

METHODOLOGY

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# Effects of capture and GPS-tagging in spring on migration timing and reproduction in Pink-footed geese *Anser brachyrhynchus*

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## Abstract

**Background** GPS-transmitters enable detailed study of animal behaviour but may impact the animals. Impacts vary from short-term stress and habituation to longer-term effects on e.g., migration and reproduction. To study impacts, ideally, true controls (i.e., uncaptured or untagged animals) are used, but unbiased assessments of their migration timing and breeding performance are challenging, especially in remote areas. Alternatively, quasi-controls can be used: individuals tagged longer ago, or the same tagged individuals but in later years. Quasi-controls reveal tagging effects that differ between the first and following years.

**Results** We captured Pink-footed geese (*Anser brachyrhynchus*) in spring and summer and deployed GPS-transmitter neckbands. In spring, geese were caught with cannon or clap nets on stopovers in Norway and Finland, 2 weeks before departure to breeding areas in Svalbard and Novaya Zemlya. In summer, geese were rounded up during wing moult in Svalbard. First, we compared geese tagged recently in spring with geese tagged in spring or summer 1–4 years prior. Newly tagged geese migrated significantly later, by 2 days, than previously tagged geese, both at departure from the spring stopover and arrival to the breeding grounds, while migration duration did not differ. Breeding propensity and laying date did not differ, but nesting success tended to be lowered, resulting in a significantly lower annual probability to produce hatchlings in recently tagged geese than in previously tagged geese. Second, within individuals tagged in spring, spring migration advanced in their next year, suggesting delay in their first spring. This was likely not an ageing effect, as geese tagged in summer showed no advancing spring migration timing over the years. Third, in Svalbard, observed brood sizes of geese tagged in summer and untagged geese did not differ 1 year after tagging.

**Conclusions** The capture and GPS-tagging of geese 2 weeks before spring departure delayed their spring migration and lowered their probability to produce hatchlings in that year. These effects lasted longer than previously reported week-long effects of GPS-tagging on time budgets in summer and of neck-banding on spring body condition. Additional study is needed to evaluate longer-term or permanent effects which remain undetected with quasi-controls.

**Keywords** Arrival, Breeding success, Departure, Device, Neckband, Nesting, Propensity, Stopover, Tracking, Transmitter

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## Background

The study of animal behaviour has benefited from modern biologging technologies, which enable us to collect detailed year-round data on the location and activity of animals [1]. However, with such data we can only make unbiased inferences about the study population if the devices do not impact the animals, or at least the parameters of interest. No impact is hardly ever the case and thus the use of transmitters should always be accompanied by an evaluation of the effect on the animals [2, 3].

The most immediate potential effects of capture and marking on animals are injury and stress during capture. After release, these effects can cause the animal to be less mobile, making it easy prey (e.g., [4, 5]). More generally, animals may behave abnormally for a short term post-catch, because they are not yet at ease with wearing the device. Specifically, they show antagonistic behaviour towards the tag and increase the proportion of time spent preening [6, 7]. The latter may be a redirected behaviour, where the general frustration is expressed in preening, as the bird is unable to remove the tag [8].

All these factors—*injury, stress, tag habituation*—contribute to a quick drop in body condition [9], which may be enhanced by the lost foraging time due to capture. Compensating for this body condition loss also takes time, which can be pressing during periods when animals are preparing for migration and breeding. This can translate into a later migration timing (e.g., [10]) and/or a lower reproduction (e.g., [11]). Effects on migration and reproduction could be long-lasting, if not permanent, because tagged individuals may have a lower foraging efficiency [12] and higher flight costs [13] and as a result also a lower nest attendance [14]. Finally, they can experience a higher divorce rate [15].

In case of GPS-tagged Pink-footed geese (*Anser brachy-rhynchus*), besides mapping migration and breeding distribution, we were interested in breeding success in relation to their timing. Hence, we focus on the effects of capture and GPS-tagging on the timing of migration and breeding variables such as breeding propensity and success.

To evaluate the effects of capture and tagging, one could use a control group of geese that are: (1) not captured nor tagged (e.g., [11]), (2) captured but instead of tagged, identifiable with only a small mark (e.g., [11, 45]) or geolocator (e.g., [16]), (3) a quasi-control group, namely captured and tagged but longer ago (e.g., [9] for normal neckbands). The third option can also refer to the same individual in subsequent years. The first option would be ideal but complicates the estimation of migration timing as geese cannot be followed individually. Alternatives to following individuals, such as counts on stopovers, are not straightforward since flock

composition is unknown (e.g., with respect to age) and numbers present are the combined result of arrival and departure (e.g., [10]). Estimating breeding success in unmarked geese is possible by surveying nests in the field but is impractical in remote areas. Breeding propensity is also challenging to estimate by field observations, also when geese are marked, because non-breeders may leave the study area. Thus, GPS-tracking may provide less-biased results of propensity than traditional field methods, provided that marked individuals are not impacted [17, 18]. Therefore, we mainly follow the third option here (for a comparison of migration timing, breeding propensity and success and laying date), but also the first option (for a comparison of brood size). With the third option, we compare between individuals, geese that were tagged recently with geese tagged longer ago (1–4 years prior). We also compare within individuals their first and subsequent years with the tag. Thus, we evaluate those effects of capture and marking that differ between the first months after capture and several years after capture.

## Methods

### Study area, capture and tagging of geese

We studied Pink-footed Geese of the Svalbard and Novaya Zemlya breeding populations. Svalbard geese traditionally winter in Belgium, the Netherlands and west and north Denmark, and migrate via Norway in spring. Recently, increasing numbers migrate via a new route via Sweden and Finland to Svalbard but also to newly colonised Novaya Zemlya [19]. Novaya Zemlya geese winter in the traditional areas mentioned above, but also in eastern Denmark and southern Sweden [19, 20].

Geese were caught and GPS-tagged (or ‘tagged’ in short) during two moult catches in Isfjorden, Svalbard in 2018 ( $n=33$  females, 2 males; Isdammen N 78° 12′, E 15° 48′ on 31 July, and Daudmannsøyra N 78° 13′, E 13° 04′ on 1 August), near Oulu, western Finland with a cannon net during three catches (28 April 2018, 27 April and 1 May 2019;  $n=16$  females, 5 males; Oulu N 64° 49′, E 25° 33′) and with two clap nets in Trøndelag, Norway during eight catches (24–29 April 2022;  $n=51$  females; Levanger N 63° 43′, E 11° 14′). Each capture took only a part of the flock present. We mainly tagged females since our main aim was to study breeding biology [20, 21] and in (Pink-footed) geese all incubation is done by females [22]. Other processed geese got normal plastic neckbands ( $n=8$  females, 38 males), except in Norway where untagged birds only got metal leg rings ( $n=11$  females, 75 males). In the weeks after capture, 71% of GPS-tagged birds turned out to be paired to neckbanded birds (13 out of 15 on Isdammen; 6 out of 19 in Finland) or to other GPS-tagged geese (2 out of 15 on Isdammen; 4 out of 19 in Finland). More details on catching procedures are

given in [7, 20]. Handling the geese took in total 1–3 h per catch. Geese were measured, weighed, marked, blood sampled (medial metatarsal vein) and sexed. In Finland and Svalbard, we also assessed behavioural traits [20], and in Svalbard and Norway we also took cloacal swaps. Sexing was validated molecularly [23], using blood and primer pair 2550F/2718R, the PCR-program of [24], running results on a 2% agarose gel.

