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Migratory connectivity and potential nonbreeding sexual segregation in Gray Vireos (*Vireo vicinior*)

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ABSTRACT

Nonbreeding distributions of most migratory North American breeding birds are relatively well-defined, but population- and sex-specific nonbreeding dispersion is poorly understood. Nonbreeding factors can limit population growth and manifest differently among populations and sexes across the full annual cycle. Thus, unraveling complex patterns mediating life history processes is crucial for targeted conservation of migratory animals. The Gray Vireo (*Vireo vicinior*) is a short-distance (i.e., ~1,000 km) migratory songbird of the southwestern United States and western Mexico for which data on migration ecology and migratory connectivity are lacking. We used light-level geolocators (48 deployed, 15 retrieved) to track migration and estimate nonbreeding locations of female and male Gray Vireos from two breeding sites in New Mexico and one breeding site in Utah, USA. Our data suggest weak-to-moderate spatial migratory connectivity ($r_M = 0.3$), with birds from one New Mexico site wintering 600–1,000 km east of the other two populations, incongruent with geographic breeding-site dispersion. Our data also suggest that females overwintered farther north (~520 km; ~4.7° latitude; 95% CI [1.6°, 7.8°]) than males, suggesting potential sexual segregation during the stationary nonbreeding season, which may be explained by larger body size in females than males. Our results provide important details on the nonbreeding ecology of an under-studied dryland songbird, as well as suggest potential differential migration patterns, all of which warrant further study.

KEYWORDS
Body-size hypothesis; differential migration; female songbird; full annual cycle; light-level geolocator; migration ecology

PALABRAS CLAVE
Ciclo anual completo; ecología de la migración; geolocalizadores de nivel de luz; hembras de aves canoras; hipótesis del tamaño corporal; migración diferencial

Conectividad migratoria y potencial segregación sexual no-reproductiva en *Vireo vicinior*

RESUMEN

La distribución no-reproductiva de la mayoría de las aves que anidan en Norteamérica está relativamente bien definida, si bien la dispersión no-reproductiva por sexo y población es escasamente conocida.

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Factores no-reproductivos pueden limitar el crecimiento poblacional y manifestarse de manera diferente entre poblaciones y sexos a lo largo del ciclo anual completo. Por ello, resolver los complejos patrones que modulan procesos en historias de vida es crucial para la conservación de animales migratorios. *Vireo vicinior*es un ave canora migratoria de corta distancia (i.e., ~1,000 km) del suroeste de los Estados Unidos y el oeste de México para la cual carecemos de datos de su ecología de la migración y conectividad migratoria. Usamos geolocalizadores de nivel de luz (48 montados, 15 recuperados) para dar seguimiento a la migración y estimar las localidades no-reproductivas de hembras y machos de esta ave de dos sitios de anidación en Nuevo México y un sitio de anidación en Utah, EUA. Nuestros datos sugieren una débil-a-moderada conectividad migratoria espacial (r_M = 0.3), con aves de un sitio en Nuevo México pasando el invierno 600–1,000 km al este de las otras dos poblaciones, incongruente con la dispersión geográfica de sitio deanidación. Nuestros datos sugieren que las hembras pasaron el invierno más al norte (~520 km; ~4.7° latitud; IC 95% [1.6°,7.8°]) que los machos, lo que sugiere una potencial segregación sexual durante el periodo estacionario de la temporada no-reproductiva, la cual puede ser explicada por el mayor tamaño de las hembras que el de los machos. Nuestros resultados proveen detalles importantes de la ecología no-reproductiva de un ave canora de regiones áridas poco estudiada, además de sugerir diferentes patrones de migración, las cuales justifican mayor estudio.

Tracking migratory animals across their full annual cycles is critical for filling knowledge gaps, determining causes of variation in population trends, and implementing effective conservation actions (Sherry and Holmes 1996; Calvert et al. 2009). In particular, many migratory songbirds are declining worldwide and may be more susceptible to the effects of a changing climate compared to resident species, partly because of their reliance on multiple landscapes at different times throughout their full annual cycle (Both et al. 2010; Klaassen et al. 2012). Yet, knowledge about most migratory songbirds is biased with respect to the full annual cycle, with most research being nesting season- and/or male-centric, leading to potentially nescient scientific conclusions or misinformed management and conservation efforts (Faaborg et al. 2010; Streby et al. 2014; Bennett et al. 2019; Haines et al. 2020).

Most Nearctic-Neotropical migratory songbirds spend ≤1/3 of their annual cycle breeding, with the remainder spent migrating or at stationary nonbreeding locations (Sillett and Holmes 2002; Faaborg et al. 2010), which are often the least-studied stages (Marra et al. 2015). Previous research has revealed limiting factors to population growth outside of the breeding season, demonstrating the importance of considering the full annual cycle when identifying mechanisms mediating declines and targeting specific locations to concentrate limited conservation resources (Sherry and Holmes 1996; Calvert et al. 2009; Gilroy et al. 2016; Hewson et al. 2016; Kramer et al. 2018).

Differential migration occurs when intraspecific subgroups (e.g., sexes or age classes) exhibit differences in migration timing (Bell et al. 2021; Neate-Clegg and Tingley 2023) and/or migration distance (e.g., sexual segregation; Cristol et al. 1999; Briedis and Bauer 2018; Bell et al. 2021). Thus, individuals that breed together can overwinter considerable distances apart (Cristol et al. 1999; Briedis and Bauer 2018). In species with sex-based differential migration, males and females from different breeding populations are often still observed together at nonbreeding sites (Catry et al. 2006), necessitating knowledge of individual migration distances for detecting differential migration. There are several non-exclusive hypotheses for drivers of differential migration (e.g., the arrival time, body-size, and social dominance hypotheses; Ketterson and Nolan 1976; Cristol et al. 1999; Catry et al. 2006), but differentiating among these hypotheses can be difficult because their predictions are often the same (Boyle 2008). Beyond sex-based patterns, other differences in migratory behavior (e.g., routes, timing, duration) and migratory connectivity may manifest among populations, potentially driving overall population trends with ecological and evolutionary implications (Hewson et al. 2016; Kramer et al. 2017, 2018; Briedis and Bauer 2018; Fraser et al. 2019).

Migratory connectivity describes the degree of spatiotemporal dispersion and mixing among populations across the full annual cycle and is generally described along a spectrum of strong to weak (Webster et al. 2002; Finch et al. 2015; Knight et al. 2021). Strong migratory connectivity, or a high degree of population-specific geographic isolation throughout the annual cycle, is thought to be relatively uncommon in songbirds but has been observed (e.g., *Vermivora* warblers; Kramer et al. 2017, 2018). On the other extreme, weak migratory connectivity is putatively more common in songbirds, occurring when there is broad nonbreeding overlap or mixing among distinct breeding populations (Finch et al. 2017; Hagelin et al. 2021). Species with moderate-to-strong migratory connectivity may be particularly susceptible to localized factors impacting fitness across the annual cycle, which can drive breeding population trends (Kramer et al. 2018).

