sites was supported, and to test whether headwinds resulted in an accumulation effect at the tip of the peninsula but not at the more inland site. This analysis provides the first published analysis of monarch population trends for Canada.

Materials and Methods

Study Sites. Long Point, Ontario, is a narrow sand peninsula that extends 32 km (20 miles) eastward from the Canadian north shore of Lake Erie (42° 35′ N, 80° 25′ W; Fig. 1). Including wetlands, Long Point is ∼16,000 ha (39,500 acres) and is composed of sandy beaches, dunes, expansive wetlands, meadows, savannahs, and forests (Gartshore et al. 1987). Because of the large numbers of monarchs passing through the area each year, Long Point was designated an International Monarch Butterfly Reserve by the Canadian government in 1995 (Anon 1995). The area is also recognized as a World Biosphere Reserve, a Ramsar wetlands site of international significance, and an Important Bird Area of global significance.

Fall migration of monarch butterflies was monitored at two sites on Long Point from 1995–2014: the Tip, at the eastern end of Long Point, and Breakwater, about 15 km west of the Tip and closer to the base of the peninsula (Fig. 1). The habitat at both sites has remained relatively stable over the past half-century. However, the two sites differ in habitat structure. The Tip site is dominated by early-successional, dry, open eastern cottonwood-red cedar savannahs, separated by wet interdunal swales, meadows, and dry (sparsely vegetated) sand dunes. Important monarch larval host and nectaring plants, including milkweed and cylindrical blazing star (*Liatris cylindracea*), are common in the meadows at this site. Conversely, the Breakwater study site is dominated by a mid-successional, open, oak-maple savannah that has a well-developed ground cover dominated by various grasses. While milkweed is fairly common, it is not as abundant at Breakwater as it is at the Tip, and blazing star is virtually absent.

Data Collection. Every fall since 1995, a standardized daily count (census) of migrating monarchs has been carried out at the Tip and Breakwater sites by volunteer surveyors. Standardized counts consisted of a 1-h afternoon walking census conducted between 1300–1700 hours along a delineated path, during which a single surveyor counted the number of monarchs seen foraging or passing through the count area. Surveyors varied within and among years, and because skill level was not recorded, observer skill was assumed to vary randomly and not systematically over time. The census was not carried out during rain or extreme weather (storm) events. Surveys began at the beginning of August and continued until the end of September at Breakwater and until late October at the Tip. Access to Breakwater beyond about 22 September each year was restricted, and as a result, the entire fall migration was not monitored at that site. Weather variables, including estimated percent cloud cover (0–100 in 10% intervals), wind direction (16-point scale), wind speed (Beaufort scale), and temperature (°C), were also collected daily at each site.

Data Analysis. We used R (version 3.0.0; R Core Team 2013) to fit all models in a Bayesian framework using Integrated Nested Laplace Approximation (R-INLA; Rue et al. 2009, 2014). Compared to fitting complex hierarchical models using an Markov Chain Monte Carlo (MCMC) approach, the INLA program is more easily implemented and accessible to ecologists, and requires a fraction of the time (Rue et al. 2009, Ross et al. 2012). Further, instead of relying on arbitrary *P*-values, the ability to sample the posterior distribution of an effect allows the estimation of specific probabilities, for example, the probability that the estimated year effect (trend) was less than or greater than zero. The INLA approach also provides a means to compare models fit in a Bayesian framework through the calculation of a Deviance Information Criterion (DIC; Rue et al. 2009).

We restricted our analyses to data collected during August and September, to ensure both sites had the same seasonal coverage. We used DIC to compare the fit of four regression models (Table 1). The base model, which was similar among all models compared (Table 1), assumed counts on day i, at site j, in year t (y_{ijt}) resulted from a negative binomial distribution, and were fit using a log-linear regression model that included a continuous year effect to estimate a log-linear rate of change (trend), and hierarchical first-order autoregressive (AR1) terms to model the temporal autocorrelation structure of residuals among 1) days in a season, nested within year and site, and 2) years, nested within site (sample R code in Supp. App. 1 [online only]). A negative binomial data model with hierarchical AR1 effects for year to estimate population trend using the INLA program is described in more detail by Ross et al. (2012). Our base model also included first- and second-order day terms to model the seasonal pattern of migration, a categorical effect for cloud cover (0–20, 30–50, 60–80, and 90–100%), and first- and second-order effects for temperature and wind direction and speed to model variation in the number of monarchs migrating and counted due to local weather conditions. For our analyses, we transformed wind speed into km/h using the midpoint along the range of values for each Beaufort wind score. Wind speed was then combined with wind direction to create east and south wind vectors (EV and SV, respectively) such that wind speed increased from 0 along each vector in two directions. For the EV, negative values represented west winds and positive values represented east winds. For the SV, negative values represented north winds, and positive values represented south winds. For wind directions that did not fall directly on either vector (e.g., ENE), we used vector addition to assign a wind speed to both the EV and SV. Polynomial terms for day, temperature, EV, and SV were calculated using a Legendre transformation, which results in orthogonal and therefore uncorrelated and independent first- and second-order covariates. Year was also centered for analysis by subtracting the mean. We included the

