Ecology

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

Ivan Pokrovsky ✉, **Teja Curk, Andreas Dietz, Ivan Fufachev, Olga Kulikova, Sebastian Rößler, Martin Wikelski**

Department of Migration, Max Planck Institute of Animal Behavior, Radolfzell, Germany • Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany • Deutsches Zentrum für Luft- und Raumfahrt e.V. (DLR), Wessling, Germany • Institute of Plant and Animal Ecology, Yekaterinburg, Russia • Institute of Biological Problems of the North, Magadan, Russia • Centre for the Advanced Study of Collective Behaviour, University of Konstanz, 78457 Konstanz, Germany

Reviewed Preprint

Revised by authors after peer review.

About eLife's process

Reviewed preprint version 2
April 26, 2024 (this version)

Reviewed preprint version 1
July 3, 2023

Sent for peer review
April 1, 2023

Posted to preprint server
March 15, 2023

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.

eLife assessment

This work presents a **useful** finding on non-breeding itinerant behavior of a migratory raptor. With its extensive dataset and analytical framework, this work is of interest to researchers investigating the ecological drivers of bird migration. However, the main claim on a novel migration pattern (so-called 'fox-trot migration') is **incomplete** in light of current knowledge on bird migratory behavior.

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**).

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-

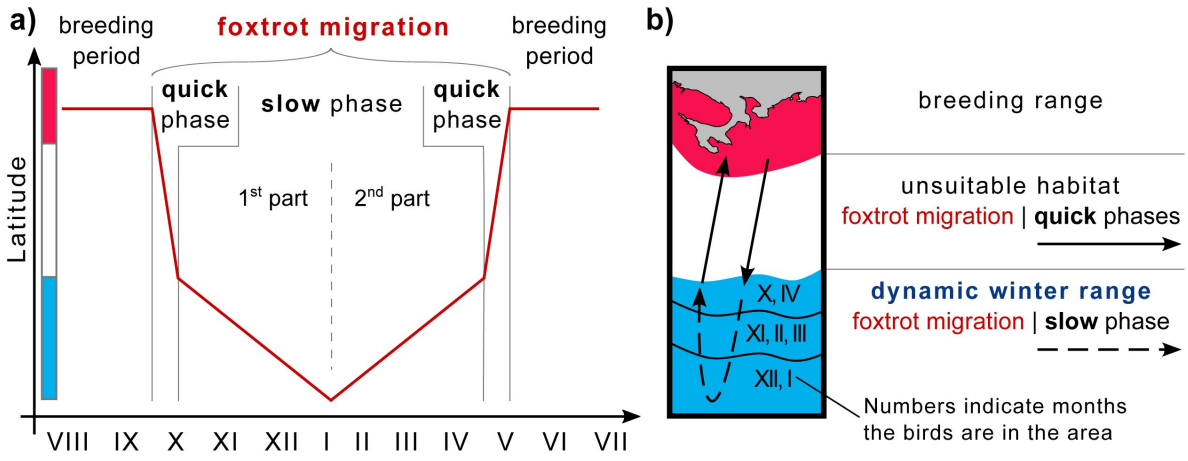

Figure 1.

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.

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 1st part of the slow phase, and the movement from the lowest point of latitude to the starting point of the spring migration as the 2nd 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)1st part of winter, 4) 2nd 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 bird' arrival at their traditionally recognized 'wintering ground' (**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).

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 1st slow phase until mid-winter. After that, they turned back to the NEE direction (57±2 deg) and performed their 2nd 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).