Compared to most North American birds, data are limited for dryland (i.e., semi-arid and arid lands) birds and other western USA songbirds (Carlisle et al. 2009; McKinnon and Love 2018; Hedley 2019; Fischer et al. 2022), which have experienced community-wide declines over the past century (Iknayan and Beissinger 2018; Riddell et al. 2021). Within these species and others, regarding free-living populations and museum specimens, data are even more sparse for females compared to males (Bennett et al. 2019; Cooper et al. 2019; Haines et al. 2020). Some demographic groups may contribute disproportionately to population growth (e.g., songbird populations are often female-limited; Dale 2001), underscoring the value of understanding sex-based differences in behavior, survival, and habitat associations throughout the annual cycle (Catry et al. 2006; Briedis and Bauer 2018).

The Gray Vireo (*Vireo vicinior*) is a small (~11–14 g), migratory songbird that breeds primarily in juniper (*Juniperus* spp.) savannas and structurally similar dryland landscapes in the southwestern USA and northwestern Mexico (Barlow et al. 1999). This under-studied species (ranks in the 36th percentile of research effort among North American songbirds; see Fischer et al. 2025) occurs at relatively low densities within a patchy breeding distribution (DeLong and Williams 2006; Schlossberg 2006; Hargrove and Unitt 2017), with significant, previously unstudied breeding (e.g., the northern Baja California Peninsula, Mexico; Hargrove et al. 2023) and nonbreeding populations (e.g., southern California, USA; Unitt 2000) still being described. Reliable range-wide population trend estimates do not exist for Gray Vireos because during the entirety of their annual cycle, they primarily occupy remote areas away from roads and are therefore poorly surveyed with standard methods (Schlossberg and Bollinger 2006; Hargrove and Unitt 2017; Fischer et al. 2022), such as the US Geological Survey (USGS) Breeding Bird Survey (BBS; Pardieck et al. 2019). Gray Vireos are listed as Threatened and as a Species of Greatest Conservation Concern in New Mexico, USA (NMDGF 2007, 2018) and are considered of conservation concern by the US Fish and Wildlife Service (USFWS 2008) and Partners in Flight (Rosenberg et al. 2016).

Despite some important studies on the nonbreeding ecology of Gray Vireos (Bates 1987, 1992a, 1992b), dispersion of the sexes from individual breeding populations and of individuals from different breeding populations throughout the annual cycle is not documented. Anecdotally, Gray Vireos overwinter in coastal drylands that support high densities of fruiting elephant trees (*Bursera microphylla*; Bates 1987, 1992a, 1992b; Unitt 2000). The current description of their nonbreeding distribution extends through the southern half of the Baja California Peninsula, Mexico, and east to southern Arizona, USA and Sonora, Mexico, with small, disjointed nonbreeding populations at Big Bend National Park, Texas and in southern California, USA (Barlow and Wauer 1971; Bates 1987, 1992a, 1992b; Unitt 2000). However, current knowledge of their nonbreeding distribution is likely incomplete (Unitt 2000) and biased by patterns of human occurrence, sampling effort (e.g., Ferrer et al. 2006), and potentially by human preferences toward seeking and reporting more aesthetically appealing species (e.g., species with brightly colored plumage; Echeverri et al. 2020; see also Fischer et al. 2025). Bates (1987, 1992b) described nonbreeding territorial behavior in both females and males and, based on museum specimens collected in a portion of their nonbreeding range (i.e., Sonora, Mexico), hypothesized that sexual segregation does not occur on the nonbreeding grounds in this species.

Gray Vireos are interesting candidates for evaluating whether sex-based body size differences could be associated with nonbreeding dispersion (i.e., the body-size hypothesis). The body-size hypothesis suggests that in sexually segregated, dimorphic species—in mass and morphometric measurements, not necessarily dichromatism—the larger-bodied sex migrates shorter distances than the smaller-bodied sex (Ketterson and Nolan 1976; Cristol et al. 1999). This phenomenon, first described in Dark-eyed Juncos (*Junco hyemalis*), is putatively related to the ability of larger-bodied individuals to withstand lower ambient temperatures associated with higher latitudes or elevations (Ketterson and Nolan 1976, 1983; Cristol et al. 1999). However, in Gray Vireos, such differences in nonbreeding dispersion may be driven by factors other than those previously hypothesized (e.g., cold tolerance) because their nonbreeding distribution is smaller and covers less of a thermal cline than that of the Dark-eyed Junco. Additionally, in systems where species are physiologically adapted to extreme conditions (e.g., drylands), differences in body size could evolve across a narrower range of conditions associated with demands on mass-specific water budget balancing (Albright et al. 2017) or heat dissipation (Hegemann et al. 2019) rather than fasting endurance (e.g., during inclement, cold weather as hypothesized in Dark-eyed Juncos). Gray Vireos are also an interesting system for studying among-population migratory connectivity because they occur within relatively isolated sky island (i.e., mountain ranges characterized by isolation; McCormack et al. 2009) breeding sites and exhibit strong breeding site fidelity (Johnson et al. 2014).

We used archival light-level geolocators (hereafter, geolocators), devices that record ambient light levels at regular intervals throughout the full annual cycle (Stutchbury et al. 2009), to estimate stationary nonbreeding locations and describe timing and duration of seasonal migrations for adult female and male Gray Vireos from three breeding sites in the eastern portion of their breeding distribution. We tested the hypothesis that the larger-bodied females overwinter farther north than males, consistent with the body-size hypothesis of differential migration, and we investigated whether populations exhibited weak, moderate, or strong spatial migratory connectivity between breeding and nonbreeding areas. We did not have a consensus expectation regarding potential differential migration because, despite females being larger than males, previous observations and museum specimens suggest that sexual segregation may not occur during the nonbreeding period in Gray Vireos (Bates 1987, 1992b). Regarding population-level spatial migratory connectivity, we expected distinct breeding populations of Gray Vireos to mix and co-occur during the nonbreeding period because most migratory songbirds studied to-date exhibit weak migratory connectivity (Finch et al. 2017).

