

RESEARCH ARTICLE

Migratory swans individually adjust their autumn migration and winter range to a warming climate

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Abstract

In response to climate warming, migratory animals can alter their migration so that different events in the annual cycle are better aligned in space and time with suitable environmental conditions. Although such responses have been studied extensively during spring migration and the breeding season, much less is known about the influence of temperature on movements throughout autumn migration and how those movements result in a winter range and shifts therein. We use multi-year GPS tracking data to quantify how daily autumn movement and annual winter distance from the breeding grounds are related to temperature in the Western Palearctic Bewick's swan, a long-lived migratory waterbird whose winter range has shifted more than 350 km closer to the breeding grounds since 1970 due to individuals increasingly 'short-stopping' their autumn migration. We show that the migratory movement of swans is driven by lower temperatures throughout the autumn season, with individuals during late autumn moving only substantially when temperatures drop below freezing. As a result, there is large flexibility in their annual winter distance as a response to winter temperature. On average, individuals overwinter 118 km closer to the breeding grounds per 1°C increase in mean December–January temperature. Given the observed temperature increase in the Bewick's swan winter range during the last decades, our results imply that the observed range shift is for a substantial part driven by individual responses to a warming climate. We thus present an example of individual flexibility towards climatic conditions driving the range shift of a migratory species. Our study adds to the understanding of the processes that shape autumn migration decisions, winter ranges and shifts therein, which is crucial to be able to predict how climate change may impact these processes in the future.

KEYWORDS

climate change, frost wave, individual flexibility, migration ontogeny, range shift, species distribution, stopover, waterbird

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1 | INTRODUCTION

Climate warming threatens the persistence of species and ecosystems across the globe (Parmesan, 2006; Urban, 2015; Walther et al., 2002; Wong & Candolin, 2015) and migratory animals may be especially vulnerable since they inhabit at least two different geographical areas where the extent and rate of change can differ (Culp et al., 2017; La Sorte et al., 2019; Runge et al., 2014). A way for migrants to respond to climate warming is through changing their migration such that different events in their annual cycle are better aligned with the environmental conditions at the time and location of those events. Such responses have been studied extensively for spring migration and the breeding season, where they predominantly entail changes in timing. For example, many migrants have advanced their spring migration (Haest et al., 2018; Jonzén et al., 2006; Knudsen et al., 2011), arriving at the breeding grounds earlier in an attempt to keep up with the advancement of spring and its associated food availability peak (e.g. Both & Visser, 2001; Lameris et al., 2018). On the other hand, far less research has focused on the effects of climate change in the autumn and winter season (Gallinat et al., 2015), despite the fact that migration timing and destination in the non-breeding season are likely driven by different decisions than in spring (Burnside et al., 2021) and responses to climate warming may thus be profoundly different. Animals leave their breeding grounds in autumn primarily to increase their chance of survival until the next breeding season (Alerstam, 1993; Somveille et al., 2015) and are not constrained by having to reach a predetermined breeding site in time. For species that do not have winter territories and whose foraging and habitat requirements allow a wide geographical range to be used during non-breeding (e.g. waterfowl and waders using wetlands and agricultural land), there is therefore room for spatial flexibility towards resource availability and environmental conditions in that period (Teitelbaum et al., 2023). Whereas in spring animals generally migrate towards the breeding grounds as soon and fast as local conditions allow (e.g. Bischof et al., 2012; Duriez et al., 2009; Nuijten et al., 2014; Van Wijk et al., 2011) in order to get the best territories (Kokko, 1999), in autumn such species might migrate when impelled to do so by deteriorating conditions (instead of being 'pulled towards' the winter range they are rather 'pushed away' from the breeding grounds; e.g. Xu & Si, 2019). In the non-breeding season there might therefore be more room for spatial responses to climate warming, for example in the form of range shifts. Although winter range shifts have been described in various migratory species (e.g. La Sorte & Thompson, 2007; Lehikoinen et al., 2013; Nuijten et al., 2020; Visser et al., 2009), few studies have quantified climate effects on migratory movements throughout autumn and considered the eventual winter destination as a result of those movements. We thus have limited understanding of how and to which extent individuals can respond to climate change by shortening their migration route and altering their winter range. Only by tracking individuals throughout autumn, determining how they respond to prevailing climatic conditions at different stages of their migration and linking those responses with the eventual winter range for multiple years in a row, can we better understand how winter range shifts arise and to what extent they are a response to climate warming.

Furthermore, little is known about the type of mechanism that drives shifts in winter range. Both individual and generational mechanisms have been described (Gill et al., 2014, 2019). The former are mechanisms that operate on the individual level, such as environment-driven flexibility in site use during the lives of individuals. The latter operate between generations, when the frequencies of individuals with different migratory schedules shift over time due to changes in the conditions that determine the success of those schedules, while individuals do not change within their lives. Generational mechanisms have been hypothesized to be the main driver of species range shifts (Gill et al., 2019), but it remains to be tested whether this holds true across species that differ in for example the extent to which they learn their migration from older conspecifics (e.g. Byholm et al., 2022; Nuijten et al., 2020; Teitelbaum et al., 2016).

