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Source: The Condor, 119(2) : 289-297

Published By: American Ornithological Society

URL: https://doi.org/10.1650/CONDOR-16-180.1

THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 119, 2017, pp. 289–297
DOI: 10.1650/CONDOR-16-180.1

RESEARCH ARTICLE

Mixed effects of geolocators on reproduction and survival of Cerulean Warblers, a canopy-dwelling, long-distance migrant

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Submitted September 20, 2016; Accepted February 23, 2017; Published May 3, 2017

ABSTRACT
Light-level geolocators, miniature devices used for tracking avian migration over the full annual cycle, are being widely deployed on small migratory passerines. However, the effects of carrying geolocators on the breeding biology of songbirds are unclear, and variable species- and guild-specific conclusions have been drawn regarding their effects on return rates (apparent annual survival). In particular, there is a lack of published information on the effects of geolocators on Nearctic–Neotropical migrant warblers and canopy-dwelling bird species, which limits our ability to determine whether this technology is appropriate for use on species within these groups. During 2014 and 2015, we deployed geolocators on 49 adult male Cerulean Warblers (*Setophaga cerulea*) in Pennsylvania, Missouri, and Arkansas, USA. We monitored the effects of geolocators across the full annual cycle by comparing apparent within-breeding-season survival (within-season ϕ), nestling provisioning rates, nest survival, and return rates between geolocator-tagged adult males and color-banded controls. We found no negative effects of geolocators during the breeding season of geolocator deployment, but the return rate of geolocator-tagged birds was lower than that of control birds (16% $\pm$ 5% vs. 35% $\pm$ 7%). We found no strong evidence that the differential return rate between the 2 groups was influenced by breeding region, body mass, bird age, year of geolocator deployment, or method of attachment. Although finding no effect of geolocators during the breeding season is encouraging, the lower return rate of geolocator-tagged birds warrants further investigation in the field. If further improvements in the design or attachment methods of geolocators are not technologically possible, the potential for increased mortality (or dispersal) of geolocator-tagged birds should be weighed against the potential conservation gains that could be made by identification of critical stopover, wintering, and breeding habitats for populations of interest.

Keywords: migration, breeding, provisioning, survival, Cerulean Warbler, *Setophaga cerulea*

Efectos mixtos de los geo-localizadores en la reproducción y la supervivencia de *Setophaga cerulea*, un migrante de larga distancia habitante del dosel

RESUMEN
Los geo-localizadores en miniatura y de bajo peso que se usan para el seguimiento de las migraciones de las aves a lo largo de todo el ciclo anual están siendo ampliamente colocados en pequeños paserinos migratorios. Sin embargo, no está claro el efecto de la colocación de los geo-localizadores en la biología reproductiva de las aves canoras, y se han sacado conclusiones variables para especies y gremios específicos sobre sus efectos en las tasas de retorno (supervivencia anual aparente). En particular, hay una falta de información publicada sobre los efectos de los geo-localizadores sobre especies de aves migratorias Neárticas-Neotropicales de currucas y habitantes del dosel, lo que limita nuestra capacidad para determinar si esta tecnología es apropiada para especies adentro de estos grupos. Durante 2014 y 2015, colocados geo-localizadores en 49 machos adultos de *Setophaga cerulea* en Pensilvania, Missouri y Arkansas. Seguimos los efectos de los geo-localizadores a lo largo de todo el ciclo anual comparando la supervivencia aparente adentro de la estación reproductiva (ϕ adentro de la estación), las tasas de aprovisionamiento de los polluelos, la supervivencia del nido y las tasas de retorno entre machos adultos con geo-localizador y controles marcados con anillos de color. No encontraos efectos negativos de la colocación de los geo-localizadores durante la estación reproductiva, pero la tasa de retorno de las aves marcadas con geo-localizadores fue más baja que la de las aves control (16 $\pm$ 5% vs 35 $\pm$ 7%). No encontramos una fuerte evidencia de que estas tasas diferenciales entre los dos grupos estuvieran influenciadas por la región de cría, la masa corporal, la edad del ave, el año de colocación del geo-localizador o el método de fijación. Aunque el hecho de no haber hallado un efecto del geo-localizador durante la estación reproductiva es alentador, la menor tasa de retorno de las aves marcadas con geo-localizadores justifica más investigaciones en este tema. Si no es tecnológicamente posible mejorar aún más el diseño o la colocación de los geo-localizadores, el aumento potencial de la mortalidad (o de la dispersión) de las aves marcadas con geo-localizadores

debería ser sopesado con el aumento del potencial de conservación que se obtiene con la identificación de los hábitats críticos de parada, invernada y de cría para las poblaciones de interés.

