VERSITA

Estimating geolocator accuracy for a migratory songbird using live ground-truthing in tropical forest

Abstract

Miniaturized light-level geolocators allow year-round tracking of small migratory birds, but most studies use calibration only at breeding sites to estimate geographic positions. Ground-truthing of positions in tropical habitat is needed to determine how accurate breeding site calibrations (i.e. sun elevations) are for estimating location of winter sites. We tested the accuracy of geographic assignments using geolocator data collected from Wood Thrushes (*Hylocichla mustelina*) in Central America. For a given light threshold, sun elevation angle was higher in the tropics than at breeding sites and also varied significantly at tropical winter sites between wet (Oct-Dec) and dry (Jan-Mar) seasons. However, estimation of Wood Thrush territory latitude did not differ significantly when using breeding or tropical dry season sun elevation. Average error in assignment to tropical sites was 365 ± 97 km (0.2-4.4°) in latitude. To obtain the best latitude estimates in the tropics with geolocators, we recommend using locations during the dry season where sun elevations are closer to those measured at breeding sites. We emphasize the importance of longitude in assigning forest birds to unknown sites; longitude estimates for Wood Thrushes in the tropics were, on average, within 66 ± 13 km (0-0.6°) of actual longitude. Latitude estimates were more accurate (180 ± 48 km) when assigning birds to breeding sites using deployments of geolocators in the tropics. Studies of species that are territorial in winter could collect more accurate migratory connectivity data by deploying geolocators at tropical wintering sites.

Emily A. McKinnon[1]*,
Calandra Q. Stanley[1],
Kevin C. Fraser[1],
Maggie M. MacPherson[1],
Garth Casbourn[1],

Peter P. Marra[2],
Colin E. Studds[3],
Nora Diggs[2],
Bridget J. M. Stutchbury[1]

[1]Dept. of Biology, York University,
4700 Keele St., Toronto, Ontario,
Canada, M3J 1P3

[2]Smithsonian Conservation Biology Institute,
Migratory Bird Center, National Zoological
Park, Washington, D.C., USA, 20008

[3]ARC Centre of Excellence for Environmental
Decisions, the NERP Environmental
Decisions Hub, Centre for Biodiversity
& Conservation Science,
University of Queensland,
Brisbane, Queensland 4072

Introduction

Tracking migration of small (<80g) songbirds has been limited to following small-scale movements using radio-telemetry [e.g., 1] or rare recoveries of banded birds [e.g., 2]. The recent surge in the use of miniaturized light-level geolocators has provided novel information on year-round movements of small, long-distance migratory birds [3-13]. Geolocators detect and archive light levels continually relative to an internal clock; thus, day length and noon/midnight times can be estimated upon retrieval to determine approximate latitude and longitude. Geographic assignments from geolocators are invaluable for determining patterns of migratory connectivity between breeding and wintering populations thousands of kilometres apart [14], identifying stopover regions [15], and informing effective conservation and management across broad spatial and temporal scales [16-18].

Differences in vegetation type, topography, and daily and seasonal weather cause variance in the ambient light levels detected by geolocators, producing error in location estimates [19,20]. Geolocators have been used successfully on birds that inhabit open environments, such as seabirds [21,22], open-country raptors [23], and songbirds [7,12,24]. Increasingly, researchers are deploying geolocators on forest-dwelling songbirds [5,6] and ground-truthing is essential to validate the usefulness of this method. Developing methods for improving geolocator accuracy for forest-dwelling species is important because many of these species are experiencing long-term population declines and geolocators have the potential to be an important tool to inform conservation priorities [25].

The most commonly used method for analysing light data from geolocators is the 'threshold method', in which geolocators must be calibrated at known locations so that the light threshold chosen to define sunrise and sunset can be associated with an accurate sun angle relative to the horizon ('sun elevation'). Latitude assignments using geolocator data are sensitive to

* E-mail: emilymck@yorku.ca

sun elevation because they are based on total day length (i.e. lower sun elevations = relatively longer day length). In contrast, longitude assignments are not sensitive to sun elevation changes. Longitude assignments are determined by the time midway between the sunrise and sunset, relative to an internal clock. As long as the sunrise and sunset are determined by the same light level (threshold), longitude assignments using geolocators are inherently more accurate than latitude assignments.

To date, tests of geolocator accuracy in terrestrial environments have been performed using (1) live deployments on a non-migratory species and assessing accuracy across the year [19], (2) static deployments (i.e., not on live birds) to assess geographic differences in accuracy across a range of sites in Europe [19], (3) static deployments across habitat types on the breeding grounds [20], and (4) comparisons of geolocator accuracy at the breeding grounds using live deployments on species that differ greatly in ecology and behaviour [20]. Most geolocator studies aim to estimate the position of a bird when it is hundreds or, more typically, thousands of kilometres away from the deployment site. A remaining critical gap in our knowledge of geolocator accuracy is the extent to which sun elevation measured at a known breeding site provides a good estimate of location for a bird at its unknown wintering site and vice versa.

Methods for geolocator tracking of long-distance migratory songbirds have been based on calibrations from breeding sites in North America [3,5,6] or Europe [4,19]. Using a breeding-site calibration for sun elevation assumes similar sun elevation angles are encountered during the non-breeding period (during migration and at winter sites). This assumption is typically made for logistical reasons; however, given that bird behaviour, climate, and habitat differ greatly between breeding and non-breeding sites, the sun elevation angles at which a given light threshold is achieved are expected to differ for individuals occupying temperate versus tropical forests.

We calculated sun elevation angles from light data downloaded from geolocators deployed on Wood Thrush (*Hylocichla mustelina*), a long-distance migratory bird that breeds in temperate deciduous forest in eastern North America and migrates to tropical wet forest in Central America. To mimic the assignment of a bird to an unknown location, we estimated latitude for birds during stationary breeding and wintering periods using both the breeding- and winter-derived sun elevations. We then calculated the accuracy of each sun elevation by comparing latitude estimates to the actual latitude. We predicted that tropical forests, which are more heavily shaded than temperate forests, would have significantly higher sun elevation values (i.e. the sun must be higher on the horizon to achieve the same ambient light level) and thus season-specific sun elevations would provide the best accuracy (lowest error) in mapping locations of migratory birds. This study is the first to report ground-truthing of sun elevations for both breeding and wintering sites and to quantify how the use of breeding-ground sun elevations affects accuracy of wintering site latitude estimates.

