



UvA-DARE (Digital Academic Repository)

Bewick's swans in a changing world

Species responses and the need for dynamic nature conservation

Nuijten, R.J.M.

Publication date

2020

Document Version

Other version

License

Other

[Link to publication](#)

Citation for published version (APA):

Nuijten, R. J. M. (2020). *Bewick's swans in a changing world: Species responses and the need for dynamic nature conservation*. [Thesis, externally prepared, Universiteit van Amsterdam].

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.



Chapter 6

Concurrent shifts in wintering distribution and phenology in migratory swans: individual and generational effects

Rascha J.M. Nuijten, Kevin A. Wood, Trinus Haitjema, Eileen C. Rees, Bart A. Nolet

Abstract

Range shifts and phenological change are two processes by which organisms respond to environmental warming. Understanding the mechanisms that drive these changes is key for optimal conservation and management. Here we study both processes in the migratory Bewick's swan (*Cygnus columbianus bewickii*) using different methods, analysing nearly 50 years of resighting data (1970-2017). In this period the wintering area of the Bewick's swans shifted eastwards ("short-stopping") at a rate of $>12.5 \text{ km y}^{-1}$, thereby shortening individual migration distance on average by 353 km. Concurrently, the time spent at the wintering grounds has reduced ("short-staying") by ~ 38 days since 1989. We show that individuals are consistent in their migratory timing in winter, indicating that the frequency of individuals with different migratory schedules has changed over time (a generational shift). In contrast, for short-stopping we found evidence for both individual plasticity (individuals decrease their migration distances over their lifetime) and generational shift. Additional analysis of swan resightings with temperature data showed that, throughout the winter, Bewick's swans frequent areas where air temperatures are $c. 5.5^{\circ}\text{C}$. These areas have also shifted eastwards over time, hinting that climate warming is a contributing factor behind the observed changes in the swans' distribution. The occurrence of winter short-stopping and short-staying suggests that this species is to some extent able to adjust to climate warming, but benefits or repercussions at other times of the annual cycle need to be assessed. Furthermore, these phenomena could lead to changes in abundance in certain areas, with resulting monitoring and conservation implications. Understanding the processes and driving mechanisms behind population changes therefore is important for population management, both locally and across the species range.

Introduction

Rapid global environmental change is affecting ecosystems, communities and species worldwide (Walther et al., 2002). Changes in temperature are of particular importance because of their influence on species' distribution (Chen et al., 2011; Hickling et al., 2006; Maclean et al., 2008; Parmesan and Yohe, 2003), abundance (Pounds, 2001; WWF, 2018), phenology (Visser and Both, 2005) and extinction risk (Thomas et al., 2004).

For migratory species that visit geographically discrete areas during their annual cycle, differing rates of change and the unpredictability of favourable conditions among these areas can create severe challenges (Robinson et al., 2009). If rates of change are not correlated between the areas these animals frequent, it is impossible for them to predict the time and place with optimal conditions (Kölzsch et al., 2015). This can lead to a mismatch with optimal circumstances (i.e. peak food abundance) because the cues they use change at a different rate (i.e. temperature at staging sites; Both, Bijlsma, & Visser, 2005), or do not change at all (i.e. day length; Post & Forchhammer, 2008). It has been found that migratory species that are declining tend to also be those that are showing weak or no phenological changes (Møller et al., 2008), especially when migratory diversity within a species is small (Gilroy et al., 2016). Changes in the distribution and/or phenology of a population can be the result of individual plasticity in the use of space and time. In the absence of individual plasticity, generational change must be the mechanism driving shifts in space or time (Gill et al., 2019). Generational change can arise from recruits consistently using different schedules than the previous generations, or by differential mortality. Both change the frequency of individuals with a certain state (e.g. distribution or timing), leading to an observed population change in this property (Gill et al. 2019).

Range shifts have been documented for many taxa (Chen et al., 2011; Parmesan and Yohe, 2003). One specific form of a range shift in migratory species is "short-stopping": "*A range shift that involves shortening of the migratory route, and is qualified by season (winter or breeding) and degree (full or partial)*" (Elmberg et al., 2014). Partial winter short-stopping has been suggested to be driven by climate warming, and has been documented in a variety of ways in waterfowl (Fox et al., 2016; Lehikoinen et al., 2013; Pavón-Jordán et al., 2019; Podhrázký et al., 2017). Fitness benefits may arise from shorter migration distances, as the annual cycle becomes less time-constrained (Tomotani et al., 2018) and individuals can make better predictions of environmental conditions in geographic areas further along their route (Visser et al., 2009). However, unforeseen harsh conditions in the areas closer to the breeding grounds could also be a risk and lead to high mortality (Suter and van Eerden, 1992).

In addition to changing distributions, migratory species can also show shifts in phenology in response to changing conditions (Diehl, 2019; Jonzén et al., 2006). Phenological changes can be studied in all aspects of the annual cycle (Tomotani et al., 2018) such as breeding (Dunn and Winkler, 2010) and the onset of migration (Cotton, 2003; Tombre et al., 2008). When phenological changes concern departure or arrival in a certain area (e.g. breeding or wintering), this can lead to a longer or shorter duration of time spent in an area. For the latter, we will use the term "short-staying" throughout this paper, in line with the term short-stopping as defined by Elmberg et al. (2014), comprising "*A phenological change in arrival or departure*

(or both) that involves shortening of the duration of time spent in a certain area". Arrival or departure have been studied mainly with regard to the breeding area of birds (e.g. Jonzén et al., 2006; Xu & Si, 2019), but changes in the wintering area are relevant too (Stirnemann et al., 2012), as most migratory species are bound to a tight annual cycle and could thus benefit from shortening the time spent in their winter quarters if warming would permit them to do so (Norris and Taylor, 2005).

Apart from assessing that changes are taking place, it is important to identify the drivers and mechanisms behind such changes. In this context "drivers" refer to the environmental steering factors such as temperature (Lehikoinen et al., 2013; Visser et al., 2009) or precipitation (Jónsson and Afton, 2015), acting either directly or indirectly (for example via food abundance) on where and when individuals are present. Alternatively, "mechanism" refers to individual plasticity or generational shifts which are behind the changes observed at the population level. Individual plasticity can cause population level changes when the drivers to which individuals respond change consistently in a specific direction (Gienapp, Teplitsky, Alho, Mills, & Merilä, 2008). Generational shifts can cause changes in the spatial or temporal distribution of a population when the frequency of individuals with a certain spatial or temporal state changes, such as when environmental conditions alter the frequency of recruits with differing states, or the mortality rates associated with these states (Gill, Alves, & Gunnarsson, 2019). Both may change the frequency of individuals with a certain state (e.g. distribution or timing).

For instance, individual black-tailed godwits (*Limosa limosa islandica*) are consistent in their migration timing over their lifetime but the proportion of juveniles recruiting into two stopover sites changed, leading to a population pattern of advanced spring arrival (Gill et al., 2013). In another population of black-tailed godwits (*Limosa limosa limosa*), juveniles started using a stop-over site proportionally more than adults and continued using these sites into adulthood, leading to an observed distribution shift at the population level over time (Verhoeven et al., 2018). Gill et al. (2019) concluded that the observed changes in distribution and phenology of migratory species likely result from generational shifts, as opposed to individual plasticity, as individual fidelity in the use of space and time is thought to be strong (Winger et al., 2019). However, we expect that generational shifts are less prevalent in species that migrate in families where young individuals follow their parents and thus 'copy' their routes and schedules ('states') in early life. Shifts in range and phenology could arise in such a system through individual plasticity at any life stage, recruits changing state once independent of their parents, or through changes in mortality across individual states.

The Bewick's swan (*Cygnus columbianus bewickii*) is one of the largest migratory bird species using an energy-intensive flapping flight mode, which requires stopovers for refuelling during migration, resulting in a tight annual cycle (Hedenstrom and Alerstam, 1998; Nuijten et al., 2014). A major decrease in numbers for the population which winters in NW Europe and breeds on the European Russian tundra, resulted in the development of an International Single Species Action Plan (Nagy et al., 2012) which identified threats to the population through expert assessment and called for research to determine the cause of the decline. Studies to date indicate that neither annual survival nor reproduction seem to have been solely responsible for the decline (Wood et al., 2018; Wood, Newth, Hilton, Nolet, & Rees, 2016), which has shifted the attention to the wintering grounds. Given the strong family bonds and site fidelity in this species (Rees, 2006), it was long thought that there would be relatively little flexibility in the use of wintering sites over the lifetime of individuals and their offspring. Recent

drastic declines in numbers at some traditional wintering areas, and an absence of conclusive reasons for these trends, gave greater weight to the hypothesis that the swans were short-stopping in their wintering range (Augst et al., 2019; Wahl & Degen, 2009; Wood et al., 2019). International census data revealed that Bewick's swans wintered further north but not east in milder winters, but, although numbers significantly decreased at the western edge and increased at the eastern edge, did not result in conclusive evidence for a north-easterly shift in winter distribution over time, perhaps because counts were conducted only once every five years and hence the study had limited statistical power with which to detect such shifts (Beekman et al., 2019). In this study we use ring-resightings as a more powerful data source with hundreds of sightings every year, to analyse whether concurrent occurrences of winter short-stopping and short-staying are evident in this avian migrant, based on the hypotheses that the swans currently arrive later, depart earlier and stay further east (i.e. closer to the breeding grounds) in winter than before. Importantly, the ring-resightings also enable us to analyse whether individual plasticity or generational shifts provide the mechanism for changes in the birds' phenological patterns. In addition we test the hypothesis that climate warming is the environmental driver for the observed changes by determining the mean air temperature where individual Bewick's swans occur, and comparing the shifts in this temperature with their range and phenology shifts.

Methods

Ringling schemes

We used two long-term monitoring programmes for Bewick's swans, one for leg-rings and one for neck-bands. In both schemes individuals were aged at capture as either juvenile, yearling or adult based on the presence or absence of grey plumage, respectively (Rees, 2006). The leg-ring programme, which commenced in 1970, was led by the Wildfowl & Wetlands Trust (WWT) in the UK. Rings were fitted both at wintering sites in the UK and on the breeding grounds in northern Russia. A total of 3998 individuals are present in this dataset, which were resighted 36,933 times outside the WWT's wetland reserves. The sightings within WWT reserves were explicitly excluded for this study, due to a different detection method (bill pattern rather than neck- or leg-ring ID). The neck-band ringling programme was initiated by TH (since 1989) and continued by NIOO-KNAW (since 2005), and neck-bands were applied in the Netherlands and Germany. In total, 843 individuals fitted with neck-bands were resighted 38,148 times. A network of professional and amateur ornithologists across the winter range in northwest Europe resighted the marked birds and the scheme organisers collated reports of these resightings into a database. The resighting numbers in this study represent unique resightings per swan per day; if a swan was registered more than once a day (for example by multiple observers) only one sighting was included in the analyses. The resighting probability of tagged individuals differs between the two ringling schemes because the larger neck-bands generally are easier to read in the field than leg-rings: leg-rings have a mean (\pm 95% CI) resighting probability of 0.70 (\pm 0.02) and neck-bands 0.91 (\pm 0.01), with no apparent trends over time (Wood et al., 2018). In this study we combined data from all individuals of both ringling schemes. Since we were interested in the overall patterns in the presence of the swans in time and space, the difference in resighting probability between swans marked with leg-rings versus those with neck-bands was not likely to influence the results. Where differences in the outcomes could occur, we analysed resightings of leg-rings and neck-bands separately, to determine whether the results were consistent irrespective of the marking method.

