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REVIEW

Ten years tracking the migrations of small landbirds: Lessons learned in the golden age of bio-logging

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ABSTRACT

In 2007, the first miniature light-level geolocators were deployed on small landbirds, revolutionizing the study of migration. In this paper, we review studies that have used geolocators to track small landbirds with the goal of summarizing research themes and identifying remaining important gaps in understanding. We also highlight research and opportunities using 2 recently developed tracking technologies: archival GPS tags and automated radio-telemetry systems. In our review, we found that most (54%) geolocator studies focused on quantifying natural history of migration, such as identifying migration routes, nonbreeding range, and migration timing. Studies of behavioral ecology (20%) uncovered proximate drivers of movements, including en route habitat quality; that migration routes, but not timing, may be flexible in some species; and different age and sex classes show significant differences in migration strategy. Studies of the evolution of migration (9%) have illustrated that migration is a potential barrier to hybridizing species or subspecies, and some work has correlated gene polymorphisms and methylation patterns with migration behavior. Studies of migratory connectivity (11%) have shown that a moderate level of connectivity is common, although variability across and within species exists. Studies of seasonal interactions (7%) have found mixed results: in some cases, carryover effects have been identified; in other cases, carryover effects are buffered during intervening stages of the annual cycle. Archival GPS tags provide unprecedented precision in locations of nonbreeding sites and migration routes, and will continue to improve understanding of migration across large spatial scales. Automated radio-telemetry systems are revolutionizing our knowledge of migratory stopover biology, and have led to discoveries of previously unknown stopover behaviors. Together, these tracking technologies will continue to provide insight into small migratory landbird movements and contribute important information for conservation of this rapidly declining group.

Keywords: geolocation, geo-logging, method, movement, songbird, tracking

Diez años siguiendo las migraciones de aves terrestres pequeñas: Lecciones aprendidas en la edad de oro de los bio-registros

RESUMEN

En 2007, los primeros geo-localizadores de nivel de luz en miniatura fueron colocados en aves terrestres pequeñas, revolucionando el estudio de las migraciones. En este artículo, revisamos los estudios que han usado geo-localizadores para seguir aves terrestres pequeñas con el objetivo de resumir los temas de investigación e identificar los vacíos de conocimiento que aún perduran. También destacamos investigaciones y oportunidades dadas por el uso de dos tecnologías de seguimiento recientemente desarrolladas: etiquetas GPS de archivo y sistemas de radio telemetría automatizados. En nuestra revisión, encontramos que la mayoría (54%) de los estudios de geo-localización se enfocaron en cuantificar la historia natural de la migración, como identificar las rutas de migración, el rango no reproductivo y el tiempo de migración. Los estudios de ecología del comportamiento (20%) revelaron las causas inmediatas de los movimientos, incluyendo la calidad del hábitat de la ruta; que las rutas migratorias, pero no el tiempo, pueden ser flexibles en algunas especies; y que diferentes clases de edad y sexo muestran diferencias significativas en la estrategia migratoria. Los estudios de la evolución de la migración (9%) han mostrado que la migración es una barrera potencial para hibridar especies o sub-especies, y algún trabajo ha correlacionado los polimorfismos genéticos y los patrones de metilación con el comportamiento migratorio. Los estudios de conectividad migratoria (11%) han mostrado que un nivel moderado de conectividad es común, aunque existe variabilidad entre y adentro de las especies. Los estudios de interacciones estacionales (7%) han encontrado resultados mixtos: en algunos casos, se han identificado efectos de arrastre, y en otros casos, los efectos de arrastre se amortiguan durante las etapas intermedias del ciclo anual. Las etiquetas GPS de archivo brindan una precisión sin precedentes en la ubicación de los sitios no reproductivos y las rutas migratorias, y continuarán mejorando el entendimiento de la migración a través de grandes escalas espaciales. Los sistemas de radio telemetría automatizados están revolucionando nuestro conocimiento de la biología de los sitios migratorios de parada y han permitido descubrir comportamientos de parada previamente desconocidos. En conjunto, estas tecnologías de seguimiento continuarán brindando perspectivas sobre los movimientos migratorios de las aves terrestres pequeñas y proveyendo importante información para la conservación de este grupo que disminuye rápidamente.

Palabras clave: ave canora, geolocalización, geo-registros, método, movimiento, seguimiento

INTRODUCTION

We have now entered a golden age of bio-logging (Wilmers et al. 2015), where tracking technology has become both smaller and more sophisticated, allowing unprecedented studies of movements of individual animals (Kays et al. 2015). For birds under 100 g in weight, the behavior and ecology of the migration period and full-annual cycle habitat use is rapidly being revealed with the widespread application of miniaturized tracking devices (McKinnon et al. 2013a). We now have examples of songbirds that show weak and strong migratory connectivity patterns (Fraser et al. 2012, Cormier et al. 2013, Hahn et al. 2013, Hallworth et al. 2015, Stanley et al. 2015, Koleček et al. 2016, Ouwehand et al. 2016), comparisons of start-to-finish migration strategy by different sex and age classes (Tøttrup et al. 2012b, McKinnon et al. 2014, 2016; Evens et al. 2017a), analysis of the flexibility of route choice and migration timing (Stanley et al. 2012, Smolinsky et al. 2013, Sjöberg et al. 2015, Streby et al. 2015, Woodworth et al. 2015), and examples of the influence of extreme weather on migration (Tøttrup et al. 2012a, Fraser et al. 2013, Streby et al. 2015, Briedis et al. 2017). These insights would not have been possible without the miniaturization of a simple light-level logging tag, first deployed on small passerines in 2007 (Stutchbury et al. 2009). Despite the logistical challenges of applying geolocators (i.e. the tags must be retrieved to recover data, analysis is prone to relatively large latitudinal errors, some studies experience high rates of tag or harness failure), researchers have persisted, and consequently gained enormous insights into bird migration. Over 100 studies have now been published using light-level geolocators to answer various questions related to migration ecology and full-life cycle biology of small landbirds (up to 2012 cited in McKinnon et al. 2013a, more recent studies in Appendix A), as well as studies of the effects of tags (see list in Appendix B), and a recent tracking-data meta-analysis of migratory connectivity (Finch et al. 2017).

Since the miniaturization of geolocators, there have been several new technological developments that have increased the capacity for tracking small birds. Platform transmitter terminals (PTTs), which transmit data regularly via communication with Argos satellites, are now <5 g (e.g., 3.5 g PinPoint tag; www.Lotek.com), and are generating important insights into locations of mortality over the annual cycle for birds as small as the European Cuckoo (*Cuculus canorus*, 115 g; Hewson et al. 2016). However, these satellite tags are still much too large for most small landbirds. Archival Global Positioning Systems (GPS) tags are now as lightweight as the first geolocators and can be applied to many small landbirds (Table 1, Figure 1). These tags record information from GPS satellites to a high degree of accuracy (i.e. within 10 m) and are within the acceptable weight limits to deploy on birds under 50 g (based on a 3–5% body-mass rule). Like geolocators, they do not transmit data, but must be recovered and downloaded. New SWIFT-fix archival GPS tags as small as 1 g can record up to 100 precise geographic locations, a vast improvement over original models that collected only 10 points (Hallworth and Marra 2015, Fraser et al. 2017).

Another rapidly emerging tool for tracking movements of small landbirds is the use of automated-telemetry systems. Digitally coded radio telemetry allows many tagged individuals to be detected on the same radio frequency, in contrast to a traditional "beeper" radio tag, which requires time-consuming frequency scrolling. By combining these digitally coded tags (Table 1, Figure 1) and a static array of radio-receivers dispersed over the landscape of interest, movements of many individual birds can be simultaneously tracked over a large area, such as a major migratory stopover region. One of the biggest projects involving this technology is the Canada-based Motus Wildlife Tracking System (www.motus-wts.org; *Motus* being the Latin word for movement), which currently has over 200 receiving towers active throughout the Americas (Taylor et al. 2017). A similar large-scale automated-telemetry system has been proposed for major stopover sites in Egypt (Rerucha et al. 2015), and many smaller arrays of receivers are being used for individual research projects. Stopover biology appears to be one of the best applications of this technology, which has led to key insights in to how small landbirds are using stopovers (Mills et al. 2011, Sjöberg et al. 2015, Woodworth et al. 2015, Gomez et al. 2017), and even discoveries of previously unknown stopover behaviors (Brown and Taylor 2015).

Here, we examine 3 currently available tracking technologies—geolocators, GPS loggers, and automated telemetry systems—which can all be deployed on small migratory landbirds to track movements. Each of these tracking technologies has limitations and logistical considerations that must be taken into account in order to

TABLE 1. Types of tracking tags available for determining movements of small landbirds.

Tag (manufacturers)	Smallest weight (g)	Stalk/Other	Approximate cost (USD)	Transmit?	Battery life	Important considerations	Example studies
Light-level geolocators (Lotek/biotrack, MigrateTech, Swiss Ornithological Institute)	0.35	Angled stalk of varying lengths, or vertical "light pipe"	200	No	0.5–2 yr	• Size of study species • Habitat types – more open habitats generally provide better resolution • Foraging behavior – dense foraging substrate may cause excessive shading, aerial foragers may be more affected by drag • Location of bird during equinoxes – if migration occurs during equinox, resolution of routes will always be poor • Longitudinal distribution – species moving along a north-to-south axis may be problematic as latitudinal error is relatively high • Analysis is increasingly complex (e.g., Bayesian approaches to route estimation during equinox)	Cooper et al. 2017
GPS-loggers (Lotek/biotrack, PathTrack Ltd)	1.0	Short whip-antenna	400	Some	1–2 yr	• Size of study species • Can study species reach whip antenna and pull it off? • Care must be taken during programming to make sure points are taken in the period of interest; some prior knowledge of annual timing required • Points can be taken at night or during day – roosting habitat could obscure satellites resulting in low probability of fixes; conversely, roosting sites may not be of as much interest as foraging sites • No post-hoc analysis needed; location is directly recorded • Tags may have high failure rates	Fraser et al. 2017
Digitally coded radio-tags (Lotek/biotrack)	0.26	Long antenna	200	Yes	10 days to >1 yr	• Location of towers • Foraging location – aerial species are picked up more easily by stationary towers than ground-foragers • Time tracked – smallest tags may only last 2–3 mo • Some post-hoc analyses, for example, if directionality of flight or exact location of individuals is important (i.e. examining signal strength dissipation on different antennas on a single tower, or triangulating positions between various antennae)	Gomez et al. 2017

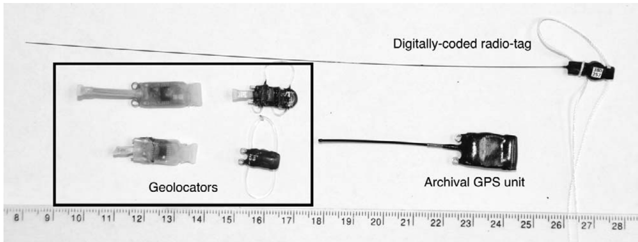

FIGURE 1. Examples of tracking tags deployed on small landbirds, including 4 models of geolocators (3 stalked, 1 unstalked in bottom right), an archival GPS unit, and a digitally coded radio-tag. Note that not all tags shown include the harness, which must be built and added. Usually string (shown on radio-tag) or elastic beading cord (shown on 2 geolocators on right-hand side of box) are used to create a leg-loop harness. Scale bar shows centimeters.

effectively answer questions by using these tools. Given the substantial cost of the tags (generally >US$200 per unit), it is critical that researchers consider the specific questions they are interested in as well as the limitations of the tags and the most appropriate study species.

Our objectives were to (1) summarize the studies using geolocators to track migrations of small landbirds, (2) highlight new tracking work that uses archival miniature GPS and automated radio-telemetry to track movements of small landbirds, and (3) provide guidelines as to which tags are best employed for answering which questions, so that researchers can invest in tracking that gives them the best value and data in the safest way possible for their study species. From geolocator studies, we were interested in the major objectives of the study, the study system, and the geographic scope of the research. Given that there is already a meta-analyses of tag effects published (Costantini and Moller 2013), and a second in preparation (P. Prochazka personal communication), we did not include in our review papers explicitly testing for effects of geolocators, although we provide a list of these studies (Appendix C). Based on the results of our literature search, we then outline gaps in tracking research on migratory landbirds that can be filled by using currently available and upcoming tracking technology.

METHODS

Geolocator Literature Review

We searched "geolocator*" as a topic in ISI Web of Science Core Collections. From the resulting list of studies ($n = 344$ as of February 27, 2018), we omitted those that were not focused on passerine (Passeriformes) or small (defined as <160 g) near-passerine landbirds (e.g., Piciformes, Coraciiformes); hereafter, we refer to the group of interest as "small landbirds." The average weight of the species tracked in our database was 37 g, with a minimum of 8.7 g and a maximum of 157 g. The 3 largest species we included were European Roller (*Coracias garrulus*, 136–143 g), Ring Ouzel (*Turdus torquatus,* 101 g), and Northern Flicker (*Colaptes auratus,* 157 g); all other species were less than 85 g. Although this excluded many interesting and important migration-tracking studies of shorebirds, seabirds, raptors, and other taxonomic groups, for the purposes of the current study, we were primarily interested in orders of birds that were un-trackable before the advent of <2 g geolocators, which includes most small passerines. In contrast, many species of raptor are large enough that satellite tags have been used to track individuals since the 1990s (Nowak and Berthold 1987), and we anticipated migration behavior, ecology, and effects of tracking tags for smaller raptors (which do require miniature geolocators) would be more comparable with studies of their larger relatives than to the many passerines and near-passerine landbirds.

After excluding studies of non-landbirds, we also excluded papers dealing exclusively with data-analysis methods (e.g., McKinnon et al. 2013b, Korner-Nievergelt et al. 2017), as well as 2 reviews of tracking studies (McKinnon et al. 2013a, Lopez-Lopez 2016) and a meta-analysis (Finch et al. 2017). We excluded from further analysis studies of the effects of geolocators on fitness parameters of small landbirds ($n = 13$, plus a comment and rebuttal), but they are listed (Appendix C). We also searched the terms "geolocation + bird" ($n = 130$ results). We used a more broad search to identify any remaining studies, using the topics "track* AND bird AND migrat*", omitting topics "seabird* OR raptor* OR shorebird*" and limiting results to studies published after 2010 (final $n = 609$ studies). We also searched by hand for studies using geolocators on small landbirds in journals that are not indexed by Web of Science, including *Animal Migration* ($n = 5$), *BMC Ecology* ($n = 1$), *Western Birds* ($n = 1$), *Limosa* ($n = 1$), and *Ornis Svecica* ($n = 1$). Finally, we manually searched all papers published in the top ornithological journals (*The Auk: Ornithological Advances*, *The Condor: Ornithological Applications*, *Journal of Avian Biology*, *Ibis*, *Journal of Field Ornithology*, and *Journal of Ornithology*) from October 2017 to February 2018 for advanced publication of studies using geolocators to study migration of small landbirds that had not yet been indexed by Web of Science.

