

# Evolution of leapfrog migration: A test of competition-based hypotheses

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## Abstract

Leapfrog migration is a common migration pattern in birds where the breeding and wintering latitudes between populations are in reversed latitudinal sequence. Competition for wintering and breeding sites has been suggested to be an ultimate factor, and several competitor-based hypotheses have been proposed to explain this pattern. If wintering sites close to the breeding sites are favored, competitive exclusion could force subdominant individuals to winter further away. Competitive exclusion could be mediated either through body size or by prior occupancy. The alternative “spring predictability” hypothesis assumes competition for sufficiently close wintering areas, allowing the birds to use autocorrelated weather cues to optimally time spring migration departure. To test predictions and assumptions of these hypotheses, we combined morphometrics, migration, and weather data from four populations of common ringed plover breeding along a latitudinal (56–68° N) and climatic gradient (temperate to Arctic). Critical for our evaluation was that two populations were breeding on the same latitude in subarctic Sweden with the same distance to the closest potential wintering site, but differed in breeding phenology, and wintered in West Africa and Europe, respectively. Thus, while breeding on the same latitude, their winter distribution overlapped with that of an Arctic and temperate population. Body size was largest within the temperate population, but there was no size difference between the two subarctic populations. Populations wintering in Europe arrived there before populations wintering in Africa. The largest variation in the arrival of meteorological spring occurred at the temperate breeding site, while there was almost no difference among the other sites. In general, temperatures at the northernmost wintering area correlated well with each breeding site prior to breeding site-specific spring arrival. Based on these observations, we conclude that competitive exclusion through body-size-related dominance cannot explain leapfrog migration. Furthermore, the assumptions on which the “spring predictability” hypothesis is based did not match the observed wintering ranges either. However, we could not reject the hypothesis that competitive exclusion mediated by prior occupancy in the wintering area could lead to

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leapfrog migration, and therefore, this hypothesis should be retained as working hypothesis for further work.

#### KEYWORDS

body size, common ringed plover, leapfrog migration, migration timing, prior occupancy, spring predictability

## INTRODUCTION

Migration distance and redistribution patterns often differ between populations in migratory bird species (Newton, 2008). While the fitness benefits of migration are relatively well understood (Gauthreaux, 1982; Lack, 1968; von Haartman, 1968), drivers of variation in migration distance and the relative locations of breeding and nonbreeding areas are less so. Disentangling putative ecological factors that determine the evolution of seasonal distribution patterns in migrants will contribute to our understanding of the evolution of migration in general (Alerstam & Hedenström, 1998) and may help predict potential range shifts in response to future environmental change. One particular pattern that has received much attention is *leapfrog migration*, in which different populations' breeding and nonbreeding latitudes are in reverse sequence from each other (Palmén, 1874; Salomonsen, 1955); that is, populations breeding at the highest latitudes winter at the lowest latitudes.

Competition has been identified as one of the ultimate factors driving seasonal geographic segregation (i.e., nonoverlapping distribution ranges) of birds in general (Cox, 1968; Gauthreaux, 1978; Ketterson & Nolan, 1983; Salomonsen, 1955) and constitutes the basis for several hypotheses aiming to explain the evolution of *leapfrog migration*. The “competition,” or “dominance,” hypothesis generally assumes that individuals attempt to minimize migration distance due to the cost of migration (Pienkowski et al., 1985; Pienkowski & Evans, 1985), and given that any nonbreeding area can only sustain a certain number of individuals, subordinate individuals are forced to disperse farther away. The individual ability to defend or control resources is assumed to be asymmetric (Smith & Parker, 1976), and hence, subordinate individuals are forced to move (Sutherland & Parker, 1985). In the “dominance” hypothesis, two proximate mechanisms, body size and prior occupancy, have been suggested to mediate the ability to outcompete conspecifics (Ketterson & Nolan, 1983; Pienkowski & Evans, 1985; Piper, 1997). In theory, both mechanisms can lead to the evolution of leapfrog migration (Holmgren & Lundberg, 1993; Lundberg & Alerstam, 1986). The alternative “spring predictability” hypothesis involves both competition in the

nonbreeding areas and competition for breeding recurses as drivers to select wintering area (Alerstam & Högstedt, 1980). However, this hypothesis relies on the ability of birds to use spatially autocorrelated weather cues between the breeding and wintering ranges to make informative decisions on when to depart from the wintering area in spring. These cues can be seen as a proximate mechanism to match an optimal arrival time to the breeding area with respect to the availability of food resources and habitat (Alerstam & Högstedt, 1980). Alerstam and Högstedt (1980) assumed that the onset of spring varies more in temperate areas than at higher latitudes and that the ability to use autocorrelated weather cues is reduced with distance from the breeding area. Thus, temperate breeding populations should stay close to their breeding area (preferably in the same climatic zone) provided that suitable nonbreeding habitat is available, to be able to use local weather cues to optimally time spring migration. However, populations migrating out from the climate zone in which they breed, do not share this benefit, and should therefore continue to more southerly wintering areas, which may provide higher survival probabilities and avoid competition with temperate breeding/wintering populations (Alerstam & Högstedt, 1980). Instead of local weather cues, individuals of populations wintering at low latitudes should rely on their internal clock to time departure on spring migration (Alerstam & Högstedt, 1980).