Short-stopping

To assess the occurrence and extent of short-stopping in this migratory species, we used three different methods. For the first two methods we selected resightings only for the months December and January in each winter season, to prevent short-staying from influencing the results. In this subset, 3865 individuals with in total 26,366 resightings were present (leg-ring: N = 3216 / 15,364; neck-band: N = 649 / 11,002 for individuals and resightings respectively). For the third method, all resightings in the winter half-year (October-March) were included.

In the first method (M1), we calculated the mean average geographic location of the resightings per winter season, and tested whether longitude and/or latitude showed a directional change towards the north and/or east over time (see Fox et al., 2016) with the following model

$$Lat_i \sim \beta_0 + \beta_1 Y_i + \varepsilon_{0i} \quad (6.1a)$$

$$Lon_i \sim \beta_0 + \beta_1 Y_i + \varepsilon_{0i} \quad (6.1b)$$

where *Lat* and *Lon* represents latitude (for assessing a northward shift) and longitude (for assessing an eastward shift), respectively, β_0 represents the intercept, β_1 the slope for the dependency and *Y* the winter season, and where subscript *i* refers to the winter season of the measurement and ε_{0ij} is the residual error term.

For the second method (M2), we created a grid with cells of 0.5° x 0.5° (lower left corner - 10.5°W, 50.5°N; upper right corner 11.5°E, 58.5°N; WGS84; Supplementary material S.3) and counted the proportion of resightings per year in each gridcell for every winter season during the study period. Only winter seasons in which > 5 gridcells contained resightings were included in the analysis (in total 44 winter seasons), to allow for an evaluation of the overall pattern in the winter area. We then calculated the trend in the proportion of observations within each gridcell that had resightings in > 5 seasons (to be able to detect such a trend). The slope of this trend for each of the gridcells, weighted by the SE of the slope, was tested against longitude to see whether gridcells towards the east had more positive slopes (indicating an increase in the proportion of resightings in those locations) than gridcells in the west with the model

$$S \sim \beta_0 + \beta_1 Lon + \varepsilon_0 \quad (6.2)$$

where *S* represents the slope within a gridcell, and *Lon* represents the longitude of that gridcell. Outlier Slimbridge was excluded from the analysis (see Discussion).

Thirdly (M3), we calculated the distance from each wintering location (i.e. each resighting) to the breeding grounds (see Podhrázký et al., 2017), as this corresponds directly to the definition of short-stopping (Elmberg et al., 2014). We used a fixed location in the breeding area (Narjan-Mar: 53.1°N, 67.7°E) and calculated the great-circle (orthodromic) distance between each resighting recorded during the winter half-year (Oct-Mar) and this point. The distances were limited to < 4000 km (i.e. the western boundary of Ireland) and > 1700 km (i.e. the distance to a known stop-over site in Estonia). We selected the maximum distance for each individual for each winter season and analysed both the within- and between individual variation in these distances over time (eqn. 6.3; N = 3839 individuals, 14302 resightings)

$$MD_{ij} \sim \beta_0 + \beta_W(Y_{ij} - Y_j) + \beta_B Y_j + u_{0j} + \epsilon_{0ij} \quad (6.3)$$

where MD is the maximum migration distance per individual per winter season Y , β_0 is the intercept, β_W is the estimate for within-individual changes, Y_{ij} is measurement in year i from individual j , Y_j is the average year of measurement for individual j , β_B is the estimate for between-individual changes, and u_{0j} is the random intercept (van de Pol and Wright, 2009).

Short-staying

To test whether Bewick's swans changed their winter phenology by shortening their duration of stay in the wintering grounds, we also used the resighting database described earlier, including both leg-ringed and neck-banded birds. To reduce the underestimation of wintering duration based on resightings (since the resighting rate is never a 100%) we only included individuals that were recorded > 9 times in a winter season (Oct-Mar). We used this selection (43% of all resightings) to ensure that only birds for which the resighting data provided an overview of their presence in a particular winter season were included in the analysis, thus excluding birds with occasional resightings or with observations concentrated on a few days only. We defined the wintering range, and thus the area that the birds arrived at or departed from, as the area west of 12°E because this boundary included almost all winter resightings (see Fig. 6.2) whilst being distanced from the first well-known migratory stop-over sites (i.e. in the Baltic states). The first resighting of an individual to the west of this boundary was labelled as 'arrival', and the last as 'departure', for that particular swan and winter season. All departures in November/December ($N = 29$) and all arrivals in January/February ($N = 188$) were removed from the resulting dataset, on the basis that they were attributable to (a lack of) individual observations, rather than to the timing of the birds' movements. In total 672 individuals and 1634 unique swan-season combinations were included in this analysis. We analysed both the within- and between-individual variation in arrival, departure and winter duration over time (eqn. 6.4; $N = 672$ individuals, 1634 observations)

$$D_{ij} \sim \beta_0 + \beta_W(Y_{ij} - Y_j) + \beta_B Y_j + u_{0j} + \epsilon_{0ij} \quad (6.4)$$

where D is the response variable (either arrival, departure or duration) per individual per winter season, β_0 is the intercept, β_W is the estimate for within-individual changes, Y_{ij} is measurement i from individual j , Y_j is the average year of measurement for individual j and β_B is the estimate for between-individual changes (van de Pol & Wright 2009).

Mechanisms behind short-stopping and short-staying

To study potential mechanisms behind short-stopping and short-staying, we compared the average population change in migration distance or winter duration respectively, with the rate of change in these variables in individuals over their lifetime within the study (see Gill et al., 2019). We used the statistical models provided by van de Pol & Wright (2009) to study within- and between individual variation for migration distance and winter duration (eqn. 6.3 and 6.4). In addition, we applied the following models

$$MD_{ij} \sim \beta_0 + \beta_W Y_{ij} + (\beta_B - \beta_W) Y_j + u_{0j} + \epsilon_{0ij} \quad (6.5)$$

$$D_{ij} \sim \beta_0 + \beta_W Y_{ij} + (\beta_B - \beta_W) Y_j + u_{0j} + \epsilon_{0ij} \quad (6.6)$$

in which the $(\beta_B - \beta_W)$ term now assesses whether β_B and β_W are significantly different from each other (van de Pol and Wright, 2009). We interpreted a significant result for β_W as support for individual plasticity in the trait. In the absence of individual plasticity, generational shifts have to be causing a population shift.

When evidence for either of the mechanisms was found, we applied the same models (eqn. 6.3 and 6.5 for migration distance; eqn. 6.4 and 6.6 for winter duration) to the age classes (age determined at capture) separately to see whether there were particular groups of individuals driving the observed changes in either migration distance or winter duration. Lastly, we also analysed data of individuals with data in both their year of capture and the year thereafter because we hypothesized that if individual plasticity plays a role, particularly the yearlings would be prone to show this since adult Bewick's swan are believed to be site-faithful and juveniles migrate with their parents and consequently follow their migratory schedule (Rees 2006).

Temperature as an environmental driver

To study our hypothesis that climate warming drives the observed population changes in the Bewick's swan population we looked at air temperature as a proxy. For this we matched all resightings west of 12°E in each winter season to the mean daily temperature recorded at the specific time and place of the resighting, using the R package RNCEP (Kemp et al., 2012). Additionally, we collected temperature data for the whole of the wintering range and modelled the position of the isotherms over time to see if changes therein would match a shift in the swans' distribution. For the isotherm modelling we used the E_OBS v18.0e dataset with 0.1°x0.1° resolution grids with daily mean temperatures (Cornes et al., 2018), and averaged all daily maps for each winter (December and January) over the study period (1970-2017) and predicted the temperatures based on a regression model:

$$T_i \sim \beta_0 + \beta_1 Lat_i + \beta_2 Lon_i + \beta_3 Lat_i^2 + \beta_4 Lon_i^2 + \beta_5 Y + \beta_6 Lon_i * Y + \epsilon_0 \quad (6.7)$$

where T is the mean average winter temperature in °C, Lat and Lon represent the latitude and longitude of the 0.1° x 0.1° gridcell i , and Y is the winter season (1970-2017; 1970 representing the winter of 1970-1971).

Results

Short-stopping and underlying mechanism

Based on the mean resighting location for each winter (M1, Fig. 6.1), the mean location of the wintering population of Bewick's swans in NW Europe shifted, both in latitude ($F_{1,46} = 29.63$, $p \ll 0.001$) and longitude ($F_{1,46} = 218.8$, $p \ll 0.001$) (Table S6.2). Over the 48 years of the study, the slopes of the shifts in degrees latitude and longitude amounted to 0.015 ± 0.003 (mean \pm se) and 0.192 ± 0.013 (mean \pm se), respectively. Estimating the first and the last locations based on this regression and calculating the great circle distance between them equals a north-eastward shift of 618 km, corresponding to a mean short-stopping rate of 12.9 km y^{-1} . The sample sizes per winter season can be found in Supplementary material S.1; a similar analysis conducted for the two ringing schemes separately is presented in S.2. The latter analyses confirmed that swans in both ringing schemes show a similar eastward shift (longitude); however, the northward shift (latitude) was absent in the neck-band dataset. In- or

excluding birds ringed in the breeding grounds rather than the wintering grounds did not change the results (S.2), thus they were included.

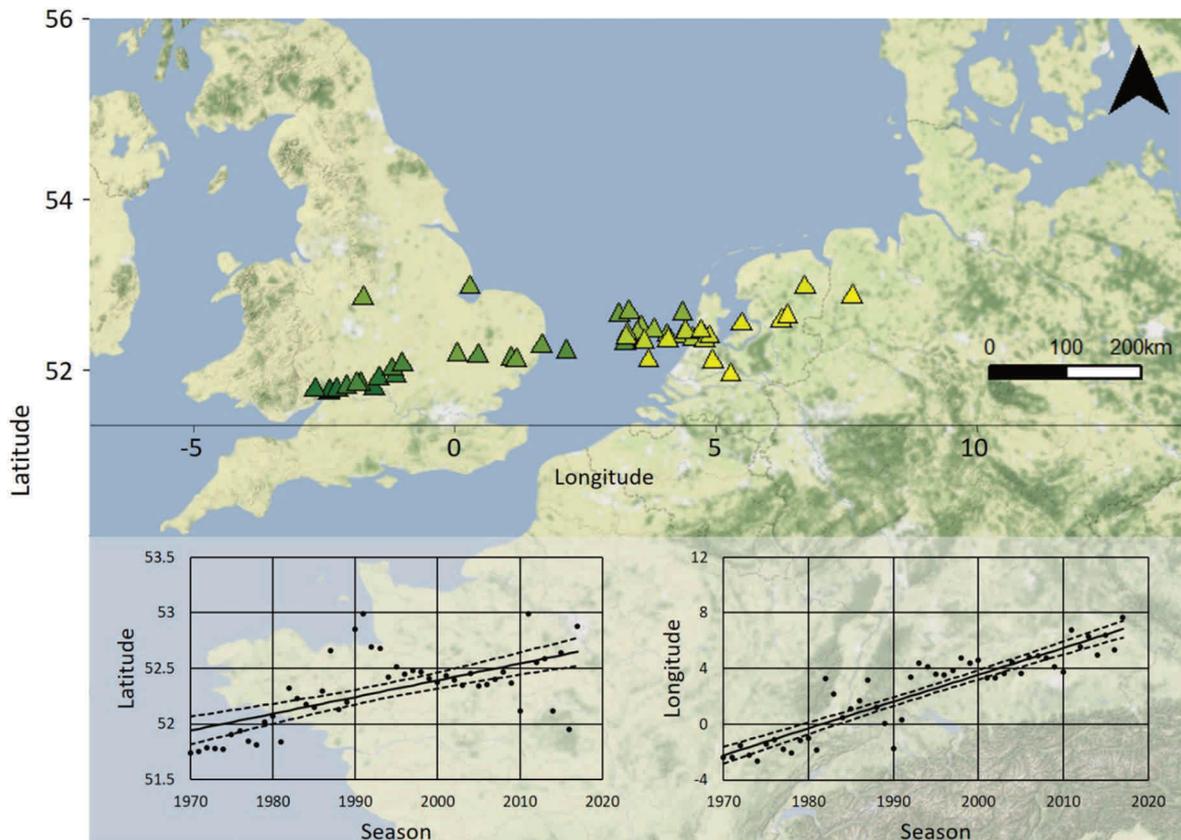


Figure 6.1: Mean winter location of mid-winter (Dec-Jan) resightings in winter seasons 1970/71-2017/18 (M1 in main text). The colour gradient represents time, where dark green is the first winter (1970/71) and yellow is the last winter in the analysis (2017/18). Sample size (resightings per year) ranged between 48 and 1539 (see Table S6.1 for an overview per season). The panel shows the latitudinal (left) and longitudinal (right) shift over time, with a regression (solid line) and 95% CI of the regression line (dashed lines). Both shifts are significant (see text).

