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RESEARCH ARTICLE

# Earlier springs increase goose breeding propensity and nesting success at Arctic but not at temperate latitudes

Michiel P. Boom[1,2,3] | Kees H. T. Schreven[2,3] | Nelleke H. Buitendijk[2,3] |
Sander Moonen[4,5,6] | Bart A. Nolet[2,3] | Götz Eichhorn[1,2] |
Henk P. van der Jeugd[1,2] | Thomas K. Lameris[7]

[1]Vogeltrekstation—Dutch Centre for Avian Migration and Demography (NIOO-KNAW), Wageningen, The Netherlands; [2]Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands; [3]Theoretical and Computational Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands; [4]Wageningen Environmental Reseach (WEnR), Wageningen, The Netherlands; [5]Institute of Avian Research, Wilhelmshaven, Germany; [6]Institute for Wetlands and Waterbird Research e.V., Verden (Aller), Germany and [7]NIOZ Royal Netherlands Institute for Sea Research, Den Burg, The Netherlands

**Correspondence**
Michiel P. Boom
Email: chiel.boom@gmail.com

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## Abstract

1. Intermittent breeding is an important tactic in long-lived species that trade off survival and reproduction to maximize lifetime reproductive success. When breeding conditions are unfavourable, individuals are expected to skip reproduction to ensure their own survival.
2. Breeding propensity (i.e. the probability for a mature female to breed in a given year) is an essential parameter in determining reproductive output and population dynamics, but is not often studied in birds because it is difficult to obtain unbiased estimates. Breeding conditions are especially variable at high latitudes, potentially resulting in a large effect on breeding propensity of Arctic-breeding migratory birds, such as geese.
3. With a novel approach, we used GPS-tracking data to determine nest locations, breeding propensity and nesting success of barnacle geese, and studied how these varied with breeding latitude and timing of arrival on the breeding grounds relative to local onset of spring.
4. Onset of spring at the breeding grounds was a better predictor of breeding propensity and nesting success than relative timing of arrival. At Arctic latitudes (>66° N), breeding propensity decreased from 0.89 (95% CI: 0.65–0.97) in early springs to 0.22 (95% CI: 0.06–0.55) in late springs, while at temperate latitudes, it varied between 0.75 (95% CI: 0.38–0.93) and 0.89 (95% CI: 0.41–0.99) regardless of spring phenology. Nesting success followed a similar pattern and was lower in later springs at Arctic latitudes, but not at temperate latitudes. In early springs, a larger proportion of geese started breeding despite arriving late relative to the

onset of spring, possibly because the early spring enabled them to use local resources to fuel egg laying and incubation.

5. While earlier springs due to climate warming are considered to have mostly negative repercussions on reproductive success through phenological mismatches, our results suggest that these effects may partly be offset by higher breeding propensity and nesting success.

KEYWORDS

*Branta leucopsis*, breeding success, climate change, migration, phenology, telemetry, tracking

## 1 | INTRODUCTION

Environmental seasonality increases with latitude and results in spatiotemporal variation in resource availability. In response, animals have evolved various life-history strategies to cope with seasonality. Migration is a striking example of a life-history tactic that enables animals to exploit seasonally occurring food peaks, while avoiding periods of scarcity (Holt & Fryxell, 2011; Newton, 2008). In order for migration to be a successful tactic, the gain in reproductive output must equal or outweigh the additional annual mortality associated with it (Stearns, 2000). Reproductive success is determined by a chain of events (including breeding propensity, clutch size, nesting success, hatchling and fledgeling survival) that each may be affected differently by the environmental conditions (Nolet et al., 2020). Given that environmental and climatic conditions are changing at unprecedented rates, especially in the Arctic, understanding the impact of environmental variation on the components of reproductive success, and how this might vary with latitude, is crucial to evaluate the viability of populations adopting different life-history strategies.

An essential component of reproductive success is the decision to breed or not, known as breeding propensity (i.e. the probability for a mature female to breed in a given year). By foregoing annual reproduction when breeding conditions are unfavourable and successful reproduction becomes unlikely, individuals avoid compromising survival up to the next breeding season (Chastel, 1995; Spaans et al., 1998; Wooller et al., 1990). This is an important tactic in long-lived species to maximize lifetime reproductive success (Stearns, 2000). The proportion of breeding adults has a strong effect on the annual reproductive output of the population and population dynamics (Cam et al., 1998; Coulson, 2010). By using a modelling approach, Lee et al. (2017) show that failing to account for non-breeders affects the estimates of demographic parameters, which are essential in determining the stability and viability of animal populations. However, while many studies on birds have focussed on the hatching, growing and fledging stages of the breeding cycle (e.g. Boom et al., 2022; Dickey et al., 2008; Lameris et al., 2019), breeding propensity is one of the least known demographic parameters, because it is difficult to estimate (Etterson et al., 2011; Sedinger et al., 2008; Souchay et al., 2014). Compared to breeding individuals, non-breeding birds are usually less conspicuous in behaviour and therefore often overlooked (Reed et al., 2004; Sedinger et al., 2008), or can be absent from breeding colonies (Chastel, 1995; Tavera et al., 2020).

Variation in environmental conditions on the breeding grounds is thus expected to result in variation in breeding propensity and ultimately reproductive output. Breeding numbers are indeed found to vary in response to environmental variation such as food availability: Red-footed boobies (*Sula sula*) were more likely to skip breeding in years with an El Niño event, probably because higher sea surface temperatures resulted in decreased food supply (Cubaynes et al., 2011); Arctic-breeding predators like snowy owls (*Bubo scandiacus*) and Arctic foxes (*Vulpes lagopus*) are known to reproduce in higher numbers in years with high food abundance, often related to lemming peaks (Gilg et al., 2006); and large groups of geese were observed as non-breeders in years with late snowmelt on their breeding grounds, presumably because forage plants were inaccessible and nesting sites limited (Dickey et al., 2008; Reed et al., 2004).