Methods

We analyzed light data from 59 geolocators (50 model MK14S, and 9 MK10S, British Antarctic Survey - BAS) deployed on birds at five breeding sites (Pennsylvania, North Carolina, Virginia, and Vermont, USA; and in Ontario, Canada) and two winter sites (Belize and Costa Rica) from 2007 to 2011 (see Table 1 for coordinates of sites). We collected light data from geolocators retrieved after bi-annual migrations (n = 43) (i.e., ~ 1 year post-deployment) and from birds that were recaptured within the same summer or winter prior to migration (n = 16) by downloading data without removing the geolocator ('live downloads'). At our main study sites in Pennsylvania, Belize, and Costa Rica, return rates for geolocator-tagged birds (14-38%, depending on site and sex) were higher or equal to return rates for birds that were banded only (BJM Stutchbury, CQ Stanley, and EA McKinnon, *unpubl. data*).

We calculated sun elevations using light data from all individuals captured, including some birds captured in more than one year (Pennsylvania n = 5, Costa Rica n = 2) and 2 birds that had 'live downloads' and were recaptured the following season (Belize n = 2). Samples from the same individual were always from different years (e.g. winter 2010/11 and winter 2011/12), and we therefore treated each as independent.

We examined how average sun elevation changed seasonally within a site due to predictable differences in foliage emergence, bird behaviour, and rainfall. At breeding sites, sun elevation angles were calculated separately for arrival (1-15 May), breeding (Jun-Jul), and moult (15 Aug – 14 Sept) periods, which correspond with vegetation changes as deciduous forests experience leaf-out and as birds become reclusive during moult in late summer and early fall [15,26]. Sun elevation angles were determined for winter sites in Central America from both the

Table 1. *Sun elevation average ± 95% confidence interval from geolocators on birds at breeding sites in North America in July-Aug, and winter sites in Central America during the dry season from Jan-Mar.*

Deployment Site	Lat	Long	n	Live calibration sun elevation
Vermont, USA	44.4	72.9	2	-2.65
Ontario, Canada	43.3	80.5	4	-1.39
Pennsylvania, USA	41.8	79.9	24	-2.10 ± 0.31
Virginia, USA	38.7	77.1	1	-1.90
North Carolina, USA	35.4	83.1	5	-1.98
Breeding site mean			5	-2.01
Belize	16.5	88.7	17	-1.05 ± 0.43
Costa Rica	10.4	84.0	25	-0.04 ± 0.83
Winter site mean			2	-0.55

rainy season (Oct-Dec) and dry season (Jan-Mar) to account for vegetation and weather changes between these two periods. Sample size for each seasonal period varied owing to the deployment date of the geolocator. For example, birds captured and tagged with a geolocator in late March and recaptured in November may not have had any useable light data for the dry season (Jan-Mar); but individuals captured in March with a geolocator from the previous winter had data from both wet season (Oct-Dec) and dry season (Jan-Mar).

All light data were adjusted for clock drift if necessary (1-3 minutes) using the program Decompressor (British Antarctic Survey, BAS). False sunrises and sunsets were deleted (see Supplemental Material Figure S1) and remaining light transitions were scored based on comparisons with light data from open habitat static calibrations (both at breeding and winter sites) using the programs TransEdit (BAS) or TransEdit2 (BAS) (Supplemental Material Figure S2). In open habitat, light data from static calibrations show smooth curves at sunset and sunrise; data from birds that showed a similar smooth curve were scored as high-quality transitions (Figure S2). Data with light peaks prior to the threshold for sunrise or after the threshold for sunset has passed were scored as poor-quality and removed from all analyses.

Changes in geolocator technology since the original deployments in 2007 resulted in our data being collected from a variety of geolocator light-sensitivities and stalk-lengths. In 2010, geolocators were manufactured with a higher light sensitivity and we determined from open habitat calibration that a light threshold of 5 corresponded to a threshold of 16 with the original MK14S geolocators. We tested for an effect of geolocator sensitivity and stalk-length on sun elevations at known sites for these light thresholds and found no significant effect on breeding and winter sun elevations across sites (one-way ANOVA, breeding $F_{1,34} = 2.41$, P = 0.13, winter $F_{1,26} = 0.25$, P = 0.61) or within a single site (Pennsylvania) where four geolocator types were used (one-way ANOVA, $F_{1,22} = 2.17$, P = 0.15). Thus all geolocators were grouped for subsequent analysis.

We calculated sun elevations using the average of all sites rather than the average of all individuals because sample sizes varied across sites and our goal was to obtain a sun elevation that best represented conditions across the breeding or wintering range for Wood Thrush. We did not weight our average using sample size because a single site could have a bias due to topography or habitat that would skew sun elevation in a particular direction [20]. We did not use an individual bird's sun elevation to calculate its later locations because as soon as an individual departs on migration (or its behaviour or habitat changes) sun elevation angle will likely also change. Instead, we calculated average sun elevation for each site using multiple individuals.

To test the accuracy of latitude estimation of known-site birds, we used the program Locator (BAS) to determine latitude for each bird using a given sun elevation. In all analyses, we included both midnight and noon locations to determine average locations since Wood Thrushes are territorial and stationary during

breeding and wintering periods. We calculated latitude and error for each individual's known breeding or wintering site using both breeding- and winter-derived sun elevations. To assign birds to breeding sites, we used locations from the months of June and July since all Wood Thrushes at our Pennsylvania breeding site were stationary at this time (assessed using geolocator data, radio-tracking data, and observation/captures at the sites). We used January and February locations to assign birds to winter sites because all Wood Thrushes from Belize and Costa Rica were stationary during this period (assessed using geolocator data, radio-tracking data, and observation/captures at the sites) and fewer days during this season (dry season) were omitted due to poor quality light transitions.

