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No short- or long-term effects of geolocator attachment detected in Pied Flycatchers *Ficedula hypoleuca*

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Tracking small passerines using miniaturized location tags is a rapidly expanding field of study. In a 1-year study, we tested whether there were any short- or longer-term effects of fitting geolocators weighing 3% of body mass on male Pied Flycatchers *Ficedula hypoleuca*. In the deployment year, we compared adult provisioning rates to nestlings, nestling growth and nest success between nesting attempts in which adult males were fitted with a geolocator, with control nests where males had the same capture history but were not tagged. We found no difference between treatments in provisioning effort by males or their associated female 2 days after geolocator fitting, in terms of nestling growth, subsequent brood reduction or nest success. Return rate, arrival date on territories, nest timing and breeding parameters were compared between tagged and untagged males in the following breeding season. We found no difference in return rate or arrival date, and no difference in nest timing, fecundity or outcome. Our study suggests that fitting lightweight tags to small passerines need not affect behaviour, breeding or apparent between-year survival. However, tagging new species should still require assessment and comparison with well-matched control cohorts, and it should be recognized that tag effects could vary between years and populations, mediated by environmental conditions.

Keywords: arrival date, brood mass, carry-over effect, datalogger, provisioning, recruitment, tag effect.

Recent miniaturization of tracking devices is leading to a proliferation of bird movement studies, helping to redress the imbalance in our ecological understanding of the complete annual cycle of migratory birds (Marra *et al.* 2015). Light-recording archival tags (geolocators, henceforward tags), now weighing < 0.4 g, potentially enable tracking of many passerine species (Bridge *et al.* 2011). It is important that tracking devices do not compromise individual survival or reproduction, and that they provide data that represent true behaviour that is not influenced by the fitting or carrying of devices (Costantini & Møller 2013). Studies of the effects of tags have until recently been limited to larger birds (for reviews see Barron *et al.* 2010, Sergio *et al.* 2015) and studies of passerines and other small birds are still few (Scandolara *et al.* 2014, Peterson *et al.* 2015, Streby *et al.* 2015, Blackburn *et al.* 2016, Weiser *et al.* 2016, van Wijk *et al.* 2016), with suitable control groups of un-tagged individuals rarely included in tracking work.

Tags may affect individuals by increasing drag or flight load, shifting the centre of gravity or reducing fat mass, or from constriction or rubbing by the harness (Barron *et al.* 2010, Bowlin *et al.* 2010, Pennycuick *et al.* 2012, Casas *et al.* 2015, Blackburn *et al.* 2016, Matyjasiak *et al.* 2016). Tagging may reduce apparent survival, which

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would be evident in reduced return rates to breeding grounds, but may also limit investment in other life stages. For example, leg-mounted tags fitted to incubating birds can result in egg breakage during incubation (Becker *et al.* 2016). In addition to direct tag effects, handling time is longer when tagging birds compared with standard ringing handling times, potentially increasing stress-related reductions in survival (Casas *et al.* 2015), nest desertion or altered behaviours affecting investment in reproduction. While studies of tag effects have mainly focused on apparent survival probabilities (Barron *et al.* 2010), there has been limited study of potential 'carry-over' effects of additional tag load on arrival dates to breeding grounds, timing of breeding or investment in clutch size (Arlt *et al.* 2013, Gómez *et al.* 2014). Studies examining the impacts of tags on dependent young are particularly limited (although see Rodriguez *et al.* 2009, Atema *et al.* 2016, Rodríguez-Ruiz *et al.* 2016, Weiser *et al.* 2016), with only two such studies on migratory passerine birds (Arlt *et al.* 2013, Scandolara *et al.* 2014). This paucity partly results from passerine tracking studies being conducted on adult birds that are not associated with a monitored nest. For passerines, studies of tag effects are equivocal, with some finding negative effects (Arlt *et al.* 2013, Scandolara *et al.* 2014, Blackburn *et al.* 2016, Ouwehand & Both 2017), some finding effects that are not detected in every year or population (Ouwehand *et al.* 2016, Rodríguez-Ruiz *et al.* 2016, van Wijk *et al.* 2016, Snijders *et al.* 2017), and some finding no effects at all (Gómez *et al.* 2014).

We investigated short-term (within a single breeding season) and longer-term (between two breeding seasons) effects of deploying geolocators on male Pied Flycatchers *Ficedula hypoleuca*, among the smallest and lightest species (averaging 13 g) to which tracking devices have been deployed to date. The Pied Flycatcher migrates from wintering grounds in sub-Saharan Africa to breed across north-west Europe and is a popular study species that is tolerant of disturbance and which readily breeds in nestboxes at high densities, enabling close monitoring and easy capture of breeding adults and nestlings. Pied Flycatcher is one of the most-studied migratory passerines in the Afro-Palaearctic flyway (Lundberg & Alatalo 1992), and many future tracking-based studies are likely to focus on Pied Flycatchers and other similar-sized species.

We tested the effect of fitting breeding adult male Pied Flycatchers with geolocators weighing 0.36 g (including attachment harness), approximately 3% of bodyweight. We compared male provisioning rates and provisioning rates of their associated female with those of a randomly allocated control group of un-tagged breeding pairs in a replicated experiment. We also tested for effects on nestlings by comparing their weight, growth rate and fledging success between the two treatments. To examine longer-term effects, we then compared the return rates and arrival times of tagged and control individuals in the following spring, and the timing and outcome of these nesting attempts.

