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LIGHT-LEVEL GEOLOCATORS REVEAL STRONG MIGRATORY CONNECTIVITY AND WITHIN-WINTER MOVEMENTS FOR A COASTAL CALIFORNIA SWAINSON'S THRUSH (*CATHARUS USTULATUS*) POPULATION

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ABSTRACT.—We used light-level geolocators to describe the migratory geography of Swainson's Thrushes (*Catharus ustulatus*) from a breeding population in central coastal California. Between 11 June and 20 July 2010, we attached geocator tags to 35 Swainson's Thrushes at three sites in Marin County, California, and recovered 12 in the following two breeding seasons. All 12 birds spent the winter in Mexico, north of the Isthmus of Tehuantepec. Eleven of the birds went to the Jalisco region in western Mexico, but two of those birds (18% of total) moved east in midwinter to either the Sierra Madre Oriental or Sierra Madre del Sur; the 12th bird went directly to one of the latter regions. The return rate over the next 2 years for tagged birds (34%) was not statistically lower than that for control birds (45%). We combined our results with the results of an earlier study that used geolocators on Swainson's Thrushes from British Columbia to quantify the strength of migratory connectivity using Mantel's correlation coefficient. Our estimate of the strength of migratory connectivity for Swainson's Thrushes ($r_m = 0.72$) was much stronger than that reported using band returns of Barn Swallows (*Hirundo rustica*) in the Eastern Hemisphere ($r_m = 0.03$). To our knowledge, this is the first quantitative measure of migratory connectivity derived from geolocators. Received 4 December 2012, accepted 15 March 2013.

Key words: *Catharus ustulatus*, Mantel's correlation coefficient, Mexico, Neotropical, Palomarin, Swainson's Thrush, tag effects.

Geocalizadores Basados en Niveles de Luz Revelan Conectividad Migratoria Fuerte y Movimientos durante el Invierno en una Población Costera de *Catharus ustulatus* en California

RESUMEN.—Usamos geocalizadores basados en niveles de luz para describir la geografía migratoria de una población reproductiva de *Catharus ustulatus* de la costa central de California. Entre el 11 de junio y el 20 de julio de 2010 marcamos con geocalizadores a 35 individuos en tres sitios en el condado Marin, California, y recuperamos 12 de éstos en las dos temporadas reproductivas siguientes. Las 12 aves pasaron el invierno en México, al norte del istmo de Tehuantepec. Once de las aves fueron a la región de Jalisco en el occidente de México, pero dos de ellas (18% del total) se movieron al oriente en la mitad del invierno, hacia la Sierra Madre Oriental o a la Sierra Madre del Sur; el ave restante fue directamente hacia una de las anteriores regiones. La tasa de retorno durante los dos años siguientes para las aves marcadas (34%) no fue estadísticamente más baja que la de las aves control (45%). Combinamos nuestros resultados con los de un estudio anterior que usó geocalizadores en *C. ustulatus* de Columbia Británica para cuantificar la fuerza de la conectividad migratoria usando el coeficiente de correlación de Mantel. Nuestro estimado de la fuerza de la conectividad migratoria en *C. ustulatus* ($r_m = 0.72$) fue mucho mayor que el reportado usando recapturas de individuos de la especie *Hirundo rustica* marcados con anillos en el hemisferio oriental ($r_m = 0.03$). De acuerdo a lo que conocemos, esta es la primera medida cuantitativa de la conectividad migratoria derivada de geocalizadores.

IN THE CONTEXT of rapid climate change and ongoing habitat loss, any successful strategy for conserving migratory birds must address their full life cycle, including breeding, wintering, and migration (Sherry and Holmes 1996, Faaborg et al. 2010, Small-Lorenz et al. 2013) and the carryover effects among them (e.g., Reudink et al. 2009). To address this requires an understanding of the spatial linkages throughout the year (Martin et al. 2007). Our ability to link the breeding, migration stopover, and wintering locations of migratory songbirds is being transformed by

information from banding returns, isotopic and genetic variation, and, most recently, light-level geolocators (e.g., Ruegg and Smith 2002, Norris et al. 2006, Stutchbury et al. 2009, Seavy et al. 2012, Tøttrup et al. 2012). Furthermore, by combining results from studies across multiple geographic locations, we are beginning to build a sophisticated understanding of migratory connectivity (i.e., the degree to which individuals that breed in one area migrate to the same non-breeding area; Webster et al. 2002) for some species (Kelly et al. 2005, Martin et al. 2007).

