

Biological Observations of Monarch Butterfly Behavior at a Migratory Stopover Site: Results from a Long-term Tagging Study in Coastal South Carolina

John W. McCord · Andrew K. Davis

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Abstract Like most migratory species, monarch butterflies (*Danaus plexippus*) must stop frequently during their long southward migration to rest and refuel, and the places where they stop are important for the success of the migration. The behavior of monarch butterflies at migratory stopover sites has never been examined in detail. Here we present results of a long-term study of monarchs at one stopover site in coastal South Carolina where over 12,000 monarchs have been captured, measured and tagged (with numbered stickers to track recovery rates) over 13 years. Only 3 monarchs (0.023%) were recovered at the monarchs' overwintering sites in Mexico, which is consistent with other tagging studies on the eastern coast. The migration season was longer at this site than at inland locations and monarchs continued to be captured in November and December, when most monarchs had already arrived at the overwintering areas in Mexico. In addition, there were 94 monarchs captured between Jan 1 and Mar 15, indicating that some monarchs overwinter at this site. Of all monarchs captured during the migration season, 80% were captured while nectaring and 10% while roosting. Others were basking, resting, flying and even mating. The sex ratio was male biased by three to one in all behavior categories except those captured mating. Roosting and nectaring monarchs had fresher wings than those in other behavior categories, suggesting that these are younger individuals. There were 13 observations of females ovipositing on non-native *Asclepias curassavica* during the fall months, which speaks to the potential for this plant to pull monarchs out of the migratory pool. Aside from these insights, this study also serves as an example of the potential that monarch tagging studies have to advance scientific understanding of monarch migration.

Keywords Monarch butterfly · *Danaus plexippus* · migration · tagging · behavior

J. W. McCord
South Carolina Department of Natural Resources, PO Box 12559, Charleston, SC 29422, USA

A. K. Davis (✉)
Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, USA
e-mail: akdavis@uga.edu

Introduction

The fall migration of monarch butterflies (*Danaus plexippus*) in eastern North America to a select few mountaintop overwintering sites in central Mexico is one of the most fascinating displays of insect behavior on Earth. The journey lasts nearly 3 months, can span up to 3,000 km, and involves millions of individuals each year (Malcolm and Zalucki 1993; Oberhauser and Solensky 2004). The monarch migration can be characterized by alternating bouts of flying and stopping as the butterflies rest or build up their fat reserves (by nectaring and transforming sugars to fat), with the fat reserves used to sustain the insects during migration and, more importantly, during the four-month overwintering period (Brower et al. 2006). At some stopover sites, monarchs form nocturnal roosts in shrubs and trees, with such roosts sometimes including thousands of individuals (Urquhart and Urquhart 1979; Howard and Davis 2009). Although the fall monarch migration has intrigued scientists for decades, even before the overwintering destination became known in the 1970s (e.g. Williams et al. 1942; Beall 1948; Urquhart 1960; Brown and Chippendale 1974), there are still many unanswered questions regarding the nature of this migration, especially with respect to the behavior of monarchs at migratory stopover sites, for which there is virtually no published information (Davis and Garland 2004).

Several recent findings have advanced our understanding of the fall migration of this population considerably. Using citizen-scientist observations of migratory roosts, Howard and Davis (2009) showed that there are essentially two fall migratory flyways in eastern North America, one large flyway in the central states that leads directly to the Mexican overwintering sites, and a second, smaller flyway along the Atlantic seaboard that lags behind the central flyway in timing, and does not point to Mexico. In addition, Brindza et al. (2008) showed that monarchs migrating in coastal locations have a reduced chance of being recovered in Mexico than those migrating inland, which can be taken to mean that these coastal butterflies are migrating to locations other than the Mexican overwintering sites, or that they have a higher rate of mortality than those migrating inland. There is evidence that the former explanation is true, since some monarchs from eastern North America end up in Cuba (Dockx et al. 2004), and some are believed to assimilate into the small non-migratory population in south Florida (Knight and Brower 2009; Altizer and Davis 2010). There are also reports from citizen-scientists of monarchs wintering in coastal areas of the United States' gulf coast (Howard et al. In Press). However, the alternative explanation, that coastal monarchs suffer higher mortality, may also hold true, as Brindza et al. (2008) showed that coastal monarchs tend to have smaller fat reserves than inland-migrating monarchs. Suffice it to say, there is mounting evidence indicating that monarchs which migrate along the east coast of North America may represent a unique subset of the collective migratory population, for several reasons.

