

# Long-Term Monitoring and Fall Migration Patterns of the Monarch Butterfly in Cape May, New Jersey

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**ABSTRACT** Each year in eastern North America, monarch butterflies, *Danaus plexippus* (L.) (Lepidoptera: Nymphalidae), undergo an annual migration to wintering sites in central Mexico. We used monarch migration census data from Cape May, NJ, over a 13-yr period (1992–2004) to test for annual and within-season variation in the numbers of monarchs seen during daily censuses and to examine the timing and patterns of migration waves. Across all years, the total number of monarchs counted over the 60-d season ranged from 452 to 15,751 with a 13-yr average of 3,490 monarchs yr<sup>-1</sup>. There was significant annual, diurnal, and within-season temporal variation in the census counts. Within seasons, monarch numbers increased during September up until early October, and gradually declined thereafter. Comparison of season averages across years, which we consider indices of population size in the northeastern United States, indicated a highly fluctuating population size with the lowest year on record in 2004. We also found that greater than average daily counts, which we termed “notable migration days,” were reported for an average of 19 d per season. On average, seven “migration waves” occurred each year, defined as a period of one or more notable migration days separated by below average days. Waves lasted an average of 3 d and were separated from others by ≈6 d. There was no significant interannual variation in wave duration or time between waves. Our 13-yr study is the longest standardized census of the monarch’s fall migration, and we believe its continued operation can provide insights into the population trends of monarchs in the northeastern United States, which may reflect long-term trends from other populations in North America.

**KEY WORDS** population census, *Danaus plexippus*, seasonal migration, North America, endangered biological phenomenon

NATIVE AND INTRODUCED MONARCH butterflies, *Danaus plexippus* (L.), populate islands and continents worldwide (Ackery and Vane-Wright 1984), and in parts of their range they undergo an annual, bird-like two-way migration (Urquhart and Urquhart 1978, Brower 1995). Each fall in eastern North America, monarchs undergo the longest annual migration of any insect species, traveling distances of up to 4,300 km from Canada and Maine to coniferous forests in the transvolcanic mountains of central Mexico (Brower and Malcolm 1991). Monarchs arrive at wintering sites from late October to November and aggregate in dense colonies that harbor tens of millions of individuals (Calvert and Lawton 1993). In February and March, these same butterflies mate and fly north to recolonize their breeding range (Van Hook 1993, Howard and Davis 2004), an additional distance of up to 2,100 km.

Monarch butterflies that breed in eastern North America face an uncertain future because their fates are strongly tied to the health of overwintering sites

that are rapidly being degraded by deforestation (Brower et al. 2002, 2005, Oberhauser and Peterson 2003). Because literally the entire eastern North American population overwinters in a few small areas of high-altitude fir forests, disturbances to these areas have dramatic influences on the survival of the overwintering monarchs (Brower et al. 2004). Because additional crises face the food resources for monarch larvae in their breeding range (Brower 1999, Oberhauser 2004, Schappert 2004), the well-known migration to and from these overwintering areas has clearly become an endangered biological phenomenon (Brower and Malcolm 1991).

Ironically, of all the life history stages of the monarch butterfly, we know the least about its fall migration. Both recent and historical studies have identified general directions that migrating monarchs travel (Urquhart and Urquhart 1977), cues used in navigation (Perez et al. 1997, Mouritsen and Frost 2002), and the influence of weather on census counts during fall migration (Brower 1995, Davis and Garland 2004, Meitner et al. 2004). For example, monarchs fly only during daylight and stop frequently to use nectar resources (Alonso-Mejia et al. 1997, Davis and Garland 2004). These stopover sites likely represent important habitats for migrating monarchs, particularly during

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inclement weather, including rain and unfavorable winds (Davis and Garland 2004). Furthermore, during their southward migration, monarchs can become concentrated by geographic features such as mountains (Calvert 2001) and peninsulas next to water barriers (Garland and Davis 2002, Meitner et al. 2004), which they are reluctant to cross if wind conditions are unsuitable (Schmidt-Koenig 1985). These accumulations can last for several days (Davis and Garland 2004), during which the butterflies drink nectar from the local flora and use trees and shrubs for roosting upon during nights and inclement weather.

Cape May, NJ, is a peninsula along the mid-Atlantic region of eastern North America bordered by the Atlantic Ocean and the Delaware Bay. Large numbers of monarchs migrating southward along the east coast accumulate at this site each fall, and a pilot project to census their daily numbers was begun in 1991. In 1992, a standardized monitoring protocol was established and has continued unchanged every fall through 2004. Data from 1991 to 1994 were used to demonstrate that the annual numbers of migrating monarchs counted at Cape May correlate positively with the size of the breeding population east of the Appalachians and to the north of the site (Walton and Brower 1996).