Environmental conditions are more variable at high latitudes both within and between years (Lisovski et al., 2017) and might therefore have a stronger impact on the breeding propensity of Arctic-breeding populations. Timing of snowmelt and onset of spring can show considerable year to year variation. Additionally, many Arctic-breeding species are migratory, which means they will have to predict conditions on the breeding grounds from a distance (Knudsen et al., 2011; Shariati-Najafabadi et al., 2016). Herbivorous species such as geese depend on the timing of vegetation development, which is strongly influenced by environmental conditions (van der Graaf et al., 2006). Kölzsch et al. (2015), show that predictability of conditions on stopover sites and the breeding grounds is affected by ecological barriers, and that arrival of geese was better matched with spring phenology when predictability was high. Arriving too early at the breeding grounds can be costly, potentially affecting survival and reproductive output through smaller clutch size, increased egg predation risk and lower breeding probability (Bêty et al., 2004; Lepage et al., 2000). Arriving too late on the other hand might result in a phenological mismatch, compromising the growth and survival of offspring (Doiron et al., 2015; Lameris, van der Jeugd, et al., 2018; Lindholm et al., 1994; van der Jeugd et al., 2009). It is therefore possible that spring phenology and relative timing of arrival affect the decision to breed, especially at high latitudes. Consequently, variation in breeding propensity might contribute to the observed variability in breeding output of Arctic-nesting geese (Fox & Leafloor, 2018), and understanding the influence of conditions on the breeding grounds on breeding propensity is essential to assess the impact of climatic changes on population dynamics. In addition, with ongoing range shifts in goose populations (Feige et al., 2008; Pennington, 2000), it is of interest to study whether breeding propensity may vary with breeding location.

In this study, we use a novel method to estimate breeding propensity of barnacle geese (*Branta leucopsis*) breeding along a latitudinal gradient based on GPS tracking data. By using tracking data, we omit the observation bias introduced by detection issues of non-breeding birds. Additionally, it allows for estimating breeding attempts over the entire breeding range of the barnacle goose. The original breeding grounds of the barnacle goose were restricted to the Arctic region, but over the past decades, the species has expanded its breeding range to the south-west, along their migratory route. The current breeding range spans over 20° of latitude, from the temperate region in the South-West of the Netherlands up to Novaya Zemlya in the high Arctic. Geese breeding in the Arctic remain long-distance migrants, whereas geese breeding in the temperate zone shortened their migration distance or became residents. In addition to breeding propensity, we use tracking data to estimate nesting success. Nesting success is an important fitness component which can give insight in the chance of successful breeding, which is expected to play a role in the decision to breed. We test if onset of spring on the breeding grounds and relative timing of arrival have a positive or negative effect on breeding propensity and nesting success, and study whether these relationships change with latitude.

## 2 | METHODS

We collated tracking data (GPS and accelerometer when available) of 96 adult female barnacle geese. This data set includes geese with various life-history tactics, ranging from long-distance migrants breeding in the Arctic (above 66° N) to short-distance migrants and residents in the temperate zone (between 51° N and 66° N). Birds were caught and equipped with GPS transmitters on the breeding grounds in the Arctic in 2014 and 2018 ($N = 6$; 68°34′ N, 52°18′ E), on breeding grounds in the temperate zone (residents) in 2015–2018 ($N = 7$; 51°47′ N, 4°08′ E) and on the wintering grounds in the North of the Netherlands and North Germany in 2016–2020 ($N = 72$). Additionally, we retrieved tracking data from Kölzsch et al. (2015) gathered in 2008–2010 ($N = 11$), which is published on movebank.org (van der Jeugd et al., 2014). In winter, geese were caught using cannon-nets, while in summer, geese were captured either on the nest using clap-nets or by rounding geese up in a catching pen during the wing moult when geese are flightless. Throughout the study period, geese were equipped with different transmitter types: Milsar (24 g, GSMRadioTag, Milsar Technologies S.R.L.; $N = 1$), UvA-BiTS (19 g, Bouten et al., 2013; $N = 11$), Madebytheo (27 g, $N = 24$), Ornitela (25 g, $N = 47$) and solar Argos/GPS PTTs (30 g, $N = 13$, Kölzsch et al., 2015). Transmitters were attached using a 16-gram Teflon harness (Lameris et al., 2017), with total mass of transmitter and harness being <3% of the average body mass of a female barnacle goose. The GPS-tags used by Kölzsch et al. (2015) were attached using a comparable nylon harness. The use of this harness did not appear to affect migration timing or breeding propensity of local moulting birds (see Supplementary Materials and Lameris, Müskens, et al., 2018). Lameris, Müskens, et al. (2018) do report a lower return rate for birds equipped with harnesses, which could be an indication of reduced breeding propensity due to harness attachment (Reed et al., 2005), but in barnacle geese, this effect appeared to be limited (0.45 compared to 0.55 for the control group).

### 2.1 | Determining nest locations

We followed methods outlined in Schreven et al. (2021) to determine nest locations based on GPS locations and, when available, accelerometer (ACC) data. This method uses the typical behaviour of incubating geese: low mobility (daily variation in location) as well as little body motion (dynamic body acceleration) to identify the location where a female goose had a nest.

