QUANTIFYING THE EFFECT OF TIME ON GEOLOCATION ACCURACY IN SEABIRDS

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ABSTRACT

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Light-based geolocation can be an effective tool for understanding movements and distributions of free-ranging seabirds, particularly during migrations and long-distance foraging trips. The light levels recorded by geolocators (global location sensors; GLS loggers) are used to infer latitude and longitude of individuals from day length and time of local midday relative to UTC (Coordinated Universal Time), respectively. However, there is an associated inaccuracy in these location estimates, associated with both systematic and random error. Previous studies have quantified this error by calculating distances to locations over the same time period derived from more accurate devices such as satellite transmitters (platform terminal transmitters; PTTs) or GPS devices. These approaches to quantifying error have focussed on twice daily or daily locations, whereas the aims of many studies using geolocation can be achieved by identifying areas used over long time periods, typically during the non-breeding season. We reanalysed data from a previous study where 12 Black-browed Albatrosses *Thalassarche melanophris* were tracked simultaneously with GLS loggers and PTTs. Rather than assessing location error over individual half-days or days, we took advantage of the principle of central tendency and calculated the distances between centroids obtained from GLS loggers and PTTs over different time periods. Our results show that overall geolocation error decreases with an increase in the number of days of data (Δ centroid distance: 76.5 ± 3.9 km [mean ± standard error] when using 30 d of location data), most likely due to a reduction in random error. Centroids are still subject to residual error, but researchers can have confidence that their accuracy is sufficient to answer many research questions for seabirds.

Key words: biologging; location estimation; geolocation error; seabirds; space use

INTRODUCTION

Geolocation is a widespread and effective tool for monitoring mid- to large-scale movements in free-ranging seabirds (Lisovski et al., 2020). Estimation of location using light levels recorded at known times by global location sensor loggers (GLS loggers; also termed geolocators) can provide crucial data to quantify space use, migrations, and other movements. Since the miniaturisation of GLS loggers in the early 2000s, they have been deployed on numerous seabird species (e.g., Egevang et al., 2010; Guilford et al., 2009; Militão et al., 2022; Swindells, 2019). However, there are limitations in the suitable applications and the inferences that may be drawn from light-based geolocation, as the locations are subject to inherent error, including random error, as well as systematic error associated with bird behaviour, shading of the sensor, proximity to the equinox, and other factors, including latitude (Halpin et al., 2021; Hill, 1994). This has driven the development of a variety of methodologies and packages that may improve accuracy through incorporation of environmental data, particularly sea-surface temperature (Lisovski et al., 2020; Merkel et al., 2016).

The few studies that have attempted to quantify the error associated with geolocation estimates for seabirds have compared locations twice-daily or daily with those from much more accurate tracking devices (Argos satellite transmitters or GPS loggers). These studies have reported substantial mean errors (408 ± 473 km, Halpin et al., 2021; 186 ± 114 km, Phillips et al., 2004; 202 ± 171 km, Shaffer et al., 2005). However, studies of animal movement using GLS loggers often focus on research questions over longer temporal scales, such as the areas used for part or all of the non-breeding season (Atkins et al., 2023; Pelletier et al., 2020). In such contexts, daily location information may not be required. Random error associated with the process of geolocation should be temporally and spatially unbiased, and so a mean location over time should account for at least some of the daily-scale variation in location accuracy through the principle of central tendency. However, the effect of averaging locations over time has yet to be quantified.

One approach commonly used to visualise and quantify space use by an individual or population over time is to calculate the centroid, which is the geometric centre of a cloud of locations over a number of days (Phillips et al., 2005). Centroids are commonly used to compare the regions used by individual seabirds or populations of seabirds over timescales greater than a single day (Atkins et al., 2023, Pelletier et al., 2020). They are most useful when preliminary analysis indicates that locations are clustered in the same general area over the period of interest, i.e., birds are not moving large distances between two or more distinct regions. The clustering of successive locations over one or a few days may form part of the pipeline for smoothing locations to decrease geolocation error (Phillips et al., 2004; Porter & Smith, 2013); however, whether clustering over a prolonged period reduces geolocation error has not been tested, despite the likely reduction in random error due to the general principle of central tendency. Instead, studies that present centroids or smoothed data frequently cite error estimates for daily or twice daily locations and assume these apply to multiday datasets (Franklin et al., 2022; Zajková et al., 2017); however, this may overestimate the random error and influence how location data are used and interpreted.

To investigate how the accuracy of centroids derived from GLS data may change with the number of days of data collected, we reanalysed data presented in Phillips et al. (2004), in which 12 Black-browed Albatrosses *Thalassarche melanophris* were tracked simultaneously with both GLS loggers and satellite transmitters (platform terminal transmitters; PTTs). Our objective was to test the extent to which accuracy of centroids may be improved by the inclusion of a greater number of location estimates (days of data).