Methods

Study species and area

We studied Gray Vireos breeding in New Mexico ($n = 2$ sites) and Utah ($n = 1$ site), USA during 2017–2018. These juniper savanna sites are sky islands and are surrounded by lower-elevation landscapes of different vegetation communities (e.g., Chihuahuan Desert grassland) not occupied by Gray Vireos. Sevilleta National Wildlife Refuge (hereafter, "Sevilleta;" 34.391°N, −106.562°W;) and Kirtland Air Force Base (hereafter, "Kirtland;" 35.005°, −106.409°W,) are in the northern Chihuahuan Desert of central New Mexico and are separated by ~90 km. The Utah site was in the southern foothills of the Abajo Mountains (hereafter, "Abajos;" 37.562°N, −109.784°W) in southeast Utah, at ~1,900 m elevation. The New Mexico study sites occurred at ~1800 m elevation along the foothills of Los Pinos Mountains (Sevilleta; Fischer 2020; Fischer et al. 2022) and ~2,000 m elevation in the Manzanita Mountains (Kirtland; Johnson et al. 2014; Harris et al. 2020).

Capture and geolocator deployment

We captured and handled Gray Vireos in compliance with Institutional Animal Care and Use Committee (IACUC) protocols at the University of Toledo (#108708) and the University of New Mexico Museum of Southwestern Biology (MSB; #16200406MC), annual Sevilleta Special Use Permits, NMDGF Permits (#3673 and #3217), a USFWS Permit (MB094297), and USGS Bird Banding Permits (#24072 and #20617).

During May through July 2017, we broadcasted recordings of conspecific songs and other vocalizations and used 12 m mist nets to capture adult female and male Gray Vireos on their breeding territories. We marked each bird with an aluminum USGS numbered band and a unique combination of one to three plastic color bands, recorded body mass (0.01 g) and morphometric measurements (1 mm), and determined phenotypic sex of each individual based on a combination of behavior (e.g., song differences, breeding behaviors, resighting during intensive breeding study; Fischer 2020) and presence of cloacal protuberance or brood patch (this species is monochromatic; Pyle 1997).

We deployed 48 0.41 g geolocators at all three sites (Sevilleta and Abajos: Intigeo W55Z9-DIPv9, Migrate Technology Ltd, Cambridge, UK; Kirtland: Lotek model #ML6340, Lotek UK Ltd, Wareham, UK). Geolocators recorded ambient light levels at regular intervals of 2 and 5 min for Lotek and Intigeo models, respectively. Data quality does not differ between these two light-sampling rates and both tag types are regularly used in bird migration studies (Lisovski et al. 2020).

At Sevilleta, we color-banded an additional sample of Gray Vireos as a control group to test for potential geolocator marker effects. Gray Vireos in the control group were captured,

Figure 1. Full annual cycle ecology of the Gray Vireo (*Vireo vicinior*), including the breeding season, migration, and the nonbreeding season (a). Adult female Gray Vireo marked with a light-level geolocator (b). Oneseed juniper (*Juniperus monosperma*) savanna at Sevilleta National Wildlife Refuge, New Mexico, USA (c). Photos and illustration by Silas E. Fischer.

handled, banded, and measured using identical methods as geolocator-marked individuals except those in the control group were not marked with a geolocator. Geolocator-marked and control individuals at Sevilleta were part of a demographic study focused on nesting and post-fledging ecology of Gray Vireos during both years of this study (see Stevens and Fischer 2018; Di Liberto et al. 2022; Fischer et al. 2022). We attached geolocators using a modified figure-eight leg-loop harness made of elastic jewelry cord (Fig. 1; Stretch Magic: Pepperell Braiding Company, Pepperell, MA USA; Rappole and Tipton 1991; Streby et al. 2015). Including the harness, geolocator units were ~3.5% of the average mass of adult Gray Vireos ($\bar{x}_{\text{vireo mass}} = 12.4$ g ± 0.8 SD).

Geolocator recovery

During the following breeding season (i.e., May–Jul 2018), we systematically searched for returning geolocator-marked Gray Vireos at all three sites and for control individuals at Sevilleta. At Sevilleta and Kirtland, we searched an area of ~500 m radius around initial capture locations and made repeated visits at different times of the day to minimize the chance of a returned Gray Vireo going undetected (Kramer et al. 2018). Our intensive search efforts at Sevilleta and Kirtland occurred from spring arrival through the breeding season and were evenly distributed at Sevilleta among all geolocator-marked and control birds. Due to logistical constraints, our search effort for returned birds at Abajos was limited to 3 days of intensive searching at the beginning of the nesting season.

Upon detecting returning geolocator-marked or control Gray Vireos in 2018, we used identical methods described above to lure individuals into mist nets. Due to difficulties recapturing some geolocator-marked Gray Vireos using song and call broadcasts (e.g., likely due to net avoidance behavior in previously captured individuals [Roche et al. 2013;

Camacho et al. 2017]), we also set and monitored nets around trees in which marked individuals were nesting to allow for passive capture. We were unable to capture three geolocator-marked Gray Vireos in mist nets; these individuals were thus collected by Museum of Southwestern Biology (MSB) personnel and were deposited as specimens in the MSB, University of New Mexico, USA.

Testing for marker effects

Upon release of geolocator-marked Gray Vireos in 2017, we monitored each individual for ~20 min for potential short-term marker effects on movement or other behaviors. We tested for marker effects on annual survival by comparing the apparent return rates in control and geolocator-marked individuals using Fisher's exact test of independence. To test for evidence of geolocators causing variable selection on morphological traits (e.g., Taff et al. 2018), we used a logistic regression to compare the 2017 (i.e., deployment year) mass and wing chord between geolocator-marked vireos that returned in 2018 and those that did not return or were not detected.

Geolocator analysis

We downloaded light-level data from each geolocator using software provided by the manufacturers (Migrate Technology Ltd, Cambridge, UK; BASTrak, Lotek UK Ltd, Wareham, UK). We analyzed all light-level data in *R* (R Core Team 2018). Specifically, we processed the data using the TwGeos package (Lisovski et al. 2016) to define sunrise and sunset transition periods (hereafter, "twilights") and to reformat drift-adjusted.lux files (Intigeo units) and.lig files (Lotek units) into "TAGS" format using the BAStag package (Wotherspoon et al. 2016). We used a twilight threshold of "1" for all tags (i.e., the lowest value above nighttime noise in the data; Lisovski et al. 2020).

