USING GEOLOGGERS TO INVESTIGATE BIMODAL ISOTOPE PATTERNS IN PAINTED BUNTINGS (*PASSERINA CIRIS*)

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ABSTRACT.—Painted Buntings (*Passerina ciris*) that breed in Oklahoma and molt in Sinaloa, Mexico, demonstrate a clear bimodal pattern of stable isotope ratios in their flight feathers. Some birds had a C3 carbon signature in primary 1 (P1, the first feather replaced during wing molt) and a C4 carbon signature in primary 9 (P9, the last primary to molt), whereas other sympatric birds evinced a C4-based diet throughout feather molt. The bimodal pattern of stable isotope ratios in flight feathers suggests that some birds may initiate molt immediately upon arrival in northwestern Mexico (and carry a C3 signature with them from the breeding grounds) whereas others may delay molt (and grow feathers solely from C4 plants of Sinaloa). From 2010 to 2012, we used geologger tags to test whether differences in the timing and route of fall migration movements were related to stable isotope signatures in primary feathers. We analyzed stable isotopes of hydrogen and carbon in P1 and P9 from 25 individuals fitted with geologger tags in two consecutive years. Of these, 60% changed the diet (C3 vs. C4) that was used to grow P1 between years. We also observed variation among individuals in migration routes, wherein birds from the same breeding population differed greatly in their use of molting and wintering locations. However, we did not find a relationship between isotope signatures and the timing or route of fall migration. We speculate that the bimodal isotope signature we observed represents a carryover effect related to local landscapes (grassland or agriculture vs. shrubland) used during the late breeding season and early molting period, and that these effects diminish as molt progresses. If this is the case, there is the potential for breeding-season diet to directly affect plumage quality in this molt migrant. *Received 4 January 2013, accepted 19 March 2013.*

Key words: carryover effects, GeoLight, geolocator, geologger, migration, molt, Painted Bunting, *Passerina ciris*, stable isotope ratio, tripEstimation.

Utilizando Geologgers Para Investigar El Isótopo Bimodal Patrones En Pintado Empavesados (Passerina Ciris)

RESUMEN.—Placados empavesados (Passerina ciris) que se reproducen en Oklahoma y muda en Sinaloa, México, demuestran un patrón claro bimodal de las proporciones de isótopos estables en las plumas de vuelo. Algunas aves tenían una firma de carbono C3 en primaria 1 (P1, la primera pluma reemplazada durante la muda del ala) y una firma de carbono C4 en primaria 9 (P9, la última primaria mudar), mientras que otras aves simpátricas demostraron una dieta a base de C4 a lo largo de la muda de la pluma. El patrón bimodal de las proporciones de isótopos estables en plumas de vuelo sugiere que algunas aves pueden iniciar la muda inmediatamente a su llegada en noroeste de México (y llevar un C3 firma con ellos de los criaderos) mientras que otros pueden retrasar la muda (y crecen plumas únicamente de las plantas de C4 de Sinaloa). Entre 2010 y 2012, utilizamos etiquetas geologger para comprobar si estaban relacionadas con las diferencias en el momento y la vía de los movimientos de la migración de otoño estable firmas isotópicas en plumas primarias. Analizamos los isótopos estables de hidrógeno y carbono en P1 y P9 de 25 individuos provistos de etiquetas geologger en dos años consecutivos. De éstos, el 60% cambió la dieta (C3 y C4) que se utilizó para crecer P1 entre años. También observamos la variación entre individuos en rutas de migración, donde aves de la misma población de cría difieren considerablemente en su uso de muda y de invernada. Sin embargo, no se encontró una relación entre firmas isotópicas y el tiempo o la ruta de migración de otoño. Especulamos que la firma de isótopo bimodal observamos representa un efecto de arrastre relacionadas con paisajes locales (praderas o agricultura vs matorrales) utilizados durante la última época de cría y período de muda, y que estos efectos disminuyen como muda progresa. Si esto sucede, existe el potencial para la dieta de la época de cría para afectan directamente la calidad de plumaje en este migrante muda. Si esto sucede, existe el potencial para la dieta de la época de cría para afectan directamente la calidad de plumaje en este migrante muda.

