Trends Observed in Fall Migrant Monarch Butterflies (Lepidoptera: Nymphalidae) East of the Appalachian Mountains at an Inland Stopover in Southern Pennsylvania over an Eighteen Year Period

GAYLE STEFFY[1]

16 Fresh Meadow Drive, Lancaster, PA 17603.

Ann. Entomol. Soc. Am. 1–11 (2015); DOI: 10.1093/aesa/sav046

ABSTRACT In total, 11,333 fall migrant monarch butterflies were captured, measured, tagged, and released in southern Pennsylvania over an 18-yr period from 1992 to 2009, excluding 1996 and 2004. Fifty-six (0.494%) were recovered at the Mexican overwintering sites. Hind wing tags had a much higher recovery rate (1.13%) than forewing tags (0.138%). When compared with published recovery rates east of the Appalachians using the same tag type, Pennsylvania was higher than all coastal sites but similar to that of inland Virginia, indicating that inland migrants are more successful. Six U.S. recoveries indicate that monarchs experience considerable eastward wind displacement after leaving the tagging sites. The wild monarchs were divided into three groups for analysis: early (20 Aug–9 Sep), middle (10 Sep–1 Oct), and late (2 Oct–20 Oct) to determine temporal trends. The average forewing length decreased over time, while the percentage of female migrants increased. These trends were not seen in a comparison set of raised monarchs originating from the same general area. As over half the Mexican recoveries came from storm-killed fall 2003 migrants, recoveries were analyzed with and without 2003, and for 2003 alone. More early than middle migrants and no late migrants were recovered. Female migrants were more likely to be recovered from 2003 and overall, but not when 2003 was excluded. The recovery data suggest that males are less likely to make it to Mexico and suffer higher mortality once there during normal overwintering seasons. It also suggests that while early migration is beneficial to both genders, it is even more beneficial for females.

KEY WORDS monarch butterfly, *Danaus plexippus*, migration, size, gender

The migration of monarch butterflies east of the Rocky Mountains is a fascinating but endangered phenomenon. Over the past 3 yr, the population at the overwintering sites in the Transverse Neovolcanic Range in central Mexico dropped to the lowest levels since counts began in 1993 (World Wildlife Fund [WWF] 2014), leading to the monarch being under review for an endangered species listing by the U.S. Fish and Wildlife Service (U.S. Fish & Wildlife Service [USFWS] 2015). Much of this decline is the result of extensive habitat loss, particularly in the Midwest (Pleasants et al. 2012, Brower et al. 2011).

Despite the drastic decline of the overwintering population, the number of monarchs migrating along the Atlantic coast through Cape May Point, NJ, has remained relatively stable over the past 20 yr (Davis 2012, MMP 2014), a fact that has major conservation implications and suggests that these coastal migrants either suffer extremely high mortality along the migration route or are traveling to alternate destinations.

Monarchs use two major flyways to reach their overwintering sites in the Transverse Neovolcanic Range in central Mexico. Those migrating west of the Appalachians travel via a large central flyway that leads directly to Mexico, while those migrating east of the Appalachians use a smaller, later flyway that moves through the eastern and coastal states before appearing to dissipate at lower latitudes (Howard and Davis 2009).

Some of these eastern monarchs eventually turn west and travel along the Gulf coast and then through eastern Texas to Mexico (Texas Monarch Watch 2014). Aggregations of monarchs on oil rigs in the Gulf of Mexico suggest that some attempt a more direct route across the Gulf, although it is unclear whether any survive the journey (Ross 2010). There is also evidence that some of these migrants continue south and assimilate into the Florida resident population (Knight and Brower 2009) or travel to Cuba (Dockx et al. 2004) and even the Bahamas (Monarch Monitoring Project 2014).

Most previous studies of monarch migration east of the Appalachians have taken place in coastal areas where large aggregations of monarchs are common, including Cape May, NJ (Walton et al. 2005), Chincoteague, VA (Garland and Davis 2002), the lower

[1] Corresponding author, e-mail: Gsteffy1@yahoo.com.

Delmarva Peninsula (Brindza et al. 2008), and Folly Beach, NC (McCord and Davis 2010). Coastal migrants, facing a harsher environment and the possibility of being blown out to sea, presumably, suffer higher mortality than those migrating inland. A previous study of monarchs tagged at coastal and inland locations in Virginia found that inland migrants had an eightfold higher Mexican recovery rate than coastal migrants, and the authors proposed that monarchs migrating inland along the piedmont may be as successful as those migrating west of the Appalachians at reaching Mexico (Brindza et al. 2008).

This study of 11,333 monarchs tagged along the Susquehanna River in southern Pennsylvania over an 18-yr period from 1992 to 2009, excluding 1996 and 2004, provides an opportunity to further examine inland migration east of the Appalachians.

The goals of this study were to tag as many monarchs as possible and to collect additional data for later analysis. The recovery data will be compared with other sites east of the Appalachians to determine whether monarchs tagged at this location are more or less successful at reaching Mexico. The additional data, including wing measurements and gender, can determine how these characteristics interact with timing and geography to determine migratory success. As a control for understanding factors that might influence variation in size and gender, these characteristics were also examined in a set of 3,056 raised monarchs, which were found as larvae in the general vicinity of the study sites and emerged during the migration period.

Previous studies have found male monarchs to be larger on average than females based on forewing length (Gibo and McCurdy 1993, Herman 1998, Borland et al. 2004, Altizer and Davis 2010, McCord and Davis 2010). There is also some evidence that the average size of monarchs migrating through an area decreases over time (Becker 2008, McCord and Davis 2010), possibly because larger monarchs migrate faster (Becker 2008). The wing measurements from this study were divided into early, middle, and late groups for analysis to determine temporal trends.

The gender ratio was also examined for temporal trends. Several previous studies have reported a lower percentage of female migrants captured while nectaring than the expected 50/50 ratio (Garland and Davis 2002, Brindza et al. 2008, Borland et al. 2004, McCord and Davis 2010). Some previous studies report an increase in the percentage of female migrants later in the migration (Herman 1988). An overall downward trend in the percentage of female migrants has also been observed in recent years (Davis and Rendon-Salinas 2010).

Over half of the recovered tags from this study were from monarchs tagged in the fall of 2003 and killed by a winter storm in early 2004, which killed ∼70% of the overwintering population (Monarch Watch Update, March 2004). While the storm was devastating to the monarchs, it provided a unique opportunity to obtain data from monarchs that would ordinarily have survived the winter. Therefore, the fall 2003 recoveries were also analyzed separately and compared with those from typical years when the main causes of death were starvation or predation.