Palabras clave: aprovisionamiento, cría, migración, *Setophaga cerúlea*, supervivencia

INTRODUCTION

The use of light-level geolocation devices (geolocators) to identify migration routes, timing of migration, stopover sites, and breeding or wintering locations for individual birds has recently become widespread in ornithology (Stutchbury et al. 2009, Bridge et al. 2013). Geolocators, composed minimally of a light sensor, a battery, and a microcomputer, can be attached to birds prior to their migration. They function by recording ambient light levels along with time stamps at regular intervals. Times of sunrise and sunset as well as day length are used to estimate the longitude and latitude of the geolocator-tagged bird on a daily basis throughout the annual cycle (Bridge et al. 2013). To obtain data from the devices, birds must be recaptured, usually when they return to the location at which they were originally captured and marked. Miniature geolocators, now weighing <0.4 g, have been used successfully on birds as small as 9-g Golden-winged Warblers (*Vermivora chrysoptera*) and 12-g Blackpoll Warblers (*Setophaga striata*; DeLuca et al. 2015, Peterson et al. 2015).

On passerines, geolocators are usually attached over the synsacrum using some form of leg-loop harness (Rappole and Tipton 1991, Bridge et al. 2013, Streby et al. 2015). A variety of geolocator types and harness materials have been used, and return rates have been highly variable across studies (Bowlin et al. 2010, Bridge et al. 2013). Although annual return rates are commonly reported for both geolocator-tagged and color-banded control birds, it is becoming apparent that the effects of these devices are species- (or guild-) specific. For example, geolocators (and other tracking devices) are more of a burden on aerial insectivores (Stutchbury et al. 2009, Bowlin et al. 2010, Gómez et al. 2014; but see Matyjasiak et al. 2016) and may be more detrimental to species that make longer migratory flights (Bridge et al. 2013). Because abiotic (e.g., microclimate, wind, weather events) and biotic (e.g., predators, prey) pressures likely differ among microhabitats (e.g., canopy vs. understory), geolocators may also differentially affect birds that occupy these dissimilar environments.

In addition to the potential for context-dependent impacts on return rates, geolocators may also influence breeding biology (Schmaljohann et al. 2012, Arlt et al. 2013, Bridge et al. 2013, Gómez et al. 2014). Studies of the effects of radio-transmitters on the breeding activities of Golden-winged and Hooded (*Setophaga citrina*) warblers indicated that there were no negative effects on nestling provisioning rates, incubation times, or seasonal productivity (Neudorf and Pitcher 1997, Streby et al. 2013). However, a meta-analysis and a literature review of the effects of transmitters and related tracking devices suggested that attached devices can have negative impacts on a number of aspects of a bird's life, such as energy expenditure, reproductive success, and the probability of nesting (Calvo and Furness 1992, Barron et al. 2010), and negative effects of tracking devices on birds are likely underreported (Hill and Elphick 2011). Finally, although geolocators have similarities to radio-transmitters in harnessing method (for songbirds), they differ in that their attachment methods are more permanent, and thus they may affect birds differently compared with radio-transmitters (Bridge et al. 2013, Streby et al. 2015).

Here, we evaluated the effects of geolocators on several components of fitness within the breeding season (within-season apparent survival, nestling provisioning rate, and nest survival) and across seasons (return rate) for a declining, canopy-dwelling, Nearctic–Neotropical migrant, the Cerulean Warbler (*Setophaga cerulea*). Although the benefits of understanding migratory timing, pathways, and connectivity for the conservation of this species (and other songbirds) are substantial (Hostetler et al. 2015, Marra et al. 2015), the potential for deleterious effects caused by the attachment of tracking devices should be evaluated and reported to reduce unintended mortality, limit impacts on reproductive performance, and provide insights that may guide technical improvements in the devices or their deployment.

