

# No short-term effects of geolocators on flight performance of an aerial insectivorous bird, the Barn Swallow (*Hirundo rustica*)

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**Abstract** Miniaturized light-level geolocators are becoming increasingly popular devices for the study of avian migration. However, the effects of these devices on birds' flight behaviour, and hence fitness components, are poorly known. We investigated the effect of miniaturized geolocators on flight performance of the Barn Swallow (*Hirundo rustica*), which may be especially susceptible to geocator deployment as it is a small (~20 g), aerially insectivorous, long-distance migratory species. We tested whether miniaturized geolocators (~3.5 % of body mass) affected short-term flight performance traits of breeding males by comparing flight manoeuvrability, velocity and acceleration of geocator-equipped versus control (handled only) birds in flight tunnels. We used a robust experimental design wherein the within-individual change in flight performance was compared between geocator-equipped birds (after allowing for a period of acclimation) and control birds (that were also tested twice). We found no statistically significant evidence that short-term flight performance traits were affected by geocator deployment. Here we discuss the implications of our findings for

the deployment of geolocators in studies of migratory behaviour of small birds.

**Keywords** Barn Swallow · Bird flight · Datalogger · External transmitter · Flight performance · Light-level geocator · Locomotion

## Zusammenfassung

**Geolokatoren haben keine kurzfristigen Auswirkungen auf die Flugleistung der in der Luft nach Insekten jagenden Rauchschwalbe *Hirundo rustica***

Miniaturisierte Helldunkelgeolokatoren werden zunehmend für Untersuchungen des Vogelzugs eingesetzt. Die Auswirkungen dieser Geräte auf das Flugverhalten und somit auf gewisse Fitnesskomponenten der Vögel sind jedoch nur schlecht verstanden. Wir haben den Einfluss von miniaturisierten Geolokatoren auf die Flugleistung der Rauchschwalbe (*Hirundo rustica*) untersucht, die als kleiner (20 g), in der Luft nach Insekten jagender Langstreckenzieher besonders empfindlich auf den Einsatz von Geolokatoren reagieren könnte. Wir haben getestet, ob miniaturisierte Geolokatoren (3.5 % der Körpermasse) die Flugleistung brütender Männchen kurzfristig beeinflussen. Hierfür haben wir in Windtunneln die Manövrierfähigkeit, Geschwindigkeit und Beschleunigung von mit Geolokatoren ausgestatteten Vögeln und Kontrollvögeln, die lediglich gehandhabt wurden, verglichen. Wir haben ein robustes experimentelles Design verwendet, bei dem die individuelle Änderung der Flugleistung von mit Geolokatoren ausgestatteten Vögeln (d.h. vor Anbringung des Geräts und nachdem sich das Tier an das Gerät gewöhnt hatte) und Kontrollvögeln (die ebenfalls zweimal getestet wurden) verglichen wurde. Wir fanden keine statistisch signifikanten

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Hinweise darauf, dass die Flugleistung kurzfristig durch den Geolokatoreinsatz beeinträchtigt wurde. Wir diskutieren die Folgen unserer Befunde für den Geolokatoreinsatz in Studien des Zugverhaltens von Kleinvögeln.

## Introduction

The development of miniaturized tracking devices has revolutionized the study of bird migration ecology, life-history strategies and conservation biology, as it has given researchers previously unattainable possibilities for investigating bird movements across broad spatial and temporal scales (Robinson et al. 2009; Bridge et al. 2011; Guilford et al. 2011). Increasingly popular and relatively cheap devices to track migrating birds on a continental scale are small (0.5–2 g) light-level dataloggers, or geolocators (Bridge et al. 2011, 2013; McKinnon et al. 2013). Geolocators record light levels over time, thereby allowing researchers to estimate the global position of the bird with an accuracy on the order of  $10^2$ – $10^3$  km. Thanks to their small size and weight, geolocators have already been used to identify migration routes (including staging areas) and wintering areas of a number of small birds (up to 50 g) that are too small to carry satellite- or GPS/GSM-assisted tags (Stutchbury et al. 2009; Åkesson et al. 2012; Fraser et al. 2012; Schmaljohann et al. 2012a, b; Stach et al. 2012; Salewski et al. 2013; Hobson et al. 2015; Liechti et al. 2015).

