# Quick-quick-slow: the foxtrot migration and dynamic non-breeding range

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# ABSTRACT

Advancements in tracking technologies have revolutionized our understanding of bird migrations, revealing a diverse array of migratory behaviors. We propose a new pattern of migratory behavior termed 'foxtrot migration,' characterized by alternating quick and slow phases during the non-breeding period. This behavior involves directional and continuous movements, distinct from traditional seasonal itinerancy or forage-on-fly migration. Using the Rough-legged buzzard as a model species, we confirmed the presence of foxtrot migration and 'dynamic non-breeding ranges', driven by environmental factors such as snow cover dynamics. We advocate for accurate representation of dynamic ranges on maps and emphasize the need to consider range dynamics when assessing species conservation status. Our findings underscore the importance of understanding complex migratory behaviors in the face of environmental change, facilitated by advancements in tracking technologies. This knowledge is crucial for effective conservation strategies amid ongoing global environmental challenges.



Keywords: *migration patterns, bird movement ecology, bird migration, types of migration, conservation, climate change, species ranges, non-breeding range, snow cover, dynamic range, foxtrot migration.*

# INTRODUCTION

In recent decades, advanced tracking technology has greatly improved our knowledge of bird migrations (Wikelski *et al.* 2007; Jetz *et al.* 2022; Kays & Wikelski 2023). In the 19th century, the finding of a White stork *(Ciconia ciconia)* in Germany with an African arrow led to the discovery that birds did not hibernate at the bottom of water bodies during the winter but rather made extensive seasonal migrations (Richter & Bick 2018). Subsequent studies of bird migration in the 20th century using ringing techniques revealed a diversity of seasonal migratory behaviors, including 1) propensity to migrate (migrants, residents, partial migrants), 2) differences among populations (leapfrog, chain, parallel migrations), 3) connectivity and philopatry (constancy of breeding and non-breeding locations), 4) length of migration routes (long-distance and short-distance migrants), 5) variations in flight paces during migration (with stopovers, forage-on-fly, nonstop), and 6) tendencies to move within a single season (breeding and non-breeding itinerancy) (Alerstam, Hedenström & Åkesson 2003; Newton 2008; Alerstam 2011; Berthold, Gwinner & Sonnenschein 2013). Different combinations of these behaviors contribute to a wide variety of bird migration patterns (Chapman *et al.* 2014; Alerstam & Bäckman 2018; Lislevand *et al.* 2020). However, the advent of 21st-century technology, such as GPS transmitters, provides a higher resolution of movement and the ability to observe more details of migratory behavior (Wikelski *et al.* 2007; Jetz *et al.* 2022). Just as advances in image resolution allow us to see finer details in images, improvements in bird tracking technology now allow us to identify previously undiscovered migratory behaviors, revealing new patterns.

Current technologies allow observing forms of migratory behavior that are intermediate or integrative to those described above. Itinerancy was initially defined as the movements of Afro-Palearctic migrants during the non-breeding season in the Sahel, with a combination of stopovers and flights in between (Moreau 1972). Subsequently, researchers investigated this behavior for multiple species wintering in Africa, attributing their movements during the non-breeding season to changes in food availability predicted by NDVI (Zwarts *et al.* 2012; Schlaich *et al.* 2016; Thorup *et al.* 2017; Verhoeven *et al.* 2021). In 1998, Garcia and Arroyo hypothesized that certain species, like the Montagu's harrier *(Circus pygargus)*, might not only cover tens to hundreds of kilometers between various sites in their winter range but could also demonstrate directional, continuous movement throughout the entire non-breeding season. This movement may span a distance similar to their migration distance (ca. 1000 km), essentially indicating a prolonged, slower-paced continuation of migration (García & Arroyo 1998). Because this behavior is intermediate between seasonal movement (itinerancy) and the actual

migration process, we can describe it as either ‘persistent directional non-breeding itinerancy’ or ‘very slow forage-on-fly migration in the non-breeding area’. Both options are clumsy and can confuse. We suggest naming this behavior with a new term to avoid confusion with established terms such as ‘itinerancy’ for any seasonal movement and ‘forage-on-fly’ denoting movement from breeding to non-breeding sites (Alerstam, Hake & Kjellén 2006; Alerstam 2011; Lopez-Ricaurte *et al.* 2024). Considering this behavior as an extension of migration and looking at the complete life cycle of such species, it includes a quick phase during the transition between breeding and non-breeding areas, followed by a slow phase of directed and seasonal movement within the non-breeding area, and finally another quick phase towards the breeding area. Analogous to the alternating fast and slow movements of the foxtrot dance, we propose the term ‘foxtrot migration’ for this seasonal movement to provide a concise and easily understandable description (Figure 1a). Consequently, we suggest to term the non-breeding range of species exhibiting this migration type as ‘dynamic range’ (Figure 1b).

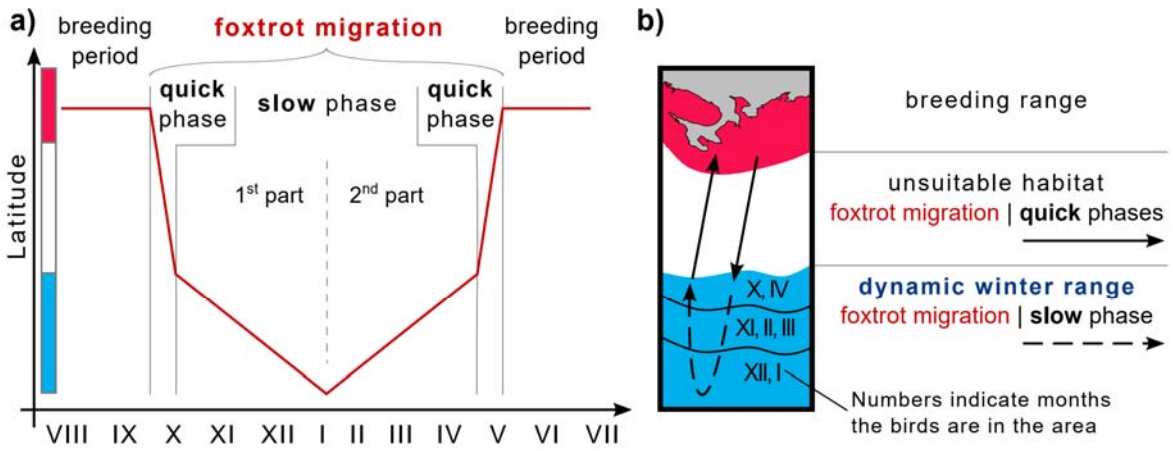


**Figure 1. Foxtrot migration and dynamic winter range scheme.** a) Foxtrot migration. The color bar along the y-axis corresponds to the color coding of the habitats in panel b of the chart on the right. b) Dynamic winter range.

The concept of dynamic range, derived from foxtrot migration, is critical to understanding the current range declines and shifts observed in many species. Typically, a species' range is divided into areas of common and uncommon, with temporal heterogeneity limited to breeding and non-breeding distinctions (Keller *et al.* 2020; Billerman *et al.* 2024). However, suppose a species exhibits a foxtrot migration, moving gradually in one direction and back again during the non-breeding season. In this case, it becomes inaccurate to represent its non-breeding range as static. This discrepancy is particularly pronounced when ranges are mapped using mid-winter surveys, such as Christmas counts. During this period, the species may

be present at the outer limits of its non-breeding range, leading to a false classification as common in that area when, in fact, it is rare if the entire non-breeding season is considered. Similarly, extended negative population dynamics of a species in a particular part of its non-breeding range could be misinterpreted as a threat to the entire population. Indeed, if this species has a foxtrot migration, range dynamics may have changed, possibly resulting in the species ceasing to migrate to that particular part of its range. Advanced technologies now make it possible the identification of foxtrot migration and range dynamics. This, in turn, facilitates accurate range mapping and proper assessment of threats to the species.