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Swainson's Thrush (*Catharus ustulatus*) has emerged as one of the models for understanding the ecology and migratory connectivity of Neotropical migrants (Ruegg and Smith 2002, Gardali et al. 2003, Kelly et al. 2005, Delmore et al. 2012, LaManna et al. 2012). Swainson's Thrushes breed along the west coast, in sections of the Rocky Mountains, and throughout the northern continental interior of North America and winter in southern Mexico and Central and South America (Mack and Yong 2000). Using stable isotopes, Ruegg and Smith (2002) found that migratory patterns in Swainson's Thrush track shifts in habitat that occurred during the Late Pleistocene. The zone of contact between the two recognized subspecies groups, the russet- and olive-backed groups, forms a migratory divide, with birds on either side having radically different migration strategies, as illustrated recently with light-level geolocators (Delmore et al. 2012).

Despite this relatively extensive body of work, our knowledge of the migratory connectivity of Swainson's Thrushes remains incomplete. Individuals from the western- and northernmost portions of the Swainson's Thrush wintering range were not sampled in any of the studies cited above, leaving the origin of these birds undocumented. None of the ~34,000 Swainson's Thrushes banded or recovered in California have definitively shown a link between breeding and wintering locations for an individual (U.S. Bird Banding Lab and PRBO Conservation Science unpubl. data). Furthermore, there has been relatively little investigation into whether males and females winter in different regions, a pattern observed in some songbirds (Ketterson and Nolan 1976, Komar et al. 2005, Mazerolle and Hobson 2007). Finally, recent geolocator work suggests that individuals of some species of Neotropical migrants may have two distinct wintering locations (Heckscher et al. 2011), including Swainson's Thrushes (Delmore et al. 2012), but the prevalence of this pattern is unknown.

To investigate the migratory connectivity of Swainson's Thrush, we used light-level geolocators to map the species' migratory geography from three breeding sites north of San Francisco Bay in central coastal California. Our objectives were to (1) identify the wintering grounds of individuals breeding in this region, (2) evaluate whether males and females use different wintering areas, (3) assess potential tag effects on these individuals, and (4) assess the strength of migratory connectivity for this species, using results from this and other studies.

METHODS

Study location and field methods.—We attached archival geolocators to 35 Swainson's Thrushes captured in mist nets at three sites in Marin County, California. Thirteen birds were tagged at PRBO Conservation Science's (hereafter PRBO) Palomarin Field Station (latitude 37.93°, longitude -122.74°) and 11 birds at Muddy Hollow (38.05°, -122.87°), both in Point Reyes National Seashore; also, 11 birds were tagged at Pine Gulch Creek (37.92°, -122.69°) in Marin County Open Space District's Bolinas Lagoon Open Space Preserve. Palomarin is characterized by a mix of coastal scrub, dominated by Coyotebrush (*Baccharis pilularis*), Douglas-fir (*Pseudotsuga menziesii*), and mixed evergreen hardwood forest dominated by Coastal Live Oak (*Quercus agrifolia*) and California Laurel (*Umbellularia californica*). Both Muddy Hollow and Pine Gulch are riparian sites dominated by Arroyo Willow (*Salix lasiolepis*) and Red Alder (*Alnus rubra*), with an understory of

blackberries (*Rubus ursinus* and *R. armeniacus*) and other species (for detailed descriptions, see Samuels et al. 2005, Jennings et al. 2009).