There has been increasing concern, however, that external tracking devices might be harmful in terms of viability or other life-history traits, that they might negatively affect bird flight performance, and that observed migratory behaviour may not reflect natural behaviour in the absence of geolocators (Barron et al. 2010; Costantini and Møller 2013), therefore potentially producing bias in tracking data. Because of the ethical, conservation and scientific implications, the deployment of such devices should therefore be associated to the assessment of their impact on birds (e.g. Arlt et al. 2013; Scandola et al. 2014; Peterson et al. 2015).

Recent meta-analyses have shown that external tracking devices cause a significant increase in energy expenditure and a reduction in reproductive output and survival (Barron et al. 2010; Costantini and Møller 2013), yet the evidence of negative geocator effects on flight performance from empirical tests is very sparse. By testing taxidermic specimens in a wind tunnel, Bowlin et al. (2010) provided evidence that geolocators increase drag by increasing the body frontal area. Pennycuik et al. (2012) used wind tunnel tests with living birds and showed that external

radio-transmitters significantly increased the drag coefficient by triggering separation of the boundary layer over the posterior end of the body. They also found that sloping antennas of transmitters (or light-sensing stalks in the case of geolocators) contributed markedly to elevated drag coefficient. In both of these studies, aerodynamic calculations showed that increased aerodynamic drag could translate into impaired long-distance flight performance and hence reduced flight range. In addition, increased drag was believed to result in reduced flight velocity (Bowlin et al. 2010).

The added body mass and frontal area from external tracking devices can impair flight manoeuvrability and acceleration (Hedenström 1992). The consequences of such negative influence of tags on flight performance are thought to be particularly severe in birds that spend large amounts of time on the wing and rely on manoeuvrable and agile flight while hunting for insects in the air or diving for invertebrates or fish. Indeed, Costantini and Møller (2013), in their meta-analytic study, showed a greater negative effect of geolocators on survival of aerial foragers compared to other birds. We are aware of two additional studies in which the effect of external transmitters on bird flight performance was investigated: Gessaman and Nagy (1988) and Irvine et al. (2007) showed that backpack radio tags significantly reduced velocity in racing pigeons (*Columba livia*) during homing flight. To date, however, no study has empirically investigated the effect of geolocators on flight performance in small birds.

Here, we experimentally assessed the impact of miniaturized geolocators on short-term flight performance traits (manoeuvrability, velocity and acceleration) in a passerine bird, the Barn Swallow (*Hirundo rustica*). Barn swallows are small ( $\sim 18$  g, wing span  $\sim 0.34$  m), aerially insectivorous long-distance migratory birds (Møller 1994; Turner 2006). Breeding male Barn Swallows were fitted with geolocators, which were deployed using a leg-loop harness. Short-term flight performance of tagged and control birds was measured in a standardized manner in flight tunnels (Rowe et al. 2001; Bowlin and Winkler 2004; Matyjasiak et al. 2004, 2009; Bro-Jørgensen et al. 2007), using a robust experimental design in which the within-individual change in flight performance was compared between birds that were equipped with a geocator (after allowing for a period of acclimation) and control birds (that were also tested twice) without geolocators. We predicted that geocator birds would suffer a decline in flight performance traits in the post- versus pre-deployment trial, whereas this change was not expected among controls. Specifically, we expected a reduction in manoeuvrability and a decrease in flight velocity and acceleration.

## Methods

### Study area and general methods

The study was carried out in 2014 in two Barn Swallow colonies (ca. 30 and 20 breeding pairs) located in two nearby horse stables in the Łomianki commune near Warsaw (52°22'N, 20°53'E, elevation 75 m), central Poland. Further details on the study area and the study population are given in Matyjasiak (2013) and Matyjasiak et al. (2013).

