Conserving bird populations in the Anthropocene: the significance of non-breeding movements

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ABSTRACT

Background

To conserve bird species threatened by climate change, it is important to understand how environmental factors affected by climate change, such as snow cover, impact their ranges. While this problem is fairly well understood for breeding areas, it remains poorly understood for non-breeding areas. In non-breeding areas, seasonal cycles can strongly influence the distribution of resources during winter. If birds adapt to such changes, they may result in seasonal and directional movement of birds within their non-breeding range. In this case, birds would experience a unique migration pattern - rapid migration between breeding and non-breeding habitats versus a slow migration pattern within their non-breeding range. Their non-breeding range would therefore be dynamic, with potentially important consequences for our understanding of population densities and non-breeding ranges.

Methods

Between 2013-2021, we tracked 43 adult Rough-legged buzzards with solar GPS-GSM loggers. We analyzed their behavior, determined whether the birds showed any directional return migrations during the non-breeding season, and evaluated the differences between the slow migration within their winter range and the quick migration between breeding and non-breeding areas. We also analyzed the vegetation cover of the areas crossed during quick and slow migrations and the role of snow cover in winter migrations.

Results

Our findings revealed that after a quick fall migration through the taiga zone, Rough-legged buzzards continue to migrate during the non-breeding season, albeit at a slower pace across the wooded fields they select as habitat. They avoid complete snow cover and move to escape the progression of the snow cover line from northeast to southwest and back during the winter. As a consequence, Rough-legged buzzards have a dynamic winter range. Thus, the migration pattern of these birds comprises alternating quick and slow phases, resembling the foxtrot dance, which we have named the ‘foxtrot’ migration pattern. Due to this pattern, their winter range displays a dynamic shift of the seasonal center of the population distribution over 1000 km towards the southwest and back throughout the winter.

Conclusions

Our study uncovered a novel bird migration pattern postulated to exist before but poorly understood. This ´foxtrot migration´ likely occurs in many migratory species inhabiting winter areas with pronounced seasonal cycles. Our findings have implications for conservation efforts in the Anthropocene, where environmental factors such as snow cover can change rapidly and have cascading effects on bird migration. We recommend presenting dynamic winter ranges in species descriptions and range maps so ecologists can use them to develop effective conservation strategies.

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

INTRODUCTION

Global climate change significantly impacts organisms and regions worldwide, with the Arctic experiencing more pronounced effects (Davy & Outten 2020; Previdi, Smith & Polvani 2021). These changes are potentially responsible for the decline in the numbers and ranges of many species and populations (Post *et al.* 2009; Gilg *et al.* 2012; Schmidt *et al.* 2012). Understanding the impact of environmental factors highly susceptible to climate change variation, such as snow cover, is critical for species conservation planning (Lawler 2009; Groves *et al.* 2012; Reside, Butt & Adams 2018). However, determining the distribution range and the seasonal changes in the local density of highly mobile taxa such as birds can be challenging. Many bird species undergo seasonal migrations, traditionally dividing their range into breeding and non-breeding areas. Most studies of climate change's impact on bird species have focused on changes in the breeding range, with less emphasis on the non-breeding range (Schmidt *et al.* 2012). This is primarily because the breeding range is easy to determine from nest counts and does not change during the season. In contrast, the non-breeding range is difficult to define as birds are not tied to any one location, despite spending most of their annual cycle within this range. Moreover, environmental factors affected by climate change can significantly influence the dynamics of the non-breeding range. In recent decades, advanced tracking technology has greatly improved our ability to study bird ecology. We can now follow birds throughout their life cycle and study the influence of environmental factors on the dynamic of their non-breeding range (Wikelski *et al.* 2007; Flack *et al.* 2022; Jetz *et al.* 2022).

The non-breeding range of many bird species can experience dramatic seasonal changes in food availability due to environmental conditions, such as the progressive snow cover line (Bildstein 2006). This line moves – at least in most north-temperate areas exposed to the northwesterly wind systems – from north (-east) to south (-west) and back again in many mid-latitude areas between October and May, affecting food availability for many bird species (Sonerud 1986; Vansteelant, Faveyts & Buckens 2011). We propose that species dependent on this environmental factor move gradually away from the snow cover during the winter and then gradually move in the opposite direction, resulting in a directed and seasonal movement of their winter range. Considering the complete life cycle of such species, they would exhibit a quick migration phase when moving between breeding and non-breeding ranges, followed by a slow migration phase with directed and seasonal movement within the non-breeding range, and finally, another quick migration phase towards the breeding range. Many insectivore bird species wintering in Africa exhibit a similar pattern – relatively fast migration across the Sahara desert

