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Low breeding propensity in a declining Arctic-breeding swan revealed by telemetry data

TOHAR TAL,*[1] BART A. NOLET,[1,2] TOM S.L. VERSLUIJS,[3,4] JUDY Z. SHAMOUN-BARANES,[1] GÖTZ EICHHORN,[5] SABINE URBAN[5] & HANS LINSSEN[1,2]

[1]*Department of Theoretical and Computational Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands*

[2]*Department of Animal Ecology, Netherlands Institute of Ecology, Wageningen, The Netherlands*

[3]*Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, Den Burg, The Netherlands*

[4]*Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands*

[5]*Michael-Otto-Institut im NABU, Bergenhusen, Germany*

Many migratory bird populations are declining in the face of habitat degradation and climate change, making it important to identify which stages of their annual cycle are most affected in order to guide conservation measures. The Bewick's Swan *Cygnus columbianus bewickii*, an Arctic-breeding waterfowl species, has suffered a dramatic population decline (from approximately 30 000 individuals in 1995 to around 13 000 in 2020) due to low reproductive output. However, it is unknown which component of reproduction (breeding propensity, nesting success and post-hatching survival) is the underlying cause. We analysed GPS tracking and accelerometer data from over 60 adult female Bewick's Swans collected over 8 years, to derive breeding propensity (i.e. the decision to breed or not) and nesting success (i.e. completing incubation) at the individual level, and assess how these metrics are influenced by onset of spring and migration timing. The odds of breeding increased by 3.9% (estimate = −0.04, se = 0.02, $P = 0.04$) for each day that the swans arrived earlier at the breeding grounds. The odds of successfully nesting increased by 5.8% (estimate = −0.06, se = 0.03, $P = 0.06$) per day of earlier snowmelt anomaly, suggesting a slight positive effect of climate warming on nesting. However, the proportion of breeding females was consistently low throughout the study period, suggesting that other factors may be driving the long-term population decline of the species by negatively impacting breeding propensity. Our study shows that distinguishing between different phases of the reproductive cycle is critical for a better understanding of the causes of migratory population declines in a changing world.

Keywords: Arctic warming, bio-logging, incubation, migration, waterfowl.

Migratory birds face the challenge of navigating multiple habitats, biomes or even entire continents each year, while encountering pressures from human activity (McCulloch *et al.* 1992, Nemes *et al.* 2023), habitat degradation (Ockendon *et al.* 2012, Walther 2016) and environmental change (Lameris *et al.* 2018, Robertson *et al.* 2024) throughout their journey. These pressures are reflected in the fact that approximately half of all migratory species are threatened or declining (Kirby *et al.* 2008, Bairlein 2016, Zurell *et al.* 2018, Lees *et al.* 2022). To address these concerns effectively, it is crucial to identify which stages of the annual cycle are negatively impacted and to understand how these stages influence one another (Martin *et al.* 2007, Reynolds *et al.* 2017, Nolet *et al.* 2020, Schindler *et al.* 2024, Pöysä 2025).

*Corresponding author.
Email: tohar@hotmail.nl

Twitter id: @Tohar_Tal

Long-distance Arctic migrants that breed at higher latitudes are often thought to be of particular concern (Hof *et al.* 2017, Wauchope *et al.* 2017, Kubelka *et al.* 2022) because global warming occurs much faster in the Arctic than at lower latitudes ('Arctic amplification', Pithan & Mauritsen 2014, Rantanen *et al.* 2022). Warming causes an advancement in the onset of spring, which can lead to a mismatch between the timing of reproduction and local resource availability (Tulp & Schekkerman 2008, Thackeray *et al.* 2016, Inouye 2022), potentially impairing reproductive success (Lameris *et al.* 2018). However, the remoteness of their breeding ranges, where some Arctic migrants spend up to half of the annual cycle, makes it particularly challenging to monitor key aspects of their life history that drive population dynamics.

The reproductive output of a population depends on successful reproduction by individual birds, which in turn relies on a sequence of steps, each contingent on the previous one: breeding propensity (the decision to breed or not), nesting success (completion of incubation until hatching) and hatchling or fledgling survival, with overall productivity being the product of these components (Nolet *et al.* 2020). While nesting success and offspring survival are among the most studied aspects of bird population biology, breeding propensity, despite its influence on population dynamics (Acker *et al.* 2022), has received less attention (Nicol-Harper *et al.* 2023), largely due to the inherent difficulty of identifying non-breeding birds and investigating potential reasons for why those birds did not breed.

In Arctic migrants, breeding propensity can be influenced by environmental conditions on the breeding grounds (Reed *et al.* 2004, Dickey *et al.* 2008, Anderson *et al.* 2015, Boom *et al.* 2023), predator pressure (Spaans *et al.* 1998), competition (Catlin *et al.* 2019, Acker *et al.* 2022), or intrinsic factors such as age or breeding success in previous years (Cam *et al.* 1998, Pradel *et al.* 2012, Warren *et al.* 2014). Especially in long-lived species, individuals may purposefully abstain from breeding in years when conditions are unfavourable (Nichols *et al.* 1994, Spaans *et al.* 1998, Syroechkovsky *et al.* 2002, Shaw & Levin 2013, Souchay *et al.* 2014, Tavera *et al.* 2020, Grandmont *et al.* 2023) to maximize their survival until the next season and thereby their lifetime reproductive success (Stearns 2000). Especially in the context of declining populations and rapid environmental change, incorporating breeding propensity into studies of breeding success is crucial when identifying key drivers of decline and understanding long-term population viability.

Advanced animal tracking technologies allow for the collection of detailed data on animal movement and behaviour throughout the annual cycle, including in remote regions (Kays *et al.* 2015, Shamoun-Baranes & Camphuysen 2025). This has made it possible to monitor various reproductive phases of Arctic-breeding birds, for example, to identify breeding attempts and derive nesting success (Picardi *et al.* 2020, Schreven *et al.* 2021, Ozsanlav-Harris *et al.* 2022, Boom *et al.* 2023, Cunningham *et al.* 2023, Ferraz *et al.* 2024, Oppel *et al.* 2025), thereby enabling population-level estimates of reproductive metrics (Murgatroyd *et al.* 2023, Solovyeva *et al.* 2025). Such approaches have opened a previously unavailable window of opportunity for understanding and addressing declines in Arctic-breeding bird populations, by enabling separate assessment of key reproductive phases and identifying where potential conservation efforts are needed the most.

The Bewick's Swan *Cygnus columbianus bewickii* is a long-lived migratory bird, with the Western Palearctic flyway population breeding on the coastal tundra of European Russia and wintering in northwestern Europe. This population of Bewick's Swans has declined strongly from approximately 30 000 individuals in 1995 to around 13 000 in 2020 (Rees & Beekman 2010, Beekman *et al.* 2019, Rees & Clausen 2024, Koffijberg *et al.* 2025). Studying the reproductive cycle of Bewick's Swans in their breeding area is highly challenging due to its inaccessibility and the low density of nests (Mineyev 1991, Rees 2006a), and any efforts to monitor trends and densities across a larger spatial extent have relied on aerial counts (Shchadilov *et al.* 2002, Rees & Rozenfeld 2020, Solovyeva *et al.* 2023). An integrated population model based on 50 years of individual mark-resighting data from the non-breeding grounds, combined with winter counts of adults and juveniles, identified declining reproductive success as the major driver of the population decline (Nuijten *et al.* 2020a). Another study used such winter counts to examine the factors influencing breeding success at the population level and found that fewer young were produced

in years with lower summer temperatures and higher estimated predator abundance (Wood *et al.* 2016). The proportion of juveniles on the wintering grounds showed no long-term trend between 1964 and 2014, but low productivity explained a decline in numbers observed between 2010 and 2020, a decline that has probably continued at least until 2024 (Koffijberg *et al.* 2025). While these studies suggest that climate factors may negatively affect the population through impacting breeding success, they relied solely on observational data from the wintering grounds. Therefore, what drives reproductive success at the individual level, and especially which stages of the breeding period are affected, remains unknown.

