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Use of multiple South American nonbreeding regions and seasonally distinct migration routes by an individual Scarlet Tanager (*Piranga olivacea*)

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ABSTRACT—Tracking individual migratory birds can help researchers link populations across breeding and nonbreeding regions and explore the frequency, locations, and durations of stopovers and other stationary periods. In May–June 2014, we deployed 15 light-level geolocators on male Scarlet Tanagers (*Piranga olivacea*) in Pennsylvania, USA, and in 2015 we retrieved location data from a single recaptured individual. This individual used 2 disjunct stationary nonbreeding locations in South America: one near the border region of Peru, Bolivia, and Brazil (57.5 d), and the other in northern Peru and the border region with Colombia and Ecuador (77 d). He exhibited a loop migration that included a likely flight over a portion of the Pacific Ocean from Ecuador/southwestern Colombia to Central America in April, and he made at least 12 multi-day (2–10.5 d) stopovers on all legs of migration, in North, Central, and South America (minimum of 6 southbound stopovers and 6 northbound stopovers). His postbreeding migration lasted approximately 32 d, the 2 stationary nonbreeding periods lasted a combined 135 d, and his

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pre-breeding migration lasted between 30 d and 38 d. His complex migration route, with many stopovers, highlights the need for further investigation into the full annual ecology of this declining omnivorous species. *Received 22 August 2023. Accepted 13 August 2024.*

Key words: full annual cycle, long-distance, Nearctic-Neotropical migrant, passerine, stopover.

Uso de múltiples regiones no reproductivas de Sudamérica y rutas migratorias estacionales diferenciadas por un individuo de tángara *Piranga olivecea*

RESUMEN (Spanish)—El rastreo individual de aves migratorias puede ayudar a los investigadores a hacer la conección de poblaciones de regiones reproductivas y no reproductivas y explorar la frecuencia, sitios y duración de las paradas migratorias y otros periodos estacionarios. En mayo-junio 2014, desplegamos 15 geolocalizadores de nivel de luz en machos de tángara *Piranga olivacea* en Pennsylvania, Estados Unidos, y en 2015 recuperamos los datos de localización de un único individuo capturado. Este individuo utilizó 2 localidades disyuntas no repoductivas estacionales en Sudamérica: una cerca de la región fronteriza entre Perú, Bolivia y Brasil (57.5 d) y otra en el norte de Perú, en la región fronteriza con Colombia y Ecuador (77 d). El ave mostró una migración en bucle que incluyó un vuelo probable sobre parte del Océano Pacífico desde el Ecuador/suroeste de Colombia hacia América Central en abril e hizo al menos 12 paradas de varios días (2–10.5 d) en todas las etapas de migración en Norte, Centro y Sur América (mínimo 6 paradas migratorias hacia el sur y 6 paradas migratorias hacia el norte). Su migración post-reproductiva duró aproximademante 32 d, los 2 periodos estacionarios duraron 135 d al combinarlos y su migración pre reproductiva duró entre 30 y 38 d. Su ruta de migración compleja, con muchas paradas de migración, resalta la necesidad de examinar a mayor profundidad la ecología anual completa de especies omnívoras en declive.

Palabras clave: ciclo completo anual, larga distancia, migratorio Neartico, Neotropical, parada migratoria, paserino.

Long-distance Nearctic–Neotropical migrants that spend the nonbreeding season in South America represent one of the most rapidly declining groups of birds that breed in North America, having lost approximately 40% of their global population (Rosenberg et al. 2019). One of these long-distance Nearctic–Neotropical migrant species is the Scarlet Tanager (*Piranga olivacea*). Although still common in much of its range, this charismatic species has been declining globally for the past 4 decades (Sauer et al. 2020, Fink et al. 2022) and is listed as a priority species of conservation concern at regional (AMJV 2019) and state levels (e.g., PGC 2015).

Scarlet Tanagers breed in mature temperate hardwood forests of the eastern half of the United States and portions of southern Canada, and usually spend the nonbreeding season in Panama and northwestern South America from Colombia to Bolivia (eBird 2023). During the nonbreeding period, Scarlet Tanagers are either solitary or found in mixed-species flocks and are found in mature forest (Robinson et al. 1995, Vallely et al. 2023), urban greenspaces (Garizabal Carmona 2020, Giraldo 2020), remnant gallery forest (Ocampo-Peñuela 2010, Roselli et al. 2020), and early successional forest (Stiles and Bohorquez 2000).

