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Comparing inferences of solar geolocation data against high-precision GPS data: annual movements of a double-tagged black-tailed godwit

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Abstract

Annual routines of migratory birds inferred from archival solar geolocation devices have never before been confirmed using GPS technologies. A female black-tailed godwit *Limosa limosa limosa* captured on the breeding grounds in The Netherlands in 2013 and recaptured in 2014 was outfitted with both an Intigeo geolocator and an UvA-BiTS GPS-tracker. The GPS positions show that, after its breeding season in 2013, the godwit flew 2035 km nonstop from The Netherlands to southern Spain. It then spent the entire nonbreeding season in the southern part of the Iberian Peninsula before returning to The Netherlands the following spring, stopping for 7 days in the delta of the Ebro River in Spain, and again for a day in central Belgium. To compare the geolocation and GPS data, we analysed the geolocation data with two open-source software packages: one using a threshold method (GeoLight) and the other a template-fit approach (FLightR). Estimates using GeoLight, on average, deviated from the individual's true position by 495.5 ± 1031.2 km (great circle distance with equinoxes excluded), while FLightR estimates deviated by 43.3 ± 51.5 km (great circle distance with equinoxes included). Arrival and departure schedules estimated by FLightR were within 12 hours of those determined by the GPS tracker, whereas GeoLight's estimates were less precise. For the analysed track, FLightR represents an improvement over GeoLight; if true for other species and conditions, FLightR will hopefully help establish more precise and accurate uses of geolocation data in tracking studies. To aid future improvements in the analysis of solar geolocation data, we also provide the GPS and geolocation data files together with our R scripts as supplementary material.

Introduction

Technological advances in bird tracking during the last decade have generated many new insights into the migration patterns and geographical distribution of long-distance migratory birds (Gill et al. 2009, Stutchbury et al. 2009, Conklin et al. 2010, Tottrup et al. 2012). Archival solar geolocation devices (hereafter, "geolocators") are currently the lightest and cheapest of these tracking methods. The lightness of geolocators (currently ~0.32 g) allows for the study of annual routines in species for which other tracking devices are too heavy, while their relatively low price enables multi-individual multi-year studies (Senner et al. 2014, McKinnon et al. 2014). These devices do not estimate and log positions, however, but only periodically measure and store light irradiance levels, which leaves the calculation of positions to researchers.

Despite the widespread use of geolocators, the methods developed for the estimation of positions using geolocation-generated data have rarely been ground-truthed; to the best of our knowledge, this has never been done for a migratory bird. The majority of the existing efforts to assess the precision of geolocators placed on birds have come from studies of penguins and albatrosses (Phillips et al. 2004, Shaffer et al. 2005), which found that the average bias of calculated locations was 186 ± 114 km. Despite validating the utility of geolocators for tracking birds, these studies had a number of significant drawbacks: position estimation was done using proprietary software, they included a number of undocumented steps, and the original data are not readily available for reanalysis with currently available software. More recent studies have attempted to improve upon these early efforts by standardizing the analysis process. For instance, Fudickar et al. (2012) placed geolocators on non-migratory European blackbirds, *Turdus merula* in central Europe and estimated the average latitudinal and longitudinal bias of positions during the wintering period at 132 ± 75 km and 50 ± 34 km, respectively. Lisovski et al. (2012a) additionally compared biases among

different species during the breeding season, but reported errors in time, not space. While these two studies are transparent, they still rely on proprietary software and do not make the original data available.

Recently a number of research groups have worked toward the development of open-source software for the analysis of geolocation data in the R computing environment (R Core Team 2015). The first packages to become available — trackit (Nielsen and Sibert 2007) and tripEstimation (Sumner et al. 2009) — were both developed to study marine animals, and the latter has been used to trackbirds as well (Seavy et al. 2012, Contina et al. 2013). More recently, Lisovski et al. (2012b) developed the GeoLight package, which is functionally similar to the BirdTracker/Locator program within the BASTrak suite, which was a proprietary software developed by the British Antarctic Survey. GeoLight is a general program useful for geolocators deployed across avian taxa, and currently the most popular open-source software in the field. Released in 2015 the latest in the line of open-source software is another bird-oriented package — FLightR (Rakhimberdiev et al. 2015). There are therefore at least three packages currently available for the analysis of solar geolocation data. As tripEstimation is in the process of being replaced (S. Lisovski, pers. comm.), we focus here on GeoLight and FLightR.

