Geolocation by light: accuracy and precision affected by environmental factors

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Summary

1. Geolocation by light allows for tracking animal movements, based on measurements of light intensity over time by a data-logging device ('geolocator'). Recent developments of ultra-light devices (< 2 g) broadened the range of target species and boosted the number of studies using geolocators. However, an inherent problem of geolocators is that any factor or process that changes the natural light intensity pattern also affects the positions calculated from these light patterns. Although the most important factors have been identified, estimation of their effect on the accuracy and precision of positions estimated has been lacking but is very important for the analyses and interpretation of geolocator data.

2. The 'threshold method' is mainly used to derive positions by defining sunrise and sunset times from the light intensity pattern for each recorded day. This method requires calibration: a predefined sun elevation angle for estimating latitude by fitting the recorded day/night lengths to theoretical values across latitudes. Therewith, almost constant shading can be corrected for by finding the appropriate sun elevation angle.

3. Weather, topography and vegetation are the most important factors that influence light intensities. We demonstrated their effect on the measurement of day/night length, time of solar midnight/noon and the resulting position estimates using light measurements from stationary geolocators at known places and from geolocators mounted on birds. Furthermore, we investigated the influence of different calibration methods on the accuracy of the latitudinal positions.

4. All three environmental factors can influence the light intensity pattern significantly. Weather and an animal's behaviour result in increased noise in positioning, whereas topography and vegetation result in systematic shading and biased positions. Calibration can significantly shift the estimated latitudes and potentially increase the accuracy, but detailed knowledge about the particular confounding factors and the behaviour of the studied animal is crucial for the choice of the most appropriate calibration method.

Key-words: animal movement, calibration methods, geolocation, migration, tracking

Introduction

Geolocation by light is based on measurements of sunlight intensity over time. This information is saved on a data-logging device ('geolocator'), and after data download, daily positions of an individual can be reconstructed using astronomical equations. In the first applications of geolocators, movements of elephant seals (Delong, Steward, & Hill 1992), seabirds (Croxall *et al*. 2005; Phillips *et al*. 2005), fish (Block *et al*. 1998) and sea turtles (Fuller *et al*. 2008) were determined. Recently, ultra-light geolocators (< 2 g) have been developed, greatly broadening the range of potential target species and boosting the number of studies using this technique (Bridge *et al*. 2011). Current studies on small-sized birds like waders (Conklin *et al*. 2010; Minton *et al*. 2010; Niles *et al*. 2010;

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Klaassen *et al.* 2011), hoopoes (Bächler *et al.* 2010) and passerine birds (Stutchbury *et al.* 2009; Tøttrup *et al.* 2011) show the enormous potential of this technique for the collection of novel information on the movements of individual birds.

There are two main methods to derive position estimates from light-level records – the 'threshold method' and the 'template fit method'. The simplest and most frequently used method is the 'threshold method' (for details, see Hill & Braun 2001; Ekstrom 2004), where only a single time point per twilight event is used to derive location estimates. Sunrise and sunset are defined as the times when the solar irradiance reaches a threshold level. The longitude follows directly from the time of local solar noon (or local solar midnight), but latitude needs to be approximated from day length (or night length), that is, the period between sunrise and sunset (or between sunset and sunrise). For the latitude estimates, the light-level threshold should be matched with a specific sun elevation angle (position of the sun above/below the horizon), with a lower threshold value corresponds to a lower sun elevation angle (Fig. 1a). Hence, selecting an inappropriate sun elevation angle may result in incorrect estimates for latitude, and this error is most pronounced around the equinoxes (Fig. 1b).

The 'template fit method' uses the shape of the light transition during sunset and sunrise periods to estimate positions (Ekstrom 2004, 2007). Herein, a template function for the temporal change in light intensity is fitted to the observed light-level pattern for a particular day. Positions are derived by finding the best-fitting model, which is described by four parameters: latitude, longitude, sunrise and sunset with correction for apparent cloudiness during each twilight period. This method results in more accurate estimates for latitude owing to the implemented cloudiness factor and because the sun passes specific sun angles more slowly at high latitudes compared to the equator where twilight periods are relatively short. The template fit method can only be applied if the full range of light intensities is recorded, that is, from darkness to the daily plateaus, which, however, most currently available geolocators cannot do for reasons of data storage and sensor sensitivity.