From each geolocator study in our database (final $n = 127$), we extracted the following variables: study species (and average weight of study individuals, if reported), the number of individuals tracked, category of the publishing journal type (ornithological, broad science, zoology, or ecology/evolution), specific objectives, and overall purpose of the study. We used the BirdLife International flyways (http://www.birdlife.org/worldwide/programme-additional-info/migratory-birds-and-flyways) to define the

TABLE 2. Research topics addressed using miniature tracking devices on small landbirds.

Category (*n*, percent of total *n*)	Example objectives	Example studies
Natural history of migration ($n = 59$; 54%)	• identify migration routes/nonbreeding/breeding sites • describe full-annual cycle timing • determine if and how birds cross barriers • determine use of cavity roosts during migration • refine nonbreeding ranges • document within-winter movements • document molting sites • confirm resident/migratory status • describe nonbreeding habitat	Bravo et al. 2017
Seasonal interactions ($n = 7$, 5.5%)	• test for carryover effects of nonbreeding habitat on spring migration and breeding success • test for carryover effects of breeding events on fall migration • test for year-round timing dependencies	van Wijk et al. 2017
Behavioral ecology ($n = 26$, 20.5%)	• determine proximate controls of migration timing (e.g., habitat quality, weather, phenological matching) • assess flexibility in migration timing and route by repeat-tracking individuals • describe response of individuals to severe weather (storms, droughts) • determine social aspects of migration (do pairs stay together all year?)	Wellbrock et al. 2017
Evolution of migration patterns ($n = 11$, 9%)	• examine migration patterns/nonbreeding sites/timing as a pre-zygotic barrier to hybridizing species/sub-species • test hypotheses for differential migration by age/sex classes • quantify the genetic basis for migration • correlate morphology with migration strategy (ecomorphology)	Haché et al. 2017
Migratory connectivity ($n = 14$, 11%)	• document how individuals from multiple breeding populations disperse across wintering range and vice versa	Koloček et al. 2016

geographic scope of each study. We further categorized each study into 4 broader categories: (1) natural history of migration, (2) evolution of migration, (3) behavioral ecology of migration, (4) migratory connectivity, and (5) seasonal interactions (Table 2).

We additionally searched for papers that tracked small landbirds using archival GPS units and automated radio-telemetry systems. We used the following search terms for archival GPS studies: "tracking", "migrat*", "bird", "GPS"; and for automated-telemetry studies: "automated radio telemetry", "bird". We eliminated non–small landbird studies and methods papers, as per our search for geolocator studies detailed above. Additionally, we focused on telemetry studies dealing with aspects of migration, as opposed to tracking work during stationary periods of the life cycle (i.e. breeding territoriality). Since there were far fewer studies using archival GPS and automated telemetry systems, we discuss them broadly. We found 3 studies that used archival GPS tags to track small birds (Hallworth and Marra 2015, Siegel et al. 2016, Fraser et al. 2017), and one that used both geolocators and archival GPS tags (Evens et al. 2017b). There were 20 studies using automated radio-telemetry systems (Appendix B) to study migration behavior of small landbirds and 2 studies describing automated-telemetry as a tool (Rerucha et al. 2015, Taylor et al. 2017).

RESULTS

The number of studies published that used geolocators on small landbirds has increased steadily since 2010. Of 127 papers in total (Appendix A), 44% were published in 2016 or 2017, and an additional 3 papers published in 2018 by February bring this up to 46%. Papers were most commonly published in ornithological journals (49%) followed by broad science (25%), ecology and evolution (16%), and zoological journals (10%). In the last 3 yr, the number of papers in broad scientific journals has declined (29% in 2015, 20% in 2016, 13% in 2017) while the number of papers in ornithological journals has increased (43% in 2015, 52% in 2016, 61% in 2017). Most studies focused on aspects of the natural history of migration (54%), followed by behavioral ecology (21%), migratory connectivity (11%), evolution of migration (9%), and seasonal interactions (6%) (Figure 2). The average sample size in terms of individuals tracked was 24 $\pm$ 36 (standard deviation), although about half the studies (51%) tracked fewer than 10 individuals (range 1–222). Most studies tracked birds in one of two major flyways,

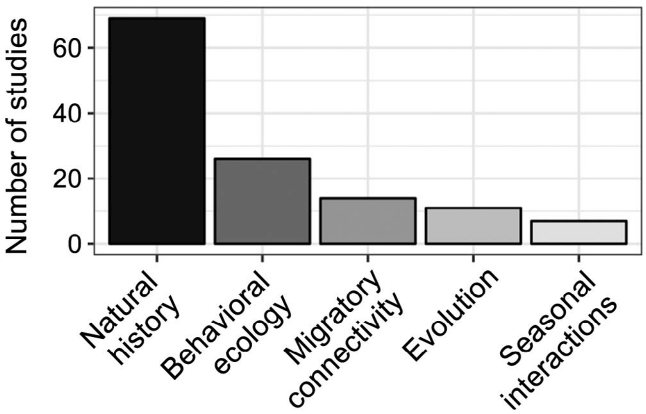

FIGURE 2. The number of publications using geolocators deployed on small landbirds since 2009 filtered by major research topic ($n = 127$ studies). Each bar shows the number of studies published in each of 5 broad categories.

East Atlantic and Atlantic Americas (33% and 20% of all studies; Figure 3); followed by the Central Americas (20%), Black Sea/Mediterranean (13%), and Pacific Americas (7%). Fewer than 5 studies tracked birds within South America, East Asia/Australasia, Central Asia, East Asia/East Africa, or Europe (total for all ~7%). Twenty papers used automated telemetry systems (i.e. Motus) to study migratory movements of small landbirds (Appendix B).

DISCUSSION

The number of papers using tracking technology to study movements of small landbirds has increased significantly over the last 10 yr. There are currently 127 studies published on movements of small landbirds with geolocators alone (Figure 2), not including papers on analysis approaches (e.g., Lisovski et al. 2012), testing accuracy of geolocators compared with other tracking techniques (e.g., Korner-Nievergelt et al. 2012, Hallworth et al. 2013, Rakhimberdiev et al. 2016), or testing the effects of geolocators on fitness ($n = 13$ plus 2 commentaries; Appendix C). In contrast to the growing body of geolocator-tracking literature, there are only 3 studies published to date that exclusively use miniature archival GPS tags (Hallworth and Marra 2015, Siegel et al. 2016, Fraser et al. 2017); however, we expect this number will increase in the next year or two.

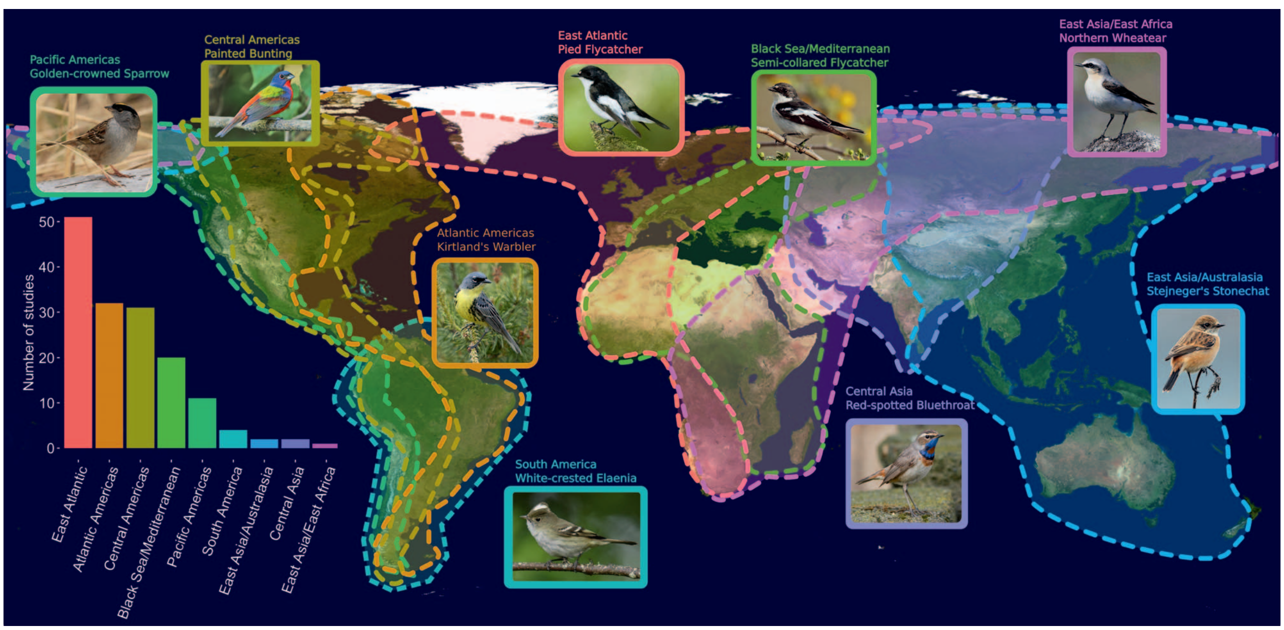

FIGURE 3. Major global flyways (modified from descriptions in BirdLife Flyways Programme, www.birdlife.org) and example species that have been tracked by using geolocators in each flyway. Colors framing photos indicate the flyway. Inset histogram counts the number of studies that have tracked birds in each flyway. If a study covered more than one flyway, it was counted once in each. Studies tracking bird migration within Europe ($n = 2$) have been omitted for simplicity. Photo credits: Kirtland's Warbler – Ron Austing; Painted Bunting – David Hollie; Pied Flycatcher – Andy Sands; Semi-collared Flycatcher – John A. Thompson; Northern Wheatear – Mark Peck; Stejneger's Stonechat – Robin Newlin; Red-spotted Bluethroat – Martyn Sidwell; Golden-crowned Sparrow – George Pagos; White-crested Elaenia – Luis R. Figuerosa. NASA Goddard Space Flight Center Image by Reto Stöckli (land surface, shallow water, clouds). Enhancements by Robert Simmon (ocean color, compositing, 3D globes, animation). Data and technical support: MODIS Land Group; MODIS Science Data Support Team; MODIS Atmosphere Group; MODIS Ocean Group. Additional data: USGS EROS Data Center (topography); USGS Terrestrial Remote Sensing Flagstaff Field Center (Antarctica); Defense Meteorological Satellite Program (city lights).

Automated radio-telemetry has been used as an extension of traditional radio-telemetry for examining territorial behaviors of birds at breeding sites, and provided important insights into previously under-studied or unknown behavior, such as nocturnal forays, nighttime predation, and dispersal of brood parasites (Ward et al. 2014, DeGregorio et al. 2015, Louder et al. 2015). Automated-telemetry is also filling an important gap in our understanding of migratory initiation and stopover behaviors ($n = 21$ studies, Appendix B). Wright et al. (2018) examine in detail the stopover biology of a species at risk, the Rusty Blackbird (*Euphagus carolinus*). They discovered a pattern of extended stays (25 days on average) in both spring and fall; correlations between stopover duration, molt, and body condition; and nocturnal migration over water; all important information for conservation and management, as well as shedding light onto stopover biology in general. The application of automated telemetry as a broad-scale movement ecology tool is also gaining momentum with the growing array of passive receiving towers across the Americas. For example, Gray-cheeked Thrushes (*Catharus minimus*) captured at a stopover site in Colombia were recorded at their subsequent stopovers in North America, allowing inferences about fat accumulation at the tropical stopover site and subsequent flight strategy (Gomez et al. 2017).

Despite the interest in and widespread use of geolocators, archival GPS tags, and automated telemetry systems, there is nonetheless a strong geographic bias toward tracking birds in the Atlantic Americas and East Atlantic flyways (together, 53% of all studies; Figure 3). Very few studies have occurred in the Central or East Asian flyways (1% each), and migration within South America is still largely unstudied (3%). In addition, there are no known studies tracking intra-African landbird migration. While we have gained important insights into migration from studies of the Atlantic Americas and East Atlantic flyways, generalization of results to other systems is not straightforward. For example, the Gulf of Mexico is a major barrier that shapes the migration strategies of migratory birds in the Atlantic and Central Americas flyways, and the deserts of the Sahara shape migration strategies of many East Atlantic and Black Sea/Mediterranean migrants (Newton 2008). The major barriers to birds migrating within South America, for example, or along the Central Asian flyways, and how that has shaped their migration strategy, are areas that require more investigation. More tracking within these under-studied systems would surely provide some insights into the evolution of migration, as well as important data for conservation.

The overarching purpose stated in most studies tracking small migratory landbirds is to fill important and often large information gaps in what we know about nonbreeding ecology and behavior of these species (Faaborg et al. 2010). Thus, about 54% of all geolocator studies can be broadly categorized as "natural history of migration" and about half (49%) are published in primarily ornithological journals (Figure 2). In a few studies, authors also named conservation as the raison d'être for their tracking work (e.g., Salewski et al. 2013). Specifically testing ecological or behavioral theory (e.g., optimal migration theory, Schmaljohann et al. 2012; niche-following theory, Hahn et al. 2013) by using individual-based tracking is still relatively rare, as the number of individuals tracked in each study is small. On average, a given geolocator study has information only from 24 $\pm$ 3.2 individuals (mean $\pm$ SE), with most studies having far fewer (mode $=$ 3 individuals). There are certainly exceptions from well-studied species such as the Purple Martin (*Progne subis*), where migration data are now available for over 200 individuals (Stutchbury et al. 2016a, 2016b).

Geolocator studies are also biased toward tracking males ($\sim$26% of studies explicitly track only males; another 14% do not report sex of individuals tracked), likely because in many species of passerines they tend to be slightly larger than females, and they respond more aggressively to audio lures, making capture easier. In studies which attempted to track both sexes (60%), most have far fewer samples from females. When both sexes were tracked, results suggest that a male bias could be problematic. For example, Saino et al. (2017b) tracked both males and females to study carryover effects of nonbreeding conditions, and found a strong effect on fitness parameters for females, but not males. This suggests there could be important differences in the behavior and ecology of birds that would be missed by tracking only males. Many species exhibit differential migration strategy by sex or age class (Fudickar et al. 2013, McKinnon et al. 2014, Woodworth et al. 2016), therefore understanding migration overall requires tracking individuals from across demographic groups. It is also interesting that effects of tags appear more severe for females than males (Scandolara et al. 2014); this suggests differences in energetics of migration could be at play, and that researchers should consider tagging males and females with different tags (i.e. lighter weight for females). Researchers should carefully consider the questions they are interested in and whether sex differences are predicted to occur, and how best to capture and track females. To our knowledge, no studies have specifically deployed smaller or lighter tags on only females; this might be warranted to increase information return and reduce any effects of the tags.

For the remainder of the discussion we summarize some of the key findings in each of the main research topics we identified: natural history of migration, migratory connectivity, seasonal interactions, behavioral ecology, and evolution of migration.

Natural History of Migration

There are now geolocator-tracking studies of the natural history of migration for 63 species of small landbirds (see Appendix A). Long-standing knowledge gaps pertaining to migration and overwintering sites are only now being filled in with information from geolocator tracking. For example, the globally threatened Aquatic Warbler (*Acrocephalus paludicola*) was found to use an unexpected migration route (Salewski et al. 2013), and Connecticut Warblers (*Oporornis agilis*) were shown to make a previously undocumented 2-day transatlantic flight during fall migration (McKinnon et al. 2017). In other species, long-hypothesized behaviors, such as molt migration, open-ocean flights, and nocturnal migrants using daytime flight to cross barriers, have been confirmed by using light-level geolocators (DeLuca et al. 2015, Adamík et al. 2016, Pillar et al. 2016). Many studies with small sample sizes have laid the groundwork for future tracking of those species to test more specific hypotheses, although the basic natural history information even from only a small sample of individuals can sometimes lead to new questions and directions. We suggest that further tracking efforts focus on understudied flyways and species, especially where species of conservation concern can safely carry geolocator or archival GPS tags.

