Migration Patterns and Environmental Effects on Stopover of Monarch Butterflies (Lepidoptera, Nymphalidae) at Peninsula Point, Michigan

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ABSTRACT Since 1996, the numbers of migrating monarch butterflies stopping over at Peninsula Point, Michigan, have been monitored by volunteers during the fall migration with standardized daily counts. In this study, we describe this project and examine: 1) general patterns of migration and stopover of monarchs at this site, and 2) how environmental conditions influence monarch stopover frequency. We tested for yearly, seasonal, and diurnal variation in monarch counts within each season. We further combined these data with basic weather information recorded at the time of each count to explore the effects of wind direction and speed, temperature, and cloud cover on monarch stopover abundance. A total of 22,539 monarchs was counted over 7 yr, with yearly totals ranging from 757 in 1998 to 6,638 in 1997. Over the 7-yr period, an average of 29 monarchs was recorded per count at Peninsula Point. Interestingly, in the migration season immediately following a major population decline at overwintering sites in Mexico, the total number of monarchs counted at Peninsula Point was not significantly different from long-term average counts. The timing of the peak of migration was not consistent from year to year, and there were few consistent temporal trends within seasons. More monarchs were counted with walking transects during the day than with a roost count in the early morning. Furthermore, more monarchs were counted earlier in the season than later. Of the environmental variables we examined, wind direction had a significant influence on the number of monarchs recorded on each count with higher counts during north winds. Cloud cover also influenced monarch counts, so that the number of monarchs observed increased with temperature and decreased with cloud cover. Based on the large numbers of monarchs that stop there each fall, we suggest that Peninsula Point represents an important monarch stopover site, and thus has the potential to increase our knowledge of monarch migration and stopover ecology greatly.

KEY WORDS monarchs, migration, stopover, weather, timing

The biology and conservation of monarch butterflies (*Danaus plexippus*) in eastern North America have received much attention in recent years, in part because of the shrinking of overwintering habitat in Mexico (Brower et al. 2002), and interactions between agricultural practices and monarch breeding biology (Oberhauser et al. 2001, Sears et al. 2001). Much of this attention, however, has been focused on either the breeding or overwintering phases of monarch life cycles, while few studies have examined aspects of monarch migration. Furthermore, although the general migration patterns and routes of travel have been described for the eastern population as a whole (Urquhart and Urquhart 1977, 1979; Brower 1995, 1996), many questions relating to monarch migration and stopover ecology remain that can only be answered with long-term monitoring from specific locations along the migration route (Walton and Brower 1996, Davis and Garland 2004).

Their visibility and ease of identification make monarch butterflies a popular species for population monitoring. As such, numerous long-term monitoring programs have been established at the state or local level by citizens or butterfly organizations in which counts of breeding monarchs (and often other butterfly species) are obtained annually and posted to online websites (e.g., North American Butterfly Association 2003, Ohio Lepidopterists Society 2003). Such volunteer-derived data have been found useful by the scientific community to show how monarch population sizes in the breeding season fluctuate widely among years (Swengel 1995). Adding to this fluctuation are episodes of catastrophic mortality at monarch butterfly overwintering sites, which can periodically reduce the size of the eastern migratory population, including the recent 2002 mortality in which 75–80% of the overwintering population died (Brower et al., 2004). However, estimating annual fluctuations in the size of the entire monarch population east of the Rocky Mountains is challenging, in part because of the wide geographic area over which monarchs breed during the summer months.

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Faced with similar problems of quantifying whole bird populations, ornithologists routinely use data from many long-term bird migration monitoring stations to estimate trends and fluctuations in songbird population sizes (Hussell et al. 1992, Hussell 1997). By trapping and counting birds in a standardized fashion as they migrate through a fixed location each year, annual indices of abundance can be derived. This has been shown to be possible with data from monarch monitoring stations as well (Walton and Brower 1996). Aside from detecting long-term trends in numbers, data from bird migration monitoring stations have also been used to address questions relating to the stopover ecology of migrants (Davis 2001, Gannes 2001, Gellin and Morris 2001, Jones et al. 2002). When birds migrate, most species make frequent stops throughout their journey to rest, forage, or avoid inclement weather (Rappole and Warner 1976). Because it is known that the presence of adequate stopover sites throughout the migration range is crucial for successful migrations (Hutto 1998), determining where birds choose to stop and the factors that make a suitable stopover site are important questions in the field of avian stopover ecology. Counts from bird migration monitoring stations can also be used to examine what environmental factors are associated with greater migration activity.

