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ORIGINAL ARTICLE

Effects of geolocators on reproductive performance and annual return rates of a migratory songbird

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Abstract Our understanding of the annual life-cycle movements of small migratory birds has advanced rapidly with the advent of light-weight geographical positioning devices (i.e., geolocators), yet the effects of geolocators on reproduction and survival have not been adequately quantified. We tested for impacts of attaching a 1-g geolocator (using a harness around the legs and back, anterior to the tail) to adult Tree Swallows (*Tachycineta bicolor*) on parental feeding behavior, nestling growth and size, fledging success, and return rates between 2011 and 2012. At one breeding site, we compared feeding visits, nestling growth, and nestling size between paired nest boxes where one parent was marked at the 'geolocator' box with a 'control' nest box where neither parent was marked. We detected no differences between geolocator and control nests in either the frequency of feeding visits to nestlings or the amount of time spent at nests. Birds marked with geolocators fed nestlings as frequently as their unmarked mates. Likewise, nestlings raised at geolocator nests grew at similar rates to those at control nests, and had similar structural size and body mass at fledging. At three widely-separated sites across the Tree Swallow breeding range in Canada, we also found that fledging success was similar for geolocator and control nests. Although we found no evidence for short-term negative impacts of geolocators, the return rates of geolocator-marked Tree Swallows tended to be significantly lower than those of unmarked control birds. Thus, we found little evidence for short-term impacts of geolocators on reproduction but our study does suggest that long-term impacts of geolocators could be manifested in terms of lower survival, higher emigration rates, or lower breeding propensity.

Keywords Feeding rate · Fledging success · Migration · Nestling growth · *Tachycineta bicolor* · Tree Swallow

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Zusammenfassung

Der Einfluss von Geolokatoren auf Bruterfolg und jährliche Rückkehrraten eines ziehenden Singvogels

Unsere Kenntnis der alljährlichen Wanderungen kleiner Zugvögel hat mit der Einführung kleiner, leichter Geräte zur geographischen Positionierung (Geolokatoren) stark zugenommen. Allerdings wurden die Auswirkungen dieser Geräte auf Fortpflanzung und Überleben bisher nur unzureichend getestet. Wir untersuchten die Auswirkung eines 1 g schweren Geolokators (befestigt mit Gurt um

Beine und Rücken, vor dem Schwanz) auf erwachsenen Sumpfschwalben (*Tachycineta bicolor*) auf Fütterverhalten der Eltern, Wachstumsrate und Größe der Küken, Ausfliegeerfolg und Rückkehrraten zwischen 2011 und 2012. An einem Brutplatz wurden zudem Fütterraten, Kükenwachstum und Kükengröße zwischen paarigen Nistkästen verglichen, wo an einem Nest jeweils ein Partner mit Geolokator markiert war (Geolokator-Nistkasten), am zweiten Nest jedoch zwei unmarkierte Partner brüteten (Kontrolle). Wir fanden zwischen den beiden Gruppen keine Unterschiede in der Häufigkeit der Fütterungen oder der Zeit, die Elterntiere am Nest verbrachten. Die mit Geolokator markierten Vögel fütterten ihre Küken ebenso häufig wie ihre unmarkierten Brutpartner. Küken aus Geolokator-Nestern hatten eine ähnliche Wachstumsrate wie Küken aus Kontroll-Nestern. Obwohl wir keine kurzfristigen negativen Einflüsse fanden, waren die Rückkehrraten der mit Geolokator markierten Sumpfschwalben signifikant niedriger, als die der unmarkierten Kontrollvögel. Insgesamt fanden wir wenige Hinweise, dass Geolokatoren auf kurze Sicht die Reproduktion beeinflussen, aber auf lange Sicht fanden wir, dass Geolokatoren höhere Sterblichkeit, Auswanderung oder geringere Brutwahrscheinlichkeit bedingten.