One of the major breakthroughs with the application of small tracking technology to small birds has been the documentation of extensive within-season movements of birds previously assumed to be territorial/sedentary outside of the migratory period. Veeries (*Catharus fuscescens*) use up to 3 distinct overwintering sites, separated by migratory-like flights of hundreds of kilometers (Heckscher et al. 2011, 2015). Conversely, Common Redstarts (*Phoenicurus phoenicurus*) were expected to show nonbreeding itinerancy, but geolocator tracking indicated that they were in fact quite sedentary during the overwintering period (Kristensen et al. 2013). Bobolink (*Dolichonyx oryzivorus*), Purple Martin, Veery, and several Austral migrants (White-crested Elaenia [*Elaenia albiceps chilensis*], Fork-tailed Flycatcher [*Tyrannus savana*]) all appear to have multiple nonbreeding residency sites within continental South America (Jahn et al. 2013, 2016; Renfrew et al. 2013, Stutchbury et al. 2016b, Bravo et al. 2017). It is likely that other South American wintering migrants or Austral migrants make large within-winter movements, but this remains to be investigated for more species. Intra-African migratory landbirds are also presumed to be "rain" migrants, departing sites at the end of the rainy season (Nwaogu and Cresswell 2016); however, to date there have been no tracking studies of any species of small landbird in this system.

The scale of these within-season movements (hundreds of kilometers) would have been undetectable with traditional radio-tags and hand-held radio receivers, mark–recapture, or other intrinsic markers such as stable isotope analysis. Relatively small-scale movements can often be detected by using geolocators (Fudickar et al. 2013), if the movements are of sufficient distance that they are larger than the expected error of the tag, which varies depending on species, habitat, tag type, and other factors. Archival GPS tags can provide more specific details on within-season movements, especially when those movements occur on a smaller scale. For example, geolocator tracking did not reveal any obvious within-winter movements in Wood Thrushes (*Hylocichla mustelina*; Stutchbury et al. 2009); however, follow-up work using archival GPS tags indicated that in late winter, many individuals traveled to "new" overwintering sites, prior to departure on northbound spring migration (C. Stanley personal observation). These movements in late winter were previously obscured by equinox effects on latitude estimates from geolocators.

Digitally coded radio-tags (e.g. Lotek NanoTags) and passive radio receiving arrays are very well suited to the study of nomadic and irruptive movements of small landbirds—both topics which have received very little attention. While this technique has been available for some time and provided important insights into migration behavior already (Smolinsky et al. 2013), the rapid expansion of the Motus automated receiving array across North America and beyond (Taylor et al. 2017) is building momentum for studies using this technology at greater spatial scales. Many northern-breeding finches, buntings, and sparrows are known to roam throughout their overwintering range, but little is understood about the causes and consequences of these movements (Newton 2008), or even the basic range and demographics of individuals moving. While geolocators or archival GPS tags can provide some insight into nomadic movements, they require that individuals are recaptured to obtain the archived data. This may be difficult for species that are irruptive and not faithful to breeding sites, or which breed in relatively inaccessible sites. For these species, automated telemetry arrays are ideal, as individuals can be trapped at a single site within the array, and movements within the area of the towers can be detected. To date this method has shown promise in determining the abiotic drivers of nomadism in Snow Buntings (*Plectrophenax nivalis*; E. A. McKinnon personal observation), and this method could also be applied to irruptive species such as grosbeaks, crossbills, or even smaller species such as redpolls. Given that these cold-adapted species are on the front lines of climate change, both at their high-latitude breeding sites and because of warming temperate winters, testing phenomenological and mechanistic hypotheses for winter movements is important for predicting effects of climate change on these species.

Migratory Connectivity

Determining the degree of migratory connectivity (Webster et al. 2002) was one of the first major questions addressed by many researchers deploying tracking tags on small landbirds (reviewed in McKinnon et al. 2013a). For example, quantifying the degree of mixing and relative spread of breeding populations at nonbreeding sites (Finch et al. 2017) is key for predicting population responses to habitat loss (Taylor and Norris 2010, Taylor and Stutchbury 2015), identifying priority areas for conservation (Stanley et al. 2015), and exploring causes for observed breeding ground population trends (Fraser et al. 2012, Hewson et al. 2016). Despite the widespread interest in describing and quantifying the degree of migratory connectivity, few geolocator studies have the geographic scope and sample size to actually measure migratory connectivity. Indeed, only 11% of the studies we reviewed quantified migratory connectivity (Figure 2). Even within this group, most studies combined tracking data with other sources of connectivity information, such as band recoveries and or stable-isotope analysis of feathers (e.g., Macdonald et al. 2012, Hallworth et al. 2015, Ouwehand et al. 2016). For species that have been tracked extensively, collaborative projects have provided enough individual tracking data to quantify migratory connectivity (Fraser et al. 2012, Finch et al. 2015, Stanley et al. 2015, Koleček et al. 2016). This highlights the importance of collaborations for answering range-wide questions about migratory connectivity that have critical implications for conservation.

Currently, the most appropriate tags for studying migratory connectivity are archival logging tags—geolocators and GPS-loggers. For precision of nonbreeding sites, GPS-loggers provide the most complete information (Hallworth and Marra 2015, Fraser et al. 2017), although they are slightly larger than the smallest available geolocators (Table 1) and at present may have relatively high tag-failure rates (K. C. Fraser personal observation). For birds that are currently still too small for the smallest GPS-loggers, geolocators can provide a more general nonbreeding location, although care must be taken to deploy tags with sufficient battery life to last until birds arrive at their wintering sites (Table 1).

Despite widespread understanding of the concept of migratory connectivity, there remain some key points that should be considered when designing a study of migratory connectivity using direct-tracking technology. First, individuals must be tracked from different populations, ideally from across the entire range. This is because connectivity consists of 2 components: mixing of individuals from different populations, and the spread of individuals across the range of the species (Finch et al. 2017). The former requires tracking data from multiple populations; the latter can be determined by tracking only from one site. Conclusions can be very different depending on the populations included. For example, Iberian Peninsula–breeding European Rollers showed "weak" connectivity based on mixing of individuals from 2 breeding populations at nonbreeding sites (Rodriguez-Ruiz et al. 2014). However, a range-wide connectivity study of the same species found significant spatial structure between breeding and wintering sites, and an overall "moderate" level of migratory connectivity (Finch et al. 2015). The latter study combined satellite tags, geolocators, and banding data to provide a more complete picture of species-level connectivity. Combining techniques can be an effective strategy, given the need for range-wide data for proper assessment of migratory connectivity at the species level (Macdonald et al. 2012, Hobson and Kardynal 2016). Combining techniques can also address the issue of sample size. Given variability in the accuracy of tracking tags such as geolocators, and potentially large individual variation in migration behavior (Wellbrock et al. 2017), caution must be used when making conclusions about migratory connectivity from only a few individuals. A recent meta-analysis of tracking data suggests that strong connectivity may in fact be quite rare for small migratory landbirds (Finch et al. 2017).

Hallworth et al. (2015) incorporated abundance of Ovenbirds into measures of migratory connectivity. A recently published R package, MigConnectivity, expands on this approach and allows researchers to estimate migratory connectivity taking into account uncertainty and unequal sampling distribution across populations in a modified Mantel correlation (Cohen et al. 2018). This quantitative approach to measuring connectivity will facilitate intra-species comparisons, and allow insight into the evolution and ecological drivers of observed patterns. Bracey et al. (2018) show how different abundance scenarios of Common Terns (*Sterna hirundo*) affect calculations of migratory connectivity based on broad-scale geolocator tracking, and that overall this species shows a low or weak degree of connectivity, with extensive mixing at winter sites of birds from widespread breeding colonies.

Seasonal Interactions

How events and processes in one season affect fitness in subsequent seasons has been an expanding area of research in the past 10 yr (Norris 2005, Harrison et al. 2011). Geolocators have allowed researchers to explicitly track carryover effects for small migratory landbirds, although to date there are only 7 studies that have used geolocators to address seasonal interactions. Many studies have looked an environmental drivers of carryover effects, such as habitat quality. In Wood Thrushes, dry conditions at wintering sites delayed spring migration departure, but not arrival at breeding sites (McKinnon et al. 2015). Similarly, in Red-backed Shrikes (*Lanius collurio*), carryover effects of winter environmental conditions on spring migration departure did not affect breeding arrival dates (Pedersen et al. 2016). Extreme weather events do undoubtedly affect migration of landbirds (see Behavioral Ecology section below for a summary). However, nonlethal carryover effects of more typical conditions appear to have negligible detectable effects. One interesting exception so far is in Barn Swallows (*Hirundo rustica*), where Saino et al. (2017b) found that carryover effects of migration phenology and overwintering habitat were strong predictors of fecundity in females, but not males.

There are several studies that found significant carryover effects of breeding outcomes on subsequent migrations. Late breeding and molting delayed fall migration departure of Wood Thrushes, but not arrival at wintering sites (Stutchbury et al. 2011). Similarly, Eurasian Hoopoes (*Upupa epops*) were able to compensate for initial migration delays caused by late breeding (van Wijk et al. 2017). However, female Veeries that experienced reproductive failure were significantly delayed on fall migration, and this carried over to delay their arrival at, and affected the latitude of, their first overwintering site (Heckscher et al. 2017). It is interesting that this effect appeared to be female-specific, and justifies again the importance of tracking both males and females.

Digitally coded radio-tags (i.e. Nanotags) are filling in an important gap in examining carryover effects from breeding to migration departure. For example, Mitchell et al. (2012) found that timing of breeding and local weather conditions explained more than 95% of the variation in adult Savannah Sparrow (*Passerculus sandwichensis*) fall migration departure dates. As the network of Motus towers expands, theoretically one could track birds with known breeding history during fall migration. However, archival GPS and geolocator tags are currently better suited for collecting information on start-to-finish migrations in the context of carryover effects. The key is that information on the birds' breeding or overwintering conditions must be known in order to test for carryover effects (Harrison et al. 2011). In many geolocator studies, birds are simply captured, tagged, and released; detailed study of birds during their stationary periods would allow further investigation of the importance of carryover effects on subsequent life-history stages and overall, on fitness.

Behavioral Ecology of Migration

Studies that explicitly tested hypotheses about the behavioral ecology of migration (20.5%) have provided important insights into the proximate controls of migration, age and sex-class differences, flexibility of migration, and social aspects of migration. Several studies have tested the hypothesis that birds are optimally following resource abundance, either within-winter or over the entire annual cycle, by using remote sensing of vegetation (e.g., Normalized Vegetation Difference Index) (Kristensen et al. 2013, Renfrew et al. 2013, Bridge et al. 2016, Thorup et al. 2017, Van Loon et al. 2017). In general, there is support for the idea that birds are following the "green wave" (but see Kristensen et al. 2013), but this remains to be tested in many species that show seasonal shifts in residency. For example, in the Purple Martin, factors such as density-dependence at roost sites may be more important predictors of intra-tropical migrations than rainfall or habitat (Stutchbury et al. 2016b).

One of the most valuable sources of information on migration behavior comes from repeat-tracking of the same individuals and comparing migrations in different years. In many cases, repeated collection of migration data was not intentional, but a by-product of retrieving the tag 2 yr post-deployment (e.g., Evens et al. 2017a). However, we suggest that researchers should consider repeat-tracking individuals as part of study design, as it provides critical insight into individual schedules vs. population-level variation, as well as the degree of phenotypic plasticity to environmental conditions. Common Swifts (*Apus apus*) appear to be highly faithful to individually distinct stopover and wintering sites year after year (Wellbrock et al. 2017). A European Nightjar (*Caprimulgus europaeus*) showed changes in its migration behavior from its first migrations (as a juvenile bird) to its second migrations (Evens et al. 2017a); a pattern supporting the idea that age-related variation in migration strategy may be adaptive, as has been found in other work (McKinnon et al. 2014). In contrast, repeat-tracks of both adult and juvenile (first-time migrant) Eurasian Hoopoes showed similar patterns in both age groups: fall migration timing was highly repeatable, wintering regions were similar, and spring migration timing not very repeatable (van Wijk et al. 2016). This also contrasts with information from Wood Thrushes, where spring migration timing was the most repeatable metric (Stanley et al. 2012). Overall these studies suggest that more repeat-tracking is needed to determine how flexible various aspects of migratory biology are across and within individuals.

In several extreme cases, birds do appear quite flexible in migration behavior. Golden-winged Warblers (*Vermivora chrysoptera*) apparently abandoned their breeding sites and reverse-migrated over 1,000 km to avoid a tornado-producing storm (Streby et al. 2015). Although the latter study has been met with some skepticism owing to the latitudinal error-prone location estimates from geolocators (Lisovski et al. 2018; but see rebuttal by Streby et al. 2018), there are now several examples of birds showing a surprising degree of migratory flexibility. A drought at a major stopover site in Africa caused delays in breeding-site arrival in 2 species of European birds (Tøttrup et al. 2012a), and a cold snap during late spring migration delayed, and reduced apparent survival of, Semi-collared Flycatchers (*Ficedula hypoleuca*; Briedis et al. 2017). While migratory birds appear to be negatively affected by encountering adverse weather, in the case of a warmer-than-average spring, Purple Martins did not increase their migration pace or arrive earlier (Fraser et al. 2013). As such, some species may be constrained by departure from the wintering grounds, limiting flexibility in response to conditions encountered en route (Ouwehand and Both 2017).

To date, detailed information on start-to-finish migration behavior can only be determined for small landbirds by using archival tags and, for most species, geolocators remain the best option. Geolocators, while relatively low in spatial resolution, can theoretically provide an estimate of location and thus timing of movements for each day the tag is collecting light data. For $\sim$1 g tags, this generally means an entire year of data can be collected, and timing of movements, duration of residency at overwintering sites, and timing of stopover events during migration, can usually be determined. The limitation is that many species migrate during the equinox periods, when day length is similar across latitudes and elucidating a position based on light levels can be difficult or impossible. However, new analysis approaches (Rakhimberdiev et al. 2016) are providing methods to statistically estimate the latitudinal positions of individuals during the equinoxes based on movement models. Also it is important to note that longitude estimates are not affected by the equinox at all and can often be used to detect timing of movements, even if the actual latitudinal position is not known (Fudickar et al. 2012). Even the best Bayesian models to estimate locations from geolocators can be strongly affected by model parameters chosen by the researcher (i.e. priors, landmasks, and other settings) and care should be taken not to overinterpret results.

Archival GPS tags can be used to collect precise and accurate information on migratory timing, for example, if they are programmed to record daily positions for the duration of spring migration. Newly developed *SWIFT* GPS tags small enough to be carried by thrushes (1 g PinPoint tags, Lotek) can collect up to 100 fixes, and if some information about migration initiation is known, then the tags can be programmed to attempt to collect locations for every day during this period, giving a precise level of detail for migration timing. However, GPS tags are still not able to collect continuous data like geolocators, and at around double the cost (Table 1) they may be preferable only for some situations (i.e. where both detailed routes and timing are required).

