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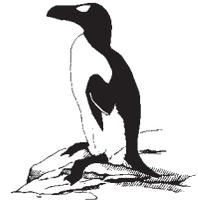
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PERSPECTIVES IN ORNITHOLOGY

NEW DISCOVERIES IN LANDBIRD MIGRATION USING GEOLOCATORS, AND A FLIGHT PLAN FOR THE FUTURE

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BIRD MIGRATION IS a spectacular natural phenomenon that has generated wonder and interest for centuries. Feats of migration inspire amazement—individual birds that weigh less than 200 g may log more than 80,000 km annually (Egevang et al. 2010), travel more than 600 km day⁻¹ (Stutchbury et al. 2009, Åkesson et al. 2012), and cross huge geographic barriers such as oceans (Bairlein et al. 2012) and inhospitable deserts (Tøttrup et al. 2012b). Despite the vast geography covered during migration, many birds return to the same territories year after year. Although incredible progress has been made in our understanding of bird migration (Newton 2008), many gaps remain in our knowledge of the migration of small birds.

The development of miniaturized tracking technology has produced a wave of research into the migratory behavior of small birds (Fig. 1). The inaugural application of miniaturized geolocators (or “geologgers”) on small songbirds in 2007 (Stutchbury et al. 2009) initiated a rapid increase in the number of studies of small landbird migration; there are currently more than 100 permits in North America alone for attaching geolocators to small birds. This technology has been so enthusiastically applied because it provides information critical to conservation and management of declining songbird populations (Faaborg et al. 2010a), as well as the opportunity to test long-standing hypotheses related to endogenous control mechanisms, navigation, and energetics (Robinson et al. 2010). Although more accurate devices may someday be available for tracking small birds, geolocators are currently the only option for migrants that weigh <50 g (Bridge et al. 2011).

The main goal of many geocator studies to date has been the description of little-known migratory routes and wintering sites (e.g., Beason et al. 2012, Stach et al. 2012). As this technique becomes more widely applied (both geographically within species and taxonomically across a broad spectrum of small landbirds),

researchers can begin to test hypotheses about migration, non-breeding ecology, and behavior to inform conservation measures. Many migratory species are declining; thus, a comprehensive understanding of the annual cycle is timely and important for management of species at risk. The purpose of our review is to summarize, for the first time, patterns emerging from geocator studies. We review new data on (1) migratory connectivity, (2) migratory routes and stopovers, (3) intratropical migration of wintering birds, and (4) migration schedules. We then explore questions that can be answered with emerging geocator studies, and provide a “flight plan” for future work as direct-tracking technology becomes increasingly smaller and more broadly applied.

GEOLOCATOR PRIMER

Geolocators are archival light-recording devices that are mounted on the lower back (for most small birds) following the Rappole and Tipton (1991) leg-loop harness design. The tags record light levels in relation to an internal timer. This allows the determination of sunrise and sunset times and, thus, day length and solar midday and midnight upon retrieval of the tag from the bird after it has completed its migration, usually the next year. Latitude and longitude are estimated from these light data, typically with a computer program such as LOCATOR (British Antarctic Survey) or tripEstimation in R (Sumner et al. 2009). Locations are determined using the “threshold method,” which uses calibration to determine the average sun elevation angle (the angle of the sun on the horizon) when a sunrise or sunset transition is defined, or using a “template-matching” method (Sumner et al. 2009, Lisovski et al. 2012). For more details on analysis methods, see Bridge et al. (2011), Lisovski et al. (2012), and McKinnon et al. (2013).

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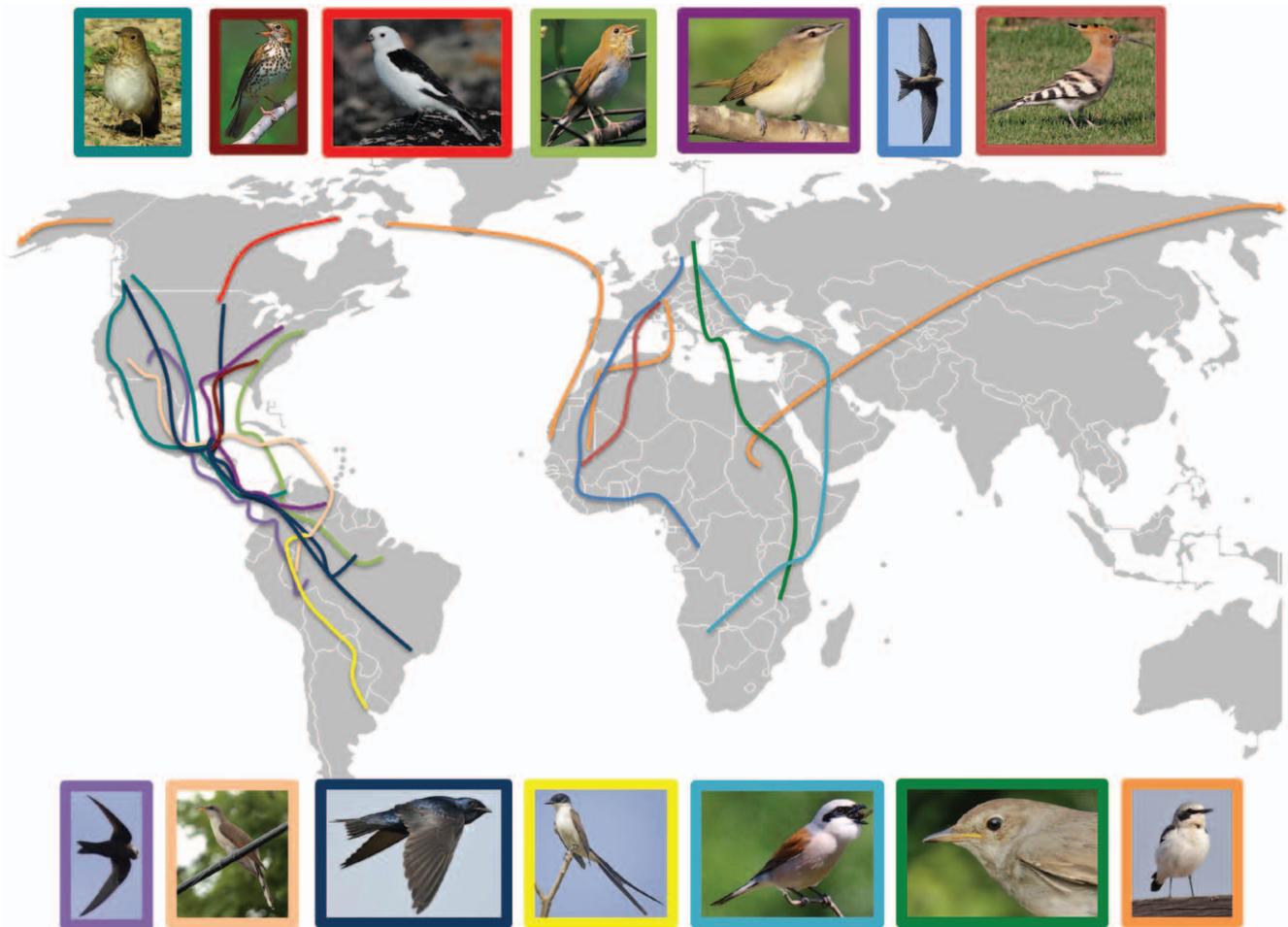


