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Northward range expansion in spring-staging barnacle geese is a response to climate change and population growth, mediated by individual experience

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Abstract

All long-distance migrants must cope with changing environments, but species differ greatly in how they do so. In some species, individuals might be able to adjust by learning from individual experiences and by copying others. This could greatly speed up the process of adjustment, but evidence from the wild is scarce. Here, we investigated the processes by which a rapidly growing population of barnacle geese (*Branta leucopsis*) responded to strong environmental changes on spring-staging areas in Norway. One area, Helgeland, has been the traditional site. Since the mid-1990s, an increasing number of geese stage in another area 250 km further north, Vesterålen. We collected data on goose numbers and weather conditions from 1975 to 2017 to explore the extent to which the increase in population size and a warmer climate contributed to this change in staging area use. During the study period, the estimated onset of grass growth advanced on average by 0.54 days/year in each of the two areas. The total production of digestible biomass for barnacle geese during the staging period increased in Vesterålen but remained stable in Helgeland. The goose population has doubled in size during the past 25 years, with most of the growth being accommodated in Vesterålen. The observations suggest that this dramatic increase would not have happened without higher temperatures in Vesterålen. Records of individually marked geese indicate that from the initial years of colonization onwards, especially young geese tended to switch to Vesterålen, thereby predominating in the flocks at Vesterålen. Older birds had a lower probability of switching to Vesterålen, but over the years, the probability increased for all ages. Our findings suggest that barnacle geese integrate socially learned behaviour with adjustments to individual experiences, allowing the population to respond rapidly and accurately to global change.

KEYWORDS
age effects, dynamic strategies, explorative behaviour, food quality, population increase, range shift, spring migration

1 | INTRODUCTION

Many organisms currently face rapidly changing environments due to global warming (Blunden, Arndt, & Hartfield, 2018; Lowry et al., 2013; Tilman et al., 2001), which force them to adjust their behaviour if they are to survive. This is especially true for long-distance migrants, which depend on spatially separated environments that may change in different ways and at different rates. Behavioural responses are common, particularly in birds, and include adjustments in the timing of migration (Bauer, Van Dinther, Høgda, Klaassen, & Madsen, 2008; Kölzsch et al., 2015; Tombre et al., 2008) and egg laying dates (Both et al., 2004; Crick & Sparks, 1999). Moreover, birds' spatial distributions change in winter (Ambrosini et al., 2011; Barbet-Massin, Walther, Thuiller, Rahbek, & Jiguet, 2009; Ramo et al., 2015), during breeding (Guillemain & Hearn, 2017; Huntley et al., 2006) and during migration (Clausen, Madsen, Cottaar, Kuijken, & Verscheure, 2018; Prop, Black, Shimmings, & Owen, 1998).

At present, there is limited knowledge about how such responses actually come about, even though they are essential to predict the timing, speed and extent that migratory traits in a population are adjusted to changing conditions. New migratory behaviour in passerines has been proposed to arise through genetic changes (Berthold & Pulido, 1994; Pulido, Berthold, Mohr, & Querner, 2001). Although associations have been found between genetic polymorphisms and migratory decisions among populations (Lundberg et al., 2017; Mueller, Pulido, & Kempenaers, 2011), actual evidence for genetic changes with functional effects on migratory behaviour is lacking. Alternatively, changes can result from individually or collectively adjusted migratory choices in direct response to a changing environment (Berdahl et al., 2018; Clausen et al., 2018). These choices may then be inherited and spread through the population via social learning, which provides the possibility of cultural evolution in addition to genetic evolution (Aplin, 2019). Social learning of migratory behaviour has been proposed for several bird species, including cranes (Mueller, O'Hara, Converse, Urbanek, & Fagan, 2013), storks (Flack, Nagy, Fiedler, Couzin, & Wikelski, 2018) and bustards (Palacín, Alonso, Alonso, Magaña, & Martin, 2011). However, also here, actual evidence that cultural evolution causes populations to adjust their migratory behaviour is limited.
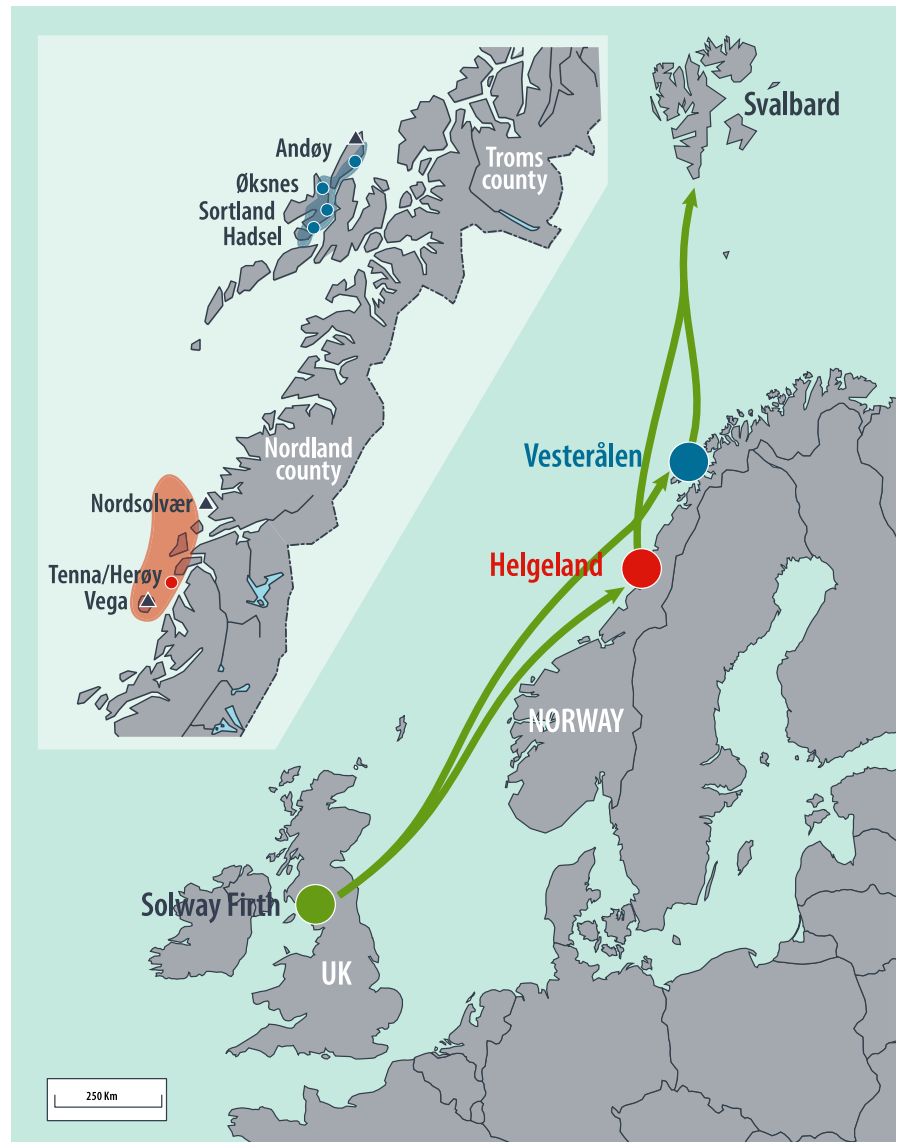
A primary candidate for further study of these questions is the adjustment of migration strategies by arctic-breeding geese. Typically, geese on spring migration make use of several staging sites to forage and thereby build up body reserves. These reserves are not only vital for maintenance and for the final migration leg (Ebbinge & Spaans, 1995; Prop & Black, 1998) but also for breeding because the availability of food is generally restricted when the geese arrive at the breeding grounds (Madsen et al., 2007; Prop & de Vries, 1993). Changes in food availability in the staging areas influence reproductive success, and happen due to climate change (Bauer et al., 2008; Lameris et al., 2017), changes in agricultural practice (Tombre, Madsen, Tømmervik, Haugen, & Eythórsson, 2005), and resource competition due to population growth (Aaron, Krapu, & Cox, 2013).

