

Light-level geolocator analyses: A user's guide

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Abstract

1. Light-level geolocator tags use ambient light recordings to estimate the whereabouts of an individual over the time it carried the device. Over the past decade, these tags have emerged as an important tool and have been used extensively for tracking animal migrations, most commonly small birds.
2. Analysing geolocator data can be daunting to new and experienced scientists alike. Over the past decades, several methods with fundamental differences in the analytical approach have been developed to cope with the various caveats and the often complicated data.
3. Here, we explain the concepts behind the analyses of geolocator data and provide a practical guide for the common steps encompassing most analyses – annotation of twilights, calibration, estimating and refining locations, and extraction of movement patterns – describing good practices and common pitfalls for each step.
4. We discuss criteria for deciding whether or not geolocators can answer proposed research questions, provide guidance in choosing an appropriate analysis method and introduce key features of the newest open-source analysis tools.
5. We provide advice for how to interpret and report results, highlighting parameters that should be reported in publications and included in data archiving.
6. Finally, we introduce a comprehensive supplementary online manual that applies the concepts to several datasets, demonstrates the use of open-source analysis

tools with step-by-step instructions and code and details our recommendations for interpreting, reporting and archiving.

KEYWORDS

animal tracking, archival tags, FLIGHTR, GeoLight, Movebank, probGLS, SGAT, solar geolocation

1 | INTRODUCTION

Light-level data loggers, or geolocators, have been used to track animals since the early 1990s (Wilson, Ducamp, Rees, Culik, & Niekamp, 1992) but it has been the advent of lightweight devices some 10 years later that made this technology a tremendous success story. Their weight (<0.5 g) and relatively low cost compared, for example, to satellite transmitters have made them applicable in large numbers to animals weighing as little as 10 g (Bridge et al., 2011). Although the use of geolocators comes with obvious ethical and logistical challenges, such as the potential impact on the animal (Brlik et al., 2019) and the need to retrieve the device, these devices have been applied to thousands of animals to answer a diverse range of questions relating to migration patterns (Briedis et al., 2019; Finch, Butler, Franco, & Cresswell, 2017; Stutchbury et al., 2009), species–habitat relationships (e.g. MacPherson et al., 2018), identification of breeding locations (Johnson et al., 2010; Lisovski, Gosbell, Hassell, & Minton, 2016), delineation of wintering distributions (Bracey et al., 2018; Egevang et al., 2010), migration stopover behaviour (Salewski et al., 2013; Yamaura et al., 2017) and general migration strategies (Briedis et al., 2019; Knight et al., 2018). Light-level geolocation has already provided unprecedented insights into migratory behaviour and annual movements of animals (McKinnon & Love, 2018) and will continue to do so in the future.

The fundamental underlying principle of light-level geolocators is to estimate geographic locations from patterns of ambient light, allowing researchers to infer the general location and movement patterns of an individual over the time it carried the device. A fundamental but often unrecognized challenge is the translation of light levels into geographic locations. The simplest geocator analysis derives latitude from day length and longitude from solar noon, which is relatively straightforward (Hill, 1994). Less obvious is how to minimize and estimate errors in location data caused by variability and ambiguity in the light data that originate from a variety of causes, including weather, habitat, behaviour and time of year (for detailed description on the accuracy and precision of geocator estimates see: Fudickar, Wikelski, & Partecke, 2012; Lisovski et al., 2012; Merkel et al., 2016; Phillips, Silk, Croxall, Afanasyev, & Briggs, 2004; Rakhimberdiev et al., 2016; Shaffer et al., 2005). Researchers regularly struggle with the analytical steps to obtain, interpret and present location estimates.

Over the last decade, a range of tools have been developed to analyse geocator data. Choosing the right tools, performing a scientifically sound analysis and presenting the results in a transparent

manner requires a thorough understanding of the concepts behind geolocation and the methodological differences between the available tools. We aim to (a) describe the concepts and provide practical guidelines for the general procedure of analysing geocator data, (b) outline key criteria for matching research questions to appropriate analysis and tools and (c) highlight the most important limitations and pitfalls of geocator analyses and discuss how to address them. As an additional aid, we provide a comprehensive supplementary online manual that includes example data and code for state of the art analyses, examples of common problems and their solutions, and details our guidelines for interpretation, reporting and archiving.

2 | FROM LIGHT-LEVEL RECORDINGS TO LOCATION ESTIMATES: GENERAL METHODS

Methods of light-level geolocation can be classified into threshold methods and curve-fitting methods (also known as “template-fit methods”; Figure 1).

Threshold methods produce a single location based on the estimated times of two successive twilights events, that is, the times at which the recorded light level crosses a predetermined threshold. Standard astronomical formulae then determine the position of terminator at these two times. In astronomical terms, *the terminator* is the transition between the illuminated (day) and non-illuminated (night) faces of the planet. Assuming the tag has been stationary in the intervening period, it must be located at the intersection of these two curves (Figure 1a). By considering the alternating sequence of sunrise/sunset and sunset/sunrise pairs, two locations can be estimated per 24 hr.

Curve-fitting methods produce a location estimate from a single twilight. The location of the terminator is derived from the estimated time of twilight, and the location of the tag on the terminator is determined by the rate of change in light level during the twilight period, that is, the interval of rapidly increasing/decreasing light (Figure 1b). Although the Earth itself revolves at a constant rate, simple geometry requires that the speed at which the terminator passes over the Earth's surface is greater at low latitudes than at high latitudes. Consequently, variation in the rate of illumination change can be used to locate the tag along the terminator.

Independent of method, twilight times and periods are a focal point of geocator analyses. Defining discrete twilight events – sunrise and sunset times – from raw light recordings (“twilight

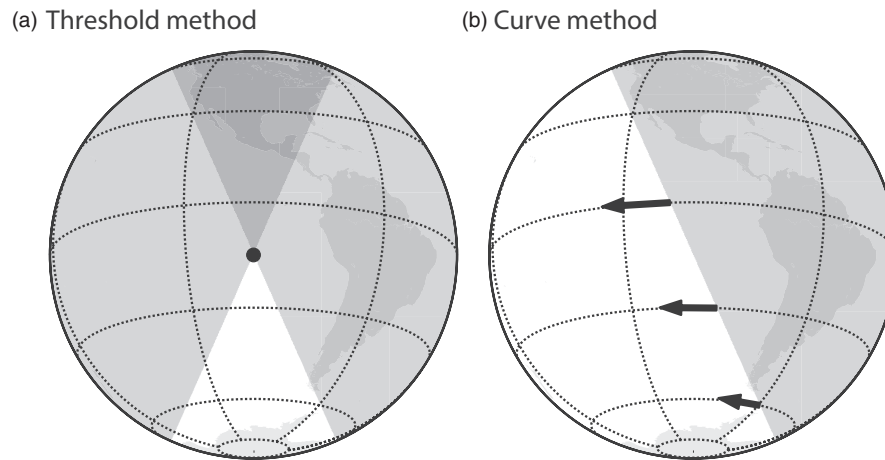


FIGURE 1 The principle behind location estimates from light recordings. Two broad methods exist, the threshold method and the curve method. Any observer experiencing a twilight must be located on the terminator—the boundary between the illuminated and the non-illuminated surface of the Earth. The threshold method (a) produces a single location for two successive twilights estimated via the times at which the recorded light level crosses a predetermined threshold. The curve-fitting method (b) produces a location for a single twilight based on the position of the terminator and the rate of change in light levels. This rate of change varies with latitude, as indicated by the arrows (arrow size is roughly proportional to rate of change)

annotation”) is, therefore, the first important step for all analyses. Once twilight times are defined, one can obtain quick but crude location estimates and apply more sophisticated modelling approaches to refine these initial location estimates. Particularly for the latter, a diverse range of analytical tools has been developed in recent years.