Between 11 June and 20 July 2010, we attached geolocators to 19 male and 16 female Swainson's Thrushes. We used Mk12-S ($n = 29$) and Mk10-S ($n = 6$) geolocators developed by the British Antarctic Survey (BAS) with 15-mm-long stalks positioned at a 30° angle. We attached tags with a leg-loop harness (Rappole and Tipton 1991) of Kevlar 450-gauge ($n = 22$) or 800-gauge ($n = 13$) thread. The average mass of the harness and tag together was 0.9 g (0.7–1.6 g), 3% of the bird's mass. Each bird was banded with a federal band and a color band. We determined the age of each bird (only adults were tagged) and weighed the bird to the nearest 0.1 g before and after the geolocator tag was attached. We determined the sex of tagged birds using the presence of a brood patch (female) or cloacal protuberance (male). Upon recapture of the birds in the following two springs, we removed the geolocator tag and collected the same data as during the initial capture.

We captured an additional 29 control Swainson's Thrushes at the three sites during the same period and collected all the same data, fitting each individual with an aluminum band but no geolocator tag or color band.

Data analysis.—To test for differences in return rates between geolocator-tagged and control birds, we used a Pearson's chi-square test and compared birds that were recaptured in either 2011 or 2012 with those that were not recaptured.

The geolocators we used measured light intensity every 1 min and recorded the maximum measurement every 2 min (Mk12-S) or 10 min (Mk10-S). Light intensity was recorded on an arbitrary scale between zero and 64. We used BASTRAK software (BAS) to download light data. Because the light intensity records of the twilight transitions were influenced by significant shading, we began by taking the 2-min data sets and collapsed them to the maximum light level recorded over 10 min. Although this reduced the temporal resolution of the data, it had the benefits of making the time interval comparable between the Mk12-S and Mk10-S tags and simplifying the process of scoring the twilight transitions.

To analyze the data, we used the threshold method performed with the GeoLight package (Lisovski and Hahn 2012) in R, version 2.15.2 (R Development Core Team 2008). The threshold method is based on sunrise and sunset times that are identified as the time points when the light intensity passes a specific threshold. We used a threshold value of 1.1 to identify sunrise and sunset times. For most birds ($n = 10$), we determined the sun elevation value using a post-deployment (on bird) calibration period from 20 July to 31 July 2010. For the other two birds (tag nos. 13310 and 21022), we used a slightly later calibration period (15–30 August 2010) because the pattern of shading during the winter twilight transitions was more similar to the pattern in August than to that in July. Calculated sun elevation angles ranged between -3.6 and -0.2, and we used the elevation angle calculated for each individual for the analyses.

To summarize temporal trends in longitude, we used a loess smoothing function (span = 0.2, degrees = 2) in R and plotted the smoothed line as a function of date for all individuals. We then visually inferred migration and wintering periods on the basis of changes and stabilization of longitude estimates. Because we relied only on longitude to infer migration periods, our estimates of the beginning and end of migration movements should

be interpreted cautiously; they may be misleading if birds made substantial movements that were primarily north–south. To test for differences in migration rates between fall and spring (sexes combined within each season) and to compare the rate of fall migration for males with that of females, we used Welch's *t*-test.

We found that there was substantial error in latitude, especially around the equinox periods. To reduce this variability when mapping the wintering locations, we omitted latitude estimates within 15 days of fall and spring equinoxes and further reduced the variation in latitude by using the "distanceFilter" function in the GeoLight package (Lisovski and Hahn 2012) to remove all locations in which the distance between two twilight periods exceeded what could be covered by a bird traveling 50 km hour⁻¹.

Using the filtered latitude and longitude estimates, we followed Bairlein et al. (2012) and mapped the wintering areas with kernel densities that encompassed 50% of the maximum density for each wintering period. We performed the kernel estimation on a 40 × 40 grid using the R package "adehabitat" with the ad hoc method for estimating the smoothing parameter and the bivariate normal kernel (Calenge 2006).

We combined our results with those of Delmore et al. (2012) to generate a spatial matrix of the pairwise distance between breeding locations for all individuals and then a second matrix with the pairwise distance between the wintering locations for all individuals. For individuals that moved in midwinter, we used the location during the later winter period, because all individuals that moved spent the most time at the second winter location. We then quantified the correlation between these two matrices using a Mantel test, following the procedure for quantifying the strength of migratory connectivity described by Ambrosini et al. (2009). We performed the Mantel test with the R package "ade4" and used 9,999 random permutations to evaluate the statistical significance of the correlation coefficient (Dray and Dufour 2007). Statistics are reported as means ± SD.

