

## COMPARATIVE SUCCESS OF MONARCH BUTTERFLY MIGRATION TO OVERWINTERING SITES IN MEXICO FROM INLAND AND COASTAL SITES IN VIRGINIA

LARRY J. BRINDZA,  
9701 Harr Court, Burke, VA 22015

LINCOLN P. BROWER,  
Department of Biology, Sweet Briar College, Sweet Briar, VA 24595; email: brower@sbcc.edu

ANDREW K. DAVIS,  
Warnell School of Forestry and Natural Resources, University of Georgia, Athens GA 30602

AND

TONYA VAN HOOK  
Department of Biology, Sweet Briar College, Sweet Briar, VA 24595

**ABSTRACT.** Prior tagging studies at Atlantic coastal sites in New Jersey and Virginia suggested that fall migrant monarch butterflies (*Danaus plexippus* L., Nymphalidae: Danainae) of the eastern North American population have lower recovery rates at overwintering sites in Mexico compared to the overall recovery rates reported by Monarch Watch for monarchs tagged throughout the late summer breeding range. Here we present the results of the first quantitative study that compares the probability of recapture in Mexico of monarchs tagged at coastal sites with inland sites that are east of the Appalachian Mountains. During the 2001–2006 fall migrations, we tagged 1,008 monarchs along the Appalachian piedmont in Virginia, of which 13 (1.29%) were recovered in Mexico. In contrast, out of 1,216 tagged at Atlantic coastal locations in Virginia, only 2 (0.16%) were recovered. This eightfold lower recapture rate of the coastal monarchs is highly significant. The data also indicated that monarchs migrating along the piedmont on the eastern side of the Appalachians are nearly as likely to reach Mexico as are those that migrate west of the Appalachians. We conclude that migrating along the Atlantic coast per se is more risky than migrating inland either east or west of the Appalachians. The recovery data also determined that both sexes of the piedmont migrants reached Mexico, but, for unknown reasons, females were more successful. Since coastal migration occurs regularly and involves very large numbers of monarchs, the Atlantic coast is not an aberrant migratory route as the Urquhart maintained. Why then do fewer coastal migrants reach Mexico? Some continue southward and may become incorporated in and help sustain breeding populations in south Florida, Cuba and perhaps in other Caribbean islands and the Yucatan. To explore other possible reasons for the lower success of coastal monarchs in reaching Mexico, we compared wing lengths and wet masses of 483 inland with more than 140 coastal monarchs. The latter had slightly but significantly smaller wing lengths and, even after accounting for variation in wing length, they weighed less than the inland monarchs. The lower wet mass reflects lower lipid and/or lower water contents which we argue may be a consequence of anthropogenic degradation of much of the native flora and nectar sources along the Atlantic coast. We consider various hypotheses that may account for the coastal migrants' smaller wings than the inland migrants, including the controversial idea that the longer winged migrants may be blown out to sea.

**Additional key words:** tagging and recapture rates, wet mass, wing length, nectar availability; Atlantic coastal ecosystem deterioration, risky fall migration route.

Qualitative knowledge derived from the recoveries of tagged fall migrant monarch butterflies (*Danaus plexippus*, L.) has indicated that their success in reaching the overwintering areas in Mexico is substantially greater when the butterflies are tagged west compared to those tagged east of the Appalachian Mountains (Urquhart & Urquhart 1979a, b; Urquhart 1987; Monarch Watch 2006). An unexplored aspect of this difference is whether monarchs migrating along the Atlantic coast per se have a lower probability of reaching Mexico, or whether all monarchs migrating east of the Appalachians, including the piedmont and the coastal areas, are less successful.

To obtain quantitative data on the fall migration along

the Atlantic coast, Walton (1999), Walton & Brower (1999) and collaborators initiated a tagging program in Cape May Point, New Jersey. In the fall of 1998, they tagged 7,541 monarchs (number corrected by Brower *et al.* in prep), of which seven were subsequently found at the Mexico overwintering sites, a recapture frequency of 0.093%. In 1998 Garland & Davis (2002) started a second coastal tagging program on the southern tip of the Delmarva Peninsula in Virginia. They released 2,190 monarchs over three years (1998–2000), of which one was found in Mexico, a recapture frequency of 0.046%. In contrast, of an estimated 1.1 million monarchs tagged by Monarch Watch participants from 1992 through 2006 in the eastern US and southern

Canada, 12,000 to 14,000 were recaptured in Mexico, a recovery rate of 1.09% to 1.27% (Taylor pers. com. 2007; Monarch Watch 2006). Using Monarch Watch's lowest recovery rate as a rough estimate of the overall eastern rate and dividing it by each of the above coastal rates ( $1.09\% / 0.093\% = 11.7$ ; and  $1.09\% / 0.046\% = 23.7$ ) indicates that the coastal monarchs have only 1/12th to 1/24th of the chance of being recaptured in Mexico (see also Taylor, in McNeil 2006).

This much lower probability of coastal monarchs reaching Mexico raises four questions that we address in this paper. First, are all monarchs that migrate along the eastern side of the Appalachians less likely to reach Mexico than monarchs that migrate west of the Appalachians? Or, second, do those monarchs that migrate along the piedmont that stretches eastwards from the Appalachians to the coastal plain (Atwood 1940; Raisz 1957) have a success rate similar to migrants west of the Appalachians? Third, if the coastal migrants per se are less successful, do these monarchs exhibit differences in physical properties from the inland piedmont migrants? Fourth, if there are physical differences between the coastal and inland piedmont

monarchs, what factors might account for the differences?

To answer the first two questions, we compared the number of recaptures in Mexico of monarchs collected and tagged along the eastern edge of the Appalachian piedmont in northern Virginia with recaptures of monarchs collected and tagged during the same years along the Atlantic coast in southern Virginia. We addressed the third question by comparing wing lengths and adult weights (wet mass) of sub-samples of the tagged inland and coastal monarchs. We addressed the fourth question by relating the wing length findings to greater coastal losses due to wind and possible other causes, and by relating the wet mass findings to anthropogenic changes in habitat quality along the Atlantic coast.

#### MATERIALS AND METHODS

**Collecting sites.** Over six years (2001–2006) between the last week of August and the last week of October, Brindza collected fall migrant monarchs from one or more coastal and inland sites in Virginia. The collection dates overlapped with the timing of the fall



FIG. 1. Location of coastal and inland study sites in eastern Virginia and average wet masses of fall migrant monarchs in eastern North America. The coastal sites were located on the southern tip of the Delmarva Peninsula (small square in the lower inset box). The inland sites were centered around the town of Woodbridge on the piedmont of the Appalachians (small circle in the lower inset box). The numbers on the map indicate average wet masses (mg) of males and females combined of fall migrant monarchs from this study and from other published studies (Brown and Chippendale 1974; Gibo and McCurdy 1993; Borland *et al.* 2004). The upper left inset shows the approximate range of the eastern North American monarch population, with the location of the Mexican overwintering area.

migration along both the Atlantic coast in Virginia (Garland & Davis 2002; Gibbs *et al.* 2006) and through an inland site on the eastern edge of the Blue Ridge Mountains at Sweet Briar College, Virginia, about 275 km west of the coastal area (Brower *et al.* 2006). In the fall of 2001, Brindza concentrated on tagging the butterflies and, from 2002 through 2006, he also weighed and measured the forewing lengths of sub-samples of those that he tagged and released.

The coastal samples were collected at Kiptopeke State Park, on the Eastern Shore of Virginia National Wildlife Refuge and Fisherman Island National Wildlife Refuge. These areas are surrounded to the west by Chesapeake Bay and to the east and south by the Atlantic Ocean (Fig. 1). Both are good locations for capturing migrating monarchs because of the funneling effect of the peninsula (Garland & Davis 2002).