METHODS

Study Area

We captured male Cerulean Warblers and deployed geolocators across 2 regions within the Cerulean Warbler's breeding range: on the Allegheny Plateau in northwestern Pennsylvania and on the Ozark Plateau in Missouri and Arkansas, USA (Figure 1). In Pennsylvania, sites were located within the State Game Lands No. 86 (41.8°N, 79.3°W) along the Allegheny River and within the adjacent Allegheny National Forest (41.6°N, 79.3°W). In the Ozark region, individual sites were located within the Buffalo National River (36.0°N, 92.6°W), Cherry Bend Recreation Area in the Ozark National Forest (35.7°N, 93.8°W), and along the Eleven Point River in the Mark Twain National Forest (36.7°N, 91.2°W).

Field Methods

In 2014, we attached geolocators (Intigeo-W30, stalkless; Migrate Technology, Coton, Cambridge, UK) to 10 adult

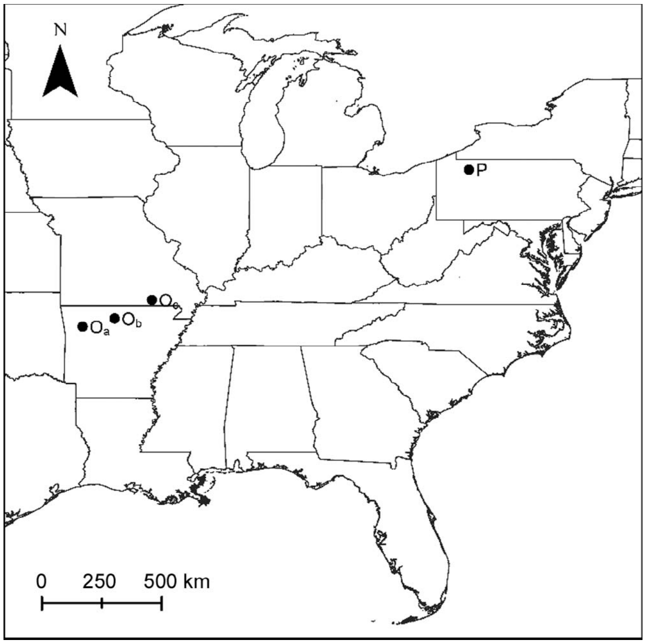

FIGURE 1. Study sites in the Ozarks (O), located in Missouri and Arkansas, and Pennsylvania (P), USA, where we fitted geolocators to Cerulean Warblers to investigate effects on reproduction and survival. O_a = Cherry Bend Recreation Area, Ozark National Forest; O_b = Buffalo National River; O_c = Eleven Point River, Mark Twain National Forest; and P = Pennsylvania State Game Lands 86 and adjacent Allegheny National Forest.

male Cerulean Warblers in Pennsylvania. The birds were captured in mist nets, lured in by playback of Cerulean Warbler vocalizations and painted wooden decoys. Upon capture, we banded each male with a U.S. Geological Survey (USGS) aluminum leg band and a unique combination of 1–3 color bands to enable the identification of individuals without recapture. The mass, age (determined by molt limits; Pyle 1997), and wing chord of each bird was recorded. We attached geolocators using an adaptation of the leg-loop method recommended by the manufacturer (and Rappole and Tipton 1991), utilizing Stretch Magic (Pepperell Braiding Company, Pepperell, Massachusetts, USA) beading cord as harness material and securing the harness with jewelry crimp beads. The weight of each geolocator with harness was 0.36 g, which was 3.6–4.0% of bird body weight. We captured and color-banded an additional 14 adult males in the same sites as the birds fitted with geolocators to serve as controls.

In 2015, we deployed 19 geolocators on adult males in the Pennsylvania sites and 20 geolocators on males in the Ozark study sites (ML 6040, stalkless; Biotrack, Wareham, UK; 0.48 g including harness weight). We used a slightly different geolocator attachment method in this year; we superglued the harness to the device prior to deployment on a bird (following Streby et al. 2015). We also captured and color-banded an additional 18 males in the Pennsylvania sites and 20 males in the Ozark sites to use as controls.