This pattern of behavior has been proposed in species that overwinter in Africa, where non-breeding movements are primarily related to the distribution of insect abundance (García & Arroyo 1998). At the same time, it is reasonable to assume that this behavior may also be characteristic of species that spend the non-breeding season in mid-latitudes, where food availability may be linked to snow cover dynamics. These dynamics have changed particularly rapidly in recent decades due to global warming (Davy & Outten 2020; Previdi, Smith & Polvani 2021). As a result, global climate change may significantly affect birds that breed in the Arctic and winter in mid-latitudes. The Arctic is experiencing more pronounced effects of global change than other regions, with declines in the abundance and range of several species and populations (Post *et al.* 2009; Gilg *et al.* 2012; Schmidt *et al.* 2012). Therefore, understanding how snow cover dynamics affect Arctic species across habitats throughout the annual cycle is essential today. Furthermore, elucidating the foxtrot migration and dynamic non-breeding range of mid-latitude wintering Arctic birds may provide valuable information on expected future changes in their non-breeding range.

We used the Rough-legged buzzard *(Buteo lagopus)* as a model species to investigate this phenomenon. The Rough-legged buzzard is an Arctic breeding and mid-latitude wintering raptor (Ferguson-Lees & Christie 2001; Bechard & Swem 2002). Rough-legged buzzards feed mainly on small rodents in the Arctic and its wintering grounds (Tast, Kaikusalo & Lagerström 2010; Pokrovsky *et al.* 2014). They prefer open areas for hunting, and trees and tall bushes or uplands for resting. In the Arctic, such areas are the southern and typical tundra (Walker *et al.* 2005), and in the mid-latitudes, areas with fields and patches of forests (wooded fields). The taiga zone, where there is little open space, is unsuitable for them, although they may nest in the northern taiga zone on the border with the tundra zone (Sundell *et al.* 2004). Snow cover and day length play an important role in their life (Terraube *et al.* 2015; Curk *et al.* 2020; Pokrovsky *et al.* 2021). Rough-legged buzzards can only hunt during the day (Pokrovsky *et al.* 2021), and heavy

snow cover makes hunting for small rodents problematic (Sonerud 1986; Vansteelant, Faveyts & Buckens 2011). These two environmental factors, therefore, affect the availability of prey for Rough-legged buzzards. At the same time, these factors vary considerably in mid-latitudes during winter. Thus, prey availability for Rough-legged buzzards in the mid-latitudes increases until mid-winter if they migrate southwards and after mid-winter if they migrate northwards. We, therefore, assume that Rough-legged buzzards could track prey availability and experience a foxtrot migration and dynamic non-breeding range.

For this study, we hypothesized that Rough-legged buzzards undertake a combined foxtrot migration and dynamic non-breeding range in response to seasonal changes in mid-latitude environmental factors. We made the following predictions. 1) Buzzards would exhibit a directional and seasonal movement pattern during the non-breeding period, moving from the northeast to the southwest and back again. This would result in a dynamic non-breeding range that would continue to move geographically throughout the season. 2) Non-breeding movements would occur in suitable open habitats, whereas fall and spring migrations would occur in unfitting forested areas. 3) Non-breeding movements would differ from fall and spring migrations in duration, extent, speed, and direction, however would continue throughout the season. 4) During non-breeding movements, Rough-legged buzzards will experience less snow cover than if they had stayed where they arrived at the end of the fall migration.

In the following, we will refer to the spring and fall migrations as the quick phase, the non-breeding movement to the lowest point of latitude as the 1$^{st}$ part of the slow phase, and the movement from the lowest point of latitude to the starting point of the spring migration as the 2$^{nd}$ part of the slow phase (Figure 1).

# MATERIAL AND METHODS

## Dataset

For this study, we tracked 43 adult Rough-legged buzzards (35 females and eight males) with the solar GPS-GSM loggers (e-obs GmbH and UKn – University of Konstanz). The fieldwork was carried out in the Russian Arctic in 2013-2019 at four study sites: Kolguev Island (69°16′N, 48°87′E), Nenetsky Nature Reserve (68°20′N, 53°18′E), Vaigach Island (69°43′N, 60°08′E), and Yamal Peninsula (68°12′N, 68°59′E). For details on capture methods and tag parameters, see Curk *et al.* (2022); for detailed study descriptions, see Pokrovsky *et al.* (2015) for Kolguev and Pokrovsky *et al.* (2019) for Yamal and Nenetsky.

During data pre-processing, we estimated the date of death using the accelerometer or GPS data and removed the tracking data if the bird was dead. We then removed duplicated timestamps and calculated the mean daily positions of each individual. We partitioned the resulting dataset into several periods: 1) breeding, 2) fall migration, 3)1$^{st}$ part of winter, 4) 2$^{nd}$ part of winter, and 5) spring migration. We estimated the migration dates – the start and stop dates of the spring and fall migrations – using an iterative search procedure for piecewise regression described by Crawley (2007). We estimated the date between winter's first and second parts as the day when the mean daily latitude was minimum.

## Data analysis

First, we used linear mixed-effects models (R function 'lmer' in the library 'lme4' (Bates *et al.* 2015)) to investigate whether or not Rough-legged buzzards migrated during winter. Latitude was the response variable, day of the year was a fixed effect, and individuals and year were included as random effects. Analyses were conducted separately for each migration period (fall, first phase of winter, second phase of winter, and spring). For both phases of the winter migration, we analyzed two additional models with longitude as the response variable instead of latitude. Likelihood ratio tests were used to compare candidate models. The year was not a calendar year but a year between two consecutive breeding seasons. Thus, fall migration, consecutive winter, and consecutive spring have the same value for the year. The day of the year was recalculated consecutively.

Second, we used linear mixed-effects models (R function 'lmer' in the library 'lme4') to investigate whether migrations' parameters differ between the migration periods. We analyzed four migration parameters: distance, duration, speed, and direction. The distance was calculated as the distance between two coordinates (start and end of migration) using the R function 'distm' in the library 'geosphere' (Hijmans 2016). The duration was calculated as the number of days between the start and end of migration. Speed was calculated as the ratio of distance to duration. The direction was calculated as the bearing from the start of the migration coordinates to the end of the migration coordinates using the R function 'bearing' in the library 'geosphere' (Hijmans 2016). The migration parameter was used as the response variable, the type of migration as a fixed factor, and individuals as a random factor. Likelihood ratio tests were used to compare candidate models. We considered four different parameters of migration (distance, duration, speed, and direction) and four types of migration (fall, first phase of winter, second phase of

winter, and spring). The analysis was done separately for each of the migration parameters. Then, we used post hoc comparisons using the R function ‘emmeans’ in the library ‘emmeans’ (Lenth *et al.* 2019) to compare the estimated means. In some raptor species, adult females disperse further than males (Mearns & Newton 1984; Serrano *et al.* 2001; Bildstein 2006; Whitfield *et al.* 2009). Therefore, we conducted an additional analysis on the effect of sex on migration length using linear mixed-effects models (R function ‘lmer’ in the library ‘lme4’). The migration distance was used as the response variable, sex as a fixed factor, and individuals as a random factor.

Third, we investigated whether vegetation land cover differed between areas crossed during the quick (fall and spring) and slow (winter) migrations. We used the combined Terra and Aqua Moderate Resolution Imaging Spectroradiometer (MODIS) Land Cover Climate Modelling Grid (CMG) (MCD12C1) version 6 dataset (Friedl & Sulla-Menashe 2015). We used a modified Leaf Area Index (LAI) as a classification scheme. We combined all four forest types and savannas into one category (forest) and excluded the categories: water bodies, and unclassified. We, therefore, had five types of vegetation cover: forest, grassland, cropland, shrubland, and urban. We annotated the mean daily positions with the vegetation cover type using the Env-DATA tool (Dodge *et al.* 2013). We used general linear mixed effects models with a binomial distribution (R function ‘glmer’ in the library ‘lme4’) to investigate whether vegetation cover types differ between migration periods. Presence/absence of the studied vegetation land cover type was used as a response variable, migration type as a fixed factor, and individuals as a random factor. The analysis was done separately for each of the vegetation land cover types.