Table 1. Models compared using DIC for best fit to counts of migrating monarch butterflies at two sites on Long Point, Ontario, Canada (1995–2014)

Model	Model Name	Model Parameters			
1	Year + Wind Int	Base	+ S*EV	+ S*SV	+ S*Y
2	Year Int	Base			+ S*Y
3	Wind Int	Base	+ S*EV	+ S*SV	
4	No Year/Wind Int	Base			

Base: $Y + S + D + D^2 + S*D + S*D^2 + EV + EV^2 + SV + SV^2 + C + T + T^2$.

Models tested 1) whether trend varied between sites by comparing models with (models 1 and 2) and without (models 3 and 4) an interaction between year and site, and 2) whether headwinds resulted in a bottleneck effect at the Tip but not at Breakwater by comparing models with (**models** 1 and 3) and without (**models** 2 and 4) interactions between site and wind. The base model (model 4), to which wind and year interactions were added, included a continuous effect of year (Y), first- and second-order effects of day (D, D^2), east wind vector (EV, EV^2), south wind vector (SV, SV^2), and temperature (T, T^2), categorical effects of site (S) and cloud cover (C), and interactions between site and day.

above weather covariates in all competing models because the effect of cloud cover, temperature, and wind on monarch migration counts has been well documented at this and other sites (Gibo and Pallett 1979, Brower 1995, Davis and Garland 2002, Meitner et al. 2004, Crewe et al. 2007).

Using DIC, we tested whether trend varied between the Tip and Breakwater sites by comparing 1) models that allowed slope to vary with site (models 1 and 2; Table 1), and 2) models with a single slope to estimate an overall population trend across sites (models 3 and 4; Table 1). Second, for each of the above two scenarios (same or differing trends across sites), we tested whether the effect of wind on migration counts varied between sites by comparing models that did (models 1 and 3; Table 1) or did not (models 2 and 4; Table 1) include an interaction between site and the two wind vectors. The interaction between site and wind allowed us to test whether a bottleneck effect occurs at Long Point during west headwinds, which would result in monarchs accumulating at the tip of the peninsula, with more highly inflated counts at the Tip site compared to at Breakwater. The four models were compared using DIC for the full 20-yr monitoring period (1995–2014), as well as for the first (1995–2005) and last (2004–2014) 11 yr of data collected, to test whether the more recent 10-yr trend varied from the trend observed over the entire time series and from the first 11 yr of data collection. Such 10-yr population trends are often used to assess the conservation status of species (e.g., International Union for Conservation of Nature (IUCN) 2013). For our purposes, we considered models to be competing when the difference in DIC scores was less than two from the top-ranked model. In all cases, the year coefficients and credible intervals were transformed into constant rates of population change using $100 \times (\exp(estimate) - 1)$. We visualized the effect of wind speed and direction on monarch counts at each site by applying a bivariate interpolation (interp, akima package; R version 3.0.0) to a loess fit (loess; R version 3.0.0) of the log of predicted counts (+1) against the east and south wind vectors. Predicted counts were derived from the top model, as suggested by DIC, for the full 20-yr monitoring period (1995–2014).

Results

Using DIC, a model that assumed a single population trend across sites had comparable support to the top-ranked model that assumed trend varied between sites, with DIC differences of ≤ 0.52 for all three time periods (Table 2). Further, for all three time periods, 95% credible intervals (CI) for the interaction between site and year included zero (Year:Tip; Tables 3–5). Together, these results suggest that evidence for a difference in rate of population change between sites was not strong. Using the second-ranked models for each time period, which assumed a single rate of population change across sites, a decline of $5.11\%yr^{-1}$ (CI $= -9.70\%yr^{-1}$, $-0.20\%yr^{-1}$) was detected over the full 20-yr sampling period, with a posterior probability of 0.97 that the trend was negative (Fig. 2). During the first 11 yr, a change in monarch counts was not supported ($1.82\%yr^{-1}$, CI $= -9.19\%yr^{-1}$, $15.05\%yr^{-1}$), with a posterior probability of 0.64 that the trend was positive. However, during the last 11 yr, monarch counts declined by $5.73\%yr^{-1}$ (CI $= -12.06\%yr^{-1}$, $1.14\%yr^{-1}$), with a posterior probability of 0.96 that the trend across sites was indeed negative.