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 %,

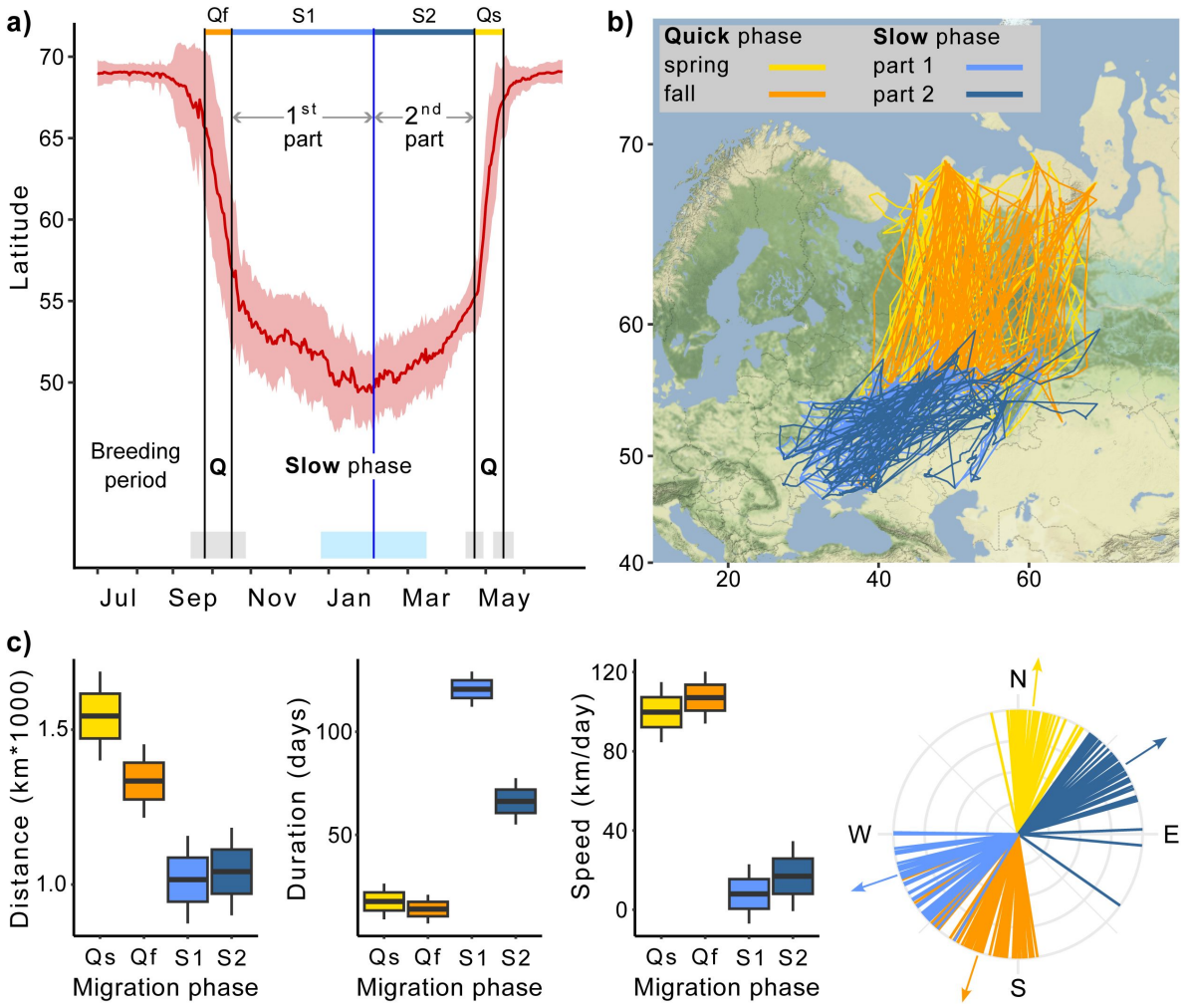

Figure 2.

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.

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

Table 1.

Parameters of the rough-legged buzzards' migration.

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.

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**).

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

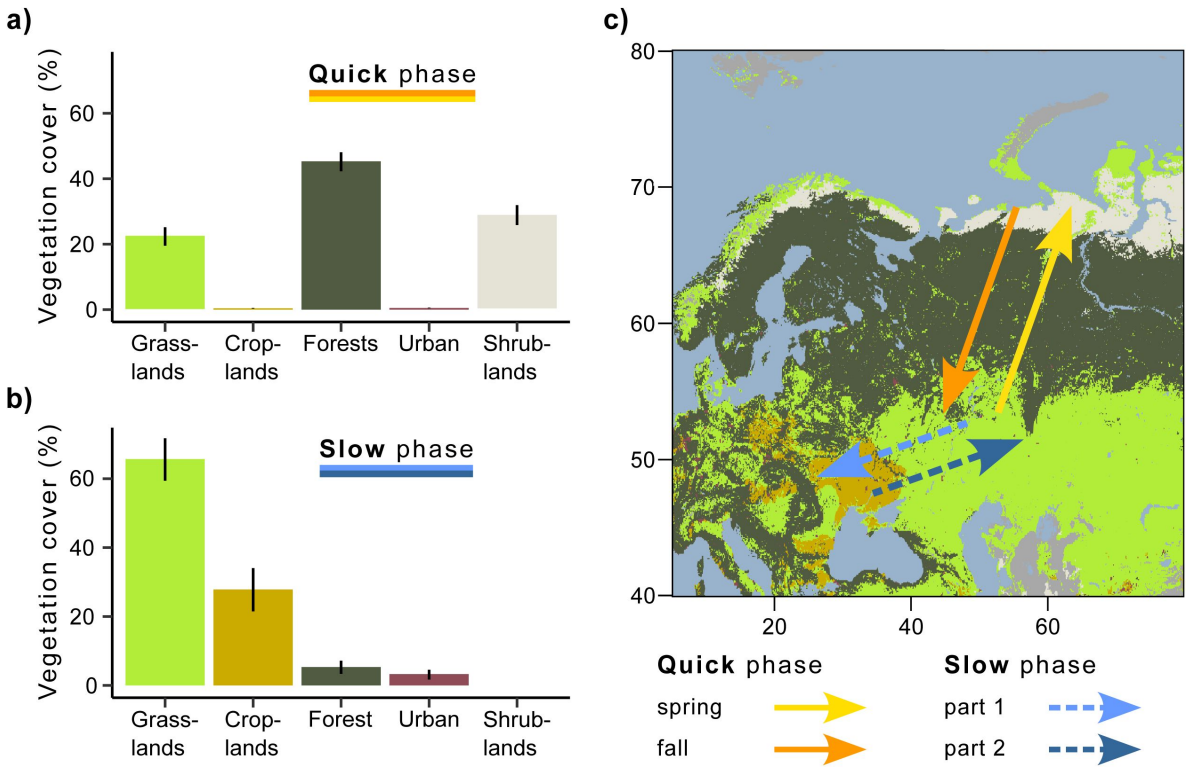

Figure 3.

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.