Here, we use 8 years of GPS tracking and accelerometer data to quantify Bewick's Swan breeding propensity and nesting success in the context of a changing climate. Deriving these metrics in Bewick's Swans is complicated by the fact that males also spend a significant amount of time sitting on the nest (25–50%), meaning that females are not near-continuously on the nest (Kondratiev 1991, Rees 2006b), which makes the use of simple metrics such as the female daily median body acceleration (Schreven *et al.* 2021) insufficient. We present a method that integrates GPS and accelerometer data to derive separate estimates of breeding propensity and nesting success for individual Bewick's Swans. By comparing these estimates to winter count data of juveniles, we additionally infer the population-level survival of juveniles from hatching to the first winter. We then assess how breeding propensity and nesting success relate to departure date from the wintering grounds, arrival at the breeding grounds and the timing of spring onset. We expect that earlier-arriving individuals show higher breeding propensity, given the narrow window for breeding in the Arctic, and that nesting success increases with an earlier onset of spring, due to the indirect effects such as higher temperatures and food availability for incubating parents. Finally, we relate these patterns to the long-term population decline and discuss their impact compared with other pressures faced by Bewick's Swans along their flyway.

METHODS

Catching and tagging

Bewick's Swans were caught with cannon nets in the Netherlands and Germany in the winters of 2016/17–2022/23 while flock-feeding on agricultural fields. More details of these catches are provided in Nuijten and Nolet *et al.* (2020) and Linssen *et al.* (2023). We fitted a total of 102 Bewick's Swans (61 adults, 18 yearlings (ca. 1.5 years) and 23 juveniles (ca. 0.5 years)) with GPS-GSM transmitters attached as neckbands. The transmitters were solar-powered and weighed 70 g (2016/17–2019/20; MadebyTheo, custom-made) or 65 g (2020/21–2022/23; Ornitela, OrniTrack-N55), which amounted to 1.0–1.6% of the body mass of the birds. They collected GPS locations and tri-axial accelerometer data (2-s burst, 20 Hz; hereafter ACC), the latter used as a measure of body activity (Nuijten *et al.* 2020b), at intervals ranging from 2 h to every 5 min depending on the battery charge. We analysed data from the period between 1 May and 31 July, encompassing the entire nesting period since birds do not arrive at the breeding grounds before May and start their post-breeding moult at the end of July or early August. Our dataset contains all breeding seasons from 2017 to 2024.

Sex was determined from blood samples using molecular sexing (Fridolfsson & Ellegren 1999) with some modifications to the PCR thermal cycling profile (step 1: 94°C for 1.30 min; Step 2: 48°C for 0.45 s; Step 3: 72°C for 0.45 s; Step 4: 94°C for 0.30 s; repeat 34 × from Step 2; 48°C for 1.00 min; 72°C for 5.00 min), and using a 2% instead of 3% agarose gel to separate PCR products.

Deriving breeding propensity and nesting success

Various methods have been developed to identify breeding attempts in female birds using GPS data alone (e.g. Picardi *et al.* 2020) or in combination with ACC data (Schreven *et al.* 2021, Ozsanlav-Harris *et al.* 2022, Wolfson *et al.* 2022). These approaches generally assume that females are solely responsible for incubation, remaining on the nest almost continuously for the whole incubation period and making simple movement metrics (e.g. median displacement) suitable indicators of incubation. In Bewick's Swans, however, males also spend a significant amount of time sitting on the nest (roughly 25–50% of the time, Kondratiev 1991, Rees 2006a). Although this behaviour probably has a different function than true incubation by females (Hawkins 1986), it makes identifying incubation from the female's movement data

less straightforward. To account for the reduced nest attendance of female Bewick's Swans, we adapted the method from Schreven *et al.* (2021) that integrates GPS and ACC data (see Supporting Information Fig. S1, for a schematic overview of our workflow).

We identified breeding attempts in females aged 3 years (4th calendar year) or older, that is adult females (Rees 2006c), based on age at capture. Males were excluded because we tracked relatively few of them, and because short (i.e. failed) nesting attempts (lasting only a few days) were difficult to detect from their limited daily time spent on the nest compared with females. Including males could therefore have biased the dataset towards (near-) successful nesting attempts. Only females with data recorded at intervals of 30 min or shorter throughout the breeding period were included, and tracks with any temporal gaps (>30 min) in data (e.g. because of device or battery failure) were excluded ($n = 11$ excluded bird summers). We first calculated the overall dynamic body acceleration (ODBA) for each ACC burst:

$$\mathrm{ODBA} = \sum\left(|a_x - \overline{a}_x| + |a_y - \overline{a}_y| + |a_z - \overline{a}_z|\right)$$

where a_i represents the raw acceleration for axis i (x, y or z). From the ODBA, we derived two metrics to detect breeding attempts. First, we calculated the daily 0.25 quantile ODBA. Secondly, we identified 'stationary periods', defined as periods where ACC bursts consistently had an ODBA lower than 1 g (gravitational acceleration) for at least 20 min, indicative of prolonged body inactivity. Using only data from stationary periods, we calculated the daily median deviation of the latitude from its daily mean, as an indication of how spatially clustered the stationary periods were each day (strong clustering indicating probable nest attendance).

We combined these two metrics to identify breeding attempts as follows. To assign the onset of a breeding attempt, we took the first three consecutive days during which the daily 0.25 quartile ODBA remained below 1 g (Supporting Information Fig. S2a–c). Within this 3-day period, the first day on which the median deviation from the daily mean latitude was below 0.001° was marked as the start of incubation (Supporting Information Fig. S2d–f). The end of incubation was defined as the first instance of the daily 0.25 quartile ODBA remaining above 1 g for 3 days, or the first day where the median deviation from the daily mean latitude was above 0.001°. We visually confirmed that the daily mean latitude remained stable over the identified period (Supporting Information Fig. S2g–i). The nest location was determined as the median longitude and latitude of all stationary periods between the start and end of incubation. Nesting success was defined as a nesting period lasting 29 days or longer, indicative of complete incubation (Kondratiev 1991, Rees 2006a, Schreven *et al.* 2021). Because we could not with certainty exclude cases where birds continued incubating unfertilized or failed eggs, our proportion of nesting success may be slightly overestimated. Individuals that met none of the above criteria were classified as non-breeders (Supporting Information Fig. S2).

We validated our method using six summer tracks from adult females known from field observations to have returned to the wintering grounds with juveniles, all of which were correctly classified as successful breeders. We also applied the method to all our tracks of yearling females ($n = 21$), which are too young to breed (Rees 2006a); all were correctly classified as non-breeding. When applied to all adult female tracks, the birds clearly fell into breeding or non-breeding with no ambiguous cases.