Because monarchs in eastern North America undertake a migration equally as long as songbirds, they too must stop frequently during their migration (Davis and Garland 2004). It is well known that temporary roosts of hundreds or thousands of monarchs can form each fall throughout the migration route, but few of these are known to occur with regularity each year (Urquhart and Urquhart 1979). From what is known of avian stopover ecology, these temporary roost sites can be considered monarch stopover sites, because while they are at these sites, their migration is temporarily stopped, and ground resources (i.e., roost trees) are being used temporarily (Davis and Garland 2004). However, for the most part, we know very little about what monarchs do other than roost during these temporary intervals when they pause their migrations. Furthermore, except for the documented overnight roosting locations, we also do not know where the most important stopover sites are located or what makes a suitable stopover site for monarchs. Thus, there is an immediate need for research describing the locations and characteristics of important monarch stopover areas, and what factors determine when monarchs are likely to use these areas.

Peninsula Point, Michigan, located at the north shore of Lake Michigan, acts to concentrate large numbers of migrating monarch butterflies that form large roosts and stopover for short intervals each fall. Since 1996, members of the Monarch Butterfly Project have conducted three daily counts each fall of the numbers of monarch butterflies stopping over at Peninsula Point. Furthermore, along with the daily monarch counts, the project personnel also routinely record wind speed and direction, temperature, and cloud cover during each count. Combined, these data allow for questions to be addressed relating to the effects of weather conditions on monarch stopover abundance.

In this work, our first objective was to characterize the general migration patterns at Peninsula Point using the data gathered over the first 7 yr of this project. We examined variation among years, and whether seasonal components within years resulted in larger numbers of monarchs earlier versus later in the migratory period. We also examined diurnal variation in monarch abundance. Our second objective was to determine whether the daily numbers of monarchs stopping over at the site were influenced by any of the environmental variables collected, including wind direction, wind speed, temperature, and cloud cover.

Materials and Methods

Study Site. The Peninsula Point recreation area, administered by the United States Department of Agriculture/Forest Service, is a 48.5-ha area of land that juts into the northern shore of Lake Michigan (Fig. 1). Most of the peninsula is wooded with cedar, aspen, or paper birch. At the southern end of the peninsula, the forest is cleared around a lighthouse tower. An interpretive 4-km-long nature trail passes through the southern clearing and the wooded area. In small sections on the peninsula, there are patches of goldenrod, in which monarchs are commonly seen nectaring during the fall (unpublished data).

Monitoring Protocol. Monarchs were counted each year between the second week of August and the third week of September. Each day, volunteer observers conducted three counts as follows: at 6 a.m. the number of monarchs roosting on or near the lighthouse were counted, and at 9 a.m. and 1 p.m. walking counts were conducted along a standardized transect on the 4-km-long trail surrounding the lighthouse and southern tip of the peninsula. For the roost count, because monarchs were counted while they remained still on the sides of the lighthouse or nearby vegetation, there was no set time limit, and observers remained in the roost area until they had counted all monarchs present. On the walking transects, observers recorded all monarchs (active, roosting, or both) seen while walking on the peninsula trail at a standardized pace without stopping, and these counts lasted an average of 45 min per transect. As the path is wooded over ≈75% of the trail, the overhead sky is obscured for the majority of this transect. Therefore, this survey targeted monarchs that were on or flying near the ground, and not monarchs flying overhead. For this reason, and because the 6 a.m. roost count targets monarchs that had stayed the night, we assume that the majority of the monarchs recorded at Peninsula Point with either count method were not actively migrating, but were engaged in stopover activities (foraging, resting, roosting, or seeking shelter).