and then experiencing gradual directional movements during the non-breeding period (Stach *et al.* 2012; Jacobsen *et al.* 2017). Researchers propose that this movement is a consequence of a shift in the insect peak, which is, in turn, influenced by seasonal changes in precipitation (Stach *et al.* 2012). This type of movement can be compared to the foxtrot dance, which also involves alternating quick and slow phases of movement, both forward and backward. We, therefore, refer to this putative migration as the 'foxtrot' migration (Figure 1a) to allow for a quick and easily understandable description. The winter range in species exhibiting this type of migration will then have a dynamic structure that shifts with the ongoing non-breeding migration over time (Figure 1b).

This concept of 'foxtrot' migration synthesizes migrating and non-breeding movements. Traditionally, studies of bird movement ecology fall into two broad categories: migration studies and studies of movements within breeding and non-breeding ranges (Newton 2008; Berthold, Gwinner & Sonnenschein 2013). Migration studies have focused on the directed seasonal return movements between breeding and non-breeding ranges (Alerstam, Hedenström & Åkesson 2003; Bildstein 2006; Curk *et al.* 2020). This includes studies of different aspects of migration behavior: reasons for migration (McKinnon *et al.* 2010; Somveille, Rodrigues & Manica 2018; Pokrovsky *et al.* 2021), the timing of migration (Lameris *et al.* 2018; Lehikoinen *et al.* 2019), duration and length of migration routes (Nilsson *et al.* 2013), and other aspects. The variability in these characteristics gives rise to a wide range of migratory patterns, which vary greatly in the time taken to migrate. Some species migrate non-stop to their wintering grounds (Battley *et al.* 2012), some species experience a 'fly-and-forage' strategy, where birds hunt during migration and reduce their stopover time (Strandberg and Alerstam 2007), some make long stops to refuel (Shimada *et al.* 2014). Research in this area has also examined the influence of external environmental factors such as wind, rain, temperature, and day length on bird migration, revealing how these factors can limit food availability and shape migration patterns (Liechti & Bruderer 1998; Alerstam, Hedenström & Åkesson 2003; Curk *et al.* 2020; Pokrovsky *et al.* 2021). The second area of research focuses on daily routine movements, dispersal movements, nomadism, and habitat selection within breeding and non-breeding habitats (Greenwood & Harvey 1982; Lenz *et al.* 2015; Curk *et al.* 2022). In these studies, it is common to observe long movements in time and distance that are non-directional and non-returning as birds search for food or suitable nesting sites. At the same time, seasonal cycles can significantly affect resource distribution across the wintering range of species. This, in turn, can lead to directional and seasonal bird movements within the wintering range, commonly referred to as migratory

behavior. We hypothesize that such a migration pattern and dynamic winter range could be observed in mid-latitude wintering Arctic raptors.

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 wintering distribution.

For this study, we hypothesized that Rough-legged buzzards would undertake a combined ‘foxtrot’ migration and dynamic winter 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 winter, moving from the northeast to the southwest and back again. This would result in a dynamic winter range that would continue to move geographically throughout the season. 2) Winter migrations would differ from fall and spring migrations in duration, extent, speed, and direction. 3) Winter migrations would occur in suitable open habitats, whereas fall and spring migrations would occur in unfitting forested areas. 4) The snow conditions experienced by the Rough-legged buzzards during their winter migration would differ from those in the areas of their winter range where they arrived after their autumn migration, with less snow cover encountered during their winter migration than if they had remained where they arrived at the end of their fall migration.

In the following, we will refer to the spring and fall migrations as the quick migration, the winter migration to the lowest point of latitude as the 1st phase of the slow migration, and the migration from the lowest point of latitude to the starting point of the spring migration as the 2nd phase of the slow migration (Figure 1a).

