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Correspondence

Response to Lisovski *et al*.

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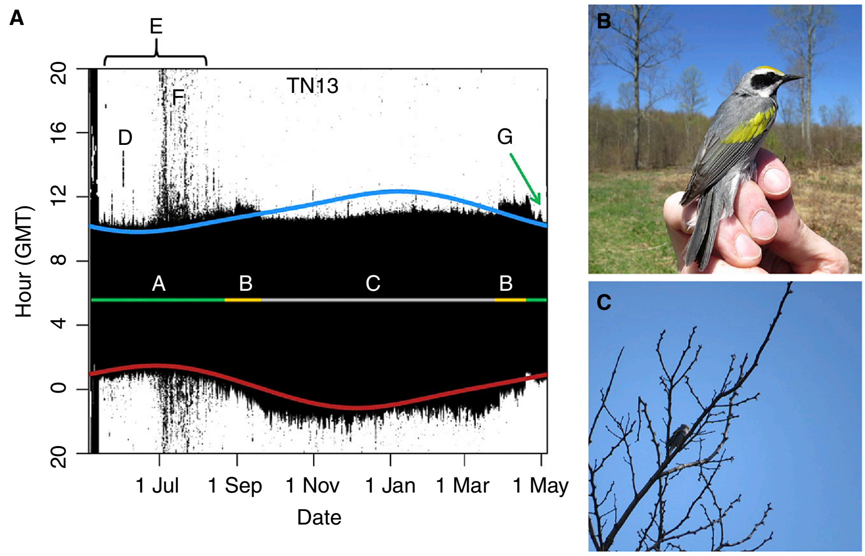

Figure 1. Recorded and observed lack of environmental shading during the evacuation period in our 2015 report.
(A) One year of raw light-level data (light levels are unitless and range from 0–64) from a representative Golden-winged Warbler (TN13) breeding in Tennessee, USA. Periods with no ambient light are black and periods of light are white. Curved lines represent the expected timing of dawn (blue line) and dusk (red line) assuming the bird never left its breeding site. Various departures from these expected transition times came during the nesting and post-fledging ('A')' migration ('B')' and nonbreeding ('C') periods. Environmental shading that occurs during the daytime can be intense enough to achieve full darkness ('D') and is likely caused by combined changes in weather and behavior and does not influence location estimates, but that which occurs during dawn or dusk can impact estimates of the timing of those transitions. Relatively intense environmental shading ('E') occurs at dusk and dawn from mid-May through July in geolocator data from Golden-winged Warblers and likely represents shifts from singing and defending territories to the use of increasingly foliated and dense vegetation for feeding nestlings (May) and rearing fledglings (May and June) and then molting (July). The evacuation period ('G') in our 2015 report occurred prior to the breeding season (a period for which there are no comparable data from the deployment year) and was not associated with signals of environmental shading during dusk or dawn transitions, in contrast with that present throughout the deployment season data that Lisovski *et al*. [1] used to inform their analyses. Panel (B) shows the lack of leaves or other vegetation characteristics likely to cause shading at our study site on 3 May 2014, *after* the period in our 2015 report during which Lisovski *et al.* assert that dense vegetation caused shading that influenced our geolocator data, and panel (C) shows the blue sky and sun shining on one of the few birds that remained on our site at 0806 hr on 30 April 2014, during the period when Lisovski *et al.* assert that shading from regional atmospheric precipitable moisture influenced dawn and dusk transition estimates in our geolocator data.

Lisovski *et al*. [1] describe the widely recognized limitations of light-level geolocator data for identifying short-distance latitudinal movements, recommend that caution be used when interpreting such data, intimated that we did not use such caution and argued that environmental shading likely explained the Golden-winged Warbler (*Vermivora chrysoptera*) movements described in our 2015 report [2]. Lisovski *et al*. [1] conclude that the bird movements we reported could not be disentangled from estimation error in stationary animals caused by environmental shading. We argue that, to the contrary, these hypotheses can easily be disentangled because the premise that environmental shading caused synchronous and parallel error among geolocators is false. With their assertion that our location estimates could be biased by >3,500 km on a day with no observable local sources of shading, Lisovski *et al.* [1] have taken a position of incredulity toward all geolocator-based animal movement data published to date.

We agree that data derived from light-level geolocators are inherently prone to error caused by environmental shading and require careful interpretation. However, we disagree that environmental shading could explain the movements we reported in Golden-winged Warblers [2], primarily based on the lack of environmental shading at our study site during most of the period of interest and secondarily based on the movements we observed being variable among birds in timing, distance, and direction, which is inconsistent with shading error. Ultimately, we find that the analysis by Lisovski *et al*. [1] largely confirms our original interpretation that Golden-winged Warblers evacuated their breeding sites one to two days before any atmospheric changes associated with the unusually strong supercell storm that developed days earlier and hundreds of kilometers away and produced 84 confirmed tornados over the course of four days in the southeastern United States.

The criticism of Lisovski *et al*. [1] relies on the assumption that there was substantial environmental shading at our study site that caused shade-related error in our geolocator data over several days. Environmental shading in geolocator data is typically attributed to either cloud cover or dense vegetation. Lisovski *et al*. [1] assert that there was environmental shading from cloud cover based on interpolated regional atmospheric precipitable water levels, but provided no evidence that interpolated levels actually resulted in local cloud cover. Although the massive storm took several days to traverse the southeastern United States, cloud cover from the storm was present at our study site for <24 hours [2], and transitions during the evacuation period showed no signs of shading (Figure 1).

