Nemes Claire (Orcid ID: 0000-0001-6910-5191)
Zenzal Theodore Joseph (Orcid ID: 0000-0001-7342-1373)
Dossman Bryant (Orcid ID: 0000-0001-9454-1518)
Cohen Emily B (Orcid ID: 0000-0002-4978-4278)

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Springing forward: Migrating songbirds catch up with the start of spring in North America

Claire E. Nemes[1], Peter P. Marra[2], Theodore J. Zenzal Jr.[3], Samantha A. Collins[4,11], Bryant C. Dossman[5,12], Alexander R. Gerson[6], Camila Gómez[7], Ana M. González[7, 8, 13], Mariamar Gutierrez Ramirez[6,9,14], Sarah A. Hamer[10], Joseph Marty[4,15], Phillip L. Vasseur[4], Emily B. Cohen[1]

[1] University of Maryland Center for Environmental Science, Appalachian Laboratory, 301 Braddock Rd., Frostburg, MD 21532, USA

[2] Department of Biology and McCourt School of Public Policy, Georgetown University, Washington, DC 20057, USA

[3] U.S. Geological Survey, Wetland and Aquatic Research Center, 700 Cajundome Blvd., Lafayette, LA 70506, USA

[4] Louisiana Department of Wildlife and Fisheries, Rockefeller Wildlife Refuge, Grand Chenier, LA 70643, USA

[5] Department of Natural Resources and the Environment, Cornell University, Ithaca, NY 14850, USA

[6] Department of Biology, University of Massachusetts, Amherst, MA 01003, USA

[7] SELVA: Investigación para la Conservación en el Neotrópico, Bogotá, Colombia

[8] Department of Biology, University of Saskatchewan, Saskatoon, SK S7N 5C9, Canada

[9] Organismic and Evolutionary Biology Program, University of Massachusetts Amherst, Amherst, MA 01003, USA

[10] Schubot Center for Avian Health, Department of Veterinary Pathobiology, Texas A&M University, College Station, TX 77843, USA

[11] Current address: The Wetlands Institute, Stone Harbor, NJ 08247, USA

[12] Current address: Department of Biology, Georgetown University, Washington, DC 20057, USA

[13] Current address: Canadian Wildlife Service, Pacific Wildlife Research Centre, Delta, BC, Canada

[14] Current address: National Park Service, Cuyahoga Valley National Park, Brecksville, Ohio 44141, USA

[15] Current address: U.S. Fish and Wildlife Service, Texas Chenier Plain NWR Complex, Anahuac, TX 77514, USA

Correspondence: Claire E. Nemes, claire.nemes@umces.edu

ABSTRACT

1. In temperate regions, the annual pattern of spring onset can be envisioned as a “green wave” of emerging vegetation that moves across continents from low to high latitudes, signifying increasing food availability for consumers.
2. Many herbivorous migrants “surf” such resource waves, timing their movements to exploit peak vegetation resources in early spring. Though less well studied at the individual level, secondary consumers such as insectivorous songbirds can track vegetation phenology during migration as well.

3. We hypothesized that four species of ground-foraging songbirds in eastern North America – two warblers and two thrushes – time their spring migrations to coincide with later phases of vegetation phenology, corresponding to increased arthropod prey, and predicted they would match their migration rate to the green wave but trail behind it rather than surfing its leading edge.

4. We further hypothesized that the rate at which spring onset progresses across the continent influences bird migration rates, such that individuals adjust migration timing within North America to phenological conditions they experience *en route*.

5. To test our hypotheses, we used a continent-wide automated radio telemetry network to track individual songbirds on spring migration between the U.S. Gulf Coast region and northern locations closer to their breeding grounds.

6. We measured vegetation phenology using two metrics of spring onset, the spring index first leaf date and the normalized difference vegetation index (NDVI), then calculated the rate and timing of spring onset relative to bird detections.

7. All individuals arrived in the southeastern U.S. well after local spring onset. Counter to our expectations, we found that songbirds exhibited a "catching up" pattern: individuals migrated faster than the green wave of spring onset, effectively closing in on the start of spring as they approached breeding areas.

8. While surfing of resource waves is a well-documented migration strategy for herbivorous waterfowl and ungulates, individual songbirds in our study migrated faster than the green wave and increasingly caught up to its leading edge *en route*.

9. Consequently, songbirds experience a range of vegetation phenophases while migrating through North America, suggesting flexibility in their capacity to exploit variable resources in spring.

RESUMEN

1. En las regiones templadas, el patrón anual de aparición de la primavera puede concebirse como una "ola verde" de vegetación emergente que se desplaza por los continentes desde las latitudes bajas a las altas, lo que significa una mayor disponibilidad de alimentos para los consumidores.
2. Muchos herbívoros migratorios "surfean" estas olas de recursos, programando sus movimientos para explotar los picos de vegetación a principios de primavera. Aunque menos estudiados a nivel individual, los consumidores secundarios, como las aves terrestres insectívoros, también pueden seguir la fenología de la vegetación durante la migración.
3. Nuestra hipótesis es que cuatro especies de aves terrestres que se alimentan en el suelo en el este de Norteamérica – dos currucas y dos zorzales – programan sus migraciones primaverales para que coincidan con las fases más tardías de la fenología de la vegetación, que se corresponden con un aumento de las presas artrópodas, y predijimos que igualarían su ritmo de migración a la onda verde, pero que irían detrás de ella en lugar de surfear su borde delantero.
4. También planteamos la hipótesis de que el ritmo al que avanza la primavera en el continente influye en las tasas de migración de las aves, de modo que los individuos ajustan el calendario de migración dentro de Norteamérica a las condiciones fenológicas que experimentan en ruta.
5. Para comprobar nuestras hipótesis, utilizamos una red automatizada de radiotelemetría a escala continental para seguir a aves terrestres individuales en su migración primaveral

entre la región de la costa del Golfo de EEUU y las localidades septentrionales más cercanas a sus zonas de cría.

