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# Variation in wing characteristics of monarch butterflies during migration: Earlier migrants have redder and more elongated wings

**Abstract:** The migration of monarch butterflies (*Danaus plexippus*) in North America has a number of parallels with long-distance bird migration, including the fact that migratory populations of monarchs have larger and more elongated forewings than residents. These characteristics likely serve to optimize flight performance in monarchs, as they also do with birds. A question that has rarely been addressed thus far in birds or monarchs is if and how wing characteristics vary within a migration season. Individuals with superior flight performance should migrate quickly, and/or with minimal stopovers, and these individuals should be at the forefront of the migratory cohort. Conversely, individuals with poor flight performance and/or low endurance would be more likely to fall behind, and these would comprise the latest migrants. Here we examined how the wing morphology of migrating monarchs varies to determine if wing characteristics of early migrants differ from late migrants. We measured forewing area, elongation (length/width), and redness, which has been shown to predict flight endurance in monarchs. Based on a collection of 75 monarchs made one entire season (fall 2010), results showed that the earliest migrants ( $n = 20$ ) in this cohort had significantly redder and more elongated forewings than the latest migrants ( $n = 17$ ). There was also a non-significant tendency for early migrants to have larger forewing areas. These results suggest that the pace of migration in monarchs is at least partly dependent on the properties of their wings. Moreover, these data also raise a number of questions about the ultimate fate of monarchs that fall behind.

**Keywords:** Monarch butterfly, *Danaus plexippus*, migration, wing morphology, wing color

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## 1 Introduction

The success of any animal migration depends heavily on the timing and pace of the journey. Slower migration would prolong exposure to the inherent dangers of the journey, ultimately leading to a lower chance of survival. By extension, those animals that migrate early (or faster) should be more likely to survive the journey. Furthermore, these animals should also have characteristics better suited for long-distance (or more efficient) flight, compared to late-migrating individuals, although this idea has rarely been examined, and thus far only in migratory birds [1,2]. One study of Dark-eyed Juncos (*Junco hyemalis*) showed significant variation in wing shape over the course of a migration although this was attributed to differential timing of age classes [3]. Other work showed early-migrating Swainson's Thrushes (*Catharus ustulatus*) tended to have more pointed wings [1], consistent with the idea that early- or fast-migrating individuals have optimal wing characteristics for flight. With birds, longer and more pointed wings have been shown to be an adaptation for optimal energy expenditure during long-distance flight [4-6]. Further, comparisons of migratory and non-migratory bird populations also reveal these differences in wing shape (i.e. migratory populations have longer wings [7-10]), which further demonstrates the importance of optimal wing characteristics for long-distance flight.

In this study we examined the relationship between wing characteristics and migration timing for the first time in a migratory insect, the monarch butterfly (*Danaus plexippus*, Fig. 1). There are a number of parallels between the monarch migration and that of birds. Monarchs in North America undergo an annual long-distance journey and in large numbers; every fall, millions of monarchs fly from breeding sites in Canada and the northern United States to overwintering sites in Central Mexico (a 3000+ km journey). This famous migration is inherently risky, as monarchs must pass a gauntlet of water barriers, severe storms and roadways [11,12], all while finding enough

nectar to power their flight and build fat reserves for winter survival [13]. As with birds, this annual migration appears to select for specific wing traits that confer aerodynamic advantages in flight: monarchs from migratory populations tend to have larger and more elongated wings than those from non-migratory populations [14,15].

One feature of monarch migration that differs from birds is the unusual association between wing pigmentation and flight propensity in this species. Recent work indicated migratory monarchs in the fall tend to be redder than non-migratory generations [16], and that wing redness is positively associated with flight endurance in captive settings [17]. Other work also demonstrated that wing color (forewing saturation) is associated with migratory distance in spring-migrating monarchs [18]. While the underlying mechanism for all of these studies remains unknown (wing pigmentation may simply be a correlate of individual quality), it is clear that the shade of orange on monarch wings is a predictor of flight ability, and thus should be included in analyses of flight performance.