Throughout the study, the used tags were solar-powered GPS-GSM transmitter neckbands (type OrniTrack-N38, Ornitela UAB, Lithuania), weighing 38 g with inner diameter 38 mm. These recorded a GPS-position along with GPS-speed and tri-axial accelerometer data (a burst of 2 s at 20 Hz) every 10–60 min, depending on battery charge. All GPS-tags were white with a black two-digit individual code, readable from a distance up to 900 m with a telescope under good conditions.

### Experimental and (quasi-)control groups

As our catches were spread out over 4 years, we could compare the performance of geese that had recently been GPS-tagged, and geese that were tagged 1–4 years prior. To evaluate the effect of recent tagging on migration timing and propensity, timing and success of breeding, we defined the experimental group (i.e., recently tagged) as the geese caught in Oulu in spring 2019 and in Trøndelag in spring 2022. The between-individual quasi-control group (i.e., geese tagged years prior) consisted of all previously tagged geese migrating via the same stopover in the same year as the recently tagged geese, i.e., via Oulu in spring 2019 and via Trøndelag in spring 2022 (see Additional file 1: Table S1 for sample sizes).

In addition, we compared the migration timing of geese in their first tagged spring versus following springs, to look at within-individual changes over the years after tagging (2018–2023). Here, we included all spring tracks of all geese, to see whether this longitudinal change differed between geese that were tagged in spring (Oulu 2018, 2019; Trøndelag 2022) and geese tagged in summer (Svalbard 2018; see Additional file 1: Table S2 for sample sizes).

We subset the data to only adult geese (at least 3rd calendar year at the time of comparison, excluding two 2nd calendar year males in Oulu, 2018), as younger geese do not breed yet [25] and all geese older than 2nd calendar year cannot be distinguished based on plumage during capture [26]. We did not subset our data to paired geese (as observed after capture), because losing a partner may be a consequence of capture and tagging, so should be included in the variation that is studied. In each year, we only included independent tracks by excluding tagged partners that migrated along (in two pairs from Oulu).

For brood size, we defined the experimental group as geese GPS-tagged at Isdammen in 2018, and the control group as untagged geese in the same area (see [Brood size](#) for details).

### Timing of migration

Departure was taken as the last moment when a goose was at the stopover, not flying (GPS-speed < 15 km/h, [27]). Stopovers were defined by a radius around a midpoint (100 km for Trøndelag, 50 km for Oulu). The midpoints were defined as the average GPS-coordinates of the tagged geese in the general area (i.e., not flying, GPS-speed < 15 km/h, Oulu: N 64.820, E 25.508; Trøndelag: N 63.928, E 11.437; [20]). The arrival in the breeding grounds was defined as the first moment when a goose reached the main breeding archipelagos, i.e., when latitude > 76.5640° (for Svalbard), or when longitude > 51.4432° (for Novaya Zemlya). We also calculated the duration between departure and arrival.

### Location, timing and success of nesting

Nesting attempts were identified following the method of [21], based on simultaneous GPS and accelerometer data.

The breeding propensity was defined as a binary variable, with nesting as “1” and no nesting as “0”. Nesting was defined as having at least 3 consecutive days with > 75% daily nest attendance (time spent within 50 m from nest location). The nest location was defined as the median coordinates of GPS-fixes at which the goose was sitting still, on days when the goose was mostly sitting still [21].

The egg laying date was taken as the first day with > 75% nest attendance, given that geese start nest building and egg laying immediately after the pair has selected a nesting site [22].

The nesting success was defined as a binary variable, with “1” indicating successful (i.e., at least one egg hatched) and “0” unsuccessful (no eggs hatched). Successful was assigned when the goose showed a nesting duration of 28–35 consecutive nesting days (each with > 75% nest attendance). This criterium was widened from the original 30–34 days mentioned in [21] based on new validation data in the current study: two GPS-tagged geese were observed with a family in summer or autumn 2022 and their nesting duration had been 28 and 35 days, respectively.

The annual probability to produce hatchlings was defined as the overall probability that a goose which arrives at the breeding grounds will nest successfully. It is a multiplication of breeding propensity and nesting success as defined above and, therefore, also binary, with “1” indicating the production of at least one hatchling and “0” no hatchling production.

### Brood size

Clutch size and brood size could not be derived from tracking data. Therefore, we observed GPS-tagged and untagged geese from a distance in Svalbard, to see how many goslings were accompanying each adult. We did this in one area, Adventdalen, targeting the area around Isdammen, east of Longyearbyen, where the available GSM reception around the village enabled the tags to transfer tracking data, enabling us to find GPS-tracked geese more easily in the field. In the same places as where we found these GPS-tagged geese, we surveyed untagged geese. This was done on 3–9 August 2019 and 23–24 July 2022. Double counts within a year were avoided by comparing the total composition of each observed flock (flock size, brood sizes, marked individuals), and including each similar flock only once. We included 10 flocks (144 family units) in 2019 and 4 flocks (61 family units) in 2022. A family unit was defined as an adult pair, or singleton, including their offspring if present. See Additional file 1: Table S3 for sample sizes.

### Statistical analysis

As outlined above, we evaluated tagging effects in three analyses: (1) a between-individual comparison based on GPS-tracks; (2) a within-individual comparison based on GPS-tracks; (3) and a between-individual comparison based on field observations.

In the first analysis, we compared the recently tagged geese with the previously tagged geese. For departure date, arrival date, migration duration and egg laying date, we used linear mixed models (LMM) in the package 'lme4' [28] and the Satterthwaite's method in the package 'lmerTest' to calculate degrees of freedom and *p*-values [29]. For breeding propensity, nesting success and annual probability to produce hatchlings, we used binomial generalized linear mixed models (GLMM). We always included a fixed effect of breeding area (Svalbard or Novaya Zemlya) and a random effect of year (2019 or 2022, which also covered the difference between stopovers).