3 | WHAT DETERMINES THE CHOICE OF TOOLS FOR MY ANALYSIS?

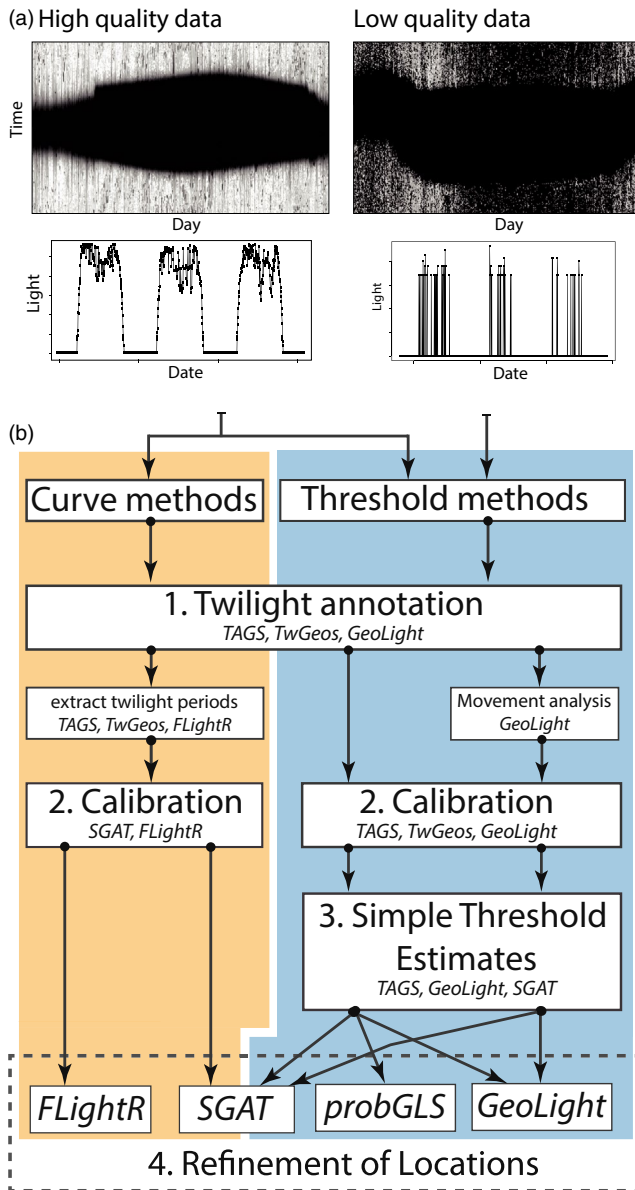
We here recommend a suite of six frequently used open-source tools, for geolocator analyses and discuss their requirements in terms of data quality, user experience and computing power: the online platform TAGS (https://tags.shinyapps.io/tags_shiny), the R packages *TwGeos* (Lisovski, Sumner, & Wotherspoon, 2015), *GeoLight* (Lisovski & Hahn, 2012), *probGLS* (Merkel et al., 2016), *SGAT* (Wotherspoon, Sumner, & Lisovski, 2013a) and *FlightR* (Rakhimberdiev, Saveliev, Piersma, & Karagicheva, 2017). We omit three other open-source R packages *Ukfss* (Nielsen, Bigelow, Musyl, & Sibert, 2006), *Trackit* (Nielsen & Sibert, 2007) and *PolarGeolocation* (Lisovski, 2018), as the first two are specialized tools for analysis of fish movements and the last one addresses a relatively specific problem of estimating locations during polar summer under 24-hr daylight.

No tool or method should be considered a silver bullet for the analysis of geolocator data. The choice of analysis method will ultimately depend on the overall research question, the type of tag used, the life history and behaviour of the animals studied, and researchers' available time and experience. For instance, is the user looking for coarse estimates of breeding and non-breeding locations or finer-scale stopover locations and durations? Is the animal living in dense forests where shading is expected to be high during some periods of the year?

In the following section, we discuss these trade-offs based on the different analysis steps needed and the availability and limitations of methods for each step (Figure 2 and Table 1). In addition, there are important considerations to take into account before using geolocators in an animal movement study. For example, light-level geolocators cannot be used to answer research questions about movements less than ~200 km, because these movements are less than the typical error of all methods (Lisovski et al., 2012). Similarly, if an animal mainly moves latitudinally during the periods around the equinoxes, when location error is largest, estimating migration routes and stopover sites for these animals is hardly or not possible, though breeding or non-breeding ranges can still be estimated (Briedis et al., 2016). Thus, there are limitations to the use of geolocators to answer questions about migratory animals that cannot be overcome by even the most sophisticated analysis and should, therefore, be considered prior to the beginning of any study.

The open-source tools that are currently available implement the steps of light-level geolocation analysis in slightly different ways (Figure 2b, Table 1). For example, the first step for analysing light-level data is to annotate the twilight events (**step 1**) that can be done in TAGS, *TwGeos* and *GeoLight*. For curve-fitting methods implemented in *TwGeos* and *FlightR*, one should use the twilight events predefined in one of the above-mentioned packages to extract twilight periods from raw light-level data using functions in *FLightR* or *TwGeos*. Calibration functions (**step 2**) are included in all tools except SGAT. Methods to estimate locations (**step 3**), refine these estimates (**step 4**) and extract movement patterns (**step 5**) are implemented in *GeoLight*, *probGLS*, SGAT and *FLightR*. In sum, these tools are as follows:

- TAGS is an online platform that allows users to upload raw light-level data, annotate twilights, perform calibration and perform a simple threshold-based analysis. Although most steps are based on *GeoLight*, the advantage of this tool is a graphical user interface



to visualize the raw light-level recordings with different zoom options, fast processing and a user-friendly interface that does not require users to write code.