New migration strategies in goose populations have previously been demonstrated to spread relatively fast within the population (Clausen et al., 2018; Eichhorn, Drent, Stahl, Leito, & Alerstam, 2009; Feige et al., 2008; Larsson, Forslund, Gustafsson, & Ebbinge, 1988). This may be attributed to individuals switching strategies in response to previous experiences, and additionally to social learning by juvenile and older geese. Indeed, several studies have demonstrated increased explorative behaviour in response to changing environmental conditions (Clausen et al., 2018; Eichhorn et al., 2009; Flint, Meixell, & Mallek, 2014; Prop et al., 1998). However, the extent to which environmental changes actually influence the probability of individual geese to switch migration strategy, whether switching is age dependent, and the extent to which these effects are responsible for population-level changes in migratory behaviour is unknown.

To answer these questions, we investigated the performance of spring-staging barnacle geese (*Branta leucopsis*) in Norway. These geese breed in the high-arctic archipelago of Svalbard, and winter on the Solway Firth, United Kingdom. The number of geese in this population has substantially increased over the previous seven decades (Griffin, 2018; Owen & Black, 1999; Wildfowl and Wetlands Trust (WWT), 2017). Currently, barnacle geese in this population have two main staging areas in northern parts of Norway (Shimmings, Bakken, & Carlsen, 2017; Tombre, Eythórsson, & Madsen, 2013; Tombre et al., 2008; Figure 1). The southernmost area, on the coast of Helgeland, has long been known to be the traditional spring-staging site (Gullestad, Owen, & Nugent, 1984), whereas an area 250 km further north, Vesterålen, has been increasingly used over the past 25 years (Tombre et al., 2013).

Here, we studied the temporal relation between the population sizes of staging barnacle geese in both staging areas and the local environmental conditions, and to what extent this relation has been mediated by the annually changing choices of new recruits in the population, and by older individuals that change their migratory strategy later in life. To this end, we first quantified annual numbers of barnacle geese both in Helgeland and in Vesterålen from 1975 to 2017, using counts of numbers of geese during spring staging as well as annual estimates of total flyway population size in winter (Griffin, 2018; Owen & Norderhaug, 1977; WWT, 2017). Second, we explored whether climate change was a potential reason for the observed change in distribution, by estimating annual foraging conditions at both staging areas. Within the Helgeland area, barnacle geese have already expanded their range northwards presumably due to warmer spring temperatures and improved food conditions (Prop et al., 1998). Here, we estimate local food conditions in both staging areas on a daily basis by using an existing simulation model for grass leaf growth (Bonesmo & Bélanger, 2002a, 2002b), based on local estimates of temperature and global radiation. This allowed us to determine whether the increasing proportion of birds visiting Vesterålen can be understood as a response to the relative change in food conditions in both staging areas, and/or to increasing competition due to population growth. Concurrently, we analysed whether this response resulted from a higher recruitment of young birds

FIGURE 1 The spring migration routes of the Svalbard-breeding population of barnacle geese. The inset shows the main staging areas of geese in Helgeland (red shading) and Vesterålen (blue shading). Triangles indicate the location of weather stations from which data on temperature and cloud cover were derived

in Vesterålen, and/or from a switch in the area choices of experienced individuals from Helgeland to Vesterålen. Addressing these questions was made possible by a large data set of observations of individually marked geese with known age, collected in Helgeland as well as in Vesterålen from the very first years of colonization onwards. These data also allowed us to assess whether the age composition in both staging areas differed, and whether the probability of switching staging area between years changed with age and over time.

2 | MATERIALS AND METHODS

2.1 | Focal population and study areas

The Svalbard-breeding population of barnacle geese has increased from only a few hundred individuals in 1948 to 42,600 in 2017 due to a combination of protection from hunting along the flyway and improved foraging conditions during the

non-breeding period on intensively managed grasslands, arable crops and stubbles (Griffin, 2018; Owen & Norderhaug, 1977; WWT, 2017). The geese spend the winter and spring on the Solway Firth, United Kingdom. They utilize areas in Norway for spring staging, and breed on the high-arctic archipelago of Svalbard (Figure 1; Owen & Black, 1999). Recently, a small but increasing number of barnacle geese spend the pre-migratory period on the Solway before heading directly towards Svalbard (LG, unpublished), which was disregarded in the current study due to a lack of quantitative data. At the spring-staging areas, geese use habitats that are dominated by cultivated grassland traditionally used for hay (timothy grass *Phleum pratense* among the main species grown), sheep and cattle grazing, but geese may also forage on natural habitats and seashore vegetation. In Helgeland, the southernmost staging area (centred at 65°45′N, 12°E), the main agricultural areas used by geese are the larger islands of Tenna, Sør-Herøy and Nord-Herøy, but geese also utilize the surrounding islets and skerries (Prop et al., 1998; Figure 1). In Vesterålen

(centred at 68°74′N, 15°E), geese almost exclusively forage on grass and pasture fields as most of the available goose habitats are cultivated (Tombre, Tømmervik, & Madsen, 2005). During the spring-staging period in May, there is almost 24 hr daylight in this part of Norway, and geese can spend most of their time foraging.