Comparison with field observations and winter count data

Since the absence of breeding attempts can be caused by females not having a partner, we checked whether the tracked females had been recorded as paired or unpaired in the winter range during each calendar year (i.e. for each summer season, during the months of January–December of that same year) by volunteer field observers (data extracted from https://submit.cr-birding.org/). Although recording pair status in the field is challenging and prone to misclassification, particularly when individuals are mistakenly classified as unpaired, the data provided us with a rough estimate of the number of adult females with and without a partner.

Additionally, each December, a large network of volunteers count the proportion of juveniles and the average brood size for Bewick's Swans across their northwest European winter range to monitor breeding success over time (Tijsen & Koffijberg 2022, Prior *et al.* 2023, Koffijberg 2024, Koffijberg *et al.* 2025). Since these counts are done after autumn migration, they reflect the combined result of breeding propensity, nesting success and

juvenile survival until the first winter at the population level. As such, they offer a more complete measure of 'ultimate breeding success' (i.e. the percentage of females that successfully raised one or more juveniles to their first winter), albeit only at the population level. We used the annual juvenile proportion and average brood size from the aforementioned winter counts to back-calculate the proportion of adult females that achieved ultimate breeding success (for method, see Supporting Information Appendix S1). This allowed us to contextualize our telemetry-based estimates of breeding propensity and nesting success; namely, the difference between our nesting success estimate and the count-based ultimate breeding success indicates a population-level estimate of post-hatching juvenile mortality.

Factors influencing breeding propensity

We aimed to assess the extent to which breeding propensity was influenced by departure date from the wintering grounds, arrival at the breeding grounds, timing of spring onset on the breeding grounds and the interval between arrival and spring onset on the breeding grounds ('relative arrival').

Inherent to studying breeding propensity is that for individuals that did not attempt to breed, there is no nest-site, and the breeding ground is in principle unknown. Nevertheless, to be able to include spatial variation in spring onset into our model of breeding propensity, we split the breeding range into two main regions: (1) mainland Russia and Kolguyev island (hereafter 'mainland'), and (2) the southern island of the Novaya Zemlya archipelago (Yuzhny Island) and Vaygach Island (hereafter 'Novaya Zemlya'; Fig. 1). This division reflects consistent differences in bioclimatic characteristics based on the Circumpolar Arctic Vegetation Map, with the mainland region classified as Low Arctic and the Novaya Zemlya region as High Arctic (Ahlenius 2010), and in the energy expenditure needed to reach and start breeding in the respective breeding regions (e.g. Schreven *et al.* 2026). We assigned each individual summer track, regardless of breeding status, to the region that contained the majority of GPS fixes during the second and third weeks of June. This period excludes stopovers on the mainland by birds migrating to Novaya Zemlya (which occur from mid-May to early June at the latest) but includes the nesting period even for the earliest breeders (mid-May to mid-June, this study, Rees 2006b). This allowed us to assign a summer region to both breeders and non-breeders for our analysis of breeding propensity. We thereby assumed that breeding status does not influence the choice of summer region, that is that individuals return to the same region, whether they breed or not. We tested this assumption by looking at the summer regions of individuals with multi-year tracking data ($n = 34$ individuals; Fig. 2); none of these switched regions between years, supporting the validity of our approach.

Migration departure and arrival

We calculated departure from the wintering grounds as the latest day on which an individual's location was west of 15°E longitude, a threshold that encompasses the current Bewick's Swan winter range (Nuijten *et al.* 2020c, Linssen *et al.* 2025) but excludes the first major staging area in the Baltic region (Nuijten *et al.* 2014). Arrival at the breeding grounds was determined as the first day on which a bird was within its summer region (region polygons presented in Fig. 1a).

Onset of spring

We used the regional date of snowmelt as a proxy for the timing of spring onset. To arrive at a region-level estimate of the date of snowmelt, we first determined annual snowmelt dates (first day with less than 50% snow cover) for the individual nest-sites detected in each region during the study period (2017–2024), using satellite imagery (Copernicus Sentinel-2, European Space Agency 2021) and the approach described in Supporting Information Appendix S2. We averaged the snowmelt dates of the individual nests per region and year. We then calculated the annual deviation of the regional date of snowmelt from the mean of that region over the study period ('regional snowmelt anomaly'), positive values indicating a late snowmelt and negative values indicating an early snowmelt relative for the region. Thus, per summer track, we included both a region variable (i.e. mainland or Novaya Zemlya) and a region snowmelt anomaly variable, to distinguish between the effects of consistent region differences and interannual variation in the onset of spring on breeding propensity. Additionally, we calculated the arrival of an individual relative to spring onset as the number of days between arrival at the breeding grounds and the regional date of snowmelt.

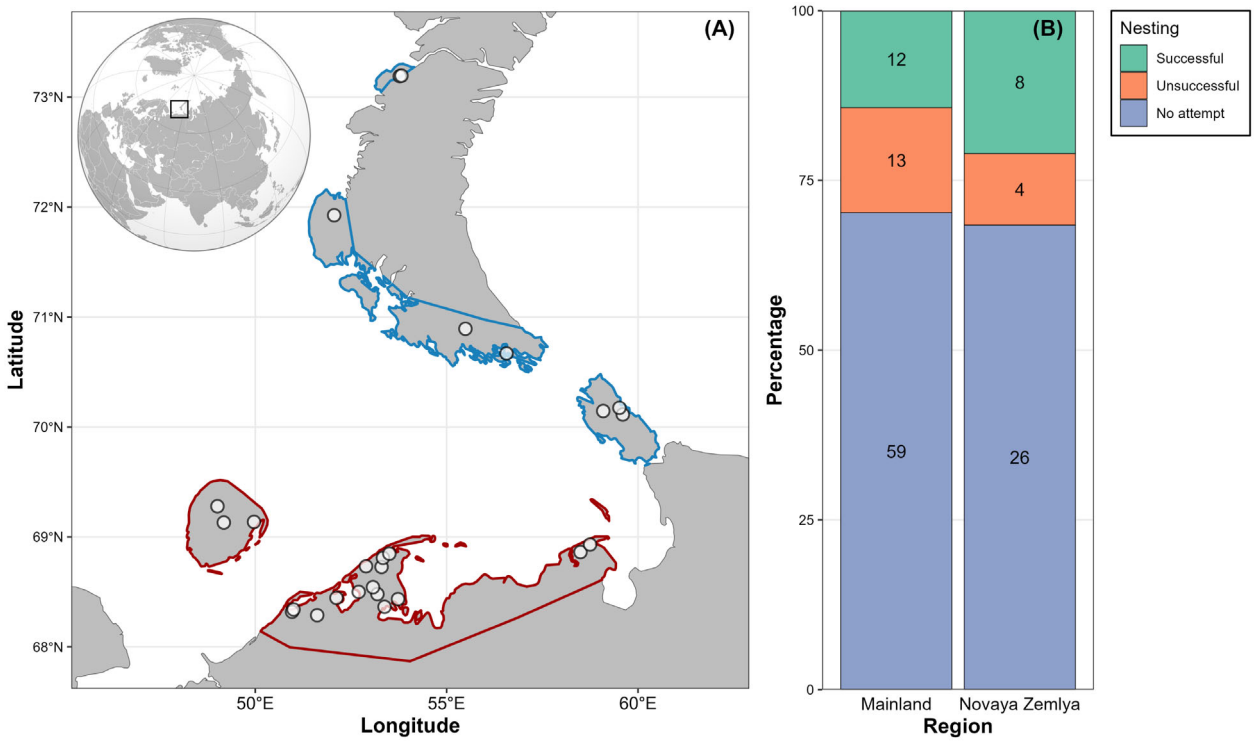

Figure 1. (a) Nest-sites of Bewick's Swans from the Western Palearctic flyway population tracked between 2017 and 2024 (indicated by white circles), with polygons indicating the two regions distinguished in our analysis: mainland (including Kolguyev Island; red) and Novaya Zemlya (including Vaygach Island; blue). (b) The percentage of successful (green) and unsuccessful (orange) breeding attempts and non-breeding attempts (purple) per region across the study period. Numbers indicate sample sizes for each category.