- The R package *TwGeos* provides tools to import raw light-level recordings from various tags, a set of functions to plot and investigate the raw data, and an interactive interface for twilight annotation and extraction of twilight times and twilight periods.
- The R package *GeoLight* provides simple threshold-based location estimates and movement analysis. Grouped methods, which provide single location estimates with uncertainty based on a series of twilight times during stationary behaviour, have recently been included (Hiemer, Salewski, Fiedler, Hahn, & Lisovski, 2018; and supplementary online manual Chapter 5 "Movement analysis").
- The R package *probGLS* uses iterative probability sampling to estimate numerous trajectories based on threshold-based twilight

FIGURE 2 Example of high- and low-quality data (a). The quality can be affected by many factors such as the sensitivity of the sensor, the tag settings (recording frequency), the individual's behavior and the habitat (ground dwelling vs. open landscape species), as well as by weather and topography. The left high-quality data was recorded on a black-tailed godwit using a logging interval of 5 minutes and a sensor that is able to resolve the entire light range (data from Rakhimberdiev et al., 2016). The right low-quality data has been recorded on a Common Rosefinch (*Carpodacus erythrinus*) with a recording interval of 10 minutes and a sensor that only resolves dim light values (early/late sunrise/sunset times). The major difference is that there are clear sunrise and sunset times in the high-quality data, which record more than 5 readings during the twilight periods (unpublished data). These periods are not resolved in the low-quality data due to the longer interval between recordings and presence of light values of zero even during the day, probably due to heavy shading caused by trees and shrubs at the non-breeding location. The quality of the data is a major determinant for the method and the tool that can be used for the analysis (b). While curve methods require good quality data around twilight and at least a couple of recordings during the increasing and decreasing light, threshold methods can deal with (almost) all data with a clear difference between night and day. The flowchart shows subsequent steps and available analysis tools for each

events and additional inputs such as the twilight error, movement and spatial masks. These can be used to derive a most likely track and location-specific uncertainties (see supplementary online manual Chapter 6 for example of a Brünnich's guillemot (*Uria lomvia*) track).

- The R package *SGAT* uses a metropolis sampling process to create Markov chain Monte Carlo simulation of movement trajectories (Sumner, Wotherspoon, & Hindell, 2009). Both threshold and curve methods can be implemented, and location estimates are refined using a twilight and movement model as well as a spatial mask.
- The R package *FLightR* uses the curve method and a particle filter to estimate actual movement. Its starting point is the spatially explicit likelihood for each twilight, which is calculated based on the value and the variation of the slope of observed versus expected light intensities during the calibration period, when geographic location of a tag is known. Using a movement model and a spatial mask, the particle filter gradually progresses through the spatially explicit likelihoods in time, weighing possible movement trajectories to derive a probability distribution, which can ultimately be used to calculate the median track and its credible intervals (Rakhimberdiev et al., 2015).

4 | ANALYSING LIGHT-LEVEL GEOLOCATOR DATA

4.1 | Step 1: Twilight annotation

Defining twilight events typically requires a light intensity threshold. The time when light levels exceed this threshold in the morning and

TABLE 1 A brief characterization of six open-source tools for the analysis of geolocator data

	TAGS	TwGeos*	GeoLight	probGLS	SGAT**	FLightR
Software capability						
1. Twilight annotation						
Define twilight events	✓	✓	✓			
Extract twilight periods	✓	✓				✓
2. Calibration						
Threshold method	✓	✓	✓	✓		
Curve method		✓			✓	✓
3. Location estimation						
Method (Threshold/Curve)	T		T	T	T/C	C
Uncertainty estimates			(✓)	✓	✓	✓
4. Refinement of locations						
Grouped Analysis***			✓		✓	
Track optimization				Probability sampling	MCMC	Particle filter
Inputs: Twilight error				✓	✓	✓
Movement model				✓	✓	✓
Spatial mask			✓	✓	✓	✓
5. Movement analysis						
Movement versus Residency			✓			✓
Requirements						
Data quality						
Tolerance to shading			•••	••	••	•
Minimum recording frequency			1/10 min	1/10 min	1/10 min	1/5 min****
Full light range required						✓
Coding experience			••	••	•••	•
Calculation time (track estimation)			Minutes	Minutes	Minutes	Hours

Note: The tools differ in which analytical steps they cover, complexity and requirements as to data quality and researcher experience (see text for detail).

*based on *BAStag* (Wotherspoon, Sumner, & Lisovski, 2013b) with extra functionalities.

**further development of the R package *tripEstimation* (Sumner et al., 2009).

***Single location estimates for stationary periods (series of twilight events).

****In some cases, notably under low shading, FLightR can deal with 1/10 min frequency.

fall below it in the evening are defined as sunrise and sunset, respectively. Although these **twilight events** are the sole parameters used for the threshold method, they are also used as an intermediate step to calculate **twilight periods** to apply curve-fitting methods. During this first step of the analysis, we strongly recommend taking the time to visually review the raw light data to identify parts of the time series that might be strongly affected by shading (Figure 2a; due to, for example, feather growth, monsoons or breeding behaviour) and to identify data gaps or light recording errors associated with device malfunction. Becoming familiar with the data provides a rough idea of the overall data quality and which methods are feasible (see Figure 2 and Table 1). The online platform TAGS and the R package TwGeos provide the most convenient procedures to define twilight

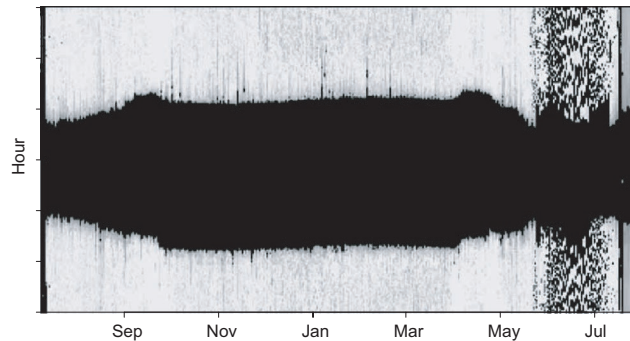
events. Both TAGS and TwGeos allow interactive visualization and editing of twilight events. In addition, they keep track of user actions and thus document the choice of twilight events (or their exclusion) for repeatability.

Two frequent questions troubling researchers are (a) what is a good threshold? and (b) should one edit potentially false twilight times? Regarding the threshold, one should choose the lowest value that is consistently above noise in the night-time light levels. It is important to realize that any threshold is tag- and species-specific. The prospect of editing twilight is a far more sensitive issue. There are procedures in TAGS and TwGeos that automatically determine twilight events (see Box 1 and Chapter 4 in the supplementary online manual). However, shading during the twilight periods may lead to

BOX 1 Annotating twilight times using the R package TwGeos

The function `lightImage` provides an overview plot of light data recorded (data: European bee-eater, see supplementary online manual Chapter 1).

```
library(TwGeos)
raw <- readMTlux(`LightRecordings.lux`)
offset = 12 # the offset for the vertical axis in hours.
lightImage(raw, offset = offset, zlim = 12)
```

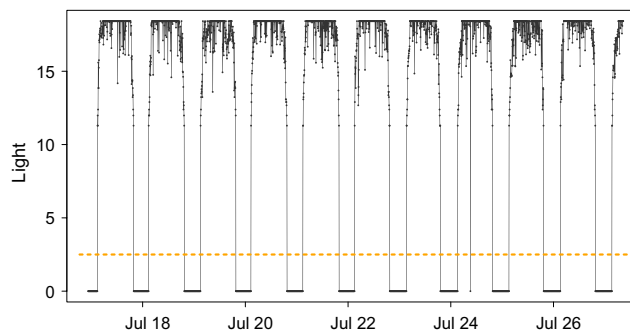


In this plot, each day is represented by a thin horizontal line that plots light values as grayscale pixels (dark = low light and white = maximum light).

```
threshold <- 2.5 # slightly above night recordings
twl <- preprocessLight(raw, threshold=threshold, offset=offset)
```

To visualize the quality of the data (e.g. clean light transitions during the twilight times) and to define a light-level threshold we can plot parts of the light recordings.

```
with(raw[2000:5000,], plot(Date, Light))
abline(h=threshold, col="grey80", lty = 2, lwd = 2)
```



a time series wherein the light values cross the threshold multiple times during a short period of time, and automated processes may pick the wrong sunrise/sunset time. One has the option here of adjusting or deleting such twilight events. We recommend a conservative approach to editing, meaning that it is better to have some noise in the dataset than to erroneously remove good data points or informative data that might convey rapid long-distance movements. Also, the criteria for editing or removing poorly classified twilights will depend on the method that is further used to infer locations. During periods of limited movement, for curve-fitting methods, day-to-day consistency in the shape of the curve around sunrise or sunset is

most important, while for threshold methods the day-to-day consistency in the twilight events is important (Figure 3).