There has been great enthusiasm in applying digitally coded radio-tags to small landbirds within arrays of passive receiving towers for understanding movements of small landbirds (e.g., NAOC 2016 symposium). This technology is particularly amenable to studying departure decisions of migrants, either from breeding or stopover sites (Sjöberg and Nilsson 2015, Woodworth et al. 2015, Dossman et al. 2016). Because the towers are passive, this approach works well in locations where the natural geography concentrates birds into a particular area where a tower can be installed (e.g., along the shore of Lake Erie; see Wright et al. 2018), or where a radio-receiver "fence" can be created to detect any passing individual. This method has been used with great success to determine the timing of Gulf of Mexico crossings for landbirds by deploying Nanotags at the north coast of the Gulf and creating a "fence" of receiving towers along the Yucatán Peninsula of Mexico (Deppe et al. 2015). Similarly, in the Palearctic migratory system, automated radio-telemetry has been used to study departure decisions of small birds from the Falsterbo Peninsula in Sweden across the Baltic Sea (Sjöberg et al. 2015). Towers deployed at breeding sites (particularly breeding sites on islands, where any departure route can reasonably be covered by a receiving tower array) can be used to test the hypothesis that breeding events carry over to influence fall migration timing (Mitchell et al. 2012). Automated telemetry systems are valuable for studying departure decisions of hatch-year birds (Woodworth et al. 2014, Mitchell et al. 2015, Crysler et al. 2016), which are important in the context of the development of migration behavior, and until this technology was available, extremely difficult to study.

Automated radio-telemetry has provided new insight into orientation behavior of birds at major ecological barriers (Woodworth et al. 2015), as well as intriguing patterns of indirect, large-scale "exploratory" movements in hatch-year birds prior to fall migration that remain to be fully explained (Brown and Taylor 2015). The rapid expansion of the automated telemetry network in North America is allowing users to track the orientation of individuals beyond the footprint of a single receiving tower.

Evolution of Migration Strategies

Individual- and population-level variation in migration behavior are apparent in many tracking studies. Migration is presumably under strong genetic control (Liedvogel et al. 2011) and we can now explore the contribution of genetic and environmental factors to migration behavior. A recent geolocator study of Barn Swallows found a correlation between polymorphisms of the *Clock* gene and migration phenology (Bazzi et al. 2015). Following up on this work, Saino et al. (2017a) found that methylation patterns on *Clock* were also significant predictors of migration timing in Barn Swallows. These amazing insights into the underlying genetic basis of migration timing would not have been possible without the detailed start-to-finish migration tracking of individuals by using geolocators. Whether polymorphisms or methylation of *Clock* (or other candidate genes) are responsible for variation in migration strategy in other small landbird species remains to be investigated, and is an exciting area of research.

Several studies have also examined whether migratory behavior can act as a reproductive barrier, reducing fitness of hybrids that use suboptimal migration routes. In both Hermit Thrushes (*Catharus guttatus*) and Swainson's Thrushes (*Catharus ustulatus*), it appears that hybrids migrate and overwinter in areas that result in lower return rates (Delmore et al. 2012, Alvarado et al. 2014, Delmore and Irwin 2014); thus population-level differences in migratory behavior could be preventing fusion of these groups. In Ovenbirds (*Seiurus aurocapilla*), tracking of individuals with geolocators revealed mixing of populations during the nonbreeding season; this complemented genetic analyses indicating that boreal and hemi-boreal breeding Ovenbirds are panmictic (Haché et al. 2017).

Only one study to date has examined the evolution of bird morphology in relation to migration (e.g., how morphological variation is related to migration performance) with direct-tracking data for individuals: Lam et al. (2015) found that variation in Purple Martin wing length did not predict migration speed, stopover duration, or timing. Determining how selection pressures have shaped migratory birds can provide insights into flexibility of migratory species in response to climate change. A recent comparative study suggests that bird species with wings highly adapted to long-distance flying (i.e. high aspect ratio) exhibit less advancement of spring arrival (Moller et al. 2017), a pattern that could be further explored by using tracking technology to examine the correlations between start-to-finish migration timing and wing morphology across species.

Conclusion

Many small landbirds are experiencing population declines, particularly those which migrate long distances. It is now well understood that conservation efforts must take into account full-annual cycle habitat needs, and an important application of tracking tags is identifying priority habitats for conservation for at-risk species or populations. Many species of landbirds show variability in population trends across their breeding range; tracking can be used to test the hypothesis that differential migration routes or winter sites for separate breeding populations are driving the observed population declines. In Wood Thrushes, tracking by using light-level geolocators revealed that most individuals used a narrow region of the Gulf of Mexico coast for stopover during spring migration (Stanley et al. 2015), highlighting the importance of this area for conservation of this species. Geolocators have been the main tracking tool for endangered landbird species, since they provide information both on migratory periods and overwintering locations (Cooper et al. 2017, Kramer et al. 2017). Given that appropriate pilot testing can be conducted to minimize potential negative effects of tags on survival of at-risk species, geolocators remain an important tool for documenting year-round habitat requirements of small landbirds.

In the near future (estimated by 2019), researchers will also be able to track birds from the International Space Station, via an ambitious project called the International Cooperation for Animal Research Using Space (ICARUS; http://icarusinitiative.org/). ICARUS tags are anticipated to be quite large (5 g) and costly (~700 Euros per tag); however, as with geolocators, the size and cost will only decline as more users participate. ICARUS will undoubtedly provide important insights into movements of birds and, for the first time, will be able to give detailed resolution of movements without the bias toward surviving individuals. We may finally determine the fate of songbirds that do not make it back to their original tagging sites.

Tracking work has broad public appeal, and stories of epic bird migrations provide an excellent way to engage non-scientists and even non-birders in understanding the many threats small migratory landbirds face. This must be considered as another tangible benefit to tracking work, in an era where science is often undervalued and misunderstood, and funding increasingly comes from nontraditional sources. With continued technological innovations, such as the upcoming ICARUS program, the end of the golden age of bio-logging is not yet in sight; hopefully to the benefit of our many declining migratory birds.

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LITERATURE CITED

Adamík, P., T. Emmenegger, M. Briedis, L. Gustafsson, I. Henshaw, and M. Krist (2016). Barrier crossing in small avian migrants: Individual tracking reveals prolonged nocturnal flights into the day as a common migratory strategy. Scientific Reports 6:21560.

Alvarado, A. H., T. L. Fuller, and T. B. Smith (2014). Integrative tracking methods elucidate the evolutionary dynamics of a migratory divide. Ecology and Evolution 4:3456–3469.

Bazzi, G., R. Ambrosini, M. Caprioli, A. Costanzo, F. Liechti, E. Gatti, L. Gianfranceschi, S. Podofillini, A. Romano, M. Romano, C. Scandolara, et al. (2015). Clock gene polymorphism and scheduling of migration: A geolocator study of the barn swallow *Hirundo rustica*. Scientific Reports 5:12443.

Bracey, A., S. Lisovski, D. Moore, A. McKellar, E. Craig, S. Matteson, F. Strand, J. Costa, C. Pekarik, P. Curtis, G. Niemi, and F. Cuthbert (2018). Migratory routes and wintering locations of declining inland North American Common Terns. The Auk: Ornithological Advances 135:385–399.

Bravo, S. P., V. R. Cueto, and C. A. Gorosito (2017). Migratory timing, rate, routes and wintering areas of White-crested Elaenia (*Elaenia albiceps chilensis*), a key seed disperser for Patagonian forest regeneration. PLOS One 12:e0170188.

Bridge, E. S., J. D. Ross, A. J. Contina, and J. F. Kelly (2016). Do molt-migrant songbirds optimize migration routes based on primary productivity? Behavioral Ecology 27:784–792.

Briedis, M., S. Hahn, and P. Adamík (2017). Cold spell en route delays spring arrival and decreases apparent survival in a long-distance migratory songbird. BMC Ecology 17:11.

Brown, J. M., and P. D. Taylor (2015). Adult and hatch-year blackpoll warblers exhibit radically different regional-scale movements during post-fledging dispersal. Biology Letters 11:20150593.

Cohen, E. B., J. A. Hostetler, M. T. Hallworth, C. S. Rushing, T. S. Sillett, and P. P. Marra (2018). Quantifying the strength of migratory connectivity. Methods in Ecology and Evolution 9: 513–524.

Cooper, N. W., M. T. Hallworth, and P. P. Marra (2017). Light-level geolocation reveals wintering distribution, migration routes, and primary stopover locations of an endangered long-distance migratory songbird. Journal of Avian Biology 48: 209–219.

Cormier, R. L., D. L. Humple, T. Gardali, and N. E. Seavy (2013). Light-level geologgers reveal strong migratory connectivity and within-winter movements for a coastal California Swainson's Thrush (*Catharus ustulatus*) population. The Auk 130:283–290.

Costantini, D., and A. P. Moller (2013). A meta-analysis of the effects of geolocator application on birds. Current Zoology 59:697–706.

Crysler, Z. J., R. A. Ronconi, and P. D. Taylor (2016). Differential fall migratory routes of adult and juvenile Ipswich Sparrows (*Passerculus sandwichensis princeps*). Movement Ecology 4:3.

DeGregorio, B. A., J. H. Sperry, M. P. Ward, P. J. Weatherhead, and E. Heberts (2015). Wait until dark? Daily activity patterns and nest predation by snakes. Ethology 121:1225–1234.

Delmore, K. E., and D. E. Irwin (2014). Hybrid songbirds employ intermediate routes in a migratory divide. Ecology Letters 17: 1211–1218.

Delmore, K. E., J. W. Fox, and D. E. Irwin (2012). Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators. Proceedings of the Royal Society B-Biological Sciences 279: 4582–4589.

DeLuca, W. V., B. K. Woodworth, C. C. Rimmer, P. P. Marra, P. D. Taylor, K. P. McFarland, S. A. Mackenzie, and D. R. Norris (2015). Transoceanic migration by a 12 g songbird. Biology Letters 11:20141045.

Deppe, J. L., M. P. Ward, R. T. Bolus, R. H. Diehl, A. Celis-Murillo, T. J. Zenzal, Jr., F. R. Moore, T. J. Benson, J. A. Smolinsky, L. N. Schofield, D. A. Enstrom, et al. (2015). Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. Proceedings of the National Academy of Sciences USA 112:E6331–E6338.

Dossman, B. C., G. W. Mitchell, D. R. Norris, P. D. Taylor, C. G. Guglielmo, S. N. Matthews, and P. G. Rodewald (2016). The effects of wind and fuel stores on stopover departure behavior across a migratory barrier. Behavioral Ecology 27: 567–574.

Evens, R., N. Beenaerts, N. Witters, and T. Artois (2017a). Repeated migration of a juvenile European Nightjar *Caprimulgus europaeus*. Journal of Ornithology 158:881–886.

Evens, R., G. J. Conway, I. G. Henderson, B. Cresswell, F. Jiguet, C. Moussey, D. Sénécal, N. Witters, N. Beenaerts, and T. Artois (2017b). Migratory pathways, stopover zones and wintering destinations of Western European Nightjars *Caprimulgus europaeus*. Ibis 159:680–686.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, et al. (2010). Conserving migratory land birds in the New World: Do we know enough? Ecological Applications 20:398–418.

Finch, T., S. J. Butler, A. M. A. Franco, and W. Cresswell (2017). Low migratory connectivity is common in long-distance migrant birds. Journal of Animal Ecology 86:662–673.

Finch, T., P. Saunders, J. Miguel Aviles, A. Bermejo, I. Catry, J. de la Puente, T. Emmenegger, I. Mardega, P. Mayet, D. Parejo, E. Racinskis, et al. (2015). A pan-European, multipopulation assessment of migratory connectivity in a near-threatened migrant bird. Diversity and Distributions 21:1051–1062.

Fraser, K. C., A. Shave, A. Savage, A. Ritchie, K. Bell, J. Siegrist, J. D. Ray, K. Applegate, and M. Pearman (2017). Determining fine-scale migratory connectivity and habitat selection for a migratory songbird by using new GPS technology. Journal of Avian Biology 48:339–345.

Fraser, K. C., C. Silverio, P. Kramer, N. Mickle, R. Aeppli, and B. J. Stutchbury (2013). A trans-hemispheric migratory songbird does not advance spring schedules or increase migration rate in response to record-setting temperatures at breeding sites. PLOS One 8:e64587.

Fraser, K. C., B. J. M. Stutchbury, C. Silverio, P. M. Kramer, J. Barrow, D. Newstead, N. Mickle, B. F. Cousens, J. C. Lee, D. M. Morrison, T. Shaheen, et al. (2012). Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. Proceedings of the Royal Society B-Biological Sciences 279:4901–4906.

Fudickar, A. M., A. Schmidt, M. Hau, M. Quetting, and J. Partecke (2013). Female-biased obligate strategies in a partially migratory population. Journal of Animal Ecology 82:863–871.

Fudickar, A. M., M. Wikelski, and J. Partecke (2012). Tracking migratory songbirds: Accuracy of light-level loggers (geolocators) in forest habitats. Methods in Ecology and Evolution 3:47–52.

Gomez, C., N. J. Bayly, D. R. Norris, S. A. Mackenzie, K. V. Rosenberg, P. D. Taylor, K. A. Hobson, and C. D. Cadena (2017). Fuel loads acquired at a stopover site influence the pace of intercontinental migration in a boreal songbird. Scientific Reports 7:11.

Haché, S., E. M. Bayne, M.-A. Villard, H. Proctor, C. S. Davis, D. Stralberg, J. K. Janes, M. T. Hallworth, K. R. Foster, E. Chidambara-vasi, A. A. Grossi, et al. (2017). Phylogeography of a migratory songbird across its Canadian breeding range: Implications for conservation units. Ecology and Evolution 7: 6078–6088.

Hahn, S., V. Amrhein, P. Zehtindijev, and F. Liechti (2013). Strong migratory connectivity and seasonally shifting isotopic niches in geographically separated populations of a long-distance migrating songbird. Oecologia 173:1217–1225.

Hallworth, M. T., and P. P. Marra (2015). Miniaturized GPS tags identify non-breeding territories of a small breeding migratory songbird. Scientific Reports 5:6.

Hallworth, M. T., T. S. Sillett, S. L. Van Wilgenburg, K. A. Hobson, and P. P. Marra (2015). Migratory connectivity of a Neotropical migratory songbird revealed by archival light-level geolocators. Ecological Applications 25:336–347.

Hallworth, M. T., C. E. Studds, T. S. Sillett, and P. P. Marra (2013). Do archival light-level geolocators and stable hydrogen isotopes provide comparable estimates of breeding-ground origin? The Auk 130:273–282.

Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop (2011). Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology 80:4–18.

Heckscher, C. M., M. R. Halley, and P. M. Stampul (2015). Intratropical migration of a Nearctic–Neotropical migratory songbird (*Catharus fuscescens*) in South America with implications for migration theory. Journal of Tropical Ecology 31:285–289.

