ACCEPTED BIRD STUDY 29TH OCTOBER 2019

Light stalks increase the precision and accuracy of non-breeding locations calculated from geolocator tags: a field test from a long-distance migrant

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Capsule: There is a substantial gain in precision and accuracy of geolocator locations when using a light stalk.

Aims: Light stalks or tubes increase the accuracy of geolocators when tracking migrant birds because they reduce potential shading of the light sensor by feathers but may increase detrimental tag effects. We aimed to determine how adding light stalks to geolocator tags increased accuracy and precision of locations.

Methods: We quantified how precision and accuracy of geolocator locations was affected by comparing variation of sunrise and sunset times from tags with variable length light stalks (6 of 0 mm, 8 of 5 mm and 21 of 10 mm). Tags were fitted to Whinchats *Saxicola rubetra* in central Nigeria (the known location to compare accuracy), and variance in latitude and longitude of geolocator estimated locations were also compared across light stalk lengths during spring migration stationary locations, and at breeding sites in Eastern Europe, for both Geolight and FlightR methods.

Results: Without a light stalk, the standard deviation of sunset and sunrise times increased by 50% and 100% respectively (i.e. less precise): confidence intervals for latitude were larger by about 4.3 degrees at non-breeding low latitudes and 1.8 degrees at stop-over latitudes, or confidence intervals for longitude were larger by 2.3 degrees, dependent on analysis method. Estimated sun elevation angles were significantly less accurate and so calculated non-breeding locations were significantly less accurate by about 8 degrees of latitude. Precision in sunrise, sunset times, latitude and longitude, was similar when using a 5mm or 10mm stalk.

Conclusions: The results show a substantial gain in precision and accuracy of low latitude geolocator locations when using a light stalk that brings the sensor above covering feathers. There is no advantage from longer light stalk lengths than those necessary to just expose the light sensor above the feathers, at least for small passerines.

Geolocators are being used widely to track small migrants but some tag designs may impact on the survival and behaviour of a tagged bird (Bowlin et al. 2010, Costantini and Moller 2013, Weiser et al. 2016). Light stalks are one aspect of geolocator design that can vary in both presence and in size. Light stalks are fitted to geolocator tags to increase the accuracy of light readings because they place the light sensor above potential shading by the feathers (Bridge et al. 2013). Similarly, some geolocators use protruding light tubes that direct light onto a sensor positioned on the logger. Accurate records of light intensity are needed because locations are determined by sunrise and sunset times (Lisovski and Hahn 2012), and shading of the sensor can lead to later and earlier apparent sunrise and sunset times respectively (Lisovski et al. 2012), potentially leading to locations being calculated with greater error (Fudickar et al. 2012, McKinnon et al. 2012). Overall, precision of geolocators is important because gelocators are the current means by which non-breeding and stop-over locations are identified for a large number of small migrant bird species (Stutchbury et al. 2009, McKinnon et al. 2013) that are undergoing large scale declines possibly associated with where they spend the non-breeding season (Sanderson et al. 2006, Vickery et al. 2014).

Light stalks or tubes, and other protruding parts of tags, however, may increase detrimental tag effects by increasing drag and weight (Dougill et al. 2000, Pennycuick et al. 2012, Bodey et al. 2018) and may even interfere with nesting in enclosed areas (Gow et al. 2015). Although some studies show no impact of light stalks on survival (Blackburn et al. 2016, Peterson et al. 2015), light stalks have been shown to impose costs in some species (Scandolara et al. 2014, Morganti et al. 2018). It is therefore important to identify how these costs can be reduced or eliminated while still allowing meaningful data collection. Not only can these impacts lead to biased or misleading data because of tag effects changing bird behaviour or survival, but also for ethical reasons and because geolocators are often used to study declining species. Nevertheless, if light stalks increase data precision and accuracy their use can be warranted, particularly if costs are shown to be low (Raybuck et al. 2017). The perceived benefits, i.e. the increase in precision of locations by using a light stalk, have rarely been tested in the field, and not in low latitudes during the non-breeding season (e.g. see Peterson et al. 2015), the main region of their utility, i.e. to determine where northern temperate species spend the non-breeding season (e.g. the studies reviewed in Finch et al. 2017). This is particularly important because variation in day length with latitude is small at low latitudes (Shaw and Cresswell 2014) and sun elevation and light intensities at mid-day are much higher. Consequently, the relative advantage of light stalks may well be dependent on latitude (McKinnon et al. 2012).

Precision of locations should only be compared during stationary periods when multiple imprecise values can be averaged to gain an estimate of the true mean. But stationary periods are defined by the variance of the geolocator data themselves, making a circularity (Lisovski and Hahn 2012). Long distance migrants are, however, likely to have long stationary periods during the non-breeding season (i.e. their wintering territory Newton 2008, Cresswell 2014) and during the breeding season (i.e. their summering territory). Similarly, during the clearly defined spring migration period when birds are between breeding and non-breeding areas, any comparison of accuracy of location stop-over periods is likely to be subject to the same bias in defining stationary periods, so allowing a like-for-like comparison of the effect of light stalk length.

Here we deploy geolocator tags on Whinchats *Saxicola rubetra* from the non-breeding season through the spring migration period from West Africa to breeding in Eastern Europe. Tags had variable light stalk lengths, 0mm (i.e. no light stalk), 5mm and 10mm. We compared the precision and accuracy of recorded sunrise and sunset times, and corresponding locations, calculated from the tags with different light stalk lengths during stationary periods (during non-breeding, when sunrise, sunset and location was known, during breeding and during major stop-overs of more than two days during spring migration). We expect longer light stalks to have greater precision and accuracy. We also test whether any of this precision and accuracy variation dependent on light stalk length varied with latitude or longitude. We expect light stalks to have a greater effect on precision and accuracy at lower latitudes, when differences in day length are much smaller, or further away from areas used for calibration.

Methods

The study took place between February 2013 and November 2013 (Year 1) and February 2014 until April 2015 (Year 2) during the dry season (early September to late April) on the Jos Plateau in the guinea savannah zone of central Nigeria, West Africa (N09°53', E08°59', approximately 1250 m altitude). Some colour-ringed only Whinchats were captured outside of these months (i.e. earlier in the wintering period or were colour-ringed birds that had returned from previous winters) to evaluate whether the geolocators affected survival (see Blackburn et al. 2016). Whinchats were captured within an area of approximately 5 x 8 km; full site details are described in Blackburn and Cresswell (2016).

Whinchats were caught with spring traps and mist nets in late February and March in 2013 or 2014. Birds were aged and sexed (Jenni and Winkler 1994), ringed with unique combinations of colour-rings, and fitted with a geolocator. In Year 1, we deployed 49 and in Year 2 we deployed 130 geolocators fitted using leg-loop ‘Rappole-Tipton’ (also called backpack) harnesses (Rappole and Tipton 1991). Full details of tag and harness design are given in Blackburn et al. (2016). Tags weighed on average 0.63 g (0.01SE), representing 4.1 % of average body mass (mean body mass of Whinchats in the study was 15.2 ± 0.05 SE g; N = 471). There was no overall significant reduction in between-year resighting rate (our proxy for survival, Blackburn and Cresswell 2016) comparing tagged and untagged birds in either year (Blackburn et al. 2016). There was no strong evidence for an effect of light stalk length on survival rate (Blackburn et al. 2016).