Relatively close to the equator, geolocators record many latitude outliers because of shorter dawn and dusk twilight periods as well as greater shading in dense tropical forests. We excluded unrealistic latitudes in our winter assignments by filtering latitudes that fell outside the possible winter range for Wood Thrushes (7.2°N to 21.0°N). This filter was not necessary for breeding assignments since all latitudes fell within the Wood Thrush breeding range.

To determine if sun elevation varied within a site, we compared sun elevations using one-way ANOVA (pre-breeding, breeding, or moulting period) or a Student's t-test (rainy vs. dry season in winter). The accuracy (measured in km of error) of assigning birds to known breeding and winter sites using season-specific sun elevations was compared using Student's t-test with sun elevation as the dependent variable. All statistical analyses were conducted using the software R (version 2.14.0, R Development Core Team, R Foundation for Statistical Computing, http://www.r-project.org/) and means are reported ± standard error unless otherwise specified.

Results

Within-season sun elevation differences.-Sun elevations during spring arrival at breeding sites in North America (early May; n = 25, mean -2.31±0.19) and peak breeding (June-July; n = 36, mean -2.03±0.14) periods were significantly different from sun elevation during the moult period (Aug-Sept; n = 37, mean -0.51±0.22) (one-way ANOVA, $F_{2,91} = 27.31$, $P<0.0001$) (Figure 1a). At Central American tropical sites, sun elevations during the rainy season (n = 23, mean 0.81±0.33) were significantly higher than during the dry season (n = 42, mean -0.45±0.28) (t-test, t = -2.94, df = 50.73, P = 0.005) (Figure 1b).

Between-season sun elevation differences.-As expected, sun elevations were higher at tropical forest 'wintering' sites in Central America than at deciduous forest breeding sites in North America (Table 1). Within the tropics, sun elevation angle in secondary rain forest in Belize (~11 year old forest regrowth after hurricane damage) was significantly lower (i.e. less shady environment) than in primary rain forest in Costa Rica (t = -2.12, df = 33.99, P = 0.04; Table 1).

Sun elevation and geolocator error.-When estimating winter locations of birds that received geolocators in Belize and Costa
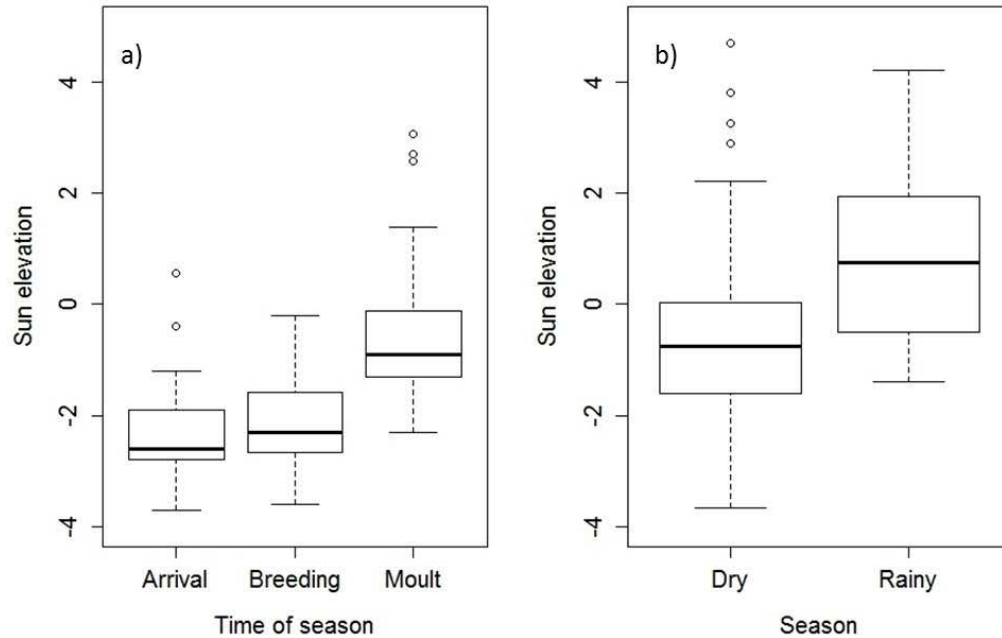
Figure 1. Within-season variation in sun elevation angles at known locations in a) eastern North America (see Table 1 for location coordinates) and b) Central America (Costa Rica and Belize). Arrival = 1-15 May (n = 25 individuals), breeding = 1 Jun - 31 Jul (n = 36), moult = 15 Aug – 14 Sept (n = 37). Dry season = Jan-Mar (n = 42), rainy season = Oct-Dec (n = 23). Mean is indicated by a dark line, and boxes extend to 25th and 75th quartiles, with whiskers extending to maximum and minimum values, and outliers indicated by open circles.

Rica, geolocator error in latitude was similar using breeding (Jun-Jul) and winter dry season sun elevations (t = 0.55, df=46.6, P = 0.58) (Figure 2a, Figure 3) (Table 2). The breeding sun elevation averaged across sites (-2.01) resulted in latitude estimates in the tropics within 0.3° and 4.4° of actual latitude for Belize and Costa Rica, respectively (Table 2). Winter sun elevation calculated from the dry season (-0.55) resulted in latitude estimates that differed on average from actual locations by 2.7° in Belize and 1.5° in Costa Rica. Longitude estimates were highly accurate during the dry season for both wintering sites (average distance error 66 km, 0.6°; Table 2, Figure 3).