Heckscher, C. M., M. G. Ramirez, and A. H. Kneidel (2017). Reproductive outcomes determine the timing of arrival and settlement of a single-brooded Nearctic–Neotropical migrant songbird (*Catharus fuscescens*) in South America. The Auk: Ornithological Advances 134:842–856.

Heckscher, C. M., S. M. Taylor, J. W. Fox, and V. Afanasyev (2011). Veery (*Catharus fucescens*) wintering locations, migratory connectivity, and a revision of its winter range using geolocator technology. The Auk 128:531–542.

Hewson, C. M., K. Thorup, J. W. Pearce-Higgins, and P. W. Atkinson (2016). Population decline is linked to migration route in the Common Cuckoo. Nature Communications 7:8.

Hobson, K. A., and K. J. Kardynal (2016). An isotope (delta S-34) filter and geolocator results constrain a dual feather isoscape (delta H-2, delta C-13) to identify the wintering grounds of North American Barn Swallows. The Auk: Ornithological Advances 133:86–98.

Jahn, A. E., D. Levey, V. Cueto, J. Pinto Ledezma, D. Tuero, J. Fox, and D. Masson (2013). Long-distance bird migration within South America revealed by light-level geolocators. The Auk 130:223–229.

Jahn, A. E., N. E. Seavy, V. Bejarano, M. B. Guzman, I. C. C. Provinciato, M. A. Pizo, and M. MacPherson (2016). Intratropical migration and wintering areas of Fork-tailed Flycatchers (*Tyrannus savana*) breeding in São Paulo, Brazil. Revista Brasileira de Ornitologia 24:116–121.

Kays, R., M. C. Crofoot, W. Jetz, and M. Wikelski (2015). Terrestrial animal tracking as an eye on life and planet. Science 348(6240):aaa2478.

Koleček, J., P. Prochazka, N. El-Arabany, M. Tarka, M. Ilieva, S. Hahn, M. Honza, J. de la Puente, A. Bermejo, A. Gursoy, S. Bensch, et al. (2016). Cross-continental migratory connectivity and spatiotemporal migratory patterns in the great reed warbler. Journal of Avian Biology 47:756–767.

Korner-Nievergelt, F., L. Jenni, A. P. Tottrup, and G. Pasinelli (2012). Departure directions, migratory timing and non-breeding distribution of the Red-backed Shrike *Lanius collurio*: Do ring re-encounters and light-based geolocator data tell the same story? Ringing & Migration 27:83–93.

Korner-Nievergelt, F., C. Prévot, S. Hahn, L. Jenni, and F. Liechti (2017). The integration of mark re-encounter and tracking data to quantify migratory connectivity. Ecological Modelling 344:87–94.

Kramer, G. R., H. M. Streby, S. M. Peterson, J. A. Lehman, D. A. Buehler, P. B. Wood, D. J. McNeil, J. L. Larkin, and D. E. Andersen (2017). Nonbreeding isolation and population-specific migration patterns among three populations of Golden-winged Warblers. The Condor: Ornithological Applications 119:108–121.

Kristensen, M. W., A. P. Tottrup, and K. Thorup (2013). Migration of the Common Redstart (*Phoenicurus phoenicurus*): A Eurasian songbird wintering in highly seasonal conditions in the West African Sahel. The Auk 130:258–264.

Lam, L., E. A. McKinnon, J. D. Ray, M. Pearman, G. T. Hvenegaard, J. Mejeur, L. Moscar, M. Pearson, K. Applegate, P. Mammenga, J. Tautin, and K. C. Fraser (2015). The influence of morphological variation on migration performance in a trans-hemispheric migratory songbird. Animal Migration 2(1). doi:10.1515/ami-2015-0005

Liedvogel, M., S. Åkesson, and S. Bensch (2011). The genetics of migration on the move. Trends in Ecology & Evolution 26: 561–569.

Lisovski, S., C. M. Hewson, R. H. G. Klaassen, F. Korner-Nievergelt, M. W. Kristensen, and S. Hahn (2012). Geolocation by light: Accuracy and precision affected by environmental factors. Methods in Ecology and Evolution 3:603–612.

Lisovski, S., H. Schmaljohann, E. S. Bridge, S. Bauer, A. Farnsworth, S. A. Gauthreaux, S. Hahn, M. T. Hallworth, C. M. Hewson, J. F. Kelly, F. Liechti, et al. (2018). Inherent limits of light-level geolocators may lead to over-interpretation. Current Biology 28:R99–R100.

Lopez-Lopez, P. (2016). Individual-based tracking systems in ornithology: Welcome to the era of big data. Ardeola 63:103–136.

Louder, M. I. M., M. P. Ward, W. M. Schelsky, M. E. Hauber, and J. P. Hoover (2015). Out on their own: A test of adult-assisted dispersal in fledgling brood parasites reveals solitary departures from hosts. Animal Behaviour 110:29–37.

Macdonald, C. A., K. C. Fraser, H. G. Gilchrist, T. K. Kyser, J. W. Fox, and O. P. Love (2012). Strong migratory connectivity in a declining Arctic passerine. Animal Migration 1:23–30.

McKinnon, E. A., C. A. Artuso, and O. P. Love (2017). The mystery of the missing warbler. Ecology 98:1970–1972.

McKinnon, E. A., K. C. Fraser, C. Q. Stanley, and B. J. M. Stutchbury (2014). Tracking from the Tropics reveals behaviour of juvenile songbirds on their first spring migration. PLOS One 9:e105605.

McKinnon, E. A., K. C. Fraser, and B. J. M. Stutchbury (2013a). New discoveries in landbird migration using geolocators and a flight plan for the future. The Auk 130:1–12.

McKinnon, E. A., C. M. Macdonald, H. G. Gilchrist, and O. P. Love (2016). Spring and fall migration phenology of an Arctic-breeding passerine. Journal of Ornithology 157:681–693.

McKinnon, E. A., C. Q. Stanley, K. C. Fraser, M. MacPherson, G. Casbourn, P. P. Marra, C. E. Studds, N. Diggs, and B. J. M. Stutchbury (2013b). Estimating geolocator accuracy for a migratory songbird using live ground-truthing in tropical forest. Animal Migration 1:31–38.

McKinnon, E. A., C. Q. Stanley, and B. J. M. Stutchbury (2015). Carry-over effects of nonbreeding habitat on start-to-finish spring migration performance of a songbird. PLOS One 10: e0141580.

Mills, A. M., B. G. Thurber, S. A. Mackenzie, and P. D. Taylor (2011). Passerines use nocturnal flights for landscape-scale movements during migration stopover. The Condor 113:597–607.
Mitchell, G. W., A. E. M. Newman, M. Wikelski, and D. R. Norris (2012). Timing of breeding carries over to influence migratory departure in a songbird: An automated radiotracking study. Journal of Animal Ecology 81:1024–1033.
Mitchell, G. W., B. K. Woodworth, P. D. Taylor, and D. R. Norris (2015). Automated telemetry reveals age specific differences in flight duration and speed are driven by wind conditions in a migratory songbird. Movement Ecology 3:19.
Moller, A. P., D. Rubolini, and N. Saino (2017). Morphological constraints on changing avian migration phenology. Journal of Evolutionary Biology 30:1177–1184.
Newton, I. (2008). The Migration Ecology of Birds. Academic Press, London, UK.
Norris, D. R. (2005). Carry-over effects and habitat quality in migratory populations. Oikos 109:178–186.
Nowak, E., and P. Berthold (1987). Satellite telemetry in the study of animal migration - A review. Journal Für Ornithologie 128: 405–422.
Nwaogu, C. J., and W. Cresswell (2016). Body reserves in intra-African migrants. Journal of Ornithology 157:125–135.
Ouwehand, J., and C. Both (2017). African departure rather than migration speed determines variation in spring arrival in pied flycatchers. Journal of Animal Ecology 86:88–97.
Ouwehand, J., M. P. Ahola, A. N. M. A. Ausems, E. S. Bridge, M. Burgess, S. Hahn, C. M. Hewson, R. H. G. Klaassen, T. Laaksonen, H. M. Lampe, W. Velmala, and C. Both (2016). Light-level geolocators reveal migratory connectivity in European populations of pied flycatchers *Ficedula hypoleuca*. Journal of Avian Biology 47:69–83.
Pedersen, L., K. C. Fraser, T. K. Kyser, and A. P. Tøttrup (2016). Combining direct and indirect tracking techniques to assess the impact of sub-Saharan conditions on cross-continental songbird migration. Journal of Ornithology 157:1037–1047.
Pillar, A. G., P. P. Marra, N. J. Flood, and M. W. Reudink (2016). Moult migration in Bullock's orioles (*Icterus bullockii*) confirmed by geolocators and stable isotope analysis. Journal of Ornithology 157:265–275.
Rakhimberdiev, E., N. R. Senner, M. A. Verhoeven, D. W. Winkler, W. Bouten, and T. Piersma (2016). Comparing inferences of solar geolocation data against high-precision GPS data: Annual movements of a double-tagged black-tailed godwit. Journal of Avian Biology 47:589–596.
Renfrew, R. B., D. Kim, N. Perlut, J. A. Smith, J. Fox, and P. P. Marra (2013). Phenological matching across hemispheres in a long-distance migratory bird. Diversity and Distributions 19:1–12.
Rerucha, S., T. Bartonicka, P. Jedlicka, M. Cizek, O. Hlousa, R. Lucan, and I. Horacek (2015). The BAARA (Biological AutomAted RAdiotracking) System: A new approach in ecological field studies. PLOS One 10:e0116785.
Rodriguez-Ruiz, J., J. de la Puente, D. Parejo, F. Valera, M. A. Calero-Torralbo, J. M. Reyes-Gonzalez, Z. Zajkova, A. Bermejo, and J. M. Aviles (2014). Disentangling migratory routes and wintering grounds of Iberian near-threatened European Rollers *Coracias garrulus*. PLOS One 9:e115615.
Saino, N., R. Ambrosini, B. Albetti, M. Caprioli, B. De Giorgio, E. Gatti, F. Liechti, M. Parolini, A. Romano, M. Romano, C. Scandolara, et al. (2017a). Migration phenology and breeding success are predicted by methylation of a photoperiodic gene in the barn swallow. Scientific Reports 7:45412.
Saino, N., R. Ambrosini, M. Caprioli, A. Romano, M. Romano, D. Rubolini, C. Scandolara, and F. Liechti (2017b). Sex-dependent carry-over effects on timing of reproduction and fecundity of a migratory bird. Journal of Animal Ecology 86: 239–249.
Salewski, V., M. Flade, A. Poluda, G. Kiljan, F. Liechti, S. Lisovski, and S. Hahn (2013). An unknown migration route of the 'globally threatened' Aquatic Warbler revealed by geolocators. Journal of Ornithology 154:549–552.
Scandolara, C., D. Rubolini, R. Ambrosini, M. Caprioli, S. Hahn, F. Liechti, A. Romano, M. Romano, B. Sicurella, and N. Saino (2014). Impact of miniaturized geolocators on barn swallow *Hirundo rustica* fitness traits. Journal of Avian Biology 45:417–423.
Schmaljohann, H., M. Buchmann, J. W. Fox, and F. Bairlein (2012). Tracking migration routes and the annual cycle of a trans-Sahara songbird migrant. Behavioral Ecology and Sociobiology 66:915–922.
Siegel, R. B., R. Taylor, J. F. Saracco, L. Helton, and S. Stock (2016). GPS-tracking reveals non-breeding locations and apparent molt migration of a Black-headed Grosbeak. Journal of Field Ornithology 87:196–203.
Sjöberg, S., and C. Nilsson (2015). Nocturnal migratory songbirds adjust their travelling direction aloft: Evidence from a radiotelemetry and radar study. Biology Letters 11:20150337.
Sjöberg, S., T. Alerstam, S. Åkesson, A. Schulz, A. Weidauer, T. Coppack, and R. Muheim (2015). Weather and fuel reserves determine departure and flight decisions in passerines migrating across the Baltic Sea. Animal Behaviour 104:59–68.
Smolinsky, J. A., R. H. Diehl, T. A. Radzio, D. K. Delaney, and F. R. Moore (2013). Factors influencing the movement biology of migrant songbirds confronted with an ecological barrier. Behavioral Ecology and Sociobiology 67:2041–2051.
Stanley, C. Q., M. M. MacPherson, K. C. Fraser, E. A. McKinnon, and B. J. Stutchbury (2012). Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. PLOS One 7:e40688.
Stanley, C. Q., E. A. McKinnon, K. C. Fraser, M. P. MacPherson, G. Casbourn, L. Friesen, P. P. Marra, C. E. Studds, T. B. Ryder, N. Diggs, and B. J. M. Stutchbury (2015). Connectivity of Wood Thrush breeding, wintering, and migration sites based on range-wide tracking. Conservation Biology 29:164–174.
Streby, H. M., G. R. Kramer, S. M. Peterson, J. A. Lehman, D. A. Buehler, and D. E. Andersen (2015). Tornadic storm avoidance behavior in breeding songbirds. Current Biology 25:98–102.
Streby, H. M., G. R. Kramer, S. M. Peterson, J. A. Lehman, D. A. Buehler, and D. E. Andersen (2018). Response to Lisovski et al. Current Biology 28:R102.
Stutchbury, B. J. M., K. C. Fraser, C. Silverio, P. Kramer, B. Aeppli, N. Mickle, M. Pearman, A. Savage, and J. Mejeur (2016a). Tracking mated pairs in a long-distance migratory songbird: Migration schedules are not synchronized within pairs. Animal Behaviour 114:63–68.
Stutchbury, B. J. M., E. A. Gow, T. Done, M. MacPherson, J. W. Fox, and V. Afanasyev (2011). Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. Proceedings of the Royal Society B-Biological Sciences 278:131–137.

Stutchbury, B. J. M., R. Siddiqui, K. Applegate, G. T. Hvenegaard, P. Mammenga, N. Mickle, M. Pearman, J. D. Ray, A. Savage, T. Shaheen, and K. C. Fraser (2016b). Ecological causes and consequences of intratropical migration in temperate-breeding migratory birds. American Naturalist 188:S28–S40.

Stutchbury, B. J. M., S. A. Tarof, T. Done, E. Gow, P. M. Kramer, J. Tautin, J. W. Fox, and V. Afanasyev (2009). Tracking long-distance songbird migration by using geolocators. Science 323:896.

Taylor, C. M., and D. R. Norris (2010). Population dynamics in migratory networks. Theoretical Ecology 3:65–73.

Taylor, C. M., and B. J. M. Stutchbury (2015). Effects of breeding versus winter habitat loss and fragmentation on the population dynamics of a migratory songbird. Ecological Applications 26:424–437.

Taylor, P. D., T. L. Crewe, S. A. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, C. M. Francis, C. G. Guglielmo, D. J. Hamilton, R. L. Holberton, et al. (2017). The Motus Wildlife Tracking System: A collaborative research network to enhance the understanding of wildlife movement. Avian Conservation and Ecology 12:11.

Thorup, K., A. P. Tøttrup, M. Willemoes, R. H. G. Klaassen, R. Strandberg, and M. L. Vega (2017). Resource tracking within and across continents in long-distance bird migrants. Science Advances 3:e1601360.