Materials and Methods

Study Sites. Fall migrant monarch butterflies were captured, tagged, measured, and released at two sites along the Susquehanna River in southern Pennsylvania (Fig. 1). Both sites, located ∼2 miles apart, featured an

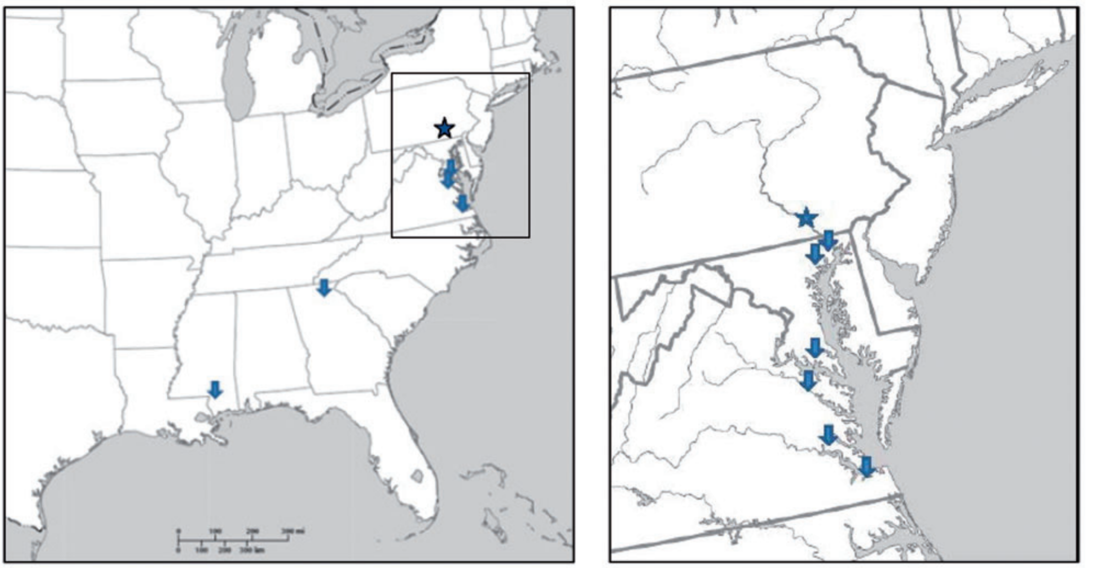

Fig. 1. Location of tagging sites and U.S. recoveries. The star indicates the location of the tagging sites along the Susquehanna River in southern Pennsylvania (39.5 N; −76.2 W). Arrows mark the location of U.S. recoveries. The close-up shows the recoveries in more detail and includes additional recoveries of raised monarchs.

abundance of *Buddleia davidii* Franchet, which attracted monarchs to the sites.

The Holtwood site was an unused strip of land near the Holtwood Hydroelectric Plant owned by Pennsylvania Power and Light. The Wissler Run site was located near the Muddy Run Pumped Storage Facility owned by Exelon Corporation. At both areas, monarchs tended to enter the *buddleia* area from the downwind side, and to move upwind while nectaring.

Unfortunately, the Wissler Run site suffered major habitat deterioration over the course of the study. Herbicide application periodically destroyed a large percentage of the *Buddleia*, which would usually grow back the following year. In later years, herbicide applications became more frequent, and by 2010, very few *Buddleia* remained and monarchs seldom visited the site. The Holtwood site remained more or less the same until 2010, when it was bulldozed. The destruction of both sites forced this study to end after the 2009 migration.

Some data from the first four years of this study were published previously in an article discussing the feasibility of using the number of monarchs tagged per hour as a census method (Steffy 1998).

Data Collection. Data were collected during the fall migration from 1992 to 2009, excluding 1996 and 2004, when I was tagging monarchs in Cape May, NJ, for the Monarch Monitoring Project (Walton et al. 2005). The choice of tagging locations was based on monarch availability. The Holtwood site usually attracted more monarchs early in the day, but the *Buddleia* became shaded by nearby trees around 4 p.m., causing monarch numbers to dwindle, especially on cool days. Tagging often continued at the Wissler Run site until untagged monarchs stopped arriving or the butterflies began to roost. Most monarchs roosted singly—only one group roost was observed during the course of this study.

Time, temperature, wind direction, and cloud cover were recorded upon arrival at the site. The time was recorded every 15 min throughout the tagging sessions, which were often longer when monarchs were plentiful than when they were scarce. Nectaring monarch butterflies were captured with a net or plucked by hand from the *buddleia* blooms, then measured, tagged, and released immediately.

Three different tags were used during the study: Steffy, Brower, and Monarch Watch. Tag choice was based on availability, and different types were often used in the same year. Steffy tags were used in 1992–1999, 2001, and 2002; Brower tags in 2002, 2003, and 2005; and Monarch Watch tags in 1998–2000, 2003, and 2005–2009. Steffy and Brower tags were rectangular and applied to the forewing using the Urquhart method, which involved rubbing a patch of scales from the upper and lower surfaces of the forewing, folding the adhesive tag before removing the backing, and then placing the creased tag over the cleared area on the leading edge of the forewing. Gentle pressure was applied to adhere the tag to both sides of the forewing. Monarch Watch tags were applied by removing the round polypropylene tag from its backing and adhering it to the discal cell of the underside of the hind wing using gentle pressure. Scales were not removed using this method.

Forewing measurements were taken from 1998 on. A transparent ruler was used to measure the distance from the white spot on the thorax nearest to the base of the forewing to the apex of the forewing to the nearest millimeter (Fig. 2). This method is similar to the standardized method (Van Hook et al. 2012), with three important exceptions: 1) the wing measurements for this study were taken on the left forewing instead of the right, unless the left wingtip was frayed. 2) The measurements were started at the 0-cm point on the ruler instead of the 1-cm point, and 3) if the wing measurement fell between 2 mm lines, the distance was estimated, and distances of 0.1–0.4 mm were rounded to the lower number, and distances of 0.5–0.9 mm were rounded to the higher number. All butterflies were measured in the field, tagged and released immediately.

For analysis, the data collected were divided into three segments representing early (20 Aug–9 Sep), middle (10 Sep–1 Oct), and late (2 Oct–20 Oct) migrants through the study sites. This division was based on the period of time monarchs were tagged in this study, and may not necessarily represent the actual migration through the area. The *Buddleia* was an excellent attractant for monarchs during late summer and early fall, but generally began to deteriorate by late September and had lost much of its ability to attract monarchs by early mid-October. Although the timing of the deterioration varied based on weather conditions, it is likely that many late migrants bypassed the sites and that migration through the area extended past 20 October. The peak migration dates for 40°N latitude according to Monarch Watch are 9/12–9/24 (Monarch Watch 2014), which encompasses the midpoint of this study (9/20).

Raised Monarchs. A separate group 3,056 raised monarchs was examined to determine whether temporal changes in the size and gender ratio of the wild monarchs tagged at the study sites were caused by a difference in the characteristics of monarchs emerging early and later in the migration period. Most of these monarchs were collected from the wild as fourth- or fifth-instar caterpillars as part of a parasitoid study for the Monarch Larva Monitoring Project (Oberhauser

Fig. 2. Nectaring monarch butterfly. The forewing measurement is illustrated by the white line.