In this study, we used 13 yr of census data (1992–2004) from the Cape May monitoring project to 1) describe the longer term population trends of the northeastern monarch population, and 2) contribute to our understanding of monarch autumn migration patterns at a long known Atlantic coastal site. Specifically, we asked to what extent do total numbers of migrating monarchs vary across years and within seasons? We also examined the timing of migration to ask how many pulses of monarchs pass through Cape May each year and to examine annual variation in the timing and duration of these waves. Characterizing patterns of migrating monarchs at this site can help identify long-term trends of the monarch population in the northeastern United States and also can provide information on the window(s) of time during which monarchs might use resources at this point along their migration route.

### Materials and Methods

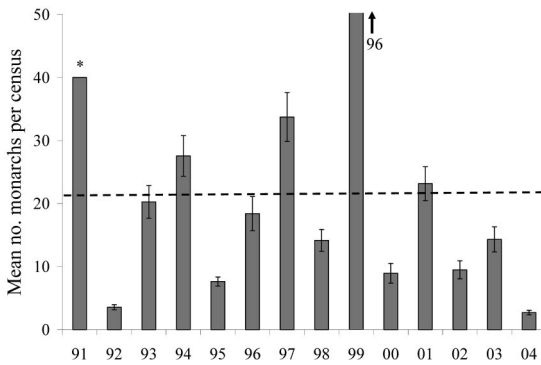
Details of the study site and the methods of data collection at Cape May, NJ, were described previously in Walton and Brower (1996). The researchers conducted driving censuses and recorded all monarchs seen while driving standardized 8-km transects at  $\approx 32\text{--}40\text{ km h}^{-1}$  from 1 September to 31 October. The transect route encompassed several different habitats, including beach dunes, agricultural fields, and residential neighborhoods at the south end of the Cape May peninsula. Censuses lasted  $\approx 17$  min, and a single observer counted all monarchs seen flying, nectar feeding, or resting from within the vehicle (R.K.W., unpublished data). Weather permitting, censuses were initiated at 9 A.M., 11 A.M., and 3 P.M. on all days until 15 October, when, because of the shortened daylength, counts were reduced to 11 A.M. and 2 P.M.

for the remainder of the season. Note that for analyses purposes, the data from these 2 P.M. censuses were pooled with the 3 P.M. census data. No counts were conducted on days with heavy rain or storms. Because censuses were conducted in the same manner each year (i.e., same number of daily censuses, same route, and census duration), we considered the daily mean number of monarchs seen per census as our test variable for analyses of monarch abundance in this study.

**Statistical Analysis.** *Variation in Monarch Abundance.* To test for variation in monarch numbers within and among years, we performed a univariate analysis of variance (ANOVA) by using the number of monarchs counted per census ( $n + 1$ , log-transformed) as the dependent variable, with year and using census number (i.e., first, second, or third census of the day) as independent variables. Julian day (number of days since 1 September) was included as a covariate to control for within-season variation. Comparison of nested regression models indicated that the relationship between Julian day and monarch abundance was best described by a quadratic curve; therefore, the square of Julian day also was added to the model as a final covariate (model:  $\log \text{count} = \text{year} + \text{census number} + \text{Julian day} + \text{Julian day}^2 + \text{year} * \text{census number} + \text{year} * \text{Julian day} + \text{year} * \text{Julian day}^2$ ).

*Comparing Within-Season Migration Patterns.* Because the total number of monarchs seen at Cape May varied from year to year, temporal migration patterns were not easily compared between years without first accounting for this annual variation in abundance. Our approach was as follows. Because the number of daily censuses varied throughout the season (i.e., either two or three censuses were conducted), we first calculated the average number of monarchs counted per census per day. We then added all these daily average census values together for the entire season to create a temporary "season total." Note that this value is not the same as the total number of monarchs actually counted each season. We next divided each day's average census value by the temporary season total (and multiplied by 100); this value reflected the relative numbers (i.e., the percentage) of monarchs seen per census each day based on the total numbers seen that season. These daily percentages were comparable across years and allowed the relative within-season migration patterns to be examined, regardless of the natural variation in the total number of monarchs counted each year.

We used these data to examine the frequency and duration of "migration waves" and peaks each year, where a migration wave was defined as one or more than one successive days when the daily percentage value (defined above) was greater than or equal to the average daily census percentage (in this case, 1.6%, or 100% divided by 60 d, the length of our migration survey). We called these above-average census days "notable migration days." We defined a migration wave as one or more notable days separated by one or more below average days. We then tested for annual variation in wave duration (days) and for annual variation in the time between waves (days) by using



\* Extrapolated from data provided in Walton and Brower (1996)

Fig. 1. Annual variation in monarch abundance at Cape May. Shown are the average numbers of monarchs seen per census each year. Dashed line shows the 1992–2004 average (21.5 monarchs per census). Error bars represent standard errors.

one-way ANOVAs with year as the independent variable in both cases. Both wave duration and the time between waves variables were log-transformed before analyses to normalize the error variance. Additionally, we defined “peak migration days” as those when the relative number of monarchs per census exceeded the annual mean percentage (1.6%) plus the average annual standard deviation (2.4%), that is, when the percentage of monarchs per census exceeded 4% of the season’s total. We then recorded the number of peak migration days seen per season and the percentage of each season’s census counts that were observed on peak days.