Tøttrup, A. P., R. H. G. Klaassen, M. W. Kristensen, R. Strandberg, Y. Vardanis, A. Lindstrom, C. Rahbek, T. Alerstam, and K. Thorup (2012a). Drought in Africa caused delayed arrival of European songbirds. Science 338:1307.

Tøttrup, A. P., R. H. G. Klaassen, R. Strandberg, K. Thorup, M. W. Kristensen, P. S. Jørgensen, J. Fox, V. Afanasyev, C. Rahbek, and T. Alerstam (2012b). The annual cycle of a trans-equatorial Eurasian–African passerine migrant: Different spatio-temporal strategies for autumn and spring migration. Proceedings of the Royal Society B-Biological Sciences 279: 1008–1016.

Van Loon, A., J. D. Ray, A. Savage, J. Mejeur, L. Moscar, M. Pearson, M. Pearman, G. T. Hvenegaard, N. Mickle, K. Applegate, and K. C. Fraser (2017). Migratory stopover timing is predicted by breeding latitude, not habitat quality, in a long-distance migratory songbird. Journal of Ornithology 158:745–752.

van Wijk, R. E., S. Bauer, and M. Schaub (2016). Repeatability of individual migration routes, wintering sites, and timing in a long-distance migrant bird. Ecology and Evolution 6:8679–8685.

van Wijk, R. E., M. Schaub, and S. Bauer (2017). Dependencies in the timing of activities weaken over the annual cycle in a long-distance migratory bird. Behavioral Ecology and Sociobiology 71:73.

Ward, M. P., M. Alessi, T. J. Benson, and S. J. Chiavacci (2014). The active nightlife of diurnal birds: Extraterritorial forays and nocturnal activity patterns. Animal Behaviour 88:175–184.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes (2002). Links between worlds: Unraveling migratory connectivity. Trends in Ecology & Evolution 17:76–83.

Wellbrock, A. H. J., C. Bauch, J. Rozman, and K. Witte (2017). 'Same procedure as last year?' Repeatedly tracked swifts show individual consistency in migration pattern in successive years. Journal of Avian Biology 48:897–903.

Wilmers, C. C., B. Nickel, C. M. Bryce, J. A. Smith, R. E. Wheat, and V. Yovovich (2015). The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. Ecology 96:1741–1753.

Woodworth, B. K., C. M. Francis, and P. D. Taylor (2014). Inland flights of young red-eyed vireos *Vireo olivaceus* in relation to survival and habitat in a coastal stopover landscape. Journal of Avian Biology 45:387–395.

Woodworth, B. K., G. W. Mitchell, D. R. Norris, C. M. Francis, and P. D. Taylor (2015). Patterns and correlates of songbird movements at an ecological barrier during autumn migration assessed using landscape- and regional-scale automated radiotelemetry. Ibis 157:326–339.

Woodworth, B. K., A. E. M. Newman, S. P. Turbek, B. C. Dossman, K. A. Hobson, L. I. Wassenaar, G. W. Mitchell, N. T. Wheelwright, and D. R. Norris (2016). Differential migration and the link between winter latitude, timing of migration, and breeding in a songbird. Oecologia 181:413–422.

Wright, J. R., L. L. Powell, and C. M. Tonra (2018). Automated telemetry reveals staging behavior in a declining migratory passerine. The Auk: Ornithological Advances 135:461–476.

APPENDIX A. List of studies that have used geolocators to track movements of small landbirds.

Adamík, P., T. Emmenegger, M. Briedis, L. Gustafsson, I. Henshaw, and M. Krist (2016). Barrier crossing in small avian migrants: Individual tracking reveals prolonged nocturnal flights into the day as a common migratory strategy. Scientific Reports 6:21560.

Åkesson, S., G. Bianco, and A. Hedenstrom (2016). Negotiating an ecological barrier: Crossing the Sahara in relation to winds by common swifts. Philosophical Transactions of the Royal Society B-Biological Sciences 371:20150393.

Åkesson, S., R. Klaassen, J. Holmgren, J. W. Fox, and A. Hedenström (2012). Migration routes and strategies in a highly aerial migrant, the Common Swift *Apus apus*, revealed by light-level geolocators. PLOS One 7:e41195.

Alonso, D., J. Arizaga, C. M. Meier, and F. Liechti (2017). Light-level geolocators confirm resident status of a Southern European Common Crossbill population. Journal of Ornithology 158:75–81.

Alvarado, A. H., T. L. Fuller, and T. B. Smith (2014). Integrative tracking methods elucidate the evolutionary dynamics of a migratory divide. Ecology and Evolution 4:3456–3469.

Arizaga, J., M. Willemoes, E. Unamuno, J. M. Unamuno, and K. Thorup (2015). Following year-round movements in Barn Swallows using geolocators: Could breeding pairs remain together during the winter? Bird Study 62:141–145.

Arlt, D., P. Olsson, J. W. Fox, M. Low, and T. Part (2015). Prolonged stopover duration characterises migration strategy and constraints of a long-distance migrant

songbird. Animal Migration 2. doi:10.1515/ami-2015-0002.

Bächler, E., S. Hahn, M. Schaub, R. Arlettaz, L. Jenni, J. W. Fox, V. Afanasyev, and F. Liechti (2010). Year-round tracking of small trans-Saharan migrants using light-level geolocators. PLOS One 5:e9566.

Bairlein, F., D. R. Norris, R. Nagel, M. Bulte, C. C. Voight, J. W. Fox, D. J. T. Hussell, and H. Schmaljohann (2012). Cross-hemisphere migration of a 25 g songbird. Biology Letters 2012:505–507.

Bazzi, G., R. Ambrosini, M. Caprioli, A. Costanzo, F. Liechti, E. Gatti, L. Gianfranceschi, S. Podofillini, A. Romano, M. Romano, C. Scandolara, et al. (2015). Clock gene polymorphism and scheduling of migration: A geolocator study of the barn swallow *Hirundo rustica*. Scientific Reports 5:12443.

Beason, J. P., C. Gunn, K. M. Potter, R. A. Sparks, and J. W. Fox (2012). The northern Black Swift: Migration path and wintering area revealed. The Wilson Journal of Ornithology 124:1–8.

Bennett, R. E., S. B. Swarthout, J. S. Bolsinger, A. D. Rodewald, K. V. Rosenberg, and R. W. Rohrbaugh (2017). Extreme genetic similarity does not predict non-breeding distribution of two closely related warblers. Journal of Field Ornithology 88:156–168.

Blackburn, E., M. Burgess, B. Freeman, A. Risely, A. Izang, S. Ivande, C. Hewson, and W. Cresswell (2017). Low and annually variable migratory connectivity in a long-distance migrant: Whinchats *Saxicola rubetra* may show a bet-hedging strategy. Ibis 159:902–918.

Bradley, D. W., R. G. Clark, P. O. Dunn, A. J. Laughlin, C. M. Taylor, C. Vleck, L. A. Whittingham, D. W. Winkler, and D. R. Norris (2014). Trans-Gulf of Mexico loop migration of tree swallows revealed by solar geolocation. Current Zoology 60:653–659.

Bravo, S. P., V. R. Cueto, and C. A. Gorosito (2017). Migratory timing, rate, routes and wintering areas of White-crested Elaenia (*Elaenia albiceps chilensis*), a key seed disperser for Patagonian forest regeneration. PLOS One 12:e0170188.

Bridge, E. S., J. D. Ross, A. J. Contina, and J. F. Kelly (2016). Do molt-migrant songbirds optimize migration routes based on primary productivity? Behavioral Ecology 27:784–792.

Briedis, M., V. Beran, S. Hahn, and P. Adamik (2016). Annual cycle and migration strategies of a habitat specialist, the Tawny Pipit *Anthus campestris*, revealed by geolocators. Journal of Ornithology 157:619–626.

Briedis, M., S. Hahn, and P. Adamík (2017). Cold spell en route delays spring arrival and decreases apparent survival in a long-distance migratory songbird. BMC Ecology 17:11.

Briedis, M., S. Hahn, L. Gustafsson, I. Henshaw, J. Träff, M. Král, and P. Adamík (2016). Breeding latitude leads to different temporal but not spatial organization of the annual cycle in a long-distance migrant. Journal of Avian Biology 47:743–748.

Briedis, M., J. Traff, S. Hahn, M. Ilieva, M. Kral, S. Peev, and P. Adamik (2016). Year-round spatiotemporal distribution of the enigmatic Semi-collared Flycatcher *Ficedula semitorquata*. Journal of Ornithology 157:895–900.

Callo, P. A., E. S. Morton, and B. J. M. Stutchbury (2013). Prolonged spring migration in the Red-eyed Vireo (*Vireo olivaceus*). The Auk 130:240–246.

Catry, I., T. Catry, J. P. Granadeiro, A. M. A. Franco, and F. Moreira (2014). Unravelling migration routes and wintering grounds of European Rollers using light-level geolocators. Journal of Ornithology 155:1071–1075.

Contina, A., E. S. Bridge, N. E. Seavy, J. M. Duckles, and J. F. Kelly (2013). Using geologgers to investigate bimodal isotope patterns in Painted Buntings (*Passerina ciris*). The Auk 130:265–272.

Cooper, N. W., M. T. Hallworth, and P. P. Marra (2017). Light-level geolocation reveals wintering distribution, migration routes, and primary stopover locations of an endangered long-distance migratory songbird. Journal of Avian Biology 48:209–219.

Cormier, R. L., D. L. Humple, T. Gardali, and N. E. Seavy (2013). Light-level geologgers reveal strong migratory connectivity and within-winter movements for a coastal California Swainson's Thrush (*Catharus ustulatus*) population. The Auk 130:283–290.

Cresswell, B., and D. Edwards (2013). Geolocators reveal wintering areas of European Nightjar (*Caprimulgus europaeus*). Bird Study 60:77–86.

Delmore, K. E., and D. E. Irwin (2014). Hybrid songbirds employ intermediate routes in a migratory divide. Ecology Letters 17:1211–1218.

Delmore, K. E., J. W. Fox, and D. E. Irwin (2012). Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators. Proceedings of the Royal Society B-Biological Sciences 279:4582–4589.

DeLuca, W. V., B. K. Woodworth, C. C. Rimmer, P. P. Marra, P. D. Taylor, K. P. McFarland, S. A. Mackenzie, and D. R. Norris (2015). Transoceanic migration by a 12 g songbird. Biology Letters 11.

Emmenegger, T., S. Hahn, R. Arlettaz, V. Amrhein, P. Zehtindjiev, and S. Bauer (2016). Shifts in vegetation phenology along flyways entail varying risks of mistiming in a migratory songbird. Ecosphere 7(6):e01385.

Emmenegger, T., P. Mayet, O. Duriez, and S. Hahn (2014). Directional shifts in migration pattern of rollers (*Coracias garrulus*) from a western European population. Journal of Ornithology 155:427–433.

English, P. A., A. M. Mills, M. D. Cadman, A. E. Heagy, G. J. Rand, D. J. Green, and J. J. Nocera (2017). Tracking the migration of a nocturnal aerial insectivore in the Americas. BMC Zoology 2:5.

Evens, R., N. Beenaerts, N. Witters, and T. Artois (2017). Repeated migration of a juvenile European Nightjar *Caprimulgus europaeus*. Journal of Ornithology 158:881–886.

Evens, R., G. J. Conway, I. G. Henderson, B. Cresswell, F. Jiguet, C. Moussey, D. Sénécal, N. Witters, N. Beenaerts, and T. Artois (2017). Migratory pathways, stopover zones and wintering destinations of Western European Nightjars *Caprimulgus europaeus*. Ibis 159:680–686.

Finch, T., P. Saunders, J. Miguel Aviles, A. Bermejo, I. Catry, J. de la Puente, T. Emmenegger, I. Mardega, P. Mayet, D. Parejo, E. Racinskis, et al. (2015). A pan-European, multipopulation assessment of migratory connectivity in a near-threatened migrant bird. Diversity and Distributions 21:1051–1062.

Fraser, K. C., C. Silverio, P. Kramer, N. Mickle, R. Aeppli, and B. J. Stutchbury (2013). A trans-hemispheric migratory songbird does not advance spring schedules or increase migration rate in response to record-setting temperatures at breeding sites. PLOS One 8:e64587.

Fraser, K. C., B. J. M. Stutchbury, P. Kramer, C. Silverio, J. Barrow, D. Newstead, N. Mickle, T. Shaheen, P. Mammenga, K. Applegate, E. Bridge, and J. Tautin (2013). Consistent range-wide pattern in fall migration strategy of Purple Martin (*Progne subis*), despite different migration routes at the Gulf of Mexico. The Auk 130:291–296.

Fraser, K. C., B. J. M. Stutchbury, C. Silverio, P. M. Kramer, J. Barrow, D. Newstead, N. Mickle, N. B. F. Cousens, J. C. Lee, D. M. Morrison, T. Shaheen, et al. (2012). Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. Proceedings of the Royal Society B-Biological Sciences 279:4901–4906.

Fudickar, A. M., A. Schmidt, M. Hau, M. Quetting, and J. Partecke (2013). Female-biased obligate strategies in a partially migratory population. Journal of Animal Ecology 82:863–871.

Gow, E. A., and K. L. Wiebe (2014). Males migrate farther than females in a differential migrant: An examination of the fasting endurance hypothesis. Royal Society Open Science 1:140346.

Gow, E. A., K. L. Wiebe, and J. W. Fox (2015). Cavity use throughout the annual cycle of a migratory woodpecker revealed by geolocators. Ibis 157:167–170.

Haché, S., E. M. Bayne, M.-A. Villard, H. Proctor, C. S. Davis, D. Stralberg, J. K. Janes, M. T. Hallworth, K. R. Foster, E. Chidambara-vasi, A. A. Grossi, et al. (2017). Phylogeography of a migratory songbird across its Canadian breeding range: Implications for conservation units. Ecology and Evolution 7:6078–6088.

Hahn, S., V. Amrhein, P. Zehtindijev, and F. Liechti (2013). Strong migratory connectivity and seasonally shifting isotopic niches in geographically separated populations of a long-distance migrating songbird. Oecologia 173:1217–1225.

Hahn, S., T. Emmenegger, S. Lisovski, V. Amrhein, P. Zehtindjiev, and F. Liechti (2014). Variable detours in long-distance migration across ecological barriers and their relation to habitat availability at ground. Ecology and Evolution 4:4150–4160.

Hallworth, M. T., T. S. Sillett, S. L. Van Wilgenburg, K. A. Hobson, and P. P. Marra (2015). Migratory connectivity of a Neotropical migratory songbird revealed by archival light-level geolocators. Ecological Applications 25:336–347.

Hasselquist, D., T. Montras-Janer, M. Tarka, and B. Hansson (2017). Individual consistency of long-distance migration in a songbird: Significant repeatability of autumn route, stopovers and wintering sites but not in timing of migration. Journal of Avian Biology 48:91–102.

Heckscher, C. M., M. R. Halley, and P. M. Stampul (2015). Intratropical migration of a Nearctic–Neotropical migratory songbird (*Catharus fuscescens*) in South America with implications for migration theory. Journal of Tropical Ecology 31:285–289.

Heckscher, C. M., M. G. Ramirez, and A. H. Kneidel (2017). Reproductive outcomes determine the timing of arrival and settlement of a single-brooded Nearctic–Neotropical migrant songbird (*Catharus fuscescens*) in South America. The Auk: Ornithological Advances 134:842–856.