The inland monarchs were collected along the Piedmont about 190 km northwest of the coastal area within a 10 km radius of Woodbridge, VA (38° 38' 08" N, 77° 15' 44" W), 20–30 km SW of Washington, D.C. (Fig 1.). The collecting site in 2001 was solely in Lorton, while from 2002–2006, the butterflies were collected in Lorton, Gunston Cove, the Occoquan Bay National Wildlife Refuge and Mason Neck State Park.

**Collecting methods.** Brindza netted most monarchs while they were nectaring on several species of composites growing in open fields or in flowerbeds, and on cultivated and native shrubs. About 2% were collected from roosts. Immediately after capture, he removed each monarch from the net and placed it in a 5.1 × 7.6 cm glassine envelope. Successive captures were accumulated for about 10 minutes in a small plastic box and kept out of direct sunlight.

Brindza made all plant identifications based on Newcomb (1977), Peterson & McKenny (1968) and Lobstein (1990). We followed the USDA plant data

base to standardize the common and scientific nomenclature (Anon. 2007a). Composites (Asteraceae), on which many butterflies were nectaring, included bearded beggar ticks (*Bidens aristosa* (Michx.) Britt.), woodland sunflower (*Helianthus divaricatus* L.), bull thistle (*Cirsium vulgare* (Savi) Ten.), other thistles (*Cirsium* spp.), false boneset (*Brickellia eupatorioides* [L.] Shinners), white snakeroot (*Eupatorium rugosum* = *Ageratina altissima* (L.) King & H.E. Robins), seaside goldenrod (*Solidago sempervirens* L.), *Solidago* spp., hyssopleaf thoroughwort (*Eupatorium hyssopifolium* L.), late flowering thoroughwort (*Eupatorium serotinum* Michx.), orange cosmos (*Cosmos sulphureus* Cav.) and garden cosmos (*C. bipinnatus* Cav.). The shrubs on which they were nectaring included butterfly bush (*Buddleia davidii* L., Buddleiaceae), Russian olive (*Elaeagnus angustifolia* L., Elaeagnaceae), abelia (*Abelia abelia* R. Br., Caprifoliaceae), lantana, (*Lantana camara* L., Verbenaceae) and groundsel tree (eastern baccharis, *Baccharis halimifolia* L., Asteraceae).

**Tagging.** Brindza tagged the butterflies within 10 minutes of capture using numbered adhesive tags provided by Monarch Watch. Over the six years, he tagged and released 1,216 monarchs in the coastal sites and 1,008 in the inland sites (Table 1). We subsequently determined those recovered at the overwintering sites in Mexico by consulting the Monarch Watch tag recovery data base (<http://www.monarchwatch.com/tagmig/recoveries.htm>).

**Weighing and measuring.** During 2002–2006, Brindza measured the left forewing length and wet mass of sub-samples of the monarchs that he tagged (Figure 2). He measured left forewing length following the protocol of Brower & Van Hook (in prep.). This measures (mm) the straight line distance on the ventral surface of the forewing from the forewing tip to the white dot on the base of the wing where the wing

TABLE 1. Summary of the number of monarch butterflies tagged during this study at coastal and inland sites in Virginia.

| Year         | Coastal |         |       |          | Inland |         |       |          | Grand Total |
|--------------|---------|---------|-------|----------|--------|---------|-------|----------|-------------|
|              | Males   | Females | Total | % Female | Males  | Females | Total | % Female |             |
| 2001         | 231     | 182     | 413   | 44.1     | 374    | 151     | 525   | 28.8     | 938         |
| 2002         | 67      | 18      | 85    | 21.2     | 41     | 22      | 63    | 34.9     | 148         |
| 2003         | 34      | 20      | 54    | 37.0     | 35     | 21      | 56    | 37.5     | 110         |
| 2004         | 7       | 4       | 11    | 36.4     | 2      | 0       | 2     | 0.0      | 13          |
| 2005         | 14      | 17      | 31    | 54.8     | 99     | 64      | 163   | 39.3     | 194         |
| 2006         | 370     | 252     | 622   | 40.5     | 134    | 65      | 199   | 32.7     | 821         |
| Total Tagged | 723     | 493     | 1216  | 40.5     | 685    | 323     | 1008  | 32.0     | 2224        |

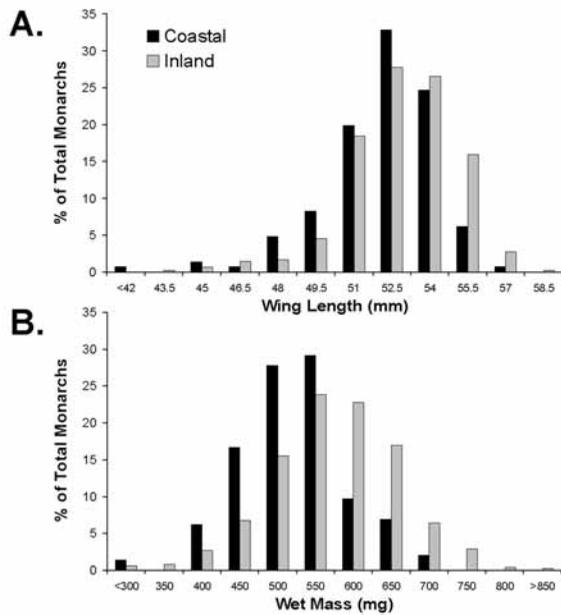


FIG. 2. Distribution of (A) forewing lengths (mm) and (B) wet masses (mg) of the coastal and inland monarchs.

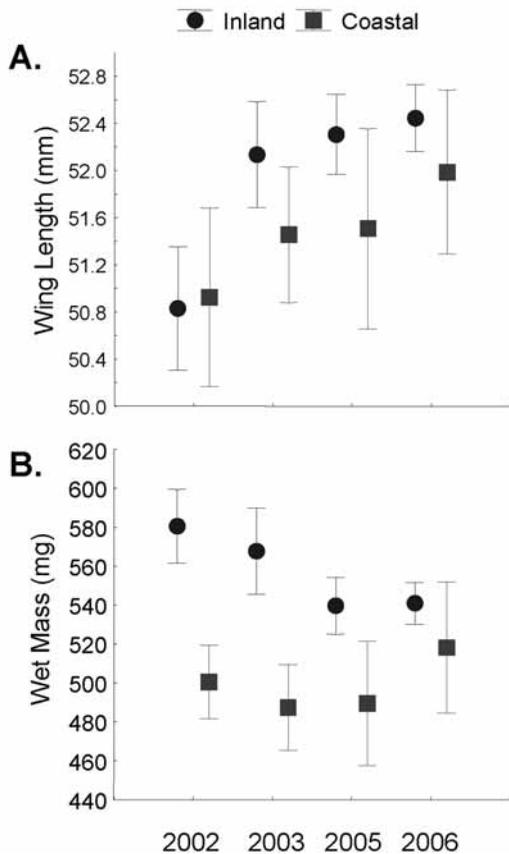


FIG. 3. (A) Average wing length and (B) average wet mass of monarchs for the four years (2002–2006, excluding 2004) for both inland and coastal sites. Bars indicate 95% confidence intervals.

attaches to the thorax. All measurements were made to the nearest 0.1 mm with handheld Mitutoyo digital calipers (Ben Meadows Co., Janesville, WI). Brindza also measured wet mass, rounded to the nearest mg, using a portable electronic balance with an accuracy of 0.001 g (Acculab, Model PP2060D, Sartorius Group, Göttingen, Germany). The balance was recalibrated on each day of use. Throughout the study, the length of time between capture and measuring and weighing individual monarchs did not exceed 15 minutes. Weighing them as soon as possible after capture is imperative to avoid mass (weight) loss through desiccation.