At the beginning of each count, observers recorded environmental variables, including wind direction (as either north, northeast, east, southeast, south, southwest, west, or northwest, based on the direction the

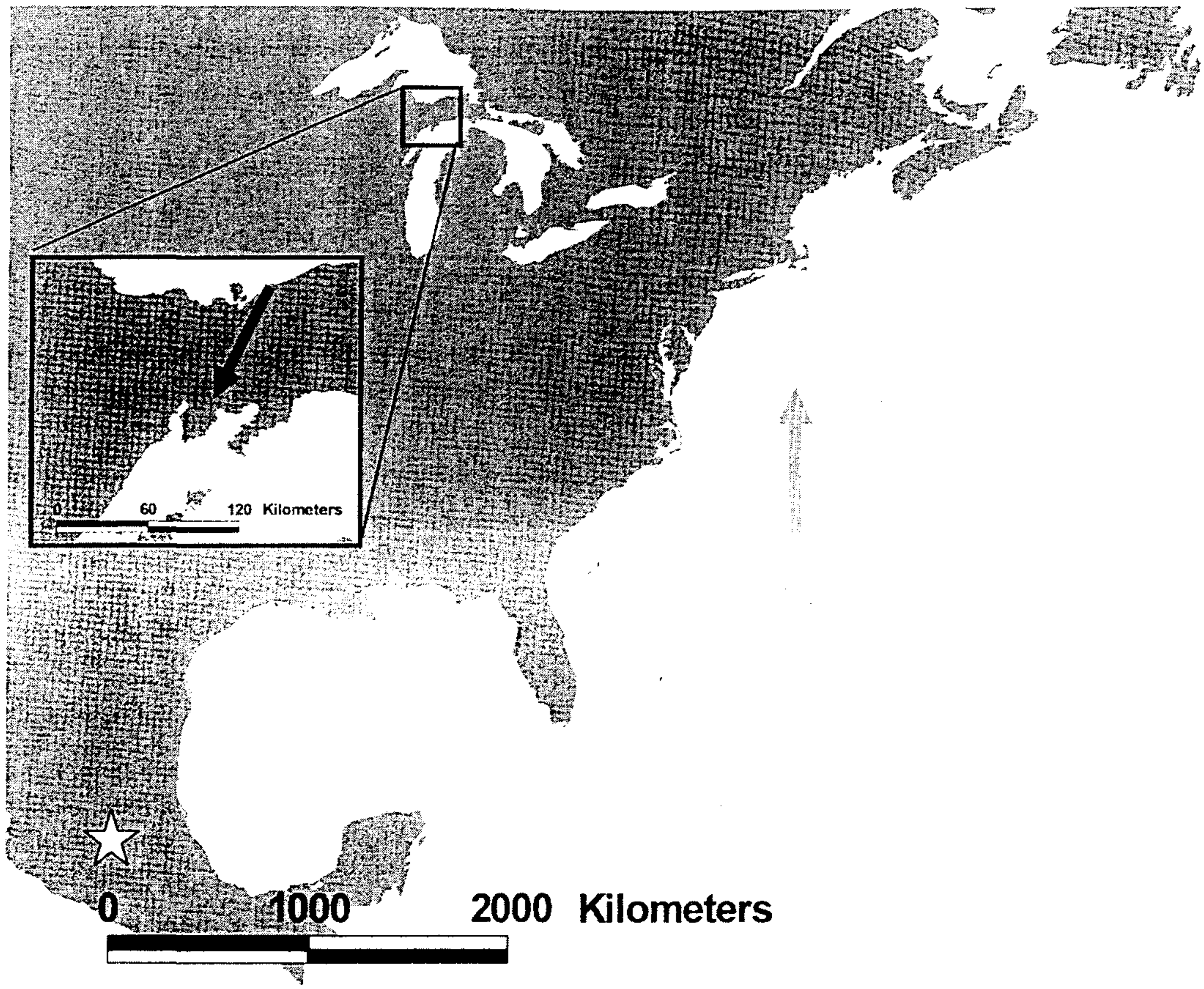

Fig. 1. Location of Peninsula Point, Michigan (solid arrow), 45.6°N 86.9°W. Mexican overwintering location (star) shown for reference.

wind was blowing from) and wind speed (on the Beaufort wind scale, with 0 indicating no winds and 6 representing storm-force winds). The temperature was also recorded, as was the amount of cloud cover. For this variable, the observer recorded the amount of the sun that was obscured by clouds on a five-point scale.

