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Effects of light-level geolocators on return rates and inter-annual territory fidelity of Prairie Warblers *Setophaga discolor*

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ABSTRACT

Capsule: In a single-year study, attaching geolocators to male Prairie Warblers *Setophaga discolor*, one of the smallest species to date to carry geolocators, decreased return rates but had no effect on inter-annual territory fidelity.

Aims: To examine the effects of light-level geolocators on return rates and inter-annual territory fidelity of adult, male Prairie Warblers migrating to and from their non-breeding grounds.

Methods: During the 2016 breeding season we captured adult male Prairie Warblers at two sites in northeastern USA and attached geolocators and colour rings to one group of birds, and only colour rings to another group of birds. During the 2017 breeding season, we estimated return rates to the sites and inter-annual territory fidelity (i.e. distance between territory locations from one year to the next) for the birds that returned to the sites. We compared return rates and territory fidelity between birds with and without geolocators.

Results: Geolocators significantly decreased return rates of male Prairie Warblers to the study sites by 0.18 (95% credible interval [CI]: −0.37 to 0.01) from 2016 to 2017. Birds that returned exhibited a range of distances between estimated locations of territories in each year (7–2104 m), but the differences in distances between birds with and without geolocators were not statistically significant.

Conclusion: Although return rates were lower for Prairie Warblers with geolocators, these effects should not necessarily disqualify their use. Rather, the magnitude of the negative effects on individuals needs to be considered against the benefits and reliability of the information gained for the population or species. We recommend the effects of geolocators and other tracking tags should be studied and reported in conjunction with the main objectives of the study for which the tags are being used.

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Archival light-level geolocators (hereafter 'geolocators') have been miniaturized to the extent that they can be used to track the daily locations of small migratory birds across their full annual cycle (Bridge *et al.* 2013). Use of this technology has enabled researchers to gather unprecedented data on the movements of individuals of numerous species, whose migratory ecologies previously were based on the limited information that could be gained from ring recoveries and sightings. Geolocator data have provided valuable insights into migration routes and non-breeding areas (Stutchbury *et al.* 2009, DeLuca *et al.* 2015, Cooper *et al.* 2017), patterns of migratory connectivity (Fraser *et al.* 2012, Hallworth *et al.* 2015, Kramer *et al.* 2018), variation in migration strategies by sex and age classes (Tøttrup *et al.* 2012, McKinnon *et al.* 2014, McKinnon *et al.* 2016), flexibility in migration routes and timing (Stanley *et al.* 2012, Streby *et al.* 2015a, Ouwehand & Both 2017), and carry-over effects between non-breeding and breeding sites (Pedersen *et al.* 2016).

As is the case with any device attached to a bird, the use of geolocators raises ethical questions about the potential effects of the device on the welfare of the individuals carrying them (e.g. changes in survival, reproduction, condition, behaviour, and other life history traits) and on their populations (Barron *et al.* 2010). These potential effects are of additional concern if the devices influence the behaviour under investigation (Wilson & McMahon 2006, Jewell 2013). For example, in a study of migratory behaviour, it would be undesirable if the physiological cost (e.g. higher stress or energy expenditure) of carrying a geolocator limits migration distance or induces a change in migration routes or timing. Thus, it is

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important to assess and understand the effects of geolocators (Bodey *et al.* 2018, Brlík *et al.* 2020).

A recent meta-analysis of the effects of geolocators on small (< 100 g) bird species found an overall weak negative effect of geolocators on apparent survival and no clear effect on condition, phenology, or breeding performance (Brlík *et al.* 2020; see also Weiser *et al.* 2016). The effects, however, were highly variable across and even within species. Some studies found lower return rates, later arrival dates, delayed onset of reproduction, decreased nesting success, and poorer body condition in birds equipped with geolocators (Arlt *et al.* 2013, Gómez *et al.* 2014, Scandolara *et al.* 2014, Weiser *et al.* 2016), while others found no difference in these measures between birds with and without geolocators (Fairhurst *et al.* 2015, Pakanen *et al.* 2015, Peterson *et al.* 2015, van Wijk *et al.* 2016, Blackburn *et al.* 2016, Bell *et al.* 2017, Cooper *et al.* 2017). The variability in these results has variously been attributed to factors such as relative tag load, tag type, attachment method, taxa, flight type, foraging behaviour, migratory route, migration distances, and spatial and temporal variations in habitat quality (Costantini & Møller 2013, Weiser *et al.* 2016, Bodey *et al.* 2018, Brlík *et al.* 2020). Nevertheless, even these factors are not consistent in their effects, which have made it difficult to develop generally applicable guidelines for small bird species (Schacter & Jones 2017) and calls into question whether adopting such guidelines is even realistic or safe. As such, the effects of geolocators should continue to be investigated, especially for species to which geolocators are being attached for the first time.