If wing characteristics are important for migration success for monarchs, we postulated that monarchs migrating early in the migration would have greater wing area, more elongated forewings, and have redder wings compared to late-migrating monarchs. These individuals should have wing features that would allow for fast flight and/or would require minimal stopovers (they would have greater endurance), and because of this, these individuals should maintain a fast migratory pace. Therefore, these monarchs would tend to comprise the earliest migrants.

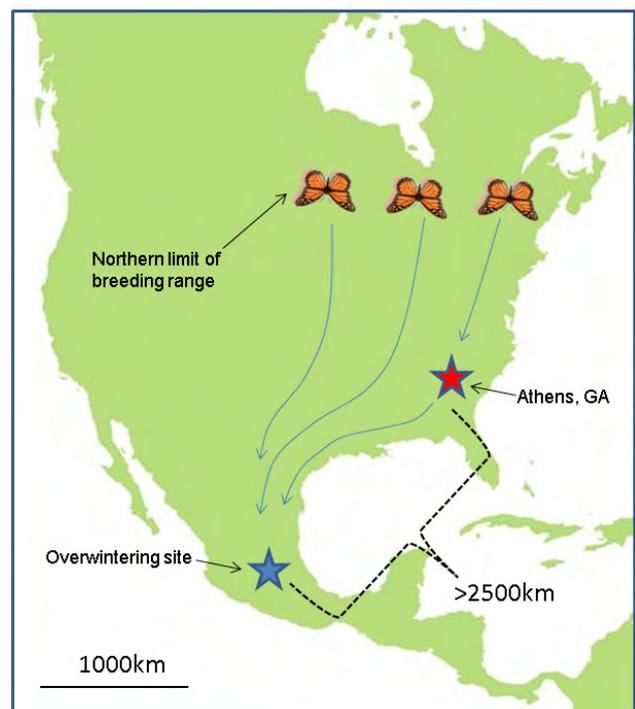


**Figure 1:** Male monarch butterfly, *Danaus plexippus*, photographed by A. Davis. Dashed lines indicate forewing length and width measurements (obtained from digital scans of monarch wings), which are used to calculate aspect ratio. Solid white arrow points to central wing cell where orange color was measured.

In contrast, those monarchs with smaller, less elongated and paler wings would eventually fall behind and would be more likely to be observed late in the migratory season. To test this idea, we captured fall-migrating monarchs across an entire fall migration season and examined wing characteristics in detail to obtain precise measures of forewing size, shape and color throughout the season.

## 2 Methods

*Capturing monarchs.*- We captured migrating monarchs using hand-held insect nets at 6 sites in Athens, GA, USA (33.96°N, 83.37°W; Fig. 2) from late September through mid-November (2010), when the main pulse of migratory monarchs tends to pass through northern Georgia (Davis, *pers. obs.*). This location is approximately midway along the migration journey to the overwintering site in central Mexico (Fig. 2). Following capture, each monarch was examined to determine sex and the level of wing wear, which represents the degree of scale loss across wings based on a 1-5 ordinal scale. We also determined the level of infection with the protozoan parasite *Ophryocystis elektroscirrha* in each monarch using methods outlined in



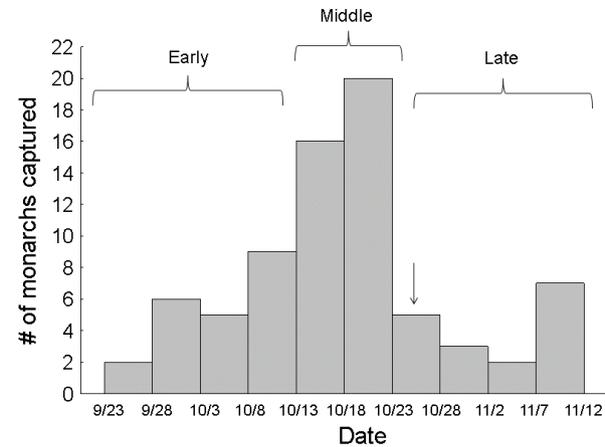
**Figure 2:** Generalized map of the migration route of monarchs in eastern North America, showing location of the study site in Athens, GA (red star) and the location of the monarch overwintering site in Mexico (blue star). The overland distance from Athens to the overwintering site is over 2500 km.