Statistical analysis

To assess how migration phenology and onset of spring relate to breeding propensity, we fitted generalized linear mixed models using a logit-link function and combinations of the following predictors: departure date from the wintering grounds, arrival date at the breeding grounds, (summer) region, regional snowmelt anomaly and relative arrival (all models listed in Table S1). To test for within-model multicollinearity among predictor variables, we calculated variance inflation factors (VIFs) using the check_collinearity() function from the 'performance' R package (Lüdecke *et al.* 2021). VIFs indicated low multicollinearity among predictors across models of both breeding propensity (range 1.00–2.90) and nesting success (range 1.03–4.25). Individual was included as a random intercept in all models (categorical variable based on tag ID). Year was not included as a random effect as it is indirectly included through snowmelt anomaly, which varies per year, making year itself redundant. Nor did we include year as a fixed effect since we considered our annual sample sizes too small to reliably detect potential linear trends in breeding propensity over 8 years of tracking. We selected the best model by comparing AIC_c values (second-order Akaike information criterion, Akaike 1973), favouring the most parsimonious model within 2 ΔAIC_c from the lowest AIC_c value among all models (Arnold 2010).

Factors influencing nesting success

For those birds that attempted breeding, we aimed to assess how their nesting success was influenced by the departure date from the wintering grounds, arrival date at the breeding grounds and the timing of snowmelt at the breeding grounds. In contrast to the analysis of breeding propensity, we did not include relative arrival and departure date from the wintering grounds as predictors of nesting success. Since those variables primarily impact the time available for foraging upon arrival, we expected that those variables could have a

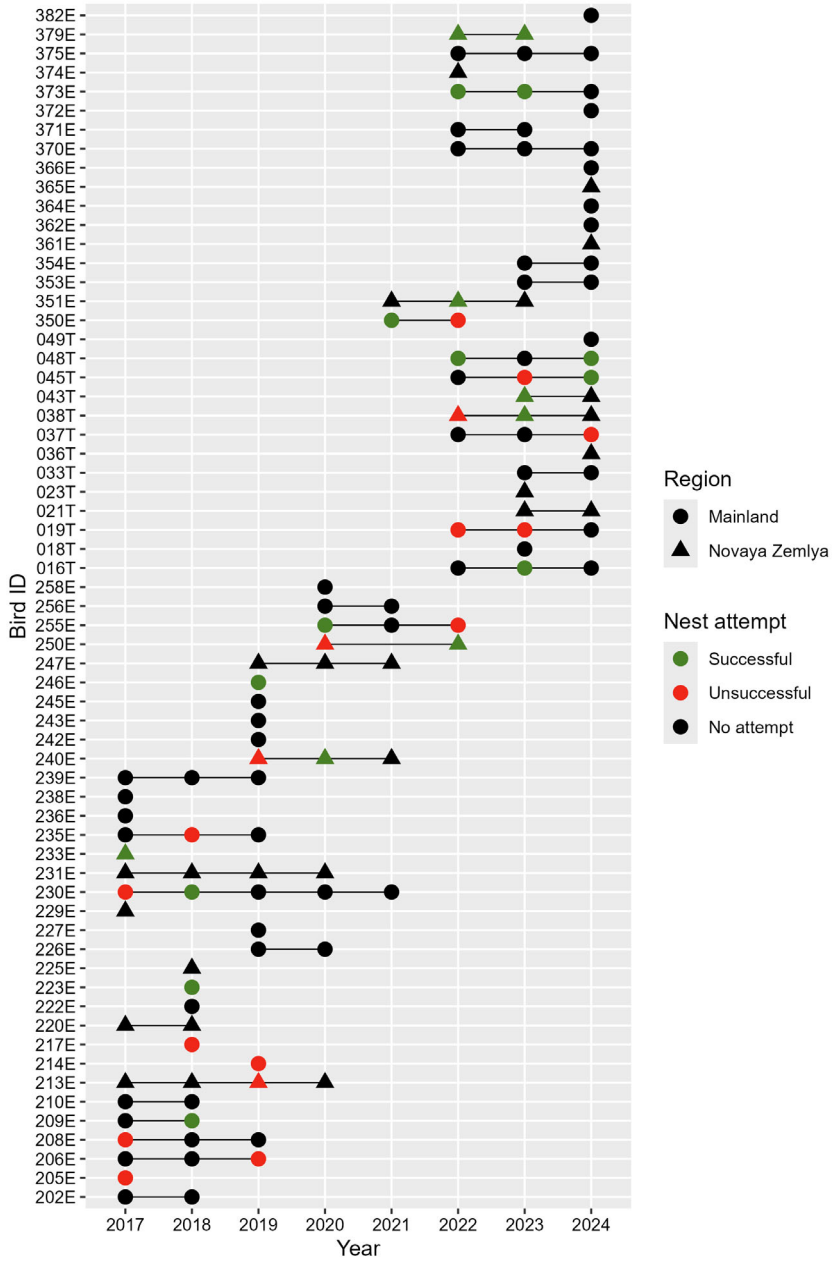

Figure 2. Summer region and nesting attempts of GPS-tracked adult female Bewick's Swans, illustrating regional fidelity of breeding propensity within individuals. The shape indicates whether the individual spent the summer on the Mainland (circle) or on Novaya Zemlya (triangle) (based on the proportion of GPS fixes during the first and second week of June). The colour indicates whether the individual made a nesting attempt (green = yes, successful; red = yes, unsuccessful; black = no attempt).

potential effect on the decision to attempt breeding, but not on the probability of successful hatching once eggs have been laid. For individuals where we tracked breeding attempts across multiple years, we used the GPS coordinates of the first attempt also for all following years, because birds generally nest in very close proximity to their previous sites (Supporting Information Fig. S3, see also Syroechkovsky *et al.* 2002).

The explanatory variables in the analysis of nesting success were similar to those in the analysis of breeding propensity, except that we used the

snowmelt variables per nest-site instead of the aggregated values per region (Supporting Information Appendix S2), as each individual in the former analysis was assigned to an exact nest-site. We split the date of snowmelt into two predictors: (1) the mean date of snowmelt for each nest-site across the study period ('mean snowmelt'), and (2) the annual deviation from that mean ('snowmelt anomaly'). In this way, each summer track was assigned one value representing the long-term average timing of spring at its nest-site, and one value representing relatively how early or late snowmelt occurred in that particular year, allowing us to capture both spatial and temporal variation in spring onset.