Other aspects of our understanding of the fall migration are changing in light of recent evidence. It was once thought that all fall migrating monarchs were in a physiological state of 'reproductive diapause', in that they were delaying their mating and breeding behavior until after the overwintering phase (Herman 1985). However, evidence from a field study in Texas showed that over 17% of the

migratory monarchs captured there had already mated (Borland et al. 2004). It was not evident whether these monarchs had broken their diapause stage after arriving in Texas or if they simply never entered diapause before initiating migration. Interestingly, in this same study, the authors found that wing lengths decreased over time during the migration, suggesting that slower-migrating monarchs tend to be small. This idea is consistent with two other studies that also showed that later migrants tend to be smaller than those in earlier portions of the fall migration period (Herman 1988; Gibo and McCurdy 1993).

Perhaps the most interesting recent finding in relation to monarch migration is that for some reason, male monarchs largely outnumber female monarchs in migratory collections (Brower et al. 2006; Brindza et al. 2008). This led Davis and Rendón-Salinas (2010) to examine historical records of monarch collections to determine the sex-ratio for this population. In doing so, they discovered that the proportion of females in this population has been declining over the past 30 years in both the overwintering and fall migratory phases. This may explain the low percentage of females in recent fall collections. However, it is not known to what degree this decline is caused by sex-related differences in ‘catchability’ (i.e. if males are more likely to fly at ground level, or visit flowers where they are easily captured).

Since 1996, migrating monarchs have been studied each fall at a stopover site in coastal South Carolina by the lead author (JWM). The goal of this project has been to capture and measure as many monarchs as possible and to tag them with uniquely numbered stickers from the MonarchWatch program (MonarchWatch 2008). In 13 years, JWM has captured over 12,000 monarchs, and maintained detailed notes about the behavior of each monarch upon capture, as well as the butterflies’ size (forewing length) and wing condition. This data set provides an excellent opportunity to address several outstanding questions about stopover behavior of monarchs. These questions include: what is the distribution of wing length and wing condition throughout the fall migration; what types of behaviors (i.e. nectaring, roosting, basking, etc.) are most frequently observed during stopover; and are the sex ratios of each behavior different? Here, we present the results from this exploration, along with many other observations which we hope will address the paucity of information on this important and understudied phase of the monarch life cycle.

Methods

Study Site The data from this project come from a long-term study of monarch butterfly migration at Folly Beach, SC (32.6°N, -79.9°W), which is an approximately 10 km×1 km barrier island, oriented northeast—southwest, on the central South Carolina coast in Charleston County. Folly Beach is connected to the mainland (James Island) via the SC highway 171 causeway and is approximately 15 km from the city of Charleston (Fig. 1). The vast majority of the island is under residential development with a small, localized business district near the island center. The central, upland portion of the island is in maritime forest cover, with typical tree species including live oak (*Quercus virginiana*), Darlington oak (*Q. hemisphaerica*), southern magnolia (*Magnolia grandiflora*), loblolly pine (*Pinus*