Altizer et al. [15]. Infection with this pathogen has been shown to reduce flight performance in a previous study [20]. All monarchs were frozen at -12°C after processing.

**Measuring wings.**— At the end of the season all monarch specimens were thawed and their left and right forewings were removed and scanned with a flatbed scanner at 300 dpi with no image correction. We used image analysis software to measure the area, length, width and hue of each forewing (see Fig. 1). Wing aspect ratio was calculated as wing length/width [16]. Wing hue, an index of the degree of redness, was obtained as the average pixel hue score of the central cell of each wing [17,18,21]. For monarchs, this method produces values ranging from 20-40 degrees (with redder being lower), which is equivalent to measures of hue using a spectrophotometer between 580- 780 nm [18]. For each specimen, the average of right and left forewing measurements was used for further analyses.

**Migration timing groups.**— Monarchs were assigned to one of three groups based on capture date: early (Sept. 28-Oct. 11), middle (Oct. 12-Oct. 25) and late (Oct. 26-Nov. 10). These divisions were chosen based on the observed frequency of captures over time (i.e. so that the middle group overlapped with the peak of migration, see results). Moreover, these cutoff dates resulted in each

group representing a time span of approximately two weeks. Similar groupings (but with different start and end dates) have been used in previous investigations into monarch butterfly migration [13,22] and are effective at differentiating distinct cohorts of migrants.



**Figure 3:** Frequency distribution of monarch captures during fall 2010 in Athens, GA. Monarchs were assigned as early, middle or late migrants based on the date of capture. Note that the bars in this figure represent 5-day intervals and the cutoff date between the middle and late groups (Oct 26, shown with arrow) falls within one bar.

**Table 1:** Summary of ANOVA models examining factors associated with each forewing parameter. Migration timing (early, middle or late) was included as a continuous predictor variable to account for the ordinal nature of the categories. Models with main effects only are shown as none of the two-way interaction terms were significant in any model. Note that monarchs with moderate to severe wing fading (n = 13) were not included in analysis of wing color.

Response Variable	Predictor Variables	df	MS	F	p
<b>Forewing Area</b>	Sex	1	9964	1.93	0.1686
	Infection status	1	221	0.04	0.8364
	Migration timing	1	9523	1.85	0.1782
	Error	71	5151		
	Total	74			
<b>Forewing Elongation (Aspect Ratio)</b>	Sex	1	0.005	2.51	0.1179
	Infection status	1	0.000	0.15	0.6952
	Migration timing	1	0.012	6.36	0.0139
	Error	71	0.002		
	Total	74			
<b>Forewing Redness (Hue Score)</b>	Sex	1	134.11	26.64	0.0000
	Infection status	1	0.30	0.06	0.8089
	Migration timing	1	20.05	3.98	0.0507
	Error	58	5.04		
	Total	61			