RESULTS

Wintering areas.—Eleven of the 12 tagged birds migrated to the region around the western Mexican states of Nayarit, Jalisco, and Colima (hereafter "Jalisco region"; Fig. 1 and Appendix). Two of the 11 individuals moved from the Jalisco region east to either the Sierra Madre Oriental region or the Sierra Madre del Sur region (Fig. 1G, K); one was a male from Pine Gulch that stayed in the Jalisco region from approximately 26 October to 8 December 2010 before migrating farther east, where he spent most of the winter (Fig. 1G). This bird moved again in March, westward and perhaps back to the same general location in the Jalisco region, where he remained from 19 March to 13 April before migrating north. The other within-winter movement was a female from Palomarin that stayed in the Jalisco region from approximately 29 September to 6 November 2010 before moving east, where she stayed from approximately 2 December 2010 to at least 12 April 2011, when the tag battery died (Fig. 1K). One bird, a male from Pine Gulch, migrated directly to the eastern area (the only individual from all sites to do so) and spent the entire winter either in the Sierra Madre Oriental or the Sierra Madre del Sur (Fig. 1F). There were no apparent differences in wintering locations by sex or breeding site (Fig. 1).

Timing of migration.—On the basis of longitude, tagged male Swainson's Thrushes (*n* = 7) departed the breeding grounds

between 2 September and 1 October 2010, and females (*n* = 5) departed from 15 to 30 September. Males arrived on the wintering grounds between 30 September and 18 October 2010 (15–31 days later), whereas females arrived from 29 September to 18 October (14–18 days later). Males took an average of 18.9 ± 5.7 days and females an average of 15.8 ± 2.0 days, a difference that was not significant (*t* = 1.42, *df* = 6, *P* = 0.20). All but four of the batteries from the recovered geolocators died before spring migration (3 males and 1 female). The males departed the winter grounds between 6 and 15 April 2011 and arrived on the breeding grounds between 21 April and 28 May: 15, 20, and 43 days later. The female departed on approximately 19 April and arrived on the breeding grounds on approximately 11 May, taking 22 days to complete her trip north. We combined sexes and found no significant difference between migration rates in fall versus spring (*t* = -1.17, *df* = 3, *P* = 0.32).

Strength of migratory connectivity.—By combining our results with those published by Delmore et al. (2012; Fig. 2), we generated matrices of distances for breeding locations and wintering locations of 21 individual Swainson's Thrushes. The Mantel correlation coefficient (*r_m*) for these matrices was 0.72 (*P* < 0.001).

Effects of geolocators on return rates.—We recaptured 11 tagged birds in 2011 and 1 in 2012. Thus, we recaptured 12 of the tagged birds (34% of 35) and 13 of the untagged control birds (45% of 29); the rates of return did not differ statistically between treatments (χ^2 = 0.36, *df* = 1, *P* = 0.55). The date of initial recapture in 2011 was similar for both groups, ranging from 5 May to 22 July for tagged individuals and from 5 May to 21 July for control birds. Average original body mass of the 12 tagged birds that eventually returned with geolocators (mean = 30.3 ± 1.7 g) was similar to the average original body mass of the 23 tagged individuals that did not return (mean = 30.1 ± 2.0 g).