**Statistical analyses.** We used Statistica 6.1 software (Statistica 2003) for our analyses. We used chi-square to test for significant differences in the numbers of recaptures in Mexico of monarchs tagged at the inland vs the coastal sites. We also used chi-square to test for differences in the numbers of tagged males and females in reaching Mexico. We used ANOVA to explore the factors influencing variation in monarch wing lengths and wet masses. With wing length or wet mass as the dependent variable, we included site (inland and coastal), sex (male and female), and year (2002, 2003, 2005 and 2006) as categorical independent variables. The 2004 data were excluded from the analyses because of the very small sample sizes. All two-way and three-way interactions were initially included in the model, and dropped if not significant. We used analysis of covariance to examine the factors affecting monarch mass, with wing length as a covariate to account for the fact that mass is influenced by butterfly size (*i.e.* forewing length).

RESULTS

**Recaptures in Mexico.** Thirteen of the 1,008 (1.29%) butterflies tagged at the inland sites were recaptured while only 2 of 1,216 (0.16%) were recaptured from the coastal sites (Tables 1 and 3). This eight-fold difference in recapture rate is statistically significant (chi-square = 10.41, 1 df,  $P < 0.001$ ). Our data thus indicate that monarchs migrating inland across the piedmont east of the Appalachians have a much higher probability of being recaptured in Mexico than do those migrating along the Atlantic coast.

Our low coastal recapture rate was 1.8 times higher than that found by Walton & Brower (1999) in Cape May (0.093%) and 3.6 times higher than that found by Garland and Davis (2002), on the southern tip of the Delmarva Peninsula in Virginia (0.046%). Our higher value is likely due to the fact that the majority of our monarchs were tagged during the fall preceding the January 2002 storm that killed nearly one quarter of a

billion monarchs in two colonies (Brower *et al.* 2004) and resulted in an all time high tag recovery rate in Mexico (Monarch Watch 2006).

There was a deficiency of females each year in all samples except for the coastal sample in 2005 (Table 1). For the inland samples tagged in 2001, there were 374 males and 151 females, *i.e.* 29% females. Of the 12 inland monarchs recaptured in Mexico that season, 7 of 12, *i.e.* 58% were females. Thus there was a reversal in the sex ratio with twice the frequency of tagged females recaptured (chi-square = 5.12, 1 d.f.,  $P < 0.025$ ) indicating that both sexes reached Mexico from the inland route, but that females were substantially more successful than males in doing so.

**Wing length.** The data for the coastal and inland samples are shown in Figs. 2A and 3A. Two way ANOVA (Figure 4) analyzed differences for site, year and sex for the 617 monarchs that we measured. We found no significant ( $P > 0.10$ ) two-way interaction terms. When these were dropped, the main effects revealed significant effects of both year ( $F_{3,611}=10.5$ ,  $p<0.001$ ) and site ( $F_{1,611}=4.0$ ,  $p=0.046$ ). Tukey's post-hoc comparisons indicated that monarchs captured in 2002 were significantly smaller than in all other years. The effect of site is evident in Figure 3A, with monarchs slightly but significantly larger at the inland sites on average and for three of the four years. At the inland sites, the average for both sexes was 52.1 mm, while at coastal sites it was 51.3 mm, a difference of about 1.5%.

**Body mass.** The data for the coastal and inland samples are shown in Figs. 2B and 3B. For wet body mass, the final model contained several highly

significant main effects and interaction terms (Table 5), most notably, the main effects of year ( $F_{3,602}=8.6$ ,  $p<0.001$ ), sex ( $F_{1,602}=4.4$ ,  $p<0.037$ ), and wing length ( $F_{1,602}=182.5$ ,  $p<0.001$ ). Males weighed significantly more than females (Table 2B), 552 mg vs 511 mg overall), and not surprisingly, the effect of wing length was positive (*i.e.* monarchs with longer wings also had greater mass). There was a significant interaction of site\*year ( $F_{3,602}=5.7$ ,  $p=0.001$ , Table 5). This interaction effect is evident in Fig. 3B, in that the monarchs from the coastal site weighed less than those from the inland, but the magnitude of this effect depended on the year, being smaller in 2006 than in 2002. Further, the difference in wet mass between sites was not due to the size difference in monarchs, as indicated by an analysis of covariance in which the effect of wing size was included in the mass model. To elucidate this point further, we plotted (Fig. 4) the average residual mass (from the significant linear regression of mass *versus* wing length) of both sites so that the difference in weights, after wing length is accounted for, can be seen. Thus when size is removed, the difference in mean residual mass between sites is significant (t-test,  $df = 625$ ,  $t = 2.31$ ,  $p = 0.021$ ). Thus the average wet mass of the coastal migrants (496 mg) was 9.6% less than the inland migrants (549 mg) and was lower than that found in several other studies (Brown & Chippendale 1974; Gibo & McCurdy 1993; Borland *et al.* 2004) as shown in Figure 1.

DISCUSSION

The data from this study in Virginia demonstrate that monarchs captured during the fall migration along the Atlantic coast differed in three significant ways from those migrating inland across the piedmont between the Appalachians and the coast. Relatively few of the coastal migrants succeeded in reaching the overwintering sites in Mexico, they had slightly smaller wing lengths and they had lower wet masses. These results have major implications for a more complete understanding of the fall migration of the eastern North American population of the monarch butterfly.

**Migration east and west of the Appalachians.** Based on their tagging studies, Urquhart & Urquhart (1979a, b) and Urquhart (1987) maintained that monarch migration along the Atlantic coast is "aberrant". Briefly, they contended that variable numbers of fall migrants are blown by westerly winds over the Appalachians to the east coast. They reasoned that these avoid flying over the ocean with most continuing to migrate south along the coast into Florida and thence into the Caribbean, without reaching the overwintering sites in Mexico. The Urquharts' aberrant

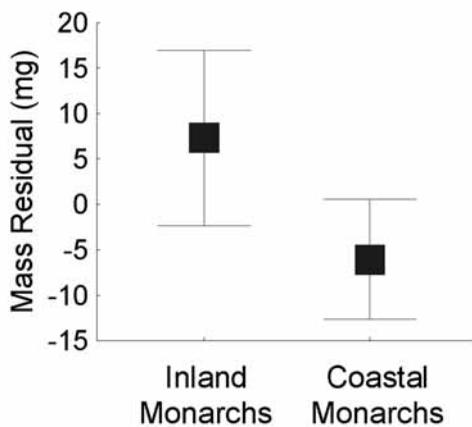


FIG. 4. Comparison of average residual mass (residuals from a linear regression of mass versus wing length) of monarchs from both inland and coastal sites. The difference is significant (t-test,  $df=625$ ,  $t=2.31$ ,  $p=0.021$ ). Bars indicate 95% confidence intervals.

migration hypothesis, together with the much lower frequencies of recaptures in Mexico of monarchs tagged east compared to those tagged west of the Appalachians by Monarch Watch (Taylor pers. comm.. 2007; Monarch Watch 2006), has led to the general assumption that monarch migration anywhere east of the Appalachians is a less successful strategy in reaching Mexico. This contention was reinforced by an analysis of 40 years of recapture data (Rogg *et al.* 1999) showing that migrants west of the Appalachians likely do get blown eastwards, but they are in some way able to compensate for this wind drift and, as some birds and dragonflies do (Richardson 1990; Syrgley 2004), they reorient to a southwesterly course leading them to Mexico (see also Howard 2007).

Based on the results of our study, this general model requires modification. We have determined that migration east of the Appalachians along the piedmont may be as successful as the migration west of the Appalachians. In contrast, as maintained in the past and

as we have confirmed, migration along the coast *per se* is far less successful. However, being less successful does not necessarily mean that the coastal migration is aberrant, a descriptor that we consider misleading.