Despite the newness of the field and the seeming simplicity of geolocation data, both GeoLight and FlightR are complex programs. They also differ considerably from each other in a number of important respects (see Rakhimberdiev et al. 2015 for a more complete review): for example, GeoLight uses a more traditional, 'threshold method' (Hill and Braun 2001), while FLightR uses a 'template fit' (Ekstrom 2004, 2007). The threshold method estimates positions from a single point per twilight period at which the sun irradiance reaches a specified threshold, whereas our implementation of the template fit method uses the slope of the linear regression of the log of 'measured' versus the log of 'expected' light irradiance

during each twilight period. The template fit is therefore less sensitive to variable shading during twilight; i.e., if an individual animal randomly obscures its geolocator during a twilight period, even if just for a brief time, the threshold method might falsely recognize this as either a sunrise or sunset and inaccurately estimate its geographic position. The template fit method does not suffer from such limitations, as it focuses on the pattern of changes in light levels over time and not on their absolute minute-by-minute values.

A second important distinction between the two packages is that FLightR optimizes a hidden Markov model over the entire period during which an individual was tracked. This means two things: First, that FLightR weighs all of the data generated by an individual together to determine the most probable location for an individual on a given day and, second, that it is possible to determine whether or not an individual changed locations between consecutive twilight periods. In contrast, GeoLight calculates each position from two neighbouring twilights, which is only accurate if an individual is assumed to have remained stationary during the intervening period. As a result, both packages are able to provide daily estimates of an individual's position, but only FLightR is able to accompany those positions with credible intervals, which denote the amount of uncertainty surrounding each location even during migration.

Although each new methodology developed has seemingly represented an improvement over previous methodologies, no formal tests have been undertaken to measure these improvements. In an effort to generate a dataset that will allow for the direct testing of both current and future methodologies, we outfitted an individual female black-tailed godwit, *Limosa limosa limosa* (hereafter, "godwit") breeding in The Netherlands with two tracking devices — a high-precision GPS tracker and a geolocator. These two tags enable us to compare the individual's geolocation-generated positions with its "true" positions throughout its annual cycle. Our use of a migratory bird is particularly important, as migration, especially

when it overlaps with an equinox, has represented the weakest component of previous analytical methodologies (Lisovski et al. 2012b). Black-tailed godwits make long-distance migrations during both the spring and fall equinoxes (Hooijmeijer et al. 2013), making them appropriate for the evaluation of any method analysing geolocation data.

Here we present a comparison between the positions recorded by a GPS tracker and an analysis of light level data undertaken with FLightR and GeoLight. We examine whether it is possible to make a spatial and temporal inference of the positions of a migratory animal with current open-source software and compare the relative precision of the two packages. We hope that our analyses and simultaneous publication of the underlying tracking data will provide a baseline for the improvement of future studies making use of geolocation data.

Methods

Study Species

The continental subspecies of the black-tailed godwit breeds predominantly in The Netherlands (Thorup 2004) and spends the nonbreeding season either in West Africa — especially Guinea Bissau and Senegal — or on the Iberian Peninsula, along the southern coasts of Spain and Portugal (Hooijmeijer et al. 2013). Southward migration occurs from late May to late September, while northward migration takes place from early December to early May. Godwits spending the nonbreeding season in West Africa typically migrate northward in two steps, first flying from West Africa to the Iberian Peninsula, where they join the rest of the population and stage for as long as 90 d (Lourenço et al. 2010, Masero et al. 2011), before moving on to The Netherlands as early as the beginning of March (Senner et al. 2015). Between the Iberian Peninsula and The Netherlands, some individuals may make as many as four stops, lasting from 1 – 7 d. Arrival in The Netherlands ranges from early March through the beginning of May (Senner et al. 2015).

Field Efforts

As a part of a larger, ongoing effort to monitor godwit migration, we placed Intigeo C65 1.0 g
geolocators (produced by Migrate Technology Ltd, UK) on 182 adult godwits from 2009 –
2015 and high-precision 7.2 g UvA-BiTS GPS trackers (The University of Amsterdam;
Bouten et al. 2013) on 21 individuals in 2013. Five females were outfitted with both a
geolocator and tracker; one of these returned and was recaptured (B3RLLL). On all
individuals, geolocators were attached to a flag placed on the tibia along with two other rings,
while the GPS tracker was attached using a leg-loop harness made of 2 mm nylon rope (see
Senner et al. 2015 for more details). Combined, the rings, geolocator, harness, and GPS
tracker weighed ~12 g, representing ~3.6% of an individual's mass at the time of initial
capture. B3RLLL was first captured on 27 May 2013 while incubating eggs in the Haanmeer
Polder (52.9226º N, 5.4336º E) and recaptured the following year on 11 Jun 2014 while
incubating eggs in the neighbouring Gellehuister Polder (52.9297º N, 5.4278º E). In both
years, B3RLLL successfully hatched her eggs, but the chicks did not survive until fledging
(N.R. Senner unpubl. data).