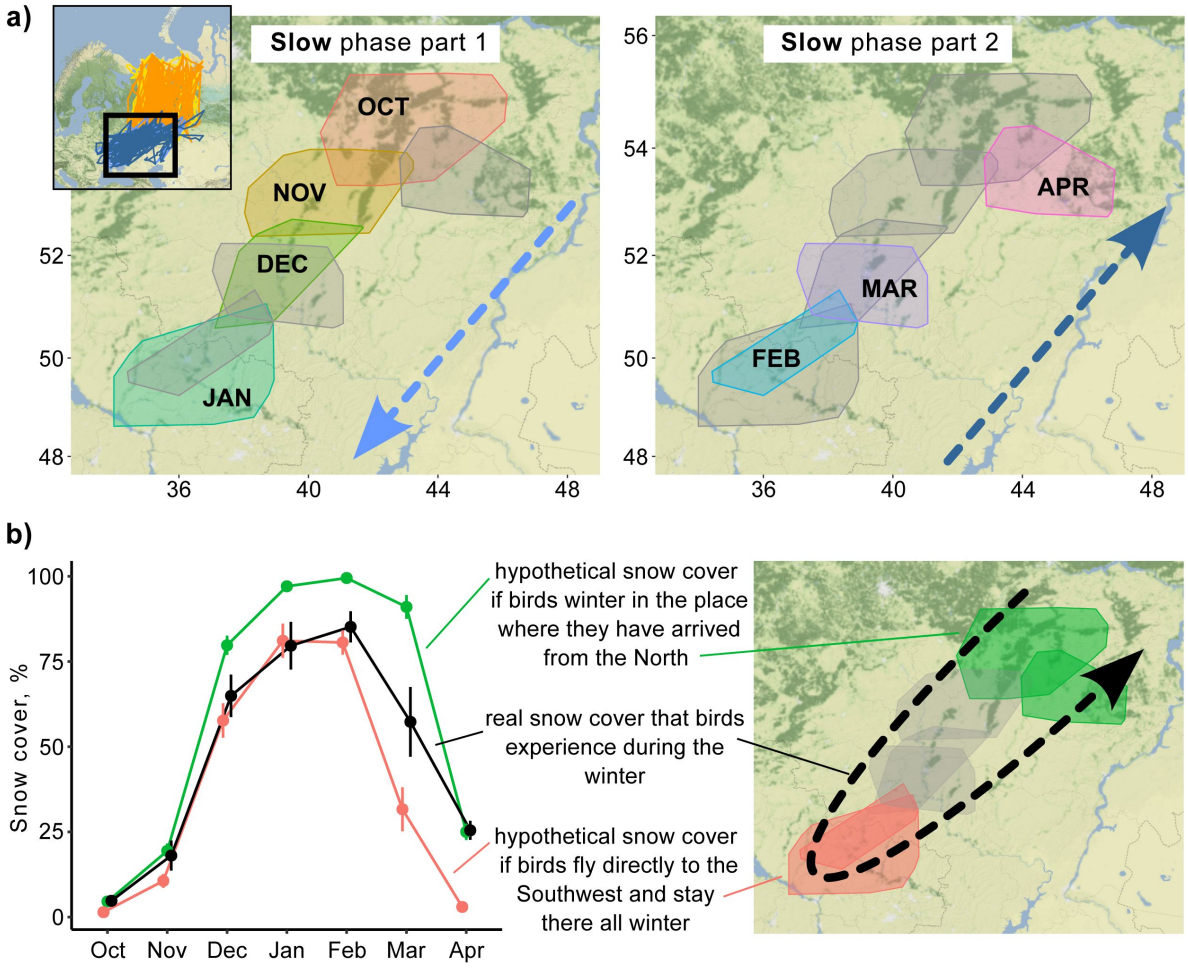

Figure 4.

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.

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**).

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.

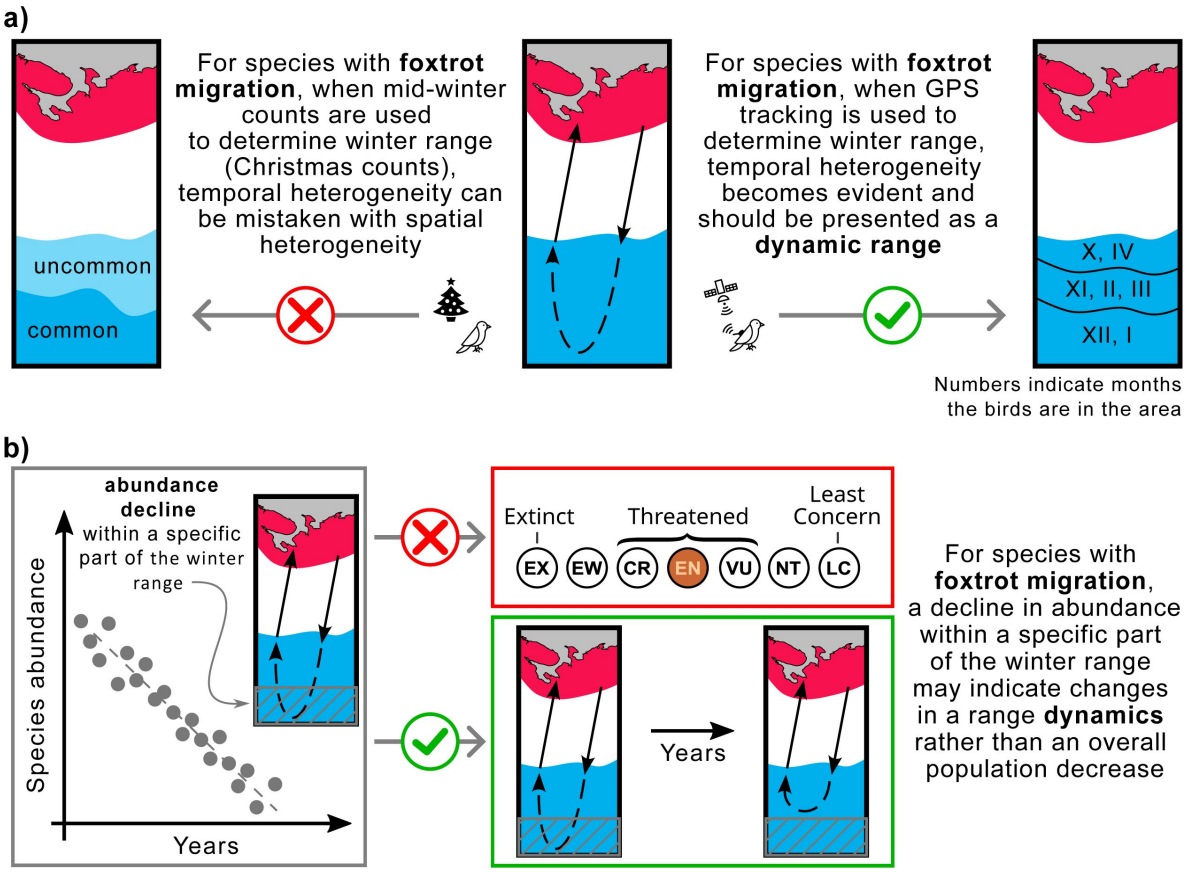

Figure 5.