There have been few studies of the effects of geolocators on very small (< 12 g) bird species, whose tag loads approach or exceed the general guideline that the device should weigh less than 5% of total body mass (Kenward 2001). Golden-winged Warblers *Vermivora chrysoptera* showed no measurable effect of geolocators on return rates, inter-annual territory fidelity, or body mass (Peterson *et al.* 2015). Cerulean Warblers *Setophaga cerulea* showed no effect of geolocators during the breeding season of deployment but had lower return rates (Raybuck *et al.* 2017). Similarly, Common Yellowthroats *Geothlypis trichas* carrying geolocators had lower return rates (Taff *et al.* 2018). Although the findings from these studies suggest that variability in effects applies to very small bird species as well, the number of these species studied so far is small. More study is needed on very small species to see if the effects are similarly variable to larger bird species, or if a different pattern emerges.

We deployed geolocators on male Prairie Warblers *Setophaga discolor* from two populations that breed in globally-rare inland pitch pine *pinus rigida*–scrub oak *querus* spp. barrens in the northeastern United States of America to track their movements to and from their non-breeding grounds in the Caribbean. We examined the effects of geolocators as part of our study because this is the first time that geolocators have been attached to Prairie Warblers, and because this species is one of the smallest (< 9 g) to carry geolocators to date. Specifically, we measured the effects of the geolocators on two aspects of the species' ecology – return rate and inter-annual territory fidelity – by comparing these measures in groups of birds with and without geolocators. We examined return rate because it serves as a proxy for survival, which is an important concern when considering the effects of geolocators for individuals and their populations. We examined inter-annual territory fidelity (i.e. the distance between territory locations from one year to the next) to see if geolocators affect the likelihood that a bird will settle in its previous territory. If geolocators cause birds to change territory locations, birds could be put at a disadvantage in terms of survival and reproductive success because of unfamiliarity with local conditions and/or lower habitat quality of the new territory (Danchin & Cam 2002, Brown *et al.* 2008). We predicted that birds with geolocators would experience lower return rates and decreased territory fidelity (i.e. greater distances between territories) relative to birds without geolocators. We also predicted that covariates such as wing length and age would moderate the effects of geolocators on return rates because longer wings are related to increased flight efficiency (Norberg 1995, Pennycuick 2008) and older individuals are socially dominant and tend to be more experienced in meeting energy demands, navigating barriers and avoiding risks during migration (Faaborg *et al.* 2010). Lastly, we examined the effects of breeding sites on return rates and territory fidelity to account for geographic differences unrelated to birds (e.g. habitat, weather, and methods), but we did not predict directional differences between sites.

Methods

Study areas

We attached geolocators to Prairie Warblers breeding in the Albany Pine Bush Preserve (APBP) in eastern New York (42.719°N 73.865°W) and the Montague Plains Wildlife Management Area (MPWMA) in western Massachusetts (42.567°N 72.517°W). These areas are more than 100 km from each other and occur near the northern edge of the species' breeding range in the United States, which extends from southern Maine to Florida and west to eastern Texas and Oklahoma. Both areas protect remnants of inland pine barrens ecosystems that contain globally-rare pitch pine–scrub oak barrens, pitch pine–scrub oak thickets, successional northern sandplain grasslands, and other ecological communities (Edinger *et al.* 2014, Swain 2016) used by Prairie Warblers during their breeding season. Both areas are actively managed using tree removal and prescribed fire, mowing, and herbicide regimes to restore and maintain these ecosystems and their constituent plant and animal communities. At the time of the study, APBP and MPWMA each contained about 500 ha of breeding habitat for Prairie Warblers. There was an additional 50 ha of breeding habitat along powerline corridors within 5 km of MPWMA, but there was very little breeding habitat within the 5000 ha surrounding APBP.

Geolocators and harnesses

We used geolocators that were manufactured without stalks to elevate the light sensor and without tubes or loops to hold a harness (model ML6040 from Biotrack Ltd). To further minimize geolocator weight, we clipped approximately 1 mm from the connection nodes. We constructed harnesses following the methods of Streby *et al.* (2015b), which were based on the figure-of-eight, leg-loop harness of Rappole & Tipton (1991). Specifically, we tied 0.5 mm black Stretch Magic® jewellery cord into a figure-of-eight with loops that were 14.5 mm in length when straightened but not stretched. We affixed each harness to the underside of a geolocator using small beads of cyanoacrylate glue (Loctite Gel Control; Henkel Corporation, Rocky Hill, Connecticut, USA). The final weight of each modified geolocator with a harness was 0.45–0.47 g.