2.2 | Temperatures and plant growth

For each day during the staging period between 1975 and 2017, we downloaded daily average, minimum and maximum temperatures and cloud cover from the Norwegian Meteorological Institute (www.eklima.met.no) from two weather stations located in Helgeland (Nordsolvær up to 1991, and Vega from 1992 onwards) and one weather station in Vesterålen (Andøy). In addition, hourly values of global irradiation on the horizontal plane at ground level (GHI, W hr/m^2) from 2004 to 2017 were downloaded from the Copernicus Atmosphere Monitoring Service (http://www.soda-pro.com/web-services/radiation/cams-radiation-service) and summed per day. Daily GHI values in both staging areas in the years from 1975 to 2003 were estimated by using hourly values of irradiation at the top of the atmosphere (W hr/m^2, also downloaded from the Copernicus website), daily minimum and maximum temperatures and daily mean cloud cover (for details see Methods S1). Using these data, we estimated the annual cumulative growth of digestible leaf biomass in both staging areas and for each year from 1975 to 2017.

First, we estimated the annual onset of grass growth in spring as the first day of the year at which the cumulative growth degree-days (starting at 1 January) surpassed a critical temperature (GDD$_c$) (Botta, Viovy, Ciais, Friedlingstein, & Monfray, 2000). Daily growth degrees were calculated as the positive difference between mean daily temperature and a threshold temperature (T_{base}). T_{base} and GDD$_c$ were estimated as −1.14 and 194°C, respectively, in Helgeland, and as −1.86 and 202°C at Vesterålen (for details see Methods S2).

Second, we calculated the daily growth of digestible grass biomass available to barnacle geese using the Canadian timothy growth model (CATIMO; Bonesmo & Bélanger, 2002a, 2002b). This model incorporates daily minimum, maximum and mean temperatures and daily GHI to estimate the daily growth of grass stems and leaves (dry mass in g/m^2) separately (Bonesmo & Bélanger, 2002a). The model also estimates the daily proportions of cell wall and cell content in leaves and stems (Bonesmo & Bélanger, 2002b). We assumed that geese only forage on grass leaves and digest 15.6% and 63.8% of cell wall and cell content respectively (Prop & Vulink, 1992). We further assumed that nitrogen and water conditions were optimal for growth (Baveco et al., 2017), even though some of the foraging areas, mostly in Helgeland, include salt marshes and older less intensively managed pastures.

We tested whether annual environmental conditions during staging differed between staging areas and over time by comparing the AIC$_c$ values of linear models (lm in R version 3.5.1; R Core Team, 2018) with and without the factor Area (either Helgeland or Vesterålen),

continuous variable Year (1975–2017) and their interaction. This model comparison was performed independently for three different response variables: annual mean daily temperatures shortly before and during the staging period (1 April–20 May), the annual start of grass growth (day of the year), and the digestible grass biomass production during the staging period (taken as 1–20 May).

2.3 | Goose numbers

The Svalbard barnacle goose population has been monitored since the early 1950s (Owen, 1982). We used counts from the years 1975–2017. The size of the total flyway population (N_{total}) was estimated by regular counts in the wintering area by WWT. Counts in Helgeland from 1994 onwards were a continuation of the previous work from the earliest barnacle goose studies in Norway (from 1975 onwards; Gullestad et al., 1984), with the focus of observations on the islands of Tenna, Sør-Herøy and Nord-Herøy (Figure 1). Abundance of geese in Vesterålen could be adequately covered by using the network of roads. Geese are concentrated in four municipalities in the Vesterålen region; Andøy, Hadsel, Sortland and Øksnes (Figure 1). Observations were made from suitable vantage points, mostly from a car in order to reduce disturbance to feeding flocks. Systematic counts were made at daily intervals within the time period 27 April to 23 May. Further details on the inventories and handling of the counts are given in Methods S3.

Growth rates of the local and flyway populations were estimated by the regression of the natural logarithm of numbers over time (Sibly, Hone, & Clutton-Brock, 2003). Local and flyway population growth rates were estimated for the years before and during colonization of Vesterålen (1975–2000) and for the period after colonization (2000–2017) separately. To describe the development of numbers for the period 1975–2017, loess smoothers (package gam in R) were applied. The optimal span width was based on the AIC of models varying in width from 0.1 to 0.9, incrementing by 0.1.

2.4 | Marking and resightings

The first barnacle geese were colour marked on Svalbard in 1962 (Norderhaug, 1984), and have since 1973 been regularly individually colour marked (Owen & Black, 1999). We used a total of 32,100 ring observations of 4,200 individuals collected in Norway from 1994 to 2017. Identification was by a combination of two or three characters (letters or digits) on coloured leg rings (five colours used). The codes can typically be read by telescopes at distances of 300 m when weather conditions are optimal, and rings are sufficiently durable to record individuals throughout their lives (on average 10 years, occasionally exceeding 20 years, Black, Prop, & Larsson, 2014). Geese were caught and marked in summer on the breeding grounds on Svalbard, on the wintering grounds in the United Kingdom and at staging sites in Helgeland. At capture, sex and age of each goose were determined: juveniles (0 year birds) were distinguished in summer, winter and spring, and yearlings (1 year olds) were distinguished in summer catches (see methods in Owen, Drent, Ogilvie, & van

Spanje, 1978). All other individuals were determined as adult (older than 1 year). Analyses that included age as one of the explanatory variables were restricted to individuals with known birth year, those who were juvenile or yearling at first capture. There were only a few geese observed that were older than 20 years (1.3% of 3,415 records), and to reduce the number of age classes, these individuals were classified as 20 year olds.

2.5 | Choice of staging areas

Analysis of the choice by geese for either area was based on resightings of all individuals with known age. When an individual had been spotted in both areas in the same year (which occurred in 1.8% of the 11,618 cases), the area with observations closest to the date of peak numbers (12 May) was classified as the staging area.

To examine variation in the probability to stage in Vesterålen (rather than in Helgeland), a binomial generalized linear mixed model (GLMM) was run using the function glmmPQL in the MASS package of R (Venables & Ripley, 2002). Goose age and year of observation were taken as continuous variables (covariates) in the fixed part of the models. To obtain meaningful intercepts, both variables were centred to the mean. As we expected that area choice during the first years of life was potentially affected by the choice made by the parents (youngsters may be associated with their parents for a year, Black et al., 2014), we added an additional factor to the fixed part of the models that reflected the development stage of the birds; coded as 0 for 0 year old birds, 1 for 1 year olds and 2 for older individuals. The random part of the models was composed of the factors *Sex* and *Individual*. Sex was taken as a random variable to cope with heterogeneity in the data due to the occurrence of pairs in which both partners were marked. GLMMs do not provide an AIC$_c$ value for model selection. Instead, we followed a backward elimination strategy (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Starting with a biologically meaningful model, containing the main terms and the interaction between year and age, nonsignificant terms were dropped to arrive at the final model.