FIG. 1. Since their deployment on the first migratory landbirds in 2007, geolocators have been used to track individual birds in the Palearctic–Tropical, Nearctic–Neotropical, and Austral migratory systems. Colors that frame the photographs match the colors that indicate migratory routes. One individual's spring migration is shown for each subspecies (two subspecies are shown for Purple Martin and Swainson's Thrush, and three for Northern Wheatear), except for Fork-tailed Flycatcher (yellow) and Thrush Nightingale (bright green), whose fall migrations are shown. Maps are modified from references in Table 1. Photo credits: Red-eyed Vireo, Wood Thrush, and Veery: Lang Elliot; Swainson's Thrush: Darren Irwin; Red-backed Shrike: Per Eckberg; Purple Martin and Fork-tailed Flycatcher: Harold Stiver; Yellow-billed Cuckoo: Karthryn Mann; Snow Bunting: Sebastien Descamps; Northern Black Swift: Steven Daly; Common Swift: Steve James; Eurasian Hoopoe, Northern Wheatear, and Thrush Nightingale: Mikkel W. Kristensen.

Geocator accuracy varies, depending on bird behavior, geographic location, habitat, and weather (Fudickar et al. 2012, Lisovski et al. 2012). Ground truthing at multiple sites prior to fall migration found that geolocators mapped 91% (83 of 91) of Purple Martins accurately to within 100 km latitude and longitude (Fraser et al. 2012; scientific names of species not provided in the text can be found in Table 1). Ground-truthing tests with stationary forest birds on their tropical wintering grounds have shown that geolocators can place birds within a few degrees of latitude (365 km) and $<1^\circ$ of longitude (66 km) of actual locations (McKinnon et al. 2013). These levels of accuracy are sufficient to elucidate unambiguous patterns of connectivity, migration timing, and so on for most species. Determination of finer-scale movements (e.g., within ~ 100 km) and finer-scale mapping of birds while stationary at non-breeding sites is currently limited by technology. Geolocators, by relying on day length to determine latitude, are not able

to determine the location of birds near the vernal and autumnal equinoxes (approximately 20 March and 22 September, respectively) when day length is the same everywhere. However, longitude during this time is still as accurate as at other times of the annual cycle (Fudickar et al. 2012).

Aside from the accuracy and analysis issues detailed above (see also Fudickar et al. 2012, Lisovski et al. 2012, McKinnon et al. 2013), researchers have encountered several shortcomings of geocator studies on small birds in terms of field work and study design. One of the first limitations for geocator studies was harness and geocator failure. This has become solvable for many species as geocator models and harness designs continue to be refined on the basis of field and laboratory data (Bowlin et al. 2010). We encourage the publication of details of successful and failed geocator attachment methods to improve future studies. Battery failure occurs even with the most reliable small geocator models (e.g., 10–15% failure rate for British

TABLE 1. Summary of migration variables obtained from small landbirds using geolocators. Species are listed by increasing body size. Question marks indicate areas where patterns are suggestive but sample size small. Information not available is indicated by NA.

Species	Body size (g)	Number of geolocator deployment sites	Loop migration ^a	Multiple winter sites (n)	Long stops ^b	Migratory connectivity ^c	Percentage of year at non-breeding sites ^d	References
Common Redstart (<i>Phoenicurus phoenicurus</i>)	16	1	Yes	No	Yes (fall and spring)	Weak	61	Kristensen et al. 2013
Red-eyed Vireo (<i>Vireo olivaceus</i>)	19	1	Yes	No	Yes (spring)	NA	NA	Callo et al. 2013
Bobolink (<i>Dolichonyx oryzivorus</i>)	25	3	NA	Yes	Yes (fall)	Weak	NA	Renfrew et al. 2013
Northern Wheatear (<i>Oenanthe oenanthe</i>)	26	3	Yes	No	No	Strong	76 (AK) 62 (Ger) 64 (Can)	Schmaljohann et al. 2012a Schmaljohann et al. 2012b Bairlein et al. 2012 Stach et al. 2012
Thrush Nightingale (<i>Luscinia luscinia</i>)	27	2	NA	Yes (3)	Yes (fall)	Strong?	NA	Stach et al. 2012
Fork-tailed Flycatcher (<i>Tyrannus savana</i>)	30	1	NA	Yes (2)	NA	NA	NA	Jahn et al. 2013b
Veery (<i>Catharus fuscescens</i>)	30	1	Yes	Yes (2)	Yes (fall)	NA	69	Heckscher et al. 2011
Swainson's Thrush (coastal; <i>C. ustulatus</i>)	30	2	Yes	Yes (2)	Yes (spring)	Strong	84	Delmore et al. 2012
Swainson's Thrush (inland; <i>C. ustulatus</i>)	30	1	Yes	No	Yes (spring)	Strong	81	Cormier et al. 2013 Delmore et al. 2012
Red-backed Shrike (<i>Lanius collurio</i>)	30	3	Yes	No	Yes (fall)	Weak?	NA	Tøttrup et al. 2012b
Eastern Kingbird (<i>T. tyrannus</i>)	40	2	Yes	Yes (2)	No	NA	69	Jahn et al. 2013a
Western Kingbird (<i>T. verticalis</i>)	40	1	NA	Yes (2)	Yes (fall)	NA	78	Jahn et al. 2013a
Scissor-tailed Flycatcher (<i>T. forficatus</i>)	40	1	NA	No	No	NA	44	Jahn et al. 2013a
Golden-crowned Sparrow (<i>Zonotrichia atricapilla</i>)	32	1	NA	No	NA	NA	70	Seavy et al. 2012
Snow Bunting (<i>Plectrophenax nivalis</i>)	35	1	NA	Yes	Yes (spring)	Weak (sub-sp.) Strong (sp.)	68	Macdonald et al. 2012
Common Swift (<i>Apus apus</i>)	44	2	No	Some individuals (2)	Yes (fall)	Weak? Strong (including banding data)	81	Åkesson et al. 2012
Gray Catbird (<i>Dumetella carolinensis</i>)	45	1	NA	No	NA	Strong (including banding data)	NA	Ryder et al. 2011
Wood Thrush (<i>Hylocichla mustelina</i>)	45	8	Yes	No	Yes (fall)	Strong	59	C. Q. Stanley et al. unpubl. data Stanley et al. 2012 Stutchbury et al. 2009, 2011
Northern Black Swift (<i>Cypseloides niger borealis</i>)	46	1	NA	NA	NA	NA	71	Beason et al. 2012
Purple Martin (<i>Progne subis</i>)	55	7	Yes	Yes (1–4)	Yes (fall)	Weak (sub-sp.) Strong (sp.)	66	Fraser et al. 2012