Statistical Analysis. For this study, we were interested in examining not only basic patterns of migration, but environmental effects as well. We therefore examined all effects simultaneously using an analysis-of-variance test on the number of monarchs seen on any given count. Monarch counts were log transformed ($\log_{10} + 1$) to normalize the error variance before this test. To examine the influence of environmental variables and temporal or seasonal effects on the number of monarchs seen at Peninsula Point, we included in the test effects of wind direction, wind speed, cloud cover (all included as categorical fixed factors), and temperature included as a covariate. We addressed effects of within-season timing by adding a continuous covariate that indicated the number of days since 1 August. Year was included (categorical variable) to test for annual differences in monarch numbers. Finally, we included a binomial variable to test for differences between the roost count and the walking counts. We had previously determined that there was no statistical difference between counts made by either the 9 a.m. or 1 p.m. walking census (two-sample t test, df = 560, t = −0.203, P = 0.840); therefore, these two counts were pooled. All analyses were performed using SPSS software (SPSS 2001).

Results

A total of 22,539 monarchs was counted over the first 7 yr (1996–2002) of this project at Peninsula Point (Table 1). A large number of monarchs appeared to stop at Peninsula Point each year, although the total number of monarchs counted each year varied considerably, ranging from 6,817 in 1997 to 757 in 1998. The overall mean number of monarchs counted per year at Peninsula Point was 3,184 (95% CI = 1276–5093). As a convenient way to summarize and compare the migration timing between years, in Table 1 each season is broken down into 5-d intervals that begin and end on the same calendar days each year. Furthermore, percentages of the seasonal total are presented for comparison instead of the actual count totals to account for differences among years in the

Table 1. Summary of monarchs seen during fall monitoring at Peninsula Point, Michigan, from 1996 to 2002, divided into 5-d intervals

Interval	Date range	1996	1997	1998	1999	2000	2001	2002	All years
1	5–10 Aug	*	54.4	3.6	5.7	24.9	31.1	3.6	28.3
2	11–15 Aug	2.7	8.8	6.3	22.0	10.0	20.8	4.9	12.0
3	16–20 Aug	7.0	12.4	11.8	5.2	31.9	14.6	12.3	15.4
4	21–25 Aug	34.3	4.7	7.9	1.5	0.3	3.2	7.4	4.9
5	25–30 Aug	1.6	5.4	21.0	10.3	8.3	1.8	2.5	5.8
6	31 Aug–4 Sept	6.5	10.0	27.6	13.7	5.5	23.5	4.7	11.9
7	5–10 Sept	27.0	0.8	11.5	41.6	0.2	2.0	3.5	7.3
8	11–15 Sept	20.8	0.6	3.0	*	16.6	2.1	20.9	7.4
9	16–20 Sept	*	2.7	2.9	*	2.3	0.4	4.4	2.0
10	21–25 Sept	*	0.1	4.4	*	0.1	0.5	35.8	5.1
	Season total	918	6,817	757	2,523	4,163	4,336	3,025	22,539
	Total No. counts	85	132	127	90	132	89	132	787
	Monarchs/Count	10.8	51.6	6.0	28.0	31.5	48.7	22.9	28.6

Percentage (of the season total) of monarchs seen in each 5-d interval shown. Intervals in which no monitoring occurred are indicated (asterisk).

volume of migration. For example, Table 1 suggests that the timing of the within-season migration peak varied among years. In 1997, most monarchs were recorded during the first 5 d of monitoring, whereas in 2002 the peak migration counts were toward the end of the monitoring period. In fact, in most years, there was at least one, and sometimes two, 5-d intervals in which over one-quarter of the monarchs for the season passed through Peninsula Point.

For logistical reasons, the total number of counts performed each year was not consistent (Table 1). Because of this inconsistency, included in Table 1 is the yearly number of monarchs per count (total monarchs seen divided by total number of counts). Similar to the seasonal totals, the number seen per count varied considerably between years, ranging from 6 in 1998 to 52 in 1997. Although these annual estimates say nothing of any potential within-season variation in monarch abundance, they each provide useful indices of annual abundance, standardized for effort, for comparison between years or with other sites with similar survey protocols.