Field methods

We captured birds throughout each study area using mobile mist nets arrays between 2 June–1 July 2016 at APBP and 29 April–20 June 2016 at MPWMA. Mist net arrays consisted of one or more nets used in combination with Prairie Warbler song playbacks and a male decoy. For all newly-captured birds, we applied a United States Geological Survey (USGS) numbered aluminium ring and a unique combination of three plastic colour rings. If a captured bird was already colour-ringed from a previous study (Akresh *et al.* 2015, Gifford unpublished data), we noted its colour combination. We determined the sex and age class (second-year [SY] or after second-year [ASY]) of each captured individual based on plumage, breeding condition, and moult limits (Pyle 1997). We measured wing chord in mm and mass to the nearest 0.25 g using a spring scale at APBP and the nearest 0.01 g at MPWMA using an electronic scale.

We attached geolocators to 25 males (80% ASY) at APBP and 22 males (59% ASY) at MPWMA (Figure 1) that weighed close to or more than 8 g (range: 7.75–8.83 g, 91% of birds were $\geq$ 8.00 g; Table 1). The weight threshold was based on the permit requirements of the USGS Bird Banding Lab which authorized the research. Male birds of all weights (range: 7.00–8.48 g, 87% of birds were < 8.00 g; Table 1) with only aluminium and colour rings served as a control group ($n = 30$ [87% ASY] at APBP and $n = 25$ [44% ASY] at MPWMA). The higher weight threshold for tagged birds caused the initial weights of birds with geolocators to be on average 0.5 g more than birds without geolocators ($t = 9.63$, $P < 0.001$). However, wing lengths of birds with and without geolocators were not significantly different ($t = 1.68$, $P = 0.09$; Table 1). We limited our consideration to males because capture rates of females using our methods were low (7% at APBP) and females generally have very low annual return rates (26% at MPWMA [Byers *et al.* 2015] and 19% in Indiana [Nolan 1978]). The combination of these low rates would have resulted in insufficient sample sizes for females.

Between 1 May–25 June 2017 at APBP and 30 April–29 June 2017 at MPWMA, we searched the study areas for returning birds. At APBP, we started our search efforts within 100 m of the location where birds were captured the previous year and expanded the spatial extent of our searches to all parts of the preserve with breeding habitat if a bird was not found. We typically would look for a bird every 2–5 days until it was found. At MPWMA, we searched most areas in the site early in the season every 2–5 days, with less frequent searches in late May and June. We also searched all breeding habitat (e.g. powerline corridors) within 3 km of MPWMA once during late May using playbacks of Prairie Warbler songs. When we located a bird carrying a geolocator, we attempted to recapture it using mist nets in combination with song playbacks and a decoy. If we recaptured the bird, we removed its geolocator. When birds with only colour rings were located, we either recaptured them or just recorded them as having returned.

To estimate territory locations, we used hand-held global positioning system (GPS) units to record the

Figure 1. Prairie Warbler with a geolocator attached using a figure-of-eight leg-loop harness.

locations where birds were captured or seen in 2016 and 2017. At APBP, we only recorded the locations where birds were initially captured or seen in each year. At MPWMA, we followed birds through part of the breeding season to obtain multiple locations and obtained an average of 2.2 locations per bird (range =

Table 1. Frequencies and body measurements of male Prairie Warblers captured in 2016, frequencies of birds that returned in 2017, and deployment durations of geolocators. Birds are grouped based on site (APB*P* = Albany Pine Bush Preserve, MPWMA = Montague Plains Wildlife Management Area), whether or not they were carrying a geolocator, and Age (SY = second-year, ASY = after second-year).

			2016					2017				
				Mass (g)		Wing length (mm)		Returned			Deployment duration (days)	
Site	Geolocator	Age	Capture	Mean	Sd	Mean	Sd	Capture	Sight	%	Mean	sd
APBP	Yes	SY	5	8.2	0.27	56.2	2.95	2	1[a]	60.0	319.7	7.77
	No	SY	4	7.7	0.08	55.8	0.96	3	0	75.0	–	–
	Yes	ASY	19	8.1	0.19	57.4	1.08	8	0	42.1	329.6	20.18
	No	ASY	26	7.6	0.21	57.3	1.39	15	3	69.2	–	–
	Total		54[b]	7.8	0.32	57.1	1.50	28	4	59.3	326.9	17.9
MPWMA	Yes	SY	9	8.3	0.30	56.3	1.00	2	0	22.2	383.5	36.06
	No	SY	14	7.9	0.28	55.8	1.31	3	4	50.0	–	–
	Yes	ASY	13	8.1	0.14	58.2	1.24	7	0	53.8	363.3	15.38
	No	ASY	11	7.7	0.25	57.3	1.27	0	5	45.5	–	–
	Total		47	8.0	0.32	56.9	1.50	12	9	44.7	367.8	20.5

[a]This bird could not be recaptured in 2017 so the geolocator was not removed. To determine a deployment period, the period was considered to have ended when the bird was resighted in 2017. The bird was captured in 2018 and the geolocator was removed.
[b]55 birds were initially captured, but one bird was excluded from analysis because it dropped its geolocator.

