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Scope for waterfowl to speed up migration to a warming Arctic

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Climate change is causing an earlier onset of spring, requiring migratory birds to accelerate their spring migration to avoid arriving late at the breeding grounds. This acceleration hinges on the capacity to shorten the time spent building energy reserves (fuelling) for migratory flight, which is currently thought to be very limited. Combining multiyear global-positioning-system tracking and body mass data from five large-bodied Arctic-breeding waterfowl species, we demonstrate that there is considerable scope for the studied species to migrate faster by shortening the fuelling time, either before departure or at stopovers. With the exception of one species (brent goose), populations were able to largely or fully offset their spring departure date with subsequent fuelling time en route. Still, under the current rates of Arctic warming, this may allow them to mediate only a few more decades of spring advance by migrating faster.

Climate change is affecting organisms and their ecology around the globe[1,2]. Importantly, the annual onset of spring is advancing through earlier temperature increase[3], combined with earlier ice and snowmelt[4] in higher-latitude and higher-altitude regions. While primary producers appear readily able to track this advance, higher-order consumers such as birds need to make more complex adjustments to their annual cycle to follow suit and many struggle to do so[5–8]. These changes are arguably the most complex for long-distance migratory birds, which have to travel each spring from their non-breeding range to their breeding grounds before they can start reproduction[9]. Arriving late relative to local spring phenology can lead to reduced reproductive performance[10] and potentially severe repercussions on fitness[11–14]. Keeping up with the advancing onset of spring requires migrants to migrate shorter distances by wintering closer to the breeding grounds, migrate earlier or migrate faster[15].

Migrating faster seems a primary mechanism through which birds are responding to climate change[10,15,16]. Still, few studies have

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investigated how much scope there is for migrants to speed up their migration[17]. This is crucial to assess the extent to which an ongoing spring advance can be mediated by migrating faster[18,19] and when other mechanisms (for example, migrating earlier[20] or shortening the migration route[21,22]) will be required to mitigate the possible consequences of arriving and breeding late. Since flight makes up only a small proportion of the total migration duration, faster migration will have to come from spending less time on stopovers[23,24]. If a bird is to reduce stopover time while arriving on the breeding grounds with the same energy stores, it must fuel faster[25]. A previous study of tracking data from a wide range of migratory bird species examined the relationship between time spent on spring stopover sites (fuelling) and migration speed[17]. It found that migrants had very little scope to migrate faster, since any substantial decrease in the duration of migration would require 50% or even 100% reductions in fuelling time. However, it did not include fuelling before departure from the non-breeding area ('predeparture fuelling') into the calculation of fuelling time. Predeparture fuelling is crucial for species that accumulate energy required for migratory flight and breeding before departing the non-breeding range[23,25] (that is, capital migrants, as opposed to income migrants which spread the fulfilment of their energy requirements across their migratory journey[26]). Including predeparture fuelling is therefore essential for accurately assessing the scope to migrate faster, as omitting this phase can severely overestimate the reductions in fuelling time, or increases in fuelling rate, required[25]. However, determining the duration of predeparture fuelling requires identifying the onset of fuelling. That remains a challenge since data on fuel deposition are difficult to obtain in wild animals. Whereas foraging activity, associated with body mass increase, can be inferred from tri-axial accelerometers[27,28,29], not all species show marked changes in activity budgets since other adjustments can also be made, such as switching to higher quality food[30]. Instead, direct measurements of body mass are a good indicator of fuel deposition[31–33] and can be a predictor of migration speed and survival[34,35].

Here we reassess how much scope there is to speed up spring migration for a range of large-bodied, herbivorous avian migrants, incorporating predeparture fuelling time in our analysis. We combine two types of data for this: global positioning system (GPS) tracks of spring migration and spring body mass trajectories compiled from wild-caught birds at their non-breeding grounds. Tracks yield departure and fuelling time en route at the individual level. Body mass trajectories, on the other hand, enable pinpointing the onset of fuelling for a population and thus making an estimation of the average predeparture fuelling period. We calculate total migration duration, speed and fuelling times while including this period. From the fuelling times we determine the hypothetical requirements, in terms of decreasing the fuelling time (or increasing fuelling rate), to speed up migration. We then use data from individuals that were tracked for multiple years to empirically assess the within-individual variation in fuelling time and the influence of spring onset on fuelling time and arrival date. Finally, we consider the empirical variability in fuelling time in the context of current rates of spring advance.

Onset of fuelling and migration speed

We study five waterfowl species that winter in Northwestern Europe and breed in the Eurasian Arctic: dark-bellied brent goose *Branta bernicla bernicla* (hereafter, brent goose), barnacle goose *Branta leucopsis*, greater white-fronted goose *Anser albifrons albifrons* (hereafter, white-fronted goose), pink-footed goose *Anser brachyrhynchus* and Bewick's swan *Cygnus columbianus bewickii* (Fig. 1 and Extended Data Table 1). Ideally, the onset of predeparture fuelling would be determined at the individual level using repeated measurements across the season. Since those data are unavailable, we determined the onset of fuelling at the population level, by compiling body mass data collected from wild-caught adult birds in Northwestern Europe between 1972 and 2024 (Fig. 2a–e). We fitted segmented regressions[36] of body mass over the day of the year (DOY) for each population separately, taking all years together and performing 5,000 bootstrap iterations. This revealed a range in the onset of fuelling between DOY 52 (21 February; 95% confidence interval (CI) 40–58) for white-fronted geese and DOY 112 (21 April; 95% CI 100–119) for brent geese (Fig. 2a–e; details and fuelling rate estimates in Supplementary Table 1). Spring departure at the individual level was derived from the tracking data, by taking the last day each bird was present in the non-breeding area (defined as southwest of 58° N, 12.85° E; Fig. 1a). Taking the time between the population-level onset of fuelling and each individual's departure gave us an estimate of the predeparture fuelling period. We thereby made two assumptions: first, that individuals of a population start fuelling at roughly the same time, or at least that the spread in the onset of fuelling is much smaller than the spread in departure. Second, that the onset of fuelling has not advanced over the decades during which the body mass data were collected to an extent that would qualitatively impact our results (Supplementary Fig. 1). Both assumptions are reasonable since fuelling onset in large waterfowl appears to be constrained largely by daylength[28,29], not temperature (Supplementary Fig. 1; Methods). Predeparture fuelling varied greatly, with barnacle geese departing 58 ± 10.1 days (mean ± s.d.) after the onset of fuelling but pink-footed geese on average not fuelling at all before departure (−2.8 ± 11.6 days; Fig. 2f). A total of 51 of 116 pink-footed geese, 13 of 118 Bewick's swans and 1 of 110 white-fronted geese departed for spring migration before the population mean onset of fuelling; we considered these individuals not to have fuelled before departure.

We delineated stopovers en route from the tracking data, by identifying the periods after departure where a bird moved less than 100 km between subsequent days for at least 2 days in a row. This provided us with an estimate of en route fuelling time. Together, predeparture fuelling and en route fuelling make up the 'total fuelling time', which, combined with the flying time, makes up the total migration duration[23] (Table 1). Predeparture fuelling accounted for a large part of the migration duration in barnacle (75%) and brent geese (55%), suggesting a capital migration strategy compared with the other species (Fig. 2g). Consequently, including predeparture fuelling led to substantially lower estimates of migration speed compared with ignoring it, especially for barnacle and brent geese (Fig. 2h).