As is the case for many long-distance migrants, knowledge gaps during the migration and nonbreeding seasons have made reversing Scarlet Tanager population decline difficult, as it is unclear where limitations to their populations exist. Thus, studies that identify migratory pathways, frequency and duration of stopovers, migratory timing, and stationary nonbreeding locations are valuable to prioritizing conservation strategies for this species. To bolster our understanding of Scarlet Tanager movements across their annual cycle, we deployed archival light-level geolocators to track the movements of individuals that spent the breeding season in northwestern Pennsylvania, USA. Although we were only able to recover data from a single individual, the novel information we gleaned from this bird provides a tantalizing snapshot into Scarlet Tanagers' complex migrations and offers motivation for future research on the migratory and nonbreeding behavior of this species.

Methods

We conducted field work on the Allegheny Plateau in the Allegheny National Forest and State Game Lands No. 86 in Pennsylvania, USA (41.88°N, 79.38°W), in the north-central portion of the Scarlet Tanager breeding range, where the species is a common breeder. We targeted Scarlet Tanagers where we encountered them within sites selected for a concurrent study, in hardwood forest stands containing mature trees, with canopy cover and tree density ranging from closed-canopy forest conditions to shelterwood stands (Raybuck et al. 2020). During the breeding season of 2014 (May–Jul), we captured 20 adult male Scarlet Tanagers using mist nets and audio playback of song vocalizations and fitted them with unique color combinations of leg bands. We fitted 15 of

the 20 birds with archival light-level geolocators (Intigeo-P50Z11-7-dip with 7 mm light pipe, Migrate Technology, Coton, Cambridge, UK) and the other 5 birds served as controls. We did not attempt to tag females because we did not feel confident that we would be able to recapture them. We attached the devices via a leg-loop harness (Rappole and Tipton 1991) constructed from Stretch Magic beading cord (Pepperell Braiding Company, Pepperell, Massachusetts, USA) tailored to fit on-bird and secured with jewelry crimp beads. Including its harness, each geolocator weighed ~0.5 g, which represented, on average, approximately 2% of an individual's body mass. During the following breeding season, we attempted to resight and recapture all returning individuals. Recapture efforts also used audio playback of songs at mist nets either raised with extension poles or raised into the canopy with a rope and pulley system, a strategy that was nearly 100% effective at recapturing tagged Cerulean Warblers (*Setophaga cerulea*; Raybuck et al. 2022).

Geolocator data analysis

We estimated geographic locations from the light-level data in a similar manner to Raybuck et al. (2022). First, we defined sunrise and sunset times using the *preprocessLight* function in the *TwGeos* package (Wotherspoon et al. 2016) in R (R Core Team 2022). We used an on-bird calibration period starting the day after the bird was outfitted with a geolocator (19 Jun) and ending 31 July to obtain twilight error distributions that account for shading effects due to variation in weather and local vegetation and terrain conditions (Lisovski et al. 2018). We calculated zenith angles for each twilight using the calibration period data in the R package *SGAT* (Solar/Satellite Geolocation for Animal Tracking; Wotherspoon and Sumner 2014). We performed Hill-Ekstrom calibrations (Lisovski et al. 2020) to examine whether the zenith angles at stationary nonbreeding locations differed from the zenith angles at the breeding location, which can affect latitudinal estimates (McKinnon et al. 2013). These calibrations resulted in similar zenith angles during the breeding (93.5°) and second stationary nonbreeding period (93.3°), and the Hill-Ekstrom calibration was not successful for the first stationary nonbreeding period, so we used the breeding angle calculated during the breeding season calibration period for the entire annual cycle. Next, we built models that included the twilight error distribution and a flight speed distribution behavioral model as priors to Markov Chain Monte Carlo (MCMC) simulations in *SGAT* (Lisovski et al. 2020). We used a gamma flight speed distribution (shape = 1.0, scale = 0.06) to allow for a maximum flight speed >80 km/h and most likely average flight speeds <20 km/h (Pennycuick et al. 2013). We then ran 60,000 MCMC iterations for burn-in and 60,000 iterations for tuning, followed by 3 chains of 40,000 iterations to derive posterior location estimates and to visually confirm model convergence.