An inherent problem of geolocation is that sunlight hardly ever reaches the earth's surface without interference. Factors that may influence the light regime are extremely diverse, but all cause some sort of shading, resulting in spuriously shorter days. The most fundamental confounding factor is refraction near the horizon that influences the perceived sunrise/sunset by up to ±0·32° of sun elevation angle depending on the composition of the atmosphere and weather conditions (Schaefer & Liller 1990). Weather conditions in general may change perceived light conditions, for example shading by cloud cover. Shadows cast by terrain (topography) or vegetation are further factors influencing the observed light intensities especially in terrestrial habitats. The effect of these different factors is usually constant neither throughout the year nor in the short term, resulting in variation in the length of the day (night) and time of local solar midday (midnight), therefore affecting the accuracy and precision of location estimates. The behaviour of the tracked animals may amplify the effects of these factors; for
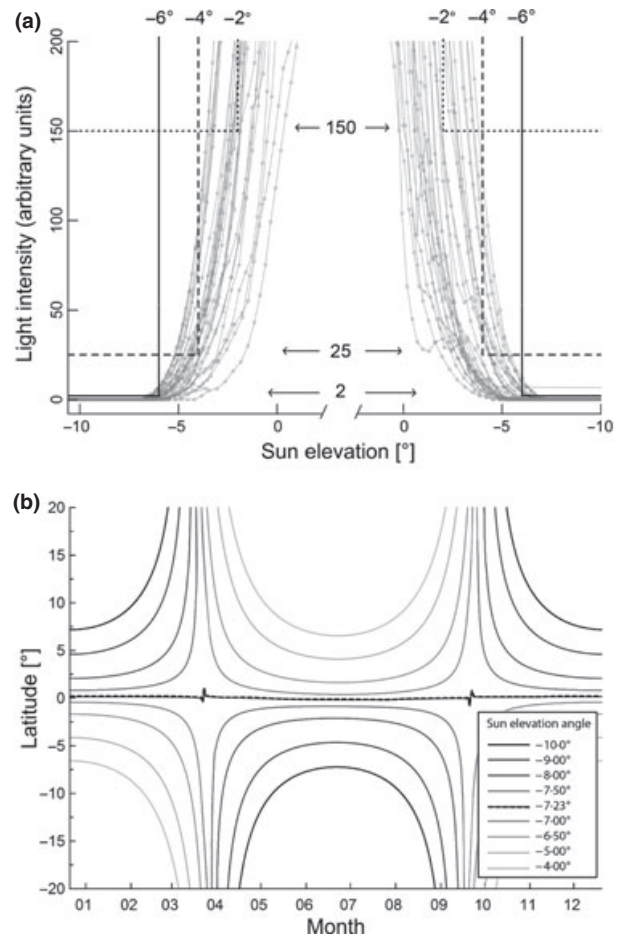

Fig. 1. The relationship between the 'light intensity threshold' and the 'sun elevation threshold'. Sun intensity measurements of one month at known location (weather: site 1) plotted over sun elevation angles (a). For each example light intensity threshold (2, 25 and 150), the sun elevation threshold that results in the best latitudinal calculation is indicated. The lower graph (b) shows the latitudinal positions over one year derived through different sun elevation angles. Day lengths corresponding to the equator with constant deviation of 10 min were used. Increasing mismatch between light intensity threshold and sun elevation threshold results in a decreasing accuracy in latitudinal estimation.

example, individuals might use different habitats throughout the year or even switch habitats between consecutive twilight periods.

Even if shading was equal over a certain period, the accuracy of latitudinal positions need not be the same. The error in the estimate for latitude varies with date according to astronomical-based calculations: it is smallest during times and for places where day length strongly varies with latitude, that is, during mid-summer and mid-winter and at high latitudes (Fig. 2, see also: Hill 1994). In contrast, the estimation of latitude is inherently highly imprecise around vernal and autumnal equinox, when day length is similar around the globe (Hill 1994; Ekstrom 2004), and near the equator where there is little variation in day length. However, calibration can, to some extent, account for such systematic deviations in day/night length by matching the correct sun elevation angle to the chosen light
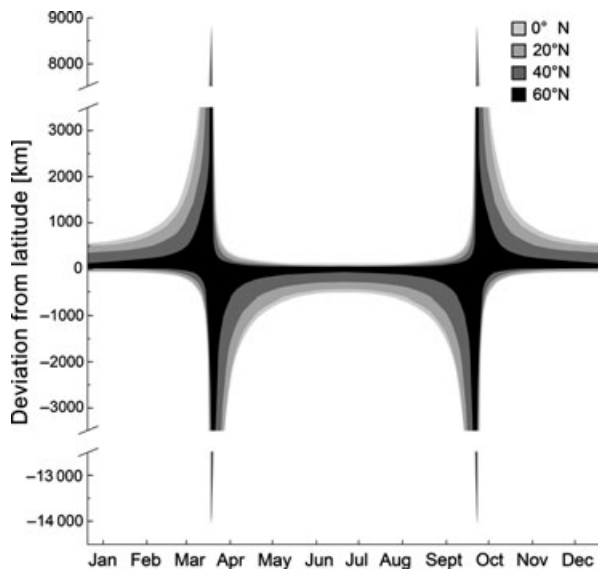
Fig. 2. The discrepancy between true latitude and latitude estimated by the threshold method where day length has a constant deviation. The deviation in kilometres is calculated for different latitudes and is drawn as a range, which approximately reflects the 90 and 10 percentiles in deviation owing to weather effects (2–17 min).

intensity threshold (Fig. 1b). Unfortunately, it is unlikely that in practice, shading is equal over longer periods, and this challenges the use of a single sun elevation threshold. Longitudinal position estimates, on the other hand, are little affected over the course of the year even in the presence of small measurement errors during twilight periods (Hill 1994; Fudickar, Wikelski, & Partecke 2011).

Although these patterns of positional error owing to true latitude and time of the year are well documented (Wilson *et al.* 1992; Hill 1994; Hill & Braun 2001; Ekstrom 2004, 2007), only a few case studies exist that compare the accuracy of geolocation by light with positions simultaneously derived by more accurate methods such as satellite telemetry. Shaffer *et al.* (2005) report that the mean error of geolocation by light was 400 ± 298 km (SD, great circle distance) for two different periods in marine habitat. Phillips *et al.* (2004) described an average deviation from the correct position of 186 ± 114 km (SD, great circle distance) after the usage of several *ad hoc* filters that reduce the error on positioning. More recently, Fudickar, Wikelski, & Partecke (2011) presented an elaborate study describing the accuracy in forest habitats during an almost complete annual cycle. Stationary geolocators in this study showed an average error of 201 ± 43 km (±95% CI) in latitude and 12 ± 03 km in longitude estimates. Geolocators mounted on birds showed lower errors, owing to the use of different calibrations (143 ± 62–132 ± 75 km in latitude; 50 ± 34 km in longitude, Fudickar, Wikelski, & Partecke 2011).