Within-season Survival

In Pennsylvania, we searched for all geolocator-tagged and control birds throughout their territories at least once per week during the nesting season of initial capture to monitor within-season apparent survival (within-season ϕ). If an individual was not located passively (by following singing individuals and verifying color-band combinations with binoculars), then song playback was used as an aid to locate and identify focal birds. Because the majority of nests had either failed or fledged by June 21, after which some males dispersed, resighting data from after this date were excluded. After excluding males captured later than June 15 (because the final week of resighting data was June 15–21), our resulting sample consisted of 27 geolocator-tagged and 26 color-banded control males. Decreased within-season ϕ of geolocator-tagged birds (vs. controls) could indicate either reduced survival or abandonment of the breeding territory following geolocator attachment. Within-season ϕ was not monitored in the Ozark study sites.

Nest Survival and Provisioning Rates

In 2014 and 2015, we searched for nests in the Pennsylvania study sites, attempting to locate nests associated with all color-banded males. We monitored these nests ($n = 40$) every 1–3 days with binoculars or spotting scopes to determine nest fate. We confirmed successful nests by observing fledging events or by locating fledglings out of nests (e.g., by following begging calls). We also documented provisioning rates by filming nests that survived to the late nestling period ($n = 24$; ~7–9 days posthatching, 2–3 hr per nest).

Return Rates

To assess return rates in Pennsylvania, we extensively searched for all geolocator-tagged birds ($n = 29$) and control birds ($n = 32$) with equal effort throughout the 2015 and 2016 nesting seasons (May 8–July 2) until found or until the last nest fledged and territories broke down. We focused on a 1-km radius area centered on each bird's original capture location; we chose this distance based upon our experience resighting color-banded Cerulean Warblers (e.g., Boves et al. 2013, S. H. Stoleson personal observation). During this study, no banded individuals were detected outside this radius during either nesting season. We had ample opportunity to detect any dispersing individuals during our extensive daily fieldwork across the larger study area. In addition, in >20 yr of combined experience marking this species, we have encountered only a single case of a banded returning bird shifting its territory >1 km between breeding seasons. Typically, individuals that return to the general study area have high site fidelity (<200 m dispersal distance), although long-distance dispersal between years is a possibility (Girvan et al. 2007).

In the Ozark study sites, where birds arrived ~10 days earlier than in Pennsylvania, we searched for each marked individual (20 geolocator-tagged and 20 banded control birds) from April 24 to June 1 until found (and geolocator-tagged birds recaptured) or considered to be absent due to mortality or dispersal from the local community. Because of time and personnel constraints, our resighting effort in the Ozarks was less intensive than in Pennsylvania; we used song playback in attempts to sight all birds (still with equal effort for each bird, control or geolocator-tagged) within a 500-m radius of the capture location, repeated twice for each individual and with at least a week between surveys.

Data Analysis

To evaluate the potential for geolocators to decrease within-season ϕ, we constructed Cormack-Jolly-Seber models (Lebreton et al. 1992) in program MARK (White and Burnham 1999) with 5 weekly resighting intervals. We tested for goodness-of-fit of the most parameterized model in program RELEASE and also checked the Fletcher c-hat ($\hat{c}$), estimated by MARK, for potential overdispersion (Cooch and White 2006). We then built a variety of models, all of which included a detectability parameter, and compared them using Akaike's Information Criterion adjusted for small sample size (AIC_c). These included a constant survival (null) model, a univariate 'group' effect model (geolocator or control), and multiple models that included all possible additive combinations of group effect, age, mass, year, and site. We considered all models with ΔAIC_c values ≤ 2 to be equivalent (Burnham and Anderson 2002), and we estimated within-season ϕ and return rates using model averaging of all top equivalent models. If 'group' was included in one of the top models, we compared survival rates between the 2 groups by examining 95% confidence intervals (CIs). If 95% CIs overlapped, we considered there to be no evidence for a difference in survival between geolocator-tagged and control birds.

To evaluate the potential effect of geolocators on nest survival (successful nests defined as fledging at least one young), we constructed and compared models in a similar fashion as described above using the nest survival module in program MARK (Dinsmore and Dinsmore 2003). If 'group' was included in a top model, we again compared daily nest survival rates (DSR) between geolocator and control groups by assessing overlap of 95% CIs. Nestling provisioning rates for each brood were estimated from videos by calculating the number of male visits with food per number of nestlings per min of video.