Over the same time period, the proportion of resightings was more likely to increase over time in the eastern gridcells as compared to the western gridcells in the grid-analysis (M2; $F_{1,114} = 5.372$, $p = 0.022$; Fig. 6.2; S4), confirming an eastward shift of the population between 1970 and 2017.

Migration distances recorded for individual Bewick's swans decreased significantly over the study period (by -7.3 km per year; Fig. 6.3a; see Table 6.1 for detailed model output), with mean distances of 3324 km (estimate based on model output; Fig. 6.3a) during the first season (1970/71), declining to 2977 km in the last season of the study (2017/18). On average, based on this analysis (M3), the swans' migration is now 353 km shorter than in the early 1970s. The individual rate of change was significantly different from zero (-22 km y^{-1} , $p < 0.001$; Fig. 6.3b) but did not change over the study period ($F_{1,2050} = 0.240$, $p < 0.001$; Fig 3b; Table S6.5). When analysing the age classes separately for the difference in their migration distance between the

year of their capture and the next year, both adults and yearlings decreased their migration distance significantly, juveniles did not (Table S6.8).

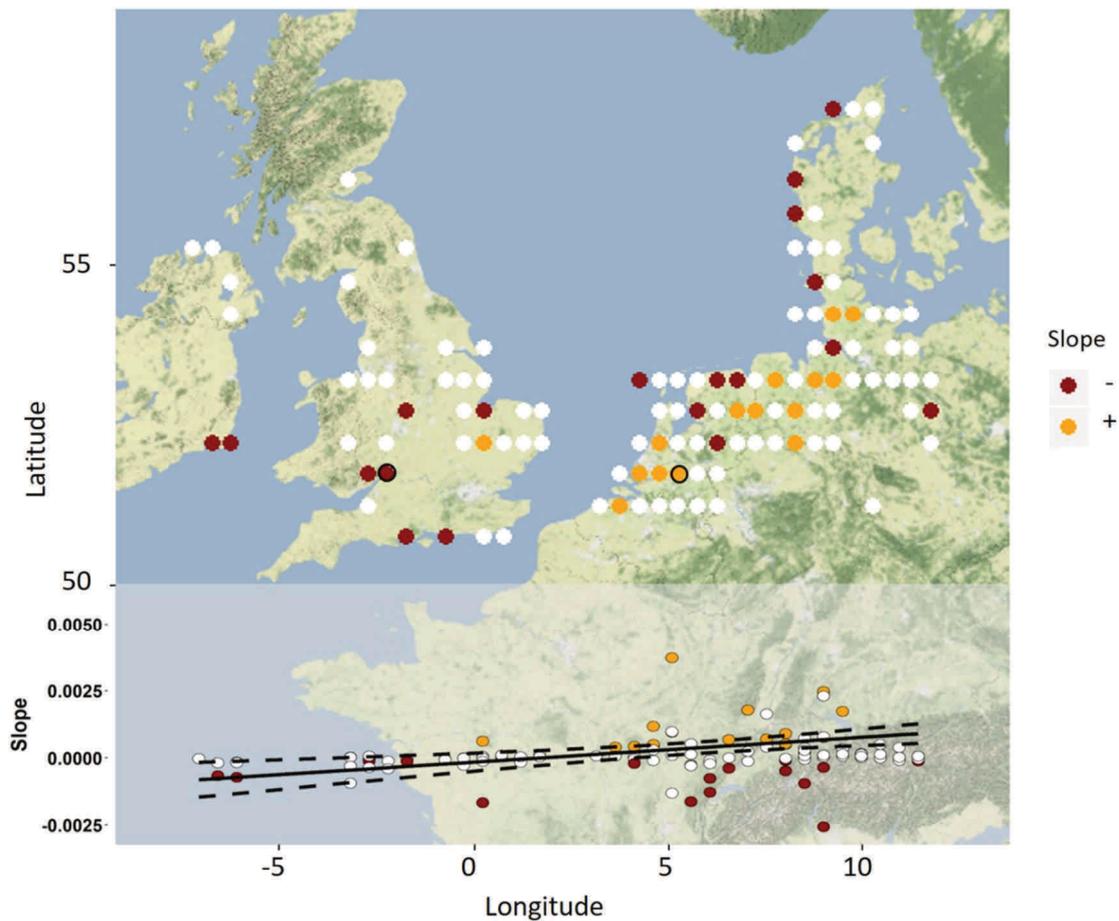


Figure 6.2: Trend of the proportion of resightings done per year in winter (Dec-Jan) in a theoretical grid over NW Europe (M2 in main text). Coloured dots represent gridcells with resightings in > 5 seasons within the study period. The colour shows the trend of the slope of the proportion of resightings in that gridcell over time, with red being a significant ($p < 0.05$) negative slope (-) and orange a significant positive slope; white dots have non-significant slopes. Slope values are visualized in the bottom panel of the figure, where the colours again indicate the significant trends. The solid black line in the bottom panel indicates a significant increase in the (weighted) slope value from west to east (see text). Dashed black lines represent the 95% CI of the regression. The red location with the black outline (main figure) is Slimbridge, a WWT site and the location with the largest decrease in proportion of resightings over time (slope -0.0166 ; excluded from bottom graph and analysis). The orange location with the black outline is in the province of Noord-Brabant in the Netherlands, where the largest increase in the proportion of resightings took place (slope 0.0037).

Short-staying and underlying mechanism

The timing of arrival and departure in the wintering area changed markedly over the study period. During the years in which there were sufficient resightings for individuals seen outside WWT wetland reserves the mean individual arrival date in the wintering grounds became progressively later (by 1.1 day y^{-1} ; $p < 0.001$; Fig 6.4a; Table 6.1a), while departure on spring migration advanced (by 0.36 day y^{-1} ; $p < 0.001$; Fig. 6.4a; Table 6.1a). Overall, the duration of

stay on the wintering grounds for the whole population was significantly reduced by 38.4 days since the winter of 1989-1990 ($p < 0.001$; Fig. 6.4b; Table 6.1a). However, individuals did not change their winter duration over their lifetime ($F_{1,212} = 2.403$, $p = 0.123$; Fig. 6.4c; Table S6.7).

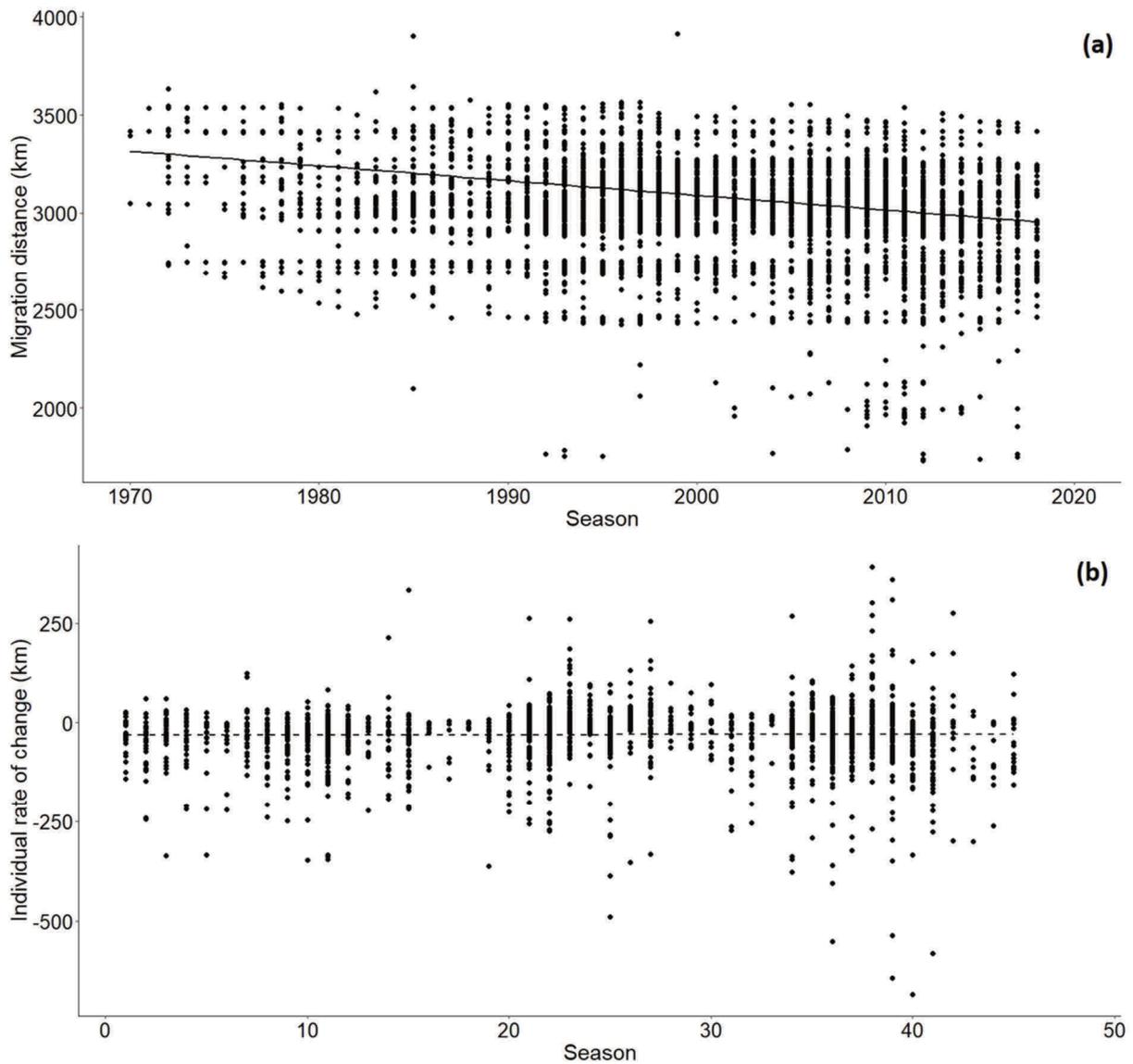


Figure 6.3: (a) Maximum migration distance of swans over time (M3). (b) Individual rate of change in maximum migration distance for individuals seen in >2 winter (Oct-Mar) seasons, each datapoint represents the slope of all observed migration distances for 1 individual over its lifetime in the study. Datapoints are weighted for number of seasons and plotted at the year of the first season (x-axis). Detailed model output for both analyses is provided in Table S6.4 and S6.5.