2012), although some were raised from eggs or collected as smaller larvae. All were collected at ~40° N, −76° W between 1993 and 2012 and raised indoors until adulthood. Those not parasitized were tagged, measured, and released on the day of emergence or the next day. The raised monarchs were divided into early (8/13–9/12), middle (9/13–9/24), and late (9/25–10/15) groups by the date they emerged. As migration probably does not begin immediately after emergence, dates 1 wk earlier than the wild groupings were used.

Statistical Analysis. All statistical analysis was performed using Minitab version 16 (Minitab 2010). Analysis of variance (ANOVA; general linear model) was used to determine the significance of time period (early, middle, and late) gender, year, and recovery on forewing length. All terms and interactions were originally included in the model and dropped if not significant. Linear regression was used to examine trends in wing length over time. Because size varies by gender, males and females were examined separately. Regression was performed for each year separately, and then for all years combined. A series of one-way ANOVAs were run to determine if recovered monarchs differed significantly in size from those not recovered when analyzed separately by gender. This analysis was repeated using only the 2003 data. Chi-square analysis was used to compare gender ratio between time periods. Because of the small number of recoveries, Fisher's exact tests were used for all comparisons involving recovery data. For all statistical analysis, 95% confidence levels were used.

Results

Recoveries. Five of the 11,333 monarchs tagged at the study sites and three from the comparison set of raised monarchs were recovered in the United States (Fig. 1). Fifty-six were recovered at the overwintering sites in the Transverse Neovolcanic Range in central Mexico. Of these, 47 were recovered at El Rosario, six at Cerro Pelon and three at Sierra Chincua. The abundance of tags recovered from El Rosario was probably because of more people searching for and selling tags there than actual distribution across sites. As the percentage of females was found to be similar among the nine overwintering colonies (Davis and Rendon-Salinas 2010), it is unlikely that colony selection has an effect on the overall gender ratios reported in this study.

Hind wing (Monarch Watch) tags had a significantly higher Mexican recovery rate than forewing (Steffy/Brower) tags ($P < 0.001$). To ensure that the high number of recoveries and predominant use of Monarch Watch tags in 2003 did not skew results, the analysis was repeated with the 2003 recoveries excluded and still showed a significantly higher ($P = 0.002$) recovery rate for hind wing tags.

Table 1 compares the Pennsylvania recovery rate with that of other tagging studies east of the Appalachians. Because of the significant difference in recovery rate between tag types, separate recovery rates were calculated for each tag type and only like tag types were compared. The PA recovery rate was not significantly different from that of Cape May, NJ, or inland Virginia, but was significantly higher than those from three other coastal sites located farther south.

More early (0.8%) than middle (0.4%) and no late migrants were recovered (Fig. 5a). This difference is significant ($P = 0.033$). Early female migrants had a significantly higher chance of being recovered than early males ($P = 0.041$). For middle migrants, there was no significant gender difference in recovery rate ($P = 0.237$). The high percentage of early female recoveries was mostly because of an astounding 15.6% recovery rate for early female 2003 migrants (Fig. 5b). When 2003 was excluded, males and females were recovered nearly equally (Fig. 5c). No late migrants were recovered.

Gender. The gender ratio of the migrants was skewed toward males for all three time periods, with

Table 1. Comparison of tag recoveries from sites east of the Appalachian Mountains

Location	Total tagged	Recoveries (Mexico)	Percent recovered	Percent of Pennsylvania recovery	P (Fisher's exact test)
Inland Pennsylvania	7,272 (forewing)	10	0.138		
	4,061 (hind wing)	46	1.13		
	11,333 (total)	56	0.494		
Cape May (L. Zemaitis personal communication.)	62,244 (forewing)	61	0.098	71.0	0.328
Coastal Virginia (Garland and Davis, 2002)	2,190 (hind wing)	1	0.045	3.98	<0.001
Coastal Virginia (Brindza et al, 2008)	1,216 (hind wing)	2	0.16	14.2	0.001
Inland Virginia (Brindza et al, 2008)	1,008 (hind wing)	13	1.29	114	0.626
Coastal South Carolina (McCord and Davis, 2010)	12,281 (hind wing)	3	0.023	2.04	<0.001
Raised Pennsylvania	1127 (forewing)	1	0.089	65.0	1.000
	1,929 (hind wing)	1	0.052	4.60	<0.001
	3,056 (total)	2	0.065	13.2	<0.001

The percentage of tagged monarchs recovered at the Mexican overwintering sites from various locations along the eastern flyway was compared to the Pennsylvania recovery rate. Because the recovery rate varied significantly between tag types ($P < 0.001$), recoveries from other studies were only compared to the Pennsylvania rate using the same tag type. The Pennsylvania rate was significantly higher than all coastal sites except Cape May, NJ. There was not a significant difference between Pennsylvania and inland Virginia.