METHODS

Data collection

Devices were deployed in late January 2002 on 12 Black-browed Albatrosses just after the brooding stage on Bird Island, South Georgia (54°00′S, 038°03′W). Birds were fitted with a GLS logger weighing 9 g, a 30-g PTT (Microwave Telemetry) and a 17-g radio transmitter (Sirtrack). PTTs were attached to mantle feathers using Tesa tape. GLS loggers and radio transmitters were attached using a plastic ring on either leg. All devices were retrieved from birds 50–60 d after deployment, except for one bird that failed breeding early and whose devices were removed in the following year (see Phillips et al., 2004). The focus of our current study was limited to the data from GLS loggers and PTTs only, available from Phillips (2002). Although the albatrosses were commuting long distances to and from a central place (the breeding site), these are the only data of which we are aware with which assessment of geolocation error over an extended time period can be made. Moreover, the data are from a species having an overall foraging area during breeding that is comparable in size to many other seabirds during the non-breeding season, i.e., hundreds of kilometres.

Device processing

We used the processed and filtered GLS data presented in Phillips et al. (2004) to allow for a direct comparison to the oft-cited value for location accuracy in that study. In brief, GLS loggers sampled light intensity every 60 s and recorded the maximum light level sensed in each 10-min window. The light data were then analysed using MultiTrace software (Jensen Software Systems) to identify transitions between daylight and darkness, resulting in two locations per day. These were filtered to remove locations on either side of the equinox (when light-based latitudes are unreliable), those associated with light-level interference, and any that failed an iterative speed filter (see Phillips et al., 2004, for details). We also ran a speed filter on the data from the PTTs and then averaged these data to generate the mean positions during each daylight and darkness period. After processing, daily location estimates from the two devices were available for between 26 and 48 d for each individual bird (mean ± standard deviation = 29 ± 9 d).

Statistical analysis

All analyses were undertaken in the statistical software R Version 4.3.1 (R Core Team, 2023). Visual examination of all filtered locations indicated a single cluster of points for each individual, thus supporting the use of centroids. We estimated mean centroids for each albatross for both GLS and PTT data using the R package "sf" (Pebesma & Bivand, 2023). We estimated these centroids using an increasing number of days of data, from one up to the total number of consecutive days, with data from both devices for each individual. For each number of days to be included, we randomly selected that number of consecutive days without replacement from the data set, using the same set of days for each device type. We then derived the centroid for each device with that set of days and then calculated the distance between the centroids. We then repeated this process 1,000 times in a resampling procedure and calculated the distances between the centroids that were calculated for each device type for each individual for each number of days in each iteration.

After initial inspection of the data, we modelled the relationship between the number of days with location data and centroid distance using non-linear least squares regression according to the following function, where "*a*" is the maximum distance value and "*b*" is the scale parameter for each resampled draw: $\textit{Centroid distance} \approx a \times \textit{number of days}^{b}$.

We included individual ID as a random intercept to account for any individual-level variation in the relationship between the number of days with location data and accuracy. We checked model residual plots to confirm that the distribution of residuals was random and compared residuals against fitted values and model covariates (Zuur et al., 2014). We then extracted the model estimates and associated confidence intervals across the models through model averaging; we calculated the weighted average and associated confidence intervals via Akaike information criterion (AIC) comparison. We determined the extrapolated model prediction curve to have reached an approximated asymptote when the extracted slope—i.e., the improvement in distance between mean centroids for one additional day of data—was < 0.2. All means are shown ± 1 standard deviation unless otherwise specified. All plots were produced using the R package "ggplot2" (Wickham, 2016).

Ethics statement

The tagging was approved by the British Antarctic Survey Animal Welfare and Ethics Committee and carried out with the permission of the Government of South Georgia and the South Sandwich Islands.

RESULTS

As expected from the principle of central tendency, the greater the number of days of data, the smaller the distance between the centroids calculated for each device type, i.e., the geolocation error (Fig. 1). The rate of change in the distance between mean centroids declined with the inclusion of more days of data.

The constants from the model are as follows:

$$\textit{Centroid distance} \approx 223.52 \times \textit{number of days}^{-0.32}$$

There was variation among individual birds in the absolute geolocation error. However, data from all individuals showed the same overall relationship: i.e., a decline in the mean distance with an increasing number of days with location data. When extrapolated, this relationship reached an asymptote after 86 d of data when the predicted error was 54.9 km ± 2.3 km.