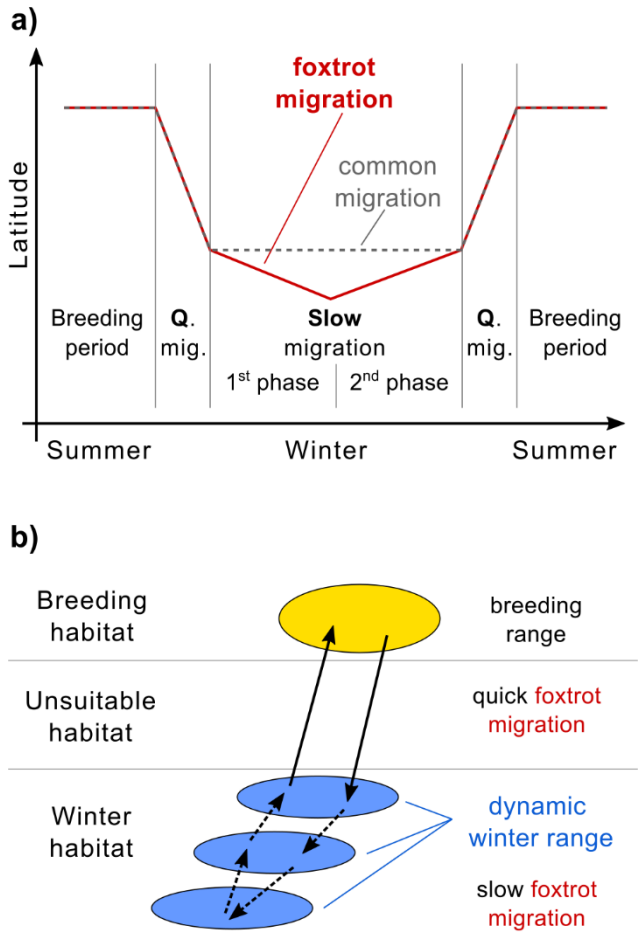

Figure 1. Hypothetical foxtrot migration and dynamic winter range scheme. a) Foxtrot migration, Q. mig. – Quick migration (spring and fall migrations). b) Dynamic winter range.

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)1st phase of winter, 4) 2nd phase 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 phases 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 migrations, 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 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°. 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 phase of the slow winter migration, the birds returned to 55.52±2.63° latitude and 49.79±8.24° longitude to start the spring migration. 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).