Required and observed variability in fuelling time

Whereas the outcome of migrating faster is an earlier arrival in days, the relevant requirement for the individual is a relative decrease in fuelling time (which should ideally be achieved by increasing the fuelling rate[25]). We therefore calculated the relationship between a decrease in migration duration in days and the required decrease in total fuelling time as a percentage, for each tracked spring migration (Fig. 3a, thin solid lines). For example, if an individual had a total fuelling time of 50 days, a 1% decrease in total fuelling time would yield a 0.5-day decrease in migration duration, a 2% decrease would yield 1 day and so on. The relationship between decrease in migration duration (day) and decrease in total fuelling time (%) would have a slope of 0.5 for this individual. These relationships varied among populations, being flatter (that is, more demanding for the birds) for species that have a shorter total fuelling time. For example, to decrease the total duration of migration by 10 days would require pink-footed geese to decrease their total fuelling time (and accordingly increase their fuelling rate) by roughly 23%, compared with 11% for white-fronted geese (Fig. 3a, thick dashed lines for median individuals per population). When predeparture fuelling was ignored, birds appeared more limited in their scope to speed up spring migration, particularly barnacle and brent geese (see Extended Data Fig. 1 for a comparison).

To assess the actual scope for speeding up spring migration, the question remains as to how capable birds really are of decreasing their total fuelling time, compared with these hypothetical requirements. We used individuals that were tracked for multiple years to empirically

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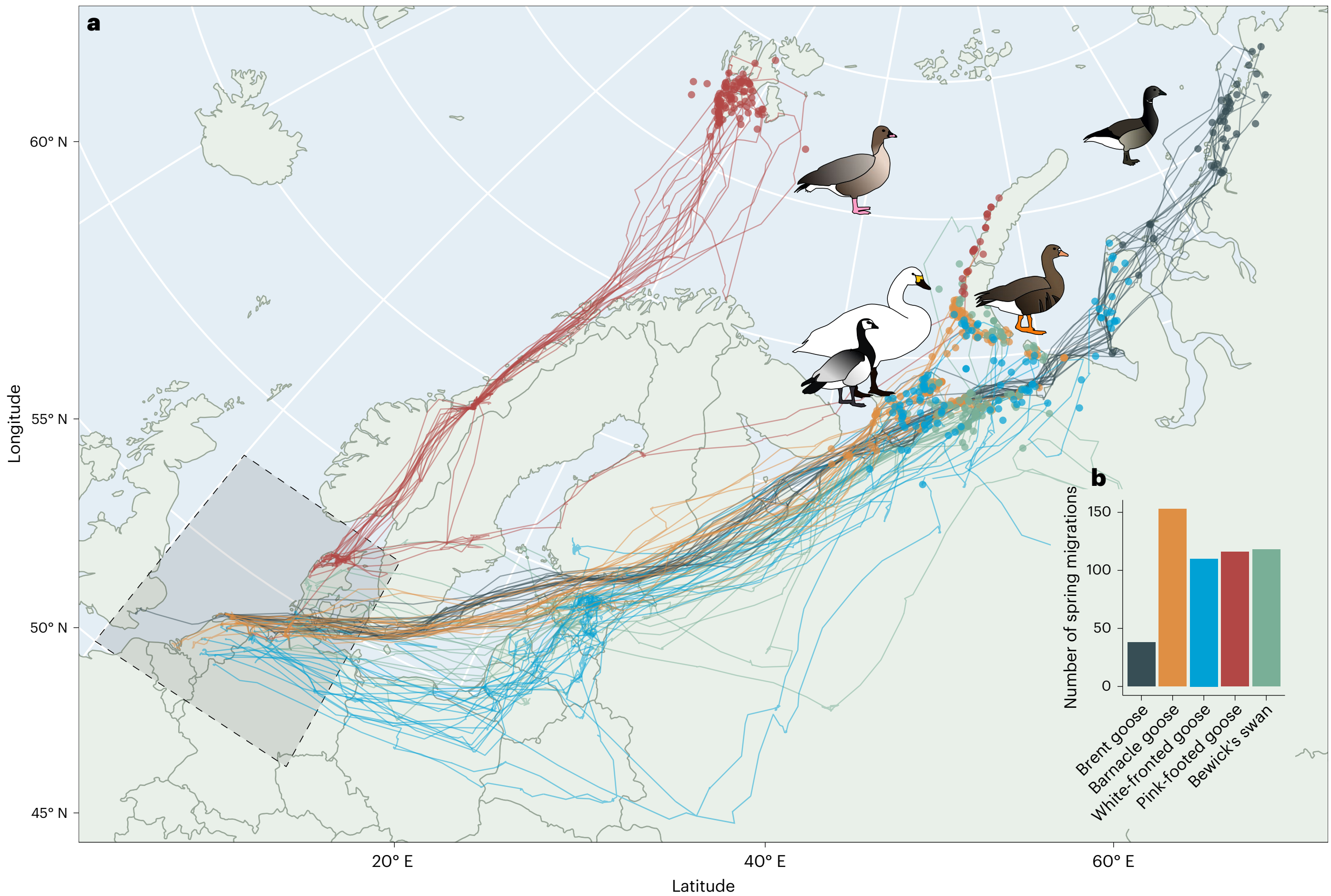

Fig. 1 | Spring migrations and tracking data of five Arctic-breeding waterfowl species. a, Spring migration tracks (only 20 randomly chosen tracks are shown per species for clarity). Dots denote summer centroids of all tracks in the analysis, which we used to determine arrival at the breeding grounds. The grey rectangle was used as the non-breeding area for all study species; we defined spring departure as the last day an individual was within that area. **b**, Numbers of tracked spring migrations per species and true sample sizes used in the analysis. Basemap in **a** from Natural Earth. Bird icons in **a** created with inkscape (https://inkscape.org/about/license).

determine the phenotypic variability in total fuelling time, by comparing the migrations with the longest and shortest total fuelling time for each individual (Fig. 3b,c; Supplementary Table 2 gives a detailed overview of sample sizes). Individuals showed a decrease between their longest and shortest total fuelling time ranging from 6.4 ± 4.5 days (mean ± s.d.) for barnacle geese to 9.7 ± 7.4 days for white-fronted geese and 9.7 ± 5.9 days for Bewick's swans (Fig. 3b). Expressed as percentages decrease, barnacle geese showed the lowest decrease (8.4% ± 5.6) and brent geese the highest (15.0 ± 13.8) (Fig. 3c).

Finally, we examined the extent to which fuelling time and arrival at the breeding grounds are a result of the onset of spring, which would further indicate scope to speed up under climate warming. We therefore modelled the effects of departure date from the non-breeding grounds and date of snowmelt on the breeding grounds, on the en route fuelling time and arrival date (Fig. 4), separating within- and between-individual effects using the method of within-subject centring[37]. Here we use en route instead of total fuelling time because birds cannot predict from the non-breeding grounds whether spring on the breeding grounds will be early or late[38], but along the way they increasingly can[39,40]; and because it enables us to test whether they can offset their departure timing with fuelling time on subsequent stopovers. Similar to previous findings in other taxa[41–43], individuals from all populations except brent geese were able to largely or fully offset their spring departure date with subsequent time spent fuelling en route (Fig. 4b and Extended Data Table 2). For each day that birds departed earlier, they spent almost one day longer at stopovers (within-individual effects: brent geese, 1.04 ± 0.69 days (mean ± s.e.); barnacle geese, 0.73 ± 0.09 days; white-fronted geese, 0.90 ± 0.14 days; pink-footed geese, 1.02 ± 0.09 days; and Bewick's swan, 1.03 ± 0.08 days; Extended Data Table 2). As a result, there was no correlation between departure and arrival within individuals, except slightly for barnacle geese (0.33 ± 0.10) (Fig. 4a, thin lines). This suggests that variation in departure date is, at least to some extent, offset by body condition at departure, and that individuals start fuelling for spring migration more or less simultaneously when environmental conditions allow (Extended Data Fig. 2).The study populations responded variably to the date of snowmelt. White-fronted geese and Bewick's swans spent less time fuelling en route in years with early snowmelt than they did in late years (within-individual effects, respectively, 0.31 ± 0.10 days and 0.25 ± 0.07 days less fuelling per day earlier snowmelt ($d\,d^{-1}$)), whereas the relation for barnacle geese was only present between individuals (between-individual effect 0.22 ± 0.03 $d\,d^{-1}$; Fig. 4d and Extended Data Table 2). As a result, barnacle geese, white-fronted geese and Bewick's swans arrived earlier at the breeding grounds in years with earlier snowmelt (respectively, 0.26, 0.38 and 0.37 $d\,d^{-1}$; Fig. 4c and Extended Data Table 2).