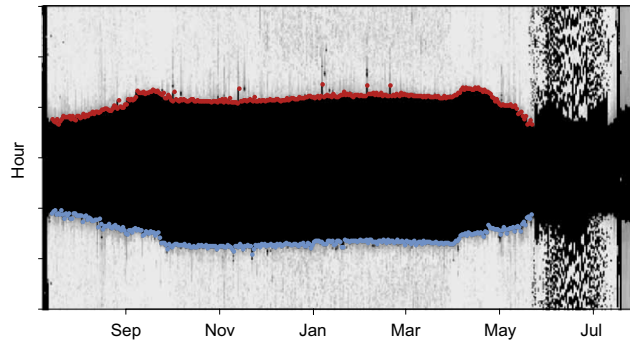
4.2 | Step 2: Calibration

Geolocators vary in the way they measure light and other information. Most importantly, tags can have different data logging schedules and (arbitrary) units for light-level data. Therefore, calibration is needed to relate observed and expected light levels. This procedure is the most important step in any geolocator analysis as it accounts for two types of errors: (a) the device-specific accuracy to measure true

BOX 1 (Continued)

We can call the interactive process to define twilight times using the function `preprocessLight` (see supplementary material for details). Finally, we can plot the sunrise and sunset times into the light image:

```
lightImage( tagdata = raw, offset = offset, zlim = 12)
tsimagePoints(twl$Twilight, offset = offset, pch = 16, cex = 1.2,
col = ifelse(twl$Deleted, "grey20", ifelse(twl$Rise, "firebrick", "cornflowerblue")))
```



And extract the twilight periods using the function `extractCrepuscular`.

Detailed explanation on how to annotate twilight, common pitfalls and best practice recommendations are available in supplementary online manual Chapter 4.

light intensities and (b) the level of shading an animal experienced in its typical habitat and performing its typical behaviour. To this end, a period is often selected when the animal was at a known location in its preferred habitat for at least a couple of weeks, for example, at the site of deployment, and light levels recorded during this period are compared to those expected for the known location. For the “threshold method”, the calibration process determines a single best reference sun elevation angle, which is the position of the sun (e.g. 5 degrees below the horizon) during the twilight events across all calibration recordings. Note that some analyses (e.g. SGAT) require zenith angle, defined as the angle from the zenith, instead of sun elevation angle which is the angle of the sun in relation to the horizon. For the “curve-fitting method”, the calibration provides the slope of recorded versus expected change in light during the twilight periods.

Given the importance of calibration, it is crucial to plan the study, for example deployment timing, to ensure that geolocator recordings include an appropriate calibration period at a known location. Such a calibration is best performed as “in-habitat calibration”, wherein the device is attached to the animal to be tracked while it is in its typical environment. This form of calibration accounts for the influence of behaviour and habitat on data quality and might be particularly useful for species that live in shaded habitats or those whose behaviour leads to frequent shading. In reality, however, many birds are tagged during the breeding period, where behaviour and habitat may differ from the rest of the annual cycle. For example, birds may use nest boxes resulting in misdetections of the true time of sunrise or sunset, causing the light pattern recorded in the breeding season to be different from the light pattern recorded throughout the rest of the year, when the

bird is not using a nest box (Meier et al., 2018). Though the breeding location may therefore not be qualified as “typical” behaviour, in many cases it will be the only known location for the tagged bird that can be used to calibrate the data. If cavity or burrow nesting is apparent in the tagged bird, it is not recommended to use this nesting period for calibration. Similarly, when geolocators are mounted on the leg, this may also introduce shading events during the calibration period, for example when the legs are covered or submerged.

To account for such sources of error, the calibration can potentially be done using recordings of a short period after the nesting while individuals remain at the breeding location. However, if calibration of geolocators on animals is not possible, as an alternative or in addition to an “in-habitat” calibration, it is recommended to perform a “rooftop calibration”, where each device is simply placed in a stationary location (e.g. a rooftop), for one or 2 weeks prior to, or after, the deployment. This form of calibration helps to estimate the device-specific inaccuracy. *FlightR* provides an optional process in which calibration can be calculated for stationary periods in unknown locations (supplementary online manual Chapter 8 “Calibration”). For threshold methods, this can also be done using a “Hill-Ekstrom calibration” (Box 3 and supplementary online manual Chapter 5 “Hill-Ekstrom calibration”).

4.3 | Step 3: Simple threshold estimates

After identifying twilight events and performing calibration, the next step is to estimate geographic locations. We recommend starting with a simple procedure based on the threshold-based analysis (see

