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# Effects of harness-attached tracking devices on survival, migration, and reproduction in three species of migratory waterfowl

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## Abstract

**Background:** Tracking devices have enabled researchers to study unique aspects of behavior in birds. However, it has become clear that attaching these devices to birds often affects their survival and behavior. While most studies only focus on negative effects on return rates, tracking devices can also affect the behavior under study, and it is therefore important to measure potential negative effects of tracking device attachment on the full range of behavioral aspects of birds. At the same time, we should aim to improve our current attachment methods to reduce these effects.

**Results:** We used a modified harness to attach tracking devices to a total of 111 individuals of three goose species (Greater White-fronted Geese, Brent Geese, and Barnacle Geese) to study their migratory behavior. By creating control groups of birds marked with colored leg bands, geolocators, and/or neck collars, we were able to compare return rates, body condition, and migratory and reproductive behavior, thus allowing a much broader comparison than return rates alone. Birds with harness-attached tracking devices had lower return rates, which could partly be explained by increased rates of divorce, but is likely also the result of reduced survival induced by the harness and device. A comparison between Barnacle Geese equipped with harness-attached tracking devices and individuals fitted with geolocators attached to leg bands showed that birds equipped with tracking devices were only slightly delayed in timing of migration and reproduction and otherwise were not affected in reproductive output.

**Conclusions:** We argue that tracking devices can be used for studies on migration timing. Nevertheless, given the effect of tracking devices on survival and divorce rate, which may differ between sexes and species, we stress that researchers should carefully consider which birds to tag in order to reduce potential negative effects.

**Keywords:** GPS tracking, Tag effects, Geolocators, Barnacle Goose, Brent Goose, Greater White-fronted Goose

## Background

With the rise of advanced electronic tracking devices, such as satellite transmitters and GPS-loggers, scientists can now gather detailed data on movement of birds, allowing unique insights into their ecology and behavior [23, 36]. However, attaching tracking devices potentially harms the survival of birds or affects their behavior [2], and the recorded data of tracking devices may thus be influenced by the tracking device itself. It is challenging

to test for these potential negative effects. While negative effects of tracking devices remain ubiquitous in tracking studies, reporting rates of these effects have gone down over the past decades [26]. To ensure that tracking data reflects the natural behavior of birds, it is critical to apply rigorous tests for potential effects of tracking devices and to develop attachment methods that reduce the negative effects.

Modern solar-powered tracking devices collect data for multiple years, which requires an external and long-lasting attachment of the device to the bird. In such cases, harness attachment has been the method of choice for larger birds, including raptors [24, 38] and waterfowl [17,

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26]. Unfortunately, harnesses often have negative effects on birds, including reduced survival rates and reproductive success [16, 39], reduced migratory flight speed [20], and changes in behavior [17]. Although many studies report on negative effects of harness attachment on a single behavioral aspect, few studies have addressed multiple potential negative effects simultaneously (but see [19]), such that the full range of potential negative effects can be explored. Most notably, negative effects on migration are difficult to study, as tracking devices often are the main approach for measuring individual behavior during migration in the first place, and hence device effects on this behavior have hardly been studied [2]. However, it is important to study effects on multiple behavioral aspects, as negative effects can also carry over across parts of the annual cycle. For example, timing of migration can be strongly linked to timing of reproduction, and relatively small effects early in the season can thus ultimately affect the fitness of a bird.

Some of the negative effects of harness-attached tracking devices seem related to the harness attachment itself. Because migratory birds vary in body mass during the year [1], harnesses may become too tight or too loose, which can cause irritation to the bird [7] and abrasion of the skin [5]. The type of harness and its fitting to the individual bird can be pivotal in reducing the influence on the bird [7] and thus how representative the tracking data are for normal behavior [41].

We aimed to design a harness that can be easily tailored to individual birds, improving on an existing design. We examined the potential negative effects of this harness attachment for a set of behavioral aspects, including survival, migration, and reproduction, in order to gain a complete overview of the potential negative effects of this harness attachment. We used the harness to attach tracking devices to three Arctic-nesting migratory species of geese: greater white-fronted geese, *Anser albifrons*; Dark-bellied brent geese, *Branta bernicla bernicla*; and barnacle geese, *Branta leucopsis*. We additionally created control groups of birds equipped with color bands and neck collars, including color bands with attached geolocators to record migration timing. Effect sizes between tagged birds and their control groups were compared for survival, for timing of migration and reproduction, and for reproductive output.