Introduction

Tracking the movements of migratory birds between their breeding and non-breeding grounds is critical for understanding life-history trade-offs (Jahn et al. 2010; Boyle et al. 2011), factors that influence fitness and population abundance (Webster et al. 2002; Norris et al. 2004), and for developing effective conservation and management plans (Martin et al. 2007; Klaassen et al. 2008; Sheehy et al. 2010). Despite the importance of understanding migration pathways, tracking small migratory birds has been extremely challenging because banded individuals are rarely recaptured (Reichlin et al. 2009; Korner-Nievergelt et al. 2012), satellite transmitters are too heavy for most species (Bridge et al. 2011), and intrinsic markers, such as stable isotopes (Hobson and Wassenaar 2008), have limited resolution and are unable to provide data on migration routes. However, recent advances in the use of light-logging geolocators have now allowed researchers to track the migration routes of birds weighing as little as few decagrams (e.g., Rodríguez et al. 2009a; Stutchbury et al. 2009; Bächler et al. 2010; Egevang et al. 2010; Åkesson et al. 2012; Bairlein et al. 2012; Stach et al. 2012; Stanley et al. 2012). Geolocators use integrated measurements of ambient light and time to provide daily estimates of latitude and longitude (Hill 1994). Although this technology provides unique information on long-distance movements (Heckscher et al. 2011), there has yet to be a formal evaluation of the potential impacts of geolocators on small, free-ranging songbirds. Barron et al.'s (2010) review of avian transmitter effects reported negative impacts on many aspects of behavior and ecology, and geolocators have been shown to influence body mass and breeding success in raptors and seabirds, respectively (Rodríguez et al. 2009b; Elliott et al. 2012).

Geolocators are often attached to songbirds in the same way as similar-sized radio transmitters: a harness attached to the device loops around the legs so the geolocator rests on the back of the individual between the wings (Rappole and Tipton 1991; Stutchbury et al. 2009). Although most previous research on radio transmitters has found little evidence for negative effects on foraging or survival (Rae et al. 2009; Gow et al. 2011; Townsend et al. 2012), this may not be similar for geolocators. For instance, some radio transmitter attachments are designed to fall off after several weeks or months, so overall impacts could be reduced. In a wind tunnel experiment, the geolocator's light-sensing stalk, which usually protrudes 2–6 mm from the main device, increases drag (Bowlin et al. 2010), which could interfere with normal activities and flight, aerobic performance, or result in lower survival rates. Lower survival or site fidelity rates are of particular concern because one major drawback of using geolocators is that individuals must be recaptured at some later point in time, typically the following year, to retrieve location data. Thus, there is the possibility that geolocators may provide biased information on migratory movements if a non-random sample of individuals is recaptured.

Here, we examine the effects of geolocators on the reproductive performance and return rates in adult Tree Swallows (*Tachycineta bicolor*), a small ($\sim$20 g) migratory aerial insectivore that breeds in temperate areas of North America and winters in the southeastern United States, the Caribbean, Mexico and Central America (Winkler et al. 2011). We examined the hypothesis that geolocators compromise the success of adults by lowering current reproductive performance and reducing the probability of returning to breed the following season. At one breeding site, we compared nestling feeding rates, nestling size and nestling growth rates at geolocator nest boxes where one adult was marked with a geolocator to boxes attended by unmarked control birds. At the same site, and at two additional breeding sites spanning the breeding range of Tree Swallows in Canada, we compared breeding success and return rates of adults with and without geolocators.

Methods

Study areas

Field work was conducted during 2011–2012 at three widely-separated Tree swallow breeding sites in Canada:

Saskatchewan (SK), Ontario (ON) and British Columbia (BC). The 385-ha St. Denis National Wildlife Area (NWA; 52°13′N, 106°04′W) is located 40 km east of Saskatoon, SK. The NWA consists of small groves of trees, mainly aspen (*Populus tremuloides*), separated by areas of cropland, native and planted grasslands, shrubs, and wetlands (Shutler and Clark 2003). In ON, data were collected near Long Point (42°39′N, 80°26′W), an area consisting of hayfields, sand dunes, lake shorelines and a disused sewage lagoon (Hussell 2003). The BC site was near Prince George (53°50′N, 122°57′W) and characterized by hayfields interspersed among areas of mature and regenerating forest (Dawson 2008). For all three sites, we present data related to fledging success and adult return rates. At the SK site only, we analyzed the influence of geolocators on parental feeding behavior and nestling sizes and growth rates.