While credible intervals for the interaction between site and year included zero for all three time periods, the posterior probability that the rate of change detected at the Tip differed from the rate of change detected at Breakwater was 0.88 over the full time period and 0.94 for the first and last 11-yr periods, providing some support for differences in trend between sites. During the 20-yr monitoring period the top ranked model, which assumed slope varied between sites (Table 2), supported a decline of $7.78\%yr^{-1}$ (CI $= -13.84\%yr^{-1}$, $-1.16\%yr^{-1}$) at Breakwater, with a posterior probability of 0.99 that the trend was negative, and a less severe decline of $2.74\%yr^{-1}$ (CI $= -8.83\%yr^{-1}$, $3.95\%yr^{-1}$) at the Tip, with credible intervals that include zero, but a posterior probability of 0.8 that the trend was negative (Fig. 3; Table 3). Credible intervals for the site-specific 20-yr trend estimates overlapped, which lends support that the constant rate of change was comparable across sites over the long term. However, the trajectory or pattern of change did vary between sites (Fig. 3). During the first 11 yr, the top ranked model included an interaction

Table 2. DIC scores, DIC differences (ΔDIC), effective number of parameters (P Eff), and model rank, for models compared for fit to daily counts of migrating monarch butterflies detected at two sites at Long Point, Ontario, Canada, over three time periods between 1995–2014

Years	Model name	P Eff	DIC	ΔDIC	Rank
1995–2014	Year + Wind Int	304.5	11334.44	0.00	1*
	Year Int	301.9	11339.31	4.87	3
	Wind Int	304.4	11334.96	0.52	2*
	No Year/Wind Int	301.8	11339.89	5.45	4
1995–2005	Year + Wind Int	188.4	6665.83	0.00	1*
	Year Int	185.4	6668.16	2.34	3
	Wind Int	185.8	6666.02	0.19	2*
	No Year/Wind Int	184.5	6668.26	2.44	4
2004–2014	Year + Wind Int	265.0	5658.68	3.60	3
	Year Int	268.4	5655.08	0.00	1*
	Wind Int	265.7	5659.38	4.30	4
	No Year/Wind Int	263.4	5655.35	0.26	2*

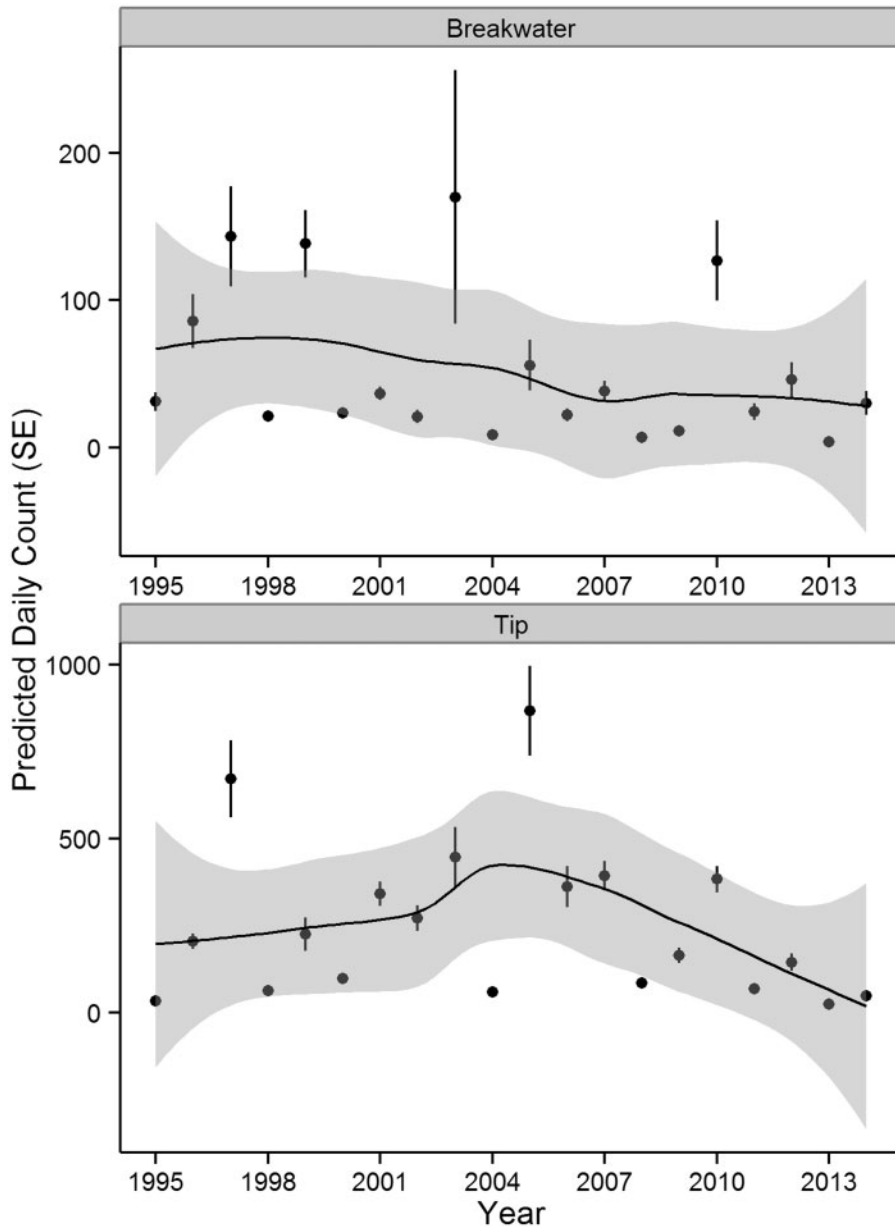* Suggests models considered competing, with ΔDIC < 2.
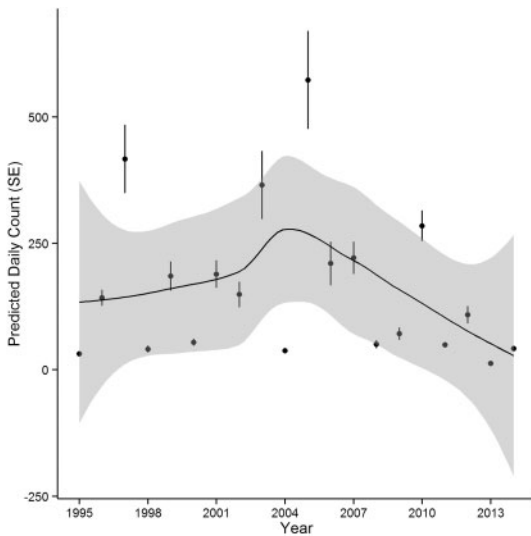
Fig. 2. Mean of predicted daily counts (black points, $\pm$ SE) of monarchs detected on migration across two sites on the Long Point peninsula in Ontario, Canada (1995–2014), where predicted counts were derived from the second-ranked model using DIC, which assumed trend did not vary between sites. A decline in annual indices of 5.1%yr^{-1} (CI = -9.81%yr^{-1}, -0.06%yr^{-1}) was detected. Overall trend is depicted by a loess curve (black line, gray shading) fit to the SE estimates of mean predicted counts.

