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RESEARCH ARTICLE

Global temperature homogenization can obliterate temporal isolation in migratory animals with potential loss of population structure

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Abstract

Climate change is expected to increase the spatial autocorrelation of temperature, resulting in greater synchronization of climate variables worldwide. Possibly such 'homogenization of the world' leads to elevated risks of extinction and loss of biodiversity. In this study, we develop an empirical example on how increasing synchrony of global temperatures can affect population structure in migratory animals. We studied two subspecies of bar-tailed godwits *Limosa lapponica* breeding in tundra regions in Siberia: *yamalensis* in the west and *taymyrensis* further east and north. These subspecies share pre- and post-breeding stopover areas, thus being partially sympatric, but exhibiting temporal segregation. The latter is believed to facilitate reproductive isolation. Using satellite tracking data, we show that migration timing of both subspecies is correlated with the date of snowmelt in their respective breeding sites (later at the *taymyrensis* breeding range). Snow-cover satellite images demonstrate that the breeding ranges are on different climate trajectories and become more synchronized over time: between 1997 and 2020, the date of snowmelt advanced on average by 0.5 days/year in the *taymyrensis* breeding range, while it remained stable in the *yamalensis* breeding range. Previous findings showed how *taymyrensis* responded to earlier snowmelt by advancing arrival and clutch initiation. In the predicted absence of such advancements in *yamalensis*, we expect that the two populations will be synchronized by 2036–2040. Since bar-tailed godwits are social migrants, this raises the possibility of population exchange and prompts the question whether the two subspecies can maintain their geographic and morphological differences and population-specific

migratory routines. The proposed scenario may apply to a wide range of (social) migrants as temporal segregation is crucial for promoting and maintaining reproductive isolation in many (partially sympatric) migratory populations. Homogenization of previously isolated populations could be an important consequence of increasing synchronized environments and hence climate change.

KEYWORDS
climate change, *Limosa lapponica taymyrensis*, *Limosa lapponica yamalensis*, long-distance migration, snowmelt, temporal segregation

1 | INTRODUCTION

Climate change is expected to lead to an increase in the spatial autocorrelation of temperatures (Di Cecco & Gouhier, 2018; Wang & Dillon, 2014). Consequently, temperatures, as well as related environmental variables, are expected to become more similar to each other at local, regional and global scales, with potentially far-reaching ecological and evolutionary consequences. For instance, there is an increased risk of extinction in populations, since synchrony in dynamics raises the likelihood of simultaneous extinctions (Heino et al., 1997; Palmqvist & Lundberg, 1998). Likewise, a greater homogeneity in temperature may encourage species dispersal, thereby undermining coexistence and diversity (Amarasekare & Nisbet, 2001; Mouquet & Loreau, 2003).

Here we suggest another potential effect of the 'homogenization of the world': the loss of population structure in migratory animals. We reason that the phenological timing of these animals, moving between non-breeding and reproduction sites annually, will become more synchronous because (i) populations of migratory species match the timing of migration with the phenology of resources in the reproduction, stopover or wintering areas (e.g., Alerstam et al., 2003; Rakhimberdiev et al., 2018) and (ii) migratory animals tend to adjust the timing of migration and reproduction with changing resource phenology (e.g., Charmantier et al., 2008; Gill et al., 2014; Gordo, 2007; Lameris et al., 2021). Migratory species often contain multiple populations or subspecies with different populations having spatially overlapping (sympatric) wintering, stopover, or reproductive areas (e.g., Alves et al., 2010; Bearhop et al., 2005; Briedis et al., 2016). Temporal segregation has been identified as an important mechanism for promoting and maintaining reproductive isolation in sympatric populations (Bauer et al., 2016; Hendry & Day, 2005; Monteiro & Furness, 1998). For instance, in population with overlapping non-breeding sites, temporal segregration may prevent population exchange if the species is a social migrant (Kölzsch et al., 2019). Likewise, in populations with shared breeding grounds, temporal segregation may enhance assortative mating (Bearhop et al., 2005). Thus, with increasing synchrony of global temperatures the temporal segregation of migratory animals may be obliterated, which may have important consequences for migration routines and population dynamics.

We examine the potential (consequences of) temporal synchronization in the onset of spring in two subspecies of bar-tailed godwits *Limosa lapponica yamalensis* and *Limosa lapponica taymyrensis* (Bom et al., 2022). The two subspecies breed in adjacent tundra regions in Russia, respectively in Yamal (*yamalensis*) in the west and Taimyr further east and north (*taymyrensis*). They are indistinguishable in neutral genetic markers, but their morphologically distinctiveness suggests that there is little or no gene flow (i.e., exchange of individuals) between populations (Bom et al., 2022). The two subspecies have different wintering areas, in the Middle East and West Africa, respectively, but they have two shared stopover areas, being therefore partially sympatric (Bom et al., 2022). One, the 'spring overlap area' is at—and south of—the Yamal Peninsula (Figure 1). In this overlap area, *yamalensis* stops and breeds and *taymyrensis* frequently stops before continuing to its breeding sites. In the second overlap area, that is, the 'summer overlap area' north of the Yamal Peninsula, particularly at Belyy Island, individuals of both populations regularly stop after the breeding season. *Yamalensis* godwits arrive about 10 days earlier than *taymyrensis* godwits in the overlapping stopover areas and breeding sites. The