Migratory connectivity mapping can also be accomplished by deploying geolocators on the wintering grounds and estimating breeding location. Geolocators were more accurate for estimating breeding site location when the breeding sun elevation, rather than the winter dry season sun elevation, was used. For the Pennsylvania population, the breeding sun elevation (-2.01) resulted in an average latitude 1.2° north of the actual breeding site (Table 2, Figure 3). However, use of winter dry season sun elevation from Belize and Costa Rica doubled the latitude error and over-estimated breeding latitude for the Pennsylvania population by an average of 2.6° (Figure 3) and resulted in a significantly larger average distance error (t = -3.3, df = 43.8, P = 0.002) (Figure 2b).

Regardless of sun elevation angle used, latitude error was higher at Central American sites relative to North American sites. In contrast to latitude, longitude had lower error at Central American sites (Table 2).

Discussion

The use of miniaturized geolocators is providing remarkable new insights into migratory connectivity, migration routes, and within-season movements of songbirds [3-12,15]. Most studies to date have used breeding-site calibrated sun elevations at deployment sites to estimate latitude at unknown locations during the non-breeding season. Our results show that data from geolocators could be used with breeding-ground sun elevation calibration to assign a forest songbird to winter sites in Central America with good accuracy (for Wood Thrushes, within 0.2-4.4° of actual latitude, and within 0-0.6 ° of actual longitude, on average).

Obtaining ground-truthed geolocator data in the tropics is logistically impractical for many species, particularly those that are not territorial in winter or those inhabiting relatively remote regions. Another proposed method for calibrating sun elevation angles without having ground-truthing data is the Hill-Ekstrom calibration [20]. This method relies on the fact that latitude estimates deviate more from true latitude as the equinoxes approach, and by plotting latitude over time using several different sun elevation angles, the sun elevation that causes the smallest deviation in latitude is apparent. However, a major assumption of this method, outlined by [20], is that shading must be equal throughout the stationary period of the bird. Our results show that sun elevation angles differ within stationary periods at both breeding and wintering sites (Figure 1). Sun elevation was significantly higher in the wet season than the dry season in the Neotropics (Figure 1b). Heavy and frequent rainfall during
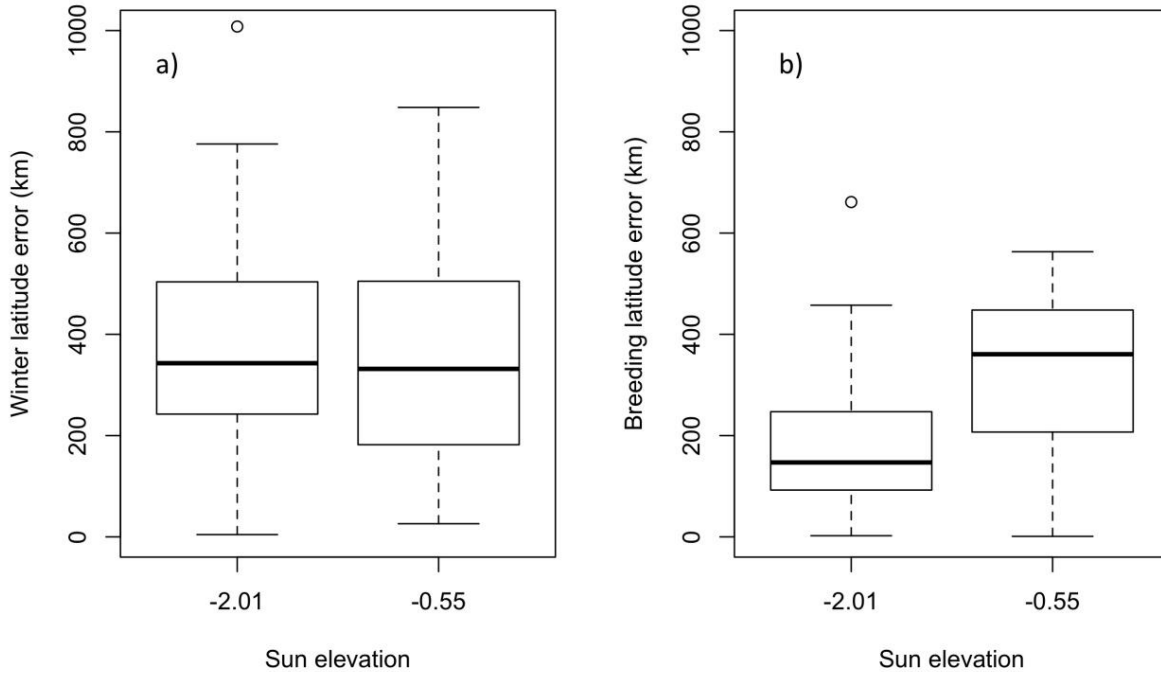
Figure 2. *Latitude error in km from sun elevations derived from breeding habitat (-2.01, n = 5 sites) and dry season wintering habitat (-0.55) for Wood Thrushes at known locations in a) Central American tropical lowland forest (n = 23), and b) eastern North American deciduous forest (n = 35). Mean is indicated by a dark line, and boxes extend to 25th and 75th quartiles, with whiskers extending to maximum and minimum values, and outliers indicated by open circles.*
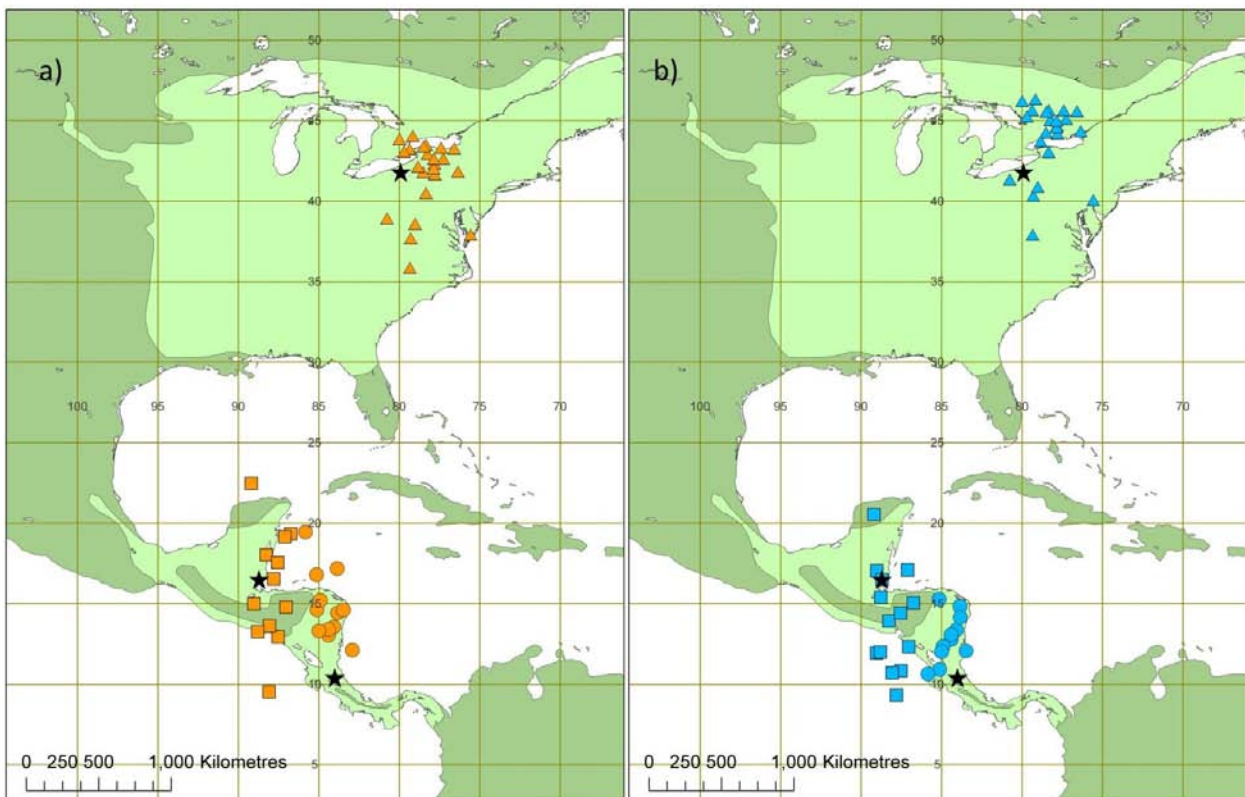