Different individual Whinchats were fitted with slightly different tag designs, with variation in the length of the light stalk protruding from the tag, at an angle of 45 degrees (36 x 0 mm light stalks, 47 x 5 mm light stalks and 96 x 10 mm light stalk: Figure 1 and see Blackburn et al. 2016 for full tag details). Geolocators without stalks (0 mm) were completely covered by back feathers after deployment and could not be seen at all on good views of perched birds after release. Geolocators with 5mm stalks, had visible stalks just protruding above the back feathers on good views of perched birds after release, although occasionally the stalks were seen to be obscured by the primary feathers when the wings were folded. Geolocators with 10mm stalks, always had visible stalks protruding well above the back and wing feathers on good views of perched birds after release.

Attempts were made to recapture any returning tagged bird resighted in the following winter. Upon recapture, geolocators were removed by cutting the harness and birds were released unharmed after briefly assessing body condition (see Blackburn et al. 2016). Sample sizes in this paper are less than the number of individuals that returned with geolocators because 18/39 returning birds in 2014 could not be recaptured (because many had become extremely wary of spring-traps and mist-nets), two individuals had lost their loggers because of harness failure, and four loggers in 2013, and one in 2014 suffered battery failure before the birds reached the breeding ground (data from their non-breeding ground and for as much of migration as possible were used in these cases). Overall, we include all possible data from 35 individuals (35 tags were recovered, 6 with 0 mm, 8 with 5 mm and 21 with 10 mm light stalks – the difference in frequency representing unequal numbers of the different length light stalk tags deployed).

Analyses

Three sets of analyses were carried out. First, we examined whether presence of a light stalk affected the variation in recorded sunrise and sunset times. The six tags recovered without light stalks were matched with six tags recovered with 5mm light stalks and six tags recovered with 10mm light stalks. These tags were chosen so that sample sizes of tags were the same in each light stalk group, with individual tags selected on the basis that they had data available on all 10 days of the period (matching with other tags with light stalks does not change the results qualitatively). Consequently, a 10 day period from March 31st until April 9th 2014 was chosen because all birds in the sample had been tagged by then and the first Whinchat in the sample left the study site on the 10th April. Each raw data file (containing light intensity readings every 2 minutes) from each tag was then examined using an R script. This identified the time of the first and last non-zero light reading on each of the 10 days (a value above zero, preceded at sunrise (time < 08:00) or followed at sunset (time > 16:00) by at least 20 zero values, representing 40 minutes). Real sunrise and sunset times calculated for the latitude and longitude of the tagging site for each day, with a typical recorded solar zenith angle of 92, were then subtracted from these times to give an error. The mean sunrise and sunset time difference, and the standard deviation of this difference, for each logger was then calculated resulting in two mean differences (errors) and their standard deviations for each of 6 loggers, of the three different light stalk types (N = 36). A General Linear Model was then run to predict the mean difference in terms of light stalk type (3 way factor), sunrise or sunset (2 way factor) and their interaction. A second identical model used the standard deviation of the time difference as the dependent variable.

Time difference or SD of difference ~ light stalk type + (sunrise/sunset) + light stalk type(sunrise/sunset)*

Second, we analysed variation in location data calculated using a standard methodology for geolocators based on the R 3.6.0 (R Development Core Team 2014) library Geolight (Lisovski and Hahn 2012), and how location then varied in the presence of a light stalk. Data from all 35 available tags were used. Raw data were downloaded, viewed and preliminarily cleaned using the BASTrack software suite (British Antarctic Survey, Cambridge, UK; see Fox 2010 for an overview of the following processes). We adjusted for clock drift, assuming that any drift was linear. We used the Transedit2 software that is part of the BASTrack software to view raw data as light curves over time. We used a threshold value of 2-5 to define sunrise dependent on individual bird records at the known location of the non-breeding site.

False twilight events due to shading from weather or vegetation were identified and removed with the 'minimum dark period' filter (we used 4 hours), which removes any impossible sunrise and sunset events (for a review and exploration of the effects of enviromental factors on geolocator data, see Lisovski et al. 2012). Data were then visually inspected to ensure that only one sunrise and sunset occurred within any 24-hour period.

Because conditions away from the wintering grounds are unknown, we used four different values of sun elevation angle (SEA value) to calculate latitude: note results do not change depending on which set of SEA values we use. First, we used a sun elevation angle of -4.5 for all loggers in both years. This is a reasonable median value and although some loggers will have had lower values and some higher, this would simply increase the error of estimating locations but should not introduce any systematic bias. The value of -4.5 was chosen because this gave the most biologically sensible plots of locations immediately after crossing the Sahara (i.e. all locations were on land in North Africa or Europe rather than in the Mediterranean Sea, within 2 standard errors of the mean of latitude for the stop-over period); see Blackburn et al. (2018). Second, we used an average SEA value of -4, the mean location calculated for each bird for sun elevation angles -2 to -6 at 0.5 increments (i.e. 9 mean locations), then averaged across these 9 locations, applied to all birds regardless of year. Third we used the sun elevation angle for each individual that best reflected their known wintering location on tagging (range of values -3.5 to -5.9, mean -4.6); we used the LocatorAid software from the BASTrack software suite, which uses known residency times and wintering location to calculate the corresponding wintering ground SEA value. Fourth, we attempted to find the correct summer angle using the Hill-Ekstrom (H-E) calibration method (Hill & Braun 2001, Ekstrom 2004, see Tottrup et al. 2012) in which we selected the SEA value that gave the least amount of variation in latitude during the first two weeks in June when all individuals were very likely to be stationary on their breeding grounds (see Blackburn et al. 2017 for further details and validation of this approach). If the calibration was not successful, we used the mean value for all the loggers for which the calibration had been successful, calculated for each year separately (range of values -2 to -4.5, mean -3.8). We used these SEA values to calculate noon and midnight locations derived from sunrise and sunset times using the 'coord' function in Geolight. Because of the uncertainty introduced by not knowing the SEA value for any stationary period, we analysed the locations with each of the four different sets of SEA values. Results are biologically and statistically very similar in all cases. Here we present the results in detail from the most reasonable assumption of SEA value (i.e. -4.5 for all birds), but also include the range of values obtained from the analyses using the other three sets of SEA values to demonstrate the similarity. Note that longitude is not affected by choice of SEA value.

Stationary periods (stop-overs of more than two days or breeding locations) were determined using the function ‘ChangeLight’ in Geolight (quantile = 0.95, day = 2) and confirmatory visual inspection of latitude and longitude changes with date (see Blackburn et al. 2018). Data analysis to identify stationary periods was restricted to the spring migration period (i.e. late March to early June). All periods identified as migratory periods (through large daily changes in sunrise and sunset time) were confirmed first by checking how the product of 5-day moving average standard deviations for latitude and longitude also varied (all peaks were coincident with the periods identified by Geolight), and by manual visual inspection of latitude and longitude with date (as a Whinchat migrates longitude and latitude change suddenly, with the latter increasing very sharply, particularly for the onset of migration across the Sahara, see example trace, Figure 1 in Blackburn et al. 2018). Occasionally, the Geolight ‘ChangeLight’ function indicated a non-stationary period after an individual was very likely to have reached the breeding ground (after the second week in May) and when there was no other supporting evidence for a migration. An analysis of variance to compare locations in periods either side of the Geolight non-stationary period confirmed whether locations had changed: when the mean locations were not significantly different the Geolight identified migratory period was ignored.