In the second analysis, we focused on spring migration timing (departure, arrival, duration) and compared the first recorded spring and following springs, within individuals. We tested whether this change was the same for geese tagged in spring (migrating via Oulu or Trøndelag) and geese tagged in summer (migrating via Trøndelag). The geese tagged in summer were captured and tagged 9.5 months before their first recorded spring departure, whereas geese tagged in spring were tagged only 2 weeks prior to their first recorded spring departure. Given this difference, we predicted that geese tagged in spring would show a delay in their first migration compared to their subsequent migrations, while geese tagged

in summer would show no, or less, delay in their first spring. We again used LMMs and the Satterthwaite's method. We included fixed effects of stopover (Oulu or Trøndelag) and an interacting effect of tagging season (spring or summer) and spring group (i.e., first/following spring for each individual; a factor with two levels), plus random effects of individual and year. A significant interaction of tagging season  $\times$  spring group would indicate that the change in migration timing between years varies with the moment of tagging (spring versus summer). This would mean that any change in migration timing of geese tagged in spring cannot simply be explained by individual improvements with increasing age (e.g., earlier and faster migration). We did not apply this longitudinal analysis to breeding parameters, as they are largely influenced by environmental phenology on the breeding grounds which varies greatly between years, resulting in low power with our small sample.

In the third analysis, we compared observed brood sizes of tagged and untagged geese using a Poisson GLMM, including a random effect of year (2019 and 2022), which also covered the two-week difference in observation date between the years.

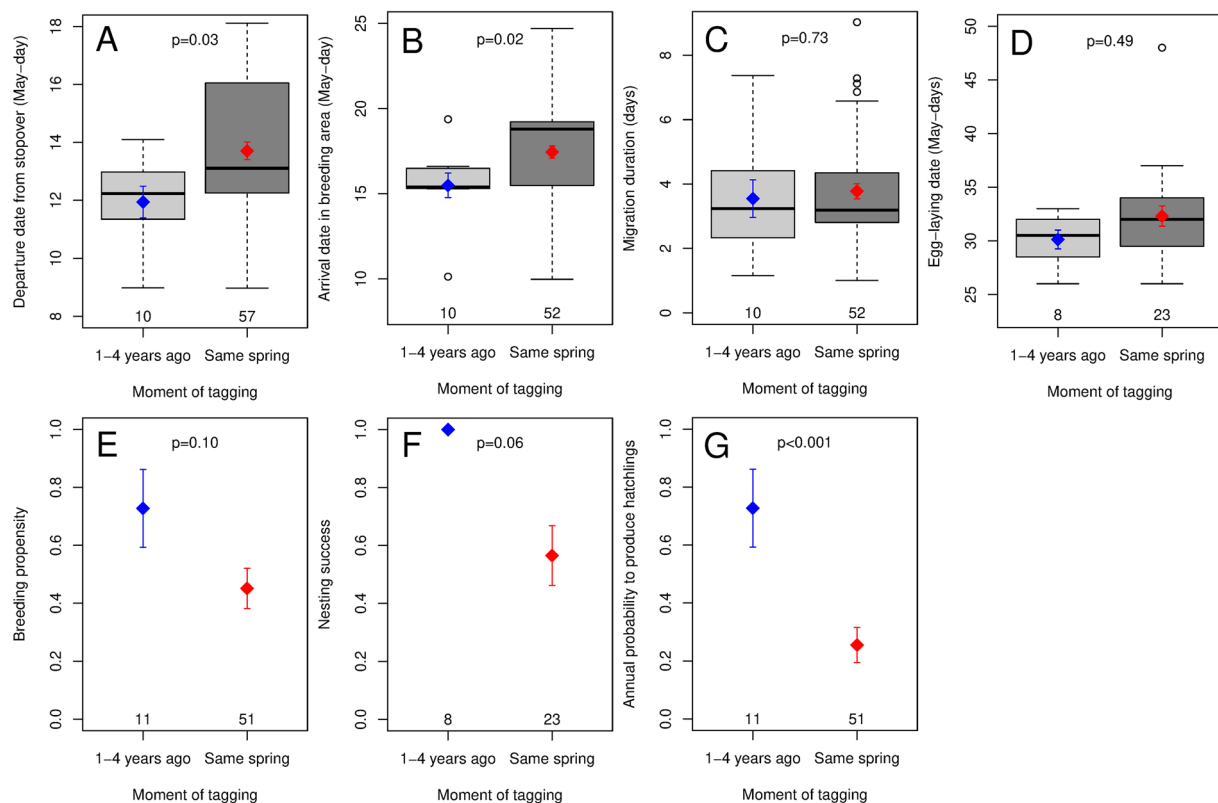
All tests were done in R, version 4.2.1 [30].

## Results

### Migration from spring stopovers to breeding area

In 2019, all eleven newly tagged geese departed from Oulu, as did all three previously tagged geese that still migrated through Oulu. In 2022, not all newly tagged geese (46) departed from Trøndelag, as three geese died shortly within 3 days after capture (Additional file 1: Table S4), while departure of another two remained unknown due to incomplete data. All eight previously tagged geese that migrated through Trøndelag survived this period in 2022.

The departure date from Oulu and Trøndelag of newly tagged geese was significantly delayed compared to geese tagged in previous years, by 1.6 days ( $\beta_{\text{Tagged recently-Tagged previously}} = 1.610 \text{ d} \pm \text{SE } 0.723$ ,  $\text{df} = 63.1$ ,  $t = 2.227$ ,  $p = 0.030$ ; Fig. 1A), when correcting for breeding area ( $\beta_{\text{Svalbard-Novaya Zemlya}} = -2.691 \text{ d} \pm \text{SE } 1.196$ ,  $\text{df} = 50.9$ ,  $t = -2.249$ ,  $p = 0.029$ ). The arrival date in the breeding area was also significantly delayed, by 1.8 days ( $\beta_{\text{Tagged recently-Tagged previously}} = 1.841 \text{ d} \pm \text{SE } 0.775$ ,  $\text{df} = 58.1$ ,  $t = 2.374$ ,  $p = 0.021$ ; Fig. 1B), when correcting for breeding area ( $\beta_{\text{Svalbard-Novaya Zemlya}} = -4.606 \text{ d} \pm \text{SE } 1.445$ ,  $\text{df} = 53.3$ ,  $t = -3.188$ ,  $p = 0.002$ ). The migration duration from stopover to breeding area was not significantly longer ( $\beta_{\text{Tagged recently-Tagged previously}} = 0.204 \text{ d} \pm \text{SE } 0.578$ ,  $\text{df} = 58.3$ ,  $t = 0.354$ ,  $p = 0.725$ ; Fig. 1C) when correcting for breeding area ( $\beta_{\text{Svalbard-Novaya Zemlya}} = -1.896 \text{ d} \pm \text{SE } 1.013$ ,  $\text{df} = 20.0$ ,  $t = -1.872$ ,  $p = 0.076$ ).