between year and site (Table 2), and supported a decline of 6.56%yr^{-1} (CI = -20.21%yr^{-1}, 10.37%yr^{-1}) at Breakwater, with a 0.81 probability that the trend was negative, but an increase of 10.04%yr^{-1} (CI = -5.40%yr^{-1}, 29.82%yr^{-1}) at the Tip, with a 0.90 probability that the trend was positive (Table 4). Using the last 11 yr of data collected, the top ranked model also included a site by year interaction (Table 2), and did not support a change in monarch counts at Breakwater (0.71%yr^{-1}, CI = -12.87%yr^{-1}, 16.58%yr^{-1}; posterior probability of 0.54 that the trend was positive), but monarch counts declined by 11.47%yr^{-1} (CI = -23.06%yr^{-1}, 1.87%yr^{-1}) at the Tip, with a posterior probability of 0.97 that the trend was negative (Table 5).

Further, the size of the negative binomial observations ("NB Size," Tables 3–5) provides an estimate of count overdispersion, such that as NB Size increases, variance will approach the mean, and counts will approximate a Poisson distribution (Bolker 2008). Thus, the observed increase in NB Size between the first and last 11-yr periods (Tables 4 and 5) suggests that monarch migration counts at Long Point became less variable and overdispersed over time. In addition, first-order temporal autocorrelation (Rho) of the random year effect declined from a negative correlation of 0.4 to ~0 between the first and last 11-yr periods (Tables 4 and 5), which suggests a potential dampening of the magnitude of change between population peaks and lows in recent years compared to that observed during the first 11 yr of data collection (Figs. 2 and 3). The extremely large precision of the random temporal autocorrelation effect for year during the latter 11 yr also suggests that the AR1 effect did not converge and was over parameterized (not necessary) for this time period (Table 5). Removal of the annual AR1 effect from the model did not impact the DIC model ranking, sizes of fixed and random effects nor the interpretation of trends. Estimates for the first-order autocorrelation in the temporal random effect for day were ≥ 0.84 across all time periods and competing models, which suggests strong interdependence of daily counts.

Both top-ranked models for the full 20-yr period and the first 11-yr period included interactions between site and the two wind vectors (Table 2). While credible intervals for the interaction effects included zero (Tables 3 and 4), the inclusion of the interaction in both top models lends support for a difference in the effect of wind on monarch counts between sites. In general, monarch counts were highest during strong west winds at Breakwater and during intermediate to strong west and northwest winds at the Tip site (Fig. 4). During the latter 11-yr period, a difference in the effect of wind on monarch counts between sites was not supported by either of the top two competing models (Table 2). Monarch counts also increased with temperature and were lowest during high (>90%) cloud cover (Tables 3–5).