1–6, sd = 1.2) in 2016 and 7.2 locations per bird (range = 1–19, sd = 5.5) in 2017.

Analysis

We categorized birds as having returned in 2017 ($y_R = 1$) or not ($y_R = 0$). The distribution of this binary response was assumed to be binomial with a probability of 'success' being represented as the probability of returning or return rate ($\pi_R = P(y_R = 1)$). We examined the effects of geolocators (β_G), wing chord (β_W), site (β_S), and individual's age at the time of initial capture (β_A) on return rates using a generalized linear model with a logit link ($\mathrm{logit}(\pi_R) = \alpha + \beta_G Geo + \beta_W Wing + \beta_S Site + \beta_A Age$). The variables *Geo*, *Site* and *Age* are indicator variables that take on values of 0 or 1, depending on if a bird was carrying a geolocator (1) or not (0), was from MPWMA (1) or APBP (0), and was age ASY (1) or SY (0). *Wing* is a continuous variable that ranges between the minimum and maximum wing chords of birds in the sample. We initially included interaction terms between *Geo* and *Age* and *Geo* and *Wing* in the model to account for the possibility that a bird's experience or size would moderate the effects of geolocators, but neither term was significant (i.e. 95% credible interval included zero, see below) so we excluded them from the final model.

For birds that returned to each study site, we measured inter-annual territory fidelity (y_T) as the distance between each bird's territory locations in 2016 and 2017. We estimated territory locations in the most robust way possible given the data that were available for each bird. At APBP, we had only a single capture location for a bird in each year to use as estimates of territory locations. At MPWMA, we had multiple locations for each bird, so we used the centroids of each bird's locations in each year as estimates of territory locations. For birds with less than five observations per year (95% in 2016 and 48% in 2017), we used the average of the coordinates of the individual points from each year as centroids. For birds with five or more observations, we used the centroids of 95% minimum convex polygons from each year instead of an average to avoid issues caused by outliers or repeat observations of birds at the same points (e.g. singing perch). The distributions of distances were positively skewed and goodness of fit tests indicated log-normal distributions were appropriate (i.e. $\ln(y_T) \sim N(\mu_T, \sigma^2)$). Therefore, we examined the effects of geolocators (β_G) and site (β_S) on territory fidelity using a log-normal model ($\mu_T = \alpha + \beta_G Geo + \beta_S Site$), where *Geo* and *Site* are indicator variables that are defined in the same way as in the model for return rates. Age was excluded from this model due to the low number of SY birds in the samples (Table 1). Additionally, we excluded four birds from APBP (2 with geolocators and 2 without) from this analysis because they occurred in areas that were managed by mowing and/or burning between the 2016 and 2017 breeding seasons. As such, we could not determine if the movements resulted from disturbance (Akresh *et al.* 2015) or the influence of geolocators.

We fitted models using Bayesian analyses because small sample sizes made it likely that we would not meet the asymptotic assumptions of frequentist methods and because uncertainty could be easily propagated to effect sizes and other derived quantities (Kéry 2010). For both models, we specified non-informative normal prior distributions ($N[0, 1000]$) for each parameter (i.e. α, β_G, β_W, β_S, β_A). For the territory fidelity model, we also specified a non-informative uniform distribution (*Unif*[0, 100]) for the standard deviation of the residuals. For both models, we constructed posterior distributions for each parameter estimate using 30,000 samples from three independent Markov chains of 10,000 samples that were retained after discarding an initial 10,000 samples from chains of 30,000 samples and thinning the chains by 2. We checked for model convergence by inspecting time-series plots of the chains and by confirming that Gelman-Rubin statistics were less than 1.1 (Gelman *et al.* 2004). We fitted models with JAGS (Plummer 2003, 2017) implemented in R (R Development Core Team 2018) with the R2jags package (Su & Yajima 2015).

For parameter estimates with a predicted directional effect (i.e. β_G, β_W, β_A), we determined the effect to be statistically significant if >95% of its posterior distribution fell above or below zero in the predicted direction. For parameter estimates for which we did not predict a directional effect (i.e. β_S), we determined statistical significance if >97.5% of the posterior distribution was above or below zero in either direction (or equivalently if the 95% credible interval excluded zero). To aid the interpretation of results from each model, we also derived effect sizes on their original scale with 95% credible intervals. For return rates, effect sizes of geolocators, site, and age are expressed as differences in return rates caused by each effect for birds with average wing lengths (57.2 mm). The effect size of wing length assumes a linear relationship (i.e. constant slope) over the range of wing lengths and is represented as change in return rates for a 1 mm increase in wing length. For territory fidelity, effect sizes of geolocators and site are expressed as multiplicative changes in distance.