**Fig. 1** Migration and breeding of Pink-footed geese that were GPS-tagged recently (in the same spring) versus 1–4 years ago (in spring or summer). Recently tagged geese were tagged in Oulu, 2019 and Trøndelag, 2022. Previously, geese were tagged in Oulu, spring 2018 and in Svalbard, summer 2018. Recently tagged geese had a later departure (**A**) and arrival date (**B**), and a lower annual probability to produce hatchlings (**G**) than previously tagged geese, while there was no difference in migration duration (**C**), laying date (**D**) and breeding propensity (**E**), and a tendency for a lowered nesting success (**F**). Note that G is the product of E and F. Boxplots and/or means  $\pm$  SE are given. The p-value is given on the top and was based on LMMs (for **A–D**) and on binomial GLMMs (for **D–G**), all including breeding area (Svalbard, Novaya Zemlya) and a random effect of year (2019, 2022). Sample sizes are given on the bottom as number of individuals

When comparing the timing of the first versus following spring migrations within individuals, the change was not the same for geese tagged in summer (migrating via Trøndelag) and geese tagged in spring (migrating via Trøndelag or Oulu). Compared to summer-tagged geese, spring-tagged geese departed with a 2.4 day delay in their first tracked spring (interaction tagging season  $\times$  spring group:  $\beta = 2.353$  d  $\pm$  SE 0.717,  $df = 131.1$ ,  $t = 3.280$ ,  $p = 0.001$ ) and arrived with a 2.8 day delay (interaction:  $\beta = 2.823$  d  $\pm$  SE 0.983,  $df = 119.0$ ,  $t = 2.873$ ,  $p = 0.005$ ), while migration duration was not significantly lengthened (interaction:  $\beta = 0.426$  d  $\pm$  SE 0.628,  $df = 37.9$ ,  $t = 0.679$ ,  $p = 0.501$ ; Fig. 2).

### Breeding propensity

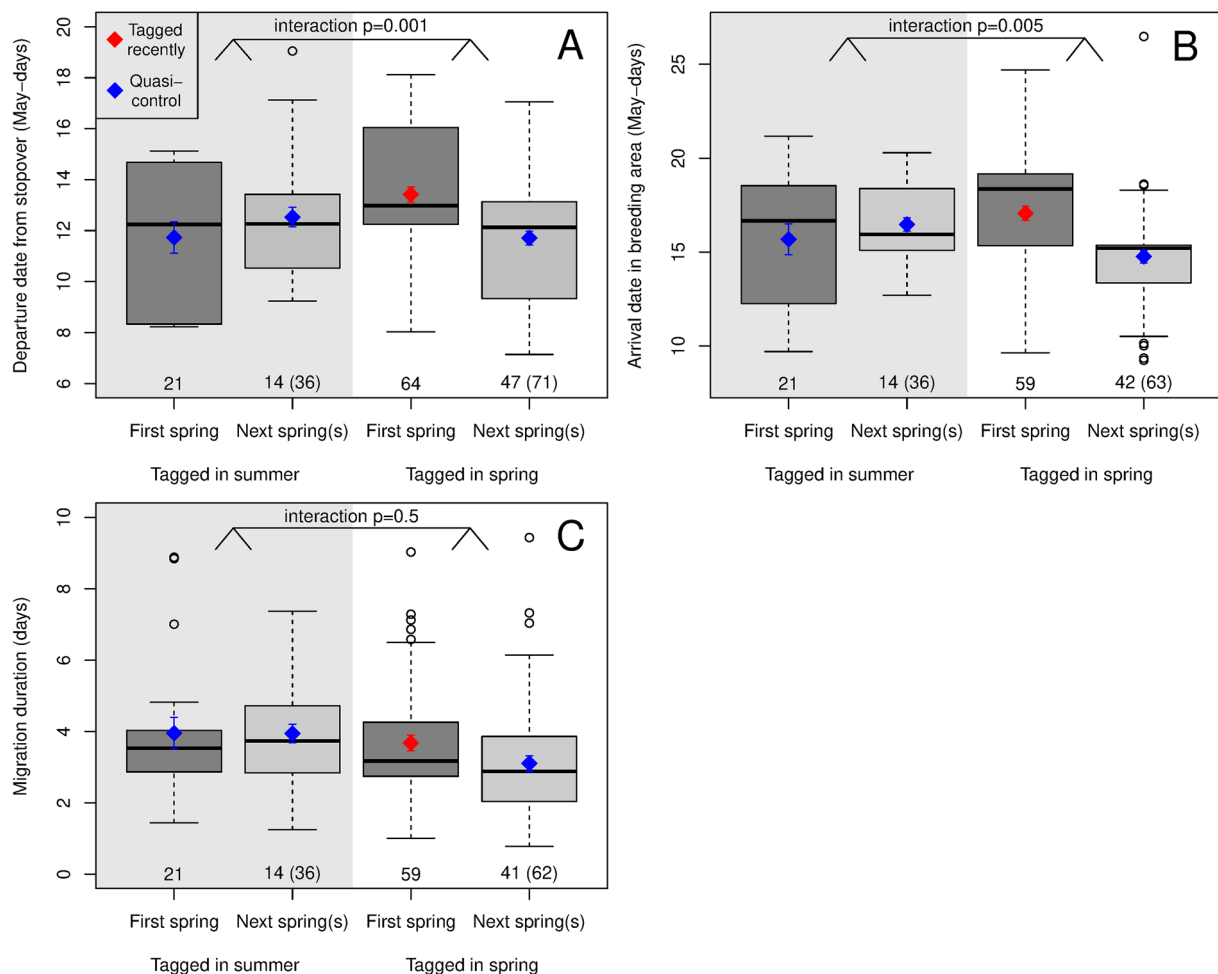
In Svalbard, nesting locations of previously tagged geese were concentrated west and centrally, around Is-fjorden, while recently tagged geese were more spread out from the south to the north, overlapping in the central Isfjorden region (Additional file 1: Fig.

S1). In Novaya Zemlya, nest sites of recently tagged geese overlapped with those of previously tagged geese but occurred also in the southern edge of Severnaya Zemlya.

The breeding propensity of recently tagged geese was not significantly lower than of geese tagged previously ( $\beta_{\text{Tagged recently-Tagged previously}} = -1.254 \pm \text{SE } 0.7503$ ,  $z = -1.672$ ,  $p = 0.095$ ; Fig. 1E), while correcting for breeding area ( $\beta_{\text{Svalbard-Novaya Zemlya}} = 0.925 \pm \text{SE } 0.791$ ,  $z = 1.170$ ,  $p = 0.242$ ).

### Egg laying date

The egg laying date of recently tagged geese was not significantly delayed compared to geese tagged previously ( $\beta_{\text{Tagged recently-Tagged previously}} = 0.972$  d  $\pm$  SE 1.394,  $df = 27.2$ ,  $t = 0.697$ ,  $p = 0.492$ ; Fig. 1D), while correcting for breeding area ( $\beta_{\text{Svalbard-Novaya Zemlya}} = -3.833$  d  $\pm$  SE 3.362,  $df = 9.4$ ,  $t = -1.140$ ,  $p = 0.283$ ).