The inconsistency between years in the number of monarchs observed stopping over at Peninsula Point was also apparent in the results of our analysis-of-variance test; there was a significant effect of year (entered as a categorical variable) on the number of monarchs counted at Peninsula Point ($F = 5.84$, df = 6, $P < 0.001$; Table 2). Interestingly, a Tukey post hoc test indicated that counts for 2002 (in the year after a dramatic decline at overwintering sites) were statistically similar to four other years.

There was a significant difference between the numbers of monarchs counted with the roost and walking census methods ($F = 53.36$, df = 2, $P < 0.001$; Table 2; Fig. 2). The roost count was significantly smaller than the walking transect counts. Finally, there was a significant effect of time within season on the numbers of monarchs counted ($F = 32.12$, df = 1, $P < 0.001$), and this effect was negative (Fig. 3).

Of the environmental variables we tested, there were significant effects of wind direction ($F = 4.40$, df = 9, $P < 0.001$) and cloud cover ($F = 5.84$, df = 4, $P < 0.001$) on the numbers of monarchs counted, but no effects of wind speed, temperature, and the interaction between wind speed and direction (Table 2). Tukey post hoc tests indicated that north winds were associated with the highest monarch counts, and south and southeast winds were associated with the lowest monarch counts (Fig. 4). Cloud cover was associated with monarch counts such that during days with low

Table 2. Results of ANOVA test on the number of monarchs seen on each census (log transformed) at Peninsula Point

Variable	S.S	df	F	P
Year	12.07	6	5.84	<0.001
Census type[a]	18.38	2	53.36	<0.001
Day within season	11.06	1	32.12	<0.001
Cloud cover	8.04	4	5.84	0.001
Wind direction	12.03	9	4.40	<0.001
Wind speed[b]	3.11	6	1.50	0.174
Temperature	0.81	1	2.36	0.125
Wind speed × direction	18.37	42	1.27	0.121
Error	240.72	699		
Total	869.52	769		

Independent variables included year, wind direction, wind speed, census type (all categorical), temperature, and a day-within-season variable as numerical covariates.

[a] Roost count or walking transect.

[b] Recorded in Beaufort wind scale units (0–6).

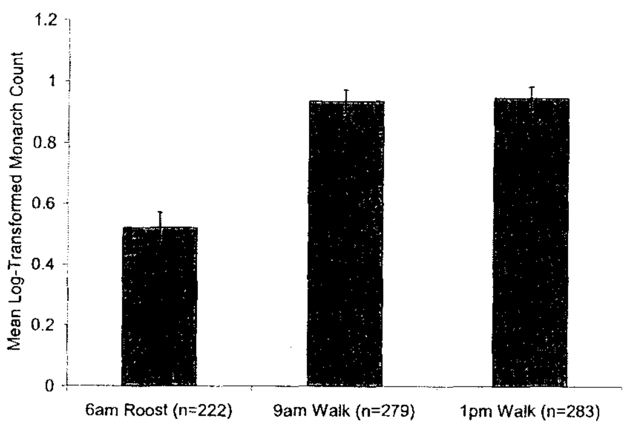

Fig. 2. Average number of monarchs (log transformed) seen during each count type at Peninsula Point.

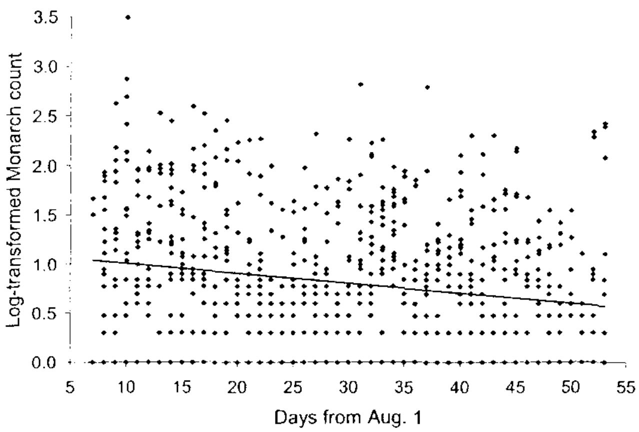

Fig. 3. Seasonal variation in monarch abundance at Peninsula Point. Mean log-transformed number of monarchs is plotted against the day within season (number of days from 1 August). Linear regression line shown.

visibility (50% or more of the sun was obscured by clouds), monarch counts were notably lower than during days with high solar visibility (Fig. 5).