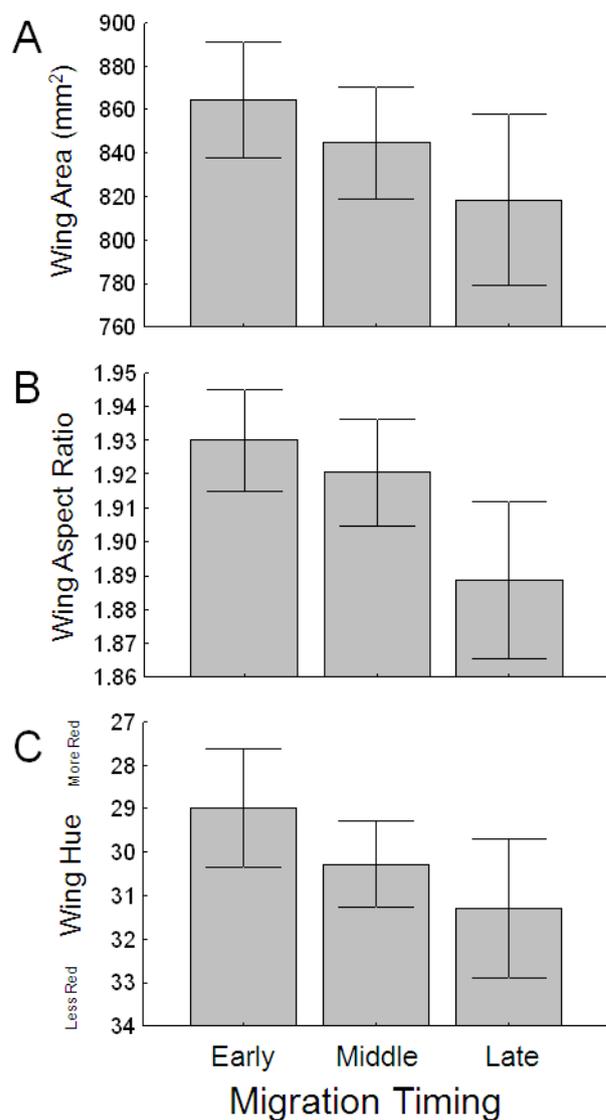
**Data analysis.**— We used analysis-of-variance to separately assess if the three monarch wing variables (wing area, aspect ratio and hue) differed between males and females (sex); between infected or uninfected monarchs (infection with OE); and across migration timing groups (early, middle and late migrants). We included migration timing as a continuous predictor to account for the ordinal nature of these groups. Two-way interaction terms for all predictors were included in the starting models but removed if their effect was not significant. For analyses of wing hue, we did not include monarchs with moderate to severe wing scale loss (i.e., with a wing wear score  $\geq 3$ ), as this can affect color measurements (Davis, *unpubl. data*). All variables were normally-distributed. All analyses were done using the Statistica 6.1 software package [23].

### 3 Results

A total of 75 monarchs were captured and measured across the entire fall sampling period (51 males, 24 females), with the most monarchs captured during the middle of the migration season (Fig. 3). The final sample sizes for the early, middle and late groups were 20, 38 and 17 monarchs. Wing area did not significantly differ between males and females, with infection status, or across migration timing groups (Table 1). However, visual inspection of wing area for early, middle and late migrants did show a gradual decline over time (Fig. 4A). Wing aspect ratio differed significantly among migration timing groups ( $p = 0.0139$ , Table 1), with the earliest migrants tending to have the most elongated forewings (Fig. 4B). Neither sex nor OE infection status were significant predictors of wing aspect ratio (Table 1). Wing hue also differed significantly among migrating timing groups ( $p = 0.0507$ , Table 1), with the earliest monarchs showing redder or more orange wings (lower hue score; Fig. 4C). Male monarchs also tended to be redder than females ( $p < 0.0001$ ), consistent with previous findings [18]. Wing hue did not differ between infected and uninfected monarchs (Table 1).