We selected data from the period between 1st April and 31st July, during which barnacle geese of different breeding populations initiate nesting (van der Jeugd et al., 2009). We subsampled data to 1 GPS-fix every 15 min to make transmitters with different sampling regimes comparable. All tracks had tracking information for at least 112 days within the 122-day period. ACC data were not available for all tracks, due to differences in transmitter type as well as settings used. When ACC data were available (Ornitela, UvA-BiTS; 78 tracks), we defined a potential nest location as the median coordinates of GPS-fixes at which the goose was motionless, on days when the goose was mostly motionless (see Schreven et al., 2021). We used ACC measurements which were taken simultaneously with GPS positions, or if ACC was not measured simultaneously, we took the nearest ACC-measurement with maximum 10 min time difference. We used VeDBA as measure of activity (Dokter et al., 2018). To deal with the differences in accelerometer types as well as burst length and burst frequency (see Supplementary Information), the threshold in VeDBA below which a goose was categorized as motionless was set per transmitter type, at: 24 (Milsar), 16.5 (Ornitela) and 26.5 (UvA-BiTS) following methods by Boom, Lameris, et al. (2023). For tracks where ACC-measurements were not available (78 of 154 tracks), we used the GPS-only method (see Schreven et al., 2021, who showed that this method worked well in comparison with the GPS- and ACC-based nest detection), defining a potential nest location as the median coordinates of GPS-fixes on days when the standard deviation in latitude was below 50 m. For each potential nest location, we calculated the time spent per day within 50 m of the nest. These locations were classified as nest when at least 4 subsequent days had >75% attendance within 50 m, allowing for differentiation between non-breeding and early nest failure (after first 4 days). Tracks of geese for which no nesting location could be determined (because no nest location was assigned which the goose attended for at least 4 days) were considered non-breeding tracks ($N = 81$).

## 2.2 | Nesting success

The start of breeding was defined as the first day with >75% attendance within 50 m of the assigned nest location. When nest attendance was >75% for 26 days or longer, the nest was considered to have hatched, because 26 days was determined as the minimum required incubation period for barnacle geese (Cramp & Simmons, 1979; Eichhorn et al., 2010). In the case of a long incubation period likely due to non-viable eggs, the nest was categorized as hatched for this analysis, because the female was capable of completing the incubation period.

## 2.3 | Potential nest locations of non-breeders

In addition to information on the locations of breeding birds, analysing differences in breeding propensity in relation to latitude and local spring conditions requires information on the potential nest location of each non-breeding bird as well. To retrieve information on location (latitude), timing of arrival and spring phenology for non-breeding bird tracks ($N = 81$), we therefore needed to estimate the most likely potential nest location of non-breeding birds (hereafter referred to as 'potential nest location'). Although site fidelity in Arctic-breeding waterfowl is considered to be high (Owen & Black, 1991), the majority of the birds in our data set were captured on the wintering grounds and, therefore, we lack prior information on breeding locations. Furthermore, long-range shifts in breeding location have been observed in this species (Lameris, 2020). To determine the potential nest locations, we therefore calculated for each non-breeding bird the similarity between its track and the tracks of breeding birds (i.e. those with an assigned nest, $N = 73$), which were considered to represent the potential breeding range. Tracks were subset to the period April–June and mean locations per day were taken, to decrease computation time. This period includes the periods of nest initiation for the whole latitudinal range (van der Jeugd et al., 2009). We used dynamic time warping (DTW), using the R package 'dtw' (Giorgino, 2009) to calculate trajectory similarities (Janoska, 2014). This method calculates the dissimilarity ('dtw distance') between two tracks based on the best alignment in the time dimension and was shown to outperform alternative approaches in a simulation study evaluating five common measures of trajectory similarity (Cleasby et al., 2019). The potential nest location of non-breeding birds was determined as the nest location of the most similar breeding bird (track of the bird with the lowest 'distance' as determined by the DTW-analysis). By making this assumption, we assign non-breeders to nesting locations in areas where geese do actually breed, and thereby avoid the assignment of unlikely breeding locations. Track dissimilarity was 0 for breeding birds (by definition, as the most similar track of a breeding bird was their own track) and ranged from 0.04 till 2.4 between non-breeding birds and the most similar breeding bird (Figure S1). After assigning the potential nest locations based on the DTW-analysis, we confirmed that, with this method, non-breeding tracks of birds that were found to be breeding in another year received the nest location of their breeding track as potential nest location (18 of 25 tracks).

## 2.4 | Arrival date

It is possible that birds either arrived too early or too late to be successful and skip breeding in a given year. We therefore needed to determine the date of arrival at the potential or real nest location for breeding and non-breeding birds respectively. For every track, arrival date was determined as the first day a goose was within 35 km of its assigned nest location (for breeders) or potential nest location (for non-breeders). A 35-km radius was considered to be sufficient, because over this distance, geese will probably get a reliable indication of the phenology at the nesting location (Shariati-Najafabadi et al., 2016). For all breeding birds, we calculated the interval between the date of arrival and the start of breeding. Not all non-breeding birds came within 35 km of the potential nest location. We concluded that for these 14 birds ($N = 13$ assigned to a nesting area 68° N or higher, $N = 1$ to 60° N), determination of a potential nest location was not reliable, and therefore, these birds were excluded from the analysis. The remaining non-breeding tracks had plausible potential nesting locations based on visual inspection of the non-breeding and most similar breeding track (Figure S2).