Scope for speeding up migration

In contrast to previous work[17], we show that there is scope to speed up spring migration for several Arctic-breeding waterfowl by reducing the time spent fuelling. The required reductions in fuelling time,

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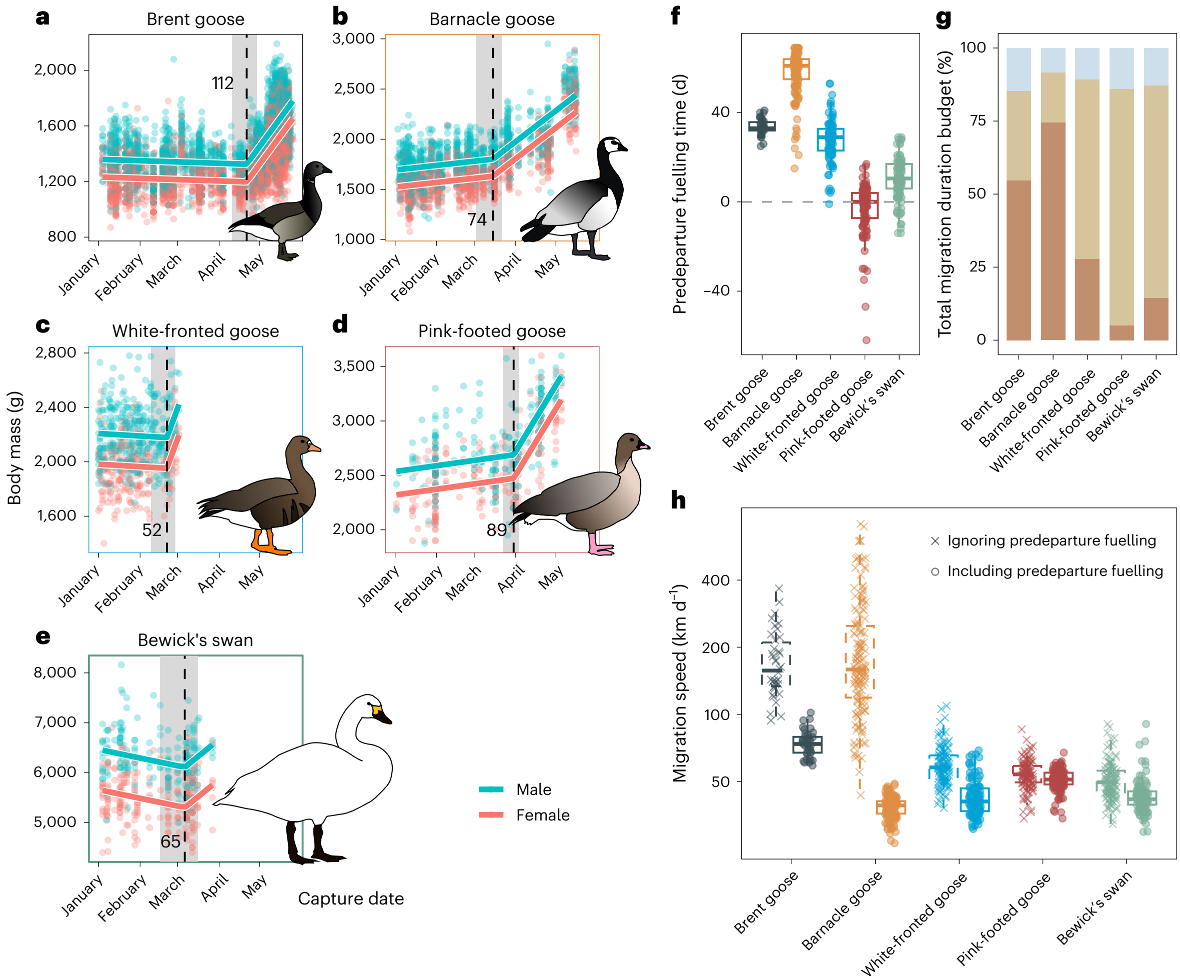

Fig. 2 | Onset of fuelling, migration budgets and migration speed for five Arctic-breeding waterfowl species, in order of increasing body mass. **a**–**e**, Body mass of wild-captured adult birds (brent goose (**a**), barnacle goose (**b**), white-fronted goose (**c**), pink-footed goose (**d**) and Bewick's swan (**e**)) at their non-breeding grounds in Northwestern Europe and derived onsets of fuelling at the population level. Solid lines are segmented linear regressions with a different intercept for females (red) and males (blue). Dashed vertical lines and shaded areas indicate the estimated onset of fuelling and 95% CI, with numbers indicating the corresponding day of the year. **f**, Predeparture fuelling time for each tracked spring migration (the interval between the population-level onset of fuelling, **a**–**e**, and individual-level spring departure). Negative numbers indicate individuals that departed migration before the onset of fuelling; we assumed a predeparture fuelling time of 0 in those cases. Boxplots indicate median and interquartile ranges, with whiskers further extending 1.5× the interquartile range. Sample sizes: brent goose, 33 individuals; barnacle goose, 88; white-fronted goose, 70; pink-footed goose, 55; and Bewick's swan, 61. **g**, Proportional contribution of predeparture fuelling (brown), en route fuelling (beige) and flying time (blue) to the total migration duration, averaged per population. For standard errors, see Supplementary Fig. 2. **h**, Migration speeds for tracked spring migrations when ignoring (crosses) or including (circles) predeparture fuelling. Boxplots indicate median and interquartile ranges, with whiskers further extending 1.5× the interquartile range. Note that the *y* axis is on a log scale. See **f** for sample sizes. Bird icons in **a**–**e** created with inkscape (https://inkscape.org/about/license).

Table 1 | Migration characteristics of the five study populations

	Migration distance (km)	Total migration duration (d)	Predeparture fuelling time (d)	En route fuelling time (d)	Flying time (d)	Total fuelling: flight time ratio	Migration speed (km d^{-1})
Brent goose	4,614±444	63.0±9.6	33.6±3.5	20.3±9.8	9.1±2.0	6.1±1.4	74.4±10.3
Barnacle goose	2,977±305	77.9±6.7	57.8±10.1	13.6±10.7	6.5±1.9	11.8±3.4	38.4±4.2
White-fronted goose	4,229±921	99.2±10.0	27.5±9.1	61.1±11.4	10.6±3.4	9.1±2.6	42.7±8.3
Pink-footed goose	2,692±341	53.7±11.1	2.4±3.6	43.9±11.7	7.4±2.1	6.6±1.6	50.9±5.5
Bewick's swan	3,378±583	79.0±8.7	11.1±7.4	57.9±12.0	10.0±2.6	7.4±2.0	43.1±8.1

Values represent the mean±s.d. Migration speed was calculated per spring migration by dividing its migration distance (the distance along the daily-interval migration path between departure and arrival) by total migration duration, which consists of predeparture fuelling, en route fuelling and flying time (shown as proportions in Fig. 2g). Sample sizes are presented in Extended Data Table 1.

or increases in fuelling rate, varied substantially between species (Fig. 3a), with those species that spend less time fuelling having to make larger relative reductions to their fuelling time. These differences thus depend on the migration characteristics of a population and we show that including predeparture fuelling is critical in assessing the scope for migrating faster[25].