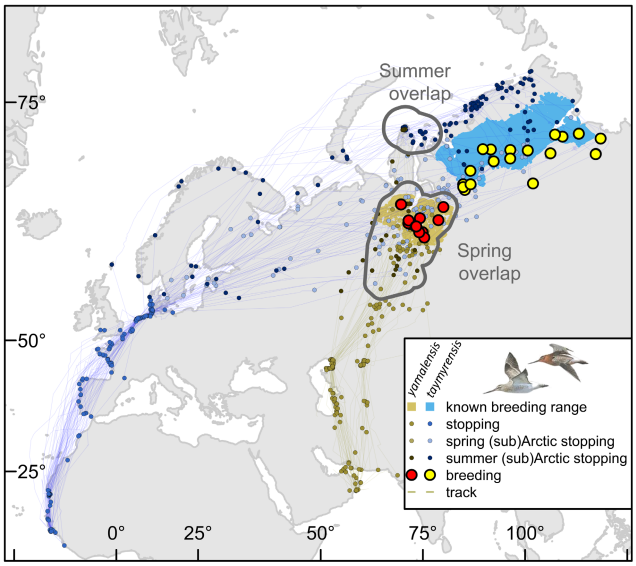

FIGURE 1 Tracks and stopping and breeding sites of *yamalensis* and *taymyrensis* bar-tailed godwit obtained from Argos PTT tracking devices between 2016 and 2020 as well as the spring and summer overlap areas and known breeding range of both subspecies. Map in Mercator projection. Breeding range is based on Lappo et al. (2012).

difference in timing is probably related to the date of snowmelt in each population breeding area (i.e., later at Taimyr than at Yamal) and is thought to facilitate reproductive isolation (Bom et al., 2022).

In the breeding range of *taymyrensis*, the date of snowmelt has shifted forward with 0.73 days per year from 1992 to 2016 (Rakhimberdiev et al., 2018). Over this same period, *taymyrensis* bar-tailed godwits advanced their arrival 0.28 days per year, whereas the laying date of the first egg advanced by 0.70 days per year (Rakhimberdiev et al., 2018). There are no indications that the date of snowmelt has changed in the *yamalensis* breeding range or that these godwits have changed their timing of migration. This could mean that the temporal segregation between *yamalensis* and *taymyrensis* is now less distinct than in past times and could eventually become synchronized in the (near) future.

In this study, we investigate whether the timing of snowmelt in breeding ranges of *yamalensis* and *taymyrensis* indeed became more synchronized between 1997 and 2020 and predict on how this may affect the timing of migration and the temporal segregation between the two populations. We use satellite tracking data to study the spatiotemporal movements of the two populations in relation to the date of snowmelt, which we obtained from NOAA satellite imageries. We first test how the two populations synchronize timing of migration with the local date of snowmelt in the breeding ranges. Next, we analyze how the local date of snowmelt at the breeding ranges changed over the last 24 years. We then assess if and how the timing of individuals of the two populations would change with respect to the use of the spring and summer overlap areas.

2 | METHODS

2.1 | Tracking data

Details on how we obtained and processed the tracking data are given in Bom et al. (2022) and summarized here. We deployed 54 solar-powered 4.5-g Argos Platform Terminal Transmitters (PTTs, Microwave Technology Inc., Columbia, MD, USA), 10 on *yamalensis* and 44 on *taymyrensis*. We captured and tagged *yamalensis* godwits at Barr Al Hikman in the Sultanate of Oman in 2015. *Taymyrensis* godwits were caught and tracked from the Wadden Sea in Netherlands (in 2016, $n = 10$), Banc d'Arguin in Mauritania (in 2015, 2017 and 2018; $n = 8$) and the Bijagós Archipelago in Guinea-Bissau (in 2018 and 2019; $n = 26$). We almost exclusively tagged female birds (92% of all birds), since female bar-tailed godwits are larger than males and presumably can better cope with the added device weight. Transmitters were deployed using a leg-loop harness made of 0.075-inch (1.9-mm) tubular Teflon tape, weighing approximately 1.5 g. For none of the birds, the tag plus harness weighed more than 3% of the birds' body mass. PTTs applied in 2015–2018 were programmed to operate on a duty cycle of 10 h 'on' for transmitting locations, followed by 25 h 'off' for charging of batteries; PTTs applied in 2019 were programmed to operate continuously when sufficiently charged. Locations were received from the Argos system and are referred to as Argos locations. The tagging work was carried out with permission of the local authorities in each country.

2.2 | Site identification

To classify breeding and (other) stopping sites, we followed the procedures developed by Chan et al. (2019) and applied earlier on the same data set by Bom et al. (2022). In this procedure, we (1) filtered Argos locations for implausible locations (i.e., Argos location classes 0, A, B and Z and a maximum rate of movement of 120 km/h); (2) classified retained Argos locations either as stationary or flight, the latter included all Argos locations where the maximum rate of movement was >20 km/h and all Argos locations that were >50 km away from the shoreline; (3) grouped stationary locations into discrete sites using a hierarchical clustering analysis. This was done by calculating, for each tracked individual separately, a distance matrix from which the optimal number of clusters was determined by maximizing distances between clusters (sites) and minimized distance between Argos locations; (4) classified each site either as a breeding or stopping site. Based on current knowledge on the natural history of the species (Piersma et al., 1996), we classified (sub)Arctic sites (latitude >56° N) as a breeding sites, if a bird remained there for more than 18 days between 23 May and 23 June. All other sites where classified as stopping sites. We further differentiated (sub)Arctic spring and summer stopping sites by classifying sites with a latitude greater than 56° N as (sub)Arctic. The distinction between spring and summer was based on whether site-arrival time was before or after 19 June respectively, which coincides with the first departure from the breeding sites. The duration of tracking differed between individuals and ranged between a few days to 5 years (Bom et al., 2022; Table 1).

All data processing was performed in the R computing environment (R Core Team, 2020). The distance matrix that was used to perform the cluster analysis was constructed with the

TABLE 1 Number of observations on arrival time for the different sites relevant for this study.

Site		*yamalensis*	*taymyrensis*
Breeding	*n* birds	7	12
	n total	23	13
Spring (sub)Arctic	*n* birds	9	20
	n total	26	24
Spring overlap	*n* birds	9	9
	n total	26	11
Summer (sub)Arctic	*n* birds	7	15
	n total	15	17
Summer overlap	*n* birds	2	7
	n total	4	8

Note: A differentiation is made between the number of birds and the total number of observations, as several birds could be tracked for more than 1 year.