Figure 3. *Geolocator-derived mean locations for breeding (n = 23) and wintering birds (n = 11 Costa Rica, n = 14 Belize) stationary at deployment sites (indicated by black stars) in Pennsylvania, USA (triangles), Belize (squares) and Costa Rica (circles), using two different sun elevation angles: a) breeding sun elevation angle (-2.01), b) winter sun elevation angle (-0.55). Light green shading indicates the breeding and winter range for Wood Thrushes. Maps were generated using ArcGIS 10 (ERSI).*

Table 2. *Estimated locations and error using the breeding season (Jun-Jul; -2.01) versus winter dry season (Jan-Mar; -0.55) sun elevations for Wood Thrushes breeding in Pennsylvania (n = 23) and wintering in Costa Rica (n = 13) and Belize (n = 15). Note that longitude is not affected by sun elevation; thus, only one longitude value is shown per site. Error is calculated by comparing the estimated location from the geolocator with the known location of the bird. Values shown are means and 95% confidence intervals. Blank boxes indicate where values were not applicable.*

Site	Breeding sun elevation (-2.01)		Winter sun elevation (-0.55)		Longitude estimate (°W)	Longitude error (km)
	Latitude Estimate (°N)	Error (km)	Latitude Estimate (°N)	Error (km)		
Belize 16.5°N 88.7°W	16.0±2.0	315±125	13.8±4.1	400±135	88.1±0.4	64±24
Costa Rica 10.4°N 84.0°W	14.8±1.2	491±131	11.95±2.0	327±141	84.0±1.0	67±46
Both winter sites		403±96		365±97		66±13
Pennsylvania 41.8°N 79.9°W	41.6±0.9	188±67	44.3±0.9	344±64	78.3±0.5	105±29

the wet season likely caused higher sun elevation angles owing to cloud cover during dawn and dusk, such that the sun would have to be higher on the horizon to produce the same light levels. Furthermore, vegetation is fuller during the rainy season as plants grow in response to precipitation. Because of these seasonal differences, the Hill-Ekstrom calibration may be more appropriately applied within season to obtain accurate results.

We also found that sun elevation angles varied within the breeding season between early arrival, breeding, and moulting periods. As expected, sun elevation angles were lowest in early May, when fewer leaves on the trees would result in less shading from habitat, and highest in Aug-Sept, when Wood Thrushes begin moult [26]. Many forest-dwelling birds use structurally complex and dense habitats during the post-fledging/moulting period [27], and exhibit cryptic behaviour. Thus, higher sun elevations in Aug-Sept are probably due to both micro-scale habitat selection and behaviour. Data collected from geolocators deployed on European Blackbirds (*Turdus merula*) had larger latitudinal error during the birds' moulting period; this likely reflects similar habitat selection and or cryptic behaviour for this species [19]. For connectivity maps, using only locations from periods matching the calibration period (i.e., June and July) would improve accuracy.

Most studies deploy geolocators on the breeding grounds, and our study suggests that mapping wintering sites during the dry season, when sun elevation is most similar to breeding site calibrations, will give the most accurate winter site latitude. For species that undertake intra-tropical migrations [5,9], mapping locations from the entire non-breeding period is important. Latitude estimates for birds are likely to differ to some extent due to sun elevation over the non-breeding period if the birds experience strong seasonality (wet and dry season) or if they change habitat type. Birds can be confirmed as sedentary during both the wet and dry season using longitude estimates. It is useful to have multiple ways to confirm that birds are stationary versus

migrating; a function in the R package GeoLight ('changelight') can also be used to confirm that birds are stationary [28], although to our knowledge, the analyses in this package have not been ground-truthed.