GPS Data

UvA-BiTS GPS trackers provide a flexible, accurate, and relatively precise system with
which to track the movements of migratory animals (Bouten et al. 2013). Locations are
typically accurate to within ± 5 m of an individual's true position. Once deployed, the device
can transmit previously collected data or receive new settings when they are within ~1 km of
a base station or related receiving device. However, once a device is out of range of a base
station, it is impossible to either download data or upload new settings, and the individual's
locations are stored until the tracker is again within range of a receiving device. We therefore
employed different data collection settings for different portions of the godwit annual cycle.
During the 2013 breeding season, when individuals were within range of our base station,

trackers recorded an individual's position once every 5-10 min depending on its battery

charge; during the rest of the year, trackers collected position data once every 15-30 min

depending on charge. Because they are charged by solar panels, UvA-BiTS trackers can

occasionally experience gaps in the data resulting from poor weather or feather-shading. The

data of B3RLLL, however, exhibited no such gaps. Complete GPS data are available as

Supplementary Materials A1 (also available at

https://raw.githubusercontent.com/eldarrak/FLightR/master/examples/Black-

Tailed_Godwit_JAB_example/A1_GPS_positions.csv) and the raw geolocator ".lux" file as

A2 (also available at

https://raw.githubusercontent.com/eldarrak/FLightR/master/examples/Black-

Tailed_Godwit_JAB_example/A2_raw_data.lux).

Analysis

The first step in our analysis of the geolocation data was to detect and truth the twilights. This

step was done in the BAStag R package (Wotherspoon et al. 2013). We chose a light

threshold value of 1.5 and used this value to automatically demarcate all sunrises and sunsets.

This step was followed by a visual inspection of each individual sunrise and sunset identified

by BAStag. Twilight periods exhibiting non-random changes in shading were excluded. For

instance, when the geolocator was strongly shaded during the beginning of a twilight period

and then quickly transitioned to full light at the end of the period or *vice versa*. [The rule of

thumb is to exclude twilights that have a strongly biased slope of light over time.] Following

the completion of the visual assessment of each twilight period, the annotated light data were

input into both GeoLight (ver. 2.01) and FLightR (ver. 0.3.6). The BAStag output is available

as Supplementary Materials file A3 (also available at

https://raw.githubusercontent.com/eldarrak/FLightR/master/examples/Black-

Tailed_Godwit_JAB_example/A3_TAGS_format.csv) and the R script explaining the

workflow in the BAStag package as Supplementary Materials file A4 (also available at

https://github.com/eldarrak/FLightR/blob/master/examples/Black-

Tailed_Godwit_JAB_example/A4_BAStag_routine.Rmd).

For analyses with both GeoLight and FLightR, we used the period from tag attachment

on 16 June to 5 July 2013 as a calibration period, as B3RLLL was known to be near her

breeding territory in southwest Friesland throughout this time (< 20 km from 52.93ºN,

5.43ºE). An additional calibration period from 5 to 15 of May 2014 was used for FLightR,

when B3RLLL was again on the breeding grounds. Using this calibration period, GeoLight

calculated a threshold sun angle of -6.115; this value was then used in all subsequent analyses

with the program. Within FLightR, all analyses were run without land or behavioural masks,

but positions were spatially constrained to the areas between 14ºW – 13ºE and 30 – 57ºN

because of their biological plausibility (Hooijmeijer et al. 2013, Senner et al. 2015). We also

limited the maximum flight distance between twilights to 1500 km. Finally, we optimised the

FLightR model with 1 million particles and without an automated outlier exclusion. The

detailed script for the GeoLight analysis can be found in Supplementary Materials file A5

(also available at https://github.com/eldarrak/FLightR/blob/master/examples/Black-

Tailed_Godwit_JAB_example/A5_GeoLight_analysis.Rmd) and for FLightR in A6

(https://github.com/eldarrak/FLightR/blob/master/examples/Black-

Tailed_Godwit_JAB_example/A6_FLightR_analysis.Rmd).

To compare the GPS track with GeoLight- and FLightR-based reconstructions we

linearly interpolated GPS positions to the time of midday (midnight) for GeoLight and

twilight time for FLightR. We then separately calculated the deviation and bias of estimated

positions. We calculated the deviation by taking the mean great circle distance between each

pair of estimated geolocation positions and GPS locations (Phillips et al. 2004). Monthly

biases of estimates were calculated separately for latitude and longitude as the mean and

standard deviation of the shift (in degrees) of the estimated positions from the corresponding GPS locations and then converted to kilometres (based on Fudickar et al. 2012). As solar geolocation is often used to determine an individual's wintering grounds we also estimated the mean and median positions for the entire wintering period.