6. Medimos la fenología de la vegetación utilizando dos métricas del inicio de la primavera, la fecha de la primera hoja del índice primaveral y la fecha de la primera hoja del índice primaveral.
7. Todos los individuos llegaron al sureste de EEUU bastante después del inicio de la primavera local. En contra de nuestras expectativas, descubrimos que las aves terrestres mostraban un patrón de "puesta al día": los individuos migraban más rápido que la ola verde del inicio de la primavera, acercándose efectivamente al inicio de la primavera a medida que se acercaban a las zonas de cría.
8. Mientras que el surfing de las olas de recursos es una estrategia migratoria bien documentada para las aves acuáticas herbívoras y los ungulados, los individuos de aves canoras de nuestro estudio migraron más rápido que la ola verde y alcanzaron cada vez más su borde de ataque en ruta.
9. En consecuencia, las aves terrestres experimentan una serie de fenofases de vegetación mientras migran a través de Norteamérica, lo que sugiere flexibilidad en su capacidad para explotar recursos variables en primavera.

INTRODUCTION

Migratory behavior has evolved in response to predictable seasonal fluctuations in resources and environmental conditions throughout an animal's annual cycle (Alerstam et al., 2003). In long-distance migratory birds, migration timing is governed by evolved circadian and circannual rhythms tied to photoperiod and fine-tuned by environmental conditions, allowing individuals to access resources at the appropriate time both at the destination and *en route* (Carey, 2009; Gwinner, 1996). However, the exact timing of seasonal transitions such as green-up and green-down varies from year to year, affecting when resources become available to consumers (Liu & Zhang, 2020; Melaas et al., 2013). A migratory songbird that arrives to its temperate breeding grounds on the same calendar day each year may find the forest verdant and flush with caterpillars in some springs, but find bare trees and a dusting of snow in others. While arriving to the breeding grounds earlier than competitors has substantial reproductive benefits (Kokko, 1999; Smith & Moore, 2005), arriving too early can impose physiological or survival costs (Briedis et al., 2017; Youngflesh et al., 2023). Consequently, long-distance migratory birds are expected to adjust the pace of migration in response to the environmental conditions they encounter *en route* (Ahola et al., 2004; Bauer et al., 2020; Tøttrup et al., 2010). Plasticity in adjusting migration rate to annual variations in environmental phenology may prove even more important because spring is arriving earlier across the temperate zone due to climate change, with increasing variation in spring onset (Liu & Zhang, 2020; Schwartz et al., 2013).

Many migratory taxa time their migrations depending on resource phenology *en route* (Drent et al., 1978). In temperate regions, spring onset can be envisioned as a "green wave" of new plant growth that sweeps across the continent from low to high latitudes and elevations as days lengthen and temperatures rise (Schwartz, 1998). This flush of emerging vegetation or "green-up" is followed by a profusion of animal life, including both vertebrate and invertebrate herbivores that directly consume plant growth (Harrington et al. 1999). For herbivores, nutritional quality in foliage peaks with green-up in early spring and may only be available for a limited time at any given location (Aikens et al., 2020; van der Graaf et al., 2006). Many migratory herbivores therefore synchronize their movements to track these trophic or resource "waves" of peak nutrition, a strategy described as "surfing" under the green wave hypothesis (Aikens et al., 2017; Drent et al., 1978; van der Graaf et al., 2006). Some consumers travel slightly ahead of or behind this peak (Shariatinajafabadi et al., 2014), while others overtake it, effectively jumping over the green wave (Bischof et al., 2012; Kölzsch et al., 2015). The specific pattern (see Fig. 1) may depend on when individuals derive the greatest benefit from high-quality new vegetation growth, either for themselves or their offspring (Abrahms et al., 2021; Armstrong et al., 2016; van der Graaf et al., 2006).

Migrants at higher trophic levels may also synchronize their seasonal movements based on patterns of vegetation growth (La Sorte & Graham, 2021; Thorup et al., 2017; Youngflesh et al., 2021). Temperature changes and plant growth in spring drive emergence of herbivorous caterpillars and other arthropods (Cayton et al., 2015; van Asch & Visser, 2007), which in turn serve as fuel for insectivorous songbirds during their northward migrations (Graber & Graber, 1983; Strode, 2015; Wood & Pidgeon, 2015). Thus, increasing primary productivity serves as a proxy for food availability for insectivorous songbirds (Pettorelli et al., 2011), which can adjust their migration timing depending on spring temperature or vegetation phenology *en route* (Thorup et al., 2017; Tøttrup et al., 2008, 2010; Youngflesh et al., 2021).

Whereas for migratory herbivores peak forage quality at a given location is ephemeral, facilitating a surfing pattern (Aikens et al., 2020), many insectivorous songbirds use a variety of food sources during spring migration (Parrish, 2000). As a result, they may not experience the same narrow windows of peak food quality that constrains the migration timing of some herbivore populations. However, the abundance and palatability of some arthropod prey such as caterpillars is related to leaf development in spring (Strode, 2015; van Asch & Visser, 2007), and migrating wood-warblers in spring prefer to forage in trees during earlier stages of flowering and leaf phenology that presumably confer higher prey abundance or accessibility (Wood & Pidgeon, 2015). Consequently, insectivorous songbirds may benefit from adjusting their migration to track stage(s) of vegetation phenology that support nutritious developmental stages of prey or high prey abundance.

In North America, annual variability in the timing of songbird migration between the southern and northern U.S. supports *en route* adjustment to the pace of migration, with faster rates of migration and earlier passage during warmer springs when plants, and presumably insect prey, develop earlier (Horton et al., 2023; Hurlbert & Liang, 2012; Marra et al., 2005). Advancement in spring migration timing within North America measured by weather radar is correlated with increasing spring temperatures linked to climate change (Horton et al., 2020), yet migrants' arrival timing *into* North America in spring has not advanced for birds traversing the Gulf of Mexico (Cohen et al., 2015; Horton et al., 2019). Taken together, these findings suggest that individual birds fine-tune their migration rate within temperate North America based on environmental phenology *en route* (Cohen et al., 2015; Horton et al., 2020; Marra et al., 2005).

Confirmation that individual plasticity is responsible for observed population-level changes in migration rate and timing requires tracking individuals as they migrate (Charmantier & Gienapp, 2014; Schmaljohann et al., 2017; Thorup et al., 2017). This offers advantages over 1) using arrival dates from banding stations or eBird observations, which obscure individual movements and could potentially mask population-specific effects, and 2) continental-scale weather radar observations, which do not differentiate between species or populations. We used tracking data from four species of Nearctic-Neotropical migratory songbirds to determine if individuals adjust their migration rate and timing in accordance with changing vegetation phenology within North America.