Discussion

Annual Population Estimates. From the large numbers of monarchs counted each year, it is clear that Peninsula Point appears to be an important annual stopover site for migrating monarchs. Overall, ≈29 monarchs were seen on an average count at Peninsula Point, based on all 7 yr, and the mean number of monarchs that were counted each season was 3,184. Sites such as Peninsula Point, where large numbers of migrating monarchs are known to occur predictably each fall, are rare in North America (Urquhart and Urquhart 1979) and represent ideal sites for research in monarch stopover ecology (Garland and Davis 2002). Furthermore, if monitored in a consistent manner for many years, as it is at Peninsula Point, these sites have the potential to provide not only information on monarch stopover ecology, but also long-term indices of fall population size. This has been shown to

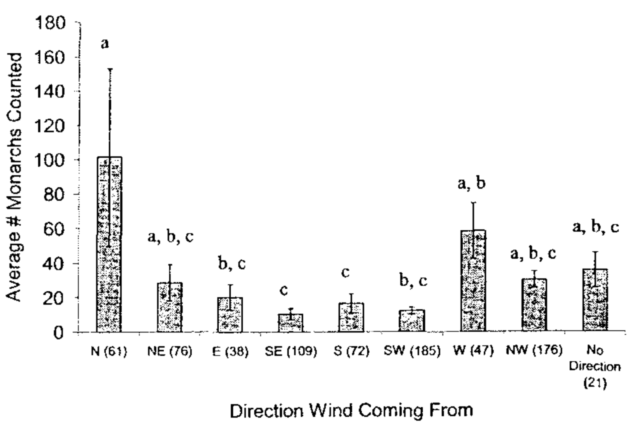

Fig. 4. Mean number of monarchs seen with each wind direction. Standard error bars shown. Number of counts made with each wind direction shown in parentheses. Homogeneous subgroups indicated.

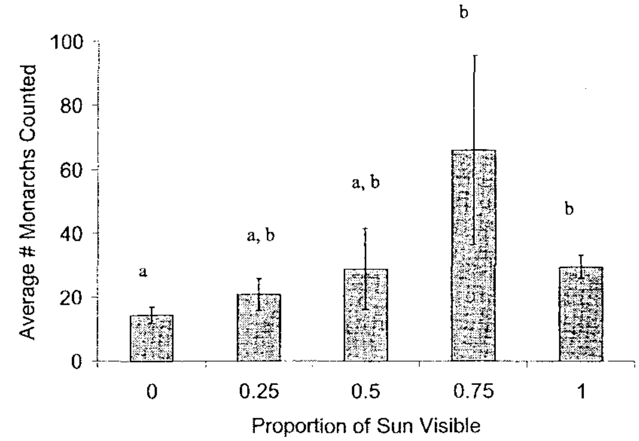

Fig. 5. Effect of cloud cover on numbers of monarchs seen at Peninsula Point. Average number of monarchs in each category is shown, with standard error bars. Cloud cover was measured by the proportion of the sun that was visible. A "0" was given when the sun was completely obscured by clouds, and a "1" indicated that the sun was completely visible. Homogeneous subgroups indicated.

be true at Cape May, New Jersey. At that site, Walton and Brower (1996) showed that annual monarch migration counts closely matched the annual breeding counts for that geographic area (northeastern United States). If the annual migration data from Peninsula Point also reflect the number of monarchs that breed each summer at least in the immediate geographic area surrounding Peninsula Point as it does in Cape May, then the annual numbers of monarchs counted at Peninsula Point indicate a widely fluctuating (postbreeding) population size in this area.