Recent winter range shifts towards the breeding grounds have been established in a range of migratory bird species (Visser et al., 2009) including waders (Austin & Rehfish, 2005; Maclean et al., 2008), ducks (Lehikoinen et al., 2013; Pavón-Jordán et al., 2015) and geese and swans (Nuijten et al., 2020; Podhrázký et al., 2017; Ward et al., 2009). However, these large-scale responses to climate were based on ring resightings and counts, and not studied by following individuals and examining their within- and between-year movements throughout the migratory journey from breeding grounds to winter range. Conversely, several studies have tracked individuals to examine the climatic drivers of timing of autumn migration but separately from the eventual wintering area choice or a shift therein. For example, waterfowl departure from autumn stopover sites was affected by freezing temperatures (Weller et al., 2022; Xu & Si, 2019) and birds delayed their autumn migration with higher cumulative temperatures (Lehikoinen & Jaatinen, 2012). The effect of temperature on winter range at a large spatiotemporal scale and on migratory movement in autumn at a small spatiotemporal scale should be linked to each other by studying them from the perspective of the migrating individual bird.

Here, we study how migratory movement in autumn and annual winter distance relate to temperature in the Bewick's swan (*Cygnus columbianus bewickii*), a large migratory waterbird whose Western Palearctic population breeds on the coastal tundra of north-western Russia and winters in north-western Europe (Rees et al., 2019). Its autumn migration proceeds faster than its spring migration because in spring ice cover restricts northward travel (Nuijten et al., 2014) and birds capitalize on bringing the energy stores required for breeding with them to the breeding grounds (capital breeding; Nolet, 2006). Like many waterfowl species (Geisler et al., 2022; Kölzsch et al., 2016; Xu & Si, 2019), Bewick's swans make use of favourable winds to facilitate their migration (Beekman et al., 2002; Evans, 1979; Klaassen et al., 2004). Five-yearly international population censuses indicated that more Bewick's swans winter further north in warmer winters (Beekman et al., 2019). Furthermore, analysis of ring resightings showed that their winter range has shifted more than 350 km closer to the breeding grounds since 1970 due to individuals 'short-stopping', that is, ceasing autumn migration at increasingly north-eastern latitudes and longitudes (Nuijten et al., 2020). This was due

to both a generational shift (the frequency of individuals with different migratory destinations changing over time; Gill et al., 2019) and individual flexibility (individuals shortening their migration during their lifetime). Note that we use the term individual *flexibility* instead of *plasticity* (Gill et al., 2019) because variation in annual winter distance comprises an explicitly reversible response to conditions that vary over time (Piersma & Lindström, 1997), even if the response is in practice generally unidirectional over time (i.e. birds on average decrease their winter distance throughout their lives). The winter range shift was spatially concurrent with a shifting 5°C thermocline over the same period, suggesting that climate change is a driver (Nuijten et al., 2020). However, it is unknown (1) to what extent temperature drives migratory movement throughout the autumn season, and thus short-stopping, (2) to what extent individual flexibility in annual winter distance is related to winter temperature and (3) to what extent individual flexibility in winter distance related to temperature can explain the observed winter range shift at the population level. Answering these questions requires repeated migration tracking of multiple individuals.

We use GPS tracks of 55 Bewick's swans, spanning 13 years in total, to test the influence of temperature on daily movements throughout autumn and, emerging from this, annual winter distance (the distance from the breeding grounds during winter) at the individual level. First, using autumn tracks, we examine the extent to which daily movement away from the breeding grounds is related to temperature and wind assistance throughout the autumn season. We expect that short-stopping is driven by temperature in the sense that, within a geographical area that birds consider potentially suitable for overwintering based on innate, social or experiential knowledge, individuals migrate away when temperatures become unsuitable for wintering, but stay as long as temperatures do not deteriorate. This would imply a temperature effect on movement which is largely constant throughout the autumn season, as opposed to declining towards the end of autumn. We expect the effect of wind assistance, on the other hand, to decline throughout the season, such that birds are largely unresponsive to beneficial winds later in the season, when they have already reached suitable areas for wintering. Second, using winter tracks, we examine the relation between winter temperature and individual annual winter distance across multiple years. We thereby specifically quantify individual flexibility in annual winter distance as a response to winter temperature. Based on our results, we discuss climate warming as a driver of the observed population shift in winter distance and the role of individual flexibility therein.