During both spring and fall migration, longitude can indicate movements and stopovers regions with a high degree of accuracy relative to latitude [7,12,19]. For species that winter in Central America, like the Wood Thrush, longitude alone can distinguish wintering locations of individuals because of the east-west orientation of the land bridge (Figure 3), and relatively high accuracy of longitude estimates in Central America (Table 2). Longitude estimates for birds wintering in Belize versus Costa Rica did not overlap (Figure 3), although latitude estimates did overlap extensively (Table 2).

Although longitude estimates had very low error compared with latitude, micro-scale habitat use differences between sunrise and sunset or local topography can result in bias in longitude estimates. The eastward bias in estimated locations of the Pennsylvania birds (Figure 3) are likely a result of the local topography of the field site- a west-facing slope. A similar eastward bias (although much smaller) can be seen in birds from Belize (Figure 3), and is likely an effect of a slight rise in elevation (west-facing) at the site relative to a local river. Topography can also affect latitude estimates. Individuals with unusually southerly latitude estimates from Pennsylvania or northerly latitude estimates from tropical sites (Figure 3) may have occupied territories on high ridges or in stream valleys where apparent day length would be longer or shorter than day length recorded at ground level.

Relatively few studies deploy geolocators on the wintering grounds, but it also must be determined whether sun elevation at deployment sites is similar to sun elevation in the opposite season. Overall error in latitude assignment for geolocators was much higher at Central American sites (365 ± 97 km 95% CI) than at North American breeding sites (180 ± 48 km). This is due

in part to latitude estimation becoming inherently less accurate toward the equator. In contrast, longitude assignment was more accurate in Central America (66 ± 13 km) than in North America (113 ± 31 km). For long-distance migratory forest birds that shift from temperate to tropical forest, deployment of geolocators in the tropics, when possible, is expected to result in more accurate migratory connectivity mapping for latitude than deployment of geolocators on the breeding grounds. However, return rates of birds in the tropics may be lower than at breeding sites (15-25% for Wood Thrushes, versus 30-60% return rate at breeding sites), because of high mortality rates of first-year birds and lower site fidelity, thus requiring more geolocator deployments to achieve a sufficient sample size in returns.

Geolocators currently provide the most accurate method to remotely assign small (<80g) forest-dwelling landbirds to non-breeding sites in the tropics. Using live calibrations from birds at tropical sites, we show for the first time that sun elevation angles calibrated at breeding sites provided accurate assignment of birds to winter sites. Longitude estimates from geolocators were more accurate than latitude estimates, and therefore geolocators will provide more accurate migratory connectivity information for forest-dwelling birds with an east-west winter distribution. Our results also indicate that for territorial species with good winter return rates, deployment of geolocators in the tropics would result in accurate assignments to breeding sites in temperate areas using a breeding-site calibrated sun elevation.

Acknowledgements

References

[1] Cochran W.W., Wikelski M., Individual migratory tactics of New World Catharus thrushes, In: Greenberg R. and Marra P.P. (Eds.), Birds of Two Worlds, The Johns Hopkins University Press, Baltimore, MA, 2005

[2] Rimmer C.C., McFarland K.P., Known breeding and wintering sites of a Bicknell's Thrush, Wilson Bull., 2001, 113, 234-236.

[3] Stutchbury B.J.M., Tarof S.A., Done T., Gow E., Kramer P.M., Tautin J., et al., Tracking long-distance songbird migration by using geolocators, Science, 2009, 323, 896, doi:10.1126/science.1166664.

[4] Bächler E., Hahn S., Schaub M., Arlettaz R., Jenni L., Fox J.W., et al., Year-round tracking of small trans-saharan migrants using light-level geolocators, PLOS ONE, 2010, 5, 4, doi:e9566 10.1371/journal.pone.0009566.

[5] Heckscher C.M., Taylor S.M., Fox J.W., Afanasyev V., Veery (*Catharus fucescens*) wintering locations, migratory connectivity, and a revision of its winter range using geolocator technology, Auk, 2011, 128, 531-542, doi:10.1525/auk.2011.10280.

[6] Ryder T.B., Fox J.W., Marra P.P., Estimating migratory connectivity of Gray Catbirds (*Dumetella carolinensis*) using geolocator and mark-recapture data Auk, 2011, 128, 448-453, doi:10.1525/auk.2011.11091.

[7] Schmaljohann H., Buchmann M., Fox J.W., Bairlein F., Tracking migration routes and the annual cycle of a trans-Sahara songbird migrant, Behav. Ecol. Sociobiol., 2012, 66, 915-922, doi:10.1007/s00265-012-1340-5.

[8] Seavy N.E., Humple D.L., Cormier R.L., Gardali T., Establishing the breeding provenance of a temperate-wintering North American passerine, the Golden-Crowned Sparrow, using light-level geolocation, PLOS ONE, 2012, 7, doi:e34886 10.1371/journal.pone.0034886.

[9] Stach R., Jakobsson S., Kullberg C., Fransson T., Geolocators reveal three consecutive wintering areas in the thrush nightingale, Animal Migration, 2012, 1, 1-7, doi:10.2478/ami-2012-0001.

[10] Beason J.P., Gunn C., Potter K.M., Sparks R.A., Fox J.W., The northern Black Swift: Migration path and wintering area revealed Wilson J. Ornithol., 2012, 124, 1-8, doi:http://dx.doi.org/10.1676/11-146.1.

[11] Åkesson S., Klaassen R., Holmgren J., Fox J.W., Hedenström A., Migration routes and strategies in a highly aerial migrant, the Common Swift *Apus apus*, revealed by light-level geolocators, PLOS ONE, 2012, 7, e41195, doi:e41195 10.1371/journal.pone.0041195.

[12] Bairlein F., Norris D.R., Nagel R., Bulte M., Voight C.C., Fox J.W., et al., Cross-hemisphere migration of a 25g songbird, Biol. Lett., 2012, 2012, 505-507, doi:10.1098/rsbl.2011.1223.

[13] Delmore K.E., Fox J.W., Irwin D.E., Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators, Proc. R. Soc. B-Biol. Sci., 2012, Published Online 26 Sept, doi:10.1098/rspb.2012.1229.