Table 6.1: (a) Model estimates for response variables individual migration distance, arrival day, departure day and winter duration with Year as explanatory variable, either individually centred (β_B) or based on the individual mean (β_W). See eqn. 6.3 and 6.4. (b) model estimates for the same response variables but with Year as explanatory variables and a slope estimate for $\beta_B - \beta_W$, see eqn. 6.5 and 6.6. As the model controls for all other effects in the model, Year in this model is equal to the estimate for within-individual variation (β_W) in table 6.1a. The $\beta_B - \beta_W$ effect in table 6.1b now represents the difference between the within- and between individual variation (van de Pol & Wright 2009).

(a)

Model	Parameter	Estimate	SE	df	t	p
Mig. distance	Intercept	17842.54	410.884	4156.0	43.42	<.001
	β_W	-14.83	0.626	11237.1	-23.69	<.001
	β_B	-7.37	0.206	4148.4	-35.82	<.001
Arrival	Intercept	287.56	2.642	545.5	108.8	<.001
	β_W	-0.09	0.241	1099.8	-0.4	0.721
	β_B	1.11	0.077	607.4	14.4	<.001
Departure	Intercept	74.74	2.735	583.5	27.3	<.001
	β_W	0.28	0.241	1109.6	1.1	0.252
	β_B	-0.36	0.080	643.9	-4.6	<.001
winter duration	Intercept	152.11	3.599	593.8	42.3	<.001
	β_W	0.36	0.318	1119.8	1.1	0.252
	β_B	-1.47	0.105	654.7	-14.0	<.001

(b)

Model	Parameter	Estimate	SE	df	t	p
Mig. distance	Intercept	17842.50	410.884	4156.0	43.4	<.001
	Year	-14.83	0.626	11237.1	-23.7	<.001
	$\beta_B - \beta_W$	7.46	0.659	12981.6	11.3	<.001
Arrival	Intercept	287.56	2.642	545.5	108.8	<.001
	Year	-0.09	0.241	1099.8	-0.4	0.721
	$\beta_B - \beta_W$	1.20	0.253	1295.1	4.7	<.001
Departure	Intercept	74.74	2.735	583.5	27.3	<.001
	Year	0.28	0.241	1109.6	1.1	0.252
	$\beta_W - \beta_B$	-0.64	0.254	1309.1	-2.5	0.012
winter duration	Intercept	152.11	3.599	593.8	42.3	<.001
	Year	0.36	0.318	1119.8	1.1	0.252
	$\beta_B - \beta_W$	-1.83	0.335	1316.4	-5.5	<.001

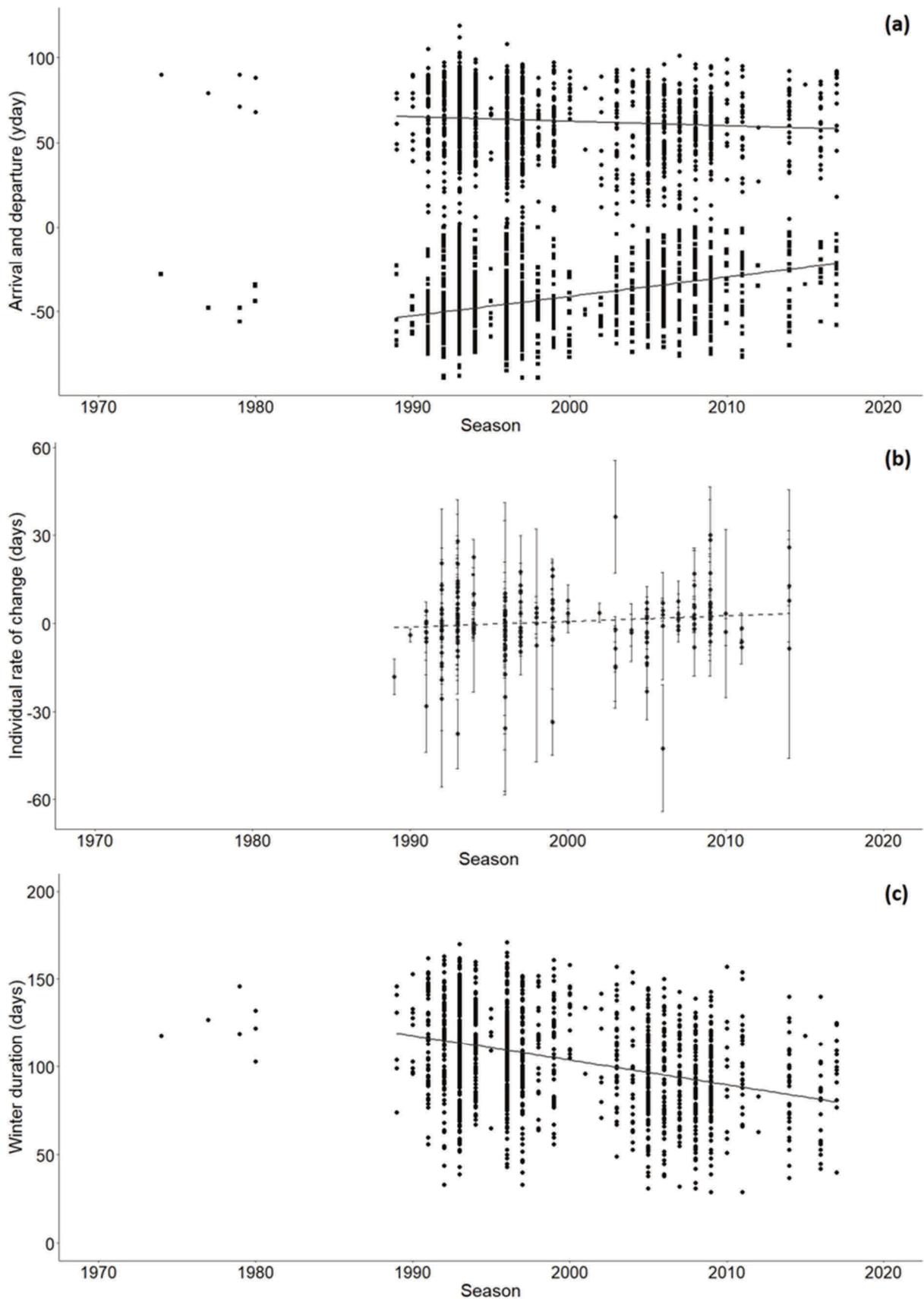


Figure 6.4: (a) Timing of arrival (bottom of figure a; < 0) and departure (top of figure a; > 0) for each winter season (x axis) for individually marked Bewicks swans resighted in the wintering area (west of 12°E). Days (y-axis) are indicated as Julian days of the year counting the number

of days from the first of January (1), with negative numbers indicating arrival days in December and November of the previous year. Solid lines show a significant later arrival ($N = 1634$, $p < 0.001$) and earlier departure ($N = 1634$, $p < 0.001$) over time. (b) Individual rate of change in winter duration for individuals seen in > 2 winter seasons. Each datapoint represents the slope ($\pm se$) of recorded winter durations over the lifetime of individual swans and is plotted on the first year this individual was seen (x-axis). Individuals did not change their winter duration over their lifetime (see main text and Table S6.7 for detailed model output). (c) Winter duration of Bewick's swans over time (in number of days spent west of $12^{\circ}E$). Winter duration significantly decreased over the study period from 118.2 days to 79.8 days (see text and Table S6.5 and S6.6 for detailed model output).

Temperature as an environmental driver

The temperatures at the resighting locations over the study period were remarkably similar (Fig. S6.8). Median temperatures did not show a trend over time ($F_{1,46} = 1.557$, $p = 0.218$; Table S6.11), and the swans thus seem to be present at a temperature of c. $5.5^{\circ}C$ over the whole study period. Both the actual and the modelled temperatures in NW Europe showed increases over time, with isotherms shifting eastwards (Fig. 6.5). For the $5^{\circ}C$ isotherm of the modelled temperatures, which is closest to the temperature where the swans stage, this shift comprised 429.5 km over our study period (48 years), corresponding to 9.1 km y^{-1} (based on a fixed latitude of $52^{\circ}N$; Table S6.12).

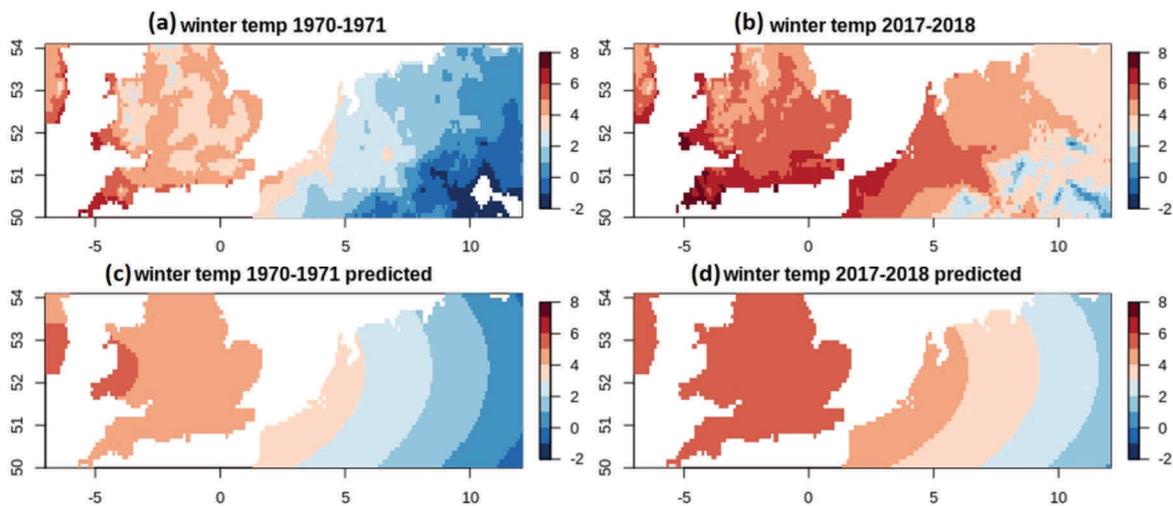


Figure 6.5: Actual (a,b) and modelled (c,d) isotherms in the first (1970/71; a,c) and the last (2017/18; b,d) winter season in our analysis. A comparison of c and d shows that the isotherms have shifted eastward.

Discussion

Our results confirm the hypotheses that the Bewick's swan population now arrives later, departs earlier and stays further east in winter when compared to half a century ago, thus confirming both short-staying and short-stopping in winter. When both processes are taking place concurrently, as in the present study, it is difficult to study them in isolation because to measure the changes in one, the other has to be fixed. For instance, to analyse short-stopping one needs to fix the timing of winter in order to determine whether individuals change their

location within this season, but this makes it by definition impossible to detect short-staying. On the other hand, for short-staying, the location of the wintering area needs to be fixed to allow detection of arrival and departure dates within this area, rendering it impossible to detect partial short-stopping. To identify both processes separately, we only included mid-winter resightings (i.e. resightings in December and January) in the first two analyses of short-stopping, to prevent a change in the timing of arrival and departure from having an effect on our assessment of the swans' location. For the analyses of short-staying, we fixed the wintering area as 'west of 12°E' for the whole study period. This boundary included almost all winter resightings (Fig. 6.2), while being distanced from the first well-known stop-over area of the swans (in the Baltic States). Moving this boundary to either 10°E or 15°E had little effect on the results (data not shown).