## 2.5 | Local onset of spring and relative timing of arrival

We derived information on the local onset of spring from temperature data for all years between 2008 and 2020. We used the R package RNCEP (Kemp et al., 2012) to retrieve temperature data from 1st January till 30th September for all assigned (breeders) and potential (non-breeders) nest locations. Air temperature (2 m above the surface) was retrieved from a 2.5° × 2.5° gridded data set with 6 h temporal resolution and interpolated using planar interpolation. We calculated the growing degree days (GDD) for every nest location. Due to the wide latitudinal range in our study, the threshold used to determine the GDD was latitude dependent, following a linear relationship ($T_{\mathrm{threshold}} = -0.25 \times \mathrm{Latitude} + 13$; see van Wijk et al., 2012). Subsequently, we fitted a sigmoid curve and derived the GDD jerk (third derivative) following van Wijk et al. (2012). The GDD jerk represents the acceleration of the spring temperature increase. By solving the derivative of the GDD jerk to zero, we determined the date of peak spring temperature acceleration (referred to as 'local onset of spring' from here on), which was found to correlate well with the timing of goose migration, snowmelt (van Wijk et al., 2012) and vegetation development (Smith et al., 2020), suggesting that it is an accurate predictor of the onset of spring.

To correct for variation in timing of onset of spring with latitude, local onset of spring was standardized. We calculated the local onset of spring for all years in the whole study period for every potential and real nest location, and subsequently calculated the mean and standard deviation for each location (Figure S3). Standardization was done by subtracting this mean from the local onset of spring in the tracked year and dividing this by the standard deviation.

The relative timing of arrival was calculated for every track by subtracting the date of the local onset of spring from the date of arrival at the potential or real nest location for breeding and non-breeding birds, respectively (hereafter referred to as 'relative arrival'), resulting in negative values for birds arriving before the local onset of spring and positive values for birds arriving later than the local onset of spring. Because resident birds stay close to the breeding grounds year round, they were excluded from analyses with relative arrival.

## 2.6 | Statistical analysis

All statistical analyses were performed in R 4.0.5 (R Development Core Team, 2021), within the R-studio platform. To test whether local onset of spring or relative arrival had a positive or negative effect on breeding propensity, and whether this effect varied with latitude we constructed Mixed Effects logistic regression models using the 'lme4' package in R (Bates et al., 2014), using a LogitLink function. The binary variable describing breeding attempt (yes/no) was used as a dependent variable. All explanatory variables (latitude, local onset of spring, relative arrival) were included as continuous variables and were standardized to avoid scaling problems: Local onset of spring was standardized for each location over the study period (see above); latitude and relative arrival were standardized within the data set. We constructed separate models for relative arrival and local onset of spring, because the variables are likely to be correlated, especially at higher latitudes. We included quadratic terms for local onset of spring and relative arrival to allow for a potential optimum. Interactions between latitude and relative arrival, and latitude and local onset of spring were included in the models. Individual (Bird_ID) was included as random effect. We performed model selection using AICc favouring the most parsimonious model within two ΔAIC from the best model. We first ran the model selection on a data set excluding the resident birds, to see if relative arrival was an important predictor. When relative arrival appeared less important than local onset of spring, we reran the model selection using the whole data set on the models without relative arrival.

To determine the effect of latitude and local onset of spring on nesting success, we analysed data from the breeding birds only. We constructed similar models as described for breeding propensity, this time with hatching (yes/no) as dependent variable. Including a random effect for individual (Bird_ID) resulted in singular models, because only a few birds in our data set were breeding in multiple years. We therefore omitted the mixed effect structure and excluded the random effect.

# 3 | RESULTS

The 96 tagged females gave a total of 154 tracks to the breeding grounds. After exclusion of the tracks that did not yield a reliable potential breeding location, 140 tracks remained. Of these 140 tracks, we determined 73 nest locations, of which 14 where located in the temperate zone and 59 above the Arctic Circle (Figure 1), and 67 potential breeding locations of non-breeding birds, of which three where located in the temperate zone and 64 above the Arctic Circle.

## 3.1 | Breeding propensity

The onset of spring (whether spring started early or late) was a more important predictor of breeding propensity than relative arrival (whether birds arrived early or late relative to the onset of spring), as all models containing local onset of spring outperformed models with relative arrival (Table S1). The best model (based on analysis of the whole data set including resident birds) included latitude, local onset of spring and their interaction (Table 1, Table S2), indicating that the effect of local onset of spring depended on latitude. In the Arctic, breeding propensity decreased rapidly in later springs, with a stronger decrease with increasing latitude varying between 0.89 (95% CI: 0.65–0.97) and 0.22 (95% CI: 0.06–0.55) at 68° N, and between 0.88 (95% CI: 0.64–0.97) and 0.02 (95% CI:

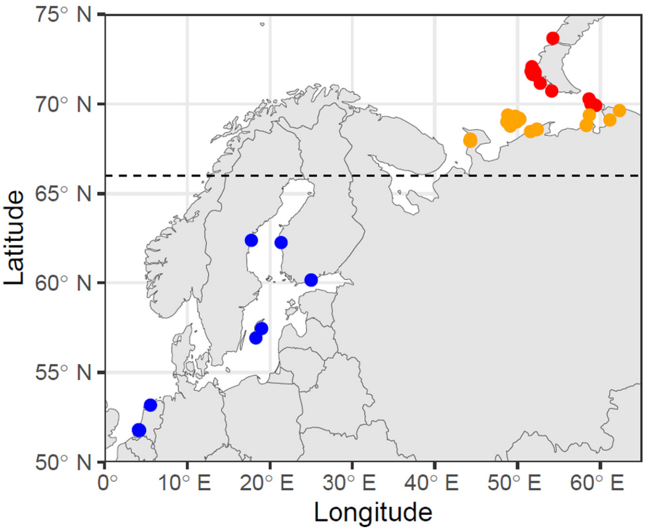

FIGURE 1 Map (Mercator projection) depicting the 73 breeding locations determined based on tracking data. Blue points (14) represent the nests in the temperate zone (51°–66° N), yellow points (32) nests in the Arctic on Kolguev island and the Russian mainland (66°–70° N), red points (27) nests on Vaigach and Novaya Zemlya (70°–74° N). The dashed line indicates the Arctic Circle. Note that points may overlap. Note that latitude was included as continuous variable in the analysis and colours are used for visualization purposes only.