Results

Return rates

Over the single year of our study (2016–2017), 11 of 24 male Prairie Warblers with geolocators (45.8%) and 21 of 30 without geolocators (70%) returned to APBP (Table 1). At MPWMA, nine of 22 male Prairie Warblers with geolocators (40.9%) and 12 of 25 without geolocators (48%) returned (Table 1). The number of birds at APBP with geolocators excludes a bird that returned without its geolocator. Because we did not know when the bird shed its geolocator, we removed that bird from all analyses. Additionally, we were unable to recapture one bird carrying a geolocator at APBP but were able to visually confirm that it was still carrying its geolocator. (We recaptured the bird and recovered the geolocator in 2018.) Mean deployment time of geolocators was 327 days (sd = 17.9) at APBP and 368 days (sd = 20.5) at MPWMA.

Geolocators significantly decreased return rates of male Prairie Warblers (97% of posterior distribution [PD] of $\beta_G < 0$; Table 2). Estimated return rates of birds with geolocators were 0.18 (95% credible interval [CI]: −0.37 to 0.01) lower than those of birds without geolocators (Figure 2). For example, for ASY birds of average wing length, estimated return rates were 0.49 (95% CI: 0.32 to 0.67) for birds with geolocators and 0.67 (95% CI: 0.51 to 0.81) for birds without geolocators at APBP. Similarly, estimated return rates were 0.35 (95% CI: 0.17 to 0.57) and 0.53 (95% CI: 0.33 to 0.73) for ASY birds with and without geolocators, respectively, at MPWMA.

Estimated return rates were 0.14 lower at MPWMA than APBP; this difference, although suggestive of an effect, was not significant (91% PD of $\beta_S < 0$; Table 2). The effects of wing length and age on return rates were not significant (83% PD of $\beta_W > 0$ and 45% of PD of $\beta_A > 0$; Table 2).

Table 2. Means (95% credible interval) of the posterior distributions for parameter estimates, percentages of posterior distribution above or below zero in the predicted direction, and effect sizes (95% credible intervals) for the effects of geolocators, wing length, site, and age on return rates and territory fidelity of male Prairie Warblers at the Albany Pine Bush Preserve and Montague Plains Wildlife Management Area (MPWMA), 2016–2017.

Variable	Effect	Prediction	Parameter	Estimate	%PD	Effect size[a]
Return rate	Intercept		α	−7.60 (−25.53–9.37)		
	Geolocator	−	β_G	−0.78 (−1.63–0.06)	96.5	−0.18 (−0.37–0.01)
	Wing length	+	β_W	0.15 (−0.16–0.47)	82.6	0.04 (−0.04–0.11)
	Site (MPWMA)	+/−	β_S	−0.61 (−1.50–0.28)	91.2	−0.14 (−0.34–0.06)
	Age (ASY)	+	β_A	−0.07 (−1.15–1.00)	44.9	−0.02 (−0.26–0.23)
Territory fidelity	Intercept		α	4.90 (4.32–5.48)		
	Geolocator	+[b]	β_G	0.39 (−0.42–1.21)	82.9	1.62 (0.66–3.37)
	Site (MPWMA)	+/−	β_S	−0.58 (−1.38–0.22)	92.4	0.61 (0.25–1.25)

[a]For return rates, effect sizes of geolocators, site, and age are expressed as differences in return rates based on birds with average wing lengths. Effect size of wing length assumes a linear relationship over the range of wing lengths and is represented as change in return rate for a 1 mm increase in wing length. For territory fidelity, effect sizes are the multiplicative effect on distances caused by geolocators and site.

[b]Territory fidelity is measured as distance between an individual's estimated territory locations in 2016 and 2017. Geolocators are predicted to increase distances between territory locations (i.e. decrease territory fidelity).