2.6 | Probabilities to switch staging areas

To analyse switching rates between staging areas, the program MARK (White & Burnham, 1999) was used within the RMark interface (Laake, 2019), which is a package working in the R environment (R Core Team, 2018). Movements were analysed by multistrata models (Brownie, Hines, Nichols, Pollock, & Hestbeck, 1983). These models are constructed to estimate movement probabilities from one stratum to another (in our case switching from Helgeland to Vesterålen, or the other way, between years), in conjunction with estimating survival and resighting probabilities for each stratum. We constructed annual resighting histories for each individual observed in Norway during the study period, indicating whether the individual had been seen at all ('0' flagging the years when not observed), and where the individual occurred ('H' for Helgeland and 'V' for Vesterålen).

Concurrent with low goose abundance in Vesterålen before 2000, numbers of ring resightings in the area were small (varying between 0 and 36 resightings each year). This caused convergence problems in estimating model parameters, and therefore, analyses of switching rates were restricted to the years from 2000 onwards. After 2000, the annual number of resightings was on average 1,002 (*SD* = 293) in Helgeland and 472 (*SD* = 256) in Vesterålen. The numbers of unique individuals identified per year were on average 305 (*SD* = 85) and 261 (*SD* = 151) respectively.

As geese operate in pairs throughout the year, and both partners may have been marked, we chose to restrict analyses to one of the sexes (females were arbitrarily chosen). The only exception was the analysis of movements during the first years of life (see below). Moreover, analyses were restricted to individuals of known age (marked as 0 or 1 year old). As geese were not necessarily observed in Norway in the first year following marking, the data were structured to include age at first observation in Norway as a group. The design data for each of the parameters (rate of resighting, survival and movement) were then modified by incrementing age by the value of the age group. As birds rarely survived more than 20 years, the groups in the observation data and in the design data were restricted to ages of 0–20. Any older birds (whether observed or modelled) were included in the group of 20 year olds.

To account for overdispersion in the observation data, we estimated an inflation factor ('c-hat') by the application U-CARE (Choquet, Lebreton, Gimenez, Reboulet, & Pradel, 2009) using the option specifically designed for multistrata models. We found inflation factor values of 2.2 (model including male and female) and 2.0 (all other models), for which model selection criteria (AIC$_c$, see below) and the variance of the estimates were corrected.

To select appropriate models, we followed a sequential strategy (Cam, Oro, Pradel, & Jimenez, 2004; Zuur et al., 2009). First, the most suitable structure of resighting probabilities (*p*) was solved from a set of candidate models with an extensive set of survival and switching probabilities (three-way interaction term of *Year*, *Age* and *Area* and all lower order terms) but that varied in *p* (any combination of the two-way interaction term of *Year* and *Area* and main effects). *Year* was either handled as a factor or as a covariate (i.e. a linear relationship over the years). The model with the lowest QAIC$_c$ (corrected for small sample sizes and overdispersion) was taken as the preferred model (Burnham & Anderson, 2002). Subsequently, the most suitable structure of the survival parameters (*S*) was solved in a similar way, taking the structure of resighting probability found at the first step. Variables that were explored for an effect on survival rate were *Area*, *Year* and *Age*. Age was handled as a covariate, as survival is known to decline with age (Black & Owen, 1995). Model selection regarding resighting rate and survival are summarized in Tables S3 and S5. After establishing the structure of *p* and *S*, the switch probabilities were modelled with all combinations (up to second-order interactions) of *Area*, *Year* and *Age*.

We expected only a potential sex effect in 0 year birds, that is in the year that juveniles become independent of their parents

and before they find a suitable mate (Black & Owen, 1995). To focus the analysis on the younger age groups and restrict the degrees of freedom, we constructed an age group *Age5* with five levels: birds in their first year of life, second, third, fourth and those which are older. To explore sex effects, we started with the preferred model on switching probabilities (see above), replaced *Age* by *Age5* and tested effects of sex on each of the switching probability terms.

Any models in the candidate sets with a Delta QAIC$_c$ <2 were considered as competitive, and were averaged to obtain model averaged parameter estimates using the package MuMIn (Barton, 2018) or Rmark. Means are given ±1 *SE*, unless otherwise stated.

2.7 | Balance of movements

The annual number of geese switching areas (Helgeland or Vesterålen) between years was calculated from the products of switching probability (Psi) and number of geese (*N*) for each year *t* as:

$$\text{Switching.area} = (1/17) \times \sum_{t=2000}^{2016} \text{Psi}_{\text{area}.t} \times N_{\text{area}.t}. \qquad (1)$$

The net number of movements between Helgeland and Vesterålen was calculated as Switching.Helgeland minus Switching.Vesterålen. The average change in population size per area was calculated as the difference between numbers in the last (2017) and first (2000) year of the main study period divided by the length of the period.

3 | RESULTS

3.1 | Temperature and plant growth

Mean daily temperatures during the staging period (1 April–20 May) increased by an average of 0.044°C/year (±0.0097; Figure 2a; Table 1). Temperatures were on average 2.2°C higher in Helgeland than in Vesterålen, and the increase showed no difference between the areas (Table 1; and model selection in Table S1). Local regression analysis indicated that the increase was not uniform over time but exhibited a sudden acceleration in the early 2000s (Figure 2a).

As a consequence of the increasing temperatures, the estimated start of grass growth advanced on average by 0.54 days/year (±0.14), adding up to approximately 3 weeks between 1975 and 2017 (Figure 2b; Table 1; Table S1). The start was on average 27.3 days earlier in Helgeland than in Vesterålen, and this difference showed no change throughout the study period (Figure 2b; model 2 in Table S1).