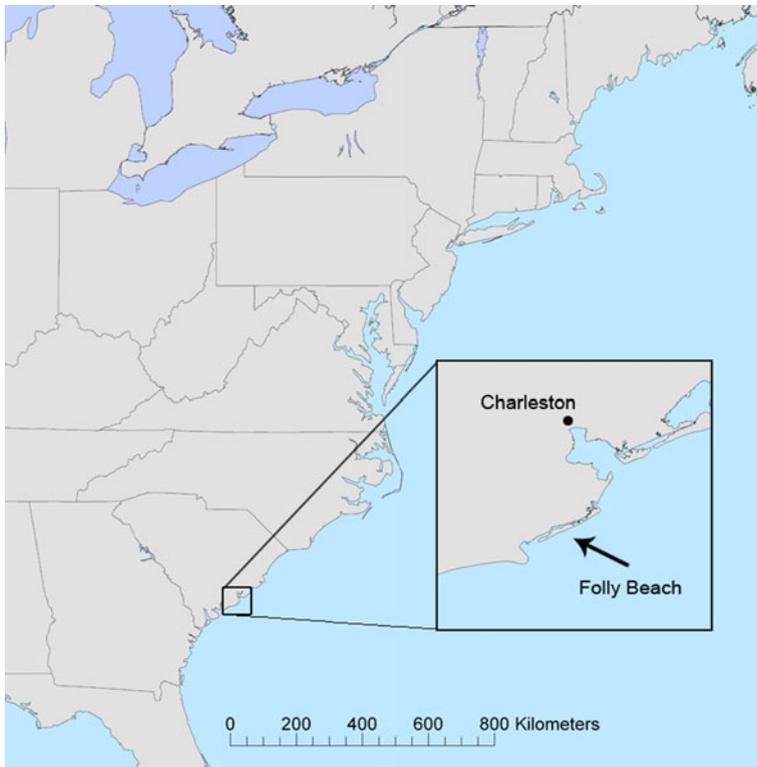


Fig. 1 Map of study site (Folly Beach) in coastal South Carolina, USA

taeda) and slash pine (*P. elliotii*). Typical shrubs and small trees include southern red cedar (*Juniperus virginiana* var. *silicicola*), cabbage palmetto (*Sabal palmetto*), Carolina laurelcherry (*Prunus caroliniana*), red bay (*Persea borbonia*), wax myrtle (*Morella cerifera*) and yaupon holly (*Ilex vomitoria*). The extreme northeast and southwest portions of the island are undeveloped and are under public property management. On the northeast end of the island is Lighthouse Inlet Heritage Preserve (~13.5 hectares composed of maritime forest, maritime shrub thicket and maritime grassland), which is managed by the South Carolina Department of Natural Resources and the Charleston County Parks and Recreation Commission. Folly Beach County Park incorporates the southwest end of the island and includes ~3.5 hectares of maritime forest, maritime shrub thicket and maritime grassland. These natural areas, and to a lesser extent developed portions of the island, support a variety of native fall-blooming monarch nectar sources, including seaside goldenrod (*Solidago sempervirens*), dune camphorweed (*Heterotheca subaxillaris*), beach blanket-flower (*Gaillardia pulchella* var. *drummondii*), spotted beebalm (*Monarda punctata*) and groundsel tree or eastern baccharis (*Baccharis halimifolia*). In addition, many non-native landscaping plants are included in developed portions of the island, including monarch nectar sources such as loquat (*Eriobotrya japonica*), thorny olive (*Elaeagnus pungens*), lantana (*Lantana camara*) and crimson bottlebrush (*Callistemon citrinus*). Some landscape plantings include the non-native

bloodflower or tropical milkweed (*Asclepias curassavica*) (milkweeds are the larval host plants of monarchs) which retains foliage capable of supporting monarch larvae throughout fall (JWM, *pers. obs.*).

Capturing and Processing Monarchs Unlike some other monarch migration projects along the Atlantic coast (Walton et al. 2005; Gibbs et al. 2006), this long-term project has no standardized censusing component. This project's primary goal is to capture and measure migrating monarchs throughout the migratory period as they pass through the study site. As such, there is no specific survey route, nor is the capture effort standardized each year. The primary focus of tagging is to maximize the number of marked individuals in order to enhance the likelihood of recoveries and to characterize migration routes and destinations. Accordingly, JWM expended more effort in attempting to capture monarchs when the insects were most numerous or when expectation of captures was greatest. In general, beginning in August, JWM visited the site at least several times per week when time allowed. Attempts were generally made to capture monarchs opportunistically (using standard butterfly nets), but emphasis was also placed on attempting to capture butterflies displaying the broadest possible range of activities or behaviors. Importantly, after monarchs were captured, McCord recorded the behavior of the individual just prior to capture, as one of seven possible behavior categories. These were roosting, nectaring, flying, basking, resting, mating and ovipositing.