Third, we analysed variation in location data calculated using another standard methodology for geolocators based on the R library FlightR (Rakhimberdiev et al. 2015, Rakhimberdiev and Saveliev 2019), and how location then varied in the presence of a light stalk. Again, data from all available tags were used (although including one fewer of the tags that failed very early than the Geolight analysis because FlightR requires more data to calculate accurate locations). Light and dark periods were visualised using the ‘lightImage’ function and the predicted twilights for the non-breeding, tagging location at Jos were fitted. These were then adjusted to fit the observed tagging location twilights by setting the zenith by eye, usually with a value of 94. The function ‘preprocessLight’ was then used to set the analysis period to three weeks before migration in the spring (4 weeks if this was early coincident with the equinox) to three to five weeks after arrival on the breeding grounds (typically end of March to mid-June). 12 seed positions (that showed clear sunrise/sunset boundaries) were set (4 before, 4 during and 4 after migration); non-defined twilights were set if necessary and then all recorded twilight times were accepted without further editing in all cases. Calibration periods were set as a three-week period before 4 days before the start of first migration away from the non-breeding, tagging site. The possible grid was set at (0,5,60,65) with a minimum distance from land used of 200km, and a minimum distance from land allowed to stay at 50km. Locations were then calculated with 'nParticles' set at 10,000 and 'decision' at 0.05. Stationary migration periods were defined with a probability cut-off of 0.1 and for a minimum stay of 3 days.

A final set of latitude and longitude data with their confidence limits was thus obtained for both the Geolight and the FlightR analyses: one for each stationary period, from non-breeding ground (although for FlightR this tagging location was not used because this was the calibration period) to breeding ground, for each individual; some individuals had several stop-overs (thus several migratory legs), others made an apparently continuous flight to the breeding ground without any stop-overs of more than one day (thus only one migratory leg); some tags failed on route (Blackburn et al. 2018). For the Geolight analyses, the final data set for analysis for precision consisted of the confidence intervals of latitudes and longitudes for 125 stationary periods (35 wintering locations, 34 first and 26 second migratory stop-over periods of more than two days, and 30 breeding locations) from 35 individuals. Six individuals had a 3rd stop-over stationary period but these were not included in the data set here to maintain balanced sample sizes (inclusion does not change any results). For the FlightR analyses, the final data set for analysis for precision consisted of the confidence intervals of latitudes and longitudes for 87 stationary periods (32 first and 25 second migratory stop-over periods of more than two days, and 30 breeding locations) from 34 individuals. Eight individuals had a 3rd stop-over stationary period, and one a 4th and 5th, but these were not included in the data set here to maintain balanced sample sizes (inclusion does not change any results). The final data set for analysis of accuracy came only from the Geolight analysis because the non-breeding location was used as the calibration location for the FlightR analysis and consisted of 256 wintering locations, from 30 individuals (some tags were fitted too close to the equinox to provide usable initial wintering locations), 6 with no light stalks, 8 with 5mm light stalks and 16 with 10mm light stalks. These data were then analysed using General Linear Mixed Models in R assuming a normal distribution of error residuals and include individual Whinchat identity as a random effect in all models.

For precision: the 95% confidence interval range (i.e. upper CI – lower CI) of latitude and longitude for each stationary period was tested against stalk length (3-way factor, 0, 5 and 10mm), latitude and longitude of the stationary period and the interaction of latitude and longitude with stalk length:

*CI range of latitude or longitude ~ light stalk length + latitude + longitude + stalk length*latitude + stalk length*longitude + (1|id as a random effect)*

For the Geolight analyses, four models were fitted for latitude to explore the effects of varying SEA values. E.g., the confidence interval range of latitude assuming (1) SEA value of -4.5, (2) average SEA value of -4, (3) SEA value for the wintering location of -3.8 and (4) SEA value for the breeding location of -4.6. Only one model was run for longitude, or for latitude and longitude in the FlightR analysis because the calculations of these values does not depend on sun elevation angle (at least after initial calibration).

All models were then repeated using just the stationary periods during migration (i.e. just major stop-overs located before and after the Mediterranean), to remove any potential confounding effects of non-breeding periods being influenced by their proximity to the equinox (and so biased towards inaccurate locations at low latitudes) and those of the breeding periods being heavily influenced by the certainty that these periods were much more likely to be stationary compared to the non-breeding locations (and so biased towards accurate locations at high latitudes). These models just tested for the main effects of stalk length to give one representative average effect. We confirmed a lack of bias in defining a stationary period dependent on light stalk length by modelling the number of stationary periods by light stalk length in a GLM assuming a normal distribution of the error residuals.

For accuracy: the latitude calculated from tag data during the period birds were on the study site prior to migration, using the SEA estimated by the Hills-Ekstrom calibration, was tested against stalk length (3-way factor, 0, 5 and 10mm). Latitude was calculated for each tag using a different SEA angle of 1 to 6 at 0.5 increments (11 sets of values), from the day the tag was fitted to last day before the tagged individual left the study site (no values were calculated when too close to equinox, i.e. using only values with a confidence value of 9). The mean and standard deviation of all values for the 11 SEAs was then calculated for each tag. The mean latitude value for the SEA with the lowest standard deviation (i.e. as per the Hills-Ekstrom calibration) was selected for each tag and the difference between it and the real latitude calculated (“Calibration Error”). The difference between this SEA and the SEA required to place the tag on the correct latitude was also calculated. Variation in “Calibration Error” and SEA difference were then tested across stalk lengths with the expectation that both would be larger with shorter light stalks (both models included individual as a random factor and assumed a normal distribution of error residuals).

For all models, non-significant interactions were removed and model improvement checked by comparing AIC values. Model fits were evaluated from diagnostic model plots, and assumptions were reasonably met in all models presented here (Crawley 2007). Predicted values were calculated from models using the predict function in MuMIn library in R (Barton 2019) and using median values for all other variables in the model. Maps were plotted using the raster, rgdal, rgeos and mapproj libraries in R (R Development Core Team 2014).

Results

The precision of determining sunrise and sunset time was affected by the presence of a light stalk (Table 1) primarily because the occurrence of false negative dark records were higher for tags without light stalks (e.g. see Figure 2). The size of the standard deviation was reduced by 54% and 31% at sunrise and sunset respectively (Table 1, Figure 3). On average, the presence of a light stalk resulted in sunrise and sunset being recorded 12-13 minutes earlier or later respectively showing their greater sensitivity to low light. Tukey post-hoc contrast tests by stalk length found no significant differences between the effects of 5 and 10mm stalks in any models ($P > 0.89$).

The precision of latitude estimation was increased by the presence of a light stalk when using a Geolight analysis approach (Table 2A&B). When all stationary periods were considered, the confidence interval decreased about 4.3 degrees of latitude with a light stalk at low latitudes (Table 2A, Figure 4), equivalent to about 480 km in the non-breeding area in West Africa, but confidence intervals were little affected at high latitudes (the breeding area in Europe). There was a highly significant decrease on average in latitude confidence interval by about 1.8 degrees when considering only stop-over periods during migration with a light stalk (equivalent to about 120 km range decrease around the Mediterranean; Table 2B, Figure 5). Tukey post-hoc contrast tests by stalk length found no significant differences between the effects of 5 and 10mm stalks in any models ($P > 0.43$). Precision of longitude estimation was not affected by stalk length across all stationary periods (Table 3A) or during migratory stop-over periods only (Table 3B). The estimated number of stop-overs during spring migration calculated using Geolight was not affected by stalk length, i.e. no bias in identifying stop-overs dependent on stalk length ($F_{2,31} = 1.6$, $P= 0.22$).