R function *distm* in the *geosphere* package (Hijmans et al., 2017) and the cluster analysis performed with the *NbClust* R package (Charrad et al., 2014). We used the *Complete aggregation* method and the *silhouette index* to determine the optimal number of clusters (Charrad et al., 2014). The maximum rate of movement was calculated using a Great Circle distance, which we calculated using the *spDistsN1* function in the R package *sp* (Pebesma & Bivand, 2005).

2.3 | Site arrival time

In this study, we were interested in the arrival time at breeding and stopping areas. Because of their duty cycle, tags were repeatedly off for 25 h, the arrival time at a site could not be classified at a sufficient temporal detail solely based on Argos locations. We therefore estimated the arrival time for each site as follows: We identified the initial "stationary" point at a site. If the previous Argos location was classified as "flight", we estimated arrival time by extrapolating the average speed of a nonstop flight (57 km/h; Piersma & Jukema, 1990) over the intervening great circle route between Argos locations. If the previous Argos location was classified as "stationary" we first calculated the estimated flight time between the two Argos locations. We assumed that this flight occurred midway along the time interval between the two, so in these cases the arrival time was calculated as the midpoint between the two timestamps minus half of the flight time between the two Argos locations.

2.4 | Breeding-site arrival dates in relation to dates of snowmelt

In order to test if the local date of snowmelt could explain the arrival to the breeding sites, we obtained, for each breeding site identified from the tracking data, the local date of snowmelt for the tracking year. We used the NOAA Climate Data Record estimates of snow cover extend on a 24 × 24 km grid based on remote sensing data (U.S. National Ice Center, 2008). We then calculated the difference (in days) between date of breeding-site arrival and date of snowmelt. Negative values mean arrival before the local date of snowmelt. We tested if the two populations differed in their breeding-site arrival time relative to the Julian day and to the date of snowmelt. Since the data were not normally distributed, we used an exact two-sample Kolmogorov–Smirnov test. For individuals that were tracked for multiple years (Table 1) we used the mean Julian day and arrival day relative to the date of snowmelt for each individual. For visualization purposes, we plotted boxplots of the arrival dates and arrival dates relative to the snowmelt for either population and include and visualize data from birds tracked over multiple years.

2.5 | Change in dates of snowmelt in the breeding ranges

In order to test if the date of snowmelt has changed in the breeding ranges of either population, we calculated the change in date of snowmelt for each identified breeding site for the period 1997–2020. We again used the NOAA Climate Data Record estimates of extent of snow cover on a 24 × 24 km grid (U.S. National Ice Center, 2008). For each grid cell falling in the breeding range (mapped during the 20th and early 21st century by Lappo et al., 2012), the snowmelt date was estimated as the next day after continuous snow cover period. We fitted a linear model to the date snowmelt as the dependent variable and year as the explanatory continuous and breeding area as categorical variables.

We also tested if the change in date of snowmelt differed between the breeding sites as recorded by the satellite tags as these were partly outside the known breeding ranges (Bom et al., 2022). Differences were computed as in the previous analysis; for visualization purposes we plot the boxplots of the slopes (change in date of snowmelt) for either population and include data from birds tracked over multiple years.

2.6 | Temporal synchronicity at overlap areas

We measured the temporal synchronicity of both subspecies in the overlap areas by analyzing arrival time. The overlap areas were mapped on the basis of distance between the two subspecies. The tracking data indicated two distinct overlap areas (Bom et al., 2022; Figure 1) so we separately determined spring and summer overlap areas. The spring overlap area was determined by selecting those spring (sub)Arctic sites and breeding sites that were within 150 km of the same sites of the other subspecies. We subsequently computed a concave polygon around these sites and, for visualization purposes, buffered this polygon by 150 km. The summer overlap area was calculated in the same way for the summer (sub)Arctic sites (Figure 1). We used the tracking data to determine the arrival time in the overlap areas for the (tracking) years 2016–2020 by extracting, for each year, the first arrival time of each individual that entered an overlap area. Furthermore, to measure the importance of the overlap areas, we provide the number of individuals tracked into the overlap areas and compare them with the total number of individuals tracked into (sub)Arctic spring and breeding and summer stopping sites. The concave polygon was constructed using the *concave* function from the *concaveman* R package (Gombin et al., 2020). All other spatial calculations were computed with the *sf* R package (Pebesma, 2018).

For each observed arrival time in the overlap areas, we conducted hindcasting and forecasting for both past (1996–2000) and future (2036–2040) arrival time at these overlapping sites. This was based on the reasoning that (i) both populations of bar-tailed godwits have synchronized the timing of migration with the day of snowmelt

in their respective breeding areas (see Section 3) and (ii) *taymyrensis* godwits were observed to adjust their timing of migration and nest initiation in accordance with the changing onset of snowmelt in their breeding areas (Rakhimberdiev et al., 2018).

Because the rate of change in snowmelt differed in two breeding areas, the past and future arrival times at the overlapping sites were calculated differently between the two subspecies. For *yamalensis*, we found no change in the date of snowmelt in the breeding areas, so we simply assumed that arrival time in the overlap areas has not and will not change for this subspecies (see Section 3).

For *taymyrensis*, we found that the date of snowmelt in the breeding areas has changed by 0.5 days per year (see Section 3). During more or less the same period (i.e., 1992–2016), *taymyrensis* godwits were observed to advance arrival time to a breeding site by 0.28 days per year (Rakhimberdiev et al., 2018). We assumed that the arrival time at the spring stopover area has changed at the same rate of the observed breeding-site arrival time advancement of 0.28 days per year. Thus, for each observed arrival time to the spring overlap area, we subtracted and added $0.28 \times 20 = 5.6$ days to predict the arrival time 20 years prior and past the observed arrival time respectively.