METHODS

Study site and monitoring

The study was conducted in the spring of 2015 and 2016 in a predominantly Sessile Oak *Quercus petraea* woodland at Yarner Wood and Neadon Cleave, both within East Dartmoor National Nature Reserve, south-west England (50°36′N, 3°43′W), which has a long established breeding Pied Flycatcher population (Burgess 2014). Adult male between-year return rates of Pied Flycatchers to Yarner Wood from 2008–2009 to 2015–2016 averaged 44 ± 3% se (Burgess & Hewson 2015). Arrival dates of individual males on territories were recorded from the first week of April, when the first males returned to the study site. Pied Flycatchers migrate and arrive at night (Ouwehand & Both 2016), and select territories the following morning. Territorial activity, such as singing, alarm calling and inspection of nestboxes, was observed by a 'slow-walk' past each nestbox every other morning, and for each bird seen, the presence, colour and position of any rings and variable plumage characteristics such as forehead patch size were recorded. These were cross-referenced against males captured at the same nestboxes later in the breeding season, when ring numbers could be read to confirm each male's identity. Male arrival date on a territory was taken as the mid-point date between the slow-walk survey prior to the first observation of a male and the survey when first observed.

Pied Flycatcher nests were monitored twice each week to determine first egg-laying date and clutch size. After 12 days of incubation, nests were inspected daily to determine exact hatch dates (1 April = day 1), as provisioning effort and reproductive success may be affected by seasonal food availability (Both & Visser 2005, Burger *et al.* 2012, Tomás 2015, Whytock *et al.* 2015, Samplonius *et al.* 2016). Nestlings were weighed collectively at 7 days old and individually at 12 days old. Runt nestlings found at 7 days old were also weighed individually. Nest outcomes were determined by checking nests within 7 days after the expected fledging date (fledging from 15 days old) and the numbers of chicks fledged and found dead were recorded.

Adults were caught in nestboxes, females mostly while incubating eggs and males when provisioning nestlings. Wing, tarsus length and weight were recorded at capture, as was a categorical Drost plumage score for males, which characterizes the degree and pattern of black plumage and is an indicator of individual quality (Drost 1936, Sirkiä *et al.* 2015). In the tagging year, across the combined total of 20 treatment and 19 control nests, 23 males had been ringed as nestlings and were of exact known age, and six were a minimum of 2 years old, first having been ringed as adults in earlier years. The remaining 10 males were unmarked, and were ringed with a uniquely numbered ring upon first capture (tagged = 4, control = 6). These were aged as a minimum age of 1 year, because they were entering the breeding population as either first- or second-year birds, as male breeding dispersal between woodlands does not occur in the species, and breeding dispersal between woodlands is rare (Eeva *et al.* 2008). Therefore, unmarked individuals were very unlikely to have been breeding dispersers from other woodlands, or natal recruits from the study population, as nearly all individuals that had bred in or fledged from the study population in earlier years had previously been captured and marked.

Geolocators

Due to licensing constraints, geolocators were only fitted to male Pied Flycatchers. Males were captured when nestlings were 10 days old, and randomly allocated to the geolocator group (tagged, $n = 20$) or to the control group (no geolocator, $n = 19$). We alternated selection of tagged and control males, giving seasonally matched samples. For cohort identification in the field the following breeding season, all males were marked with a single coloured anodized uniquely numbered metal ID ring: blue for males fitted with a geolocator and red for controls. Any previous ring was removed (with permission from the British Trust for Ornithology) so all males wore a single ring. Handling time was a maximum of 5 min for males fitted with a geolocator and 2 min for control males.

Geolocators weighing 0.32 g (Intigeo-W30Z11-DIP, Migrate Technology) with no light tube or stalk (which could potentially impede access through the 32-mm-diameter nestbox entrance holes) were attached using a Rappole-Tipton leg loop harness (Rappole & Tipton 1991) made from 0.7-mm-diameter elastan. Harness span was determined based on previous deployments on Pied Flycatchers and body mass at capture (Ouwehand *et al.* 2016), with several pre-assembled geolocators and harnesses available at deployment to reduce processing time. Geolocator fit was assessed with the bird held only by the legs, allowing the wings to move freely. In all cases the fit was acceptable on the first attempt, with no need for replacement. Geolocators together with harness weighed 0.36 g, a mean of 2.93% of body weight (range 2.73–3.13%).

Provisioning behaviour

In the tagging year, provisioning rates were observed at all nests when nestlings were 7 and 12 days old, 3 days before and 2 days after geolocator fitting, providing a before and after tagging comparison. The first provisioning watch was carried out on 24 May and the last on 18 June 2015, with half the watches carried out by 5 June. We recorded the number of provisioning visits made by males and females, separable by their sexually dimorphic plumage. Although no females were tagged, we were interested in quantifying any change in female provisioning rates, as they may compensate for changes in provisioning behaviour by their associated males (Alatalo *et al.* 1988) as a result of tagging. The observer settled into position a minimum of 10 m from nests and waited at least 5 min before starting watches to allow any alarmed adults time to resume normal behaviour. Although Pied Flycatcher provisioning rates are considered to vary little during the day (Lundberg & Alatalo 1992), we restricted all watches to between 08:30 and 13:45 h in case provisioning differed between morning and afternoon in our study population. Weather, particularly rainfall, is likely to affect provisioning rate (Radford *et al.* 2001), so we only conducted watches when no rainfall occurred. Provisioning was observed for 30 min, during which time we recorded the count of male and female visits to nests with food for the nestlings. Food was usually delivered inside nestboxes, but at some nests at the day 12 watch, food was delivered from the nestbox entrance. Nestling number and mass were recorded at the end of each provisioning watch.