The species in our study are insectivorous, ground-foraging long-distance migrants that primarily breed across forested regions of North America (Fig. 2). The two thrush species – Swainson's Thrushes (*Catharus ustulatus*) and Gray-cheeked Thrushes (*Catharus minimus*) – spend the stationary non-breeding period in South America (Mack & Yong, 2020; Whitaker et al., 2020), while two warbler species – Northern Waterthrushes (*Parkesia novaeboracensis*) and Ovenbirds (*Seiurus aurocapilla*) – migrate south to Mexico, Central America, and the Caribeean (Porneluzi et al., 2020; Whitaker & Eaton, 2020). All are broadly associated with the forest understory and forage for arthropods on or near the ground during spring stopover in North America (Lott et al., 2006). During spring migration our study species pass through the U.S. Gulf of Mexico coast region, where individuals often stop to refuel before continuing northward towards their breeding areas (Cohen et al., 2017).

Using the Motus automated radio telemetry network (Taylor et al., 2017), we tracked individuals of these four species in spring as they migrated from the U.S. Gulf Coast region to receiver stations further north approaching their breeding destinations, allowing us to measure migration rate and timing relative to spring onset for each individual. We used several metrics characterizing vegetation phenology to assess (1) if individual songbirds adjust migration rate in response to phenological conditions *en route,* and (2) if their migrations are characterized by a particular pattern such as surfing or jumping over the green wave (Fig. 1). We further sought to identify how the strength of birds' relationships with spring onset might vary over the course of the season, reflecting changes in the relative importance of exogenous and endogenous drivers of migration phenology (Jenni & Schaub, 2003; Tøttrup et al., 2010). We do not suggest that the spring onset day of year – the day on which the green wave "arrives" at a given location – represents an absolute stage of resource phenology that migrating birds should optimally track. Rather, we use spring onset as a relative measure of the timing of vegetation development (a proxy for food availability) at different locations, i.e., a yardstick against which to compare songbird migration phenology (Visser & Both, 2005).

We expected individuals to adjust migration rate in response to the rate that the green wave travels across the continent in spring. Unlike herbivorous waterfowl that synchronize their migration timing to track vegetation emergence in early spring (Fig. 1, Surfing - Leading Edge), we predicted that the ground-foraging insectivores in our study would instead migrate behind the leading edge of the green wave of spring onset (Fig.1, Surfing - Trailing), tracking later stages of leaf development that correspond to increased arthropod prey (Cayton et al., 2015; Mayor et al., 2017; van Asch & Visser, 2007). Alternative strategies are possible when individuals migrate faster between points on the landscape than the progression of spring onset; they may begin by trailing behind the green wave but then close in on its leading edge (Fig.1, Catching Up) or even overtake it (Fig. 1, Jumping). Conversely, individuals might increasingly lag behind spring onset as they travel from south to north, for example if spring phenology at high latitudes advances faster than low latitudes with climate change (Mayor et al., 2017). We also hypothesized that the survival cost of *en route* phenological mismatch is higher early in the spring and predicted that early individuals would be more sensitive to the green wave rate when adjusting their migration rate. In contrast, we predicted that later individuals would migrate faster to minimize migration time because of the potential reproductive costs of arriving late to the breeding grounds.

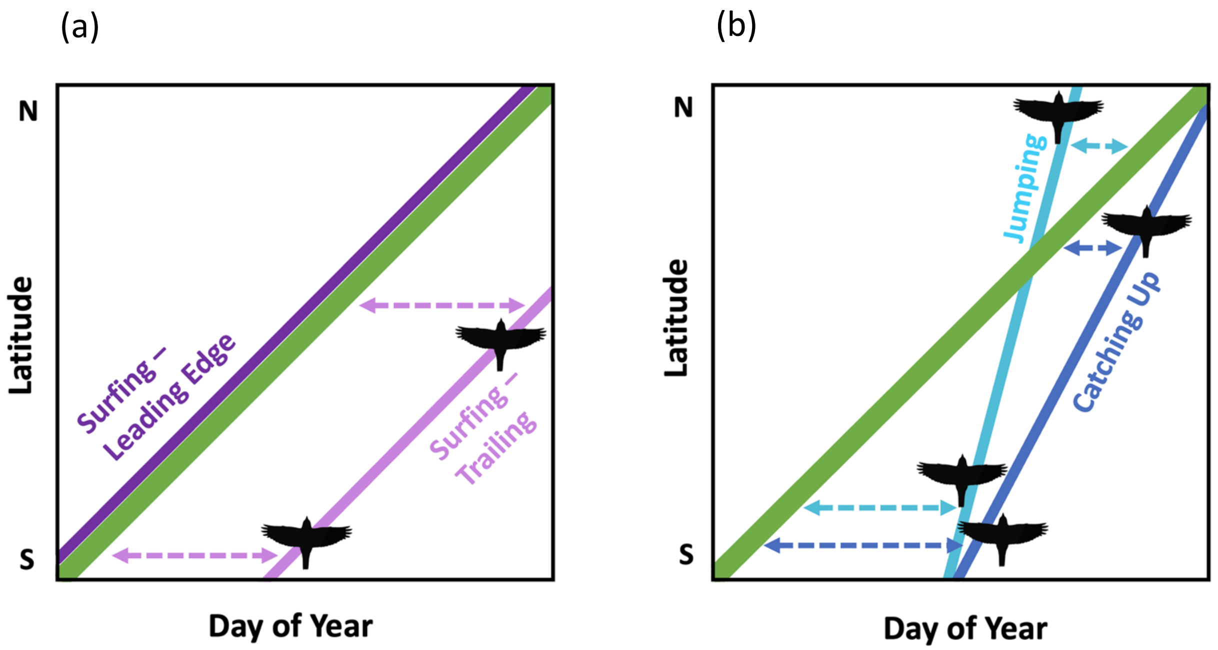

Figure 1. Four potential patterns of insectivorous songbird migration relative to vegetation phenology. Birds are assumed to experience different extents of vegetation development and hence food availability depending on their migration timing relative to spring onset day, which signifies the arrival of the green wave (solid green line). The phenological interval (dashed horizontal arrows) is the day of year of the bird's passage minus the day of year of local spring onset. If migration rate matches the green wave rate (a), then the phenological interval will not change as birds move from south to north, although they may migrate with the leading edge of the green wave (Surfing - Leading Edge) or trail behind it (Surfing - Trailing). If birds migrate faster than the green wave (b), the phenological interval will decrease as they travel from south to north, allowing migrants to catch up to the green wave (Catching Up) or overtake it (Jumping). Birds might also lag increasingly far behind the green wave as they migrate, with the phenological interval increasing from south to north (not pictured). Note that we use the green wave as a benchmark against which to assess bird migration phenology, rather than as an absolute measure of optimal timing.