Fig. 3. Mean of predicted daily counts (black points, ± SE) of monarchs detected on migration at the Breakwater (top panel) and Tip (bottom panel) sites on the Long Point peninsula in Ontario, Canada (1995–2014), where predicted counts were derived from the top-ranked model using DIC, which assumed trend varied between sites. Declines of 7.78%yr^{-1} (CI = −13.84%yr^{-1}, −1.16%yr^{-1}) and 2.74%yr^{-1} (CI = −8.83%yr^{-1}, 3.95%yr^{-1}) were detected at Breakwater and the Tip, respectively. Overall trend at each site is depicted by a loess curve (black line, gray shading) fit to the SE estimates of mean predicted counts.

Discussion

In recent years, there has been an increasing amount of interest and concern surrounding the susceptibility of the eastern North American monarch butterfly population's migratory phenomenon to the loss and degradation of the Mexican overwintering and North American breeding habitats. Evidence to support a

decline in the monarch population, however, has varied among datasets, with a reported decline in the number of monarchs overwintering in Mexico from 1994 through 2011 (Brower et al. 2012), but no significant change in the number of monarchs migrating through Cape May, New Jersey (1992–2010) or Peninsula Point, Michigan (1996–2010) during similar time periods

Table 3. Mean (95% credible interval) of fixed and random effects for the top two competing models fit to daily monarch counts collected from 1995–2014 at two sites at Long Point, Ontario, Canada

Effect type	Parameter	Model 1: Year + Wind Int		Model 3: Wind Int	
		Mean	95% CI	Mean	95% CI
Fixed	Year	−0.08	(−0.15,−0.01)	−0.05	(−0.10,0.00)
	Year:Tip	0.05	(−0.04,0.14)		
	Breakwater	3.25	(2.22,4.27)	3.25	(2.22,4.28)
	Tip	2.31	(1.38,3.23)	2.30	(1.37,3.23)
	Day	1.31	(−0.56,3.16)	1.33	(−0.57,3.18)
	Day^2	−0.24	(−1.71,1.22)	−0.23	(−1.69,1.23)
	EV	−1.18	(−1.57,−0.79)	−1.18	(−1.57,−0.79)
	EV^2	−0.30	(−0.64,0.05)	−0.30	(−0.64,0.05)
	SV	0.03	(−0.28,0.33)	0.03	(−0.28,0.33)
	SV^2	−0.20	(−0.49,0.11)	−0.19	(−0.49,0.11)
	Cloud 30–50%	0.10	(−0.07,0.27)	0.10	(−0.07,0.27)
	Cloud 60–80%	0.06	(−0.13,0.25)	0.06	(−0.13,0.25)
	Cloud 90–100%	−0.25	(−0.42,−0.08)	−0.25	(−0.42,−0.08)
	Temp	−0.53	(−0.97,−0.11)	−0.53	(−0.97,−0.11)
	$Temp^2$	−0.28	(−0.71,0.16)	−0.28	(−0.71,0.16)
	Tip:Day	−5.70	(−7.41,−3.99)	−5.69	(−7.40,−3.99)
	$Tip:Day^2$	−3.32	(−4.70,−1.94)	−3.32	(−4.70,−1.94)
	Tip:EV	0.31	(−0.16,0.78)	0.31	(−0.16,0.78)
	Tip:SV	−0.31	(−0.70,0.09)	−0.30	(−0.70,0.09)
Random	NB size	1.59	(1.42,1.77)	1.59	(1.42,1.77)
	Precision-Year	1.62	(0.83,2.87)	1.55	(0.81,2.66)
	Rho-Year	−0.29	(−0.67,0.19)	−0.24	(−0.65,0.21)
	Precision-Day	1.05	(0.72,1.45)	1.06	(0.74,1.47)
	Rho-Day	0.87	(0.81,0.92)	0.87	(0.81,0.92)

Both models included continuous effects for year, first- and second-order effects for day, east wind vector (EV), south wind vector (SV) and temperature, a categorical effect of cloud cover (0–20%, 30–50%, 60–80%, 90–100%), and interactions between site and day and site and the two wind vectors. An interaction between site and year was also included in the top ranked model. The slope for year describes the log-linear rate of change observed at Breakwater, and the interaction Year:Tip is the difference in rate between Breakwater and the Tip. "NB size" is the size of the negative binomial observations, and precision and Rho for year and day are estimates of the first-order autoregressive hierarchical effects fit to year and day, where Rho is the estimated temporal autocorrelation of residuals.

(Davis 2012). Using counts of monarchs migrating through two sites on the Long Point peninsula in Ontario, Canada, a decline in monarch counts over the 20-yr monitoring period was supported by declines at both sites and when sites were combined to estimate a single rate of population change. However, while credible intervals for the site-specific 20-yr trends overlapped, the trajectory or pattern of change varied between sites, with evidence for a more constant decline at Breakwater, but an increase in the first 11 yr and a decline in the last 11 yr at the Tip.