To determine onset and cessation of pre-breeding and post-breeding migrations, we inspected twice-daily modeled location estimates and considered the initiation of migration (from breeding grounds and from stationary nonbreeding periods) to be the first of 10 consecutive twilight locations (5 d) for which the location estimates differed by at least 2° longitude (~170–222 km) or by at least 4° latitude (~444 km) from the capture location/median stationary nonbreeding location. These thresholds were chosen based on our interquartile ranges (IQR) of nonbreeding location estimates. The end of pre-breeding and post-breeding migration periods were similarly determined by the first of 10 or more twilight events in succession that fell within both 2° longitude and 4° latitude from the capture location or the median nonbreeding location. We defined stopovers as periods >2 d, during which median location estimates did not differ by greater than thresholds of 2° longitude or 4° latitude (Raybuck et al. 2022). Thus, our defined stopovers represent coarse resolution as local movements up to ~220 km E–W or ~440 km N–S were possible during the defined stopover periods. Stationary nonbreeding regions were defined using the same methods that we used to define stopover locations. Accuracy of light-level geolocator data from ground-truthed Wood Thrush (*Hylocichla mustelina*) locations in Central American tropical forests (McKinnon et al. 2013) was also higher for longitude (66 ± 13 km) than for latitude (365 ± 97 km) and comparable to our ~220 km and ~440 km thresholds.

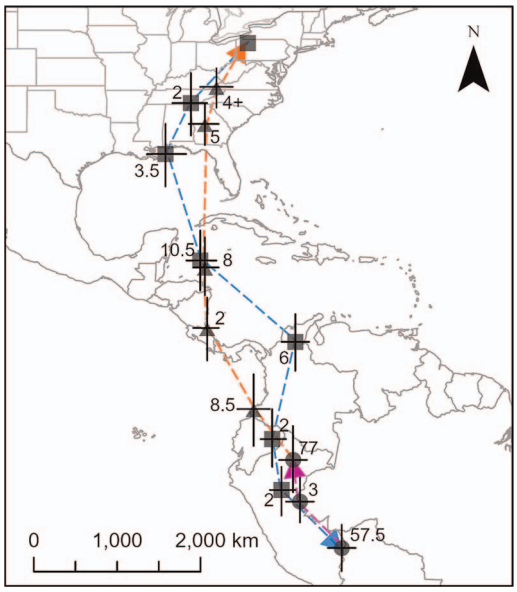

Figure 1. Stationary migratory stopovers and stationary nonbreeding locations used by a male Scarlet Tanager across the 2014–2015 annual cycle. This individual was captured and tagged with a geolocator in Pennsylvania, USA. Squares (breeding and post-breeding migration), circles (nonbreeding), and triangles (pre-breeding migration) represent median locations within stopover and stationary nonbreeding regions and crosses represent interquartile ranges of location estimates during these periods. Stopover durations are listed as numbers that represent the number of days spent at each location. Dashed lines temporally connect stationary locations and do not necessarily represent actual routes.

Results

We resighted 5 of the 15 (30%) tagged individuals in 2015 and one of the 5 (20%) control birds, but we were only able to recapture one tagged bird despite numerous efforts. The one recaptured individual was originally captured and marked on 17 June 2014 (as a second-year male) and recaptured on 16 May 2015.

Post-breeding migration

The tracked male Scarlet Tanager stayed in northwestern Pennsylvania until 18 October, and then moved and briefly stopped over on the Cumberland Plateau in the southeastern United States (2.0 d) and the U.S. coast of the Gulf of Mexico (3.5 d; Fig. 1). After crossing the Gulf of Mexico, he spent 10.5 d in Central America, or potentially, but less likely, western Cuba, before crossing the Caribbean Sea to northern Colombia where he stayed for 6 d. The bird resumed his migration and made 2 additional 2 d stops in Ecuador/Peru before arriving at his first (and most southern) stationary nonbreeding location near the border region of Peru, Bolivia, and Brazil. The entire post-breeding migration period lasted approximately 32 d.