Nest monitoring

Tree Swallows readily use nest boxes because natural nest cavities may be limited (Shutler and Clark 2003). Nest boxes and general monitoring protocols are described by Shutler and Clark (2003) and Shutler et al. (2006). Briefly, nest boxes were placed 1.5 m above ground on metal T-bars or fence posts and spaced approximately 30 m apart. From early May to July, nests were visited daily or every other day to monitor timing of breeding (i.e., first egg dates), clutch size, and hatching and fledging success.

We captured adults within a few days of the last egg hatching in each clutch, banded (except recaptured birds), weighed [nearest 0.25 g with a Pesola scale (SK, BC), 0.1 g with a digital balance (ON)], and we recorded unflattened wing chord and 9th primary (nearest 1 mm with a wing ruler) lengths, and head-bill (nearest 0.05 mm with calipers) length (Pyle et al. 1987). Adults were sexed by presence or absence of a brood patch (only females incubate) or cloacal protuberance (Pyle et al. 1987; Winkler et al. 2011). Birds at geolocator nests were recaptured when their nestlings were >7 days old (mean age = 10 ± 3.3 days SD), weighed again, and geolocators were attached. At the SK site, we used measurements recorded at the first capture to compare body mass and wing length of males and females in the control and geolocator groups. In SK, nestling measurements were taken at 12 and 16 days post-hatching using methods described above for adults (except head-bill length because of low repeatability), enabling us to determine growth between 12 and 16 days of age.

Geolocators and attachment method

All adults equipped with geolocators had been previously banded at the same study site, had active nests in the year geolocators were attached, and weighed >19.5 g. These individuals were equipped with a 0.67-g light-sensing geolocator (Lotek Wireless model MK12-S in 2011, MK5-S in 2012), attached using a backpack harness (Stutchbury et al. 2009; 0.96 g with harness, <5 % of body weight). Attachment involved a figure-eight harness that loops around the legs and over the back. The geolocator sat just in front of the tail, and did not directly impede movement of the wings. Harnesses were fabricated from 1-mm-diameter ethylenepropylene-diene rubber O-rings (O-Rings West, Seattle, WA, USA), which were cut into different lengths to ensure a proper fit. The resulting exposed harness loop lengths varied between 38 and 40 mm. During attachment, we placed a small amount of cyanoacrylate adhesive (Krazy Glue®, Columbus, OH, USA) between the geolocator and the contour feather on the bird's back, with additional feathers arranged to cover the geolocator and reduce drag. Different adult Tree Swallows were marked with geolocators in 2011 and 2012.

Monitoring adult provisioning behavior

In 2011 and 2012 at the SK site, we monitored parental feeding rates as they provisioned 16-day-old nestlings. Two observers monitored all nests, alternating between control and geolocator nests (where one parent had a geolocator). Number of visits and time spent (nearest sec) at the nest box were recorded. Observations began at randomly selected times between 0900 and 1500 hours and lasted 40 min (see Bortolotti et al. 2011 for rationale). We tried to reduce disturbance by arriving 5–10 min before the start time and observing nests using a spotting scope or binoculars from a sitting position >50 m from nests. An average of 5 days (range 2–9 days) elapsed between the date that geolocators were attached to birds and the nest observation period. In 2012, we marked one adult with a geolocator and the other member of the pair was temporarily marked on the outermost tail feathers with nontoxic typewriter correction fluid, enabling us to determine which bird(s) fed nestlings.

Fledging success

In both years at all sites, the number of nestlings was recorded for each brood at hatch, and nests were visited again 20–21 days post-hatch after young had fledged. The percent of young that fledged successfully from each nest was estimated as number of young that fledged divided by the number hatched.

Return rates

At all sites, adults that had been recaptured (i.e., band-only or geolocator-marked adults) in 2011 were classified as recaptured or not in 2012. Banded adults with no geolocators that had raised nestlings during the same span of nesting dates as geolocator-marked birds were included in the control group. Return rates should not be interpreted as representing true survival rates because Tree Swallows marked with geolocators could have lower breeding propensity or higher emigration rate.