The sex of each captured monarch was noted, its forewing length recorded to the nearest millimeter, and the condition of its wings was subjectively scored on a 1–5 scale. In this system, 5 = excellent condition, no, or practically no, wear or damage; 4 = minimal damage/wear that presumably causes little immediate reduction in flying efficiency; 3 = moderate, damage significant enough to likely cause some reduction in flying efficiency; 2 = significant damage (often one wing-tip missing), causing labored flight; and 1 = major damage, flight extremely labored (usually with portion of both forewing tips missing and often with hindwing damage as well). Note that this scale is opposite that of the sometimes-used MonarchLab 'wing wear' scoring system, where 5 = the highest level of wing wear and 1 the lowest (MonarchLab Website 2008). Furthermore, this method incorporates both wing wear and wing damage into one scale. Finally, each captured monarch was tagged with a numbered MonarchWatch tag on its hindwing (Fig. 2), so that it could be tracked by personnel at MonarchWatch, who report recoveries of tagged monarchs at the Mexican overwintering site or elsewhere (MonarchWatch 2008).

Data Analyses To allow ease of interpretation and analyses, the dates of capture were grouped into eight two-week time periods throughout the fall, starting in late August and ending in late December. With these groupings we examined seasonal variation in wing lengths using ANOVA, where time period was a categorical explanatory variable. Sex was also included in this model to account for the larger size of male monarchs (Borland et al. 2004; Altizer and Davis 2010). This same design was used to examine seasonal variation in wing condition scores, which we treated as a continuous variable. Thus, time period and sex were explanatory variables in this model, and here, wing length was included as a continuous covariate. We also used ANOVA to examine wing size variation across behavior

Fig. 2 Photo of a monarch butterfly that has been marked with a uniquely numbered MonarchWatch tag (www.monarchwatch.org)



categories (with sex included), and to examine wing condition across behavior categories (with sex and wing length included). Since few monarchs were captured in one of the behavior categories (oviposition), this category was excluded from these analyses. All analyses in this study were conducted using Statistica 6.1 software (Statistica 2003) and in all cases, significance was accepted when $p < 0.05$.

Results

General From 1996 to 2008 (13 years), a total of 12,821 monarchs were captured and tagged at Folly Beach (Table 1). Of these, only 3 (0.023%) were subsequently recovered at the Mexican overwintering sites. The majority of monarchs (nearly 50%) were captured in the final half of October, and another 34% were captured in the first 2 weeks of November. Collectively then, nearly 84% of monarchs were captured between October 15 and November 14 at this site. Interestingly, monarchs were still being captured in December. By mid-October, monarchs in the central flyway of North America have already begun arriving at Mexican overwintering sites. There was also a decidedly male-bias to the captures, with 34% being female overall, and with males outnumbering females in most two-week time periods by nearly 3 to 1 (Table 1). The exception to this was during the first 2 weeks of October, when the sex ratio was close to 1 to 1. In addition, there were multiple observations of both mating and oviposition at this site throughout the fall migration (Table 1). Overall, 2.4% of all monarchs were captured while mating, with the highest percentage being in the initial time period (before August 31). Meanwhile, the number of monarchs captured while ovipositing, although only a small fraction of the total numbers captured (<1%), pointed to two periods of oviposition activity at this site, one in the early phase of migration (August through September), and the other in late November and December.

Seasonal Variation in Wing Length and Condition As has been shown in other investigations (Altizer and Davis 2010), wing lengths of males captured at Folly

Table 1 Summary of fall monarch captures at the migratory stopover site in coastal South Carolina from 1996 to 2008

Time Period	Date Range	% Females	% Mating	% Ovipositing	Total Captured*
1	<Aug 31	25.9	11.1	1.8	54 (0.4%)
2	Sept 1–Sept 14	16.7	0.0	1.0	96 (0.7%)
3	Sept 15–Sept 30	35.8	0.0	4.5	67 (0.5%)
4	Oct 1–Oct 14	49.1	4.2	0.0	617 (4.8%)
5	Oct 15–Oct 31	36.3	2.4	0.0	6,262 (48.8%)
6	Nov 1–Nov 14	32.2	2.4	<0.1	4,352 (33.9%)
7	Nov 15–Nov 30	32.9	1.4	0.4	1,120 (8.7%)
8	Dec 1–Dec 31	36.8	0.8	0.8	253 (2.0%)
Combined		35.1	2.4	0.1	12,821