Heckscher, C. M., S. M. Taylor, J. W. Fox, and V. Afanasyev (2011). Veery (*Catharus fucescens*) wintering locations, migratory connectivity, and a revision of its winter range using geolocator technology. The Auk 128:531–542.

Hedenstrom, A., G. Norevik, K. Warfvinge, A. Andersson, J. Backman, and S. Akesson (2016). Annual 10-month aerial life phase in the Common Swift *Apus apus*. Current Biology 26:3066–3070.

Hiemer, D., V. Salewski, W. Fiedler, S. Hahn, and S. Lisovski (2018). First tracks of individual Blackcaps suggest a complex migration pattern. Journal of Ornithology 159:205–210.

Hobson, K. A., and K. J. Kardynal (2015). Western Veeries use an eastern shortest-distance pathway: New insights to migration routes and phenology using light-level geolocators. The Auk: Ornithological Advances 132:540–550.

Hobson, K. A., and K. J. Kardynal (2016). An isotope (delta S-34) filter and geolocator results constrain a dual feather isoscape (delta H-2, delta C-13) to identify the wintering grounds of North American Barn Swallows. The Auk: Ornithological Advances 133:86–98.

Hobson, K. A., K. J. Kardynal, S. L. Van Wilgenburg, G. Albrecht, A. Salvadori, M. D. Cadman, F. Liechti, and J. W. Fox (2015). A continent-wide migratory divide in North American breeding Barn Swallows (*Hirundo rustica*). PLOS One 10:e0129340.

Horns, J. J., E. Buechley, M. Chynoweth, L. Aktay, E. Çoban, M. A. Kırpık, J. M. Herman, Y. Şaşmaz, and Ç. H. Şekercioğlu (2016). Geolocator tracking of Great Reed-Warblers (*Acrocephalus arundinaceus*) identifies key regions for migratory wetland specialists in the Middle East and sub-Saharan East Africa. The Condor: Ornithological Applications 118:835–849.

Jahn, A. E., V. R. Cueto, J. W. Fox, M. S. Husak, D. H. Kim, D. V. Landoll, J. P. Ledezma, H. K. LePage, D. J. Levey, M. T. Murphy, and R. B. Renfrew (2013). Migration timing and wintering areas of three species of flycatchers (*Tyrannus*) breeding in the Great Plains of North America. The Auk 130:247–257.

Jahn, A. E., D. Levey, V. Cueto, J. Pinto Ledezma, D. Tuero, J. Fox, and D. Masson (2013). Long-distance bird migration within South America revealed by light-level geolocators. The Auk 130:223–229.

Jahn, A. E., N. E. Seavy, V. Bejarano, M. B. Guzman, I. C. C. Provinciato, M. A. Pizo, and M. MacPherson (2016). Intra-tropical migration and wintering areas of Fork-tailed Flycatchers (*Tyrannus savana*) breeding in São Paulo, Brazil. Revista Brasileira de Ornitologia 24:116–121.

Jimenez, J. E., A. E. Jahn, R. Rozzi, and N. E. Seavy (2016). First documented migration of individual White-Crested Elaenias (*Elaenia albiceps chilensis*) in South America. The Wilson Journal of Ornithology 128:419–425.

Johnson, J. A., S. M. Matsuoka, D. F. Tessler, R. Greenberg, and J. W. Fox (2012). Identifying migratory pathways used by Rusty Blackbirds breeding in southcentral Alaska. The Wilson Journal of Ornithology 124:698–703.

Klvaňa, P., J. Cepák, P. Munclinger, R. Michálková, O. Tomášek, and T. Albrecht (2018). Around the Mediterranean: An extreme example of loop migration in a long-distance migratory passerine. Journal of Avian Biology 49:jav-01595.

Koike, S., N. Hijikata, and H. Higuchi (2016). Migration and wintering of Chestnut-cheeked Starlings *Agropsar philippensis*. Ornithological Science 15:63–74.

Koleček, J., S. Hahn, T. Emmenegger, and P. Prochazka (2018). Intra-tropical movements as a beneficial strategy for Palearctic migratory birds. Royal Society Open Science 5:171675.

Koleček, J., P. Prochazka, N. El-Arabany, M. Tarka, M. Ilieva, S. Hahn, M. Honza, J. de la Puente, A. Bermejo, A. Gursoy, S. Bensch, et al. (2016). Cross-continental migratory connectivity and spatiotemporal migratory patterns in the great reed warbler. Journal of Avian Biology 47:756–767.

Kramer, G. R., H. M. Streby, S. M. Peterson, J. A. Lehman, D. A. Buehler, P. B. Wood, D. J. McNeil, J. L. Larkin, and D. E. Andersen (2017). Nonbreeding isolation and population-specific migration patterns among three populations of Golden-winged Warblers. The Condor: Ornithological Applications 119:108–121.

Kristensen, M. W., A. P. Tottrup, and K. Thorup (2013). Migration of the Common Redstart (*Phoenicurus phoenicurus*): A Eurasian songbird wintering in highly seasonal conditions in the West African Sahel. The Auk 130:258–264.

Lam, L., E. A. McKinnon, J. D. Ray, M. Pearman, G. T. Hvenegaard, J. Mejeur, L. Moscar, M. Pearson, K. Applegate, P. Mammenga, J. Tautin, and K. C. Fraser (2015). The influence of morphological variation on migration performance in a trans-hemispheric migratory songbird. Animal Migration 2(1). doi:10.1515/ami-2015-0005.

Laughlin, A. J., C. M. Taylor, D. W. Bradley, D. LeClair, R. G. Clark, R. D. Dawson, P. O. Dunn, A. Horn, M. Leonard, D. R. Sheldon, D. Shutler, et al. (2013). Integrating information from geolocators, weather radar, and citizen science to uncover a key stopover area of an aerial insectivore. The Auk 130:230–239.

Lemke, H. W., M. Tarka, H. G. Klaassen, M. Akesson, S. Bencsch, D. Hasselquist, and B. Hansson (2013). Annual cycle and migration strategies of a trans-Saharan migratory songbird: A geolocator study on the Great Reed Warbler. PLOS One 8:e79209.

Lerche-Jørgensen, M., M. Willemoes, A. P. Tottrup, K. R. S. Snell, and K. Thorup (2017). No apparent gain from continuing migration for more than 3000 kilometres: Willow warblers breeding in Denmark winter across the entire northern Savannah as revealed by geolocators. Movement Ecology 5:17.

Liechti, F., C. Scandolara, D. Rubolini, R. Ambrosini, F. Korner-Nievergelt, S. Hahn, R. Lardelli, M. Romano, M. Caprioli, A. Romano, B. Sicurella, and N. Saino (2015). Timing of migration and residence areas during the non-breeding period of barn swallows *Hirundo rustica* in relation to sex and population. Journal of Avian Biology 46:254–265.

Lislevand, T., B. Chutný, I. Byrkjedal, V. Pavel, M. Briedis, P. Adamik, and S. Hahn (2015). Red-spotted Bluethroats *Luscinia s. svecica* migrate along the Indo-European flyway: A geolocator study. Bird Study 62:508–515.

Macdonald, C. A., K. C. Fraser, H. G. Gilchrist, T. K. Kyser, J. W. Fox, and O. P. Love (2012). Strong migratory connectivity in a declining Arctic passerine. Animal Migration 1:23–30.

Macdonald, C. A., E. A. McKinnon, H. G. Gilchrist, and O. P. Love (2015). Cold tolerance, and not earlier arrival on breeding grounds, explains why males winter further north in an Arctic-breeding songbird. Journal of Avian Biology 47:7–15.

McKinnon, E. A., K. C. Fraser, C. Q. Stanley, and B. J. M. Stutchbury (2014). Tracking from the Tropics reveals behaviour of juvenile songbirds on their first spring migration. PLOS One 9:e105605.

McKinnon, E. A., C. M. Macdonald, H. G. Gilchrist, and O. P. Love (2016). Spring and fall migration phenology of an Arctic-breeding passerine. Journal of Ornithology 157:681–693.

McKinnon, E. A., C. Q. Stanley, and B. J. M. Stutchbury (2015). Carry-over effects of nonbreeding habitat on start-to-finish spring migration performance of a songbird. PLOS One 10:e0141580.

Nelson, A. R., R. L. Cormier, D. L. Humple, J. C. Scullen, R. Sehgal, and N. E. Seavy (2016). Migration patterns of San Francisco Bay Area Hermit Thrushes differ across a fine spatial scale. Animal Migration 3:1–13.

Norevik, G., S. Åkesson, and A. Hedenström (2017). Migration strategies and annual space-use in an Afro-Palaearctic aerial insectivore – the European nightjar *Caprimulgus europaeus*. Journal of Avian Biology 48:738–747.

Ouwehand, J., and C. Both (2016). Alternate non-stop migration strategies of pied flycatchers to cross the Sahara desert. Biology Letters 12:4.

Ouwehand, J., and C. Both (2017). African departure rather than migration speed determines variation in spring arrival in pied flycatchers. Journal of Animal Ecology 86:88–97.

Ouwehand, J., M. P. Ahola, A. N. M. A. Ausems, E. S. Bridge, M. Burgess, S. Hahn, C. M. Hewson, R. H. G. Klaassen, T. Laaksonen, H. M. Lampe, W. Velmala, and C. Both (2016). Light-level geolocators reveal migratory connectivity in European populations of pied flycatchers *Ficedula hypoleuca*. Journal of Avian Biology 47:69–83.

Pedersen, L., K. C. Fraser, T. K. Kyser, and A. P. Tøttrup (2016). Combining direct and indirect tracking techniques to assess the impact of sub-Saharan conditions on cross-continental songbird migration. Journal of Ornithology 157:1037–1047.

Pillar, A. G., P. P. Marra, N. J. Flood, and M. W. Reudink (2016). Moult migration in Bullock's orioles (*Icterus bullockii*) confirmed by geolocators and stable isotope analysis. Journal of Ornithology 157:265–275.

Procházka, P., S. Hahn, S. Rolland, H. van der Jeugd, T. Csörgő, F. Jiguet, T. Mokwa, F. Liechti, D. Vangeluwe, and F. Korner-Nievergelt (2017). Delineating large-scale migratory connectivity of reed warblers using integrated multistate models. Diversity and Distributions 23:27–40.

Renfrew, R. B., D. Kim, N. Perlut, J. A. Smith, J. Fox, and P. P. Marra (2013). Phenological matching across hemispheres in a long-distance migratory bird. Diversity and Distributions 19:1–12.

Rodriguez-Ruiz, J., J. de la Puente, D. Parejo, F. Valera, M. A. Calero-Torralbo, J. M. Reyes-Gonzalez, Z. Zajkova, A. Bermejo, and J. M. Aviles (2014). Disentangling migratory routes and wintering grounds of Iberian near-threatened European Rollers *Coracias garrulus*. PLOS One 9:e115615.

Röseler, D., H. Schmaljohann, and F. Bairlein (2017). Timing of migration, routes and wintering grounds of a short-distance diurnal migrant revealed by geolocation: A case study of Linnets *Carduelis cannabina*. Journal of Ornithology 158:875–880.

Ross, J. D., E. S. Bridge, M. J. Rozmarynowycz, and V. P. Bingman (2014). Individual variation in migratory path and behaviour among Eastern Lark Sparrows. Animal Migration 2:29–33.

Ryder, T. B., J. W. Fox, and P. P. Marra (2011). Estimating migratory connectivity of Gray Catbirds (*Dumetella carolinensis*) using geolocator and mark–recapture data. The Auk 128:448–453.

Saino, N., R. Ambrosini, B. Albetti, M. Caprioli, B. De Giorgio, E. Gatti, F. Liechti, M. Parolini, A. Romano, M. Romano, C. Scandolara, et al. (2017). Migration phenology and breeding success are predicted by methylation of a photoperiodic gene in the barn swallow. Scientific Reports 7:45412.

Saino, N., R. Ambrosini, M. Caprioli, A. Romano, M. Romano, D. Rubolini, C. Scandolara, and F. Liechti (2017). Sex-dependent carry-over effects on timing of reproduction and fecundity of a migratory bird. Journal of Animal Ecology 86:239–249.

Saino, N., D. Rubolini, R. Ambrosini, M. Romano, C. Scandolara, G. D. Fairhurst, M. Caprioli, A. Romano, B. Sicurella, and F. Liechti (2015). Light-level geolocators reveal covariation between winter plumage molt and phenology in a trans-Saharan migratory bird. Oecologia 178:1105–1112.

Salewski, V., M. Flade, A. Poluda, G. Kiljan, F. Liechti, S. Lisovski, and S. Hahn (2013). An unknown migration route of the 'globally threatened' Aquatic Warbler revealed by geolocators. Journal of Ornithology 154:549–552.

Schmaljohann, H., M. Buchmann, J. W. Fox, and F. Bairlein (2012). Tracking migration routes and the annual cycle of a trans-Sahara songbird migrant. Behavioral Ecology and Sociobiology 66:915–922.

Schmaljohann, H., J. W. Fox, and F. Bairlein (2012). Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world. Animal Behaviour 84:623–640.

Schmaljohann, H., C. Meier, D. Arlt, F. Bairlein, H. van Oosten, Y. E. Morbey, S. Akesson, M. Buchmann, N. Chernetsov, R. Desaever, J. Elliott, et al. (2016). Proximate causes of avian protandry differ between subspecies with contrasting migration challenges. Behavioral Ecology 27:321–331.

Seavy, N. E., D. L. Humple, R. L. Cormier, and T. Gardali (2012). Establishing the breeding provenance of a temperate-wintering North American passerine, the Golden-Crowned Sparrow, using light-level geolocation. PLOS One 7:e34886.

Sechrist, J. D., E. H. Paxton, D. D. Ahlers, R. H. Doster, and V. M. Ryan (2012). One year of migration data for a Western Yellow-billed Cuckoo. Western Birds 43:2–11.

Selstam, G., J. Sondell, and P. Olsson (2015). Wintering area and migration routes for Ortolan Buntings *Emberiza hortulana* from Sweden determined with light-geologgers. Ornis Svecica 25:3–14.

Sim, I. M. W., M. Green, G. W. Rebecca, and M. D. Burgess (2015). Geolocators reveal new insights into Ring Ouzel *Turdus torquatus* migration routes and non-breeding areas. Bird Study 62:561–565.

Stach, R., S. Jakobsson, C. Kullberg, and T. Fransson (2012). Geolocators reveal three consecutive wintering areas in the thrush nightingale. Animal Migration 1:1–7.

Stach, R., C. Kullberg, S. Jakobsson, K. Strom, and T. Fransson (2016). Migration routes and timing in a bird wintering in South Asia, the Common Rosefinch *Carpodacus erythrinus*. Journal of Ornithology 157:671–679.

Stanley, C. Q., M. M. MacPherson, K. C. Fraser, E. A. McKinnon, and B. J. Stutchbury (2012). Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. PLOS One 7:e40688.

Stanley, C. Q., E. A. McKinnon, K. C. Fraser, M. P. MacPherson, G. Casbourn, L. Friesen, P. P. Marra, C. E. Studds, T. B. Ryder, N. Diggs, and B. J. M. Stutchbury (2015). Connectivity of Wood Thrush breeding, wintering, and migration sites based on range-wide tracking. Conservation Biology 29:164–174.