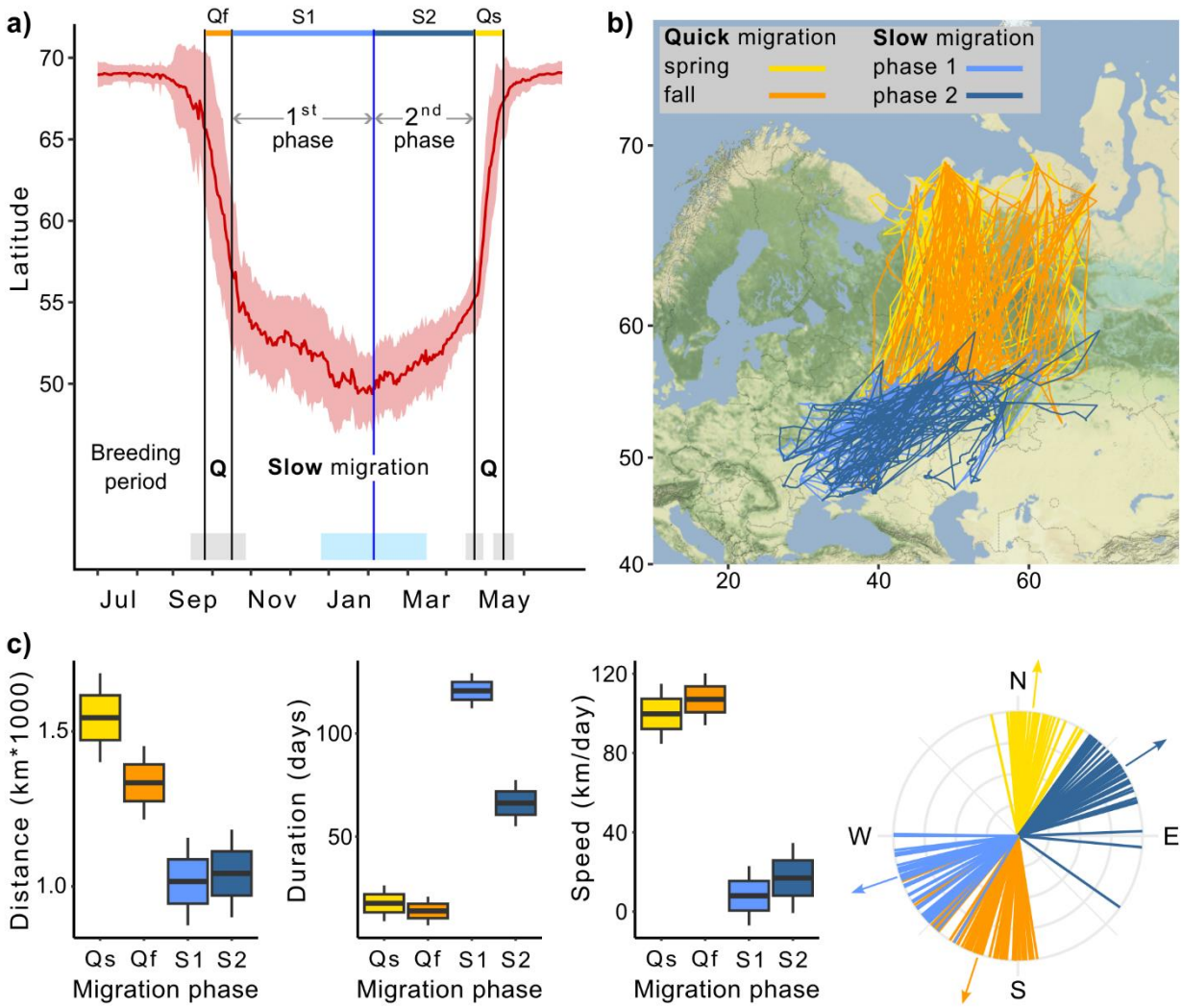

Figure 2. Quick and slow migration patterns of Rough-legged buzzards throughout an annual cycle, termed ´foxtrot migration´ for quick referencing. Q – quick migration. Qf – Quick fall migration (orange), Qs – Quick spring migration (yellow), S1 – Slow migration, 1st phase (light blue), S2 – Slow migration, 2nd phase (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 periods. Lines on the direction plot (down, right) represent the mean value for each bird; arrows represent the mean direction.

Quick-slow migration features comparison

During quick migration, individual birds flew greater distances in a shorter time, i.e., at a faster rate, than during slow migration. After arriving at what is traditionally known as the wintering grounds, the direction of migration changed, so the direction of quick and slow migration also differed (Table 1, Figure 2c). The quick migration was 1415±50 km long, whereas the slow migration (one phase) was 1026±55 km, i.e., 389±60 km shorter ($p<0.001$, Table S4, Figure 2c). During quick migration, birds flew for 15±3 days, and one phase of slow migration lasted 100±4 days, i.e., 85±5 days longer ($p<0.001$, Table S5, Figure 2c). At the same time, the second phase of slow migration 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 1st slow phase until mid-winter. After that, they turned back to the NEE direction (57±2 deg) and performed their 2nd slow migration 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	
	1st 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 fast migrations, Rough-legged buzzards cross the forest zone, while during slow migrations, 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 migration, the three most common vegetation land cover types were forest (44.5±2.9 %, hereafter, percentage of all mean daily positions during migration annotated with the given vegetation type), shrublands (29.9±3 %), and grasslands (24.7±2.8 %, Figure 3a). During slow migration, 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 migration periods ($p<0.001$, Table S9), except for the urban lands. Urban lands were more common during the slow than quick migration (Figure 3). However, this type has been annotated for too few birds to make an adequate comparison.