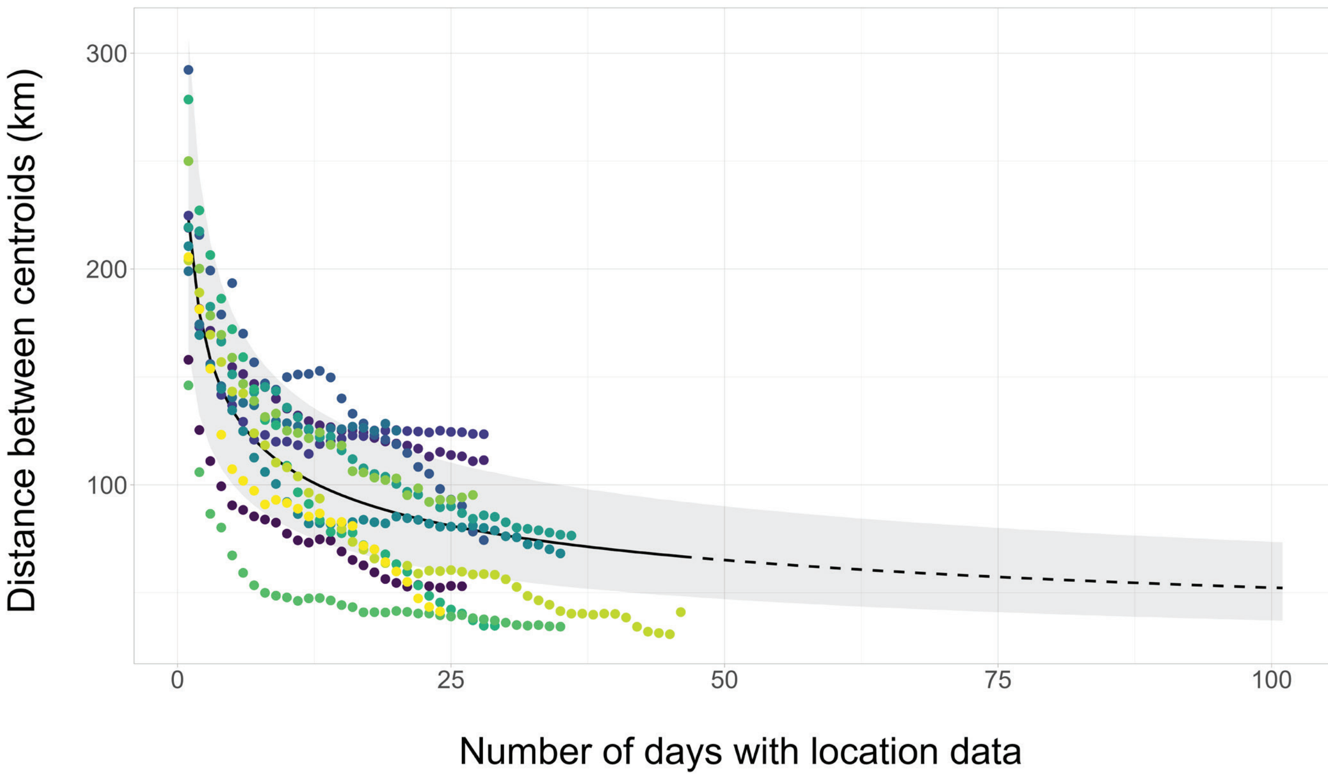

Fig. 1. Data and predictions from non-linear least squares models of the relationship between the number of days with location data and the distance between centroids derived from global location sensor loggers and platform terminal transmitters deployed on Black-browed Albatrosses *Thalassarche melanophris*. The dashed line is the model prediction beyond the bounds of the observations, and the shaded area indicates the 95% confidence intervals. Symbol colours indicate data for each tracked individual.

On average, increasing the time period over which the centroid was calculated from one to 30 d reduced the error by 60.0%. An increase from one to five days led to a reduction of over 30.1% (Table 1, Fig. 2).

DISCUSSION

We have shown that the more days of GLS data used to estimate centroids of distribution, the greater the accuracy of this average location. This was particularly apparent as the sample size increased from one to ~12 d of data at the point of maximum curvature (Fig. 1). The mean distance of 193.5 km between daily locations derived here from the GLS and PTT data for single data points is very similar to the mean of 186 km presented in Phillips et al. (2004). However, the improvements in accuracy for the estimation of mean centroids obtained from more days of data that we identify were greater than the improvements shown through increased iterative smoothing (by repeated interpolation of intermediate fixes between successive locations) in Phillips et al. In that study, smoothing eight times reduced the error by an average of ~24 km. Importantly, the mean geolocation error associated with the use of

TABLE 1
Non-linear least squares model predictions of the mean error across individuals in the distance between centroids calculated from increasing days of data from GLS loggers and platform terminal transmitters