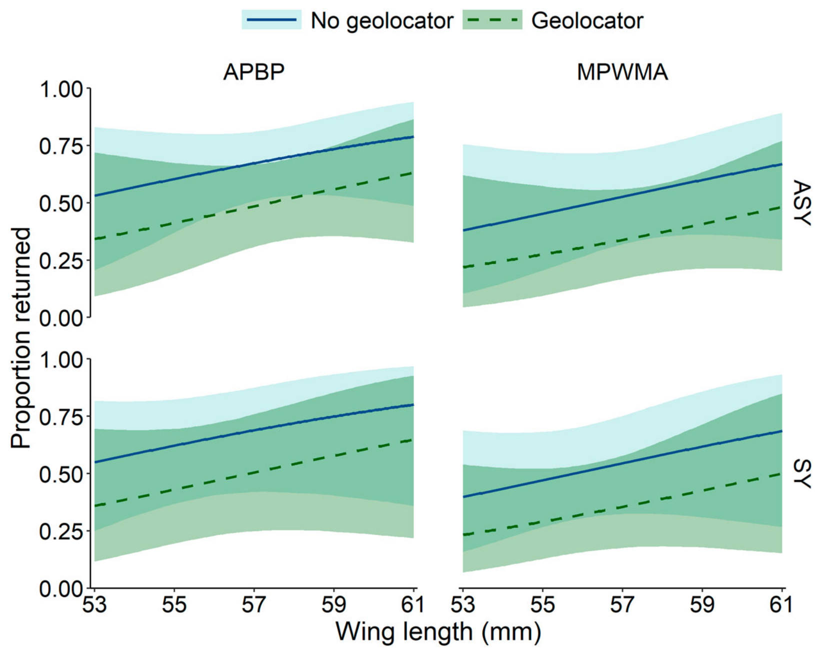

Figure 2. Estimated return rates of second-year (SY) and after second-year (ASY) Prairie Warblers with and without geolocators between 2016 and 2017 at the Albany Pine Bush Preserve (APBP) and Montague Plains Wildlife Management Area (MPWMA). Ages and wing lengths are from the time of their initial capture in 2016. Shaded areas represent the 95% credible intervals around the mean predicted relationship.

Inter-annual territory fidelity

At both sites, birds with and without geolocators exhibited a range of distances between estimated locations of territories in each year (APBP: 7–2104 m, MPWMA: 7–1192 m). At APBP, the model-predicted median distance between capture locations of birds with geolocators was 215 m (95% CI: 93–428 m) compared to 140 m (95% CI: 75–239 m) for birds without geolocators, whereas at MPWMA, median distances between territory centroids were 120 m (95% CI: 52–238 m) and 80 m (95% CI: 37–152 m) for birds with and without geolocators, respectively (Figure 3). Differences between groups, however, were not statistically significant. Geolocators did not significantly reduce territory fidelity (i.e. increase distances between territories; 83% PD of $\beta_G > 0$; Table 2). Likewise, territory fidelity did not significantly differ by site, but estimates suggested that distances moved at MPWMA were 0.61 times lower than those at APBP (92% PD of $\beta_S < 0$; Table 2).

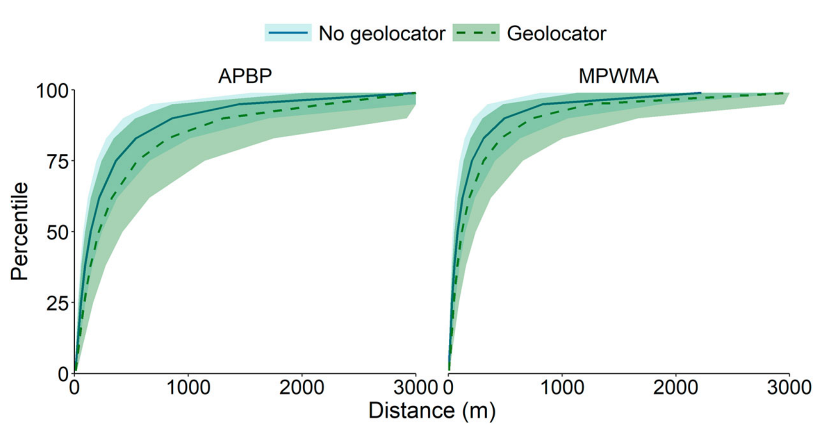

Figure 3. Estimated cumulative distribution of inter-annual distances between 2016 and 2017 territory locations of Prairie Warblers with and without geolocators at the Albany Pine Bush Preserve (APBP) and Montague Plains Wildlife Management Area (MPWMA). At APBP, distances were between capture locations and at MPWMA distances were between territory centroids. Larger distances represent lower territory fidelity.

Discussion

Our results from attaching geolocators to adult male Prairie Warblers – one of the smallest bird species equipped with geolocators to date – were generally consistent with findings from recent meta-analyses on the effects of geolocators and other tags on birds under 100 g (Costantini & Møller 2013, Bodey *et al.* 2018, Brlík *et al.* 2020). These meta-analyses found a weak negative effect of tags on apparent survival and no clear effect on the condition and other aspects of their ecology. In our study, we observed a statistically significant negative effect of geolocators on return rates, but no significant negative effects on inter-annual territory fidelity among birds that returned to the study area.