To derive estimated stationary nonbreeding locations and associated uncertainty from geolocators, we used the template-fit method and movement models in FLightR (Rakhimberdiev et al. 2017) generally following the workflow outlined by Rakhimberdiev et al. (2016) and used in Kramer et al. (2017, 2018). We used the period during which we knew an individual Gray Vireo was at its breeding site to select calibration periods (i.e., the time when an individual was stationary at a known breeding location) and by visually inspecting light images (i.e., a visual depiction of each individual tag's light regime throughout the annual cycle) and location slopes (Lisovski et al. 2020). We constrained location estimates in movement models to a rectangular area that encompassed the breeding and nonbreeding distribution of Gray Vireos (18 – 43°N and -121 – -100°W) and used spatial masks that prevented them from remaining stationary (i.e., landing) on water bodies (Rakhimberdiev et al. 2016, 2017). However, we allowed individual movement locations to occur overwater and we allowed mean likelihood surface estimates for wintering locations to occur over water because there were islands in the region, and we did not want to bias otherwise objective nonbreeding estimates by forcing them toward the mainland. We also limited the maximum flight distance between subsequent twilights to 1200 km based on estimates derived from initial model runs (Rakhimberdiev et al. 2016; Lisovski et al. 2020). Final movement models were run with one million particles and automated outlier exclusion (Rakhimberdiev et al. 2016).

We derived spatially explicit likelihood surfaces (Kramer et al. 2017; Delancey et al. 2020) for all twilights between 1 November 28 February ($n = 238$ twilights), or the subset of time when we assumed the bird was stationary at the nonbreeding site (because both female and male Gray Vireos defend winter territories; Bates 1987, 1992b). Some individuals ($n = 5$) appeared to experience environmental shading or light sensor occlusion during portions of the 1 November–28 February window; in those cases, we used a subset or different window of consecutive twilights during the nonbreeding period that were free of apparent shading or occlusion to derive more biologically plausible estimates (Kramer et al. 2017, 2018). We then averaged all likelihood surfaces and divided by the sum of the surface to create nonbreeding probability density functions to visualize the most parsimonious nonbreeding location for each individual with associated error (Kramer et al. 2017, 2018).

We estimated the nonbreeding location for each Gray Vireo by extracting the latitude and longitude coordinates from the highest probability cell (0.5 × 0.5° resolution) in the probability density function (Kramer et al. 2018; Delancey et al. 2020). We then averaged probability density functions for individuals from each breeding population to visualize population-level spatial patterns during the nonbreeding period. For normally distributed data, we used one-way ANOVAs and Tukey HSD post-hoc tests in *R* (R Core Team 2018) to compare characteristics of nonbreeding distribution and migration among the three breeding populations. Spring migration length and fall departure dates were not normally distributed (Shapiro-Wilk; $P < 0.05$); thus, we used Kruskal-Wallis tests in *R* to compare these characteristics among populations.

We estimated when each individual crossed latitude or longitude boundaries >±2° (Lisovski et al. 2020) from the corresponding breeding or nonbreeding site to determine migration timing (i.e., departure and arrival dates to and from the breeding and nonbreeding grounds) and associated variance. Most often, we used a longitude boundary because longitude is usually more accurate than latitude in geolocator analyses, especially around the equinoxes (Rakhimberdiev et al. 2016, 2017). However, when there was aberrant noise in longitude data during migration, we also used latitude boundaries. We used the "stationary.migration.summary" function in FLightR to identify probable stopovers, or periods during migration in which birds were stationary (i.e., locations ≥ 2 days using a probability cutoff of 0.1; Rakhimberdiev et al. 2016). The movement model is more generous in detecting movement and stopovers with smaller probability cutoffs (0.1 compared). For one individual we increased the probability cutoff to 0.2 to obtain a biologically reasonable estimate due to noise in the data (Rakhimberdiev et al. 2016; Lisovski et al. 2020).

Morphometric comparison of females and males

To confirm body-size differences between female and male Gray Vireos, we compared body mass, wing chord, and tail length measurements we collected over three years (2017–2019) at Sevilleta as part of a larger study. We averaged morphological measurements for individuals that we captured and measured in two or more years. We assessed data normality using Shapiro-Wilk tests. We used a Welch's two-sample *t*-test to compare female and male body mass. Wing chord of both females and males, as well as male tail length, were not normally distributed (Shapiro-Wilk; $P < 0.05$); thus, we used Mann-Whitney tests to compare wing chord and tail length of females and males. We included only females that were known to be weighed outside of the laying period in the comparison of mass between the sexes because the mass of a Gray Vireo egg ($\bar{x} = 1.9$ g, range 1.8–2.1 g; Hanna 1944; Barlow et al. 1999) can be ~17% of body mass and could inflate female mass measurements.

Testing for sex-based differential migration

To test for differences in female and male nonbreeding latitudes, and whether nonbreeding distribution patterns could be associated with differences in morphology between the sexes (Ketterson and Nolan 1983), we compared the nonbreeding latitude estimates (extracted from the highest probability cell of the probability density function; see above) between females and males using a Welch's two-sample *t*-test. Our sample sizes of nonbreeding location estimates were modest for female ($n = 3$) and male ($n = 9$; see results) vireos. The typical statistical concern with small sample sizes is Type II error (i.e., not detecting a difference that is in fact present; Zar 2010). However, to address the possibility of a Type I error (i.e., detecting a difference when it is in fact not present), we simulated additional female nonbreeding locations to increase the sample size. Specifically, we incrementally (i.e., one at a time) added 20 simulated female locations to a single latitude that was 2° latitude into the male latitudinal range (i.e., 4.6° south of the southernmost female highest probability cell and 2° south of the northernmost male highest probability cell) to test if a larger sample size of females, even with substantial overlap into the male latitudinal range (which we did not detect in real data) would affect our inference. Between females and males, we compared nonbreeding longitude, fall migration duration, spring migration departure date, breeding and nonbreeding arrival dates, and time spent on the nonbreeding grounds, all with Welch's two-sample *t*-tests. Fall departure date and spring migration duration were not normally distributed (Shapiro-Wilk; $P < 0.05$); therefore, we used Mann-Whitney tests for these two comparisons.

Testing for sex-based bias in light regimes

To assess whether differences in nonbreeding latitude estimates between females and males could be attributed to biased geolocator data rather than differential migration, we calculated the mean log-transformed daytime light level (i.e., light levels > 0) during the nonbreeding period for each geolocator-marked individual. We compared light intensity between females and males and to assess whether the sexes exhibited differences in daytime light regimes (i.e., differences in habitat associations or behavior leading to the use of more shaded areas by one sex) that could bias location estimates and cause artificial differences between sexes. We excluded Kirtland birds from these calculations because Lotek geolocators (.lig files) record a light index (max = 64 arbitrary units) rather than the full light spectrum as Intigeo geolocators do (.lux files; max ~70,000 lux; Lisovski et al. 2020), complicating comparisons of the relative light levels between Lotek and Intigeo tags. We used Welch's two-sample *t*-test to compare light intensity between females and males.