**Fig. 2** Migration of Pink-footed geese in their first GPS-tracked spring and following springs. The individual change in spring migration timing, from the first to the following springs, differed between geese tagged in summer (Svalbard, migrating via Trøndelag; left half of each panel, with shaded background) and geese tagged in spring (Oulu and Trøndelag; right half of each panel). Geese tagged in summer showed no delay in their migration timing when we compare their first versus next springs, but geese tagged in spring did. This pattern was visible in the departure date (A), the arrival date (B), but not the migration duration (C). The pattern indicates that the initial delay (red diamond) is not simply an effect of ageing (i.e., delayed migration at younger age), but more likely a tagging effect. Sample sizes are given on the bottom as number of individuals, with the number of tracks in brackets (as some individuals migrated in multiple following springs, more detail in Additional file 1: Table S2). Boxplots and means  $\pm$  SE are given. The  $p$ -value of the interaction tagging season  $\times$  spring group is given on the top and was based on LMMs including a fixed effect of stopover and random effects of individual and year

### Nesting success

The nesting success of recently tagged geese tended to be lowered compared to geese tagged previously, but not significantly ( $\beta_{\text{Tagged recently-Tagged previously}} = -0.328 \pm \text{SE } 0.164$ ,  $\text{df} = 27.3$ ,  $t = -1.998$ ,  $p = 0.056$ ; Fig. 1F), while correcting for breeding area ( $\beta_{\text{Svalbard-Novaya Zemlya}} = 0.222 \pm \text{SE } 0.392$ ,  $\text{df} = 8.3$ ,  $t = 0.567$ ,  $p = 0.585$ ).

### Annual probability to produce hatchlings

The overall probability that a goose arriving in the breeding area will nest successfully, was significantly lower in recently tagged geese than previously tagged geese

( $\beta_{\text{Tagged recently-Tagged previously}} = -0.512 \pm \text{SE } 0.137$ ,  $\text{df} = 58.2$ ,  $t = -3.738$ ,  $p = 0.0004$ ; Fig. 1G), while correcting for breeding area ( $\beta_{\text{Svalbard-Novaya Zemlya}} = 0.053 \pm \text{SE } 0.251$ ,  $\text{df} = 20.2$ ,  $t = 0.212$ ,  $p = 0.834$ ).

### Brood size

On Svalbard, August 2019 (1 year post-tagging), the observed brood size of the geese that were GPS-tagged on Isdammen in 2018 was on average 0.38 (range 0–2,  $n = 8$  pairs) while untagged geese in the same area had an average brood size of 0.83 (range 0–8,  $n = 136$ ). In July 2022 (4 years post-tagging), it was 2.67 for GPS-tagged

geese (range 1–7,  $n=6$  pairs) and 1.00 for untagged geese (range 0–6,  $n=55$ ). Combined, there was no significant effect of tagging on brood size (Poisson GLMM:  $\beta_{\text{Tagged-Untagged}}=0.403 \pm \text{SE } 0.243$ ,  $z=1.656$ ,  $p=0.098$ ; Fig. 3, Additional file 1: Table S3), nor when only including 2019 (Poisson GLM:  $\beta_{\text{Tagged-Untagged}}=-0.796 \pm \text{SE } 0.585$ ,  $z=1.360$ ,  $p=0.173$ ). Also when including only families with chicks, no significant differences were found (both years:  $\beta_{\text{Tagged-Untagged}}=-0.069 \pm \text{SE } 0.242$ ,  $z=0.286$ ,  $p=0.775$ ; only 2019:  $\beta_{\text{Tagged-Untagged}}=-0.493 \pm \text{SE } 0.585$ ,  $z=0.843$ ,  $p=0.399$ ).

## Discussion

We found that the migration timing of recently captured and GPS-tagged geese was delayed by on average 1.6 days, compared to previously tagged geese as quasi-controls. This difference was found in the departure from the stopover and the arrival at the breeding area. No differences were found in the duration of migration between stopover and breeding grounds, nor in breeding propensity, laying date and brood size, but nesting success tended to be lowered and the annual probability to produce hatchlings was lowered. Also, with our longitudinal approach (comparing first and following spring migrations within individuals) we found that geese were delayed in the spring of tagging, on average by 2.4–2.8 days. This could not simply be an effect of ageing (i.e., delayed migration at earlier age), since geese tagged in summer did not show such a delay in their first spring migration. Finally, we found that tagged and untagged

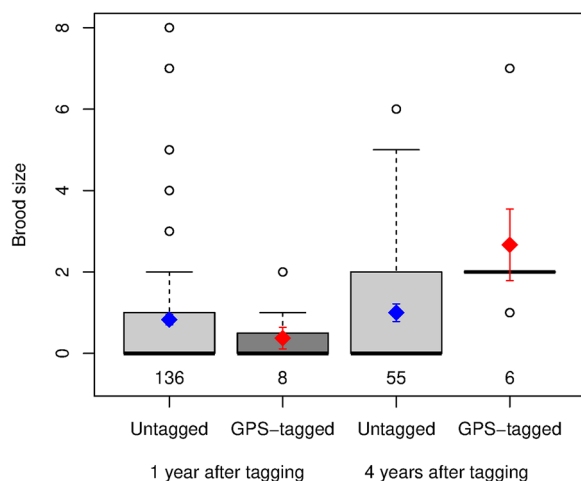
geese had no different brood sizes during moult 1 year after tagging.

The result that newly tagged geese got around 2 days behind on schedule likely resulted from the loss of time and energy, due to: (1) lost foraging time due to capture and tag habituation, (2) recovery from injury or stress caused by the capture, and (3) efforts to find back the partner if the pair was split during capture. Injury may have been the indirect cause of death for 2–3 geese within 3 days post-catch in Norway (Additional file 1: Table S4). These injuries (skin rupture due to net entanglement) were associated with the use of one particular net, which was not used anymore after injuries were noticed. The absence of an effect of recent tagging on migration duration suggests that the effect of potential injury was limited in other individuals. These casualties indicate that capture can impair survival, since all previously tagged geese survived the same stopover period (although data were limited).

A previous study on a more southern stopover (Jutland, Denmark) found that newly captured and neckbanded geese had a significantly lower body condition for about a week after capture than geese captured in previous years [9]. Although we did not study the body condition of geese, the delayed departure around 2 weeks after capture, suggests that a similar, but longer, effect plays on these northern stopovers. In spring, geese have higher energy gain rates in northern than southern stopovers sites [31, 32]. Therefore, capture and tagging effects may last longer on a more northern stopover (see Additional file 1: Fig. S2). Body stores are a likely factor to determine the departure from stopovers in combination with vegetation growth and date itself [33]. Further, energy intake rate is an important determinant of fitness, especially on the more northern stopovers, later in the spring [34]. Thus, if energy intake has been lowered by capture, geese may decide to stay longer on the stopover to compensate and increase their chances of reproduction, before migrating to the breeding grounds.

A delay of the timing of departure in the spring of tagging was also found in our longitudinal analysis. This cannot be explained by coincidental variation in the start of spring. Spring was not particularly early in Trøndelag in 2019 (first spring of quasi-controls), nor was it particularly late in Oulu in 2018–2019, nor in Trøndelag in 2022 (first springs of newly tagged geese; [20]). Moreover, based on field counts and ring readings, the departure date from Trøndelag and Oulu is not related to spring phenology [20, 35].