(Continued)

TABLE 1. Continued.

Species	Body size (g)	Number of geolocator deployment sites	Loop migration ^a	Multiple winter sites (n)	Long stops ^b	Migratory connectivity ^c	Percentage of year at non-breeding sites ^d	References
Western Yellow-billed Cuckoo (<i>Coccyzus americanus occidentalis</i>)	60	1	Yes	No	Yes (spring and fall)	NA	79	Sechrist et al. 2012
Eurasian Hoopoe (<i>Upupa epops epops</i>)	68	1	Yes	No	Yes (fall)	Weak	70	Bächler et al. 2010

^a Loop migration: this category includes species in which spring migration was east or west of fall migration.

^b Long stopover = any stopover >7 days, on average.

^c Migratory connectivity: defined as overlap of wintering sites for individuals from different breeding populations. Weak = individuals from multiple breeding populations wintering together; strong = individuals from distinct breeding populations with distinct wintering ranges. Question marks indicate studies with minimal data or no clear pattern.

^d Percentage of year at non-breeding sites includes days spent at stopovers, on migration, and at wintering sites.

Antarctic Survey MK 10 and 16 on songbirds). Researchers must take into account not only return rates of the individual birds, but also potential rates of harness or geolocator failure when determining how many geolocators should be deployed.

Another important issue to consider is the impact on the study species. Most geolocator studies assume little impact on survival or behavior of the birds tracked. Although true tests of effects of geolocators on migratory behavior are not possible, evidence suggests that return rates of birds with geolocators are not significantly lower than those without geolocators (E. S. Bridge et al. unpubl. data). For sensitive species, low returns may be solvable through changes in geolocator or harness design (e.g., Purple Martins had very low return rates in the first 2 years, but shortening the light stalk of the geolocator solved the problem; B. J. M. Stutchbury et al. unpubl. data). Pilot testing with dummy geolocators and various harness types is a low-cost way to establish whether negative effects occur before time, effort, and money are invested into real geolocator deployments.

In some cases, the retrieval rate of birds wearing geolocators is low because of low site fidelity (i.e., deployments on juveniles or at stopover sites). Whether or not deployment on species or demographic groups with low return rates is valuable or ethical depends on the study species and questions.

In sum, the collective experience gained around the world from tracking small birds with geolocators in the past 5 years means that most researchers should be able to confidently proceed with geolocator tracking of small birds because they can (1) identify appropriate questions, species, study sites, and methods needed to get migration data; (2) understand the inherent limitations of geolocators (battery failure, temporal and spatial accuracy, shading, equinox issues with latitude, and data from survivors only); (3) ensure that they monitor possible effects on birds and conduct pilot studies in advance; and (4) anticipate return and retrieval rates in order to determine *a priori* feasibility of obtaining adequate sample sizes and statistical power for the questions posed.

MIGRATORY CONNECTIVITY

One of the primary goals of tracking migratory birds between breeding and wintering areas is to determine migratory

connectivity. Migratory connectivity is defined from a breeding-grounds perspective as the amount of overlap in wintering locations of individual birds from geographically distinct breeding populations (Webster et al. 2002, Boulet and Norris 2006). The degree of linkage between populations in different seasons has direct implications for density-dependent population dynamics (Norris and Marra 2007, Taylor and Norris 2010) and, therefore, conservation of migratory birds (Martin et al. 2007, Marra et al. 2011).

Broad patterns of migratory connectivity have been determined for some species by using stable isotope analysis of feathers grown at the site of interest (Hobson and Wassenaar 1997, Marra et al. 1998, Rubenstein et al. 2002), by mapping genetic structure (Clegg et al. 2003), or by using a combination of these techniques (Chabot et al. 2012). Geolocators can reveal fine-scale connectivity patterns (i.e., locations of birds within 100–500 km) that, in most cases, cannot be elucidated by examining stable isotopes or genetic structure, which can only map birds to broad isoscapes available in the environment or to the level of genetically distinct groups (Irwin et al. 2011). An under-used source of fine-scale connectivity data is the North American bird-banding database (Ryder et al. 2011). However, for many species, band recoveries, if they exist, are too sparse to draw conclusions about migratory connectivity (e.g., Northern Black Swift [Beason et al. 2012] and Purple Martin [Fraser et al. 2012]).