Estimating spatial migratory connectivity

We estimated the degree of spatial migratory connectivity among breeding and nonbreeding populations by calculating the Mantel correlation coefficient (r_M; Ambrosini et al. 2009) using the "calcMantel" function in the MigConnectivity package in *R* (Cohen et al. 2018).

The Mantel correlation compares the relationship between pairwise distance matrices in two subsequent periods of the full annual cycle (i.e., breeding locations and geolocator-derived maximum likelihood nonbreeding locations; see above). Populations with r_M values approaching −1 exhibit patterned dispersion in which individuals that breed closer together occur farther apart during the nonbreeding period. Strong migratory connectivity occurs in populations with r_M values near 1 wherein individuals from proximate breeding locations also occur closer together during the nonbreeding period. Values of r_M near 0 indicate weak migratory connectivity wherein individuals from distinct breeding populations mix and co-occur during the nonbreeding period (Cohen et al. 2018).

We assessed data normality (and thus whether data meet the assumptions of parametric tests) using Shapiro-Wilk tests. For analysis of variance (ANOVAs), *t*-tests, Mann-Whitney tests, Kruskal-Wallis tests, and logistic regression, we considered $\alpha = 0.05$ to indicate statistical significance. Estimates are presented as means ± SD unless specified otherwise.

Results

We marked 48 Gray Vireos from three breeding sites with geolocators in 2017 (Table 1). Of these 48 individuals, we re-sighted 38% in 2018 ($n = 18$; Table 1), excluding one geolocator-marked male that returned carrying only the harness and was censored from all analyses because we could not determine when the individual lost the geolocator. We retrieved 15 geolocators across all three sites ($n = 9$ at Sevilleta, $n = 4$ at Kirtland, and $n = 2$ at Abajos; Table 1) and recovered usable data from 12 units ($n = 7$ Sevilleta, $n = 3$ Kirtland, $n = 2$ Abajos), of which 3 were from females ($n = 2$ Sevilleta, $n = 1$ Abajos) and 9 were from males ($n = 5$ Sevilleta, $n = 3$ Kirtland, $n = 1$ Abajos). Three geolocator-marked individuals ($n = 1$ female Sevilleta, $n = 1$ male Kirtland, $n = 1$ male Abajos) returned and were detected in 2018 but were not recaptured.

Marker effects

Most geolocator-marked Gray Vireos did not exhibit behavioral changes in the 20 min observation period after marking. Some individuals took up to 5 min to acclimate to geolocators after release, exhibiting behaviors such as preening and picking at the harness, but all quickly returned to behaviors indistinguishable from pre-marking activities. Of the 50 control individuals we banded at Sevilleta in 2017, 52% were observed to have returned in 2018 ($n = 26$). We detected no difference between the apparent return rates of Sevilleta geolocator-marked individuals (43%; Table 1) and control individuals (Fisher's exact test odds ratio = 0.7, $P = 0.62$). Apparent return rates

Table 1. Sample sizes and apparent return rates for light-level geolocator-marked Gray Vireos (*Vireo vicinior*) from three breeding populations: Sevilleta National Wildlife Refuge, New Mexico, USA; Abajos Mountains, Utah, USA; and Kirtland Air Force Base, New Mexico, USA.

	Sevilleta, NM		Abajos, UT		Kirtland, NM	
Sex	Marked	Returned (Recaptured)	Marked	Returned (Recaptured)	Marked	Returned (Recaptured)
Female	7	3 (2)	3	1 (1)	0	N/A
Male	16	7 (7)	9	2 (1)	13	5 (4)
Total	23	10 (9)	12	3 (2)	13	5 (4)

were also similar between geolocator-marked and control individuals when considering sexes independently (female odds ratio = 0.8, $P > 0.95$; male odds ratio = 0.8, $P = 0.75$). Of the geolocator-marked individuals at Sevilleta, mass and wing chord at the time of geolocator deployment had no apparent association with return rate the following year ($\beta_{\text{mass}} = 0.2 \pm 0.3$ SE, $P = 0.51$; $\beta_{\text{wing}} = -0.3 \pm 0.2$ SE, $P = 0.08$), providing no evidence for a relationship between morphology and apparent return rate for Gray Vireos carrying geolocators.

Nonbreeding location estimates

We estimated that Gray Vireos from Sevilleta occurred along the Baja California Peninsula, Mexico and possibly the surrounding islands during the nonbreeding season. We estimated that individuals breeding at Kirtland occurred generally in Sonora, Mexico and those breeding at Abajos occurred on or near Guadalupe Island, Mexico and in southern California, USA during the stationary nonbreeding season (Fig. 2).

Morphometric comparison of females and males

Body mass of non-gravid female Gray Vireos ($\bar{x}_{\text{female}} = 13.0 \pm 0.8$ g, $n = 23$) was 0.7 g (~6%) greater than males ($\bar{x}_{\text{male}} = 12.3 \pm 0.7$ g, $n = 84$; $t = 3.6$, df = 33.3, $P < 0.01$). Female wing chord ($\bar{x}_{\text{female}} = 64.0 \pm 1.5$ mm, $n = 51$) was 0.6 mm (~1%) shorter than male wing chord ($\bar{x}_{\text{male}} = 64.6 \pm 1.8$ mm, $n = 82$; $W = 1673$, $P = 0.04$). Tail length was similar between females ($\bar{x}_{\text{female}} = 60.3 \pm 2.6$ mm, $n = 34$) and males ($\bar{x}_{\text{male}} = 60.4 \pm 3$ mm, $n = 69$; $W = 1204$, $P = 0.93$). These results indicate that female Gray Vireos are larger-bodied than males, but the difference is primarily in body mass and not in flight-feather length.