Statistical analyses

First, we assessed whether males and females differed between treatment groups in ways that might influence their provisioning rate. We tested for differences in wing and tarsus length using *t*-tests, and differences in minimum age and Drost plumage score using Wilcoxon tests, as these data were not normally distributed. To compare adult weights between treatments, mixed effects models were run for males and females separately, with 'treatment' as a fixed effect and 'nestling age' as a random effect to account for adult weight variation during the nestling stage (Askenmo 1977).

Provisioning rates of males and females at day 7 and day 12 were each modelled separately with respect to tagging treatment, with brood size and the date of the provisioning watch included as covariates, using generalized linear models (GLMs) with a quasi-Poisson error structure and log link. Models were simplified by sequential removal of insignificant terms (Crawley 2013). To test whether provisioning rates differed between 7- and 12-day-old nestlings for each of the four adult classes (control and tagged, for both male and female), and whether provisioning rates differed between sexes within a pair at both nestling ages, paired Wilcoxon tests were used to compare the count data, which were not normally distributed. To account for potential effects of brood size, we also tested a response variable expressed as the provisioning rate per nestling using the number of provisioning visits divided by brood size.

Differences between treatments in average nestling mass at 7 and 12 days old, and the growth of nestling mass between 7 and 12 days old, were tested with brood size and hatch date as covariates using Gaussian GLMs with an identity link. To test whether the treatment affected successful fledging probability, the outcome of each nestling was predicted by treatment, brood size and hatch date, with 'nest identity' as a random effect using a mixed effects model with a binomial error structure and logit link. In both cases, model simplification was carried out as above.

Return rates of the 2015 tagged and control males were calculated as the percentages that were recaptured at the study site in 2016. Return rates were a measure of apparent survival, which for the highly philopatric Pied Flycatcher (Eeva *et al.* 2008) is likely to be close to actual survival, particularly for males, which rarely disperse > 1 km between years (Harvey *et al.* 1984), and in our study population because of a high adult detection rate due to breeding almost exclusively in nestboxes. The effect size of a tag-induced reduction in apparent survival was calculated as the return rate of tagged males divided by the return rate of untagged control males, subtracted from 1. The 2015 tag treatment was tested as a predictor of male arrival date and the first egg-laying date of the associated 2016 breeding attempt using a GLM with a Gaussian error structure. Clutch size and the number of fledglings of 2016 nest attempts were also tested against the 2015 tag treatment using GLMs with a Poisson error structure and log link. Three recaptured tagged males had lost their geolocators over the year and so were excluded from all longer-term effect analyses, as we did not know when geolocators were lost. All analyses were carried out using R (R Development Core Team 2013) with mixed effects models run using the lme4 package (Bates *et al.* 2015) and a 90% confidence limit for the standardized mean difference in return rates (effect size) calculated using the ci.smd function in the MBESS package (Kelley 2016). All estimates are given with standard errors.

RESULTS

All 20 tagged males were observed feeding nestlings after the fitting of geolocators in 2015. One control nest and two nests with a male fitted with a geolocator failed when nestlings were between 10 and 12 days old; all other nests produced at least one fledgling. Treatment groups did not differ significantly in morphology or plumage, with the exception that geolocator-fitted males had slightly longer tarsi (Table 1). The following breeding season (2016), 60 pairs of Pied Flycatchers attempted to breed, from which 56 males and 59 females were captured. Captures in 2016 included 10

Table 1. Adult (a) and nest (b) sample sizes and descriptive statistics. Adult weights were compared by linear mixed effects models with treatment as a fixed effect and nestling age as a random effect. Only nests of experimental treatment males are compared. Twenty males were allocated to the tagging group and 19 to the control group, but constraints such as inclement weather on the scheduled provisioning watch day or subsequent nest failure meant sample sizes were not always 20 : 19. Tag females were mates of males fitted with geolocators.

		Control			Tag				
(a) Adult measures	Sex	Mean	se	*n*	Mean	se	*n*	Test value	*P*
Wing length (mm)	Male	78.89	0.44	19	79.13	0.41	16	−0.38	0.71
	Female	76.46	0.33	19	76.42	0.38	20	0.08	0.93
Weight (g)	Male	11.91	0.14	19	12.24	0.13	20	1.47	0.15
	Female	13.43	0.39	17	13.31	0.32	19	1.64	0.11
Tarsus length (mm)	Male	17.13	0.11	16	17.43	0.11	15	−2.19	0.04
	Female	17.28	0.16	11	17.25	0.14	16	0.14	0.88
Age (years)	Male	2.11	0.38	19	1.65	0.17	20	201.0	0.75
Drost plumage score	Male	4.53	0.38	17	4.44	0.37	18	155.0	0.96

		Control			Tag		
(b) Nest measures	Nestling age (days)	Mean	se	*n*	Mean	se	*n*
Mean brood size	7	6.17	0.22	18	5.84	0.39	19
	12	5.88	0.37	17	5.44	0.43	18
Mean brood mass	7	67.09	3.35	17	59.35	4.33	18
	12	77.94	5.89	16	72.22	5.86	18
Number fledged		105 (5.53/nest)			92 (4.60/nest)		

tagged and nine control males from 2015, and 10 and 13 females that had paired with tagged and control males in 2015, respectively.