Stationary nonbreeding periods

The bird spent nearly 2 months (20 Nov to 17 Jan) near the border region of Bolivia, Brazil, and Peru, with location estimates centered in the Peruvian Bolivian Andes (Fig. 1). On 18 January, he left this location and moved northwest ~1,200 km (with a 3 d stop in between) to the border region of Peru, Ecuador, and Colombia (Fig. 1) where he remained for 2.5 months (20 Jan to 7 Apr). In total, the 2 stationary nonbreeding periods lasted approximately 135 d.

Pre-breeding migration

The bird initiated his pre-breeding migration on 7 April and made his first stopover in western Ecuador or Colombia for 8.5 d (7–15 Apr). He then made a ~1,100 km journey that may have included a flight over a portion of the Pacific Ocean, with arrival in Central America (location estimates centered in Costa Rica) on 17–18 April. Although we also used 16 April location estimates that suggested this overwater flight, because single-day location estimates are less reliable due to potential shading effects in light-level geolocator data, it is also possible that he followed a more indirect overland route through Colombia and Panama between 15 April and 17 April. After this initial 2 d stop in or near Costa Rica, the bird spent 8 d near the Caribbean coast of Nicaragua, Honduras, or western Cuba before crossing the Caribbean Sea and Gulf of Mexico between 27 April and 30 April. After spending 5 d in or near Georgia, USA (30 Apr to 4 May), he stopped in the central Appalachian region (eastern United States) for at least 4 d before the geolocator stopped collecting usable data (8 May). The duration of pre-breeding migration was between 30 d and 38 d, as the bird was first resighted on the breeding grounds in Pennsylvania 16 May.

Discussion

The migratory route and nonbreeding locations of the individual we tracked represent the first year-long individual-level migration track for a Scarlet Tanager and suggest several annual cycle strategies of interest. First, this bird left his breeding grounds in northwestern Pennsylvania on 18 October, which is later than expected based on previous observations. For example, it has been suggested that most Scarlet Tanagers departed central Wisconsin by 20 September (Robbins 1991). More recently, citizen science data suggest most Scarlet Tanagers depart northwestern Pennsylvania by early October, with only a few records in the region in mid-October (eBird 2023). It is possible the departure of our tagged individual was later than usual, or late-October departures may be more common than recognized, given that these birds are more difficult to detect and identify in October when males have molted into cryptic basic plumage and are no longer singing (Pyle 1997).

Secondly, and importantly from a conservation standpoint, we documented the use of multiple extended stationary nonbreeding regions in South America. While this strategy has not been suggested to occur in Scarlet Tanagers previously, it is proving to be more common in migratory birds than previously thought (Ruiz-Gutierrez et al. 2016). Advances in miniaturized tracking technology over the past ~15 years and a growing focus on nonbreeding ecology of Nearctic–Neotropical migrants in recent decades have highlighted a number of songbird species that use multiple nonbreeding locations lasting <2–3 months. These species include: Veery (*Catharus fuscescens*; Heckscher et al. 2011), Red-eyed Vireo (*Vireo olivaceus*; Callo et al. 2013), Swainson's Thrush (*Catharus ustulatus*; Delmore et al. 2012), Eastern Kingbird (*Tyrannus tyrannus*; Jahn et al. 2013), and Bobolink (*Dolichonyx oryzivorus*; Renfrew et al. 2020; termed "split migration"). This pattern also occurs for some austral migrants (e.g., White-crested Elaenia; *Elaenia albiceps chilensis*; Bravo et al. 2017). Several of these studies suggest that the birds (e.g., Red-eyed Vireos, Eastern Kingbirds, and Bobolinks) might use multiple stationary nonbreeding regions to take advantage of temporally and spatially variable rainfall and food resources, moving to a second region with ample fruit sources to complete molts into alternate plumage (Callo et al. 2013, Jahn et al. 2013, Renfrew et al. 2020), as we discuss below for Scarlet Tanager.

Thirdly, we found a pre-breeding migration movement to the Pacific coast and apparent crossing of the Pacific Ocean to access Central America as a stopover, which was unexpected because flights over this portion of the Pacific have not been well-documented in other songbird migrants (but see figure 1 in Jahn et al. [2013]). This individual took a trans-Gulf of Mexico and trans-Caribbean route in October and November and an apparent overwater crossing of a portion of the Pacific, followed by a trans-Caribbean and trans-Gulf of Mexico route in April. The apparent overwater flight from the second South American stationary nonbreeding region to Central America warrants further investigation to assess the prevalence of this loop migration strategy in Scarlet Tanagers and other species. If it is common, it may be especially important to identify and conserve stopover locations that birds use prior to crossing this migratory barrier.