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.

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.

Acknowledgements

We are very grateful to everyone who helped us collect data in the field. This study was funded by the Max-Planck Institute of Animal Behavior and the German Air and Space Administration (DLR). We also acknowledge partial funding by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germany's Excellence Strategy – EXC 2117 – 422037984.

References

Alerstam T (2011) **Optimal bird migration revisited** *Journal of Ornithology* **152**:5–23

Alerstam T., Bäckman J (2018) **Ecology of animal migration** *Current Biology* **28**:R968–R972

Alerstam T., Hake M., Kjellén N (2006) **Temporal and spatial patterns of repeated migratory journeys by ospreys** *Journal of Animal Behaviour* **71**:555–566

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

Bates D., Mächler M., Bolker B., Walker S (2015) **Fitting Linear Mixed-Effects Models Using lme4** *Journal of Statistical Software* **67**

Bechard M.J., Swem T.R, Poole A. (2002) **Rough-legged Hawk (Buteo lagopus), The Birds of North America Online**

Berthold P., Gwinner E., Sonnenschein E. (2013) **Avian migration1**

Bildstein K.L (2006) **Migrating raptors of the world: their ecology & conservation**

Billerman S.M., Keeney B.K., Rodewald P.G., Schulenberg T.S (2024) **Birds of the World**

Calenge C (2006) **The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals** *Ecological Modelling* **197**:516–519

Chapman B.B., Hulthén K., Wellenreuther M., Hansson L.-A., Nilsson J.-Å., Brönmark C, Hansson L.-A., Susanne Å. (2014) **Patterns of animal migration. Animal movement across scales** :11–35

Crawley M.J (2007) **The R Book**

Curk T., Kulikova O., Fufachev I., Wikelski M., Safi K., Pokrovsky I (2022) **Arctic Migratory Raptor Selects Nesting Area During the Previous Breeding Season** *Frontiers in Ecology and Evolution* **10**

Curk T. *et al.* (2020) **Arctic avian predators synchronise their spring migration with the northern progression of snowmelt** *Scientific Reports* **10**

Davy R., Outten S (2020) **The Arctic surface climate in CMIP6: status and developments since CMIP5** *Journal of Climate* **33**:8047–8068

Dietz A.J., Kuenzer C., Dech S (2015) **Global SnowPack: a new set of snow cover parameters for studying status and dynamics of the planetary snow cover extent** *Remote Sensing Letters* **6**:844–853

Dodge S., Bohrer G., Weinzierl R., Davidson S.C., Kays R., Douglas D., Cruz S., Han J., Brandes D., Wikelski M (2013) **The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data** *Movement Ecology* **1**

Ferguson-Lees J., Christie D (2001) **Raptors of the World**

Friedl M., Sulla-Menashe D. (2015) **MCD12C1 MODIS/Terra+Aqua Land Cover Type Yearly L3 Global 0.05Deg CMG V006.**

García J.T., Arroyo B.E (1998) **Migratory movements of western European Montagu's Harrier Circus pygargus: a review** *Bird Study* **45**:188–194

Gilg O. *et al.* (2012) **Climate change and the ecology and evolution of Arctic vertebrates** *Annals of the New York Academy of Sciences* **1249**:166–190

Hijmans R.J (2016) **geosphere: Spherical Trigonometry** *R package version* **1**:5–5

Hijmans R.J., van Etten J. (2023) **raster: Geographic data analysis and modeling** *R package version*

Hornman M., Boele A., van Winden E. (2022) **Ruigpootbuizerd: steeds schaarser, behalve in piekjaren** *Nature Today*

Jetz W. *et al.* (2022) **Biological Earth observation with animal sensors** *Trends in Ecology & Evolution* **37**:293–298

Kays R., Wikelski M (2023) **The Internet of Animals: what it is, what it could be** *Trends in Ecology & Evolution*

Keller V. *et al.* (2020) **European Breeding Bird Atlas 2: Distribution, Abundance and Change.**

Lenth R., Singmann H., Love J., Buerkner P., Herve M. (2019) **Package 'emmeans'.**

Lislevand T., Hahn S., Rislaa S., Briedis M (2020) **First records of complete annual cycles in water rails Rallus aquaticus show evidence of itinerant breeding and a complex migration system** *Journal of Avian Biology* **51**

Lopez-Ricaurte L., Vansteelant W.M.G., Hernández-Pliego J., García-Silveira D., Casado S., Garcés-Toledano F., Martínez-Dalmau J., Ortega A., Rodríguez-Moreno B., Bustamante J (2024) **Itinerant lifestyle and congregation of lesser kestrels in West Africa** *Journal of Avian Biology* **2024**

Mearns R., Newton I (1984) **Turnover and dispersal in a peregrine Falco peregrinus population** *Ibis* **126**:347–355

Moreau R.E (1972) **The Palaearctic-African Bird Migration Systems**

Newton I (2008) **The Migration Ecology of Birds**

Pokrovsky I., Ehrich D., Fufachev I., Ims R.A., Kulikova O., Sokolov A., Sokolova N., Sokolov V., Yoccoz N.G (2019) **Nest association between two predators as a behavioral response to the low density of rodents** *The Auk* **137**

Pokrovsky I., Ehrich D., Ims R., Kulikova O., Lecomte N., Yoccoz N (2014) **Diet, nesting density, and breeding success of rough-legged buzzards (Buteo lagopus) on the Nenetsky Ridge, Arctic Russia** *Polar Biology* **37**:447–457