2002 Season. Although it was not the primary goal of this study, the data for the 2002 season deserve comment, as it was the first fall migration after a severe overwintering population crash in Mexico (Brower et al., 2004). As much as 75–80% of the eastern population may have been killed by an ice storm during this time. We therefore expected to find few monarchs at Peninsula Point during the season immediately after this decline. Contrary to our expectations, the total number of monarchs observed that season was similar to the 7-yr average for this site. This could indicate that the population in Michigan and surrounding areas was not substantially depressed in that year. We can offer several possible explanations for this result. It may be that the data collected from Peninsula Point each fall (i.e., annual numbers of monarchs stopping over) are not truly indicative of the annual numbers of monarchs breeding in the upper Midwestern monarch population, and by random chance the data for 2002 showed a larger number of monarchs than would have been expected based on the size of the monarch breeding population that year. Alternatively, it may be that when the few remaining monarchs returned to the Midwest in the 2002 breeding season, the population in this area was able to rebound so that the subsequent postbreeding numbers observed at Peninsula Point were not greatly affected. In either case, the data from Peninsula Point suggest that the 2002 fall monarch numbers in this area were not substantially lower than in the majority of years over which data were collected.

Basic Migration Patterns. Besides the annual fluctuations in the numbers of monarchs counted at Peninsula Point, we observed considerable variation in the within-season timing of migration through the site. There was little consistency in the timing of the peak of migration from year to year. This fact underscores the importance of consistent, standardized monitoring throughout the migration season, because the timing of peak migration activity (beyond knowing what months to monitor) cannot be predicted. We did detect a small, but significant temporal pattern such that the numbers of monarchs counted declined as the season progressed each year (Fig. 3). However, even this pattern may not hold true for all years, because in 2002, 35.8% of the season's monarchs were counted during the final week of the monitoring period.

The inconsistency in migration timing points to a potential problem in the annual starting and ending dates of the monitoring program at Peninsula Point. In 1997 and again in 2001, the peak of the migration for those years was observed during the first 5 d of the monitoring, which may indicate that some monarchs had already passed through before the monitoring started for that year. Furthermore, in 2002, the most monarchs were counted during the final 5-d interval, suggesting that some were missed after the end of monitoring for that year. For this reason, to ensure that the entire migration is captured by surveys, we suggest that future monitoring programs at this and other stopover sites include at least 10 more days of monitoring (start 5 d earlier and end 5 d later) than the Peninsula Point program if at all logistically possible. Because at Peninsula Point it is possible for over half of the annual total number of monarchs to pass through the site in one 5-d interval, and given that the timing of this peak varies annually, it is essential that all potential migration times be encompassed by monitoring to ensure accurate yearly estimates of abundance.

Another pattern we detected was a significant difference in the number of monarchs counted between the roost count and the walking transect counts. This result was not surprising, as previous comparisons of similar monitoring methods have shown that differences in the resulting counts can exist (Davis and Garland 2002). Each of the census methods used at Peninsula Point targets different stopover behaviors. The roost count, because it is conducted early in the morning, reflects the number of monarchs that roosted at the site during the previous night, while the walking censuses target monarchs engaged in nectaring or low-flying activities at the site. The larger number of monarchs counted at Peninsula Point during the day with the walking transects could be caused by the monarchs' increased activity and visibility at this time, or may reflect a pattern whereby more monarchs arrive at the site during the day, which leads to increasing numbers counted.

Environmental Effects on Stopover. Wind direction appeared to influence greatly the number of monarchs that were counted at Peninsula Point on any given day, a result that is consistent with previous research (Schmidt-Koenig 1985, Davis and Garland 2002, Davis and Garland 2004). However, the fact that the most monarchs were counted with north winds was not expected, as this direction should be the most favorable for active migration in this area, and thus few monarchs should have been detected at stopover sites at these times. Previous studies have demonstrated that the most unfavorable wind directions (i.e., headwinds) tend to cause large accumulations of monarchs at stopover sites (Schmidt-Koenig 1985, Davis and Garland 2004). It may be that at Peninsula Point, the favorable north winds were simply causing more monarchs to be migrating in general during those days, and that many of these monarchs stopped for brief periods during the day at Peninsula Point, causing large numbers to be reported. If this was indeed the case, then the north winds may not have been causing the accumulations of monarchs at the site per se; rather, the large numbers of monarchs stopping over at Peninsula Point simply coincided with large waves of actively migrating monarchs.