Fourth, we investigated whether snow cover could drive the slow migration phenomenon. We then compared the snow cover conditions the birds experienced during the winter with two hypothetical snow cover conditions that the birds would have experienced if they had not migrated during the winter. The first hypothetical snow cover condition would have happened if the birds had stayed where they arrived from the north (i.e., where their fall migration ended). To estimate this parameter, we calculated the winter dynamics of the average snow cover at the minimum convex polygons (MCP) occupied by the birds in October and April (northeast of their winter range). A second hypothetical snow cover condition would be if the birds flew immediately to the southwest and spent the whole winter there. To evaluate this, we calculated the winter dynamics of average snow cover on the MCPs occupied by the birds in January and February (southwest of their winter range). We then compared the values obtained for the real

snow cover and two hypothetical snow covers using general linear mixed effects models with a binomial distribution (R function 'glmer' in the 'lme4' library). Presence/absence of snow cover was used as a response variable, type of snow cover (real, 1st hypothetical, or 2nd hypothetical) as a fixed factor, and years as a random factor. The analysis was done separately for each month. We then used post hoc comparisons to compare the estimated means, using the R function ‘emmeans’ in the ‘emmeans’ library (Lenth *et al.* 2019).

We obtained monthly snow cover data with a spatial resolution of ca 500 meters (Global SnowPack MODIS) from the German Aerospace Center (DLR). This product is based on the Moderate Resolution Imaging Spectroradiometer (MODIS) daily snow cover products MOD10A1 and MYD10A1 (version 6 as provided by the National Snow and Ice Data Center NSIDC), which have been processed to remove the gaps due to cloud cover and polar darkness (Dietz, Kuenzer & Dech 2015). These processing steps include a combination of data available from different satellites (Aqua and Terra), 3-day temporal moving window filtering, a regional snow line elevation interpolation relying on a Digital Elevation Model (DEM), and a seasonal filter running through the time series for the whole hydrological year (1st of September through August 31st). The proportion of days in which one pixel is snow-covered per month is referred to here as fractional snow cover and is derived from these daily gap-filled rasters. Five MODIS tiles (h19v03, h20v03, h20v04, h21v03 and h21v04) were mosaicked and re-projected to WGS84. Then, for each month from October to April, we calculated 95% minimum convex polygons (MCPs) for the distribution of Rough-legged buzzards using the R function ‘mcp’ in library ‘adehabitatHR’ (Calenge 2006). We extracted mean snow cover values from each MCP from every monthly snow cover raster separately, using the R library 'raster' (Hijmans & van Etten 2023).

All calculations were performed using R version 4.2.2 ‘Innocent and Trusting’ (R Development Core Team 2022) and RStudio version 353 ‘Elsbeth Geranium’ (Posit team 2022).

# RESULTS

## Foxtrot migration – always on the move

Except during the breeding season, Rough-legged buzzard migration continues throughout the year, even after the birds´ arrival at their traditionally recognized ´wintering grounds´ (Figure 2a, b). For both quick and slow phases of the foxtrot migration, linear mixed-effects models with the season as a fixed factor received higher support from the likelihood ratio test ($p < 0.001$, Tables S1-S3). Rough-legged buzzards started their fall migration (quick phase) on 28 September

(hereafter mean±sd for the day of the year: 271±11, n=31) and ended on 12 October (285±11, n=33). The mean latitude/longitude where the birds ended their fall migration was 55.57±1.92°/49.35±5.63° (Figure 2a). During the winter, birds continued to migrate at a slower pace down to 49.53±2.01° latitude (on 5 February, 36±40, n=23) and 34.29±5.11° longitude (on 24 January, 24±47, n=23). Afterward, during the second part of the slow phase, the birds returned to 55.52±2.63° latitude and 49.79±8.24° longitude to start the spring migration (Figure 2a). Rough-legged buzzards started their spring migration to the Arctic on 27 April (117±7, n=27) and arrived at the breeding grounds on 15 May (135±8, n=18).

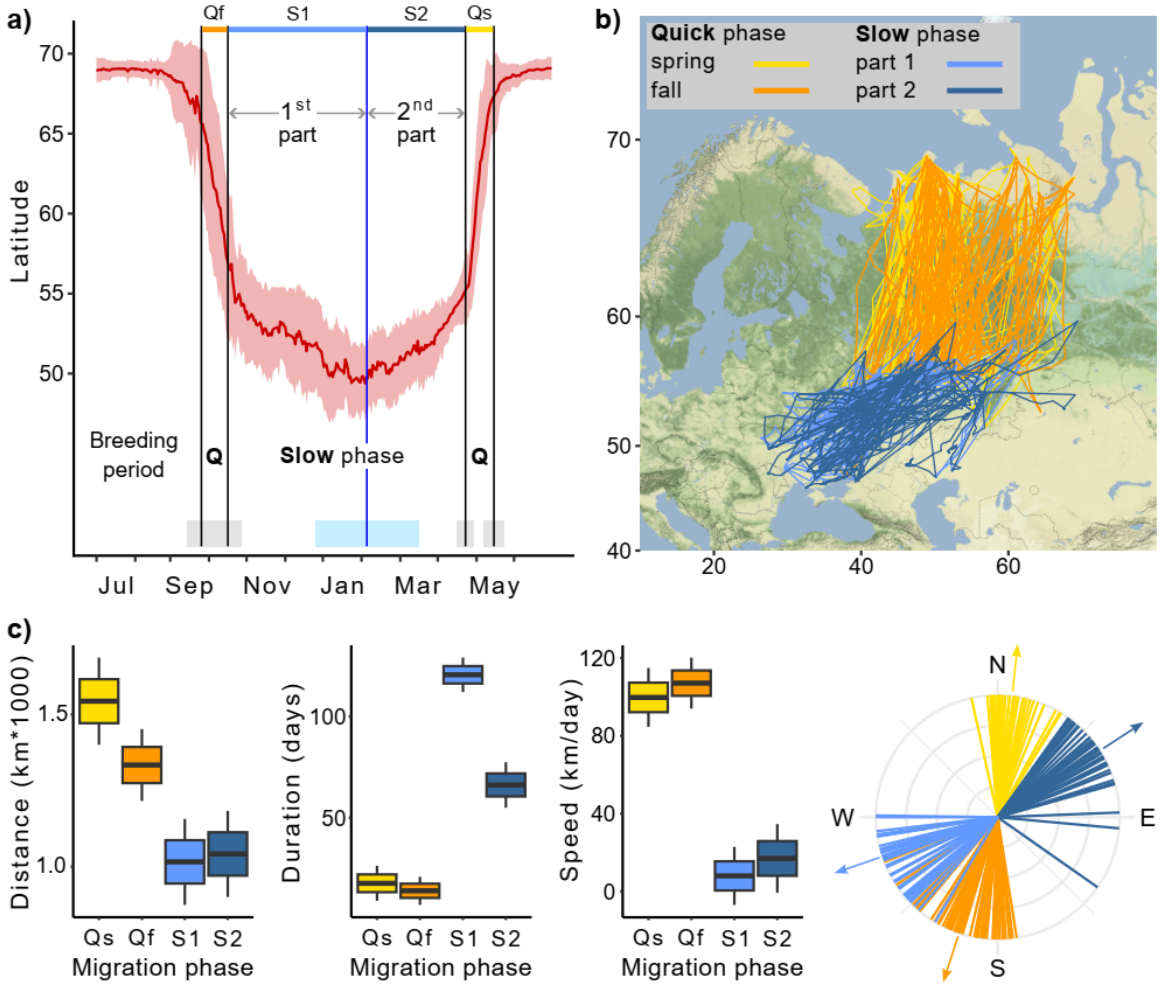


**Figure 2. Foxtrot migration of Rough-legged buzzards.** Q – quick phase. Qf – Quick fall phase (orange), Qs – Quick spring phase (yellow), S1 – Slow phase, 1st part (light blue), S2 – Slow phase, 2nd part (dark blue). a) Change in the latitude of 43 Rough-legged buzzards during the year, red line – mean latitude of all birds, black vertical lines – mean dates of start and end of the migration phases, blue vertical line – mean date of the minimum latitude. Grey, sky blue, and

piggy pink shaded areas – standard deviation of the means. b) Migration map. c) Difference in the migration parameters between the migration phases. Lines on the direction plot (down, right) represent the mean value for each bird; arrows represent the mean direction.