0.00–0.19) at 72° N. This effect was consistent in models based on Arctic-breeding birds only (Table S3). At temperate latitudes, breeding propensity remained stable (between 0.75 [95% CI: 0.38–0.93) and 0.89 (95% CI: 0.41–0.99]) regardless of spring phenology (Figure 2).

**TABLE 1** Model results of the best performing logistic regression models explaining the breeding propensity and nesting success in relation to latitude and local onset of spring (standardized GDD jerk), based on the full dataset. Significant values ($p < 0.05$) are indicated in bold. Note that the model for nesting success did not have a random effect structure.

| Breeding propensity | Estimate | s.e. | *z*-value | *p*-value |
|---|---|---|---|---|
| (Intercept) | 0.12 | 0.31 | 0.68 | 0.660 |
| Latitude | −1.44 | 0.63 | −2.3 | **0.021** |
| GDD jerk | −0.93 | 0.38 | −2.46 | **0.014** |
| Latitude × GDD jerk | −1.28 | 0.63 | −2.03 | **0.043** |

*Random effects: Bird_ID (variance = 1.27; SD = 1.13), N = 140, Bird_ID = 90*

| Nesting success | Estimate | s.e. | *z*-value | *p*-value |
|---|---|---|---|---|
| (Intercept) | 0.84 | 0.35 | 2.41 | **0.016** |
| latitude | −1.3 | 0.78 | −1.68 | 0.094 |
| GDD jerk | −0.37 | 0.3 | −1.22 | 0.220 |
| latitude × GDD jerk | −1.4 | 0.71 | −1.91 | 0.057 |

*Note*: N = 73.

## 3.2 | Nesting success

The patterns for nesting success were similar to those found for breeding propensity; models containing local onset of spring generally outperformed the models containing relative arrival as explanatory variable (Table S4). The best performing model (based on analysis of the whole data set including resident birds) contained local onset of spring, latitude and their interaction (Table 1, Table S5). Like breeding propensity, nesting success showed a decrease with later onset of spring at Arctic latitudes (Figure 3). This effect was not consistent in models based on Arctic-breeding birds only (Table S6), indicating that the effect of onset of spring was similar across Arctic latitudes. At temperate latitudes, nesting success appeared lower in early springs (see discussion), but was generally high, regardless of spring phenology.

# 4 | DISCUSSION

Our analysis shows that, in the Arctic, breeding propensity and nesting success of barnacle geese are higher in earlier springs, but are not affected by relative time of arrival on the breeding grounds. This effect of spring phenology is dependent on latitude: within the Arctic, the effects of local onset of spring become stronger at higher latitudes, whereas breeding propensity and nesting success are generally high in temperate breeding regions where the effect of spring phenology appeared less important.

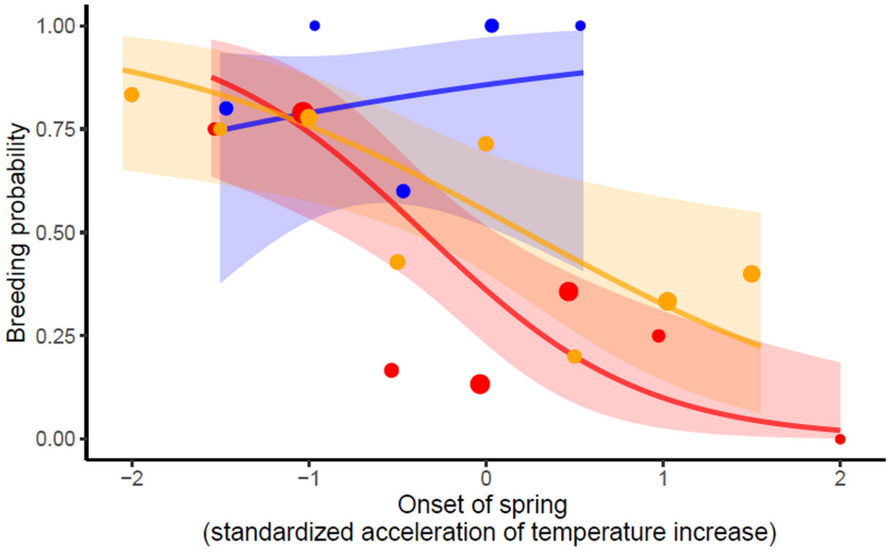

**FIGURE 2** Breeding propensity (probability of breeding) in relation to local onset of spring at three different latitudes (grouped for visualization purposes). Onset of spring was determined as the standardized GDD jerk (acceleration of temperature increase, see main text). Points correspond to the average probability of breeding in 0.5 wide bins of standardized GDD jerk, with size indicating sample size (smallest = 1, largest = 19). Colours of the points represent the latitudinal range 51°–66° N (blue), 66°–70° N (yellow) and 70°–74° N (red). Lines (including 95%-confidence bands) are based on the predictions from the most parsimonious model including local onset of spring, latitude and their interaction for three different latitudes: 62° N (blue), 68° N (yellow) and 71° N (red).

