



No detectable effect of light-level geolocators on the behaviour and fitness of a long-distance migratory seabird

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Abstract

Light-level geolocators are increasingly popular devices for tracking migratory birds. However, to ensure that data on migratory behaviour represent natural behaviour that is not affected by potentially harmful effects of carrying such a device, their effects on behaviour and fitness should be assessed. A review of studies that tested for effects of tarsus-mounted light-level geolocators on seabirds showed that results are equivocal and often difficult to interpret due to the inclusion of only few traits and/or the lack of a proper experimental design. We therefore experimentally tested whether tarsus-mounted light-level geolocators affected a long-distance migratory seabird, the Common Tern *Sterna hirundo*. Using a well-matched treatment and control group, including both males and females, we tested whether light-level geolocators, deployed in the second half of incubation, affected the subsequent share of incubation, provisioning rate, reproductive performance, phenology or survival of tagged birds or their partners. In the year of deployment, we found no evidence for the behaviour of tagged birds or their partners to be affected by the geolocators. Moreover, we found no effect on their reproductive performance and departure date from the breeding colony. Finally, neither local survival to the next season, nor arrival date to the breeding colony in that season differed between tagged birds or their partners and control birds. These results suggest that a year of carrying a light-level geocator attached to the tarsus has negligible effects on Common Terns and that such a device can be used to study their migratory behaviour without causing problems or introducing bias.

Keywords Tracking device · Geolocation · GLS · Animal movement · Bird migration · Common Tern

Zusammenfassung

Keine nachweisbaren Effekte von Helldunkelgeolokatoren auf das Verhalten und die Fitness eines langstreckenziehenden Seevogels

Helldunkelgeolokatoren werden immer häufiger für das Aufzeichnen der Wanderwege von Zugvögeln eingesetzt. Um sicherzustellen, dass die Daten zur Wanderung ein natürliches Verhalten wiedergeben, sollten die potentiellen Effekte des Tragens eines Geolokators auf das Verhalten und die Fitness der Vögel vorab untersucht werden. Eine Begutachtung von wissenschaftlichen Studien, in denen die Effekte eines am Bein befestigten Helldunkelgeolokators auf verschiedene Seevögel untersucht wurden, zeigte, dass die Ergebnisse nicht eindeutig und oft schwierig zu interpretieren sind. Dies liegt vor allem

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daran, dass nur wenige Merkmale untersucht wurden und/oder kein geeignetes experimentelles Design vorlag. Deshalb untersuchten wir, ob ein am Bein befestigter Helldunkelgeolokator einen Effekt auf einen langstreckenziehenden Seevogel, die Flussseseschwalbe (*Sterna hirundo*), hat. Hierzu führten wir ein Experiment durch, in dem die Untersuchungs- und Kontrollgruppe ausgewogen waren und beide Geschlechter enthielten. Die aus der Untersuchungsgruppe ausgewählten Vögel wurden in der zweiten Hälfte der Inkubationszeit belogget. So testeten wir, ob Helldunkelgeolokatoren den anschließenden Anteil der Inkubation, die Versorgungsrate der Küken, die Reproduktionsleistung, die Phänologie oder das Überleben der beloggeten Vögel oder das ihrer nicht-beloggeten Partner beeinflussten. In dem Jahr der Beloggerung fanden wir keinen Hinweis darauf, dass das Verhalten der beloggeten Vögel oder das ihrer Partner durch die Geolokatoren beeinflusst wurde. Darüber hinaus fanden wir keinen Effekt auf die Reproduktionsleistung und den Abzugszeitpunkt von der Brutkolonie. In der darauffolgenden Saison unterschieden sich weder die lokale Überlebensrate noch der Ankunftszeitpunkt in der Brutkolonie zwischen den beloggeten Vögeln oder ihren Partnern und den Kontrollvögeln. Diese Ergebnisse legen nahe, dass die Beloggerung mit einem Helldunkelgeolokator für den Zeitraum von einem Jahr vernachlässigbare Effekte auf Flussseseschwalben hat. Daher gehen wir davon aus, dass ein solcher Logger für die Untersuchung des Wanderverhaltens verwendet werden kann, ohne die Vögel zu beeinträchtigen oder die Ergebnisse zu beeinflussen.