If birds are to perform faster migration while arriving with the same body stores, decreasing the fuelling time will require increasing

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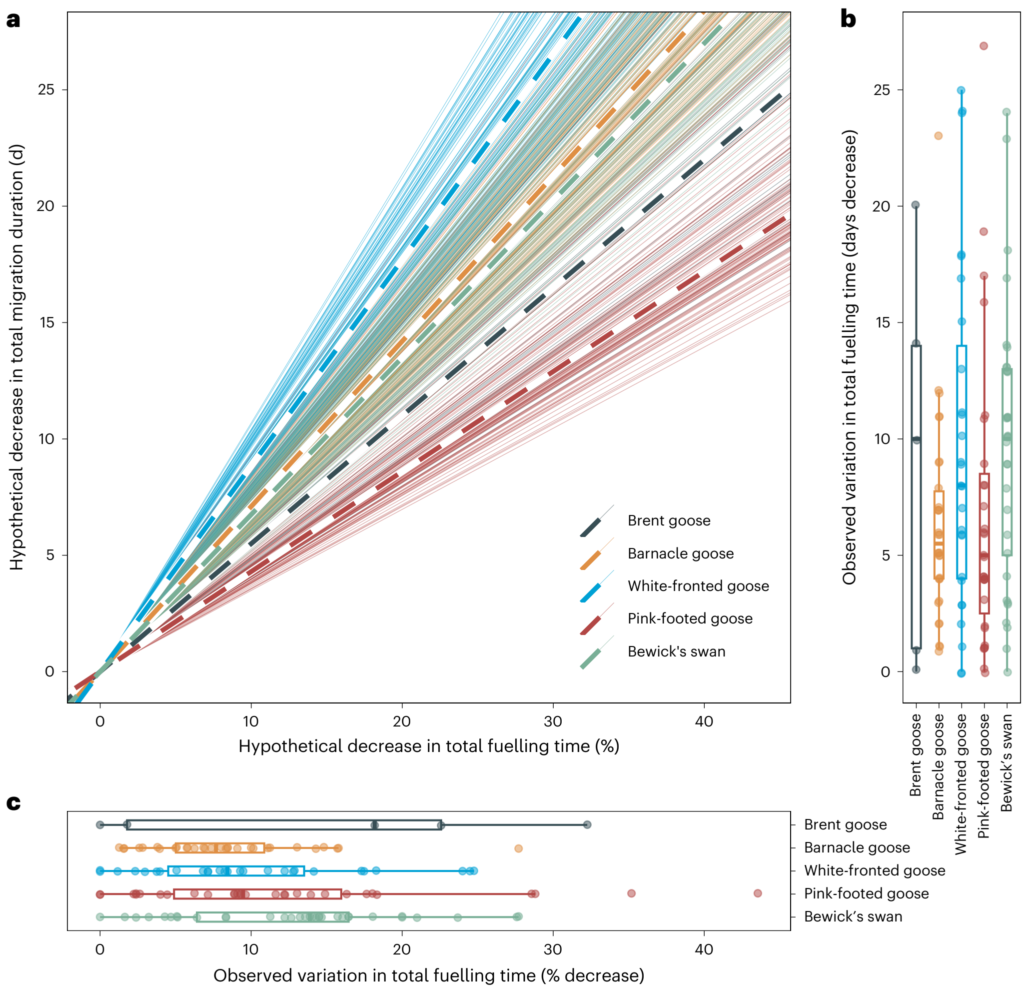

Fig. 3 | Required and observed variability in fuelling time for five Arctic-breeding waterfowl species. a, Relationships between a hypothetical decrease in migration duration (days) and the required hypothetical decrease in total fuelling time (%). Each thin line represents one tracked spring migration and indicates how much that migration would have been shortened (in days) by a certain percentage decrease in fuelling time. For example, if an individual had a total fuelling time of 50 days, a 1% decrease in total fuelling time would yield a 0.5-day decrease in migration duration, a 2% decrease would yield 1 day and so on, yielding a slope of 0.5. Thick dashed lines indicate the median slope per population. Note that total fuelling time includes predeparture fuelling; a comparison without predeparture fuelling is made in Extended Data Fig. 1. **b**,**c**, Observed within-individual variation in total fuelling time of individuals that were tracked for multiple years, shown both as days decrease (**b**) and percentage decrease (**c**) between the longest and shortest total fuelling time (each point represents one individual and each individual is visualized in **b**,**c**). Boxplots indicate median and interquartile ranges, with whiskers further extending 1.5× the interquartile range. A single data point of a pink-footed goose (decrease 54.3%) was omitted from the plot for visualization purposes. Sample sizes: brent goose, 5 individuals; barnacle goose, 30; white-fronted goose, 27; pink-footed goose, 31; and Bewick's swan, 33.

the fuelling rate. The large variation in fuelling time within and between our study animals probably results in part from variation in fuelling rate, both on the non-breeding grounds and en route. Fuelling rates can vary greatly depending on food quality[44,45] and abundance[16,31] and higher fuelling rates can enable earlier departure in waterfowl[46] and other birds[31,47,48]. For example, agricultural pastures currently present an equally suitable or even better foraging habitat than traditional salt marshes for spring-staging barnacle and brent geese, leading to earlier departure among pasture-foraging birds[46,49,50]. Earlier springs due to a warming climate will probably contribute to earlier availability of high-quality forage along the flyway, at least for herbivores[51] and thereby facilitate earlier departure, faster fuelling and faster migration in the future[19]. Pink-footed geese have already shown a shift in recent decades from fuelling at the non-breeding grounds towards postponing their fuelling until the first major stopover in Norway[52], which is apparent in our results (Fig. 2f). This could provide further scope for adjusting migration to spring advance, given that conditions at the non-breeding grounds are advancing too. Future conditions might therefore enable birds to achieve even faster migrations than their current degree of variability, which we use here, suggests.

Moreover, birds may also adjust their en route fuelling time in response to the timing of spring, as seen in barnacle geese, white-fronted geese and Bewick's swans in this study. White-fronted geese and Bewick's swans make more stopovers than the other species and do not make large sea-crossings, which provides them with more and better opportunities to monitor the development of spring underway and may explain their higher responsiveness to spring onset on the breeding ground[39,53,54]. This could mean that pink-footed and brent geese, appearing insensitive to the development of spring while underway, can only keep track of advancing springs in the breeding range if springs are sufficiently advancing in the non-breeding range too.

Migrating faster will have a limit. Although our study populations (except brent geese) were able to effectively resolve differences in spring departure en route, such that early- and late-departed migrations had a similar arrival at the breeding grounds, we do not know the actual fuelling rates and the body condition in which birds arrived. It seems unlikely that birds are capable of fully compensating for shorter