Short-stopping

We found a major (> 600 km) eastward shift in the swans' distribution over 48 years, corresponding to ~13 km y⁻¹ (Fig. 6.1). Winter range shifts of a similar order of magnitude have been documented in waders (~110 km in 20 years; Maclean et al., 2008). The extent of the swans' relocation can be partly but not entirely attributed to the fact that the North Sea between the UK and the Netherlands is unsuitable wintering habitat for the birds. Over the course of our study period, the majority of the population stopped crossing the North Sea, and thus the mean winter location shifted to the east. The slight northward (latitudinal) shift (Fig. 6.1) is probably influenced by migration direction. Analysing data from the two ringing schemes separately did not change the main result: both the leg-ringed (1970-2017) and neck-banded birds (1989-2017) stayed further east in more recent years, although only leg-ringed birds also shifted significantly northwards (S2).

Significant decreases in the proportion of resightings at particular locations (Fig. 6.2) match information reported in other studies. For example Slimbridge, in southwest England, showed the strongest decrease in this analysis, and numbers of Bewick's swans are also decreasing at other sites in Britain, such as Ouse Washes (Wood et al., 2019), and only very small numbers are still visiting Ireland (Worden et al., 2006). In the Netherlands there has been a decrease of the swans' use of northern areas such as the Lauwersmeer and parts of Friesland (Tijssen and Koffijberg, 2015) in recent years (corresponding to the 2 red points in the North of the Netherlands in Fig. 6.2). This is in line with the view that swans staging in the northern parts of the Netherlands used to cross the North Sea to winter in the UK, whereas birds staging further south generally do not do so (Tijssen and Koffijberg, 2015). Changes in habitat use and availability may also play a role (Clausen et al., 2018a), and an increase in maize-feeding may explain the proportional increase in the province of Noord-Brabant (Koffijberg and Tijssen, 2018), in the south of the Netherlands, where the largest increase in the proportion of resightings was recorded (Fig. 6.2). The finding that an increasing proportion of the resightings took place in northwest Germany (particularly the states Lower Saxony and Schleswig-Holstein) is in line with observations made by Wahl & Degen (2009), and more recently by Augst et al. (2019), who reported that this region is increasingly being used as a wintering area by Bewick's swans.

In agreement with the definition of short-stopping provided by Elmberg et al. (2014), we found a significant shortening of the population migration distance to the breeding grounds, of > 350 km over the study period (Fig. 6.3). This corresponds to 11-13% of the total migration distance and could potentially reduce constraints on the swans' annual cycle, leaving them with more

opportunity to respond to changing circumstances. It was notable to us that the largest maximum distances did not seem to change too much over the study period. We believe that this may be due to the historically-fixed location of the long-term monitoring scheme at WWT Slimbridge in the UK, so that swans that visit this place have a high chance of being recorded. In addition, swans that are caught and subsequently resighted at or near Slimbridge, which particularly in recent years is towards the western edge of the swans' wintering range, provide the maximum distance data included in the analysis. If the level of short-stopping showed in this study continues, we are aware that that our catch locations may not provide a representative subset of the population in future years.

The analyses of migration distances (Fig. 6.3a) assume that the swans' breeding site did not change significantly over the study period. There is some evidence for migratory bird species that breeding ranges are shifting northwards (Hitch and Leberg, 2007; Lehikoinen and Virkkala, 2016). Additionally, bioclimate modelling predicts a major shift in potential breeding range of many European breeding birds towards the end of the 21st century (Huntley et al., 2007). However, for Arctic breeding birds there is not much opportunity for a north-ward shift, due to the absence of landmass north of the current breeding areas (Huntley et al., 2007). Data on breeding distribution for the Bewick's swan is limited. Since resightings in the breeding area are rare, and surveys are only done post-breeding and irregularly (Mineyev, 1991), assessing such a shift of the breeding range is difficult, but first results of the European Breeding Bird Atlas do not indicate a shift (E.C. Rees and S. Rozenfeld, *unpublished data*). Results from tracking studies also do not suggest major changes (Nuijten et al., 2014; R.J.M. Nuijten et al. *unpublished data*).

We found evidence for both individual plasticity and generational change when assessing within- and between-individual variation in migration distance over time. This means that individuals do change their migration distance over their lifetime, possibly in response to climate warming (Fig. 6.5). It has always been thought that Bewick's swans are very site-faithful (Rees, 2006), and further research is required to study whether the observed change in migration distance reflects individuals not using parts of their range that they have previously used (in the west), but remaining site-faithful to the sites that are used or whether they actually explore new areas. In addition to these individual effects, the frequency of individuals using sites in the west or east changed over time resulting in an overall observed population change (generational effect). Range shifts such as short-stopping resulting from generational shifts can also be driven by environmental changes, for example when recruits respond differently to the circumstances than their predecessors or when the changes cause selective (dis)appearance of individuals. Both mechanisms (individual plasticity and generational shifts) have been found to co-occur in barnacle geese as well where it was found that especially juvenile geese tended to switch to another staging area. Older geese were less likely to switch, but this probability did increase over time, suggesting individual plasticity (Tombre et al., 2019). We found no clear differences between adults and yearlings, both age classes shortened their migration between the year of catch and the year after, suggesting that the between-individual short-stopping was driven by selective (dis)appearance. Whether selective disappearance (in the west) or selective appearance (in the east) takes place requires further research.

The three analyses of short-stopping (Fig. 6.1, 6.2, 6.3a) show strong evidence for this process; however, the observed changes could potentially (at least partly) be due to changes in observer effort in time and space (Buckland et al., 2005). Unfortunately, we cannot control

effectively for this confounding factor, but count data both from some key Bewick's swan wintering sites as mentioned above and from systematic five-year censuses show trends in numbers which correspond to our findings (Beekman et al., 2019). If changes in observer effort in time and space did occur, and it is indeed likely that they did, these trends support that this potential observer effect did not influence our analyses to the extent that incorrect conclusions were drawn. Interestingly, it was shown before that resighting probabilities for the different ringing schemes did not show a directional change over time (Fig. 6.4 in Wood et al. 2018), which supports our idea that changes in observer effort are of minor importance.

Short-staying

In addition to shifting their winter distribution, we also found evidence that time spent in the wintering ground has shortened (Fig. 6.4). Between 1989 and 2017, the time that the Bewick's swans spent west of 12°E has declined by an average of ~38 days. Extrapolation suggests that over the study period the swans shortened their wintering period by two months. As with short-stopping, this could potentially make the annual cycle of these migrants less time constraint. Whether this is indeed the case, and whether potential benefits or repercussions at other times of the annual cycle do occur needs further investigation.

Although (spring) arrival dates are frequently studied in migratory birds (Hüppop and Hüppop, 2003; Jonzén et al., 2006), less emphasis is put on the duration of stay in the non-breeding range. Gordo & Sanz (2006) did however mention the importance of this measure of phenology and showed that two of the five migratory bird species included in their study changed the duration of stay in Spain. When different phases of the annual cycle shift with differing rates, this can lead to overlapping or diverting phases (Tomotani et al., 2018). Concerning the Bewick's swans in this study, we found a shortening of the wintering phase due to a later arrival in autumn and earlier departure in spring. Although autumn arrival changed by a larger extent, spring departure is thought to have more consequences for fitness as it could lead to more flexibility in timing during spring migration and enable early arrival on the breeding grounds, which could be beneficial in the light of current climate change given that early onset of breeding is associated with higher breeding propensity, increased clutch sizes and higher nesting success in waterbirds (Nolet et al., 2020). However, environmental changes and potential population responses during spring migration and breeding season should be studied to substantiate this potential effect (Norris and Taylor, 2005).

In two populations of black-tailed godwits it was found that, although individual birds did not change their phenology and site use over the years, new recruits in the population did (Gill et al., 2013; Verhoeven et al., 2018), suggesting generational shifts to be a mechanism behind the population change (Gill et al. 2019). Similarly, we did not find evidence for individual plasticity for short-staying, suggesting that a generational shift is steering the observed changes on the population level (Fig. 6.4). The observed changes are of the same magnitude as (spring departure) or higher than (autumn arrival) changes in spring arrival dates in a range of bird species that were considered to be within the range of potential micro-evolutionary change, but these bird species were much smaller and will have shorter generation times than Bewick's swans (Charmantier & Gienapp, 2014; Gienapp, Leimu, & Merilä, 2007). In order to assess whether micro-evolutionary change can account for such rapid changes information on heritability of the trait (i.e. pedigree information) and fitness differences (if any) between phenotypes need to be known (Gienapp et al., 2008; Merilä & Hendry, 2014). Since we do not

have this information available for this population, we focused on individual behaviour here and assessing micro-evolutionary change is beyond the scope of this study.

Potential drivers

The 5°C isotherm, which is close to the air temperature where Bewick's swans were resighted, shifted in the same direction and with the same magnitude as the swans' wintering location. Shifts in this order of magnitude have been confirmed before for isotherms in Europe (Beniston et al. 2014). This suggests that the swans' short-stopping and perhaps also short-staying is driven by a change in temperature. If so, it could be a direct effect through for example decreased costs of thermoregulation in areas with higher temperatures, enabling the swans to winter further northeast than before. Although Bewick's swans are relatively large birds, with wide thermoneutral zones, studies in other swan species suggest that these birds have thermoregulation costs below 5°C (Bech, 1980; Nespolo et al., 2008). Alternatively, the correspondence with temperature could represent an indirect effect such as via food availability, as frozen water and fields during periods of < 0°C temperatures may prevent swans from feeding on aquatic and terrestrial plants, respectively. An earlier study including Bewick's swans based on count data did not find a distributional shift nor a relationship with milder winters (Pavón-Jordán et al., 2019), but this may have been influenced by a grouping of both species and weather data in the analysis.

While changes in habitat availability are also known to be important for the distribution of waterfowl (Clausen et al., 2018; Fox et al., 2005), long-term habitat data covering NW Europe were not available for studying this at the continental level. Future research could focus on the influence of habitat availability on within-winter movements of Bewick's swans, to gain further insights into this factor (Nolet et al., 2002).

Conclusion

The results of this study provide strong evidence for short-stopping and short-staying by Bewick's swans wintering in northwest Europe, and these spatial and temporal changes may have important consequences for our understanding of the dynamics of this population. In Bewick's swans winter area use (short-stopping) was changing by individual plasticity and generational shifts, whereas arrival and departure in the winter area (short-staying) was changing by generational shifts. This led to changes in abundance in both time and space (Augst et al., 2019; Beekman et al., 2019). Understanding the processes behind the rapid changes in abundance is therefore important for population monitoring, management and conservation.

Acknowledgements - We are immensely grateful to all those involved in ringing Bewick's swans across Europe over the years which has made this study possible, especially staff and volunteers at the Wildfowl & Wetlands Trust Centres, and the Nenetskiy State Nature Reserve (notably Andrey Glotov and Yulia Leonova), and also including Dmitri Boiko (in Russia in 2010) and Maria Wieloch (in Russia in 2011), for the ringing scheme by TH (notably Axel Degen, Bart Ebginge, Ben Koks, Bernard Spaans and Wim Tijsen), for the ringing scheme by NIOO-KNAW (notably Gerard Müskens, Kees Oosterbeek, Wim Tijsen, Peter de Vries, Erik Kleyheeg and Youri van der Horst). We also thank the dedicated observers of Bewick's Swans in the NW European flyway, many of who are volunteers, whose ring resightings have provided the data needed for the analyses. Particular thanks are extended to those who have been involved in processing the ringing and resightings data over the decades, including Mary Matthews (who initiated computerisation of the ring resightings data in the early 1980s), John Bowler, Julia Newth, Jenny Earle, Sue Carman, Steve Heaven, Alison Bloor, Kane Brides, Peter de Vries and Yke van Randen (www.geese.org). We thank Emiel van Loon for kindly helping out with the temperature modelling, Martijn van de Pol for his advice on the statistical modelling and Peter de Vries and Sibrand Rinzema for the GIS analyses. We thank M.E. Visser, J.A. Gill, three anonymous reviewers and the subject editor for their constructive comments on earlier versions of this manuscript. We also acknowledge the E-OBS dataset from the EU-FP6 project UERRA (<http://www.uerra.eu>) and the Copernicus Climate Change Service, and the data providers in the ECA&D project (<https://www.ecad.eu>). RJMN was supported by NWO-NPP grant 866.15.206 awarded to BAN.