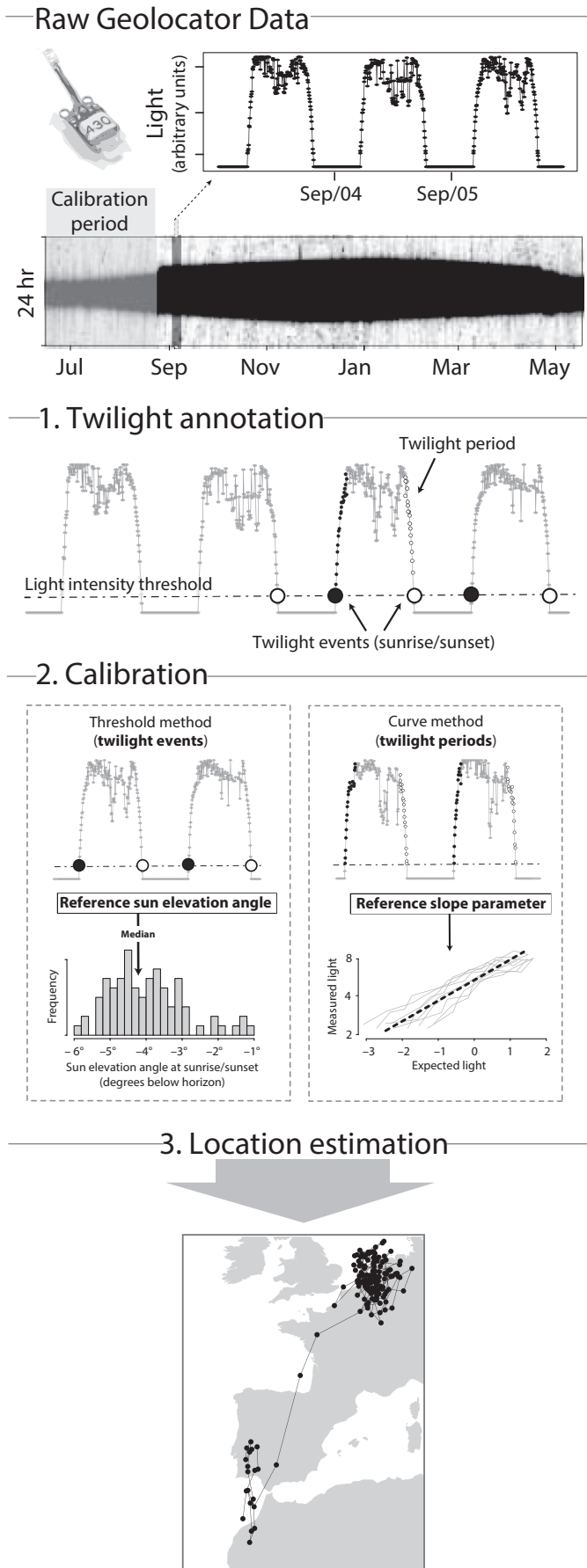


FIGURE 3 A schematic over view of the analytical steps required to translate raw light-level geolocator recordings to simple location estimates. Geolocator record ambient light levels over time (top panel) resulting in a time series of daylight patterns. In an initial step (1), discrete sunrise and sunset times (twilight times) are defined using a light intensity threshold. While these twilight events are used to obtain location estimates with the “threshold method”, twilight periods that follow a sunrise and precede a sunset are used in “curve methods”. Using light recordings from a known location (e.g. after the deployment of the logger), the calibration process (2) establishes the relationship between observed and expected light levels. This calibration provides a reference sun elevation angle for the “threshold method” and a reference slope parameter for the “curve methods” that can then be used to estimate two discrete locations per day. The exemplary data shown have been recorded on a Bar-tailed godwit (*Limosa limosa*) and were described in Rakhimberdiev et al. (2016). Simple location estimates were calculated using the R package *GeoLight*

Box 2 and Figure 2). Even if a more sophisticated analysis is planned, a quick threshold-based analysis provides a first impression of the track and can reveal data-quality issues that may have escaped earlier scrutiny. An initial threshold analysis can also serve as a sanity check for further analysis. It is unlikely that any successive modelling approach will dramatically change the general movement pattern revealed by a simple threshold analysis. In fact, if the modelling does produce dramatically different results, then something went wrong with the analysis (e.g. erroneous calibration, poor movement/behavioural model, inappropriate spatial mask). Finally, a simple threshold-based analysis provides an opportunity to evaluate the influence of the calibration parameters, particularly the reference sun angle. Although experimenting with parameter settings sounds very subjective, we recommend performing several preliminary threshold analyses to evaluate the effects of changes in the reference sun elevation angle on the results/track. For example, the amount of shading experienced by an animal often varies across the tracking period as the habitats used for breeding, stopover and non-breeding may differ in topography, foliage and local weather that can have differentially influence on location estimates during distinct periods. In such cases, going back to the calibration step and applying alternative methods such as the “Hill-Ekstrom calibration” (Lisovski et al., 2012) might be required. See Box 3 and supplementary online manual Chapter 5 (“Hill-Ekstrom calibration”) for examples investigating such issues as well as options that may allow accounting for and even correcting them.

The results of a simple threshold analysis provide a pilot overview, but often show large and unrealistic movements (Box 2) over short time periods due to variable shading. Furthermore, around the equinoxes daylength is similar across the globe, and even small deviations in sunrise or sunset times or slope will result in large spatial errors, particularly in latitude. Therefore, it is often desirable to refine these crude location estimates by incorporating knowledge about the tracked animal, such as its movement capabilities and what habitat (e.g. ocean vs. land) it is likely to use.

Box 2 Simple location estimation using *GeoLight*

Starting with the table that contains the annotated twilight times (see Box 1), we can estimate the reference sun elevation angle. Here, we use a specific range of the recordings, after making sure that the bird has been stationary at the deployment site (51.32°N, 11.96°E) during this period (e.g. breeding time).

First, we export the table into the required *GeoLight* format:

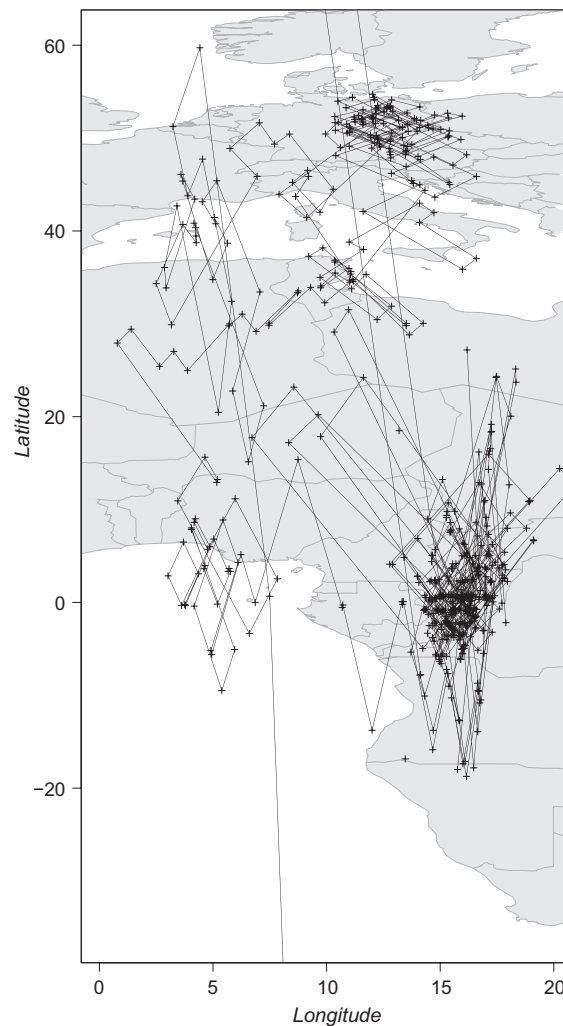
```
library(GeoLight)
twl.gl <- export2GeoLight(twl) # export the table into the required GeoLight format
```

Next, we perform calibration:

```
lon.calib <- 11.96
lat.calib <- 51.32
tm.calib <- as.POSIXct(c("2015-07-20", "2015-08-29"), tz = "GMT")
twl.calib <- subset(twl.gl, tFirst>=tm.calib[1] & tSecond<=tm.calib[2])
gE <- getElevation(twl = twl.calib,
                  known.coord = c(lon.calib, lat.calib))
```

Using the reference zenith angle (93.50°), we can estimate and plot locations:

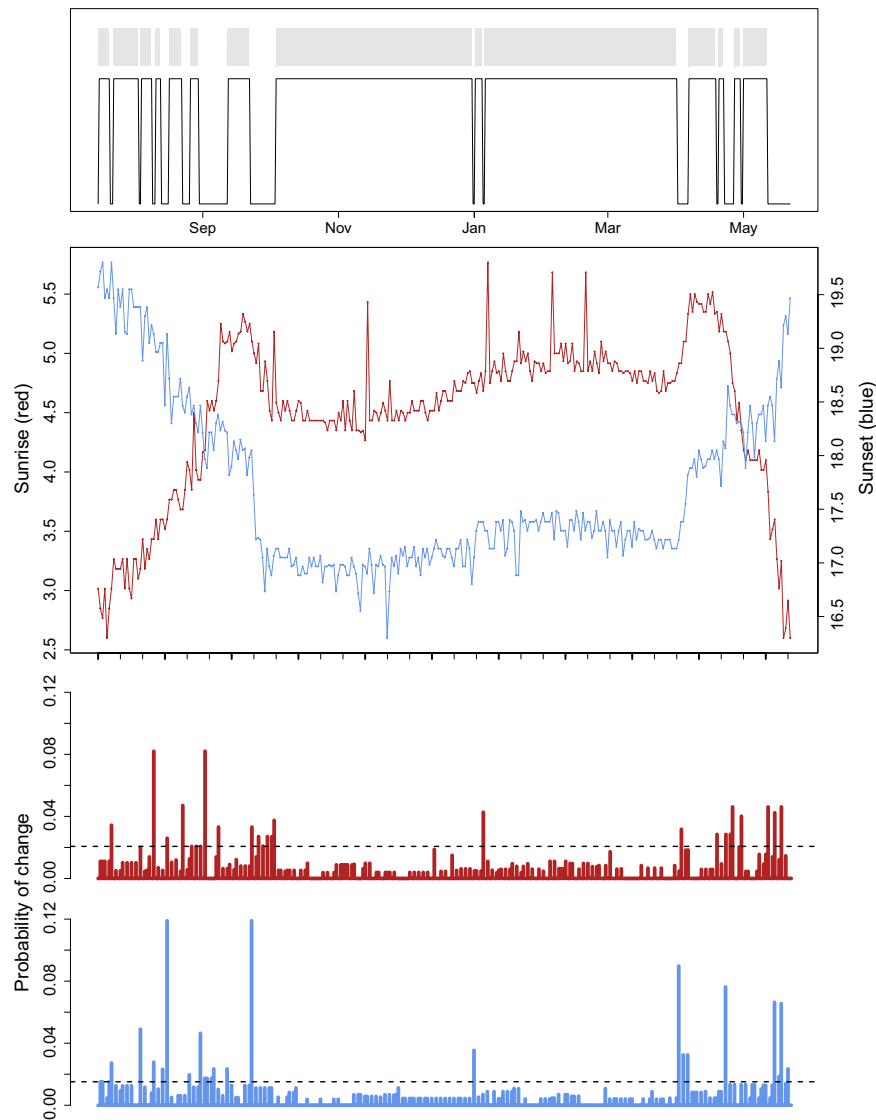
```
crds <- coord(twl.gl, degElevation = 90 - gE[1])
tripMap(crds, ylim = c(-35, 60),
        xlim = c(0, 20), equinox = FALSE)
```



Box 3 Movement analysis and “Hill-Ekstrom” calibration

GeoLight offers tools to distinguish between periods of movement and periods of residency. The `changeLight` function uses the twilight times (not the location estimates) that are unaffected by, for example, the equinox and searches for sudden changes that indicate changes in the location of the animal.

```
library(GeoLight)
cL <- changeLight(twl = twl.gl, quantile = 0.85)
```



4.4 | Step 4: Refinement of locations

Location estimates are typically refined via a statistical modelling effort that incorporates at least three components: (a) a twilight model, (b) a movement model and (c) a spatial mask. The **twilight model** is basically an extension of the calibration that not only determines one overall best sun elevation angle or single slope across the whole calibration period, but also considers variation of the daily light pattern within the calibration period. Incorporating the twilight

error distribution allows calculation of a spatial likelihood for each twilight (Figure 4) via the known distribution of the twilight events or from the variation in the slope parameter of the twilight periods (e.g. standard deviation of slope).

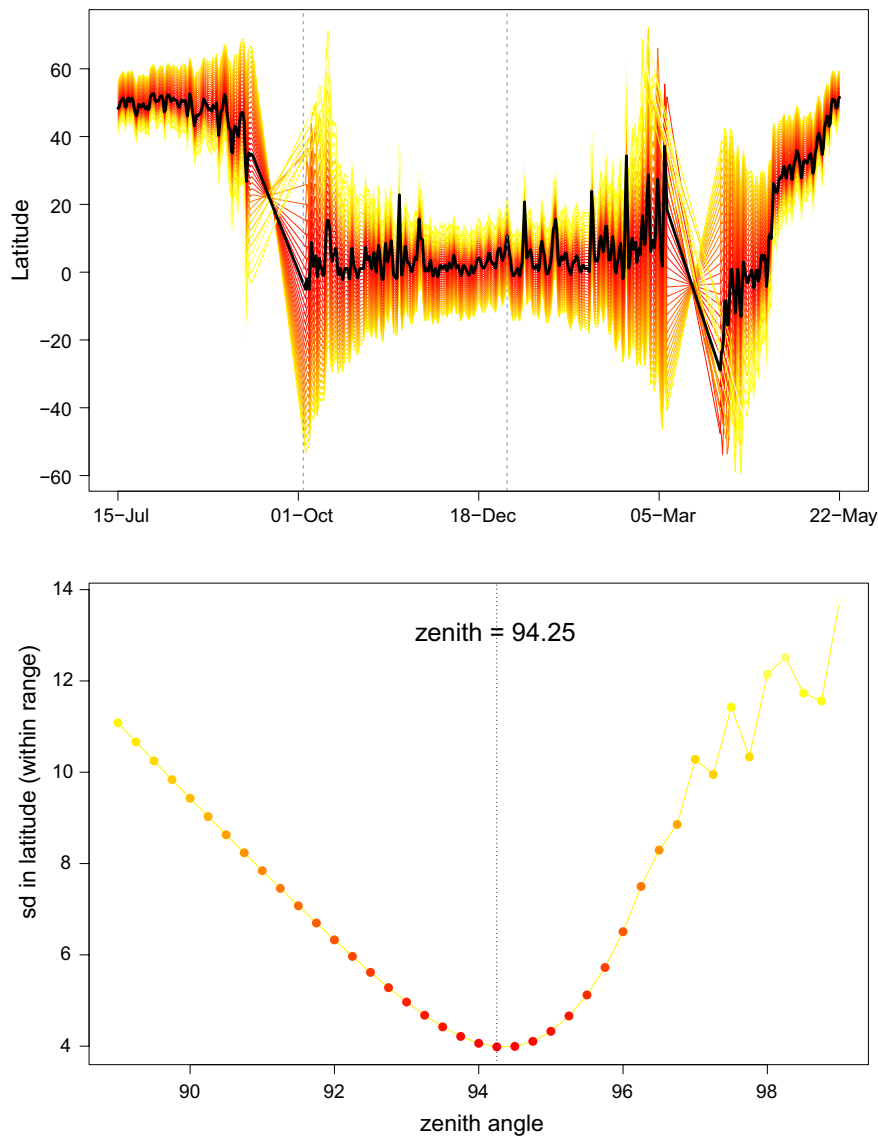
A **movement model** aims to limit the occurrence of unrealistic locations by constraining length and frequency of long-distance movements in accordance with what is known (or assumed) about a species' propensity for movement. Various possibilities for specific movement models exist that differ in level of complexity and assumptions;

BOX 3 (Continued)

The output plot shows the twilight times (sunrise in red and sunset in blue) in the center plot, the probabilities of change in the lower plot and the resulting sequence of movements and periods of residency.