We compared nestling provisioning rates (as the dependent variable) between control and geolocator-tagged males using a mixed model analysis of covariance (ANCOVA) while controlling for year, ordinal date, and nestling age (as random effects) in R 3.2.3 (R Core Team 2016). After selecting top models, we tested that assumptions of homogeneity of variance and normal distribution of residuals were met by assessing residual plots. Because 8 filmed nests were associated with males of unknown age (i.e. unbanded males), provisioning rates between banded and unbanded birds, and between banded second-year (SY) and after-second-year (ASY) birds, were compared using 2-sample *t*-tests to determine whether parental age affected provisioning rates (and whether parental age needed to be accounted for in our analysis). We considered the groups to be different if $P < 0.05$.

To evaluate the potential for geolocators to decrease return rates (i.e. apparent annual survival), we constructed binomial general linear models (glm) in R, with 0 indicating no return to the search area and 1 indicating that a bird returned. We used this method instead of Cormack-Jolly-Seber models because we had just 1 recapture occasion and could not estimate detectability. We included the predictors of group effect, year (2014 or 2015), age (SY or ASY), mass, and region (Pennsylvania or Ozarks). Interactions of group effect with mass, year, age, and region were also tested in the models. We again compared models using AIC_c, and assessed the strength of any potential group effect by examining the 95% CI of the estimate (β) for that variable (if included in an equivalent top model). We also ensured that the annual return rate data from our most parameterized glm were not largely overdispersed ($\hat{c} = 1.15$; 109.1 residual deviance on 95 df for the global model). Values for all parameter estimates are reported as the mean $\pm$ 1 SE.

RESULTS

Within-season Survival

Four models were equivalent, with none including 'group' (Table 1), indicating no support for a geolocator-marking effect on within-season ϕ. The model-averaged weekly ϕ, estimated from the top 4 models, was 0.968 ± 0.026 ($n = 53$ for the combined groups); across the entire breeding season, this was equivalent to an apparent seasonal survival rate of 85% ($0.968^{5\ \text{weeks}}$). Note that this is apparent survival rate, including dispersal as well as mortality.

Nest Survival and Provisioning Rates

The top model describing daily nest survival rate (DSR) was the null model, indicating that geolocators did not affect nest survival. The DSR 95% CI of geolocator-tagged males (0.940–0.978; $n = 21$) overlapped with that of control males (0.928–0.977, $n = 19$; Table 2).

TABLE 1. Comparison of top equivalent models ($\Delta AIC_c < 2.00$) for apparent weekly survival of male Cerulean Warblers in Pennsylvania, USA, 2014 and 2015, using Akaike's Information Criterion adjusted for small sample size (AIC_c). K = the number of parameters, w_i = model weight, and Dev = model deviance. The top model that included the variable 'group' (which indicates the influence of geolocators; the 2 groups were geolocator-tagged birds and color-banded control birds) and the null model are shown for comparison.

Model	K	ΔAIC_c	w_i	Dev
Age + Mass	3	0.00 [a]	0.27	116.73
Age + Mass + Site	4	0.17	0.25	114.67
Age	2	0.41	0.22	119.31
Age + Site	3	1.59	0.12	118.32
Group + Age + Mass + Site	5	2.08	0.10	114.31
Constant (null)	1	4.08	0.04	125.12

[a] $AIC_c = 125.16$.

Nestling provisioning rates did not differ between banded (2.37 ± 0.43 visits per nestling per hr) and unbanded control males (2.26 ± 0.34 visits per nestling per hr; $t_{22} = -0.18$, $P = 0.86$), nor between SY (2.50 ± 0.48 visits per nestling per hr) and ASY banded control males (2.26 ± 0.77 visits per nestling per hr; $t_{12} = 0.27$, $P = 0.80$). Thus, to maximize our sample size at 9 geolocator-tagged and 15 control birds, unbanded (age unknown) control birds were included and parental age was not accounted for in our models. The null model was the sole top model ($\Delta AIC_c = -2.91$), providing no support for geolocator-marking influencing provisioning rates (geolocator-tagged birds = 2.47 ± 0.70 visits per nestling per hr; control birds = 2.24 ± 0.27 visits per nestling per hr; Table 2).