Sex-based differences in migration

Our nonbreeding location estimates suggested that all female Gray Vireos we monitored occurred north of all males we monitored (Fig. 3). We estimated that female Gray Vireos occurred on average 4.7° latitude (95% CI [1.6°, 7.8°]; ~520 km) north of males during the nonbreeding season ($\bar{x}_{\text{female latitude}} = 32.4° \pm 1.3$, 95%CI [29.1°, 35.7°]; $\bar{x}_{\text{male latitude}} = 27.7° \pm 2.2$, 95%CI [26.0°, 29.4°]; $t = 4.4$, df = 6.2, $P < 0.01$; Fig. 3). Incrementally adding 20 simulated female nonbreeding locations outside of the observed female latitudinal range that we observed and substantially overlapping into the male latitudinal range (i.e., at 28.7°, or 2° south of the northernmost male) did not change the results of the statistical test ($p < 0.03$), suggesting our results are robust despite modest sample sizes. We found no difference in nonbreeding longitude between females and males ($\bar{x}_{\text{female longitude}} = -115.4° \pm 3.6$; $\bar{x}_{\text{male longitude}} = -113.5° \pm 4.2$; $t = -0.8$, df = 4.1, $P = 0.47$; Fig. 2). Between females and males, we found no evidence for a difference in fall migration duration ($\bar{x}_{\text{female}} = 30 \pm 22$ days; $\bar{x}_{\text{male}} = 25 \pm 18$ days; $t = 0.4$, df = 2.9, $P = 0.75$), spring migration duration ($\bar{x}_{\text{female}} = 18 \pm 7$ days; $\bar{x}_{\text{male}} = 23 \pm 21$ days; $W = 13$, $P = 0.92$), migration departure or arrival dates ($p > 0.05$ for all comparisons), or length of time spent on the nonbreeding grounds ($\bar{x}_{\text{female}} = 224 \pm 21$ days; $\bar{x}_{\text{male}} = 194 \pm 22$ days; $t = 2.0$, df = 3.8, $P = 0.11$). We found no evidence for a difference in log-transformed light levels during the nonbreeding period between females and males ($\bar{x}_{\text{female}} = 2.2 \pm 0.5$; $\bar{x}_{\text{male}} = 3.1 \pm 0.8$; $t = -2.0$; df = 5.7; $P = 0.10$), indicating that observed differences in the nonbreeding latitude location

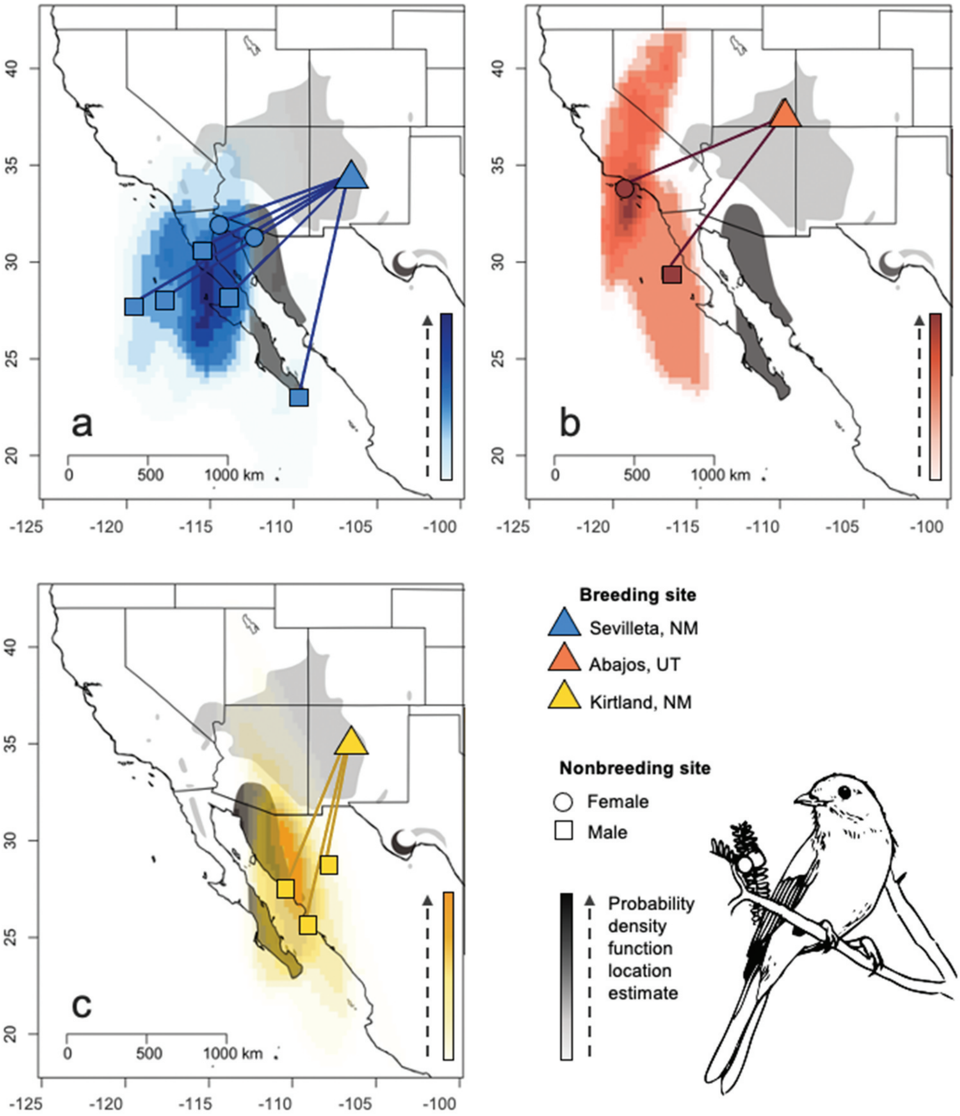

Figure 2. Estimated nonbreeding locations of 12 Gray Vireos (*Vireo vicinior*) from three breeding populations: Sevilleta National Wildlife Refuge, New Mexico (a), Abajo Mountains, Utah (b), and Kirtland Air Force Base, New Mexico, USA (c). Population-level average nonbreeding probability density functions are presented (color heatmaps). Individual nonbreeding location estimates are indicated and represent the highest probability cell extracted from individual female (circles) and male (squares) nonbreeding probability density functions. We derived population-level average nonbreeding probability density functions by averaging the 25th percentile probability density functions of individuals from the same population to aid in visualization of core use areas. Lines between breeding populations and individuals emphasize general directionality and dispersion, not actual migration routes. Locations are plotted on distribution maps accessed from BirdLife International and Handbook of the Birds of the World (2021), which notably does not include recently confirmed breeding and nonbreeding location for this species (see Methods).