Introduction

Billions of animals of taxonomic groups as diverse as insects, fishes, reptiles, birds and mammals undertake structured annual movements, ranging from only a few to many thousands of kilometres (Dingle 1996; Newton 2008; Ueda and Tsukamoto 2013). Despite the enormous number of migratory animals, large gaps remain in our knowledge of the causes, mechanisms and consequences of migration, partly due to the difficulties associated with following individual animals across their annual cycle.

The development of tracking devices, such as global positioning systems (GPS) and archival light-level geolocators (hereafter referred to as ‘geolocators’), has, however, enabled the year-round tracking of, and thus the collection of migratory data for, many different animals, including migratory birds. Geolocators are small electronic devices that continually detect and record light-level data, which, upon extraction, can be used to estimate an animal’s position on the globe by using the internal clock to determine the timing of sunrise and sunset (Wilson et al. 1992). Since geolocators are steadily miniaturized and can be attached to rings, it has become possible to track a much broader range of bird species than with e.g. GPS devices, which, at ≥ 3.5 g (Lotek), are currently still too heavy for many bird species (e.g. Bridge et al. 2011). Geolocators have therefore become increasingly popular, especially in studies of small elusive bird species for which direct observation is difficult (for reviews see e.g. Bridge et al. 2013; McKinnon and Love 2018).

To ensure that data on natural migratory behaviour are collected, however, it is important to know whether geolocator deployment affects its carriers. Recent reviews and meta-analyses evaluating the effects of geolocators (e.g. Costantini and Møller 2013; Brlík et al. 2019) and other tracking devices (e.g. Barron et al. 2010; Vandenabeele

et al. 2011; Bodey et al. 2018; Geen et al. 2019) suggested various effects on different bird species. We reviewed the literature on seabirds and found 50 studies that statistically tested for effects of tarsus-mounted geolocators on at least one of three different fitness proxies: (1) return and/or survival rate, (2) body condition and (3) reproductive performance (Table S1). Of the 14 studies testing for potential effects on the return and/or survival rate of birds, 2 (i.e. 14%) found a negative effect of geolocator deployment, while 6 out of 36 (i.e. 17%) and 3 out of 23 (i.e. 13%) of the studies found a negative effect on body condition and reproductive performance, respectively (Fig. 1, Table S1). Such variable results may be due to methodological issues, such as (1) small sample sizes, (2) a focus on only one or a few traits, (3) observer bias (e.g. selection of high quality individuals for tracking device deployment or less effort in searching for control birds) or (4) differences in the study site of tagged and control birds. Moreover, they could be due to biological issues, such as different behaviour of the different study species and/or the size and weight of the tracking device relative to that of its carrier. Either way, the equivocal results show that results cannot easily be extrapolated and that more experimental studies assessing a multitude of traits in a way that excludes observer bias are needed.

Using a robust experimental design with a well-matched treatment and control group, including both males and females, we therefore evaluated potential effects of tarsus-mounted geolocators on several traits of a long-distance migratory seabird, the Common Tern *Sterna hirundo*. By comparing birds carrying a geolocator and control birds, all of known identity and life history, we tested whether the geolocator affected the share of incubation, provisioning rate, reproductive performance, phenology or survival to the next year. To take into account the fact that negative effects do not need to be limited to the geolocator-deployed bird itself, we also tested for potential compensation behaviour of partners, as well as effects on their phenology and survival.

