Introduction

Major divisions in migratory behavior occur both within and across Neotropical migratory songbirds. In temperate North America there is a notable divergence in migratory behavior, which corresponds to the east/west continental divide. Whereas >74% of “Eastern” songbirds remain on breeding grounds to undergo feather molt and subsequently make relatively direct autumn migrations to wintering grounds, >53% of “Western” songbirds depart breeding grounds before molt ([1]; S. Rohwer, personal communication) and many of these interrupt autumn migration to replace feathers at traditional molting grounds, often within the North American Monsoon region (NAMR) [2-4]. Rohwer et al. [2] hypothesized that Western “molt-migrants” are responding to the interplay between a “push” away from drying breeding grounds that lack resources for energy-demanding prebasic molt, and a “pull” to late-summer resource pulses in the NAMR [5].

The breeding ranges of a few Western Neotropical migrants extend into typically Eastern habitats. One example is the Lark Sparrow (Chondestes grammacus), a Neotropical migrant that breeds primarily in western North America but also occupies grassland patches in the American Midwest [6-7]. This species has been characterized as a molt-migrant [3]; however, it is unknown whether typical Western molt-migration behavior (e.g., pre-molt breeding ground departure, interrupted migration) occurs among Eastern Lark Sparrows. From 2005 to 2011 we monitored a population of Lark Sparrows in Ohio (i.e., an eastern population) and observed that the species disappeared relatively early compared to other local, migratory songbird species (i.e., by August 10), with no flight feather molt detected among 58 adult and juvenile Lark Sparrows captured there during July (J. Ross, unpublished data). These observations raised the question of whether the migratory behavior of Lark Sparrows in Ohio resembled that of Western molt-migrants, including western Lark Sparrows, despite the fact that their breeding location was located in the eastern United States, far from the NAMR.
To address this question, we used light-level geolocation data loggers (geolocators) to ascertain migratory timing and routes of individual Eastern Lark Sparrows breeding in Ohio. The recent miniaturization of light-level geolocators has rapidly advanced our understanding of individual variation in migratory life-cycles among small songbirds [8-9], including some Western Neotropical migrants [10-12]. According to recent phylogenetic analysis, Lark Sparrows from our Ohio population appear to have descended from ancestors of the central North American Great Plains [7]. Having observed possible behavioral remnants of their Western ancestry (e.g., early departure from breeding grounds), we predicted that Ohio Lark Sparrow migration tracks would reveal early fall migration with interruptions to accommodate feather molt. The alternative possibility was delayed post-breeding departure (to molt in situ) followed by direct migration to wintering grounds typical of Eastern migratory species [2-4].

2 Methods

We manufactured 0.7-0.8 gram archival geolocators programmed to log mean light levels over 10 min intervals. During May-July 2011 we mist-netted 21 breeding adult Lark Sparrows (9 males, 12 females) in Lucas Co., Ohio and tagged each with a geolocator and unique color leg-band combination. We attached geolocators using a leg-loop harness [13] of Stretch Magic beading thread (0.7 mm diameter; Pepperell Braiding Company, Pepperell, MA, USA). In 2012 we recaptured individuals using mist nets and removed geolocators for subsequent data download. This work was approved by the University of Oklahoma Institutional Animal Care and Use Committee (Protocol #R12019).

We visualized and edited light-level data using the R-package GeoLight [14]. This program estimates daily geographic location from light levels using a simple light-threshold interpolation. We used a light threshold value of 5.1, which corresponded with sun angles of -3.875° to -0.550° below the horizon, depending on the tag. During GeoLight analysis we excluded apparent aberrations such as false twilights and voltage spikes.

We conducted an alternate analysis of light-level data using the R-package tripEstimation [15], which implements a simple movement model within a Bayesian likelihood framework to estimate daily geographic positions. This approach allowed for uncertainty in daily location estimates, limits on movement speed, and landscape feature masking (e.g., oceans) to estimate the likely migratory path. We calibrated tripEstimation relative to ≥ 10d of light data at the release or recapture location. Other model settings were: x and y sigma estimates = 0.1; k sigma = 5; light sigma = 3; behavior mean (s.d.) = 12 (2); ekstrom limits = -5,1,3; behavior distribution = gamma; thin (down-sampling) = 10; burn-in iterations = 5x10⁴; and model iterations = 10⁴. We exported mean estimates (± 99% C.I.) of daily locations for mapping and further analysis. An example tripEstimation script is provided as Supplementary Material. In addition, raw light-level data and GeoLight and tripEstimation outputs used in this study are available in Movebank (http://movebank.org, study name “Geolocator-tracked variation in migratory behavior of Lark Sparrows”) and are published in the Movebank Data Repository with DOI: 10.5441/001/1.5jd56s8h.