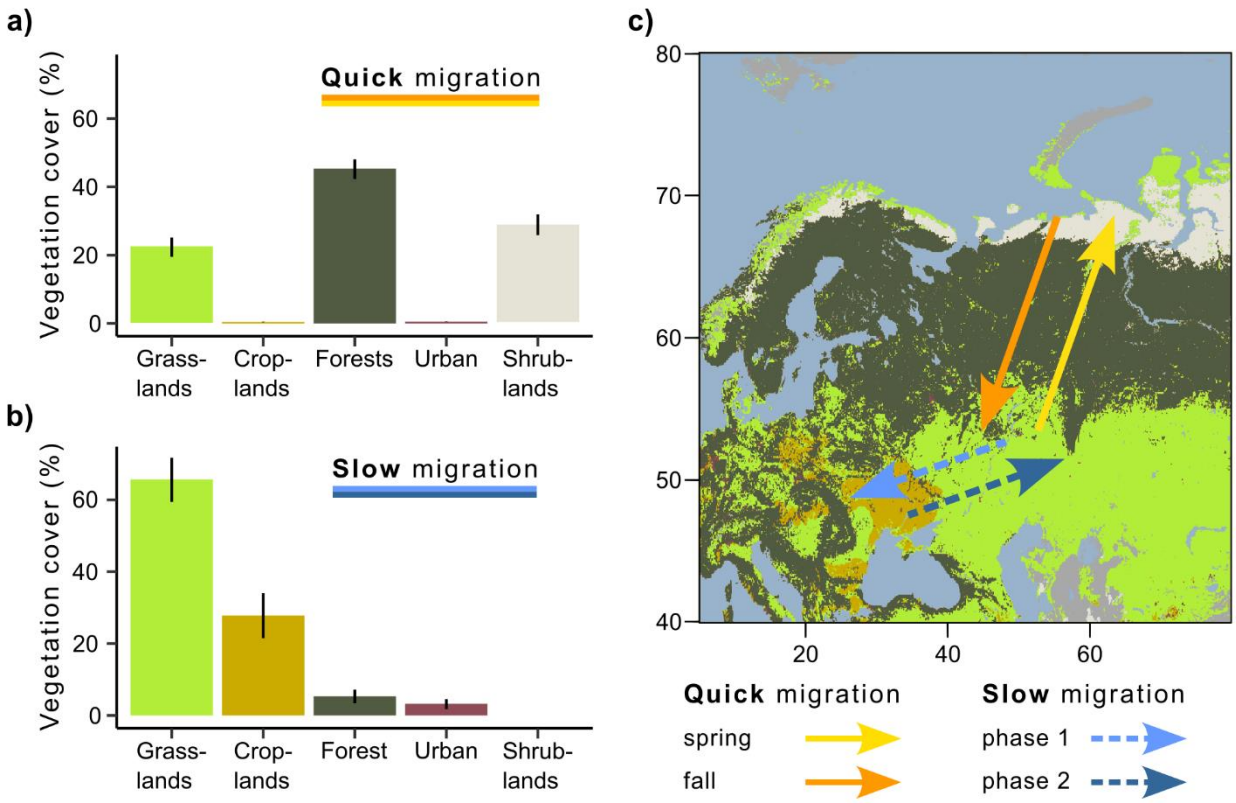

Figure 3. Vegetation land cover during quick and slow migration. a) Quick migration. Spring and fall migration together. b) Slow migration. 1st and 2nd phases of the slow migrations together. c) Migration map.

Snow cover – the main reason for the dynamic winter range

During the slow winter 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).