DISCUSSION

Our results provide information about the migratory connectivity of coastal California Swainson's Thrushes that was not described in analyses of band recoveries, genetics, or stable isotopes (Ruegg and Smith 2002, Kelly et al. 2005, U.S. Bird Banding Lab and PRBO unpubl. data). All but one of the birds in our geolocator study went to the same general region in western Mexico, although two birds eventually moved to a second winter location. The primary winter location for birds from our study was around the states of Nayarit, Jalisco, and Colima (which we refer to as the "Jalisco region"). Although the kernels showing the estimated winter area in our study often extend far beyond this region, we were able to narrow our focus to areas within our kernel estimates that are part of the Swainson's Thrush winter range because of earlier work that determined details of that range (Phillips 1991, Howell and Webb 1995). In the Jalisco region of Mexico, Swainson's Thrushes are considered fairly common to uncommon throughout the winter and occur primarily between 300 and 2,000 m in elevation (Howell and Webb 1995) and in relatively humid forests and shade-grown coffee plantations (S. N. G. Howell pers. comm.). There was only one bird that did not appear to go to the Jalisco region but instead went northwest of the Isthmus of Tehuantepec, either to the Sierra Madre Oriental or the Sierra Madre del Sur region.

Our results and those of Delmore et al. (2012) are suggestive of strong migratory connectivity (Fig. 2), but how strong is it? By combining data from our study and that of Delmore et al.