## Quick-slow phase features comparison

During quick phase, individual birds flew greater distances in a shorter time, i.e., at a faster rate, than during slow phase. After arriving at what is traditionally known as the wintering grounds, the direction of migration changed, so the direction of quick and slow phases also differed (Table 1, Figure 2c). The quick phase was 1415±50 km long, whereas the slow phase (one part) was 1026±55 km, i.e., 389±60 km shorter ($p<0.001$, Table S4, Figure 2c). During quick phase, birds flew for 15±3 days, and one part of slow phase lasted 100±4 days, i.e., 85±5 days longer ($p<0.001$, Table S5, Figure 2c). At the same time, the second part of slow phase was 54±7 days shorter than the first ($p<0.001$, Table S5, Figure 2c). The migration speed was 104±6 km/day during the quick phase and 12±7 km/day during the slow phase, i.e., about eight times higher ($p<0.001$, Table S6, Figure 2c). During the fall migration, birds moved in the SSW direction (7±2 deg), then turned 50±3 deg ($p<0.001$, Table S7, Figure 2c) to the west and started their 1$^{st}$ slow phase until mid-winter. After that, they turned back to the NEE direction (57±2 deg) and performed their 2$^{nd}$ slow phase for several months until they turned 54±3 deg ($p<0.001$, Table S7, Figure 2c) to the north and started their spring migration. As a result of additional analysis of the effect of sex on migration length, we found no significant difference between the migration distances of males and females (Table S8).

**Table 1.** Parameters of the rough-legged buzzards' migration.

| Phase of migration | Sub-phase of migration | Distance (km) | Duration (days) | Speed (km/day) | Direction (deg) |
|---|---|---|---|---|---|
| Quick | | 1415±50 | 15±3 | 104±6 | |
| | Spring | 1544±72 | 18±4 | 100±8 | 7±2 |
| | Fall | 1334±59 | 14±4 | 107±7 | 198±3 |
| Slow | | 1026±55 | 100±4 | 12±7 | |
| | 1$^{st}$ phase | 1016±71 | 121±4 | 8±7 | 251±3 |

| | | | | |
|---|---|---|---|---|
| 2nd phase | 1042±71 | 66±6 | 17±9 | 57±2 |

## Vegetation land cover during migration

During quick phases, Rough-legged buzzards cross the forest zone, while during slow phase, they migrate within the grassland and cropland zone (Figure 3). Rough-legged buzzards migrated fast across the tundra zone on the north in the Arctic and then through the taiga zone. Therefore, during quick phase, the three most common vegetation land cover types were forest (44.5±2.9 %, hereafter, percentage of all mean daily positions annotated with the given vegetation type), shrublands (29.9±3 %), and grasslands (24.7±2.8 %, Figure 3a). During slow phase, the three most common vegetation land cover types were grasslands (65.1±6.2 %), croplands (26.9±6.3 %), and forests (4.9±1.4 %, Figure 3b). According to the linear mixed-effects models, the percentage of all vegetation land cover types differed between the slow and quick phases ($p<0.001$, Table S9), except for the urban lands. Urban lands were more common during the slow than quick phase (Figure 3). However, this type has been annotated for too few birds to make an adequate comparison.

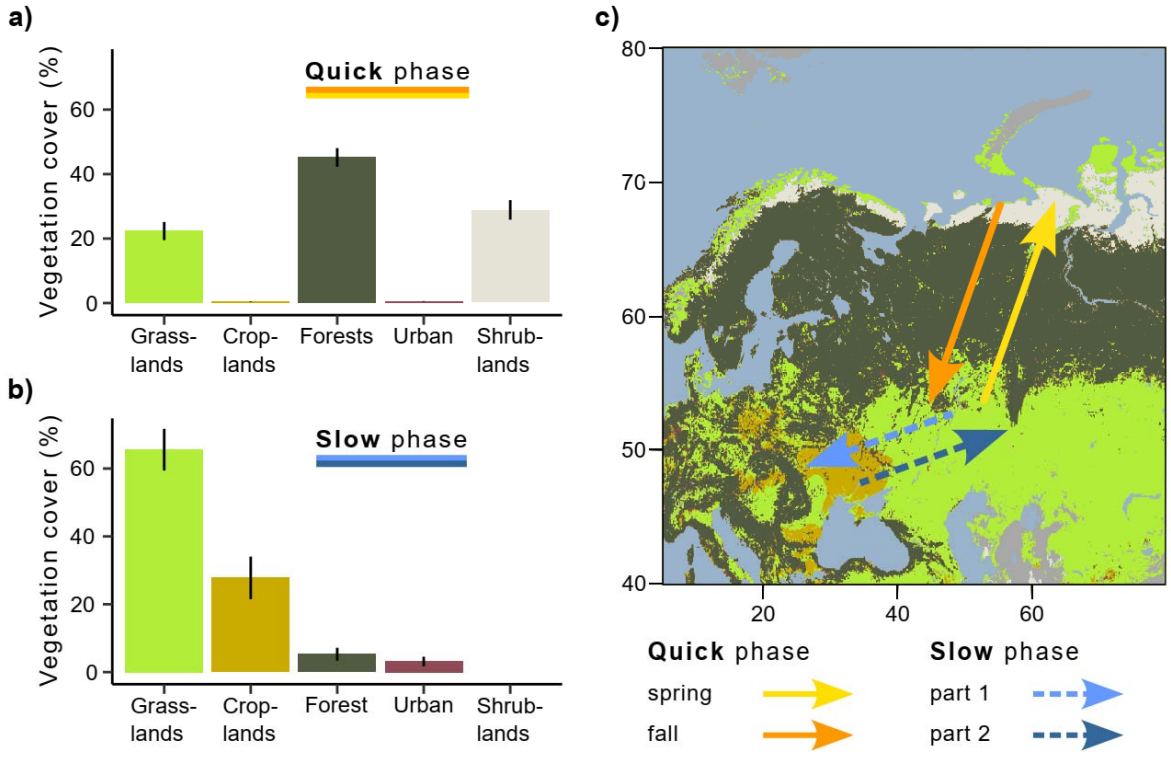

**Figure 3. Vegetation land cover during quick and slow phases.** a) Quick phase (spring and fall periods together). b) Slow phase (1st and 2nd parts together). c) Migration map.

## Snow cover – the main reason for the dynamic winter range

During the slow phase of the foxtrot migration, Rough-legged buzzards experienced snow cover ranging from 4.8±1.0% in October to 85.2±4.6% in February (Figure 4). If birds spent the winter in the place where they arrived after the fall migration, they would experience snow cover conditions ranging from 4.6±0.6% in October to 99.5±0.1% in February (Figure 4). And if birds fly directly to the southeast and stay there for the whole winter, they would experience snow cover conditions ranging from 1.4±0.2 % in October to 81.1±5.0 % in January (Figure 4). Thus, if birds fly immediately to the southwest and stay there until the end of the winter, they will find conditions with less snow cover in spring ($p<0.001$, Table S10). And if birds stay where they ended the fall migration, they will find themselves in situations with more snow cover ($p<0.001$, Table S10). In the latter case, the difference between real and hypothetical situations is not as pronounced (85.2% vs. 99.5%), but more means that snow cover will be close to 100% for several months in this hypothetical situation (Figure 4b).