2 | MATERIALS AND METHODS

2.1 | Animals and tracking data

Bewick's swans were caught in the Netherlands in the winters (December–January) of 2009/10–2010/11 and 2016/17–2020/21, on agricultural fields using cannon nets. More details of the catches

up until 2011 are provided in Nuijten et al. (2014), and of those up until 2018 in Nuijten and Nolet (2020). We fitted a total of 105 Bewick's swans (86 adults, 4 yearlings (ca. 1.5 years old) and 15 juveniles (ca. 0.5 years old)) with GPS-GSM transmitter neckbands (2009/10: 23, 2010/11: 13, 2016/17: 30, 2017/18: 6, 2018/19: 20, 2019/20: 7, 2020/21: 7). Transmitters from the first two winters were battery-powered, those from 2016/17 onwards solar-powered. The neckbands weighed 75 g (2009/10–2010/11), 70 g (2016/17–2019/20) (both MadebyTheo, custom-made) or 65 g (2020/21; Ornitela, OrniTrack-N55), which amounted to 1.0–1.6% of the body mass of the swans equipped with those transmitters. The neckbands collected GPS locations at intervals ranging from four times per day for the oldest, non-rechargeable devices up to every 5 min for the newest solar-powered devices under good sunlight conditions. We deleted all GPS data from within 3 days of catching, to exclude possible effects of catching and handling on the swans' behaviour from our analysis. In a single instance of two identical tracks from an adult bird and their young, we removed the autumn and winter track of the young for that season to avoid pseudo-replication.

2.2 | Drivers of daily autumn movement

2.2.1 | Calculating daily autumn movement

We used the tracking data to examine the extent to which temperature drives migratory movement throughout the autumn season. We quantified this movement in a number of steps. First, we subset all GPS locations between 1 August and 31 December, thereby including the months in which Bewick's swans make the largest part of their movement away from the breeding grounds (October–November) and the month in which migratory movements become smaller and the distance from the breeding grounds plateaus (Dec, Figure S1). Second, we deleted all GPS locations northeast of Mezen Bay (66.5°N, 43°E) from the autumn tracks to exclude the breeding area and autumn migration departure from the analysis. When Bewick's swans depart for autumn migration they largely skip the White Sea, unlike during spring, and fly their first stretch all the way to the Baltic states (Beekman et al., 2002; unpublished tracking data), suggesting that, once departed, the first few hundreds of kilometres of the migration route are not a flexible response to external conditions. The *timing* of autumn departure from the breeding range itself, on the other hand, is driven by a range of internal and external factors (e.g. Lehikoinen & Jaatinen, 2012; Nuijten et al., 2014; Xu & Si, 2019), but we considered that to be outside the scope of our study. Third, we used step lengths and time intervals between subsequent locations to calculate ground speeds, and removed those locations with a ground speed of >3 m/s to both the previous and next location (2.7% of all locations). We thereby excluded flying behaviour from the data and retained only non-flying locations to focus on the environmental influence on movements between those locations. Fourth, we downsampled the non-flight locations to one location per day by selecting the first GPS location on each day ($n = 5229$ daily locations

from 67 individuals). Fifth, we calculated for each daily location the distance to a fixed location central in the breeding grounds (Naryan-Mar: 67.7°N, 53.1°E, following Nuijten et al. (2020)). We calculated this distance along the rhumb line (i.e. loxodrome), which maintains a constant geographical bearing and is a better descriptor of the migration route within this flyway than the great-circle distance (see also Green et al., 2002). Finally, we calculated for each daily location the change in distance compared to the next day. We used this daily change as our response variable of interest and refer to it as 'daily autumn movement' (in km; a negative value would indicate movement back towards the breeding grounds).

2.2.2 | Annotating variables

We annotated the daily autumn locations with temperature, wind assistance for travelling towards the winter range and day in the season. Temperature at surface level and *u*- and *v*-components of wind at 100m level (the level most relevant for migrating Bewick's swans; Klaassen et al., 2004) were downloaded from the ECMWF Reanalysis v5 (ERA5) Climate Data Store (<https://cds.climate.copernicus.eu>; Hersbach et al., 2020). Following Piersma and Jukema (1990), we combined the wind *u*- and *v*-components with a fixed air speed to calculate, for each location, the wind assistance for travelling in the direction of the winter range, would the individual decide to leave at that point. We thereby took the track direction to the winter range (49°N, 8°W) as a proxy for the preferred direction of travel. We estimated the fixed air speed by taking all flying locations (ground speed >10m/s) from our full GPS tracking data set at times when there was no wind (wind speed <1m/s, meaning that the recorded ground speed resulted solely from flying effort of the swans and was therefore identical to the air speed). We used a more conservative threshold of 10m/s for assigning flight rather than the previous 3m/s (Section 2.2.1) to select more strictly for flying behaviour and since data loss was a smaller concern for this step in the analysis. This selection yielded locations with an average speed of 15.75 m/s (± 2.41 SD), which we used as our fixed air speed in calculating wind assistance. The covariates temperature, wind assistance and day in the season were not collinear (variance inflation factor = 1.32, 1.26 and 1.19 respectively).

2.2.3 | Statistical analysis

We tested how daily autumn movement relates to temperature, wind assistance and day of the season by constructing generalized additive mixed models (GAMMs). We chose GAMMs to enable detecting non-linear effects of the predictor variables on the response variable, such as a temperature threshold for moving away. We modelled daily autumn movement with all possible combinations between the three predictors as either a main effect or in a two-way interaction with another predictor (Table S1). The predictors were always included as smoothed terms, using penalized regression

splines, and each model included individual bird and autumn season as random effects. We selected the best model by comparing AIC values (Akaike information criterion; Akaike, 1973), favouring the most parsimonious model within 2 Δ AIC from the lowest AIC value among all models (Arnold, 2010).