METHODS

Migration rate

We tracked individual Swainson's Thrushes, Gray-cheeked Thrushes, Northern Waterthrushes, and Ovenbirds during spring migration in years 2016 - 2019. Birds were captured and tagged either in stationary non-breeding areas (central Colombia; Jamaica) or during spring stopover (northern Colombia; U.S. Gulf of Mexico Coast in Texas, Louisiana, and Florida; Fig. 2). For detailed site and banding information, see Supporting Information. Individuals that met minimum mass requirements received digitally coded "nanotag" radio transmitters (Lotek Wireless, Ontario, Canada; Table S1) registered with the Motus Wildlife Tracking System, a collaborative network of automated radio telemetry stations distributed across the Americas (motus.org; Fig. 2). Receiver stations continuously "listen" for signals on a common frequency and record any tags that pass within the detection radius (up to ~15 km; Taylor et al., 2017), allowing individuals to be tracked with high temporal precision as they migrate.

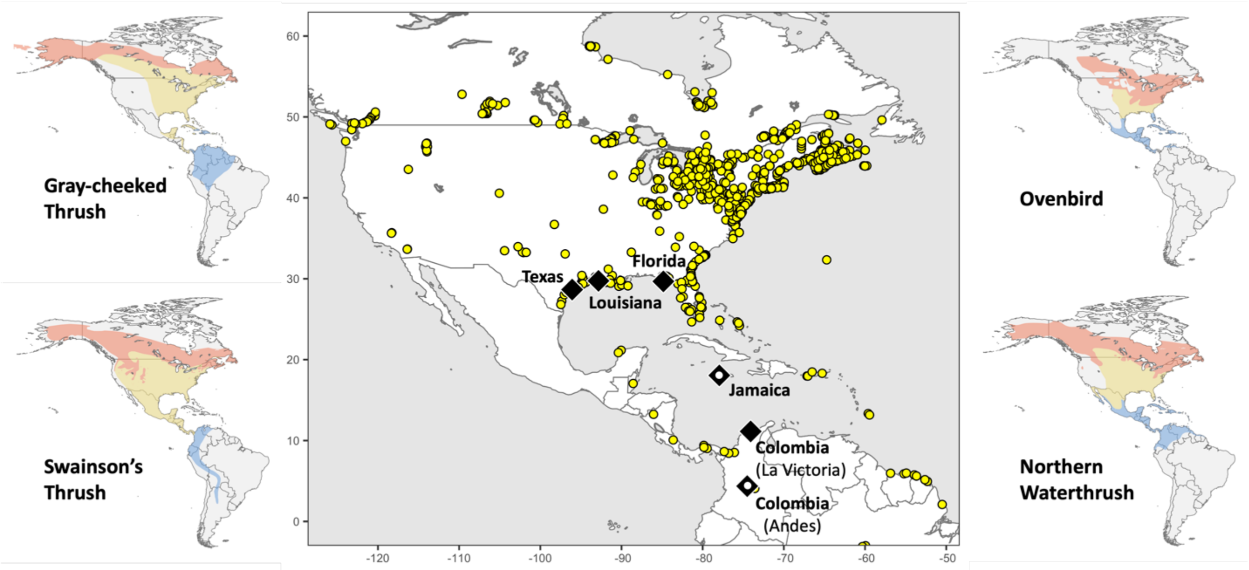

Figure 2. Center: Bird tagging locations at spring migration stopover sites (solid black diamonds) and stationary non-breeding sites (black diamonds with white dots). Yellow points show the positions of all Motus receivers deployed between 2016 - 2019 within the migration and breeding ranges of the four study species. Sidebars: Range maps for the four migratory songbirds tracked in this study, including breeding ranges (pink), stationary non-

breeding ranges (blue), and migration passage areas (yellow). Species distribution maps courtesy of BirdLife International and Handbook of Birds of the World (2022).

Animal capture and handling adhered to institutional care and use standards and was approved by the Smithsonian Institution Animal Care and Use Committee (#18-09), the University of Massachusetts Amherst Institutional Animal Care and Use Committee (#2015-0019), the University of Saskatchewan Animal Research Ethics Board (#20100084), the University of Southern Mississippi Institutional Animal Care and Use Committee (#17081101), and the Universidad de los Andes animal care and ethics committee - CICUAL (Acta 293, C.FUA_14-016). Research permits were issued by the U.S. Geological Survey (USGS) Bird Banding Laboratory (permit numbers 06669, 09700, 24101, and 23979), Texas Parks and Wildlife Department (Scientific Permit SPR-0312-042), The Nature Conservancy Texas Chapter (Scientific Investigation and Collection Permit), Florida Fish and Wildlife Conservation Commission (Permit LSSC-16-00033), Louisiana Department of Wildlife and Fisheries (Scientific Research and Collecting Permits LNHP-18-020 and WDP-19-005), Agencia Nacional de Licencias Ambientales, Colombia (Res. 0597), and Jamaican National Environment and Planning Agency (Ref# 18/27).

We used detections of individual nanotagged birds as they migrated into temperate North America, primarily along the Gulf Coast in the southeastern U.S., and again as they approached their breeding destinations during the same spring. Thus, each individual bird had paired detection locations and dates in southern and northern portions of North America during the same migration (Fig. 3a). All detection data were screened and possible false positives removed following recommendations in Crewe et al. (2018); details provided in Supporting Information.

Average **bird migration rate** (km/d), inclusive of flight and stopover, was calculated as the great circle distance between each individual's detection locations (obtained using the motus R package; Birds Canada, 2022) divided by the days elapsed between detections. This produced a conservative estimate of the minimum rate at which each bird could have migrated. To validate the use of Motus data for calculating average migration rate, we also estimated flight speeds (m/s) by estimating the total hours spent in flight based on a theoretical 1:7 ratio of time in flight : time on stopover (Hedenström & Alerstam, 1997). We then divided distance traveled by estimated hours in flight to obtain a coarse estimate of average flight speed.