We did not find an effect of recent GPS-tagging on the migration duration from the stopovers to the breeding areas. In flight, aerodynamic drag due to tags may be expected [36], but this would be a permanent effect, thus



**Fig. 3** Brood size of GPS-tagged and untagged geese observed in Adventdalen, Svalbard. Geese were tagged here in July 2018 and observed in the same area in August 2019 and July 2022. The number of goslings in summer did not differ significantly between tagged and untagged geese (not in 2019 only, nor when combining 2019 and 2022). Boxplots and means  $\pm$  SE are given

undetectable by comparing geese tagged recently or long ago. However, drag is thought to be small for neckband tags compared to e.g., backpacks [2]. When migrating over the Barents Sea, Pink-footed geese were found to be influenced by wind, causing them to drift off route and sometimes pause on the water [27]. Tagged geese may be more susceptible to wind effects if drag is large, but on the other hand, geese migrate in flocks and individuals may benefit from the uplift that the preceding goose creates [37–39] and migratory decisions may also depend on the behaviour of the flock, which is mainly untagged.

Arrival to the breeding grounds was delayed in recently tagged geese. This is in line with [10] showing that, 2 months after tagging, Pink-footed geese that were captured and tagged in Denmark migrated slightly later through northern Norway than unringed geese. The fact that we detected this effect with quasi-control indicates that the effect is (at least partly) temporary. This is confirmed by [40], showing that 1 year after tagging GPS-tagged geese and untagged geese had similar timing on pre-breeding sites in Svalbard.

Once arrived at the breeding grounds, geese that were tagged recently or previously did not differ significantly in breeding propensity. Other studies did find an effect of tagging on breeding propensity, e.g., in Emperor geese (*Chen canagica*, [11]). Possibly, statistical power was limited, or Pink-footed geese recovered and compensated for their energy loss within a month, as was also demonstrated on spring stopovers [9]. However, an experimental study in Greater snow geese (*Anser caerulescens atlanticus*) showed that the main factor determining the effect of capture on goose breeding success was time spent in captivity (0–4 days, > 1 week before departure), rather than food supplementation even when it allowed birds to maintain body mass [41]. This effect was only present in years with normal or adverse breeding conditions and worked via breeding propensity rather than laying date or clutch size [42]. In our data, a tendency for a negative effect may be present, but severe effects on breeding propensity due to mate loss (e.g., [15]) seem absent.

Those newly tagged geese that decided to breed, did so at a similar timing to geese tagged in previous years. This may indicate that geese may only start to breed when they are capable to do so at a normal timing, as laying later has associated costs, e.g., lower clutch survival [43] and limited chick growth due to a possible mismatch (e.g., [44]). In other studies, tagged geese were found to lay eggs later than untagged geese, e.g., by 3–4 days (Greater snow geese, [15]) and 2–3 days (Barnacle geese *Branta leucopsis*, [16]). In our study, power may have been limited, although the effect size also seemed smaller (only 1 day, not significant), which could indicate that a

tagging effect on laying date is more difficult to detect with quasi-controls.

The nesting success of newly tagged geese tended to be lowered (as in [15] and see [45] for normal neckbands). Nesting success is strongly determined by nest attendance, which in turn depends on energy reserves [46, 47]. Although our result was not significant, it may point again towards lost body stores by capture and tagging which were not fully compensated.

However, combining the non-significant effects on both breeding propensity and nesting success, we found that the annual probability to produce hatchlings was significantly lowered in recently tagged geese. This is in line with previous studies (e.g., [41, 42]) and seemed to play only in the same breeding season directly following tagging in spring. One year after tagging, the brood size during moult was not different between tagged and untagged geese. It must be noted that this test had a low power due to some unbalanced and small sample sizes. Still, such potential fading of the tagging effect over the years post-tagging also explains why we could detect an effect of tagging on newly tagged geese by comparing them with quasi-controls. Nevertheless, in other studies, tagging effects on breeding are found to last longer than a year. For example, in [15], the laying date, clutch size and nesting success of geese tagged 10 and 22 months ago did not differ but was lower than that of untagged geese.

In all analyses that we performed with quasi-controls, one must bear in mind that we could only study those geese that survived, which may lead to a bias. These surviving geese might be of 'higher quality' for two reasons: (1) individual survival is often correlated with other life-history traits such as reproductive success [48]; and (2) individual performance may also improve with age (e.g., [49]). Thus, using these potentially high-quality birds as a reference may lead to an overstatement of the tagging effect, although we showed for geese tagged in summer that their spring migration did not advance between the first and following springs. On the other hand, tagging effects are likely to be larger than what appears from an analysis with quasi-controls, because mortality itself may be a tagging effect (e.g., [11, 16]), and other permanent effects remain undetected.

Working with quasi-controls is a way to reveal short- and medium-term tagging effects. This is especially valuable for studies in which not enough birds were captured to warrant the creation of true control groups (i.e., untagged birds). When only small numbers of birds are captured, creating untagged control groups does not give enough statistical power to detect (small) tagging effects, but does come at the expense of the sample size of tagged birds, potentially impairing statistically sound inferences from tracking. Thus, this is an example typical of animal



experiments, where there is a balance of a ‘partial loss’ due to discomfort with a ‘total loss’ due to insufficient sample sizes, see e.g., [50].

Still, true controls are necessary to evaluate permanent effects. This is especially important for studies that use tracking to derive population parameters, e.g., as input for population modeling, rather than studies that focus solely on differences between groups within the tagged sample. Creating true controls is only feasible at larger sample sizes, because of the trade-off mentioned in the previous paragraph but also because methods of observing controls (with marks which are thought to have no effect, e.g., small tarsal bands [11, 45]) have a lower reporting rate because the bird’s location is unknown beforehand, and its mark less conspicuous.

Although it is difficult to assess the breeding and migration parameters of this study in controls with only a small mark, it is possible to still assess reproductive success in autumn [20], thus in less remote areas, as juveniles travel with their parents [51]. Also in spring, the abdominal profile [31], a proxy of fitness [52], can be assessed to reveal tagging effects [9]. Both these parameters can also be assessed in unmarked individuals. Lastly, other parameters can be screened for tagging effects, by comparing tagged versus marked control birds, such as survival based on recoveries or re-sightings [11, 16].

In any case, our results suggest that, to maximize the usefulness of tracking data, birds should be tagged long enough before the parameter of interest is assessed, to allow tagging effects to fade. In this study, catching in late spring to obtain data on spring migration and breeding turned out not to be optimal, at least not in the birds’ first tracking season.

## Conclusions

In conclusion, our results show that the capture and GPS-tagging of geese 2 weeks before spring departure on average delays them from their migration schedule, and lowers their probability to produce hatchlings in that year. One year after tagging, breeding performance of tagged and untagged geese was similar. Further study is needed to evaluate permanent effects of tagging as our current approach with quasi-controls cannot detect life-long impacts.