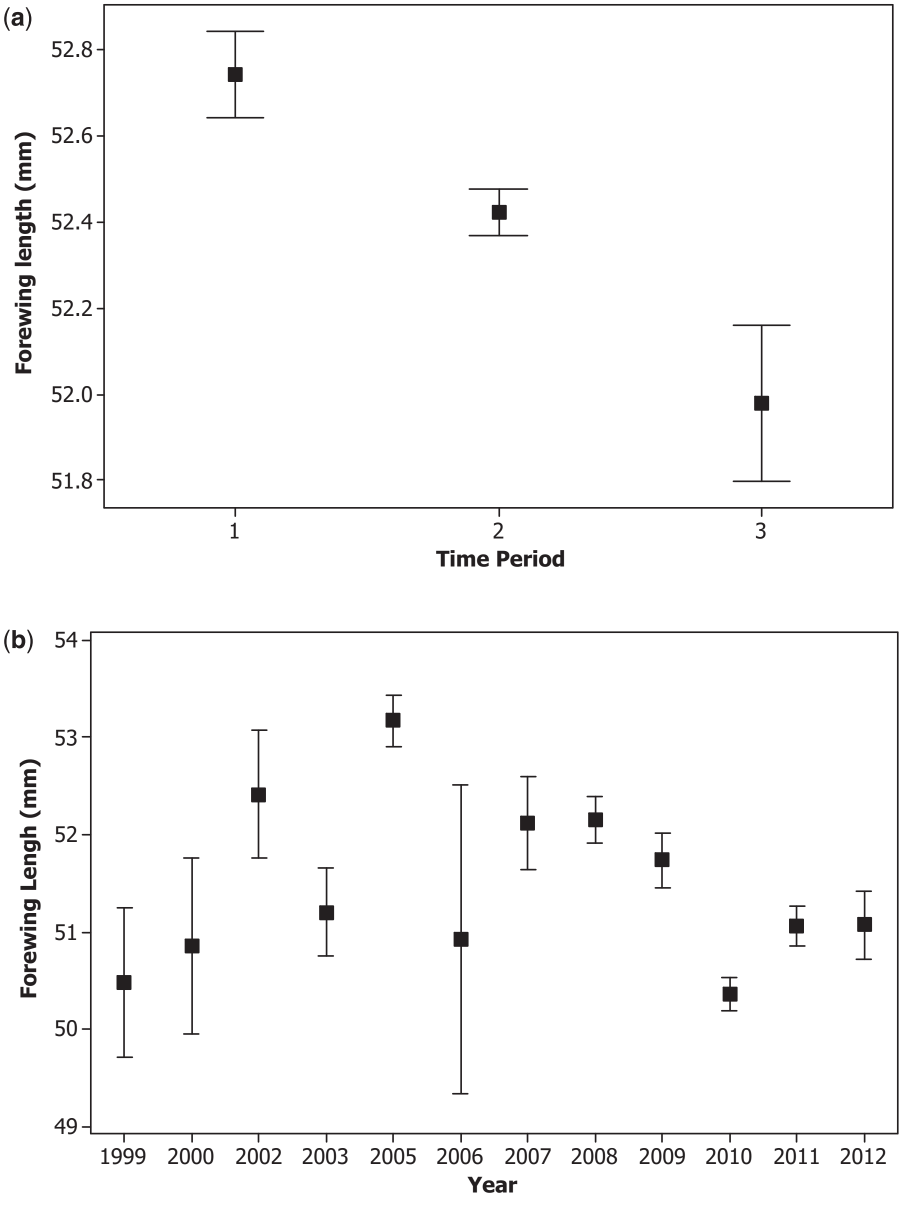

Fig. 3. Forewing length in wild monarchs was influenced by (a) migration time (1 = early, 2 = middle, and 3 = late) and (b) year. Mean and 95% CIs are shown.

only 28% of the overall total being female (Table 2). Although the percentage of female migrants varied, sometimes dramatically, from day to day and from year to year, linear regression analysis showed no significant long-term trend in the overall percentage of females captured over the 18 yr of the study (% female = 433–0.202*year; $F_{(1,14)} = 0.54$, $R^2 = 3.7\%$; $P = 0.473$).

When the gender ratio was compared for the early, middle, and late migrants, it became evident that the percentage of females captured increased as fall progressed (Table 2). A chi-square test on the number of each gender captured during each time period showed that the increase in females was significant ($\chi^2 = 88.536$; df = 2; $P < 0.001$). To determine if this difference occurred between all time periods, the analysis was repeated for early versus middle ($\chi^2 = 44.769$; df = 1; $P < 0.001$) and middle versus late ($\chi^2 = 31.268$; df = 1; $P < 0.001$). When this analysis was repeated for the raised monarchs, the gender ratio remained close to 50/50 during all three time periods with no significant difference between periods.

Forewing Length. Forewing measurements for 7,284 of the wild monarchs were examined by ANOVA for the effect of time period, year, gender, and recovery in Mexico. Recovery and all interactions between terms were found to be insignificant and dropped. The final

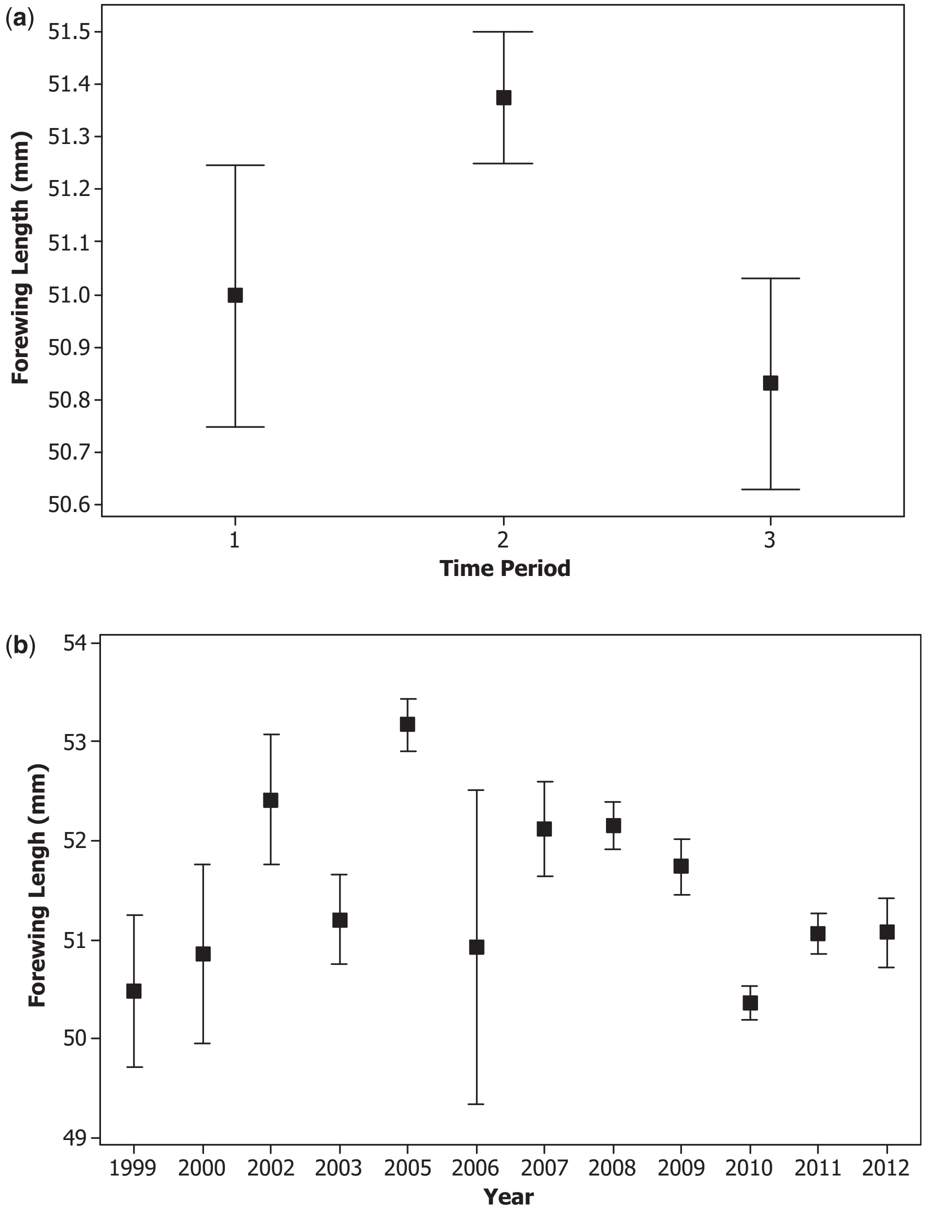

Fig. 4. Forewing length in raised monarchs was influenced by (a) time emerged (1 = early, 2 = middle and 3 = late) and (b) year. Mean and 95% CIs are shown. The trend seen in the wild monarchs toward decreasing forewing size throughout the migration was not seen in the raised monarchs. The raised monarchs were smaller than their wild counterparts during all time periods.

model showed significant effects of time period ($F = 11.94$; df = 2; $P < 0.001$), year ($F = 18.32$; df = 10; $P < 0.001$), and gender ($F = 95.27$; df = 1; $P < 0.001$) on forewing length (Fig. 3a and b). Males were larger than females during all three time periods, and forewing length decreased as fall progressed.