The assumptions and predictions on which the competition-related hypotheses are based have been evaluated and discussed on several occasions (Alerstam & Högstedt, 1985; Bell, 2005; Hockey et al., 1992; Pienkowski et al., 1985; Pienkowski & Evans, 1985), and the predictions are seldom mutually exclusive, as have also been found when applied on differential migration patterns between sex and age groups (Cristol et al., 1999; Ketterson & Nolan, 1983). Ideally, an experimental approach would be needed to critically evaluate these hypotheses, but such an approach is difficult to implement on the large geographical scales that apply to migrating birds. An alternative is to find a system where a comparative approach can be taken with characteristics that makes it a natural experiment (Diamond, 1986; Piersma, 2007). Here, we use this approach to evaluate

long-standing, competition-based hypotheses aiming to explain leapfrog migration using the common ringed plover (*Charadrius hiaticula*). The common ringed plover (henceforth ringed plover) has a wide latitudinal breeding range (Davidson & Scott, 2009) and constitutes a textbook example of a leapfrog migrant (Berthold, 2001; Newton, 2008). In Europe, Arctic breeding populations migrate to Africa, primarily wintering south of the Sahara, whereas temperate breeding populations mainly winter in Western Europe and as far south as northern Morocco (Figure 1A) (Hedh et al., 2022; Hedh & Hedenström, 2020; Lislevand et al., 2016; Taylor, 1980; Thorisson et al., 2012), although some temperate populations are more or less sedentary on the British Isles (Salomonsen, 1955; Taylor, 1980).

Specifically, we make use of annual spatiotemporal data obtained from light-level geolocators and morphometrics from four populations of ringed plovers breeding in Sweden. Crucial for our evaluation of the hypotheses is that the breeding populations cover a large latitudinal gradient, and two of them breed on the same latitude in the subarctic (~65° N, Figure 1A). These two populations have similar distances to the closest potential wintering areas (Davidson & Scott, 2009), but there is a slight shift in the onset of the breeding season so that the coastal population starts ~10 days earlier than the alpine population (Väisänen, 1977). Thus, this difference in initiation of breeding could facilitate earlier departure date and arrival at potential wintering sites. This arrangement provides an opportunity to disentangle otherwise non-mutually exclusive predictions and underlying assumptions of the hypotheses outlined above. The two remaining populations are located in southern temperate (~56° N) and northern Arctic (~68° N) Sweden, respectively, which represent a typical leapfrog pattern (Figure 1A) (Hedh et al., 2022).

To evaluate the competition-based hypotheses, we derived the following predictions. Based on the “dominance” hypothesis, we predict that populations wintering in Europe have a larger body size and/or gain competitive advantage at wintering sites by prior occupancy (Figure 1C). Thus, we predict that populations wintering in Europe depart earlier from the breeding area than populations wintering in sub-Saharan Africa, they arrive earlier in stopover sites in northern Europe (outside the Scandinavian peninsula), and they arrive in their wintering areas before, or at the same time as populations wintering farther south reach their European stopover sites. Furthermore, we evaluate whether individuals from populations wintering in Africa and Europe, respectively, potentially meet on European wintering sites and thus may be exposed to competitive interactions. For the “spring predictability” hypothesis, we evaluate the

assumption that breeding sites of populations wintering in Europe are subject to more variable interannual onset of spring and that the temperature prior to spring migration shows a stronger correlation between those breeding sites and the European wintering range, compared with the breeding sites of populations wintering in Africa (Figure 1C).