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The Painted Bunting (*Passerina ciris*) is a Neotropical migrant with two geographically disjunct breeding areas in North America that differ markedly in their patterns of migration and molt (Fig. 1; Thompson 1991a). Individuals that breed in the southern Midwest of the United States are molt migrants, which means that they have prolonged stopover periods in late summer associated with feather replacement at locations distant from breeding and wintering areas (Thompson 1991b). These birds depart the breeding grounds in late July and, presumably, move westward to molt in northern Mexico before continuing to winter locations in southern Mexico or northern Central America (Rohwer et al. 2009a, b). Individuals from the eastern population molt on the breeding grounds along the Atlantic coast of the United States (Fig. 1) before migrating to wintering areas in southern Florida and the Caribbean in late September or October (Sykes et al. 2007). The existence of two fundamentally different migration strategies within a single species provides an opportunity to understand the life-history implications of migration and prompted us to examine variation in molt and migration behavior using stable isotope ratios in primary feathers and light-level geolocation tags (hereafter "geologgers").

One important element of migration and molt strategies is the ability of birds to track seasonal shifts in food availability (Stach et al. 2012; but for other taxa, also see Bischof et al. 2012,
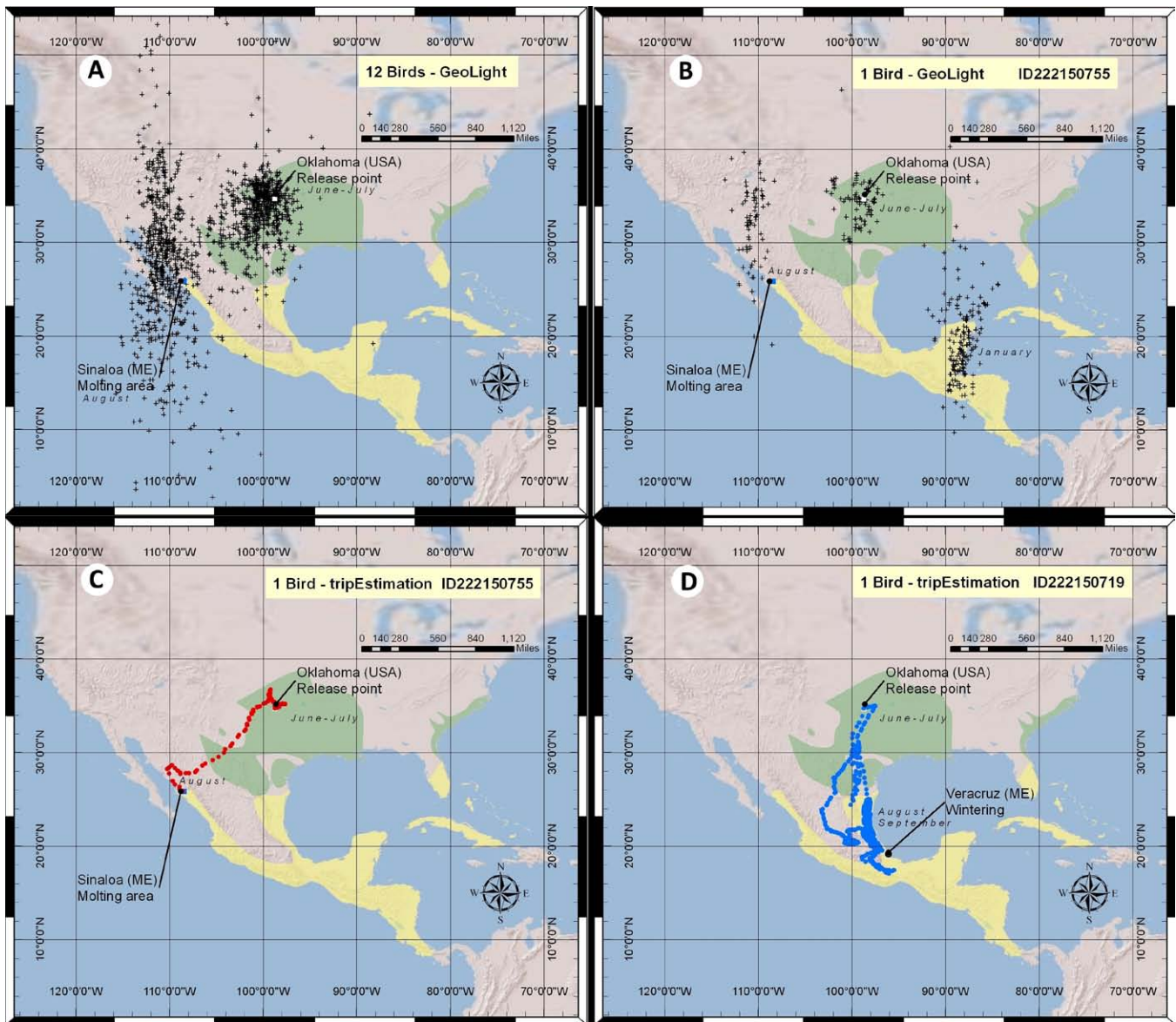