Number of days with data	Mean centroid distance error ± standard error (km)
1	193.5 ± 12.9
5	134.1 ± 3.7
15	94.5 ± 3.7
30	76.5 ± 3.9

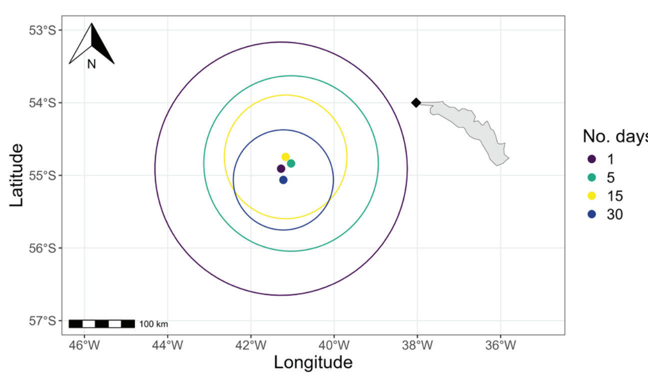

Fig. 2. The distance between mean centroids of data from global location sensor loggers and platform terminal transmitters (PTTs) deployed on Black-browed Albatrosses *Thalassarche melanophris* breeding on Bird Island (diamond) using a varying number of days with location data. The color-matched circle around each point shows the associated error around the centroid of the PTT data for the indicated number of days.

centroids is much lower than that associated with twice-daily or daily locations in previous studies (Halpin et al., 2021; Phillips et al., 2004; Shaffer et al., 2005). Consequently, researchers should have confidence that centroids can accurately represent the general area used by an individual over a number of days. While the largest reductions in error (> 60%) were found when increasing the number of days of data from very small sample sizes (i.e., < 10), the error continued to decrease with the inclusion of up to 86 d of data. Using centroids will tend to reduce the random error, although there will always be some residual systematic error attributable to bird behaviour (e.g., shading), latitude, time of year, and other factors, as highlighted by the asymptote in Figure 1 not reaching zero.

In this study, the daily geolocation estimates were produced with a fairly unsophisticated workflow that did not incorporate data from other sensors such as sea-surface temperature, which can increase location accuracy if birds are in well-stratified water masses (Shaffer et al., 2005). Many more recent R packages and methodologies reduce apparent geolocation errors by incorporation of species-specific information on movement speeds, environmental data, and smoothing (Lisovski & Hahn, 2012; Merkel et al., 2016; Rakhimberdiev et al., 2017). Consequently, the overall error associated with using a centroid might be even lower using these improved processing algorithms. Centroids may be particularly useful for comparing the main areas used by individuals if the annual cycle of the study species includes periods of residence in stopover or wintering areas, as seen in most seabirds during the non-breeding season (Atkins et al., 2023; Bennett et al., 2024; Tranquilla et al., 2013). Centroids are less suitable for birds that use multiple, distinct stopover or wintering areas, which should be straightforward to determine by visualisation of individual locations. Knowledge of species behaviour and matching the analytical approach to any given research question is also useful in determining the most appropriate technique to quantify space use in each case. In our study, birds were tracked in the chick-rearing period when undertaking long flights to and from the colony with relatively fast travel speeds. Were our study to be repeated on birds not subject to a central-place foraging constraint (i.e., not undertaking movements at this scale) it is possible that the level of error would decrease further.

Reduced error associated with centroids calculated over longer time periods demonstrates the general principle of central tendency. However, it must be acknowledged that centroids are not appropriate for answering research questions relating to space use at fine temporal or spatial scales, and the advantages and disadvantages differ across species and datasets. Locations are of course still subject to residual error that depends on species, latitude, bird behaviour, and environmental factors (Halpin et al., 2021; Lisovski et al., 2012). Studies using geolocation will need to remain cautious about these inherent biases, as they may lead to erroneous conclusions. Consequently, we would recommend that the results of this study be used as a guiding principle rather than the mean values be quoted verbatim as metrics of geolocation accuracy, a caution that would also be wisely applied to all published errors for daily locations. Overall, we show that centroids derived from GLS data may provide an accurate indication of the area used by an individual seabird over a prolonged period, since the error is considerably lower than for twice daily or daily location estimates. Future research should determine if our conclusions also apply to other species and regions and whether error is further reduced by using other processing routines and would benefit from applying new technologies to collect concurrent GPS and GLS for long periods during the non-breeding season.

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AUTHOR CONTRIBUTIONS

SB and JAG conceived the ideas and designed the experimental methodology; RAP collected the data; SB analysed the data, supported by JAG; SB led the writing of the manuscript, supported by RAP and JAG. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The PTT data used in this study are available for download from the BirdLife International Seabird Tracking Database (Phillips, 2002).

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