Nevertheless, knowledge of factors that influence accuracy is urgently required for any interpretation of light-based geolocator data. Such knowledge is particularly important for terrestrial studies, where light conditions are probably much more variable than in marine habitats owing to shading from topography and vegetation (habitat). Once we have identified the factors and quantified their effect on perceived light conditions, we can select adequate methods for reducing their errors. Therefore, we aim at (1) demonstrating the effects of environmental conditions, for example weather, topography and vegetation, on the accuracy and precision of position estimates derived from geolocators, (2) giving examples of these effects using representative migratory species that differ in their basic ecology and live in different types of habitats and (3) discussing simple methods for reducing some of the errors (calibration).

Materials and methods

DATA COLLECTION

First, we identified the effects of weather, topography and vegetation on the accuracy and precision of geolocator measurements by analysing light-level data from logger devices installed at fixed position. We ensured that no artificial light sources that may affect the results were present. Secondly, for studying the combined effects of bird behaviour, habitat and weather on positioning by geolocation, we used data from geolocators mounted on free-living birds during their stationary breeding period at known localities. Finally, we give examples of the effects of different calibration methods on positioning by using two data sets, one data set from a logger installed at a fixed location and one data set from a logger mounted on a bird which was stationary within the same habitat type at an unknown location. Sample sizes and recording periods are summarized in Table 1.

Weather

We measured light intensity simultaneously at two sites approximately 1000 km apart, by putting geolocators (SOI-GDL1·0, Swiss Ornithological Institute) on rooftops at Sempach, Switzerland (Site 1: 8°12′ E, 47°08′ N), and Nyiregyháza, Hungary (Site 2: 21°42′ E,

Table 1. Number of geolocators and periods of measurement used for the analyses

	N	Days
Stationary geolocators		
Weather		
Site 1	1	226
Site 2	1	215
Topography*		
Valley	1	165
Mountain top	1	167
Vegetation		
Solitary tree**	2	22
Shrub**	2	42
Reed**	2	86
Woodland**	2	26
On-bird geolocators		
Arctic tern	2	59
Common Nightingale	2	92
European Hoopoe	2	92
Great Reed Warbler	1	94

47°58′ N). Light intensities were recorded from December 2009 to August 2010 with a measurement interval of 2 min (as in all other SOI-GDL1·0 devices used here). The precisions of the two data sets were compared with cloudiness parameter provided by Movebank (Wikelski & Kays 2010) using raw data from the NOAA (National Oceanic & Atmospheric Administration: Kanamitsu *et al.* 2002). Therewith, we tested the correlation between cloud cover and deviation of each twilight event using a linear regression allowing for temporal autocorrelation of first order (autoregressive model AR1). The generalized least square method was used to fit the model.

Topography

The influence of topography was studied at Scuol, Switzerland (10°18′ E, 64°48′ N), in a steep Alpine valley, facing eastwards and being characterized by a mountain chain up to 3100 m high, located approximately 4 km to the south. Geolocators (SOI-GDL1·0) were placed on rooftops at two different altitudes; in the valley at 1320 m and on the mountaintop at 2050 m. Measurements were recorded from December 2009 to July 2010.

Vegetation

The effect of vegetation was simultaneously measured at four sites in Sempach, all within a 100-m circle. The sites (shrub, solitary tree, reed bed and deciduous woodland) represent the spectrum from open to densely vegetated terrestrial habitats. Two geolocators (SOI-GDL1·0) were placed in each habitat in heights between 1 m (for reed and woodland) and 2 m (for shrub and tree) from September 2010 to October 2010.

Habitat and behaviour

Light intensity data from geolocators on birds were studied with respect to habitat effects. Geolocator data were collected from breeding Arctic Terns (*Sterna paradisaea*), European Hopooes (*Upupa epops*) and Common Nightingales (*Luscinia megarhynchos*). These birds represent species breeding in open landscape, open woodland and woodland habitats, respectively. We analysed light-level records during the breeding period (July) when individuals were stationary and positions were known. For each species, two individuals were equipped with geolocators: terns with Mk14-S from the British Antarctic Survey (BAS) at their breeding site in Sweden (14°38′ E 55°97′ N), and hoopoes and nightingales with SOI-GDL1·0 at their breeding sites in Switzerland (7°15′ E 46°11′ N) and Bulgaria (27°51E, 42°5N), respectively. BAS data loggers measured light intensities every minute but only store the maximum level of 10-min intervals.

Calibration

For illustrating the effects of different calibration methods on positioning, we calculated positions for two data sets: data from a stationary geolocator (SOI-GDL1·0) placed in a reed bed at Sempach during the time period from September 2010 to December 2010 and data of an individual Great Reed Warbler (*Acrocephalus arundinaceus;* BAS Mk10B-S) during its stationary wintering period from February 2009 to April 2009. Stationary period was defined as the period during which day/night length and time of solar midnight/noon were relatively stable. We compared latitudinal positions derived from both data sets using different calibration methods, that is, 'civil twilight calibration', 'rooftop calibration', 'in-habitat calibration' and 'Hill–Ekstrom calibration'.