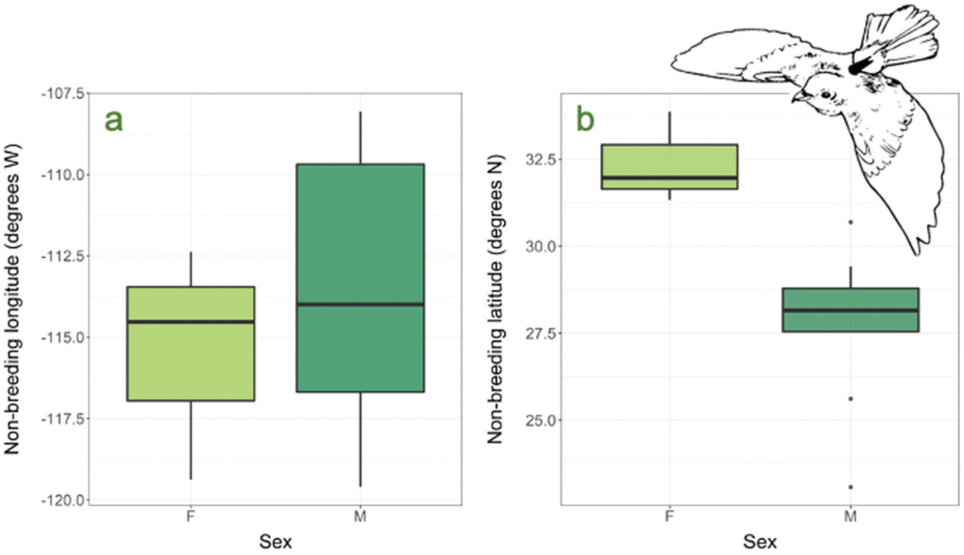

Figure 3. Geolocator-derived estimates (i.e., extracted highest probability cells from nonbreeding probability density functions) of nonbreeding longitude (a) and nonbreeding latitude (b) of Gray Vireo (vireo vicinior) females ($n = 3$; light green) from two populations (Sevilleta National Wildlife Refuge, New Mexico; Abajo Mountains, Utah, USA) and males ($n = 9$; dark green) from three populations (Sevilleta National Wildlife Refuge, New Mexico; Abajo Mountains, Utah; Kirtland Air Force Base, New Mexico, USA) tracked from 2017–2018.

estimates between sexes were likely not attributable to artifacts of habitat-related shading in the light-level data.

Population spatial migratory connectivity

Kirtland Gray Vireos occurred on average 5.5° longitude (95% CI [0.1°, 11.0°]; ~600 km) east of those from Sevilleta (one-way ANOVA, $F_{2,9} = 6.6$, $P = 0.02$; post-hoc Tukey test, $P = 0.05$) and 8.8° longitude (95% CI [1.6°, 16.0°]; ~1000 km) east of those from Abajos during the stationary nonbreeding season (post-hoc Tukey test, $P = 0.02$). Gray Vireos from Abajos and Sevilleta occupied similar nonbreeding longitudes (post-hoc Tukey test, $P = 0.37$). We found no differences among populations in nonbreeding latitude (one-way ANOVA, $F_{2,9} = 1.4$, $P = 0.28$). Regardless of population, deployment longitude and latitude were not significantly associated with nonbreeding latitude (one-way ANOVA; $F_{1,10} = 1.7$, $P = 0.22$) or longitude (one-way ANOVA; $F_{1,10} = 3.0$, $P = 0.12$). We estimated that the spatial migratory connectivity of Gray Vireos between breeding and nonbreeding sites was weak-to-moderate ($r_M = 0.3$).

Migration characteristics

Gray Vireos that bred farther north (i.e., at Abajos) spent more time on the nonbreeding grounds (one-way ANOVA, $F_{2,8} = 5.8$, $P = 0.03$) compared to Kirtland (Post-hoc Tukey test, $P = 0.03$) and Sevilleta (Post-hoc Tukey test, $P = 0.05$), a pattern that appears to be driven by a non-significant but potentially meaningful trend in which Abajos vireos departed from the nonbreeding grounds almost one month later (one-way ANOVA, $F_{2,8} = 4.2$, $P = 0.06$). We did not find evidence for population-level differences in migration duration or spring or fall migration arrival timing (all comparisons $P > 0.05$).

For all populations combined, the average breeding-grounds departure date (i.e., fall migration initiation date) was 7 September ±22 days; fall migration took an average of 26 ± 18 days ($n = 12$). The average nonbreeding site arrival of Gray Vireos from all populations combined was 3 October ± 12 days. Average nonbreeding site departure date (i.e., spring migration initiation date) was 22 April ±17 days; spring migration took an average of 22 ± 18 days ($n = 11$). Average breeding-season arrival date for Gray Vireos was 14 May ± 19 days ($n = 11$). We estimated that five of twelve (42%) Gray Vireos made stopovers during fall migration and that five of eleven (45%) made stopovers during spring migration. Of the 11 individuals carrying geolocators that recorded both fall and spring migration, we estimated that three (27%) made stopovers during both fall and spring migrations.

Discussion

We used light-level geolocators to track the annual migratory movements and estimate nonbreeding locations of Gray Vireos from three breeding sites in New Mexico and Utah, USA. We found no evidence that carrying a geolocator reduced the apparent return rate of Gray Vireos or that apparent return rate was associated with morphological characteristics of geolocator-marked individuals. With the caveat that our sample size was modest, female Gray Vireos we tracked appeared to overwinter ~5° latitude north of males from the same breeding populations. Our data suggest that, regardless of sex, Gray Vireos from the three populations we monitored exhibited nuanced nonbreeding dispersion patterns wherein the more distantly separated populations (i.e., Sevilleta and Abajos) wintered more closely together than the two nearest breeding populations (i.e., Sevilleta and Kirtland), which we estimated overwintered in distinct regions separated by the Gulf of California.

In general, we found a southwestward movement pattern from breeding to nonbreeding locations in Gray Vireos. This pattern contrasts with the southeastward movement pattern in two congeners, the Cassin's Vireo (*Vireo cassinii*; Hedley 2019) and Red-eyed Vireo (*V. olivaceus*; Callo et al. 2013). Migration duration in Gray and Cassin's vireos appears to be similar (Hedley 2019). We attempted to describe migration stopover patterns, but it appears that most Gray Vireos either do not make many stopovers or that, because they are relatively short-distance migrants, stopovers can be difficult to detect using geolocator data, especially compared to longer-distance migrants (see information about stopover detection; Lisovski et al. 2020). Even using conservative cutoff probabilities, we did not detect many apparent stopovers, consistent with previous predictions in the species (Bates 1987; Unitt 2000). Nevertheless, Gray Vireos did not appear to congregate at staging areas or bottlenecks (Warnock 2010). However, more information is needed on finer-scale migratory movements for this species, which may not be possible with light-level geolocators and may require, for example, barometric pressure geolocators (Rhyne et al. 2024).