## Methods

We modified an existing full-body harness design (e.g., [24]) with a neck and body loop (Fig. 1). Straps consisted of three materials (Teflon, Tygon, and nylon) to create a sturdy, but smooth, harness that was tubular in shape. We included sliding cramping rings, so we could quickly adjust the size of the neck and body loops when fitting

the harness on different-sized birds and could easily fixate the loops by squeezing the rings with a pair of pliers. Stainless steel rings were used to connect the harness to the tracking device. Harnesses can be tailored to different-sized species or individuals by adjusting the length of the straps. Full methods and instructions on how to construct and deploy the harness can be found in Lameris et al. [27].

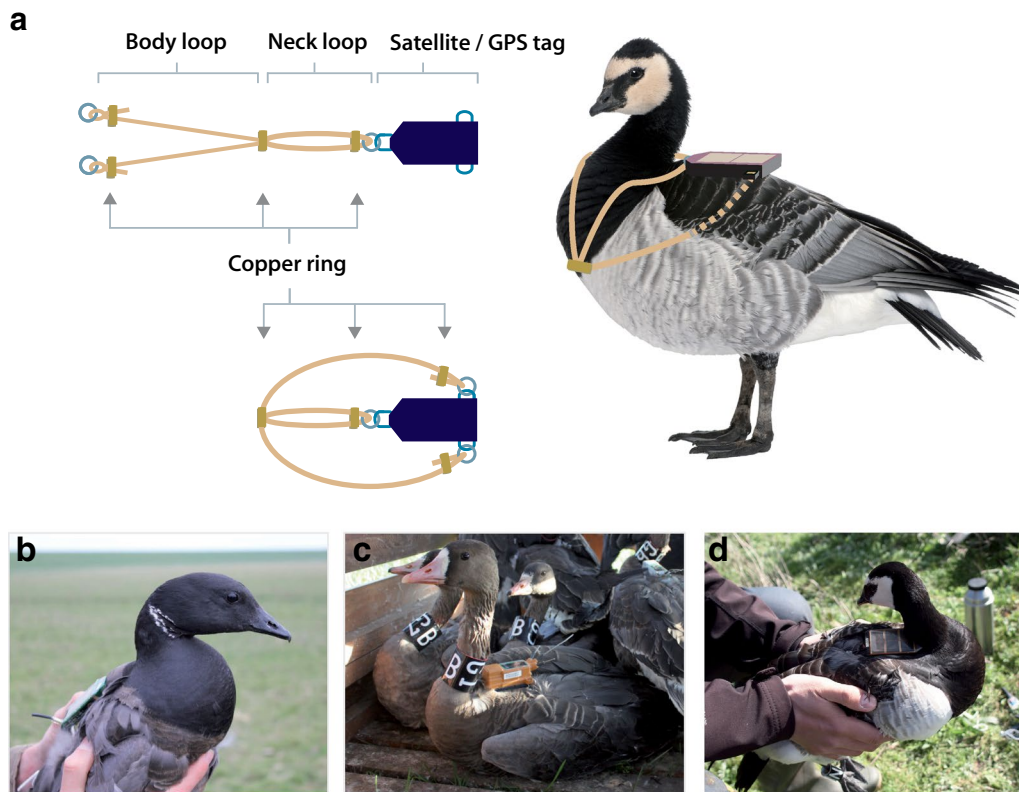
## Study species and capture methods

From 2012 to 2014, we equipped in total 111 geese with tracking devices using this harness. Apart from a tracking device, all birds received metal and color bands for identification in the field. A larger sample of birds was equipped with only colored legbands or neck collars as control group.