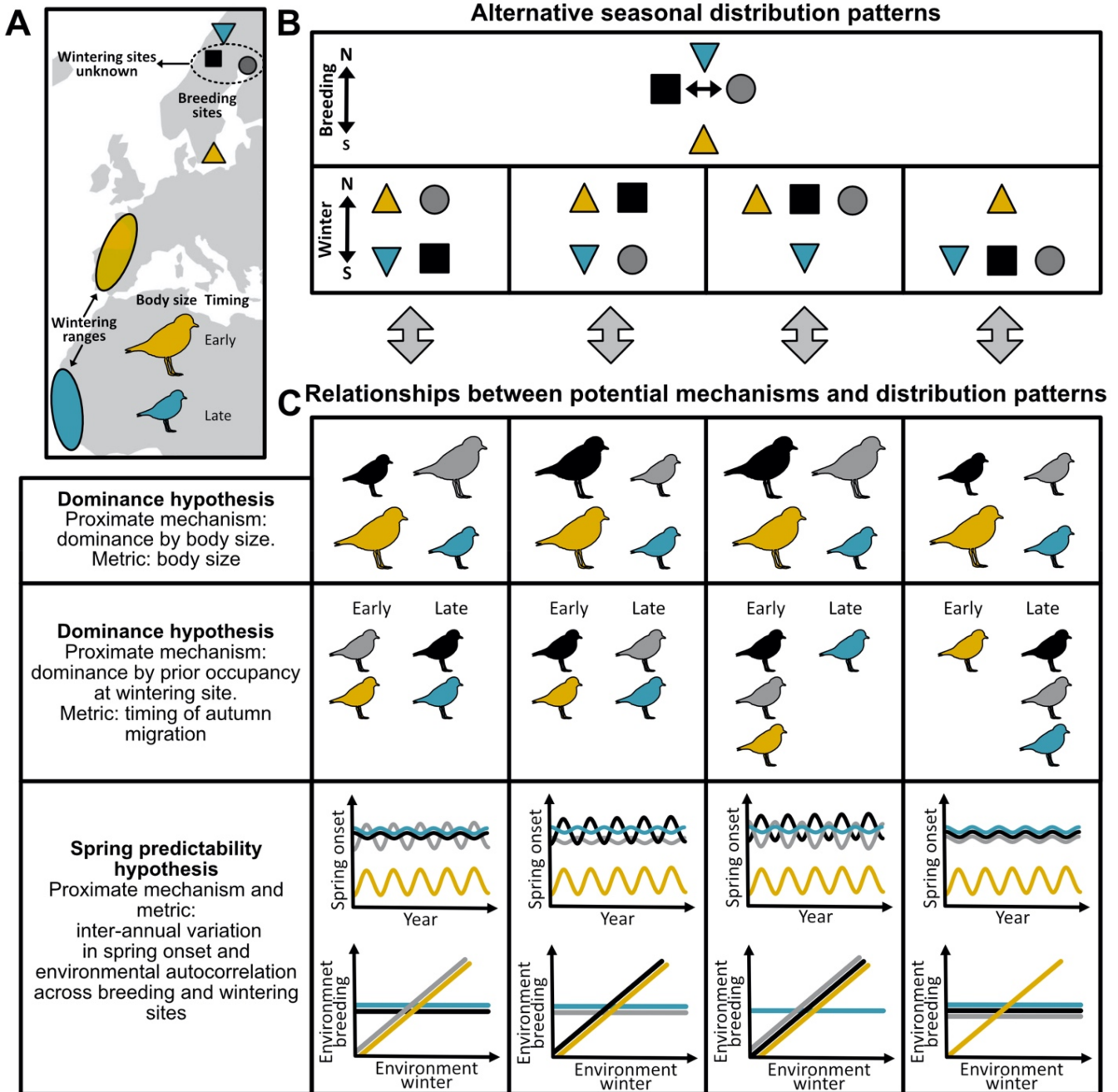
## METHODS

### Study system and field procedures

Between 2013 and 2021, ringed plovers were caught during the breeding seasons at four sites in Sweden. The sites were spanning a latitudinal range of 12° to include temperate (Ottenby), subarctic (Ammarnäs and Malören), and Arctic (Abisko) climate zones (Table 1). Birds were caught on the nest using a walk-in trap or a spring trap (Bub, 1991). Upon trapping, each individual was banded with a numbered metal band and a unique combination of color bands for identification in the field. The wing was measured to the nearest 0.5 mm using the maximum chord method (Svensson, 1992), and tarsus and total head length to the nearest 0.1 mm using a caliper (Green, 1980). Individuals were equipped with light-level geolocators of model MK10s (in 2013 without “stalk”) from Migrate Technology Ltd. The geolocators were attached with a leg-loop harness made of braided nylon string. The total mass of the device (1.6 g) constituted on average 1.4% of the birds’ mass at capture. In total, 149 geolocators were deployed at four locations and 54 were retrieved (distributed on 44 individuals) during subsequent years (Table 1).

### Analysis of geocator data

Light data were initially corrected for clock drift and twilights were defined using the R-package *TwGeos* (Lisovski et al., 2015) using a threshold value of 5 lx. For positioning, we used a threshold-based method, and light data were translated into two daily positions using the R-package *GeoLight* (Lisovski & Hahn, 2012). For each geocator, we conducted a “Hill–Ekstrom” calibration to find the sun angle corresponding to the set threshold value (Ekstrom, 2004), which was subsequently used to calculate coordinates. This was done by modeling latitudes against alternative sun elevation angles with increments of 0.1°. We then selected the sun elevation angle that minimized the error in latitude around the autumn and spring equinoxes and generated stable latitudinal positions over the wintering period.



**FIGURE 1** Hypothetical winter distributions of common ringed plovers (*Charadrius hiaticula*) breeding at different latitudes and under different environmental conditions in Sweden. (A) Natural experimental setup: Two populations breeding on the same latitude (black and gray) with previously unknown winter distributions, and two populations breeding in the Arctic and temperate zone (blue and yellow), respectively. For the latter two, the wintering distribution, body size, and timing of migration are known (Hedh et al., 2022). (B) Possible winter distributions (breeding latitudes are known) of the two experimental populations in relation to the arctic and temperate breeding populations. (C) Predictions (columns) based on alternative mechanisms of competitive exclusion explaining leapfrog migration. The body-size-related dominance hypothesis predicts that populations wintering in Europe should be larger than those wintering in Africa. The prior occupancy dominance hypothesis predicts that populations wintering in Europe that arrive earlier at their preferred wintering sites have a competitive advantage. The “spring predictability” hypothesis assumes that the onset of spring is more variable in temperate breeding sites than that in the Arctic and that weather cues are autocorrelated between European wintering sites and the corresponding breeding sites allowing birds to use cues at their wintering sites to time departure on spring migration.



**TABLE 1** Overview of available tracks from four different populations of common ringed plover (*Charadrius hiaticula*) breeding in Sweden.

Population	Climatic zone	Coordinates	No. deployed loggers	No. retrieved loggers	Deployment		
					No. individuals	No. tracks	period
Abisko	Arctic	68.4° N, 18.5° E	27	11	8	12	2014–2016
Ammarnäs	Subarctic	66° N, 16.2° E	46	11	10	13	2019–2020
Malören	Subarctic	65.5° N, 23.6° E	23	7	5	7	2019–2020
Ottenby	Temperate	56.2° N, 16.4° E	53	25	21	34	2013–2016

## Defining migratory timing, stationary positions, and wintering range

Departure and arrival times, which define start and termination of migratory and stationary periods, were primarily identified by visually inspecting plots of latitudes and longitudes (Hedh & Hedenström, 2020; Machín et al., 2015). Due to close to 24-h daylight during the breeding period experienced by the three populations breeding at high latitudes, it was not always possible to determine departure from breeding sites. As a solution, we raised the light threshold to 550 lx and repeated the process of calibration and positioning for those individuals. Using this method made it possible to connect autumn departure with light-derived positions at the breeding sites. This correction did not work during spring migration for the Arctic and one subarctic population, which migrated in May/June (see *Results*), when 24-h daylight prevails. Instead, we added 0.5 days flight time to the time for the last derived position (usually found over southern Sweden or Norway).

Stationary periods during migration (i.e., stopovers) were only defined (and calculated, see below) for stops lasting  $\geq 3$  days. For individuals wintering in Africa (south of the Sahara), individual wintering periods were defined as any stationary period  $\geq 30$  days south of the Sahara, and for individuals wintering in Europe/Morocco, wintering periods were defined as any stationary period  $\geq 30$  days outside the breeding season (i.e., between departure and arrival at the breeding area). One exception was made for an individual wintering in France, making a 36-day stopover in the German and Danish Wadden Sea, which was not defined as a wintering period. The breeding period was defined as the time between arrival at and departure from the breeding area. Geographical positions of stationary periods were estimated by averaging the daily derived coordinates within the defined time periods. Individuals changed wintering site within the same season on 16 occasions, but as none of those switched between major wintering areas (i.e., between Europe/Morocco and sub-Saharan Africa or vice versa), we include all wintering sites when defining a complete wintering range. Total wintering ranges for each population were estimated and

presented by calculating the 75% kernel density of the estimated average wintering positions, using the R-package *adehabitatHR* (Calenge, 2006).