[14] Fraser K.C., Stutchbury B.J.M., Silverio C., Kramer P.M., Barrow J., Newstead D., et al., Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore, Proc. R. Soc. B-Biol. Sci., 2013, 279, 4901-4906.

[15] Stutchbury B.J.M., Gow E.A., Done T., MacPherson M., Fox J.W., Afanasyev V., Effects of post-breeding moult and energetic condition on timing of songbird migration into the

tropics, Proc. R. Soc. B-Biol. Sci., 2011, 278, 131-137, doi:10.1098/rspb.2010.1220.

[16] Martin T.G., Chades I., Arcese P., Marra P.P., Possingham H.P., Norris D.R., Optimal conservation of migratory species, PLOS ONE, 2007, 2, e751, doi:e751 10.1371/journal. pone.0000751.

[17] Sheehy J., Taylor C.M., McCann K.S., Norris D.R., Optimal conservation planning for migratory animals: integrating demographic information across seasons, Conserv Lett, 2010, 3, 192-202, doi:Doi 10.1111/J.1755-263x.2010.00100.X.

[18] Marra P.P., Hunter D., Perrault A.M., Migratory connectivity and the conservation of migratory animals, Environmental Law. Lewis and Clark., 2011, 41, 317-354.

[19] Fudickar A.M., Wikelski M., Partecke J., Tracking migratory songbirds: accuracy of light-level loggers (geolocators) in forest habitats, Methods in Ecology and Evolution, 2012, 3, 47-52, doi:10.1111/J.2041-210x.2011.00136.X.

[20] Lisovski S., Hewson C.M., Klaassen R.H.G., Korner-Nievergelt F., Kristensen M.W., Hahn S., Geolocation by light: accuracy and precision affected by environmental factors, Methods in Ecology and Evolution, 2012, 3, 603-612, doi:10.1111/j.2041-210X.2012.00185.x.

[21] Harris M.P., Daunt F., Newell M., Phillips R.A., Wanless S., Wintering areas of adult Atlantic puffins *Fratercula arctica* from a North Sea colony as revealed by geolocation technology, Mar Biol, 2010, 157, 827-836, doi:10.1007/s00227-009-1365-0.

[22] Nisbet I.C.T., Mostello C.S., Veit R.R., Fox J.W., Afanasyev V., Migrations and winter quarters of five Common Terns tracked using geolocators, Waterbirds, 2011, 34, 32-39.

[23] Rodriguez A., Negro J.J., Bustamante J., Fox J.W., Afanasyev V., Geolocators map the wintering grounds of threatened Lesser Kestrels in Africa, Divers Distrib, 2009, 15, 1010-1016.

[24] Tøttrup A.P., Klaassen R.H.G., Strandberg R., Thorup K., Kristensen M.W., Jørgensen P.S., et al., The annual cycle of a trans-equatorial Eurasian-African passerine migrant: different spatio-temporal strategies for autumn and spring migration, Proc. R. Soc. B-Biol. Sci., 2012, 279, 1008-1016, doi:Doi 10.1098/Rspb.2011.1323.

[25] Faaborg J., Holmes R.T., Anders A.D., Bildstein K.L., Dugger K.M., Gauthreaux S.A., et al., Conserving migratory land birds in the New World: Do we know enough?, Ecological Applications, 2010, 20, 398-418.

[26] Vega Rivera J.H., McShea W.J., Rappole J.H., Haas C.A., Pattern and chronology of prebasic molt for the Wood Thrush and its relation to reproduction and migration departure, Wilson Bull., 1998, 110, 384-392.

[27] Chandler C.C., King D.I., Chandler R.B., Do mature forest birds prefer early-successional habitat during the post-fledging period?, Forest Ecol Manag, 2012, 264, 1-9, doi:10.1016/j.foreco.2011.09.018.

[28] Lisovski S., Bauer S., Emmenegger T., Analysis of light based geolocator data, 1.02, 2012, CRAN, cran.r-project.org/web/packages/GeoLight/GeoLight.pdf

Supplemental Material:
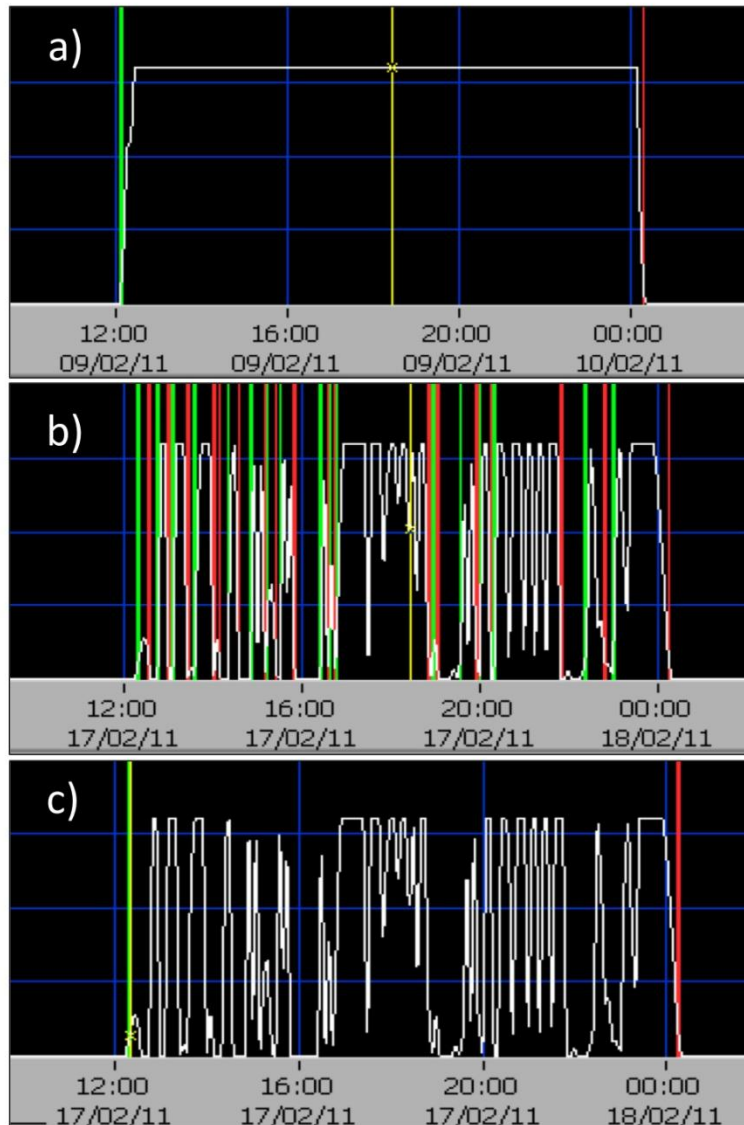# Methods for light analysis for geolocators on Wood Thrushes