Return rates

Reduced return rates in small birds have been linked to high tag loads (Weiser *et al.* 2016, Bodey *et al.* 2018, Brlík *et al.* 2020). This relationship held for Prairie Warblers; tag loads were relatively high (mean = 5.6%, sd = 0.15%) and return rates were reduced by 18%. Because the weights of the tags (~0.46 g) were greater than the average of individual body mass changes observed in Prairie Warblers captured previously at each of the sites (APBP: mean = 0.41 g, sd = 0.45 g, n = 28, Gifford, unpublished data; MPWMA: mean = 0.33 g, sd = 0.30 g, n = 83, Akresh, unpublished data), the tags likely posed a burden in excess of normal weight fluctuations for at least some individuals. Further, carrying the extra weight of a tag on its lower back (Streby *et al.* 2015b) is likely more cumbersome than having the same weight distributed either centrally, as with fat stored in the furcular region, or across the bird's body as with subcutaneous fat. It is also possible that other aspects of the tag (e.g. shape and harness type) may have led to changes in behaviour, higher stress, or greater energy expenditure (e.g. increased drag during flight) that resulted in lower return rates (Bowlin *et al.* 2010, Pennycuick *et al.* 2012, Scandolara *et al.* 2014, but see Fairhurst *et al.* 2015). For example, Scandolara *et al.* (2014) found that shortening the light stalk slightly reduced geolocator weight and drag and enhanced the survival of female Barn Swallows *Hirundo rustica*.

Although tag loads for Prairie Warblers were among the highest of any species studied so far, the size of the effect of geolocators on return rates was within the range of many other species with lower tag loads (Bridge *et al.* 2013, Brlik et al. 2020). One possibility for this result is that we may have minimized the effects of geolocators by attaching them to birds that were heavier than birds without geolocators (Table 1). If larger birds were in better condition and/or better able to handle a geolocator, then our sample of birds may have been *a priori* biased to reduce the effects of geolocators (Brlík *et al.* 2020). It is also possible that other factors were likely to be important in mitigating the effects of increased load. Aerodynamic properties of a bird (e.g. wing loading, wing aspect ratios, and flight type) could be important in determining its ability to tolerate additional weight of geolocators (Caccamise & Hedin 1985, Vincze *et al.* 2019). Prairie Warblers have relatively low wing loading (approximately 0.15 g/cm^2; Nolan & Mumford 1965) and may be better able to tolerate the additional weight of tags compared to birds that are closer to maximum wing loading (2.5 g/cm^2). Differences in migration strategy may also play a role. Longer-distance migrants, such as Prairie Warblers, may incur smaller costs for the additional mass of a geolocator because their physiology is adapted to carrying varying levels of fat during migration (Costantini & Møller 2013, Wesier et al. 2016). Furthermore, their autumn and spring migrations occur mostly over land; they fly over the eastern United States and 'island hop' across Caribbean islands (Meehan et al. 2022). Frequent stops to refuel during migration may allow them to meet increases in energy requirements caused by geolocators and lead to lower mortality and higher return rates than birds that make extreme, long-distance flights over water (e.g. Blackpoll Warblers *Setophaga striata*; DeLuca *et al.* 2015).

The lower return rates we observed in birds with geolocators were unlikely to have resulted from factors unrelated to the geolocator. The geolocator data from these birds indicated that the populations from APBP and MPWMA are strongly connected to non-breeding grounds in Hispaniola (Campbell & Akresh, unpublished data). Therefore, birds with and without geolocators likely faced similar risks during migratory and non-breeding periods. It was also unlikely that we put geolocators disproportionately on birds that were inherently more vulnerable to risk factors. The initial weight of a bird was the only criterion used in the decisions for attaching geolocators, so birds were expected to be a random sample from the population for all other intrinsic factors that may affect their vulnerability to external risk factors. If anything, the decision to put geolocators on heavier birds should have decreased, not increased, their vulnerability to risks.

Inter-annual territory fidelity

For Prairie Warblers that returned to the study areas, the distances between territory locations in subsequent years of birds with geolocators were not significantly different than those of birds without geolocators. Thus, it is unlikely that the geolocators negatively affected inter-annual territory fidelity. The lack of an effect was consistent with the findings from two other studies that examined the effects of geolocators on territory fidelity. Golden-winged Warblers with and without geolocators showed no difference in inter-annual territory fidelity as measured by changes in capture locations between years (Peterson *et al.* 2015). Similarly, geolocators did not affect breeding movements of Arctic-nesting shorebirds as measured by nest locations in consecutive years (Weiser *et al.* 2016).