Statistical analyses

All analyses were performed in SAS (SAS Institute 2003). Body mass, head-bill and wing length measurements of male and female Tree Swallows in the control and geolocator nests were compared with generalized linear models (Proc GLM), with fixed effects of sex and marking group, an interaction between sex and marking group, and controlling possible effects of measurement date. When possible, at all three sites, we matched nests by hatch date (±1 day) and number of nestlings (±1 nestling) where one adult had been marked with a geolocator with control nests attended by unmarked adults. At SK, number of visits and time spent (cube root transformed to improve normality for analyses only) at nest boxes in each group were compared using paired *t* tests in 2011; in 2012, there were data for five pairs of geolocator and control boxes, and Wilcoxon signed ranks tests were used for all comparisons (Siegel and Castellan 1988). Comparisons of nestling size and growth in 2011 were analyzed with mixed-effects models to account for clustering of nestlings within families, i.e., nest box as the random effect, and marking group, brood size and measurement date as fixed effects (Proc Mixed). For all three sites, we used Wilcoxon tests to compare percent fledging success between boxes attended by geolocator-marked and unmarked birds, and return rates were compared using *G* tests and logistic regression. Unless indicated otherwise, we present least squares means (LSM) and 95 % confidence intervals (95 % CI).

Results

After controlling for effects of measurement date at the SK site, neither body mass nor morphological measurements of adult males and females differed between control and geolocator groups (all Ps > 0.39), nor was there an interaction between sex and marking group (all Ps > 0.13). Therefore, parents in these groups had similar characteristics when captured immediately post-hatch ($n = 88$ adults).

Feeding observations, and nestling size and growth

At SK in 2011, no differences were detected between geolocator and control nests in terms of number of feeding visits (paired $t_{22} = 0.61$, $P = 0.55$) or time spent at nest boxes (paired $t_{22} = 0.32$, $P = 0.75$) by adult Tree Swallows (Fig. 1); parents in the control and geolocator-marked nests visited nests with similar frequency during the 40-min observation period (controls: LSM = 17, 95 % CI = 14–19 visits; geolocators: LSM = 18, 95 % CI = 15–21 visits) and, overall, parents were at nests for about 5 min (controls: LSM = 295 s, 95 % CI = 195–395 s; geolocators: LSM = 313 s, 95 % CI = 213–413 s).

In 2012 at SK, there were similar numbers of total visits made to nests attended by control (median 21 visits, range 17–41) and geolocator (median 30 visits, range 23–40) adults, and the amount of time (control: median = 324 s, range = 131–615 s; geolocator: median = 221 s, range = 117–348 s) spent in nest boxes did not differ (Wilcoxon signed ranks tests, $P = 0.19$ and $P > 0.50$, $n = 5$ pairs of nests). Likewise, at five geolocator nest boxes where one parent was marked with white correction fluid, geolocator-marked birds visited nests (median 10 visits, range 9–24) as frequently as their mates marked temporarily with correction fluid (median 13 visits, range 2–17) and the amount of time spent at nests (geolocator: median = 86 s, range = 53–112 s; white: median = 97 s, range = 5–165 s) was also similar (Wilcoxon signed ranks tests, both Ps > 0.50).

Body size measurements and growth rates of nestlings were similar in each marking group in 2011 at SK (Table 1), after controlling for nest box effects (Ps < 0.001) in mixed model analyses. Size of 16-day-old nestlings was unrelated to whether or not a parent was marked with a geolocator (Ps > 0.44), and there was