Pokrovsky I., Ehrich D., Ims R.A., Kondratyev A.V., Kruckenberg H., Kulikova O., Mihnevich J., Pokrovskaya L., Shienok A (2015) **Rough-Legged Buzzards, Arctic Foxes and Red Foxes in a Tundra Ecosystem without Rodents** *Plos One* **10**

Pokrovsky I., Kölzsch A., Sherub S., Fiedler W., Glazov P., Kulikova O., Wikelski M., Flack A (2021) **Longer days enable higher diurnal activity for migratory birds** *Journal of Animal Ecology* **90**:2161–2171

Posit team (2022) **RStudio: Integrated Development Environment for R** *Posit Software, PBC, Boston, MA*

Post E. *et al.* (2009) **Ecological Dynamics Across the Arctic Associated with Recent Climate Change** *Science* **325**:1355–1358

Previdi M., Smith K.L., Polvani L.M (2021) **Arctic amplification of climate change: a review of underlying mechanisms** *Environmental Research Letters* **16**

R Development Core Team (2022) **R: A language and environment for statistical computing**

Richter S., Bick A, Beck L.A. (2018) **ROSTOCK: The Zoological Collection of the University of Rostock. Zoological Collections of Germany: The Animal Kingdom in its Amazing Plenty at Museums and Universities** :583–589

Schlaich A.E., Klaassen R.H.G., Bouten W., Bretagnolle V., Koks B.J., Villers A., Both C (2016) **How individual Montagu's Harriers cope with Moreau's Paradox during the Sahelian winter** *Journal of Animal Ecology* **85**:1491–1501

Schmidt N.M., Ims R.A., Hoye T.T., Gilg O., Hansen L.H., Hansen J., Lund M., Fuglei E., Forchhammer M.C., Sittler B (2012) **Response of an arctic predator guild to collapsing lemming cycles** *Proceedings of the Royal Society B-Biological Sciences* **279**:4417–4422

Serrano D., Tella J.L., Forero M.G., Donazar J.A (2001) **Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues** *Journal of Animal Ecology* **70**:568–578

Sonerud G.A (1986) **Effect of snow cover on seasonal changes in diet, habitat, and regional distribution of raptors that prey on small mammals in boreal zones of Fennoscandia** *Ecography* **9**:33–47

Sumasgutner P., Buij R., McClure C.J.W., Shaw P., Dykstra C.R., Kumar N., Rutz C (2021) **Raptor research during the COVID-19 pandemic provides invaluable opportunities for conservation biology** *Biological Conservation* **260**

Sundell J., Huitu O., Henttonen H., Kaikusalo A., Korpimaki E., Pietiainen H., Saurola P., Hanski I (2004) **Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators** *Journal of Animal Ecology* **73**:167–178

Tast J., Kaikusalo A., Lagerström M (2010) **Diet composition of breeding rough-legged buzzards Buteo lagopus at Kilpisjärvi** *NW Finnish Lapland. Kilpisjärvi Notes* **22**:10–18

Terraube J., Villers A., Ruffino L., Iso-Iivari L., Henttonen H., Oksanen T., Korpimäki E (2015) **Coping with fast climate change in northern ecosystems: mechanisms underlying the population-level response of a specialist avian predator** *Ecography* **38**:690–699

Thorup K., Tøttrup A.P., Willemoes M., Klaassen R.H.G., Strandberg R., Vega M.L., Dasari H.P., Araújo M.B., Wikelski M., Rahbek C (2017) **Resource tracking within and across continents in long-distance bird migrants** *Science advances* **3**

Tucker M.A. *et al.* (2018) **Moving in the Anthropocene: Global reductions in terrestrial mammalian movements** *Science* **359**:466–469

Vansteelant W., Faveyts W., Buckens J (2011) **Opmerkelijke Ruigpootbuizerdinvasie in de winter 2010-2011: oorzaken in een historische en Europese context** *Natuur.oriolus* **77**:87–98

Verhoeven M.A., Loonstra A.H.J., McBride A.D., Both C., Senner N.R., Piersma T (2021) **Migration route, stopping sites, and non-breeding destinations of adult Black-tailed Godwits breeding in southwest Fryslân, The Netherlands** *Journal of Ornithology* **162**:61–76

Walker D.A. *et al.* (2005) **The Circumpolar Arctic vegetation map** *Journal of Vegetation Science* **16**:267–282

Whitfield D.P., Duffy K., McLeod D.R., Evans R.J., MacLennan A.M., Reid R., Sexton D., Wilson J.D., Douse A (2009) **Juvenile dispersal of white-tailed eagles in western Scotland** *Journal of Raptor Research* **43**:110–120

Wikelski M., Kays R.W., Kasdin N.J., Thorup K., Smith J.A., Swenson G.W (2007) **Going wild: what a global small-animal tracking system could do for experimental biologists** *Journal of Experimental Biology* **210**:181–186

Zwarts L., Bijlsma R.G., van der Kamp J., Wymenga E (2012) **Living on the Edge: Wetlands and Birds in a Changing Sahel. KNNV Publishing**

Article and author information

Ivan Pokrovsky
Department of Migration, Max Planck Institute of Animal Behavior, Radolfzell, Germany
For correspondence: ipokrovsky@ab.mpg.de
ORCID iD: 0000-0002-6533-674X

Teja Curk
Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany
ORCID iD: 0000-0002-9082-6433

Andreas Dietz
Deutsches Zentrum für Luft- und Raumfahrt e.V. (DLR), Wessling, Germany
ORCID iD: 0000-0002-5733-7136

Ivan Fufachev
Institute of Plant and Animal Ecology, Yekaterinburg, Russia
ORCID iD: 0000-0002-9531-3127