Estimates of the annual total production of digestible leaf biomass during the staging period, that is, staging period vegetation quality, increased in Vesterålen by 0.33 g m^{-2} year^{-1} (±0.101; Figure 2c; Table 1), but not in Helgeland where the increase did not differ from zero (0.02 ± 0.099 g m^{-2} year^{-1}; Figure 2c; Table 1; model selection in Table S1). As a consequence, the mean staging period vegetation quality in the two areas was similar in recent years
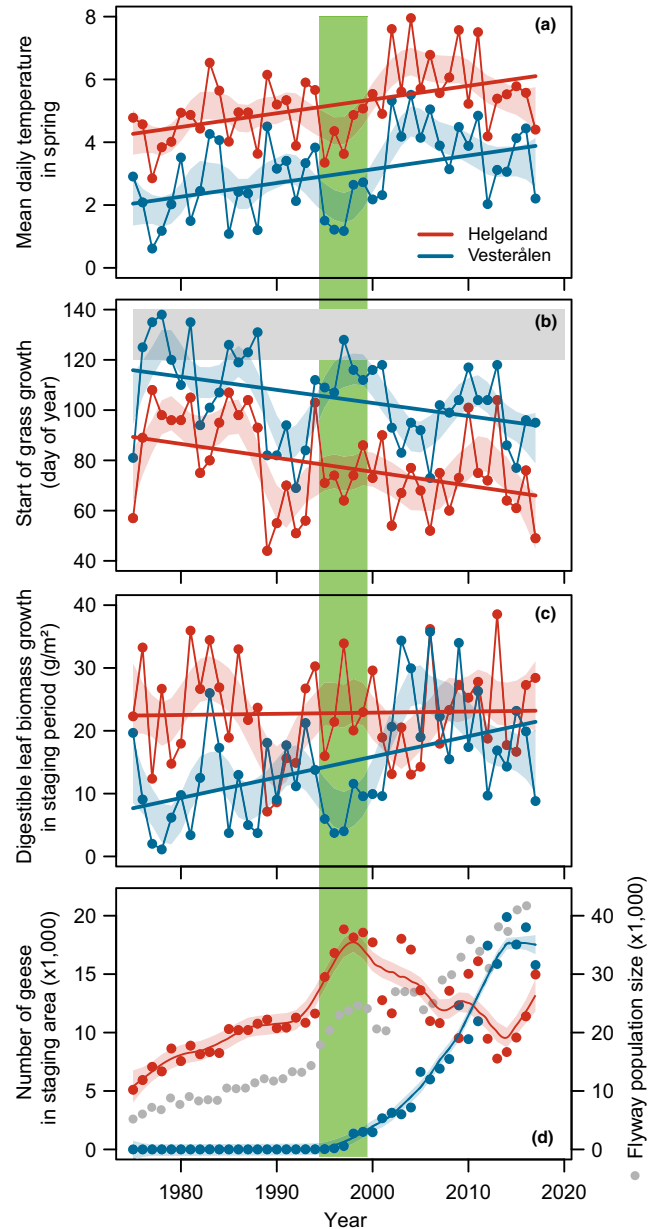

FIGURE 2 Mean daily temperature (a), start of grass growth (b) and mean daily digestible leaf biomass growth (c) in spring at two staging areas for barnacle geese in Norway, Helgeland (red) and Vesterålen (blue), 1975–2017. Lines show predictions of the linear models (Table 1). The bottom panel (d) shows annual peak numbers of barnacle geese (left axis) in Helgeland and Vesterålen, and the total flyway population size (grey dots, right axis). Shaded bands are standard errors from local regression analyses (loess, span = 0.2). For ease of comparison, the goose staging period has been shaded grey (panel b), and the years when geese colonized Vesterålen are indicated by the vertical green box

(Figure 2c). Local regression analyses indicated that the trends in both areas were not uniform, and that fluctuations differed considerably between both areas (Figure 2c). Most strikingly, Vesterålen showed a sudden increase in staging period vegetation quality in the early 2000s, whereas Helgeland did not.

TABLE 1 Model estimates of the best linear models for three response variables: mean daily temperature from 1 April to 20 May (Temp, in °C), onset of spring growth (Onset, day of the year) and mean daily digestible leaf biomass growth during the staging period (Growth, in g/m²). Explanatory variables were year (from 1975 to 2017, centred to the mean) and area (either Helgeland [H] or Vesterålen [V])

Model	Parameter	Estimate	SE	t	p
Temp	Intercept	5.19	0.170	30.5	<.001
	Year	0.04	0.097	4.5	<.001
	Area-V	−2.22	0.241	−9.2	<.001
Onset	Intercept	77.67	2.584	30.1	<.001
	Year	−0.54	0.147	−3.6	<.001
	Area-V	27.26	3.654	7.5	<.001
Growth	Intercept	22.81	1.227	18.6	<.001
	Year	0.02	0.099	0.2	.854
	Area-V	−8.26	1.735	−4.8	<.001
	Year × area-V	0.31	0.140	2.2	.029

3.2 | Goose numbers

The number of barnacle geese in the two spring-staging areas has changed markedly over the study period. From 1975 until 2000, goose numbers in Helgeland grew rapidly by 4.5% (±0.24) annually, fuelled by an increasing flyway population size (Figure 2d). After the first flocks of geese had been seen in Vesterålen in the early 1990s, numbers there built up in the second half of the 1990s to 1,500 individuals at the end of that decade. From 2000 onwards, the flyway population continued to increase by 3.8% (±0.39) annually. At the same time, numbers in Helgeland dropped at a rate of 3.9% (±1.24). In contrast, numbers in Vesterålen increased by on average 14.2% (±1.12) annually, such that from 2012 onwards, numbers in Vesterålen exceeded those in Helgeland (Figure 2d).

During the main study period (1994–2017), number of geese in Vesterålen exhibited a strong correlation (r = .90) with the total flyway population size. The slope of the relationship between numbers in Vesterålen and flyway numbers (0.84 ± 0.086; Figure 3a) indicates that much of the flyway population increase was accommodated in Vesterålen. Detrended numbers were not correlated (Figure 3b), which suggests that additional factors besides population size affected annual variation in goose abundance in Vesterålen. However, neither date of onset of grass growth nor amount of digestible biomass added significantly to a linear model (Table S2). This was partly because the years that geese colonized Vesterålen (1994–1999) were strikingly colder than preceding years, with a late onset of grass growth and low biomass production. Nevertheless, the changes in the onset of grass growth are likely to have allowed the geese to colonize Vesterålen. Taking the date of onset of grass growth as an indicator of improved foraging conditions in Vesterålen, 8 of the 20 years before geese started to colonize Vesterålen (1994) were late growth seasons (i.e. the grass only started to grow during the typical Norwegian staging period), whereas late growth seasons did not occur after colonization (from 2000 onwards; χ_1^2 = 6.87; p < .01; Figure 2b).