## Results

**Annual Variation in Census Counts.** From 1992 to 2004, a total of 45,368 monarchs were counted during 2,113 standardized census runs along the monitoring transect in Cape May. Across these 13 yr, the total number of monarchs counted per season ranged from 452 to 15,751 (a 35-fold difference), with a 13-yr average of 3,490 monarchs per season. The average numbers of monarchs per census per day are shown in Appendix for all years (rounded to the nearest individual). The annual average number of monarchs counted per driving census (i.e., mean for all censuses in a given year) ranged from three to 96 monarchs per census, with a 13-yr average of 21 monarchs per census. Figure 1 shows these annual census averages across all years, including an extrapolated average for 1991 based on data provided in Walton and Brower (1996). (Note, however, that the 1991 data were not included in our tests and are merely provided in this figure to visualize long-term trends).

There was a significant effect of year ( $F = 28.36$ ;  $df = 12, 2,084$ ;  $P < 0.001$ ; Table 1) on the average number of monarchs counted per census each season as demonstrated by the large variation shown in Fig. 1. Tukey’s post hoc tests at the 0.05 level confirmed

Table 1. Results of ANOVA test examining variation in the number of monarchs counted per census at Cape May from 1992 to 2004

Variable	df	Mean square	<i>F</i>	Significance
Yr	12	8.106	28.363	<0.001
Census no.	2	3.125	10.935	<0.001
Julian day	1	62.039	217.070	<0.001
Julian day <sup>2</sup>	1	67.905	237.592	<0.001
Yr × Julian day <sup>2</sup>	12	2.575	9.011	<0.001
Error	2,084	0.286		

The interaction effect of year × census number was not significant and was therefore removed from the final model.

Comparison of nested regression models indicated that the relationship between Julian day and monarch abundance was best described by a quadratic curve.

that 1999 had the highest number of monarchs seen (average of 96 monarchs per census). Furthermore, Fig. 1 shows that the five above-average years (1991, 1994, 1997, 1999, and 2001) were immediately followed by years where monarch counts were substantially below average. Below-average numbers of monarchs were recorded for 2002, 2003, and 2004; 2004 showed the lowest monarch census counts recorded to date.

**Within-Season Variation in Census Counts.** There was a significant effect of daily census number (i.e., first, second, or third daily census of the day) on the number of monarchs seen ( $F = 10.94$ ;  $df = 2, 2,084$ ;  $P < 0.001$ ), indicating a diurnal trend in monarch abundance at Cape May. On average, 16.6 monarchs were seen during the 9 a.m. census, 29.8 were seen during the 11 a.m. census, and 20.2 were seen during the afternoon census. There was also a significant effect of Julian day on monarch abundance ( $F = 237.59$ ;  $df = 1, 2,084$ ;  $P < 0.001$ ), indicating substantial within-season variation. This variation can be seen in Fig. 2, where the mean daily percentage of monarchs seen per census (averaged across all years) is plotted over the entire season. These long-term averages showed a gradual increase in monarch abundance in the first third of the season, a peak in census counts between the last week of September and the first week of October, and a gradual decrease during the final 3 wk of the census counts.

**Within-Season Patterns.** Differences between years in the timing of migration patterns become apparent when each season’s data are viewed after standardizing for variation in annual numbers. Figure 3 shows the days when the numbers of monarchs counted exceeded 1.6% of season totals (notable migration days) and 4% of season totals (peak migration days). Across all years, we observed an average of 19 notable days per season, with a range of 12–26 d (Table 2). Moreover, counts of consecutive notable days (migration waves) showed an average of 7.1 waves per year, with a range of 4–12 (Table 2). We observed no significant variation in wave duration among years ( $F_{12, 80} = 0.302$ ;  $P = 0.987$ ), with waves averaging 2.8 d each season. There were on average 6.1 d between migration waves each season, and again we found no significant annual variation in this measure ( $F_{12, 78} =$

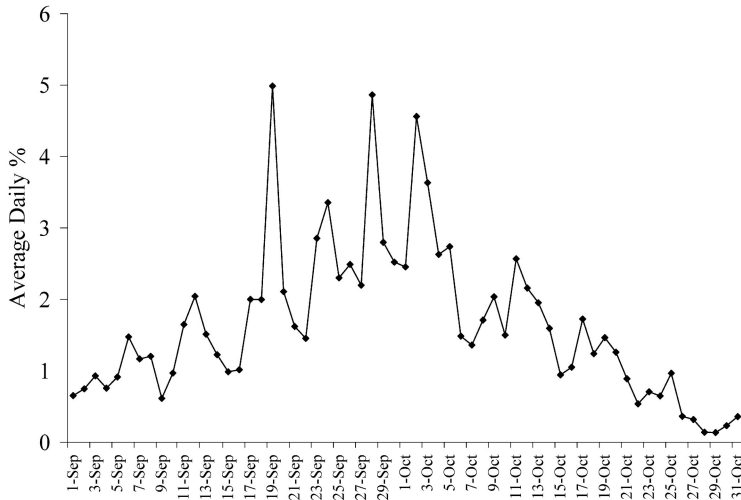


Fig. 2. The 13-yr average (1992–2004) of the daily percentages of each season's total for all days during the monitoring period (1 Sept.–31 Oct.).