### 4 Discussion

Results from this study demonstrated that wing characteristics of migrating monarch butterflies differ within the migration season; early-migrants tend to have more elongated and redder forewings. We interpret this to mean that these wing characteristics provide the most efficient flight performance, leading to an overall faster migration pace in the early migrants. This idea would be consistent with prior work showing that redness



**Figure 4:** Variation in forewing morphology measures across migration timing groups. Sample sizes for groups in A and B were 20, 38 and 17 (for early, middle and late, respectively), and for C were 15, 34 and 13.

predicts flight distance and endurance in monarchs [18,19]. Because of their higher endurance, the reddest individuals may not require frequent or lengthy stopovers to rest or refuel, giving them an advantage in terms of migration pace. By extension, it also makes sense that less red individuals would fall behind in the migratory journey if they were forced to rest more frequently (because of poorer flight performance or reduced endurance). Such individuals may also be less efficient foragers during migratory stopovers, and may remain longer per given stopover, leading to a slower overall migratory pace. These results are also consistent with other work on

migrating monarchs that showed the earliest migrants tend to have more robust immune condition than the latest migrants [24]. Combined, these studies all lead to the same conclusion; that the earliest monarch migrants tend to be the highest-quality individuals.

There are two alternative explanations for the temporal patterns we observed in wing characteristics. The first is that late-migrating monarchs could show differences in wing characteristics simply because they emerged from their pupal stage late in the season. This could occur if their eggs had been laid late in the season, or if cooler temperatures late in the growing season prolonged their larval development. This idea seems plausible, since any monarch larvae grown during such times may also experience food shortages, which could result in smaller adult size [25]. Unpublished data from a prior experiment may shed some light into this issue. As part of an earlier effort to uncover effects of larval rearing temperature on adult wing pigmentation [26], monarch larvae from eastern North America were reared at different temperatures until eclosion, and the wings of adults were examined using image analysis similar to the current study. Results showed monarchs reared in cool temperatures (19°C,  $n = 58$ ) had significantly larger forewings, and their hue scores were significantly lower (i.e. redder) than those reared at 26°C ( $n = 48$ ), based on Student's T-tests ( $p < 0.05$  for both). If rearing temperature can be considered a proxy for eclosion timing, then based on these data, any monarch that emerges late in the breeding season should actually be larger and more red than early-emerging monarchs, which is not consistent with what we observed. Thus, the patterns we observed in wing characteristics over time in migrating monarchs are likely not due to differences in eclosion timing.

The second explanation for the temporal patterns we found is that different cohorts in our collection (early, middle and late migrants) reflect varying distances travelled by each cohort. In other words, late migrants could have simply originated from further north than the early migrants. This explanation is not unreasonable, especially since other work with migratory birds has demonstrated this phenomenon occurs [27]. Unlike the prior idea above, we do not have information from this or other studies to disprove this possibility; nor do we know the distance any of the monarchs we captured had travelled by the time they arrived in Athens, GA. However, we believe this idea unlikely; if this were true, it would imply that monarchs originating from the most northern latitudes (which would be the latest migratory cohort in this scenario) tend to be small, less elongated and pale, which are all characteristics of poor flight performance

in this species. If anything, the most northerly monarchs (with the farthest to travel) should have the most well-adapted flight characteristics of any monarch population, as the demands of the long-distance travel should select for such traits over time. In fact, there is some evidence in support of this for monarchs; comparisons of forewing length between fall migrants in Minnesota and Texas in the same season showed northern monarchs were significantly larger [28].

While tangential to the original goals of this study, results concerning OE infection and wing characteristics merit comment. Infected monarchs did not show significant differences in wing area or wing aspect ratio compared to healthy monarchs—a finding that is consistent with a previous study examining wing morphology and OE infection [20]. Further, infected monarchs in our study also did not show differences in wing redness, which is thought to be a predictor of flight ability. In contrast, the previous study indicated that infected monarchs exhibit reduced flight performance, such as decreased flight speed and distance, compared to uninfected individuals [20]. Our results corroborate the conclusion put forth by Bradley and Altizer [20], that OE infection affects flight through physiological rather than morphological mechanisms, such that infected migrants suffer reduced flight performance due to, for example, desiccation, and not due to poorer wing quality.