To assess how migration phenology and onset of spring relate to the probability of the female completing incubation to the hatching period, we fit generalized linear mixed models of nesting success, using a logit-link function and combinations of the following predictors: arrival date at the breeding grounds, (summer) region, nest-site-specific mean snowmelt and nest-site-specific snowmelt anomaly (all models listed in Table S2). We included the region of the nest-site (mainland or Novaya Zemlya) to test for differences in nesting success between the regions that are unrelated to weather (e.g. predation). Individual was included as a random intercept (categorical variable based on tag ID) in all models. Year was not included as a random or fixed effect based on the same reasons mentioned for the analysis of breeding propensity. Model selection was done similar to the analysis of breeding propensity. We visually inspected residual diagnostics, including residuals versus fitted values and assessment of the distribution of residuals, to verify that model assumptions, including the normality of residuals, were satisfied. All analyses were carried out in R 4.2.3 (R Core Team 2023) using glmmTMB (Brooks *et al.* 2017) for model fitting and ggplot2 (Wickham 2016) for data visualization.

RESULTS

In total, 63 adult female Bewick's Swans provided sufficient data to analyse breeding attempts and nesting success, resulting in 122 individual summer tracks in total (Table S3). We derived 37 breeding attempts from 26 individuals from those tracks (overall breeding propensity = 30%), spanning eight breeding seasons (2017–2024; Figs. 1b–3, Table S4). Of these attempts, 20 were successful (nesting duration ≥29 days; overall nesting success = 16%; Figs. 1b and 2, Table S4). Although breeding propensity and nesting success showed relatively high annual variability, warranting some caution for interpretation, they were consistently low across years, with breeding propensity exceeding 40% ($n = 9$ individuals) only once, in 2022, during the study period (Fig. 3, Table S4).

Breeding propensity and nesting success were overall slightly higher in the Novaya Zemlya region (32% and 21%, respectively) than in the mainland region (30% and 14%, respectively, Fig. 1b), but the difference was not statistically significant (Fisher's exact test of breeding status proportions: $P = 0.570$). Individuals showed strong fidelity to their summer region, spending summers consistently in either the mainland or Novaya Zemlya region regardless of breeding status (Fig. 2).

Comparison with field observations and winter count data

In 28% (15 out of 53) of those bird summers where no breeding attempt was made and pair status was recorded in winter during that same calendar year, the tracked female was reported as unpaired by volunteer field observers (Table S3).

Annual variation in breeding propensity and nesting success, calculated at the individual level from our GPS-tracked birds, corresponded with the ultimate breeding success, inferred at the population level from annual brood counts in the wintering range (Pearson's r for breeding propensity = 0.72, $P = 0.043$; for nesting success: $r = 0.87$, $P = 0.005$; Fig. 3, Table S4), but note that this could only be assessed for a relatively short temporal period of eight consecutive years (i.e. breeding seasons). Comparing the telemetry-based average nesting success estimate over our study period (16.6%) with the count-based average ultimate breeding success over that same period (11.5%) indicates that roughly 30% of parents that succesfully completed incubation, hatching one or more chicks, arrived without any chicks on the wintering grounds. That is, at least 30% of hatchlings did not survive until their first winter, but probably more since initial clutch sizes tend to be larger (roughly three on

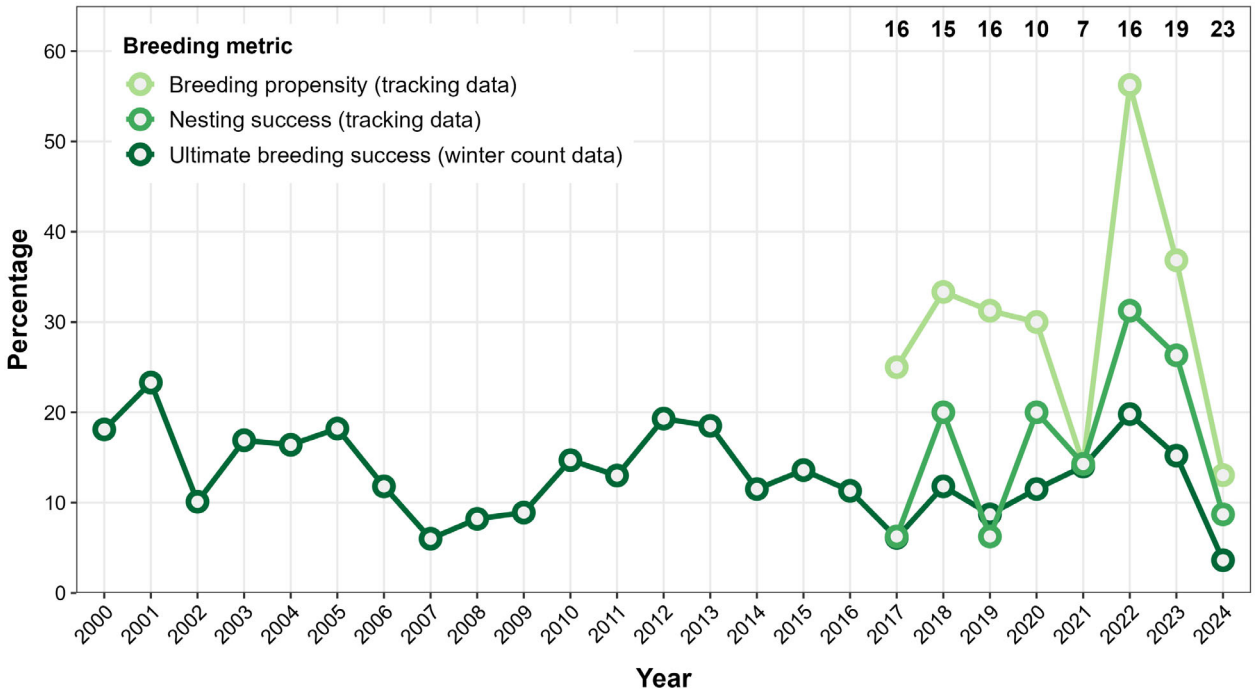

Figure 3. Breeding propensity (light green), nesting success (medium dark green) and ultimate breeding success (dark green) of adult female Bewick's Swans across the years. Ultimate breeding success refers to the percentage of females that successfully raised one or more juveniles to their first winter. Breeding propensity and nesting success were derived at the individual level from GPS-tracked adult females; ultimate breeding success was derived at the population level from winter count data (see section Comparison with winter count data). Numbers along the top indicate annual sample sizes of individual summer tracks. For the raw numbers underlying this figure, see Supporting Information Table S4.

average, Rees 2006b) than brood sizes recorded during the winter counts.

Drivers of breeding propensity

We identified six competing top models ($\Delta AIC_c < 2$) of breeding propensity, all of which included arrival date as a predictor (Table S1). The explanatory power of the models was generally weak, with the variables explaining some 10–15% of the variation in breeding propensity (Table S1). The model with arrival date as the sole predictor performed best, having the fewest degrees of freedom (Table 1, see also Supporting Information Table S1). The odds of breeding increased by 3.9% ($\beta = -0.04$, se = 0.02, $P = 0.04$; Fig. 4, Table 1) for each day that the swans arrived earlier at the breeding grounds, although note the effect size was rather small (Fig. 4). The closest competing model, with the lowest AIC_c but higher degrees of freedom, included both region and arrival date, where only the latter was significant (Supporting Information Table S1). Nevertheless, modelled breeding propensity was generally low, with predictions staying below 50% even for the earliest arrivals in our dataset (Fig. 4).