Green wave rate and spring onset timing

The green wave concept describes the progression of vegetation emergence (spring onset) over time and space at the continental scale (Schwartz, 1998). We therefore used **spring onset day** (ordinal day) as a static measure of the green wave's timing of arrival to a location. We calculated the **green wave rate** (km/d) as the distance between bird detection locations divided by the difference in spring onset between them. The green wave rate is thus directly comparable with the average migration rate (km/d) of each individual because it is calculated between the same points on the landscape.

We characterized spring onset with two independent methods based on temperature and remotely-sensed measures of vegetation phenology (Polgar & Primack, 2011), using vegetation growth as an indicator of prey available to insectivorous migrants (van Asch & Visser, 2007). Satellite-derived remote sensing products, including the normalized difference vegetation index (NDVI), directly measure vegetation greenness, whereas temperature-based metrics such as cumulative growing degree-days record thermal sums as proxies for plant development (Pettorelli et al., 2005; Polgar & Primack, 2011; Schwartz et al., 2013). Though not our intention to formally compare the ability of different phenology estimators to predict songbird migration, we were interested to see if general patterns were consistent between approaches. We discuss the first method of characterizing spring onset in detail below and describe the NDVI-based method in the Supporting Information.

The temperature-based estimate of spring onset, the U.S. National Phenology Network (USA-NPN) Extended Spring Index First Leaf Date, uses growing degree-day thresholds to predict timing of leaf-out across the United States and Canada (Schwartz et al., 2013). Spring index models are calibrated and validated on lilac (*Syringa*) and honeysuckle (*Lonicera* spp.) cultivars (Ault et al., 2015) and serve as a proxy for spring onset day of year in temperature-sensitive plant species (Schwartz et al., 2013). We used the USA-NPN's "first leaf" product as a relative benchmark of spring onset day in each of the four years in which birds were tracked. We also downloaded historical data for each site and calculated the average spring onset day at the site in the 30 years prior to each individual's migration tracking year.

Phenological interval

The migratory pattern (Fig. 1) is determined by both the migration rate and the **phenological interval** – the number of days' difference between a bird's migratory passage and spring onset day of year (Mayor et al., 2017) – along the migration route. Phenological interval values are positive when migrating birds arrive at a location after spring onset (i.e., after the green wave arrives) and negative when they arrive before it. Phenological interval may remain relatively constant along the route (with a value of zero or a constant positive value in "Leading Edge" and "Trailing" surfing patterns, respectively). Conversely, it may decrease along the migration route, corresponding to shorter times between migratory passage and spring onset with increasing latitude (“Catching Up” or “Jumping” patterns). Individuals that “jump” over the green wave switch from a positive phenological interval to a negative one.

Migration phenology models

To investigate the effect of green wave rate on bird migration rate, we fitted generalized linear mixed-effects models (GLMMs) with bird migration rate (km/d) as the response variable, using a Gamma distribution with a log link to constrain the response to be positive. As predictors, we included green wave rate, species, and time of season (the day of year that the bird was detected migrating through the southeastern U.S., mostly in the Gulf Coast region (Fig. 3a) between 28.6 - 31.8°N latitude [mean = 29.7°N, n = 28 receiver locations.]) Time of season was centered by species to account for different mean passage dates between species. We included a random intercept of south receiver ID to account for detections of more than one individual at a given receiver. Time of season and the green wave rate were scaled to facilitate model convergence. To test the hypothesis that the relationship between the green wave rate and migration rate depends on whether a bird is an earlier or later season migrant, we included an interaction term between green wave rate and time of season.

To test our expectation that the insectivorous birds in our study use a Surfing - Trailing migration strategy, we fitted linear mixed-effects models with phenological interval as the response variable and detection location (factor with two levels: southern receiver or northern receiver; Fig. 2) as a predictor variable. We included year and species (each a four-level factor) as fixed effects and individual as a random intercept to account for paired observations.

For each question, we fitted separate models for spring onset estimated by the USA-NPN extended spring index of first leaf (hereafter **first leaf spring onset**) and spring onset estimated by vegetation greenness change (hereafter **NDVI spring onset**). We verified model assumptions by visually inspecting residual plots using base R and R package ‘performance’ (Lüdecke et al., 2021). If residuals showed heteroscedasticity, we evaluated different weights for the variance covariate(s) and selected the optimal variance structure based on AIC values and improvement in residual plots (Pinheiro et al., 2020; Zuur et al., 2009). Collinear predictor variables (VIF >5) were removed. To obtain the overall effect of factors with multiple levels, we used likelihood ratio tests to compare nested models (Zuur et al., 2009). We plotted predictions from fitted models with packages ‘visreg’, ‘ggeffects’, and ‘ggplot2’ (Breheny & Burchett, 2017; Lüdecke, 2018; Wickham, 2016). All analyses were performed using R version 3.6.3 (R Core Team, 2020). For model results, we report mean ± SE unless noted otherwise.

In most cases, results were qualitatively similar regardless of which method (first leaf or NDVI) was used to characterize spring phenology. We thus present the results of first leaf spring onset models in detail below, noting differences from NDVI models where they occur, and provide full NDVI and first leaf model results in the Supporting Information (Tables S3 - S6).

RESULTS

From 2016 - 2019, we tracked 102 individuals during spring migration within North America (Fig. 3a, Table 1). Birds migrated through the U.S. Gulf of Mexico Coast region between 5 April and 29 May and were detected further north, approaching breeding areas, between 28 April and 10 June. Average northward migration rate was fastest for Ovenbird followed by Gray-cheeked Thrush and Swainson’s Thrush, with Northern Waterthrush migrating the slowest (Table 1). We report age and sex summaries in Supporting Information (Table S1).

Table 1. Spring migration tracking results of four Nearctic-Neotropical songbird species captured at three sites along the U.S. Gulf of Mexico coast, two in Columbia, and one in Jamaica between 2016 - 2019. Migration rates

and flight speeds are reported as mean ± SD. Annual variation in migration rate by species is shown in Supporting Information (Fig. S5 - S6).