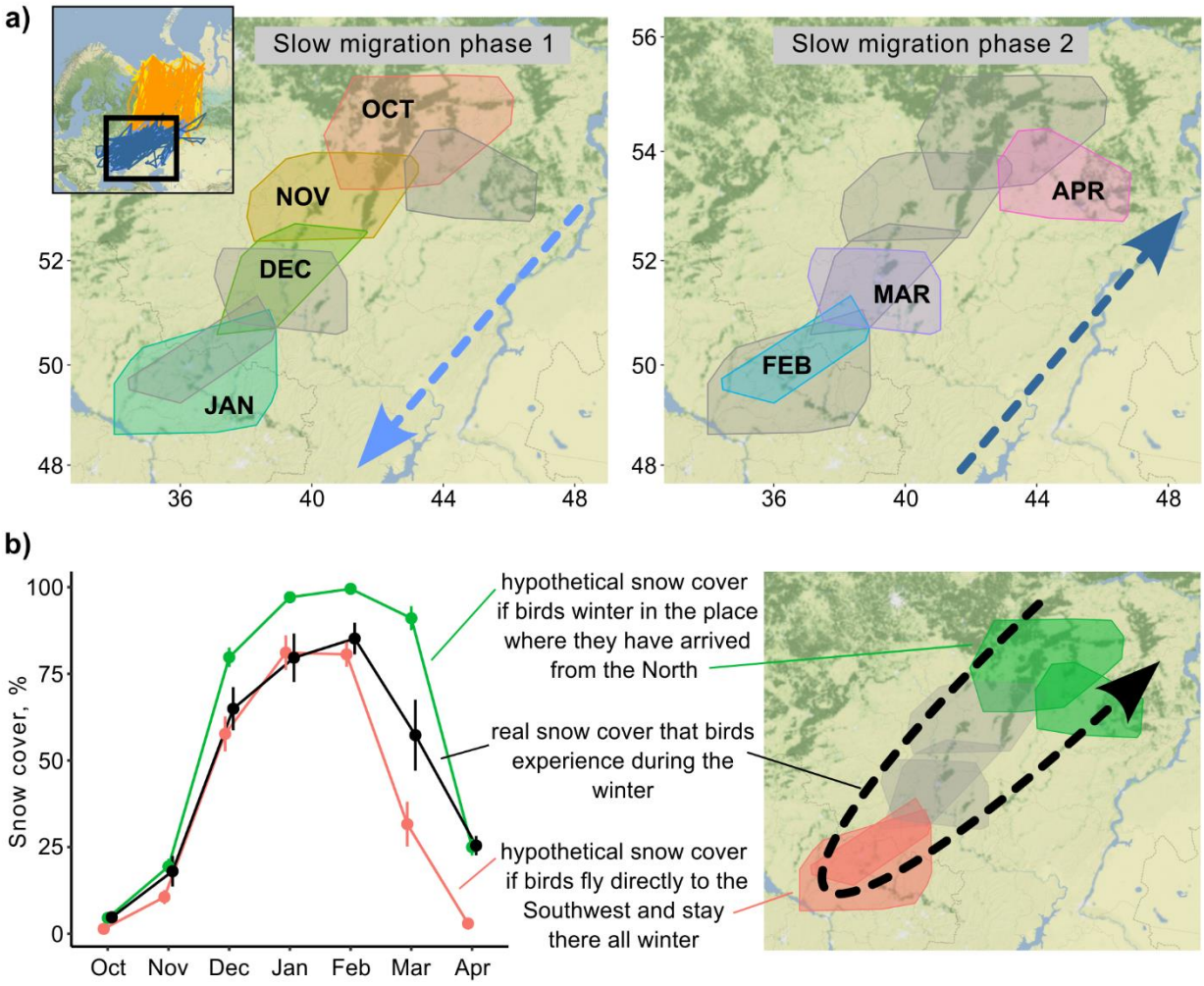

Figure 4. Slow migration and snow cover conditions. a) 95% Minimum convex polygons (MCPs) of Rough-legged buzzards during winter. Arrows indicate the direction of the movement across months. OCT – October, NOV – November, DEC – December, JAN – January, FEB – February, MAR – March, APR – April. b) Snow 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.

DISCUSSION

Our study has revealed a novel bird migration pattern that likely occurs in many migratory species inhabiting winter areas with pronounced seasonal cycles. This pattern results in the dynamic shift of the birds' non-breeding range by hundreds of kilometers. In contrast to traditional migration patterns where birds settle in a single location after the initial rapid migration phase in the fall (Bildstein 2006; Newton 2008), the quick-and-slow migration involves a continuous migration at a slower pace through the winter range, followed by a swift return to the breeding site (Figures 2a, b; 4a; 5a). This pattern features a consistent, directional return migration throughout the winter, which is repeated annually, unlike the nomadic movements observed in some bird species during winter (Eng & Schladweiler 1972; Roth & Vetter 2008; Heckscher *et al.* 2011). We, therefore, termed this migration pattern 'foxtrot' migration – a quick movement followed by slow movements in different directions – for quick referencing. Also, unlike the 'fly-and-forage' migration pattern (Strandberg & Alerstam 2007) and long stopovers during migrations (Shimada *et al.* 2014) caused by physiological needs, in this case, birds are moving primarily due to external factors that are changing rapidly in the present-day world as a result of climate change. Therefore, this pattern is potentially subject to significant change during the Anthropocene, a change that could have cascading effects on species distributions.

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 hypothesis. We suggest that population changes of highly mobile organisms in many non-breeding areas around the world could be similarly explained by a more or less continuous movement of individuals in response to climate alterations.

Understanding the dynamic range and migration pattern of Rough-legged buzzards is crucial for developing effective conservation strategies for this, but also for other species. In

conservation planning, balancing prohibited management activities within the species' range and the benefits of such activities is a key consideration (Beatley 1992; Jones, Pejchar & Kiesecker 2015; Harfoot *et al.* 2018; Carrell, Hammill & Edwards 2022). By understanding the dynamic range of the species, a more optimal trade-off can be identified, allowing management activities to be carried out when the species is not present. We recommend that researchers working on species distribution atlases and range maps take this important aspect of a species´ biology into account. In most of the bird atlases and web resources of today (Keller *et al.* 2020; Audubon 2022), the winter range is usually depicted as a single entity or an area where the species may be present in varying densities (Figure 5b, c), indicating spatial heterogeneity. We propose that temporal heterogeneity be identified as separate zones, indicating periods when the species is abundant, perhaps beyond a threshold value, in the area. To differentiate from spatial heterogeneity, we suggest using lines to define the boundaries of these zones instead of using color shading (Figure 5c) or arrows to show the migration phases (Figure 5a). It is important to note that when mid-winter counts (e.g., Christmas counts) are used to determine the winter range, the spatial heterogeneity observed may be due to temporal heterogeneity. This study indicates that the fact that the majority of birds are far from the northern limit of their winter range in mid-winter does not necessarily mean that they are less abundant there throughout the winter compared to other parts of their winter range.