Drivers of nesting success

We identified four competing top models ($\Delta AIC_c < 2$) of nesting success, all of which included snowmelt anomaly (i.e. annual snowmelt deviation from the mean across the study period) as a predictor (Table S2). The model with snowmelt anomaly as the sole predictor performed best, having the fewest degrees of freedom (Supporting Information Table S2, Table 2). The odds of successfully nesting increased by 5.8% ($\beta = -0.06$, se = 0.03, $P = 0.06$; Fig. 5; Table 2) per day of earlier snowmelt anomaly, although note that the model output indicated that this effect was only marginally insignificant (Table 2). The closest competing model, with the lowest AIC_c but higher degrees of freedom, included both snowmelt anomaly and arrival date, with only the former being significant (Supporting Information Table S2).

DISCUSSION

Using GPS and accelerometer data, we examined breeding propensity and nesting success separately across eight breeding seasons in a declining population of Bewick's Swans. Birds that arrived early on their breeding grounds appeared more likely to attempt breeding, and nesting success appeared higher in years with an early snowmelt, suggesting slight positive effects of the climate change-induced advancement of spring onset. Nevertheless, breeding propensity was consistently low throughout the study period. These findings suggest that factors other than spring onset and changes therein are responsible for the persistently low proportion of breeding adults, presumably contributing to the ongoing population decline.

Aerial surveys covering the core part of the Western Palearctic breeding range found that 38–56% of Bewick's Swans occupied breeding territories in 1980, 1981 and 1991, while a variable 65%, 71% and 20% of territorial pairs attempted to breed in 1991, 1998 and 1999, respectively (note that the two measures were recorded in different years, Shchadilov *et al.* 2002). Although deferral of breeding under unfavourable conditions is a common strategy for long-lived species to increase their survival and lifetime reproductive success (Spaans *et al.* 1998, McCleery *et al.* 2002, Shaw & Levin 2013, Cunningham *et al.* 2023), the fact that the Bewick's Swan population size started decreasing in the mid-1990s may indicate that the breeding propensity rates estimated in that period of time were already insufficient to maintain a stable population. Our telemetry data suggest that breeding propensity has since remained low and potentially declined even further, in line with the overall population size (Beekman *et al.* 2019, Koffijberg *et al.* 2025), with an average of 30% of adult females attempting to breed over 8 years. Although neck collars have been reported to reduce breeding propensity in Greater Snow Geese *Chen caerulescens* (Reed *et al.* 2005) and Brent Geese *Branta bernicla* (Lensink 1968), Bewick's Swans are much larger-bodied, making collars only 1–1.5% of their body mass. Furthermore, neck-banded Bewick's Swans showed no altered behaviour after just a few weeks (Nuijten *et al.* 2014), similar to findings in Black Swans *Cygnus atratus* (Guay & Mulder 2009). We therefore consider it unlikely that our low breeding propensity estimates are the consequence of tagging.

Maintaining a stable population ultimately depends on a combination of sufficient breeding success and survival, the latter of which is generally high in Bewick's Swans (>0.873 on average across all ages, Nuijten *et al.* 2020a). Determining the minimum breeding propensity required for population stability would require a dedicated modelling study (e.g. Koons *et al.* 2017). Our results are, however, similar to previous findings that overall breeding success was low over the past 25 years (Nuijten *et al.* 2020a, Koffijberg *et al.* 2025), suggesting that the current levels of breeding propensity are below those necessary to sustain the population, potentially driving its decline.

Bewick's Swans were more likely to attempt breeding when arriving earlier at their breeding grounds. Most of the top competing models ($\Delta AIC_c < 2$) of breeding propensity also included either day of snowmelt or relative arrival (the interval between arrival and snowmelt, Supporting Information Table S1), suggesting that the onset of spring plays a role, with earlier springs linked to higher breeding propensity. Correspondingly, nesting success was higher during years with earlier snowmelt. These findings are similar to those of a field study of Bewick's Swans nesting on Vaygach Island, which reported lower nest density and nesting success in colder years (Syroechkovsky *et al.* 2002). Similar patterns have been observed in Mute Swans *Cygnus olor* (Kouzov *et al.* 2024a), Barnacle Geese *Branta leucopsis* (Prop & de Vries 1993, Layton-Matthews *et al.* 2020, Boom *et al.* 2023), Pink-footed Geese *Anser brachyrhynchus* (Madsen *et al.* 2007, Anderson

Table 1. Summary statistics from the best-performing GLMM of breeding propensity (i.e. the model with the lowest df within 2 ΔAIC_c of the lowest-AIC_c model), which includes day of arrival at the breeding grounds (arrival) as a predictor and a random effect for individual bird. We report parameter estimates, standard errors, Wald *Z* statistics with associated *P*-values, and the degree of variance explained by the model using the marginal and conditional *R*-squared. An overview of all candidate models considered in the AIC_c-based model selected is provided in Supporting Information Table S1.

	Estimate	Std. error	*Z* value	*P*-value	R^2_C	R^2_M
Intercept	5.48	3.01	1.82	0.07	0.106	0.064
Arrival	−0.04	0.02	−2.09	0.04		

Random intercept: individual (variance = 0.1551; sd = 0.3939), $n_{tracks} = 122$, $n_{individuals} = 63$.

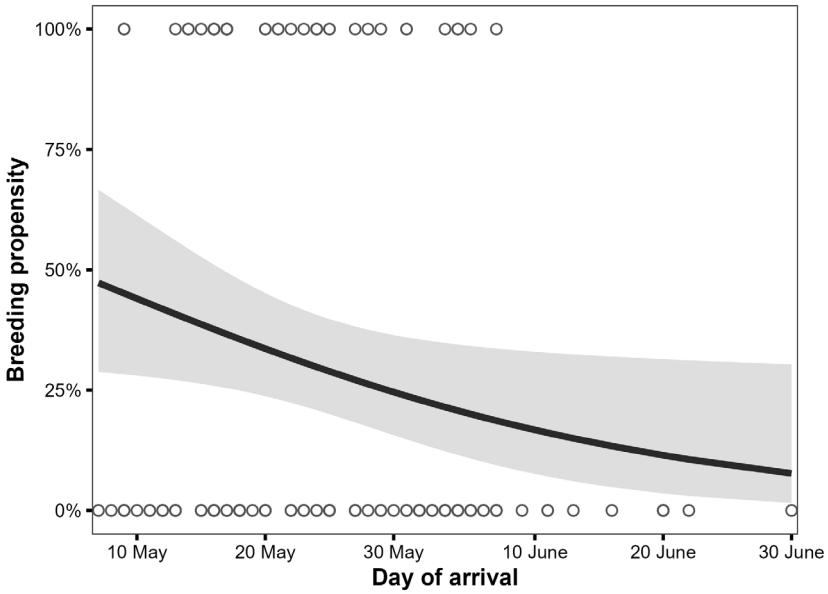

Figure 4. Relationship between breeding propensity and day of arrival at the breeding grounds. Circles along the top and bottom represent raw data points (breeding attempt: yes or no). There were no overlapping data points. The black line shows the GLMM prediction with the grey band representing the 95% confidence interval.

Table 2. Summary statistics from the best-performing GLMM of nesting success (i.e. the model with the lowest df within 2 ΔAIC_c of the lowest-ΔAIC_c model), which includes snowmelt anomaly as a predictor and a random effect for individual bird. We report parameter estimates, standard errors, Wald *Z* statistics with associated *P*-values, and the degree of variance explained by the model using the marginal and conditional *R*-squared. An overview of all candidate models considered in the AIC_c-based model selected is provided in Supporting Information Table S2.