0.420;  $P = 0.951$ ). Finally, we recorded an average of 7.3 peak days each season (days for which the average percentage of monarchs per census exceeded 4%), and the number of peak days ranged from 4 to 10 (Table 2). When the percentages for these peak days were summed, we found that peak days accounted for an average of 50.7% of each season's total counts (range 21.5–75.5%; Table 2).

### Discussion

**Annual Variation in Census Counts.** A previous analysis based on 4 yr of migration census data in Cape May, NJ, showed that the total numbers of monarchs counted each year were positively associated with the numbers of monarchs breeding during midsummer in the northeastern United States (Walton and Brower 1996). Our results based on 13 yr of migration data from this same site show a fluctuating pattern of annual population size in the northeastern United States (Fig. 1). This observation is consistent with Swengel (1995), who showed fluctuating monarch population sizes based on annual midsummer counts. Such large fluctuations mean that detecting positive or negative long-term population trends in this population will be difficult and will require a longer set of data than the 14 yr presented here. Furthermore, it means that periodic low-census years should not necessarily be cause for concern. For example, in 1992 an extremely low number of monarchs was recorded at Cape May, but just 2 yr later the numbers were well above average, and 7 yr later, the numbers were at a 14-yr high. This pattern points to the resiliency of monarch populations.

The 14-yr trends shown in Fig. 1 provide insight into future population dynamics of monarchs in the northeastern United States. To begin, average or above-average years seem to be always followed immediately by below-average years. Put another way, we never

recorded two consecutive years with above-average monarch numbers. Further, when the population census was extremely low (as during 1992 and 1995) recovery to above-average numbers took 2 yr or longer. Thus, if the numbers of monarchs counted in subsequent years do not recover after the low in 2004 as they did after 1992, then this recent trend could signify the beginnings of the population collapse foretold in Brower and Malcolm (1991) as the likely combined result of overwintering habitat destruction (Brower et al. 2002, Brower et al. 2005) and widespread pesticide use in breeding areas (Brower 1999, Oberhauser 2004, Schappert 2004).

**Within-Season Migration Patterns.** The lack of temporal consistency between years in within-season census patterns was similar to that found at an inland migration monitoring site at Peninsula Point, MI (Meitner et al. 2004). In both sites, the migration peaks seemed to be sporadic and unpredictable during the migration season, with few similarities in timing between years. However, it is interesting to note that even though different methods were used to census monarchs in the Peninsula Point and Cape May studies (walking versus driving censuses, respectively), the 7-yr average number of monarchs counted per census at Peninsula Point was 29 (Meitner et al. 2004), whereas the 13-yr average at Cape May was 21. This may simply be a coincidence; however, censuses in both locations covered observation areas that were similar in size, and it will be interesting to compare these numbers to migration counts from additional sites in eastern North America to determine whether similar numbers are observed elsewhere.

Despite the unpredictability in the timing of migration at Cape May, general within-season temporal patterns became evident when the graphs of each season were compared. First, seasonal trends averaged across all years (Fig. 2) indicate that the bulk of the migration was captured by our 60-d census period and