During the winters of 2013/2014 and 2014/2015 in Noord Brabant, The Netherlands, 35 greater white-fronted geese (7 males, 7 females, 21 juveniles) were caught in family groups using a remote-controlled clap net (see [25]). Each bird was equipped with a plastic, numbered neck collar and a 45-g e-obs GPS-GSM transmitter with the described harness. Another 92 birds were captured and equipped only with neck collars.

On the islands Terschelling and Schiermonnikoog, The Netherlands in April and May 2012, brent geese were caught using canon nets. From these catches, 30 male geese (21 on Terschelling, 9 on Schiermonnikoog) were equipped with plastic, numbered colored legbands and 16-g UvA-BiTS GPS-loggers [3] attached with a prototype of the harness, while a control group was equipped with colored legbands only. The prototype differed from the latter type by lacking the outer layer of Teflon and having attachment rings made of carbon steel instead of stainless steel. In 2014, brent geese were caught using canon nets on Terschelling, and 6 female brent geese were equipped with 19-g UvA-BiTS GPS-loggers and the standard version of the harness (as described above: including an outer layer of Teflon and with attachment rings made of stainless steel). For our analysis on return rates, only geese caught on Terschelling were used as observation effort on Schiermonnikoog was too low.

At the Kolokolkova Bay, Russia, in June and July 2014, 40 adult female barnacle geese were caught on the nest during incubation using a remote-controlled clap net and equipped with plastic color legband and 19-g GPS-loggers (UvA-BiTS, [3]) with the described harness. A control group of 40 adult female geese was either similarly caught on the nest (22 birds) or caught by rounding up flightless geese during molt (18 birds). The birds in the control group were equipped with two plastic color bands (6.6 g total) and an Intigeo C-65 Migrate Tech geolocator (1 g) attached to the left colored legband.



**Fig. 1** Schematic design of the harness attachment design and study species. **a** A schematic design of the harness attachment design with locations indicated where cramping rings are placed. Before deployment, the harness is attached to the front end of the tracking device (upper picture). During deployment, the harness is fastened on the goose by placing the neck loop over the head and attaching the ends of the body loop to the sides of the tracking device (under the wing of the bird). The cramping rings are used to adjust the size of the harness to fit the individual bird. **b–d** The study species equipped with tracking devices and the harness: **b** a male Brent Goose; **c** a family of greater white-fronted geese, and **d** a female Barnacle Goose

Because the geolocator weighed only a small fraction of the total weight of the two colored legbands, we assume that geese equipped with colored legbands and a geolocator would not differ in any behavior from geese with only colored legbands. As some of the geese in the control group were caught during catches during the molt period rather than on the nest, we ran analyses separate for the complete control group (40 geese) and the subset of geese caught on the nest (22 geese, in similar state as the geese with GPS-loggers).

#### Comparison of parameters

To calculate one-year return rates, we collected all resighting data from the focal birds from [www.geese.org](http://www.geese.org), an online platform where observers can submit sightings of individually marked geese and swans. Observations made by many volunteer band readers as well as those made by the researchers themselves were included. For barnacle geese, we calculated return rates based on birds caught during the molting period one year after

equipping the birds with transmitters, as resightings of birds with GPS-loggers were biased, since we used GPS tracking data to find birds in the field.

We compared the timing of departure and migration speed of barnacle geese with harness attachments and those with geolocators as a control group. Data were retrieved at our study site in the Kolokolkova Bay, Russia, in the summer of 2015. Data from UvA-BiTS GPS-loggers were downloaded remotely using a Zigbee two-way receiver unit in the tracker connecting to a base station and six relays [3], after which these data were stored at the UvA-BiTS database. From this database, we downloaded the data as text files with latitude and longitude positions. The GPS-loggers had stored 48 to 288 accurate GPS locations (mean stationary error = 3.23 m, [3]) per day. The Intigeo C-65 geolocators were retrieved from shot birds or by rounding up flightless birds during the molting period. After retrieving geolocators, data were downloaded and processed using the program Intipro (Migrate technology 2014). Further analysis was

carried out using the package ‘GeoLight’ [30] in R 3.0.2 [34]. The geolocators had recorded light intensity every 5 min. Twilight events were identified using the ‘threshold method’ [11] at a light intensity value of 2 [31] and used to calculate two longitude positions per day (error of 140–400 km, [31]). For both spring migration tracks acquired using GPS-loggers and geolocators, we determined the moment of departure from wintering site in the Wadden Sea area (first position with longitude > 9°) and the moment of departure from the Baltic Sea region (first position with longitude > 30°). For those geese that did not stop in the Baltic Sea region but migrated straight to the Arctic, the latter position was absent from geolocator data. For these geese, we took the day after the last day at which we could obtain a longitude position as the day of leaving the Baltic region. We calculated the speed of migration as the number of days between departure from the wintering grounds and departure from the Baltic region.