Nesting success	Estimate	Std. error	*Z* value	*P*-value	R^2_C	R^2_M
(intercept)	0.12	0.35	0.33	0.74	NA	0.128
Snowmelt anomaly	−0.06	0.03	−1.86	0.06		

Random intercept: individual (variance = 3.2e-09; sd = 5.6e-05), $n_{tracks} = 37$, $n_{individuals} = 26$.

et al. 2015) and Snow Geese (Reed *et al.* 2004, Dickey *et al.* 2008), where early springs were likewise associated with a higher likelihood of breeding and nesting success.

It is striking that our model selection indicated that breeding propensity was better predicted by arrival date than by the timing of snowmelt, or even arrival relative to snowmelt. Bewick's Swans partially adjust their arrival timing in response to spring onset, arriving earlier in years with an early spring (Lameris *et al.* 2025, Linssen *et al.* 2025). Hence, the earlier arrivals in our study probably reflect, at least in part, a flexible response to earlier springs. Nonetheless, our results suggest that the environmental effects of arrival timing may be less important than, or at least act in concert with, direct benefits of early arrival, such as securing a better breeding territory (Kokko 1999). This is particularly relevant for paired Bewick's Swans to secure the territory of the previous year, and such pairs may even start nesting while the tundra is still covered with snow and ice (Rees & Belousova 2006, Rees 2006b). Finally, early arrival may also provide swans with more time to replenish energy reserves before breeding begins, enhancing resource accumulation with potential carry-over effects affecting subsequent breeding propensity (Ebbinge & Spaans 1995, Drent 2006, Spaans *et al.* 2007).

Spring is generally advancing under the influence of current climate change (Thackeray *et al.* 2016, Inouye 2022), leading to an increased frequency of early springs, which in our study population are associated with higher breeding propensity through earlier arrival and higher

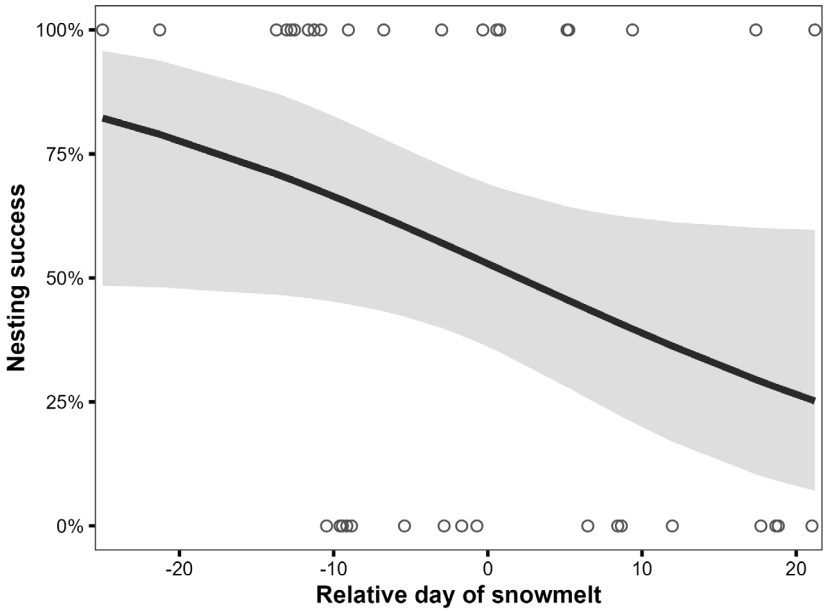

Figure 5. Relationship between nesting success and the snowmelt anomaly (the day of snowmelt relative to the mean for the nest-site across 2017–2024). Circles along the top and bottom represent raw data points (nesting success: yes or no) with some horizontal jitter to show overlapping points. The black line shows the GLMM prediction with the grey band representing the 95% confidence interval. Note that the modelled nesting success applies only to females that attempted to breed, so predictions range from 0% to 100% and are higher than the overall nesting success reported in the results, which is based on the total number of adult females.

breeding success. Spring onset in the Russian Arctic has advanced by a long-term average of 0.35 days per year (Linssen *et al.* 2025). Although our modelled effect of snowmelt appears relatively modest given this trend, this may benefit breeding propensity over the course of several decades. For example, 30 years of advancing spring onset would be associated with an increase in breeding propensity of roughly 5–10% (Fig. 4). Thus, the ongoing decline of the Bewick's Swan population since the mid-1990s is probably caused by other factors than the advancing onset of spring at the breeding grounds.

Low breeding propensity may result from interspecific competition at various stages of the annual cycle. The final stopover sites during spring migration are critical for Bewick's Swans to accumulate sufficient energy to complete the last leg of their migration, and to arrive at the breeding site with enough resources for breeding (Rees & Bowler 1991, Nolet *et al.* 2001, Nolet 2006, Nuijten & Nolet 2020). In contrast to the winter period, when interspecific competition at feeding sites is probably reduced due to an abundance of food resources (Wood *et al.* 2021), food availability at staging sites is more limited and competition with Whooper Swans *Cygnus cygnus* in particular may occur as this species also feeds on below-ground parts of aquatic macrophytes (Nolet & Drent 1998, Mikhailov *et al.* 2024, Kouzov *et al.* 2024b, 2024c). Furthermore, on the breeding grounds, Bewick's Swans face increasing numbers of breeding Whooper Swans (Shchadilov *et al.* 2002, Kritsov & Mineyev 2013, Rees *et al.* 2019) and moulting Mute Swans (Petr Glazov pers. comm., Syroechkovski 2002, Rees *et al.* 2019). Potential negative effects of competition are supported by a modelling study based on winter counts (Nuijten *et al.* 2020a), which found a negative correlation between Bewick's Swan breeding success and Whooper Swan abundance, although the effect was relatively small.

Despite the species being protected across its range, Bewick's Swans experience high hunting pressure, probably concentrated in the northern part of their flyway (Newth *et al.* 2019, 2022). We hypothesize that increased hunting pressure may reduce breeding propensity of the species and explain the relatively modest explanatory power of the current environmental variables considered in

our analysis. A striking 33% of Bewick's Swans (n = 46) caught between 2017 and 2022 in The Netherlands carried embedded shotgun pellets in their tissues (Buij *et al.* 2026). In the UK, 23% of wintering Bewick's Swans since 2000 had embedded pellets (31% when counting since the 1970s, Newth *et al.* 2011). Moreover, adults carrying shotgun pellets appeared in poorer condition when caught in the UK (Newth *et al.* 2011), probably months or more after most of the injuries had been inflicted. A study on Greater Snow Geese found that fewer females nested in years with spring hunting (Mainguy *et al.* 2002). Similarly, research on Common Eiders *Somateria molissima* showed that sudden environmental disturbances (albeit associated with food shortage) led to reduced breeding propensity, demonstrating that stress factors can cause females to defer breeding (Legagneux *et al.* 2016). Paradoxically, annual survival in Bewick's Swans is high across age groups (0.87–0.94, Nuijten *et al.* 2020a). Although this suggests that being shot is often non-lethal, we hypothesize that disturbances and certainly injuries caused by shooting during late spring migration or upon arriving at the breeding grounds may lead to reduced body condition and, subsequently, deferred breeding in Bewick's Swans. We currently lack sufficient data on the incidence of embedded pellets among our tagged individuals to test for an effect on breeding performance, but we highly recommend that future studies investigate potential links between pellet injury and reproductive success, while simultaneously increasing efforts to reduce hunting and disturbance at key stopover and breeding sites.