Birds were captured by mist-netting conducted from 15 May to 15 June, sexed according to Svensson (1984), ringed with a numbered aluminium leg ring, and individually marked with a combination of colour leg rings. Since breeding pairs and unmated males were intensively ringed in 2013, we were able to classify marked birds as “after second-year” (ASY), meaning birds in at least their second breeding season, while unmarked birds or birds ringed as nestlings in the previous year were classified as second-year (SY), or birds hatched the previous year and in their first breeding season. This approach is justified on the basis of high breeding philopatry in this species (Møller 1994) and on our own capture–recapture data. We measured the length of the wing (from the carpal joint to the tip of the longest primary feather) and tail to the nearest 1 mm using a ruler. Keel and tarsus lengths were measured to the nearest 0.1 mm using a pair of callipers. Body mass was measured to the nearest 0.5 g with a Pesola spring balance. All measurements were taken by PM. After measurements and ringing, the birds were immediately released.

### Deployment of geolocators

We recaptured birds for geocator deployment between 28 June and 10 July. We decided to apply geolocators on males only in order to reduce the negative effect of geolocators on the survival of sample study birds, as geolocators have proven to be more harmful to female than male Barn Swallows in terms of survival (Scandolara et al. 2014). We applied miniaturized Swiss Ornithological Institute (Sempach, Switzerland) geolocators with a mean weight of 0.64 g, including harness (0.02 SD; see also Scandolara et al. 2014). The weight of geolocators constituted 3.2–4.1 % of body mass of a male Barn Swallow upon capture (mean = 3.5 %), and their light-sensing stalks protruded ca. 5 mm from the main device. We fitted these tags using a leg-loop harness (Rappole and Tipton 1991) made of an elastic silicone rubber mixture (MVQ 60 shore A). We used leg-loop harnesses with a diameter of 28 mm and a thickness of 1.25 mm (Scandolara et al. 2014). This caudal position of geolocators was conducive

to minimizing the aerodynamic drag they may cause (Bowlin et al. 2010). For pictures of tagged swallows 2–3 weeks after geocator deployment, see Figs. S1 and S2.

We assigned males from one of the two colonies to the geocator group, while males from the other colony were assigned to the control group. This protocol was chosen to avoid interfering with ongoing research being carried out concurrently in the study area. Importantly, males from the two colonies did not differ in morphological or flight performance (pre-deployment) traits (see “Statistical analysis”, below), and we have no reason to suspect that the assignment of birds from different colonies to either experimental group produced any bias in the results. We also note that our experimental design allowed us to test for any geocator deployment effect on within-individual change in flight performance.

### Measurement of short-term flight performance

Male Barn Swallows were tested twice for flight performance. Geocator birds were initially tested within 1 week before the deployment of geolocators, while post-deployment trials were performed at least 2 weeks after geocator deployment. Control birds were similarly tested twice, and the two tests were conducted 4–6 weeks apart. The first set of flight trials was performed between 20 June and 10 July (3 trial days), and the second set of trials between 10 July and 5 August (2 trial days). Birds were captured at dawn between 0430 and 0530 hours, and flight tests were performed in the morning between 0700 and 1000 hours. We chose clear days with no wind or rain (temperatures of approximately 20–25 °C) for flight tests.

Manoeuvrability performance was tested by releasing birds through a flight maze measuring 18 m × 4 m × 1.6 m (length × width × height; Matyjasiak 2013). The maze consisted of a metal frame covered in a double layer of a fine-mesh garden sunshade netting (black, shade factor 35 %). Its long axis was oriented west–east. The west end of the maze was closed and contained the release box (where the bird was kept before release into the maze; see below), while the east end was open. The first 9-m section of the maze (on the release box side) was free of obstacles and acted as an acceleration zone. The remaining 9-m section towards the exit acted as a test zone. It contained 16 successive panels of weighted vertical cotton strings suspended from the roof of the maze. Both the distance between the strings within a panel and the distances between consecutive panels decreased towards the exit. The within-panel separation of the strings decreased from 70 cm at the beginning of the test zone (roughly twice the wingspan of a Barn Swallow) to 8 cm at the exit (roughly a quarter of the