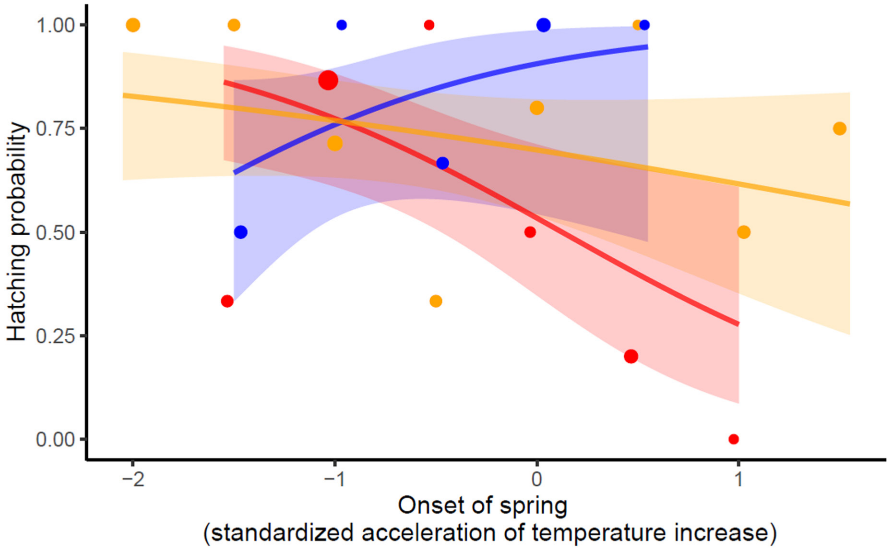

**FIGURE 3** Nesting success (probability of hatching at least 1 egg) in relation to local onset of spring at three different latitudes (grouped for visualization purposes). Onset of spring was determined as the standardized GDD jerk (acceleration of temperature increase, see main text). Points correspond to the average probability of hatching in 0.5 wide bins of standardized GDD jerk, with size indicating sample size (smallest = 1, largest = 17). Colours of the points represent the latitudinal range 51°–66° N (blue), 66°–70° N (yellow) and 70°–74° N (red). Lines (including 95%-confidence bands) are based on the predictions from the most parsimonious model including local onset of spring, latitude and their interaction for three different latitudes: 62° N (blue), 68° N (yellow) and 71° N (red).

## 4.1 | Breeding propensity

The impact of local onset of spring on breeding propensity in the Arctic increased with latitude (which was modelled as continuous variable). It is possible that wearing a harness attached GPS device affected our breeding propensity estimates, and therefore, they should be interpreted with caution. However, in barnacle geese flying 3000 km to their breeding grounds, this effect appeared limited to a lower return rate (0.45 compared to 0.55 for the control; Lameris, Müskens, et al., 2018), and 17 of 18 returning tracked geese commenced breeding (see Supplementary Information). This lower return rate could represent a reduction in breeding propensity, when non-breeding birds spent the breeding period elsewhere (Reed et al., 2005), but is not in the order of magnitude of the effect of onset of spring we found. Furthermore, the impact of wearing a tracking device is unlikely to affect the relationship with onset of spring at different latitudes. Our estimates of breeding propensity in barnacle geese breeding at Arctic latitudes are comparable with findings in greater snow geese breeding at 73° N, where breeding propensity varied between 1.0 and 0.13 and depended on the timing of snowmelt (Reed et al., 2004). The importance of spring phenology has also been suggested by Prop and de Vries (1993), who reported a larger proportion of breeding birds in a local population on Svalbard in years with early snowmelt. Similar effects of spring phenology have been found in Arctic-breeding waders, where the probability of laying a full clutch of four eggs decreased in years with later snowmelt (Weiser et al., 2018).

In seabirds, intermittent breeding is common, and the probability that birds skip a breeding season has been found to be related to food availability around the breeding area (Chastel, 1995; Cubaynes et al., 2011). For migratory waterfowl, this relation is often found to be less clear, probably because many species can use a capital strategy, using body stores accumulated on spring staging sites (Ankney & Macinnes, 1978; Gauthier et al., 2003; Jönsson, 1997). In addition to conditions at spring staging sites, conditions encountered during migration are suggested to play an important role for breeding propensity in long-distance migrants such as Arctic-breeding geese (Cunningham et al., 2023). Adverse weather conditions *en route* are known to cause mortality (Loonstra et al., 2019; Newton, 2008), delay arrival at breeding grounds and negatively affect body condition upon arrival (Drent et al., 2006; Lack, 1968; Ma et al., 2011) and can thus carry over to affect breeding propensity. For example, in common eiders, body condition upon arrival was determined as the key driver for the decision to breed or not (Legagneux et al., 2016).

However, our finding of higher breeding propensity in the Arctic in earlier springs is consistent with the idea that breeding propensity in barnacle geese is driven by local food availability and conditions prior to arrival. In years with late springs, Arctic-breeding geese rely more on capital (Hupp et al., 2018), and only individuals that arrive with sufficient body stores might be able to breed (Anderson et al., 2015). When spring is early, geese that initially arrive with insufficient body stores can use local foraging opportunities to acquire resources for egg production and incubation (Gauthier et al., 2003; Hupp et al., 2018; Klaassen et al., 2006), allowing more individuals to breed. Lameris, van der Jeugd, et al. (2018) show that in years with early springs, Arctic-breeding barnacle geese do not advance the timing of breeding as much as timing of arrival, resulting in a longer interval between arrival and breeding. The geese used this period to forage locally and allocated more local resources in their eggs. This comes at the cost of nesting later relative to the onset of spring, which might compromise gosling growth (Boom et al., 2022; Doiron et al., 2015; Nolet et al., 2020) and gosling survival through a trophic mismatch (Lameris, van der Jeugd, et al., 2018).