We measured reproductive performance of barnacle geese with harness attachments and those with geolocators at our study site at Kolokolkova Bay, Russia [37]. We searched for new nests and checked known nests every 2 to 3 days between 31 May and 25 June 2015. Eggs were marked, and the number of eggs was recorded at every visit. Nest initiation dates were determined as the day at which the first egg was laid. For incomplete clutches found during egg laying, initiation date was estimated as follows: 1 egg, day of discovery; 2 eggs, day of discovery minus 1; 3 eggs, day of discovery minus 3; 4 eggs, day of discovery minus 4 [21]. Clutch size was only determined for nests with a stable number of eggs from the third visit onwards. We measured reproductive performance of brent geese with harness attachments by observing them on their wintering grounds in the Wadden Sea, the Netherlands, and by noting whether they were accompanied by juveniles.

In July and August 2015, we captured flightless barnacle geese using herders and boats. We visually assessed condition and damage on geese carrying harness attachments. We weighed geese using a spring scale ( $\pm 10$  g).

### Statistical analyses

All analyses were conducted using R 3.0.2 [34]. We compared one-year return rates of birds with the harness attachment and the control groups. We tested for significant differences between return rates using binomial logistic regression models that included species, sex, experimental group (harness or control), and the interaction effect of experimental group and species/sex. We used one-tailed Mann–Whitney U tests (as we expected only negative effects for birds with harness attachments) to compare differences in migratory behavior (departure

date from the wintering grounds, departure date from the Baltic Sea region, migration speed) between birds with harness attachments and their control group. We used one-tailed Mann–Whitney U tests to compare the difference in reproductive parameters (nest initiation dates and clutch size) of barnacle geese equipped with harness attachments and their control group, where the control group consisted either of geese with geolocators or of birds without attached devices (i.e., only colored legbands). For some comparisons, sample sizes were low, and minor effects of harness attachments were probably not detectable. We provided 95% confidence intervals of effect sizes (Cohen’s D) for all tests, rather than conducting a post hoc power analysis [11]. Also, we refrained from statistical tests on a number of parameters where detection probability was too low (including nesting propensity and divorce rate).

## Results

### Return rates

Geese with GPS-loggers or GPS-GSM transmitters experienced reduced one-year return rates compared to their control group (effect of harness attachment:  $\beta = -1.14 \pm 0.28$  (SD);  $z = -4.0$ ;  $p < 0.001$ ; odds ratio, 0.32; Table 1). This did not differ between species and sex/age groups, as the interaction effect between attachment and species or sex/age group was not present in the highest ranking models (Table 2).

### Migratory behavior

We found no significant differences in the migratory behavior of barnacle geese with harness-attached GPS-loggers and those with geolocators. However, the effect size suggests that birds with GPS-loggers were potentially slightly delayed ( $\sim 1$  day) in moment of departure, including the moment of departure from the Wadden Sea region (GPS-logger,  $N = 18$ :  $45 \pm 6$ ; geolocator,  $N = 18$ :  $43 \pm 10$  days since 1 April;  $W = 136$ ,  $d = 0.43$ , 95% CI  $[-0.26, 1.11]$ ,  $p = 0.21$ ) and the moment of departure from the Baltic Sea region (GPS-logger,  $N = 18$ :  $50 \pm 3$ ; geolocator,  $N = 19$ :  $48 \pm 3$  days since 1 April;  $W = 138.5$ ,  $d = 0.47$ , 95% CI  $[-0.21, 1.15]$ ,  $p = 0.16$ ). There was no difference in migration speed (GPS-logger,  $N = 18$ :  $4.55 \pm 4.60$ ; geolocator,  $N = 18$ :  $5.33 \pm 7.84$  days;  $W = 162$ ,  $d = 0.22$ , 95% CI  $[-0.46, 0.90]$ ,  $p = 0.51$ ).