wingspan of a Barn Swallow). The between-panel distance decreased from 70 to 40 cm. The strings were placed so that each panel was offset from both the neighbouring panels. The birds were released (after 2 min of acclimation) from the release box at the closed end and flew through the maze to escape from the open end. The front side of the box was opened remotely with a string. We measured the time taken for a bird to negotiate the test section and recorded the number of strings collided with en route, which were used as measures of the bird's ability to cope with the obstacle course. A faster flight time and/or fewer strings hit indicated greater manoeuvrability (Rowe et al. 2001; Bro-Jørgensen et al. 2007; Matyjasiak 2013). Time taken to negotiate the stringed maze section was measured based on video images (HDV camcorder SONY HDR-HC1; filming at 25 frames  $s^{-1}$ ) obtained with the use of angled mirrors positioned in line with the first and last panels of strings. A bird's image was reflected in the first mirror as it entered the test section, and the second image was reflected in the other mirror when it left the maze. The flight time was determined by counting the number of frames between the two images and converting the result into seconds (accuracy within 0.04 s). The number of strings hit was determined based on video recordings obtained from two camcorders (SONY DCR-HC96)—one positioned in front of the maze exit and the other was at the closed end of the maze. Videos were analysed by viewing them frame-by-frame in Edius Pro 3 (Canopus, Reading, UK).

Flight acceleration and velocity were measured by releasing the birds through a second flight tunnel measuring 10 m  $\times$  1.2 m  $\times$  1.2 m (length  $\times$  width  $\times$  height; Matyjasiak 2013), which consisted of a metal frame covered in a double layer of fine-mesh netting. Birds were released from a small release box that was centred at the tunnel's closed end. A Stalker Pro ATS Ka-band radar gun (Applied Concepts Inc., Plano, TX, USA) connected to a Samsung R522 portable computer was mounted on a tripod at the tunnel exit. The radar was run with a minimum speed of 0 and a maximum of 225 kph in high range, with the peak mode off and the auto clear set to 0 s. To minimize signal noise in the radar, the flight tunnel was positioned inside an unused building, with the open end at the exit doors. Radar data were analysed using Stalker Pro ATS 4.5 (2002; Applied Concepts Inc., Plano, TX, USA) in "acceleration run" mode. The program was configured to discard any data points that occurred before the bird had been released and after it had left the tunnel. To create velocity-versus-time and acceleration-versus-time graphs in "acceleration run" mode, we used the medium digital filter setting, as recommended by Stalker (Vanman and Shorten 1997). Maximum acceleration and maximum velocity were obtained from these graphs with the graph tracer.

First, birds were tested for manoeuvrability performance in the flight maze and recaptured in a mist-net positioned at the maze exit (the distance between the last panel of strings and the mist-net was ca. 50 cm). Immediately after the manoeuvrability test, birds were released through the second tunnel for acceleration and velocity performance testing, and then released immediately. These measurements of short-term flight performance are highly repeatable, and hence they are sufficiently precise to allow use in statistical analyses (Matyjasiak 2013; see also for further information on flight test methodology adopted in this study).

### Statistical analysis

The study involved 21 control males (14 second calendar-year and 7 older) and 17 geolocator males (5 second calendar-year and 12 older). Because the age composition of the geolocator and control groups differed somewhat, and because the two age groups may differ in flight performance traits, we considered the effect of age in the statistical analyses. Sample sizes for the analyses of specific flight performance traits varied slightly compared to the above values, as not all birds completed all tasks in both the pre- and post-deployment trials or because the radar recordings were unreliable (see Table 1 for details of sample sizes). Only birds completing both trials were included in the analyses. In total, two control and three geolocator birds failed to complete one or both flight maze trials—these birds hovered and/or circled within the test zone or perched on strings rather than flying through the obstacle course. In addition, we were unable to get maximum acceleration data for seven control birds and one geolocator bird, and maximum velocity data for one control bird. In the first instance, the birds during the initial (about 0.5 s) phase of flight were indistinguishable from background noise on radar. In the second case, the bird hovered and circled within the tunnel before it flew outside.