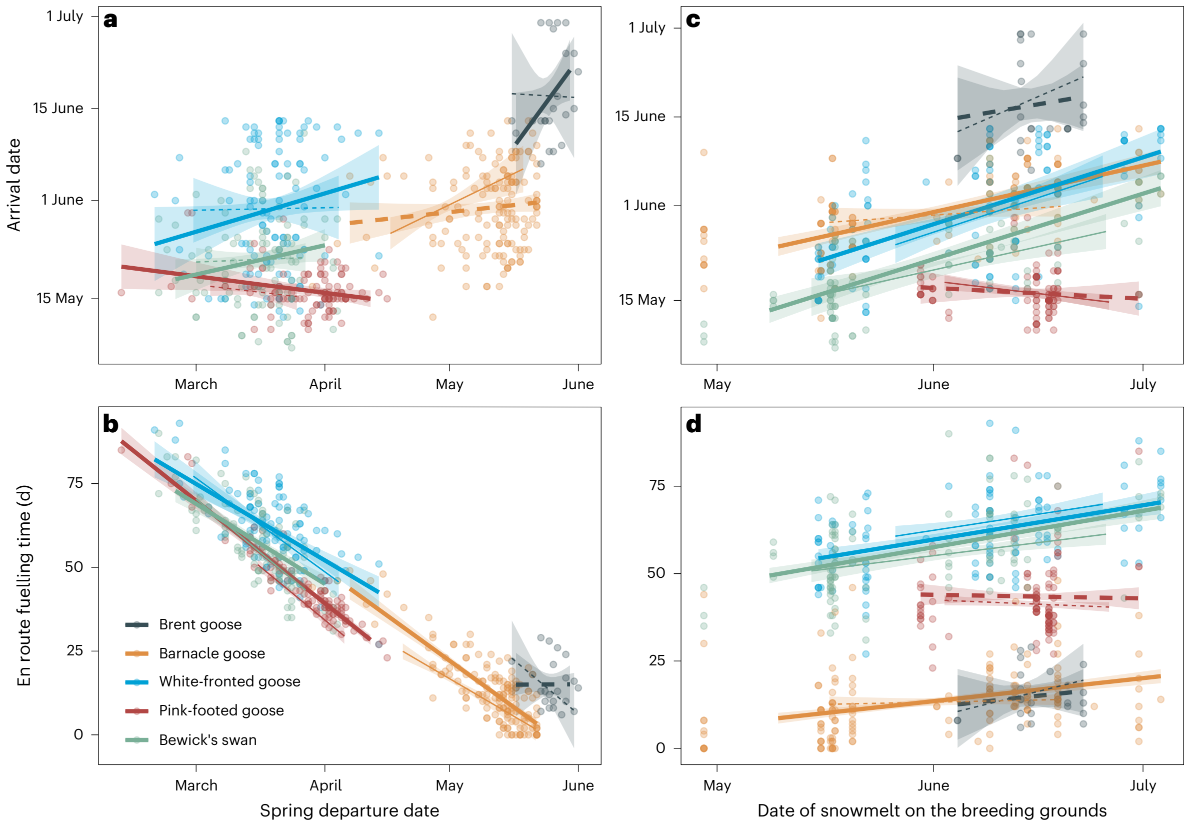

Fig. 4 | Relationships of arrival date and en route fuelling time with spring departure and date of snowmelt, for five Arctic-breeding waterfowl species. a–d, Lines show modelled effects (thick, between-individual effects; thin, within-individual effects; solid, significant; dashed, insignificant). See Extended Data Table 2 for details. Shaded bands indicate 95% confidence bands around the mean prediction. **a**,**b**, Arrival date (**a**) and en route fuelling time (**b**) in relation to spring departure. Across populations, later departure was compensated roughly one-on-one with less time spent fuelling en route. **c**,**d**, Arrival date (**c**) and en route fuelling time (**d**) in relation to the date of snowmelt on the breeding grounds.

fuelling times en route by fuelling faster[42]: for example, barnacle geese reduce their time spent on stopovers in years with early spring onset, but seem to arrive at the breeding grounds with fewer body stores[10]. Birds might thus be forced to shift their strategy away from capital migration and breeding, towards income[55]. Therefore, while we estimated the decreases in migration speed that birds seem able to achieve, negative effects might arise before they actually fulfil that potential.

To make the scope for migrating faster more tangible, we can divide the within-individual variation in total fuelling time of our study populations (Fig. 3b) by the current rates of snowmelt advance. Although the timing of snowmelt might not advance continuously as a result of an increase in precipitation in winter[56], possibly leading to more snow[57], this does provide a biological yardstick of how long our study populations might still be expected to mitigate earlier springs with faster migrations. Calculating a rate of snowmelt advance on the breeding grounds of 0.35 d yr^{-1} (average since 2000; Methods), we find that within-individual variation in total fuelling time allows to buffer some 18–28 years more of spring advance (barnacle geese, 18 years; pink-footed geese, 23; brent geese, 26; white-fronted geese, 28; Bewick's swans, 28). This suggests that some time in the second half of this century, advancing arrival will start requiring other mechanisms than migrating faster. These could be mechanisms at the individual level, such as advancing the whole migration through earlier onset of predeparture fuelling or shortening the migration route through winter range shift[21,22,58,59]; or mechanisms at the population level, such as selective disappearance of individuals with late migration schedules[60–62]. While some of these mechanisms are already at play, it remains to be seen whether they will be sufficient to help populations keep pace with advancing springs once the limits to migrating faster have been reached.

Looking ahead, the large variation in fuelling time within and between our study animals raises the questions how individuals migrate faster in some years than in others and how some individuals migrate faster than others in general. Birds might do so by simply fuelling less en route[10] or, alternatively, spending a larger part of their day fuelling[28] or selecting more favourable stopover sites[63,64] to complete faster migration without compromising body condition. For example, pink-footed geese can change migration strategies between years to improve their fuelling rate and reproductive output, suggesting that individual flexibility and learning can support rapid adjustment of migration[65]. To make further progress on these questions and move beyond the broad-scale metrics currently available, data are needed on fuelling rates at the individual level before departure and ideally also at stopovers. These would enable to test, at the individual level, the mechanisms underlying and the consequences of faster migration. Only by integrating behaviour, physiology and the environment across the full migration[66] can a deeper understanding be gained of the challenges that animals face in adjusting their schedules to a changing climate.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-025-02419-6.

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Methods

Animal ethics

All catching and tagging of geese and swans was carried out under the appropriate regulations and permits, listed in Supplementary Table 4.

Body mass data

We used body mass measurements from adult birds caught at the non-breeding grounds in Northwestern Europe to determine the onset of spring migration fuelling at the population level, for our five study populations. We collected the data from the international ringing database www.geese.org (ref. 67) and selected only measurements taken from 1 January onwards. Sample sizes ranged from 430 measurements for Bewick's swan to 7,211 for brent goose (Extended Data Table 1). The capture sites were distributed across the Netherlands, Germany, Denmark, the UK and France (Supplementary Fig. 3) and captures ranged from 1972 until 2024 with variation among the populations in how their data are distributed over the sites and years (Extended Data Table 1 and Supplementary Fig. 4). For brent geese, pink-footed geese and Bewick's swans (but not the other two species), this period extends substantially further back than the more recent period over which their tracking data were collected (see section on 'Tracking data'). We therefore experimented with using more recent subsets of the body mass data. Although a single capture can yield body mass measurements from many individuals, leading to large total sample sizes, many years had only a few or even no capture events. As a result, taking more recent subsets of the body mass data led to incomplete seasonal body mass series (Supplementary Fig. 1) and unreliable segmented regression output (see next section) and we were unable to statistically examine trends in the onset of fuelling over the decades. However, visually comparing the data from different decades did not suggest a general advance in the onset of fuelling over the decades, but rather that if there would be changes, these would be small relative to the size and spread of our calculated predeparture fuelling times (Supplementary Fig. 1). For example, many pink-footed geese departed on migration throughout the 30 days before the population mean onset of fuelling (Fig. 2f), but the body mass data do not suggest that the onset of fuelling has advanced, let alone in that order of magnitude (Supplementary Fig. 1d). This corresponds with our current understanding of the onset of fuelling being mostly constrained by daylength[28,29], which is not subject to change over the decades. Moreover, whereas departure from the non-breeding grounds has become earlier over the decades in pink-footed geese[52], the average body reserves before departure have declined (Supplementary Fig. 5 and Supplementary Table 3). This further suggests that, even though pink-footed geese and, to a lesser extent, Bewick's swans[22] advanced their spring departure, they have not simultaneously advanced the onset of fuelling, but rather postponed fuelling of their largest migratory stretch to the first or first few stopovers. We thus assumed that the onset of fuelling has not changed over the period of body mass data for brent geese, pink-footed geese and Bewick's swans, at least not to the extent that it would qualitatively impact our results. We compiled the body mass data per population across all sites and available years to construct seasonal body mass trajectories for each population. Data from pink-footed geese were overabundant from late-season catches in Denmark, but lacking in midwinter. We supplemented these with body mass data from pink-footed geese of the western flyway (breeding in Greenland or Iceland), caught in winter in the UK but with capture events spread more evenly throughout the non-breeding season. There is little exchange between the two flyways[68], but visual inspection of the data from both flyways indicated that their body mass trajectories are similar (Supplementary Fig. 6). We randomly thinned the overabundant late-season data to retain 20 measurements from each sex for each 10-day period after DOY 60, which was roughly the number of measurements per 10 days before that day (that is 20 male and female measurements between DOY 60 and 69, 20 between DOY 70 and 79, and so on). White-fronted goose data, on the other hand, were overabundant up until halfway through February and relatively scarce after, when the birds get closer to their onset of fuelling. Therefore, we randomly thinned the white-fronted goose data to retain 60 measurements from each sex for each 10-day period up until DOY 50 (roughly the number of measurements per 10 days after that day), to match the data quantities of the latest period.