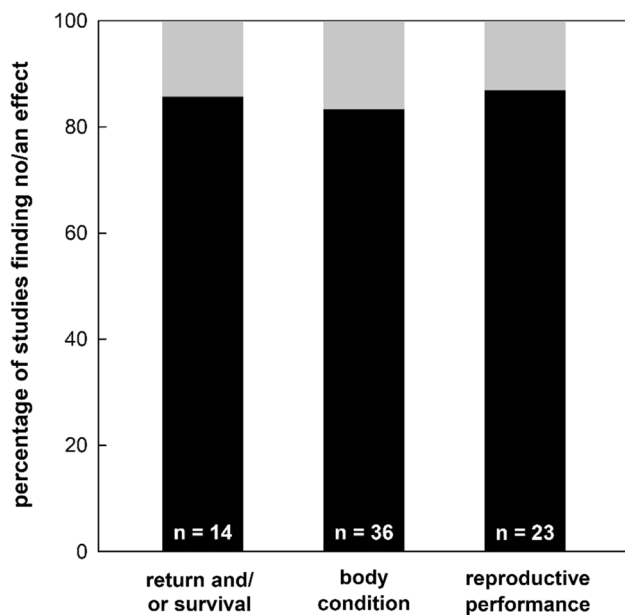


Fig. 1 Percentage of studies finding no (black) or a negative (grey) effect of seabirds carrying a leg-mounted light-level geolocator on return and/or survival rate ($n=14$), body condition ($n=36$) and reproductive performance ($n=23$)

Methods

Study species and site

The Common Tern is a Holarctic colonially breeding and long-distance migratory seabird (Becker and Ludwigs 2004). It has a clutch of two to three eggs per breeding attempt and incubation, which is shared between partners, takes c. 22 days (Becker and Ludwigs 2004). Chick mortality is high (Vedder et al. 2019) and on average only one chick fledges (Vedder and Bouwhuis 2018).

We study Common Terns from a long-term study population located at the ‘Banter See’ in Wilhelmshaven, at the German North Sea coast (53°360 N, 08°060 E). The number of breeding pairs at this colony has ranged between 90 and 740 since 1992. The colony site consists of six rectangular concrete islands, each measuring 10.7 × 4.6 m and surrounded by 60 cm high walls, which protect against flooding and prevent chicks from leaving the colony site prior to fledging. Since 1992, all locally hatched chicks are ringed within 2–3 days after hatching and subcutaneously marked with a transponder (TROVAN ID-100 BC, Trovan, Germany) just prior to fledging, which allows non-invasive life-long individual identification using an automatic antenna registration system. The antennae are located on 44 resting platforms mounted on the colony walls, as well as placed around each nest during incubation. They read transponder codes when birds are within a distance of ≤ 11 cm.

Data collection

Experimental setup

From the 1st of May 2016, we checked the colony site twice a day (mornings and afternoons) to detect 48 breeding pairs of which both pair members were ringed (i.e. of known identity and life history). These 48 pairs were alternately assigned to a geolocator or control group ($n=24$ vs. 24). Twice-a-day checks of the colony site continued to enable the collection of all eggs from these 48 pairs on the day of laying. Eggs were placed within digital incubators (Rcom max 50 and Rcom pro 20; Autoelex Co., Ltd., South Korea) with a temperature of 37.5 °C and a relative humidity of 50% (following Murk et al. 1994), and replaced with model eggs similar in size and colour, which were invariably accepted. Egg collection had two purposes: (1) to prevent potential damage to eggs after providing birds in the experimental group with a geolocator [as suggested by between-year comparisons of hatching success in Becker et al. (2016)], and (2) to monitor the development rate of embryos for another project (Vedder et al. 2017a).