Species	**n**	**Tagging locations**	**Years tracked**	**Migration rate** (km/d)	**Flight speed** (m/s)
Swainson's Thrush	72	Colombia (Andes), Texas, Louisiana, Florida	2016 - 2019	145 ± 55.6	13.4 ± 5.1
Northern Waterthrush	14	Louisiana, Florida	2016 - 2019	121 ± 44.6	11.2 ± 4.1
Gray-cheeked Thrush	9	Colombia (La Victoria, Andes), Florida	2016 - 2018	152 ± 46.6	14.1 ± 4.3
Ovenbird	7	Jamaica, Texas	2019	236 ± 103.0	21.9 ± 9.6

The range of migration rates of nanotagged birds in our study overlapped those reported elsewhere (e.g., Gómez et al., 2017). Using our migration rate (km/d) estimates and a theoretical 1:7 flight-to-stopover time ratio (Hedenström & Alerstam, 1997), we estimated flight speeds (m/s) for all species (Table 1). Comparing these with empirical flight speed measurements provides a useful validation; for example, our estimated flight speeds (m/s) for nanotagged Swainson's Thrushes were 13.4 ± 5.1 (mean ± SD, range: 5.6 - 33.3 m/s, n = 72), similar to direct flight speed measurements of *Catharus* thrushes (e.g., 13.6 - 16.6 m/s, Bowlin 2005).

In general, spring onset values estimated from the temperature-based first leaf model were earlier than those obtained using the NDVI-based model (Fig. 3c-d). At southeastern sites, annual spring onset day estimated with the first leaf method ranged from 15 January - 5 February (mean: 25 January ± 5.5 days, n = 36 unique site and year combinations ["site-years"]). Using NDVI, spring onset estimates were nearly two months later (mean: 17 March ± 9.3 days, range:

23 February - 6 April, n = 15 site-years). For the northern sites, which spanned a wider latitudinal range (35.2 - 51.8°N), first leaf spring onset day ranged from 17 February - 16 May (mean: 10 April ± 19.1 days, n = 83 site-years) while NDVI spring onset day ranged from 8 April - 13 May (mean: 21 April ± 8.3 days, n = 38 site-years).

When using first leaf to characterize spring onset, the effect of the green wave rate on migration rate depended on the time of season that birds migrated through the southeastern U.S. relative to conspecifics (Table S3). However, in contrast to our predictions, migration rate of earlier birds was negatively related to the green wave rate, whereas for later birds there was a positive relationship (Fig. S2). When using NDVI to characterize spring onset, we did not observe a significant interaction between time of season and the NDVI green wave rate (Table S4a); instead, migration rate was positively related to time of season and green wave rate separately (Fig. S3).

Birds appeared to catch up to the start of spring as they traveled across North America. All birds arrived after first leaf spring onset in the southeastern U.S. (south phenological interval: bird detection day - spring onset day = 100 ± 11.2 days, range: 67 - 117, n = 102) and were detected fewer days after spring onset as they migrated northwards (north phenological interval: bird detection day - spring onset day = 43 ± 20.0 days, range: -2 - 91, n = 102). Bird detection location (north or south) was an important predictor of the phenological interval value (likelihood ratio test: $\chi^2(1) = 248.8$, $p < 0.001$; Table S5). Northern phenological interval was substantially smaller than southern phenological interval, indicating that birds migrated faster than the green wave and were “catching up” with it as they approached their breeding destinations. Swainson’s Thrushes (n = 72) migrated through the U.S. approximately 101 ± 10.4 days after spring onset in the south and 44 ± 18.6 days after spring onset in the north (Fig. 3d).

Northern Waterthrushes (n = 14) migrated earlier than other species through both southern and northern regions (Fig. 3d, Table S5).