2.3 | Temperature as a driver of winter distance

2.3.1 | Calculating mean midwinter distance

We also used the tracking data to test the relation between temperature and annual distance from the breeding grounds during winter, again on the individual level. Examination of complete winter tracks indicated that swans generally reach the furthest distance from the breeding grounds in the months of December and January (Figures S1 and S2). For that reason, we defined December and January as 'midwinter' and used it as our period of interest (see also Nuijten et al. (2020)). We downsampled our tracking data to daily locations and selected bird-midwinters for which locations were recorded on at least 7 days in December and 7 days in January. We then selected only the bird-midwinters of those birds with tracking data from at least two midwinters. This yielded 55 bird-midwinters (2009/10: 1, 2010/11: 2, 2011/12: 1, 2016/17: 6, 2017/18: 13, 2018/19: 11, 2019/20: 9, 2020/21: 8, 2021/22: 4) from 22 individuals, including eight bird-midwinters that were the winter of catching. Forty-six of the bird-midwinters were from adults and only five from subadults and four from yearlings. For each bird-midwinter we calculated the mean rhumb line distance to the breeding grounds (Naryan-Mar: 67.7°N, 53.1°E), and defined that distance as the 'mean midwinter distance' (see Figure S3 for a map of the mean locations of those bird-midwinters).

2.3.2 | Calculating mean midwinter temperatures

To be able to test the relation between temperature and mean midwinter distance, we constructed a measure of annual winter temperature in the Bewick's swan winter range that is independent of the between- and within-year movements and decisions of individuals. First, we made a kernel density estimation (using an axis-aligned bivariate normal kernel; Venables & Ripley, 2002) of the mean locations of those bird-midwinters used in our analysis (Section 2.3.1). We took the area within the 0.01 contour line of that density estimation as a very rough approximation of the main geographical area that Bewick's swans consider as potential wintering area in December and January (Figure S3). Second, we downloaded monthly averaged temperature data at surface level from the ECMWF Reanalysis v5 (ERA5) Climate Data Store (<https://cds.climate.copernicus.eu>; Hersbach et al., 2020), removed the marine cells and cropped it with the 0.01 contour area (Figure S3). For the cropped area, we calculated mean midwinter (December–January) temperature per winter season, which we hereafter refer to as 'mean midwinter

temperature'. Using different contour lines, and therefore different areas over which to calculate mean midwinter temperature, yielded near identical results that led to the same conclusions.

2.3.3 | Statistical analysis

We fit linear mixed models (LMMs) to test how mean midwinter distance relates to mean midwinter temperature. Within our GPS tracking dataset, mean midwinter temperature and winter season were collinear (Pearson's $r = .67$, $p < .0001$), that is, midwinter temperature showed an increasing trend over the non-continuous years from which we had tracking data (Figure 1). To disentangle the effect of mean midwinter temperature from other factors that may have shown a chronological trend in the years of our tracking data, such as food availability, we made two separate models: one modelling mean midwinter distance with winter season and one modelling mean midwinter distance with mean midwinter temperature. Simply detrending our midwinter temperature data would not have solved the issue, since the trend over the non-continuous years of our data was much stronger than the actual, long-term temperature increase. An effect of the detrended midwinter temperature would therefore not be interpretable in the context of that actual, long-term increase. Both models included individual bird as a random effect. We used AIC to determine the most parsimonious model of the two. For both models, predictor significance was determined with a likelihood ratio chi-square test. To separate within-individual effects from between-individual effects and prevent erroneously generalizing a possible between-individual relation to a within-individual relation, we used the post-hoc procedure of within-subject centring (van de

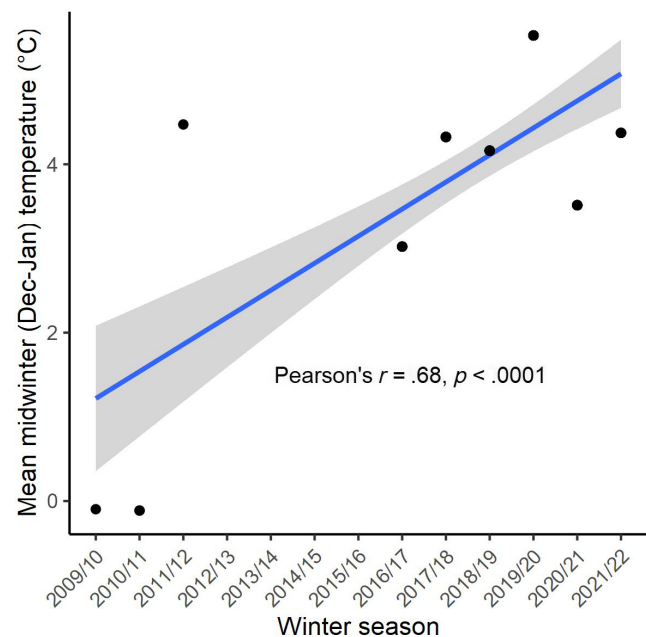


FIGURE 1 Annual trend in mean midwinter (December–January) temperature for the winter seasons that were included in our winter distance analysis.