Linear regression analysis (Table 3) showed a significant decrease in wing length over time for females when all years were pooled together, but not for each year alone. The pooled data for males also showed a significant decrease in wing length over time, as did four individual years (1999, 2005, 2006, and 2008). One year (1998) showed an increase in size over time. This year was atypical, however, with the butterflies smaller overall than other years.

Wing measurements for 2,150 raised monarchs were also examined by ANOVA for effects of time, year, and gender (Fig. 4a and b). Because only two raised monarchs were recovered in Mexico, recovery was not included. The final model showed significant effects of time period ($F = 16.43$; df = 2; $P < 0.001$), year ($F = 30.20$; df = 11; $P < 0.001$); and gender ($F = 49.75$;

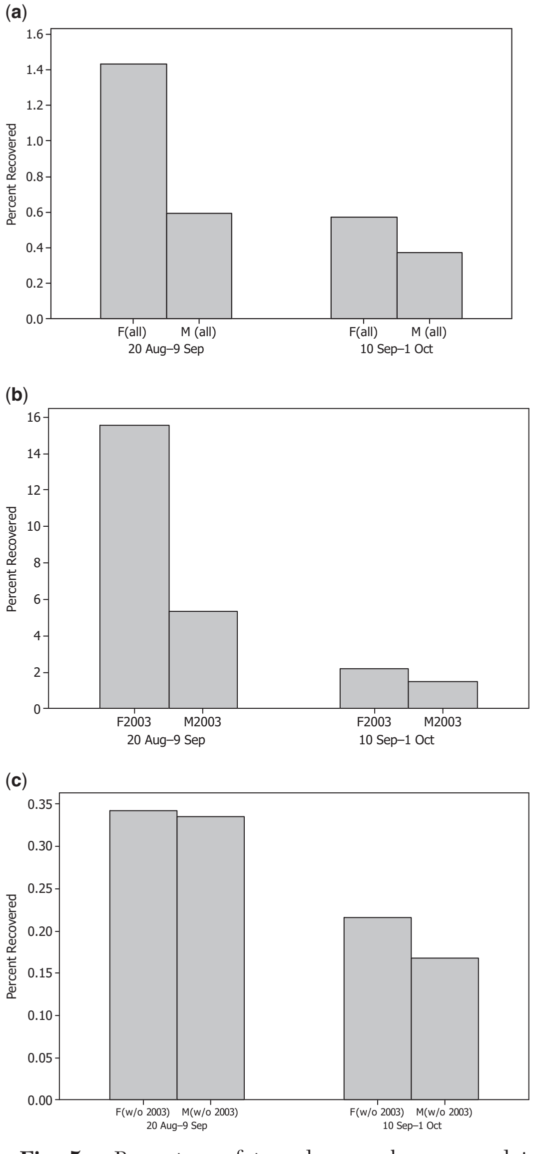

Fig. 5. Percentage of tagged monarchs recovered in Mexico by gender and time period. Data were analyzed by (a) all recoveries, (b) 2003 recoveries only, and (c) recoveries excluding 2003. More early than middle and no late migrants were recovered. Significantly more early females were recovered than males, but only when 2003 was included. With 2003 excluded, both genders were recovered equally.

df = 1; $P < 0.001$). Fisher's least significant difference method was used to compare the means of the three time periods, and found that middle monarchs were significantly larger than early or late monarchs, but that early and late monarchs were not significantly different from each other.

Recovered monarchs did not differ significantly in size from those not recovered, and no significant difference was found between recoveries from the early and middle groups of migrants.

Discussion

The results of this study indicate that the migratory success of monarchs east of the Appalachians is influenced by geography, year, timing, gender, and size. Tag type also had an influence on recovery, with hind wing (Monarch Watch) tags being several times more likely to be recovered in Mexico than forewing (Steffy/Brower) tags. However, it is unclear whether these monarchs were more successful as migrants or if hind wing tags were easier to find or sell at the overwintering sites. Because of the significant recovery difference between tag types, only the results from the same tag type were used during comparison with other studies.

Geography. When compared with other study sites east of the Appalachians, wild monarchs tagged in southern Pennsylvania were significantly more likely to be recovered in Mexico than those from all coastal locations except Cape May, NJ (Table1). The Pennsylvania rate was not significantly different from that of monarchs tagged approximately 100 miles south-southwest in inland Virginia (Brindza et al. 2008).

There are several factors to consider when comparing results across studies. Because the number of recovered monarchs is so small, they may not accurately represent the population. The studies also took place during different years and at different times during the migration season, both of which have been shown to have a significant effect on recovery. Therefore, these results need to be interpreted with caution.

Cape May is the only comparison study that used forewing tags, and was therefore compared with a different subset of the Pennsylvania monarchs that the other studies. It is likely that the difference between the two sites is larger than it appears because predominately hind wing tags were used in Pennsylvania during the year with the most recoveries (2003). The significant difference between inland and coastal sites using hind wing tags (Brindza et al. 2008) supports this conclusion. Therefore, the results from this study appear to confirm Brindza et al.'s conclusion that inland migrants east of the Appalachians are more successful at reaching Mexico than those migrating along the Atlantic coast (Brindza et al. 2008).

While monarchs leaving the tagging sites would be expected to head southwest toward Mexico, six recoveries more directly south suggest considerable wind displacement to the east (Fig. 1). Similar wind displacement has been shown to affect migrating monarchs in previous studies (Rogg et al. 1999, Urquhart 1987). The recovery locations also suggest that some Pennsylvania migrants join the coastal migration below the Delmarva Peninsula. A monarch tagged in Reinholds, PA, was recovered at the southern tip of the Delmarva Peninsula (Garland and Davis 2002), proving that monarchs from the general vicinity of the study sites have reached the coast. Although the origin of the Pennsylvania migrants is unknown, it is likely that wind displacement was also a factor before their arrival at the tagging sites and that many monarchs migrating east of the Appalachians at least initially move in a south or southeast direction.