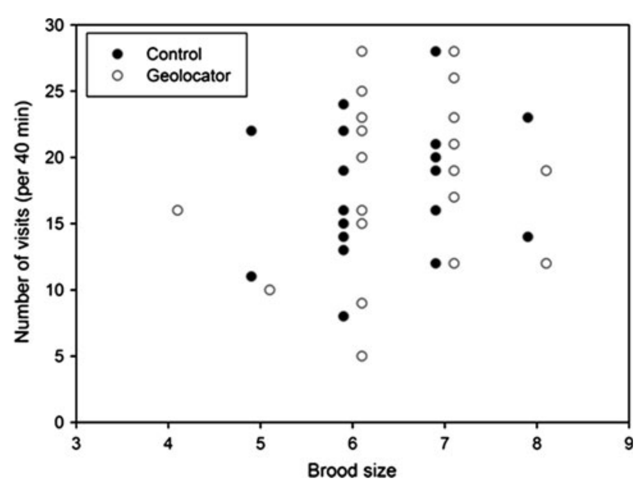

Fig. 1 Number of visits (in a 40-min observation period) to feed nestlings made by adult Tree Swallows (*Tachycineta bicolor*) marked with geolocators (one parent marked) versus unmarked controls in relation to brood size, St. Denis, Saskatchewan, Canada, 2011. Data points are slightly offset from exact brood sizes, but a few points remain hidden; $n = 23$ pairs of nests matched for hatch date and brood size

Table 1 Body size measurements at 16 days post-hatching and growth of body components from day 12 to day 16 for nestling Tree Swallows (*Tachycineta bicolor*) raised in nest boxes by unmarked parents (control) or at nests where one parent was marked with a geolocator, St. Denis, Saskatchewan, Canada, in 2011

	Control				Geolocator			
	n	Mean	Lower	Upper	*n*	Mean	Lower	Upper
Body size (day 16)								
Wing length	147	74.8	73.9	75.7	147	75.4	74.7	76.1
9th primary length	147	49.1	48.2	50.0	147	49.4	48.7	50.1
Body mass	147	22.8	22.5	23.1	147	22.6	22.4	22.9
Growth (days 12–16)								
Wing length	147	21.1	20.5	21.6	147	20.0	19.4	20.5
9th primary length	116	21.6	20.9	22.2	133	21.4	21.0	21.8
Body mass	146	−0.9	−1.1	−0.6	147	−0.8	−1.0	−0.6

Shown are sample size of nestlings (*n*), mean, and lower and upper 95 % confidence intervals of wing length (mm), 9th primary length (mm) and body mass (g). There were 23 nest boxes in each group, matched for hatching date and brood size. *Growth* refers to the difference (i.e., day 16 − day 12) in body size measurements

similarly no effect detected of geolocators on growth between day 12 and 16 (Ps > 0.10). There was no interaction between brood size and marking group in any of these analyses (all Ps > 0.25). Brood sizes did not differ between marking groups (G test, $G_3 = 0.53$, $P = 0.91$).

Fledging success

At the SK site, fledging success was 100 % in 2011 for broods in geolocator and control nests ($n = 23$ pairs of nests). Likewise, fledging success was 100 % at another 17 nests where an adult was marked with a geolocator (brood size at 12 days post-hatching ranged from 1 to 8 nestlings) but a matched control nest was not available. In 2012, fledging success was 93.8 and 88.3 % for geolocator and control nests ($n = 22$ pairs of nests), respectively, with fledging success ranging from 0 to 100 % in both groups and brood sizes ranging from 3 to 9 nestlings; no difference was detected between marking groups (Wilcoxon test, $P > 0.50$).

At the ON site in 2011, mean fledging success was 90.5 % (range 50–100 %) for 25 nests with a geolocator-marked adult and 71.7 % (range 0–100 %) for 25 control nests (Wilcoxon test, $P > 0.50$). In 2012, mean fledging success was 98.1 % (range 83.3–100 % for both groups; Wilcoxon test, $P > 0.50$) in geolocator and control boxes ($n = 9$ pairs of nests).

At the BC site, we found no differences between marking groups in either year (Wilcoxon tests, Ps > 0.40). In 2011, mean fledging success rates were 66.9 % (range 0–100 %) and 70.2 % (range 0–100 %) at 11 pairs of nests attended by geolocator and control birds, respectively; corresponding estimates for 9 pairs of nests were 91.1 % for geolocator nests (range 40–100 %) and 97.2 % for control nests (range 75–100 %) in 2012. There were no appropriate matched controls for five nests where one member of the pair had a geolocator, with three occurring in 2011 (fledging success: 0, 100, 100 %) and two in 2012 (60, 80 %).