The data that support the findings of this study are openly available on Dryad "Concurrent shifts in wintering distribution and phenology in migratory swans", reference number <https://doi.org/10.5061/dryad.dfn2z34xp>. Nuijten et al. 2020b.

Supplementary Material

1

Sample sizes

Table S6.1: Number of resightings (N) short-stopping analysis based on mean location (latitude and longitude) of resightings per winter per season (method 1 in main text).

	Season	Seasonnr	Mean.lat	Mean.lon	N
1	19701971	1	51.74055	-2.40512	156
2	19711972	2	51.75693	-2.3889	61
3	19721973	3	51.78825	-1.53601	89
4	19731974	4	51.77742	-2.24422	165
5	19741975	5	51.77258	-2.67131	48
6	19751976	6	51.90814	-1.44842	76
7	19761977	7	51.93837	-1.12551	126
8	19771978	8	51.84574	-1.79373	247
9	19781979	9	51.81055	-2.06563	314
10	19791980	10	52.02035	-1.18665	184
11	19801981	11	52.07196	-0.99282	188
12	19811982	12	51.84266	-1.87047	117
13	19821983	13	52.32209	3.271671	146
14	19831984	14	52.22631	2.1483	337
15	19841985	15	52.17919	0.458765	281
16	19851986	16	52.14845	1.091358	218
17	19861987	17	52.29695	1.681535	286
18	19871988	18	52.65615	3.164477	107
19	19881989	19	52.13287	1.186956	203
20	19891990	20	52.19713	0.052245	237
21	19901991	21	52.85175	-1.74943	480
22	19911992	22	52.98735	0.296592	510
23	19921993	23	52.68782	3.358744	652
24	19931994	24	52.67473	4.383683	919
25	19941995	25	52.41917	4.093512	1225
26	19951996	26	52.51428	3.582494	718
27	19961997	27	52.44482	3.515402	703
28	19971998	28	52.47698	3.829205	1181
29	19981999	29	52.46947	4.746665	821
30	19992000	30	52.40592	4.393268	784
31	20002001	31	52.37406	4.570991	505
32	20012002	32	52.43313	3.32205	527
33	20022003	33	52.39657	3.302281	420
34	20032004	34	52.34543	3.638763	531
35	20042005	35	52.45495	4.447601	470
36	20052006	36	52.34317	3.644572	1128

37	20062007	37	52.35402	4.803036	1248
38	20072008	38	52.4026	4.896817	1503
39	20082009	39	52.46815	4.738608	1539
40	20092010	40	52.36552	4.097582	1082
41	20102011	41	52.11678	3.730362	1116
42	20112012	42	52.9878	6.72993	792
43	20122013	43	52.55287	5.514886	622
44	20132014	44	52.58836	6.272805	527
45	20142015	45	52.11357	4.959362	658
46	20152016	46	52.63933	6.397523	394
47	20162017	47	51.95124	5.30471	977
48	20172018	48	52.87718	7.639933	748

2

Mean winter location

In the first method (M1 in main text), we calculated the mean average geographic location of the Dec-Jan resightings per winter season, and tested whether longitude and/or latitude showed a directional change towards the north and/or east over time. To assess a potential effect of marker method (leg-ring or neck-band) or catch location (winter range or breeding range), we performed the analyses on these separate groups as well. First for the neck-bands only (Fig. S2.1), second for the leg-ringed birds excluding those birds caught in Russia on the breeding grounds (Fig. S2.2) and third for the leg-ringed birds caught in Russia (Fig. S2.3). Results are presented in the text below the figures.

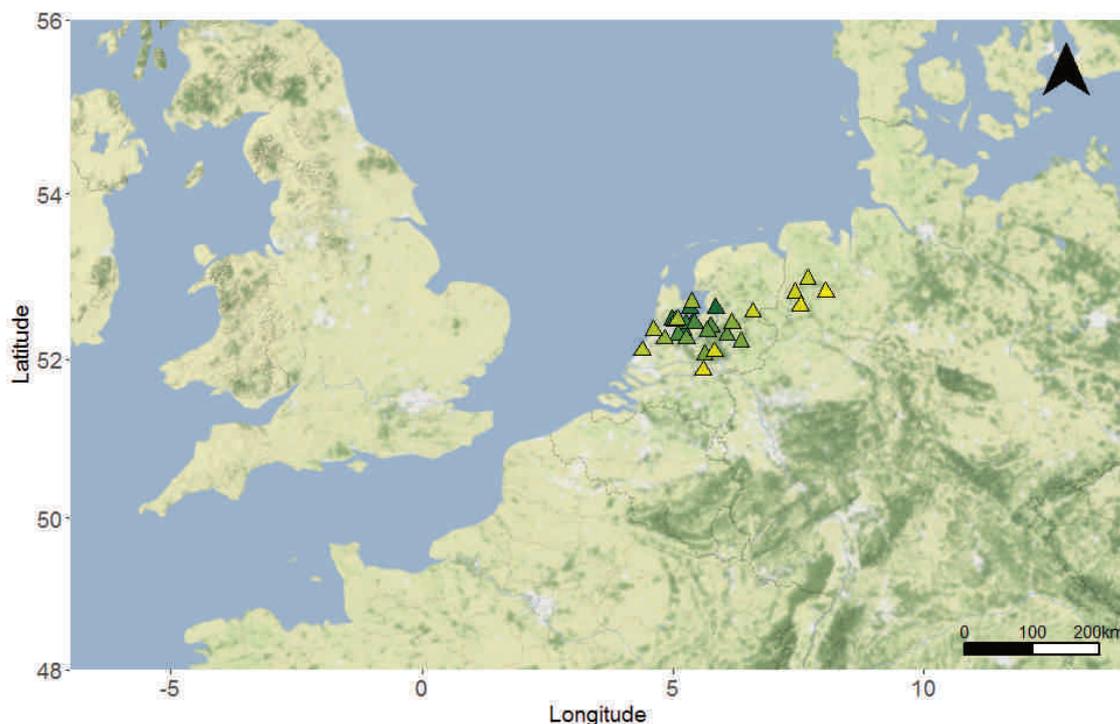


Figure S6.1: Mean winter location of swan resightings for neck-bands only (1989-2017). The colour gradient represents time where dark green is the first winter (1989/90) and yellow is the

last winter in the analysis (2017/18). Longitudinal shift was significant ($F_{1-26} = 7.5, p = 0.011$), latitudinal shift was not ($F_{1-26} = 0.0513, p = 0.823$).

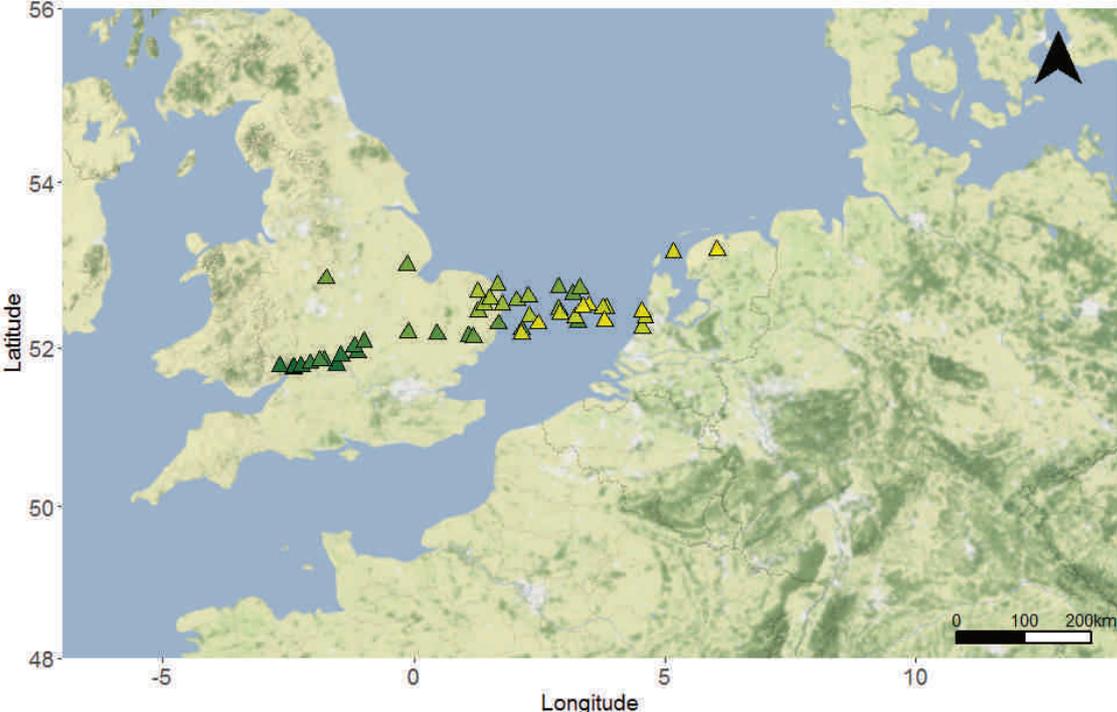


Figure S6.2: Mean winter location of swan resightings for leg-rings caught in wintering range (excluding catch sites in Russia; 1970-2017). The colour gradient represents time where dark green is the first winter (1970/71) and yellow is the last winter in the analysis (2017/18). Both latitudinal ($F_{1-46} = 31.22, p << 0.001$) and longitudinal ($F_{1-46} = 219, p << 0.001$) shifts were significant.