Within each breeding pair, one bird was randomly assigned to be the focal bird (geolocator group: $n=13$ males and 11 females; control group: $n=10$ males and 14 females), the other one to be the partner. In the geolocator group, the 24 focal birds were identified by their transponder and caught on the nest using an electronically released drop trap during incubation (Fig. 2a), on average 14 days (± 0.8 SD) after the first egg was laid. They were weighed (average body mass: 129.7 g (± 8.2 SD) using a digital balance (± 1.0 g accuracy; MAULalpha, Jakob Maul GmbH, Germany) and tagged with a light-level geolocator (Intigeo-C65, Migrate Technology, UK; Fig. 2b). The geolocator was attached to the (previously unringed) leg of the bird using a 10 mm aluminium ring. The total mass of the ring and geolocator was 1.6 g, i.e. 1.2% (± 0.1 SD) of the body mass of the birds at tagging, and thus below the recommended threshold of 3% (Kenward 2001; Fig. 2c). Total handling time was 2–8 min and all birds resumed incubation after having been trapped (i.e. no clutch was abandoned). In 2017, we re-trapped 22 out of 23 geolocator birds that returned (one did not attempt reproduction in the colony) to remove the geolocator and extract the data.

Share of incubation and provisioning rate

The focal bird of each of the 48 pairs was spray-painted with picric acid for easy remote differentiation between pair members. Spray-painting was done by SB, who was not involved in any observations, such that observations of incubation and provisioning behaviour were blind with respect to the identity, age or sex of each pair member.



Fig. 2 Pictures of a Common Tern **a** being caught with an electronically released drop trap during incubation, **b** being tagged with a light-level geolocator, and **c** sitting on a resting platform (equipped with an antenna) after tagging. Photos by SB

Observations of incubation behaviour started 1–3 days after marking the focal birds, i.e. 7–15 days after clutch completion. Each nest was observed for 3 h at three consecutive days, i.e. 9 h in total. During observations, it was registered which bird (painted or unpainted) incubated the clutch for how many minutes. The share of incubation by each pair member was calculated by dividing its total incubation duration (in minutes) by 540 min (9×60 min).

New hatchlings were removed from the incubators twice a day (at 09:00 and 16:00), ringed and returned to their nest of origin. Model eggs were removed when chicks were returned, or 1–2 days after the last chick was returned if not all eggs from a clutch had hatched. Returned chicks were readily accepted by their parents and all clutches had at least one hatchling.

Observations of provisioning behaviour were distributed across 8 days after the first chick hatched, as tern chicks are semi-precocial and can walk too far from their nest to allow reliable observations after this period (Becker and Ludwigs 2004). Chicks were temporarily marked with a small coloured sticker on the head. Each nest was observed for five 2-h sessions, i.e. 10 h in total, except for one, in which all chicks died before the observations could be completed. For this nest only 2 h of provisioning observation were included in the analysis. During observations, it was registered which bird (painted, i.e. focal bird, or unpainted, i.e. partner) fed its chicks. The provisioning rate of each pair member was calculated as the number of prey items successfully delivered per hour.

Fledging success and fledging mass

Following the alternating assignment of geolocator and control nests, models (parameter estimate \pm SE) showed that there was no significant difference in laying date (0.17 ± 0.82 SE, $\chi^2_1 = 0.04$, $p = 0.840$), clutch size (0.02 ± 0.17 SE, $\chi^2_1 = 0.01$, $p = 0.933$) or number of hatchlings (-0.07 ± 0.18

SE, $\chi^2_1 = 0.13$, $p = 0.715$) between the geolocator and control group.

Each nest was visited three times a week to assess the chicks' body mass (with a digital balance of ± 1 g accuracy; MAULalpha, Jakob Maul GmbH, Germany) and status (alive or dead) until they had fledged. Missing chicks that were not yet at a stage ready to fledge were assumed dead. Fledging success of each nest was defined as the number of fledglings divided by the number of hatchlings. Quality of the fledglings was assessed as their fledging mass (see Bouwhuis et al. 2015; Bichet et al. 2019), which was defined as their last mass prior to fledging.

Departure and arrival date

The departure date from the colony was defined as the last registration of each breeder with the antenna system in 2016, while the first registration with the antenna system in 2017 was defined as its arrival date.