For geolocators to provide information on the strength of migratory connectivity, birds should ideally be tracked from multiple breeding and/or wintering sites to determine the degree of overlap of distinct breeding populations at different points in the annual cycle (Fig. 2). To date, deployment of geolocators at such a broad scale has been relatively rare (but see Fraser et al. 2012, Laughlin et al. 2013, Renfrew et al. 2013). However, geolocators are rapidly filling in maps for single populations (or single birds; Table 1) and can be used in conjunction with other data, such as stable isotope analysis of feathers (Macdonald et al. 2012) and band recoveries (Ryder et al. 2011), to provide a snapshot of range-wide connectivity.

Two species tracked extensively using geolocators, the Wood Thrush and Purple Martin, exhibit extremes in connectivity. Wood Thrushes tracked from a single breeding population in northern Pennsylvania overwinter, almost exclusively, in a small portion of the wintering grounds in eastern Honduras and Nicaragua

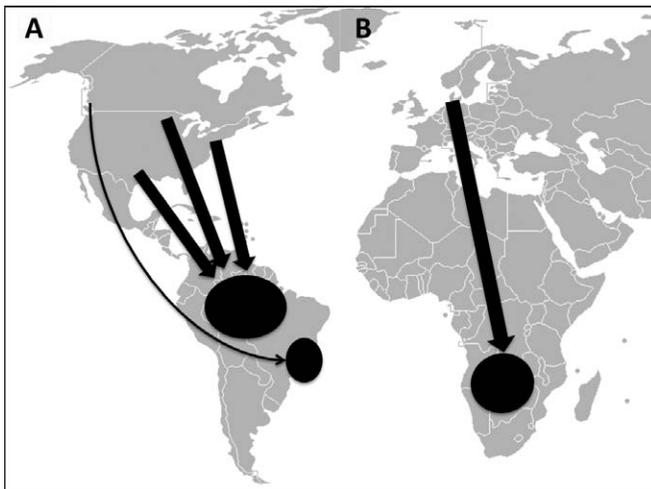


FIG. 2. Examples of migratory connectivity patterns described using geolocator data: (A) weak connectivity within subspecies of Purple Martin (eastern subspecies, *Progne subis subis*, shown by thick arrows to indicate multiple breeding sites) but strong connectivity across subspecies (*P. subis arbuticola*, shown by thin arrow) (Fraser et al. 2012); and (B) three breeding populations (shown by thick arrow) of Red-backed Shrike tracked to the same wintering region—likely weak connectivity (Tøttrup et al. 2012b). This example illustrates how multiple breeding populations are needed to determine connectivity strength.

(Stutchbury et al. 2009, 2011). Tracking from six other breeding sites and three wintering sites revealed a strong pattern of parallel leap-frog connectivity: northeastern populations (New York and Quebec) tend to winter in the southeast of their range (Costa Rica); central-eastern breeding birds (Pennsylvania and Ontario) winter in central Mesoamerica (Nicaragua and Honduras); and southern and midwestern breeding birds (e.g., Indiana, Kentucky, and North Carolina) tend to winter in the northwestern winter range (Belize and Mexico) (C. Q. Stanley et al. unpubl. data).

By contrast, there was little spatial structure in winter distributions of the eastern subspecies of Purple Martin (*Progne subis subis*; Fraser et al. 2012). Similarly, Bobolinks from across the breeding range showed extensive mixing during the non-breeding period (Renfrew et al. 2013). In Purple Martins, birds from colonies across the breeding range were found in the same core wintering region in the northern Amazon basin (Fig. 2; Fraser et al. 2012). Birds from a single breeding colony wintered, on average, 900 km apart and had overlapping winter distribution with birds from breeding colonies $\leq 2,000$ km away. This extensive mixing of breeding populations at wintering sites is a textbook example of weak migratory connectivity. However, at the subspecies level, Purple Martins exhibit strong connectivity. Purple Martins from the western North American subspecies (*P. s. arbuticola*) that were tracked using geolocators had a distinct wintering area in southeastern Brazil (Fraser et al. 2012) that did not overlap at all with the wintering range of the eastern subspecies (Fig. 2). These results emphasize the importance of scale and phylogenetics in defining patterns of connectivity.

Macdonald et al. (2012) found strong parallel connectivity, also at the scale of subspecies, in Snow Buntings, with Greenland breeding birds wintering in eastern Canada (shown through band records) and Canadian Arctic breeding birds wintering in western

Canada. Examining the banding records alone suggests a pattern of weak connectivity within subspecies: multiple breeding populations from Greenland share a broad overlapping wintering site in eastern Canada. However, geolocator data from the Canadian Arctic revealed a migratory divide at Hudson Bay. Overall, then, the species shows a broad pattern of strong connectivity (Macdonald et al. 2012). Delmore et al. (2012) studied subspecies of Swainson's Thrush at a migratory divide and found that subspecies separated by <300 km at their breeding sites had distinct migratory routes and wintering ranges. Unlike in Snow Buntings, a pattern of strong connectivity was apparent within subspecies of Swainson's Thrush; coastal birds tracked with geolocators from a breeding population in California had a distinct wintering area in relation to coastal birds tracked from British Columbia (Cormier et al. 2013).

Most studies using geolocators have focused on qualitative measures of connectivity, such as the broad patterns described above. However, as more data are collected, quantitative measures of connectivity can be explored. To quantitatively describe migratory connectivity in Purple Martins, Fraser et al. (2012) used nearest-neighbor calculations to describe the spatial relationship among wintering birds from the same breeding populations and tested for significant correlations between breeding and wintering latitude and breeding and wintering longitude. Ambrosini et al. (2009) used band returns and distance matrices to calculate Mantel's correlations between proximity of individual Barn Swallows (*Hirundo rustica*) at breeding and winter sites, testing whether the distribution of birds in one season was random (weak connectivity) or correlated with the distribution of birds in the previous season (strong connectivity). Mantel's correlation coefficient indicated very strong connectivity using geolocator data from Swainson's Thrushes (Cormier et al. 2013). Quantitative measures of connectivity patterns and strength would allow for more cross-species comparisons, which could lead to better understanding of the evolution of migratory behavior and, potentially, better predictions of patterns of connectivity in species that are too small for geolocator tracking.