### Reproduction

We found that 27 of 40 barnacle geese with harness-attached GPS-loggers returned to breed in 2015 and 20 initiated nests (17 nested successfully). Barnacle geese with geolocators also bred successfully, based on 12 found nests out of 40 tagged birds. Clutch sizes of geese with GPS-loggers did not differ between geese with

**Table 1 Return rates of birds equipped with harness-attached tracking devices (tagged birds) compared to their control groups, equipped with colored legbands or neck collars**

Species	Time frame of measurement	Sample size tagged birds	Return rate	Sample size control group	Return rate	Coefficient	Odds ratio
Greater White-fronted Goose (males)	Winter 2013/2014–winter 2014/2015 and winter 2014/2015–winter 2015/2016	7	0.43	13	0.62	−0.37	0.69
Greater White-fronted Goose (females)	Winter 2013/2014–winter 2014/2015 and winter 2014/2015–winter 2015/2016	7	0.29	13	0.69	−1.34	0.26
Greater White-fronted Goose (juveniles)	Winter 2013/2014–winter 2014/2015 and winter 2014/2015–winter 2015/2016	21	0.29	66	0.70	−1.37	0.25
Brent goose (males)	May 2012–May 2013	21	0.52	37	0.78	−0.81	0.44
Brent goose (females)	May 2014–May 2015	6	0.83	15	0.93	−0.65	0.52
Barnacle goose (females)	June 2014–August 2015	40	0.45	40	0.55	−0.40	0.67
				22 <sup>a</sup>	0.55	−0.38	0.68

For each return rate, we give the time frame of the measurement over which the return rate has been measured, the coefficient value taken from logistic regression models (representing the change in log odds) and the odds ratio

<sup>a</sup> For this comparison, only the subset of control birds caught on the nest is used as a control group

**Table 2 Final binomial logistic regression models for return rates over species (S), sex/age groups (A), attachment treatment (T), the interaction between treatment and species (T × S), and the interaction between treatment and sex/age groups (T × A)**

Return rate	Intercept	Species (S)	Sex/age (A)	Treatment (T)	Treatment × Species (T × S)	Treatment × Sex/Age (T × A)	Degrees of freedom	Δ AICc
~ S+T	0.673	0.88*		−1.14***			4	0.00
~ T	0.900			−1.14***			2	0.28
~ S+T+T*S	0.182	1.38*		−0.38	−1.17		6	12.13
~ S	−0.065	1.15**					3	12.15
~ S+A+T	0.669	1.36*	−0.64	−1.13***			6	13.12
~ S+T+S*A	0.395	1.47**		−0.71		−1.04	8	46.11

Coefficient values are given, with asterisks denoting significant effects (\* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ )

geolocators and other birds in the colony (GPS-logger:  $4.3 \pm 1.0$  eggs,  $N = 18$ ; geolocator:  $4.5 \pm 0.93$  eggs,  $N = 11$ ; colony:  $4.4 \pm 1.2$  eggs;  $N = 351$ ; GPS-logger vs geolocator:  $W = 80$ ,  $d = 0.51$ , 95% CI [−0.28, 1.31],  $p = 0.19$ ; GPS-logger vs colony:  $W = 3307$ ,  $d = 0.51$ , 95% CI [−0.36, 0.59],  $p = 0.64$ ). However, geese with GPS-loggers initiated egg laying on average 2–3 days later than geese with geolocators and other geese in the colony (GPS-loggers:  $37.1 \pm 1.9$  days since 1 May,  $N = 18$ ; geolocator:  $34.1 \pm 2.0$  days since 1 May,  $N = 8$ ; colony:  $34.7 \pm 2.4$  days since May 1st,  $N = 216$ ; GPS-logger vs geolocator:  $W = 106.5$ ,  $d = 1.35$ , 95% CI [0.39, 2.31],  $p = 0.004$ ; GPS-logger vs colony:  $W = 917.5$ ,  $d = 0.67$ , 95% CI [0.18, 1.16],  $p < 0.001$ ).