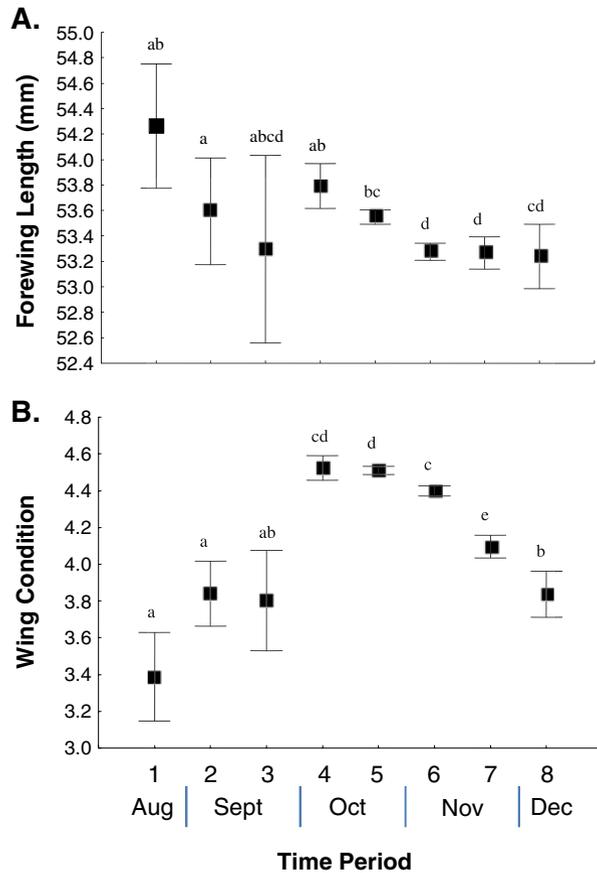
*Percentages in parentheses in this column reflect the relative number of individuals captured in this time period out of the total ($n=12,821$)

Beach were significantly larger than females ($F_{1,12567}=163.5$, $p<0.0001$). However, there was also significant variation in mean wing lengths across time periods ($F_{7,12567}=14.3$, $p<0.0001$). Tukey's post-hoc tests indicated that monarchs captured early in the migration tended to have larger wings than those captured in later periods (Fig. 3a). The ANOVA examining wing condition showed effects of sex ($F_{1,12566}=56.2$, $p<0.0001$), forewing length ($F_{1,12566}=6.9$, $p=0.009$) and time period ($F_{7,12566}=74.1$, $p<0.0001$). Although the effect of sex was significant, the actual differences in wing condition score between males and females was negligible (females=4.49, males=4.35). Similarly, the significant relationship between wing condition and length was not strong; both variables were only weakly positively related ($r=0.017$, $p=0.058$). Wing condition scores showed an approximate bell-shaped pattern when compared across time periods (Fig. 3b). Tukey's post-hoc tests showed that monarchs in the early part of the season had low wing condition scores, monarchs captured in October had the highest scores (wings were freshest and least worn), and condition scores dropped at the end of the migration.

Behavior Categories The vast majority of monarchs (80%) were captured while they were nectaring on flowering herbs and shrubs (Table 2). A further 10% were captured while roosting, which was often observed on eastern baccharis or red bay (Fig. 4). The remaining 10% of captures were spread across the five other behavior categories, including 306 monarchs (2.4% of total) that were captured while mating and 13 females that were captured while ovipositing (all on the non-native *Asclepias curassavica* plants at the site). The sex ratios of behavior categories were male-biased in all cases (by nearly 3 to 1) except the mating category, which was 50–50, as would be expected.

Wing Length and Condition Across Behavior Categories In the ANOVA examining wing lengths across behavior categories (roosting, nectaring, flying, resting, basking and mating), sex was again significant ($F_{1,12556}=147.5$, $p<0.0001$), and there was significant variation across behaviors ($F_{5,12556}=4.5$, $p=0.0004$), although the pattern

Fig. 3 Seasonal variation in wing lengths (a) and wing condition scores (b) of monarchs captured from 1997 to 2008 at the study site ($n=12,821$). Error bars represent 95% confidence intervals. Letters above error bars denote homogeneous groups based on Tukey's post-hoc tests at the level of $p<0.05$. Wing condition scores were such that a score of 5 represented perfect condition and 1 represented extremely poor condition



of this variation was not immediately clear. Basking monarchs appeared to have the largest wing sizes (Fig. 5a), although post-hoc comparisons showed these were not significantly different than those in three other categories. The analysis of wing condition across behavior categories was more easily interpretable. After accounting