Ten geolocators from the temperate and one from the Arctic population contained data on two autumn migrations and one spring migration. Two geolocators failed due to unknown (technical) reasons, two stopped collecting data during mid-winter and one did so during spring migration. As a result, 60 relevant autumn migration tracks and wintering sites were available for analyses (Table 1).

## Onset of meteorological spring and spatial autocorrelation

To estimate the variation in onset of spring at each site, we used daily temperature data from weather stations at or close to each breeding area, covering the period 1970–2019. The weather stations used were located at Ottenby (56.1957° N, 16.4010° E; 56.1977° N, 16.4005° E), Storön (65.7306° N, 23.0924° E; 65.6972° N, 23.0959° E), Hemavan (65.821° N, 15.086° E; 65.808° N, 15.085° E), and Abisko (68.354° N, 18.817° E; 68.354° N, 18.816° E), which correspond to the breeding areas at Ottenby (temperate), Malören, Ammarnäs (subarctic), and Abisko (Arctic), respectively. In all cases, the weather stations have been updated and moved a short distance (see coordinates above). All data were downloaded from the Swedish Meteorological and Hydrological Institute (SMHI; [www.smhi.se](http://www.smhi.se)). We calculated the average onset of “meteorological spring” and the coefficient of variance for each site as a measure of interannual variation. “Meteorological spring” is defined by SMHI as the day, after February 15, when the average daily temperature exceeds 0°C for seven consecutive days.

To investigate how weather data correlate between each breeding site and the European wintering area, we downloaded National Centers for Environmental Prediction (NCEP)-reanalysis sea-level temperature data (spatial resolution of 1.875°) from the period 1970 to 2019, using the R-package *RNCEP* (Kemp et al., 2012). We then calculated the average daily temperature for

each point on the grid and extrapolated this to generate a raster covering 30°–75° N and 15° W–28° E. For each breeding site, we identified the corresponding grid cell and calculated the correlation coefficient between that one and every other grid cell during a breeding site-specific time window. The critical time window for each breeding site was defined as the month before each population's spring departure date. Hence, we assume that if any local cue (temperature in this case) can inform individuals about when to depart on spring migration, this should happen within a month from departure. For the temperate, one of the subarctic and the two remaining populations we choose February, March, and April, respectively, as time window (see *Results*). We then transformed the correlation matrix to a raster by using the function *rast()* in the R-package *terra*. Temperature was specifically used because it has been shown to be used as direct cue to drive spring migration phenology in other short-to-medium-distance migratory species (e.g., Burnside et al., 2021).

## STATISTICS

To compare the overall structural body size between the four populations, we performed a principal components analysis (PCA), including wing length, total head length, and tarsus length, for all individuals caught within each population. We then compared the first principal component (PC1) as a measure of overall body size (Rising & Somers, 1989), using an ANOVA. To evaluate differences in departure from the breeding ground and arrival in continental Europe or the British Isles (i.e., stopover sites outside the Scandinavian peninsula) between populations, we constructed two linear mixed models (LMMs) for each event using the R-package *lme4* (Bates et al., 2015). The models included date (departure or arrival) entered as day number (1 January = day 1) as response variable and individual as random factor. We used the R-package *emmeans* version 1.5.5-1 (Lenth, 2024) to produce estimated marginal means, 95% CIs, and pairwise post hoc tests to compare overall structural body size (PC1) and departure and arrival dates between populations within the framework of the ANOVA and LMMs, respectively. All statistical analyses were carried out using R version 4.0.3 ([www.r-project.org](http://www.r-project.org)).

## RESULTS

### Wintering distribution and autumn stopover sites

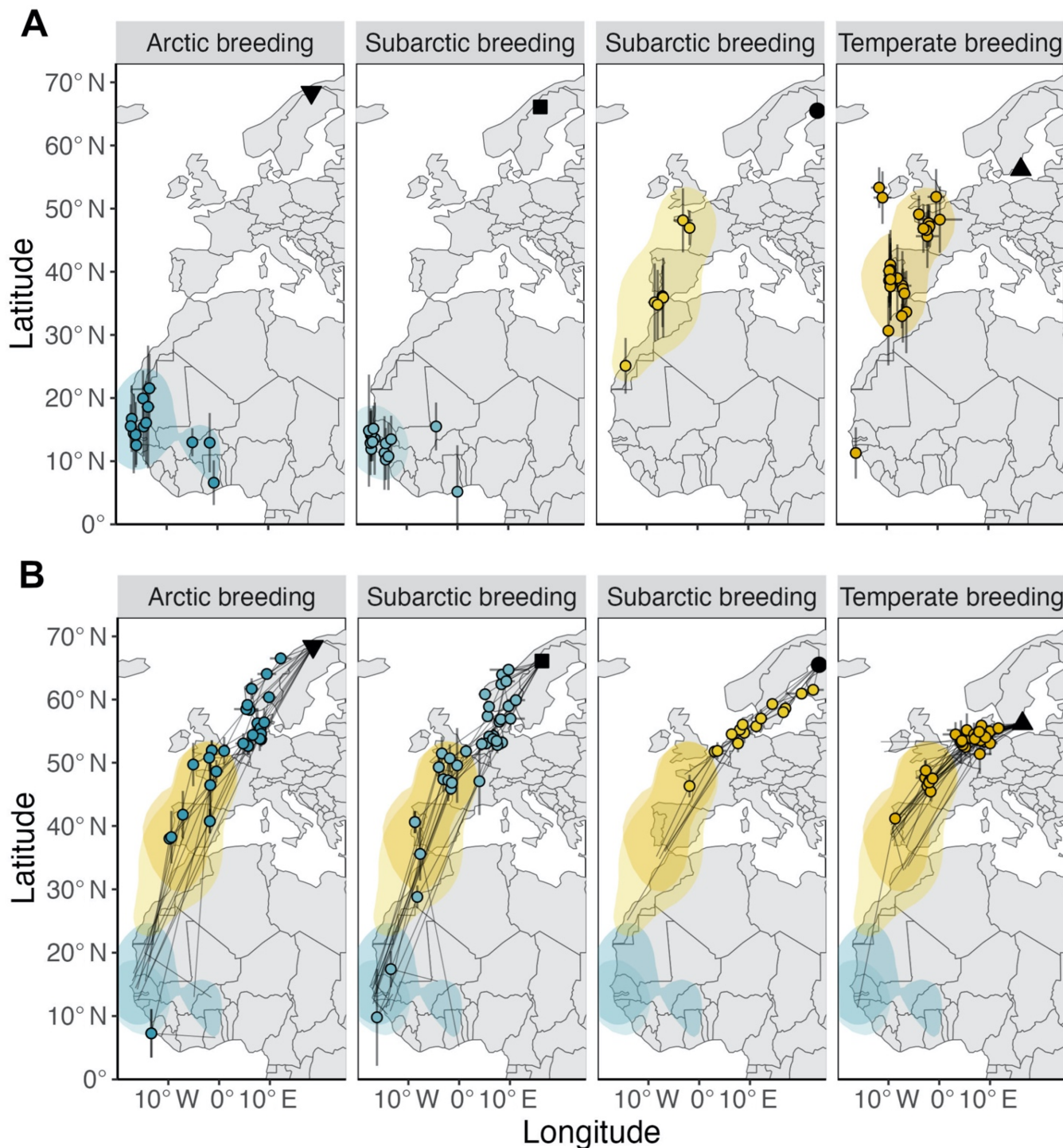
We found a clear latitudinal segregation in the wintering distributions between populations. Individuals from the