3.3 | Choice of staging areas

From 1994 to 1999, the first years of colonization of Vesterålen, the most common age classes there were 1 and 2 year olds (61%
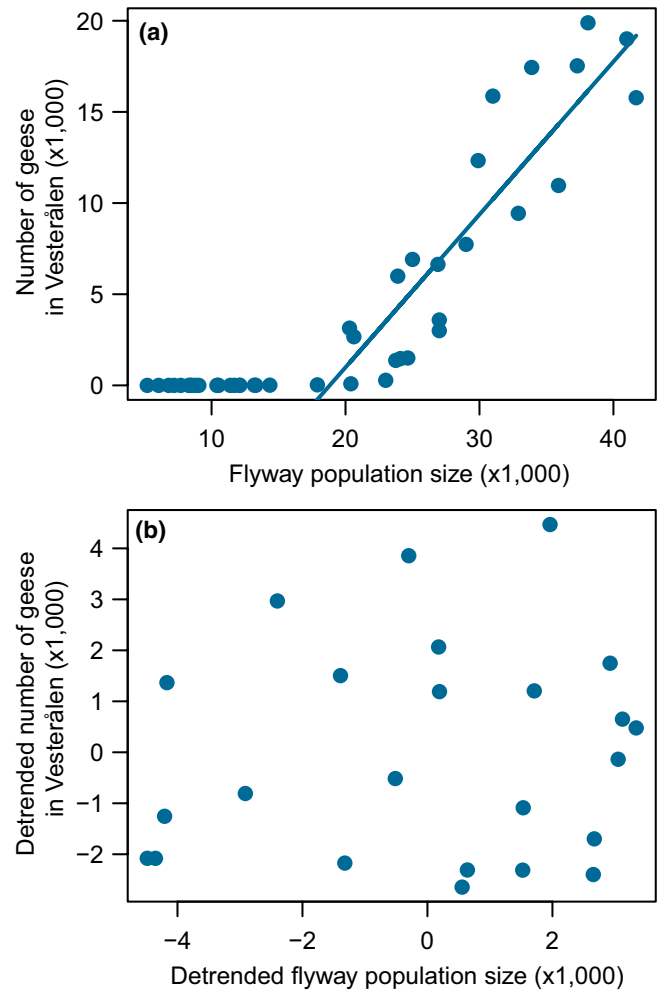

FIGURE 3 (a) Relationship between annual peak numbers in Vesterålen and the total flyway population size (estimated in the preceding winter, see Figure 2d) from 1975 to 2017. (b) The same relationship after detrending. The regression line refers to observations in the main study period (1994–2017: y = 15,780 + 0.84x, $F_{1,22}$ = 94.5, p < .001)

of the resightings, n = 28). At that time, these age classes were less prominent in the flocks at Helgeland (25%, n = 748; comparison among areas χ_1^2 = 17.39; p < .001). The prevalence of 0 year old
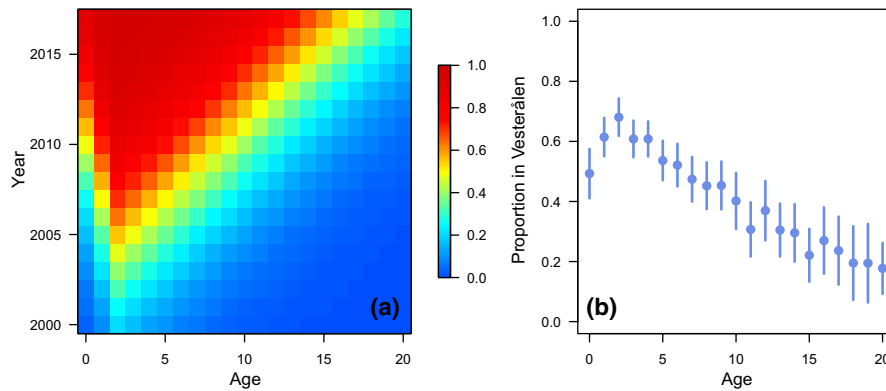
FIGURE 4 (a) Proportion of barnacle geese staging in Vesterålen (as opposed to Helgeland) in relation to age (horizontal axis) and year of observation (vertical axis). The scale and associated colours are shown on the right. Estimates are based on the model in Table 2. (b) Proportion of individual barnacle geese staging in Vesterålen (as opposed to staging in Helgeland) in relation to age. Given are the mean values with 95% confidence intervals based on all records (2000–2017)

birds was similar in Vesterålen and Helgeland (4% and 9%, respectively; χ^2_1 = 1.09, p = .36). With geese becoming more numerous in Vesterålen after 2000, the composition of the local population remained skewed towards younger birds, although the difference was less obvious than during the years of colonization (19.6% of the resightings in Vesterålen concerned 1 or 2 year olds, n = 1,354, and 10.8% in Helgeland, n = 1,285, respectively; χ^2_1 = 14.21, p < .001, combined for all years after 2000). Modelling the proportion of birds staging in Vesterålen as a function of age (0–20) and year (2000–2017) showed that the proportion increased over the years for all ages (Figure 4a; see raw data in Figure S2). Proportions dropped with age in each separate year (Figure 4a,b). Birds of 0 and 1 year old were exceptions to this trend, both showing lower proportions compared to the trend over all age classes (Figure 4a,b; Table 2). The range of ages at which most birds staged in Vesterålen broadened over the years, such that by the end of the study period, the majority of all age classes staged in Vesterålen, except the oldest birds (>16 years; Figure 4a).

3.4 | Probability of switching staging areas

The probability of switching spring-staging area in subsequent years was best explained by effects of the current staging area (Helgeland or Vesterålen), age, year and all two-way interaction terms (Table 3, model selection in Table S6). For geese staging in Helgeland, the probability of switching to Vesterålen in the next spring dropped steeply with age, but for all age classes, the probabilities increased over the years (Figure 5a). The trends in probability for the reverse were strikingly different. First, they were considerably lower (Figure 5b). Second, rather than a unidirectional trend within the relationship of age with year, an interaction between age and year became apparent (Figure 5b). Both young birds in the early 2000s and old birds in more recent years showed elevated switch rates compared to the other birds.

Male and female exhibited similar switch rates (Table S7; Figure S3). The only evidence of a sex effect was among the 0 year olds,

TABLE 2 Model estimates (fixed effects) of the proportion of barnacle geese staging in spring in Vesterålen (as opposed to Helgeland) in relation to year of observation, age and development stage (juvenile or yearling). Data were analysed by glmmPQL with a binomial distribution and logit link function. Non-significant term is not included in the final model. Age and year were centred to the mean. Dev is a factor representing development stage (being either 0 year [0], 1 year [1], or older [2]). Sex and individual were random factors
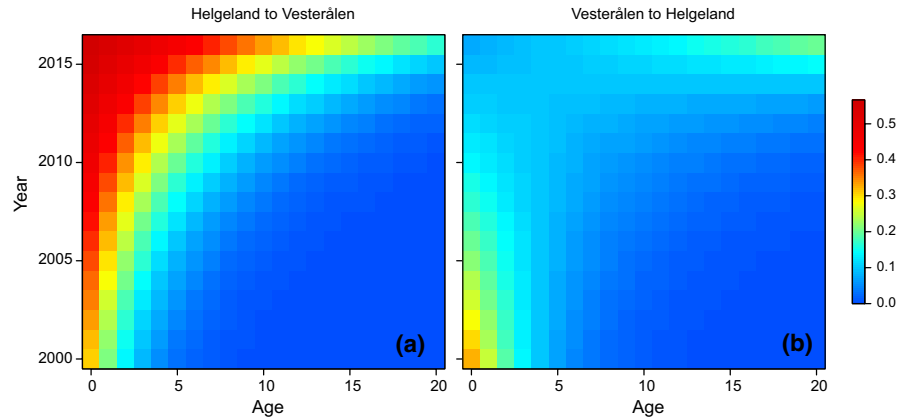
Term	Estimate	SE	df	t	p
Intercept	0.163	0.149	1,710	1.095	.274
Age	−0.263	0.021	1,710	−12.358	<.001
Year	0.336	0.019	1,710	17.859	<.001
Dev-0	−2.32	0.251	1,710	−9.249	<.001
Dev-1	−1.162	0.195	1,710	−5.96	<.001
Age × Year			1,709	1.22	.224