Of the female brent geese equipped with harness-attached GPS-loggers, three of five females that returned to the wintering grounds in 2014 nested successfully, as they were accompanied by juveniles. Tagged males did not nest successfully in 2013, but it must be noted that nesting success was generally very low this year, also for untagged geese.

#### Other effects

Twelve out of the 18 barnacle geese with harness-attached GPS-loggers which we recaptured during molt were either not damaged, or only missing some down feathers in the axillar region or had some broken back feathers below the logger. Four geese were missing

feathers in the axillar region and had broken back feathers, and two birds had suffered from more severe damage, showing old wounds in the axillar region. Body mass during molt did not differ between birds with GPS-loggers, geolocators, or only colored legbands (GPS-logger:  $1621 \pm 120$  g,  $N=18$ ; geolocator:  $1645 \pm 103$  g,  $N=22$ ; colored legbands:  $1620 \pm 137$  g;  $N=3186$ ; GPS-logger vs geolocator:  $W=237$ ,  $d=0.34$ , 95% CI  $[-0.31, 0.99]$ ,  $p=0.29$ ; GPS-logger vs colony:  $W=1720$ ,  $d=0.05$ , 95% CI  $[-0.44, 0.53]$ ,  $p=0.85$ ). The harnesses themselves were only slightly damaged and showed some wear of Teflon at the outer loops.

Although all 14 observed male brent geese with harness-attached tracking devices had a mate after the initial catch in 2012, only 36% of those males returned with their original partner in 2013 (but at least two males were able to find a new partner during that spring period). Of the six females with harness-attached tracking devices in 2014, all returned with their original partner.

Of seven families of White-fronted Geese equipped with harness-attached tracking devices, the parents of two families separated within a week after tag attachment. Only one of the six tagged juveniles in those two families was not shot or predated during spring migration. Even if juvenile survival was higher for the five other families, none of the parents of those families returned to the wintering grounds together in the following year.

## Discussion

We show that harness-attached tracking devices can have negative effects on return rates and can affect behavior, but effects can differ considerably between species and sexes. Reduced return rates of geese with harness attachment compared to a control group can be partly explained by birds not returning to their original wintering or breeding grounds, but we argue that this is largely the result of a reduced survival. More specifically, we show that tracking devices can affect multiple aspects of behavior, including a potential increase in divorce probability, but only slightly affect timing of migration and reproduction.

Return rates can be used as an index for survival, if individuals have high site fidelity and a high probability of being observed if alive. Individual brent geese return to the island of Terschelling every spring, and due to the open landscape and high observation effort, individuals have close to a 100% chance of being observed when alive. The same holds for greater white-fronted geese, due to the good visibility of the neck collars combined with a large network of voluntary ring-readers in the Netherlands. We observed female barnacle geese at their breeding colony, to which female geese are known to return every year [22], and we maximized our observation and

recapture effort in an attempt to detect all individuals present. Non-observed individuals were never detected in subsequent years, supporting the conclusion that detection rate was high and non-observed individuals were likely to be dead. Lower return rates should thus indeed represent lower survival rates.

However, male geese tend to follow the female year-round and can thus change wintering area when divorcing from their original partner. Divorce rates are extremely low for geese (average of 3% per year for several species of geese) because they benefit from long-lasting partnerships [12]. Our results suggest that divorce rates for male brent geese and greater white-fronted geese with harness-attached tracking devices were relatively high, and increased divorce rates have also been reported for female brent geese with transmitters [39] or neck collars [29]. The attachment of a tracking device might affect the quality of the bird as a partner, as found for brent geese [8, 18], and this may drive divorces between birds. Divorces may subsequently decrease reproductive output and survival [28]. The decreased return rates of male brent geese could also be affected by individuals switching to different wintering sites, as divorced birds would follow their new partners to other wintering sites. Negative effects related to divorces are therefore likely to be sex-specific, as we find high divorce rates for male brent geese but not for female Brent or barnacle geese. These effects of tracking device attachment could potentially be avoided when tagging females rather than males, and the choice of which birds are being tagged can thus importantly influence the success of a tracking study. In addition, the low return rates of male brent geese might be explained by the use of a prototype of the harness, with carbon steel rings potentially more prone to breaking after prolonged exposure to marine (salt) environments, causing (partial) harness detachment. The harnesses used later in this study were made stronger by using stainless steel rings and an outer layer of Teflon.