The two maze flight performance traits, i.e. flight time and number of strings hit, were only weakly correlated in both this ( $r = 0.16$ ,  $n = 66$  tests) and previous samples of flight trials (Matyjasiak et al. 2004, 2009). Similarly, maximum acceleration and maximum velocity were weakly correlated ( $r = 0.20$ ,  $n = 60$  tests). Because the correlations were small, all of these flight performance variables differed in their information content, and hence were all considered to be informative. Therefore, we performed separate statistical analyses for these variables. The mean values of the short-term flight performance traits in the pre-deployment trial did not differ significantly between geolocator and control birds (effect of treatment, all  $P$  values  $>0.10$ ; linear models with treatment and age as factors; see Table 1 for mean values). Similarly, the two

**Table 1** Flight performance traits (mean ± SD, sample size in parentheses) of male Barn Swallows belonging to the control and geolocator treatment groups before and after the deployment of geolocators

Flight performance variable	Control bird trials		Geolocator bird trials	
	Pre-deployment	Post-deployment	Pre-deployment	Post-deployment
Flight time through the maze (s)	2.02 ± 0.86 (19)	1.99 ± 0.74 (19)	1.98 ± 0.47 (14)	2.38 ± 1.40 (14)
Number of strings hit	2.4 ± 1.4 (19)	1.8 ± 1.2 (19)	3.0 ± 1.7 (14)	1.9 ± 1.7 (14)
Maximum acceleration (m/s <sup>2</sup> )	8.8 ± 2.5 (14)	8.5 ± 2.3 (14)	9.3 ± 2.2 (16)	8.7 ± 2.7 (16)
Maximum velocity (m/s)	7.2 ± 0.9 (20)	7.3 ± 0.8 (20)	7.7 ± 0.6 (17)	7.4 ± 0.7 (17)

treatment groups did not differ significantly in morphology (wing, tarsus, and keel length) or body mass before the flight trial (all *P* values >0.29; linear models with treatment and age as factors). Therefore, males in these groups had similar morphological and flight performance characteristics before the geolocator application.

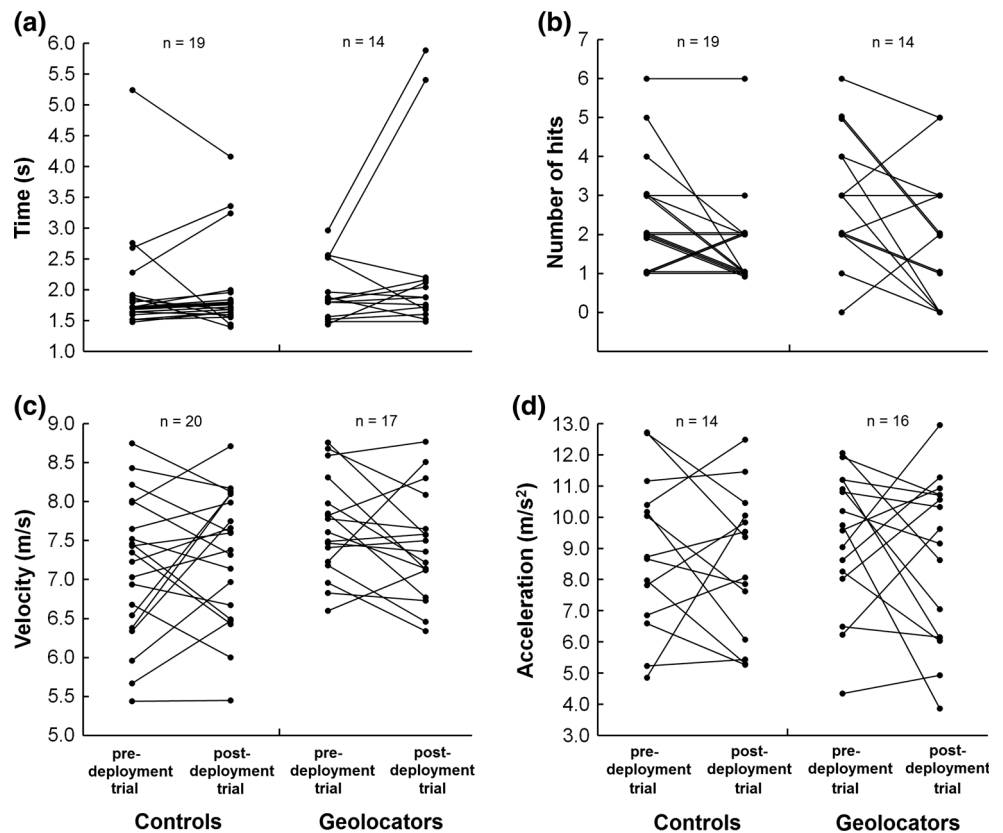
To investigate the effect of geolocator deployment on short-term flight performance, we relied on linear mixed models with bird identity as a random factor (to account for measuring the same individual twice). We ran models of each of the four flight performance traits (flight time through the maze, number of strings hit, and maximum acceleration and velocity) as a function of trial (pre-deployment vs. post-deployment), treatment (geolocator birds vs. controls) and age (second calendar-year vs. older; fixed