Although the general migratory timing and nonbreeding distribution of Scarlet Tanagers is recognized (Herzog et al. 2009, Avendaño et al. 2018, eBird 2023), little dedicated research on the species has occurred during the nonbreeding season(s) and thus there is still much to learn about its ecology (e.g., habitat preferences and diet) during migration and stationary nonbreeding periods. Our tagged bird's use of multiple stationary nonbreeding locations suggests that either (1) Scarlet Tanagers require varying resources throughout the course of the nonbreeding season or (2) required resources may not be sufficiently available in a single region throughout the totality of nonbreeding months (Oct/Nov through Mar/Apr) in South America. There is much to learn about Scarlet Tanagers' habitat needs (and whether they vary geographically or temporally) during nonbreeding periods, including stopovers and stationary periods, and much further research is warranted. Although their diet primarily consists of invertebrate prey during the breeding season, fruits are also a component (to an unquantified

and perhaps varying degree) of their diet during the post-breeding, migration (e.g., strangler *Ficus* fruit in Mexico; Coates-Estrada and Estrada 1986, and pomegranate in May in Argentina, the second documented record in the country; Torreguitar 2020), and stationary nonbreeding periods (Mowbray 2020, Torres-Ariza and Gil-T 2023). Variable seasonal fruit availability could potentially explain the use of multiple stationary nonbreeding regions. As male Scarlet Tanagers are believed to molt into their bright red alternate plumage between January and March (Pyle 1997, Herzog et al. 2009, Mowbray 2020), ample fruit resources rich in carotenoids (Brush 1967, Schafer et al. 2008) may be especially important during this period. Ecuador and northern Peru appear to harbor stationary nonbreeding habitat for a high proportion of the global Scarlet Tanager population throughout the nonbreeding period, with likely an increasing concentration in Ecuador and Colombia during the latter months (i.e., Mar and Apr) prior to pre-breeding migration through Central America, as suggested by eBird weekly abundance maps and by the route of the geolocator-tagged individual.

The route taken by the Scarlet Tanager we studied, and its many stopovers, highlight the importance of identifying and conserving habitat throughout the nonbreeding range. Additional tracking studies could potentially use the Motus network as well as archival tracking devices. Migratory connectivity could potentially be assessed by deploying Motus-registered nanotags throughout the South American range to determine breeding regions. It is important to determine whether multiple stationary nonbreeding sites are common for this species (this may require further expansion of the Motus network in South America; Teitelbaum et al. 2023). Offshore Motus towers or a study design similar to that implemented by Smetzer et al. (2017) could help determine whether a direct flight from South to Central America over a portion of the Pacific Ocean is common for this species. GPS loggers are now available that could pinpoint precise locations used at stopovers and stationary nonbreeding locations throughout the annual cycle and allow for the association of precise locations with habitat conditions, but they require researchers to recapture the birds, which proved difficult in this study. Additional options to consider for addressing these knowledge gaps are stable isotopes studies (e.g., Cardenas-Ortiz et al. [2020] found that Scarlet Tanagers captured at a stopover location in northern Colombia originated from throughout a vast area of the breeding range) and GPS transmitters (if they become available at a small enough size to deploy on Scarlet Tanagers).

Focused studies of Scarlet Tanager are needed in South America, and at stopover sites in Central America and the Caribbean, to learn more about their habitat selection and food resource utilization during the nonbreeding season. The use of multiple stationary nonbreeding regions could complicate estimation of nonbreeding survival rates if they were to be based on studies utilizing mark–recapture techniques without accounting for site emigration. Studies designed to evaluate the relationship between food availability and molt timing and large-scale nonbreeding movements would provide valuable insight on habitat quality and could potentially help explain why Scarlet Tanager, at least sometimes, uses multiple stationary nonbreeding regions.

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Data availability

The dataset generated during the current study is available in the Movebank Data Repository (https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study4353860777).

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