For the *taymyrensis* arrival time to the summer overlap sites, we assumed that past and future arrival time changes at a same rate as clutch initiation date in the breeding areas has changed. This was observed to be 0.7 days per year (at a single breeding site). This rate, however, may not apply to the entire population as we measured snowmelt to change with 0.50 days per year across the entire breeding range in *taymyrensis* godwits (see Section 3). Therefore, we suggest that this later rate is more appropriate to use as a measure of advancement in arrival time in the summer overlap area. Thus, for each observed summer-overlap arrival time, we subtracted and added $0.50 \times 20 = 10$ days to predict the arrival time 20 years prior and past the observed arrival time respectively.

We used an exact two-sample Kolmogorov–Smirnov test to test if the two populations differed in their observed and predicted past and future arrival time to overlap areas (Julian day). For individuals that were tracked for multiple years (Table 1), we used the mean arrival date for each individual. To provide a general idea of the overlap between populations, we provide the median and interquartile range (IQR) for the observed and predicted past and future arrival times at the overlap areas. For visualization purposes, we plotted the boxplots of the (predicted) arrival dates at the overlap areas for either population and include data from birds tracked over multiple years.

3 | RESULTS

Tracking data revealed that the arrival time in the breeding areas relative to the day of year differed between *yamalensis* and *taymyrensis* godwits (Exact two-sample Kolmogorov–Smirnov test on Julian day, $D = 0.69$, $p < .001$, Figure 2a); the mean Julian day was 151 for *yamalensis* godwits and 157 for *taymyrensis*. However, the arrival time relative to the local date of snowmelt did not differ between the subspecies ($D = 0.31$, $p = .40$, Figure 2b). Both subspecies arrived a few days before the date of snowmelt, with the mean arrival day relative to the local date of snowmelt being 4.4 days (SD ± 9.45 days) for *yamalensis* and 1.8 days (SD ± 10.3 days) for *taymyrensis*.

The date of snowmelt in the breeding ranges of the two subspecies increasingly synchronized between 1997 and 2020. In all years, the date of snowmelt is generally earlier in the breeding

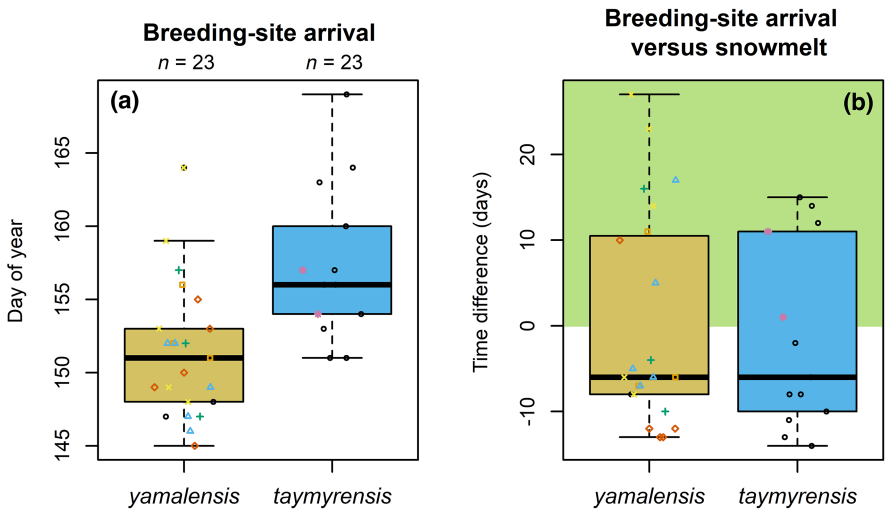

FIGURE 2 Boxplots with individual data points (jittered) showing the variation on the timing of arrival at breeding sites for *yamalensis* and *taymyrensis* godwits (a) in relation to the day of year (for reference, 1 June is day 152), and (b) in relation to the local date of snowmelt. Negative values mean arrival before the local date of snowmelt (white shaded area, defined as the next day after continuous snow cover period) and positive values after the local date snowmelt (green shaded area). Sample sizes are the same as in (a). Breeding sites were derived from tracking data and snowmelt data was obtained from NOAA satellite imagery at 24×24 km grid. Open black circles represent individuals with one breeding-site localization, while individuals with multiple breeding-site localizations are represented with different colors and symbols for each individual.

range of *yamalensis* than in the breeding range of *taymyrensis* (Figure 3a). However, the date of snowmelt strongly advanced in the breeding range of *taymyrensis* (slope = −0.48 days per year ± 0.01 SE; the intercept at year 1997 is 174, i.e., 23 June) whereas no such advancement was observed in the breeding range of *yamalensis* (slope is 0.02 days/year ± 0.03 SE; the intercept at year 1997 is 151, i.e., 31 May). In 2041, the slopes would cross on 31 May, meaning that at the current pace of change, the snowmelt phenology will be synchronized in that year. A similar pattern was observed at the breeding sites of the tracked bar-tailed godwits, with a slight delay at the *yamalensis* breeding sites (slope = 0.23 days per year ± 0.09 SE) and a strong advancement at the *taymyrensis* breeding sites (slope = −0.52 days per year ± 0.06 SE, Figure 3b).