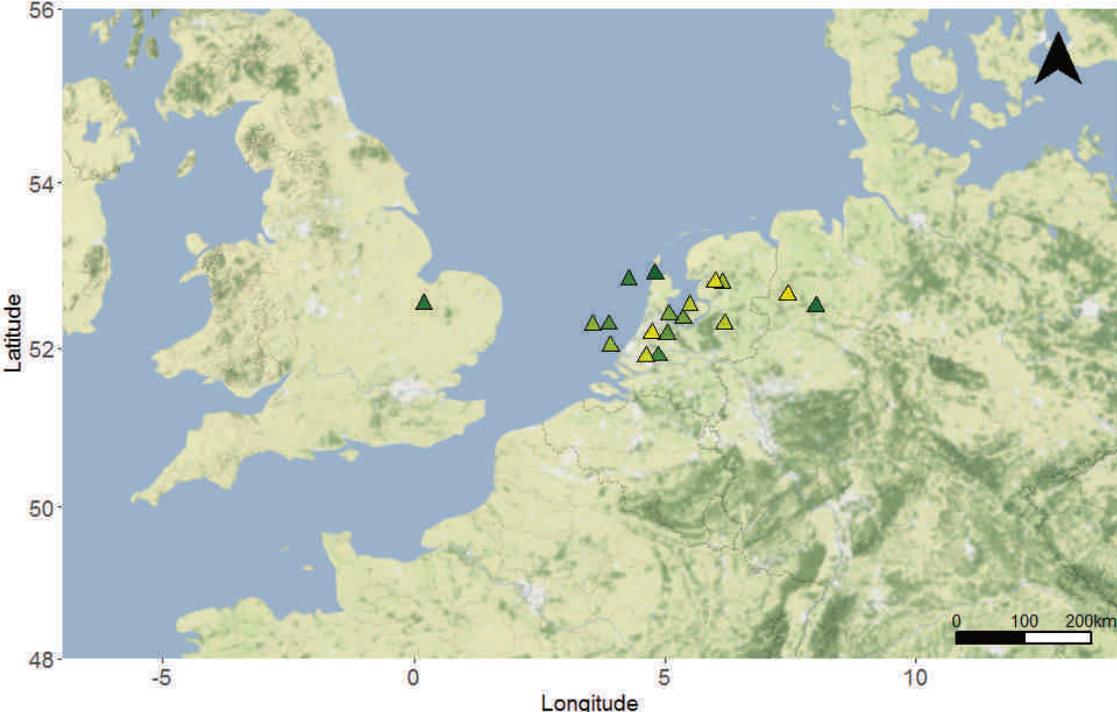


Figure S6.3: Mean winter location of swan resightings for leg-ringed birds ringed in Russia (1992-2017). The colour gradient represents time where dark green is the first winter (1992/93) and yellow is the last winter in the analysis (2017/18). Both latitude ($F_{1-16} = 0.4163$, $p = 0.528$) and longitude ($F_{1-16} = 1.855$, $p = 0.19207$) shifts were not significant. However, we noticed an odd pattern in the data, with two of the early years representing the furthest west and furthest east mean location. This might be caused by the small sample size for both number of resightings in December and January (299 individuals and 2098 resightings) and years (18 winter seasons in between 1992/93 and 2017/18) in this subset of the data. Especially in the early years (1992-2004) only five winter seasons were represented in the data, all of which had low numbers of resightings (max 19). However, if we exclude those years for the birds ringed in Russia the shifts are still not significant (latitude $p = 0.44$; longitude $p = 0.0543$), which might be caused by the short timescale (13 seasons; 2005-2017). Despite this specific group of leg-ringed birds showing no distribution shift, in- or excluding these in the main analysis did not change the overall results as presented in the main text.

3 Grid

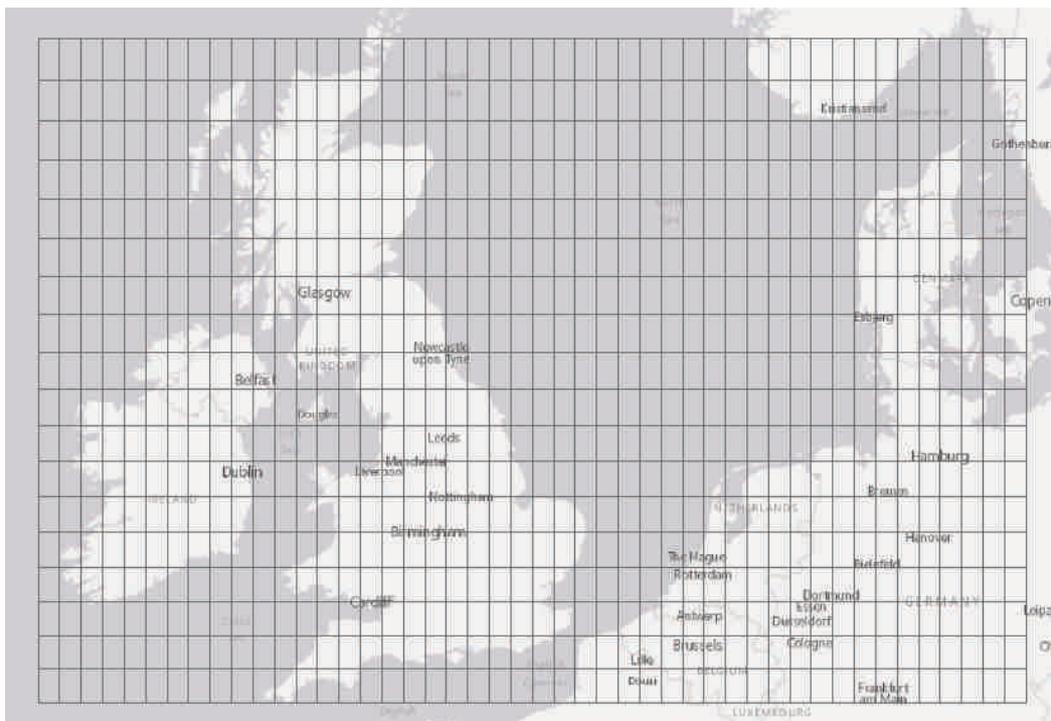


Figure S6.4: Geographical grid used in the second analyses for short-stopping. Cells are $0.5^\circ \times 0.5^\circ$. The lower left corner has coordinates -10.5°W , 50.5°N , the upper right corner has coordinates 11.5°E , 58.5°N .

4

Model output

Table S6.2: Model estimates for response variables Latitude and Longitude of the mean location of resightings explained by time (winter season, expressed as Year). M1 in main text (see eqn. 6.1a and 6.1b and Fig. 6.1).

Model	Parameter	Estimate	SE	t	p
Latitude	Intercept	51.93	0.078	670.0	<.001
	Year	0.01	0.003	5.4	<.001
Longitude	Intercept	-2.42	0.365	-6.6	<.001
	Year	0.19	0.013	14.8	<.001

Table S6.3: Model estimates for response variable slope with explanatory variable Longitude of the gridcells. M2 in main text (see eqn. 6.2 and Fig. 6.2).

Model	Parameter	Estimate	SE	t	p
Slope	Intercept	-0.0002	0.0002	-1.0	0.339
	Longitude	0.00009	0.00002	3.7	0.003

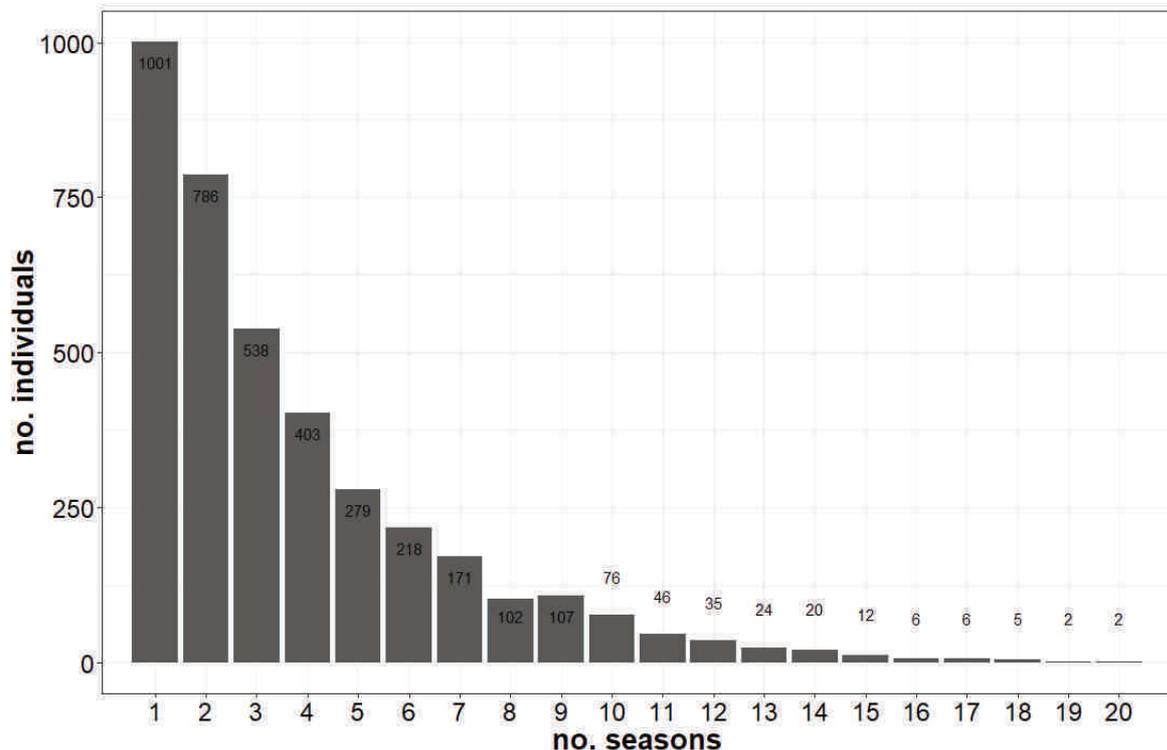


Figure S6.5: Number of years on which a migration distance for 3839 individually marked Bewick's swans has been recorded.

Table S6.4: Model estimates for response variable migration distance explained by time (winter season, expressed as Year). M3 in main text (see eqn. 6.3 and Fig. 6.3a).

Model	Parameter	Estimate	SE	t	p
Mig. distance	Intercept	18130.19	330.884	54.8	<.001
	Year	-7.5200	0.166	-45.4	<.001

Table S6.5: Model estimates for response variable individual migration distance explained by time (winter season, expressed as the first year in which a migration distance for an individual was recorded). Only individuals with a measurement in > 2 years were included for this analysis. M3 in main text (see eqn. 6.4 and Fig. 6.3b).

Model	Parameter	Estimate	SE	t	p
Ind. mig. distance	Intercept	-21.98	3.34	-6.6	<.001
	First year	-0.06	0.13	-0.5	0.625

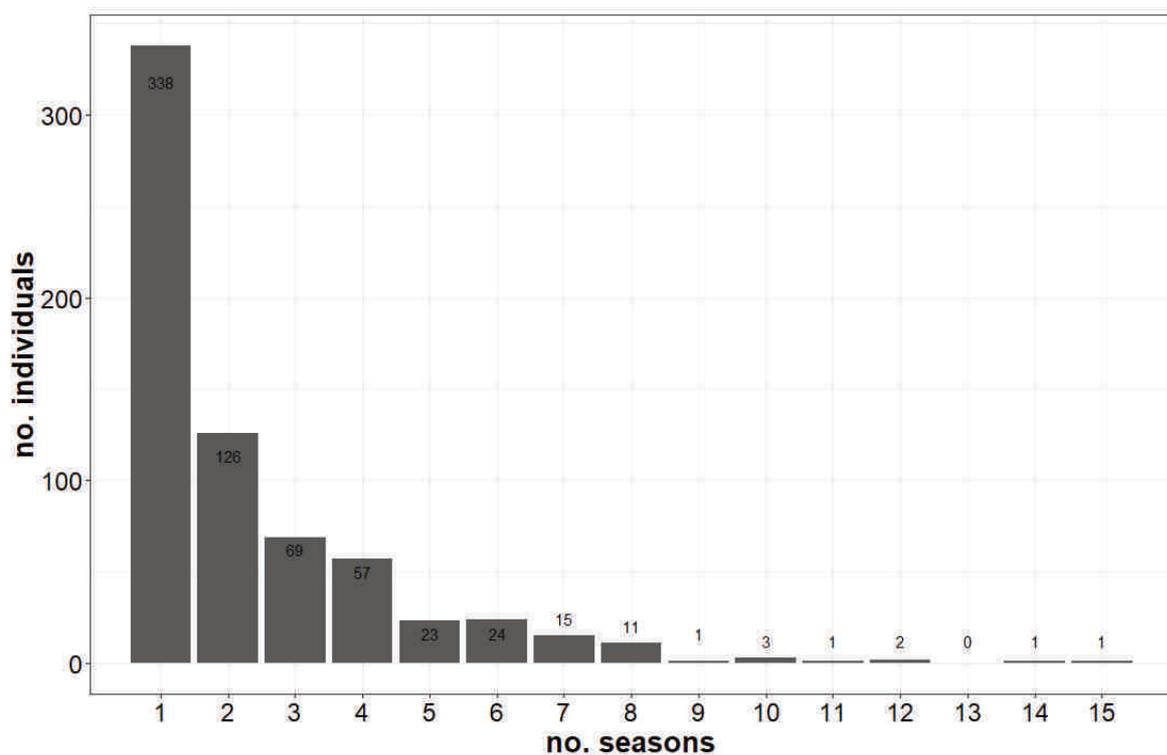


Figure S6.6: Number of years on which a winter duration 678 individually marked Bewick's swans has been recorded (1989-2017).