The precision of longitude estimation was increased by the presence of a light stalk when using a FlightR analysis approach (Table 2C & D). When all stationary periods outside of the main non-breeding (wintering) period (which is used as a calibration in FlightR) were considered, there was a highly significant decrease in the longitude confidence interval with a light stalk. The longitude confidence interval decreased on average by 2.3 degrees with a light stalk (Table 2C, Figure 6), equivalent to about 245 km in the non-breeding area in West Africa and about 140 km for the more northerly breeders in Europe. There was also a highly significant decrease on average in longitude confidence interval of 1.8 degrees with a light stalk when considering only stop-over periods during migration (Table 2D), equivalent to about 170 km around the Mediterranean. Tukey post-hoc contrast tests by stalk length found no significant differences between the effects of 5 and 10mm stalks in any models ($P > 0.22$). Precision of latitude estimation was not (or only marginally affected) affected by stalk length across all stationary periods (Table 2C) or during migratory stop-over periods only (Table 2B). The estimated number of stop-overs during spring migration calculated using FlightR was not affected by stalk length, i.e. no bias in identifying stop-overs dependent on stalk length ($F_{2,29} = 0.3$, $P= 0.78$).

The accuracy of calculated latitude on the non-breeding area increased by about 8 degrees (Figure 7A) and accuracy of SEA estimation likely increased with the presence of a light stalk (Figure 7B). The difference between calculated latitude using the Hills-Ekstrom calibration approach and actual latitude at the non-breeding site ("Calibration Error") was marginally significantly different for no light stalks (-10.0 ± 4.1 SE degrees, t_5 =-2.4, $P = 0.059$) but not for 5 mm (-1.2 ± 1.2 SE degrees, $t_7 = -0.9$, $P = 0.37$) or 10 mm stalks (-1.9 ± 2.7 SE degrees, $t_{20} = -0.7$, $P = 0.48$). The difference between the SEA required to place the tag at the correct latitude and the SEA identified by the Hills-Ekstrom calibration approach was significantly greater than zero for no light stalks (2.5 ± 0.9 SE degrees, $t_5 = 2.7$, $P = 0.043$), and 10 mm light stalks (0.93 ± 0.35 SE degrees, $t_{20} = 2.6$, $P = 0.015$), but to a marginally smaller degree compared to no light stalks (-1.5 ± 0.8 SE degrees, $t_{1,25} = -1.9$, $p = 0.066$) but was not significantly different from zero for 5 mm light stalks (-0.8 ± 0.7 SE degrees, $t_7 = -1.2$, $P = 0.27$).

Discussion

Light stalks had a biologically significant effect on location precision and accuracy in this study. When analysing using Geolight methods, latitude can be estimated more accurately on the scale of 100s of kilometres and when using FlightR methods, longitude can also be estimated more accurately on the scale of 100s of kilometres. Differences introduced by the presence or absence of a light stalk are similar for the two methods in terms of precision: the frequency of false negatives (Figure 2) and so inaccuracies in estimating twilights (Figure 3) mean that variation will always be greater in data obtained from tags without light stalks. Some of these errors can be removed by manual checking and editing, or using calibrated twilight functions, but ultimately during migration periods, particularly when there are few sunrise and sunset times available, these methods cannot fully compensate. A 10mm stalk did not confer any additional precision or accuracy compared to a 5mm stalk. This threshold effect (i.e. no effect above at least 5mm) and field observations that both stalk lengths resulted in the sensor being above the level of Whinchat body feathers, suggest that the effect of light stalk length on accuracy is a consequence of the sensor being shaded by feathers, as expected. Although sample sizes are relatively small, the results are clear, and our study is the first to look for, and find, these effects on the non-breeding grounds, where remote data from geolocators is most frequently collected. The results suggest that there is a clear benefit from using light stalks, at least in some species, to increase precision and probably accuracy of location estimates during migration and on the non-breeding ground. Whinchats are birds of open habitats and so geolocators are subject to less shading from vegetation (in addition to shading from feathers) compared to birds of shady habitats such as forest and scrub, and so the benefits of using a light stalk are likely to be even greater for birds of shady habitats.

The benefits of greater precision when using light stalks occurred mostly at lower latitudes. This may be because variation in shading due to feathers is perhaps more likely to mask the small differences in day length closer to the equator. Only one other study has explicitly compared the accuracy of locations obtained with variable length light stalks (Peterson et al. 2015) and found that there were no differences at temperate latitudes. Our study also showed this, but we also show how precision depended on latitude, with greater imprecision arising for stop-over locations and substantially lower precision when considering non-breeding locations at tropical latitudes. Again, geolocators are most frequently used to remotely collect data in these regions. The maximum scale of additional errors introduced by not using a light stalk was about 4-5 degrees of latitude on the non-breeding ground. This is about 500 km at 10 degrees North, i.e. in the central savannah zone of West Africa where many Palearctic migrants spend the non-breeding season. Whether this presents a problem worth imposing the cost of a light stalk on a tagged species depends on the hypothesis being tested. But the light stalk effect identified in our study is likely to be highly relevant because almost all geolocator studies to date have tracked birds from temperate areas (see McKinnon et al. 2012, Finch et al. 2017), to determine their stop-over sites at this resolution at lower latitudes and for non-breeding areas in tropical latitudes.

Precision in geolocators is important because we can then use fewer data to estimate stationary periods and so locations to evaluate migration distances and migration routes, and so migratory capability, flexibility and resilience (Rakhimberdiev et al. 2016, Blackburn et al. 2018). Location of accurate non-wintering areas may be in some cases perhaps not that important because many species have low connectivity (Finch et al. 2017), however some species have high connectivity and geolocator data has been used to determine non-breeding distribution (Salewski et al. 2013), and latitudinal position is important in determining bioclimatic wintering areas. Furthermore, identifying inter-annual differences depends on accuracy, and these may be key issues in the population dynamics of migrant populations in the light of anthropogenic climate and habitat change (Cresswell 2014, Blackburn et al. 2017). But it should be noted that identification of stationary periods during migration was still possible regardless of stalk length, and there was no indication that tags without light stalks were less accurate in revealing the number of stop-over periods or the timing of migration. However, geolocators *per se* are poor in identifying short stationary periods in any case.

But it is important to note that this study was carried out in 2013 and 2014 and tracking technology has moved on. For example, many geolocator models now use a light tube to direct light from above the feathers on to the light sensor positioned on the main part of the tag. Light tubes attenuate light so reducing the amount of light getting to the sensor compared to a light stalk, but as light is usually considered logarithmically this still allows for the same methods of selecting sun elevation angle. And the same issues of shading will arise if the tube is too short to protrude above the feathers. Careful attachment of harnesses so that geolocator tags sit above the feathers, and remain so for the life of the tag, may also be possible in some species rendering the use of a light stalk redundant (e.g. Streby et al. 2015). Nevertheless, geolocator tags are still being used extensively and many studies still use light stalks or tubes because of problems of feathers covering the light sensor regardless of attachment method. But even when light stalks become obsolete, our ability to interpret the accuracy of the published studies that have used light stalks of variable length will rely on studies such as this one that have experimentally measured the effects of variable light stalk length, and its use or not.