Table 2 Number of male and female monarchs captured, organized by the type of behavior during capture

Behavior	% Females	Total Captured
Nectaring	35.2	10,356 (80.7%)
Roosting	34.6	1,309 (10.2%)
Basking	22.7	458 (3.6%)
Mating	51.0	306 (2.4%)
Flight	33.8	302 (2.6%)
Resting	29.9	77 (0.6%)
Ovipositing	100.0	13 (0.1%)
Combined	35.1	12,821

Fig. 4 Photo of monarchs roosting (on red bay, *Persea borbonia*) at Folly Beach, SC



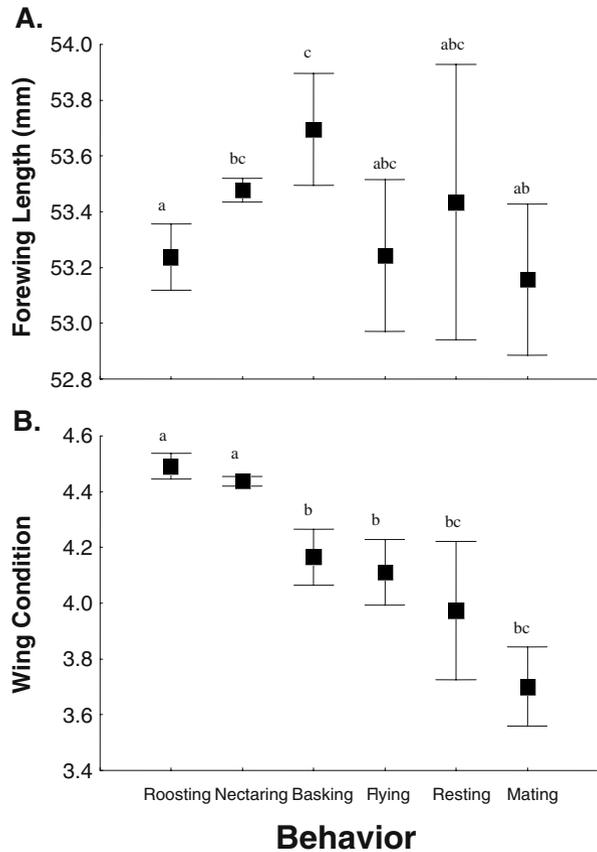
for the effect of sex ($F_{1,12555}=77.5$, $p<0.0001$) and forewing length ($F_{1,12555}=6.9$, $p=0.009$), there was significant variation in wing condition across behavior categories ($F_{5,12555}=53.1$, $p<0.0001$). Monarchs captured while roosting and nectaring had significantly higher wing condition scores than all other monarchs (Fig. 5b). Meanwhile, mating monarchs had the lowest wing condition scores.

Overwintering Monarchs While these were not included in the formal analyses in this paper, there were additional monarchs captured at this site after December, which suggest they were overwintering in the local area. Over the 13 years of this study, a total of 94 monarchs were captured between January 1 and March 15. The principal author has also observed many worn and tattered monarchs moving generally northward along the South Carolina coastal area in March and April. Bloodflower (*Asclepias curassavica*) typically remains dormant or in a winter-suppressed growth stage during spring in the South Carolina coastal region and accordingly is not widely available for monarch oviposition during these months. However, JWM has made numerous observations of monarchs ovipositing on swallow-wort (*Seutera angustifolia*) in transitional upland habitats adjacent to tidal saltmarsh within the central South Carolina coastal zone. Since the overwintering cohort from Mexico is usually just arriving in central Texas (30°N latitude) by the middle of March (Howard and Davis 2004), it is very unlikely that any monarchs present in South Carolina before, or even within a week after, mid-March could have come from the cohort that overwinters in Mexico.