Figure S1. *Typical example of a single day of light data from a) stationary geolocator in an open area; and b) and c), a Wood Thrush inhabiting tropical moist forest during the dry season Belize, Central America, shown as screenshots from the light analysis program TransEdit2 (British Antarctic Survey). Each green line indicates an increase in light levels that surpasses the threshold for defining sunrise, and each red line indicates light passing the same threshold, indicating sunset. Stationary geolocators record a single sunrise and sunset (panel a) while geolocators deployed on Wood Thrushes record many false sunrises and sets throughout the day (panel b shows 32 false transitions). These sunrises and sunsets are manually deleted to produce one sunrise and sunset per day, as shown in panel c).*
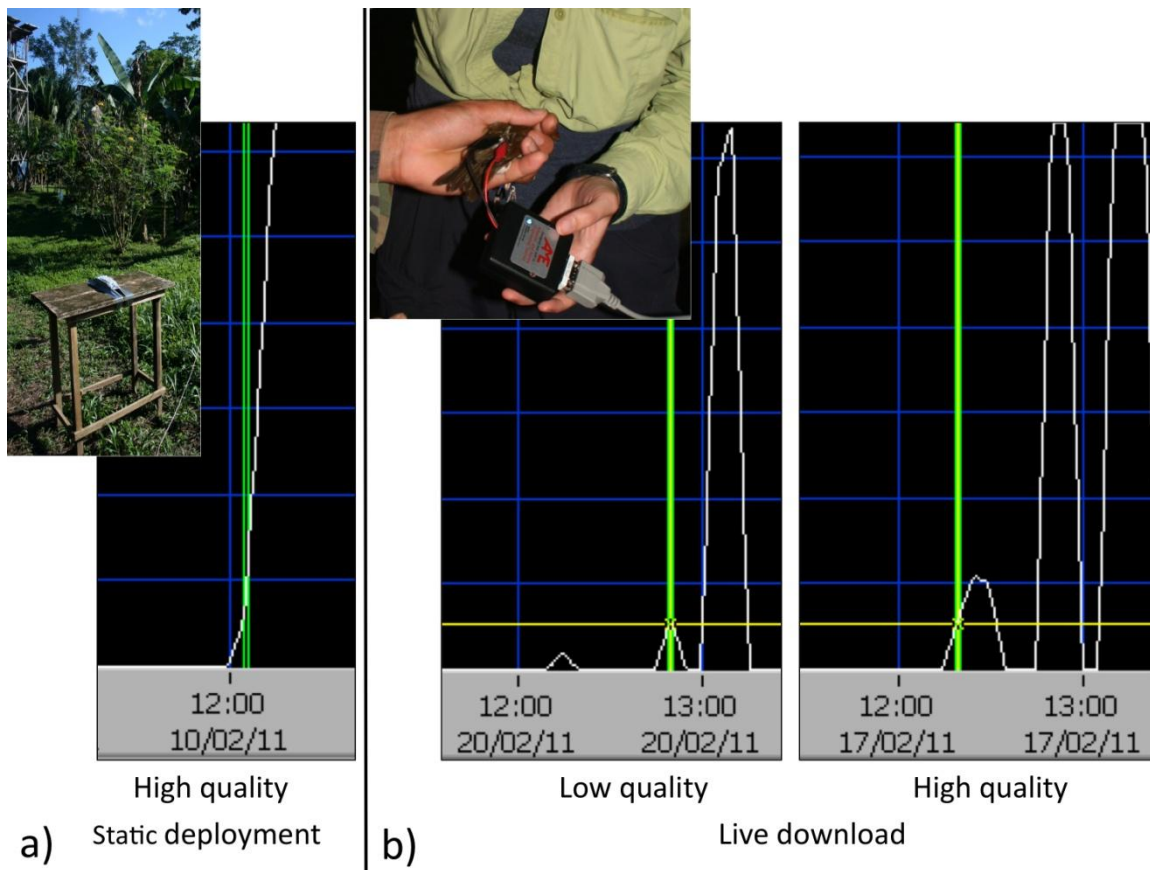
Figure S2. Examples of high and low quality sunrise transitions. Light levels are indicated by white lines; sunrise is indicated by a vertical green line. Panel a) shows a high-quality sunrise transition from static calibration, with inset photo showing geolocators on a table in an open area with full sun exposure; b) shows sunrise transitions from 'live' data downloaded from geolocator deployed on a Wood Thrush in Belize; inset photo shows Wood Thrush with geolocator and attached cables for downloading data without removing geolocator. In the 'low quality' transition in b), a small light peak is present at ca. 12:15 GMT before the threshold for sunrise is reached at ca. 12:50 GMT, about 40 minutes later. This indicates that sunrise must have occurred earlier than when the threshold was reached. In the high quality transition for the same bird a few days earlier (c): the sunrise is ca. 12:15 GMT. Low quality transitions were not used in location analyses. Note that the time of sunrise even in the high quality live download is later than in the static deployment (a; ca. 12:05 GMT), which is why sun elevations calculated from data collected from birds in their natural environment are much higher (i.e. sun must be higher on the horizon to achieve the same light threshold) than those calculated from stationary, open-habitat geolocators.