Return rates

Overall, return rates differed among sites ($G_2 = 10.50$, $P = 0.005$), being higher in ON (50.0 %, $n = 110$), intermediate (45.5 %, $n = 143$) in SK and lower in BC (31.6 %, $n = 152$). In SK, 30 % of 40 geolocator-marked adults were recaptured in 2012 (Fig. 2), but one male had shed its geolocator. At SK, return rates were lower for adults marked with geolocators (logistic regression:

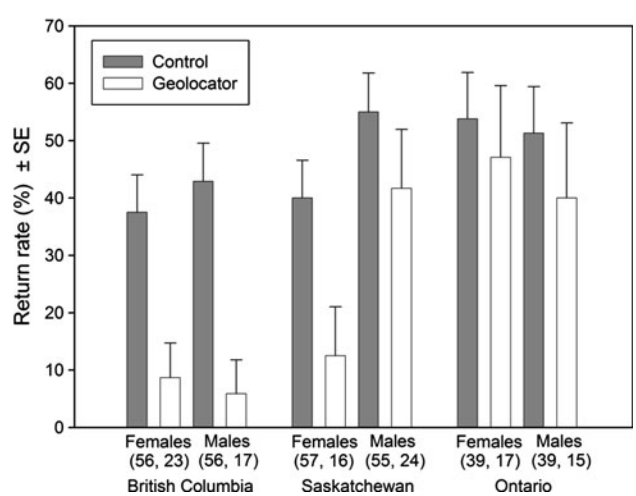

Fig. 2 Return rates (%; ±1 SE) of male and female adult Tree Swallows marked with standard leg bands (*filled bars*) or geolocators (*open bars*) at study sites in British Columbia, Saskatchewan and Ontario, Canada, 2011–2012. Sample sizes (control, geolocator) shown in *parentheses*

$\beta = -0.425 \pm 0.202$ SE, $P = 0.04$) when compared with controls, and for females ($\beta = -0.384 \pm 0.171$ SE, $P = 0.03$) when compared with male birds, but there was no evidence for a marking type × sex interaction ($P = 0.27$). In ON, return rates were similar for geolocator (48 %) and control groups (51 %; logistic regression, $P = 0.40$) and between sexes ($P = 0.68$); no marking group by sex interaction effect ($P = 0.83$) was found (Fig. 2). Only 7.5 % of birds equipped with geolocators in BC returned in 2012 (although one returning male had shed the geolocator), a rate that was significantly lower than control birds, of which 40.2 % returned (Fig. 2; logistic regression, $\beta = -1.052 \pm 0.313$, $P < 0.001$). At BC, there was no difference between sexes ($\beta = 0.083 \pm 0.184$, $P = 0.65$) and no marking group by sex interaction ($P = 0.63$).

Discussion

Adverse effects of externally-mounted markers are frequently reported (see Barron et al. 2010), but we found no evidence that placing geolocators on Tree Swallows produced any detectable short-term effects on feeding behavior, nestling growth and size, or breeding success. Likewise, Schmaljohann et al. (2012: supplementary material) detected no adverse effects of attaching geolocators to male Northern Wheatears (*Oenanthe oenanthe*) on either subsequent breeding performance or return rates (Schmaljohann et al. 2012). Because, in 2011, we only marked one adult at each nest, it is possible that unmarked birds compensated for reduced effort by their geolocator-marked mates, so that overall provisioning rates in each marking group appeared similar (Fig. 1). Although we cannot completely rule out this possibility, we observed marked birds feeding at 20 of 23 nests at Saskatchewan, sometimes frequently, so we believe that this explanation is unlikely. Furthermore, in 2012, when both sexes were marked at a subsample of nests at Saskatchewan, geolocator-marked birds fed nestlings just as often as their white color-marked mates. Finally, we did not detect an interaction between marking group and brood size in any analyses of Saskatchewan data, although previous results from mate-removal experiments (or due to natural mate loss) indicate that individual Tree Swallows are able to compensate for loss of a mate in small or average-sized broods (Leffelaar and Robertson 1986; Quinney 1986), which suggests that impacts of geolocators might be most evident in larger broods.

If marked birds had delivered smaller amounts or lower quality food at each visit, this change in provisioning was not manifested in reduced nestling growth rates or size at fledging at Saskatchewan (Table 1). Given that the Tree Swallows experienced favorable weather and foraging conditions during our study at Saskatchewan, it is possible that the Tree Swallows were able to adjust easily to any possible adverse effects imposed by the geolocators. Short-term effects of geolocators may be more evident during challenging conditions of inclement weather and food scarcity (Murray and Fuller 2000; Igual et al. 2005; Rodríguez et al. 2009b).