To conclude, although we did not identify any light stalk effects on survival in Whinchats in an earlier study (Blackburn et al. 2016), aerodynamic costs have likely been shown in more aerial species (Scandolara et al. 2014, Morganti et al. 2018). Therefore using the precautionary principle suggested by the fact that any increase in weight and or attachment to a tag will increase drag (Pennycuick et al.

2012), we recommend the use of 5mm light stalks or tubes (i.e. just sufficient to capture light from above the body feathers) when deploying geolocator tags on species similar to Whinchats. Importantly, our results show no advantage from longer light stalk lengths than those necessary to just expose the light sensor above the feathers, at least for small passerines. But it is important to note that bird species may differ in length and density of back feathers. Species will vary in how feathers sit across a geolocator and this will likely vary dependent on their activity or posture, how the wings are folded across the back, or the size and structure of the bird. And light stalks are not necessary if the geolocator is fixed onto a leg ring or other non-feathered area. The angle of the light stalk from the back will also be important with steeper angles than the 45 degrees we used requiring shorter stalks. In essence, the light stalk tip must sit above the feathers in all aspects of a bird's life style (e.g. foraging, sitting, flying etc.) to give the most accurate and precise estimates, and the length of light stalk necessary to do this will be species dependent. When light stalks are above the feathers, our results suggest that there is a substantial gain in precision and accuracy of geolocator locations, and this may be most pronounced at lower non-breeding latitudes, the principal region where geolocators are used to obtain data.

Acknowledgements

The study was carried out in Nigeria where no licences are required for the procedures used. Nevertheless this study was carried out under the ethical guidelines of the AP Leventis Ornithological Research Institute Scientific Committee (APLORI is the only ornithological research institute in Nigeria) based on the Association for the Study of Animal Behaviour guidelines and those of the British Trust for Ornithology's ringing scheme. All personnel involved in fieldwork – either catching, colour-ringing or tagging birds had BTO ringing licences. MB had been previously licensed to fit geolocators in the UK. This work was supported by the Chris Goodwin, A.P. Leventis Conservation Foundation, AP Leventis Ornithological Research Institute, the British Ornithologists' Union and the Linnean Society. This is paper number (to be completed at proof stage) from the AP Leventis Ornithological Research Institute. We thank two anonymous referees and the Editor for their helpful comments on an earlier draft of the manuscript.

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Table 1: Variation in first and last light intensity for a day dependent on light stalk length and whether it was sunrise or sunset, over a 10-day period March 31st to April 9th. A. Variation in the difference between mean sunrise and sunset time recorded by the geolocator and the actual sunrise and sunset times. Residual degrees of freedom = 28, adjusted R^2 = 0.77. B. Variation in the standard deviation of the difference between recorded mean sunrise and sunset time and actual sunrise and sunset times. Residual degrees of freedom = 30, adjusted R^2 = 0.40. Note the interaction between stalk and sunrise/sunset was not significant and so was removed (delta AIC – 3.8) and that the model is improved by pooling light stalks 5mm and 10mm together because they have very similar effects (delta AIC –1.9). In both models, no light stalk (0 mm) and sunrise were set to the intercept and both use decimal hours (i.e. 0.5 represents 30 minutes).

A. Mean difference	Estimate	SE	t value	P value
(Intercept)	0.012	0.046	0.3	0.79
5mm light stalk	-0.205	0.062	-3.3	**0.002**
10mm light stalk	-0.225	0.062	-3.6	**0.001**
Sunset	-0.007	0.064	-0.1	0.92
5mm LS * Sunset	0.421	0.088	4.8	**<0.001**
10mm LS * Sunset	0.484	0.088	5.5	**<0.001**
B. SD of difference				
(Intercept)	0.114	0.013	8.6	**<0.001**
5mm light stalk	-0.059	0.016	-3.7	**<0.001**
10mm light stalk	-0.066	0.016	-4.1	**<0.001**
Sunset	0.027	0.013	2.1	**0.042**

Table 2: Variation in confidence interval for latitude with stalk length, dependent on latitude and longitude: Geolight analysis with manual confirmation of stationary periods: A. Using stationary periods between February and June, during the non-breeding season, the breeding season and first and second stop-overs during spring migration; B. Using only the first and second stop-overs during spring migration. GLMM with individual ID as a random effect (A. N = 125 stationary periods from 35 individuals, adjusted $R^2 = 0.52$, with random effects accounting for a further 0.05 of variance; B. N = 60 stationary periods from 34 individuals, adjusted $R^2 = 0.28$, with random effects accounting for a further 0.19 of variance). The interactions between latitude or longitude and stalk length were not significant in model B and so were removed (delta AIC – 12.5). In A and B, the Estimate and SE columns give the estimates and their standard errors for the confidence intervals of the locations calculated using a sun elevation angle (SEA value) value of -4.5 which gives the most biologically sensible locations after crossing the Sahara. The range of estimates obtained using different values of SEA to calculate locations is given in the fourth column: estimates are biologically and statistically similar in significance in all analyses. FlightR analysis: C. Using the first and second stationary stop-over periods of 3 days or greater during spring migration after leaving the tagging site, and the final breeding location, all between April and June; D. Using only the first and second stop-overs during spring migration. GLMM with individual ID as a random effect (C. N = 87 stationary periods from 34 individuals, adjusted $R^2 = 0.09$, with random effects accounting for no further variance; D. N = 57 stationary periods from 32 individuals, adjusted $R^2 = 0.05$, with random effects accounting for a further 0.15 of variance). The interactions between latitude or longitude and stalk length were not significant in models C and D and so were removed (delta AIC – 17.0 and -13.8 respectively). No light stalk (0 mm) was set to the intercept in all models.

A.	Estimate	SE	Estimate range dependent on SEA value	df	t value	P value
(Intercept)	6.1	0.42	5.1 to 6.1	92.1	14.4	<0.001
5mm light stalk	-3.9	0.61	-3.9 to -3.3	109.4	-6.5	**<0.001**
10mm light stalk	-4.6	0.49	-4.6 to -3.4	95.4	-9.4	**<0.001**
Latitude	-0.081	0.013	-0.08 to -0.06	97.9	-6.2	**<0.001**
Longitude	-0.047	0.014	-0.05 to -0.03	116.4	-3.3	**0.0013**
Lat * 5mm LS	0.082	0.016	0.06 to 0.08	78.0	5.1	**<0.001**
Lat * 10mm LS	0.098	0.013	0.08 to 0.10	85.5	7.4	**<0.001**
B.						
(Intercept)	3.7	0.55	3.5 to 3.7	33.2	6.9	**<0.001**
5mm light stalk	-2.0	0.55	-2.0 to -1.9	18.4	-3.6	**0.0021**
10mm light stalk	-1.7	0.49	-1.8 to 1.6	20.4	-3.5	**0.0020**
Latitude	-0.012	0.018	-0.012 to -0.006	36.6	-0.7	0.52
Longitude	0.014	0.025	0.010 to 0.014	36.1	0.6	0.57
C.						
(Intercept)	4.8	1.3		82	3.6	**<0.001**
5mm light stalk	-0.38	0.87		82	-0.43	0.67
10mm light stalk	-1.5	0.77		82	-2.0	0.053
Latitude	0.015	0.041		82	0.363	0.72
Longitude	-0.056	0.041		82	-1.4	0.18
D.						
(Intercept)	3.3	1.8		43.0	1.8	0.08
5mm light stalk	0.45	1.3		21.7	0.3	0.74
10mm light stalk	-1.2	1.2		21.3	-1.0	0.31
Latitude	0.050	0.057		49.0	0.9	0.39
Longitude	-0.047	0.068		38.8	-0.7	0.49