An alternative explanation for why most monarchs were present on Peninsula Point during seemingly favorable winds may be that most of the monarchs that were observed at these times could no longer sustain flight and were in need of resources, despite the favorable winds. We know little of the requirements of migrating monarchs at stopover sites. The primary motivation for a bird to use a stopover site is to forage and replenish its depleted fat stores, which it uses for its next migratory flight (Cherry 1982). Brower (1985) demonstrated that monarch fat stores increase throughout the migration south. Thus, there appears to be a requirement for fat deposition in migratory monarchs, similar to migratory birds. However, the nature of this fat deposition in monarchs is unclear. Questions remain, such as what resources are required for fat deposition, are these resources dwindling or stable throughout the migration route, and how long does it take for individuals to deposit the necessary fat stores?

That most monarchs were counted when there was little cloud cover was not unexpected. It has been demonstrated previously that more monarchs generally migrate during these conditions (Schmidt-Koenig 1985). However, it has also been shown that migrating monarchs tend to soar high in the sky during sunny days (Gibo and Pallett 1979, Schmidt-Koenig 1985), and that this behavior can lead to fewer numbers of monarchs counted with monitoring methods that target ground or near-ground monarchs (Davis and Garland 2002). This may have also been the case at Peninsula Point, where a surprisingly low number of monarchs was counted when the sun was fully visible. During these times, many monarchs may have been migrating, but high over the peninsula, and possibly out of the range of sight. This possibility further emphasizes the need to ensure that monarch monitoring protocols include a ground-based count, as well as a count of monarchs flying high overhead.

Future Directions. Throughout this study, we have assumed that when monarchs were observed at Peninsula Point during the fall, the majority were not migrating at the time of observation, because most monarchs were observed nectaring, roosting, or flying low to the ground. Therefore, we have argued that all counts of monarchs at Peninsula Point, and indeed for any other monarch migration monitoring site with similar protocols, are actually estimates of the number of monarchs temporarily stopping over at the site. Whether monarchs stop for 10 min or 3 d, if they descend to the ground and use resources (i.e., nectar plants, roost trees) in any way, these events represent stopover behaviors. Ornithologists typically consider the length of time that a landbird spends at a stopover site to indicate the quality of habitat at that site (Morris et al. 1996, Dunn 2000). Through monarch tagging studies, Davis and Garland (2004) documented an average autumn stopover duration of 2 d at a coastal site in Virginia. We do not know the average duration of stopover activity at Peninsula Point. If the importance of a stopover site to migrating monarchs is related to their stopover length, then future studies at Peninsula Point, and at other monitoring sites, should involve marking and recapturing individuals during stopover and calculating average durations of stay. Furthermore, future research at all monitoring sites should address the questions relating to fat deposition in monarchs during stopovers. Such questions could easily be accomplished by capturing and weighing monarchs during migratory stopovers at monitoring sites.

We conclude that the migration of monarchs through Peninsula Point is variable in nature, with little temporal consistency from year to year other than the fact that most of the migration occurs in the same 2 mo each year. The numbers of monarchs that migrate through this area vary among years, ranging from several hundred to several thousand annually. These numbers might be considered indices of fall population size in this geographic area. Few consistent temporal patterns in the migration exist, although in general, more monarchs pass through Peninsula Point early in the migration season, and more monarchs are usually counted in the mid-morning and afternoon than in the early morning. Temporary stopovers of 1 d or less may be the norm for this site, either because the monarchs do not require longer stopovers, or because the site itself is not suitable for this. Finally, monarchs at Peninsula Point are seen most often when the wind direction is from the north, at higher rather than lower temperatures, and when there is little cloud cover. From the large number of monarchs counted annually at Peninsula Point, this site clearly represents an important annual monarch stopover area, regardless of how long monarchs stay there, and it therefore has the potential to increase our knowledge greatly of this little-known aspect of monarch life cycles.

Acknowledgments

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