We subdivided tracks into migration stages: autumn migration (deployment – September 4), wintering (November 15 – February 1), and spring migration (April 1 – recapture). To depict autumn and spring migrations, we used ArcGIS v10.1 (ESRI, Redlands, CA, USA) to plot both GeoLight estimates as points and best-path renderings from tripEstimation as solid lines. Finally, we estimated wintering locations using kernel density plots with cell sizes of 0.1° and search radiuses of 3° latitude and longitude, with exclusion of kernel densities less than three points per cell.

3 Results

Of 21 Lark Sparrows tagged with geolocators in 2011 we relocated 9 (5M, 4F) in 2012 and, of these, recaptured 5 (4M, 1F). One male had lost his geolocator and another male’s geolocator failed shortly after deployment, leaving datasets for two males (Male-1, Male-2) and one female (Female-1). We resighted an additional female in 2013 that was not seen in 2012, therefore at least 10 of 21 (47.6%) geolocator-marked individuals returned to breed in the Ohio population. During previous years (2005-08) a higher proportion of color-banded adults had returned to this population (50 of 81; 61.7%), though the apparent decline in return rate was not significant (Fisher’s exact test, p = 0.18).

Estimated autumn migratory behavior showed both similarities and differences in timing and path taken among individuals. GeoLight and tripEstimation tracks for Male-1 and Female-1 both showed movements directly south to the Gulf of Mexico coastal region, then west to Texas, and finally south to central Mexico (Figure 1a-b). These migrations were relatively fast (i.e. ≤33 days), though their timing showed almost no overlap (Table 1).
Table 1: Departure and arrival dates between breeding grounds and estimated wintering grounds for each tracked Lark Sparrow. Dates range from July 2011 to May 2012.

| Individual ID | Autumn Migration | Spring Migration |
|---------------|------------------|------------------|
|               | Breeding departure | Wintering arrival | Wintering departure | Breeding arrival |
| Male-1        | July 5           | August 7         | April 14           | April 27         |
| Female-1      | August 7         | August 26        | April 18           | May 3            |
| Male-2        | July 20          | September 2      | -                  | -                |

By contrast, GeoLight estimated that Male-2 first moved generally westward, lingered for nearly a month in the central Great Plains region, and then moved south to north-central Mexico (Figure 1c). Male-2’s tripEstimation path indicated an initial southward-sweep which, unlike the tracks of Male-1 or Female-1, partly contrasted with the GeoLight analysis. In the case of Male-2, calibrating the tripEstimation model may have been affected by relatively inconsistent light-level distributions across twilight events (raw solar geolocator data available in the Movebank; see Methods). Nonetheless, both analyses revealed a comparatively long-duration, Male-2 migration (44 days; Table 1).

Wintering distributions all appeared to occur within a narrow longitudinal range (W100-102°; Figure 1). Light data from Male-2 were muted after the autumnal equinox and eventually ceased on November 15, 2011. These technical difficulties compromised our ability to confidently estimate its terminal wintering latitude. Mid-winter data for Male-1 and Female-1, on the other hand, were high-quality and narrowed their probable wintering latitudes to between N21-23° and N19.5-21°, respectively (Figure 1a-b). The estimated wintering ranges approximately correspond to the southern Warm Desert and Southern Semi-arid Highlands ecoregions in central Mexico [16]. This region experiences mild winters, receives annual rainfall of 30-60 cm, and is predominantly xeric grassland or shrubland [16], though habitat may vary altitudinally across numerous topographic features [17]. Portions of this landscape would therefore resemble the core Lark Sparrow breeding habitats of the Great Plains ([6]; J. Ross, personal observation).