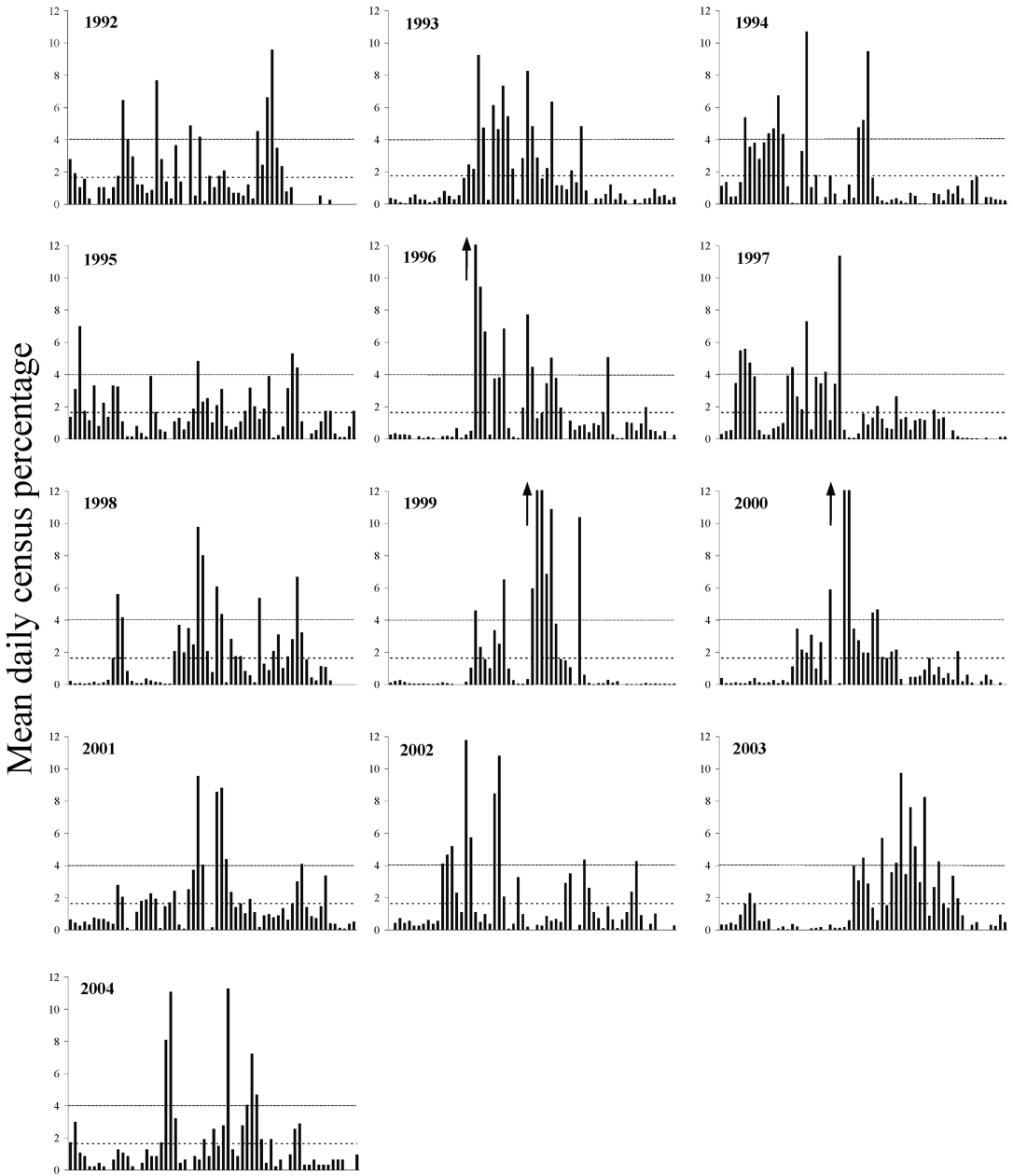


Fig. 3. Migration patterns for all years at Cape May. Shown are the average daily census percentages of each season's total (y-axes) for all days of the migration period (x-axes). The x-axis scale ranges from 1 Sept. to 31 Oct. Black short-dashed line indicates notable day threshold, or average daily census percentage (1.6%). Gray, long-dashed line indicates the peak day threshold of 4%, defined as the average census percentage plus 1 SD, (i.e.,  $1.6 + 2.4\%$ ) as described in *Materials and Methods*.

that in general more monarchs were observed during the middle portion of each migration season than during the early and late phases. When comparing patterns among years (Fig. 3), we could identify three somewhat distinct seasonal patterns from these graphs. In the most common type, the bulk of the monarch migration at Cape May seemed to occur in the middle of the sampling period (as in 1993, 1996,

1999, 2000, and 2001). In a second pattern, higher census counts were concentrated toward the beginning of the sampling period (1994, 1997, and 2002). The least common pattern was observed in 1992 and 1995, when migratory counts remained relatively steady throughout the sampling period. Differences in these seasonal patterns may result from year-to-year differences in the timing and occurrence of favorable

**Table 2.** Summary of monarch fall migration at Cape May, NJ, based on data shown in Fig. 3

Yr	No. notable days	No. waves <sup>a</sup>	Avg wave length (d)	Avg days between waves	No. peak days (% of total)
1992	20	9	2.2	3.1	8 (47.9)
1993	18	6	3.0	6.2	10 (61.8)
1994	18	6	3.0	8.5	9 (55.7)
1995	26	12	2.2	3.3	4 (21.5)
1996	16	6	2.7	6.5	8 (58.8)
1997	18	7	2.6	4.9	7 (43.0)
1998	23	7	3.3	6.0	8 (50.0)
1999	12	4	3.0	10.0	8 (75.5)
2000	20	6	3.3	8.5	5 (25.8)
2001	21	9	2.3	4.9	6 (39.4)
2002	16	7	2.3	6.1	9 (59.3)
2003	20	6	3.3	6.5	8 (49.3)
2004	18	8	2.3	4.4	6 (46.4)
Avg	19	7.1	2.7	6.1	7.3 (50.9)

Notable days were defined as days when the average daily census percentage exceeded 1.6% of the season's total (as defined in *Materials and Methods*). Waves were defined as one or more consecutive notable days separated by one or more below-average days. Peak days were defined as days when the average daily census percentage exceeded 4% of the season's total (as defined in *Materials and Methods*).