MIGRATORY ROUTES AND STOPOVERS

The documentation of individual migratory routes and stopover sites, from start to finish, is one of the most exciting and unique contributions of geolocators to the study of migration in small birds. Geolocators have revealed geographically and individually consistent patterns of loop migration within species (Tøttrup et al. 2012b), connections between New World Arctic and African ecosystems (Bairlein et al. 2012), and unexpectedly long spring stopovers (e.g., Red-eyed Vireos; Callo et al. 2013) and fall stopovers (e.g., Wood Thrushes; Stutchbury et al. 2011).

Many species tracked using geolocators have shown seasonal variation in migratory routes (i.e., loop migration; Table 1). For example, most Wood Thrushes exhibit fall migration routes consistently east of spring migration routes (Stanley et al. 2012). In the Palearctic system, Red-backed Shrikes tracked from three sites in southern Scandinavia also showed a strong pattern of loop migration, with all individuals migrating farther west in fall in relation to spring routes (Tøttrup et al. 2012b). These patterns may be related to broad-scale wind patterns or spatial variation in the quality of stopover habitat (Klaassen et al. 2010); however, these hypotheses have not been explicitly tested in small landbirds.

Some species show within-season differences in migratory routes. Coastal and inland subspecies of Swainson's Thrush differed greatly in migratory route (Delmore et al. 2012), as did Alaskan and Canadian Arctic-breeding subspecies of the Northern Wheatear (Bairlein et al. 2012). Subspecific differences might be expected, but differences within populations have been documented as well. Eurasian Hoopoes tracked from the center of their breeding range showed very different migration routes, possibly indicative of a migratory divide (Bächler et al. 2010), and Northern Wheatears tracked from Germany also exhibited within-population variation in their migratory route (Schmaljohann et al. 2012a). Within-population variation in migratory routes is also evident in the Nearctic–Neotropical migration system. Two of five Veeries tracked from a single breeding population migrated across the western Gulf of Mexico in spring, whereas three crossed the gulf from Cuba to Florida (Heckscher et al. 2011).

It is unclear whether variation (or convergence) in migratory routes of individuals in a single population is because of endogenous control (i.e., genetic and heritable traits) or is a flexible response to environmental cues en route. Schmaljohann et al. (2012b) examined weather effects on migration decisions by Northern Wheatears and found that wind and temperature affected migration decisions in fall but not in spring. Repeat-tracking of individual Wood Thrushes showed that 7 of 10 birds used a similar spring route at the Gulf of Mexico from year to year, although, at a finer geographic scale, longitude when crossing 23.4°N was not statistically repeatable (Stanley et al. 2012). Longitudinal studies (i.e., tracking the same individuals in more than one year) using geolocators are logistically difficult because of the short life span of small birds and, thus, the large number of geolocators needed to repeat-track a sufficient sample of individuals. Nevertheless, experimental design that targets repeat-tracking is very important for addressing questions about phenotypic plasticity.

Geolocators have also revealed that some species take very long stopovers (Bächler et al. 2010, Stutchbury et al. 2011, Åkesson et al. 2012, Tøttrup et al. 2012b; Table 1); these long stops exceed the time for migratory refueling expected on the basis of energetic models (Alerstam 1991). Studies of stopover ecology predict that food-rich sites will reduce stopover duration because birds can refuel faster and resume migration (Newton 2008), but geolocators have led to a new perspective on stopover ecology. In fact, the discovery (using geolocators) of these extended stopovers has called into question the definition of stopover, and researchers have made the case that stops longer than needed to refuel should be considered short-term residency periods that are as important for conservation as breeding and wintering periods (Stach et al. 2012, Tøttrup et al. 2012b).

Prolonged stopovers at sites with abundant food could be favored if they improve migratory performance or condition on arrival at breeding sites (Newton 2008, Klaassen et al. 2011). Both Swainson's Thrushes and Red-eyed Vireos are omnivorous and commonly feed on fruit, a resource that is consumed by many migrants at tropical sites before and during spring migration (Blake and Loiselle 1992). Long stationary periods during spring migration in both of these species (Delmore et al. 2012, Callo et al. 2013) could be driven by high fruit availability en route. These

sites may be important staging areas for refueling for subsequent migration, as in shorebirds, but this remains to be investigated.

MULTIPLE WINTER SITES

Another surprising discovery made with geolocators is the documentation of intratropical migrations of long-distance migratory birds within their winter range (Table 1). Although there was evidence that some species are “itinerant” in winter (Newton 2008), data from geolocators suggest that multiple distinct residency periods in winter may be fairly common (Table 1). For example, two-thirds of Purple Martins occupied more than one long-term winter site, and some individuals had up to four distinct sites $\leq 1,400$ km apart (Fraser et al. 2012). Intratropical movements complicate connectivity studies because the degree of connectivity with breeding areas could change over the non-breeding season as birds shift locations.

The discovery of multiple wintering sites is important for conservation and management of species at risk. Without direct tracking, these sites and the connections between them and links to breeding sites would remain unknown. Determining the year-round and full extent of habitat use is key in effective reserve design, as illustrated by a study of the Resplendent Quetzal (*Pharomachrus mocinno*); direct tracking revealed that birds spent most of their time at sites outside of reserves (Powell and Bjork 1995). Multiple non-breeding sites for temperate-breeding birds in the tropics can be compared to the more widely recognized intratropical and elevational migration of tropical species (Faaborg et al. 2010b) to determine why this pattern is evident in some species or individuals and not others.

MIGRATION SCHEDULES

Prior to the deployment of light-level geolocators on small songbirds, migration timing en route was estimated using mean passage dates between two or more points on migration (e.g., Marra et al. 2005, Tøttrup et al. 2008). One limitation of this approach is that multiple populations of birds are being measured and, hence, temporal changes within populations are not known (Newton 2008). Using this technique, actual migration rate (km day^{-1}) of individuals cannot be calculated. Mark-recapture is a second method used to obtain migration rates, wherein birds are banded in one location and recaptured in another (Fransson 1995). A limitation is that exactly when birds departed or arrived at each location is unknown, which influences estimates of migration rates, and such data are rare for many species and reveal only a snapshot of migration. Despite location error associated with geolocator tracking, geolocators currently provide the most accurate method to measure the specific migration rate of individual birds from start to finish and during both spring and fall migration. In this case, migration “rate” includes stopovers and flight days or nights and is usually calculated using overall migration distance divided by the number of days spent on migration. Specific migratory flight speed requires precise knowledge of stopover timing and migratory routes and is more easily obtained using geolocators for species that inhabit open landscapes with clear light data, such as the Purple Martin.