Fig. 1. Painted Bunting migration revealed by geologgers. Breeding and wintering grounds are highlighted in green and yellow, respectively. (A) Unfiltered data points for 12 birds are superimposed to show a clear westward movement and a shift in longitude (~10°) occurring at the end of July 2011. (B) Unfiltered data points for one bird migrating to the Yucatan peninsula in January 2012. (C) Migratory route for the same bird shown in panel B, but modeled for only the first part of the migration until August 2011. (D) Migratory route for one bird that migrated south, overwintered in Mexico, and returned to Oklahoma in spring 2012.

Fryxell and Avgar 2012). Focusing on a population of Painted Buntings breeding in Oklahoma, Bridge et al. (2011) found a bimodal distribution of carbon isotope ratios in primary flight feathers (P1 and P9) indicating a midmolt shift from a C3 diet (derived from C3 photosynthesis) to a C4 diet (derived from C4 photosynthesis). Such a pattern suggests that two groups of individuals in this population could have fundamentally different migratory routes, such that the two carbon signatures reflect two molting locations, one with C3 food resources and the other with C4 resources. To test this hypothesis, Bridge et al. (2011) examined carbon stable isotope ratios in newly grown feathers from birds in a single stopover molting area in Sinaloa, Mexico. Feathers at this location also had a bimodal carbon signature, which suggests that differences in molting locations are not necessary to explain the differences in diet (i.e., isotope ratios of feathers).

An alternative explanation for the bimodal pattern is that, depending on the timing and duration of migration, stable carbon isotope ratios of P1 can reflect the diet on the breeding ground, which in Oklahoma is dominated by C3 plants, or the diet at the molting location, which is dominated by C4 plants. Although the mechanism behind this relationship could take several forms, the most parsimonious explanation would be that early migrants arrive at the stopover region early and spend a week or more equilibrating with the local trophic web prior to molt, whereas late migrants begin molt immediately after arriving in the molting area, such that they grow their first primary using reserves that reflect isotope ratios from the breeding grounds. In this case, we would predict that the carbon isotope signature of P1 would be associated with the date of arrival on the molting grounds.

Here, we provide the first quantitative descriptions of the migration biology of individual Painted Buntings using data from custom-designed, low-cost geologgers. This is the smallest North American migrant tracked to date and among the first molt-migrant species to be tracked using geologgers. In particular, we used light data collected from individual Painted Buntings to estimate (1) the date of initiation of migration, (2) the number of days between initiation of migration and stopover for molt, (3) the date of arrival at the molting grounds, and (4) routes of migratory movements. We used these data to test the prediction that C3 carbon signatures in P1 occur more often in late migrants that, presumably, molt immediately after arrival on the molting grounds and that C4 carbon signatures are common in early migrants that may remain on the molting grounds for several days or weeks prior to molting. In addition, we measured stable isotope ratios in these birds' feathers in two consecutive years so that we could examine year-to-year consistency of isotope ratios in feathers, which is presumably related to consistency in diet and molting locations. On the basis of known distributions of Painted Buntings throughout the year (Lowther et al. 1999), we predicted that the migration route of birds from our study population in Oklahoma would involve a westward flight to northwestern Mexico to molt, followed by a southward movement and subsequent stationary period within the documented wintering range. If bimodal patterns in isotope values indeed arise from timing of molt, rather than differences in migratory pathways, we expected that all birds from our breeding population would follow similar migratory trajectories, but that the isotope ratios of the first primary would be related to the timing of migration.