DATA ANALYSIS

We used the threshold method (Ekstrom 2004) to calculate positions from light intensity measurements. The light intensity threshold was set slightly above the baseline value (i.e. slightly above complete darkness) for each geolocator. This threshold corresponds to a sun elevation angle of approximately −6·0°, which is defined as the 'civil twilight'. This specific light intensity threshold for each geolocator is used for all subsequent analyses and allows comparison between data set from different devices. In contrast to the fixed sun intensity threshold, the corresponding sun elevation angle can change according to the applied calibration method.

To quantify the accuracy of geolocation measurements, we calculated the differences between observed and true values of day length (deviation in day length, hereafter devDL) and solar midnight/noon (deviation in timing of midnight/noon, devMN). These measures are more independent of true latitude time of the year and not affected by calibration method than distance measures and therefore allow direct comparison of data collected at different latitudes and dates. We used mode values and the 10th and the 90th percentiles to describe the distributions of devDL and devMN. The variance reflects the precision in devDL and devMN.

We used the following four different calibration methods to analyse the data described earlier (see Appendix S2 for additional details on these calibration methods). For the 'civil twilight calibration', the sun elevation angle corresponding to the light intensity threshold level was set at −6°, irrespective of the specific conditions during the measurement. Only sunrise and/or sunset times without shading will fit to this sun elevation angle and result in a low deviation in day/night length and midnight/noon.

The variable weather conditions at a specific location are considered via the 'rooftop calibration'. The sun elevation angle is derived from a measurement of light intensities at a rooftop over a period of days (10–25 days). Each derived light intensity measurement can be assigned to the corresponding sun elevation angle (Fig. 1a). With the defined light intensity threshold, a single sun elevation angle can be calculated for each twilight event (where the light intensity exceeds the light intensity threshold) – the median of all sun angles derived in this way is subsequently used as the reference sun elevation angle. As weather potentially produces shading, the mean day length in this period is usually shorter than the true day length, and the resultant sun elevation threshold is therefore higher than −6·0°.

'In-habitat calibration' accounts for shading by vegetation (in addition to the effects of weather). In this method, measurements for calculating the sun elevation angles at times the light intensity reaches the threshold value are obtained from loggers placed inside a specific habitat.

Finally, the 'Hill–Ekstrom calibration' is developed after the basic idea from the studies of Hill & Braun (2001) and Ekstrom (2004) and allows the calibration during stationary periods at unknown latitudinal positions. The 'Hill–Ekstrom calibration' is based on the observation that the error in latitude increases with an increasing mismatch between light threshold value and inferred sun angle. This error is amplified with increasing proximity to the equinox times owing to the increasingly shallow latitudinal slope of day length variation (Figs 1b and 2). Furthermore, the sign of the error switches at the equinox, that is, latitude is overestimated before the equinox and underestimated after the equinox (or vice versa depending on autumnal/vernal equinox, hemisphere, and sign of the mismatch between light threshold value and inferred sun angle). During stationary periods, the variance in latitude is minimal if sun elevation angle fits to the defined sun intensity threshold. Furthermore, the accuracy of positions increases

with decreasing variance in latitudes (Fig. 1b). We can therefore use these patterns to identify the correct sun elevation angle for stationary periods without knowing the correct position beforehand, simply by calculating the variance in latitudes over a range of sun elevation angles. However, the method is only applicable for periods when the bird is stationary with almost stable shading intensity during the entire stationary period.

Sun elevation angles for specific locations and times were generated using R package maptools (R Development Core Team 2010). Sunset, sunrise, sun elevation angles and locations were calculated with the software GEOLOCATOR (developed by Swiss Ornithological Institute) based on standard astronomical equations (Montenbruck & Pfleger 2000). For all statistical analysis, we used R 2·8·1 (R Development Core Team 2010). All tests were two-tailed; data with skewed distributions were normalized by Box–Cox transformations before using (classic) statistical tests.

Results

WEATHER

The mean devDL (deviation in day length) was similar for study sites at Sempach and Nyiregyháza (students t-test: $t_{441} = -0.82$ $P = 0.41$). In contrast, mean devMN (deviation from solar midnight/noon) differed significantly between sites (Fig. 3a: $t_{441} = 4.1$ $P < 0.001$). Weather affected day

length by similar magnitudes at each site but resulted in different variances in the devMN (ANOVA, devDL: $F_{1,441} = 0.67$, $P = 0.441$; devMN: $F_{1,441} = 16.8$, $P < 0.001$). Finally, the mode values of devDL were −4 min at both locations, and devMN differed within a range of 1·5 min (Sempach 1·0 min; Nyiregyháza −0·5 min). The deviation from the time of true twilight was positively correlated with cloud cover at both study sites (site 1: $t_{417} = 7.04$, $P < 0.001$; site 2: $t_{438} = 6.96$, $P < 0.001$; the temporal autocorrelation was estimated to be 0·17 and 0·49, respectively). Mean cloud cover was equal at the sites (47–48% respectively; ANOVA, $F_{3,826} = 1.34$, $P = 0.25$), but at Sempach, cloud cover was often similar for two consecutive twilight periods during one day (paired t-test: $t_{200} = 0.034$, $P = 0.9$, mean difference 0·06%), whereas at site Nyiregyháza, cloud cover at sunset was significantly higher than at sunrise for the same date (mean difference −5·29%; $t_{213} = -2.77$, $P < 0.05$).