The first geolocator study of a songbird showed that migration rate, particularly in spring, was much faster than previously estimated using other methods (Stutchbury et al. 2009). Some Purple Martins traveled from South America to the northern United States at 500–600 km day⁻¹, and Wood Thrushes returned from Central America at 250 km day⁻¹, whereas previous estimates for spring migration pace in songbirds were 50–150 km day⁻¹ (Newton 2008). Subsequent studies using geolocators have confirmed that many species typically travel >200 km day⁻¹ on spring migration (Fig. 3). It has been hypothesized that birds traveling greater distances will migrate at a faster rate (Newton 2008). Using data from Table 1, we compared migration pace in spring and fall with migration distance using a linear regression (R Development Core Team 2011) and found no relationship (spring: $r^2 = 0.024$, $P = 0.28$; fall: $r^2 = -0.019$, $P = 0.40$). We also tested the hypothesis that body size is related to pace, with larger birds traveling faster (Newton 2008), but larger birds did not migrate faster than smaller birds (spring: $r^2 = -0.030$, $P = 0.44$; fall: $r^2 = -0.060$, $P = 0.65$).

With direct tracking, we can also compare both spring and fall migration rates of individual birds and species for the first time (Fig. 3). Using a paired t -test, we found that spring migration rate is significantly faster than fall rate, by species ($t = 2.88$, $df = 12$, $P = 0.01$). Many factors can influence migration speeds or rates, but it is generally predicted that birds migrate at greater rates when they are under greater pressure of time to reach their destinations (Newton 2008, Tøttrup et al. 2012b). However, the associated fitness benefits of early arrival in spring do not necessarily predict faster migration rate, because birds may also achieve earlier arrival at breeding areas by leaving tropical wintering sites earlier. Departure date from overwintering areas is, in many cases, the strongest predictor of arrival date at breeding sites, with differences in rate en route between individuals contributing relatively little to variation in arrival dates (Stanley et al. 2012, Tøttrup et al. 2012b, Callo et al. 2013, Jahn et al. 2013a). With more geolocator studies, we will be able to answer the question of what ecological factors select for a fast (e.g., Purple Martin and Wood Thrush) or a slow (e.g., Red-eyed Vireo and Swainson's Thrush) rate of spring migration.

It will also be important to establish what ecological or genetic factors constrain spring departure date and, thus, prevent individuals from departing early. Constraints on departure date may be related to habitat moisture gradients and associated insect abundance (Smith et al. 2011, Studds and Marra 2011). It is now possible, with geolocators, to test how individual condition and habitat quality, measured at wintering sites, affect not only departure date but also subsequent spring migration rate and arrival date. Fall migration departure and rate also remain largely uninvestigated; molt and food availability in late summer are likely major predictors of fall migration strategy for some species (e.g., *Tyrannus* spp.; Jahn et al. 2013a).

We can also use geolocators to examine the relative flexibility of timing of migration. It is much debated whether birds can mount flexible responses to conditions at wintering sites or on migration, or whether these are mostly under endogenous control (Knudsen et al. 2011). This is important to determine, particularly in the context of climate change, because population declines can be expected when timing of migration does not keep pace with warming trends (Both et al. 2006). Using geolocators to track the

same individual Wood Thrushes in multiple years revealed high repeatability in timing of spring migration, with individuals departing tropical non-breeding sites, on average, within 3 days of themselves in different years (Stanley et al. 2012). Such consistency of migration timing suggests that we might expect little individual flexibility in the migration schedules of some species and the strong influence of endogenous routines. By contrast, both Red-backed Shrikes and Thrush Nightingales were found to delay their spring arrival date at European breeding sites; geolocator tracking revealed that this was in response to an extensive drought and a prolonged stopover by the birds at a major stopover site in the Horn of Africa (Tøttrup et al. 2012a). This suggests that extreme weather events may induce changes in migration strategy. Heritability of departure timing, and of other migration traits, could be established via tracking of parents and offspring, but with geolocators would require large deployments and a species with high natal return rates.

FUTURE RESEARCH USING GEOLOCATORS

Geolocators have revealed the first detailed start-to-finish migrations of small landbirds. Although many studies are based on small samples sizes, they have nevertheless revealed surprises such as very prolonged stopovers in fall and spring, intratropical movements, and very rapid migration rate (Table 1 and Fig. 3). The growing number of direct-tracking studies will allow for novel comparative studies to test predictions for the ecological correlates that drive the evolution of these traits. Larger sample sizes for individual species will also allow more hypothesis-testing and information-theoretic approaches to explore migration behavior (e.g., Stutchbury et al. 2011, Stanley et al. 2012) and conservation (Fraser et al. 2012).

Optimal migration theory.—Optimal migration theory provides a predictive framework that can be tested using data from individual tracks of small migratory birds. Alerstam (2011) outlined the major areas where optimal migration theory could be applied, namely flight speed, fuel deposition, response to predation risk, stopover use, transition from migration to breeding, routes, timing (daily budgets and arrival timing), foraging and migration, wind (selectivity and drift), phenotypic flexibility, and molt schedules. For example, optimal migration theory can be used to predict duration and frequency of stopovers or which route birds should take to minimize energetic costs.