Olga Kulikova
Institute of Biological Problems of the North, Magadan, Russia
ORCID iD: 0000-0002-4029-9452

Sebastian Rößler
Deutsches Zentrum für Luft- und Raumfahrt e.V. (DLR), Wessling, Germany
ORCID iD: 0000-0001-5462-2495

Martin Wikelski
Department of Migration, Max Planck Institute of Animal Behavior, Radolfzell, Germany, Centre for the Advanced Study of Collective Behaviour, University of Konstanz, 78457 Konstanz, Germany
ORCID iD: 0000-0002-9790-7025

Copyright

Editors

Reviewing Editor
Yuuki Watanabe
Graduate University for Advanced Studies, SOKENDAI, Tokyo, Japan

Senior Editor
Detlef Weigel
Max Planck Institute for Biology Tübingen, Tübingen, Germany

Reviewer #2 (Public Review):

This preprint by Pokrovsky and coworkers is a descriptive study reporting on non-breeding itinerant behaviour of an intrapalearctic migratory raptor, the rough-legged buzzard, and relating such non-breeding movements to snow cover across the European non-breeding range. The article is based on long-term GPS tracking data from a relatively large (n=43) sample of individuals that were equipped with state-of-the-art tracking devices in the Russian Arctic during 2013-2019. The results show that, upon breeding, buzzards migrated rapidly to southern non-breeding areas, located in open areas north of the Black and Caspian seas, where they perform continuous directional movements at a slower pace, initially moving SW (Oct to Jan) and then progressively moving NE (Feb to Apr) before embarking on rapid spring migration. It is suggested that such itinerant behaviour follows variation (expansion and retreat) of snow cover across the non-breeding range.

The results are potentially useful for researchers investigating the ecological drivers of bird movement patterns. The analytical framework appears solid, although some details on the analyses (requested during the previous review round) are still unclear and have not been modified despite explicit requests. Significant weaknesses in the theoretical framework persist in the revised version, including unwarranted claiming of novelty, overselling of importance of the study, and overinterpretation of the data. Below are key points that the authors did not consider when revising their manuscript.

(1) The authors underemphasize the fact that what they term 'fox-trot' migration is actually a well-known patterns for many other migratory species, both in the Nearctic and in the Afro-Palearctic migration systems. Such behaviour has previously been identified as 'itinerant' or

'non-breeding itinerancy', involving an alternation of stopovers and movements between different short-term non-breeding residency areas, or even slow continuous movements, and it seems that the pattern the authors report for this particular species is perfectly in line with such previous evidence. For instance, this is well-documented among migratory raptors, such as the Montagu's harrier, lesser kestrels or black kites, that exploit Sahelian savannahs, where large spatio-temporal variation in greenness and hence resource availability occurs. And, besides the mentioned cuckoos and nightingales, there are studies of red-backed shrikes suggesting the same, as well as of tree swallows in the Nearctic. Therefore, the authors should avoid claiming novelty for this study and introducing unnecessary and confusing new terms in the literature (i.e. the 'fox-trot' migration patterns) when these are definitely not strictly needed as they have been previously observed and defined otherwise. Sentences such as 'We used the rough-legged buzzard as a model..." are also similarly unwarranted. This is simply a descriptive studies reporting on such behaviour in yet another migratory species. The whole introduction is pervaded by a faulty logic. The authors first introduce a new (unwarranted) term based on previous evidence from other studies (none of which felt any need to introduce and describe it); then they assume, for unclear reasons, that the species they are studying should behave in that way; even more worryingly, based on these assumptions, they make specific predictions on how this species should behave, without any sound biological reason for these predictions. I admit I hardly see any scientific logic in this approach.

(2) The species has a very standard migration for a short-distance migrant, by all means. It moves to non-breeding areas, and once there it slowly moves towards the south in autumn and back again in spring, until it departs for pre-breeding migration. This is no different from other trans-Saharan migratory raptor species that spend the non-breeding period in the Sahel. Whether the species perform any short/medium term stopover (frequenting the same are for some days) during the non-breeding stage (between end of autumn migration and onset of spring migration), as is the case of most species showing non-breeding itinerancy, is not reported. The authors only show a slower pace of movement during the non-breeding period compared to autumn and spring migration, without providing any further details. This hinders comparisons with other previous studies.

(3) The current title is unnecessarily general (it may recall rather a review or meta-analysis) and not adequately describing the content of the manuscript. In order to be informative, the title should more tightly reflect the content of the article. A valid alternative would be 'Itinerant non-breeding behaviour of an intra-Palaearctic migratory raptor', as it would be far more adequate and informative.

(4) The text, particularly the Introduction and the Discussion, would greatly benefit from profound reframing in light of the above comments. Upon reading the first sentence of the introduction, it looks surprising that the authors based their suggestion for 'fox-trot' migration based on a very outdated article on the migration of Montagu's harrier based on sparse ring recovery data which merely suggests the existence of 'movements' within the non-breeding areas (i.e. non-breeding itinerancy), while subsequent large scale satellite tracking studies of this species provided compelling evidence for non-breeding area itinerancy (and again, no mention of 'fox-trot' whatsoever). The discussion is entirely framed around potential issues related to accurate monitoring of population size and trends, which the author surprisingly refer to 'conservation implications'. As I already mentioned in my previous review, the 'conservation implications' of this study are nearly negligible. At best, it suggests that caution should be applied when interpreting population trends of migratory species based on non-breeding area counts only, a pattern that is already well known for decades (consider the long-running IWC coordinated by Wetlands International!). In addition, Christmas Bird Count, a long-term monitoring program of AOS, is mentioned without any accurate reference to what it actually is, assuming that any reader would be familiar with a very peculiar monitoring scheme of the Nearctic region.

The final paragraph epitomizes how authors are overstating the importance of this study, claiming for non-existent novelty and even 'discovery': "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".

https://doi.org/10.7554/eLife.87668.2.sa0

Author response:

The following is the authors' response to the current reviews.