The boundaries of the spring and summer overlap areas are shown in Figure 1. The spring overlap area was used by all *yamalensis* godwits that could be tracked into spring (sub)Arctic stopping sites, whereas 9 out of 20 *taymyrensis* godwits were tracked into this area (Table 1). The summer overlap area was used by two out of seven *yamalensis* godwits that could be tracked into summer (sub)Arctic stopping sites whereas seven out of 15 *taymyrensis* godwits were tracked into this area. The tracking data revealed how the arrival time at the overlap areas differed between the two subspecies for the period 2016–2020 (Figure 4). In the spring overlap area, *yamalensis* godwits arrived in general 4 days before *taymyrensis* godwits, with the median Julian day being 146 (26 May) (IQR ± 6) for *yamalensis* and 150 (30 May) (IQR ± 3 days). This difference was statistically significant ($D = 0.67$, $p = .03$). At the summer overlap area, the arrival times did not differ between *yamalensis* and *taymyrensis* ($D = 0.57$, $p = .56$; median Julian days of arrival of 176 [25 June] [IQR ± 4] for *yamalensis* and 190 [9 July] [IQR ± 25 days] for *taymyrensis*).

We hindcast that the arrival day in the spring overlap area was substantially more different between the two subspecies for the period 1996–2000 ($D = 0.89$, $p < .0001$) and forecast that this difference will disappear within 20 years by 2036–2040 ($D = 0.33$, $p = .70$). The arrival day in the summer overlap area differed significantly between the two subspecies for the period 1996–2000 ($D = 1$, $p = .03$) but not for 2036–2040 ($D = 0.43$, $p = .89$), but became more synchronized in time.

4 | DISCUSSION

We show that the date of snowmelt in two adjacent breeding ranges of two subspecies of bar-tailed godwits is converging and, under the current pace of climate change, will be fully synchronized by 2041. Based on (i) the finding that the subspecies have synchronized their migration phenology with the date of snowmelt and (ii) previous evidence showing *taymyrensis* bar-tailed godwits to have adjusted their migration to changes in date of snowmelt over the last 20 years (Rakhimberdiev et al., 2018), we expect that the timing of migration in the two subspecies will become synchronized as well. This means that in the near future the two subspecies will no longer be temporally segregated at the shared spring and summer areas. This, as we will argue now, could homogenize these previously isolated populations.

In sympatric migratory populations, temporal segregation may lead to reproductive isolation (Bearhop et al., 2005) and different pathways have been identified to promote this. If populations have shared breeding grounds, temporal segregation could limit population exchange simply because populations mate assortatively, as was shown in Blackcaps *Sylvia atricapilla* and Madeiran Storm Petrels *Oceanodroma castro* (Bearhop et al., 2005; Monteiro & Furness, 1998). In sympatric populations with shared stopover sites, just as in our study system, temporal synchronization may promote population exchange when animals from two (flyway) populations join. This was for example shown in a tracking study with

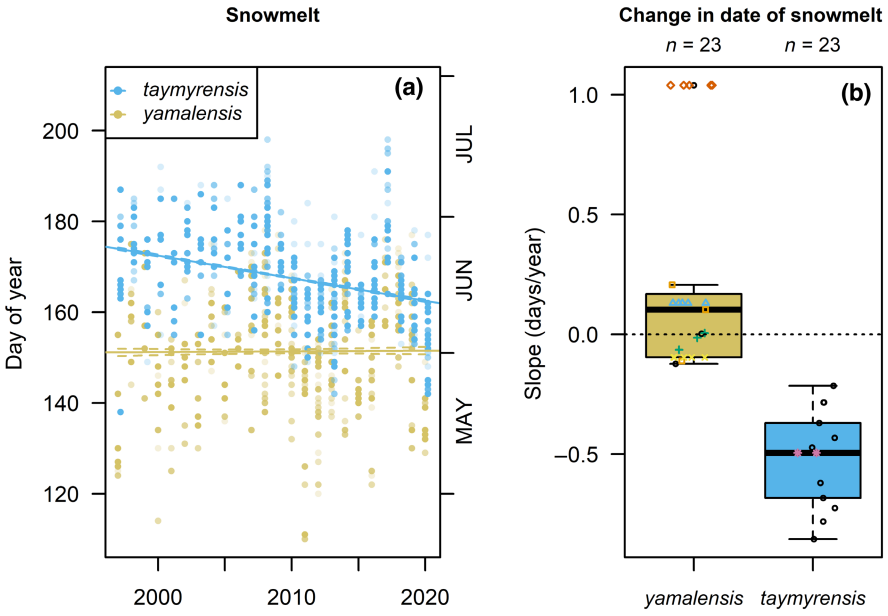

FIGURE 3 Variation in (a). Date of snowmelt across the breeding range of *yamalensis* and *taymyrensis* bar-tailed godwits between 1997 and 2020 (breeding ranges are based on Lappo et al., 2012) and date of snowmelt obtained from NOAA satellite imagery at 24 × 24 km grid) and (b) boxplots with individual data (jittered) points showing the rate of change in the date of snowmelt from 1997 to 2020 at the breeding sites (inferred from tracking data) of *yamalensis* and *taymyrensis* bar-tailed godwits. Open black circles represent individuals with one breeding-site localization, while individuals with multiple breeding-site localizations are represented with different colors and symbols for each individual.