Schmaljohann et al. (2012b) applied optimal migration theory to study the migratory schedules and routes of Northern Wheatears tracked using geolocators. In fall, the birds' ratio of flight to stopover days corresponded almost exactly with theoretical predictions, and the birds also responded to wind and air pressure in a manner consistent with theory. However, contrary to optimal migration theory, Northern Wheatears did not migrate using the shortest routes between breeding and winter sites, and in spring they did not respond to environmental factors such as wind and temperature during migration. Unexpectedly prolonged fall and spring stopovers observed in other studies (see above and Table 1) also do not conform to optimal migration theory. Small migratory birds seem to be breaking "the rules" in many respects, which will launch a reexamination of what constrains the rate of migration and drives stopover

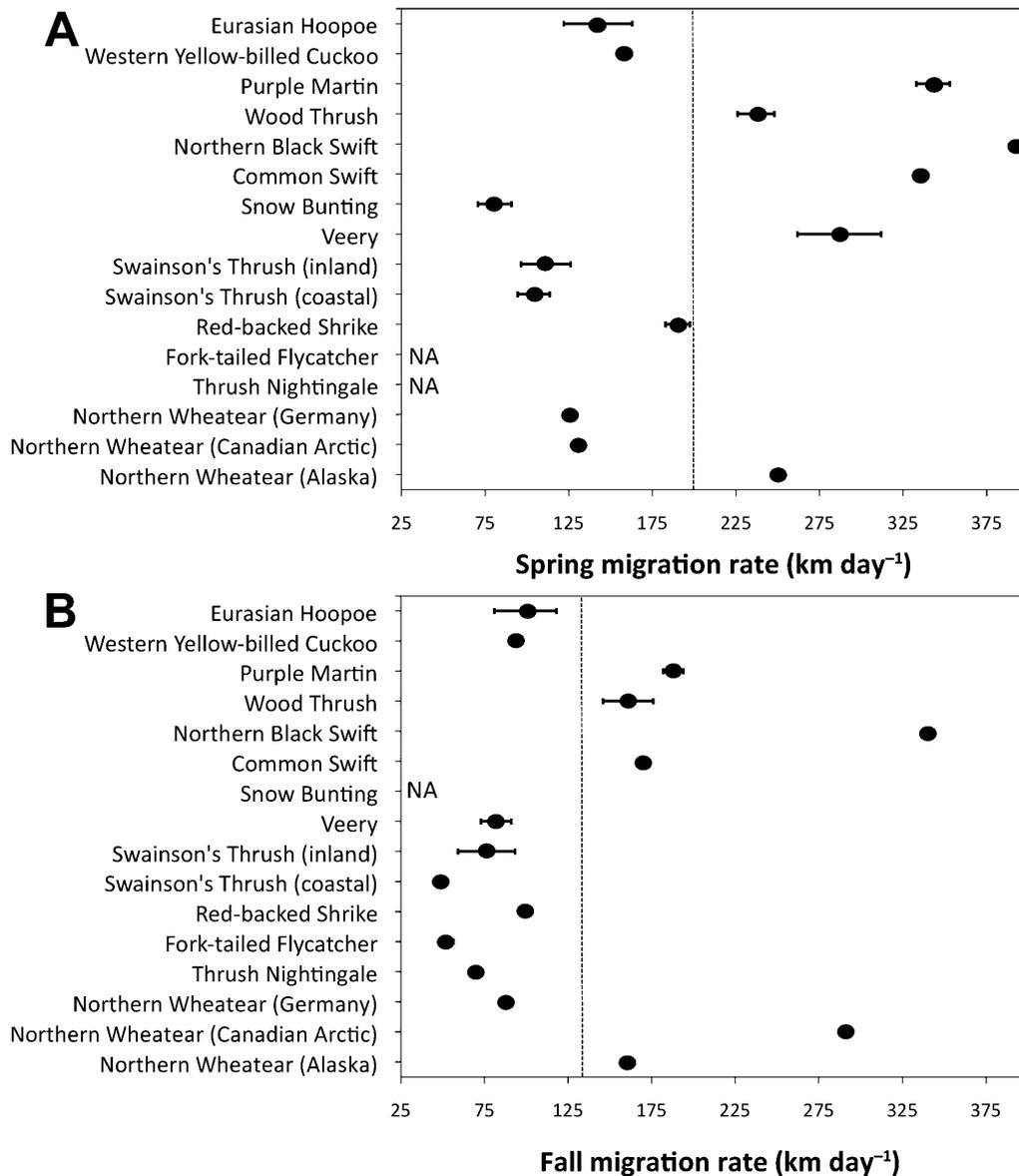


FIG. 3. Average (\pm SE where available) (A) spring migration rate ($n = 13$ species) and (B) fall migration rate ($n = 15$) for birds tracked using geolocators, in order of decreasing average body mass. Dashed lines indicate mean values (206 km day^{-1} for spring and 135 km day^{-1} for fall). Data points without error bars are from papers that did not report standard error or full data sets, with the exception of the Canadian Arctic Wheatear and Western Yellow-billed Cuckoo, which represent single individuals. Sample sizes are as follows (spring and fall, respectively, if different): Eurasian Hoopoe, $n = 2$; Western Yellow-billed Cuckoo, $n = 1$; Purple Martin, $n = 84, 89$; Wood Thrush, $n = 61, 28$; Northern Black Swift, $n = 3$; Common Swift, $n = 6$; Snow Bunting, $n = 11$ (spring only); Veery, $n = 5$; Swainson's Thrush (inland), $n = 4$; Swainson's Thrush (coastal), $n = 4, 5$; Red-backed Shrike, $n = 9$; Fork-tailed Flycatcher, $n = 5$ (fall only); Thrush Nightingale, $n = 2$ (fall only); Northern Wheatear (Germany), $n = 5$; Northern Wheatear (Canadian Arctic), $n = 1$; Northern Wheatear (Alaska), $n = 3$.

duration. A limitation is that geolocators can produce data only for survivors and, thus, it is not yet possible to understand fatal errors in migration strategy.

Sex and age patterns in migration.—Different sex- and age-specific migratory strategies could be linked to differential migration risks and energetic costs for some demographic groups, with implications for our understanding of population dynamics and applications for conservation management. Tracking of males and

females allows for tests of proximate factors that drive well-known patterns such as protandry in spring migration (Coppack and Pulido 2009), as well as little-studied patterns such as protogyny in fall (Mills 2005). Tracking of juvenile birds on their first fall migration (i.e., from the nestling stage) is currently impractical (Thorup et al. 2007) because natal return rates are poor in most species, but tracking of first spring migration is more tenable. Working in the wintering sites of migratory birds allows the deployment of

geolocators on hatch-year birds before their first spring migration and makes it possible to do field tests of hypotheses related to navigation and orientation of juvenile versus adult migratory birds. As expected, Wood Thrushes tracked on their first spring migration departed later from the tropics and arrived later to breeding sites than adults (Stanley et al. 2012); however, the details of juvenile versus adult migration tracks (including stopover behavior, flight speed or rate, and migratory route) have yet to be examined using geolocators.