The combined mass of geolocator and harness was <5 % of an adult swallow's body mass, near the recommended upper limits for devices placed on birds and several other vertebrates (Kenward 2001). However, some studies report extended foraging trip duration and reduced breeding success in birds carrying transmitters that represent only 3 % of body mass (Phillips et al. 2003). If longer foraging trips occurred in our study, presumably the number of visits would have been lower in the geolocator group but this effect was not found. The addition of a 1-g geolocator was within the range of body mass changes observed at Saskatchewan from the first captures of adults (when the last egg had hatched) to the second capture when geolocators were attached (overall, mean = -0.9 g, SD = 1.3, $n = 40$); an average of 10 days elapsed between these two capture events, so perhaps Tree Swallows are capable of short-term adjustments to higher wing loading. Finally, the attachment method we employed was designed to reduce handling time, ensure that the harness did not impede wing movement (Bowlin et al. 2010), and was explicitly tailored to fit both smaller and larger Tree Swallows. Presumably, all of these factors had the potential to reduce short-term adverse impacts on birds. Furthermore, peak nestling food demands likely occurred before we marked adults with geolocators (Zach and Mayoh 1982; McCarty 2001), so impacts on feeding behavior may be found by marking adults with geolocators when nestlings are younger.

Our study was designed to control for effects of observer bias, brood size, nestling age and daily changes in food supply. We also verified, albeit in a *post hoc* manner, that morphological characteristics of marked and unmarked adults did not differ at Saskatchewan. Therefore, preferential marking of heavier Tree Swallows did not result overall in a non-representative sample in terms of the variables we measured. However, the latest-nesting birds at our sites, possibly those of lower quality, were not marked but may be more susceptible to deleterious effects of geolocators.

Overall, we obtained no consistent evidence of adverse effects of geolocators on fledging success at any site. In 2011 at Saskatchewan, fledging success was 100 % at all nests in our study, including at 17 geolocator nests that lacked adequate controls, and indices of nestling quality were unrelated to marking group (Table 1). In 2012, fledging success exceeded 88 %, with no difference between marked and control pairs. Parent birds marked with geolocators continued to feed nestlings, suggesting that short-term marking effects were insufficient to provoke abandonment in either year. Fledging success varied annually at Ontario and particularly at British Columbia, but was unrelated to marking group. This result could signal that local breeding success was more closely related to prevailing environmental conditions such as weather and food supply. Indeed, the low return rates of Tree Swallows at British Columbia in 2012 could be related to effects of carrying geolocators during adverse conditions experienced by adults in 2011 (i.e., when they fledged fewer nestlings).

The result of greatest concern for the application of geolocators was the low return rate of adults marked with geolocators at the British Columbia and Saskatchewan sites (Fig. 2). Overall, sex-specific impacts were equivocal; only females at Saskatchewan had lower return rates than males, possibly due to their smaller size (Winkler et al. 2011) or relatively higher investment in reproduction. At the Ontario site, point estimates of return rates of geolocator-equipped Tree Swallows were only slightly lower than controls in both sex cohorts. Given that study sites were >1,000 km apart, return rates may reflect spatiotemporal differences in overwinter and spring environmental conditions that mediate individual responses to the impacts of geolocators (Tøttrup et al. 2012). Anecdotal observations from British Columbia (L.L.B.) suggest that 1–4 birds equipped with geolocators had returned to the study site, but were not recaptured; similar observations were not made at Ontario or Saskatchewan. Stutchbury et al. (2009) reported that 54 % of banded Purple Martins (*Progne subis*) were recaptured at breeding colonies, but only 10 % were recaptured after marking with geolocators. Combined with findings reported here, this suggests that survival rates, dispersal behavior or breeding propensity could be adversely affected by these devices, at least in some species of aerial insectivores. Thus, longer-term study of songbirds and other species is needed to distinguish among these explanations, as well as determine whether individuals marked with geolocators provide reliable information about timing, duration and direction of migratory movements.

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