Table 3: How the range of the confidence interval for longitude varied with stalk length dependent on latitude and longitude: Geolight analysis with manual confirmation of stationary periods: A. Using stationary periods between February and June, during the non-breeding season, the breeding season and first and second stop-overs during spring migration; B. Using only the first and second stop-overs during spring migration. GLMM with individual ID as a random effect (A. N = 125 stationary periods from 35 individuals, adjusted R^2 = 0.18, with random effects accounting for no further variance; B. N = 60 stationary periods from 34 individuals, adjusted R^2 = 0.37, with random effects accounting for a further 0.13 of variance. The interactions between latitude and stalk length and between longitude and stalk length were not significant in the model and so were removed (delta AIC – 31 and -25 respectively). FlightR analysis: C. Using the first and second stationary stop-over periods of 3 days or greater during spring migration after leaving the tagging site, and the final breeding location, all between April and June; D. Using only the first and second stop-overs during spring migration. GLMM with individual ID as a random effect (C. N = 87 stationary periods from 34 individuals, adjusted R^2 = 0.42, with random effects accounting for 0.01 further variance; D. N = 57 stationary periods from 32 individuals, adjusted R^2 = 0.39, with random effects accounting for no further variance). The interactions between latitude or longitude and stalk length were not strongly significant in models C and D and so were removed (delta AIC – 13.8 and -6.8 respectively). No light stalk (0 mm) was set to the intercept in all models.

A.	Estimate	SE	df	t value	P value
(Intercept)	0.51	0.17	120.0	3.0	0.0032
5mm light stalk	-0.29	0.19	120.0	-1.5	0.13
10mm light stalk	-0.29	0.17	120.0	-1.7	0.085
Latitude	0.022	0.0050	120.0	4.4	**<0.001**
Longitude	-0.016	0.0083	120.0	-2.0	**0.049**
B.					
(Intercept)	0.16	0.31	45.0	0.5	0.60
5mm light stalk	-0.49	0.31	34.0	-1.6	0.12
10mm light stalk	-0.38	0.28	36.0	-1.3	0.19
Latitude	0.031	0.014	45.4	2.2	**0.032**
Longitude	0.024	0.010	45.4	2.3	**0.026**
C.					
(Intercept)	-0.74	0.96	74.9	-0.8	0.44
5mm light stalk	-2.3	0.64	24.4	-3.5	**0.002**
10mm light stalk	-2.3	0.56	25.5	-4.1	**<0.001**
Latitude	0.13	0.030	77.3	4.4	**<0.001**
Longitude	-0.011	0.030	60.1	-0.4	0.73
D.					
(Intercept)	-0.73	1.0	52	-0.7	0.48
5mm light stalk	-1.7	0.72	52	-2.4	**0.022**
10mm light stalk	-1.9	0.62	52	-3.1	**0.003**
Latitude	0.13	0.033	52	3.9	**<0.001**
Longitude	-0.014	0.038	52	-0.4	0.71

Figure legends

Figure 1: Tags used in the study showing the variation in light stalk length. The black tag had no light stalk and the light sensor is visible as a pale square at the bottom: The sensor was covered by feathers when mounted on the bird. In the grey tags this sensor is mounted on the tip of the stalk protruding from the tag, so that the sensor was located above the level of the feathers when mounted on the bird. Stalks were either 5mm (middle) or 10mm (right) in length.

Figure 2: The occurrence of dark records in a daily light trace dependent on light stalk length of three typical male Whinchats in 2014. Fitted curved lines show the sunrise and sunset times at Jos, Nigeria where the birds were tagged and spent the non-breeding period (October to April). Dashed lines show the equinoxes.

Figure 3: The difference in time between values of first and last light intensity in a day and actual sunrise and sunset times dependent on stalk length, over a 10-day period of March 31st to April 9th. Mean values of the difference in minutes and their standard deviation are plotted. See Table 1 for analysis of statistical differences, but the standard deviation for no light stalk is significantly larger than that with a light stalk present, and sunrise and sunset is measured to the same degree, either significantly earlier or later, with a light stalk present.

Figure 4: The effect of light stalk length on precision (95% confidence interval) of locations dependent on latitude, using a Geolight analysis with manual confirmation of stationary periods. Graph A. plots the mean confidence interval (CI) of latitude (+/- 95% confidence intervals of this mean) predicted from the model in Table 2A with longitude set to the median value for all individuals carrying that light stalk type (0mm black circles, solid line; 5mm grey triangles, dashed line; 10mm white squares, dotted line). Map B. plots these predicted latitude ranges (i.e. the vertical lines through each point) on a map to show how the confidence intervals for 0mm light stalk (black circles) compare to those for a light stalk of 5mm (grey triangles). In general, the difference in accuracy is large in the non-breeding area but becomes trivial on the easterly, breeding ground. Predicted values for the confidence intervals for longitude (using the values from Table 3A) are also plotted (i.e. the horizontal lines through each point) but these are relatively small regardless of light stalk type.

Figure 5: The mean difference in latitude confidence interval for variable light stalk lengths considering only the major (greater than 2 days) stop-over periods during spring migration, using a Geolight analysis

with manual confirmation of stationary periods. Predicted values of the mean confidence intervals for latitude (+/- 2SE) from the model in Table 2B are plotted at median longitude.

Figure 6: The effect of light stalk length on precision (95% confidence interval) of locations dependent on latitude, using a FlightR analysis. Graph A. plots the mean confidence interval (CI) of latitude (+/- 95% confidence intervals of this mean) predicted from the model in Table 2C with longitude set to the median value for all individuals carrying that light stalk type (0mm black circles, solid line; 5mm grey triangles, dashed line; 10mm white squares, dotted line). Map B. plots the predicted latitude and longitude ranges from the model in Table 2C (i.e. the vertical lines through each point) on a map to show how the confidence intervals for 0mm light stalk (black circles) compare to those for a light stalk of 5mm (grey triangles).

Figure 7: A. The difference between A. real latitude and latitude estimated using the Hills-Ekstrom calibration method and B. the difference between the SEA required to place the tag on the correct latitude and the SEA identified by the Hills-Ekstrom calibration method for tagged birds on the study site before migration, dependent on light stalk length.