Ecological correlates of major stopovers and intratropical movements.—Now that multiple winter sites and prolonged stopovers have been documented in many species (Table 1), hypotheses related to the causes and consequences of these behaviors can be tested. Renfrew et al. (2013) provided direct evidence that large-scale intratropical movements of Bobolinks corresponded to changes in primary productivity within their non-breeding range. Heckscher et al. (2011) noted potential links among seasonal rainfall, flooding, and intratropical movement of Veeries and speculated that individuals may respond to this predictable seasonal change in resources. Stach et al. (2012) found a positive correlation between rainfall and intratropical movement of Thrush Nightingales, which suggests that birds are tracking high-quality habitat or food resources as they relocate throughout the winter. It has been proposed that rainfall may explain wintering movements of an austral migrant, the Fork-tailed Flycatcher (Jahn et al. 2013b), and of the Neotropical migrants Eastern and Western kingbirds (Jahn et al. 2013a). These hypotheses are testable by comparing weather patterns and bird movements using online tools provided by Movebank (see Acknowledgments; Bridge et al. 2011, Kranstauber et al. 2011). The utility of this database was illustrated by a comparison of Northern Wheatear movements with wind and air pressure (Schmaljohann et al. 2012b). Future studies should consider the advantages of Movebank, which include long-term data storage and spatial analysis capabilities, as well as making tracking data available to the public for educational or research purposes. Thus, Movebank can facilitate collaborative studies to test hypotheses regarding interspecific and geographic differences in migration strategy.

Åkesson et al. (2012) noted a large westward detour in the spring migration route of Common Swifts tracked using geolocators; they hypothesized that this detour capitalized on the emergence of insect prey in a small area of Liberia before the birds crossed the Sahara desert. An index of food availability in Northwest Africa (vegetation greenness) did not explain autumn stopovers in Common Redstarts (Kristensen et al. 2013). Other long stopover areas may be important sites for molt (Barry et al. 2009, Jahn et al. 2013a). Macdonald et al. (2012) proposed that long spring stopovers in Snow Buntings may be “muster” points where birds gather to forage in large groups to reduce predation by migrating Peregrine Falcons (*Falco peregrinus*). As with multiple winter sites, understanding the environmental and behavioral correlates of major stopovers for migratory birds will inform conservation and management strategies for migratory species and will require on-the-ground studies at these newly identified sites to assess food supply, extent of molt, and predation risk.

Geolocators as a conservation tool.—As connectivity maps are developed for more species, it will be important to model the effects of these spatial connections and patterns in habitat loss (or other threats) on population dynamics (Taylor and Norris 2010).

Direct tracking and associated migratory-connectivity mapping can also allow us to determine connections between breeding population trends and distant habitat use in the non-breeding season to test hypotheses that relate population decline to non-breeding habitat (e.g., Fraser et al. 2012). Webster et al. (2002) predicted that birds with strong connectivity would be more vulnerable to climate change than those with weak connectivity patterns because they are likely to contain little genetic variation, reducing their ability to undergo an evolutionary response to a warmer climate. Strong connectivity also increases vulnerability of species to habitat loss and environmental change on the wintering grounds because populations connected to areas with high rates of winter habitat loss will have relatively few individuals arriving from other intact wintering sites to buffer breeding populations from severe declines (Marra et al. 2006). For the first time, geolocators allow links between populations to be mapped so that demographics (e.g., breeding success and survival) can be measured at the breeding and wintering grounds of the same population to understand what drives population dynamics and to take conservation action at both breeding and wintering sites of the same population.

The biannual migrations of small landbirds are thought to be the most “risky” part of the annual cycle; in one species, mark-recapture data estimated that 85% of annual adult mortality occurred during migration (Sillett and Holmes 2002). Understanding where mortality occurs during migration, and why, is a critical conservation need. Geolocators cannot provide information on birds that do not survive migration, but birds that survive provide data on where and when individuals migrate and which areas are migration bottlenecks. For example, many Wood Thrushes enter the United States in spring through a very narrow range of longitude near coastal Louisiana (Stutchbury et al. 2009, Stanley et al. 2012), which suggests that this site is important for conservation of this declining species. All 10 Red-eyed Vireos tracked by Callo et al. (2013) also made landfall in this small area of Louisiana, and Tree Swallows (*Tachycineta bicolor*) from three widely separated breeding populations also shared a long stopover in this region (Laughlin et al. 2013). We can also now compare migration routes of widely separated populations and quantify the severity and nature of threats (e.g., urbanization, habitat loss, communication towers, wind turbines, and pesticide application). For example, a crucial staging area for Bobolinks, identified using geolocators, coincides with an area in northern Venezuela where seed-eating birds have been intentionally poisoned (Renfrew et al. 2013). We can also test whether migration distance is positively correlated with mortality, as is often assumed (Faaborg et al. 2010a, Taylor and Norris 2010).

CONCLUSION

A new era of bird migration research has been launched with the use of miniaturized geolocators. The newest geolocators are small enough (0.5 g), in theory, to be deployed safely on large warblers, so the taxonomic scope of migration data is broadening each year. Despite small sample sizes, geolocators have already changed major assumptions about migratory connectivity, migration routes, non-breeding sites, and migration timing. For example, a sample size of six geolocator returns for the Common Swift revealed more information about migration and non-breeding sites for this species than 100 years of bird banding (Åkesson et al. 2012).

Researchers should be encouraged that many of the hypotheses now testable using geolocators will also be applicable to studies using other direct-tracking technology. Aside from providing new testable hypotheses and fascinating questions, data from geolocators have provided a breakthrough for conservation of declining long-distance migratory birds. Until recently, conservation of migratory landbirds was limited by the “black box” of the migration period (Faaborg et al. 2010a). Now managers have an excellent tool for determining year-round habitat requirements of vulnerable species (e.g., Beason et al. 2012, Macdonald et al. 2012) and for testing hypotheses related to threats during the non-breeding season (Fraser et al. 2012).

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