Because the Tip and Breakwater sites monitor the same population of migrating butterflies, the variation in trajectory between sites suggests that one or more factors that influence the detection of migrants also varies between sites. Higher counts observed at both sites during west headwinds supports an increase in the number of monarchs blown off their overall southwesterly fall migratory course to the Mexican overwintering sites (Gibo and Pallett 1979, Brower 1995). However, while higher counts during west winds likely reflect an increase in the number of individuals actively moving past Breakwater, higher counts observed during west and northwest winds at the Tip are more likely to reflect an increase in the number of monarchs blown off course as well as the accumulation of large numbers of monarchs in a bottleneck effect until weather conditions improve. During northwest winds in particular, monarchs may remain at the Tip to avoid flight over

open water (Brattström et al. 2008). Similar accumulations of monarchs during headwinds have been observed at other coastal monarch migration count sites (Davis and Garland 2002, Meitner et al. 2004).

In their recommendations for monitoring landbird migration, Hussell and Ralph (2005) suggest placing migration count sites in poor-quality stopover habitat to reduce the probability that trends will be biased by migrants that remain on site for extended periods of time. Because the Tip acts as a bottleneck and supports an abundance of nectaring plants that monarchs can use to fuel their migration, counts conducted at Breakwater are more likely to be a random and proportional sample of the daily migratory population than counts at the Tip. Counts at Breakwater should thus better reflect the size of the annual migratory population. Indeed, the overall 80% decline in mean daily monarch count observed at Breakwater between 1995–2014 more closely reflects the 81% reduction in monarch egg production and 80% decline in agricultural milkweed estimated for the upper Midwest between 1999–2010 (Pleasants and Oberhauser 2013) than did the estimated 42% decline in mean monarch count observed at the Tip. Further, an examination of Pearson correlation of estimated overwintering population size (Rendon-Salinas et al. 2014) with mean predicted counts from the preceding fall migration at Long Point (1995–2014) suggests a stronger correlation with counts from Breakwater ($\rho = 0.42$) than with counts from the

Table 4. Mean (95% credible intervals) of fixed and random effects for the top two competing models fit to daily monarch counts collected from 1995–2005 at two sites at Long Point, Ontario, Canada

| Effect type	Parameter	Model 1: Year+Wind Int		Model 3: Wind Int	
		Mean	95% CI	Mean	95% CI
Fixed	Year	−0.07	(−0.23,0.10)	0.02	(−0.10,0.15)
	Year:Tip	0.17	(−0.04,0.39)		
	Breakwater	3.17	(1.62,4.72)	3.57	(2.07,5.07)
	Tip	3.47	(2.09,4.88)	3.14	(1.80,4.51)
	Day	0.99	(−1.38,3.34)	1.01	(−1.39,3.37)
	Day^2	−0.57	(−2.43,1.27)	−0.55	(−2.42,1.30)
	EV	−1.19	(−1.72,−0.67)	−1.19	(−1.72,−0.67)
	EV^2	−0.40	(−0.89,0.11)	−0.40	(−0.89,0.11)
	SV	0.09	(−0.31,0.50)	0.09	(−0.32,0.50)
	SV^2	−0.45	(−0.86,−0.03)	−0.45	(−0.86,−0.03)
	Cloud 30–50%	0.09	(−0.14,0.32)	0.08	(−0.15,0.32)
	Cloud 60–80%	0.12	(−0.13,0.38)	0.12	(−0.13,0.38)
	Cloud 90–100%	−0.26	(−0.49,−0.03)	−0.26	(−0.49,−0.03)
	Temp	−0.81	(−1.81,0.18)	−0.80	(−1.81,0.18)
	$Temp^2$	−0.11	(−1.03,0.84)	−0.11	(−1.04,0.83)
	Tip:Day	−4.01	(−6.31,−1.73)	−3.96	(−6.26,−1.67)
	$Tip:Day^2$	−2.36	(−4.18,−0.55)	−2.33	(−4.16,−0.50)
	Tip:EV	0.31	(−0.35,0.97)	0.32	(−0.34,0.98)
	Tip:SV	−0.38	(−0.92,0.18)	−0.37	(−0.92,0.18)
Random	NB Size	1.54	(1.32,1.78)	1.53	(1.32,1.77)
	Precision-Year	1.44	(0.66,2.66)	1.40	(0.62,2.84)
	Rho-Year	−0.43	(−0.78,0.04)	−0.37	(−0.78,0.16)
	Precision-Day	1.15	(0.77,1.64)	1.13	(0.72,1.64)
	Rho-Day	0.84	(0.75,0.91)	0.84	(0.76,0.91)

Both models included continuous effects for year, first- and second-order effects for day, east wind vector (EV), south wind vector (SV) and temperature, a categorical effect of cloud cover (0–20%, 30–50%, 60–80%, 90–100%), and interactions between site and day and site and the two wind vectors. An interaction between site and year was also included in the top ranked model. The slope for year describes the log-linear rate of change observed at Breakwater, and the interaction Year:Tip is the difference in rate between Breakwater and the Tip. "NB size" is the size of the negative binomial observations, and precision and Rho for year and day are estimates of the first-order autoregressive hierarchical effects fit to year and day, where Rho is the estimated temporal autocorrelation of residuals.