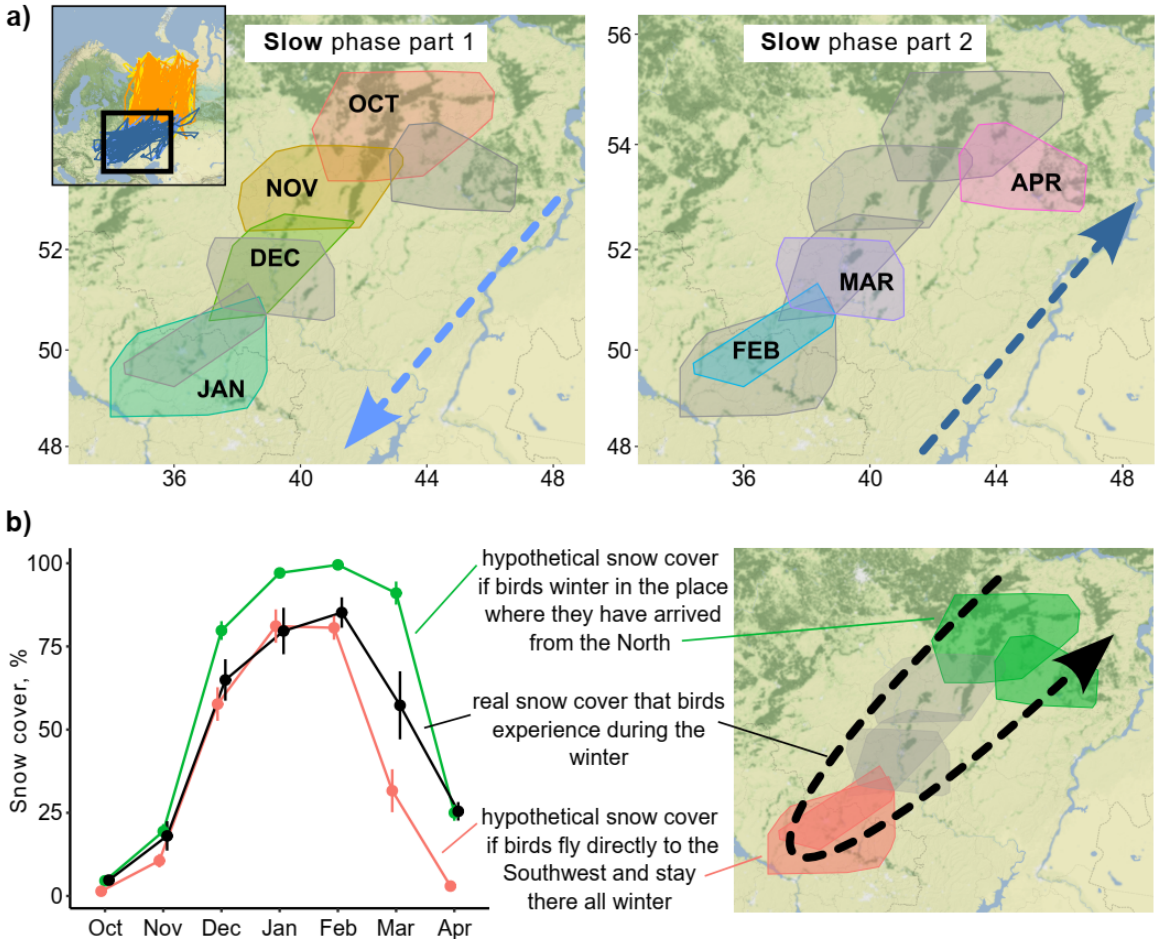


**Figure 4. Snow cover conditions during the slow phase of the foxtrot migration.** a) 95% Minimum convex polygons (MCPs) of Rough-legged buzzards during winter. Arrows indicate the direction of the movement across months. OCT – October, NOV – November, DEC – December, JAN – January, FEB – February, MAR – March, APR – April. b) Snow cover conditions for the real situation (black) and two hypothetical situations – if birds spend the winter in the place where they arrived after the fall migration (green) and if birds fly directly to the southwest and stay there all winter (red). Dots represent mean values, error lines – standard errors.

In some raptor species, adult females disperse further than males (Mearns & Newton 1984; Serrano *et al.* 2001; Bildstein 2006; Whitfield *et al.* 2009). While our analysis does not support this (Table S8), it should be acknowledged that our dataset comprises 35 females, eight males, and no juveniles. The unbalanced sex ratio and absence of immature individuals in our sample may have potential influences towards the observed movement patterns in this study.

# DISCUSSION

Our study confirmed the existence of a previously hypothesized bird migration pattern (García & Arroyo 1998) characterized by alternating quick and slow phases (Figure 1). Following the breeding season, birds quickly traverse unfavorable habitats and proceed slowly through winter in favorable environments influenced by external factors. Subsequently, they quickly cross unfavorable terrain once more to reach the breeding region in spring (Figure 2). This pattern, termed 'foxtrot migration', distinguishes itself from 'itinerancy' by featuring directional and continuous movements. Additionally, it differs from 'forage-on-fly migration' as it occurs during the non-breeding period. We propose referring to the non-breeding area as 'dynamic area', reflecting its temporal heterogeneity, where the region with the highest bird density continually changes throughout the non-breeding period.

Our study affirmed the presence of foxtrot migration and a dynamic non-breeding range in Rough-legged Buzzards. The taiga zone posed as unfavorable habitat during the quick phase of foxtrot migration (Figure 3), given the difficulty for Rough-legged Buzzards to locate open areas for hunting. Conversely, the grassland and cropland zone served as favorable habitats during the slow phase throughout the entire non-breeding period (Figure 3), offering numerous open areas for hunting. Snow cover was the external factor driving their continual 1000 km southwest movement during winter (Figure 4). Our analysis revealed that if Rough-legged Buzzards remained at their fall migration endpoint without moving southwest, they would encounter 14.4% more snow cover (99.5% vs. 85.1%, Figure 4). Although this difference may seem small (14.4%), it holds significance for rodent-hunting birds, distinguishing between complete and patchy snow cover. Simultaneously, if Rough-legged Buzzards immediately flew to the southwest and stayed there throughout winter, they would experience 25.7% less snow cover (57.3% vs. 31.6%, Figure 4). Despite a greater difference than in the first case, it doesn't compel them to adopt this strategy, as it represents the difference between various degrees of landscape openness from snow cover. This indicates ecological tipping points in the environment that are not predicted by a slight linear increase in effect size.

This pattern is likely to be observed in many migratory species with distinct seasonal cycles in their non-breeding range. In our study, we focused on an Arctic species that resides in the mid-latitudes during the non-breeding period. In general, foxtrot migration is likely to be a common feature among species where snow cover significantly influences food availability, especially those specializing in rodents. Originally proposed for birds in Africa, where seasonal changes regulate food availability, it's likely that many insectivorous birds that spend the non-

breeding season in Africa also exhibit this form of migration. This type of migration and dynamic non-breeding range is widespread both geographically and taxonomically, with obvious conservation implications.

## The conservation implications

The conservation implications of our study are twofold: 1) the use of mid-winter (Christmas) bird surveys to determine non-breeding range may yield inaccurate results for species with foxtrot migrations (Figure 5a), and 2) declines in abundance within a particular segment of the non-breeding range may indicate changes in range dynamics rather than widespread declines in species abundance (Figure. 5b).

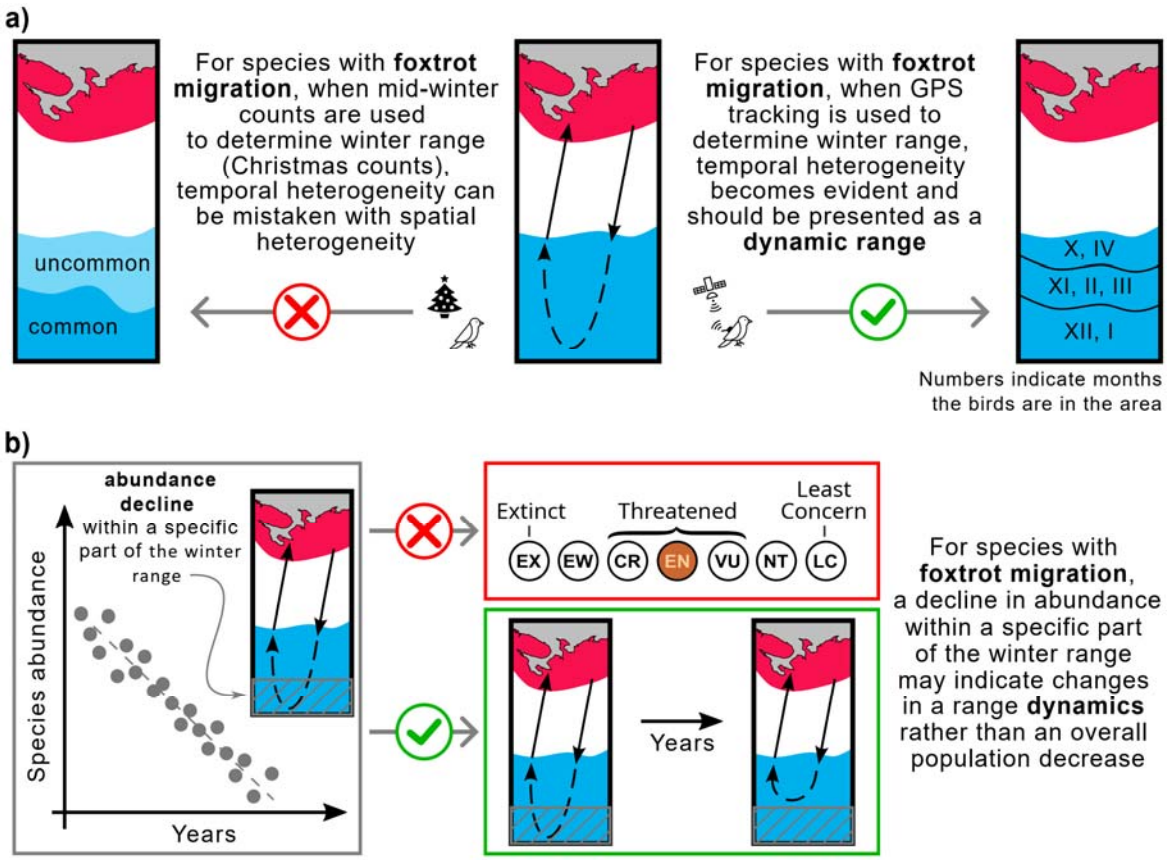


**Figure 5. The use of foxtrot migration research for the assessment of the non-breeding range and conservation status of a particular species.** a) Christmas counts, often used to determine winter range, may give a misleading representation of non-breeding range for species with foxtrot migration. b) Changing the conservation status of a species based on reduced abundance in a particular area may not be appropriate for species with foxtrot migrations. Red – breeding range, blue – winter range. Latin numbers indicate the month the birds are present in the area.

Christmas Bird Counts provide insight into the mid-winter distribution of a species. For example, based on our study of the Rough-legged Buzzard, the species is predominantly present in the southwestern portion of its non-breeding range during this period, with only a small proportion present in the rest of the region. As a result, a map of the non-breeding range may inaccurately depict the species as common in the southwest and extremely rare in the northeast. This map would be inaccurate because, during the entire non-breeding period, Rough-legged Buzzards spend both fall and spring in the northeastern part and only mid-winter in the southwesternmost part.

To address this, continuous year-round GPS tracking of the species provides a means to track bird locations throughout the non-breeding season, facilitating the creation of accurate distribution maps, particularly for species that exhibit foxtrot migrations and dynamic ranges. We advocate representing temporal heterogeneity (range dynamics) on maps as distinct zones, denoting periods when the species is abundant in a given area. To distinguish temporal from spatial heterogeneity, we recommend using lines to delineate the boundaries of these zones, rather than color shading, and incorporating numbers to denote the months of species abundance in a given zone (Figure 5a). We suggest ecologists include dynamic non-breeding ranges in descriptions and range maps for foxtrot migratory bird species.

Population counts for a species are often limited to a portion of its range. Therefore, conclusions about conservation status drawn from such counts may be misleading. A decline in abundance within a particular portion of the non-breeding range may indicate changes in range dynamics rather than a general decline in the species. For example, climate change may affect snow cover dynamics, reducing its intensity in northern regions. As a result, species whose range dynamics depend on snow cover may choose to remain in the northern areas and not migrate as far south as they traditionally have. Despite this shift in range dynamics, overall species abundance may remain unchanged. Similar patterns have affected Rough-legged Buzzards in some areas of the European non-breeding range.

A 2022 Dutch study found a decline in wintering Rough-legged buzzards over the last 40 years (Hornman, Boele & van Winden 2022). On the one hand, this may represent a conservation concern. On the other hand, applying the rationale of the foxtrot migration, the apparent local decline may simply be attributed to climate change, resulting in less comprehensive snow coverage in the northeastern wintering areas of Rough-legged buzzards relative to the Netherlands. Such a shift in snow coverage makes it less probable for the birds to migrate to the Netherlands for overwintering. This proposition is further supported by a study of

the winter population dynamics of Rough-legged buzzards in the Netherlands in 2011, showing that the main winter population peak occurred in late December, with many birds migrating (Vansteelant, Faveyts & Buckens 2011). The authors also found that the main migration occurred after heavy snowfall in northern Europe, supporting our foxtrot migration explanation for this decline. Therefore, investigating the dynamic range and foxtrot migration is critical to understanding a species' range and effectively assessing its conservation status.

Significant environmental changes, including changes in snowpack dynamics, have occurred in recent decades that may have significant impacts on bird migration (Tucker *et al.* 2018; Sumasgutner *et al.* 2021). In order to understand the effects of global environmental change on bird migration behavior, there is an urgent need for in-depth investigations into the intricate relationship between migration patterns and evolving environmental factors. The advent of new technologies in recent decades has expanded our understanding of bird migration, enabling the identification of novel behavioral patterns and facilitating the study of their susceptibility to various environmental influences. This knowledge is becoming increasingly urgent in the face of rapid climate change and anthropogenic habitat alteration, which pose threats to both wildlife and human populations.

## CONCLUSIONS

Our study has identified and characterized a new pattern of migratory behavior, the ‘foxtrot migration’, along with the associated concept of ‘dynamic range’. This discovery has significant implications for conservation strategies and adequate representation of non-breeding habitats. As animal tracking technology advances, we expect to discover more new details about animal migrations and, consequently, new patterns of migratory behavior. With these technological developments, we are gaining a clearer understanding of the complex patterns and behaviors that drive animal migrations, providing valuable insights for conservation efforts and deepening our understanding of the natural world.

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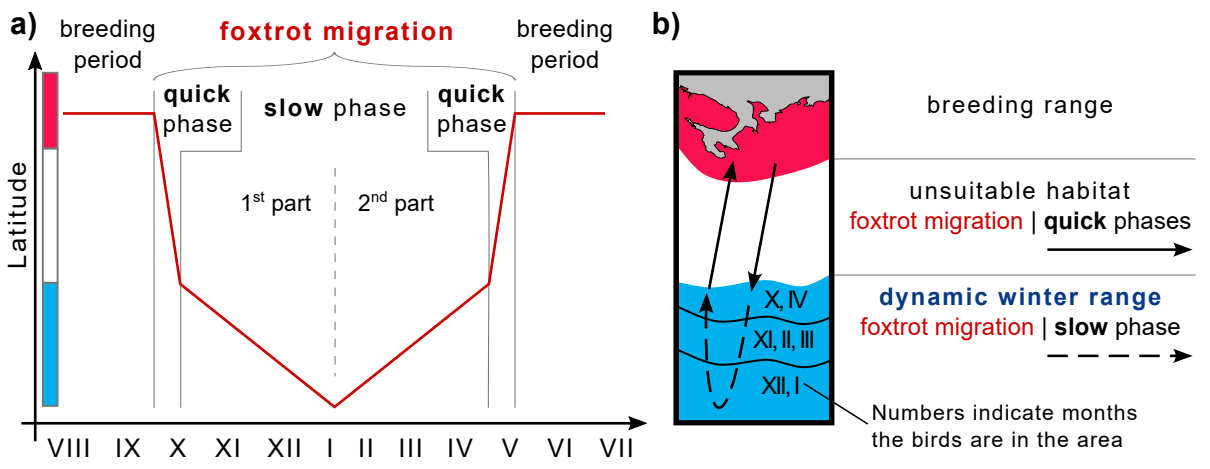
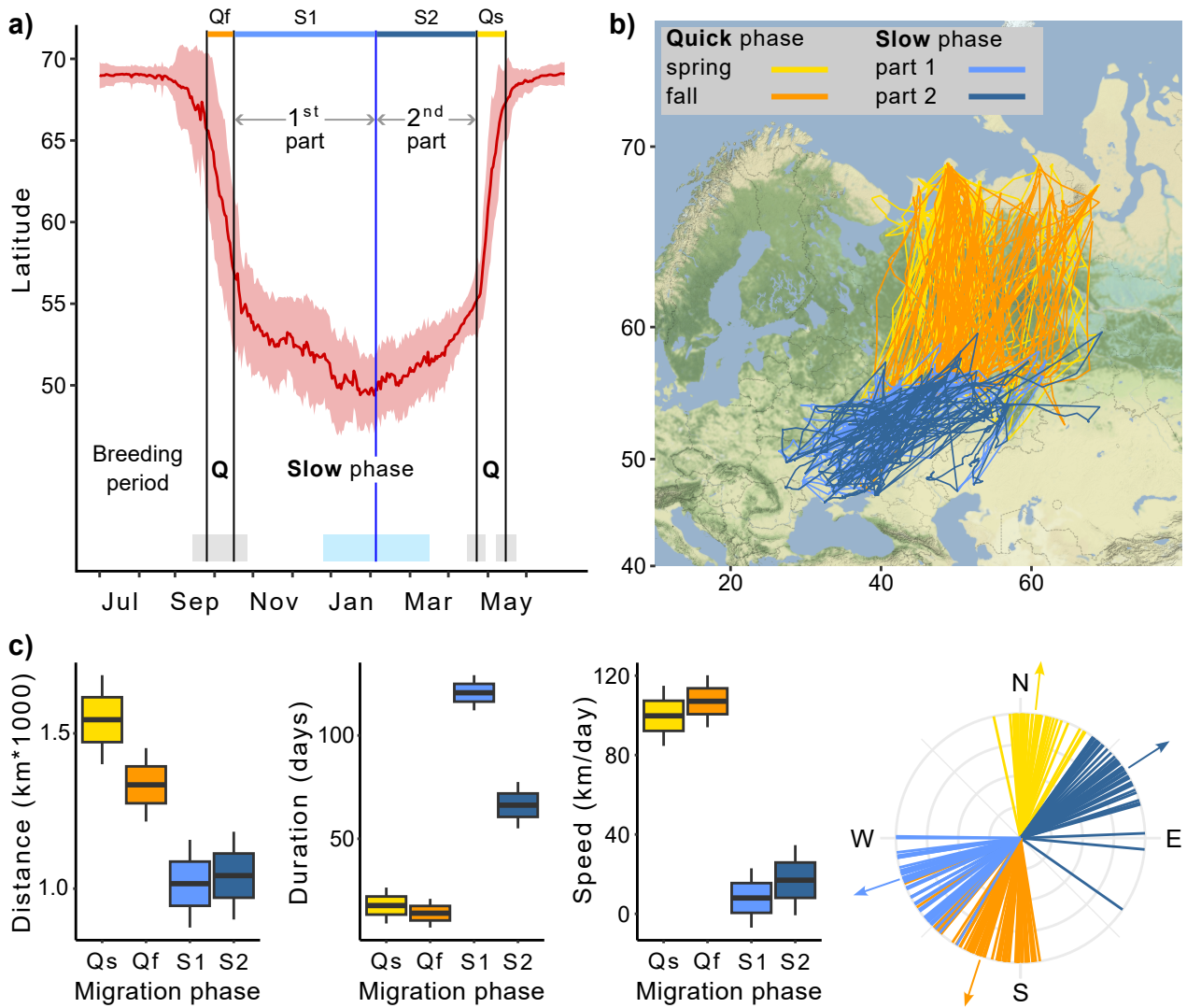

a)
breeding period
foxtrot migration
breeding period
quick phase
slow phase
quick phase
1st part
2nd part
Latitude
VIII IX X XI XII I II III IV V VI VII
b)
breeding range
unsuitable habitat
foxtrot migration | quick phases
dynamic winter range
foxtrot migration | slow phase
X, IV
XI, II, III
XII, I
Numbers indicate months the birds are in the area


a)
Qf
S1
S2
Qs
Latitude
70
65
60
55
50
1st part
2nd part
Breeding period
Q
Slow phase
Q
Jul
Sep
Nov
Jan
Mar
May
b)
Quick phase
spring
fall
Slow phase
part 1
part 2
70
60
50
40
20
40
60
c)
Distance (km*1000)
1.5
1.0
Qs
Qf
S1
S2
Migration phase
Duration (days)
100
50
Qs
Qf
S1
S2
Migration phase
Speed (km/day)
120
80
40
0
Qs
Qf
S1
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Migration phase
N
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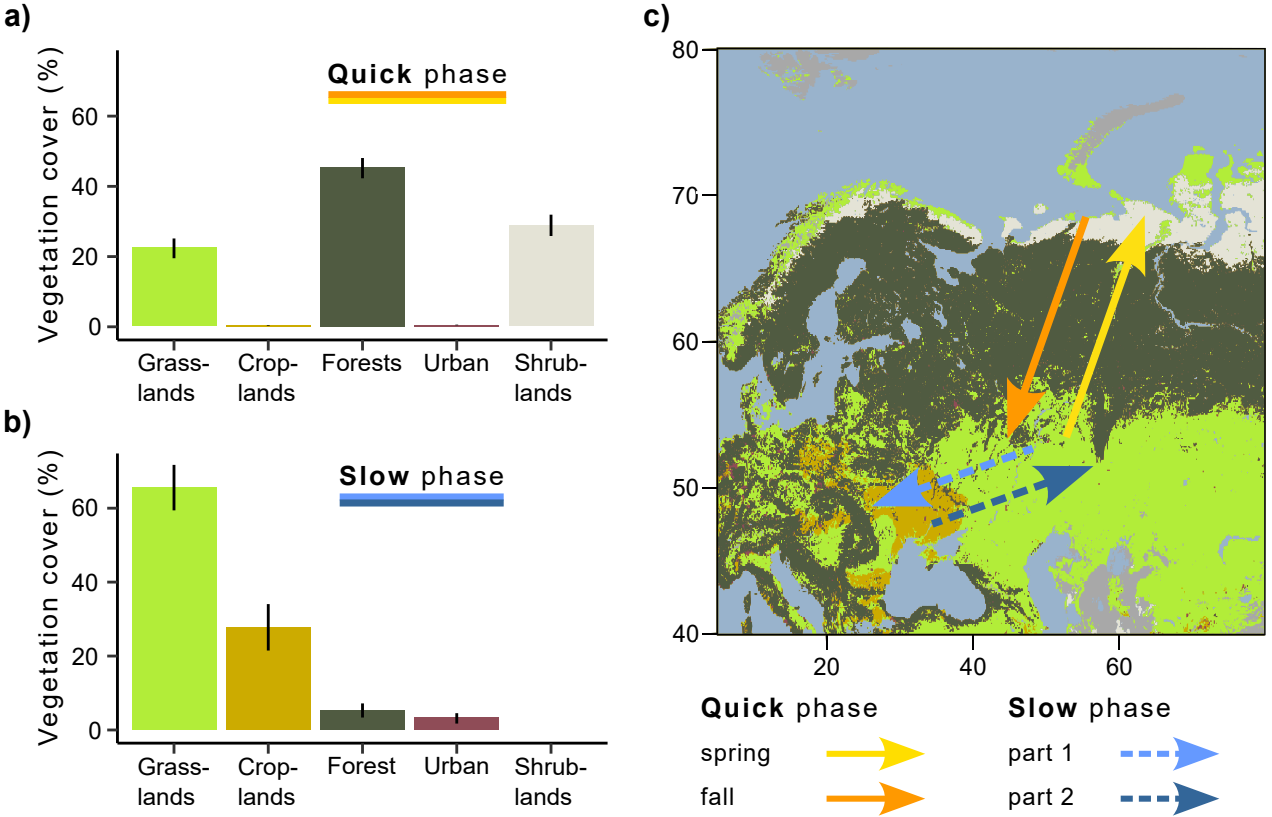
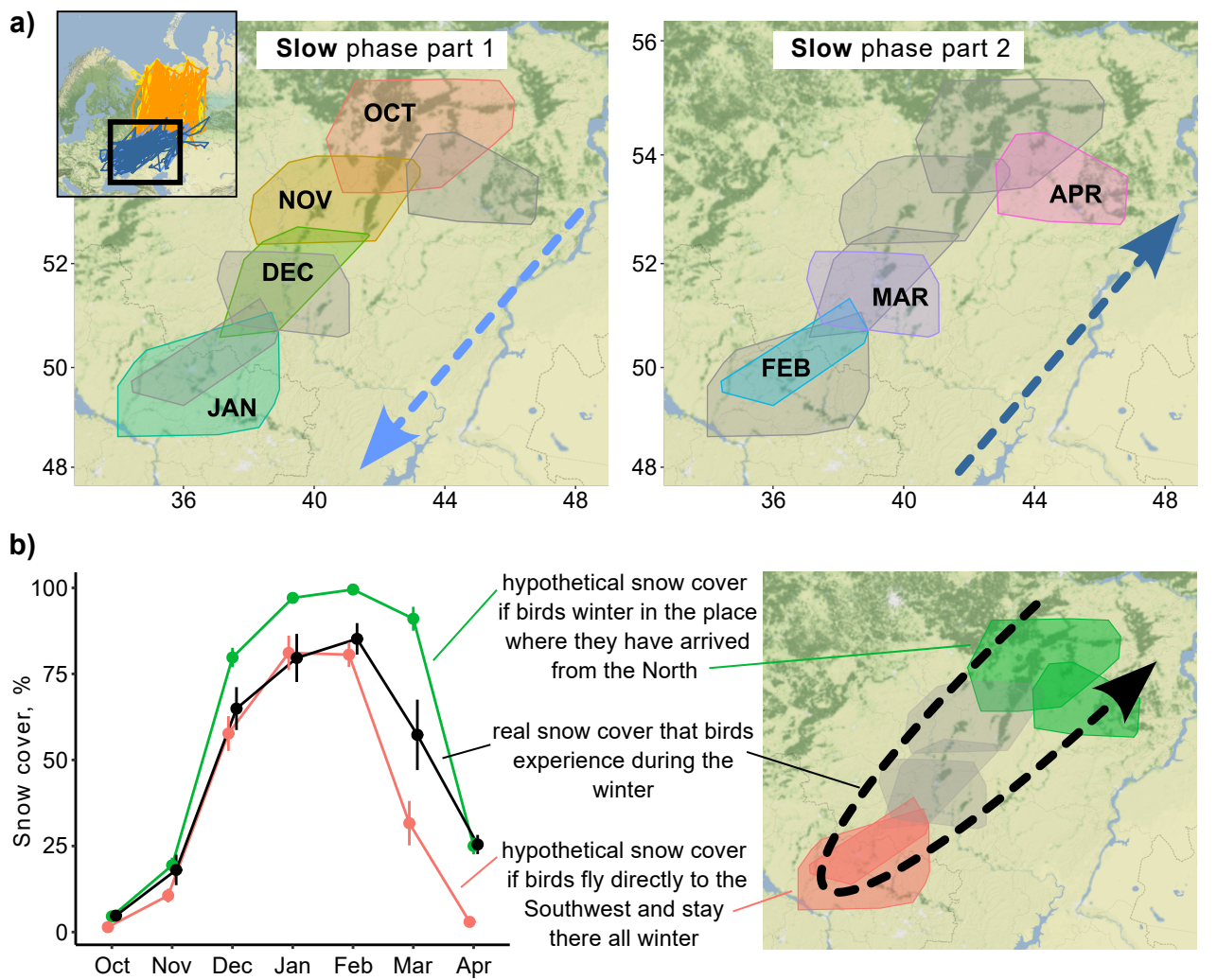
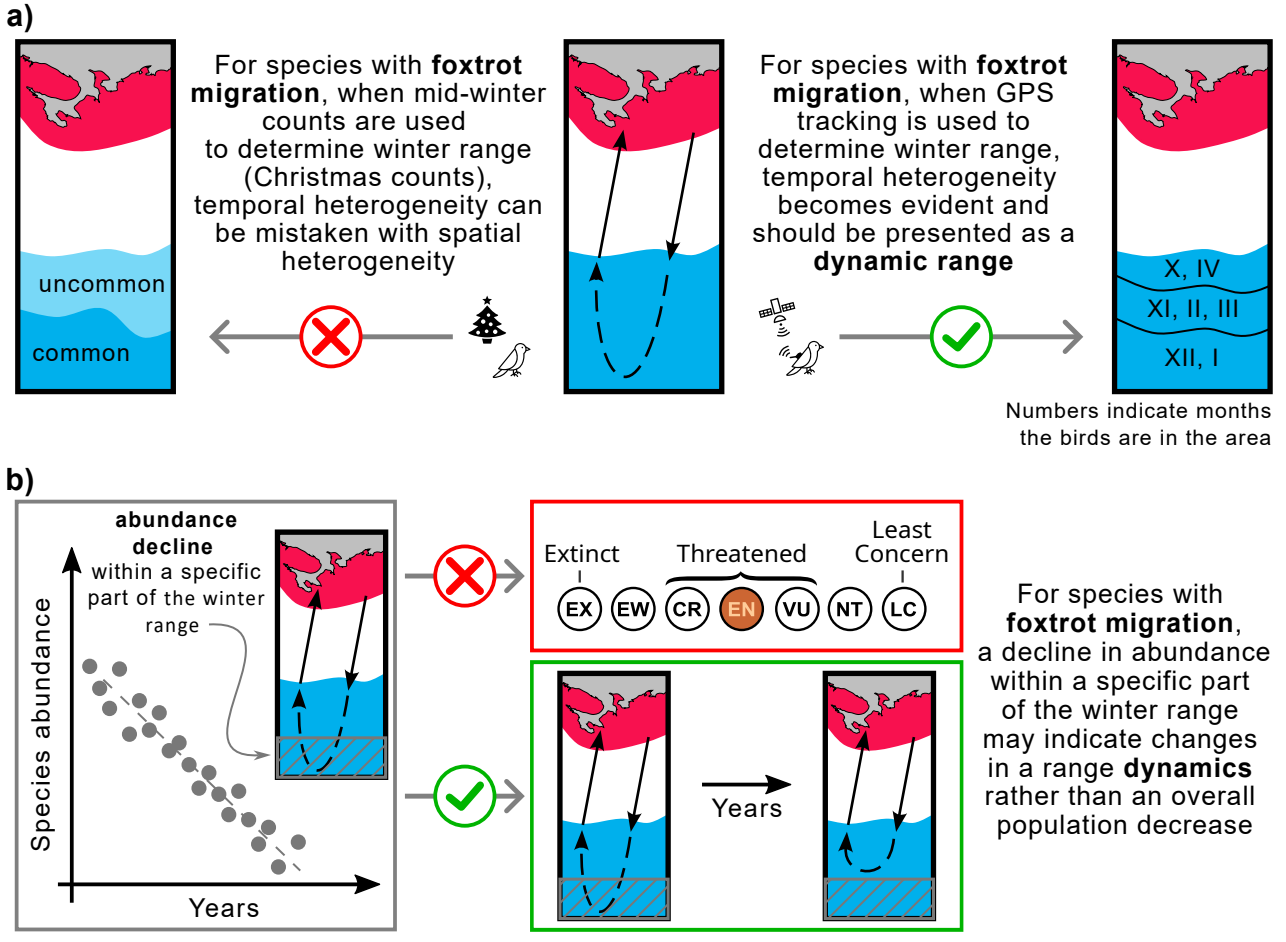

a)
Quick phase
Vegetation cover (%)
0
20
40
60
Grass-lands
Crop-lands
Forests
Urban
Shrub-lands
b)
Slow phase
Vegetation cover (%)
0
20
40
60
Grass-lands
Crop-lands
Forest
Urban
Shrub-lands
c)
80
70
60
50
40
20
40
60
Quick phase
spring
fall
Slow phase
part 1
part 2


a)
Slow phase part 1
OCT
NOV
DEC
JAN
52
50
48
36
40
44
48
Slow phase part 2
56
54
52
50
48
APR
MAR
FEB
36
40
44
48
b)
Snow cover, %
100
75
50
25
0
Oct
Nov
Dec
Jan
Feb
Mar
Apr
hypothetical snow cover if birds winter in the place where they have arrived from the North
real snow cover that birds experience during the winter
hypothetical snow cover if birds fly directly to the Southwest and stay there all winter


a)
uncommon
common
For species with **foxtrot migration**, when mid-winter counts are used to determine winter range (Christmas counts), temporal heterogeneity can be mistaken with spatial heterogeneity
For species with **foxtrot migration**, when GPS tracking is used to determine winter range, temporal heterogeneity becomes evident and should be presented as a **dynamic range**
X, IV
XI, II, III
XII, I
Numbers indicate months the birds are in the area
b)
**abundance decline** within a specific part of the winter range
Species abundance
Years
Extinct
Threatened
Least Concern
EX
EW
CR
EN
VU
NT
LC
Years
For species with **foxtrot migration**, a decline in abundance within a specific part of the winter range may indicate changes in a range **dynamics** rather than an overall population decrease