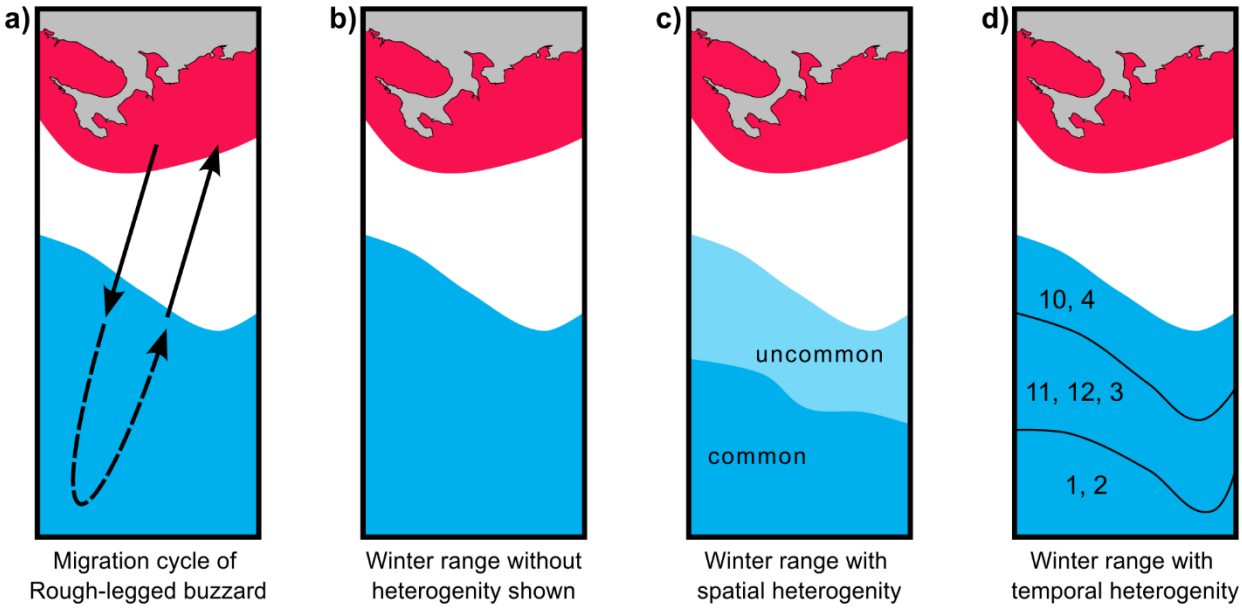

Figure 5. Winter range representations. Red – breeding range, blue – winter range. a) Migration cycle of Rough-legged buzzard; arrows represent migration (solid line – quick migration, dashed line – slow migration). b) Winter range without heterogeneity shown. c) Winter range with spatial heterogeneity. d) Winter range with temporal heterogeneity; the numbers indicate the months the birds are common in the outlined area.

While the practical importance of this migratory behavior is clear, understanding the reasons behind this pattern of migration is crucial for predicting potential changes in response to climate change. As in the case of species wintering in subtropical or tropical parts of Africa, the movement patterns are likely driven by the interplay between seasonal cycles and habitat types – similar to what we propose for the alternating periods of fast and slow migration in Rough-legged buzzards. During the quick migration phase, birds pass through habitats that are unfavorable for their survival, while during the slow migration phase, they navigate through more suitable habitats. In our study, the quick migration tracks, as shown in Figures 2 a, b and 3, traverse the taiga zone, which is not conducive to the hunting needs of Rough-legged buzzards, which require open areas for hunting (Ferguson-Lees & Christie 2001; Bechard & Swem 2002). Upon arriving in an appropriate habitat, such as a wooded field and croplands, the birds temporarily halt or slow their migration but then turn from the south to the southwest and gradually migrate in this direction as the winter progresses (Figures 2c and 4). The question arises as to why the birds turn to the southwest and do not continue their migration further south into the steppe zone, which is an open habitat, too. We assume that the lack of forests in the steppe, which serve as crucial roosting sites for Rough-legged buzzards, prevents them from doing so. Our analysis of the locations assigned to forests during the slow migration revealed a scarcity of such sites, with less than 5% of the locations being assigned to forests (Figure 3b). Despite their scarcity in these habitats, forests appear to hold significant importance for Rough-legged buzzards for nocturnal safety. Another question is why Rough-legged buzzards do not stay in places where their autumn migration has ended. Based on our analysis, we postulate that the primary driver behind the winter migration of Rough-legged buzzards is the southwestward progression of the snow line over the winter season.