Table S6.6: Model estimates for response variable winter duration explained by time (winter season), expressed as the first year a winter duration was recorded for an individual. See eqn. 6.5 and Fig. 6.4 in main text.

Model	Parameter	Estimate	SE	t	p
winter duration	Intercept	145.63	2.714	53.7	<.001
	First year	-1.37	0.087	-15.7	<.001

Table S6.7: Model estimates for response variable individual winter duration explained by time (winter season, expressed as the first year in which a winter duration for an individual was recorded). Only individuals with a measurement in >2 years were included for this analysis. See eqn. 6.4 and Fig. 6.4b in main text.

Model	Parameter	Estimate	SE	t	p
Ind. Winter duration	Intercept	-4.06	2.939	-1.4	0.169
	First year	0.15	0.099	1.6	0.123

5

Model output age classes

Table S6.8: Model estimates for the difference in migration distance (Δ MD) between the year of catch and the year after for age classes Adult, Yearling and Juvenile over time. Age was determined at capture.

Model	Parameter	Estimate	SE	t	p
Δ MD Adult	Intercept	-210.89	19.501	-10.8	<.001
	Year	2.61	0.654	4.0	<.001
Δ MD Yearling	Intercept	-318.79	57.003	-5.6	<.001
	Year	6.25	1.831	3.4	<.001
Δ MD Juvenile	Intercept	-177.73	33.251	-5.3	<.001
	Year	-0.08	1.257	-0.1	0.949

6

Additional analysis arrival, departure, winter duration

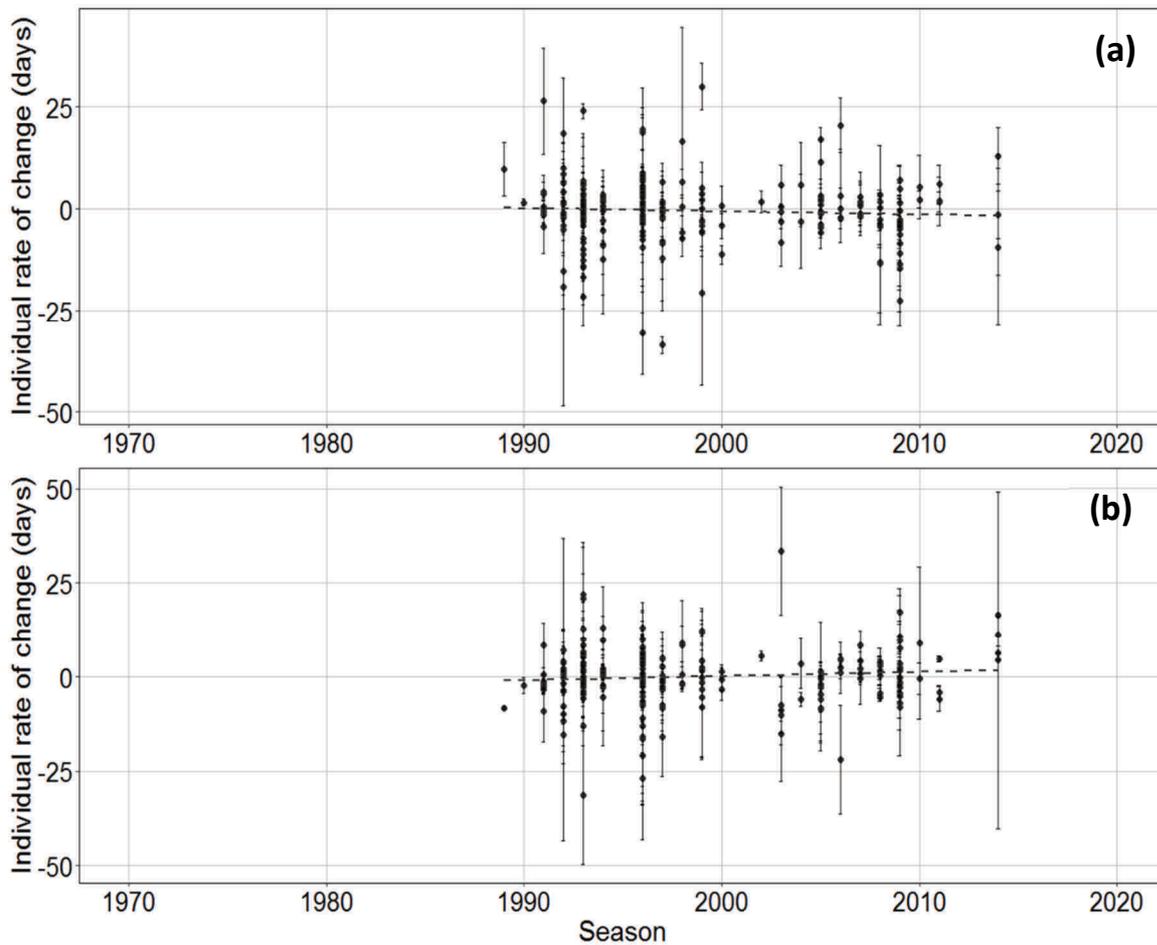


Figure S6.7: (a) Individual rate of change in arrival day, each datapoint represents the slope (\pm se) of arrival days for all seasons a specific individual was observed (data is weighted for number of seasons). Individuals did not change their arrival day over their lifetime ($N = 214$, $p = 0.393$). (b) Individual rate of change in departure day, each datapoint represents the slope (\pm se) of arrival day for all seasons a specific individual was observed (data is weighted for number of seasons). Individuals did not change their departure day over their lifetime ($N = 214$, $p = 0.233$).

Table S6.9: Model estimates for response variable individual arrival day explained by time (winter season, expressed as the first year in which a departure day for an individual was recorded). Only individuals with a measurement in >2 years were included for this analysis.

Model	Parameter	Estimate	SE	t	p
Ind. arrival	Intercept	1.61	2.235	0.7	0.471
	First year	-0.06	0.075	-0.9	0.393

Table S6.10: Model estimates for response variable individual departure day explained by time (winter season, expressed as the first year in which a departure day for an individual was recorded). Only individuals with a measurement in >2 years were included for this analysis.

Model	Parameter	Estimate	SE	t	p
Ind. departure	Intercept	-2.36	2.129	-1.1	0.272
	First year	0.086	0.072	1.2	0.233

7

Temperature at resighting locations

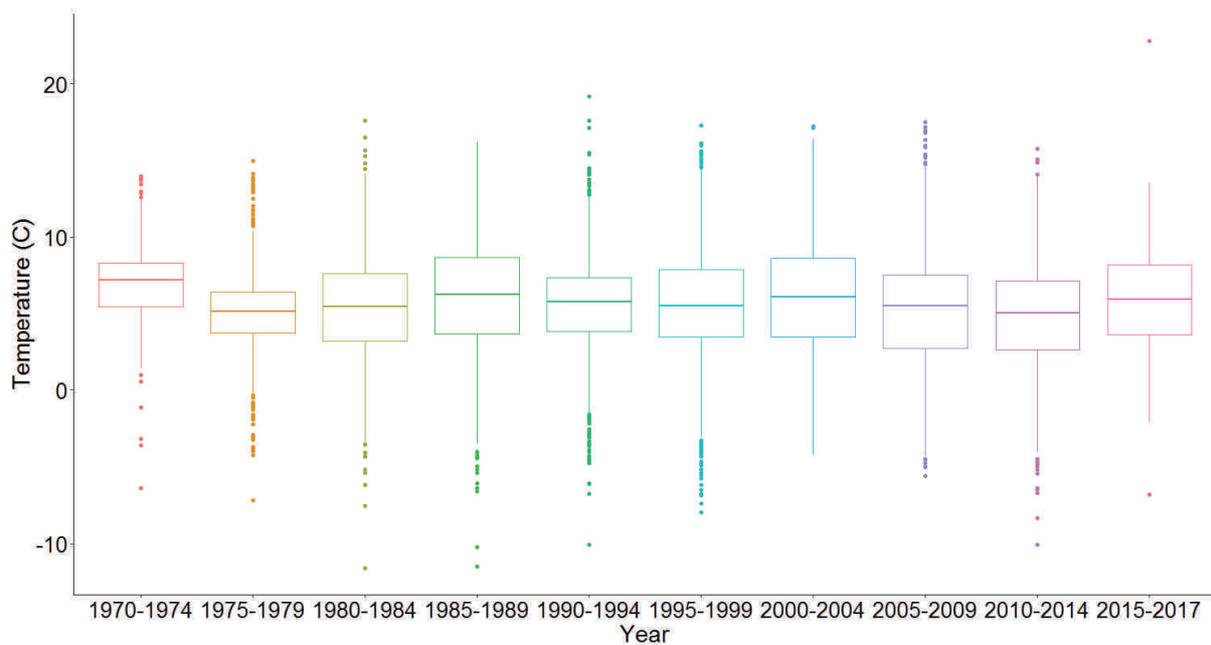


Figure S6.8: Temperatures at which individual Bewick's swans were resighted west of 12°E, presented as boxplots aggregating 5-year periods. There was no significant change over time in the median temperature of the resightings over the study period ($F_{1,46} = 1.557$, $p = 0.218$; Table S6.11).

Table S6.11: Model estimates for response variable median winter temperature of resightings to the west of 12°E with winter season (expressed as Year) as explanatory variable.

Model	Parameter	Estimate	SE	t	p
Median temp.	Intercept	38.09	26.071	1.5	0.151
	Year	-0.02	0.013	-1.2	0.218

8

Output temperature model

Based on the actual temperatures in NW Europe in winter (averages for Dec-Jan in each winter from 1970/71 to 2017/18 inclusive) provided by the E_OBS v18.0e dataset (Cornes et al., 2018), we modelled the temperatures for all these winter seasons in order to reduce the effects of extreme years and obtain smoothed isotherms, for calculating the shift of these isotherms (Fig. 6.5 in main text).

To model the temperatures, we used the regression model:

$$T_i \sim \beta_0 + \beta_1 Lat_i + \beta_2 Lon_i + \beta_3 Lat_i^2 + \beta_4 Lon_i^2 + \beta_5 Y + \beta_6 Lon_i * Y + \epsilon_0 \quad (S6.1)$$

where T is the mean average winter temperature in °C, Lat and Lon represent the latitude and longitude of the $0.1^\circ \times 0.1^\circ$ gridcell i , and Y is the winter season (1970-2017; 1970 representing the winter of 1970/71).

The model with the interaction between longitude and year (i.e. allowing longitudinal temperature changes to vary over the years) was significantly better than a model without this interaction ($p \ll 0.005$). All variables included in the model had a statistically significant effect on temperature (Table S6.12).

Table S6.12: Model estimates for response variable winter temperature of resightings to the west of $12^\circ E$ with winter season (expressed as Year) as explanatory variable.

Model	Parameter	Estimate	SE	t	p
winter temperature	Intercept	-479.30	8.913	-53.8	<.001
	Latitude	17.06	0.342	49.9	<.001
	Longitude	-1.045	0.100	-10.5	<.001
	Latitude ²	-0.163	0.0033	-49.5	<.001
	Longitude ²	-0.013	0.0002	-81.6	<.001
	Year	0.019	0.0003	55.4	<.001
	Lon:Year	0.0004	0.00005	8.7	<.001