In addition to estimating an individual's position, we also estimated migratory arrival and departure dates throughout B3RLLL's annual cycle. In FLightR, tests of such temporal and spatial hypotheses are simple, as FLightR generates each position's posterior probability as a distribution of 1×10^6 particles over a spatial grid. We estimated median arrival and departure dates for each site by determining the date by which half of the particles (5×10^5) crossed an arbitrary specified spatial boundary (for The Netherlands, we chose the boundary of 2° East and for Spain, 5° West). In GeoLight we used the `changeLight` and then `mergeSites` functions to estimate B3RLLL's migratory schedule. `changeLight` works independently from those GeoLight functions estimating an individual's position by searching for dates on which there were likely changes in the timing of either dawn or dusk (see Lisovski et al. 2012b for details and Supplementary Materials file A5 for the parameters used in the current analysis); `mergeSites` is a new GeoLight function that combines an individual's estimated positions with schedule.

Results

Migratory Movements

B3RLLL was captured on 27 May 2013 and her nest hatched on 3 June. She subsequently stayed within 1 km of her nest (likely indicating that her chicks were alive) until 12 June. From 12 June until 9 July, B3RLLL remained within 20 km of her nest; from 9 July until 25 August, she moved around the province of Friesland, never flying more than 30 km at any one time. On 25 August at 16:30 h local time, B3RLLL flew non-stop for 30.75 h and 2035 km to

her nonbreeding grounds in Spain. Having arrived in southern Spain, B3RLLL then spent the entire nonbreeding season (26 August – 21 April) along the southern coast of Portugal and Spain. During that time, she ranged between Sanlúcar de Barrameda, Spain, in the east (36.98ºN, 6.26ºW), and Faro, Portugal in the west (37.06ºN, 7.75ºW), with the majority of the period spent near Ayamonte, Spain (37.22ºN, 7.43ºW). On 21 April 2014 at around 20:45 h local time, she began migrating northward. After an initial flight of 815 km, on 22 Apr at around 10:00 h in the morning, she stopped for 7 d in the Ebro River Delta of northeast Spain. From there on 29 Apr 19:30 h local time she moved 1144 km northwards to central Belgium (50.95ºN, 2.83ºE), where she stopped over for 1 d before arriving at her breeding grounds in The Netherlands on 5 May. She was recaptured on 11 Jun while incubating a nest in the Gellehuister Polder (52.93°N, 5.43°E).

Comparison of Software Packages

Both packages successfully reconstructed the general shape of the annual routine of B3RLLL (Figs. 1, 2). Positions estimated by GeoLight had an average deviation of 495.5 ± 1031.2 km (SD, great circle distance, excluding equinoxes) from those measured by the GPS tracker, while positions estimated by FLightR had an average deviation of 43.3 ± 51.5 km (including equinoxes; Table 1). Both packages estimated longitude better than latitude, with maximum error occurring around the equinoxes and during active migration. GeoLight's longitudinal and latitudinal precision was -8.69 ± 28.13 km and -237.59 ± 1116.37 km respectively, while for FLightR it was -8.01 ± 168.3 and -18.84 ± 57.34 km. The location of B3RLLL's wintering site was estimated well, with both GeoLight and FLightR (Table 2). GeoLight's `mergeSites` function finds stationary periods and estimates the best possible location during these periods. This function greatly improved GeoLight's estimates of wintering site location (Table 2). Additionally, because FLightR provides spatially explicit credible intervals, we were able to estimate the match between actual GPS positions and the

corresponding credible intervals. For longitude, 76.9% of the GPS points were within the 95% modelled credible intervals and 67.6% within 50%. For latitude, 92.3% of the GPS points were within 95% CI and 78% within 50% CI.

Comparison of B3RLLL's real migration schedule with its estimated schedule from geolocation data also validated the utility of both packages for this type of analysis. Both GeoLight (with the `mergeSites` function) and FLightR correctly distinguished among breeding, wintering, and stopover sites. GeoLight then estimated the departure from the Netherlands 4 d earlier, arrival to Spain 1 d earlier, departure from Spain 2 d earlier and arrival to the Netherlands 1 d later than the real events. The schedules estimated with FLightR, on the other hand, were precise to within a few hours (Fig. 3).

Discussion

We provide here the first direct verification of two open-source software packages recently developed for the analysis of geolocation data using data detailing the annual routine of an individual black-tailed godwit carrying both a geolocator and a high-precision GPS tracker. Both software packages accurately estimated the majority of the individual's migratory schedule. Our results using GeoLight (Table 1) have similar biases to those of Fudickar et al. (2012) for geolocators placed on non-migratory birds. However, the FLightR package outperformed GeoLight and provided more accurate results. FLightR thus represents a step forward in analyses of geolocation data on migratory animals. We also make both the GPS and geolocator data publically available, providing a baseline against which future developments in the analysis of geolocation data can be measured.