Our results suggest weak-to-moderate spatial migratory connectivity ($r_M = 0.3$) among three Gray Vireo breeding populations, consistent with many other songbirds studied to-date (Finch et al. 2017). However, migration ecology (and thus migratory connectivity) of birds breeding in western USA is under-studied (McKinnon and Love 2018; Hedley 2019), limiting comparison among species in similar systems. Finch et al. (2017) demonstrated that species with relatively restricted nonbreeding distributions are more likely to exhibit weak migratory connectivity (as measured by the Mantel correlation coefficient, r_M) even if the spread of individuals within populations was relatively low. Similarly, Cresswell and Patchett (2024) show that species with populations that migrate shorter distances appear to exhibit greater overlap during the nonbreeding period. Gray Vireos have relatively restricted nonbreeding distributions compared to many other migratory songbirds, which could increase the probability of observing weaker estimates of migratory connectivity using the Mantel correlation coefficient. Additional information on the migratory behavior and nonbreeding dispersion of other Gray Vireo populations could add context to our results, reduce the uncertainty inherent to quantifying migratory connectivity (Cohen et al. 2018), and further characterize the strength of migratory connectivity in this species, especially because such patterns can sometimes emerge only when sampling occurs across greater spatial scales (Finch et al. 2015; Knight et al. 2021; Mancuso et al. 2021; Sharp et al. 2023).

Our results suggest that the female Gray Vireos we tracked overwintered ~5° latitude (> 500 km) north of males from the same breeding populations, indicating potential sex-based differential migration (Ketterson and Nolan 1983). This trend may initially appear to contradict previous observations that female and male Gray Vireos co-occur during the nonbreeding period (Bates 1987, 1992b). However, both patterns (i.e., potential sex-based differential migration, nonbreeding co-occurrence of sexes) could be explained if females and males co-occurring during the nonbreeding period were from different breeding populations. This nuanced pattern could be further explored by collecting genetic samples from nonbreeding Gray Vireos along a north-south transect to assess latitudinal variation in sex ratio (e.g., Ketterson and Nolan 1976).

We compared light regimes recorded by geolocators carried by females and males to assess the alternative hypothesis that our observations of females occurring farther north than males was an artifact of sex-specific light conditions (e.g., shading). Sex-specific differences in light regime could arise if sexes displayed different habitat associations (e.g., Morton 1990; Bennett et al. 2019) or behaviors that altered the amount of ambient light detected by the geolocator (e.g., a tendency for females to forage in the shaded interior of shrubs). However, female and male Gray Vireos exhibit similar nonbreeding habitat associations (Bates 1987, 1992a, 1992b), and we found no evidence of behavioral differences in the light regimes experienced by female and male Gray Vireos during the nonbreeding period. Further, our post-hoc simulation of increased sample size and forced overlap between female and male nonbreeding latitudes did not meaningfully change our results, suggesting that our initial results are robust despite modest sample sizes. However, additional tracking data are needed to confirm this sexual segregation trend, which would be intriguing because, in most other songbirds that exhibit known sexual segregation, females typically occur farther south during the nonbreeding season and thus migrate longer distances than males (Komar et al. 2005; Catry et al. 2006; MacDonald et al. 2015; Briedis and Bauer 2018).

Differential migration may manifest as differences in timing, routes, habitat associations, migratory connectivity, and nonbreeding geographic sexual segregation, and can contribute to differences in breeding population sex ratios and survival (Ketterson and Nolan 1983; Komar et al. 2005; Catry et al. 2006; Briedis and Bauer 2018). The potential sex-based pattern we observed is contrary to that of most other songbirds that exhibit sexual segregation, in which females generally occur farther south during the nonbreeding season and migrate longer distances than males (Komar et al. 2005; Catry et al. 2006; MacDonald et al. 2015; Briedis and Bauer 2018).

Females wintering farther north than males is evident in at least two other North American songbirds (i.e., Indigo Bunting [*Passerina cyanea*], Johnston 1970; Komar et al. 2005; and Painted Bunting [*Passerina ciris*]; Sharp 2021), one woodpecker (Northern Flicker [*Colaptes auratus*], Gow and Wiebe 2014), and species in several other avian orders (Cristol et al. 1999). The body-size hypothesis predicts that in songbirds, individuals of the smaller-bodied sex (i.e., often females) migrate farther because individuals of the heavier-bodied sex may be able to tolerate colder temperatures or inclement weather associated with relatively high latitudes or elevations (Ketterson and Nolan 1983; Cristol et al. 1999; Gow and Wiebe 2014). Adult female Gray Vireos in our study area weighed ~6% more than males, consistent with other data on the species (Pyle 1997; Barlow et al. 1999), making their apparently shorter migrations consistent with the body-size hypothesis. However, previous applications of the body-size hypothesis have focused on species that occur in colder regions or over broader, less geographically restricted nonbreeding distributions (e.g., Dark-eyed Juncos; Ketterson and Nolan 1979) wherein latitudinal temperature gradients are typically greater than those throughout the Gray Vireo nonbreeding distribution (see Wang et al. 2016). If differential migration does occur as our data suggest, there are likely multiple selective pressures mediating differential migration in Gray Vireos, as proposed in Dark-eyed Juncos (Ketterson and Nolan 1976, 1983). Larger sample sizes of marked female and male Gray Vireos would provide additional power to confirm this trend.

Regardless of the evolutionary factors underlying potential latitudinal segregation between female and male Gray Vireos during the nonbreeding season, the potential presence of such segregation would likely hold significant conservation implications. A “seesaw” climate pattern persists in the Baja California Peninsula during which northern Mexico is usually dry while southern Mexico is wet and vice versa (Méndez and Magaña 2010) Therefore, females and males from the same breeding populations may experience dramatically different conditions (e.g., droughts or hurricanes) on their nonbreeding grounds (Rockwell et al. 2012; Latta et al. 2016; Bennett et al. 2019). Any geographic variability in future climate conditions or land-use change between the northern and southern portions of the nonbreeding distribution could affect females and males from the same breeding population differently and could cause sex-specific population bottlenecks either through decreasing nonbreeding survival rate, or through indirect carry-over effects that reduce productivity on the breeding grounds (Harrison et al. 2011; Latta et al. 2016). The possibility of future geographic differences in environmental conditions was recently demonstrated when Hurricane Hilary made landfall on 20 August 2023 and brought record rainfall and flooding along the Baja California Peninsula and southern California but had little impact on the rest of Gray Vireo nonbreeding distribution (NASA 2023; https://www.earthobservatory.nasa.gov/; accessed 24 Aug 2023). Information from additional populations, repeat tracks of individuals among years, and greater sampling effort of both female and male Gray Vireos would further our understanding of their migratory ecology and inform full annual cycle management for this under-studied species of conservation concern.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Permits and ethics protocols

We captured and handled Gray Vireos in compliance with Institutional Animal Care and Use Committee (IACUC) protocols at the University of Toledo (#108708) and the University of New Mexico Museum of Southwestern Biology (16200406 MC), annual Sevilleta Special Use Permits, NMDGF Permits (3673 and), a USFWS Permit (MB094297), and USGS Bird Banding Permits (24072 and).

Statement on the use of generative AI

Generative AI was not used in the production of this manuscript.

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