TOPOGRAPHY

Local topography strongly affected day length with shorter days measured in the valley (Fig. 3b: $t_{325} = 6.637$ $P < 0.001$). Moreover, both at the mountain top and in the valley, devMN was less than 0, and this effect was larger for the mountain top
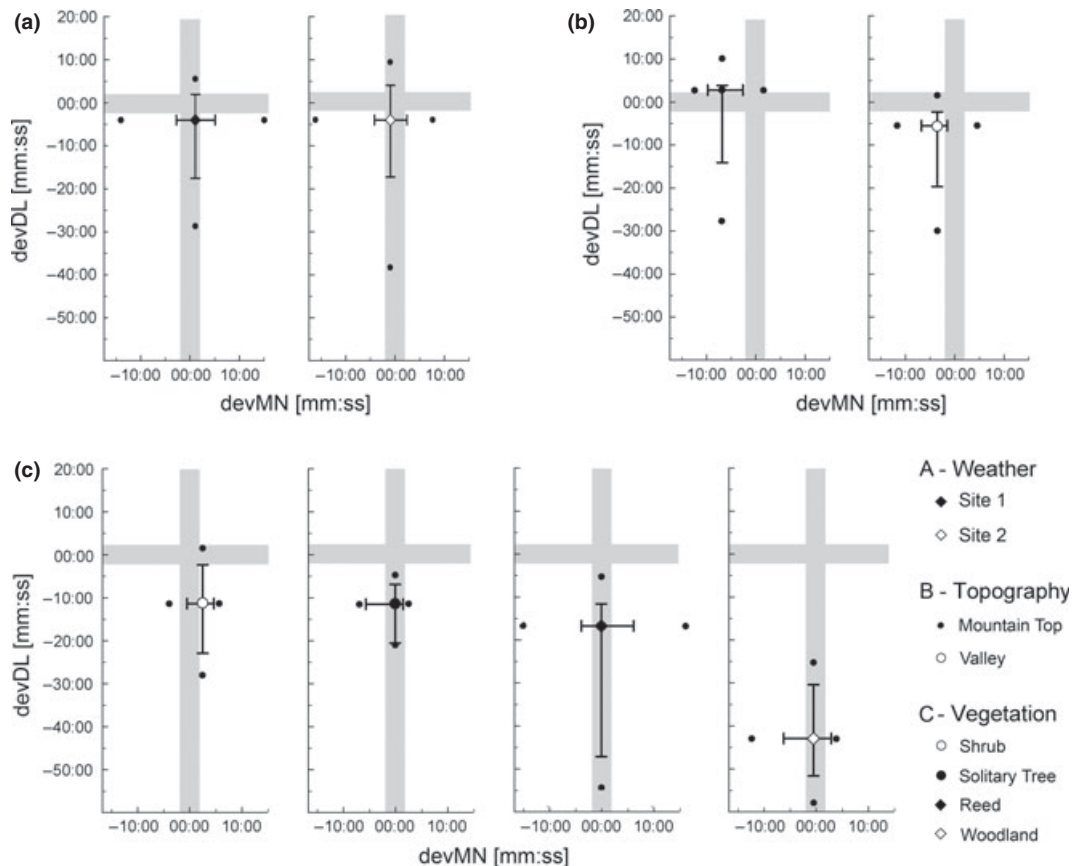

Fig. 3. Deviation from 'true' day length (devDL) and solar midnight/noon (devMN) in min:s of stationary geolocators which were exposed to the effects of (a) weather, (b) topography plus weather and (c) vegetation plus weather. For deviations, mode values and 10 and 90 percentile values are given; extremes are symbolized as dots. The grey bars indicate the range of ± 2 min, which is the potential highest accuracy of each sunrise and sunset time determined by refraction at the horizon.

than for the valley ($t_{618} = -8.1162$ $P < 0.001$). Topography did not affect the variance of devDL ($F_{1,166} = 1.29$ $P = 0.102$) but significantly affected the variance of devMN ($F_{1,329} = 1.673$ $P < 0.001$). The difference of the mode values of devDL between mountaintop and valley was 8·5 and 3·5 min for devMN.

HABITAT

Vegetation strongly affected the measured day length in the four habitats (ANOVA: $F_{3,118} = 121.9$ $P < 0.001$), with devDL being largest in woodland habitat, intermediate in reed and smallest in shrub/solitary tree (Fig. 3c). There was no such effect on devMN ($F_{3,225} = 0.264$ $P = 0.607$). However, the variances of devDL and devMN differed significantly between the four habitats (Bartlett test: $K_3^2 = 25.64$ $P < 0.001$, $K_3^2 = 43.23$ $P < 0.001$). The modes of devDL increased by about 32 min from shrub (-11.5 min), solitary tree (-13.0 min) to reed (-17.0 min) and woodland (-43.0 min). For devMN, the modes differed from zero (by 3·0 min) only in shrub (see Appendix S1 for statistical details).

BEHAVIOUR AND HABITAT

Geolocators mounted on birds showed a comparable habitat-specific pattern with significantly different devDL between species (ANOVA: $F_{2,178} = 27.24$ $P < 0.001$). The modes of devDL decreased from open-landscape species to woodland species (from tern 4·0 min; hoopoe 17·0 min; to the nightingale 24·0 min, Fig. 4). DevMN showed a large variance in terns with large positive deviations (90 percentile: 31·5 min), while its modes were similar to those of the other species and within a range of 2 min (tern 1·0 min, hoopoe 1·0 min, nightingale -1.0 min).