TABLE 3 Parameter estimates of the preferred multistrata model examining the effects of area, age and year on switching probabilities between Helgeland (H) and Vesterålen (V) by barnacle geese. Given are the lower and upper bounds of the 95% confidence intervals. Year and age are continuous variables. Note that parameter estimates are on a logit scale

	Estimate	SE	Lower	Upper
Intercept	−0.807	0.683	−2.146	0.532
Area-V	0.088	0.668	−1.221	1.397
Year	0.067	0.069	−0.068	0.203
Age	−0.516	0.129	−0.769	−0.264
Area-V × Year	−0.176	0.060	−0.293	−0.059
Year × Age	0.026	0.011	0.005	0.048
Area-V × Age	0.148	0.070	0.010	0.286

with females tending to have a higher probability of switching to Vesterålen than males (mean = 0.71 ± 0.166 and mean = 0.36 ± 0.169, respectively; overlapping 95% confidence intervals).

FIGURE 5 Probabilities that barnacle geese switch from one staging area to the other in subsequent years from Helgeland to Vesterålen (a), and the other way around (b). Probabilities are related to age (horizontal axis) and year of observation (vertical axis). The scale and associated colours are shown at the right. Estimates are based on the model in Table 3

3.5 | Balance of movements

Averaged across years, an estimated 1,120 birds changed from using Helgeland in one spring to use Vesterålen the next spring (Figure 6), whereas 595 birds are estimated to have done the opposite (note that these are partly the same birds). Thus, the overall net flux towards Vesterålen amounted to 525 birds per year. This coincided with an estimated decrease in the local number of birds in Helgeland by 160 annually (see Figure 2d), which means that the numbers in Helgeland have been supplemented by a net amount of 365 recruits annually (525–160). Similarly, the net flux to Vesterålen of 525 birds coincided with a local increase of 840 birds annually (Figure 2d), which means that switching across years between staging areas accounted for approximately 62.5% (525/840) of the population growth in Vesterålen. The remaining 37.5% of

the local population growth (840–525 = 315 birds annually) must have resulted from recruitment of birds staging in Vesterålen for the first time.

4 | DISCUSSION

The numbers of barnacle geese staging in Vesterålen increased rapidly from the 1990s onwards (Figure 3), and within 15 years after the first flocks of spring-staging barnacle geese colonized Vesterålen, the numbers surpassed those in the traditional Helgeland area. Below, we discuss which environmental changes may underlie this rapid change. We also examine which behavioural processes may have enabled the geese to adjust their migratory behaviour.

4.1 | The colonization of Vesterålen

The colonization of Vesterålen by barnacle geese in the late 1990s followed a northward expansion already apparent in the 1980s within the Helgeland area (Black et al., 2014). Two main causes were thought to underlie the northern expansion (Prop et al., 1998). First, global warming provided geese with opportunities to explore foraging grounds further north than the original spring areas. Second, with an increasing population size, the limited amount of foraging area in the traditional area had reached a carrying capacity. Our observation that barnacle geese expanded further north in the following decades, and this time in substantially larger numbers, fits well within this picture. Here, we are able to provide quantitative evidence as to how geese respond to environmental changes due to climate warming and demonstrate that the dramatic changes in distribution and size of populations occurred in association with a warming climate.

FIGURE 6 Box-and-arrow diagram demonstrating the use by barnacle geese of the spring-staging areas in Helgeland and Vesterålen, Norway. Figures in circles represent the change in goose numbers in each area over the period 2000–2017, and circle sizes are proportionate to average numbers staging. The annual number of individuals that switched from Helgeland in one spring to Vesterålen in the next spring, or the opposite, is calculated from counts and switch rates (see Section 2). Annual numbers recruiting into the local populations are added to complete the budget of goose numbers

4.2 | Warmer climate and earlier onset of grass growth

The grass growth model that we modified for this study was developed by Bonesmo and Bélanger (2002a, 2002b) based on

observations of timothy grass varieties that were available at the time of publication. Economic grass varieties are continuously being selected for an earlier growth date (Wilkins & Humphreys, 2003), and farmers have possibly used successive generations of improved grass breeds. If so, we expect a later onset of grass growth and a lower digestible leaf biomass production for the early years of this study, and the opposite for later years. This means that the actual trends may have been even stronger than our model predicted. Other simplifications that we made, such as optimal nitrogen conditions, might have resulted in an overestimation of grass production. However, we expect this effect to be more or less the same annually, which justifies using the model results as a relative measure, as we did.

A surprising result from the grass growth model was that the production of digestible biomass in Helgeland remained stable throughout the study period, in spite of strongly enhanced grass growth in the area, and unlike the observed trend in Vesterålen. This was caused by the early ageing of the grass in Helgeland, resulting in a decrease of grass digestibility. Indeed, an earlier ageing may cause the grass to be beyond its usefulness to geese, cf. the 'green wave' (van der Graaf, Stahl, Klimkowska, Bakker, & Drent, 2006). As we found no indication that digestible biomass production in the traditional area has changed, it is unlikely that the shift towards the northern staging area has been triggered by changes in food conditions in the traditional area alone. Instead, we suggest that the changed conditions at Vesterålen contributed to the observed range expansion. The spring in Vesterålen often did not start until well into the staging period in the 1990s and earlier years, but during the past 20 years, grass growth had always started before the geese arrived in Norway. In some of the recent years, the production of digestible biomass during the staging period has even been larger than in Helgeland (Figure 2c).