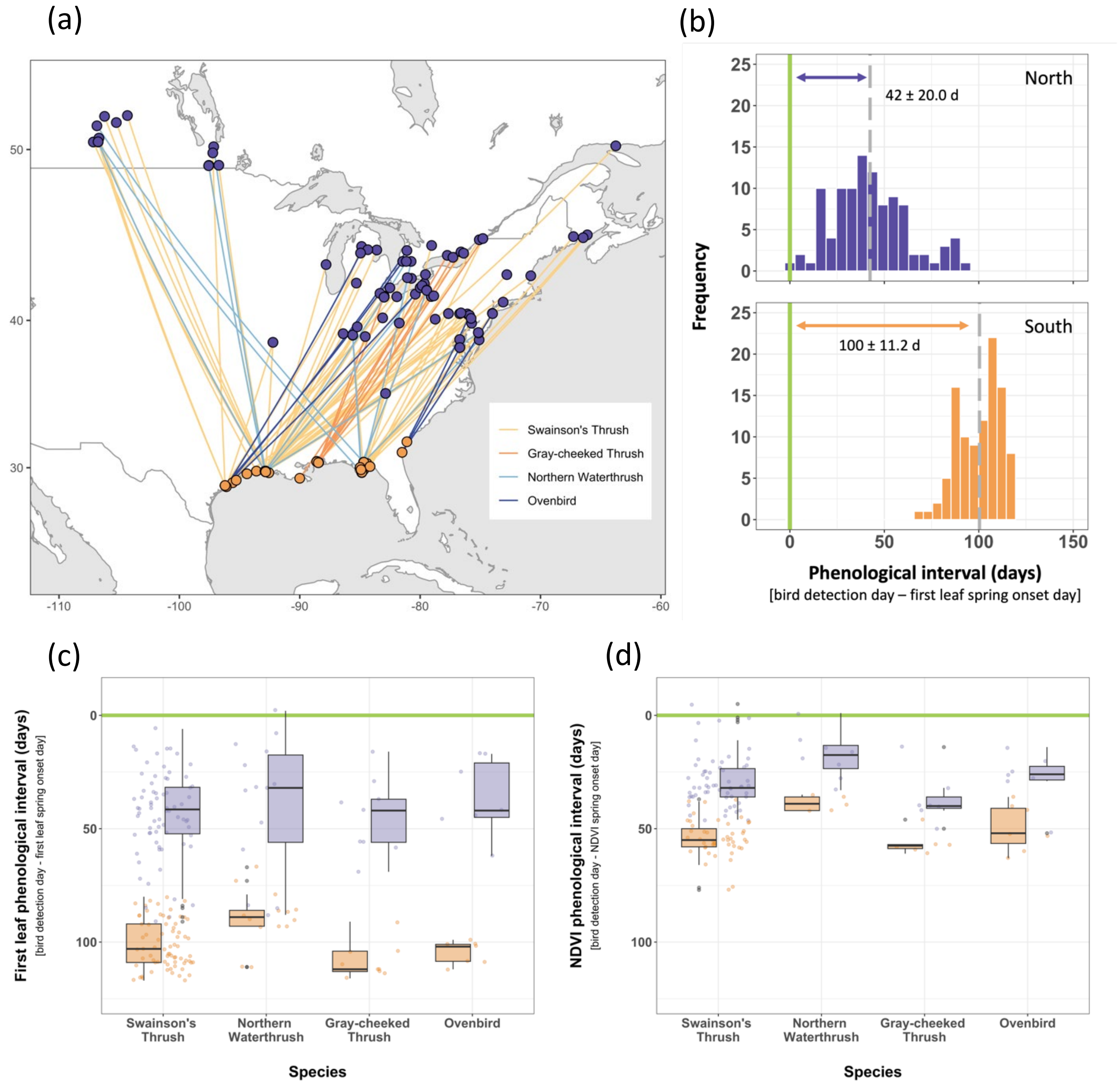

Figure 3. (a) Locations of south (orange) and north (purple) bird detection sites with lines connecting each individual's detections. Note that track lines denote the shortest distance between points and do not necessarily represent a bird's actual migration route. (b) Frequencies of phenological intervals (bird migration day relative to local spring onset day of year, here estimated using the first leaf spring index) for birds migrating through the southern U.S. (bottom, orange) versus further north in the U.S. and Canada (top, purple). Dashed vertical line represents the mean phenological interval at south and north sites. Spring onset day of year (green line) has been centered at 0 so that a positive interval means birds arrive after spring onset and a negative interval means birds arrive before it. A smaller positive phenological interval indicates that individuals migrate through an area fewer days after local spring onset and therefore experience an earlier stage of spring phenology than individuals arriving

later. Species-specific differences in phenological interval using (c) first leaf out and (d) NDVI in the south (orange) and the north (purple). Note position of y-axis scale with 0, representing spring onset, at the top.

DISCUSSION

Our study leveraged the power of the Motus Wildlife Tracking System, a unique collaborative network for studying animal movement, to track individual songbirds from multiple non-breeding and stopover sites as they migrated through North America in spring. Unlike many herbivore species, songbirds in our study did not travel at the green wave's leading edge, nor did they surf behind the green wave by timing their migrations to arrive a consistent number of days after spring onset across their routes. Instead, all birds arrived in the southern U.S. well after spring onset but traveled substantially faster than the green wave while migrating through the U.S. and Canada. Consequently, individuals caught up to the green wave's leading edge as they approached their breeding grounds, migrating through northern areas closer to the time of local spring onset (Fig. 3). This pattern was consistent whether we defined spring onset using first leaf or NDVI. Because the first leaf model estimates spring onset to occur earlier than the NDVI model, birds were generally detected "further behind" the first leaf spring onset than the NDVI spring onset at both detection points. Regardless of method, birds in our study appeared to display a catching-up pattern relative to the green wave within temperate North America.

What is the advantage of the observed pattern? It may imply that no single stage of spring vegetation phenology, corresponding to food availability or quality, is sufficiently beneficial or reliable for songbirds to track a specific vegetation phenophase throughout the entire migratory period, as occurs with surfing populations (Armstrong et al., 2016). For dietary generalist insectivores in forested ecosystems, resource waves may be composed of a variety of prey species with their own distinct phenologies that are in turn dependent on complex vegetation communities, meaning that there may be successive overlapping resource peaks or waves available to support energetic needs *en route* (Armstrong et al., 2016; Donnelly et al., 2017). Many songbirds exploit broader niches during migration, using a wider variety of food sources, foraging behaviors, and habitat types than during non-migratory periods (Parrish, 2000; Petit, 2000; Zuckerberg et al., 2016). These generalist species may therefore be less constrained to follow a particular vegetation phenophase than commonly-studied herbivores migrating through less vegetatively complex ecosystems in the arctic and subarctic (Abrahms et al., 2021).

We did not find evidence for our hypothesis that migration rate of early-migrating individuals is more sensitive to the green wave than later-migrating individuals. Instead, we observed a somewhat puzzling pattern of early birds migrating more slowly as the first leaf green wave rate increased, and later birds migrating faster as expected. We did not observe this interaction in the model using NDVI to characterize spring onset, which used a smaller sample of individuals. Instead, time of season and NDVI green wave rate positively and independently influenced migration rate (Table S4b, Fig. S3). In both cases, individuals migrating later in the season traveled faster than earlier-migrating conspecifics (Fig. S4), presumably because of increased time pressure to reach the breeding grounds (Jenni & Schaub, 2003), or the potential benefits of migrating later and faster (Gonzalez et al. 2021).

Correlation in environmental conditions along the route can substantially influence migration timing because information about phenology at the next stopover site or destination is more reliable when conditions are correlated (Abrahms et al., 2021; Bauer et al., 2020; Kölzsch et al., 2015). We did not measure the degree of phenological predictability in our study and thus cannot assess how well spring onset on the Gulf Coast predicts spring onset elsewhere *en route*. However, due to spatial correlation, migrants that travel a shorter distance within North America probably obtain more valuable information about phenology on their breeding grounds during Gulf Coast stopovers than longer distance migrants, which they use to time migratory initiation and departures (Zenzal et al., 2023). In support of this, short-distance migrants generally show greater sensitivity and adjustments to migration timing in response to phenological changes than long-distance migrants (Hurlbert & Liang, 2012; Miller-Rushing et al., 2008; Youngflesh et al., 2021).

By the time long-distance migrants reach the southeastern U.S., spring phenology is well advanced (Ault et al., 2015) and there is little danger of food limitation (Zenzal, *unpublished data,* 2023). However, because we found that birds migrated faster than spring progressed across the continent, the risk of mistiming may increase as birds travel northward. At some point, it may become more important for birds to fine-tune migration pace to avoid "overshooting" favorable conditions and possibly incurring a survival cost. At the species level, synchrony between migration timing and vegetation phenology increases with proximity to the breeding grounds (Bauer et al., 2008; Shariati-Najafabadi et al., 2016; Youngflesh et al., 2021), when matching timing to peak food resources becomes essential for successful reproduction (Smith & Moore, 2005).