Pol & Wright, 2009). Additionally, as a way of checking for potential confounding long-term temporal trends in our data, we examined the relation between *interannual change* in midwinter distance and *interannual change* in midwinter temperature (i.e. the first-order time derivatives of both variables) using a linear model. If there are no such confounding temporal trends, this relation would be similar to the relation between simply midwinter distance and midwinter temperature. All analyses were performed in R 4.0.4 (R Core Team, 2019), using the packages *mgcv* (Wood, 2010) for GAMM fitting, *lme4* (Bates et al., 2015) for LMM fitting and *MASS* (Venables & Ripley, 2002) for kernel density estimation.

3 | RESULTS

3.1 | Daily autumn movement

The best models of daily autumn movement all included interactions between wind assistance and day in the season, and most included temperature, sometimes in interaction with wind assistance or day in the season (Table S1). Daily autumn movement was best explained by two-way interactions between all three predictors: temperature, wind assistance and day in the season (Figure 2; Table 1). Movement decreased throughout the autumn season. Swans generally moved further away from the breeding grounds with lower temperatures, and especially so with beneficial winds early in the season. Later in the season, the effect of wind disappeared and swans only moved substantially further with temperatures below freezing.

3.2 | Mean midwinter distance

Individuals showed substantial variability in their annual mean midwinter distance to the breeding area, with average and maximum within-individual ranges in mean midwinter distance of 297 and 846 km respectively (see Figure S3 for the mean midwinter locations). Mean midwinter distance in our GPS tracking data showed a decreasing trend both over the winter seasons ($\beta = -39.54$ km/year, $SE = 11.86$, $p = .0013$; Table 2; Figure 3a) and with mean midwinter temperature ($\beta = -117.97$ km/°C, $SE = 22.00$, $p < .0001$; Table 2; Figure 3b). The model AICs indicated that mean midwinter temperature was a better predictor of mean midwinter distance than winter season was (AIC = 727.19 and 741.84 respectively). When excluding the relatively cold winters of 2009/10 and 2010/11, the relation between temperature and midwinter distance remained unchanged ($\beta = -118.25$ km/°C, $SE = 37.28$, $p = .0024$; Figure S4; Table S2). There was no difference between the between-individual effect and the within-individual effect of mean midwinter temperature on mean midwinter distance ($\beta = 2.67$, $SE = 44.56$, $p = .95$; Table S3), indicating that the model effect of temperature is present not only among but also within individuals. Similarly, the model effect of winter season on midwinter distance was also present both among and within individuals ($\beta = 24.44$, $SE = 40.01$, $p = .54$; Table S3). Finally, the relation between *interannual change* in

FIGURE 2 Daily autumn movement away from the breeding grounds in relation to temperature and wind assistance during early, middle and late autumn season (left to right) as predicted with the best GAMM. That model included two-way interactions between all three predictors temperature, wind assistance and day in the season. The light-shaded areas denote 95% confidence intervals. Wind assistances of -12 and 6 m/s signify strong but realistic headwinds and tailwinds respectively, -3 m/s being the average wind assistance in our data. $n = 5229$ daily bird locations.

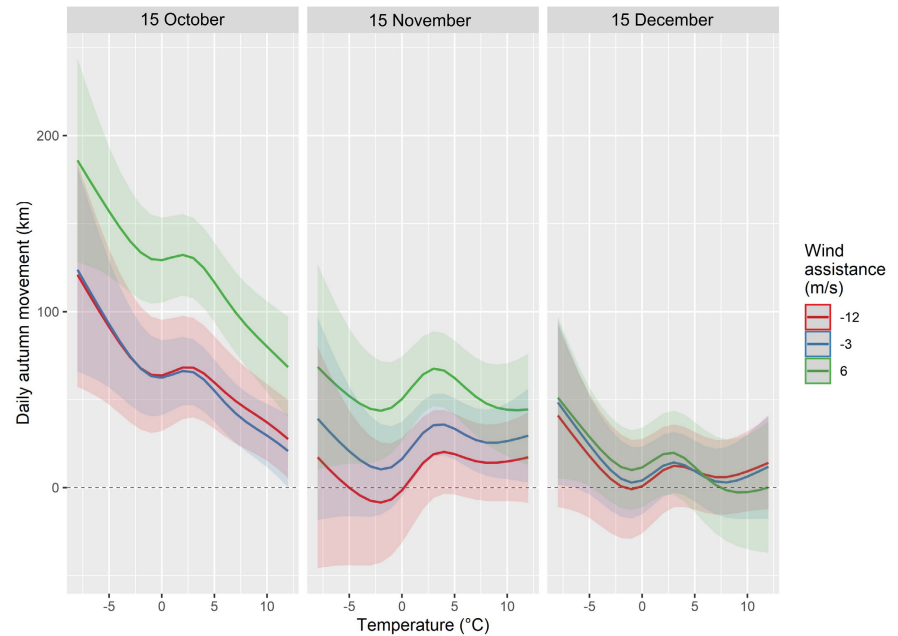


TABLE 1 Generalized additive mixed model (GAMM) of daily autumn movement (km), as selected through AIC comparison (for an overview of all models, see Table S1).

	edf	F	p
Fixed effects			
Temperature	4.94	8.62	<.0001
Wind assistance	1.03	0.01	.9645
Day in the season	1.00	0.36	.5494
Temperature × wind assistance	4.22	0.30	.0070
Temperature × day in the season	18.16	4.83	<.0001
Wind assistance × day in the season	14.31	1.78	<.0001
Random effects			
Bird	13.35	0.29	.0375
Autumn season	1.87	0.37	.1168

Note: edf of the main effects of wind assistance and day in the season are very close to one, indicating that they are linear (but nonetheless insignificant). $n = 5229$ daily bird locations.