Survival

Our automatic antenna registration system allows us to estimate local return rates with no observation bias and very precisely (i.e. a detection probability of almost 100% for breeding birds; Szostek and Becker 2012). We therefore use these return rates as an index for local survival (also see Zhang et al. 2015a, b, c; Bouwhuis et al. 2015; Vedder and Bouwhuis 2018).

Statistical analyses

For geolocator vs. control birds, we tested for effects of carrying a geolocator on their (1) share (proportion) of incubation, (2) provisioning rate, (3) offspring fledging

success, (4) offspring fledging mass, (5) departure date after breeding and (6) arrival date in the following year. Because there may be sex differences in some of these traits, or the effect of carrying a geolocator may differ between the sexes, we additionally tested for effects of sex and the interaction between sex and experimental group.

Effects on provisioning rate, arrival date and departure date were analysed using general linear models with a normal error distribution. Because some pairs fledged multiple chicks, effects on fledging mass were analysed using a general linear mixed model, with nest identity as a random effect. Effects on share of incubation and fledging success were analysed using generalized linear models with a binomial error distribution and a logit link function; with denominators of 1 and the number of hatchlings, respectively. Because the presence of the interaction term did not allow testing for the overall effect of carrying a geolocator, we used a backwards elimination approach, removing the least significant terms, starting with the interaction term, until only significant ($p < 0.05$, two-tailed) terms remained. The statistics of non-significant terms are reported as when included in the final model. Models were run in MLwiN 2.22 (Rasbash et al. 2004). Significance was assessed using the Wald statistic, which approximates the χ^2 distribution. Averages are presented \pm standard error (SE).

To test for potential compensation behaviour of partners of birds carrying a geolocator in terms of share of incubation and provisioning rate, and possible negative effects on their departure and arrival dates, we repeated the same analyses for the partners of the focal birds.

Because survival to the next year was very high (see Results) we used Fisher's exact test to test for differences in survival between geolocator and control birds and between the geolocator partners and control partners, which better accommodates the low frequency of cases of mortality. These tests were performed in SPSS 25 (IBM Corp., Armonk, NY).

Results

On average, the 48 nests were incubated 537 ± 0.5 out of 540 min. The proportion of incubation did not differ between geolocator and control birds, nor between the partners of geolocator and control birds (Fig. 3a, Table 1). After hatching, provisioning rate averaged 0.72 ± 0.05 prey/h and also did not differ between geolocator and control birds, nor between their partners (Fig. 3b, Table 1). The provisioning rate of males was, however, roughly twice that of females (0.92 ± 0.08 vs. 0.52 ± 0.05 prey/h, respectively; Table 1).

The 48 pairs hatched on average 2.5 ± 0.1 and fledged on average 1.2 ± 0.1 chicks. Fledging success and fledging mass

did not differ between offspring of geolocator and control nests and averaged 0.51 ± 0.04 and 114.6 ± 1.1 g, respectively (Table 1).

Departure date after breeding in 2016 averaged 28 July (± 2.4 days), and did not differ between geolocator and control birds, or between their partners (Table 1). One focal bird of each group (geolocator vs. control) did not return to the colony in 2017, such that local survival did not differ ($p = 1.00$). Among partners, two birds did not return, both of which were partners of a geolocator bird. This difference, however, was not statistically significant ($p = 0.49$). Among the birds that returned, arrival date at the start of the 2017 breeding season averaged 18 April (± 0.8 days) and did not