Arctic and one of the subarctic populations (Ammarnäs) wintered in West Africa, south of the Sahara, mainly in coastal areas in Senegambia, Guinea-Bissau, and Ghana, as well as at inland wetlands in Mali, Burkina Faso, Mauritania, and Ghana (Figure 2A). Individuals from the temperate and the coastal subarctic population (Malören) wintered mainly at coastal areas on the Iberian Peninsula, on the British Isles, in France, and in northern Morocco (Figure 2A). Inland wintering sites were also used on the Iberian Peninsula (Figure 2A). During autumn migration, all populations mainly utilized stopover sites on or near the European and African Atlantic coasts, from central Norway to northern Morocco (Figure 1B). Of all stopovers made in continental Europe outside the Wadden Sea and the Dutch Delta (which was a major stopover “hub” for all populations) by individuals wintering in Africa ( $n = 22$ ), only two stopovers (9%) fell outside the estimated 75% kernel density distributions representing the European wintering area (Figure 2B).

### Relative timing of migration

In autumn, the four populations differed in both departure date from the breeding sites (ANOVA:  $F_{3,45.405} = 15.829$ ,  $p < 0.001$ ; Figure 3A) and arrival at the first stopovers in continental Europe ( $F_{3,43.857} = 19.244$ ,  $p < 0.001$ ; Figure 3B). A pairwise comparison showed that individuals wintering in Europe departed from the breeding sites and arrived at the first stopovers in continental Europe approximately 2 weeks earlier than individuals wintering in Africa (Figure 3A,B, Table 2). There was also a significant difference in arrival times to wintering sites by the two populations wintering in Europe and arrival time to the first stopover in continental Europe (outside the Scandinavian peninsula) by the two populations wintering in Africa ( $F_{3,43.8} = 3.2978$ ,  $p = 0.029$ ; Figure 3C, Table 2). This difference was mainly driven by the temperate breeding population arriving to their wintering grounds earlier than individuals from the Arctic arriving to their first continental stopover sites (Figure 3C). In all other comparisons, there were no differences in arrival at either wintering site or the first continental stopover site ( $p > 0.1$ ; Table 2). Individuals wintering in Africa subsequently arrived in their wintering grounds approximately 1.5 months later than those wintering in Europe (Table 2).

In spring, there were differences in timing between the populations in both departure from wintering sites ( $F_{3,33.855} = 195.14$ ,  $p < 0.001$ ) and arrival at breeding sites ( $F_{3,35.199} = 302.46$ ,  $p < 0.001$ ). Individuals breeding at the temperate site departed from the wintering sites and arrived at the breeding site in early March (Table 2). Individuals from the subarctic population wintering in Europe departed

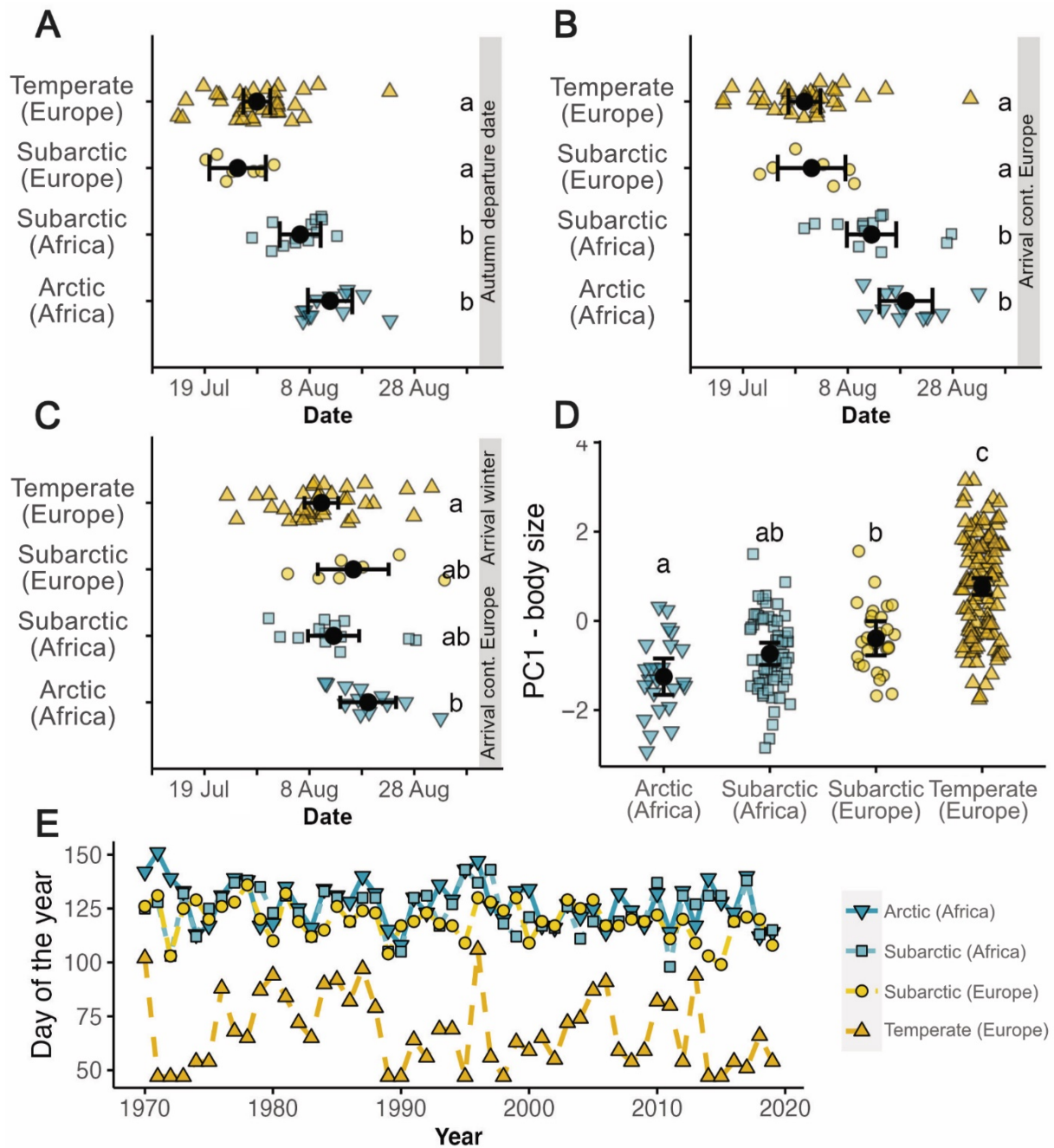


**FIGURE 2** Spatial distribution of four populations of common ringed plovers (*Charadrius hiaticula*) in different parts of the annual cycle. (A) Individual wintering positions and population-specific wintering ranges (here presented as the 75% kernel density of the individual positions). (B) Individual autumn stopover sites in relation to all wintering ranges. All positions are presented as means with SDs. Breeding locations are represented as black symbols in each panel. Note that all wintering locations are presented in panel A (including consecutive wintering locations within a single season and repeated wintering locations between years) and that all wintering ranges (kernel density surfaces) are overlaid in B. The latter is to illustrate the total wintering areas better in order to compare with individual stopover locations.

in early April, approximately 1 month later than the temperate breeding population ( $p < 0.001$ ; Table 2), and arrived in early May to the breeding site ( $p < 0.001$ ; Table 2).

Individuals wintering in Africa departed from the wintering sites in early May ( $p < 0.001$ ; Table 2) and arrived at breeding sites in early June ( $p < 0.001$ ; see Table 2).





**FIGURE 3** Autumn migration phenology, body size, and experienced onset of spring in four populations of common ringed plover (*Charadrius hiaticula*) here presented as breeding climate zone and wintering area (latter indicated within brackets). (A) Departure date from the breeding sites. (B) Arrival in continental Europe. (C) Arrival at wintering site versus in continental Europe for populations wintering in Europe and Africa, respectively. (D) Overall body size (PC1 of the composite value for wing length, total head length, and tarsus length). (E) Yearly variation of breeding site-specific onset of spring. Black symbol in (A–D) represents the model mean and error bar the 95% CI. In all figures, scatters represent individual measurement points (“Arctic (Africa)” [Abisko]: blue triangles, points down; “Subarctic (Africa)” [Ammarnäs]: blue squares; “Subarctic (Europe)” [Malören]: yellow points; and “Temperate (Europe)” [Ottenby]: yellow triangles).

## Body size

Structural body size, as estimated from the first principal component, differed significantly between the four populations ( $F_{3,225} = 47.06$ ,  $p < 0.001$ ; Figure 3D). A

pairwise Tukey’s post hoc tests revealed that there was no significant difference in body size between the populations breeding in the subarctic ( $p = 0.44$ ), or between the Arctic and the subarctic population wintering in Africa ( $p = 0.15$ ). However, individuals of the temperate



breeding population were on average larger compared to birds of all other populations ( $p < 0.001$ ), while the average body size of the subarctic population wintering in Europe was larger compared to that of the Arctic population ( $p = 0.014$ ) (Figure 3D).

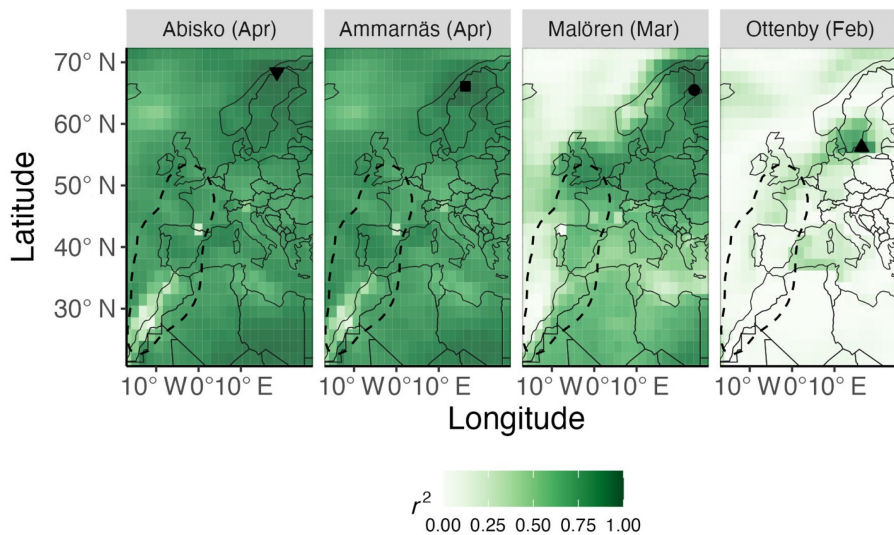
### Meteorological spring phenology and temperature correlation

Meteorological spring occurred approximately 2 months earlier at the temperate breeding site (March 9, March 5–12 95% CI) compared to all other sites (Arctic site: May 7, May 4–11, March 5–12 95% CI;  $p < 0.001$ ; sub-Arctic site, population wintering in Africa: May 4, April 29–May 7 95% CI;  $p < 0.001$ ; subarctic site, population

wintering in Europe: April 30, April 26–May 3 95% CI;  $p < 0.001$ ). There was no difference in when meteorological spring occurred between the populations breeding on the same subarctic latitude ( $p = 0.19$ ), or between the breeding sites for the populations wintering in Africa (subarctic and Arctic,  $p = 0.34$ ), but there was a significant difference between the breeding sites of the Arctic and subarctic/Europe population ( $p = 0.002$ ). The CV of the meteorological start of spring was 8.1%, 8.5%, 7%, and 25.5% at the Arctic, subarctic/Africa, subarctic/Europe, and the temperate site, respectively (Figure 3E). The average temperatures at each breeding site were in general positively correlated with the average temperatures across the European wintering range in the months prior to each populations' departure date from wintering sites (Figure 4). The  $r^2$  increased during March and April

**TABLE 2** Migration timing of four populations of common ringed plover (*Charadrius hiaticula*) breeding in Sweden.

Population	Climatic zone	No. tracks	Departure	Arrival in continental Europe (autumn only)	Arrival
<b>(a) Autumn</b>					
Abisko	Arctic	12	Aug 12 ± 2.1	Aug 19 ± 2.5	Sep 23 ± 4.9
Ammarnäs	Subarctic	13	Aug 6 ± 1.9	Aug 13 ± 2.3	Sep 24 ± 4.4
Malören	Subarctic	7	Jul 25 ± 2.7	Aug 1 ± 3.2	Aug 15 ± 6.2
Ottenby	Temperate	34	Jul 29 ± 1.3	Jul 31 ± 1.5	Aug 10 ± 3
<b>(b) Spring</b>					
Abisko	Arctic	11	May 7 ± 2.8	...	Jun 3 ± 3
Ammarnäs	Subarctic	10	May 5 ± 2.7	...	Jun 1 ± 2.8
Malören	Subarctic	5	Apr 1 ± 4	...	Apr 30 ± 4.2
Ottenby	Temperate	25	Mar 4 ± 1.8	...	Mar 10 ± 1.9



**FIGURE 4** Continent-wide autocorrelation in ambient air temperature to breeding sites at population-specific time periods, which may be critical to determine spring migration phenology. Dashed lines indicate the combined European wintering range (same as in Figure 2A).

(i.e., the months prior to departure date of individuals breeding at the subarctic/Europe [ $r^2 = 0.45$ ,  $SD = 0.24$ ], at the subarctic/Africa [ $r^2 = 0.74$ ,  $SD = 0.15$ ], and at the Arctic site [ $r^2 = 0.72$ ,  $SD = 0.17$ ]) and was as high or higher compared to February (i.e., month before departure date for individuals breeding at the temperate site [mean = 0.11,  $SD = 0.11$ ]) (Figure 4).

## DISCUSSION

Birds from the two subarctic breeding populations located at the same latitude wintered in West Africa, south of the Sahara, and temperate Europe and Morocco. The wintering ranges thus overlapped with those of an Arctic and a temperate breeding population, respectively. During autumn migration, individuals from populations wintering in Africa visited stopovers within the European wintering range, suggesting that competition for wintering sites could potentially occur with populations wintering there. However, due to the spatial resolution of light-level geolocation data, we could not identify any segregation on a finer geographical scale. Nevertheless, studies at sites within the European wintering range have reported passage migrants and winter residents at the same time, where winter residents tend to have a larger body size than those passing by (e.g., Clapham, 1978; Hortas & Cuenca, 2000). These findings suggest that single sites are indeed concurrently occupied by populations originating from a range of latitudes during autumn migration/early winter. We will now use our migration data to evaluate the alternative competition-based hypotheses proposed to explain the evolution of leapfrog migration.

### Dominance by body size

Contrary to the prediction that competitive exclusion mediated through body size is a mechanism for the evolution of leapfrog migration (Pienkowski & Evans, 1985), we found no difference in the overall body size between the populations that breed on the same latitude but winter in Europe and Africa, respectively. Furthermore, birds breeding at the temperate site were on average larger than birds of all other populations, and still birds from one of the subarctic populations overlapped in winter range, despite being smaller. Thus, in terms of body size, there is no reason why birds from the inland subarctic population, which wintered in Africa, would not also winter in Europe. Therefore, we reject competitive exclusion through body-size-related dominance as a proximate mechanism behind the evolution of leapfrog migration in this system.

### Dominance by prior occupancy

The studied populations not only showed spatial segregation during winter but also differed in their timing of autumn migration. Birds from populations wintering in Europe left their respective breeding areas and arrived in continental Europe two to three weeks before birds from both populations that wintered in Africa. Furthermore, while the two populations wintering in Africa reached their first stopover sites in continental Europe, individuals wintering in Europe had already reached their wintering sites. Hence, our observed pattern is consistent with the hypothesis that competitive exclusion through prior occupancy could lead to leapfrog migration (Figure 1C; Holmgren & Lundberg, 1993; Lundberg & Alerstam, 1986; Smith & Parker, 1976; Sutherland & Parker, 1985). However, ultimately accepting this hypothesis as an explanation requires proof that direct or indirect competition occurs and that this leads to large-scale displacements. Although competition at wintering sites seems to occur between individuals and groups (e.g., sex) in waders, leading to small-scale displacement (e.g., Alves et al., 2013; Leyrer et al., 2012), there are still few examples linking competition to displacements over larger geographic scales (e.g., Townshend, 1985).

### Spring predictability

The interannual variation in onset of meteorological spring at the temperate site was approximately three times higher than at all other sites, which all varied little in relation to each other (CV 7%–8%). This agrees with the assumption of the “spring predictability” hypothesis, which states that variation in onset of spring decreases with increasing latitude. Based on these results, one would expect individuals from all populations, except the temperate, to winter at low latitudes (Africa) far away from the breeding areas. However, this was not the case since individuals breeding at one of the subarctic sites also wintered in Europe. Importantly, this was the site with the least variation in spring onset. Also, the second assumption, that weather cues should correlate better between temperate breeding and wintering sites compared to that between temperate wintering sites and higher latitude breeding sites, did not fit the observed pattern. Our results indicate that spring temperatures at the breeding sites from populations wintering in Africa were highly correlated with areas within the European wintering range during the month prior to spring departure (see Table 2 for dates). Consequently, given the similarity in the CV of spring onset, and the correlations between breeding sites and the European wintering range, there is no reason for individuals from the two

subarctic populations at the same latitude to not winter at the same latitudes. Thus, using temperature as the proximate cue, our data do not seem to fit the assumptions underlying the “spring predictability” hypothesis.

Other cues, such as precipitation and atmospheric pressure, could potentially also be used to predict weather conditions at a given breeding site from afar. These cues are shown to impact departure decisions related to the success of the migratory journey, a process operating on a finer spatial and temporal scale (Cooper et al., 2023). However, there is a high collinearity between weather variables, particularly between temperature, atmospheric pressure, and precipitation (e.g., Yu et al., 2018), making it difficult to disentangle which variables are critical. Recently, Burnside et al. (2021) showed that individual timing of spring migration in the Asian houbara bustard (*Chlamydotis macqueenii*), from a medium distance migratory population, was best explained by local temperature at the wintering site and that the temperature between the wintering and breeding sites was correlated. This is relevant in the context of leapfrog migration and the “spring predictability” hypothesis because it seems like temperature is a reliable cue, which can be used over migration distances typical for lower latitude breeding populations in leapfrog systems. Or, as in our situation, the distance between wintering sites in Europe, which are located closer to a general breeding area in subarctic Sweden, compared to African wintering areas inhabited by populations which also breed in the same general area and latitude.

### Generality of competition-based hypotheses and noncompetition-based hypotheses

The idea that competition for wintering and breeding sites is an ultimate driver behind the evolution of different migration patterns, such as leapfrog migration, is general (Cox, 1968; Gauthreaux, 1982). But it may of course not be true for all species given the multitude of different life-history strategies and variation in habitat use throughout the annual cycle, nor may it be to the proximate mechanisms presented here (i.e., body size, prior occupancy by earlier arrival or spatial variability in spring onset, and autocorrelated weather cues), even if competition is the ultimate cause. However, assuming that competition is the main driver, we were able to reject two proximate mechanisms in the case of the ringed plover, a species that switches between Arctic tundra or sandy/rocky beaches and grassed meadows in summer for intertidal mudflats and salt marshes in winter (van de Kam et al., 2004). Many shorebird species fall into this category (Hale, 1980; van de Kam et al., 2004), which may suggest that our findings

could apply more generally for this group. Indeed, in most cases of leapfrog migration among shorebirds, the populations wintering closer to the breeding grounds tend to, as we find in the ringed plover, arrive in the most proximate wintering grounds first. For example, bar-tailed godwits (*Limos lapponica*) breeding in the Fennoscandian mountain range arrive at the Wadden Sea, where they winter, before populations breeding on the Taimyr Peninsula in the high Arctic pass by. The latter only use the Wadden Sea as a staging area before continuing to their main wintering sites in West Africa (Duijns et al., 2012).

In this study, we specifically test predictions and assumptions related to hypotheses that articulate competition for wintering and breeding sites. However, other hypotheses that do not assume any competition have been proposed. For example, Greenberg (1980) suggested a life-history trade-off where the proportion of time allocated in the breeding and nonbreeding grounds, in which the quality in terms of reproductive and survival rate at respective site varies latitudinally, is suggested to explain the evolution of leapfrog migration under certain conditions. Bell (1996, 2005) suggested that the “variation among populations in the cost of spring migration in relation to [site-specific] optimal time for the start of breeding” and wintering site-specific dynamics of food abundance are the main drivers. These hypotheses must also be evaluated before we can fully attribute the evolution of leapfrog migration in ringed plovers to either hypothesis. However, these require data on population-specific seasonal survival and reproductive rates, as well as winter site-specific food dynamics, which is currently unavailable.

### Conclusions

With the assumption that competition is a pivotal selective agent for the evolution of leapfrog migration, our data suggest that body-size-related dominance does not explain the difference in wintering sites between birds from two subarctic populations breeding at the same latitude. Given the overlap in wintering area of the population breeding at a temperate site (the largest individuals) and that of a coastal subarctic population, competitive exclusion through body-size-related dominance does not generally explain leapfrog migration in this species. However, we could not reject the hypothesis that competitive ability mediated by prior occupancy can lead to leapfrog migration. The assumptions on which the “spring predictability” hypothesis is based did not match the observed wintering ranges of the studied populations. Therefore, competition for wintering sites and prior occupancy, most likely shaped by site-specific breeding phenology, should be retained as the working hypothesis for the evolution of leapfrog migration in the ringed plover and other shorebirds of similar ecology.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Underlying data (Hedh et al., 2024a) are available in Dryad at <https://doi.org/10.5061/dryad.r4xgxd2d7>. Code (Hedh et al., 2024b) is available in Zenodo at <https://doi.org/10.5281/zenodo.5535903>. The sun elevation angles used to derive positions for each light-level geolocator (Hedh et al., 2024c) are available in Zenodo at <https://doi.org/10.5281/zenodo.5535905>.

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