Discussion

The data and observations from this long-term tagging project add to a growing body of evidence that monarchs migrating along the eastern coast of the United

Fig. 5 Average wing lengths (a) and wing condition scores (b) of monarchs from each behavior category (except the ‘ovipositing’ category, which only had 13 females). Error bars represent 95% confidence intervals. Letters above error bars denote homogeneous groups based on Tukey’s post-hoc tests at the level of $p < 0.05$. Wing condition scores were such that a score of 5 represented perfect condition and 1 represented extremely poor condition



States represent a distinct subset of the eastern migratory population. First, the relative number of tagged monarchs from this coastal South Carolina site that were recovered in Mexico was extremely minute (0.023%). This is compared to similarly-low recovery rates of 0.0093% for Cape May, New Jersey (R. Walton, *pers. comm.*) and 0.045% for the Eastern Shore of Virginia (Garland and Davis 2002). Meanwhile, the overall recovery rate for all MonarchWatch tags is approximately 1.25% (Taylor, cited in Brindza et al. 2008). Thus, monarchs migrating on the coast of South Carolina have a Mexico recovery rate that is 50 times less than the norm. Second, the overall length of the migration season at this site (late August to the end of December, or ~15–16 weeks) was much longer than that for migrants in the Midwest. The fall migration of the overall eastern population typically lasts 13 weeks, based on the timing of roost formation throughout the migration flyways from start to finish (Howard and Davis 2009). However, at this site monarchs continued to fly through (and be captured) in November and December, well after most monarchs have arrived at the Mexican overwintering site (WWF, *unpubl data*). Furthermore, a non-trivial number of monarchs were captured in the winter months. The overall impression presented by these observations is that of a long and drawn-out migration through this area, with a few monarchs even choosing to stay for the winter. This idea would be consistent with recent evidence showing that the

migration in the east coast flyway lags behind the central flyway in timing (Howard and Davis 2009).

Monarchs in the late phase of the migration tended to be smaller than those in the early and middle phases (Fig. 3a). This is consistent with prior field studies of migratory monarchs (Herman 1988; Gibo and McCurdy 1993). The reason for this trend could be that later-migrating monarchs are composed of individuals that experienced suboptimal conditions during late development, and/or cut short their larval development time, resulting in smaller body sizes as adults. Meanwhile, the seasonal variation in wing *condition* of monarchs showed a bell-shaped curve (Fig. 3b). Monarchs had the most worn wings in late August, the freshest wings in the middle portion of the migration (October), then there was a steady decline through November and December. Wing condition has been considered a proxy for age in other butterflies (e.g. Beck 2008), and if that is the case with monarchs, then this trend is more easily interpreted. The collections made at the beginning of the season may have contained some older adults that carried over from the breeding season. At least some of these insects may have originated at more inland areas of South Carolina or other areas of the Southeast and moved to coastal areas during a gradual southerly drift. Then, the shift toward very fresh wings in October may signify a new cohort of monarchs entering the migratory population, most of which undoubtedly originated well north of South Carolina but likely also includes some insects produced in the Southeast and even locally. Assuming there are no more generations after this one, this cohort then ages, and the wing condition scores throughout November and December reflect this ageing.

While only 2.4% of all monarchs captured were mating, this number likely underestimates the true proportion since mating pairs are often concealed or perched well above ground where netting is unlikely and because mating pairs tend to be rather wary and quick to seek better cover (WM, *pers. obs.*). This number is also much less than the 17% of monarchs that were estimated to have mated in collections of Texas migrants (Borland et al. 2004). It is also less than the observations of Knight and Brower (2009), who witnessed mating pairs in 29–38% of migrants along the northern Gulf coast of Florida. Nevertheless, these observations further emphasize the notion that not all migratory monarchs are in reproductive diapause, at least in the southern states.

A small number of females (13) were captured when ovipositing on the *A. curassavica* plants that are present at or near the site. This non-native *Asclepias* species is often planted for esthetic reasons in backyard gardens, and it readily attracts monarchs. However, its leaves do not die back at the end of the summer as do most native milkweed species. Because of this, there is growing concern among monarch researchers that when migrating monarchs encounter such plants in the fall, they may break diapause and lay eggs on them, which is what was observed here. This phenomenon actually occurs each year in south Florida, where arriving fall migrants from the eastern population break diapause when they encounter the warm conditions and continuously-available hostplants in south Florida (Knight and Brower 2009).

Another negative consequence of the tropical milkweeds is that spores of the monarch-specific parasite *Ophryocystis elektroscirrha* can build up on their leaves over time and then more readily spread infections to any larvae on them (Altizer et

al. 2004). This has been shown to be the reason why the non-migratory south Florida monarch population is heavily infected (over 80% of monarchs are infected) with the parasite (Altizer et al. 2000). Thus, while the number of monarchs observed ovipositing in this study relative to the total number captured appears small, this issue is clearly not trivial. Further work must be done to understand what becomes of monarchs that oviposit on these plants in the fall, and also what becomes of their progeny.