Our sample likely included a mixture of individuals from different breeding populations within each species (Cohen et al., 2017, 2019; Langin et al., 2009). Because our data did not allow us to identify specific breeding locations of individuals, we are unable to infer how proximity to the destination affected their migration rate and timing. In general, migration rate increases as birds approach their breeding areas. The relatively high migration rate and flight speeds observed in Ovenbirds could reflect the species' more southerly breeding distribution (Fig. 1), since individuals are probably closer to their breeding areas when they pass through the

U.S. Gulf Coast region than the other species in our study. Similarly, conditions in the non-breeding range can vary signficiantly between years and can affect timing of departure from stationary areas and stopover sites, fueling rates, and birds' overall speed and physical condition during migration (Studds and Marra 2011, González-Prieto and Hobson 2013, Paxton et al. 2014, Gómez et al. 2017, but see Dossman et al., 2022; González et al., 2020). With the exception of birds tagged in central Colombia and Jamaica, we could not discern where individuals in our study spent the stationary non-breeding season, and hence could not incorporate possible carryover effects resulting from exposure to different environmental conditions prior to detection in the southeastern U.S. Both species- and individual-level differences in migration rate and timing in our study could be partly attributable to differences in breeding destination, non-breeding location, and total distances traveled (Dossman et al., 2022).

Discrepancies in the ability of different spring onset metrics to predict animal migration phenology may be partly explained by differences in the biological phenomena that each approach measures (Schwartz et al., 2013; White et al., 2014). NDVI quantifies changing vegetation greenness and thus directly reflects food available to herbivores while indirectly measuring food for insectivores, such as the songbird species in our study (Pettorelli et al., 2005). In contrast, the first leaf spring index predicts leaf development based on thermal sums (Polgar & Primack, 2011). Temperature influences arthropod emergence and activity both directly, because their development is linked to temperature, and indirectly, by promoting the development of leaves upon which caterpillars and other arthropods feed (van Asch & Visser, 2007). However, in general, dates of spring onset derived from temperature-based models and remotely-sensed vegetation indices are broadly correlated (Zurita-Milla et al., 2020). Accordingly, we found similar patterns in migration rate and timing regardless of whether we characterized spring using temperature-based first leaf models or satellite-derived NDVI models, despite absolute differences in their estimates of spring onset day.

Our study made a number of simplifying assumptions. Bird tracking data consisted of "snapshot" detections at two points along each individual's migratory journey. This represents an important but incomplete segment of the migratory track; for example, if additional birds ultimately jumped over the green wave at higher latitudes, we would be unable to distinguish this from a catching up pattern because of the limited number of receiver stations operating further north. As discussed, environmental conditions at the endpoints of the track – the non-breeding departure location and the breeding destination – and at stopover sites throughout the Americas also influence migration rate and timing (González-Prieto & Hobson, 2013; Studds & Marra, 2011). Establishing additional receiver stations at stopover sites south of the Gulf of Mexico and throughout migrants' non-breeding ranges, as well as at high latitudes, could therefore be valuable for understanding migratory connectivity and *en route* variation in stopover ecology and timing (Bayly et al., 2018; Gómez et al., 2017).

Another limitation was our inability to investigate potentially important heterogeneity in the progression of migration and vegetation phenology between detection locations and through time (Ahola et al., 2004; Aikens et al., 2020; Donnelly et al., 2017). For example, the annual mean speed of the green wave in North America varies by ecoregion (O'Leary et al., 2020), reflecting a mixture of abiotic and biotic conditions unique to each region. Additional detections would have allowed us to see if migration rate and green wave rate differed between track segments, perhaps reflecting differences in stopover site resource phenology and quality that can vary between years and ecoregions. Furthermore, our sample size was too small to model effects of factors such as wind direction, age, and sex, which can be important determinants of migration rate and timing (Dossman et al., 2022; Morbey et al., 2018). Despite its limitations, automated radiotelemetry is a valuable technique for tracking small songbirds over long distances with high temporal precision, especially compared to other technologies. We also confirmed that Motus data can be used to derive plausible estimates of migration rate and flight speed consistent with empirical measurements and with theoretical predictions of time spent on stopover versus passage (Hedenström & Alerstam, 1997).

CONCLUSION

As climate change affects the timing of organisms' life history events, animals may grow increasingly out of sync with the phenology of resources in their environments (Youngflesh et al., 2023). Migratory birds are flexible enough to adjust to novel conditions *en route* and hence may be expected to cope with changing conditions better than other organisms (Charmantier & Gienapp, 2014). However, long-distance migrants may be unable to keep pace with rapid changes beyond a certain point and could suffer negative consequences (Carey, 2009; Connare & Islam, 2022; Miller-Rushing et al., 2008). The catching up pattern that we found in songbirds migrating through eastern North America may indicate that they can exploit a range of stages of vegetation phenology during migration, which we surmise corresponds to a shifting variety of arthropod food sources *en route.* In effect, these species could be considered generalists rather than specialists with regard to resource phenology during this phase of their life cycle (Abrahms et al., 2021). Flexibility and breadth in diet could help buffer songbirds from harmful effects of climate change-induced phenological mismatches during migration. Additional tracking of individual migrants and empirical assessments of their diets and food resource phenology (e.g., Di Cecco et al., 2023) on stopover is necessary to clarify the adaptive value of this pattern and if it is maintained as birds near their destinations. Future efforts to characterize spatiotemporal patterns of prey availability and quality across migration landscapes would help identify if arthropod resource waves exist across broad scales and could shed additional light on optimal strategies for migrating songbirds.

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Conflict of Interest

The authors have no conflicts of interests to declare.

Author Contributions

CEN and EBC conceived of the project and developed hypotheses. CEN conducted the analyses and wrote the manuscript. PPM, TJZ, SAC, BCD, ARG, CG, AMG, MGR, SAH, JM, PLV, and EBC conducted fieldwork and contributed Motus data. PPM and SAH provided financial support. All authors reviewed and provided feedback on the manuscript.

Data Availability Statement

Data and code are available from the Dryad Digital Repository:

https://datadryad.org/stash/share/ONiVWICLyRYea9LBss4c_DYRL62P1Y5anQ9C110-AZc

(Nemes et al. 2023)

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