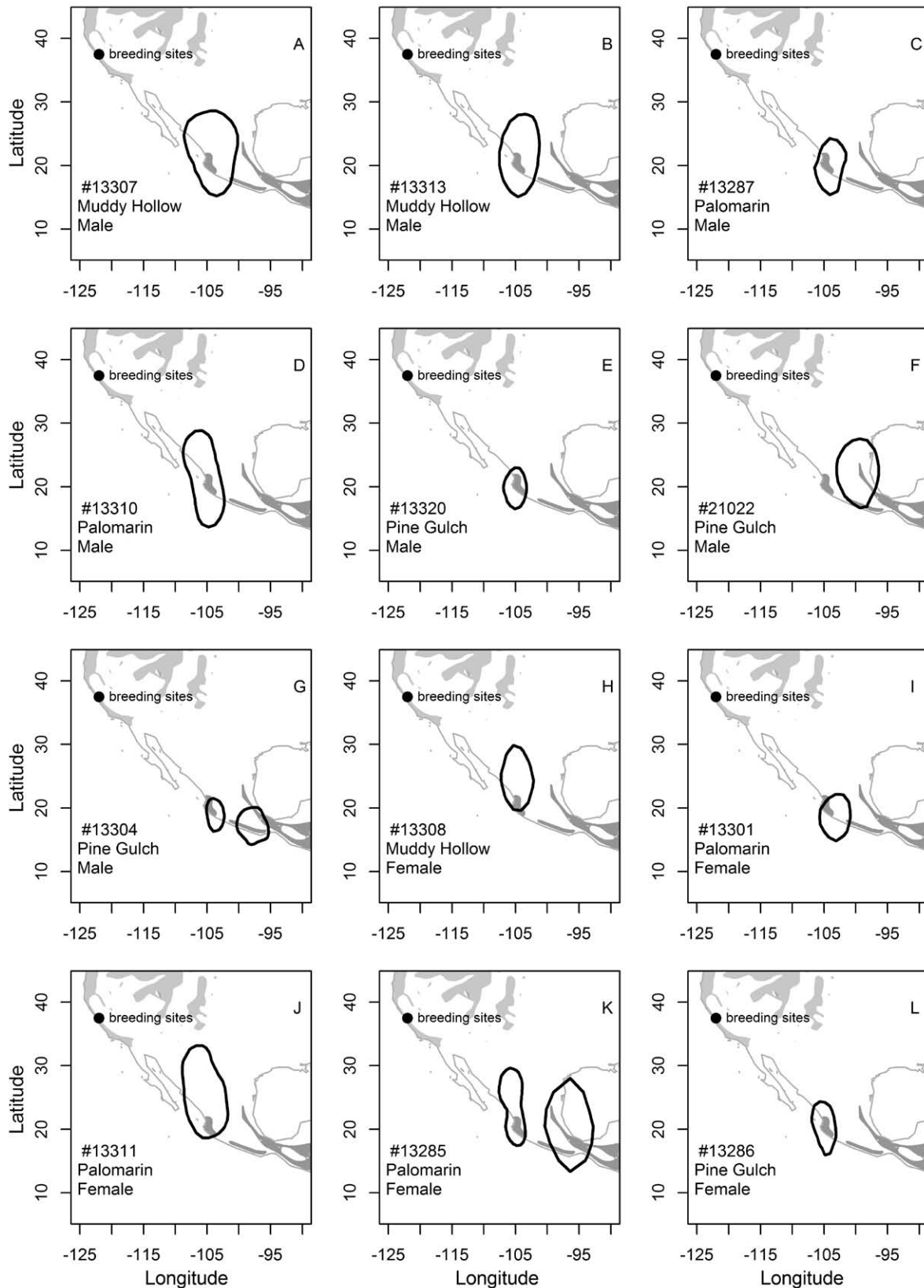


FIG. 1. Kernel density estimates encompassing 50% of the maximum density for each wintering area for 12 geolocator-tagged Swainson's Thrushes tagged in Marin County, California, in 2010. Breeding (light gray shading) and non-breeding (dark gray shading) ranges provided by NatureServe (2012).