The variation in distances between estimated locations of territories in each year (Figure 3) was consistent with previously observed territory shifts for this species at these sites. Previous studies based on mapped territories found that territories moved 10–2100 m (median = 206 m) between years at APBP (Gifford, unpublished data) and 60–2760 m (median = 253 m) between years at MPWMA (Akresh *et al.* 2015). Given that average Prairie Warbler territory size is 1–1.2 ha (Nolan 1978, Akresh *et al.* 2015), the estimated distances of territory shifts in the previous and current studies at these sites suggest that some individuals established new territories while other individuals used some or all of their previous territories. The observed variation in inter-annual territory movements is to be expected in managed pine barrens, which are characterized by a shifting mosaic of breeding habitat of varying quality that corresponds to shrubland vegetation in various stages of regeneration following periodic disturbance by mowing and/or burning (Akresh *et al.* 2015).

Although we represented territory fidelity in a manner similar to previous studies (Peterson *et al.* 2015, Weiser *et al.* 2016), our assessment of territory fidelity is limited in two ways. First, at APBP we used a single location in each year as estimates of territory locations. The reliability of this approach will depend on the likelihood that a bird was captured near the centre of its territory. If a bird was captured near the edges of its territory in one or both years (as is possible when using playback recordings to capture birds) distances moved could be biased high or low. This issue was likely less of a problem at MPWMA, where we used the centroids of multiple locations collected over each breeding seasons to estimate territory locations. Territory locations estimated in this way should be more representative, so the shorter distances observed at MPWMA may indicate shifts in territories more reliably. Second, our assessment of territory fidelity was limited to the study areas and habitats in adjacent power line corridors. Given the extensive searching of these areas, it is unlikely that birds that returned to these areas went undetected. However, if some birds survived but dispersed outside the searched areas, the larger distances between territory locations in subsequent years would be excluded and our estimates of territory fidelity would be biased high. Moreover, if this subset of birds was composed disproportionately of birds with geolocators, it could suggest a latent negative effect of geolocators on territory fidelity. While these outcomes are possible, previous surveys at MPWMA found very few colour-ringed birds in available habitat 5–15 km from the study site (Akresh, unpublished data), so we suspect that few birds dispersed past the areas that we surveyed. We also note that our inability to detect far-dispersing birds, while problematic, is inherent in all studies of territory fidelity except those that can track the survival and location of all individuals regardless of where they settle (e.g. studies using GPS satellite tags).

Conclusions

Our use of light-level geolocators on Prairie Warblers suggests that geolocators are a viable method for obtaining daily locations of very small migratory passerines across their full annual cycle (Bridge *et al.* 2013). Nevertheless, our findings and the collective evidence emerging from recent reviews (Bridge *et al.* 2013, Brlík *et al.* 2020) indicate that geolocators can have negative effects on the individual birds carrying them. In our case, we only found a significant negative effect on return rate, but it is important to note that we only examined return rate and inter-annual territory fidelity of males. Geolocators could have a negative effect on other important life history parameters that we did not examine (Arlt *et al.* 2013, Scandolara *et al.* 2014) or have different effects on females. Additionally, we only examined the effects in a single year and effects of geolocators have been shown to vary or carry-over between years (Arlt *et al.* 2013, Scandolara *et al.* 2014, van Wijk *et al.* 2016). Consequently, our study of the effects of geolocators on return rates and territory fidelity in a single year for adult males may be providing only a partial understanding of their effects.

Although some may argue against the use of geolocators if there is any potential for negative effects on the individuals carrying them, we suggest that the magnitude of the negative effects on individuals be considered against the benefits and reliability of the information gained for the population or species (Wilson & McMahon 2006, Jewell 2013, Raybuck *et al.*

2017). In our case, return rates in tagged birds was lower but a relatively high percentage of tagged Prairie Warblers still returned and provided useful and novel data about the migratory ecology of the species. Ultimately, the effects should be considered in the context of its effects on the size and rate of change of the local populations being studied. The extent of the population-level effects will depend on the proportion of the population that is tagged, return rates of tagged and untagged individuals, and the productivity of returning individuals. Thus, use of geolocators and other tags should be carefully considered for local populations of endangered birds, but their use will likely have little to no population impacts for migratory bird species with very large populations.

Future improvements in the design or attachment methods of geolocators are likely to reduce or even eliminate some of their negative effects. Nevertheless, our current level of knowledge suggests that researchers should still conduct studies of tag effects that include well-matched control groups in conjunction with the main objectives of the study. For example, our study was not designed specifically to measure tag effects, but we were able to gather data for this purpose with little additional effort as part of a larger tracking project. These studies should report not only the effects of the tags but also supplementary information that can aid the interpretation of the results (e.g. mass of bird, mass of geolocator, attachment methods, and deployment duration; Bodey *et al.* 2018). Sharing the results from these types of studies, even if for a single species over a single year, is important for other researchers studying the same or similar species and to ensure that they are included in meta-analyses (Bodey *et al.* 2018, Brlík *et al.* 2020), which can yield more robust conclusions and recommendations about the use of geolocators and other tracking devices on small birds.

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