Geolocator Precision

Although both GeoLight and FlightR represent a significant improvement over previous programs used to analyse geolocation data, they nonetheless remain relatively imprecise estimators of a migratory organism's true position. This is especially true with respect to latitudinal position estimates: on average GeoLight estimates differed by almost 500 km from GPS positions, while FLightR estimates were off by 43 km. In the periods surrounding the equinoxes, these inaccuracies were further exacerbated. As such, GeoLight does not even calculate latitudinal positions for approximately 10 days before and after each equinox (the length of these periods depends upon the calibration angle used), while FLightR positions had their highest levels of uncertainty during this period. Longitudinal position estimates are more accurate in both GeoLight and FLightR, but especially FLightR. Nonetheless, some short-distance movements are, at this point, simply indistinguishable using geolocation data. For instance, B3RLLL flew 150 km south of The Netherlands for one day during the breeding season and neither GeoLight nor FLightR identified this movement. Although these movements were mainly along an east-west axis, which should be more readily identifiable using geolocation data, the distances travelled were within the uncertainty range for both packages. Estimation of B3RLLL's wintering site, however, worked well (Table 2). This was likely a result of the fact that B3RLLL remained at a single location for several months. If B3RLLL were to have moved more frequently during this period, we would expect the precision of the location estimates to have been lower.

GeoLight and FLightR are repeatable and transparent, but they are still somewhat subjective. For example, we argue that a manual check of every twilight period, followed by the exclusion of those periods with a strong change in shading during the twilight period, is highly recommended for every dataset. This step is inherently subjective. Nonetheless, all of our exclusions are recorded in the output, and therefore remain available for reassessment. We hope that it will be possible to automate this step in the future.

One of the strengths of geolocation data, however, is its ability to identify the timing of movements within an individual's annual cycle. While such inferences have been drawn before (e.g., Senner et al. 2014), FLightR refines and improves the transparency and accuracy of these efforts. FLightR now provides the ability to assign departure probabilities to each day of the year as well as an estimate of the direction flown at take-off and the actual distance covered between twilight periods. In the case of B3RLLL, FLightR accurately identified the probable timing of arrivals and departures as having taken place within a few hours of the actual events (Fig. 3). GeoLight can generally also infer the migration schedules. For the current track GeoLight identified schedules with a precision of ± a few days (Fig. 3).

The Future of Geolocation Analysis

The key to a successful research program is a study design that maximizes the strengths and minimizes the weaknesses of its data. In the case of geolocation data, this means it is necessary to decide beforehand on the importance of latitudinal information to the questions being asked. For instance, determining the locations used by a species that migrates in a straight line along a north-south axis, and especially along a north-south coastline, may be difficult (e.g., western sandpipers, *Calidris mauri*; Warnock and Bishop 1998). On the other hand, for species such as godwits — for which each site used throughout the annual cycle differs not only in latitude, but also longitude — determining an individual's position on a given day can be done with a relatively high degree of confidence. More generally, studies focused on the timing of movements, and not the geographic location of individuals, will have the strongest power of inference using geolocation data.

The field of geolocation is still in active development, and this means that currently existing methods are likely to be improved upon and new, more precise, methods will appear

in the near future. Therefore we strongly recommend making the underlying geolocation data associated with any publication available online. After subsequent reanalysis, the conclusions made in the original articles are not likely to change, but more biological details may be inferred from the same data using the new analytical techniques. Geolocation data may currently be stored for free at Movebank (www.movebank.org, Kranstauber et al. 2011), but other less specialized archiving repositories are also available.

Conclusions

Despite the popularity of geolocators for the study of animal movement, their precision has rarely been calibrated on live animals, and never before for a migratory bird (Fudickar et al. 2012, Lisovski et al. 2012b). As a result, there remain significant concerns about the precision and accuracy of geolocation data, potentially calling into question the validity of recent studies. Our findings here show that, with the aid of the recently developed open-source software packages GeoLight and FLightR, it is possible to precisely monitor the timing of migratory movements and, with an increasing level of certainty, geographic locations of migratory animals throughout their annual cycles. While we realize that approaches to the analysis of geolocation data other than those illustrated here do exist (e.g., trackit and TripEstimation), we believe that our analysis is at the forefront of the field and represents what is currently possible. Nonetheless, we welcome reanalysis of our data and hope that our dataset will help to develop and validate new approaches for analysing geolocation data that will shift geolocation studies towards more quantitative and transparent frontiers.