The analysis of Lisovski *et al*. [1] relies on improper inference from two irrelevant periods when environmental conditions, bird behavior, and habitat use of individual Golden-winged Warblers were not comparable to those during the late-April and early-May period of interest in our 2015 report. First, Lisovski *et al*. [1] used our data [3] from a later portion of the breeding season during the previous year (i.e., nestling provisioning and post-fledging stages of 2013) to inform an expected-error model that overestimated potential shading error. Vegetation and bird breeding phenology in 2013 were among the earliest in a decade and all birds were already nesting when we marked them in May of 2013. Therefore, the data were not from the relevant pre-breeding period when vegetation was leafless and Golden-winged Warblers typically perch and sing from treetops during mornings and evenings (Figure 1). Given the differences in vegetation and bird nesting phenology between years, and that we deployed geolocators during the 2013 nesting season, the only relevant calibration data for comparison to the evacuation period are those of the 19 days in 2014 before and after the movement period when the birds were stationary at their breeding site under similar environmental conditions, which are the data we used for calibration in our 2015 report [2]. Most of the expected error in the Lisovski *et al*. [1] model is far greater than the greatest error (290 km) we observed in the relevant calibration data, demonstrating the extent to which their expected error model was inflated.

Lisovski *et al*. [1] overlaid the location estimates from our 2015 report onto that model. Notably, they demonstrated that many of our location estimates fell within the outermost, least-likely band of extreme potential shade-related error in their model. Thus, we contend that the results of Lisovski *et al*. [1] seemingly quantify the extent to which an error model must be inflated to justify the slightest shading-based skepticism about our original interpretation of the data, but only if one first accepts the false premise that such shade was present at our study site during all dawn and dusk transitions throughout the evacuation period.

In a second analysis, Lisovski *et al*. [1] compared location estimates from an even later portion of the breeding season (June 2013) to location estimates during the evacuation period (late April 2014) and claim that levels of regionally interpolated atmospheric precipitable water were associated with erroneous location estimates. However, at our study site, June is the early post-fledging period, during which adults forage for provisions and raise fledglings in dense vegetation in the understory of older, denser forest than that in which they nest [4]. In this comparison, Lisovski *et al*. [1] explained that shading error can cause apparent synchronous movements in a population of geolocator-marked birds that are stationary, and they pointed to the relatively small and synchronous errors that occurred during June 2013 when there was more environmental shading experienced by the warblers than was present during the period in 2014 when we reported that marked warblers made previously undocumented long-distance movements. Those error-based changes in latitudinal estimates during the post-deployment period of 2013 are not similar to the relatively large, extended, and variable movements among birds in our 2015 report when sources of shade were not present. Additionally, the potential latitudinal error described by Lisovski *et al*. [1] ignores the unexplained magnitude and variability of longitudinal movements we reported. The lumping of data to show similarities between the frequency distribution of light deviations during the evacuation period and during the previous summer obfuscates the unexplained variation among geolocator-marked birds in our report in timing, distance, and direction moved during the evacuation period.

Shade-related error can, by definition, only make days appear shorter by making dawn appear to occur later and dusk appear to occur earlier. This is acknowledged by Lisovski *et al*. [1] in the calculation of their expected error range when they used the earliest sunrises and latest sunsets for each geolocator as 'true events'. If some atmospheric condition on an otherwise non-unique day caused the first light of dawn to appear earlier or the last light of dusk to appear later, we would expect to see such events consistently recorded among multiple geolocators at the same site, and if both occurred on the same day, the birds in our 2015 report would have appeared to move north. In the movements we reported, dawn occurred much earlier than at our study site for some warblers on the same days that dawn occurred much later than at our study site for other warblers, and the same variability among warblers occurred in recordings of dusk. For example, on 28 April 2014, one of the warblers we tracked experienced dawn and dusk 9 and 13 minutes earlier, respectively, than those transitions occurred at our study site, while a second warbler that bred in a neighboring territory experienced dawn and dusk 41 minutes and 39 minutes later than the first warbler. The substantial differences between these locations and the timing of twilight cannot be explained by the effects of shading on or even near our study site. Lastly, the movements by the five warblers in our report resembled their individual fall migration routes. The probability that any form of shading experienced simultaneously by five warblers at one study site would coincidentally cause each warbler to appear to trace its individual fall migration route must be extremely low.

We believe that illogical arguments made by Lisovski *et al*. [1] represent an incorrect and therefore less parsimonious explanation than our original interpretation of the data. We echo their encouragement of the responsible interpretation of geolocator data, but add that such interpretation is best rooted in a detailed understanding of the ecology and behavior of the study system.

AUTHOR CONTRIBUTIONS

Conceptualization, H.M.S., G.R.K., and D.E.A.; Writing – Original Draft, H.M.S., G.R.K., and D.E.A.; Visualization, H.M.S. and G.R.K.; Writing – Review and Editing, S.M.P., D.A.B., and J.A.L.

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