Another reason to abstain from breeding is that a bird may be without a partner. Although confirming individual pair status in flocks of overwintering swans is difficult and prone to error, data from our tracked birds suggest that approximately a quarter were unpaired (Supporting Information Table S3). Studies undertaken at Slimbridge, UK, from 1963 to 1999 found that only 67% of adult Bewick's Swans were paired (Rees 2006c), indicating that unpaired birds are common and unlikely to be a notable effect of catching and tagging. This is supported by a recent study on Greater White-fronted Geese *Anser albifrons* that found no effect of neck collars on pairing status (Babkina *et al.* 2025).

Moreover, the comparison of our telemetry-based estimates of breeding propensity and nesting success with winter counts of juveniles indicated that at least 30% of hatchlings die before their first winter. Although egg predation is probably reduced because either the female or male sits on the eggs, while the attending parent bird tends to defend their nest from predators such as Arctic Foxes *Vulpes lagopus* (Syroechkovsky *et al.* 2002), fewer juveniles are generally observed on the wintering grounds following summers with higher estimated Arctic Fox abundance (Wood *et al.* 2016). This suggests that post-hatching juvenile predation contributes to the reduced reproductive output (Wood *et al.* 2016, Layton-Matthews *et al.* 2020). Our results further suggest that predation, together with unknown but potentially high mortality during the first autumn migration, probably amplifies the effect of an already low number of hatchlings on the population decline. Furthermore, shifts in vegetation communities due to climate change may alter the landscape (e.g. an increase in shrubby vegetation, Shabanov *et al.* 2021) in ways that enhance concealment of land predators such as Arctic Foxes (Johnson-Bice *et al.* 2025). To gain more insight into these processes, future studies should aim to derive hatchling survival from the tracked movement of adult breeding birds, since parents typically avoid long-distance flights while their hatchlings are still flightless (Rees 2006b). A sudden change in movement patterns, for example because they return to mobile flying behaviour, could thus indicate mortality of juveniles. Linking breeding propensity and nesting success with juvenile survival at the individual level (Ross *et al.* 2018) would allow for more accurate assessments of the key factors driving population dynamics.

CONCLUSIONS

In order to obtain a better understanding of population declines and thereby inform conservation of migratory species, it is essential to identify which stages of the annual cycle contribute most (either positively or negatively) to overall population productivity (Martin *et al.* 2007, Reynolds *et al.* 2017). Despite the fact that increasingly early springs linked to climate change are associated with higher nesting success in European Bewick's Swans, population persistence remains threatened by consistently low breeding success throughout the 21st century. Our findings suggest that low breeding propensity may be a key driver of poor reproductive

output and that factors other than climatic conditions, such as hunting of adults, impact breeding propensity. An important next step is to elucidate the relative contributions of breeding propensity, nesting success and hatchling survival to population dynamics. Identifying the minimum levels required for each to sustain the Bewick's Swan population will be crucial to effectively address the population decline and inform conservation measures across the species' flyway.

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AUTHOR CONTRIBUTIONS

Tohar Tal: Conceptualization; writing – original draft; writing – review & editing; formal analysis; methodology; visualization; investigation. **Bart A. Nolet**: Writing – review & editing; data curation; funding acquisition; conceptualization; methodology; supervision; investigation. **Tom S.L. Versluijs**: Writing – review & editing; data curation; methodology; formal analysis. **Judy Z. Shamoun–Baranes**: Writing – review & editing; supervision. **Götz Eichhorn**: Writing – review & editing; data curation. **Sabine Urban**: Writing – review & editing; data curation. **Hans Linssen**: Writing – original draft; writing – review & editing; conceptualization; formal analysis; methodology; data curation; supervision; investigation.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

ETHICAL NOTE

All catching, tagging and blood sampling were conducted with permission from the relevant authorities in the Netherlands (Dienst Regelingen permits FF/75A/2016/044; Omgevingsdienst Brabant Noord permits Z/046757 and Z/141920; Centrale Commissie Dierproeven permits 2016518 and 202114712) and Germany (Niedersächsisches Landesamt für Verbraucherschutz und Lebensmittelsicherheit (LAVES) permit AZ 20/3603).

Data Availability Statement

The data and code to reproduce the results are available at Zenodo under restricted access: https://doi.org/10.5281/zenodo.17131332.

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SUPPORTING INFORMATION

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

Figure S1: Schematic overview of the method used to extract breeding attempts and nesting success for adult ($>=4$th calendar year) female Bewick's Swan GPS and accelerometer (ACC, *g* representing gravitational acceleration) data.

Figure S2: Examples of a breeding bird with a successful breeding attempt (left row), a breeding bird with an unsuccessful breeding attempt (middle row) and an individual without a breeding attempt (right row). Nesting was defined as the period in which the daily 0.25 quartile ODBA (a–c) was below 1 *g* and the daily median deviation of the latitude from its daily mean (d–f) was below 0.001°. Daily mean latitudes (g–i) confirmed that the absolute geographical location was stable during the nesting period for breeding birds, but not for non-breeding birds.

Figure S3: Distances between nests of the 11 individuals with two different attempts in different years. Each point represents a nest-site location accompanied by a number indicating the distance between nests (in metres).

Figure S4: Correlation between snowmelt estimates derived from Sentinel-2 level 1C (top of atmosphere) and level 2A (surface reflectance) products across all nest-sites ($n = 27$) for 2019–2024. The level 1C product was used in the main analysis because level 2A data are not available for 2017–2018 at higher latitudes. Annual snowmelt estimates from both products were strongly correlated (mean Pearson's $r = 0.98$), indicating that the choice of product does not affect the conclusions.

Table S1: Comparison of models of breeding propensity, using combinations of the predictors: departure from the wintering grounds (departure), arrival at the breeding grounds (arrival), summer region (region), regional snowmelt anomaly and relative arrival. All models included individual bird as a random intercept. Models are sorted by AIC_c. The model in bold was considered best-performing (i.e. with $\Delta AIC_c < 2$ and the lowest df). Included are also the *R*-squared values, both conditional (R^2_C) and marginal (R^2_M).

Table S2: Comparison of models of nesting success, using combinations of the predictors: arrival at the breeding grounds (arrival), summer region (region), mean snowmelt and snowmelt anomaly. All models included individual bird as a random intercept. Models are sorted by AIC_c. The model in bold was considered best-performing (i.e. with $\Delta AIC_c < 2$ and the lowest df). Included are also the R-squared values, both conditional (R^2_C) and marginal (R^2_M). However, the conditional R^2 could not be calculated for most models due to the restrictive sample size.

Table S3: Overview of pairing status (0 = unpaired, 1 = paired, blank = no data), breeding attempts (0 = no attempt, 1 = attempt), nesting success (0 = unsuccessful, 1 = successful), and incubation dates and duration of GPS-tracked adult female Bewick's swans. Only seasons that yielded consistent enough data for us to assess breeding attempts and success are included (see Methods).

Table S4: Breeding propensity, nesting success and ultimate breeding success (the percentage of females that successfully raised one or more juveniles to their first winter) over the years. Breeding propensity and nesting success derived from telemetry data, ultimate breeding success derived from winter count data. *Numbers are given in percentages (%). **Average ultimate breeding success is calculated only over the years 2017–2024.

Appendix S1: Back-calculating ultimate breeding success from winter counts.

Appendix S2: Determining annual date of snowmelt.