Provisioning rate

Neither male nor female provisioning rates differed between treatments when nestlings were 7 or 12 days old (Table 2, Fig. 1a). Within pairs, males and females did not differ in provisioning rate between treatments at 7 or 12 days old (Fig. 1, tagged: day 7, $v = 87.5$, $P = 0.32$; control: $v = 63.5$, $P = 0.51$; day 12: tagged: $v = 91.5$, $P = 0.49$; control, $v = 61.5$, $P = 0.28$), or comparing the rates of same nests between 7 and 12 days old (male: tagged, $v = 100$, $P = 0.28$, control, $v = 41$, $P = 0.49$; female: paired with tagged male, $v = 68.5$, $P = 0.65$, control, $v = 28$, $P = 1$). Using a provisioning rate per nestling response variable gave similar results.

Seasonally later nests had fewer provisioning visits by males when nestlings were 7 days old irrespective of treatment, but no seasonal trend was evident for female provisioning rate or for males or females when nestlings were 12 days old (Table 2). Female provisioning rates were influenced by brood size when nestlings were 7 days old, with a greater number of provisioning visits made to larger broods in both treatment groups, but this trend was not observed when nestlings were 12 days old, nor for male provisioning at either nestling age (Table 2).

Nestling mass and nest success

There was no difference in average nestling mass between treatments when nestlings were 7 or 12 days old (Table 2, Fig. 1b). Average nestling mass increased between day 7 and 12 in all nests, with no difference between treatments (mean increase for nests of tagged males = 2.69 ± 0.30 g, nests of control males = 2.53 ± 0.24 g; Table 2). There was no seasonal or brood size effect on average brood mass gain (all $P > 0.05$; Table 2). At provisioning watches when nestlings were 12 days old, a runt was present in four control nests and five nests with tagged males; there was no difference between treatments in either mean runt mass (tagged = 10.17 ± 0.52 g, control = 10.69 ± 1.17 g, *t*-test: $P = 0.71$), or average brood mass excluding the runt (tagged = 12.41 ± 0.76 g, control = 12.40 ± 0.97 g, *t*-test: $P = 0.99$). Two nests

Table 2. Results of generalized linear models of nestling provisioning rate (PR) by parents and average nestling mass (g), when nestlings were 7 days old (*n* = 37: tagged nests = 19, control nests = 18) and 12 days old (*n* = 35: tagged nests = 18, control nests = 17). Maximal models tested the effect of tagging treatment, brood size and date (1 April = 1) of the nest. Models of provisioning rate were tested with a quasi-Poisson error structure and a log link. Models of nestling mass were tested with a Gaussian error structure. Significant minimal adequate models ($P < 0.05$) are shown in bold. Where no terms were significant, the maximal model is presented.

Nestling age	Response variable	Predictor	Intercept	Estimate	se	*t*	*P*
7 days	Male PR	Date	4.53	−0.03	0.01	−2.72	**0.01**
	Female PR	Brood size	1.42	0.15	0.05	2.84	**0.008**
	Average nestling mass	Treatment	9.32	−0.57	0.47	−1.21	0.24
		Brood size	9.32	−0.09	0.18	−0.51	0.61
		Date	9.32	0.03	0.06	0.58	0.57
12 days	Male PR	Treatment	2.23	−0.10	0.17	−0.60	0.55
		Brood size	2.23	0.001	0.05	0.02	0.98
		Date	2.23	0.004	0.02	0.20	0.85
	Female PR	Treatment	2.65	−0.05	0.13	−0.39	0.70
		Brood size	2.65	−0.01	0.04	−0.24	0.81
		Date	2.65	−0.003	0.02	−0.20	0.84
	Average nestling mass	Treatment	9.11	−0.11	0.50	−0.24	0.82
		Brood size	9.11	0.08	0.16	0.51	0.62
		Date	9.11	0.06	0.06	0.93	0.36
	Average mass gain day 7–12	Treatment	1.30	0.12	0.41	0.30	0.77
		Brood size	1.30	−0.03	0.13	−0.24	0.81
		Date	1.30	0.02	0.05	0.42	0.68