Our data set is not suitable for directly analysing the relation between the arrival-breeding interval and local onset of spring, because the large spatial variation in nest locations and varying temporal coverage of these locations introduces noise. Although we cannot formally test for a relationship between onset of spring and the arrival-breeding interval, we do observe the expected longer interval in years with relatively early springs at Arctic latitudes (Figure S4), which is consistent with findings of Lameris, van der Jeugd, et al. (2018) who only partly used the same data (13 of 154 tracks). Arrival-breeding intervals also appeared shorter at higher latitudes, consistent with findings in pied flycatchers (Nicolau et al., 2021), likely because of the strong time pressure due to the shorter breeding season further north. This can also explain the lack of detected nest attempts in years with late onset of spring above 70° N (Figure 2), when time might be insufficient to raise a brood before winter conditions set in (Barry, 1962). Alternatively, this pattern could be explained by nest-site availability. When snowmelt is late, a larger proportion of nesting sites might be covered with snow when birds arrive, thereby limiting breeding numbers (Lindberg et al., 1997).

At temperate latitudes, breeding propensity showed no clear relation to local onset of spring and varied around 0.75 (95% CI: 0.38–0.93) and 0.89 (95% CI: 0.41–0.99). It is important to note that our sample size at temperate latitudes was limited (17 tracks in total), making it impossible to further disentangle differences within temperate latitudes. At temperate latitudes, geese experience no (or at least strongly reduced) costs of migration, which might allow for a higher breeding propensity compared to Arctic latitudes. Additionally, the temperate resident population is small in comparison to the Arctic population and increasing (van der Jeugd et al., 2009), which indicates that nesting site availability is probably not limited yet. At temperate latitudes, the onset of spring is probably less crucial in determining nesting site availability and food availability. Due to the mild climate at temperate latitudes in Europe, access to food and nesting sites is usually not restricted by snow cover. Additionally, temperate breeding geese can adjust timing of breeding to spring temperatures (Clermont et al., 2018; van der Jeugd et al., 2009). Besides a milder climate, agricultural intensification increased the nutritional value of the food available for barnacle geese in the temperate region, reducing the importance of natural vegetation development (Eichhorn et al., 2012; van Eerden et al., 2005). This more stable food supply might facilitate the high breeding propensity at temperate latitudes, which is also indicated by laying dates which are late relative to the onset of spring and less synchronized than in Arctic-breeding geese (van der Jeugd et al., 2009). Furthermore, the breeding season in the temperate region is longer than in the Arctic, allowing temperate goslings enough time to reach fledging size despite growing slower than goslings in the Arctic, where daylight no longer restricts feeding time due to the 24 h polar day (Boom et al., 2022). Post-fledging survival was also found to decrease rapidly in the Arctic with hatch date, but remained high in temperate breeding geese (van der Jeugd et al., 2009). While for temperate breeding geese reproductive success thus seems independent of spring phenology, the trade-off between current and future reproduction appears strongly related to spring phenology for Arctic-breeding geese.

## 4.2 | Nesting success

The importance of spring phenology for successful breeding in the Arctic is illustrated by the decrease in nesting success with later local onset of spring. This is consistent with findings in pink-footed geese and barnacle geese breeding on Svalbard, where nesting success (determined as hatching a nest with at least 1 young) was found to decrease with later snowmelt and colder temperatures (Layton-Matthews et al., 2020; Madsen et al., 2007). Lameris et al. (2019) only found a decrease in nesting success with later snowmelt in a high Arctic barnacle goose colony (on Svalbard), but not in the low Arctic (at 68° N). In our analysis, the effect of onset of spring appeared similar across Arctic latitudes (Table S6). In years when spring is late and temperatures are lower, longer or more frequent nest recesses may be needed to maintain body condition to fuel incubation (Aldrich & Raveling, 1983), leaving nests vulnerable to predation (Bêty et al., 2002; Samelius & Alisauskas, 2000), which might explain the lower nesting success.

At temperate latitudes, nesting success was generally high, as all of the nests of resident geese were estimated to have hatched successfully. Lower nesting success at temperate latitudes mainly occurred in birds nesting around the Baltic Sea. Nest attentiveness in resident temperate breeding barnacle geese was found to be higher than in Arctic-breeding barnacle geese (Eichhorn et al., 2010), likely because the resident geese commenced incubation in better condition, which might result in lower predation risk and subsequent high nesting success. For geese breeding around the Baltic Sea, predation risk might have a large impact on nesting success. The exponential increase in White-tailed eagles (*Haliaeetus albicilla*) since 1990 (Herrmann et al., 2009) has resulted in an increased predation risk (Jonker et al., 2010), which is considered to have had a large impact on the breeding population (K. Larsson unpubl.). Eagles are capable of predating breeding pairs. Additionally, a single eagle attack can disturb multiple breeding females (who nest close together), leaving multiple nests exposed to potential egg predators like gulls (T.K. Lameris, B.A. Nolet & M.P. Boom, pers. obs.).

## 4.3 | Breeding propensity and implications for population dynamics

Our results indicate that spring phenology can have a large impact on breeding propensity and nesting success, two key parameters in determining breeding output. While other studies have estimated breeding propensity based on resighting probabilities (e.g. Schmutz and Morse (2000), Legagneux et al. (2016)), such an approach is prone to biased estimates and caution is warranted when using these estimates in demographic models (Lee et al., 2017). We show that tracking data offer a new way of estimating breeding propensity, while omitting the resighting bias. We also demonstrate the use of tracking data in estimating nesting success. The use of traditional nest monitoring data might lead to overestimating nesting success, because unsuccessful nest might have been abandoned before they are found (but see Mayfield, 1961; Verhoeven et al., 2020). Nesting success based on tracking data might therefore give a more accurate estimate.