We sincerely appreciate the reviewer's dedication to evaluating our manuscript and raising essential considerations regarding the classification of the migration behavior we described. While the reviewer suggests that this behavior aligns with the concept of itinerancy, we contend that it represents a distinct phenomenon, albeit with similarities, as both involve the non-breeding movements of birds. We acknowledge that our manuscript did not adequately address this distinction and have considered the reviewer's feedback. In our response, we clarify the difference between the described phenomenon and itinerancy. Our revised manuscript will include a new section in the Discussion to address this issue comprehensively.

In the first part of the review, the reviewer emphasizes that the pattern we are describing is consistent with itinerancy. Regardless of the terminology used, we want to highlight the existence of two different types of migratory behavior, both of which involve movement in non-breeding areas.

The first type, called itinerancy, was first described by Moreau in 1972 in "The Palaearctic-African Bird Migration Systems." As noted by the reviewer, this behavior involves an alternation of stopovers and movements between different short-term non-breeding residency areas. They usually occur in response to food scarcity in one part of the non-breeding range, causing birds to move to another part of the same range. These movements typically cover distances of 10 to 100 kilometers but are neither continuous nor directional. Moreau (1972) defined itinerancy as prolonged stopovers, normally lasting several months, primarily in tropical regions. He noted observations of certain species disappearing from his study areas in sub-Saharan Africa in December and others appearing, suggesting they may have multiple home ranges during the non-breeding season. Subsequent research, as mentioned by the reviewer, has confirmed itinerancy in many species, particularly among Palaearctic-African migrants in sub-Saharan Africa. In particular, the Montagu's Harrier has been extensively studied in this regard. The reviewer rightly points out that our study does not include recent findings on this species. In our revised version, we will include references to recent studies, such as those by Trierweiler et al. (2013, Journal of Animal Ecology, 82:107-120) and Schlaich et al. (2023, Ardea, 111:321-342), which show that Montagu's Harrier has an average of 3-4 home ranges separated by approximately 200 kilometers. These studies suggest that the species spends approximately 1.5 months at each site, with the most extended period typically observed at the last site before migrating to the breeding grounds.

In the second type, birds undertake a post-breeding migration, arrive in their non-breeding range, and then gradually move in a particular direction throughout the season. This continuous directional movement covers considerable distances and continues throughout the non-breeding period. In our study, this movement covered about 1000 km, comparable to the total migration distance of Rough-legged Buzzards of about 1500 km. As observed in our research, these movements are influenced by external factors such as snow cover. In such cases, the progression of snow cover in a south-westerly direction during winter can prevent

birds from finding food, forcing them to continue migrating in the same direction. In essence, this movement represents a prolonged phase of the migration process but at a slower pace. Similar behavior has been documented in buzzards, as reported by Strandberg et al. (2009, Ibis 151:200-206). Although several transmitters in their study stopped working in mid-winter, the authors observed a phenomenon they termed 'prolonged autumn migration.'

In the second part of the review, the reviewer questions the need to distinguish between the two behaviors we have discussed. However, we believe these behaviors differ in their structure (with the first being intermittent and often non-directional, whereas the second is continuous and directional) and in their causes (with the first being driven by seasonal food resource cycles and the second by advancing snow cover). We therefore argue that it is worth distinguishing between them. To differentiate these forms of non-breeding movement, we propose to use 'itinerancy' for the first type, as described initially by Moreau in 1972, and introduce a separate term for the second behavior. Although 'slow directional itinerancy' could be considered, we find it too cumbersome.

Moreover, 'itinerancy' in the literature refers not only to non-breeding movements but also to the use of different nesting sites, e.g., Lislevand et al. (2020, Journal of Avian Biology: e02595), reinforcing its association with movements between multiple sites within habitats. We, therefore, propose that the second behavior be given a distinct name. We acknowledge the reviewer's point that we did not adequately address this distinction in the Discussion and plan to include a separate section in our paper's revised version. In the third part of his review, the reviewer suggests an alternative title. Another reviewer, Dr Theunis Piersma, suggested the current title during the first round of reviewing, and we have chosen his version.

In the fourth part of the review, the reviewer questions whether it is appropriate to discuss the conservation aspect of this study. This type of non-breeding movement raises concerns about accurately determining non-breeding ranges and population dynamics for species that exhibit this behavior. We believe that accurate determination of range and population dynamics is critical to conservation efforts. While this may be less important for species breeding in Europe and migrating to Africa, for which monitoring breeding territories is more feasible, it's essential for Arctic and sub-Arctic breeding species. Large-scale surveys in these regions have historically been challenging and have become even more so with the end of Arctic cooperation following Russia's war with Ukraine (Koivurova, Shibata, 2023). For North America and Europe, non-breeding abundance is typically estimated once per season in mid-winter. In North America, these are the so-called Christmas counts (which take place once at the end of December), and in Europe, they are the IWC counts mentioned by the reviewer (as follows from their official website - "The IWC requires a single count at each site, which should be repeated each year. The exact dates vary slightly from region to region, but take place in January or February"). Because of such a single count in mid-winter, non-breeding habitats occupied in autumn and spring will be listed as 'uncommon' at best, while south-western habitats where birds are only present in mid-winter will be listed as 'common.' However, the situation will be reversed if we consider the time birds spend in these habitats.

The reviewer also highlights the introduction's unconventional structure and information redundancy at the beginning. We have chosen this structure and provided basic explanations to improve readability for a wider audience, given eLife's readership. At the same time, we will certainly take the reviewers' feedback into account in the revised version. We plan to include the references to modern itinerancy research mentioned above and to add a section on itinerancy to the Discussion.