Table 5. Mean (95% credible intervals) of fixed and random effects for the top two competing models fit to daily monarch counts collected from 2004–2014 at two sites at Long Point, Ontario, Canada

Effect type	Parameter	Model 2: Year Int		Model 4: No Year/Wind Int	
		Mean	95% CI	Mean	95% CI
Fixed	Year	0.01	(−0.14,0.16)	−0.06	(−0.13,0.01)
	Year:Tip	−0.14	(−0.386,0.113)		
	Breakwater	2.75	(1.01,4.48)	3.10	(1.4,4.72)
	Tip	2.68	(1.12,4.23)	2.39	(0.94,3.83)
	Day	1.46	(−1.66,4.58)	1.46	(−1.65,4.56)
	Day2	0.52	(−1.95,3.00)	0.51	(−1.96,2.97)
	Tip:Day	−6.26	(−9.76,−2.79)	−6.23	(−9.74,−2.77)
	Tip:Day2	−4.30	(−7.05,−1.56)	−4.26	(−7.01,−1.52)
	EV	−1.07	(−1.36,−0.79)	−1.07	(−1.35,−0.79)
	EV2	−0.41	(−0.83,0.01)	−0.41	(−0.82,0.01)
	SV	−0.26	(−0.49,−0.03)	−0.26	(−0.49,−0.03)
	SV2	0.06	(−0.27,0.40)	0.07	(−0.27,0.40)
	Cloud 30–50%	0.14	(−0.07,0.35)	0.14	(−0.07,0.35)
	Cloud 60–80%	−0.11	(−0.34,0.12)	−0.11	(−0.34,0.13)
	Cloud 90–100%	−0.17	(−0.37,0.04)	−0.17	(−0.37,90.04)
	Temp	−0.26	(−0.70,0.17)	−0.26	(−0.70,0.17)
	$Temp^2$	−0.01	(−0.46,0.46)	0.00	(−0.46,0.46)
Random	NB Size	3.12	(2.40,3.99)	3.10	(2.39,3.97)
	Precision-Year	21613.74	(1608.52,85685.66)	21471.72	(1589.53,82695.06)
	Rho-Year	0.00	(−0.99,0.99)	−0.01	(−0.99,0.99)
	Precision-Day	0.54	(0.37,0.72)	0.53	(0.38,0.72)
	Rho-Day	0.91	(0.86,0.94)	0.91	(0.86,0.94)

Both models included continuous effects for year, first- and second-order effects for day, east wind vector (EV), south wind vector (SV) and temperature, a categorical effect of cloud cover (0–20, 30–50, 60–80, 90–100%), and interactions between site and day. An interaction between site and year was included in the top ranked model, but interactions between site and wind were not included in either competing model. The slope for year describes the log-linear rate of change observed at Breakwater, and the interaction Year:Tip is the difference in rate between Breakwater and the Tip. "NB size" is the size of the negative binomial observations, and precision and Rho for year and day are estimates of the first-order autoregressive hierarchical effects fit to year and day, where Rho is the estimated temporal autocorrelation of residuals.
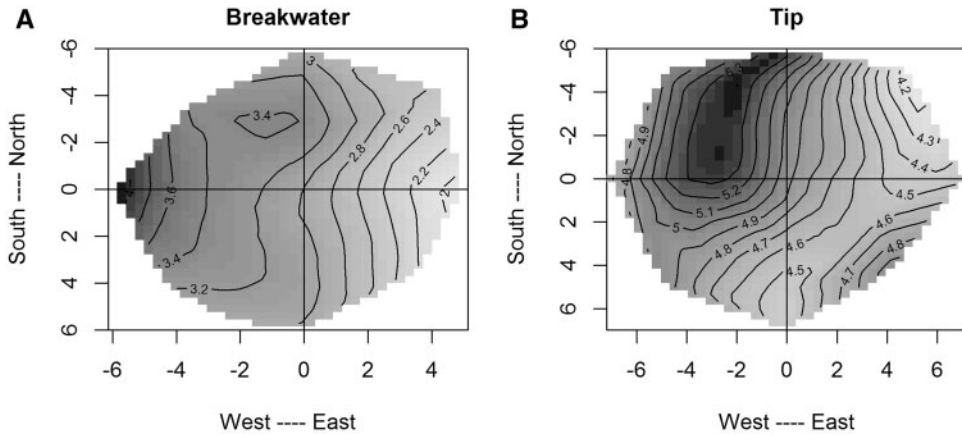
Fig. 4. Loess interpolation of log(predicted monarch counts + 1) against the south and east wind vectors for the Breakwater (A) and Tip (B) sites on the Long Point peninsula in Ontario, Canada (1995–2014). Wind speed increased from 0 along each vector in two directions, with negative values representing north and west winds along the south (vertical line) and east (horizontal line) vectors, respectively. Predicted counts were estimated using the top-ranked model using DIC, which assumed trend and the effect of wind differed between sites. Darker shading represents higher predicted counts.