Year. The percentage of tagged monarchs recovered at the overwintering sites varied significantly from year to year. Much of this variation was because of weather events at the overwintering sites. Over half (35) of the recovered monarchs migrated during the fall of 2003 and died in early 2004 from an adverse weather event that caused massive mortality among the overwintering monarchs (Taylor 2004a,b). Interestingly, a similar storm that hit the overwintering sites in early 2002, killing nearly one-fourth of a billion overwintering monarchs in two of the colonies (Brower et al. 2004), did not result in a similar spike in recoveries of fall 2001 migrants. This may be, in part, due to the low recovery rate of forewing tags, which were used exclusively during the fall 2001 migration. Other likely contributing factors to the yearly variation in recovery rate are weather conditions during the fall migration and the number of people searching for and buying tags at the overwintering sites.

Timing. The timing of migration also influences migratory success. Figure 5a shows that monarchs tagged during the early period (20 Aug–9 Sep) were significantly more likely than those tagged during the middle period (10 Sep–1 Oct) to be recovered in Mexico. Those tagged during the late period (2 Oct–20 Oct) were not recovered at all. It is possible that some later migrants are killed by the cold weather on the way south or lose their urge to migrate before reaching their destination. It is also possible that they go somewhere other than central Mexico.

Several monarchs tagged in Cape May, NJ, were recovered in southern Florida (Monarch Monitoring Project 2014), and a study has shown that some migrants assimilate into the resident Florida population (Knight and Brower 2009). Overwintering monarchs are not uncommon along the Gulf coast and coastal South Carolina (Howard and Davis 2010), and monarchs are known to travel to Cuba (Dockx et al. 2004), and even the Bahamas (Monarch Monitoring Project 2014).

Interestingly, the Mexican recovery rate for the raised monarchs was much lower than that of their wild counterparts ($P = <0.001$) and was in fact similar to that of the coastal migrants. While the cause of this lower recovery rate requires further investigation, possible contributing factors include the smaller size of the raised monarchs (Fig 4a and 4), which may have increased their chances of being displaced eastward and joining the coastal migration; exposure to artificial light, which may have delayed or prevented their entry into diapause; or that most of the raised monarchs emerged later than the ideal period for migratory success. The two raised monarchs recovered in Mexico emerged on 14 Aug and 1 Sep, earlier than the majority of the raised monarchs. As no monarchs tagged elsewhere were caught at the study sites, the age and origin of the wild migrants is unknown. It is possible

Table 2. Percentage of female migrants

Year	% F Early (*N*)	% F Mid (*N*)	% F Late (*N*)	% F All (*N*)
1992	47 (30)	20 (166)	33 (6)	25 (202)
1993	21 (321)	30 (824)	39 (56)	28 (1201)
1994	25 (371)	34 (306)	56 (9)	29 (686)
1995	29 (110)	31 (324)	39 (18)	31 (452)
1997	28 (457)	31 (895)	37 (30)	30 (1382)
1998	42 (50)	31 (168)	0 (0)[a]	33 (218)
1999	38 (66)	32 (484)	49 (65)	35 (615)
2000	33 (6)	31 (185)	0 (0)[a]	31 (191)
2001	18 (93)	32 (458)	36 (11)	30 (562)
2002	23 (75)	21 (394)	39 (128)	25 (597)
2003	28 (158)	32 (1310)	40 (177)	32 (1645)
2005	14 (727)	18 (869)	36 (14)	16 (1610)
2006	27 (37)	27 (814)	34 (86)	27 (937)
2007	14 (261)	17 (138)	0 (0)[a]	15 (399)
2008	24 (29)	35 (105)	0 (0)[a]	33 (134)
2009	29 (34)	33 (468)	0 (0)[a]	33 (502)
Total	22 (2825)	29 (7908)	40 (600)	28 (11333)
Raised	50 (768)	50 (1656)	47 (632)	49 (3056)

The percentage of female migrants varied from year to year, but increased significantly overall with each time period. Only 28% of the 11,333 migrants tagged were female. For comparison, the overall percentage of females from the raised monarchs was also included.

[a] No late monarchs were tagged.

Table 3. Effect of time on forewing length

	Female				Male			
Year	Equation	*F*	R^2	*P*	Equation	*F*	R^2	*P*
1998	$y = 49.6 + 0.053x$	$F_{(1,71)} = 3.15$	4.3%	0.08	$y = 48.9 + 0.083x$	$F_{(1,142)} = 13.56$	8.7%	**<0.001**
1999	$y = 51.5 + 0.005x$	$F_{(1,197)} = 0.14$	0.1%	0.713	$y = 54.0 - 0.064x$	$F_{(1,382)} = 27.61$	6.7%	**<0.001**
2000	$y = 53.2 - 0.040x$	$F_{(1,40)} = 0.29$	0.7%	0.592	$y = 2.0 + 0.018x$	$F_{(1,83)} = 0.16$	0.2%	0.691
2001	$y = 53.1 - 0.042x$	$F_{(1,166)} = 2.05$	1.2%	0.154	$y = 52.5 + 0.000x$	$F_{(1,390)} = 0.00$	0.0%	0.981
2002	$y = 1.0 + 0.016x$	$F_{(1,146)} = 0.73$	0.5%	0.393	$y = 52.9 - 0\ .010x$	$F_{(1,441)} = 1.13$	0.3%	0.288
2003	$y = 52.9 - 0.018x$	$F_{(1,529)} = 3.47$	0.7%	0.063	$y = 52.8 - 0.003x$	$F_{(1,1105)} = 0.16$	0.0%	0.689
2005	$y = 52.9 - 0.013x$	$F_{(1,258)} = 0.85$	0.3%	0.357	$y = 53.2 - 0.012x$	$F_{(1,1346)} = 4.77$	0.4%	**0.029**
2006	$y = 53.0 - 0.030x$	$F_{(1,252)} = 2.87$	1.1%	0.092	$y = 53.6 - 0.029x$	$F_{(1,675)} = 9.21$	1.3%	**0.002**
2007	$y = 53.0 - 0.033x$	$F_{(1,58)} = 0.41$	0.7%	0.527	$y = 53.0 - 0.021x$	$F_{(1,336)} = 1.06$	0.3%	0.305
2008	$y = 51.5 + 0.012x$	$F_{(1,41)} = 0.03$	0.1%	0.865	$y = 55.1 - 0.120x$	$F_{(1,88)} = 14.09$	13.8%	**<0.001**
2009	$y = 50.8 + 0.034x$	$F_{(1,160)} = 0.59$	0.4%	0.445	$y = 53.8 - 0.043x$	$F_{(1,335)} = 2.24$	0.7%	0.135
All	$\mathbf{y = 52.4 - 0.011x}$	$\mathbf{F_{(1,1938)} = 4.98}$	**0.3%**	**0.026**	$\mathbf{y = 53.1 - 0.016x}$	$\mathbf{F_{(1,5343)} = 37.38}$	**0.7%**	**<0.001**
Raised	$y = 0.4 + 0.013x$	$F_{(1,1060)} = 4.78$	0.4%	0.029	$y = 51.6 - 0.002x$	$F_{(1,1101)} = 0.11$	0.0%	0.736

Results of linear regression analysis of the effect of time (x) on forewing length (y) for each year separately and all years combined. As males are larger on average than females, each gender was tested separately. While the trend was not evident in most individual years, the overall result showed a significant decrease in forewing length as fall progressed. This trend was not evident for the raised monarchs.

that the majority of successful migrants originate from areas farther north. It is also possible that the majority of the raised monarchs became part of the "late" group of migrants, none of which have been recovered in Mexico. If this is true, weather conditions that delay the development of the final generation or the onset of migration could have major conservation implications, as fewer will become successful migrants.