Migration paths of Male-1 and Female-1 were similar in spring as they were in autumn, although both paths notably differed between seasons (Figure 1a-b). The ~3,000 km long spring migration routes taken by Male-1 and Female-1 initially tracked north-northeast from the wintering grounds to stopover sites in northeast Texas/southwest Arkansas, reversing part of the route used by Male-1 during its autumn migration (Figure 1a). From there it appears that both individuals quickly moved back to the breeding grounds in Ohio. Spring migration was of shorter duration than autumn migrations for both Male-1 and Female-1 (i.e., < 15 days), and the timing of their migration overlapped
much more during spring than autumn (Table 1). Estimates of mean speed of spring migration were ~11% faster for Male-1 (218 km/d) than Female-1 (196 km/d).

4 Discussion

The Lark Sparrow migratory tracks produced by our study were not only interesting descriptions of variation among individual, migratory life history, but also revealed that the timing of migratory behavior among Eastern Lark Sparrows reflected the species’ Western origins [7] or, alternatively, its Eastern breeding range.

First, autumn migration differed considerably among individuals in terms of geographic path and timing. Male-2, in particular, offered an interesting case where migration was clearly not a relatively direct and continual path between breeding and wintering grounds. The westward movement and month-long stopover of Male-2 during autumn migration resembles what one might expect for a molt-migrant from the Great Plains; that is, an initial westward migration, stopover to molt, and then continued southward movement to wintering grounds [2-3]. Stopover period rather than flight speed between stopovers appeared to dictate the duration of Male-2’s migration (Figure 1c), supporting theoretical expectations for a long-distance migrant [18]. By contrast, Male-1 and Female-1 displayed largely direct and continual movement to the wintering grounds, resembling more a typical “Eastern” bird migration.

Second, all individuals appeared to begin autumn migration before initiating molt. This finding agreed with our prior observations of early departure and a lack of flight feather molt from/on the breeding grounds in this population (see Introduction). Both Male-1 and Female-1 likely molted on the wintering grounds after the autumn migration. Male-1, in particular, was captured June 28, 2011 showing no evidence of molt, departed the breeding grounds by July 5th, and stopped only briefly during migration before arriving at its wintering grounds in central Mexico by early August (Figure 1a; Table 1). It is hard to imagine that this individual molted before reaching its wintering grounds, as molt for Passerines typically requires a sessile period ≥ 30 days [19-21]. As noted earlier, Male-2 may have undergone molt during an extended stopover in the central Great Plains, but we lack additional evidence to test this possibility (e.g., stable isotopes). First-year male Lark Sparrows also depart Ohio breeding grounds early, leaving shortly after fledging and presumably before molt (J. Ross, unpublished data). Since Eastern Lark Sparrow populations show little genetic divergence from Great Plains populations [7], ancestral propensities to depart breeding populations early could be retained to varying degrees across these regions.

Third, the wintering range of Eastern Lark Sparrows likely encompasses the semi-arid highland grasslands in central Mexico (Figure 1). Therefore, eastern populations are probably not segregated from Great Plains populations during winter but instead mix extensively within a comparatively small winter range [6]. This finding may help explain the modest gene flow that occurs between populations of these regions [7], and indicates the conservation value of these wintering habitats. Degradation of the Lark Sparrow’s geographically-restricted wintering grounds may have disproportionate demographic impacts across a wide swath of the species’ breeding range.

Finally, spring migration of Male-1 and Female-1 were rapid and nearly direct from wintering to breeding grounds (Table 1, Figure 1), suggesting that early arrival at nesting sites is favored, likely because of competition for breeding territories. Furthermore, overlapping stopovers in northeast Texas/southwest Arkansas highlight this area as possibly an important staging area for Eastern Lark Sparrows during spring migration.

Among birds, some characteristics of migratory behavior are heritable and can vary among individuals [22-32]. The genetic basis for modifying or developing migratory behavior has been well studied, yet comparatively less is known of genetic triggers for the inception of migratory events [33]. Although our sample size is small, the three autumn and two spring migration tracks reveal an interesting blend of typical Eastern and Western migratory strategies. Potential remnants of Western migratory timing among Eastern Lark Sparrows (i.e., pre-molt departure) suggest that genetic predispositions underlie differences in migratory onset between Western and Eastern Neotropical migratory birds. On the other hand, individual variation in the temporal and directional properties of fall migration suggests less constraint on migratory route and, as such, support Rohwer et al.’s [2] hypothesis that migration is facultatively adjusted relative to environmental “pushes and pulls”. This study highlights how tracking data from even a handful of individual birds can help expand our understanding of avian migration biology, and it evinces the potential for multi-population geolocator studies to revolutionize our understanding of migratory behavior evolution and songbird conservation.

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