Return Rates

The top equivalent models all included the 'group' effect, with the most parsimonious of these being the univariate 'group' effect model (Table 3). From these models with equivalent support, only the 95% CI of the β for 'group' effect did not overlap zero, indicating that geolocator status was the most important explanatory variable. Models that included body mass, either additively or as an interaction term, were not an improvement on the univariate model (body mass + group: $\Delta AIC_c = 1.14$; body mass 95% CL = −1.62, 0.53). Geolocator-tagged birds were less likely to return to their breeding sites the year after capture than were control birds (return rate = 16% ± 5%, $n = 49$, vs. 35% ± 7%, $n = 52$; Table 2).

TABLE 2. Summary of performance estimates associated with geolocator-tagged and control male Cerulean Warblers in the Ozarks (O) and Pennsylvania (P) study sites (see Figure 1 for study site locations) in 2014–2016: Mean weekly apparent survival (ϕ) over the breeding season (Pennsylvania only), daily nest survival (DSR; Pennsylvania only), nestling provisioning rates (NPR; Pennsylvania only; visits per nestling per hr), and annual return rates (Pennsylvania and Ozarks). Weekly ϕ and DSR estimates were calculated from the top model that included group (see Tables 1 and 3).

	Geolocator		Control	
Parameter	Estimate (mean ± SE)	n	Estimate (mean ± SE)	n
Weekly	0.97 ± 0.03	27	0.98 ± 0.03	26
DSR	0.96 ± 0.01	21	0.96 ± 0.01	19
NPR	2.47 ± 0.70	9	2.24 ± 0.27	15
Return rate	0.16 ± 0.05	49	0.35 ± 0.07	52

TABLE 3. Best-supported models ($\Delta AIC_c < 2.00$) for return rates of male Cerulean Warblers in Pennsylvania and the Ozarks, USA, for the 2014–2015 and 2015–2016 annual cycles, using Akaike's Information Criterion adjusted for small sample size (AIC_c). The null model is also shown for comparison. K = the number of parameters, w_i = model weight, and Dev = model deviance. The group effect refers to the influence of geolocators; the 2 groups were geolocator-tagged birds and color-banded control birds.

Model	K	ΔAIC_c	w_i	Dev
Group effect only	2	0.00 [a]	0.15	110.70
Group + Mass	3	1.14	0.09	109.71
Group + Year	3	1.46	0.07	110.04
Group*Year	4	1.94	0.06	108.34
Group + Region	3	1.96	0.06	110.53
Constant (null)	1	2.43	0.05	115.21

[a] $AIC_c = 114.82$.

DISCUSSION

Our study is among the first to evaluate the effects of geolocators on both reproduction and return rate. We found no evidence to suggest a negative effect of geolocators on apparent within-breeding-season survival, daily nest survival, or nestling provisioning rate, which suggests that reproductive output prior to migration is not likely to be hampered by the use of this technology. However, we found that birds with geolocators were less likely to return to their breeding grounds in the following year than control birds, which is cause for some concern.

Following geolocator deployment, our data and qualitative field observations suggest that Cerulean Warblers quickly made any necessary adjustments associated with carrying a geolocator, resuming normal activities (e.g., singing, territory defense, and nestling provisioning) within 24 hr. Their short-distance flights and foraging efforts did not appear to be affected, as has also been observed in Barn Swallows (*Hirundo rustica*; Matyjasiak et al. 2016). Although our statistical power was not always high, our results providing no evidence for geolocator effects on breeding activities of Cerulean Warblers are in agreement with those of similar studies that examined the effects on warblers of tagging with radio-transmitters: these devices had no effects on nestling provisioning by Hooded Warblers (Neudorf and Pitcher 1997) or on nest survival (as well as the number of fledglings produced and postfledging survival) of Golden-winged Warblers (Streby et al. 2013).