## Abbreviations

GPS	Global Positioning System
GSM	Global System for Mobile communication
GLMM	Generalised linear mixed model
LMM	Linear mixed model

## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40317-024-00365-2>.

**Additional file 1: Figure S1.** Nesting locations of different tagging cohorts on Svalbard and Novaya Zemlya. On Svalbard, Pink-footed geese that were GPS-tagged during wing moult in Svalbard nested in the area where they were tagged, while geese tagged in Finland were spread out over the center and north, and geese tagged in Norway concentrated more on the center and south. On Novaya Zemlya, only one goose from the first cohort nested, while 16 geese from the second cohort nested over a wider area. Geese that did not nest are not depicted. Number of nests is given as sample size per group. **Figure S2.** Schematic representation of changes in body condition after capture on different stopovers. The time that it takes captured geese to catch up in body condition with uncaptured geese is expected to be longer when geese are fattening up on the stopover (B), than when they are not fattening up (A), assuming constant values of body stores lost due to capture and constant fattening speed of tagged geese. **Table S1.** Sample sizes for cross-sectional analyses. For each stage (departure, arrival, breeding propensity, laying date, hatching success) the number of GPS-tagged geese is given, for the quasi-control and experimental groups, and per flyway (as specified by the stopover and breeding area). **Table S2.** Sample sizes for longitudinal analyses. For each year, the number of GPS-tagged geese is given, for departure from stopover and arrival in breeding area (separated by a “/” in each cell). Underlined numbers indicate experimental group (i.e., tagged recently), not underlined numbers the quasi-control group (i.e., tagged longer ago). **Table S3.** Brood size distribution as observed in Adventdalen, Longyearbyen, Svalbard. **Table S4.** Geese that died shortly after capture in Trøndelag, Norway, spring 2022. The moment of death was based on GPS and accelerometry: when dying on water, the Y-axis of the accelerometer (in dimension from body towards head) turned gradually negative, indicating a hanging instead of upright neck. Time is UTC + 2. One GPS-tag (code 5Z) was retrieved and deployed on a different individual in a following catch.

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## Author contributions

Conceptualisation: KS, JM, BN; fieldwork: KS, JM, BN; methodology and analysis: KS, initial writing: KS; review and editing: KS, JM, BN; funding and permits acquisition: KS, JM, BN.

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## Availability of data and materials

The datasets generated and/or analyzed during the current study are available in the DataverseNL repository (<https://doi.org/10.34894/EPEC10>) under Creative Commons licence CC-BY-NC-4.0 in the Nolet group.

## Declarations

### Ethics approval and consent to participate

Capture and marking of geese in Svalbard and Norway were approved by the Norwegian animal research authority (Mattilsynet) (reference no. 17/210528)

and by the Governor of Svalbard (reference no. 17/01420-4), granted to Aarhus University. For capture on Isdammen, Longyearbyen Lokaltstyre granted permission (reference no. 2018/347-5-X70). Capture and marking of geese in Finland were permitted by Etelä-Suomen aluehallintovirasto to Aarhus University (ESAVI/1924/2018 and ESAVI/1880/2018) and by the Varsinais-Suomen elinkeino-, liikenne- ja ympäristökeskus (to Jorma Pessa, VARELY/551/2018).

### Competing interests

The authors declare that they have no competing interests.