#### Rejection of the aberrant migration hypothesis.

In contesting the aberrant coastal migration hypothesis, Walton & Brower (1996, 1999) reported that at least some tagged coastal monarchs do succeed in making it to Mexico, as we have again shown in this paper. Walton & Brower also reemphasized that the coastal migration has occurred regularly since it was described in the 19th century and often involves spectacular numbers of butterflies (Brower 1995). This has been confirmed quantitatively by fifteen consecutive annual censuses in Cape May, New Jersey begun in 1991 (Walton & Brower 1996; Walton *et al.* 2005) and by nine annual coastal censuses in Chincoteague, Virginia, 117 km south of Cape May (Gibbs *et al.* 2006). Further evidence of the large magnitude of the coastal migration includes reports of nocturnal roosts of over 10,000

TABLE 2. **A.** Female and male mean mass (wet weight) and size (wing length) comparisons between Coastal and Inland collections sites in VA. 2002-2006. **B.** Overall mean mass and size comparisons: **1)** Coastal versus Inland, combining all years and sexes and **2)** male versus female combining all years and both Coastal and Inland sites. Data for 2004 are not included because of very small sample sizes.

| A.                      |             | WET WEIGHT (mg) |            |                 |             | WING LENGTH(mm) |             |             |             |
|-------------------------|-------------|-----------------|------------|-----------------|-------------|-----------------|-------------|-------------|-------------|
|                         |             | Females         |            | Males           |             | Females         |             | Males       |             |
|                         |             | Coastal         | Inland     | Coastal         | Inland      | Coastal         | Inland      | Coastal     | Inland      |
| Year                    |             |                 |            |                 |             |                 |             |             |             |
| 2002                    | <b>Mean</b> | <b>449</b>      | <b>557</b> | <b>524</b>      | <b>593</b>  | <b>49.9</b>     | <b>50.7</b> | <b>51.3</b> | <b>50.9</b> |
|                         | STD         | 49.7            | 83.3       | 54.4            | 68.1        | 2.3             | 2.1         | 2.7         | 2.1         |
|                         | N           | 14              | 22         | 31              | 41          | 14              | 22          | 34          | 41          |
| 2003                    | <b>Mean</b> | <b>495</b>      | <b>539</b> | <b>483</b>      | <b>585</b>  | <b>52.1</b>     | <b>51.9</b> | <b>51.1</b> | <b>52.3</b> |
|                         | STD         | 59.8            | 65         | 77              | 88.4        | 1.4             | 1.1         | 2.0         | 1.9         |
|                         | N           | 15              | 21         | 27              | 35          | 15              | 21          | 27          | 35          |
| 2005                    | <b>Mean</b> | <b>487</b>      | <b>507</b> | <b>492</b>      | <b>561</b>  | <b>52</b>       | <b>51.8</b> | <b>50.9</b> | <b>52.6</b> |
|                         | STD         | 84.6            | 95.9       | 93              | 88.2        | 2.2             | 2.5         | 2.4         | 1.9         |
|                         | N           | 17              | 64         | 14              | 99          | 17              | 64          | 14          | 99          |
| 2006                    | <b>Mean</b> | <b>521</b>      | <b>514</b> | <b>516</b>      | <b>554</b>  | <b>52.3</b>     | <b>52.3</b> | <b>51.8</b> | <b>52.5</b> |
|                         | STD         | 43.2            | 77         | 72.7            | 73.8        | 1.7             | 2.1         | 0.9         | 2.0         |
|                         | N           | 6               | 65         | 9               | 134         | 6               | 65          | 9           | 134         |
| B                       |             | WET WEIGHT (mg) |            | WING LENGTH(mm) |             |                 |             |             |             |
|                         |             | Coastal         | Inland     | Coastal         | Inland      |                 |             |             |             |
|                         |             |                 |            |                 |             |                 |             |             |             |
| 1. All Yrs & Both Sites | <b>Mean</b> | <b>496</b>      | <b>549</b> | <b>51.3</b>     | <b>52.1</b> |                 |             |             |             |
|                         | STD         | 71.4            | 85         | 2.2             | 2.1         |                 |             |             |             |
|                         | N           | 133             | 481        | 136             | 481         |                 |             |             |             |
|                         |             | Females         | Males      | Females         | Males       |                 |             |             |             |
| 2. All Yrs & Both Sexes | <b>Mean</b> | <b>511</b>      | <b>552</b> | <b>51.8</b>     | <b>52.1</b> |                 |             |             |             |
|                         | STD         | 82.8            | 82.8       | 2.2             | 2.1         |                 |             |             |             |
|                         | N           | 224             | 390        | 224             | 393         |                 |             |             |             |

monarchs on Chincoteague (Gibbs pers. comm.) and on Cape May (Smith 2007).

Given the fact that the Atlantic coastal migration is an integral part of the monarch's fall migration, what is the fate of migrants of the eastern North American population that do not make it to Mexico? Cardenolide fingerprinting indicated that some migrate into south Florida where they become incorporated into local breeding populations on the eastern edge of the Everglades (Knight 1998). Cardenolide fingerprinting together with isotope marker analyses determined that still others continue across the Caribbean to Cuba where they also become incorporated into local breeding populations (Dockx *et al.* 2004). Those that may reach the Yucatan or any of the Antillean islands (Urquhart 1987) may help sustain these tropical populations. However, the ability of all these butterflies to remigrate northwards the following spring is nil because, in becoming reproductive under the high tropical temperatures, they lose their migratory capacity and will not be able to live for the five or more months until spring arrives along the Gulf Coast (Brower 1995; Zemaitis 2005). On the other hand, some of those coastal migrants that regain the southwesterly migratory track do make it to the Mexican overwintering sites and have the opportunity to remigrate back into the southern USA the following spring.

In light of all these recent findings, we reject the aberrant migration hypothesis and we cannot agree with Taylor's contention (in McNeil Jr. 2006) that monarchs migrating along the coast are "toast." However, the lower recapture rates, shorter wing lengths and lower wet masses of the coastal migrants do indicate that there are negative factors affecting these monarchs' ability to reach Mexico. What might these negative factors be?

**Risk of being blown out to sea favors shorter wing lengths.** When one considers the distances the monarchs may fly, coastal migrants must be severely challenged by winds. The Atlantic coastal habitat extends for 2,700 miles from Maine to Florida, includes the Florida Gulf Coast, and continues westward and southward to the border of Texas and Mexico (Beatley *et al.* 2002). We propose that monarchs migrating along the coast have shorter wing lengths than those migrating inland because the larger individuals are more likely to get blown out to sea and have more difficulty flying back in than do the smaller ones. We are not advocating the idea that the coastal migrants are a sub-population that has been selected for shorter wing lengths. In fact, the likelihood of shorter wings genetically evolving is unlikely because of the random mating that occurs among the millions of individuals of the eastern population that takes place in Mexico (Brower 1995).

However, it is relevant to point out that natural selection is a strong evolutionary force that has shaped the flight dynamics of both birds and insects along coastal environments, and, on oceanic islands, has led to flightlessness in many lineages. It is also well established that insects lose control of their direction and velocity when they fly up out of the slower moving air in the boundary layer near the ground and can be carried away by the wind (pp. 298, 324, in Dudley 2000; Alexander 2002). However, Robert Dudley (pers. comm.), contends that the opposite should be true, namely that the larger winged individuals should have a better chance of fighting their way back in from the ocean to the coast. Dudley & Syrgley (2008) also found that several neotropical migrant butterflies reduce their flight speed as their lipid reserves deplete. Thus, there may be an interplay between size and mass in the coastal monarchs, resulting in the larger individuals that have a depleted lipid mass having to slow down, and therefore lowering their ability to fight the wind.

While we have no direct evidence, our wing length hypothesis is consistent with observations made by Schmidt-Koenig (1993) along the Atlantic coastline that monarchs avoid flying over large bodies of water unless the direction and speed of the winds are favorable. Gibbs (2007) also observed monarchs' strong reluctance to fly southwesterly across the Chesapeake Bay when the winds were unfavorable. That migrating monarchs are sensitive to unfavorable winds is also evident from their response to cross-winds by flying low to the ground (Schmidt-Koenig 1985; Davis & Garland 2002; Garland & Davis 2002), or by simply pausing their migration to wait for better conditions to resume flying and soaring (Schmidt-Koenig 1985; Davis & Garland 2004). Ishii *et al.* (1992), working along the Gulf Coast south of Tallahassee, Florida, counted the numbers of fall migrants that were flying over the ocean and found that the number flying inland exceeded the number flying out. They interpreted this as evidence for reluctance to sustain flight across the Gulf.