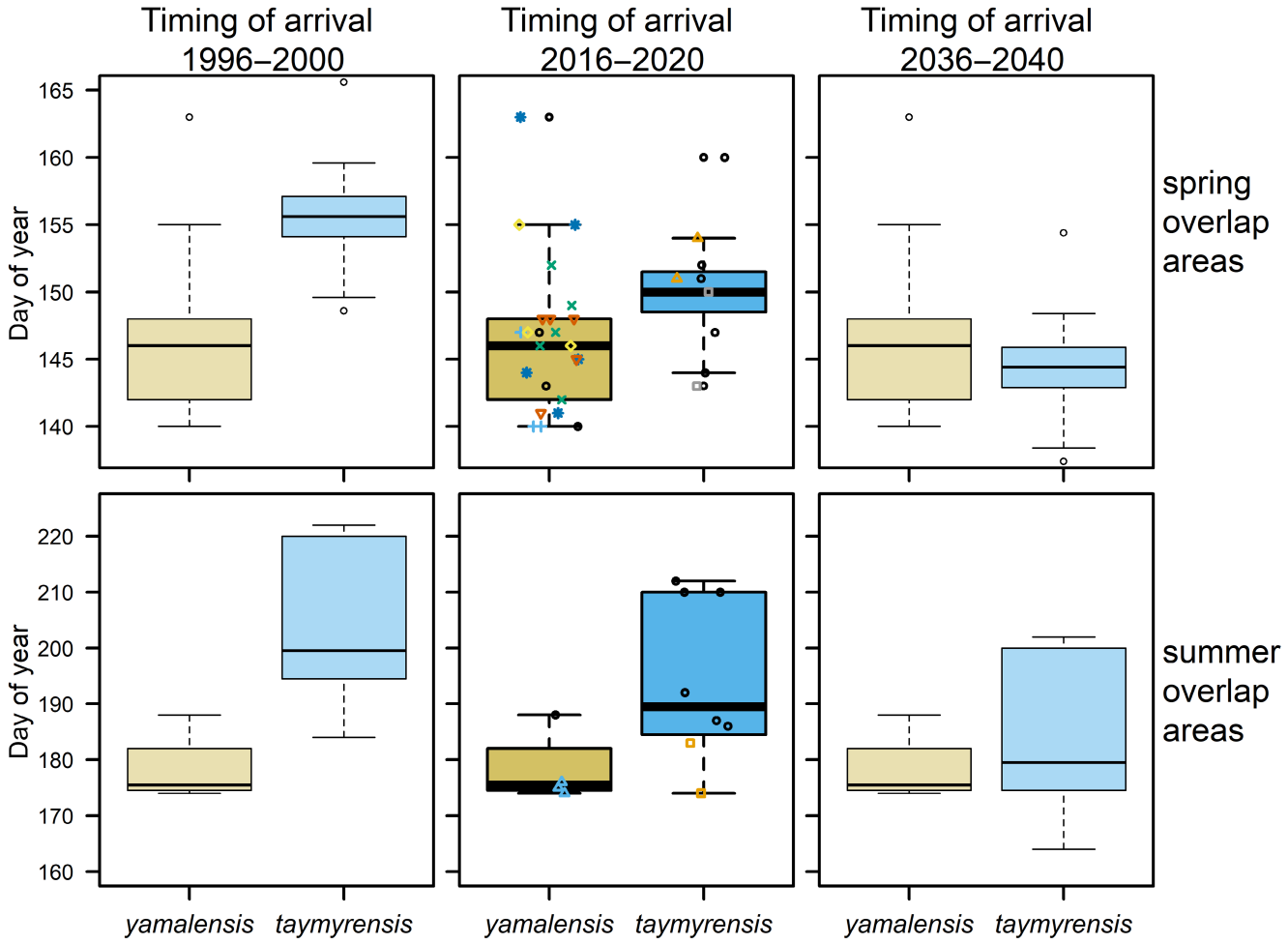

FIGURE 4 Boxplot showing the predicted and observed timing of arrival of *yamalensis* and *taymyrensis* at stopover areas across four and half decades: 1996–2005 (hindcast—left column); 2016–2020 (observations from tagged individuals—middle column); 2036–2040 (forecast—right column), in spring (top row) and summer (bottom row). Raw data (with jitter) are presented in the middle column. Open black circles represent individuals with one observation, while individuals tracked for multiple years are represented with different colors and symbols for each individual.

white-fronted geese, *Anser albifrons* (Kölzsch et al., 2019). Such exchange may only occur in social migrants in which social cues, such as the state of moult, reproductive state and fat reserves can be important sources of information to determine the routes taken (Flack et al., 2018; Gill et al., 2019; Helm et al., 2006). In birds, social migration has primarily been identified in several large non-passerine birds living in family units (Flack et al., 2018), but in fact may be widespread among other birds as well (Byholm et al., 2022; Méndez et al., 2021; Piersma et al., 2020). Certainly, bar-tailed godwits, although probably not flying in family flocks, are social migrants as they migrate in groups (Piersma et al., 1990), and socially learned migration has been experimentally demonstrated in the closely related black-tailed godwit *Limosa limosa* (Loonstra et al., 2023). We therefore expect that in our study system population exchange might be (increasingly) likely in the near future. In fact, recent population exchange may have already occurred in the studied populations of bar-tailed godwits, as we found that there is nowadays significant temporal overlap in the summer overlap sites, and that there was no genetic differentiation in mitochondrial DNA (Bom et al., 2022).

Young inexperienced birds may be especially important in initiating population exchange. For instance, Gill et al. (2019) showed that, within the population breeding in Iceland, young black-tailed godwits were the most likely to change migration destinations, while Verhoeven et al. (2018) suggested the same for shifts in staging areas during northward migration of Dutch breeding birds. Gill et al. (2019) then proposed a general mechanism by which conditions experienced at the natal stage, such as timing of hatching, influence the probability of individuals to undertake generational shifts in migration destination. In a translocation experiment, Loonstra et al. (2023) showed that naïve young Black-tailed Godwits displaced from the Netherlands to Poland adopted the spatiotemporal pattern of migration characteristic of the population at the release location rather than the birth place. We are unaware of the juvenile movements of the studied bar-tailed godwit, but if they follow the same migration routes as the adults, there is a fair chance that young birds from the two populations will increasingly meet at the summer overlap area.

Gill et al. (2019) presented a pathway by which climate change alters the distribution of individuals *within* a migratory population

of black-tailed godwits. They showed that many migratory populations consist of individuals that migrate to different wintering areas and those migrating longer distance typically have a more limited capacity to alter breeding phenology in response to climate change. If these differences are associated with fitness, the likelihood that individuals will migrate to a certain wintering area may quickly become dominant by several mechanisms, including generational shifts (Gill et al., 2014, 2019). We suggest a more dramatic *between-population* consequence of climate change, by which disappearance of temporal segregation can lead to population homogenization and thereby to the disappearance of subspecies.