In studies of the effects of geolocators on passerines besides warblers, a lack of evidence supporting a geolocator-marking effect on apparent within-season survival and fledging success has also been reported (within the season of geolocator deployment) for Tree Swallows (*Tachycineta bicolor*; >19.5 g; Gómez et al. 2014), which also had unaffected nestling provisioning rates, and Northern Wheatears (*Oenanthe oenanthe*; 21–24 g; Schmaljohann et al. 2012, Arlt et al. 2013). However, Arlt et al. (2013) documented decreased nest success (as well as a reduced return rate and later arrival and clutch initiation dates) in the subsequent breeding season in geolocator-tagged Northern Wheatears. In our case, we were unable to monitor enough nests during the breeding season following the return of individuals that bore geolocators to have adequate statistical power for a comparison, but the possibility of reduced nest survival and likelihood of mate pairing (potentially due to geolocator-related carryover effects and/or reduced migration speed) is worth future investigation.

In a study that investigated the effects of radio-tagging Great Tits (*Parus major*), the nestling provisioning rates of radio-tagged birds did not differ from those of control birds (Snijders et al. 2017). However, the authors did report a radio-tagging effect on nest desertion by adults marked during the nestling provisioning period (nest desertion by both parents increased), suggesting that marking with tracking devices during the nestling provisioning period may negatively affect reproductive output in some cases. While we did not find an overall difference in nestling provisioning rates between geolocator and control groups, we did observe 2 instances (11% of 18 nests associated with geolocator-tagged males that had nestlings) of apparent nest abandonment by males. In both cases, the birds were tagged during the nestling provisioning period, and in both cases the female continued to provision the nestlings and each nest fledged at least 2 young. In another experimental study on nonmigratory Great Tits, nestling mass was negatively associated with geolocator-tagged males, marked males increased in body mass but their wing chord decreased over the postdeployment year, and the marked males seemingly exhibited less competitive ability to secure winter roosts (Atema et al. 2016). However, once again, the marked males' survival and reproductive success were unaffected.

A decreased return rate for geolocator-tagged individuals, as found in our study, implies that geolocator-tagging causes one or more of the following: (1) displacement from the previous year's territory, potentially caused by a later arrival date or decreased aggression toward territorial intruders (one geolocator-tagged bird was resighted ~860 m from the location of his territory in the previous year, and this individual, along with 3 other marked birds, exhibited noticeably less aggression toward song playback upon return); (2) reduced site fidelity, with some birds possibly stopping elsewhere within the breeding range that involves a shorter travel distance from the wintering grounds; or (3) decreased annual survival, potentially due to increased weight or drag during long-distance flights (Bowlin et al. 2010). Although this study was not designed to distinguish among these 3 explanations, it is possible that our results were related to altered breeding dispersal by geolocator-tagged birds. However, we found no evidence that the effects of geolocators differed by site, which may be assumed if geolocator-tagged birds were attempting to reduce the cost of migration. Return rates between control and geolocator-tagged birds differed similarly in the Ozarks, in the southwestern corner of their breeding range, and in northwestern Pennsylvania, toward the northern end of the breeding distribution. However, we may have lacked adequate statistical power to show support for differential fidelity by study site through a significant interaction effect of geolocator status and site on likelihood of return. Alternatively, it is possible that the reduced return rates of geolocator-tagged birds occurred because mortality during the nonbreeding season was greater for these individuals, with the most likely period of differential mortality occurring during one of their long-distance migrations (Sillett et al. 2002, Jones et al. 2004).

Other studies that have explored the possibility that the return rates of small migratory birds are affected by geolocator-tagging have come to a variety of conclusions. In a technical review, Bridge et al. (2013) found decreased return rates for 9 of 24 (38%) bird species weighing 12–80 g, with smaller species more likely to be negatively affected. And, in a meta-analysis across study species, Costantini and Møller (2013) found that birds with small body mass were more likely to be negatively affected by carrying tracking devices. However, small body mass does not always lead to reduced return rates of geolocator-tagged migrants, as some of the smallest species marked to date, Golden-winged Warblers and Aquatic Warblers (*Acrocephalus paludicola*), were not adversely affected (Salewski et al. 2012, Peterson et al. 2015). Additionally, inclusion of body mass as a variable in our analysis did not improve the best model (geolocator status only), and Barron et al. (2010) found little support for increasingly negative impacts on survival caused by proportionally heavier devices in their meta-analysis of tracking device–related effects on birds.

Instead of mass alone, several other factors could influence the decreased return rates of Cerulean Warblers (and other small migratory birds) fitted with geolocators.