factors). All two-way interaction terms were included in the models. Mixed models were fitted using SAS 9.3 PROC MIXED (Littell et al. 2006). Degrees of freedom were estimated according to the Kenward-Roger method.

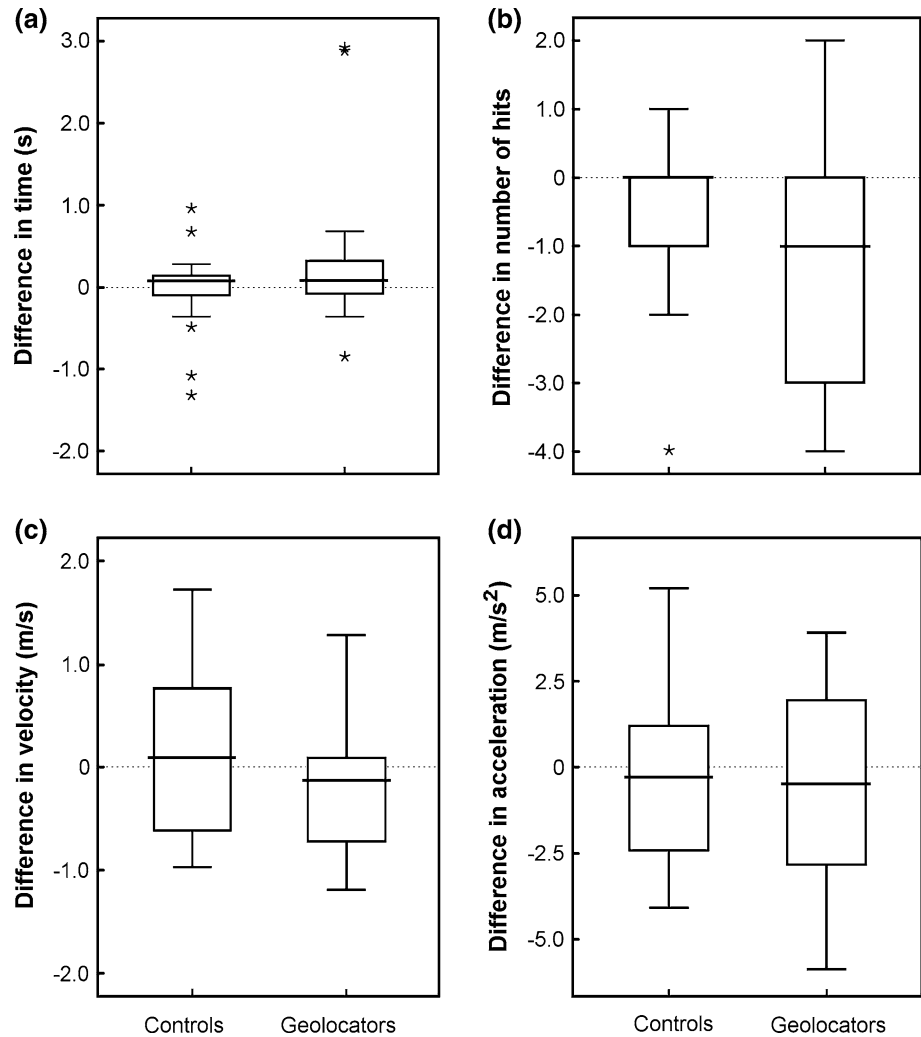
**Results**

Mean values of flight performance traits for control and geolocator individuals before and after deployment of geolocators are shown in Table 1. Within-individual changes in flight performance traits in relation to deployment of geolocators are shown in Fig. 1, and median differences in these traits are presented in Fig. 2. Deployment of geolocators did not significantly impair flight

**Fig. 1** Within-individual changes in flight performance traits of male Barn Swallows **a** flight time through the maze; **b** number of strings hit; **c** maximum velocity; and **d** maximum acceleration in relation to treatment (control birds vs. geolocator birds) and trial (pre-deployment vs. post-deployment). Raw data are shown. Data points from the same individual are connected. Sample sizes are given at the top of the panels



**Fig. 2** Within-individual differences in flight performance traits of male Barn Swallows **a** flight time through the maze; **b** number of strings hit; **c** maximum velocity; and **d** maximum acceleration in relation to treatment (control birds vs. geolocator birds). The horizontal midlines within the boxes represent the median value. Boxes depict the 25th to 75th percentile range of the data, and the whiskers extend 1.5 times beyond the interquartile range. Stars indicate outliers. The broken horizontal line represents the no-change reference value between the post- and pre-deployment trials



**Table 2** Linear mixed models of flight performance traits of male Barn Swallows (flight time through the maze, number of strings hit, and maximum acceleration and velocity) as a function of trial (pre-

deployment vs. post-deployment), treatment (geolocator birds vs. controls) and age (second calendar-year vs. older)