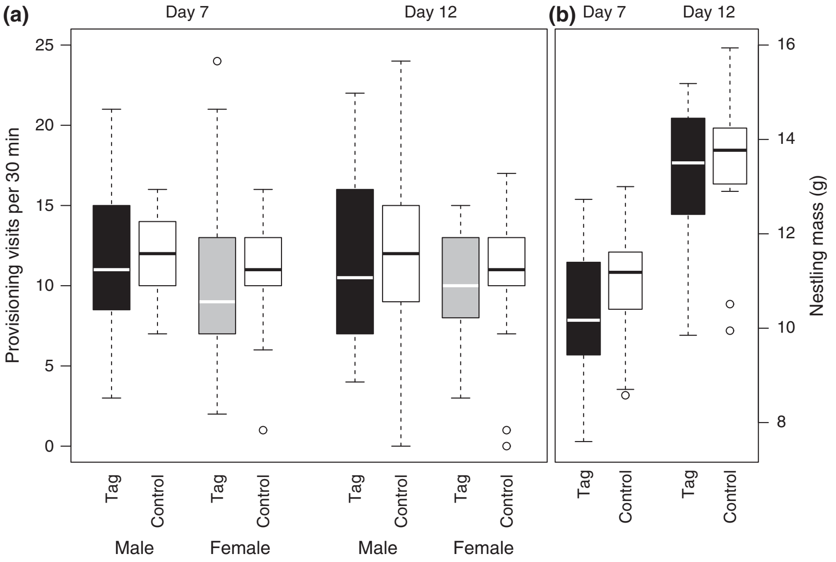

Figure 1. (a) Provisioning visits per 30 min and (b) average nestling mass of nests with geolocator-fitted males (black, with white median), their associated female (grey, with white median) and untagged control males and females (white, with black median) when nestlings were 7 days old (day 7: tagged = 19 nests, control = 18 nests) and 12 days old (day 12: tagged = 18 nests, control = 17 nests), i.e. before and after fitting geolocators when nestlings were 10 days old. The box plot shows the interquartile range (box), median (horizontal bar), the 1.5*interquartile range (whiskers) and values outside the 1.5 interquartile range (circles).

(one control and one tagged nest) suffered partial brood loss between nestling age 7 and 12 days old, both losing a single nestling. In total, eight nestlings died between 12 days old and fledging, but fledging success was not predicted by treatment ($P = 0.92$).

Return rate, arrival date, recruitment and nest success in 2016

In 2016, 10 males fitted with geolocators were recaptured, although three had lost their geolocator during the year; nine control males were recaptured. The return rate of tagged males was therefore 50% (10/20), or 41.2% when only considering those that returned with geolocators (7/17), and 47.3% (9/19) for control males. The effect size estimate of a tag-induced reduction in apparent survival was −0.06 (90% CI: −0.64 to −0.42), or 0.26 only including males returning with a geolocator (90% CI −0.64 to −0.42). Ten females paired with a tagged male in 2015 returned in 2016 (50%), compared with 13 paired with an untagged male (68%). Mean arrival date for the seven tagged males that returned with a geolocator was 16 April (range 11–26), and 16 April (range 10–20) for the nine returning control males. The difference between treatment groups was not significant ($t = 0.12$, $P = 0.91$; Table 3).

We found no longer-term effects associated with tagging on timing or reproductive parameters in the following year, as there was no effect of tagging on timing of egg-laying, clutch size or the number of fledglings (all $P > 0.2$; Table 3, Fig. 2) in 2016. A total of nine fledglings recruited from nine of the 2015 nests into the East Dartmoor breeding population in 2016, two males and three females from five nests with a tagged male, and one male and three females from four control nests.

Table 3. Results of generalized linear models of 2016 breeding parameters tested against the effect of tagging treatment in 2015. Arrival date and first egg date (1 April = 1) were tested using a Gaussian model. Clutch size and number fledged were tested with Poisson and quasi-Poisson models. In all models the control is taken as the intercept. Tagged males = 7, control males = 9.

Nesting variable	Control (se)	Tag (se)	*t*	*P*
Male arrival date	15.89 (1.20)	16.14 (1.94)	0.12	0.90
First egg-laying date	41.33 (0.75)	40.14 (1.13)	−1.05	0.31
Clutch size	7.22 (0.15)	6.43 (0.30)	−0.60	0.55
No. of fledglings	5.56 (0.65)	4.29 (0.79)	−1.25	0.23

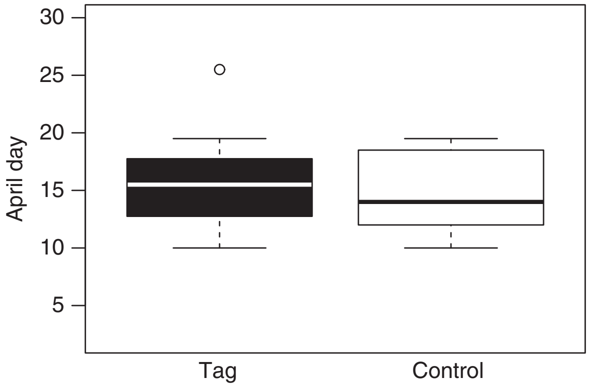

Figure 2. Comparison of mean 2016 arrival dates between males returning with geolocators and untagged control males. Mean arrival date for seven males fitted with geolocators and for nine control males was 16 April. The difference between treatment groups was non-significant ($t = 0.12$, $P = 0.91$). The box plot shows the interquartile range (box), median (horizontal bar), the 1.5*interquartile range (whiskers) and value outside the 1.5 interquartile range (circle).

DISCUSSION

We found no short- or longer-term effects of fitting adult male Pied Flycatchers with a geolocator. There were no short-term effects on male or female provisioning rates, nestling mass gain, mean pre-fledging nestling mass or nest outcome. We did not subsequently detect any impact on apparent between-year survival, male arrival date on territories the following year, the timing of 2016 nesting attempts or 2016 nest productivity. We also observed little difference in recruitment of 2015 fledglings between tagged and control nests. As our two groups of males did not differ greatly in weight, body size, age or plumage, and the two groups were seasonally matched, we are confident that tracking devices weighing *c.* 3% of body mass, using the methods described, had no short- or longer-term effect on males, associated females, nestlings, nest outcome, or recruitment over and above the effects of capture without fitting a device, under the circumstances and over the period in which the trial was conducted.

Assessing potential tag effects requires a matched control cohort of ringed-only individuals to establish that information from tagged individuals is not biased as a consequence of the tag (Costantini & Møller 2013). We are aware of only one other migratory passerine tagging study that compares provisioning rates between tagged and untagged parents (Gómez *et al.* 2014); that study assessed provisioning rates of Tree Swallow *Tachycineta bicolor* 2–9 days after geolocator deployment, but did not include before and after deployment comparisons. We quantified provisioning 3 days before and 2 days after deployment, with all males tagged when nestlings were 10 days old. Our study concurs with Gómez *et al.* (2014) in finding no tag effects on provisioning rates.