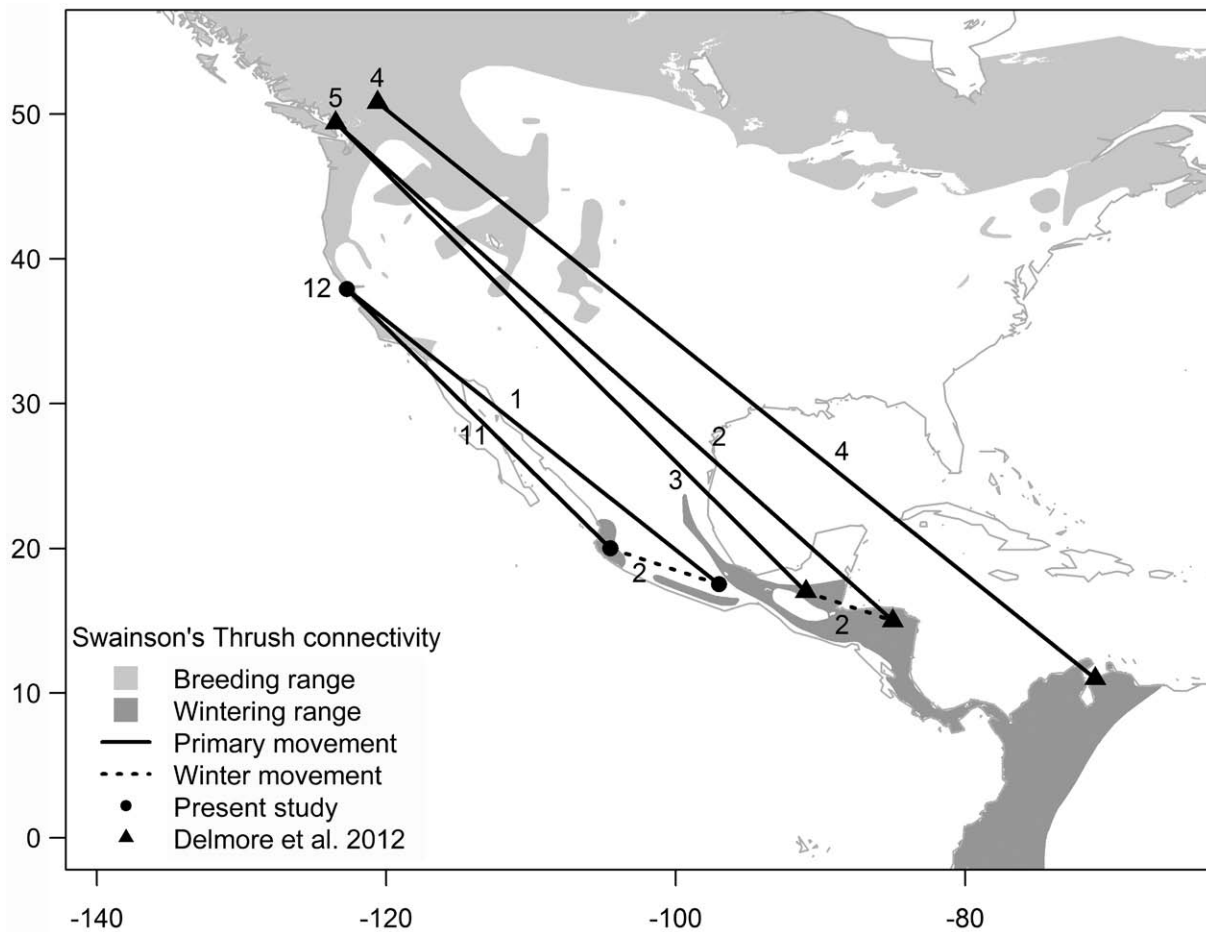


FIG. 2. Summary of two studies using geolocators to describe migratory connectivity of Swainson's Thrushes that breed in coastal California (present study) and British Columbia (Delmore et al. 2012). Wintering locations have been grouped into general regions to simplify the map. Numbers at the breeding location indicate the number of geolocator birds that were recaptured, and numbers along lines represent the number that spent the non-breeding season at the location indicated. Dashed lines represent movements from the first to a second site during the non-breeding season. Range map provided by NatureServe (2012).

(2012), we quantified the strength of migratory connectivity using the Mantel correlation coefficient to describe the similarity between the distances of individual birds on their breeding grounds and the distances between these same birds on their wintering grounds (Ambrosini et al. 2009). Using this method, the strength of migratory connectivity for Swainson's Thrushes ($r_m = 0.72$) was greater than that estimated from banding recoveries of Barn Swallows in the Eastern Hemisphere ($r_m = 0.03$; Ambrosini et al. 2009) or from satellite tracking of Montagu's Harriers (*Circus pygargus*, $r_m = 0.50$; Trierweiler 2010).

The rapid advancement of geolocator technology will necessitate the development of new tools for quantifying migratory connectivity. To our knowledge, this is the first attempt to quantitatively describe the strength of migratory connectivity using geolocator data, and one of only a few studies to use the Mantel test approach (Ambrosini et al. 2009, Trierweiler 2010). This approach is relatively simple compared to some other methods for estimating the strength of connectivity, such as estimating transition probabilities from breeding to wintering areas (Marra et al. 2006). Given this simplicity, this statistic

should be interpreted cautiously when comparing species that differ in geographic range and migratory behavior.

Although most of the birds in our study appeared to remain at their initial location for the entire winter, two birds moved east in December after spending approximately 5–6 weeks in western Mexico, one of which also appeared to move a third time, possibly back to its original wintering location in western Mexico, where it remained for 3–4 weeks before the onset of spring migration. Midwinter movements have been documented in other geolocator studies with thrushes: Delmore et al. (2012) observed 3 of 10 Swainson's Thrushes moving to a second location at the end of December among sites in southern Mexico and Northern Central America, and Heckscher et al. (2011) documented Veeries (*Catharus fuscescens*) moving to a second location within the Amazon Basin in midwinter. To date, it is only possible to document such midwinter movements and the approximate duration of time spent in each region through geolocator technology.

We did not find consistent differences in wintering locations between males and females. If sexual segregation occurs, it may be

at a finer spatial scale than we can detect with geolocators, such as by habitat or elevation (Lynch et al. 1985, Marra et al. 1993, Smith et al. 1993, Townsend et al. 2012).

Birds traveled from breeding to wintering sites in an average of 18 days in the fall, and in an average of 25 days in spring. Multiple geocator studies have found that birds migrate faster in spring than in fall (e.g., Stutchbury et al. 2009, Bächler et al. 2010, Tøttrup et al. 2012), including the Swainson's Thrush (Delmore et al. 2012); the pattern in the present study was in the opposite direction, but the difference was not significant. However, our ability to detect differences in migration speed was limited by our small sample size. We found no significant difference between males and females in the duration of fall migration. Although we found no evidence of prolonged migratory stopovers, our ability to make inferences about migratory routes and stopovers was limited because many of the twilight periods during migration were shaded and because much of fall migration occurred close to the equinox (when latitude cannot be calculated).