Onset of fuelling

We performed segmented regression[36], also known as piecewise or broken-stick regression, to determine the point in time where body mass starts increasing ('breakpoint') and use that as the population-level onset of fuelling. Analyses were performed separately for each population using the R package segmented[36], with DOY and sex included as predictors. To assess the confidence interval around the estimated breakpoints we conducted 5,000-fold non-parametric bootstrapping. In each iteration we resampled body mass values with replacement within species (retaining the original sample size) and refitted the segmented regression model (Supplementary Fig. 7). For barnacle geese, white-fronted geese and Bewick's swans, the segmented regressions concentrated around two different breakpoints, only one of which was relevant for our analysis. For example, barnacle geese showed an initial breakpoint in body mass around mid-March (relevant for our analysis) and an alternative breakpoint towards the end of April due to accelerated body mass increase around that time. We excluded the breakpoint estimates belonging to alternative breakpoints for those three species, based on visual comparison with the body mass trajectories (Supplementary Fig. 7). We used the remaining breakpoint distributions to derive a mean onset of fuelling per population and a 95% CI by taking the 0.025 and 0.975 percentiles (Supplementary Table 1). Although body mass and trends therein are a good measure of fuel deposition[33], persistent body mass differences exist between individuals with different body sizes. As a way of correcting body mass for body size we also calculated the scaled mass index[69], scaling mass by wing length and repeated the breakpoint analyses. However, wing length measurements were often lacking, leading to lower sample sizes and a more patchy distribution of the scaled mass index data across the non-breeding season (Supplementary Fig. 8). For brent goose and pink-footed goose, two species for which we had good amounts and temporal spread of scaled mass index data, the segmented regression of scaled mass index yielded breakpoints very similar to those of body mass (Supplementary Table 1). Therefore we simply used body mass for all populations to infer the onset of fuelling.

Tracking data

We used previously collected GPS tracking data from the period 2011–2024 for adult brent geese[46], barnacle geese[70,71], white-fronted geese[72], pink-footed geese[73] and Bewick's swans[74,75]. We additionally included yet unpublished GPS tracking data from brent geese, collected from the year 2023 onwards. The tracking data were extracted from Movebank[76] using the R package move2 (ref. 77). For an overview of the data, see Extended Data Table 1; for an overview of the Movebank study IDs and relevant permits and funding for tagging, see Supplementary Table 4. The birds were captured at sites in the Netherlands and Germany, except for pink-footed geese (in Finland, Central Norway and Svalbard) and white-fronted geese (in Russia in 2013, 2016 and 2018). Details on the capture methods are included in the various papers. They were equipped with loggers or transmitters, attached with backpack harnesses (brent geese before 2024; white-fronted geese in 2014; barnacle geese throughout) or as neck collars (brent geese in 2024; white-fronted geese after 2014; pink-footed geese throughout, Bewick's swans throughout). The loggers stored data that were downloaded through a blue-tooth connection and the transmitters sent their data through GSM networks. The complete tracking dataset ranged from 2011 to 2024, with some variation among the populations in how their data are distributed over the years or decades (Extended Data Table 1).

Spring migration calculations

We downsampled the tracks to one position per day by taking the daily median longitude and latitude, marking days with zero GPS fixes as gaps. We then selected the complete spring migration tracks, taking those tracks that started in the non-breeding area (defined as the area southwest of 58° N, 12.85° E; Fig. 1a), lasted until 10 July and had up to a maximum of three single-day gaps (gaps of multiple days were not tolerated). Tracks that did not start in the non-breeding area were removed (barnacle geese, 2; white-fronted geese, 1; pink-footed geese, 1; Bewick's swans, 1). Although part of the brent geese population spends the first months of the non-breeding period considerably further southwest at the French coast, the months before spring departure (those relevant for our study) are spent in the Wadden Sea. For an overview of the final sample sizes, see Extended Data Table 1. We defined spring departure as the last day on which an individual was within the non-breeding area. We calculated the predeparture fuelling period for each individual spring track (Fig. 2f) by taking the interval between the onset of fuelling (at the population level; see section on 'Onset of fuelling') and spring departure (that is, assuming a unique predeparture fuelling period for each individual). Arrival was defined as the first day on which an individual was within 200 km from its summer centroid. We calculated the summer centroid as the median longitude and latitude in the second and third weeks of June, except for brent geese (which generally breed later[78]), where we used the first two weeks of July. We delineated stopovers en route from the tracking data by identifying the periods after departure where a bird showed little displacement between subsequent days, for at least 2 days in a row[53]. We used a threshold of 100 km (instead of 30 km (ref. 53)) to reduce the chance of stopovers being split into several smaller ones, or being missed altogether as a result of birds making short detours during their staging period. Moreover, actual migratory flights between stopovers in geese and swans are generally well above 100 km. This provided us with an estimate of en route fuelling time. Together, predeparture fuelling and en route fuelling make up the 'total fuelling time' (Fig. 2g and Table 1). Migration distance, required to derive migration speeds (Fig. 2h and Table 1), was calculated as the great-circle distance along the daily-interval migration path between departure and arrival.

Modelling variability in fuelling time

For each of the five populations separately, we modelled en route fuelling time and arrival date at the breeding grounds in separate linear mixed models, with (1) spring departure date and (2) date of snowmelt in the breeding area (as a proxy for the onset of spring) as predictors (Extended Data Table 2). We included individual bird as a random effect. The brent goose model of en route fuelling time failed to converge because of a relatively small sample size compared with the number of different individuals (the random effect); instead, we fit a linear model without random effect. Five breeding area polygons were distinguished for calculating the date of snowmelt, together encompassing all the sites where our tracked birds spent their summers: Svalbard, Pechora, Novaya Zemlya, Yamal and Taymyr (Supplementary Fig. 9). We calculated the date of snowmelt for each breeding area polygon based on the 500-m MODIS Terra Surface Reflectance Daily Global product (MOD09GA, v.6.1)[79]. We conducted the analysis using the R package RGEE[80] and followed the automated workflows for the quantification of snowmelt developed by ref. 81. We extracted all satellite images between 15 March and 15 September for each polygon and all years from 2000 to 2024. We used the 1,000-m MOD35 cloud mask product[82] to mask all pixels that were labelled as clouds and used the 250-m Terra Land Water Mask dataset (MOD44W, v.6.0)[83] to mask all pixels that were labelled as water bodies (that is, ponds, rivers, lakes or oceans). We then calculated the fraction of snow-covered pixels by counting the fraction of unmasked pixels with a normalized difference snow index value larger than 0.4 (refs. 84,85). To calculate the date of snowmelt within each polygon we fit a general additive model to the annual snow fraction time series and extracted the moment when this fit first dropped below 50% snow cover.

We separated the within- and between-individual effects of departure date and date of snowmelt using the method of within-subject centring[37], effectively creating two separate predictors for departure date (one describing within-individual variation and one describing between-individual variation) and two for snowmelt date (Extended Data Table 2). We fit the models and determined predictor significance using the R package glmmTMB[86].