Our findings of converging onset of spring (snowmelt phenology) are consistent with the prediction that global temperatures, and correlated environmental variables, will be increasingly synchronized in the future (Di Cecco & Gouhier, 2018; Liu et al., 2019; Wang & Dillon, 2014). Concurrently, the two populations of bar-tailed godwits studied are just one of the many seasonal migratory animal populations with shared non-breeding sites where temporal segregation may limit population exchange. Temporal segregation in sympatric populations with overlapping non-breeding sites has been described for migratory shorebirds (Lamarre et al., 2021), seabirds (Monteiro & Furness, 1998), passerines (Bearhop et al., 2005; Briedis et al., 2016), and is probably applicable to migratory animals of other taxa such as whales (Carvalho et al., 2014). Many of these populations have adjusted their phenology to temperature or correlated environmental variables in the breeding sites (Alves et al., 2019; Briedis et al., 2016; Lamarre et al., 2021). We thus expect that the sequence of effects of climate change described here may be relevant for a large number of species, and therefore may have important consequences for migratory populations, and consequently for global biodiversity.

AUTHOR CONTRIBUTIONS

Roeland A. Bom: Conceptualization; formal analysis; writing – original draft. **Theunis Piersma:** Conceptualization; funding acquisition; supervision; writing – original draft. **José A. Alves:** Conceptualization; funding acquisition; resources; writing – review and editing. **Eldar Rakhimberdiev:** Conceptualization; formal analysis; writing – original draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The tracking data is archived at Movebank under the study name "Bar-tailed Godwit – East Atlantic Flyway – PTT" (https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study265875917 and https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study118428098). The breeding range, overlap areas, breeding and other stopping sites and snowmelt data that supports the finding are available at https://dataportal.nioz.nl/doi/10.25850/nioz/7b.b.dg.

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REFERENCES

Alerstam, T., Hedenström, A., & Åkesson, S. (2003). Long-distance migration: Evolution and determinants. *Oikos*, *103*, 247–260.

Alves, J. A., Gunnarsson, T. G., Sutherland, W. J., Potts, P. M., & Gill, J. A. (2019). Linking warming effects on phenology, demography, and range expansion in a migratory bird population. *Ecology and Evolution*, *9*, 2365–2375.

Alves, J. A., Lourenço, P. M., Piersma, T., Sutherland, W. J., & Gill, J. A. (2010). Population overlap and habitat segregation in wintering black-tailed Godwits *Limosa limosa*. *Bird Study*, *57*, 381–391.

Amarasekare, P., & Nisbet, R. M. (2001). Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. *The American Naturalist*, *158*, 572–584.

Bauer, S., Lisovski, S., & Hahn, S. (2016). Timing is crucial for consequences of migratory connectivity. *Oikos*, *125*, 605–612.

Bearhop, S., Fiedler, W., Furness, R. W., Votier, S. C., Waldron, S., Newton, J., Bowen, G. J., Berthold, P., & Farnsworth, K. (2005). Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science*, *310*, 502–504.

Bom, R. A., Conklin, J. R., Verkuil, Y. I., Alves, J. A., De Fouw, J., Dekinga, A., Hassell, C. J., Klaassen, R. H. G., Kwarteng, A. Y., Rakhimberdiev, E., Rocha, A., ten Horn, J., Tibbitts, T. L., Tomkovich, P. S., Victor, R., & Piersma, T. (2022). Central-West Siberian-breeding bar-tailed Godwits *Limosa lapponica* segregate in two morphologically distinct flyway populations. *Ibis*, *164*, 468–485.

Briedis, M., Hahn, S., Gustafsson, L., Henshaw, I., Träff, J., Král, M., & Adamík, P. (2016). Breeding latitude leads to different temporal but not spatial organization of the annual cycle in a long-distance migrant. *Journal of Avian Biology*, *47*, 743–748.

Byholm, P., Beal, M., Isaksson, N., Lötberg, U., & Åkesson, S. (2022). Paternal transmission of migration knowledge in a long-distance bird migrant. *Nature Communications*, *13*, 1566.

Carvalho, I., Loo, J., Collins, T., Barendse, J., Pomilla, C., Leslie, M. S., Ngouessono, S., Best, P. B., & Rosenbaum, H. C. (2014). Does temporal and spatial segregation explain the complex population structure of humpback whales on the coast of West Africa? *Marine Biology*, *161*, 805–819.

Chan, Y., Tibbitts, T. L., Lok, T., Hassell, C. J., Peng, H., Ma, Z., Zhang, Z., & Piersma, T. (2019). Filling knowledge gaps in a threatened shorebird flyway through satellite tracking. *Journal of Applied Ecology*, *56*, 2305–2315.

Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. B., & Sheldon, B. C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, *320*, 800–803.

Charrad, M., Ghazzali, N., Boiteau, V., & Niknafs, A. (2014). Package 'nbclust'. *Journal of Statistical Software*, *61*, 1–36.

Di Cecco, G. J., & Gouhier, T. C. (2018). Increased spatial and temporal autocorrelation of temperature under climate change. *Scientific Reports*, *8*, 14850.

Flack, A., Nagy, M., Fiedler, W., Couzin, I. D., & Wikelski, M. (2018). From local collective behavior to global migratory patterns in white storks. *Science*, *360*, 911–914.

Gill, J. A., Alves, J. A., & Gunnarsson, T. G. (2019). Mechanisms driving phenological and range change in migratory species. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *374*, 20180047.

Gill, J. A., Alves, J. A., Sutherland, W. J., Appleton, G. F., Potts, P. M., & Gunnarsson, T. G. (2014). Why is timing of bird migration advancing when individuals are not? *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20132161.