Figure 1:

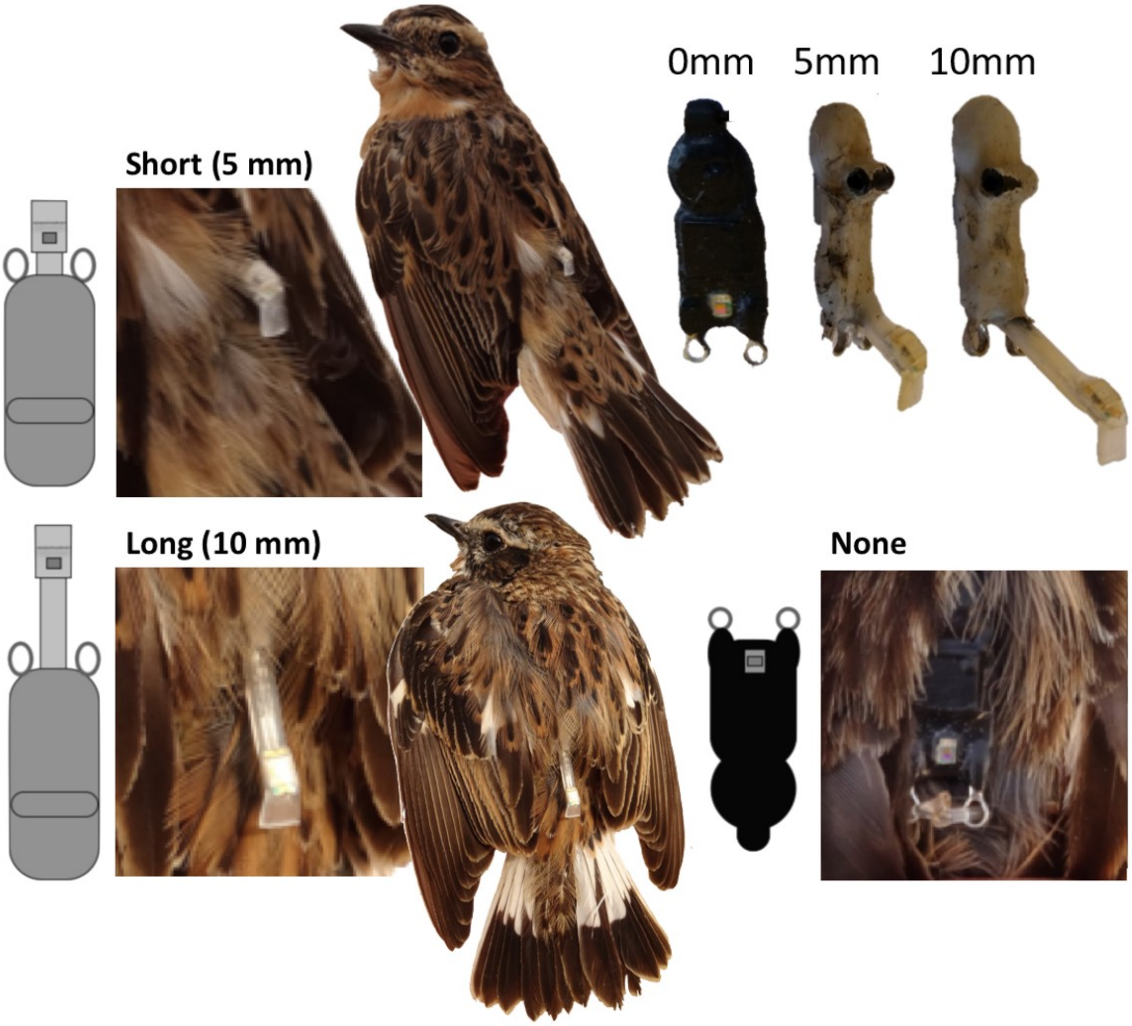

Figure 2:

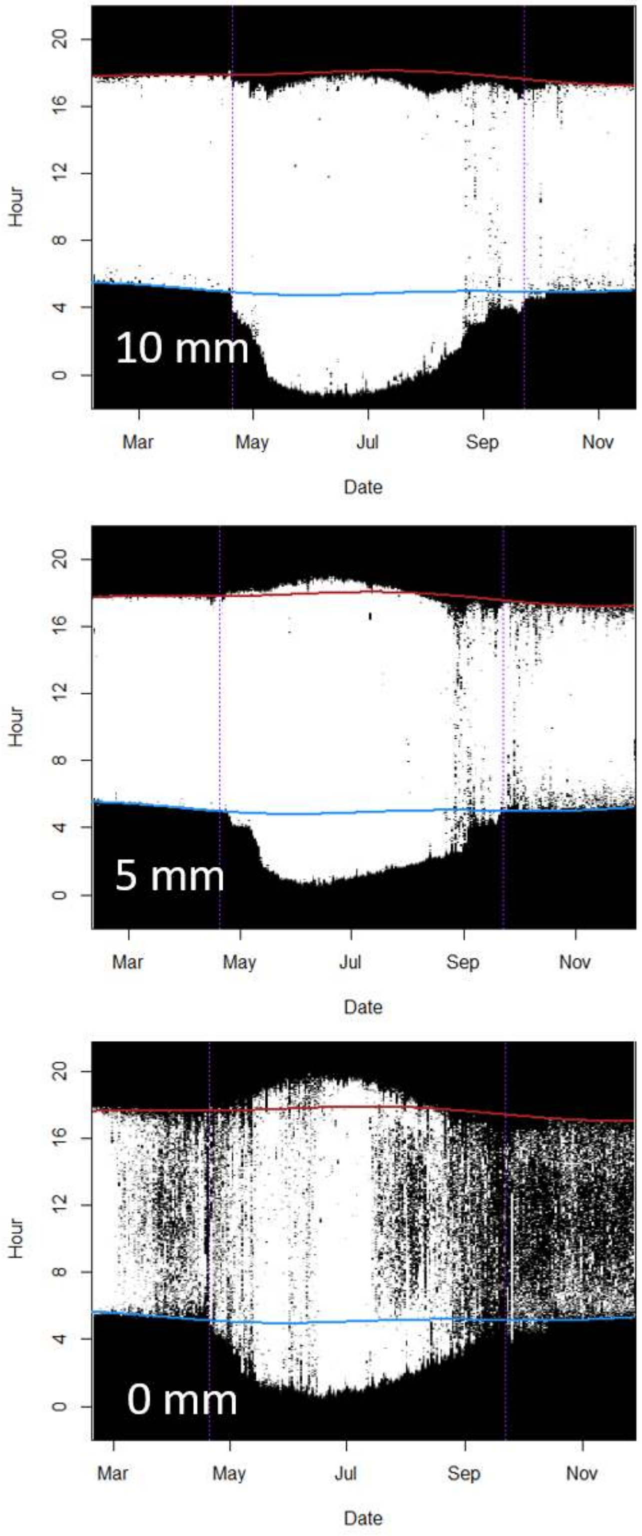
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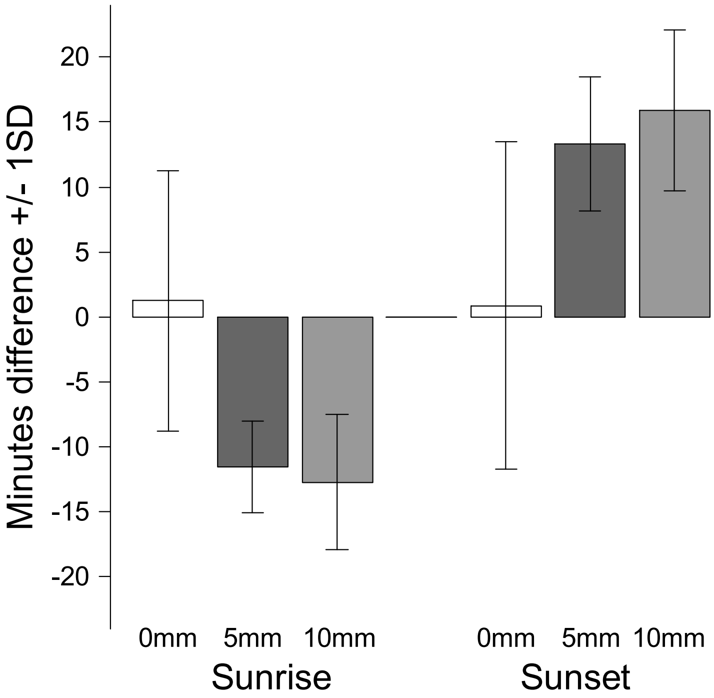
Figure 3: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Sunset