Projecting variability onto current rates of snowmelt advance

On the basis of the within-individual variation in total fuelling time (Fig. 3b), we made an estimation per population of how many years of snowmelt advance can still be mediated by migrating faster. We thereby made the general assumption that the date of snowmelt will keep advancing at the same rate as that of the last decades, at least for the coming decades (see refs. 56,57). We did this by dividing the mean within-individual variation in total fuelling time (days) of our tracked study populations (Fig. 3b) by the average rate of snowmelt advance (days per year) on their respective breeding grounds since 2000 (Supplementary Fig. 10). We fit linear models of the date of snowmelt, using all combinations of the predictors year and breeding area and their interaction (Supplementary Table 5). Model selection through small-sample corrected Akaike information criterion (AICc) comparison[87] indicated that the date of snowmelt advanced with 0.35 ± 0.10 (mean ± s.d.) days per year ($P < 0.001$) and that the trend did not differ between the regions (the model including year and breeding area in interaction had an AICc value of 3.52 higher than the model including year and area without interaction; Supplementary Tables 5 and 6).

All data processing and analyses were conducted in R v.2.3 (ref. 88).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The snowmelt data are available via *figshare* at https://doi.org/10.21942/uva.28597007 (ref. 89). The GPS tracking and body mass data used in the analysis are not openly available, but extracted from www.movebank.org and www.geese.org with permission from the concerned data owners (Supplementary Table 4). The available code includes downloading the data from Movebank for all tracking studies, given that collaborator rights to the studies are acquired. Source data are available with this paper.

Code availability

Code used to perform the analysis, including downloading the data from Movebank for all tracking studies given that collaborator rights to the studies are acquired, is available via figshare at https://doi.org/10.21942/uva.28597007 (ref. 89).

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Author contributions

H.L., B.A.N., T.K.L., M.P.B., R.J.M.N., E.E.v.L. and J.Z.S.-B. conceptualized the study. All authors, except T.S.L.V., J.Z.S.-B. and E.E.v.L., collected tracking and/or body mass data for the analysis and T.S.L.V. processed and prepared the snowmelt data for the onset of spring. H.L. prepared the tracking data and performed the analyses, with B.A.N., T.K.L., M.P.B., E.E.v.L., R.J.M.N. and J.Z.S.-B. giving crucial input. H.L. led the writing and T.K.L., M.P.B., R.J.M.N., N.H.B., A.M.D., B.S.E., G.E., J.G., T.H., A.K., H.K., J.L., J.M., C.M., S.M., G.J.D.M.M., K.H.T.S., L.V., T.S.L.V., J.Z.S.-B., E.E.v.L. and B.A.N. provided critical feedback on the paper. All authors approved the final paper. H.L. is the corresponding author.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41558-025-02419-6.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41558-025-02419-6.

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Extended Data Table 1 | Overview of study species and properties of the body mass data and spring migration tracks

	# body mass measurements	Body mass years	# GPS-tracked individuals**	# GPS-tracked spring migrations**	GPS years**
Brent goose	7211	1972 – 2024	33	38	2012 – 2024
Barnacle goose	2285	1979 – 2024	88	153	2015 – 2024
White-fronted goose	640 (7054)*	1998 – 2024	70	110	2014 – 2023
Pink-footed goose	428 (3097)*	1987 – 2023	55	116	2019 – 2024
Bewick's swan	430	1985 – 2023	61	118	2011 – 2024

*Sample sizes of white-fronted and pink-footed geese body mass measurements are after thinning; sample sizes before thinning are indicated between brackets. For an overview of the Movebank study IDs and relevant permits and funding, see Supplementary Table 4. **Sample sizes of GPS-tracked individuals and spring migrations used in the eventual analysis, that is after selecting for completeness.

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Extended Data Table 2 | Linear mixed models of en route fuelling time and arrival date at the breeding grounds

			En route fuelling time			Arrival date		
	predictor	between/within ind.	est	SE	p	est	SE	p
Brent goose	intercept	-	-21.46	102.38	0.836	1.25	96.39	0.990
	departure	between	0.01	0.50	0.988	0.93	0.47	0.049
		within	-1.04	0.69	0.147	-0.04	0.65	0.951
	snowmelt	between	0.21	0.40	0.600	0.20	0.37	0.594
		within	0.50	0.52	0.357	0.51	0.49	0.298
Barnacle goose	intercept	-	97.37	7.90	<0.001	101.52	8.14	<0.001
	departure	between	-0.90	0.05	<0.001	0.07	0.05	0.137
		within	-0.73	0.09	<0.001	0.33	0.10	0.001
	snowmelt	between	0.22	0.03	<0.001	0.26	0.03	<0.001
		within	0.04	0.05	0.430	0.08	0.06	0.157
White-fronted goose	intercept	-	67.70	11.20	<0.001	75.80	12.52	<0.001
	departure	between	-0.74	0.09	<0.001	0.20	0.10	0.048
		within	-0.90	0.14	<0.001	0.01	0.14	0.928
	snowmelt	between	0.33	0.05	<0.001	0.38	0.06	<0.001
		within	0.31	0.10	0.001	0.39	0.10	<0.001
Pink-footed goose	intercept	-	134.92	17.70	<0.001	154.94	16.12	<0.001
	departure	between	-0.99	0.04	<0.001	-0.09	0.04	0.028
		within	-1.02	0.09	<0.001	-0.08	0.09	0.356
	snowmelt	between	-0.03	0.10	0.723	-0.06	0.09	0.494
		within	-0.08	0.05	0.094	-0.14	0.05	0.002
Bewick's swan	intercept	-	63.31	9.14	<0.001	75.31	8.79	<0.001
	departure	between	-0.77	0.08	<0.001	0.15	0.08	0.042
		within	-1.03	0.08	<0.001	0.03	0.08	0.724
	snowmelt	between	0.35	0.04	<0.001	0.37	0.04	<0.001
		within	0.25	0.07	<0.001	0.26	0.07	<0.001

All models included individual bird as random effect. Only the brent goose model of en route fuelling time failed to converge due to a relatively small sample size compared with the number of different individuals (the random effect); instead, we fit a linear model without random effect (see Methods section "Modelling variability in fuelling time"). For sample sizes, see Extended Data Table 1.

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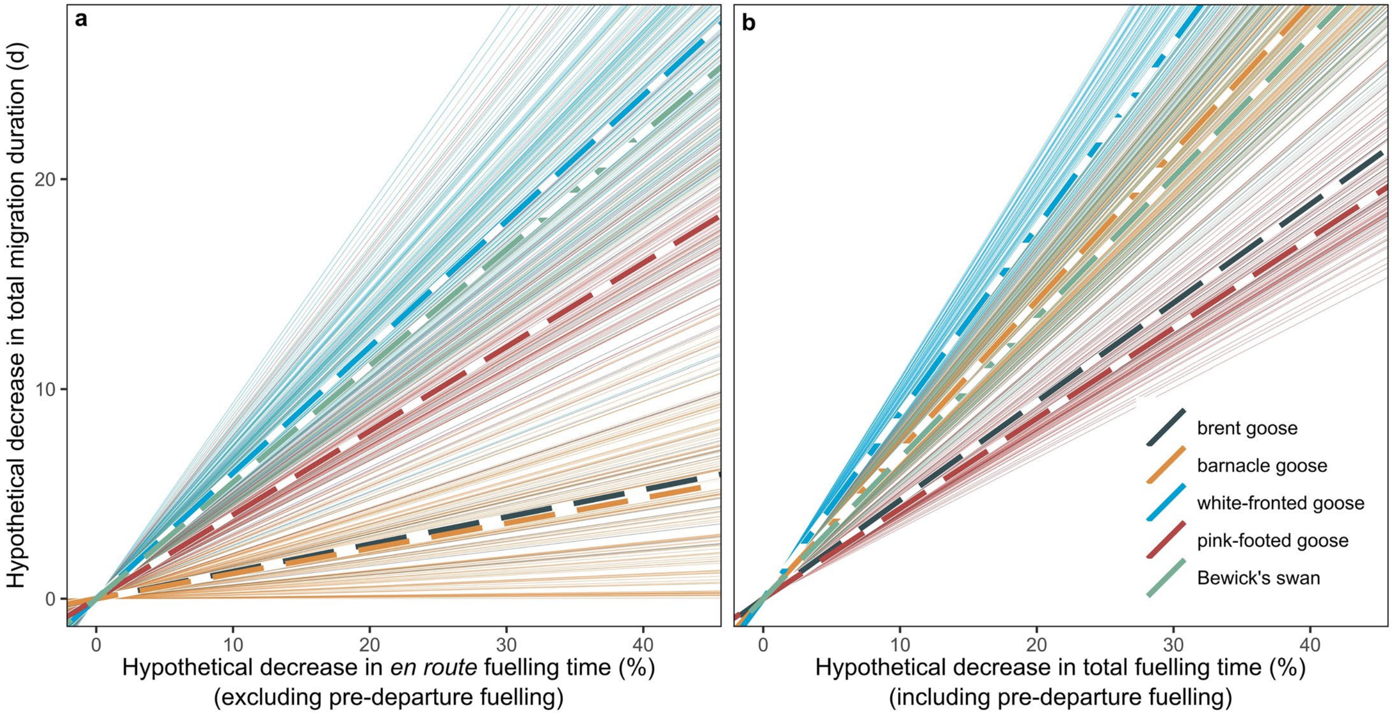