Post-tagging provisioning rates were observed only 2 days after tag deployment when nestlings were 12 days old, meaning only an immediate effect of tagging on behaviour could be observed. However, the peak demand for food by Pied Flycatcher nestlings is around 10 days old (Lundberg & Alatalo 1992), so we would expect nestlings to be especially sensitive to any change in food delivery around the time we recorded provisioning rates. Nestlings remain in the nest for 15 or more days and so fledge a minimum of 5 days after tag deployment. We found no difference in the probability of partial brood loss or nest failure between treatments. Further to this, Pied Flycatchers continue to provision young after fledging (Lundberg & Alatalo 1992). Young from tagged (five) and control (four) nests recruited into the breeding population the following year, and so we found no evidence in this small sample that suggested that the number of recruiting young from nests with a tagged male was influenced by tag fitting.

The breeding success of Pied Flycatchers is associated with a seasonal peak in invertebrate abundance in temperate woodlands (Both *et al.* 2006), but we found timing of breeding had only a limited effect on provisioning rate. For both treatments, when nestlings were 7 days old, males provisioned earlier timed nests at a higher rate, but there were no seasonal differences in female provisioning. This highlights the need for controls in studies like ours to be temporally matched. If tags did not limit the provisioning rate, but constrained optimal foraging, with prey quality or quantity reduced, we should have detected negative effects on nestling mass and growth even 2 days after tagging, which we did not. Neither brood mass nor fledging success were affected by tagging in studies of Tree Swallow, Barn Swallow *Hirundo rustica* or Black Kite *Milvus migrans* (Gómez *et al.* 2014, Scandolara *et al.* 2014, Sergio *et al.* 2015), but effects were found in one of three examined populations of European Roller *Coracias garrulus* when both parents were tagged (Rodríguez-Ruiz *et al.* 2016).

It is possible that in a short-lived species such as the Pied Flycatcher, adults may absorb short-term fitness costs by prioritizing nestling care at the expense of their own condition, and tag effects may instead reduce longer-term survival (Ouwehand *et al.* 2016). This was not the case in our study, as we found no difference in apparent survival of tagged and control individuals, and no tag effect on male arrival date or timing of breeding, contrary to two other studies (Arlt *et al.* 2013, Scandolara *et al.* 2014). A study of Pied Flycatchers breeding in the Netherlands found no effects on return rate or arrival date using the same harness type and material that we used, but there was a reduced return rate and arrival date for males tagged with a full body harness made from a non-flexible material (Ouwehand & Both 2017).

Several tag effect studies on other passerines have found long-term, but not short-term, effects. Scandolara *et al.* (2014) found lowered adult Barn Swallow return rates, delayed breeding and smaller clutches, but they used a geolocator design (protruding light stalk) and harness (leg-loop) likely to be unsuited to highly aerial feeding species. Lowered return rates, delayed arrival and breeding were also found in tagged Northern Wheatear *Oenanthe oenanthe*, thought to result from costs accumulated during migration (Arlt *et al.* 2013). A study of the aerial feeding Tree Swallow found return rates of tagged and control males differed in populations with intermediate or low return rates (Gómez *et al.* 2014). This suggests that any differences in return rates between tagged and control individuals may be population-dependent. Year and stochastic environmental effects determine the probability of individual survival, and the ability of tagged individuals to withstand the extra tag-load may be more detectable in years with unfavourable conditions (van Wijk *et al.* 2016, Snijders *et al.* 2017). Given the 'normal' return rate of control birds in our study, we may assume that non-breeding conditions were not unusually challenging in 2015–2016, and we have no reason to believe our study was conducted under especially favourable breeding conditions. In our study population overall, the mean number of fledglings per breeding attempt was 4.26 in 2015 and 4.32 in 2016, just below the 1955–2016 population average (4.69), and well within the standard deviation of 1.14. Differences in return rates of tagged and untagged birds may also be sex-dependent, as suggested in previous work on Pied Flycatchers (Ouwehand *et al.* 2016, Ouwehand & Both 2017).

Our experimental design using randomly assigned but closely matched individuals and seasonally matched nests adds to the few studies examining tag effects on small passerines in finding no short- or long-term effects. Our study suggests fitting lightweight tags to small passerines need not affect provisioning behaviour, nest success, timing of breeding, apparent between-year annual survival or recruitment. However, effects can be population- and year-specific and tagging new species or populations should still require assessment of the kind of traits and behaviours examined here by comparison with well-matched control cohorts over multiple years.

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REFERENCES

Alatalo, R.V., Gottlander, K. & Lundberg, A. 1988. Conflict or cooperation between parents in feeding nestlings in the Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scand.* **19**: 31–34.

Arlt, D., Low, M. & Pärt, T. 2013. Effect of geolocators on migration and subsequent breeding performance of a long-distance passerine migrant. *PLoS ONE* **8**: e82316.

Askenmo, C. 1977. Effects of addition and removal of nestlings on nestling weight nestling survival and female weight loss in the Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scand.* **8**: 1–8.

Atema, E., van Noordwijk, A.J., Boonekamp, J.J. & Verhulst, S. 2016. Costs of long-term carrying of extra mass in a songbird. *Behav. Ecol.* **27**: 1087–1096.