With this information, we can perform a calibration for a period with unknown location (e.g. the longest stationary period nr. 5). The function `findHEZenith` from the R package `TwGeos` analyses this period and calculates the zenith angle (sun elevation angle) that results in the lowest variation in the estimates of latitudes (for details see: Lisovski et al., 2012 and supplementary online material Chapter 5, "Hill-Ekstrom calibration").

```
library(TwGeos)
StartEnd <- range(which(twl$Twilight >= min(twl.gl$tFirst[cL$site==8]) &
                     twl$Twilight <= max(twl.gl$tFirst[cL$site==8])))
HE <- findHEZenith(twl, range = StartEnd)
```



for example, models can assume a constant velocity or a bimodal speed distribution to distinguish resident and movement behaviour (Schmaljohann, Lisovski, & Bairlein, 2017; Yamaura et al., 2017).

A *spatial mask* defines spatial likelihoods within the analysis to reduce or even prevent unrealistic location estimates, that is, where the specific animal is very unlikely to occur. Spatial masks can be

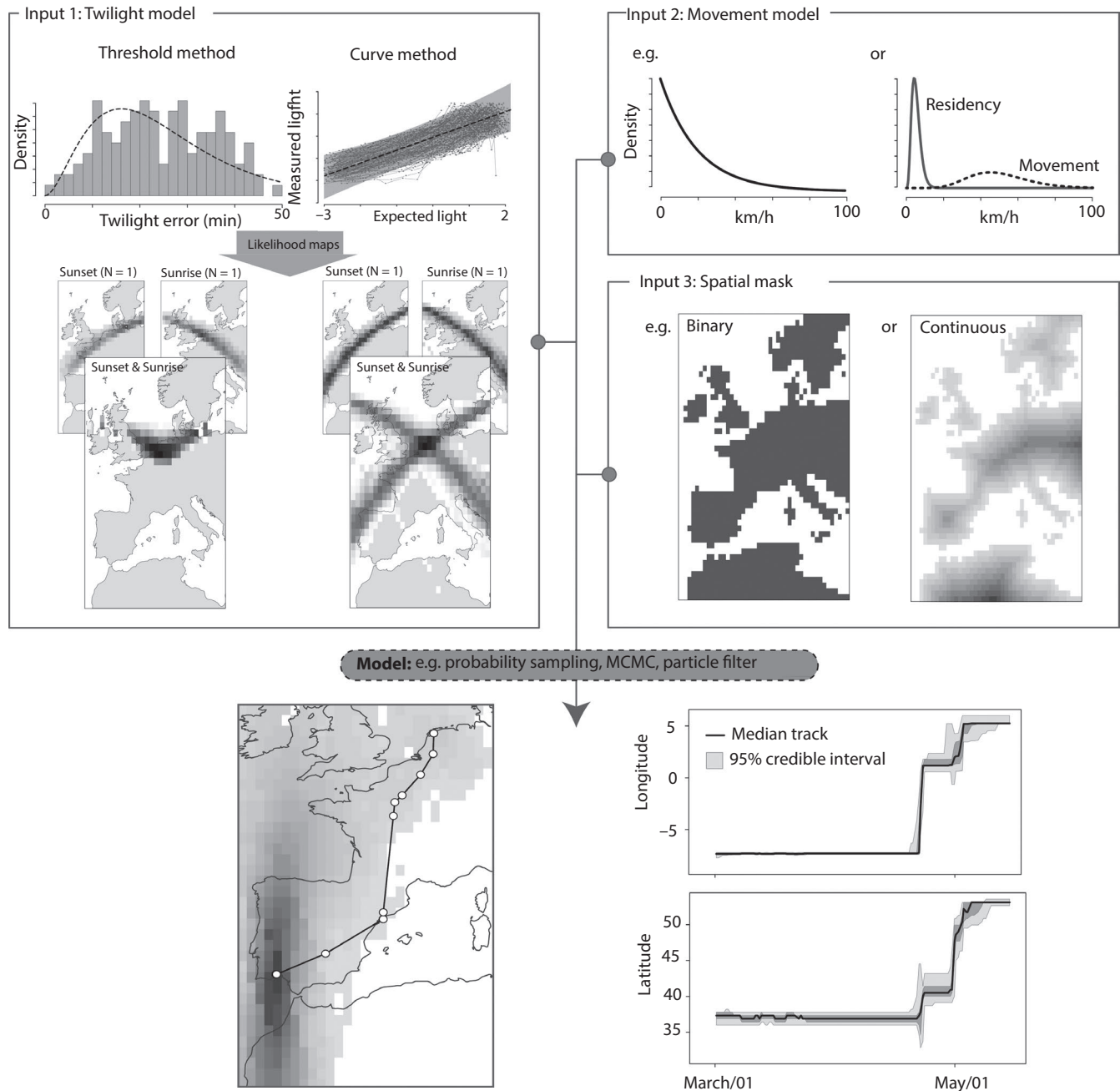


FIGURE 4 The principles behind the refining location process. Using knowledge on the variation (error distribution) in the detection of sunrise and sunset times for the “threshold method” and the variation in the slope parameter for the “curve method” allows calculation of spatially explicit likelihoods for each twilight (the twilight model). Further assumptions in the movement behaviour of the species (the movement model) and the spatial occurrence can then be incorporated in a modelling approach to estimate the most likely movement path and the associated credible intervals. The data used are again from the Bar-tailed godwit and the final results come from an analysis using the R package FLIGHTR (Rakhimberdiev et al. 2016)

as simple (binary) as restricting land animals to land by excluding oceans or large waterbodies, or more complex when considering species-specific habitat, altitudes or other preferences. They may also include measurements of other variables, such as temperature, that are sometimes recorded by multi-sensor loggers (Lam, Nielsen, & Sibert, 2010; Lavers, Lisovski, & Bond, 2019; Merkel et al., 2016; Shaffer et al., 2005; Sumner et al., 2009). The full model-based analysis combines these sources of information using the prior

distributions of probabilities from the twilight model, the movement model and the spatial mask to generate multiple (often thousands of) simulated locations for each tracking interval (see Figure 4). These simulated points are then regarded as a posterior probability distribution from which one can derive the “best” path (most probable the path that is usually the mean or median of all estimated locations within each time interval) and the associated credible intervals. “Best” in this case means that the result is the most likely

representation of the recorded geolocator data and the specified prior assumptions on twilight error distribution, movement capacities and spatial restrictions.

4.5 | Step 5: Movement analysis

In addition to deriving location data, we recommend a formal analysis of movement behaviour to delineate periods of movement and residency. This analysis can be a final step, based on posterior probabilities, or an intermediate step based on twilight times. In either situation, determining movement dates is not trivial, given the inherent limits on the accuracy and the precision of the location estimates. Different methods have been proposed and implemented in the different tools, some of which allow refining earlier steps in the analysis (e.g. calibration). An advantage to determining movement and stationary periods as an intermediate step is that it allows for grouping and classifying segments of the light-level time series. With these data categorized in this manner, we can combine the data from several successive days to derive a single location for a presumed stationary period (see supplementary online manual Chapter 5 “Movement Analysis” and Chapter 7 “The Group Model” for details and examples).