Streby, H. M., G. R. Kramer, S. M. Peterson, J. A. Lehman, D. A. Buehler, and D. E. Andersen (2015). Tornadic storm avoidance behavior in breeding songbirds. Current Biology 25:98–102.

Stutchbury, B. J. M., K. C. Fraser, C. Silverio, P. Kramer, B. Aeppli, N. Mickle, M. Pearman, A. Savage, and J. Mejeur (2016). Tracking mated pairs in a long-distance migratory songbird: Migration schedules are not synchronized within pairs. Animal Behaviour 114:63–68.

Stutchbury, B. J. M., E. A. Gow, T. Done, M. MacPherson, J. W. Fox, and V. Afanasyev (2011). Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. Proceedings of the Royal Society B-Biological Sciences 278:131–137.

Stutchbury, B. J. M., R. Siddiqui, K. Applegate, G. T. Hvenegaard, P. Mammenga, N. Mickle, M. Pearman, J. D. Ray, A. Savage, T. Shaheen, and K. C. Fraser (2016). Ecological causes and consequences of intratropical migration in temperate-breeding migratory birds. American Naturalist 188:S28–S40.

Stutchbury, B. J. M., S. A. Tarof, T. Done, E. Gow, P. M. Kramer, J. Tautin, J. W. Fox, and V. Afanasyev (2009). Tracking long-distance songbird migration by using geolocators. Science 323:896.

Szep, T., F. Liechti, K. Nagy, Z. Nagy, and S. Hahn (2017). Discovering the migration and non-breeding areas of sand martins and house martins breeding in the Pannonian basin (central-eastern Europe). Journal of Avian Biology 48:114–122.

Thorup, K., A. P. Tøttrup, M. Willemoes, R. H. G. Klaassen, R. Strandberg, and M. L. Vega (2017). Resource tracking within and across continents in long-distance bird migrants. Science Advances 3:e1601360.

Tøttrup, A. P., R. H. G. Klaassen, M. W. Kristensen, R. Strandberg, Y. Vardanis, A. Lindstrom, C. Rahbek, T. Alerstam, and K. Thorup (2012). Drought in Africa caused delayed arrival of European songbirds. Science 338:1307.

Tøttrup, A. P., R. H. G. Klaassen, R. Strandberg, K. Thorup, M. W. Kristensen, P. S. Jørgensen, J. Fox, V. Afanasyev, C. Rahbek, and T. Alerstam (2012). The annual cycle of a trans-equatorial Eurasian–African passerine migrant: Different spatio-temporal strategies for autumn and spring migration. Proceedings of the Royal Society B-Biological Sciences 279:1008–1016.

Tøttrup, A. P., L. Pedersen, A. Onrubia, R. H. G. Klaassen, and K. Thorup (2017). Migration of red-backed shrikes from the Iberian Peninsula: Optimal or sub-optimal detour? Journal of Avian Biology 48:149–154.

Van Loon, A., J. D. Ray, A. Savage, J. Mejeur, L. Moscar, M. Pearson, M. Pearman, G. T. Hvenegaard, N. Mickle, K. Applegate, and K. C. Fraser (2017). Migratory stopover timing is predicted by breeding latitude, not habitat quality, in a long-distance migratory songbird. Journal of Ornithology 158:745–752.

van Oosten, H. H., R. Versluijs, and R. van Wijk (2014). Migration routes and wintering areas of two Dutch Northern Wheatears *Oenanthe oenanthe* in the Sahel. Limosa 87:168–172.

van Wijk, R. E., S. Bauer, and M. Schaub (2016). Repeatability of individual migration routes, wintering sites, and timing in a long-distance migrant bird. Ecology and Evolution 6:8679–8685.

van Wijk, R. E., M. Schaub, and S. Bauer (2017). Dependencies in the timing of activities weaken over the annual cycle in a long-distance migratory bird. Behavioral Ecology and Sociobiology 71:73.

van Wijk, R. E., M. Schaub, D. Tolkmitt, D. Becker, and S. Hahn (2013). Short-distance migration of Wrynecks *Jynx torquilla* from Central European populations. Ibis 155:886–890.

Wellbrock, A. H. J., C. Bauch, J. Rozman, and K. Witte (2017). 'Same procedure as last year?' Repeatedly tracked swifts show individual consistency in migration pattern in successive years. Journal of Avian Biology 48:897–903.

Winkler, D. W., F. A. Gandoy, J. I. Areta, M. J. Iliff, E. Rakhimberdiev, K. J. Kardynal, and K. A. Hobson (2017). Long-distance range expansion and rapid adjustment of migration in a newly established population of Barn Swallows breeding in Argentina. Current Biology 27:1080–1084.

Wolfe, J. D., and E. I. Johnson (2015). Geolocator reveals migratory and winter movements of a Prothonotary Warbler. Journal of Field Ornithology 86:238–243.

Woodworth, B. K., A. E. M. Newman, S. P. Turbek, B. C. Dossman, K. A. Hobson, L. I. Wassenaar, G. W. Mitchell, N. T. Wheelwright, and D. R. Norris (2016). Differential migration and the link between winter latitude, timing of migration, and breeding in a songbird. Oecologia 181:413–422.

Witynski, M. L., and D. N. Bonter (2018). Crosswise migration by Yellow Warblers, Nearctic–Neotropical passerine migrants. Journal of Field Ornithology 89:37–46.

Xenophontos, M., E. Blackburn, and W. Cresswell (2017). Cyprus wheatears *Oenanthe cypriaca* likely reach sub-Saharan African wintering grounds in a single migratory flight. Journal of Avian Biology 48:529–535.

Yamaura, Y., H. Schmaljohann, S. Lisovski, M. Senzaki, K. Kawamura, Y. Fujimaki, and F. Nakamura (2017). Tracking the Stejneger's stonechat *Saxicola stejnegeri* along the East Asian–Australian Flyway from Japan via China to southeast Asia. Journal of Avian Biology 48:197–202.

APPENDIX B. Studies using automated telemetry systems to study the movements of small landbirds.

Brown, J. M., and P. D. Taylor (2015). Adult and hatch-year blackpoll warblers exhibit radically different regional-scale movements during post-fledging dispersal. Biology Letters 11:20150593.

Crysler, Z. J., R. A. Ronconi, and P. D. Taylor (2016). Differential fall migratory routes of adult and juvenile Ipswich Sparrows (*Passerculus sandwichensis princeps*). Movement Ecology 4:3.

Deppe, J. L., M. P. Ward, R. T. Bolus, R. H. Diehl, A. Celis-Murillo, T. J. Zenzal, Jr., F. R. Moore, T. J. Benson, J. A. Smolinsky, L. N. Schofield, D. A. Enstrom, et al. (2015). Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. Proceedings of the National Academy of Sciences USA 112:E6331–E6338.

Dossman, B. C., G. W. Mitchell, D. R. Norris, P. D. Taylor, C. G. Guglielmo, S. N. Matthews, and P. G. Rodewald (2016). The effects of wind and fuel stores on stopover departure behavior across a migratory barrier. Behavioral Ecology 27:567–574.

Gomez, C., N. J. Bayly, D. R. Norris, S. A. Mackenzie, K. V. Rosenberg, P. D. Taylor, K. A. Hobson, and C. D. Cadena (2017). Fuel loads acquired at a stopover site influence the pace of intercontinental migration in a boreal songbird. Scientific Reports 7:11.

Goymann, W., F. Spina, A. Ferri, and L. Fusani (2010). Body fat influences departure from stopover sites in migratory birds: Evidence from whole-island telemetry. Biology Letters 6:478–481.

Kishkinev, D., D. Heyers, B. K. Woodworth, G. W. Mitchell, K. A. Hobson, and D. R. Norris (2016). Experienced migratory songbirds do not display goal-ward orientation after release following a cross-continental displacement: An automated telemetry study. Scientific Reports 6:37326.

Mills, A. M., B. G. Thurber, S. A. Mackenzie, and P. D. Taylor (2011). Passerines use nocturnal flights for landscape-scale movements during migration stopover. The Condor 113:597–607.

Mitchell, G. W., A. E. M. Newman, M. Wikelski, and D. R. Norris (2012). Timing of breeding carries over to influence migratory departure in a songbird: An automated radiotracking study. Journal of Animal Ecology 81:1024–1033.

Mitchell, G. W., B. K. Woodworth, P. D. Taylor, and D. R. Norris (2015). Automated telemetry reveals age specific differences in flight duration and speed are driven by wind conditions in a migratory songbird. Movement Ecology 3:19.

Muller, F., P. D. Taylor, S. Sjöberg, R. Muheim, A. Tsvey, S. A. Mackenzie, and H. Schmaljohann (2016). Towards a conceptual framework for explaining variation in nocturnal departure time of songbird migrants. Movement Ecology 4:24.

Rerucha, S., T. Bartonicka, P. Jedlicka, M. Cizek, O. Hlousa, R. Lucan, and I. Horacek (2015). The BAARA (Biological AutomAted RAdiotracking) System: A new approach in ecological field studies. PLOS One 10:e0116785.

Sjöberg, S., and C. Nilsson (2015). Nocturnal migratory songbirds adjust their travelling direction aloft: Evidence from a radiotelemetry and radar study. Biology Letters 11:20150337.

Sjöberg, S., T. Alerstam, S. Åkesson, A. Schulz, A. Weidauer, T. Coppack, and R. Muheim (2015). Weather and fuel reserves determine departure and flight decisions in passerines migrating across the Baltic Sea. Animal Behaviour 104:59–68.

Smolinsky, J. A., R. H. Diehl, T. A. Radzio, D. K. Delaney, and F. R. Moore (2013). Factors influencing the movement biology of migrant songbirds confronted with an ecological barrier. Behavioral Ecology and Sociobiology 67:2041–2051.

Taylor, P. D., T. L. Crewe, S. A. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, C. M. Francis, C. G. Guglielmo, D. J. Hamilton, R. L. Holberton, et al. (2017). The Motus Wildlife Tracking System: A collaborative research network to enhance the understanding of wildlife movement. Avian Conservation and Ecology 12:11.

Taylor, P. D., S. A. Mackenzie, B. G. Thurber, A. M. Calvert, A. M. Mills, L. P. McGuire, and C. G. Guglielmo (2011). Landscape movements of migratory birds and bats reveal an expanded scale of stopover. PLOS One 6:e27054.

Woodworth, B. K., C. M. Francis, and P. D. Taylor (2014). Inland flights of young red-eyed vireos *Vireo olivaceus* in relation to survival and habitat in a coastal stopover landscape. Journal of Avian Biology 45:387–395.

Woodworth, B. K., G. W. Mitchell, D. R. Norris, C. M. Francis, and P. D. Taylor (2015). Patterns and correlates of songbird movements at an ecological barrier during autumn migration assessed using landscape- and regional-scale automated radiotelemetry. Ibis 157:326–339.

APPENDIX C. Studies of the effects of geolocators on fitness of small landbirds.

Arlt, D., M. Low, and T. Pärt (2013). Effect of geolocators on migration and subsequent breeding performance of a long-distance passerine migrant. PLOS One 8:e82316.

Bell, S. C., M. El Harouchi, C. M. Hewson, and M. D. Burgess (2017). No short- or long-term effects of geolocator attachment detected in Pied Flycatchers *Ficedula hypoleuca*. Ibis 159:734–743.

Blackburn, E., M. Burgess, B. Freeman, A. Risely, A. Izang, S. Ivande, C. Hewson, and W. Cresswell (2016). An experimental evaluation of the effects of geolocator design and attachment method on between-year survival on whinchats *Saxicola rubetra*. Journal of Avian Biology 47:530–539.

Bowlin, M. S., P. Henningsson, F. T. Muijres, R. H. E. Vleugels, F. Liechti, and A. Hedenstrom (2010). The effects of geolocator drag and weight on the flight ranges of small migrants. Methods in Ecology and Evolution 1:398–402.

Costantini, D., and A. P. Moller (2013). A meta-analysis of the effects of geolocator application on birds. Current Zoology 59:697–706.

Fairhurst, G. D., L. L. Berzins, D. W. Bradley, A. J. Laughlin, A. Romano, M. Romano, C. Scandolara, R. Ambrosini, R. D. Dawson, P. O. Dunn, K. A. Hobson, et al. (2015). Assessing costs of carrying geolocators using feather corticosterone in two species of aerial insectivore. Royal Society Open Science 2:150004.

Gomez, J., C. I. Michelson, D. W. Bradley, D. R. Norris, L. L. Berzins, R. D. Dawson, and R. G. Clark (2014). Effects of geolocators on reproductive performance and annual return rates of a migratory songbird. Journal of Ornithology 155:37–44.

Matyjasiak, P., D. Rubolini, M. Romano, and N. Saino (2016). No short-term effects of geolocators on flight performance of an aerial insectivorous bird, the Barn Swallow (*Hirundo rustica*). Journal of Ornithology 157:653–661.

Morganti, M., D. Rubolini, S. Åkesson, A. Bermejo, J. de la Puente, R. Lardelli, F. Liechti, G. Boano, E. Tomassetto, M. Ferri, M. Caffi, et al. (2018). Effect of light-level geolocators on apparent survival of two highly aerial swift species. Journal of Avian Biology 49:jav-01521.

Peterson, S. M., H. M. Streby, G. R. Kramer, J. A. Lehman, D. A. Buehler, and D. E. Andersen (2015). Geolocators on Golden-winged Warblers do not affect migratory ecology. The Condor: Ornithological Applications 117:256–261.

Raybuck, D. W., J. L. Larkin, S. H. Stoleson, and T. J. Boves (2017). Mixed effects of geolocators on reproduction and survival of Cerulean Warblers, a canopy-dwelling, long-distance migrant. The Condor: Ornithological Applications 119:289–297.

Raybuck, D. W., J. L. Larkin, S. H. Stoleson, and T. J. Boves (2017). Response to Streby and Kramer: Additional considerations for explaining differences in return rates of geolocator-tagged and control Cerulean Warblers. The Condor: Ornithological Applications 119:852–854.

Rodríguez-Ruiz, J., D. Parejo, J. de la Puente, F. Valera, M. A. Calero-Torralbo, A. Bermejo, I. Catry, J. M. Avilés, and C. Rutz (2016). Short- and long-term effects of tracking devices on the European Roller *Coracias garrulus*. Ibis 158:179–183.

Scandolara, C., D. Rubolini, R. Ambrosini, M. Caprioli, S. Hahn, F. Liechti, A. Romano, M. Romano, B. Sicurella, and N. Saino (2014). Impact of miniaturized geolocators on barn swallow *Hirundo rustica* fitness traits. Journal of Avian Biology 45:417–423.

Streby, H. M., and G. R. Kramer (2017). Comment on "Mixed effects of geolocators on reproduction and survival of Cerulean Warblers, a canopy-dwelling, long-distance migrant." The Condor: Ornithological Applications 119:848–851.

van Wijk, R. E., G. Souchay, S. Jenni-Eiermann, S. Bauer, and M. Schaub (2015). No detectable effects of lightweight geolocators on a Palaearctic–African long-distance migrant. Journal of Ornithology 157:255–264.