<sup>a</sup> Number of migration waves over the course of the season.

wind conditions during the fall, which monarchs are known to exploit during their migration (Schmidt-Koenig 1985, Davis and Garland 2002). Further examination of the census data with respect to daily environmental conditions at Cape May is planned and will highlight factors that influence these patterns.

Over an average season, there were approximately seven waves of above-average monarch numbers, and these waves tended to be spread over approximately three consecutive days each. Furthermore, an average of 19 d, or 30% of the 60-d monitoring period had the majority of the monarchs recorded each season, and about one-half of each season's monarchs were sighted during 4–10 peak days each year (Table 2). These data tell how often, and for how long, the Cape May site is likely to be used by migrating monarchs each fall.

It is important to note that we did not distinguish between actively migrating monarchs and nonmigrating, "bivouacked" monarchs in the Cape May driving census data, although driving censuses tend to reflect the numbers of grounded monarchs more so than high-flying, actively migrating monarchs (Davis and Garland 2002). Thus, on the one hand, migration waves and peaks could represent pulses of actively migrating monarchs, with each pulse taking 3 d to pass the site. Alternatively, these waves could represent 3-d accumulations of monarchs on the peninsula. In this case, monarchs could arrive at the Cape May area and stop migrating for a short time to seek shelter or nectar on the peninsula before crossing the Delaware Bay. One way to explore this issue is through tagging methods following the approach of Davis and Garland (2004). By tagging and recapturing individuals during migratory stopovers, their study established that the average stopover duration of monarchs at that site was

2 d, and differentiated between active migration waves and periods of monarch accumulation at their site. We suggest that future efforts at Cape May and at other sites could use this method to estimate the typical duration of stopovers for the site. This information would provide further insight into the importance of resources and habitat at these sites to migrating monarchs and indicate to what extent these sites are used by monarchs as a place of temporary refuge and/or as a flight corridor.

In conclusion, because of our methodological consistency, our census data can be used for long-term population monitoring and to describe the migration patterns of the monarch butterfly population in the northeastern United States. Our data suggest a highly fluctuating population size in the northeastern United States, meaning that continued monitoring in Cape May will be necessary to detect long-term positive or negative trends. The data also may elucidate how often and for how long the Cape May site is used by monarchs as a place of temporary refuge and as a flight corridor. Our data indicates that the largest numbers of monarchs are present at Cape May on  $\approx 7$  d during a given fall migration season.

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### References Cited

- Ackery, P. R., and R. I. Vane-Wright. 1984. Milkweed butterflies: their cladistics and biology. Cornell University Press. Ithaca, NY.
- Alonso-Mejia, A., E. Rendon-Salinas, E. Montesinos-Patino, and L. P. Brower. 1997. Use of lipid reserves by monarch butterflies overwintering in Mexico: implications for conservation. *Ecol. Appl.* 7: 934–947.
- Brower, L. P. 1995. Understanding and misunderstanding the migration of the monarch butterfly (Nymphalidae) in North America: 1857–1995. *J. Lepid. Soc.* 49: 304–385.
- Brower, L. P. 1999. Will biotechnology doom the monarch? *Defenders (Conserv. Mag. Defenders Wildl.)* 79: 39–41.
- Brower, L. P., and S. B. Malcol. 1991. Animal migrations: endangered phenomena. *Am. Zool.* 31: 265–276.
- Brower, L. P., G. Castilleja, A. Peralta, J. Lopez-Garcia, L. Bojorquez-Tapia, S. Diaz, D. Melgarejo, and M. Missrie. 2002. Quantitative changes in forest quality in a principal overwintering area of the monarch butterfly in Mexico, 1971–1999. *Conserv. Biol.* 16: 346–359.
- Brower, L. P., D. R. Kust, E. Rendon-Salinas, E. Garcia Serrano, K. R. Kust, J. Miller, C. Fernandez Del Rey, and K. Pape. 2004. Catastrophic winter storm mortality of