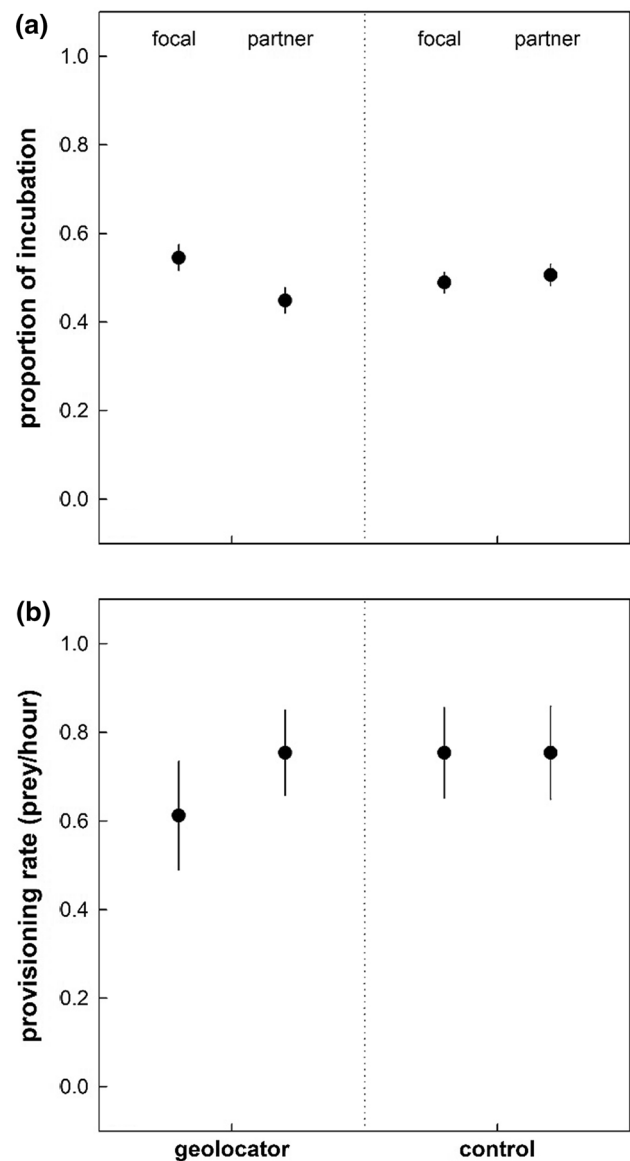


Fig. 3 Average (\pm SE) proportion of incubation (**a**) and provisioning rate (prey/h; **b**) of focal birds (geolocator vs. control) and their partners ($n = 24$ for each category)

Table 1 Summary of models testing for potential effects of carrying a geolocator (focal birds) and potential compensation in partners of geolocator birds (partners)

