

1 **ACCEPTED BIRD STUDY 29<sup>TH</sup> OCTOBER 2019**

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

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

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

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

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

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

40 Geolocators are being used widely to track small migrants but some tag designs may impact on the  
41 survival and behaviour of a tagged bird (Bowlin et al. 2010, Costantini and Moller 2013, Weiser et al.  
42 2016). Light stalks are one aspect of geolocator design that can vary in both presence and in size. Light  
43 stalks are fitted to geolocator tags to increase the accuracy of light readings because they place the  
44 light sensor above potential shading by the feathers (Bridge et al. 2013). Similarly, some geolocators  
45 use protruding light tubes that direct light onto a sensor positioned on the logger. Accurate records of  
46 light intensity are needed because locations are determined by sunrise and sunset times (Lisovski and  
47 Hahn 2012), and shading of the sensor can lead to later and earlier apparent sunrise and sunset times  
48 respectively (Lisovski et al. 2012), potentially leading to locations being calculated with greater error  
49 (Fudickar et al. 2012, McKinnon et al. 2012). Overall, precision of geolocators is important because  
50 geolocators are the current means by which non-breeding and stop-over locations are identified for a  
51 large number of small migrant bird species (Stutchbury et al. 2009, McKinnon et al. 2013) that are  
52 undergoing large scale declines possibly associated with where they spend the non-breeding season  
53 (Sanderson et al. 2006, Vickery et al. 2014).

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

69 mid-day are much higher. Consequently, the relative advantage of light stalks may well be dependent  
70 on latitude (McKinnon et al. 2012).

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

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

## 90 **Methods**

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

98 Whinchats were caught with spring traps and mist nets in late February and March in 2013 or 2014.  
99 Birds were aged and sexed (Jenni and Winkler 1994), ringed with unique combinations of colour-rings,  
100 and fitted with a geocator. In Year 1, we deployed 49 and in Year 2 we deployed 130 geolocators  
101 fitted using leg-loop 'Rappole-Tipton' (also called backpack) harnesses (Rappole and Tipton 1991). Full  
102 details of tag and harness design are given in Blackburn et al. (2016). Tags weighed on average 0.63  
103 g (0.01SE), representing 4.1 % of average body mass (mean body mass of Whinchats in the study was  
104  $15.2 \pm 0.05$  SE g; N = 471). There was no overall significant reduction in between-year resighting rate  
105 (our proxy for survival, Blackburn and Cresswell 2016) comparing tagged and untagged birds in either  
106 year (Blackburn et al. 2016). There was no strong evidence for an effect of light stalk length on survival  
107 rate (Blackburn et al. 2016).

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

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

## 128 **Analyses**

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

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

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

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

163 Because conditions away from the wintering grounds are unknown, we used four different values of sun  
164 elevation angle (SEA value) to calculate latitude: note results do not change depending on which set of  
165 SEA values we use. First, we used a sun elevation angle of -4.5 for all loggers in both years. This is a  
166 reasonable median value and although some loggers will have had lower values and some higher, this  
167 would simply increase the error of estimating locations but should not introduce any systematic bias.  
168 The value of -4.5 was chosen because this gave the most biologically sensible plots of locations  
169 immediately after crossing the Sahara (i.e. all locations were on land in North Africa or Europe rather  
170 than in the Mediterranean Sea, within 2 standard errors of the mean of latitude for the stop-over period);  
171 see Blackburn et al. (2018). Second, we used an average SEA value of -4, the mean location calculated  
172 for each bird for sun elevation angles -2 to -6 at 0.5 increments (i.e. 9 mean locations), then averaged  
173 across these 9 locations, applied to all birds regardless of year. Third we used the sun elevation angle  
174 for each individual that best reflected their known wintering location on tagging (range of values -3.5 to  
175 -5.9, mean -4.6); we used the LocatorAid software from the BASTrack software suite, which uses known  
176 residency times and wintering location to calculate the corresponding wintering ground SEA value.  
177 Fourth, we attempted to find the correct summer angle using the Hill-Ekstrom (H-E) calibration method  
178 (Hill & Braun 2001, Ekstrom 2004, see Tottrup et al. 2012) in which we selected the SEA value that  
179 gave the least amount of variation in latitude during the first two weeks in June when all individuals were  
180 very likely to be stationary on their breeding grounds (see Blackburn et al. 2017 for further details and  
181 validation of this approach). If the calibration was not successful, we used the mean value for all the  
182 loggers for which the calibration had been successful, calculated for each year separately (range of  
183 values -2 to -4.5, mean -3.8). We used these SEA values to calculate noon and midnight locations  
184 derived from sunrise and sunset times using the 'coord' function in Geolight. Because of the uncertainty  
185 introduced by not knowing the SEA value for any stationary period, we analysed the locations with each  
186 of the four different sets of SEA values. Results are biologically and statistically very similar in all cases.  
187 Here we present the results in detail from the most reasonable assumption of SEA value (i.e. -4.5 for

188 all birds), but also include the range of values obtained from the analyses using the other three sets of  
189 SEA values to demonstrate the similarity. Note that longitude is not affected by choice of SEA value.

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

205 Third, we analysed variation in location data calculated using another standard methodology for  
206 geolocators based on the R library FlightR (Rakhimberdiev et al. 2015, Rakhimberdiev and Saveliev  
207 2019), and how location then varied in the presence of a light stalk. Again, data from all available tags  
208 were used (although including one fewer of the tags that failed very early than the Geolight analysis  
209 because FlightR requires more data to calculate accurate locations). Light and dark periods were  
210 visualised using the 'lightImage' function and the predicted twilights for the non-breeding, tagging  
211 location at Jos were fitted. These were then adjusted to fit the observed tagging location twilights by  
212 setting the zenith by eye, usually with a value of 94. The function 'preprocessLight' was then used to  
213 set the analysis period to three weeks before migration in the spring (4 weeks if this was early coincident  
214 with the equinox) to three to five weeks after arrival on the breeding grounds (typically end of March to  
215 mid-June). 12 seed positions (that showed clear sunrise/sunset boundaries) were set (4 before, 4 during  
216 and 4 after migration); non-defined twilights were set if necessary and then all recorded twilight times  
217 were accepted without further editing in all cases. Calibration periods were set as a three-week period



218 before 4 days before the start of first migration away from the non-breeding, tagging site. The possible  
219 grid was set at (0,5,60,65) with a minimum distance from land used of 200km, and a minimum distance  
220 from land allowed to stay at 50km. Locations were then calculated with 'nParticles' set at 10,000 and  
221 'decision' at 0.05. Stationary migration periods were defined with a probability cut-off of 0.1 and for a  
222 minimum stay of 3 days.

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

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

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

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

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

265 For accuracy: the latitude calculated from tag data during the period birds were on the study site prior  
266 to migration, using the SEA estimated by the Hills-Ekstrom calibration, was tested against stalk length  
267 (3-way factor, 0, 5 and 10mm). Latitude was calculated for each tag using a different SEA angle of 1 to  
268 6 at 0.5 increments (11 sets of values), from the day the tag was fitted to last day before the tagged  
269 individual left the study site (no values were calculated when too close to equinox, i.e. using only values  
270 with a confidence value of 9). The mean and standard deviation of all values for the 11 SEAs was then  
271 calculated for each tag. The mean latitude value for the SEA with the lowest standard deviation (i.e. as  
272 per the Hills-Ekstrom calibration) was selected for each tag and the difference between it and the real  
273 latitude calculated ("Calibration Error"). The difference between this SEA and the SEA required to place  
274 the tag on the correct latitude was also calculated. Variation in "Calibration Error" and SEA difference  
275 were then tested across stalk lengths with the expectation that both would be larger with shorter light  
276 stalks (both models included individual as a random factor and assumed a normal distribution of error  
277 residuals).

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

## 284 **Results**

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

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

305 The precision of longitude estimation was increased by the presence of a light stalk when using a  
306 FlightR analysis approach (Table 2C & D). When all stationary periods outside of the main non-breeding

307 (wintering) period (which is used as a calibration in FlightR) were considered, there was a highly  
308 significant decrease in the longitude confidence interval with a light stalk. The longitude confidence  
309 interval decreased on average by 2.3 degrees with a light stalk (Table 2C, Figure 6), equivalent to about  
310 245 km in the non-breeding area in West Africa and about 140 km for the more northerly breeders in  
311 Europe. There was also a highly significant decrease on average in longitude confidence interval of 1.8  
312 degrees with a light stalk when considering only stop-over periods during migration (Table 2D),  
313 equivalent to about 170 km around the Mediterranean. Tukey post-hoc contrast tests by stalk length  
314 found no significant differences between the effects of 5 and 10mm stalks in any models ( $P > 0.22$ ).  
315 Precision of latitude estimation was not (or only marginally affected) affected by stalk length across all  
316 stationary periods (Table 2C) or during migratory stop-over periods only (Table 2B). The estimated  
317 number of stop-overs during spring migration calculated using FlightR was not affected by stalk length,  
318 i.e. no bias in identifying stop-overs dependent on stalk length ( $F_{2,29} = 0.3$ ,  $P = 0.78$ ).

319 The accuracy of calculated latitude on the non-breeding area increased by about 8 degrees (Figure 7A)  
320 and accuracy of SEA estimation likely increased with the presence of a light stalk (Figure 7B). The  
321 difference between calculated latitude using the Hills-Ekstrom calibration approach and actual latitude  
322 at the non-breeding site ("Calibration Error") was marginally significantly different for no light stalks ( $-$   
323  $10.0 \pm 4.1$  SE degrees,  $t_5 = -2.4$ ,  $P = 0.059$ ) but not for 5 mm ( $-1.2 \pm 1.2$  SE degrees,  $t_7 = -0.9$ ,  $P = 0.37$ )  
324 or 10 mm stalks ( $-1.9 \pm 2.7$  SE degrees,  $t_{20} = -0.7$ ,  $P = 0.48$ ). The difference between the SEA required  
325 to place the tag at the correct latitude and the SEA identified by the Hills-Ekstrom calibration approach  
326 was significantly greater than zero for no light stalks ( $2.5 \pm 0.9$  SE degrees,  $t_5 = 2.7$ ,  $P = 0.043$ ), and 10  
327 mm light stalks ( $0.93 \pm 0.35$  SE degrees,  $t_{20} = 2.6$ ,  $P = 0.015$ ), but to a marginally smaller degree  
328 compared to no light stalks ( $-1.5 \pm 0.8$  SE degrees,  $t_{1,25} = -1.9$ ,  $p = 0.066$ ) but was not significantly  
329 different from zero for 5 mm light stalks ( $-0.8 \pm 0.7$  SE degrees,  $t_7 = -1.2$ ,  $P = 0.27$ ).

## 330 **Discussion**

331 Light stalks had a biologically significant effect on location precision and accuracy in this study. When  
332 analysing using Geolight methods, latitude can be estimated more accurately on the scale of 100s of  
333 kilometres and when using FlightR methods, longitude can also be estimated more accurately on the  
334 scale of 100s of kilometres. Differences introduced by the presence or absence of a light stalk are  
335 similar for the two methods in terms of precision: the frequency of false negatives (Figure 2) and so

336 inaccuracies in estimating twilights (Figure 3) mean that variation will always be greater in data obtained  
337 from tags without light stalks. Some of these errors can be removed by manual checking and editing,  
338 or using calibrated twilight functions, but ultimately during migration periods, particularly when there are  
339 few sunrise and sunset times available, these methods cannot fully compensate. A 10mm stalk did not  
340 confer any additional precision or accuracy compared to a 5mm stalk. This threshold effect (i.e. no effect  
341 above at least 5mm) and field observations that both stalk lengths resulted in the sensor being above  
342 the level of Whinchat body feathers, suggest that the effect of light stalk length on accuracy is a  
343 consequence of the sensor being shaded by feathers, as expected. Although sample sizes are relatively  
344 small, the results are clear, and our study is the first to look for, and find, these effects on the non-  
345 breeding grounds, where remote data from geolocators is most frequently collected. The results suggest  
346 that there is a clear benefit from using light stalks, at least in some species, to increase precision and  
347 probably accuracy of location estimates during migration and on the non-breeding ground. Whinchats  
348 are birds of open habitats and so geolocators are subject to less shading from vegetation (in addition  
349 to shading from feathers) compared to birds of shady habitats such as forest and scrub, and so the  
350 benefits of using a light stalk are likely to be even greater for birds of shady habitats.

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

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

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

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

396 2012), we recommend the use of 5mm light stalks or tubes (i.e. just sufficient to capture light from above  
397 the body feathers) when deploying geolocator tags on species similar to Whinchats. Importantly, our  
398 results show no advantage from longer light stalk lengths than those necessary to just expose the light  
399 sensor above the feathers, at least for small passerines. But it is important to note that bird species may  
400 differ in length and density of back feathers. Species will vary in how feathers sit across a geolocator  
401 and this will likely vary dependent on their activity or posture, how the wings are folded across the back,  
402 or the size and structure of the bird. And light stalks are not necessary if the geolocator is fixed onto a  
403 leg ring or other non-feathered area. The angle of the light stalk from the back will also be important  
404 with steeper angles than the 45 degrees we used requiring shorter stalks. In essence, the light stalk tip  
405 must sit above the feathers in all aspects of a bird's life style (e.g. foraging, sitting, flying etc.) to give  
406 the most accurate and precise estimates, and the length of light stalk necessary to do this will be species  
407 dependent. When light stalks are above the feathers, our results suggest that there is a substantial gain  
408 in precision and accuracy of geolocator locations, and this may be most pronounced at lower non-  
409 breeding latitudes, the principal region where geolocators are used to obtain data.

#### 410 **Acknowledgements**

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

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520

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

531

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

532

533 Table 2: Variation in confidence interval for latitude with stalk length, dependent on latitude and  
534 longitude: Geolight analysis with manual confirmation of stationary periods: A. Using stationary periods  
535 between February and June, during the non-breeding season, the breeding season and first and second  
536 stop-overs during spring migration; B. Using only the first and second stop-overs during spring  
537 migration. GLMM with individual ID as a random effect (A. N = 125 stationary periods from 35  
538 individuals, adjusted  $R^2 = 0.52$ , with random effects accounting for a further 0.05 of variance; B. N = 60  
539 stationary periods from 34 individuals, adjusted  $R^2 = 0.28$ , with random effects accounting for a further  
540 0.19 of variance). The interactions between latitude or longitude and stalk length were not significant in  
541 model B and so were removed (delta AIC – 12.5). In A and B, the Estimate and SE columns give the  
542 estimates and their standard errors for the confidence intervals of the locations calculated using a sun  
543 elevation angle (SEA value) value of -4.5 which gives the most biologically sensible locations after  
544 crossing the Sahara. The range of estimates obtained using different values of SEA to calculate  
545 locations is given in the fourth column: estimates are biologically and statistically similar in significance  
546 in all analyses. FlightR analysis: C. Using the first and second stationary stop-over periods of 3 days or  
547 greater during spring migration after leaving the tagging site, and the final breeding location, all between  
548 April and June; D. Using only the first and second stop-overs during spring migration. GLMM with  
549 individual ID as a random effect (C. N = 87 stationary periods from 34 individuals, adjusted  $R^2 = 0.09$ ,  
550 with random effects accounting for no further variance; D. N = 57 stationary periods from 32 individuals,  
551 adjusted  $R^2 = 0.05$ , with random effects accounting for a further 0.15 of variance). The interactions  
552 between latitude or longitude and stalk length were not significant in models C and D and so were  
553 removed (delta AIC – 17.0 and -13.8 respectively). No light stalk (0 mm) was set to the intercept in all  
554 models.

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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	<b>&lt;0.001</b>
10mm light stalk	-4.6	0.49	-4.6 to -3.4	95.4	-9.4	<b>&lt;0.001</b>
Latitude	-0.081	0.013	-0.08 to -0.06	97.9	-6.2	<b>&lt;0.001</b>
Longitude	-0.047	0.014	-0.05 to -0.03	116.4	-3.3	<b>0.0013</b>
Lat * 5mm LS	0.082	0.016	0.06 to 0.08	78.0	5.1	<b>&lt;0.001</b>
Lat * 10mm LS	0.098	0.013	0.08 to 0.10	85.5	7.4	<b>&lt;0.001</b>
<b>B.</b>						
(Intercept)	3.7	0.55	3.5 to 3.7	33.2	6.9	<b>&lt;0.001</b>
5mm light stalk	-2.0	0.55	-2.0 to -1.9	18.4	-3.6	<b>0.0021</b>
10mm light stalk	-1.7	0.49	-1.8 to 1.6	20.4	-3.5	<b>0.0020</b>
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
<b>C.</b>						
(Intercept)	4.8	1.3		82	3.6	<b>&lt;0.001</b>
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
<b>D.</b>						
(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

558

559 Table 3: How the range of the confidence interval for longitude varied with stalk length dependent on  
560 latitude and longitude: Geolight analysis with manual confirmation of stationary periods: A. Using  
561 stationary periods between February and June, during the non-breeding season, the breeding season  
562 and first and second stop-overs during spring migration; B. Using only the first and second stop-overs  
563 during spring migration. GLMM with individual ID as a random effect (A. N = 125 stationary periods from  
564 35 individuals, adjusted  $R^2 = 0.18$ , with random effects accounting for no further variance; B. N = 60  
565 stationary periods from 34 individuals, adjusted  $R^2 = 0.37$ , with random effects accounting for a further  
566 0.13 of variance. The interactions between latitude and stalk length and between longitude and stalk  
567 length were not significant in the model and so were removed (delta AIC – 31 and -25 respectively).  
568 FlightR analysis: C. Using the first and second stationary stop-over periods of 3 days or greater during  
569 spring migration after leaving the tagging site, and the final breeding location, all between April and  
570 June; D. Using only the first and second stop-overs during spring migration. GLMM with individual ID  
571 as a random effect (C. N = 87 stationary periods from 34 individuals, adjusted  $R^2 = 0.42$ , with random  
572 effects accounting for 0.01 further variance; D. N = 57 stationary periods from 32 individuals, adjusted  
573  $R^2 = 0.39$ , with random effects accounting for no further variance). The interactions between latitude or  
574 longitude and stalk length were not strongly significant in models C and D and so were removed (delta  
575 AIC – 13.8 and -6.8 respectively). No light stalk (0 mm) was set to the intercept in all models.

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<b>A.</b>	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	<b>&lt;0.001</b>
Longitude	-0.016	0.0083	120.0	-2.0	<b>0.049</b>
<b>B.</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	<b>0.032</b>
Longitude	0.024	0.010	45.4	2.3	<b>0.026</b>
<b>C.</b>					
(Intercept)	-0.74	0.96	74.9	-0.8	0.44
5mm light stalk	-2.3	0.64	24.4	-3.5	<b>0.002</b>
10mm light stalk	-2.3	0.56	25.5	-4.1	<b>&lt;0.001</b>
Latitude	0.13	0.030	77.3	4.4	<b>&lt;0.001</b>
Longitude	-0.011	0.030	60.1	-0.4	0.73
<b>D.</b>					
(Intercept)	-0.73	1.0	52	-0.7	0.48
5mm light stalk	-1.7	0.72	52	-2.4	<b>0.022</b>
10mm light stalk	-1.9	0.62	52	-3.1	<b>0.003</b>
Latitude	0.13	0.033	52	3.9	<b>&lt;0.001</b>
Longitude	-0.014	0.038	52	-0.4	0.71

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581 **Figure legends**

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

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

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

597 Figure 4: The effect of light stalk length on precision (95% confidence interval) of locations dependent  
598 on latitude, using a Geolight analysis with manual confirmation of stationary periods. Graph A. plots the  
599 mean confidence interval (CI) of latitude (+/- 95% confidence intervals of this mean) predicted from the  
600 model in Table 2A with longitude set to the median value for all individuals carrying that light stalk type  
601 (0mm black circles, solid line; 5mm grey triangles, dashed line; 10mm white squares, dotted line). Map  
602 B. plots these predicted latitude ranges (i.e. the vertical lines through each point) on a map to show how  
603 the confidence intervals for 0mm light stalk (black circles) compare to those for a light stalk of 5mm  
604 (grey triangles). In general, the difference in accuracy is large in the non-breeding area but becomes  
605 trivial on the easterly, breeding ground. Predicted values for the confidence intervals for longitude (using  
606 the values from Table 3A) are also plotted (i.e. the horizontal lines through each point) but these are  
607 relatively small regardless of light stalk type.

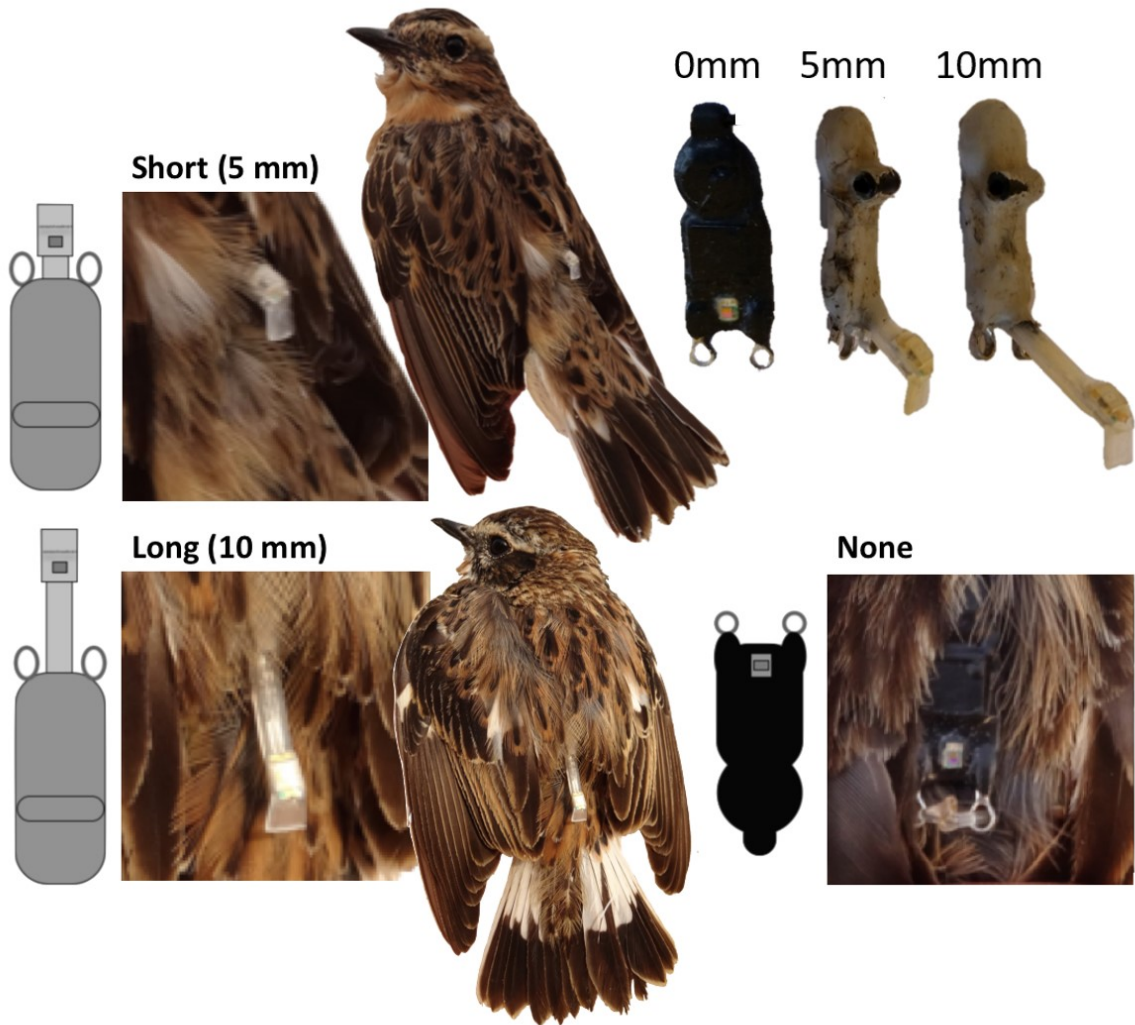
608 Figure 5: The mean difference in latitude confidence interval for variable light stalk lengths considering  
609 only the major (greater than 2 days) stop-over periods during spring migration, using a Geolight analysis

610 with manual confirmation of stationary periods. Predicted values of the mean confidence intervals for  
611 latitude ( $\pm 2SE$ ) from the model in Table 2B are plotted at median longitude.

612 Figure 6: The effect of light stalk length on precision (95% confidence interval) of locations dependent  
613 on latitude, using a FlightR analysis. Graph A. plots the mean confidence interval (CI) of latitude ( $\pm$   
614 95% confidence intervals of this mean) predicted from the model in Table 2C with longitude set to the  
615 median value for all individuals carrying that light stalk type (0mm black circles, solid line; 5mm grey  
616 triangles, dashed line; 10mm white squares, dotted line). Map B. plots the predicted latitude and  
617 longitude ranges from the model in Table 2C (i.e. the vertical lines through each point) on a map to  
618 show how the confidence intervals for 0mm light stalk (black circles) compare to those for a light stalk  
619 of 5mm (grey triangles).

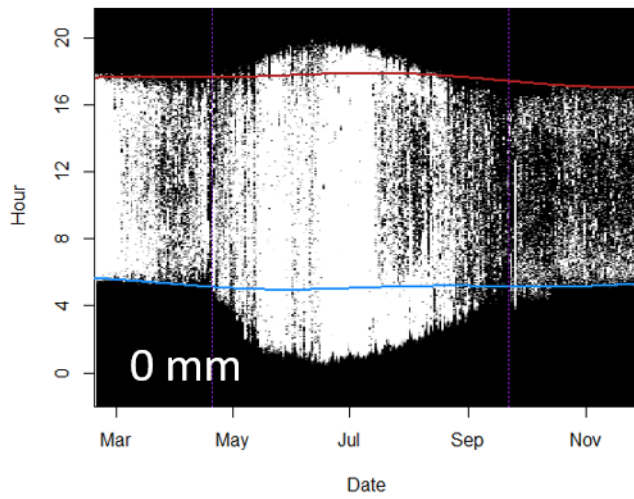
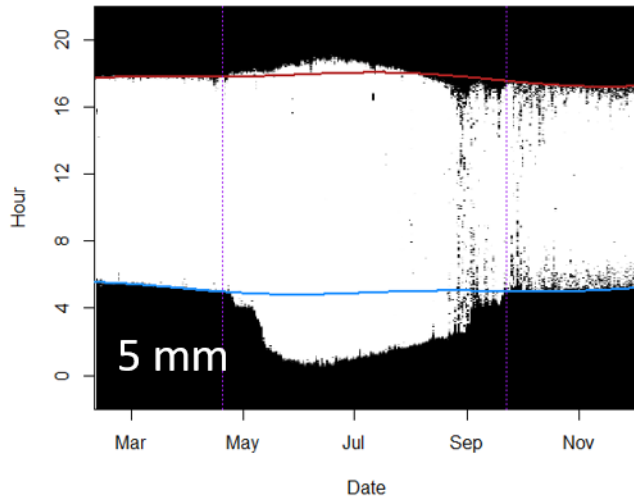
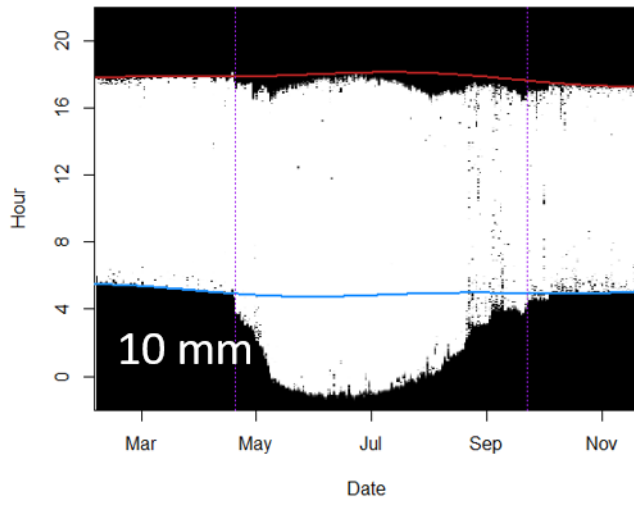
620 Figure 7: A. The difference between A. real latitude and latitude estimated using the Hills-Ekstrom  
621 calibration method and B. the difference between the SEA required to place the tag on the correct  
622 latitude and the SEA identified by the Hills-Ekstrom calibration method for tagged birds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

624 Figure 1:  
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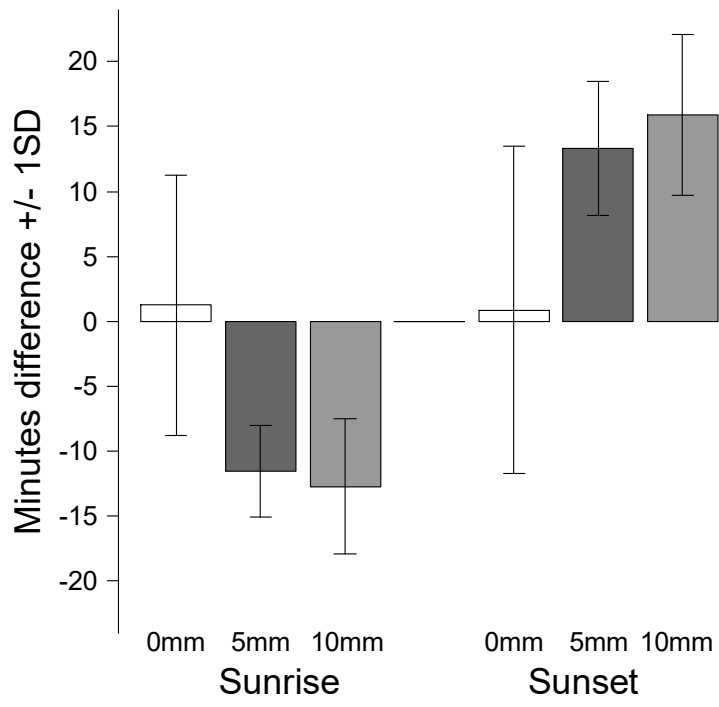
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628 Figure 2:  
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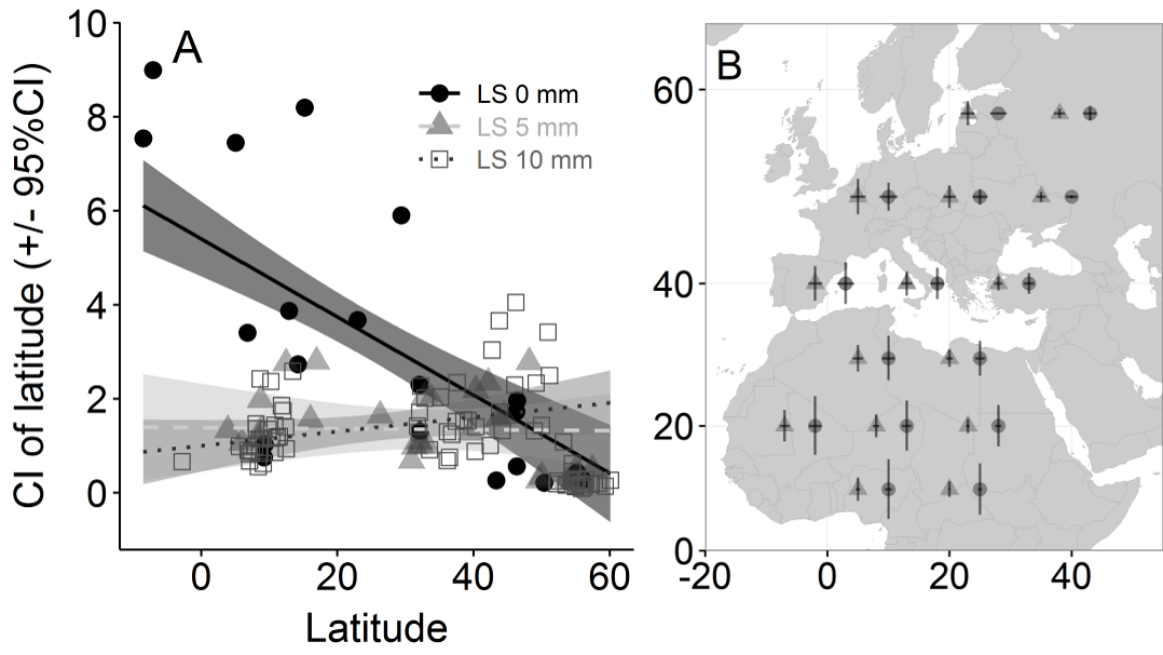
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631 Figure 3:  
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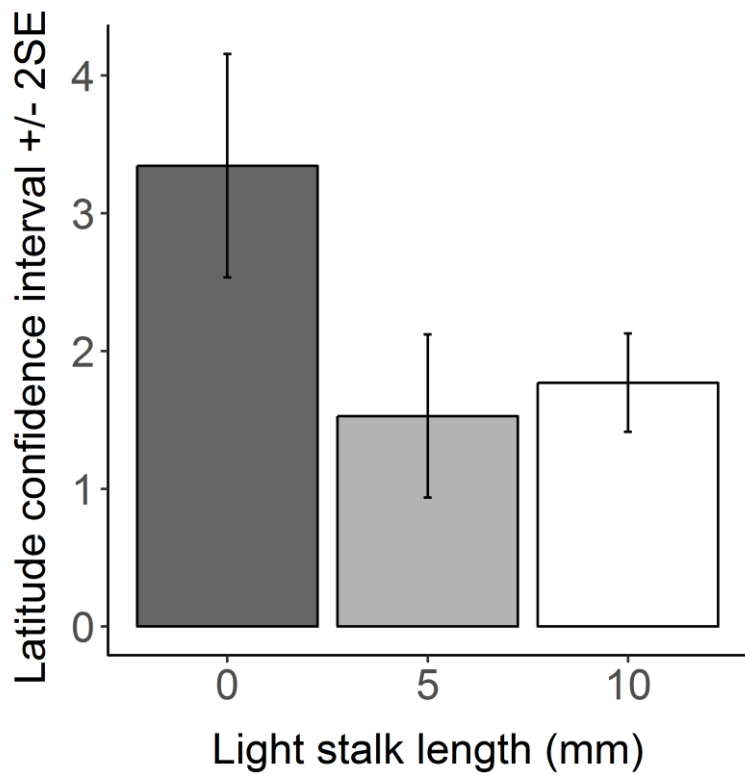
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634 Figure 4:  
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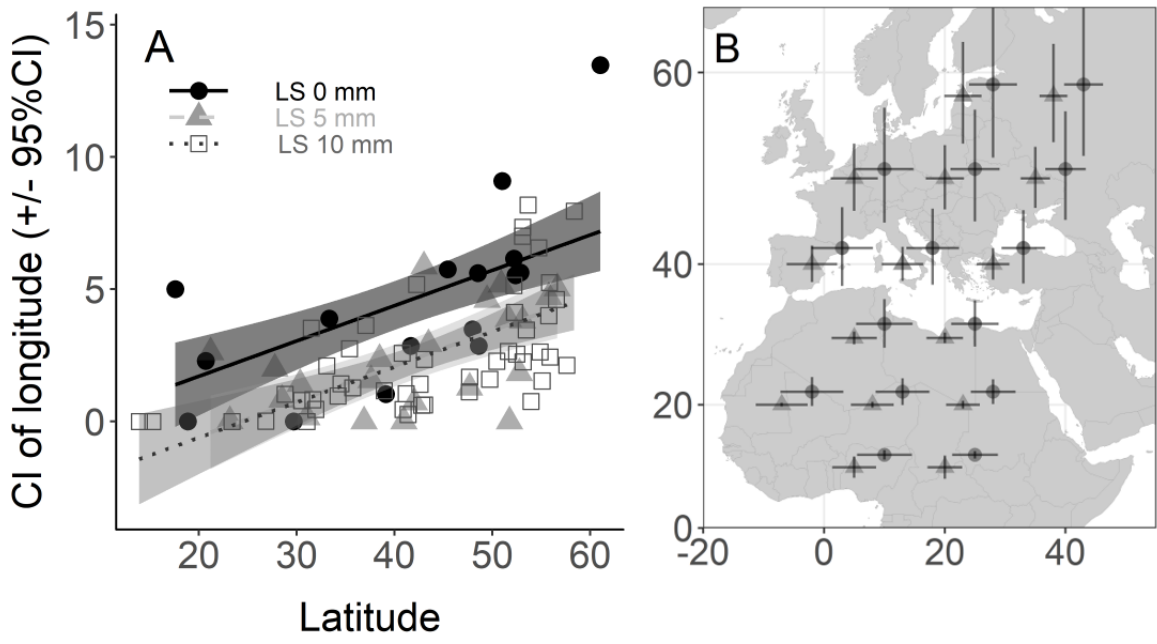
639 Figure 5:  
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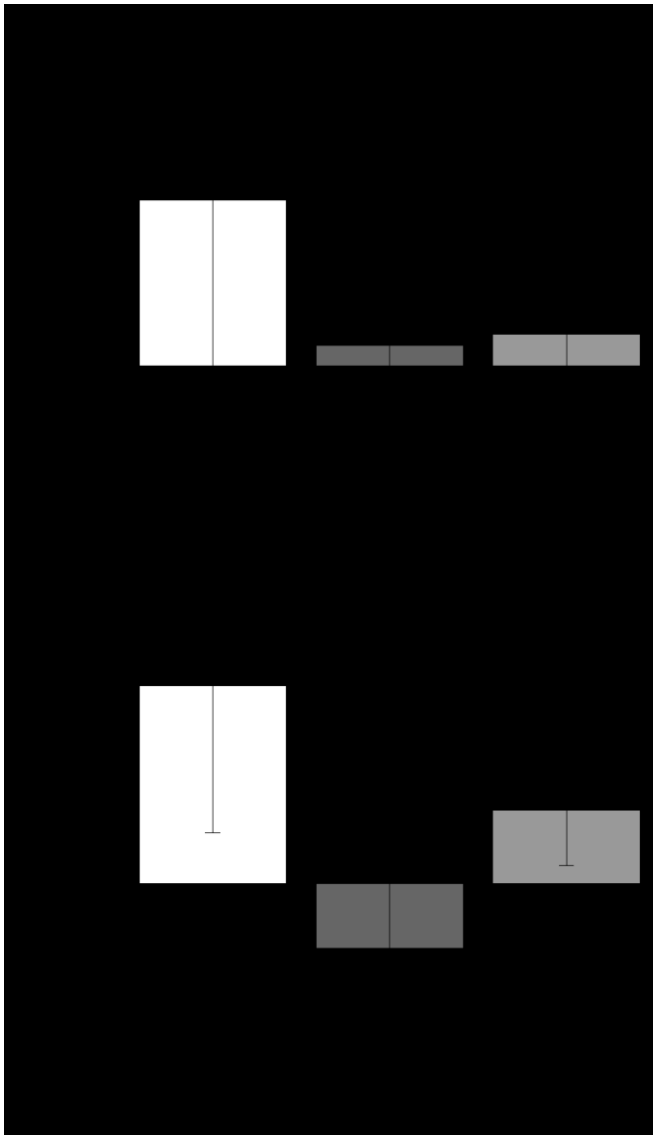


644 Figure 6:  
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648 Figure 7:  
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