4.3 | The impact of population size and carrying capacity

Spring-staging areas are important for migratory geese as a place for supplementing body stores prior to the final leg of the spring migration, egg laying and incubation (Spaans, van't Hoff, van der Veer, & Ebbinge, 2007), and performance in the staging areas has repercussions for the number of offspring produced and their survival probability (Kéry, Madsen, & Lebreton, 2006; Klaassen, Hahn, Korthals, & Madsen, 2017; Madsen, 2001; Prop, Black, & Shimmings, 2003). Thus, correspondence in the trends of numbers in Vesterålen and in the total size of the flyway population suggest that population growth in the 1990s had become limited by competition during staging in Helgeland. This finding is of interest because evidence for population limitation at staging sites is limited for migratory birds (Newton, 2007). However, it is in line with earlier findings in barnacle geese that better body condition in Helgeland increases the probability of returning to the United Kingdom with offspring (Prop & Black, 1998). This implies that the recent doubling of the population size might not have been possible without the availability of

Vesterålen as a staging area due to climate change. We cannot exclude the possibility that a growing barnacle goose population could have colonized alternative areas in the absence of climate warming, but the amount of suitable habitat in Vesterålen is much larger than anywhere else along the coast of northern Norway (Tombre, Tømmervik, Gullestad, & Madsen, 2010). That bird populations are strongly affected by changes in climate is well recognized (Crick, 2004), but to our knowledge, this is one of the few examples to provide evidence for direct and large-scale effects of global change on bird population size.

4.4 | Interactions with pink-footed geese

Vesterålen has traditionally been the main spring-staging area for pink-footed geese (*Anser brachyrhynchus*; Madsen, Cracknell, & Fox, 1999; Tombre et al., 2008). But as the number of barnacle geese has increased in Vesterålen, the number of pink-footed geese has decreased (Tombre et al., 2013). The majority of pink-footed geese now stage at another site in Mid-Norway, which is located further south than Vesterålen along their migration route from Denmark. Pink-footed geese are observed to avoid barnacle geese, probably because they cut the grass down to unprofitable lengths for the larger billed pink-footed geese (J. Madsen & I. Tombre, unpublished data). Therefore, we expect that the observed barnacle goose population dynamics are not greatly affected by the presence of pink-footed geese. Nonetheless, the presence of pink-footed geese in Vesterålen may have contributed to both the suitability of the area to barnacle geese and the likelihood of its discovery by barnacle geese. In this sense, pink-footed geese may have facilitated the colonization of Vesterålen by barnacle geese (cf. Baveco, Kuipers, & Nolet, 2011).

4.5 | Behavioural processes underlying the changes in staging area use

In a demographic sense, the population growth at Vesterålen is composed of two different processes. The first is the early developmental process of migratory behaviour; this process caused an increasing number of 0 year old birds, on their first northward migration and without any local experience, to choose Vesterålen as their staging area. Previous studies showed that approximately 18% of the 0 year old birds remained with their parents up to their first spring migration (Black et al., 2014). So, those that are still with their parents can follow them en route to the staging areas, or they can follow a 'carrier' flock of the same or different species and learn from others. There are several benefits for young birds to join birds of the same age in particular. First, due to the lower competitive abilities of younger, inexperienced birds (Black & Owen, 1987; Raveling, 1969, 1970; Stahl, Tolsma, Loonen, & Drent, 2001), it may be an effective way to reduce food competitors. Second, there is the increased opportunity of finding potential mates as the vast majority choose a partner of the same age when pairing for the first time (Black & Owen, 1995). Also geographically speaking, Helgeland is the first

area a naïve 0 year old goose will encounter heading north from the Solway and so it cannot choose between that area and Vesterålen as it has no knowledge of the area further north at this stage of its first spring migration.

The second process that explains the population growth in Vesterålen is that individuals change their choice of staging area later in life: especially 1 and 2 year old birds staging in Helgeland exhibited a relatively high probability of switching to Vesterålen in the subsequent year. Over the years, geese that switched staging area included increasingly older individuals as well. The proportion of 1 and 2 year old birds in the newly colonized area was high from the first years of colonization onwards, and since then always remained higher than in the traditional staging area.

There are several potential behavioural differences between young and adult geese that could explain the observed dissimilarity in switching rates between staging areas. One of them is that young geese may be more prone to explore new areas (Morand-Ferron, Cole, Rawles, & Quinn, 2011). Indeed, fitness costs of exploring an unsuitable area are lower for young birds, as geese only start reproducing when they are 2 years old, and generally much later (Prop, van Eerden, & Drent, 1984). At the same time, the potential fitness advantage of exploring a profitable site will be higher for young geese, as they will on average, as a long-lived species, have more future breeding seasons to benefit from the choice they make (Stearns, 1992).

Another explanation for higher switch rates in young birds is that most pair formations occur before an age of 5 years (Choudhury, Black, & Owen, 1996), and individuals may subsequently switch staging area when following their new partner. Indeed, this was the reason why younger age classes of Greenland white-fronted geese (*Anser albifrons flavirostris*) showed higher rates of switching to other wintering areas (Marchi et al., 2010).

4.6 | Cultural evolution of migratory behaviour

Colonization events in nature often remain obscure, as monitoring programs usually start in response to the event, and not in anticipation. In our case, Vesterålen is an important traditional spring-staging area for pink-footed geese, and systematic goose monitoring has been in place since 1988 (Madsen et al., 1999; Tombre et al., 2013). As a consequence, the colonization event was monitored more precisely than otherwise would have been possible. The results are highly suggestive of a complex social system, mixing social learning with individual experiences, that underlies the population-scale patterns of staging area choice by barnacle geese. This system has allowed the population to respond rapidly to increasing density dependence in the traditional staging area, as well as to changing environmental conditions as a result of a warmer climate, by colonization of a new staging area and rapid redistribution.

Cultural inheritance is likely to be an important aspect of migratory behaviour by geese in general, as they travel in groups and new behavioural strategies spread relatively fast (Clausen et al.,

2018; Larsson et al., 1988). Cultural inheritance was, for example, suggested to play an important role for the breeding distribution in light-bellied brent geese (*Branta bernicla hrota*), where individually marked birds were followed for several years and offspring recruited near to or within their natal site (Harrison et al., 2010). A similar process was also proposed earlier for barnacle geese (Eichhorn et al., 2009; Jonker et al., 2013; van der Jeugd, 2001), but our study is the first to show the link between individual decisions and population-scale patterns in any detail. In doing so, our study adds to a growing number of studies that point out the importance of social processes in the development of migratory behaviour (see, Berdahl et al., 2018 for a review). However, we stress that these behavioural processes remain largely speculative, and the size and direction of their combined effects go beyond our current understanding. Further quantitative study on these combined effects may shed more light on the respective roles of naïve juveniles and experienced adults in the colonization of new staging areas, and the evolution of migratory behaviour in general.

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