Methods

Field site and tagging effort.—We studied a population of Painted Buntings that bred at the Wichita Mountains Wildlife Refuge (N34.4–W98.4), Oklahoma. This refuge is largely dominated by mixed prairie grasses (mostly C4 species) such as Little Bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), and Switchgrass (*Panicum virgatum*), but Painted Buntings are located primarily in patches of forest characterized by oaks (*Quercus* spp.) and Eastern Redcedar (*Juniperus virginiana*) that represent an important source of dietary C3 carbon (Eskew 1938, Martin et al. 1951, Askins 1993, Carter et al. 2008).

We deployed 120 geologgers on free-ranging male Painted Buntings during summer 2010 and 2011 (May–July) and released them shortly after capture. We used solar-powered geologgers of our own design that weighed 0.6 to 0.7 g (including harness material), representing ~4% of the body mass of this species. The geologgers measured light intensity every minute and recorded the average light measurement every 10 min on an arbitrary scale from zero to 127. We mounted the tags using leg-loop harnesses (Rappole and Tipton 1991) made of 0.7-mm elastic silicon beading thread (Stretch Magic brand; Pepperell Braiding, Pepperell, Massachusetts) that were presized (see Naef-Daenzer 2007) and assembled by heat welding (rather than tying) prior to deployment. We also tagged each bird with individually numbered federal bands and plastic color bands. Adult singing males were captured in 12-m mist nets close to nests or active territories using playback calls and decoy mounts.

To study the effect of migration timing on migration route, we deployed 80 additional geologgers (40 in 2010 and another 40 in 2011) on individuals captured in May of each year and assigned to a manipulative experiment, in which birds were held in captivity under different light regimes before being fitted and released with geologgers. This manipulative experiment was designed to accelerate or decelerate the annual cycle of the birds. Half of the birds belonged to an "early" group, which was released on 1 July of each year, and the other half belonged to a "late" group that was released on 1 August (for details, see supplemental material with the online version of this article). Recaptured birds with geologgers from year 1 were fitted with new geologgers in year 2 to enable us to document migratory behavior of single individuals in consecutive years. Thus, we deployed a total of 200 geologgers over the course of the study.

Stable isotopes.—The stable isotope signatures of primary feathers reflect nutrient deposition into keratin tissue at the beginning and end of the molting period. Thus, we measured stable isotope ratios in the innermost primary (P1, first to be molted) and the outermost primary (P9, last to be molted) collected from the right wing upon each recapture event in summer 2011 and 2012. We analyzed the $^{13}C/^{12}C$ ratio ($\delta^{13}C$) and deuterium/hydrogen ratio (δD) at the University of Oklahoma following the laboratory procedures detailed in previous publications (Kelly et al. 2009, Paritte and Kelly 2009, Bridge et al. 2011). We report our results in delta notation in relation to PeeDee Belemnite for $\delta^{13}C$ and in relation to Standard Mean Ocean Water for δD (Craig 1957, 1961). We used generalized linear models to test for correlation between variables and, in particular, the association between $\delta^{13}C$ signature in P1 molted in 2011 and three explanatory variables:

(1) departure dates from the breeding ground in Oklahoma, (2) arrival dates at the molting sites in northwestern Mexico, and (3) duration of migration from Oklahoma to the molting grounds in days. All statistical analyses were performed using XLSTAT. We considered feathers with $\delta^{13}C$ values greater than –18‰ to be primarily C4 in origin, based on Bridge et al. (2011), and feathers with δD values greater than –65‰ to be of potential Mexican origin, based on our interpretation of δD distribution proposed by Hobson et al. (2009).

Light-level geolocation.—To derive location estimates from raw light-level data, we employed the threshold method implemented in the R package GeoLight (R Development Core Team 2005, Lisovski and Hahn 2012). For purposes of illustration, we also conducted an exploratory analysis to estimate migratory routes using the curve-fitting method implemented in the R package tripEstimation (Sumner et al. 2009, Sumner and Wotherspoon 2010).

Detection of twilight events is a crucial step in defining the correct location of birds with geologgers. With the threshold method, we determined twilight events for the GeoLight package using a threshold value of 6.5 on the scale of zero to 127, which corresponded to a sun angle of –3 to –4.5 (depending on the individual tag), based on an individual calibration period that corresponded to a minimum of 3 days after deployment while the birds were still resighted on the breeding grounds. The first 24 h after deployment were regarded as a behavioral equilibration period, and we did not use these data for tracking or calibration. To compute migration departure and arrival dates, we then plotted the coordinates for each data point in ARCGIS and visualized the longitudinal and latitudinal movements associated with each day of the year. A consistent longitudinal movement (e.g., ~5 consecutive data points with longitudinal shift ≥5°W) was considered a real movement and not an artifact of shading. We did not consider latitude when computing departure and arrival dates because of the high degree of error in latitude estimates.