We were surprised to find no statistically significant variation in forewing size across the migration season (Fig. 4A), especially in light of multiple prior studies that show how monarch wing lengths tend to decline during the fall [22,28,29]. The explanation may relate to methodological differences between these studies and ours. In all prior studies indicated, the forewing length of monarchs (measured with rulers or calipers) was used as the sole measure of wing size, and in no study was forewing shape considered. However, measuring forewing length alone may actually confound forewing size and shape, as two monarchs could have similar forewing lengths but considerably different forewing areas if forewing width varies. Thus, variation in forewing length observed over time could reflect a change in either forewing size or shape. In support of this, comparison of forewing length measurements with both forewing area and aspect ratio from our own data revealed positive (or near-positive) relationships with both ( $p = 0.024$ ,  $p = 0.081$ , respectively). For this reason we argue that it is more appropriate for researchers to use separate estimates of forewing area and aspect ratio to characterize both size and shape of butterfly wings, which should disentangle these two measures. Even still, the results of the prior studies using forewing

length are consistent with the current study; they suggest that late-migrating monarchs have either smaller or less elongated forewings.

The consequences of falling behind in the migration would not be favorable for monarchs. As a case in point, by our estimate any late-migrating monarchs from our site would be unlikely to complete the migration to Mexico. Our study site is approximately midway along the migration path (Fig. 2), assuming their ultimate destination is the historical overwintering sites in Central Mexico [30]. It is approximately 2539 km from Athens, GA to the northernmost overwintering site in Mexico (this was calculated as the overland distance from Athens, GA to the southwest Texas border in Laredo, TX and then from Laredo, TX straight south to the small town of Los Angeles in Michoacan, Mexico, which is close to the Cerro Altamirano overwintering site). The pace of migrating monarchs in the southern United States has recently been found to be approximately 42 km/day, based on hundreds of sightings of roosting monarchs over many years [31]. This is a rate that takes into account temporary stopovers and weather delays (and is not the same as the actual flight speed of monarchs). At this rate, it would take approximately 60 days to complete the journey to the wintering sites from Athens, GA. Therefore, the ‘early’ monarchs we captured would be arriving at the overwintering site between November 27 and December 10. This is consistent with the known arrival window for monarchs at the Mexico sites [30]. For ‘middle’ monarchs their arrival window would be between December 11 and December 24, and for ‘late’ monarchs they would be arriving (if at all) after December 25. Given that the overwintering colonies are thought to be fully formed (i.e. no new arrivals) by mid-December [30], it is logical to assume that most monarchs in the late group (and perhaps some from the middle group) at our site do not reach the overwintering sites.

If the above scenario is true for monarchs (late-migrating monarchs are unlikely to reach Mexico), then the question remains, what becomes of them? In the northern regions of their flyway, the answer is clear; they eventually succumb to advancing cold temperatures and storms [12]. However, if they fell behind anywhere near a Gulf-coast state, and could then reach a coastal location, they might be able to escape those harsh conditions. In fact, because of the mild climate along the Gulf coast and southern Atlantic coast (South Carolina, Georgia, Florida), such coastal locations are increasingly supporting local populations of continuously-breeding and/or overwintering adult monarchs [32]. It may be that these coastal populations are comprised in part from migrants

that were unable to complete the journey to Mexico. As a test of this, future efforts could examine if monarchs from these areas have wings that are smaller, less elongated and/or less red, which based on the current study and others [18], are all characteristics associated with poor migration success.

In summary, our study revealed a temporal pattern of wing characteristics in monarch butterflies during their fall migration; the earliest migrants tend to have more elongated forewings and are redder in color. They also tend to be larger in size. We interpret this pattern to be a reflection of the faster migration pace by this cohort, because of superior flight performance and/or high endurance. In contrast, those individuals with less optimal wing characteristics tended to make up the latest migrants, possibly because of poorer flight performance or lower endurance. These results add to a growing body of literature around the flight performance, migration behavior and wing morphology of monarch butterflies (e.g. [14,16,18-20]), a species for which migration is a critical stage of their life history.

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