- overwintering monarch butterflies in Mexico during January 2002, pp. 151–166. *In* K. Oberhauser and M. Solensky [eds.], *The monarch butterfly. Biology and conservation*. Cornell University Press, Ithaca, NY.
- Brower, L. P., A. Alonso, L. S. Fink, B. Frost, S. B. Malcolm, K. Oberhauser, D. Slayback, O. R. Taylor, S. B. Weiss, and M. P. Zalucki.** 2005. Reduced numbers of monarch butterflies overwintering in Mexico during the 2004–2005 season: evidence in relation to celestial and recommendations. Report to World Wildlife Fund Mexico.
- Calvert, W. H.** 2001. Monarch butterfly (*Danaus plexippus* L., Nymphalidae) fall migration: flight behavior and direction in relation to celestial and physiographic cues. *J. Lepid. Soc.* 55: 162–168.
- Calvert, W. H., and R. O. Lawton.** 1993. Comparative phenology of variation in size, weight, and water content of eastern North American monarch butterflies at five overwintering sites in Mexico, pp. 299–307. *In* S. B. Malcolm and M. P. Zalucki, [eds.], *Biology and conservation of the monarch butterfly*. Natural History Museum of Los Angeles County, Los Angeles, CA.
- Davis, A. K., and M. S. Garland.** 2002. An evaluation of three methods of counting migrating monarch butterflies in varying wind conditions. *Southeast. Nat.* 1: 55–68.
- Davis, A. K., and M. S. Garland.** 2004. Stopover ecology of monarchs in coastal Virginia: using ornithological methods to study monarch migration, pp. 89–96. *In* K. Oberhauser and M. Solensky [eds.], *The monarch butterfly. Biology and conservation*. Cornell University Press, Ithaca, NY.
- Garland, M. S., and A. K. Davis.** 2002. An examination of monarch butterfly (*Danaus plexippus*) autumn migration in coastal Virginia. *Am. Midl. Nat.* 147: 170–174.
- Howard, E., and A. K. Davis.** 2004. Documenting the spring movements of monarch butterflies with Journey North, a citizen science program, pp. 105–114. *In* K. Oberhauser and M. Solensky [eds.], *The monarch butterfly. Biology and conservation*. Cornell University Press, Ithaca, NY.
- Meitner, C. J., L. P. Brower, and A. K. Davis.** 2004. Migration patterns and environmental effects on stopover of monarch butterflies (Lepidoptera, Nymphalidae) at Peninsula Point, Michigan. *Environ. Entomol.* 33: 249–256.
- Mouritsen, H., and B. J. Frost.** 2002. Virtual migration in tethered flying monarch butterflies reveals their orientation mechanisms. *Proc. Natl. Acad. Sci. U.S.A.* 99: 10162–10166.
- Oberhauser, K. S.** 2004. Breeding biology, pp. 3–7. *In* K. Oberhauser and M. Solensky [eds.], *The monarch butterfly: biology and conservation*. Cornell University Press, Ithaca, NY.
- Oberhauser, K., and A. T. Peterson.** 2003. Modeling current and future potential wintering distributions of eastern North American monarch butterflies. *Proc. Natl. Acad. Sci. U.S.A.* 100: 14063–14068.
- Perez, S. M., O. R. Taylor, and R. Jander.** 1997. A sun compass in monarch butterflies. *Nature (Lond.)* 387: 29.
- Schappert, P.** 2004. *The monarch butterfly: saving the king of the new world*. Key Porter Books, Toronto, Ontario, Canada.
- Schmidt-Koenig, K.** 1985. Migration strategies of monarch butterflies. Pages 786–798 *in* M. A. Rankin, [ed.], *Migration: mechanisms and adaptive significance*. Univ. Texas Contrib. Marine Sci., Austin, TX, 27 (Supplement).
- Swengel, A. B.** 1995. Population fluxuations of the Monarch (*Danaus plexippus*) in the 4th of July Butterfly Count 1977–1994. *Am. Midl. Nat.* 134: 205–214.
- Urquhart, F. A., and N. R. Urquhart.** 1977. Overwintering areas and migratory routes of the monarch butterfly (*Danaus p. plexippus*, Lepidoptera: Danaidae) in North America, with special reference to the western population. *Can. Entomol.* 109: 1583–1589.
- Urquhart, F. A., and N. R. Urquhart.** 1978. Autumnal migration routes of the eastern population of the monarch butterfly (*Danaus plexippus*) (L.) (Danaidae: Lepidoptera) in North America to the overwintering site in the neovolcanic plateau of Mexico. *Can. J. Zool.* 56: 1754–1764.
- Van Hook, T.** 1993. Non-random mating in monarch butterflies overwintering in Mexico, pp. 49–60. *In* S. B. Malcolm and M. P. Zalucki [eds.], *Biology and conservation of the monarch butterfly*. Publications of the Natural History Museum of Los Angeles County, Los Angeles, CA.
- Walton, R. K., and L. P. Brower.** 1996. Monitoring the fall migration of the monarch butterfly *Danaus plexippus* L. (Nymphalidae: Danainae) in eastern North America: 1991–1994. *J. Lepid. Soc.* 50: 1–20.