Effects	Time			Number of hits			Acceleration			Velocity		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
Trial	1.60	1.30	0.22	8.65	1.30	0.006	0.84	1.27	0.37	0.15	1.34	0.70
Treatment	0.51	1.29	0.58	0.95	1.29	0.34	0.09	1.26	0.76	1.05	1.33	0.31
Age	0.25	1.29	0.62	0.11	1.29	0.74	0.16	1.26	0.69	0.49	1.33	0.49
Trial × treatment	2.09	1.30	0.16	0.84	1.30	0.37	0.52	1.27	0.48	2.32	1.34	0.14
Trial × age	0.04	1.30	0.84	0.07	1.30	0.80	1.57	1.27	0.22	0.01	1.34	0.94
Treatment × age	0.04	1.29	0.84	1.44	1.29	0.24	3.68	1.27	0.07	0.16	1.33	0.69

Bird identity was included as random intercept effect (details not shown)

performance, as indicated by the non-significant effect of the interaction between trial and treatment (pre- vs. post-deployment of geolocators; Table 2). However, a non-significant trend towards worsening of flight velocity between the pre- and post-deployment trial was observed

within geolocator individuals but not within controls (Fig. 2c). In contrast, in the case of the number of strings hit, we observed a non-significant trend towards improvement in performance in geolocator birds (Fig. 2b). There were no statistically detectable differences in flight

performance traits between second calendar-year and older birds (non-significant age effect, Table 2). Overall, flight performance traits did not significantly vary between the pre- and post-deployment trials (Table 2; Fig. 2), with the single exception of the number of strings hit, which significantly decreased in the post-deployment trial compared to the pre-deployment trial (Table 2; Fig. 2b).