We implemented tripEstimation by following the general steps described in Seavy et al. (2012). We began by truncating the 0–127 raw light measurements to measurements from 6 to 20 that captured the twilight period. We discarded all twilight transitions with substantial shading, and designated tag-specific calibrations using the same periods from the threshold method. We constrained possible locations with a land mask, the known locations of release day, and the spatial boundaries beyond which we considered locations unrealistic (values outside of latitude 0 to 40 or longitude –120 to –40). We disregarded latitudinal estimates during the equinox period (15 days on either side of the true equinoxes). For the light parameters, we used variance in light data = 2.5, variance in light attenuation = 6, an Ekstrom range of –20 to 40, and variance outside this range = 7. For our movement model, we used a log normal distribution with a mean of 2.6 km h^{-1} and variance of 1.3. We set up the Markov-chain Monte Carlo (MCMC) to start by drawing 10,000 samples for burn-in and tuning of the proposal distribution. We then repeated an MCMC from the end of the burn-in by drawing 10,000 samples and made sure that the model parameters were tuned in for each tag and that the MCMC had converged by assessing minimal migration trajectory shift from the burn-in period and the additional run of 10,000 simulations. Finally, we set up a new MCMC by drawing 10,000 simulations and then generating a last draw of 10,000 samples to describe the posterior distribution. We used the mean of the posterior distribution coordinates to plot our estimate of the most likely routes for each individual. Results are presented as means ± SD.

RESULTS

In 2011, we retrieved 13 of the 100 geologger tags deployed in 2010, but only 2 geologgers lasted to the following year of recapture to provide usable data (see online supplemental material). During summer 2012 we retrieved 32 of 100 geologger tags deployed in 2011. Of these, 24 provided usable data through fall migration (e.g., November).

Overall, of the 26 tags with usable data, 23 came from free-ranging birds tagged in 2011, 2 from birds used in our photoperiod manipulations trial carried out in 2010, and 1 from our photoperiod manipulations carried out in 2011. One individual was recaptured in consecutive years (2011, 2012).

Migratory geography.—Of the 25 birds with geologger data, 23 migrated from the breeding ground in southwestern Oklahoma toward the molting site in northwestern Mexico (Fig. 1A and supplemental material). The "noisy" light measurements yielded only approximate estimates of geographic position because, as is typical of current technology, poor weather conditions (e.g., clouds), feather shading of the light sensor, and behavior all influenced light levels recorded by the geologger. Nevertheless, the overall westward migratory pattern from Oklahoma toward Mexico was clear. There were two notable exceptions to this pattern: one unmanipulated bird migrated east to northern Louisiana (ID 251112862 in supplemental material, Fig. S1). His location after that was unknown because the geologger failed in mid-September. Another bird, a member of the "late" experimental group in 2010, migrated immediately south along the eastern edge of the Gulf of Mexico and spent the winter at or near the Isthmus of Tehuantepec before returning to the breeding ground in the spring along the same route (ID 222150719 in Fig. 1D). Some individuals appeared to stop over in southwest Texas (about a week, possibly along the Rio Grande) during their migration to the Sinaloa–Sonora region (see supplemental material).