Gender. The gender ratio of the nectaring monarchs caught at the study sites varied, sometimes dramatically, from day to day and year to year, but was consistently skewed toward males throughout (Table 2). Overall, only 28% of the monarchs captured were female, which is consistent with other studies of migrating monarchs (Gibo and McCurdy 1993, Borland et al. 2004, Brindza et al. 2008, McCord and Davis 2012). Although the percentage of females captured varied significantly from year to year, linear regression analysis showed no significant long-term trend over the 18 yr of the study (Table 3). Therefore, the significant overall decrease in the percentage of female migrants over the past 30 yr found by Davis and Rendon-Salinas (2009) was not evident in this group of migrants.

While fewer in number overall, females made up an increasing percentage of the monarchs captured from the early to middle, and middle to late time periods. This gradual increase in the percentage of female migrants as fall progresses was also seen in previous studies (Herman 1988, Gibo and McCurdy 1993, Borland et al. 2004). The gender ratio of the raised monarchs emerging throughout the migration period remained close to 50/50, indicating that the increase in females was not caused by a change in the gender ratio of late emerging monarchs.

At the overwintering sites, early female migrants were significantly more likely to be recovered than early males (Fig. 5a); however, this was only true when the storm-killed 2003 migrants were included in the analysis. When the 2003 migrants were removed, males and females were recovered equally (Fig. 5c). The analysis of 2003 recoveries alone (Fig. 5b) showed that an astounding 16% of the early females were recovered. In contrast, only 5.3% of the early males were recovered.

A similar high percentage of female recoveries was reported for inland Virginia migrants tagged in fall 2001 after the 2002 storm (Brindza et al. 2008). As most of the fall 2001 and 2003 monarchs died from the weather instead of starvation or predation, the recoveries from these years are more likely to reflect the overall makeup of the overwintering colonies. The gender ratio at the overwintering sites was found to be ~43% female on average over the past decade (Davis and Rendon-Salinas 2010), indicating that the skewed gender ratio favoring males among the migrants also exists at the overwintering sites, but to a lesser degree. This supports the conclusion that migrating females are more likely to make it to Mexico than males, especially those that migrate early.

The equal percentage of male and female recoveries when 2003 was excluded suggests that in addition to being less likely to make it to Mexico, males are more likely to die there under normal weather conditions. The sample size (21) is small, however, and another study has found no evidence of differential mortality at the overwintering sites (Davis and Rendon-Salinas 2010).

Size. Using forewing length as an estimate of size, males were significantly larger than females during all three time periods, which is consistent with other studies of migrating monarchs (Gibo and McCurdy 1993, Herman 1998, Borland et al. 2004, Altizer and Davis 2010, McCord and Davis 2010). Early wild migrants were significantly larger overall than middle migrants, which were larger than late migrants (Fig. 3a). This trend of decreasing size over time was also seen in linear regression analysis for both genders (Table 3) and has been reported for monarchs migrating through the Midwest (Becker 2008) and coastal South Carolina (McCord and Davis 2010). Interestingly, this trend was not evident for most individual years (Table 3), probably because the large size variation between individual butterflies obscured the trend in smaller sample sizes.

The average size of the monarchs also varied considerably between years. Some of the variation can be explained by the differing percentage of females between years—the two years with the lowest percentage of females (2005 and 2007) also had the longest average wing length. Other likely contributors to the size variation include differing proportions of monarchs tagged during each time period and weather conditions during larval development.

The average raised monarch was significantly smaller than the average wild monarch during all three time periods. The higher percentage of female raised monarchs explains some of the size difference, as females are smaller on average than males. Other contributing factors may be desiccation from feeding on cut milkweed or feeding on different species of milkweed.

The middle group of raised monarchs had significantly longer forewings than the early or late groups, but the early and late groups did not differ significantly from each other (Fig. 4a). The smaller size of the early group of raised monarchs may be due to overlap with the smaller summer generation, although a monarch that emerged on 8/14 was recovered at the overwintering sites, indicating that at least some of these monarchs are indeed migrants. The smaller size of the late monarchs may be due to increased desiccation because cut milkweed leaves dried out faster and were consumed slower in the lower autumn humidity and temperatures. Decreasing temperatures also increased time spent in the chrysalis, exposing them to further desiccation. The fact that all of the raised monarchs were significantly smaller than their wild counterparts suggests that desiccation was a factor throughout, but milder in the earlier time periods.

As the gradual decrease in size over time seen in the wild monarchs was not evident in the raised monarchs, it is probably not caused by a decrease in the size of butterflies emerging later in the season. Another possible explanation for the decreasing size of the later migrants is that large monarchs migrate faster than small ones. Previous research indicates monarchs with a larger wing area get more lift, which allows a longer glide period (Becker 2008). Therefore, larger monarchs are likely to use less energy during the migration, and require shorter stopover periods for refueling (Becker 2008). This idea is supported by findings from a study of monarchs at a stopover site in North Carolina (McCord and Davis 2012), which indicate that smaller monarchs remained at the site longer than larger ones.

Larger monarchs travelling faster may also explain the increase in females later in the fall, which appears to contradict the finding that early female migrants are more successful. If larger monarchs do indeed migrate faster than smaller ones, the later abundance of females may be, in part, because of their shorter forewings. The increased success of early migrants of both genders, which have longer forewings on average than later migrants, suggest that longer forewings may be advantageous for migratory success. This idea is supported by a study that found that migratory populations of monarchs have longer forewings than resident populations (Altizer and Davis 2010).

In summary, migratory success for monarch butterflies east of the Appalachians is increased by taking an inland route and migrating early. Early migration appears to be particularly beneficial to females. Although males greatly outnumbered females at the tagging sites, the females appear to be more successful as migrants. As early migrants are larger on average, longer forewings may also increase migratory success.

The biggest detriment to migratory success appears to be late migration. This has important conservation implications since global warming is likely to cause increasing numbers of late migrants. Therefore, it is important to determine the fate of the late migrants to understand why early migration is much more conducive to survival, and to determine whether a shift in the timing of migration is contributing to the drastic population decline at the overwintering sites in Mexico. Further research in this area is necessary to help guide conservation efforts.

Acknowledgments

I would like to thank Lincoln Brower, Chip Taylor, and Andy Davis for encouraging me to publish and for their valuable feedback and advice. I would also like to thank the Monarch Monitoring Project, specifically Dick Walton, Louise Zemaitis, Mark Garland, and Paige Cunningham for sharing their data and for their continuing support and friendship. Finally, I would like to thank Daniel Yocum for helping with the statistical analysis.