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Appendix. Mean number of monarchs per census ( $d^{-1}$ ) for all year at Cape May

	92	93	94	95	96	97	98	99	00	01	02	03	04	Avg
1 Sept.	5	4	16	6	3	6	2	6	2	9	0	3	3	5
2 Sept.	4	3	19	14	4	9	1	11	0	6	2	3	5	6
3 Sept.	2	1	6	32	3	10	1	14	0	3	4	4	2	6
4 Sept.	3	0	7	8	3	66	0	8	1	7	2	3	1	8
5 Sept.	1	4	19	5	2	105	1	3	0	4	3	8	0	12
6 Sept.	0	6	76	15	0	107	1	2	0	10	1	14	0	18
7 Sept.	2	3	50	4	2	90	0	2	1	9	1	19	1	14
8 Sept.	2	3	54	10	0	74	1	3	2	9	2	14	0	13
9 Sept.	1	1	40	6	1	10	2	2	1	7	3	5	0	6
10 Sept.	2	2	54	15	1	5	14	1	0	5	2	4	1	8
11 Sept.	3	4	62	15	0	5	47	3	1	38	3	6	2	15
12 Sept.	12	9	67	5	2	12	35	6	1	28	23	0	2	16
13 Sept.	8	5	96	1	2	15	7	4	0	2	26	1	1	13
14 Sept.	6	3	62	1	1	19	2	1	1	0	29	2	0	10
15 Sept.	2	6	15	4	7	75	1	0	1	15	13	0	0	11
16 Sept.	2	17	1	2	1	85	1	0	6	25	6	3	1	12
17 Sept.	1	26	0	1	3	50	3	9	18	26	65	2	2	16
18 Sept.	2	24	47	18	5	35	2	54	11	31	32	0	1	20
19 Sept.	15	100	152	8	145	139	1	241	10	27	6	0	1	65
20 Sept.	5	51	15	3	101	11	1	122	16	1	3	1	3	25
21 Sept.	3	8	25	2	71	73	0	82	5	20	5	1	13	25
22 Sept.	1	66	*	0	3	66	0	52	13	23	2	1	17	20
23 Sept.	7	50	6	5	40	80	17	177	1	33	47	0	5	38
24 Sept.	3	79	25	6	41	22	31	132	30	4	60	3	1	34
25 Sept.	*	59	9	3	73	65	17	343	0	1	11	1	1	49
26 Sept.	9	24	*	5	7	217	29	51	0	35	0	1	0	32
27 Sept.	1	3	4	9	1	11	21	14	81	51	2	1	1	16
28 Sept.	8	31	17	22	0	1	82	2	112	132	18	5	1	33
29 Sept.	0	89	6	11	21	1	67	2	18	56	5	34	3	25
30 Sept.	3	52	68	12	82	6	17	17	14	0	1	26	1	22
1 Oct.	2	31	74	5	48	30	6	314	10	2	0	38	4	43
2 Oct.	3	17	135	10	14	17	51	945	10	118	2	24	2	108
3 Oct.	4	24	23	14	17	25	37	656	23	122	1	12	4	75
4 Oct.	2	68	7	4	37	39	1	361	24	61	5	5	18	48
5 Oct.	1	12	3	3	54	24	24	573	9	32	3	48	2	62
6 Oct.	1	12	1	3	40	13	15	198	8	19	4	13	1	25
7 Oct.	1	10	4	5	21	12	15	83	10	23	3	30	4	17
8 Oct.	2	22	5	8	0	50	7	78	11	14	16	35	6	20
9 Oct.	1	14	3	15	12	23	5	56	2	26	19	83	11	21
10 Oct.	9	52	1	9	6	26	1	0	0	15	0	29	7	10
11 Oct.	5	9	10	6	9	11	45	547	2	2	2	65	3	55
12 Oct.	13	*	7	9	9	22	11	31	2	12	24	44	1	15
13 Oct.	18	4	0	18	4	24	7	4	3	13	14	25	3	11
14 Oct.	7	4	1	0	10	22	17	0	5	11	6	70	0	12
15 Oct.	5	7	0	1	9	0	26	4	8	12	4	7	1	7
16 Oct.	2	13	10	4	18	35	9	4	3	19	1	23	0	11
17 Oct.	2	3	9	15	54	24	15	14	6	9	8	36	2	15
18 Oct.	0	7	3	25	3	26	24	6	2	22	4	14	4	11
19 Oct.	0	3	13	21	1	0	56	10	4	42	1	12	5	13
20 Oct.	0	*	9	5	1	10	27	0	2	57	4	29	1	12
21 Oct.	0	3	16	0	11	3	13	2	11	20	6	17	1	8
22 Oct.	0	1	5	2	11	1	4	1	1	12	13	8	1	4
23 Oct.	1	4	*	3	6	1	2	1	3	10	24	0	1	4
24 Oct.	0	4	21	5	10	1	10	1	1	20	5	3	1	6
25 Oct.	1	10	24	8	21	1	9	5	0	47	0	4	1	10
26 Oct.	0	5	*	8	6	0	2	2	1	6	2	0	1	3
27 Oct.	0	6	6	2	5	1	0	3	3	5	6	0	1	3
28 Oct.	0	3	6	1	2	0	0	2	2	2	0	3	1	2
29 Oct.	0	5	4	1	5	0	0	3	0	1	0	2	0	2
30 Oct.	0	*	4	4	0	3	0	1	1	5	0	8	0	2
31 Oct.	*	*	3	8	3	3	0	2	0	7	2	4	2	3
Avg	4	20	28	8	18	34	14	96	9	23	9	14	3	21

\* Indicates dates when no censuses were conducted.