Most geologgers stopped collecting data while birds were still in the Sinaloa–Sonora region. However, we recovered breeding-season-to-breeding-season tracks from 2 individuals used in light manipulation trials in 2010 and a track until late January from 1 wild bird tagged in 2011. As described above, 1 bird from the "late" light manipulation treatment migrated immediately south to wintering grounds in southern Mexico and then returned to Oklahoma in spring (ID 222150719 in Fig. 1D). The other bird from the "late" light manipulation treatment and the unmanipulated bird both followed similar loop migration paths, beginning with southwestward movement to northwest Mexico (Sonora and Sinaloa regions) in late summer, followed by less rapid southward movement in late fall, and an eastward shift in early winter to southeastern Mexico (ID 222150714 in supplemental material and ID 222150755 in Fig. 1B, C, and supplemental material, respectively). There were also variations in movements associated with later stages of their migration. In particular, the bird from the 2010 light manipulation group showed an eastward movement to the Isthmus of Tehuantepec (or thereabout) and a direct northward spring migration in early May to return to the breeding site,
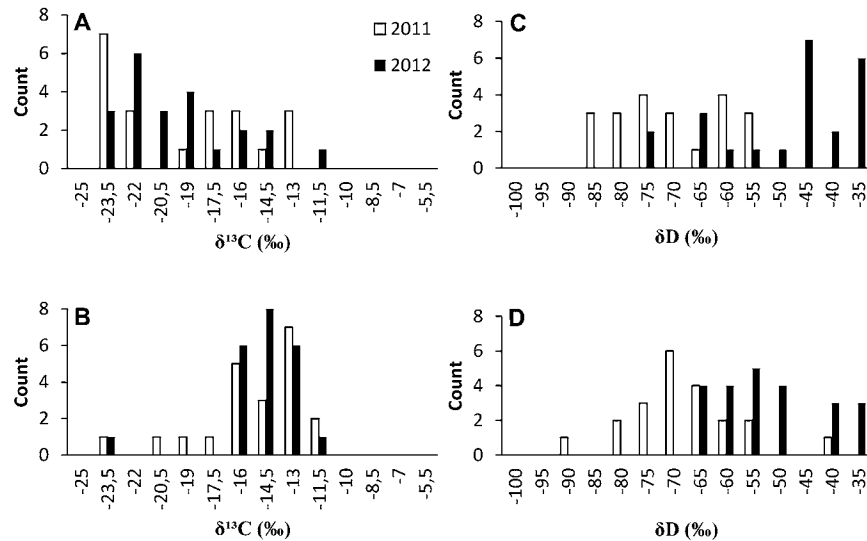
Fig. 2. Distribution of (A, B) carbon and (C, D) hydrogen stable isotope ratios in primary feathers for individual Painted Buntings sampled in two consecutive years at the breeding site in Oklahoma (Wichita Mountains Wildlife Refuge). Feathers collected in summer 2011 (white bars) were molted in 2010, and feathers collected in 2012 (black bars) were molted in 2011.

whereas the wild individual tagged in 2011 showed a longer eastward movement and wintered primarily in the Yucatan Peninsula.

Migratory timing.—Painted Buntings departed the Oklahoma breeding site from mid-July through mid-August (Table S1). In 2010, one bird migrated to the molting site in 4 days (the other migrated eastward). In 2011, the duration of migration ranged from a few days to as long as 29 days and averaged 11.4 days (Tables S1 and S2).

Migration timing and diet shifts.—The bimodal pattern in carbon isotope ratios in the first primary feathers previously observed by Bridge et al. (2011) was evident in samples from 2011 and 2012 (Figs. 2 and 3). We found no significant association between $\delta^{13}C$ signatures in primary feathers (P1) molted in 2011 and timing of migration variables when considered together in a single model or independently. The full model describing variation in $\delta^{13}C$ signature in P1 molted in 2011 as a function of departure dates from the breeding ground in Oklahoma, arrival dates at the molting sites in northwestern Mexico, and duration of this migration in days was not significant ($R^2 = 0.14$, ANOVA; $F = 0.98$, df = 3 and 17, $P = 0.421$). Similarly, $\delta^{13}C$ values in P9 molted in 2011 had no relationship with departure dates from Oklahoma, arrival dates at the molting sites in Mexico, or duration of fall migration ($R^2 = 0.16$, ANOVA; $F = 1.12$, df = 3 and 19, $P = 0.316$). We also tested each of these relationships in a univariate regression, and none was significant ($P = 0.714$, $n = 22$). The results suggest that the bimodal pattern in carbon stable isotope in P1 is not associated with departure dates from the breeding ground or pace of migration. Interestingly, comparisons of feathers taken from the same bird in consecutive years revealed that 60% of the birds switched "pattern" between years as reflected in the carbon isotope ratios of P1. For P1s molted in 2010, 50% of the birds had a carbon signature compatible with a diet based on C3 carbon sources typical of mesic plants (i.e., $< \delta^{13}C = -18$‰), whereas only 15% of the birds had a carbon signature in P9 compatible with a diet based on primarily C3 food intake. The mean $\delta^{13}C$ value for P1 molted in 2010 was -18.3 ± 4.1‰ (range: -23.3 to -12.0‰), and that for P9 molted

in 2010 was -14.2 ± 2.9‰ (range: -22.1 to -10.5‰). However, our examination of $\delta^{13}C$ signature in primary feathers molted in the same birds in 2011 showed that 80% of the birds had a carbon signature in P1 compatible with a diet based on C3 carbon sources, and only 5% had a carbon signature in P9 compatible with a diet based on C3 carbon sources. The mean $\delta^{13}C$ value for P1 molted in 2011 was -19.1 ± 5.1‰ (range: -22.6 to -10.8‰), and that for P9 molted in 2011 was 13.9 ± 3.9‰ (range: -23.0 to -11.4‰).