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Supplementary material (Appendix JAV-00891 at <www.oikosoffice.lu.se/appendix>).

Appendix 1–6.

Table 1. Average monthly biases and standard deviations (in km) estimated by GeoLight and FLightR for a black-tailed godwit carrying both an archival geolocation tracking device and high-precision GPS tracker. Calibration was done using twilights from the period 16 June – 5 Jul 2013, and for the FLightR also from 5 to 15 May 2014.

Month	Longitude					Latitude					Notes
		GeoLight		FLightR			GeoLight		FLightR		
	Truth	Mean bias	SD	Mean bias	SD	Truth	Mean bias	SD	Mean bias	SD	
1	-7.4	-15	78.8	-16.7	24	37.2	-23.8	295.5	-31.7	74.8	
2	-7.4	-19.4	99	7.5	2.1	37.2	95.8	538.4	-15.1	29.1	
3	-7.4	7.9	60.6	4.9	1.7	37.2	-1282.3	2318.7	12.5	3.7	Equinox
4	-5.2	-20.1	90.3	13.5	30.6	38.2	-197.1	398	-10.8	56.6	Migration
5	4.9	-17.7	69	7.6	53.6	52.5	-98.9	171.3	-42.7	84.6	Migration
6	5.4	-5.7	70.3	-13.9	2.7	52.9	-59.2	95.4	18.7	2.5	
7	5.4	-0.5	97.2	-13.4	6.6	53	47.4	130.9	4.5	11.3	
8	3.9	-5.4	107.7	-17.3	37.1	50.6	-47.3	175.3	-32.5	70.3	Migration
9	-7.4	-3.9	61.1	6.8	3.8	37.2	-844.3	2400.4	-9.6	10.3	Equinox
10	-7.4	-20.9	54.2	5.8	2.4	37.2	-248.6	1162.9	-12.6	5.7	
11	-7.4	-10.4	58.6	-29.6	35.5	37.2	-128.9	214.2	-102	88.4	
12	-7.4	0.5	60.3	-42.9	0.8	37.2	-101.5	208.8	3.3	4.6	

[1]Note that GeoLight excludes unreliable values close to equinox.

Table 2. Bias in wintering location estimation, means and medians of estimated locations and GPS points for a black-tailed godwit carrying both an archival geolocation tracking device and high-precision GPS tracker over the period from 27 Aug 2013 to 20 Apr 2014.

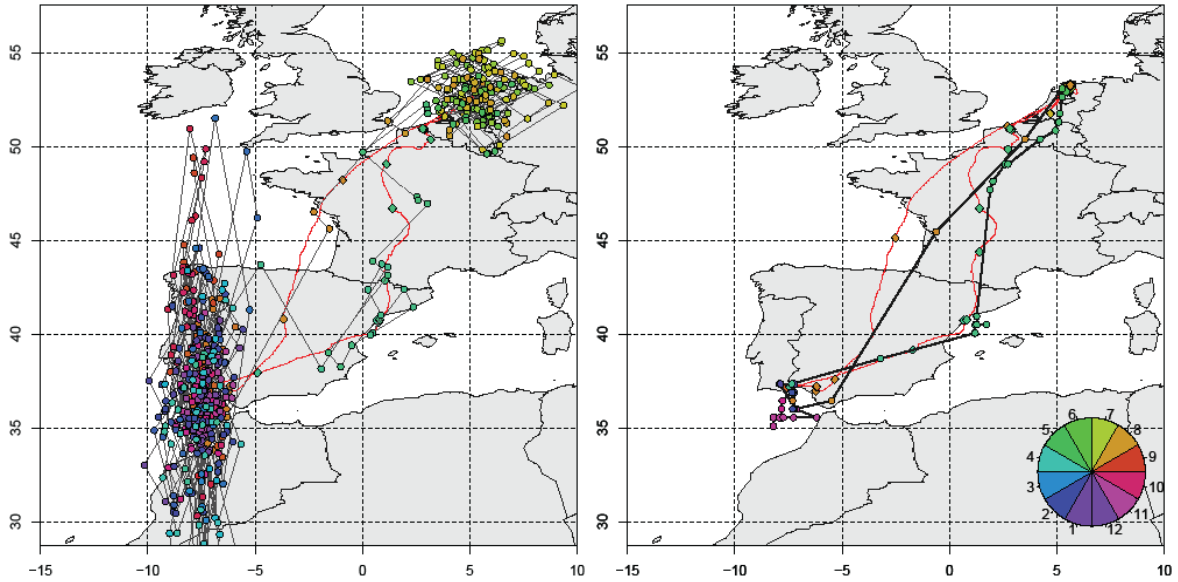|	GeoLight	FLightR
Mean of Latitude, km	332.49	27.37
Median of Latitude, km	103.67	15.16
Mean of Longitude, km	10.12	9.3
Median of Longitude, km	6.53	4.27
Mean of Latitude with mergeSites(), km	49.75	
Mean of Longitude with mergeSites(), km	6.77	