5 | AFTER THE ANALYSIS

5.1 | Interpretation

Always **consider the limitations** of the results. Regardless of the initial research aims, the geolocation data quality and migration path of the animal often require researchers to adjust the scale at which they draw conclusions. A general awareness of the precision and accuracy of geolocator tracks is always key, and it is important to realize that precision and accuracy frequently change throughout the tracking period. The high precision expected during one long shade-free period will likely not apply to a short shady period. Generally, inference becomes more challenging or even impossible when migration paths are more gradual rather than discrete, when stops are of short duration and distances are small, and for latitudinal movements close to equinox periods. In practice, with noisy geolocation data you may not always be able to accurately and reliably recover stopover sites and timing during the migration period, and it is important to communicate this uncertainty through the inclusion of error ranges in the results. Notably, such limitations are not per se uniform across analyses, since data quality and migration paths can vary, for example, between seasons, devices, sexes, populations and species. The larger the variability in data quality, devices and migration paths (timing and locations), the more the caution is warranted to prevent overestimating precision and accuracy and over-interpreting data. Caution is particularly warranted in studies investigating multiple species with different types of tags and species that occupy areas with highly variable habitats.

5.2 | Presentation

Geolocator data are often presented in maps, which are an intuitive way to show locations and migration paths. Unfortunately, in many publications, maps of the results of geolocator analysis neglect the uncertainty and assumptions in the underlying analysis, yet they are important for the validation, perception and interpretation of results. Therefore, we strongly encourage visualizations that show the precision and accuracy (uncertainty) associated with the data (e.g. Rakhimberdiev et al., 2016). For instance, summarized locations should also indicate their error. Providing separate plots of latitude versus time and longitude versus time is a simple way to make this presentation (see supplementary online manual Chapter 8 “Exploration of results”).

5.3 | Reporting

While conducting analyses, it is crucial to clearly and unambiguously document all steps taken so that your work will be reproducible. Although in many cases the standard procedures and pathways outlined above and in the supplementary material will suffice, the wealth of options in each analysis requires that methodological choices such as parameter settings, filtering or similar analytical decisions be documented. The same applies to deviations from standard procedures. The R packages described in this paper facilitate the creation of annotated and clearly documented scripts, which we recommend archiving as supplements to any published research. We recommend complete and separate analysis for each tag, rather than setting up general analyses and looping through several tags using the very same parameter settings. This recommendation especially applies to more sophisticated analyses that are often subject to tag-specific assumptions. The supplementary online manual gives an extensive overview of how to report methodological choices and present results.

5.4 | Archiving

Archiving geolocator data is not only good scientific practice, it is a precondition for publication in a growing number of journals. Proper archiving retains the value of the data for future (re-) analyses, allowing for re-analysis with new analytical methods or an overarching syntheses (Finch et al., 2017). As there are several tools that could potentially be used, and each requires specific values for a suite of parameters, it is crucial to archive both raw data and location estimates in conjunction with the code that led to the specific results.

Although several databases exist for sharing and archiving animal movement data, the foremost as a general research platform for animal movement data is *Movebank* (<https://www.movebank.org/>). *Movebank* is particularly well suited for geolocator data as it includes features tailored to tracking based on ambient light levels, supporting storage of raw light recordings, twilight annotation

tables, location estimates with credibility intervals and custom files such as R scripts or model output, along with deployment- and study-level metadata. Researchers are encouraged to publish their data in the public domain, which can be done by publishing in the *Movebank Data Repository*, wherein a dataset can acquire a digital object identifier (DOI), persistent link, licence and citation after undergoing review. For in-progress work, Movebank provides a range of sharing options, for example allowing owners to store and manage data privately, give access to specific researchers and allow the public to discover but not access the data or to download data after accepting owner-defined terms of use. We recommend storing data in *Movebank* or similar repositories even during preliminary analysis stages when the results and analyses remain unpublished. In these situations, the online archive provides a secure backup and can be discovered by other researchers who can contact the owner about potential collaboration using the data.

6 | SUPPLEMENTARY MATERIAL: THE MANUAL

This publication is accompanied by a comprehensive online manual that applies the concepts to several datasets, analyses them using the open-source tools discussed above and provides step-by-step code as well as recommendations for addressing common issues (<https://geolocationmanual.vogelwarte.ch/>). We consider this supplementary online manual to be a community endeavour for which we give here a starting point. Users can add their own experiences and analysis pathways simply by contributing to the source code of the manual via its GitHub repository (<https://github.com/slisoiski/TheGeolocationManual>). In addition, we recommend the online forum “Geolocator Discussion & Support” hosted by “ornithology exchange” (<http://ornithologyexchange.org/forums/forum/259-geolocator-discussion-support/>) as a platform for discussion and the opportunity to exchange questions and answers with the geolocator user community.

7 | OUTLOOK

Over the next decade or so, geolocators will likely remain an important tool in migration research, thanks to their low cost and light weight, which are as yet unmatched by any of the more precise GPS tags or other tracking devices.

There are several recent technological advancements that will perhaps even increase their appeal. The most important among them is probably the combination of light recording with other *en route* data, such as air pressure, acceleration, magnetism and temperature (Bäckman et al., 2017; Dhanjal-Adams et al., 2018; Sjöberg et al., 2018). These additional data can facilitate the refinement of location estimates (see step 4 in the analysis). For instance, acceleration data or changes in air pressure can distinguish movement and residency periods relatively easily, and such prior knowledge can

then be fed into the stationary location estimation (see Box 3 and Chapter 7; “The Group Model” in the supplementary online manual).

These additional sensor data also provide a wealth of complementary information on fine-scale behaviour: air pressure and temperature can be used to infer flight altitude and initiation and termination of migratory or foraging flights; acceleration data can be used to determine daily activity budgets and, given supplementary measurements, be related to energy expenditure and energy budgets; magnetic field data can be used to infer strategies in orientation and navigation during migration. Combining such behavioural information with refined, reliable and accurate location estimates can assist in identifying habitat associations of migrants or their responses to evolutionarily novel factors such as artificial light at night, sensory pollution or wind farms. This knowledge will improve our understanding of the fates of migrants and the bottlenecks they might experience at sensitive times and places, which will allow us to improve our conservation and management strategies for migratory populations.

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AUTHOR'S CONTRIBUTIONS

S.L. and S.B. wrote the first draft with significant contributions from K.L.D.-A., J.O. and E.S.B. All authors contributed to revisions and approved the final version. S.L., K.L.D.-A., M.T.H., B.M., J.K., E.R. and E.S.B. wrote the initial draft of the supplementary online manual, and all authors added and commented on the current version.

DATA ACCESSIBILITY

Code and data of online supplementary material are available via Zenodo (Lisovski et al., 2019) and via GitHub: <https://github.com/slisovski/TheGeolocationManual>. The online supplementary manual is released on <https://geolocationmanual.vogelwarte.ch>.

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