CALIBRATION METHODS

The four different calibration methods strongly affected the estimated latitudinal positions for stationary geolocators in the reed bed (ANOVA: $F_{3,268} = 97$, $P < 0.001$). The mean deviation from the correct position was largest for data calibrated with the civil twilight method (667 km), followed by 'rooftop calibration' (392 km) and 'in-habitat calibration' (68 km, Fig. 5). The 'Hill–Ekstrom calibration', using data around the equinox periods, provided the smallest errors (20 km). The mean latitudinal positions of an individual Great Reed Warbler at an unknown winter site did not differ significantly between the different calibration methods ($F_{3,346} = 0.69$, $P = 0.55$) although the median values decreased from 17·94° for the 'civil twilight calibration' to 10·33° for the 'Hill–Ekstrom calibration', which indicates a difference of 843 km. The variance also decreased from $27.2 \pm SD$ ('civil twilight calibration') to $8.6 \pm SD$ ('Hill–Ekstrom calibration').

Discussion

We demonstrated how the three most important environmental factors affect the accuracy and precision of geolocation by light. Given that threshold-based positioning relies on the correct determination of day length and time of local solar noon, shading during twilight periods can result in severe errors in positioning. The three factors which we demonstrated the potential impact of in our analyses – weather, topography and vegetation – typically contribute most to shading effects, especially in terrestrial systems. Furthermore, we investigated the extent of shading effects for birds breeding in different habitats. Finally, we applied different calibration methods to investigate how far they might compensate for shading effects and finally improve positioning estimates.
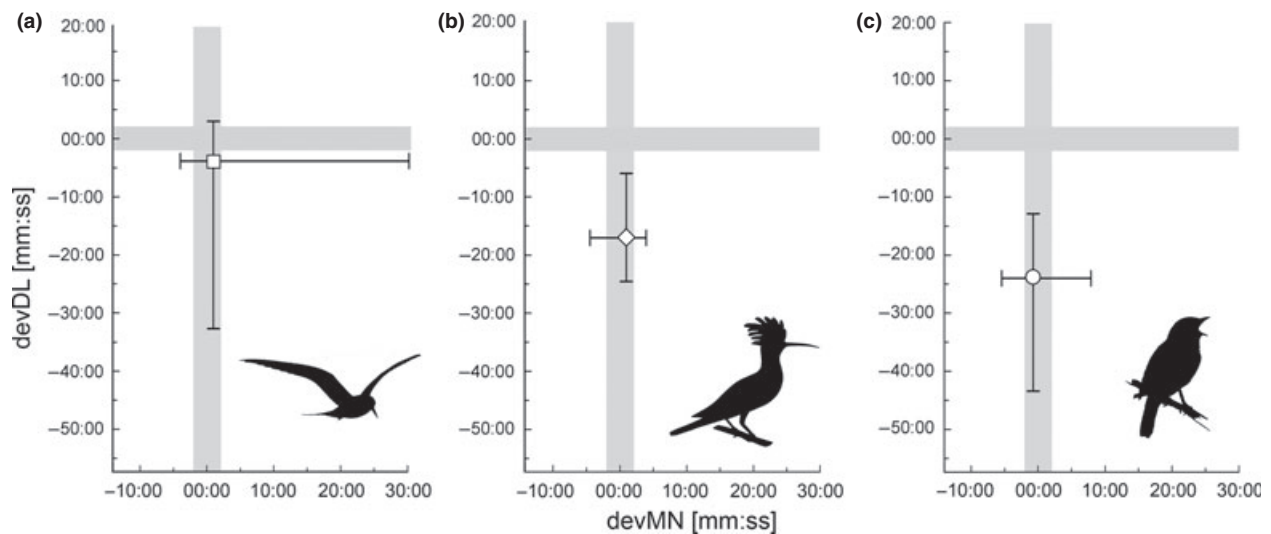

Fig. 4. Deviation (min:s) from true day length (devDL) and solar midnight/noon (devMN) for on-bird geolocators of (a) Arctic Tern for open-landscape habitat, (b) European Hoopoe for open woodland habitat and (c) Common Nightingale for woodland habitat. The grey bars indicate the range of ±2 min, which is the potential highest accuracy of each sunrise and sunset time determined by refraction at the horizon.
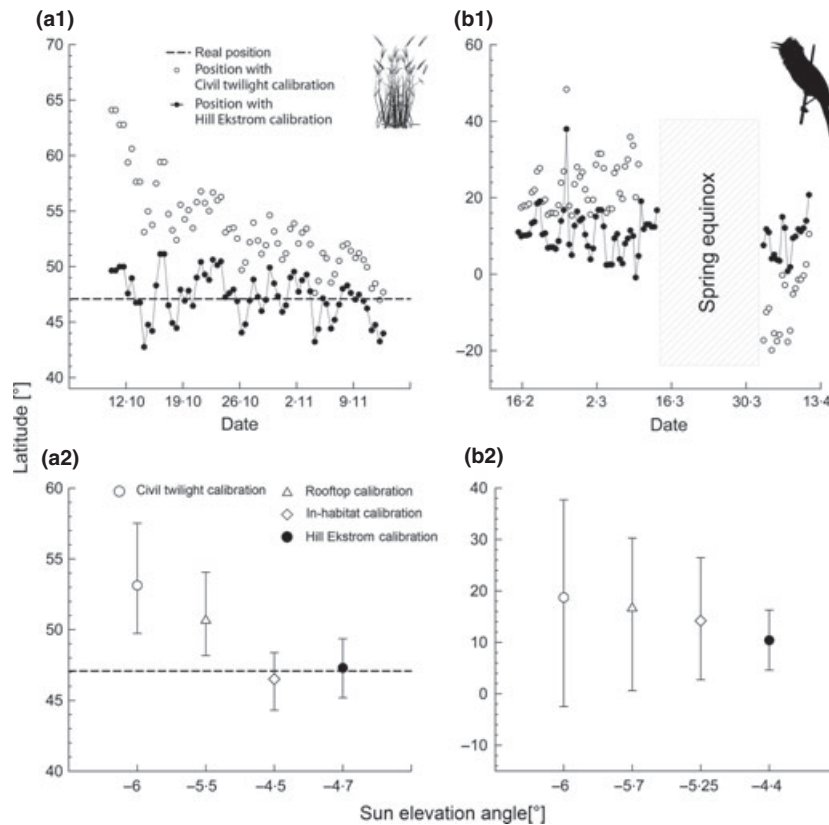
Fig. 5. Two examples of latitudinal positions calculated through different calibration methods. Data come from (a) a stationary geolocator placed within a reed bed in Switzerland and (b) a Great Reed Warbler during winter in a stationary unknown position. The upper graphs show the latitudinal positions over a specific time period. Positions were derived through 'civil twilight calibrations' (open circles) and through 'Hill–Ekstrom calibration' (black circles). In the lower graphs (a2 and b2), the latitudinal positions derived though different methods are compared. The black dotted line in a1/a2 gives the real position of the geolocator.