Barron, D.G., Brawn, J.D. & Weatherhead, P.J. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods Ecol. Evol.* **1**: 180–187.

Bates, D., Maechler, M., Bolker, B. & Walker, S. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Soft.* **67**: 1–48.

Becker, P.H., Schmaljohann, H., Riechert, J., Wagenknecht, G., Zajková, Z. & González-Solís, J. 2016. Common Terns on the East Atlantic Flyway: temporal–spatial distribution during the non-breeding period. *J. Ornithol.* **157**: 927–940.

Blackburn, E., Burgess, M., Freeman, B., Risely, A., Izang, A., Ivande, S., Hewson, C. & Cresswell, W. 2016. An experimental evaluation of the effects of geolocator design and attachment methods on between-year survival on Whinchats *Saxicola rubetra*. *J. Avian Biol.* **47**: 530–539.

Both, C. & Visser, M.E. 2005. The effect of climate change on the correlation between avian life-history traits. *Glob. Change Biol.* **11**: 1606–1613.

Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* **441**: 81–83.

Bowlin, M.S., Henningsson, P., Muijres, F.T., Vleugels, R.H.E., Liechti, F. & Hedenström, A. 2010. The effects of geolocator drag and weight on the flight ranges of small migrants. *Methods Ecol. Evol.* **1**: 398–402.

Bridge, E.S., Thorup, K., Bowlin, M.S., Chilson, P.B., Diehl, R.H., Fléron, R.W., Hartl, P., Roland, K., Kelly, J.F. & Robinson, W.D. 2011. Technology on the move: recent and forthcoming innovations for tracking migratory birds. *Bioscience* **61**: 689–698.

Burger, C., Belskii, E., Eeva, T., Laaksonen, T., Mägi, M., Mänd, R., Qvarnström, A., Slagsvold, T., Veen, T., Visser, M.E., Wiebe, K.L., Wiley, C., Wright, J. & Both, C. 2012. Climate change, breeding date and nestling diet: how temperature differentially affects seasonal changes in Pied Flycatcher diet depending on habitat variation. *J. Anim. Ecol.* **81**: 926–936.

Burgess, M.D. 2014. Restoring abandoned coppice for birds: few effects of conservation management on occupancy, fecundity and productivity of hole nesting birds. *For. Ecol. Manage.* **330**: 205–217.

Burgess, M.D. & Hewson, C.M. 2015. Migration behaviour and winter distribution of a declining long-distant migrant, the Pied Flycatcher (*Ficedula hypoleuca*). *BOU-funded Project Report:* 1–3.

Casas, F., Benítez-López, A., García, J.T., Martín, C.A., Viñuela, J. & Mougeot, F. 2015. Assessing the short-term effects of capture, handling and tagging of Sandgrouse. *Ibis* **157**: 115–124.

Costantini, D. & Møller, A. P. 2013. A meta-analysis of the effects of geolocator application on birds. *Curr. Zool.* **59**: 697–706.

Crawley, M.J. 2013. *The R book*. Chichester: John Wiley & Sons Ltd.

Drost, R. 1936. Über das Brutkleid männlicher Trauerfliegenfänger, *Muscicapa hypoleuca*. *Vogelzug* **6**: 179–186.

Eeva, T., Ahola, M., Laaksonen, T. & Lehikoinen, E. 2008. The effects of sex, age and breeding success on breeding dispersal of Pied Flycatchers along a pollution gradient. *Oecologia* **157**: 231–238.

Gómez, J., Michelson, C., Bradley, D.W., Ryan Norris, D., Berzins, L.L., Dawson, R.D. & Clark, R.G. 2014. Effects of geolocators on reproductive performance and annual return rates of a migratory songbird. *J. Ornithol.* **155**: 37–44.

Harvey, P., Greenwood, P., Campbell, B. & Stenning, M. 1984. Breeding dispersal of the Pied flycatcher (*Ficedula hypoleuca*). *J. Anim. Ecol.* **53**: 727–736.

Kelley, K. 2016. The MBESS R Package. CRAN.

Lundberg, A. & Alatalo, R.V. 1992. *The Pied Flycatcher*. London: T & A D Poyser.

Marra, P.P., Cohen, E.B., Loss, S.R., Rutter, J.E. & Tonra, C.M. 2015. A call for full annual cycle research in animal ecology. *Proc. R. Soc. Lond. B* **11**: 20150552.

Matyjasiak, P., Rubolini, D., Romano, M. & Saino, N. 2016. No short-term effects of geolocators on flight performance of an aerial insectivorous bird, the Barn Swallow (*Hirundo rustica*). *J. Ornithol.* **157**: 653–661.

Ouwehand, J. & Both, C. 2016. Alternate non-stop migration strategies of Pied Flycatchers to cross the Sahara desert. *Biol. Lett.* **12**: 20151060.

Ouwehand, J. & Both, C. 2017. African departure rather than migration speed determines variation in spring arrival in Pied Flycatchers. *J. Anim. Ecol.* **86**: 88–97.

Ouwehand, J., Ahola, M.P., Ausems, A.N.M.A., Bridge, E.S., Burgess, M., Hahn, S., Hewson, C., Klaassen, R.H.G., Laaksonen, T., Lampe, H.M., Velmala, W. & Both, C. 2016. Light-level geolocators reveal migratory connectivity in European populations of Pied Flycatchers *Ficedula hypoleuca*. *J. Avian Biol.* **47**: 69–83.