Our preliminary analysis of the light-level data from the geolocators carried by returning birds in this study has indicated long migratory flights across the Gulf of Mexico and/or the Caribbean Sea as they travel to and from their winter territories in the northern Andes Mountains. Migration strategy (including single flight distances and land cover during migration) along with weather patterns during this stage could influence whether geolocators reduce survival (Butler 2000). If geolocator weight and drag decrease maximum flight range (Bowlin et al. 2010), small long-distance migrants that make long overwater flights could be more negatively affected by geolocators than species that undertake shorter flights and stop more often (even if the cumulative trip length is equivalent). Additionally, unfavorable weather patterns or storm systems that are encountered during migration, which are more likely to occur during El Niño events (which occurred during both the fall and spring of 2015; NOAA National Weather Service 2016), may further differentially reduce return rates for individuals fitted with geolocators (again, especially for species that make overwater flights; Butler 2000). Therefore, it is possible that weather conditions during migration were more favorable in 2013–2014 (La Niña conditions during migration, and geolocator-tagged Golden-winged Warbler return rates unaffected; Peterson et al. 2015) than in 2014–2015 and 2015–2016 (reduced return rates of geolocator-tagged Cerulean Warblers in this study). As another example of long overwater flights potentially affecting the survival of geolocator-tagged birds more than untagged birds, DeLuca et al. (2015) reported a relatively low return rate for Blackpoll Warblers, which make long trans-Atlantic migratory flights, some flying overwater from the northeastern coast of the United States to stopover locations in the Caribbean Sea (minimum overwater flights of 2,270–2,770 km) before continuing to northern South America. Only 5 of 37 ($\sim$14%) geolocator-tagged Blackpoll Warblers returned to study sites in Nova Scotia or Vermont in 2013, compared with return rates of birds without tracking devices from 3 breeding sites in different years ranging from 27% to 70% in New Brunswick and New Hampshire (DeLuca et al. 2013). Brown et al. (2017) also found variation in the return rates of geolocator-tagged Semipalmated Sandpipers (*Calidris pusilla*) among breeding sites across the North American Arctic. Collectively, these studies suggest that migration strategy may be a more important predictor of the effects of geolocators on the likelihood of return than the proportional mass of the device, both at the species level and for individuals within species.

From the perspective of global conservation, reduced return rates do not preclude the continued use of geolocators to improve our understanding of the full annual cycle of Cerulean Warblers and other similarly sized birds. Although the potential for increased mortality during the nonbreeding season, or alterations to migratory timing or pathways, is of some concern, the fact that reproduction does not appear to be hampered is encouraging, particularly for a species that is short-lived (Buehler et al. 2013). Spatial and temporal data acquired from the use of geolocators has enormous conservation potential, and these benefits likely outweigh the potential cost of a relatively small number of individuals being negatively affected by carrying geolocators. The information obtained from individuals that are capable of successfully migrating with geolocators allows researchers to identify important migration stopover locations and to link breeding and nonbreeding season geographies (Stanley et al. 2015, Horns et al. 2016). In turn, such knowledge allows researchers and conservation professionals to more accurately develop full annual cycle population models, which can be used to more effectively target species- and region-specific conservation activities (Faaborg et al. 2010, Hostetler et al. 2015).

ACKNOWLEDGMENTS

We thank all of the hard-working field technicians who assisted with this study.

Funding statement: Funding for this project was provided by grants from the Pennsylvania Game Commission and the Arkansas Science and Technology Authority. In addition, the USDA Forest Service Northern Research Station, Arkansas State University Department of Biological Sciences, and Indiana University of Pennsylvania, provided equipment, vehicles, and housing. None of the funders had input into the content of the manuscript, nor did they require approval of the manuscript prior to submission or publication.

Ethics statement: We captured, handled, and marked all birds under all necessary federal and state permits, following Arkansas State University Institutional Animal Care and Use Committee Protocol No. 574486-1.

Author contributions: J.L.L., T.J.B., S.H.S., ad D.W.R. initiated this study, with J.L.L. and T.J.B. securing funding. Data was collected by D.W.R., S.H.S., and T.J.B. D.W.R. conducted the data analysis and wrote the paper with guidance from T.J.B, J.L.L., and S.H.S.

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