**Energetically contending with the coastal environment.** One hypothesis to explain the lower wet mass of the coastal monarchs compared with those collected inland is that excess exertion burns their lipids while they confront unfavorable beach winds and cross large bodies of water, including the numerous bays and sounds along the coast. Gibbs (in Gibbs *et al.* 2006; Gibbs 2007, pers. comm.) has studied coastal monarch migration through Chincoteague in Northern Virginia for 14 years (1994–2007) and she has frequently observed large numbers of monarchs being blown out to sea and others struggling against winds to return to land. She also noted that the butterflies that succeeded in

TABLE 3. Fifteen recoveries in Mexico of the 2,224 monarchs tagged by L. Brindza at inland and coastal sites in Virginia over five years (2001–2006). The tag cities are the towns closest to the tagging locations.

| Sex            | Tag Code | Tag City         | Tag Date  | Report Date | Wintering Colony |
|----------------|----------|------------------|-----------|-------------|------------------|
| <b>Inland</b>  |          |                  |           |             |                  |
| Female         | ABJ667   | Lorton, VA       | 12-Sep-01 | 06-Jan-02   | El Rosario       |
| Male           | ABJ835   | Lorton, VA       | 22-Sep-01 | 26-Feb-02   | El Rosario       |
| Female         | ABJ782   | Lorton, VA       | 13-Sep-01 | 26-Feb-02   | El Rosario       |
| Male           | ABJ388   | Lorton, VA       | 04-Sep-01 | 26-Feb-02   | El Rosario       |
| Female         | ABJ415   | Lorton, VA       | 05-Sep-01 | 20-Feb-02   | Sierra Chincua   |
| Male           | ABJ492   | Lorton, VA       | 06-Sep-01 | 27-Feb-02   | Sierra Chincua   |
| Female         | ABJ675   | Lorton, VA       | 12-Sep-01 | 27-Feb-02   | Sierra Chincua   |
| Female         | ABJ497   | Lorton, VA       | 06-Sep-01 | 12-Mar-02   | El Rosario       |
| Female         | ABJ484   | Lorton, VA       | 06-Sep-01 | 24-Mar-03*  | El Rosario       |
| Female         | ABJ682   | Lorton, VA       | 12-Sep-01 | 03-Mar-04*  | El Rosario       |
| Male           | ABJ538   | Lorton, VA       | 07-Sep-01 | 18-Mar-05*  | El Rosario       |
| Male           | ABJ757   | Lorton, VA       | 13-Sep-01 | 18-Mar-05*  | El Rosario       |
| Male           | HCM412   | Woodbridge, VA   | 03-Sep-06 | 20-Feb-07   | El Rosario       |
| <b>Coastal</b> |          |                  |           |             |                  |
| Female         | AII546   | Cape Charles, VA | 02-Oct-01 | 18-Mar-05*  | El Rosario       |
| Female         | HCM160   | Cape Charles, VA | 03-Oct-01 | 06-Jan-07   | El Rosario       |

\*Time span greater than 1 overwintering season because tag was found and held by local residents until collected by Monarch Watch officials

returning immediately began nectaring. Louise Zemaitis (pers. comm.) has made similar observations in Cape May.

Beall (1948) found that many monarchs perished while attempting to cross Lake Erie during the fall and he determined that they had a lower lipid content than monarchs that survived the crossing. It therefore seems reasonable to conclude that migrants are forced to burn more lipid while using powered and flapping flight to contend with the coastal winds and flights across water than the tenfold more energy-efficient soaring and gliding that is common in the less windy inland environment (Schmidt-Koenig 1985; Masters *et al.* 1988; Davis & Garland 2004; Brower *et al.* 2006).

**Are the diminished nectar resources and low lipid levels due to human encroachment?** As implied by our having caught most of our butterflies at flowers, monarchs frequently interrupt their fall migration to drink nectar. Sugar that is contained in nectar is converted to lipid that the butterflies store and use to fuel their flight and other activities. In a recent study, Brower *et al.* (2006) found only moderate

amounts of lipids in migrating monarchs until they reach Texas, where they then accumulate large lipid stores. Lipid stores are critical to fuel the butterflies five month overwintering period in Mexico (Alonso *et al.* 1997).

We hypothesize that our coastal monarchs were lighter than the inland monarchs because they did not have access to sufficient nectar sources and that this is due to a diminished flora caused by habitat deterioration along the Atlantic coastal migratory corridor. While the overall nectar abundance may always have been less along the coast than inland, as now discussed, this is doubtful.

**The coastal habitats.** The dynamic ecological interrelationships of coastal habitats are described in Frid & Evans (1995). They include long ribbons of barrier and sea islands that over geological time developed a series of very different habitats extending from the sea to inland (Christensen 1988). The habitats include the sandy beaches, coastal prairies, primary and secondary sand dunes and wetland swales behind the dunes (Silberhorn 1999). Further inland are saline and

TABLE 4. Results of ANOVA model explaining variation in wing length of migrating monarch butterflies. The data for the 2004 year were not included in the analysis. All two-way interactions were initially included in the model but were removed when found not significant.

| Independent | df  | MS | F    | P      |
|-------------|-----|----|------|--------|
| Site        | 1   | 17 | 4.0  | 0.046  |
| Year        | 3   | 46 | 10.5 | <0.001 |
| Sex         | 1   | 15 | 3.5  | 0.064  |
| Error       | 611 | 4  |      |        |
| Total       | 616 |    |      |        |

freshwater estuaries, lagoons, sounds and coastal forests. According to Delacourt & Delacourt (1981), this very dynamic ecosystem complex has persisted for the last 9000 years, about as long as the current monarch butterfly migration is thought to have existed (Brower 1995). Even though the various communities within this environmental can be complex and harsh (Barbour & Christensen 1993), they have specialized, productive and diverse floras (Barbour 1992; Tiner 1987, 1993; Packham & Willis 1997; Silberhorn 1999). These include numerous annual and perennial plants that serve as nectar sources for the monarch butterfly migrating through the complex of habitats each fall.

According to Bird (1985), coastal erosion through rising sea level has impacted about 70% of the planet's sandy beach environments including those along the North American Atlantic coast. Rising sea level causes the beach, coastal prairie and dune habitats to erode, but, with slow rising conditions, the habitats reestablish further inland. They then undergo ecological succession and the flora physically stabilizes the

TABLE 5. Results of ANOVA model explaining variation in wet mass of migrating monarch butterflies. The data for the 2004 year were not included in the analysis. The interactions of Site\*Sex and Year\*Sex were initially included in the model but were removed when found not significant.

| Independent     | df  | MS     | F     | p      |
|-----------------|-----|--------|-------|--------|
| Site            | 1   | 8280   | 1.9   | 0.164  |
| Year            | 3   | 36516  | 8.6   | <0.001 |
| Sex             | 1   | 18595  | 4.4   | 0.037  |
| WingLength      | 1   | 778160 | 182.5 | <0.001 |
| Sex*WingLength  | 1   | 14502  | 3.4   | 0.066  |
| Site*WingLength | 1   | 12449  | 2.9   | 0.088  |
| Site*Year       | 3   | 24216  | 5.7   | 0.001  |
| Error           | 602 | 4263   |       |        |
| Total           | 613 |        |       |        |

restored habitat. To what extent have humans diminished this environment?