Pennycuick, C., Fast, P.L., Ballerstädt, N. & Rattenborg, N. 2012. The effect of an external transmitter on the drag coefficient of a bird's body, and hence on migration range, and energy reserves after migration. *J. Ornithol.* **153**: 633–644.

Peterson, S.M., Streby, H.M., Kramer, G.R., Lehman, J.A., Buehler, D.A. & Andersen, D.E. 2015. Geolocators on Golden-winged Warblers do not affect migratory ecology. *Condor* **117**: 256–261.

R Development Core Team. 2013. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Radford, A.N., McCleery, R.H., Woodburn, R.J.W. & Morecroft, M.D. 2001. Activity patterns of parent Great Tits *Parus major* feeding their young during rainfall. *Bird Study* **48**: 214–220.

Rappole, J.H. & Tipton, A.R. 1991. New harness design for attachment of radio transmitters to small passerines. *J. Field Orn.* **62**: 335–337.

Rodriguez, A., Negro, J.J., Fox, J.W. & Afanasyev, V. 2009. Effects of geolocator attachments on breeding parameters of Lesser Kestrels. *J. Field Orn.* **80**: 399–407.

Rodríguez-Ruiz, J., Parejo, D., de la Puente, J., Valera, F., Calero-Torralbo, M.A., Bermejo, A., Catry, I. & Avilés, J.M. 2016. Short- and long-term effects of tracking devices on the European Roller *Coracias garrulus*. *Ibis* **158**: 179–183.

Samplonius, J.M., Kappers, E.F., Brands, S. & Both, C. 2016. Phenological mismatch and ontogenetic diet shifts interactively affect offspring condition in a passerine. *J. Anim. Ecol.* **85**: 1255–1264.

Scandolara, C., Rubolini, D., Ambrosini, R., Caprioli, M., Hahn, S., Liechti, F., Romano, A., Romano, M., Sicurella, B. & Saino, N. 2014. Impact of miniaturized geolocators on Barn Swallow *Hirundo rustica* fitness traits. *J. Avian Biol.* **45**: 417–423.

Sergio, F., Tavecchia, G., Tanferna, A., López Jiménez, L., Blas, J., De Stephanis, R., Marchant, T.A., Kumar, N. & Hiraldo, F. 2015. No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning and condition of its offspring. *J. Appl. Ecol.* **52**: 1665–1675.

Sirkiä, P. M., Adamik, P., Artem'ev, A. V., Belskii, E., Both, C., Bures, S., Burgess, M. D., Bushuev, A. V., Forsman, J. T., Grinkov, V., Hoffmann, D., Jarvinen, A., Kral, M., Krams, I., Lampe, H. M., Moreno, J., Magi, M., Nord, A., Potti, J., Ravussin, P. A., Sokolov, L. & Laaksonen, T. 2015. Fecundity selection on multiple male colouration traits does not vary along large geographical cline of trait means in a passerine bird. *Biol. J. Linn. Soc.* **114**: 808–827.

Snijders, L., Weme, L. E. N., de Goede, P., Savage, J. L., van Oers, K. & Naguib, M. 2017. Context-dependent effects of radio transmitter attachment on a small passerine. *J. Avian Biol.* DOI: 10.1111/jav.01148

Streby, H.M., McAllister, T.L., Peterson, S.M., Kramer, G.R., Lehman, J.A. & Andersen, D.E. 2015. Minimizing marker mass and handling time when attaching radio-transmitters and geolocators to small songbirds. *Condor* **117**: 249–255.

Tomás, G. 2015. Hatching date vs laying date: what should we look at to study avian optimal timing of reproduction? *J. Avian Biol.* **46**: 107–112.

Weiser, E.L., Lanctot, R.B., Brown, S.C., Alves, J.A., Battley, P.F., Bentzen, R., Bêty, J., Bishop, M.A., Boldenow, M., Bollache, L., Casler, B., Christie, M., Coleman, J.T., Conklin, J.R., English, W.B., Gates, H.R., Gilg, O., Giroux, M.-A., Gosbell, K., Hassell, C., Helmericks, J., Johnson, A., Katrínardóttir, B., Koivula, K., Kwon, E., Lamarre, J.-F., Lang, J., Lank, D.B., Lecomte, N., Liebezeit, J., Loverti, V., McKinnon, L., Minton, C., Mizrahi, D., Nol, E., Pakanen, V.-M., Perz, J., Porter, R., Rausch, J., Reneerkens, J., Rönkä, N., Saalfeld, S., Senner, N., Sittler, B., Smith, P.A., Sowl, K., Taylor, A., Ward, D.H., Yezerinac, S. & Sandercock, B.K. 2016. Effects of geolocators on hatching success, return rates, breeding movements, and change in body mass in 16 species of Arctic-breeding shorebirds. *Mov. Ecol.* **4**: 12.

Whytock, R.C., Davis, D., Whytock, R., Burgess, M.D., Minderman, J. & Mallord, J. 2015. Wood Warbler *Phylloscopus sibilatrix* nest provisioning rates are correlated with seasonal caterpillar availability in British Oak *Quercus* woodlands. *Bird Study* **62**: 339–347.

van Wijk, R., Souchay, G., Jenni-Eiermann, S., Bauer, S. & Schaub, M. 2016. No detectable effects of lightweight geolocators on a Palaearctic-African long-distance migrant. *J. Ornithol.* **157**: 255–264.

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