The progression of snow cover in the wintering range of Rough-legged buzzards plays a significant role in their winter migration pattern. The winter range of Rough-legged Buzzards experiences a dynamic snow cover with a gradual increase from October to January-February and a subsequent gradual decrease from February to May, moving from the northeastern part of the range to the southwestern part. Correspondingly, the buzzards also move from northeast to southwest during the winter, as if in response to the increasing snow (Figures 2b, 4a). They only partially avoid snow, with snow cover reaching 85% in the southeast of their range by mid-winter. However, they successfully avoid continuous snow cover, with snow cover reaching 100% in the northeast part of their range (Figure 4b). There is a critical limit of snow cover,

around 90%, beyond which hunting becomes infeasible. The shortening day length in the northeast compared to the southwest and the fact that Rough-legged buzzards only hunt during the day (Pokrovsky *et al.* 2021) highlights the significance of even a tiny difference in snow cover. One might wonder why the buzzards would not move to the southwest of the range in the autumn and remain there throughout the winter. This behavior might be attributed to optimizing migration energy costs, with the buzzards moving to the optimal habitat only when the prevailing conditions become unfavorable for their survival. This is in accordance with the theory of optimal migration (Alerstam & Lindström 1990; Houston 1998; Newton 2008). However, some individuals may migrate directly to the southwest, reflecting the plasticity of the migration behavior (Figure S1). The dynamics of snow cover hold a significant influence not only over the winter migration patterns but also in the entire migration cycle of Rough-legged buzzards.

Both quick and slow migration phases in Rough-legged buzzards are influenced by environmental changes that are part of seasonal cycles (Sonerud 1986; Curk *et al.* 2020). These cycles result in variations in temperature, precipitation, snow cover, and day length, which affect food availability. Latitude affects the extent of these seasonal changes. In autumn, birds in northern breeding grounds face declining temperatures, shorter days, and increased snow cover, prompting a migration to escape these adverse conditions (Alerstam 1991; Houston 1998; Alerstam, Hedenström & Åkesson 2003). However, unfavorable habitats in the southern portion of their breeding range (taiga zone) prevent gradual movement away from adverse environmental conditions. Hence, they perform quick migration to cross the forest zone. Once in favorable habitats, the birds are temporarily insulated from the negative factors they had previously fled, allowing for respite. As the influence of these negative factors eventually reaches the birds' favorable habitats in the south, they must migrate again, but at a slower pace that corresponds with the gradual approach of these factors. This delay results in a slower migration rate in the first half of winter compared to the second half (Figure 2, Table S2).

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.

The quantification of environmental changes that could prove fatal to bird species presents yet another challenge for conservation efforts in an era of rapid global change. In this study, we have demonstrated the impact of seemingly minor variations in ecological parameters

on the species' behavior. For instance, the presence of small patches of woodland in the winter range might appear crucial to the survival of the Rough-legged buzzard. Elimination of these seemingly minor elements of vegetation cover through management actions could have dire consequences for the species. Similarly, snow cover, while not necessarily a limiting factor in the distribution of a particular species, can become critical at certain thresholds and play a crucial role in shaping species' behavior. As our study shows, if Rough-legged buzzards fly southwest immediately and stay there for the whole winter, they will experience 25.7% (57.3% vs. 31.6%) less snow cover in March, but this does not force them to adopt this strategy. At the same time, if Rough-legged buzzards stay where they finished their fall migration and don't move southwest, they will experience 14.4% (99.5% vs. 85.1%) more snow cover in February, and this will force them to migrate. The point is that in this case, although the difference is not as great (14.4% vs. 25.7%), it is the difference between complete snow cover and inconsistent snow cover. This again shows that when we discuss conservation strategies, it is not necessarily important to judge such parameters in terms of numbers or percentages, but rather to understand the context of these parameters in the species' biology and their importance for the species' existence. In some contexts, significant environmental changes may not affect the species' life, but in other contexts, even small changes in the same environmental parameters may be fatal to the species: in short, there may be tipping points in environmental settings that are not predicted by a small linear increase in effect sizes.

CONCLUSIONS

The quick-and-slow migration pattern of Rough-legged buzzards (we termed them ´foxtrot migration´) results in a significant temporal shift of their winter range of over 1000 km. After the birds arrive in their ´wintering range´, they move slowly but continuously towards the southwest and back during the winter, highlighting the adaptability of birds in response to changing environments. Our findings have crucial implications for conservation efforts in the Anthropocene, where rapidly changing environmental factors can severely impact bird migration (Tucker *et al.* 2018; Sumasgutner *et al.* 2021). We suggest that ecologists should include dynamic winter ranges in species descriptions and range maps to develop effective conservation strategies for the bird species. The knowledge about dynamic range shifts is imperative in the face of rapid climate and human-induced habitat changes threatening wildlife and humans.

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