Figure 4:

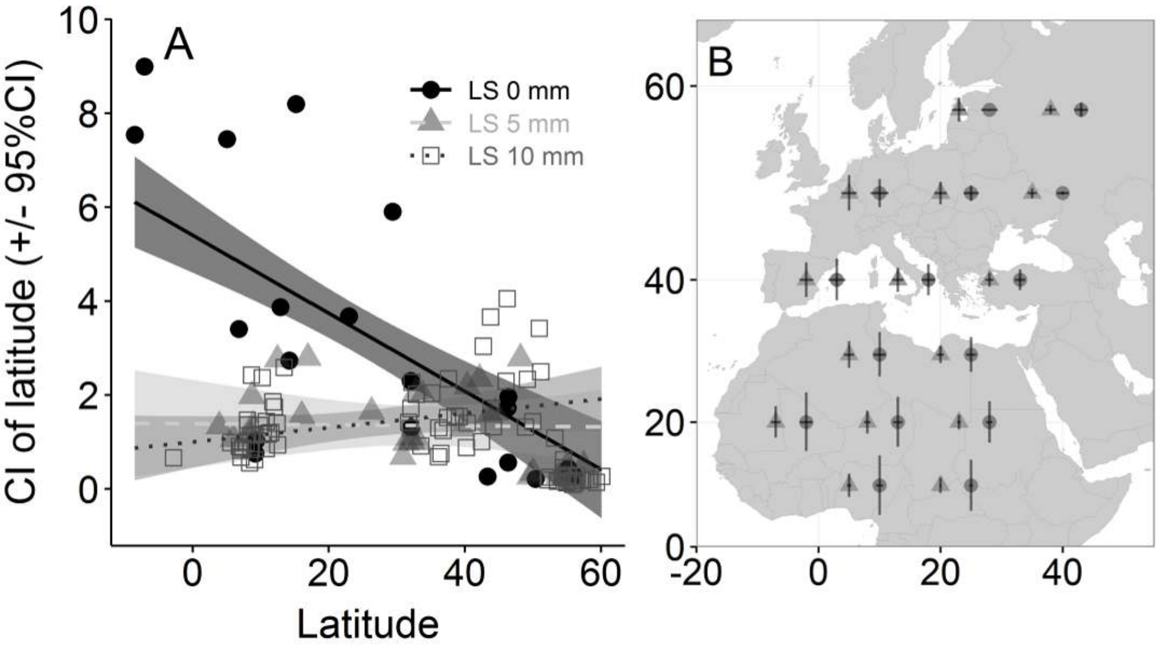
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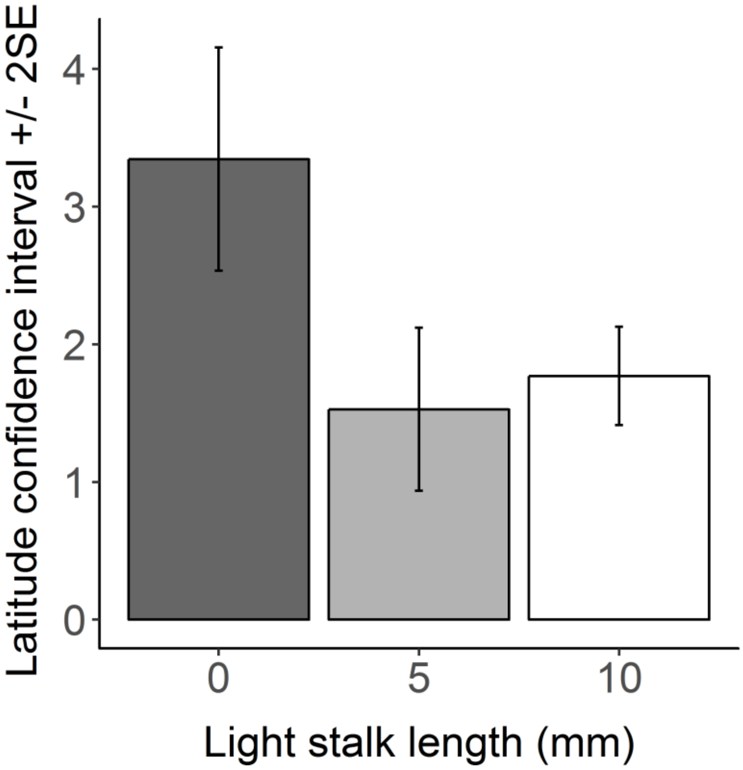
Figure 5: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Light stalk length (mm)

Figure 6:

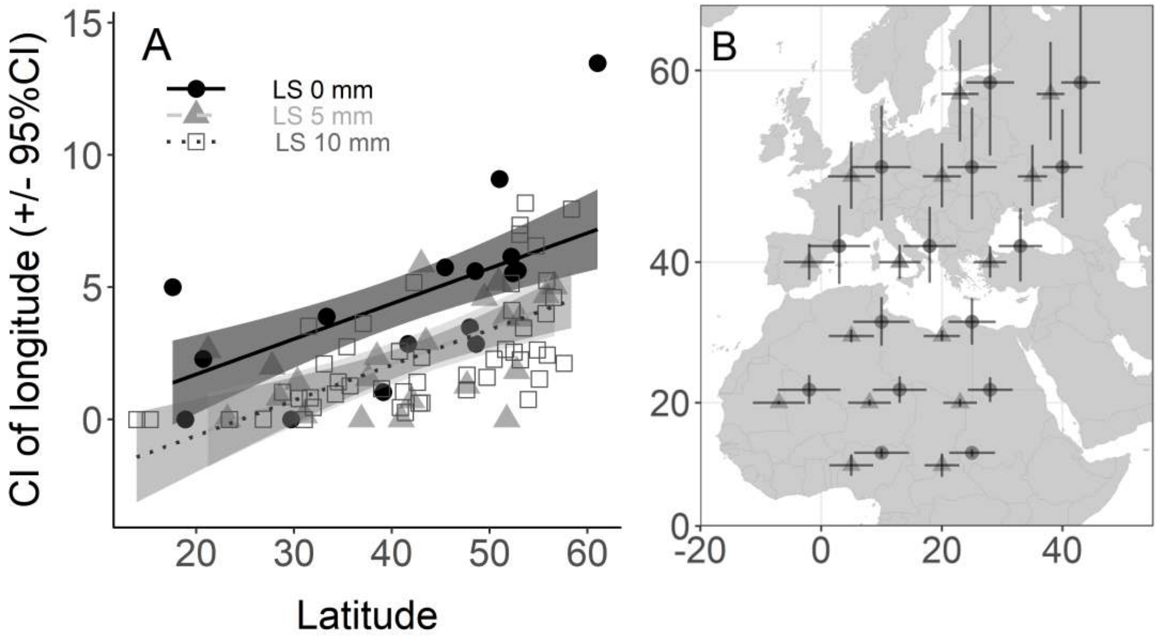
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Figure 7: