Correspondence

Inherent limits of light-level geolocation may lead to over-interpretation

Simeon Lisovski[1,2,*], Heiko Schmaljohann[3,4], Eli S. Bridge[5], Silke Bauer[1], Andrew Farnsworth[6], Sidney A. Gauthreaux, Jr.[7], Steffen Hahn[1], Michael T. Hallworth[8], Chris M. Hewson[9], Jeffrey F. Kelly[5], Felix Liechti[1], Peter P. Marra[8], Eldar Rakhimberdiev[10], Jeremy D. Ross[5], Nathaniel E. Seavy[11], Michael D. Sumner[12], Caz M. Taylor[13], David W. Winkler[14], Simon J. Wotherspoon[15], and Michael B. Wunder[16]

In their 2015 *Current Biology* paper, Streby *et al*. [1] reported that Golden-winged Warblers (*Vermivora chrysoptera*), which had just migrated to their breeding location in eastern Tennessee, performed a facultative and up to “>1,500 km roundtrip” to the Gulf of Mexico to avoid a severe tornadic storm. From light-level geolocator data, wherein geographical locations are estimated via the timing of sunrise and sunset, Streby *et al*. [1] concluded that the warblers had evacuated their breeding area approximately 24 hours before the storm and returned about five days later. The authors presented this finding as evidence that migratory birds avoid severe storms by temporarily moving long-distances. However, the tracking method employed by Streby *et al*. [1] is prone to considerable error and uncertainty. Here, we argue that this interpretation of the data oversteps the limits of the used tracking technique. By calculating the expected geographical error range for the tracked birds, we demonstrate that the hypothesized movements fell well within the geolocators’ inherent error range for this species and that such deviations in latitude occur frequently even if individuals remain stationary.

Geolocator tags record light intensity over time, allowing one to retrospectively estimate locations based on geographic variation in the daily light pattern. There are several methods to derive locations from geolocator data [2–4]. Streby *et al*. [1] used the most frequently applied and simple ‘threshold method’, whereby distinct daily sunrise and sunset times are established and, based on daylength and time of solar noon, locations are estimated [2]. A major source of error in geolocator position estimates results from shading (e.g., from clouds or dense foliage) [2]. When using a threshold method, sunrise and sunset times are defined by applying a threshold and searching for the time when the light exceeds this threshold during dawn and falls below this threshold during dusk. This threshold is associated to a specific sun elevation angle that needs to be defined for each logger device using calibration data (e.g. data recorded by the logger at a known location). Any shading during twilight causes a delayed transition of the threshold during dawn and an early transition during dusk. Thus, shading effectively ‘shortens’ the day and shifts the solar noon. Derived location estimates are thereby altered by shading. The direction and degree to which shading leads to North–South deviations in location estimates depends on the time of the year. For periods after the spring equinox (21st of March), shading of geolocators would result in location estimates that are south of the true location [2] as day lengths are shorter further south. Thus, even if the Golden-winged warblers in Streby *et al*. [1] had not moved but resided at the same location throughout, any shading, including heavy shading associated with the severe weather event, would have yielded location estimates south of the breeding sites.

Streby and colleagues [1] acknowledged the potential influence of shading on location estimates; however, they argued that shading did not influence their results. To support their argument, they cited the methodological study by Lisovski *et al*. [2], and concluded that the proposed distances travelled in avoiding the storm were substantially greater than the expected error in location estimates. However, Lisovski et al. [2] and other studies [5–7] actually demonstrated that distances as large as those between the Tennessee and the alleged evacuation locations lie well within the range of error caused by variation in weather conditions. Therefore, it seems crucial to account for the expected error range when judging whether the data support the suggested tornado-avoidance. Recently, the entire tracks and raw data of the geolocators employed by Streby *et al*. [1] were released as part of a follow-up publication [8], allowing us to perform this analysis (Supplemental information). The provided data included light levels collected during the post-deployment period of 2013, in which the birds were known to be stationary on their breeding grounds and during which shading was in the expected range of what can be attributed to weather events, e.g. cloud cover (Supplemental information). During this period, recorded sunrise and sunset times most frequently deviated from the true twilight event by 5 to 15 minutes, with maximum deviation of up to 48 minutes (Figure 1A). This maximum recorded amount of shading can potentially result in a shortening of day length of up to 96 minutes that would cause a southward deviation in latitude of 3,500 km if recorded during the period of the tornado (Supplemental information). We used the post-deployment data to calculate the error distribution expected from geolocators mounted on Golden-winged Warblers during late April. By applying this error distribution to the breeding location during the alleged evacuation period, we found that the location estimates presented lie within the expected error ranges. Hence, any southward movement, even if it occurred within the range of error, could also be explained by the effects of shading induced by the severe weather event (Figure 1B) and therefore cannot be disentangled from the inherent error of the tracking technique.

Synchronous deviations in latitude among individuals potentially indicate movements as opposed to individualistic effects of shading caused by e.g. habitat. But examination of location estimates during the 2013 post-deployment period, when birds were known to be stationary, revealed synchronous error patterns (Figure 1C) comparable to the data from April 2014. These patterns are likely due to regional weather events (*e.g*., cloud cover, rain) that affected all individuals within the breeding population similarly (Figure 1C). Note that larger deviations in latitude during the tornado period cannot be explained by larger deviations in sunrise/sunset times but by the closer proximity to the spring equinox (21st of March) when shading has larger effects on latitude estimates.

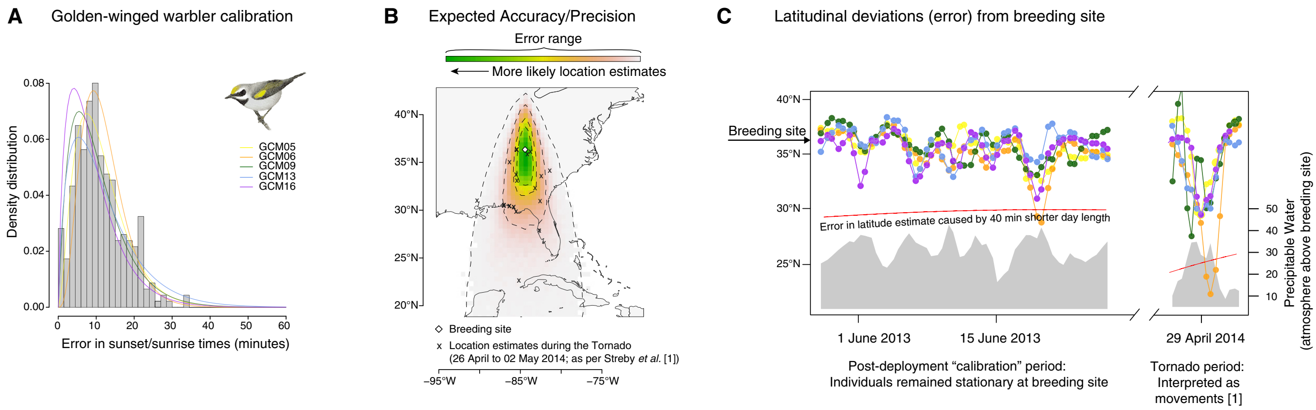

Figure 1. Error range and location estimates of light-level geolocator data from Golden-winged warblers (*Vermivora chrysoptera*) breeding in Tennessee, USA.

Same individuals and colors as in Streby *et al*. [1]. (A) Error in sunset/sunrise times; calculated deviation of recorded sunrise/sunset times (absolute values) to the true event (e.g., a deviation of 10 minutes corresponds to a sunrise detected 10 minutes later or a sunset 10 minutes earlier, caused by shading due to *e.g*. weather events or dense vegetation). The grey bars are based on pooled data from all five tracked individuals (n = 308 twilight times). Colored lines represent the best fit of a gamma density distribution for each individual dataset. (B) The expected error range for the period of the tornadic storms (26th April to 5th May 2014) based on the twilight error distribution shown in panel (A). Contour lines indicating the percentiles of location estimates (40%, 60%, 90%, 95%). The location estimates during the proposed tornado avoidance flight are shown as crosses. (C) Latitude estimates during parts of the calibration period (right) in 2013 when birds were known to be stationary and during the reported tornado period. Red line shows the expected error if sunrise and sunset times deviate by 20 minutes from the true twilight time causing the day length to be 40 minutes shorter. Due to the proximity to the spring equinox, the deviations in latitude are larger in late April than early June despite the same amount of shading. Grey polygons indicate precipitable water in the atmosphere above the breeding site and can be used as a rough proxy for cloud cover (Supplemental information).

While we still do not know what the birds really did during the tornado, and an evacuation movement within a certain radius would indeed be possible, geolocator data cannot provide evidence for such short-term behavior within the expected error range. Therefore, we argue that the most parsimonious explanation for the location estimates during the severe weather event in 2014 is that geolocators were receiving reduced light intensities caused by the weather event. Moreover, shading may have been augmented by sheltering behavior on the part of birds facing a severe storm, a behavior that can have even higher effects on the error in location estimates. Geolocation by light has proven to be an excellent tool for tracking small migratory birds. Yet, its inherent inaccuracies call for careful analysis and conservative interpretation including consideration of error ranges.

SUPPLEMENTAL INFORMATION

Supplemental Information including experimental procedures and one figure can be found with this article online at https://doi.org/10.1016/j.cub.2017.11.072.

AUTHOR CONTRIBUTIONS

All authors initiated and discussed the framework of the manuscript. S.L. performed analyses. S.L., H.S., E.S.B. and S.B. wrote the manuscript. All authors provided comments and criticism.

REFERENCES

1. Streby, H.M., Kramer, G.R., Peterson, S.M., Lehman, J.A., Buehler, D.A., and Andersen, D.E. (2015). Tornadic storm avoidance behavior in breeding songbirds. Curr. Biol. *25*, 98–102.
2. Lisovski, S., Hewson, C.M., Klaassen, R.H.G., Korner-Nievergelt, F., Kristensen, M.W., and Hahn, S. (2012). Geolocation by light: accuracy and precision affected by environmental factors. Methods Ecol. Evol. *3*, 603–612.
3. Sumner, M.D., Wotherspoon, S.J., and Hindell, M.A. (2009). Bayesian estimation of animal movement from archival and satellite tags. PLoS One *4*, e7324.
4. Rakhimberdiev, E., Saveliev, A., Piersma, T., and Karagicheva, J. (2017). FlightR: and R package for reconstructing animal paths from solar geolocation loggers. Methods Ecol. Evol. https://doi.org/10.1111/2041–210X.12765.
5. Fudickar, A.M., Wikelski, M., and Partecke, J. (2012). Tracking migratory songbirds: accuracy of light-level loggers (geolocators) in forest habitats. Methods Ecol. Evol. *3*, 47–52.
6. Liechti, F., Scandolara, C., Rubolini, D., Ambrosini, R., Korner-Nievergelt, F., Hahn, S., Lardelli, R., Romano, M., Caprioli, M., Romano, A., *et al*. (2014). Timing of migration and residence areas during the non-breeding period of barn swallows Hirundo rustica in relation to sex and population. J. Avian Biol. *45*, 1–12.
7. Ross, J.D., Bridge, E.S., Rozmarynowycz, M.J., and Bingman, V.P. (2014). Individual variation in migratory path and behavior among Eastern Lark Sparrows. Anim. Migration *2*, 29–33.
8. Kramer, G.R., Streby, H.M., Peterson, S.M., Lehman, J.A., Buehler, D.A., Wood, P.B., McNeil, D.J., Larkin, J.L., and Andersen, D.E. (2017). Nonbreeding isolation and population-specific migration patterns among three populations of Golden-winged Warblers. The Condor *119*, 108–121.

[1]Swiss Ornithological Institute, Department of Bird Migration, 6204 Sempach, Switzerland. [2]University of California, Department of Neurobiology, Physiology and Behavior, Davis, California, CA 95616, USA. [3]Institute of Avian Research "Vogelwarte Helgoland", 26386 Wilhelmshaven, Germany. [4]Faculty of Biology/ Environmental Sciences, University Oldenburg, D-26111 Oldenburg, Germany. [5]Oklahoma Biological Survey, University of Oklahoma, Norman, OK 73019, USA. [6]Information Science Program, Cornell Lab of Ornithology Ithaca, NY 14853, USA. [7]P. O. Box 9, Edisto Island, SC 29438-0009, USA. [8]Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington DC 20013, USA. [9]British Trust for Ornithology, Norfolk IP24 2PU, UK. [10]NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems and Utrecht University, Den Burg, Texel, 1790 AB, The Netherlands & Department of Vertebrate Zoology, Lomonosov Moscow State University, Moscow, 119991, Russia. [11]Point Blue Conservation Science, Petaluma, CA 94954, USA. [12]Australian Antarctic Division, Kingston TAS 7054, Australia. [13]Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA 70118, USA. [14]Department of Ecology and Evolutionary Biology, Museum of Vertebrates and Laboratory of Ornithology, Cornell University, Corson Hall, Ithaca, NY 14853, USA.[15]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, TAS 7001, Australia. [16]Department of Integrative Biology, University of Colorado, Denver, CO 80202, USA.
*E-mail: simeon.lisovski@gmail.com