**Human encroachment.** Human exploitation of the valuable economic resources offered by the dynamic coastal ecosystems and its severe impact on their natural features is documented in numerous studies (Turner *et al.* 1998; Doody 2002; Ray & McCormick-Ray 2003; Burroughs & Tebbins 2005; Feagin *et al.* 2005; Forman *et al.* 2005; Verhoeven *et al.* 2006; Martinez & Psuty 2007). The construction of buildings, dikes, parking lots, roads, etc. often squeezes the land against the ocean and blocks the natural inland sand movement. Sea currents then either wash the sandy beaches, the prairies and the dunes away, or reduce them to mere remnants with extensively diminished floras. It is estimated that 350,000 structures in the United States are located within 500 feet of the shorelines and nearly half of all coastal wetlands have been destroyed since pre-Columbian times (Beatley *et al.* 2002). Dredging and ditching in the first half of the 20th century also deteriorated much coastal habitat (Humphrey and Rockefeller 1968). Although passage of the 1972 Wetlands Act helped mitigate the losses, Beatley *et al.* (2002, p. 283) tell us: "Alarm bells are ringing everywhere as our coastal environment endures unabated development pressures and environmental degradation".

Another negative anthropogenic impact is the spraying of herbicides, including glyphosate ("Roundup", Monsanto, Inc., see Anon. 2005) and imazapyr ("Habitat", BASF Inc., see Anon. 2007b), to control marsh reed grass, *Phragmites australis* (Cav.) Trin. ex Steud. (Poaceae). These biocides, either directly or through inadvertent wind drift when applied by helicopters, can kill the nectar sources adjacent to the marshes. For example, spraying herbicides was a major issue in Cape May in 2005 (Fichter 2005) and in the Chincoteague National Wildlife Refuge in 2006. According to Denise Gibbs (pers. comm.), helicopter spraying on Chincoteague is forbidden if the wind exceeds 5 mph. However, on 2 October 2006—a peak monarch butterfly migration day—the spraying was continued with a 15 mph wind, drifting "Habitat" for at least a half a mile across a main *Solidago sempervirens* nectaring area. Yet other impacts are exemplified by helicopter spraying of malathion (see Anon. 2006) and by truck misting with the pyrethroid derivative resmethrin, ("Scourge", Aventis Environmental Science, see Anon. 2007c) for mosquito control by the Cape May County Mosquito Commission. A related synthetic pyrethroid ("Permethrin") has been found to kill monarchs in both larval and adult stages and has long term effects on the butterflies (Oberhauser *et al.* 2006).

The extent to which these various physical and chemical impacts have diminished the quantity and quality of the nectar sources in the coastal environment has not been quantified, but the losses have almost certainly affected the lipid and hydration dynamics of fall migrant monarch butterflies, as well as the nectar requirements of other animals living in and using this migratory corridor (Nabhan 2004; Brower & Pyle 2004).

**Inland habitats.** In contrast to the natural and anthropogenic hazards to monarchs flying along the coast, flight over the far more extensive inland routes with diverse and varied nectar resources may not be as stressful. Inland environments are also subject to less intense wind and, until recently, roadsides and agricultural fields provided extensive areas with wildflowers. Unfortunately, the ever-increasing use of herbicides on roadsides, and, in conjunction with the repeated spraying of corn and soybean crops that are genetically engineered to be resistant to the herbicides, are eliminating huge areas of floral resources (Brower *et al.* 2006).

**Alternative hypotheses and future research.** An alternative hypothesis to account for the smaller and lighter coastal monarchs is that fewer of their larvae had the opportunity to feed on *Asclepias syriaca* L. (Asclepiadaceae), the major food plant (Malcolm *et al.* 1989) of the monarch's eastern population and is known to be nutritionally superior to *Asclepias tuberosa* L. (Erickson 1973). The latter milkweed is widely distributed along the Atlantic coast (Woodson 1954), and it is possible that more of the coastal migrants had fed on it and ended up as smaller individuals. Thin layer chromatography analyses (Malcolm *et al.* 1989) could determine if the food plants eaten by the larvae differed among the larger and smaller individual butterflies. However, this explanation seems unlikely because, as implied above, the majority of coastal monarchs probably fed on *A. syriaca* plants growing inland before being wind-drifted to the coast.

Another possibility is that the smaller and lighter monarchs were less able than the larger and heavier ones to resist winds that blew them towards the coast. This is consistent with Beall's (1948) finding that the monarchs that drowned crossing Lake Erie were both smaller and lighter than ones he collected in roosts both north and south of the lake collections. Another possibility is that the monarchs with lower mass were more fuel and/or water stressed and therefore accumulated on the coast to nectar, while the heavier ones kept migrating south. It is important to remember that our samples were gathered in a very limited latitudinal transect. Much light could be shed on the questions by analyzing collections along the coast as the

migration progresses from Maine to Florida.

To test our habitat deterioration hypothesis, comparative measurements of the amount of nectar imbibed by monarchs (methods in Brower *et al.* in prep.) collected at inland and the coastal sites could be made. Currently, there are hundreds of citizen-scientists (Monarch Watch 2006; Prysby & Oberhauser 2004) who study, capture, tag and release monarchs each year. Direct measurements of wing length and wet mass, as done in this study without killing the individual monarchs, would help build long term comparative data sets. However, more accurate measurements of both lipid and water contents of the inland and coastal monarchs are needed. Wet mass is the sum of the water, lipid and the lean body mass. Consequently, the correlation between wet mass of the whole butterfly and the contained lipid mass is weak and confounds the masses of water and lipid. In order to measure both accurately, the monarchs must be killed by freezing, weighed, dehydrated, weighed again, and then their lipids extracted and weighed (Brower *et al.* in prep.). Citizen-scientists could collect and freeze monarch samples and have professionals carry out the lipid and water determinations in a well-coordinated project.

#### ACKNOWLEDGEMENTS

We thank the following for field assistance in Virginia: Sharna Tolfree, Randy Emmitt, David Haynes, and Elizabeth Townsend, all supported by the Coastal Virginia Wildlife Observatory. Logistic support was also provided to Brindza by the Occoquan Bay National Wildlife Refuge, Eastern Shore of Virginia National Wildlife Refuge, Mason Neck State Park, Kiptopeke State Park, and the Chesapeake Bay Bridge-Tunnel. We are grateful to Linda Fink, Richard Walton, Louise Zemaitis and two reviewers for critical comments on the manuscript, to Denise Gibbs for sharing information on the migration through Chincoteague, VA, and to Peter Raven for identifying scientists familiar with the Atlantic coastal flora, including Michael Barbour, James Morris, Gerry Moore, George Yatskievych; and to Janet Steven. We appreciate the enormous efforts of Orley Taylor in coordinating the Monarch Watch tagging program, for purchase of recovered tags in Mexico and for disseminating recapture data. Robert Dudley, though skeptical of our wind loss hypothesis, provided valuable commentary and insights. Financial support was provided over the years by The Wildlife Conservation Society, Paul and Kathy Reinhold, The October Hill Foundation, and by National Science Foundation grant DEB-0415340 to Sweet Briar College with Lincoln Brower and Linda Fink as principal investigators. AKD was supported by the D.B. Warnell School of Forestry and Natural Resources at the University of Georgia during the writing of this manuscript.

#### LITERATURE CITED

- ALEXANDER, D. E. 2002. Nature's flyers. The Johns Hopkins University Press, Baltimore, Maryland.
- ALONSO-MEJIA, A., E. RENDON-SALINAS, E. MONTESINOS-PATINO, & L. P. BROWER. 1997. Use of lipid reserves by monarch butterflies overwintering in Mexico: implications for conservation. *Ecological Applications* 7: 934-947.
- ANON. 2005. Monsanto imagine: Backgrounder history of Monsanto's glyphosate herbicides, June 2005. <http://www.monsanto.com/>

- pdf/products/roundup\_back\_history.pdf. Accessed 19 November 2007.
- \_\_\_\_\_. 2006. Cape May County Mosquito Control Commission. <http://execdeanagriculture.rutgers.edu/photos/album.asp?mosquitocontrol2006>. Accessed 19 November 2007.
- \_\_\_\_\_. 2007a. Plants database. In USDA Natural Resources Conservation Service <http://plants.usda.gov>. Accessed 11 September 2007.
- \_\_\_\_\_. 2007b. Imazapyr. Weed Control Methods Handbook, The Nature Conservancy. <http://tncweeds.ucdavis.edu/products/handbook/17.Imazapyr.pdf>. Accessed 19 November 2007.
- \_\_\_\_\_. 2007c. Scourge and mosquito control. In New York Department of Health Information Sheet "Scourge and mosquito control". <http://www.health.state.ny.us/nysdoh/westnile/education/2739.htm>. Accessed 19 November 2007.
- ATWOOD, W. W. 1940. The physiographic provinces of North America. Ginn and Company, Boston, Massachusetts.
- BARBOUR, M. G. 1992. Life at the leading edge: the beach plant syndrome. Pp. 291–307. In U. Seeliger (ed.), Coastal plant communities of Latin America. Academic Press, San Diego.
- \_\_\_\_\_, & N. L. Christensen. 1993. Vegetation. Pp. 97–131. In N. R. Morin (ed.), Flora of North America. Oxford University Press, New York.
- BEALL, G. 1948. The fat content of a butterfly, *Danaus plexippus*, as affected by migration. *Ecology* 29: 80–94.
- BEATLEY, T., D. J. BROWER, & A. K. SCHWAB. 2002. An introduction to coastal zone management, 2nd edition. Island Press, Washington, D.C.
- BIRD, E. C. F. 1985. Coastal changes: a global review. John Wiley and Sons, Chichester, UK.
- BORLAND, J., C. C. JOHNSON, T. W. CRUMPTON III, M. THOMAS, S. ALTIZER, & K. OBERHAUSER. 2004. Characteristics of fall migratory monarch butterflies, *Danaus plexippus*, in Minnesota and Texas. Pp. 97–104. In K. Oberhauser & M. Solensky (eds.), The monarch butterfly, biology and conservation. Cornell University Press, Ithaca, NY.
- BROWER, L. P. 1995. Understanding and misunderstanding the migration of the monarch butterfly (Nymphalidae) in North America: 1857–1995. *Journal of the Lepidopterists' Society* 49: 304–385.
- \_\_\_\_\_, K. R. KUST, J. MILLER, C. FERNANDEZ DEL REY, & K. PAPE. 2004. Catastrophic winter storm mortality of monarch butterflies in Mexico during January 2002. Pp. 151–166. In K. S. Oberhauser & M. J. Solensky (eds.), The monarch butterfly, biology and conservation. Cornell University Press, Ithaca.
- \_\_\_\_\_, L. S. FINK, & P. WALFORD. 2006. Fueling the fall migration of the monarch butterfly. *Integrative and Comparative Biology* 46: 1123–1142.
- \_\_\_\_\_, & R. M. PYLE. 2004. The interchange of migratory monarchs between Mexico and the western United States, and the importance of floral corridors to the fall and spring migrations. Pp. 167–178. In G. P. Nabhan (ed.), Conserving migratory pollinators and nectar corridors in western North America. The University of Arizona Press and The Arizona-Sonora Desert Museum, Tucson, AZ.
- BROWN, J. J., & G. M. CHIPPENDALE. 1974. Migration of the monarch butterfly, *Danaus plexippus*: energy sources. *Journal of Insect Physiology* 20: 1117–1130.
- BURROUGHS, S. M., & S. E. TEBBENS. 2005. Dune retreat and shoreline change on the Outer Banks of North Carolina. Abstract, December, American Geophysical Union, San Francisco. <http://www.agu.org/cgi-bin/SFgate/SFgate>
- CHRISTENSEN, N. L. 1988. Vegetation of the southeastern coastal plain. Pp. 317–363. In M. G. Barbour & W. D. Billings (eds.), North American Terrestrial Vegetation. Cambridge University Press, Cambridge, England.
- DAVIS, A.K., & M. S. GARLAND. 2002. An evaluation of three methods of counting migrating monarch butterflies in varying wind conditions. *Southeastern Naturalist* 1: 55–68.
- \_\_\_\_\_, & \_\_\_\_\_. 2004. Stopover ecology of monarchs in coastal Virginia: using ornithological methods to study monarch migration. Pp. 89–96. In K. Oberhauser & M. Solensky (eds.), The monarch butterfly. biology and conservation. Cornell University Press, Ithaca, NY.
- DELACOURT, P. A. & H. R. DELACOURT. 1981. Vegetation maps for eastern North America: 40,000 yr B.P. to the present. Pp. 123–165. In R. C. Romans (ed.). Geobotany II. Plenum Press, New York.
- DOCKX, C., L. P. BROWER, L. I. WASSENAAR & K. A. HOBSON. 2004. Do North American monarch butterflies travel to Cuba? Stable isotope and chemical tracer techniques. *Ecological Applications* 14: 1006–1114.
- DOODY, J. P. 2002. Coastal conservation and management: an ecological perspective. Kluwer Academic Publishers, Boston, Massachusetts.
- DUDLEY, R. 2000. The biomechanics of insect flight; form, function, evolution. Princeton University Press, Princeton, New Jersey.
- DUDLEY, R., & R. B. SYRLEY. 2008. Airspeed adjustment and lipid reserves in migratory Neotropical butterflies (Lepidoptera: Pieridae and Nymphalidae). *Functional Ecology* 22: 264–270.
- ERICKSON, J. M. 1973. The utilization of various *Asclepias* species by larvae of the monarch butterfly, *Danaus plexippus*. *Psyche* 80: 230–244.
- FEAGIN, R. A., D. J. SHERMAN, & W. E. GRANT. 2005. Coastal erosion, global sea-level rise, and the loss of sand dune plant habitats. *Frontiers in Ecology and the Environment* 3: 359–364.
- FICHTER, J. 2005. Herbicide spraying continues, so do worries. p. 9. In Cape May County Herald, 5 October 2005, Cape May, New Jersey.
- FORMAN, S. L., Z. SAGINTAYEV, S. M. SMITH, M. I. SULTAN, & R. BECKER. 2005. The relation between 20th century dune migration and wetland formation at Cape Cod National Seashore, MA. Abstract, December, American Geophysical Union, San Francisco. [http://www.agu.org/meetings/fm05/fm05-sessions/fm05\\_H43D.html](http://www.agu.org/meetings/fm05/fm05-sessions/fm05_H43D.html) Accessed 4 December 2007.
- FRID, C. L. J., & P. R. EVANS. 1995. Coastal habitats. Pp. 59–83. In W. J. Sutherland & D. A. Hill (eds.), Managing habitats for conservation. Cambridge University Press, Cambridge.
- GARLAND, M. S., & A. K. DAVIS. 2002. An examination of monarch butterfly (*Danaus plexippus*) autumn migration in coastal Virginia. *American Midland Naturalist* 147: 170–174.
- GIBBS, D. 2007. Assateague Island, Virginia at Chincoteague National Wildlife Refuge. Monarch Watch, Lawrence, Kansas. 2 October 2007, DPLEX-L\_digest 4012. Accessed 3 October 2007.
- \_\_\_\_\_, R. WALTON, L. BROWER, & A. K. DAVIS. 2006. Monarch butterfly (Lepidoptera, Nymphalidae) migration monitoring at Chincoteague, VA and Cape May, NJ: a comparison of long-term trends. *Journal of the Kansas Entomological Society* 79: 156–164.
- GIBO, D.L., & J. A. MCCURDY. 1993. Lipid accumulation by monarch butterflies (*Danaus plexippus* L.). *Canadian Journal of Zoology* 71: 76–82.
- HOWARD, E. 2007. (Fall migration roost formation, animated as monarchs migrate south). On: the Journey North website: <http://www.learner.org/jnorth/tm/monarch/FallMigrationTiming.html>, accessed 23 September 2007.
- HUMPHREY, H. N., & L. S. ROCKEFELLER. 1968. From sea to shining sea: a report on the American environment—our natural heritage. President Lyndon B. Johnson's Council on Recreation and Natural Beauty, Washington, D.C.
- ISHII, M., L. P. BROWER, AND T. VAN HOOK. 1992. Autumnal movements of monarch butterflies along the Gulf Coast in Florida. Page 178. In Transactions of the XIX International Congress of Entomology, Beijing, China.
- KNIGHT, A. L. 1998. A population study of monarch butterflies in north-central and south Florida. M.S. Thesis. viii +125 pp.
- LOBSTEIN, M. B. 1990. Summer and fall wildflowers of Northern Virginia: A checklist. Prince William Wildflower Society, Manassas, VA.
- MALCOLM, S. B., B. J. COCKRELL, & L. P. BROWER. 1989. Cardenolide fingerprint of monarch butterflies reared on common milkweed, *Asclepias syriaca* L. *Journal of Chemical Ecology* 15: 819–853.

- MARTINEZ, M. L., & N. P. PSUTY (eds.). 2007. Coastal dunes: ecology and conservation (ecological studies). Springer-Verlag, Berlin.
- MASTERS, A. R., S. B. MALCOLM, & L. P. BROWER. 1988. Monarch butterfly (*Danaus plexippus*) thermoregulatory behavior and adaptations for overwintering in Mexico. *Ecology* 69: 458–467.
- MCNEIL, D. G., JR. 2006. Fly away home. The monarch migration mystery. Pages D1 and D3 . In 3 October 2006 edition, New York Times, New York.
- MONARCH WATCH. 2006. Tag recovery database. <http://www.monarchwatch.org/tagmig/recoveries.htm>. Accessed 1 October 2007.
- NABHAN, G. P. 2004. Stress on pollinators during migration. Pp. 3–22. In G. P. Nabhan (ed.), *Conserving migratory pollinators and nectar corridors in western North America*. The University of Arizona Press and The Arizona-Sonora Desert Museum, Tucson AZ.
- NEWCOMB, L. 1977. *Newcomb's wildflower guide*. Little, Brown and Company, Boston.
- OBERHAUSER, K. S., S. J. BRINDA, S. WEAVER, R. D. MOON, S. A. MANWEILER, & N. READ. 2006. Growth and survival of monarch butterflies (Lepidoptera: Danaidae) after exposure to permethrin barrier treatments. *Environmental Entomology* 35: 1626–1634.
- PACKHAM, J. R., & A. J. WILLIS. 1997. *Ecology of dunes, salt marsh and shingle*. Chapman Hall, London.
- PETERSON, R. T., & M. MCKENNY. 1968. *A field guide to wildflowers of northeastern and north-central North America*. Houghton Mifflin Company, Boston and New York.
- PRYSBY, M., & K. S. OBERHAUSER. 2004. Temporal and geographic variation in monarch densities: citizen scientists document monarch population patterns. Pp. 9–20 . In K. Oberhauser & M. Solensky (eds.), *The monarch butterfly: biology and conservation*. Cornell University Press, Ithaca, NY.
- RAISZ, E. J. 1957. *Map of the landforms of the United States: to accompany Atwood's Physiographic provinces of North America*. 6th revised edition. Published by the author, Cambridge, Massachusetts.
- RAY, C. G., & J. MCCORMICK-RAY. 2003. *Coastal-marine conservation: science and policy*. Blackwell Publishing Limited.
- RICHARDSON, W. J. 1990. Wind and orientation of migrating birds: a review. *Cellular and Molecular Life Sciences* 46: 416–425.
- ROGG, K. A., O. R. TAYLOR, & 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. Pisanty, S. Price, & T. Wilkinson (eds.), in: *Paper presentations: 1997 North American Conference on the monarch butterfly (Morelia, Mexico)*. The Commission for Environmental Cooperation, Montreal, Canada.
- SCHMIDT-KOENIG, K. 1985. Migration strategies of monarch butterflies. Pp. 786–798 . In M. A. Rankin (ed.), *Migration: mechanisms and adaptive significance*. Univ. Texas Contrib. Marine Sci., Austin, TX 27 (Supplement).
- \_\_\_\_\_. 1993. Orientation of autumn migration in the monarch butterfly. Pp. 275–283 . In S. B. Malcolm & M. P. Zalucki (eds.), *Biology and conservation of the monarch butterfly*. Natural History Museum of Los Angeles County, Los Angeles, California.
- SILBERHORN, G. M. 1999. *Common plants of the mid-Atlantic coast: a field guide*, revised edition. The John Hopkins University Press.
- SMITH, B. 2007. View from the field: monarch update 10/16/07. [birdcapemay.org/sightings/](http://birdcapemay.org/sightings/) Accessed 17 October 2007.
- STATISTICA. 2003. Statistica version 6.1, Statsoft, Inc. Tulsa, OK.
- SYRIGLEY, R. B. 2004. Wind drift compensation in migrating dragonflies *Pantala* (Odonata: Libellulidae). *Journal of Insect Behavior* 16: 217–232.
- TINER, R. W. 1987. *A field guide to coastal wetland plants of the northeastern United States*. University of Massachusetts Press, Amherst, Massachusetts.
- \_\_\_\_\_. 1993. *A field guide to coastal wetland plants of the southeastern United States*. University of Massachusetts Press, Amherst, Massachusetts.
- TURNER, R. K., I. LORENZONI, N. BEAUMONT, I. J. BATEMAN, I. H. LANGFORD, & A. L. McDONALD. 1998. Coastal management for sustainable development: analysing environmental and socio-economic changes on the UK coast. *The Geographical Journal* 164: 269–281.
- URQUHART, F. A. 1987. *The monarch butterfly: international traveller*. University of Toronto Press, Toronto.
- \_\_\_\_\_ & N. R. URQUHART. 1979a. Aberrant autumnal migration of the eastern population of the monarch butterfly, *Danaus p. plexippus* (Lepidoptera: Danaidae) as it relates to the occurrence of strong westerly winds. *Canadian Entomologist* 111: 1281–1286.
- \_\_\_\_\_ & \_\_\_\_\_. 1979b. Breeding areas and overnight roosting locations in the northern range of the monarch butterfly (*Danaus plexippus plexippus*) with a summary of associated migratory routes. *The Canadian Field Naturalist* 93: 41–47.
- VERHOEVEN, J. T. A., B. BELTMAN, R. BOBBINK & D. F. WHIGHAM. 2006. *Wetlands and natural resource management (ecological studies)*. Springer.
- WALTON, D. 1999. 1998 monarch migration project: seasonal summary. *Peregrine Observer (Cape May Bird Observatory)* 21: 6–7.
- WALTON, R. K. & L. P. BROWER. 1996. Monitoring the fall migration of the monarch butterfly *Danaus plexippus* L. (Nymphalidae: Danaeinae) in eastern North America: 1991–1994. *Journal of the Lepidopterists' Society* 50: 1–20.
- \_\_\_\_\_ & \_\_\_\_\_. 1999. What we know that ain't so.....the 1998 fall Atlantic Coast monarch migration. *American Butterflies* 7: 18–25.
- \_\_\_\_\_, \_\_\_\_\_, & A. K. DAVIS. 2005. Long-term monitoring and fall migration patterns of the monarch butterfly (Nymphalidae: Danaeinae) in Cape May, NJ. *Annals of the Entomological Society of America* 98: 682–689.
- WOODSON, R. E., Jr. 1954. The North American species of *Asclepias* L. *Annals of the Missouri Botanical Garden* 41: 1–211.
- ZEMAITIS, L. 2005. Monarch monitoring project: 2004 season summary. *Peregrine Observer (Cape May Bird Observatory)* 27: 18–19.

*Received for publication 31 January 2008; revised and accepted 9 September 2008.*