Besides potential shifts in wintering grounds for divorced male geese, decreased return rates of individuals equipped with harness-attached tracking devices likely indicate a lower survival of these birds. Some studies have found that harnesses negatively affect return rates and survival in geese [10, 16, 39], but other studies did not find such negative effects [14, 15]. These latter studies measured return rates over a shorter time span. Attachment of tracking devices may increase the susceptibility of birds to being predated or shot, as shown by causes of death from tagged greater white-fronted geese in this study, of which out of 35 birds, 14 had been retrieved as shot, and 7 as predated by large birds of prey or fox during the spring migration following tag deployment. This may be caused by a change in behavior (e.g., increased

time spent preening, [13]) or reduced flight maneuverability by the cross-sectional profile of the backpack tag causing additional drag [4], and perhaps not so much hunters targeting for marked geese [6]. Although our study found negative effects on return rates, our survival rates of tagged individuals were definitively higher than in some other studies [39],

Harness attachments may have negative effects on survival, but are also likely to have non-lethal effects on migratory birds [26]. By using a control group from which we have individual data on migration timing gained from geolocators, we can show convincingly that harness attachments cause only a slight delay in timing of migration departure for barnacle geese. This effect was not significant, and there exists a high degree of variation between individuals. Also, the migration speed of these birds was not affected. For comparison, an earlier study in northern pintails *Anas acuta* found that birds with harness-attached tracking devices arrived 19 days later on the breeding grounds in comparison with the population mean [20]. This is ascribed to a higher cost of migration, which is also suggested by models from Pennycuik et al. [32]. Also, we found a 2–3-day delay in laying date for barnacle geese with harness attachments, which is minor in comparison with earlier studies on mallards *Anas platyrhynchos* with harness attachments, which were delayed between 8 and 14 days [33, 35]. We did not find effects on clutch size or on nest success, while these aspects of reproduction are susceptible to negative effects of harnesses attachment [16, 33, 35]. Although we were not able to measure differences in body stores of birds on arrival, any potential differences had disappeared after the nesting period, because we did not find a difference in body mass of female barnacle geese with harness attachment and females in control groups.

Our results are concurrent with recent reviews on the negative effects of tracking devices on birds [2, 26, 40]. We show that harness-attached transmitters can negatively affect survival but also pair-bonding, and thus the potential of birds to initiate breeding. These negative effects can have important consequences for behavior measured by tracking devices. While we find a delay in timing of reproduction and possibly timing of migration for birds with harness-attached transmitters, the delay is only minor, and other aspects of migration or reproduction are not affected. In contrast with earlier studies, which have shown strong negative effects on migration timing and reproduction for birds equipped with tracking devices [20, 33, 35], we find that tracking devices are reliable tools to study timing of migration and reproduction, and the modified harness which we have developed appears to be a reliable method to attach tracking devices on geese. Given our different results for different sexes,

we stress that researchers make a careful consideration which birds they equip with tracking devices.

#### Authors' contributions

TL, AK, AD, HvdJ, and BN conceptualized the study; TL, GM, AK, AD, and HvdJ collected the data; TL, AK, and AD analyzed the data; TL wrote the manuscript; and AK, AD, HvdJ, and BN revised the manuscript. All authors read and approved the final manuscript.

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#### Competing interests

The authors declare that they have no competing interests.

#### Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

#### Consent for publication

Not applicable.

#### Ethics approval and consent to participate

All field data were collected in compliance with national guidelines regarding animal welfare and were approved by the animal experimentation committee of the Royal Netherlands Academy of Arts and Sciences (DEC-KNAW), under protocols NIOO 12.04, NIOO 13.14, and NIOO 14.07.

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