Figure 1. The track of a black-tailed godwit as estimated from 5-min fixing interval solar geolocation data by GeoLight (left panel) and FlightR (right panel) in comparison with GPS positions (red line). Estimated midday and midnight positions for GeoLight and medians of twilight positions for FLightR with the corresponding GPS positions are coloured by month of a year. Note that no spatial or behavioural masks were used in FLightR, so positions were allowed to occur anywhere in Europe and Northern Africa.
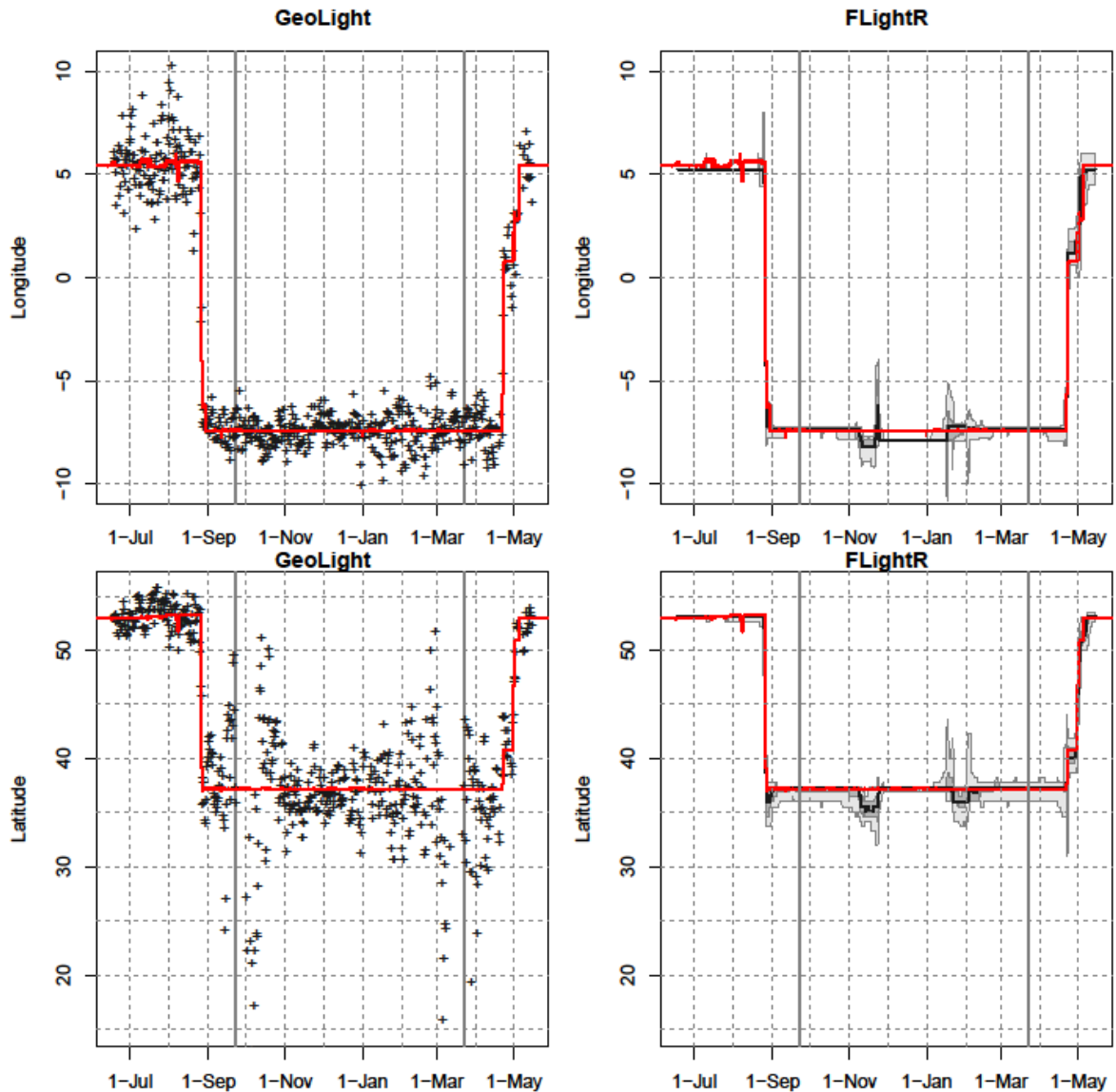
Figure 2. Longitudes (upper panels) and latitudes (lower panels) estimated by GeoLight (left panels) and FLightR (right panels) in comparison with GPS positions (red lines) of a track of a black-tailed godwit as estimated from 5-min fixing interval solar geolocation data. For FLightR the medians of twilight positions are shown with accompanying quartile ranges and 95% credible intervals. Note absence of the latitudinal positions from GeoLight during the equinoxes (shown by grey vertical lines).
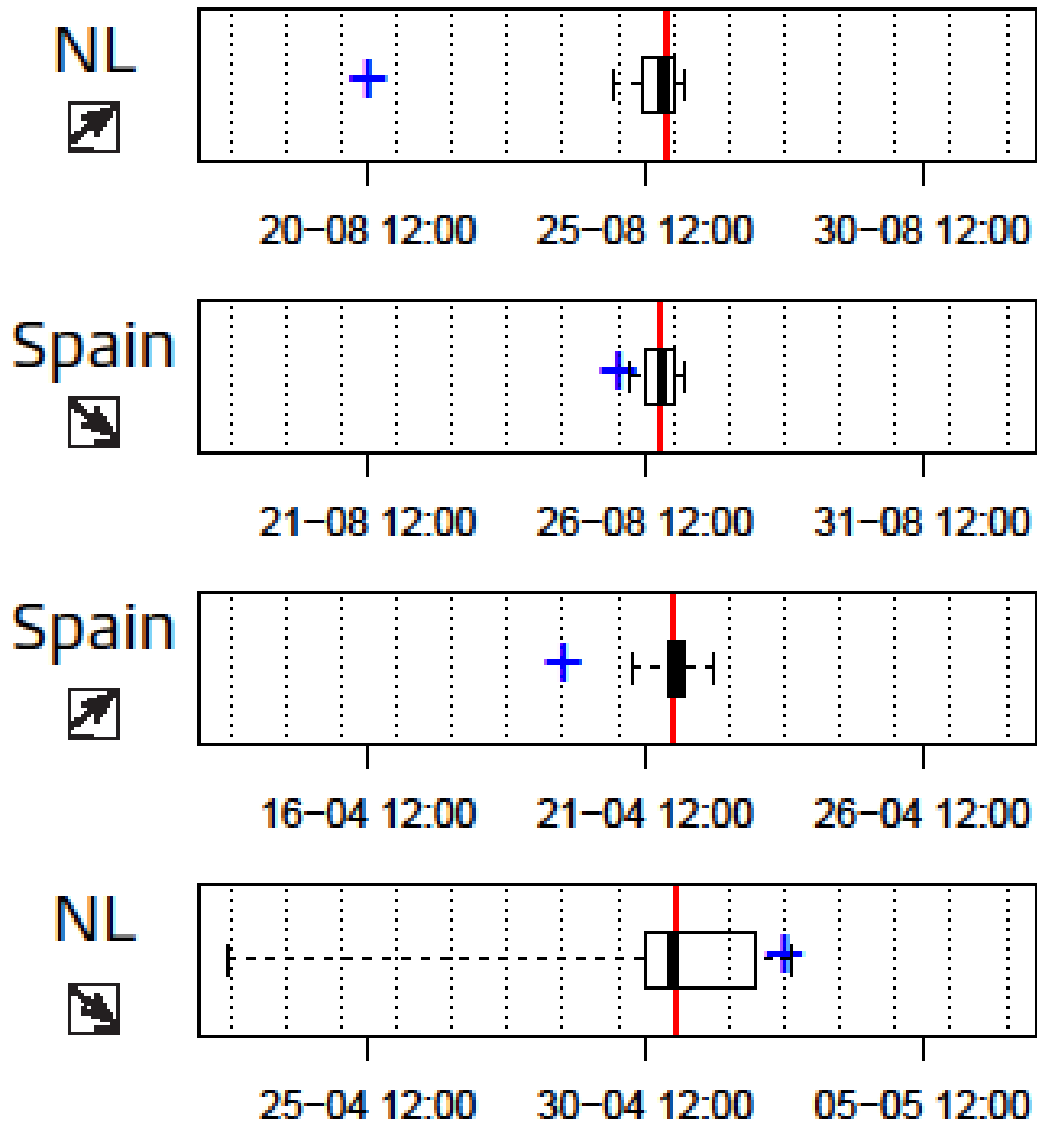
Figure 3. Departure and arrival timing of a black-tailed godwit as estimated by GeoLight (blue crosses) and FLightR (medians, quartiles and 95% credible intervals are shown with lines, boxes and whiskers respectively) in comparison with GPS-measured departure and arrival timing (red lines).