References Cited

Altizer, S., and A. K Davis. 2010. Populations of monarch butterflies with different migratory behaviors show divergence in wing morphology. Evolution 64: 1018–1028.

Becker, C. 2008. A possible Size-Determined Directional Selection in Danaus plexippus (Lepidoptera: Danaidae) with Evidence from Stable Isotope Analysis. M.S. thesis, University of Kansas, Lawrence.

Borland, J., C. C. Johnson, T. W. Crumpton III, M. Thomas, S. Altizer, and K. Oberhauser. 2004. Characteristics of fall migratory monarch butterflies, *Danaus plexippus*, in Minnesota and Texas, pp. 97–104. *In* K. Oberhauser and M. Solensky (eds.), The monarch butterfly, biology and conservation. Cornell University Press, Ithaca, NY.

Brindza, L. J., L. P. Brower, A. K. Davis, and T. Van Hook. 2008. Comparative success of monarch butterfly migration to overwintering sites in Mexico from inland and coastal sites in Virginia. J. Lepid. Soc. 62: 189–200.

Brower, L. P., K. R. Kust, J. Miller, C. Fernandez Del Rey, and K. Pape. 2004. Catastrophic winter storm mortality of monarch butterflies in Mexico during January of 2002, pp. 151–156. *In* K. S. Oberhauser and M. J. Solensky (eds.), The Monarch Butterfly, Biology and Conservation. Cornell University Press, Ithica, NY.

Brower, L. P., O. R. Taylor, E. H. Williams, D. A. Slayback, R. R. Zubieta, and M. I. Ramirez. 2011. Decline of monarch butterflies overwintering in Mexico: is the migratory phenomenon at risk? Insect Conserv. Divers doi: 10.1111/j.1752-4598.2011.00142.x.

Davis, A. K. 2012. Are migratory monarchs really declining in eastern North America? 99Examining evidence from two fall census programs. Insect Conserv. Divers. 5: 101–105.

Davis, A. K., and E. Rendon-Salinas. 2010. Are female monarch butterflies declining in eastern North America? Evidence of a 30-year change in gender ratios at Mexican overwintering sites. Biol. Lett. 6: 45–47.

Dockx, C., L. P. Brower, L. I. Wassenaar, and K. A. Hobson. 2004. Do North American monarch butterflies travel to Cuba? Stable isotope and chemical tracer techniques. Ecol. Appl. 14: 1106–1114.

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.

Gibo, D. L., and J. A. McCurdy. 1993. Lipid accumulation by monarch butterflies (Danaus plexippus L.). Can. J. Zool. 71: 76–82.

Herman, W. S. 1988. Body weight and wing length changes in Minnesota populations of the monarch butterfly. J. Lepid. Soc. 42: 32–36.

Howard, E., and A. K. Davis. 2009. The fall migration flyways of monarch butterflies in eastern North America revealed by citizen scientists. J. Insect Conserv. 13: 279–286.

Howard, E, H. Aschen, and A. K. Davis. 2010. Citizen science observations of monarch butterfly overwintering in the southern United States. Psyche 2010: 689301. doi: 10.1155/2010/689301.

Knight, A., and L. P. Brower. 2009. The influence of eastern North American autumnal migrant monarch butterflies (Danaus plexippus L.) on continuously breeding resident monarch populations in southern Florida. J. Chem. Ecol. 35: 816–823.

McCord, J. W., and A. K. Davis. 2012. Characteristics of monarch butterflies (Danaus plexippus) that stopover at a site in coastal South Carolina during fall migration. J. Res. Lepid. 45: 1–8.

McCord, J. W., and A. K Davis. 2010. Biological observations of monarch butterfly behavior at a migratory stopover site: results from a long term tagging study in coastal South Carolina. J. Insect Behav. 23: 405–418.

Minitab, Inc. 2010. Meet Minitab® 16.

Monarch Monitoring Project. 2014. (www.monarchmonitoringproject.com/recover.html) (accessed 18 May 2015).

Monarch Watch. 2014. (http://monarchwatch.org/tagmig/peak.html) (accessed 18 May 2015).

Oberhauser, K. 2012. Tachinid flies and monarch butterflies: Citizen Scientists Document Parasitism Patterns over Broad Spatial and Temporal Scales. Am. Entomol. 58: 19–22.

Pleasants, J. M., and K. S. Oberhauser. 2012. Milkweed loss in agricultural fields because of herbicide use: Effect on the monarch butterfly population. Insect Conserv. Divers. 6: 135–144.

Rogg, K. A., O. R. Taylor, and D. L. Gibo. 1999. Mark and recapture during the monarch migration: A preliminary analysis. pp. 133–138. *In* J. Hoth, L. Merino, K. Oberhauser, I. Pisantry, S. Price, and T. Wilkinson (eds.), Paper Presentations: 1997 North American Conference on the monarch butterfly (Morelia, Mexico). The Commission for Environmental Cooperation, Montreal, Canada.

Ross, G. N. 2010. The monarch's trans-gulf express: "a clockwork orange". Southern Lepid News 32: 11–24.

Steffy, G. 1998. Tagging as a method of monitoring the fall migration of the monarch butterfly. News Lepid. Soc. 40: 28–30.

Taylor, O. R. 2004a. Monarch Watch Monthly Update, February 2004, www.monarchwatch.org/update/2004/0216.html, (accessed 18 May 2015).

Taylor, O. R. 2004b. Monarch Watch Monthly Update, March 2004, www.monarchwatch.org/update/2004/0318.html, (accessed 18 May 2015).

Texas Monarch Watch, 2014. (http://www.texasento.net/flyway_analysis.htm) (accessed 18 May 2015).

Urquhart, F. A. 1987. The Monarch Butterfly: International Traveler. Chicago, IL.

(USFWS) U.S. Fish & Wildlife Service. 2015. (http://ecos.fws.gov/speciesProfile/profile/speciesProfile.action?spcode=I0WJ) (accessed 18 May 2015).

Van Hook, T., E. H. Williams, L. P. Brower, S. Borkin, and J. Hein. 2012. A standardized protocol for ruler-based measurement of wing length in monarch butterflies, Danaus plexippus L. (Nymphalidae, Danainae). Trop. Lepid. Res. 22: 42–52.

Walton, R. K., L. P. Brower, and A. K Davis. 2005. Long-term monitoring and fall migration patterns of the monarch butterfly (Nymphalidae:Danainae) in Cape May, NJ. Ann. Entomol. Soc. Am. 98: 682–689.

(WWF) World Wildlife Fund. 2014. (www.worldwildlife.org/species/monarch-butterfly) (accessed 18 May 2015).

Received 25 January 2015; accepted 29 April 2015.