Understanding migration patterns and connectivity has been a persistent challenge in ecology and conservation. New technologies such as light-level geolocation, stable isotopes, and genetics have begun to shed light on some of these mysteries. The pattern of using multiple sites during the non-breeding season has important implications for conservation of these species. These results highlight the importance of combining results from multiple studies and methods to increase our understanding of the migratory ecology and the complete annual cycle of songbirds.

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APPENDIX. Mean estimates (\pm SD) of longitude and latitude for summer and winter areas of Swainson's Thrushes outfitted and tracked with geolocators in 2010 in Marin County, California. Individuals are identified by their tag serial number (Fig. 1). Birds that made midwinter movements have "Winter2" (and "Winter3" if applicable) seasons. Start- and end-dates reflect dates used to calculate longitude and latitudes after filters for equinoxes were applied and, thus, may not represent the entire time each bird was in the area.

Individual	Season	Start date	End date	Longitude ($^{\circ}$ W)	Latitude ($^{\circ}$ N)
13285	Summer	8-Jul-10	8-Sep-10	-122.15 ± 1.06	38.01 ± 2.5
	Winter1	8-Oct-10	5-Nov-10	-105.37 ± 0.82	23.69 ± 3.84
	Winter2	3-Dec-10	3-Mar-11	-96.46 ± 1.3	21.38 ± 4.99
13286	Summer	2-Jul-10	8-Sep-10	-121.21 ± 1.18	37.32 ± 2.25
	Winter1	12-Oct-10	24-Apr-11	-104.82 ± 0.89	20.25 ± 4.02
13301	Summer	14-Jul-10	5-Sep-10	-122.22 ± 1.41	37.03 ± 3.6
	Winter1	21-Oct-10	18-Apr-11	-103.17 ± 1.46	19.69 ± 4.5
13308	Summer	22-Jun-10	8-Sep-10	-121.96 ± 1.19	36.49 ± 3.96
	Winter1	11-Oct-10	24-Apr-11	-104.9 ± 1.28	25.65 ± 5.59
13311	Summer	17-Jul-10	6-Sep-10	-122.11 ± 1.82	33.9 ± 6.81
	Winter1	12-Oct-10	5-Mar-11	-105.07 ± 2.29	27.41 ± 6.32
13287	Summer	16-Jun-10	7-Sep-10	-121.81 ± 1.36	37.13 ± 3.39
	Winter1	7-Oct-10	21-Apr-11	-103.9 ± 1.38	20.44 ± 4.31
13304	Summer	23-Jun-10	8-Sep-10	-121.94 ± 1.23	38.14 ± 3.12
	Winter1	17-Oct-10	7-Dec-10	-103.94 ± 0.88	18.71 ± 2.39
	Winter2	28-Dec-10	4-Mar-11	-97.49 ± 1.43	17.4 ± 2.8
	Winter3	4-Apr-11	10-Apr-11	-103.65 ± 0.81	24.67 ± 6.11
13307	Summer	22-Jun-10	30-Aug-10	-122.93 ± 1.61	37.18 ± 7.04
	Winter1	10-Oct-10	5-Apr-11	-103.92 ± 2.35	25.06 ± 6.54
13310	Summer	24-Jun-10	7-Sep-10	-122.2 ± 1.53	41.06 ± 4.54
	Winter1	12-Oct-10	5-Apr-11	-105.83 ± 2.05	22.85 ± 6.22
13313	Summer	12-Jun-10	8-Sep-10	-122.8 ± 1.45	38.31 ± 4.54
	Winter1	10-Oct-10	12-Apr-11	-104.35 ± 1.83	24.08 ± 6.44
13320	Summer	15-Jul-10	5-Sep-10	-122.15 ± 0.9	38.92 ± 2.42
	Winter1	20-Oct-10	17-Apr-11	-105.06 ± 0.9	19.62 ± 3.57
21022	Summer	18-Jun-10	8-Sep-10	-122.58 ± 1.6	40.43 ± 4.93
	Winter1	9-Oct-10	14-Apr-11	-99.32 ± 1.97	23.39 ± 5.3