Although our study is restricted to a subset of possible factors, we are confident that the main results capture the general patterns in shading effects of different confounding factors. Light intensities measured on rooftops without interference by neighbouring buildings or trees reflect local weather conditions. The derived median day lengths were a few minutes shorter than expected for ideal (non-interfered) circumstances, resulting from frequent cloud cover at both study sites (~50%). Similarly, an asymmetry in cloud cover between sunrise and sunset can also explain an observed shift in the timing of local noon. At site 2, for instance, more cloud cover during the afternoon leads to earlier timing of local noon. Obviously, weather conditions are highly variable in space and time. Therefore, the accuracy and precision of geolocation by light is likely to be strongly affected by variation in weather between sites, climatic zones and seasons. Weather can cause a systematic bias in positioning owing to moderate levels of shading, but high variability between twilight events (even within a single day) will impact the precision of geolocation too. Topography, especially mountainous regions, can cause complex mosaics of shadows in the valleys and exposed locations at mountaintops. The relative difference between the altitude of the eastern horizon (where the sun rises) and the western horizon (where the sun sets) can result in asymmetrical shading of

dawn and dusk times, which, most importantly, affects the estimate for longitude. Similar patterns may occur for deviations from true day length and hence influence the latitudinal positions. We showed that day length was shorter in the valley than on top of the mountain, with the latter having relatively longer days than predicted, owing to high altitude and a resulting broader horizon (Fig. 3b). In contrast to the effect of weather, the light regime in mountainous regions could produce systematic deviations resulting in lower accuracies of positions.

Vegetation had the strongest mean effect on the light intensity patterns among the factors studied here. However, its effect on light-level measurements is probably as diverse as vegetation itself. In general, vegetation density, that is, shading by plants, affected the measured day lengths and thus the accuracy of latitudinal estimation. The effect increased from shrub to deciduous forest locations and reached the most extreme median deviation of nearly 1 h in the deciduous woodland (Fig. 3c). In addition, the vegetation effect is probably only similar during short time periods (except for tropic regions), as shading effect is most prominent in the growing season (when plants and leaves are fully developed) and relaxed during autumn and winter (when leaves fall off and many plants disappear). Furthermore, vegetation has rarely a homogenous

structure, and thus, highly variable shading intensities may occur within the same habitat. In addition, local weather conditions may influence the effect of topography and vegetation by adding a variance to the positions.

These patterns in accuracy and precision only serve as examples for the particular study sites and periods but clearly show how light intensities are influenced by environmental factors in general. Our results can facilitate correct interpretation of geolocator data collected in terrestrial habitats. In addition to the environmental factors, the behaviour of the animals could also affect light intensity pattern and potentially contribute to the shading effects discussed above. However, the errors in day length and time of midnight/noon for on-bird geolocators in our study strongly resemble the errors related to the birds' specific habitats. Animals that typically inhabit open landscapes (e.g. terns) experience much less shading than animals in dense vegetation like the forest-dwelling nightingales. These results are derived from stationary periods at the breeding place, but it should be borne in mind in particular that movements can affect the shading patterns experienced, for example, if moving between different vegetation types or within a highly heterogeneous small-scale mosaic with dense vegetation plots.

In view of this, prior knowledge on the typical behaviour and habitat use during twilight of the study species is certainly an advantage for the interpretation of geolocator data. Animals might also use different habitats during different migration periods (e.g. the Sedge Warbler *Acrocephalus schoenobaenus*: Ormerod 1990; Chernetsov 1998). Furthermore, during long-distance migration, most passerines spend the twilight periods outside the vegetation with a free view to the sky to recalibrate their compass (Able & Able 1990; Åkesson, Alerstam, & Hedenstrom 1996; Cochran, Mouritsen, & Wikelski 2004; but see: Chernetsov *et al.* 2011). Such behaviours potentially lead to highly different shading between migration and resident periods. Large-scale movements such as migration itself influence the light intensity patterns depending on the travel speed and direction. For example, longitudinal movements undertaken within a day or night will affect day or night length, with movements towards the east decreasing it and those towards the west increasing it. In the same way, latitudinal movements increase or decrease the day/night length depending on the time of the year. These behavioural patterns and their variability may affect the precisions of both latitude and longitude estimates.