## Discussion

This study constitutes an empirical investigation of the effect of geolocator application on the flight behaviour of small (<20 g) birds. Our results indicate that deployment of miniaturized geolocators on male Barn Swallows did not have statistically detectable effects on their short-term flight performance during the breeding season. We also found no significant age-specific effects of geolocators on flight behaviour.

Short-term flight performance traits, especially manoeuvrability, are believed to be important for the foraging efficiency of aerial insectivores in particular (Waugh 1978) and for predator avoidance in birds in general (Metcalf and Ure 1995). Impairment of manoeuvrability from the effect of geolocators could be reflected in reduced aerial foraging efficiency, and hence reduced chick-feeding ability. Scandolaro et al. (2014) recently reported that applying geolocators (a model similar to the one we deployed in this study) to Barn Swallow parents showed no negative impacts on their subsequent reproductive performance, estimated as nestlings' body mass or fledging success. In a similar study, Gómez et al. (2014) showed that equipping Tree Swallows (*Tachycineta bicolor*) with geolocators while they were attending their broods had no significant negative impact on their nestling feeding rate, nestling's growth rate or fledging success. Our finding of no statistically significant negative impact of geolocators on the short-term flight performance of male Barn Swallows corroborates these findings. The geolocator model SOI-GDL2.11 does not seem to have a short-term negative impact (i.e. within a few weeks following the application) on Barn Swallow flight performance. Our findings also correspond well with the results of a recent study by Fairhurst et al. (2015), who measured levels of corticosterone in feathers grown after deployment of geolocators in Barn Swallows and Tree Swallows in order to evaluate energetic demands of geolocator application. They reported that geolocator-equipped birds that returned from annual migration did not appear to be handicapped due to instrumentation in terms of increased energetic costs and corticosterone levels during moult. However, the authors suggested that geolocators may have been handicapping to individuals that failed to arrive and presumably were of

lower quality in terms of the ability to manage the corticosterone physiology. A desirable step forward would be an investigation of corticosterone levels in blood plasma, for example, or in feathers regrown after experimental removal (Saino et al. 2014) in birds carrying geolocators during the breeding season compared with those without geolocators.

Bowlin et al. (2010) suggested that geolocators, and especially those with a light-stalk like the model we used here, might significantly increase drag during flight. This is believed to result in a reduced flight range and increased energetic costs of sustained flight, which could hamper fitness (Bowlin et al. 2010). Scandolaro et al. (2014) reported a significantly lower return rate of geolocator birds compared to controls after migration, an effect which was mostly evident among females. Moreover, geolocator birds showed delayed reproduction and smaller clutch sizes (Scandolaro et al. 2014). Significantly lower return rates of Tree Swallows equipped with geolocators compared to control birds were shown also by Gómez et al. (2014). The lack of statistically significant negative effects of geolocators on short-term flight performance and chick-rearing ability suggests that the negative fitness effects of geolocator deployment reported by Gómez et al. (2014) and Scandolaro et al. (2014) are related to processes acting largely outside the breeding season. These may be associated with increased drag during sustained flight (Bowlin et al. 2010) and/or impaired pre-migratory fattening from wearing a leg-loop harness. During migration, European Barn Swallows indeed cross large spans of inhospitable areas, including part of the Sahara Desert and the Mediterranean Sea, via sustained flight across such ecological barriers (Liechti et al. 2015). This could be a critical step where carrying a geolocator could make a difference in the flight energetic effort. Analysing the return rates of Barn Swallows equipped with geolocators, but following contrasting migration routes (e.g. those from Eastern Europe, which may be less susceptible to ecological barrier crossing, vs. those of Western Europe, or those from Northern Europe, which may be better suited to long-distance flight, vs. those from Southern Europe), may provide a clue to these effects. Such a study might also take into account the effect of variation in individual quality, for example, as gauged by the ability to manage physiological stress (see Fairhurst et al. 2015).

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PM. The experiments performed in this study comply with the ethical standards of Poland (Local Ethics Committee in Warsaw, statement no. 62/2013).

### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interests.

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