Abbreviation: edf, estimated degrees of freedom.

mean midwinter distance and *interannual change* in mean midwinter temperature ($\beta = -130.17$ km/°C, $p = .0003$; Figure S5; Table S4) was similar to the relation between simply mean midwinter distance and mean midwinter temperature (above). This indicates that there is no confounding long-term temporal trend in the midwinter distance data and further supports the validity of our approach.

4 | DISCUSSION

We use multi-year GPS tracking data to show that the migratory movement of individual Bewick's swans in autumn is related to

decreasing temperatures throughout the season, with movement during late autumn specifically being driven by temperatures below freezing. As a result, there is large flexibility in their annual winter distance as a response to temperature at this time of the year. This suggests that, in this long-distance arctic migrant, the ongoing multi-decadal winter range shift in the direction of the breeding grounds (i.e. 'short-stopping'), as inferred from winter resightings, is for a substantial part driven by individual responses to a warming climate. In contrast to the notion that socially migrating waterfowl are generally site-faithful in winter (Rees, 2006; Robertson & Cooke, 1999), we show that range shifts in these migratory birds can be driven by flexible responses to changing environmental conditions at the individual level.

The GPS-tracked swans moved larger distances in autumn on days with lower air temperatures, but that effect decreased throughout the autumn season, implying that birds become gradually less responsive to temperature during autumn. In late autumn birds generally moved only small distances or did not move at all; only freezing temperatures provided a stimulus for moving to the same extent as early-season movements. Xu and Si (2019) found that the probability of leaving autumn stopover sites increased after the first night where temperatures dropped below 0°C in two goose species. Our study adds to those results, but we suggest that temperature can drive movement away from the breeding grounds through different mechanisms during early and late autumn, the specific effect of frost only becoming apparent later. This corresponds with the fact that autumn-migrating Bewick's swans generally stay well ahead of the wave of ice formation at least until passing the Baltic states (Nuijten et al., 2014). The late-season effect of frost may be direct, through increasing thermoregulatory costs (Bech, 1980; Jenssen et al., 1989; Nespolo et al., 2008), or indirect: Bewick's swans fuel their autumn migration predominantly with aquatic plants (Beekman et al., 1991; Hoyer et al., 2012)

TABLE 2 Linear mixed models of mean midwinter (December–January) distance (km) from the breeding grounds. $n = 55$ bird-midwinters for both models.

	Model predictor	Estimate (β)	SE	χ^2	p	Model AIC
Model 1 ^a	Intercept	82,716.66	23,935.94	—	—	727.19
	Winter season	-39.54	11.86	10.31	.0013	
Model 2 ^b	Intercept	3403.48	91.99	—	—	741.84
	Mean midwinter temperature	-117.97	22.00	23.84	<.0001	

^aVariance estimate for individual bird = 1987.

^bVariance estimate for individual bird = 4080.