The hydrogen ratio values of both P1 (mean = -67.1 ± 10.5‰, range: -84.8 to -52.4‰) and P9 (mean = -65.2 ± 11‰, range: -88.6 to -36.8‰) grown by 60% of birds in 2010 generally
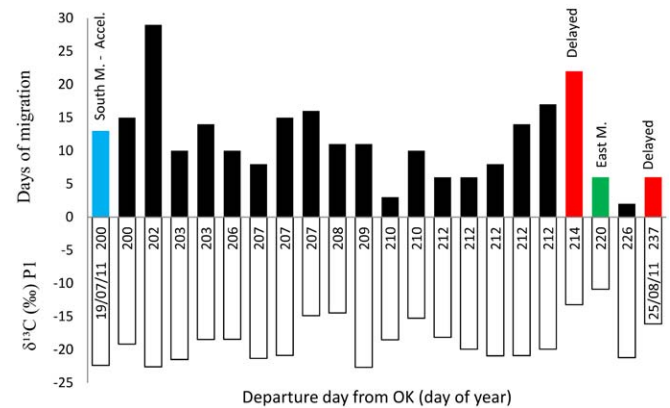

Fig. 3. Histograms indicating carbon stable isotope ratios in P1 associated with the length of migration and departure dates from the breeding ground of Painted Buntings at Wichita Mountains Wildlife Refuge in Oklahoma (OK). Black bars represent free-ranging birds, white bars represent carbon stable isotope ratios in P1, and green bar indicates east migration (Louisiana); the photoperiod-manipulation late group (migration onset delayed) is represented by red bars, and the photoperiod-manipulation early group and south migration (migration onset accelerated) are represented by blue bar. For a description of photoperiod manipulations (delayed and accelerated treatments), see details in the text.

indicated latitudes associated with the central United States (less than −65‰ δD; Bowen and Revenaugh 2003). However, δD values in primary feathers molted in the same birds during the following year all exceeded −65‰ δD (P1: mean = −37.9 ± 17.7‰, range: −64.14 to −5.9‰; P9: mean = −49.6 ± 10.5‰, range: −62.26 to −28.5‰).

Mean δ¹³C values of P1 and P9 did not differ between years (P1: $t = −0.7$, df = 19, $P = 0.43$; P9: $t = −0.4$, df = 19, $P = 0.68$). By contrast, mean δD in P1 and P9 differed significantly between years (P1: $t = −6.7$, df = 19, $P = 0.000002$; P9: $t = −4.8$, df = 19, $P = 0.00001$). High annual variation in hydrogen isotope ratios among years in the arid west has been demonstrated previously (Wunder et al. 2005).

DISCUSSION

Molting schedules can differ between populations of the same or closely related species. Examples include eastern and western populations of the Painted Bunting, along with populations of Warbling Vireos (*Vireo gilvus*) and Northern Rough-winged Swallows (*Stelgidopteryx serripennis*) (Thompson 1991a, Yuri and Rohwer 1997, Voelker and Rohwer 1998). There is also evidence that migration and molt can vary among individuals within populations (Elrod et al. 2011). For the western Painted Bunting, bimodal isotopic signatures in a sample of primary feathers from a single breeding population provided highly suggestive evidence for the existence of variation in migration behavior among individuals (Bridge et al. 2011). This variation compels testing of hypotheses regarding the causes of multiple migratory patterns and/or diverging migratory schedules within a breeding population of Painted Buntings in Oklahoma.