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### References

- Rutz C, Hays GC. New frontiers in biologging science. *Biol Lett*. 2009;5:289–92.
- Lameris TK, Kleyheeg E. Reduction in adverse effects of tracking devices on waterfowl requires better measuring and reporting. *Animal Biotelem*. 2017;5:1–14.
- Geen GR, Robinson RA, Baillie SR. Effects of tracking devices on individual birds—a review of the evidence. *J Avian Biol*. 2019;50: e01823.
- Sorenson MD. Effects of neck collar radios on female redheads (Efecto de radiotransmisores de collar en hembras de *Aythya americana*). *J Field Ornithol*. 1989;60:523–8.
- Cappelle J, Iverson SA, Takekawa JY, Newman SH, Dodman T, Gaidet N. Implementing telemetry on new species in remote areas: recommendations from a large-scale satellite tracking study of African waterfowl. *Ostrich*. 2011;82:17–26.
- Nuijten RJM, Kölsch A, Van Gils JA, Hoyer BJ, Oosterbeek K, De Vries PP, Klaassen M, Nolet BA. The exception to the rule: retreating ice front makes Bewick's swans *Cygnus columbianus* bewickii migrate slower in spring than in autumn. *J Avian Biol*. 2014;45:113–22.
- Clausen KK, Schreven KHT, Madsen J. Effects of capture and marking on the behaviour of moulting Pink-footed Geese *Anser brachyrhynchus* on Svalbard. *Wildfowl*. 2020;70:13–29.
- Duncan IJH. Frustration in the fowl. In: Freeman BM, Gordon RF, editors. *Aspects of poultry behaviour*. Edinburgh: British Poultry Science Ltd; 1970. p. 15–31.
- Clausen KK, Madsen J. Effects of neckbands on body condition of migratory geese. *J Ornithol*. 2014;155:951–8.
- Glahder CM, Fox AD, Hubner CE, Madsen J, Tombre IM. Pre-nesting site use of satellite transmitter tagged Svalbard Pink-footed Geese *Anser brachyrhynchus*. *Ardea*. 2006;94:679–90.
- Schmutz JA, Morse JA. Effects of neck collars and radiotransmitters on survival and reproduction of emperor geese. *J Wildlife Manage*. 2000;64:231–7.
- Ludynia K, Dehnhard N, Poisbleau M, Demongin L, Masello JF, Quillfeldt P. Evaluating the impact of handling and logger attachment on foraging parameters and physiology in southern rockhopper penguins. *PLoS ONE*. 2012;7: e50429.
- Vandenabeele SP, Grundy E, Friswell MI, Grogan A, Votier SC, Wilson RP. Excess baggage for birds: inappropriate placement of tags on gannets changes flight patterns. *PLoS ONE*. 2014;9: e92657.
- Whidden SE, Williams CT, Breton AR, Buck CL. Effects of transmitters on the reproductive success of Tufted Puffins. *J Field Ornithol*. 2007;78:206–12.
- Demers F, Giroux JF, Gauthier G, Bêty J. Effects of collar-attached transmitters on behaviour, pair bond and breeding success of snow geese *Anser caerulescens* atlanticus. *Wildlife Biol*. 2003;9:161–70.
- Lameris TK, Müskens GJDM, Kölsch A, Dokter AM, van der Jeugd HP, Nolet BA. Effects of harness-attached tracking devices on survival, migration, and reproduction in three species of migratory waterfowl. *Animal Biotelem*. 2018;6:1–8.
- Boom MP, Schreven KHT, Buitendijk NB, Moonen S, Nolet BA, Eichhorn G, van der Jeugd HP, Lameris TK. Earlier springs increase goose breeding propensity and nesting success at Arctic but not at temperate latitudes. *J Anim Ecol*. 2023;92:2399–411.
- Murgatroyd M, Tate G, Amar A. Using GPS tracking to monitor the breeding performance of a low-density raptor improves accuracy, and reduces long-term financial and carbon costs. *Roy Soc Open Sci*. 2023;10: 221447.
- Madsen J, Schreven KHT, Jensen GH, Johnson FA, Nilsson L, Nolet BA, Pessa J. Rapid formation of new migration route and breeding area by Arctic geese. *Curr Biol*. 2023;33:1162–1170.e4.
- Schreven KHT. Geese colonising New Land: causes and mechanisms of range expansion in an Arctic-breeding migrant. PhD thesis, Amsterdam, The Netherlands, University of Amsterdam; 2023.
- Schreven KHT, Stolz C, Madsen J, Nolet BA. Nesting attempts and success of Arctic-breeding geese can be derived with high precision from accelerometer and GPS-tracking. *Animal Biotelem*. 2021;9:1–13.
- Inglis IR. The breeding behaviour of the Pink-footed Goose: behavioural correlates of nesting success. *Anim Behav*. 1977;25:747–64.
- Fridolfsson AK, Ellegren H. A simple and universal method for molecular sexing of non-ratite birds. *J Avian Biol*. 1999;30:116–21.
- Griffiths R, Double MC, Orr K, Dawson RJ. A DNA test to sex most birds. *Mol Ecol*. 1998;7:1071–5.
- Boyd H. Statistics of the British population of the pink-footed goose. *J Anim Ecol*. 1956;25:253–73.
- Beer JV, Boyd H. Weights of Pink-footed Geese in autumn. *Bird Study*. 1962;9(2):91–9.
- Geisler J, Madsen J, Nolet BA, Schreven KHT. Sea crossings of migratory pink-footed geese: seasonal effects of winds on flying and stopping behaviour. *J Avian Biol*. 2022;10: e02985.
- Bates D, Mächler M, Bolker BM, Walker SC. Fitting linear mixed-effects models using lme4. *J Stat Softw*. 2015;67:1–48.
- Kuznetsova A, Brockhoff PB, Christensen RHB. lmerTest package: tests in linear mixed effects models. *J Stat Softw*. 2017;82:1–26.
- R Core Team. R: A language and environment for statistical computing (version 4.2.1). R Foundation for Statistical Computing, Vienna, Austria. 2022. [www.R-project.org](http://www.R-project.org). Accessed 23 Jun 2022.
- Madsen J, Klaassen M. Assessing body condition and energy budget components by scoring abdominal profiles in free-ranging pink-footed geese *Anser brachyrhynchus*. *J Avian Biol*. 2006;37:283–7.
- Chudzińska ME, Nabe-Nielsen J, Nolet BA, Madsen J. Foraging behaviour and fuel accumulation of capital breeders during spring migration as derived from a combination of satellite- and ground-based observations. *J Avian Biol*. 2016;47:563–74.
- Duriez O, Bauer S, Destin A, Madsen J, Nolet BA, Stillman RA, Klaassen M. What decision rules might pink-footed geese use to depart on migration? An individual-based model. *Behav Ecol*. 2009;20:560–9.
- Bauer S, van Dinther M, Høgda KA, Klaassen M, Madsen J. The consequences of climate-driven stop-over sites changes on migration schedules and fitness of Arctic geese. *J Anim Ecol*. 2008;77:654–60.
- Tombre IM, Høgda KA, Madsen J, Griffin LR, Kuijken E, Shimmings P, Rees E, Verschuere C. The onset of spring and timing of migration in two arctic nesting goose populations: the pink-footed goose *Anser brachyrhynchus* and the barnacle goose *Branta leucopsis*. *J Avian Biol*. 2008;39:691–703.
- Pennycuik CJ, Fast PLF, Ballerstädt N, Rattenborg N. 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*. 2012;153:633–44.
- Badgerow JP. An analysis of function in the formation flight of Canada geese. *Auk*. 1988;105:749–55.
- Weimerskirch H, Martin J, Clerquin Y, Alexandre P, Jiraskova S. Energy saving in flight formation. *Nature*. 2001;413:697–8.
- Portugal SJ, Hubel TY, Fritz J, Heese S, Trobe D, Voelkl B, Hailes S, Wilson AM, Usherwood JR. Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature*. 2014;505:399–402.
- Eischeid I, Madsen J, Ims RA, Nolet BA, Pedersen ÅØ, Schreven KHT, Soininen EM, Yoccoz NG, Ravolainen VT. Snowmelt progression drives habitat use and vegetation disturbance by an Arctic avian herbivore. *Ecosphere*. 2023;14: e4729.

41. Legagneux P, Fast PLF, Gauthier G, Bêty J. Manipulating individual state during migration provides evidence for carry-over effects modulated by environmental conditions. *P Roy Soc B-Biol Sci.* 2012;279:876–83.
42. Grandmont T, Fast PLF, Grentzmann I, Gauthier G, Bêty J, Legagneux P. Should I breed or should I go? Manipulating individual state during migration influences breeding decisions in a long-lived bird species. *Funct Ecol.* 2023;37:602–13.
43. Madsen J, Tamstorf M, Klaassen M, Eide N, Glahder C, Rigét F, Nyegaard H, Cottaar F. Effects of snow cover on the timing and success of reproduction in high-Arctic pink-footed geese *Anser brachyrhynchus*. *Polar Biol.* 2007;30:1363–72.
44. Doiron M, Gauthier G, Lévesque E. Trophic mismatch and its effects on the growth of young in an Arctic herbivore. *Glob Change Biol.* 2015;21:4364–76.
45. Lensink CJ. Neckbands as an inhibitor of reproduction in Black Brant. *J Wildlife Manage.* 1968;32:418–20.
46. Samelius G, Alisauskas RT. Deterring arctic fox predation: the role of parental nest attendance by lesser snow geese. *Can J Zoolog.* 2001;79:861–6.
47. Spaans B, van 't Hoff CA, van der Veer W, Ebginge BS. The significance of female body stores for egg laying and incubation in Dark-bellied Brent Geese *Branta bernicla bernicla*. *Ardea.* 2007;95:3–15.
48. van Noordwijk AJ, de Jong G. Acquisition and allocation of resources: their influence on variation in life history tactics. *Am Nat.* 1986;128:137–42.
49. Rockwell RF, Cooch EG, Thompson CB, Cooke F. Age and reproductive success in female lesser snow geese: experience, senescence and the cost of philopatry. *J Anim Ecol.* 1993;62:323–33.
50. National Research Council. Recognition and alleviation of distress in laboratory animals. Washington: The National Academies Press; 2008. <https://doi.org/10.17226/11931>.
51. Gupte PR, Koffijberg K, Müskens GJDM, Wikelski M, Kölzsch A. Family size dynamics in wintering geese. *J Ornithol.* 2019;160:363–75.
52. Drent R, Both C, Green M, Madsen J, Piersma T. Pay-offs and penalties of competing migratory schedules. *Oikos.* 2003;103:274–92.

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