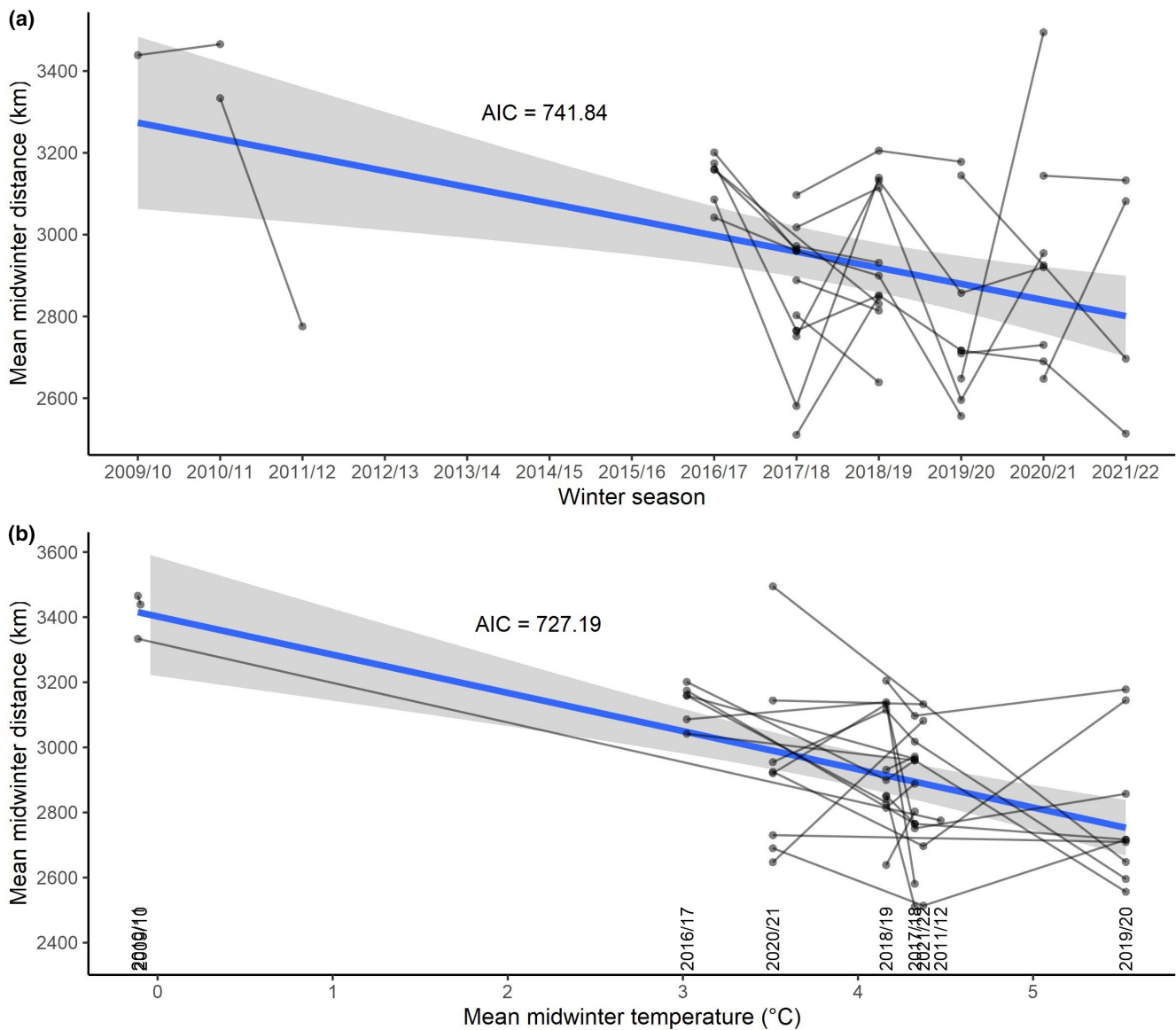


FIGURE 3 Mean midwinter (December–January) distance from the breeding grounds against (a) winter season and (b) mean midwinter temperature for GPS-tracked birds ($n = 55$ bird-midwinters). Grey lines connect midwinters that belong to the same bird. The light-shaded areas denote 95% confidence intervals. AIC values of the trend models (blue) are given in the figure, indicating that (b) was the best model. See [Figure S3](#) for a map of the locations of these bird-midwinters. The relationship between mean midwinter distance and temperature remained unchanged when excluding the relatively cold winters of 2009/10 and 2010/11 (see [Figure S4](#); [Table S2](#)).

and frost can make those unavailable (Nuijten et al., 2014). Upon arrival in the winter range aquatic plants are still the preferred food source (before depletion drives a switch to agricultural fields; Nolet

et al., 2002) and frozen water likely drives swans to explore more south-westerly areas, which are generally warmer, for those resources. Temperature can thus give rise to eventual winter distance

through cold spells, and specifically late autumn frost, driving birds further into their winter range.

Our GPS-tracked birds moved larger daily distances with beneficial winds during early autumn, an effect in the same order of magnitude as that of temperature. Wind assistance can drive higher daily distances through increasing the daily departure probability (Geisler et al., 2022; Klaassen et al., 2004; Kölzsch et al., 2016; Xu & Si, 2019) but also through facilitating faster ground speed when in flight (Kemp et al., 2010). The declining effects of temperature and wind assistance on movement throughout autumn indicate that the birds become less responsive to those climatic factors towards their eventual winter range, likely due to coming closer to and eventually reaching a geographical area that is considered a potential wintering area based on experience or social information (see Abrahms et al., 2021). Thus, individual migration destination is to some extent predetermined, as opposed to fully dependent on environmental conditions encountered throughout autumn and early winter. However, the effect of wind assistance eventually disappearing completely implies that wind is used only to facilitate migration towards a destination, whereas temperature co-determines that destination.

Indeed, we found high flexibility in the swans' annual winter distance related to winter temperature, with individuals residing on average 118 km closer to the breeding grounds in midwinter (December and January) for every 1°C increase in mean temperature in that period. Inspection of tracking data from the summer months of June and July indicated that swans did not individually shift their summer locations over the years, and hence wintering closer to the breeding area was not reflected in (or 'negated by') site choice in the breeding area, but instead indicative of a shortened migration (Figure S6; Table S5). These results enable us to add to the findings of Nuijten et al. (2020), who used ring resightings from the winter range to calculate that the winter distance of Bewick's swans has decreased with 353 km between 1970 and 2017. That decrease was due to both a generational shift, that is, a change over time in the frequencies of individuals that winter at different distances from the breeding ground, and interannual individual flexibility, that is, individuals wintering increasingly close to the breeding grounds during their lives. In our GPS tracking study, we specifically quantified without resighting bias which part of the individual flexibility in winter distance is a response to temperature, by modelling annual winter distance as a function of annual winter temperature. Average winter temperatures in the Netherlands, which is situated somewhat centrally in the Bewick's swan's winter range, increased with 2°C between 1970 and 2017 (from 2.6 to 4.6°C; Royal Netherlands Meteorological Institute, www.knmi.nl/klimaat). This increase would translate to a decrease in the winter distance of roughly 220 km based on the relation between temperature and winter distance found in this study, explaining a large part, although not all, of the observed shift since 1970 with individual flexibility related to temperature. Gill et al. (2019) showed how expansions in both the breeding and