In contrast to the accuracy in latitude estimations, we must consider noise in twilight event determination and therefore decreasing precisions in both longitude and latitude. Selection of the most suitable study species (including its habitat use throughout the year) can guarantee high-quality data. For example, if the tracked animal experiences equal shading throughout the year and the correct sun elevation angle can be determined for a period for which the location of the animal is known, the estimated positions will be relatively close to the true positions (with the exception of high latitudes and dates close the equinoxes). Such an ideal scenario certainly does not reflect those encountered in practice. Migrating animals typically cross different climate zones and experience very different and variable weather conditions. For example, Wheatears (*Oenanthe oenanthe*) migrate from polar climate via temperate climate to the tropics (Förschler & Bairlein 2011) and additionally use different types of vegetations during their journey (Glutz & Bauer 1988) with very different light conditions. These highly variable conditions challenge the determination of a single sun elevation angle for calibration especially because geolocation by light usually aims to estimate the whereabouts of the animals without prior knowledge of local conditions (i.e. habitat choice).

However, we tested different ways to derive sun elevation angles, attempting to cover a range of general circumstances of migratory species. The 'in-habitat calibration' uses the conditions experienced by the animal during breeding or at another known location. The data can be collected either with stationary logger devices in the particular habitat or by using the first part (e.g. breeding period) of the measurements on the animal at the known site additionally taking behavioural pattern into account. By using the 'in-habitat calibration', it is assumed that habitat choice and weather conditions are almost the same over the whole non-breeding period. Seasonal changes in behaviour and behavioural variability during resident periods obviously violate this assumption. In this study, we were able to illustrate how seasonal effects influence the calibration with the stationary geolocator in reed beds (Fig. 5a). Calibration during late summer underestimates the latitudes of a later period where vegetation density was decreased. The comparison of calibration methods for the Great Reed Warbler data also shows that the 'in-habitat calibration' does not necessarily reflect the shading intensity during the wintering site. Certainly, calibration through field data always works best if the light conditions experienced during calibration resemble the conditions at other times; however, this assumes that the researcher already has some knowledge about the location of the bird, which is usually the aim of the study.

The 'Hill–Ekstrom calibration' can be applied independently from data gathered in the field with no prior information (e.g. about position, habitat) being required. Moreover, this calibration leads to an accurate latitudinal estimation for each stationary period (Fig. 5), but it makes rather strong requirements, namely that (i) the animal must be resident over the applicable period and (ii) the average shading intensity for the whole period must be equal. Recent geolocator studies provided evidence that some migratory species fulfil the criteria – establish a major wintering site and remaining resident for long periods (Stutchbury *et al.* 2009; Bächler *et al.* 2010; Klaassen *et al.* 2011; Kopp *et al.* 2011; Tøttrup *et al.* 2011). But long stationary periods may also imply seasonal changes in weather conditions and/or vegetation development that alter the shading intensity. Additionally, individual behaviour may differ between the wintering sites and the breeding period, and individuals may use a broad range of habitats (Herrera 1978; Salewski & Jones 2006). Such behavioural patterns prevent the required stable shading conditions for the

'Hill–Ekstrom calibration'. Finally, the 'rooftop calibration' fits best to open-landscape species and to periods when birds are outside the vegetation, for example during migration. Again, prior knowledge about the behaviour of the focal species can assist in the choice of one or more calibration method.

Even if the best possible calibration method for a particular data set is used, positions from geolocation by light are inherently less accurate than positions from GPS ('global positioning system'). Therefore, we can only emphasize that interpretations, questions and model species must be accurately attuned to the methods. In the last two decades, studies using light-based geolocation typically tackled questions related to migration routes and schedules, foraging behaviour, and winter distributions of populations and individuals. For example, the degree of migratory connectivity can reliably be measured in species/populations that are distributed along an east–west gradient like the European hoopoe (Bächler *et al.* 2010) as the calibration method is not of high importance for the interpretation of east–west distributions. Spatiotemporal analyses of migration schedules are common procedures, but their quality highly depends on the precision of underlying data. Measurements of speed, for example, require accurate arrival and departure times, but these dates can be only detected if the positions lay outside the precision range of the anterior and posterior stationary site. This most notably compromises the correct determination of times in species with low or moderate migration speed. Additionally, longitudinal movements can provide more precise details, as estimation of longitude is more precise than estimation of latitude (Fudickar, Wikelski, & Partecke 2011). To improve such analyses of migration schedules, speed, etc. analytical methods are needed to distinguish between different stages of migration modes, that is, residency vs. movement. Detailed knowledge of accuracy and precision is also crucial if positions are combined with environmental data such as local landscape structures, weather conditions, food supply and vegetation indices (NDVI, sea-surface chlorophyll, etc.). Any mismatch between inferred and true positions can potentially lead to false conclusions. Nonetheless, light-level geolocation is a powerful tool for the investigation into large-scale movements of individual animals. It is currently the only method to track relatively small-sized migrants, but some abiotic and biotic factors can hamper its application. Understanding and consideration of the method's theoretical background and the potential limiting factors, as well as calibration issues, should guarantee new insights into the ecology of animal migration.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Statistics of stationary geolocators and the resulting deviations in latitude and longitude.

Appendix S2. Calibration.

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