Extended Data Fig. 1 | Relationships between a hypothetical decrease in migration duration (days) and the required hypothetical decrease in total fuelling time (%). **a**, ignoring pre-departure fuelling; **b**, including pre-departure fuelling. Panel **b** is identical to Fig. 3a. Each thin line represents one tracked spring migration and its slope is derived from that spring migration and indicates how much that migration would have been shortened (in days) by a certain percentage decrease in fuelling time. Thick dashed lines indicate the median slope per population. When pre-departure fuelling was ignored, birds appear more limited in their scope to speed up spring migration, particularly barnacle and brent geese.

 https://doi.org/10.1038/s41558-025-02419-6

Extended Data Fig. 2 | Schematic overview of migrated distance (solid lines) and stored energy (dotted lines) over time in spring, according to two alternative (extreme) hypotheses. Both hypotheses assume that early- and late-departing individuals have the same fuelling rate and the same net energy expenditure across their migration, that is they generally arrive at the breeding grounds in the same condition. **a**, Individuals with different departure dates have the same onset of fuelling, and thus different pre-departure fuelling times. Later departure results in higher energy stores at departure and is compensated with less time spent on stopovers, resulting in the same total time spent fuelling and the same arrival. **b**, Individuals with different departure dates have the same pre-departure fuelling time and are flexible in the onset of fuelling. Energy stores at departure are the same and later departure is not compensated with faster travel between departure and arrival, still resulting in the same total time spent fuelling (through later arrival). Our results support hypothesis a, with departure date being largely compensated with subsequent en route fuelling time across the study species (except brent goose), resulting in similar arrival among early- and late-departing migrations and individuals (Fig. 4a, b; main text).

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For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☒	☐	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
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☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	We filtered, processed and analysed the body mass data and tracking data using the code that is available on Figshare (https://doi.org/10.21942/uva.28597007).
Data analysis	All analyses were conducted in R version 4.2.3. The code used to analyse the data is available on Figshare (https://doi.org/10.21942/uva.28597007).

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

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All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
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Code used to perform the analysis and the snowmelt data are available at Figshare (www.doi.org/10.21942/uva.28597007). The GPS tracking and body mass data used in the analysis are not openly available, but extracted from www.movebank.org and www.geese.org with permission from the concerned data owners (see Supplementary Table 3). The code includes downloading the data from Movebank for all tracking studies, given that collaborator rights to the studies are acquired.

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	NA
Reporting on race, ethnicity, or other socially relevant groupings	NA
Population characteristics	NA
Recruitment	NA
Ethics oversight	NA

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Non-experimental, statistical analysis of body mass data of wintering birds and GPS tracking data of spring-migrating birds. Body mass data were used to determine an onset of mass increase. Subsequently, individual GPS tracks were used to calculate time spent fuelling during the entire migration. Finally, we used statistical models to explain variation in the time spent fuelling with departure from the winter grounds, and the timing of spring in the breeding area.
Research sample	Previously collected data from five waterfowl species that winter in northwestern Europe and breed in various regions within the Eurasian Arctic: dark-bellied brent goose (Branta bernicla bernicla), barnacle goose (Branta leucopsis), greater white-fronted goose (Anser albifrons albifrons), pink-footed goose (Anser brachyrhynchus) and Bewick's swan (Cygnus columbianus bewickii). Sample sizes ranging between 33 (brent goose) and 88 (barnacle goose) individuals per species. We chose these species because of the large amount of available information on migration (tracking data) and migration fuelling (body mass data). Body mass data were derived from www.geese.org, tracking data from www.movebank.org (see Data availability statement). We used adult individuals of both sexes. Sample sizes are large, so they are meant to represent the flyway populations from which they are derived.
Sampling strategy	All data were previously collected, so we refer to previous studies for information about sampling strategies (see references in Methods section Tracking data).
Data collection	Body mass data were directly measured during catching by many different people involved in catches over the years. Tracking data were collected automatically through GSM networks, or in the case of older devices, by manually reading out loggers (for an overview, see Supplementary Table 3).
Timing and spatial scale	Body mass data ranged from 1972 until 2024 with variation among the populations in how their data are distributed over the years. Brent geese body mass data extend furthest back (1972), whereas data from the other species is concentrated in the 90s, or between 2000 and 2024 (Supplementary Figure 3). Tracking data ranged from 2011 – 2024, with some variation among the populations in how their data are distributed over the years or decades.
Data exclusions	Juvenile birds were excluded from the analysis, since they occur in much smaller quantities in both the body mass and tracking data, whereas their migration ecology (e.g. foraging, timing) may be different from adults.
Reproducibility	Our study is non-experimental; we made statistical models of time spent fuelling with covariates departure date and timing of spring. We used an AIC model selection procedure to determine predictor importance. The analysis can be reproduced with the scripts provided on Figshare (https://doi.org/10.21942/uva.28597007).
Randomization	Not relevant to our study (non-experimental; we made statistical models of time spent fuelling with covariates departure date and timing of spring).

Blinding	Not relevant to our study (non-experimental; we made statistical models of time spent fuelling with covariates departure date and timing of spring).

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☐	☒ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☒	☐ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

Laboratory animals	The study did not involve laboratory animals
Wild animals	We used previously collected tracking data from various studies (for references, see Methods section Tracking data). The birds were captured at sites in the Netherlands and Germany, except for pink-footed geese (in Finland, Central Norway and Svalbard) and white-fronted geese (in Russia in 2013, 2016 and 2018). Details on the capture methods are included in the various papers. They were equipped with loggers or transmitters, attached with backpack harnesses (brent geese prior to 2024, barnacle geese, white-fronted geese prior to 2015) or as neck collars (brent geese in 2024, white-fronted geese from 2015 onwards, pink-footed geese, Bewick's swans).
Reporting on sex	Both sexes were included in our study to increase sample sizes, so our findings apply to both sexes. In geese and swans, pairs always stay and migrate together. Therefore, tracks of males and females can be used in the same way for our purpose; they are similarly indicative of migratory timing and fuelling.
Field-collected samples	The study did not involve samples collected from the field
Ethics oversight	Our manuscript draws from many different animal tracking studies, each of which was approved by specific relevant institutions. An overview of these institutions is given in the Supplementary information of the manuscript (Supplementary Table 3).

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Plants

Seed stocks	NA
Novel plant genotypes	NA
Authentication	NA