| | Focal birds | | | Partners | | |
|----------------------------|------------------|-----------------------|--------------|------------------|-----------------------|--------------|
| | Coefficient ± SE | χ^2_1 | <i>p</i> | Coefficient ± SE | χ^2_1 | <i>p</i> |
| Share of incubation | | (<i>n</i> = 24 + 24) | | | (<i>n</i> = 24 + 24) | |
| Geolocator | 0.22 ± 0.58 | 0.15 | 0.699 | − 0.23 ± 0.58 | 0.15 | 0.695 |
| Sex | 0.08 ± 0.58 | 0.02 | 0.890 | 0.08 ± 0.58 | 0.02 | 0.890 |
| Geolocator × sex | 0.63 ± 1.17 | 0.29 | 0.589 | 0.64 ± 1.17 | 0.29 | 0.588 |
| Provisioning rate | | (<i>n</i> = 24 + 24) | | | (<i>n</i> = 24 + 24) | |
| Geolocator | − 0.20 ± 0.14 | 1.86 | 0.172 | 0.05 ± 0.13 | 0.13 | 0.717 |
| Sex | − 0.42 ± 0.15 | 8.13 | 0.004 | − 0.37 ± 0.13 | 8.23 | 0.004 |
| Geolocator × sex | 0.37 ± 0.28 | 1.70 | 0.193 | 0.25 ± 0.26 | 0.95 | 0.329 |
| Fledging success | | (<i>n</i> = 24 + 24) | | | | |
| Geolocator | − 0.14 ± 0.367 | 0.15 | 0.696 | – | – | – |
| Sex | − 0.39 ± 0.369 | 1.09 | 0.296 | – | – | – |
| Geolocator × sex | − 0.62 ± 0.750 | 0.69 | 0.405 | – | – | – |
| Fledging mass | | (<i>n</i> = 26 + 30) | | | | |
| Geolocator | − 0.87 ± 2.17 | 0.16 | 0.687 | – | – | – |
| Sex | − 1.59 ± 2.20 | 0.52 | 0.472 | – | – | – |
| Geolocator × sex | − 2.61 ± 4.49 | 0.34 | 0.561 | – | – | – |
| Departure date | | (<i>n</i> = 22 + 19) | | | (<i>n</i> = 19 + 21) | |
| Geolocator | − 1.66 ± 7.38 | 0.05 | 0.823 | 7.53 ± 5.94 | 1.61 | 0.205 |
| Sex | 9.72 ± 7.22 | 1.81 | 0.178 | − 9.31 ± 5.88 | 2.51 | 0.113 |
| Geolocator × sex | 24.22 ± 14.04 | 2.98 | 0.084 | − 5.56 ± 11.56 | 0.23 | 0.631 |
| Arrival date | | (<i>n</i> = 22 + 18) | | | (<i>n</i> = 18 + 21) | |
| Geolocator | − 1.07 ± 2.35 | 0.22 | 0.641 | − 2.04 ± 2.23 | 0.84 | 0.360 |
| Sex | − 2.32 ± 2.32 | 1.00 | 0.317 | − 1.94 ± 2.23 | 0.75 | 0.386 |
| Geolocator × sex | − 4.41 ± 4.61 | 0.92 | 0.338 | 3.85 ± 4.46 | 0.75 | 0.388 |

Statistics of the non-significant single terms are presented as when tested separately in the final (empty) model, except for provisioning behaviour where sex was significant (as shown in bold) and included in the final model. Interactions were tested with the underlying single terms in the model. The reference category for 'sex' is male, that for 'geolocator' control. *n* number of geolocator and control individuals/nests for all traits, except for fledging mass, where it represents the number of chicks

differ between geolocator and control birds, or between their partners (Table 1).

Discussion

Light-level geolocators are increasingly popular devices for tracking migratory birds. However, to ensure that data on migratory behaviour represent natural behaviour that is not affected by potentially harmful effects of carrying such a geolocator, the effect of carrying these devices on behaviour and fitness should be assessed. Because experimental studies assessing a multitude of traits in a way that excludes observer bias are relatively rare, we used a robust experimental design to test whether leg-mounted geolocators affected the behaviour and/or fitness of Common Terns. Birds of the experimental group were caught during the second half of the incubation phase, equipped with a light-level geolocator and spray-painted with picric acid; focal birds of the control group were spray-painted only.

The subsequent share of incubation of focal birds, or that of their partners, was not affected by carrying a geolocator: eggs were incubated 99.4% of the time and pair members regularly interchanged, as is the norm in Common Terns (e.g. Wiggins and Morris 1987). Previous studies have shown that hatching success can be negatively affected when parents carry a geolocator, for example due to a reduced incubation effort of parents carrying a geolocator or by the geolocator damaging the eggs (Nisbet et al. 2011; Becker et al. 2016). In our case, we collected the eggs at the day of laying and artificially incubated them, which prevents us from drawing any conclusions on incubation intensity or damage to eggshells. Our artificial incubation, however, led to a hatching success (89%) higher than that of unmanipulated birds in our population (77%, *n* = 13,212 eggs; Vedder et al. 2017a) and we would recommend this procedure when deploying birds with a leg-mounted tracking device to a priori rule out damage to eggs (also see Becker et al. 2016).