Our investigation confirmed that the frequency distribution of carbon isotope ratios in the first primary was bimodal in Painted Buntings that molted at stopover locations in west Mexico, which indicates that some birds used primarily C3 food and others used C4 sources early in molt. This bimodal pattern contrasts with the frequency distribution of carbon isotope values in the ninth primary, which was uniformly C4 in origin. We tested whether the bimodal distribution in P1 was the result of variation in (1) migration routes or (2) migration timing, and found no support for either hypothesis. Hypotheses that remain to be tested include the possibility that the carbon isotope ratio of P1 reflects the composition of the breeding territory in Oklahoma or of habitats used in the early stages of migration, reinforcing the importance of the role played by molting behaviors and migratory patterns in processes leading to speciation (Rohwer and Irwin 2011).

The across-year consistency in δ¹³C is interesting, considering that so many birds evidently altered their use of C3 and C4 food sources between years, and suggests that local effects, as opposed to landscape effects, led to the bimodal distribution of δ¹³C. That is, the landscape was consistent between years, giving rise to similar between-year averages, but the use of particular patches within the landscape (perhaps agricultural fields vs. grasslands) may have given rise to bimodal δ¹³C population distributions. We note that in our research we focused on adult males to maximize the rate of recaptures. However, we should consider the possibility that migratory patterns of females and juveniles may differ greatly, as previously demonstrated in other species (Butler et al. 2002, Jenkins and Cristol 2002, Bai and Schmidt 2012).

Although there was temporal variation in the migratory behavior of Painted Buntings in our study population, it was not related to the bimodal distribution of δ¹³C in primary feathers. Our data also demonstrate large year-to-year variation in δ¹³C and δD in isotope ratios of primary feathers of individuals. Thus, it is evident that the different isotope profiles for P1 and P9 do not constitute genetically "hard-wired" migration or dietary strategies. We found no clear relationship between isotope signatures and migration timing. Moreover, the frequency with which birds evinced changes in dietary carbon sources between years indicates that rigid dietary preferences were not likely a cause of the bimodal distribution of isotope signatures in P1 or the transition to unimodal pattern by the end of molt.

We also documented individual variation in departure dates from the breeding ground, arrival dates in northwestern Mexico, the time used to migrate between these two sites, and the duration of short refueling stops in southwestern Texas. However, it is unclear why two adult birds of the same sex and from the same breeding population diverged so dramatically from the general migratory directional pattern shown by the other birds. Perhaps environmental instability related to the monsoons of the Sonora–Sinaloa region (Rohwer et al. 2005, Pyle et al. 2009) has promoted the evolution and maintenance of a degree of flexibility in the migratory behavior of Painted Buntings and other avian migratory species that breed in the Great Plains of the United States (Jahn et al. 2013). Also, the severe drought in southwestern Oklahoma in July 2011 (National Oceanic and Atmospheric Administration; see Acknowledgments) likely had an effect on timing of migration in Painted Buntings and many other species of grassland birds.

The power of combining light-based geolocation data and other markers such as stable isotopes is becoming increasingly evident in investigations of migratory species (González-Solís et al. 2011). Carbon stable isotopes are widely used to infer the spatial distribution of consumers and in migratory connectivity studies (Marra et al. 1998, Hobson et al. 2012). Our findings suggest that the carbon isotope signatures of primary feathers are related to diet late in the breeding season or early in migration, independent of location. This inference was possible only because we incorporated information from the geologgers. Indeed, our threshold approach provided a relatively easy procedure to extrapolate variables associated with the timing and duration of migration, but it is coarse in its resolution of movements and accuracy of locations. By contrast, our preliminary analysis of migration routes through the curve-fitting method (Fig. 1C, D) is an example of how we can estimate movements between simple data points. However, it can be computationally intensive and requires careful selection of model parameters.

In conclusion, our data suggest a marked convergence to a similar use of resources toward the end of the molting period, as evinced by stable isotope analysis of P9 feathers, and that the bimodal carbon signature in P1 (Bridge et al. 2011) is not related to variation in arrival date at the molting locations and subsequent timing of the onset of molt. The most likely remaining explanation is that P1 is grown using energy reserves acquired prior to migration. This is an intriguing possibility because this would be a quantitative and direct carryover effect from the breeding season to the migration and molting stages of the Painted Bunting's life history. Such a carryover might have ecological and evolutionary implications (Marra and Holberton 1998, Norris and Marra 2007).

For example, the degree to which plumage quality is a useful proxy in selection of breeding partners may depend on the information it contains about the ability of individuals to garner resources on the breeding ground in the previous year rather than at stopover sites encountered during migration (Keyser and Hill 2000).

Acknowledgments

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