non-breeding ranges of Icelandic black-tailed godwits (*Limosa islandica*) were driven by temporal shifts in the frequencies of individuals using different locations, whereas individuals were consistent in annual timing and space-use (Gill et al., 2014). They therefore argued that distribution shifts in migratory species likely result from generational shifts. Our results together with those of Nuijten et al. (2020) indicate that flexibility within the lives of individuals in response to temperature, and thus on a larger temporal scale to climate warming, is a major driver of the ongoing winter range shift in the socially migrating Bewick's swan.

A temperature-driven *generational shift*, on the other hand, would be represented in our model by a shifting intercept in Figure 3b, lower for later cohorts, but we did not have enough data of young birds to detect such an effect (Figure S7; Table S6). Individuals might be more responsive to temperature in their wintering site selection during early life, becoming gradually less flexible as they get older and accumulate knowledge of suitable sites in terms of habitat and food availability (Tombre et al., 2019). That way, with winters becoming increasingly mild, new cohorts would favour wintering sites closer to the breeding area more so than older cohorts would. Future analyses of tracking data that include repeated years of young birds, ideally in combination with tracks from their parents, will be able to detect or exclude such a mechanism. Additionally, the winter range shift could be partly driven by individual or generational responses to spatiotemporal changes in food availability in the winter range, where various waterfowl, including Bewick's swans, have been shifting during the last decades from feeding predominantly on grassland to arable land (Abraham et al., 2005; Beekman et al., 2019; Fox & Abraham, 2017; Wood et al., 2019) and specifically maize harvest residues (Clausen, Madsen, Nolet, & Haugaard, 2018; Koffijberg & Tijssen, 2018; Rosin et al., 2012). Abundant resources may have alleviated the need for birds to migrate further into the winter range and enabled them to remain at and return to northeasterly wintering sites throughout the years (Teitelbaum et al., 2016). Further research should look at age-related land use during autumn and winter (Hoye et al., 2012) and interannual variability therein, to examine to which extent anthropogenic changes in land use and food availability can further explain the observed range shift through individual- or generation-level mechanisms.

Waterfowl have traditionally been considered site-faithful throughout their annual cycle due to their highly social migration behaviour in early life, combined with the advantage of returning to known sites in terms of habitat suitability, food abundance and distribution of conspecifics (Rees, 2006; Robertson & Cooke, 1999; Rohwer & Anderson, 1988). Nonetheless, Clausen, Madsen, Cottaar, et al. (2018) found high variability in geographical wintering area use of pink-footed geese (*Anser brachyrhynchus*) in relation to land use, but not temperature. Here we add that individual migratory swans are highly flexible in the non-breeding season in terms of winter distance in relation to temperature. Studies across several taxa have shown interannual variability in winter distance

related to temperature at the population level, using resighting or count data (Austin & Rehfisch, 2005; Pavón-Jordán et al., 2015; Podhrázký et al., 2017; Visser et al., 2009; Ward et al., 2009). Our GPS tracking study implies that the Bewick's swan is adapting to climate change in the non-breeding season in terms of winter range selection on the individual level. Yet, it is a topic for future study whether the potential for the species to further shift their winter range might be limited by, for example, food availability (Wood, Stillman, et al., 2021), competition (Wood, Newth, et al., 2021), hunting pressure (Newth et al., 2011) or changes therein in the newly suitable parts of the winter range. Furthermore, it is unknown if there are carry-over effects of migration distance on for example timing of arrival on the breeding grounds, breeding propensity and ultimately breeding success. Only by tracking individual migrants through their seasonal environments throughout their lives can we advance our understanding of the mechanisms that underlie changes in migration and subsequent range shifts, which is crucial to predict how migration and species' ranges might be impacted by further climate change.

AUTHOR CONTRIBUTIONS

Hans Linssen: Conceptualization; data curation; formal analysis; methodology; writing – original draft; writing – review and editing. **E. Emiel van Loon:** Conceptualization; methodology; writing – review and editing. **Judy Shamoun-Baranes:** Conceptualization; methodology; writing – review and editing. **Rascha J. M. Nuijten:** Conceptualization; data curation; methodology; writing – review and editing. **Bart A. Nolet:** Conceptualization; data curation; funding acquisition; methodology; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The data and scripts that support the findings of this study are openly available in Figshare at <http://doi.org/10.21942/uva.24083703>.

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SUPPORTING INFORMATION

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

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