Tip ($\rho = 0.20$). The 42% correlation at Breakwater is comparable to the 47% correlation observed between yearly egg production and subsequent overwintering population size in the upper Midwest (Pleasants and Oberhauser 2013). Long Point falls within the portion of the upper Midwest that, according to isotope analysis, contributes 50% of the overwintering population size (Wassenaar and Hobson 1998). Thus, correspondence of population estimates is expected, and provides support that counts at Long Point, and at Breakwater in particular, do reflect broad-scale population fluctuations, as opposed to more local or regional influences.

Our results cannot exclude the possibility that estimated trends at Long Point have been biased by temporal shifts in the monarch's breeding distribution. In recent decades, poleward shifts in the breeding range of many taxa have been reported, and have been attributed primarily to climate warming (Breed et al. 2012, Paprocki et al. 2014). Loss of breeding habitat in the upper Midwest region due to the adoption of genetically modified crops (Pleasants and Oberhauser 2013) might also drive shifts in the breeding distribution of monarchs. Observed declines in migration counts at Breakwater and in egg production and agricultural milkweed abundance in the upper Midwest (Pleasants and Oberhauser 2013) were more extreme than the 65% decline in overwintering population size over a similar time period (Brower et al. 2012). Concurrently, migration counts did not change significantly at sites in northern Michigan and New Jersey (Davis 2012), which fall outside the upper Midwest region contributing the bulk of the overwintering population (Wassenaar and Hobson 1998). It is possible that these sites are now contributing a larger proportion of the overwintering population than previously estimated (Wassenaar and Hobson 1998).

Similar to the results of Davis (2012), monarch counts at Long Point were highly variable over time. Up to and including 2010, troughs in the population trajectory were consistently followed by population peaks within one or two years (Figs. 2 and 3). However, since 2010, there appears to be a dampening of the magnitude between population peaks and troughs. This dampening effect is supported by a reduction in the size, overdispersion, and temporal autocorrelation of counts during the most recent 11-yr sampling period. A decline in the magnitude of population peaks could be driving the apparent long-term population declines at these sites. Temporary collapses of population cycles are not unusual for highly variable populations, and may not signal the demise of a species (Ims et al. 2008, Allstadt et al. 2013). However, the correspondence between declines in breeding habitat, egg production, and migrating monarchs in the upper Midwest region in particular suggests that factors beyond natural variability are at play in this system. More robust statistical analyses that examine the cyclicity of monarch populations, mechanisms behind population cycles, and whether cycle period has changed significantly over time should be undertaken.

Despite reported declines in the monarch population, monarchs do have the potential to expand exponentially through the production of several successive generations in a single breeding season under ideal conditions. As a result, monarchs are likely resilient to occasional declines in the overwintering or breeding populations, and this resilience could contribute to the lack of a detected decline in the size of fall migratory populations reported elsewhere (Davis 2012). However, the monarch's resilience and ability to recover from population lows has the potential to be compromised by the combination of a sustained decline in the overwintering population, an increased likelihood of weather extremes with climate change (Intergovernmental Panel on Climate Change (IPCC) 2012), and the continued degradation and loss of breeding and overwintering habitats (Pleasants and Oberhauser 2013, Flockhart et al. 2015). The lower variability in

annual counts at Long Point in the past several years might suggest that the capacity of monarchs to rebound has in fact been compromised. Recent evidence that moderating the loss of breeding habitat would have a larger impact on monarch population recovery than mitigating the loss of overwintering habitat (Flockhart et al. 2015) suggests that conservation efforts should focus on reducing the loss of milkweed, particularly in the upper Midwest. Continued long-term monitoring of monarchs during all phases of their life cycle will provide an ideal opportunity to test whether such conservation efforts are having their anticipated effect. An integrated population analysis (Schaub and Abadi 2011) that combines data collected by monitoring programs during overwintering, breeding, and migration would also be a logical next step in the assessment of monarch population status, in order to link estimates of population change to demographic parameters, and provide additional evidence for population limitations.

Acknowledgments

Supplementary Data

Supplementary data are available at *Annals of the Entomological Society of America* online.

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