The effect of local onset of spring on breeding propensity was more pronounced at high latitudes, while at temperate latitudes, breeding propensity was high regardless of spring phenology. Climate warming is most pronounced in the Arctic, leading to earlier springs (Cohen et al., 2014; Pithan & Mauritsen, 2014). While it is often considered that earlier springs have mainly negative impacts on reproductive success through the increase in phenological mismatches (Doiron et al., 2015; Lameris, van der Jeugd, et al., 2018), these may potentially be compensated for by an increase in breeding propensity and nesting success (Nolet et al., 2020). Furthermore, earlier springs might open up additional breeding opportunities at places that were previously snow-free too late in the season, facilitating population growth (Jensen et al., 2008; Lameris et al., 2022; Madsen et al., 2023). Therefore, in order to evaluate the impact of climate warming on population viability, it is essential to consider the effect of climatic variability on all aspects determining reproductive output.

## AUTHOR CONTRIBUTIONS

Michiel P. Boom and Kees H. T. Schreven conceptualized the study; Michiel P. Boom, Nelleke H. Buitendijk, Sander Moonen, Götz Eichhorn and Thomas K. Lameris collected and provided data; Michiel P. Boom and Kees H. T. Schreven analysed the data; Bart A. Nolet, Henk P. van der Jeugd and Thomas K. Lameris advised on the analysis; Michiel P. Boom, Kees H. T. Schreven and Thomas K. Lameris discussed the interpretation of the results; Michiel P. Boom wrote the initial manuscript; all authors provided comments and contributed to the final version of the manuscript.

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## CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interests to declare.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.m63xsj47x (Boom, Schreven, et al., 2023).

## ETHICS STATEMENT

Tagging geese in the Netherlands and Russia was approved by the Animal Welfare committees of the Royal Netherlands Academy for Arts and Sciences (licence 20173788) and the St. Petersburg State University (decision nr. 131-03-2 from 3 April 2018). Approval for tagging geese in Northern Germany (Lower Saxony) was obtained from the Lower Saxony State Office for Consumer Protection and Food Safety (LAVES AZ 33.19-42502-04-15/1956 dated.15.9.2015).

## ORCID

*Michiel P. Boom* https://orcid.org/0000-0002-6448-2446
*Kees H. T. Schreven* https://orcid.org/0000-0002-0550-7447
*Nelleke H. Buitendijk* https://orcid.org/0000-0002-4476-485X
*Sander Moonen* https://orcid.org/0000-0002-7315-1593
*Bart A. Nolet* https://orcid.org/0000-0002-7437-4879
*Götz Eichhorn* https://orcid.org/0000-0003-2151-8856
*Henk P. van der Jeugd* https://orcid.org/0000-0002-5332-9526
*Thomas K. Lameris* https://orcid.org/0000-0001-7023-3406

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Figure S1.** Dissimilarities for each track and the most similar breeding track determined by the dynamic time warping analysis, ranked on dissimilarity distance. Values of 0 represent breeding tracks, with the most similar breeding track being identical.

**Figure S2.** Examples of non-breeding tracks (black) and their most similar breeding track (red) for four different dissimilarities. The red dot indicates the breeding location determined for the breeding track, and assigned to the non-breeding track. Note that the projection may obscure track differences, especially in the east-west direction at high latitudes.

**Figure S3.** Local onset of spring (mean GDD jerk ± SD) in relation to latitude (a) and longitude (b). Colours show locations in the temperate region (blue) Kolguev and the Russian mainland (yellow) and Vaigach and Novaya Zemlya (red).

**Figure S4.** Relation between local onset of spring and the arrival-breeding interval (mean ± SD) in the Arctic. Points represent the arrival-breeding interval grouped at three different latitudes for visualization purposes: 67°–68.5° N (black; $N=7$), 68.5°–70° N (yellow; $N=36$) and 70°–74° N (red; $N=16$, with 14 observation between 70° and 72° N). Dashed lines show the linear relationship between onset of spring and arrival-breeding interval (not tested for significance, see main text).

**Figure S5.** (Reproduced from Boom et al., 2023): Probability density histograms for the VeDBA of the four transmitter types used in this study. Green lines give the probability density functions, red lines show the fitted gamma distributions. Red triangles indicate the mid points of the gamma distributions for inactive and active behaviour. Dashed vertical lines indicate the thresholds used to distinguish VeDBA values indicating active and inactive behaviour (24, 16.5, 29 and 26.5 respectively).

**Table S1.** Model selection results based on the GLMMs on breeding propensity in relation to latitude, local onset of spring (GDD_jerk) and relative arrival (rel_arrival). All models included an intercept as well as random effects for individual (Bird_ID). All fixed effects were standardized (see main text). Resident birds were excluded from this analysis.

**Table S2.** Model selection results based on the GLMMs on breeding propensity in relation to latitude and local onset of spring (GDD_jerk) on the whole dataset (including resident birds). All models included an intercept as well as random effects for individual (Bird_ID). All fixed effects were standardized (see main text). The best performing (most parsimonious) model is given in bold.

**Table S3.** Model selection results based on the GLMMs on breeding propensity in relation to latitude and local onset of spring (GDD_jerk) on Arctic-breeding birds (above 66° N) only. All models included an intercept as well as random effects for individual (Bird_ID). All fixed effects were standardized (see main text). The best performing (most parsimonious) model is given in bold.

**Table S4.** Model selection results based on the GLMs on nesting success in relation to latitude, local onset of spring (GDD_jerk) and relative arrival (rel_arrival). All models included an intercept. All fixed effects were standardized (see main text). Resident birds were excluded from this analysis.

**Table S5.** Model selection results based on the GLMs on nesting success in relation to latitude and local onset of spring (GDD_jerk) on the whole dataset (including resident birds). All models included an intercept. All fixed effects were standardized (see main text). The best performing (most parsimonious) model is given in bold.

**Table S6.** Model selection results based on the GLMs on nesting success in relation to latitude and local onset of spring (GDD_jerk) on Arctic breeding birds (above 66° N) only. All models included an intercept. All fixed effects were standardized (see main text). The best performing (most parsimonious) model is given in bold.

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