Besides the mating and oviposition, the other behaviors of monarchs at capture, and associated wing measurements of the monarchs, provide several new insights into the nature of monarch stopover ecology. For example, the fact that roosting and nectaring monarchs had fresher, less worn wings than all other monarchs, including those captured while flying (Fig. 5b) is extremely interesting. If we again assume wing condition is a proxy for age (e.g. Beck 2008), this may indicate that roosting and nectaring monarchs are younger than all others. The nectaring vs. flying difference might make sense if one considers that freshly emerged monarchs (with minimal fat reserves) would be more likely to seek nectar sources. And if flying monarchs are older, they presumably would have had time to build their fat reserves, and may not require nectar sources. It would be interesting in the future to compare wet masses of each of these groups, which can be done in the field (Brindza et al. 2008). The reasons why the roosting monarchs have fresher (in fact the freshest) wings than other categories are not clear. It may be that younger monarchs are more likely to congregate with other monarchs. Alternatively, monarchs that form roosts may be less likely to engage in behaviors that cause wing damage. Brower et al. (2006) provided evidence that roosting monarchs tend to have better lipid stores than monarchs collected while nectaring, suggesting that roosting monarchs already have adequate fat stores. Collectively, these results might indicate that roosting monarchs represent a non-random (perhaps superior?) subset of the migratory population.

The sex ratios of monarchs engaging in each behavior were male biased by nearly 3 to 1, except for the mating category (Table 2), which was 1-1, as would be expected if whenever a mating pair was netted, one male and one female would be captured (although in relatively few instances one partner did escape capture). The overall percentage of females captured at this site (35.1%) is comparable to that found recently in coastal Virginia, where 37.5% of monarchs were females (Brindza et al. 2008). Importantly, roosting monarchs at the South Carolina site did not have an appreciably different sex ratio than monarchs captured flying or nectaring. If one assumes that roosting monarchs, which are usually immobile and reluctant to fly when approached, are the truest representation of the sex ratio of the population, then these data show that there is no sex-related bias in nectaring monarchs (i.e. males do not nectar more so than females), which make up the majority of most monarch collections. Thus, it is likely that there really are fewer female monarchs than males in the migratory population, and the recent discovery of declining female monarchs in the migratory generation (Davis and Rendon-Salinas 2010) appears to not be caused by any capture bias towards males.

In a more general sense, given the location of this site in coastal South Carolina, the large number of monarchs captured each year engenders many questions about their ultimate destination. At least three monarchs tagged here were later recovered at the Mexican overwintering sites. However, five monarchs tagged at Folly Beach

have also been recaptured in Florida (WM, *unpubl. data*). How reflective these recapture rates are of the relative number of monarchs that fly toward Florida versus Mexico from the South Carolina coast is not known. However, if one considers the timing of the main passage of migrants through Folly Beach (84% were captured between Oct 15 and Nov. 14), one cannot help but wonder how *any* monarchs from here would end up at the Mexico sites. Most monarchs begin arriving at those sites in early November (Calvert and Brower 1986), and any monarchs that are passing through Folly Beach still have at least 2,500 km left in their journey (the overland distance from Folly Beach to the Mexican overwintering sites). Since three tagged monarchs were recovered at those sites, it is clearly possible that monarchs *can* successfully traverse this distance in this time frame, although the extremely low tag recovery rate in Mexico indicates that few actually succeed. Future examinations of tagging and recovery data from similar coastal versus inland locations, especially in the southeastern United States, may help to clarify this issue.

Finally, aside from the many biological insights garnered by this massive data set, this study serves as an example of how much can be learned from monarch tagging activities, provided good records are kept and a few extra measurements made on each butterfly. Currently there are hundreds of people who tag thousands of monarchs each year but yet do little more than ‘tag and release’ with minimal data collection. From those activities, the most that can be gleaned from those data are recovery rates in Mexico or elsewhere. As this paper shows, if additional data is collected when the butterflies are in hand, the scientific value of the tagging data are considerably enhanced. We hope that this paper encourages other monarch taggers to consider the practice not as a hobby, but as a scientific endeavor.

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