Gombin, J., Vaidyanathan, R., & Agafonkin, V. (2020). *Concaveman: A very fast 2D concave hull algorithm*. R package version 1.1.0.

Gordo, O. (2007). Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research*, *35*, 37–58.

Heino, M., Kaitala, V., Ranta, E., & Lindström, J. (1997). Synchronous dynamics and rates of extinction in spatially structured populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *264*, 481–486.

Helm, B., Piersma, T., & van der Jeugd, H. (2006). Sociable schedules: Interplay between avian seasonal and social behaviour. *Animal Behaviour*, *72*, 245–262.

Hendry, A. P., & Day, T. (2005). Population structure attributable to reproductive time: Isolation by time and adaptation by time. *Molecular Ecology*, *14*, 901–916.

Hijmans, R. J., Williams, E., Vennes, C., & Hijmans, M. R. (2017). *Package 'geosphere'*. R package version 3.

Kölzsch, A., Müskens, G. J. D. M., Szinai, P., Moonen, S., Glazov, P., Kruckenberg, H., Wikelski, M., & Nolet, B. A. (2019). Flyway connectivity and exchange primarily driven by moult migration in geese. *Movement Ecology*, *7*, 1–11.

Lamarre, J.-F., Gauthier, G., Lanctot, R. B., Saalfeld, S. T., Love, O. P., Reed, E., Johnson, O. W., Liebezeit, J., McGuire, R., & Russell, M. (2021). Timing of breeding site availability across the North-American Arctic partly determines spring migration schedule in a long-distance Neotropical migrant. *Frontiers in Ecology and Evolution*, *9*, 710007.

Lameris, T. K., Hoekendijk, J., Aarts, G., Aarts, A., Allen, A. M., Bienfait, L., Bijleveld, A. I., Bongers, M. F., Brasseur, S., & Chan, Y.-C. (2021). Migratory vertebrates shift migration timing and distributions in a warming Arctic. *Animal Migration*, *8*, 110–131.

Lappo, E. G., Tomkovich, P. S., & Syroechkovskiy, E. (2012). *Atlas of breeding waders in the Russian Arctic*. UF Ofsetnaya Pechat.

Liu, D., Zhao, Q., Guo, S., Liu, P., Xiong, L., Yu, X., Zou, H., Zeng, Y., & Wang, Z. (2019). Variability of spatial patterns of autocorrelation and heterogeneity embedded in precipitation. *Hydrology Research*, *50*, 215–230.

Loonstra, A. H. J., Verhoeven, M. A., Both, C., & Piersma, T. (2023). Translocation of shorebird siblings shows intraspecific variation in migration routines to arise after fledging. *Current Biology*, *33*, 2535–2540.

Méndez, V., Gill, J. A., Þórisson, B., Vignisson, S. R., Gunnarsson, T. G., & Alves, J. A. (2021). Paternal effects in the initiation of migratory behaviour in birds. *Scientific Reports*, *11*, 2782.

Monteiro, L. R., & Furness, R. W. (1998). Speciation through temporal segregation of Madeiran storm petrel *Oceanodroma castro* populations in the Azores? *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *353*, 945–953.

Mouquet, N., & Loreau, M. (2003). Community patterns in source-sink metacommunities. *The American Naturalist*, *162*, 544–557.

Palmqvist, E., & Lundberg, P. (1998). Population extinctions in correlated environments. *Oikos*, *83*, 359–367.

Pebesma, E. (2018). Simple features for R: Standardized support for spatial vector data. *The R Journal*, *10*, 439–446.

Pebesma, E., & Bivand, R. S. (2005). S classes and methods for spatial data: The sp package. *R News*, *5*, 9–13.

Piersma, T., & Jukema, J. (1990). Budgeting the flight of a long-distance migrant: Changes in nutrient reserve levels of bar-tailed Godwits at successive spring staging sites. *Ardea*, *55*, 315–338.

Piersma, T., Loonstra, A. H. J., Verhoeven, M. A., & Oudman, T. (2020). Rethinking classic starling displacement experiments: Evidence for innate or for learned migratory directions? *Journal of Avian Biology*, *51*, 1–7.

Piersma, T., van Gils, J. A., & Wiersma, P. (1996). Family Scolopacidae (sandpipers, snipes and phalaropes). In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. de Juana (Eds.), *Birds of the world. Hoatzin to auks* (Vol. *3*, pp. 444–533). Lynx Edicions.

Piersma, T., Zwarts, L., & Bruggemann, J. H. (1990). Behavioural aspects of the departure of waders before long-distance flights: Flocking, vocalizations, flight paths and diurnal timing. *Ardea*, *78*, 157–184.

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rakhimberdiev, E., Duijns, S., Karagicheva, J., Camphuysen, C. J., Castricum, V. R. S., Dekinga, A., Dekker, R., Gavrilov, A., ten Horn, J., Jukema, J., Saveliev, A., Soloviev, M., Tibbitts, T. L., van Gils, J. A., & Piersma, T. (2018). Fuelling conditions at staging sites can mitigate Arctic warming effects in a migratory bird. *Nature Communications*, *9*, 4263.

U.S. National Ice Center. (2008).). *IMS daily northern hemisphere snow and ice analysis at 1 km, 4 km, and 24 km resolutions, version 1* [Data Set]. Boulder, Colorado, USA. National Snow and Ice Data Center. https://doi.org/10.7265/N52R3PMC

Verhoeven, M. A., Loonstra, A. H. J., Hooijmeijer, J. C. E. W., Masero, J. A., Piersma, T., & Senner, N. R. (2018). Generational shift in spring staging site use by a long-distance migratory bird. *Biology Letters*, *14*, 20170663.

Wang, G., & Dillon, M. E. (2014). Recent geographic convergence in diurnal and annual temperature cycling flattens global thermal profiles. *Nature Climate Change*, *4*, 988–992.

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