Carrying a geolocator did not affect the provisioning rate of our focal birds and their partners and, as expected based on this result, there was no effect of geolocator deployment on the fledging success or fledging mass of hatchlings. These results regarding fledging success are in line with those of most other leg-mounted geolocator studies on seabirds (e.g. Guilford et al. 2012; Quillfeldt et al. 2012; Meier et al. 2017), but results on fledging mass are more equivocal. Similar to our study, studies on Gould's Petrels (*Pterodroma leucoptera*; Kim et al. 2014) and Short-tailed Shearwaters (*Ardenna tenuirostris*; Carey 2011) did not find a negative effect of geolocators on fledging mass, while a study on Crested Auklets (*Aethia cristatella*; Robinson and Jones 2014) found a negative effect and a study on Whiskered Auklets (*Aethia pygmaea*; Schacter and Jones 2017) found mass gain to be reduced in chicks reared by pairs in which one parent was carrying a geolocator. We would therefore recommend future studies to monitor not only fledging success, but also fledging mass, as it is known that, among seabirds, heavier fledglings have a higher probability of survival (e.g. Coulson and Porter 1985; Perrins et al. 1973; Bichet et al. 2019).

Neither phenology (departure date after deployment and arrival date to the colony in the following year) nor local survival of geolocator birds and their partners was negatively affected by the focal bird carrying a geolocator: couples left the colony mostly at the end of July and, among the high number of returned geolocator birds and their partners (96% and 92%, respectively), arrival in the following season mainly occurred mid-April. These survival rates are slightly above the overall average local survival (90%) reported for our colony (Ezard et al. 2006; Szostek and Becker 2012), and the absence of an effect is in line with many other leg-mounted geolocator studies on seabirds (e.g. Igual et al. 2005; Harris et al. 2010, 2013; Pollet et al. 2014; Ratcliffe et al. 2014; Carneiro et al. 2016). Studies testing for effects on phenology are much rarer. In fact, we are aware of only a single other study testing for effects on arrival date and this study, which was an earlier, non-experimental pilot study in our colony, also did not find a negative effect of carrying a geolocator (Becker et al. 2016). Although effects on migratory traits, such as the number or duration of stop-overs or the specific wintering area cannot be excluded (nor tested in studies on elusive species, such as most seabirds), the absence of effects on phenology as the most accessible proxy is promising.

While we used a robust experimental design and tested for effects on a multitude of traits, our study did not include physiological measures and comprised only a single year. A previous study on Common Murres (*Uria aalge*), however, showed that year-long deployment of geolocators led to increased corticosterone levels (Elliott et al. 2012). While these levels did not translate to reduced

survival to the next year in that study either, small costs of chronic stress could potentially accumulate and affect survival in the longer run (Elliott et al. 2012). Moreover, a study on Whiskered Auklets (*Aethia pygmaea*) found between-year variation in the effects of carrying a leg-mounted geolocator on the return rate and body condition of the birds (Schacter & Jones 2017). As such, effects of geolocators should ideally be tested in more than 1 year for the results to be generalizable across time and environmental conditions. In our case, the high survival rate (see above) and relatively high fledging success (51% of geolocator birds and their partners show that the year of deployment (2016) was a good year for the terns of our population (the overall average fledging success was 46%; Vedder et al. 2017b). Whether the results would be identical in a poor year is currently unknown. Unfortunately, we could not keep up detailed monitoring of the behaviour and performance of a well-matched control group across years, but continued monitoring of the performance of geolocator birds and the remainder of the study population will allow us to ensure that our conclusion of no disturbing effects of carrying a geolocator holds across years.

In summary, using a robust experimental design, we found no negative effects of a year of carrying of a tarsus-mounted geolocator on the share of incubation, provisioning rate, reproductive performance, phenology and survival of Common Terns. As such, we believe these devices can be used to study their migratory behaviour without introducing problems or bias.

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Compliance with ethical standards

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

Ethical approval The study was performed under licenses of the city of Wilhelmshaven and the Lower Saxony State Office for Consumer Protection and Food Safety, Germany.

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