We appreciate the reviewer's input and sincerely thank them for their time and effort in reviewing our paper. While we may not fully agree on the classification of the behavior we describe, we value the opportunity to engage in discussion and believe that presenting arguments and counterarguments to the reader is beneficial to scientific progress.

The following is the authors' response to the original reviews.

> ***Reviewer #1 (Recommendations For The Authors):***
>
> *I much enjoyed reading this manuscript, that is, once I understood what it is about. Titles like "Conserving bird populations in the Anthropocene: the significance of non-breeding movements" are a claim to so-called relevance, they have NOTHING to do with the content of the paper, so once I understood that this paper was about the "Quick quick slow: the foxtrot migration of rough-legged buzzards is a response to habitat and snow" (an alternative title), it was becoming very interesting. So the start of the abstract as well as the introduction is very tedious, as clearly much trouble is taken here to establish reputability. In my eyes this is unnecessary: eLife should be interested in publishing such a wonderful description of such a wonderful migrant in a study that comes to grips with limiting factors on a continental scale!*

We sincerely appreciate your time and effort in reviewing our manuscript. Thank you for your appreciation of our study.

We agree that the focus of the article should be changed from conservation to migration patterns. We have rewritten the Introduction and Discussion as suggested. We have added the application of this pattern including conservation at the end of the Discussion by completely changing Figure 5. We have also changed the title to the suggested one.

> *Not sure that the first paragraph statements that seek to downplay what we know about wintering vs breeding areas are valid (although I see what purpose they serve). Migratory shorebirds have extensively been studied in the nonbreeding areas, for example, including movement aspects (see, as just one example, Verhoeven, M.A., Loonstra, A.H.J., McBride, A.D., Both, C., Senner, N.R. & Piersma, T. (2020) Migration route, stopping sites, and non breeding destinations of adult Black tailed Godwits breeding in southwest Fryslân, The Netherlands. Journal of Ornithology 162, 61-76) and there are very impressive studies on the winter biology of migrants across large scale (for example in Zwarts' Living on the Edge book on the Sahel wetlands). Think also about geese and swans and about seabirds!*

We have rewritten the first paragraph and it now talks about patterns of migratory behavior. We have also rewritten the second paragraph, now it is devoted to studies of movements in the non-breeding period. We explain how our pattern differs from those already studied and give references to the papers you mentioned.

> *Directional movements in nonbreeding areas as a function of food (in this case locusts) have really beautifully been described by Almut Schlaich et al in JAnimEcol for Montagu's harriers.*

We have added Montagu's harrier example in the second paragraph of the Introduction and the Discussion. We have added a reference to Schlaich and to Garcia and Arroyo, who suggested that Montagu's harriers have long directional migrations during the non-breeding period.

> *Once the paper starts talking buzzards, and the analyses of the wonderful data, all is fine. It is a very competent analysis with a description of a cool pattern.*

Thank you for your appreciation of our study. We hope the revised version is better and clearer.

> *However, i would say that it is all a question of spatial scale. The buzzards here respond to changes in food availability, but there is not an animal that doesn't. The question is how far they have to move for an adequate response: in some birds movements of 100s of meters may be enough, and then anything to the scale of rough-legged buzzards.*

In the new version of the manuscript, we emphasize that this is a large distance (about 1000 km), comparable to the distance of the fall and spring migrations (about 1400 km) in lines 70-72 of the Introduction and 379-383 of the Discussion.

> *And actually, several of the shorebirds I know best also do a foxtrot, such as red knots and bar-tailed godwits moulting in the Wadden Sea, then spending a few months in the UK estuaries, before returning to the Wadden Sea before the long migrations to Arctic breeding grounds. The publication of the rough-legged buzzard story may help researchers to summarize patterns such as this too. Mu problem with this paper is the framing. A story on the how and why of these continental movements in response to snow and other habitat features would be a grand contribution. Drop Anthropocene, and rethink whether foxtrot should be introduced as a hypothesis or a summary of cool descriptions. I prefer the latter, and recommend eLife to go with that too, rather than encourage "disconnected frames that seek 'respectability'" Good luck, theunis piersma*

We thank the reviewer again for his valuable comments and suggestions. We have changed the framing to the suggested one and removed the Anthropocene from the article.

We sincerely appreciate the time and effort you have taken to review our manuscript. We have carefully considered all of your comments, including both public and author comments, and provided detailed responses to each of them below. In addition, we would like to address the most important public comments.

We agree with the suggestion to shift the focus of the article from conservation to migration patterns. Accordingly, we have rewritten both the Introduction and Discussion sections to focus on migration behavior rather than conservation.

However, we respectfully disagree with the suggestion that the migration patterns we describe are synonymous with itinerancy. We acknowledge that our original presentation may have been unclear and may have hindered full understanding. In the revised version, we provide a detailed analysis of migratory behavior in the Introduction that describes how our pattern differs from itinerancy. We also revisit this distinction in the Discussion section. We have also carefully revised Figure 1 to improve clarity and avoid potential misunderstandings.

Regarding the applicability of the described migration pattern, we acknowledge that the Rough-legged Buzzard is not listed as an endangered species. However, we believe that our findings have practical implications. We have moved our discussion of this issue to the end of the Discussion section and have completely revised Figure 5. While the overall population of Rough-legged Buzzards is not declining, certain regions within its range are experiencing declines. We show that this decline does not warrant listing the species as endangered. Instead, it may represent a redistribution within the non-breeding range - a shift in range dynamics. We use the example of the Rough-legged Buzzard to illustrate this concept and emphasize the importance of considering such dynamics when assessing the conservation status of species in the future.

> ***Reviewer #2 (Recommendations For The Authors):***

We sincerely appreciate the time and effort you have taken to review our manuscript. We have carefully considered all of your comments, including both public and author comments, and provided detailed responses to each of them below. In addition, we would like to address the most important public comments.

We agree with the suggestion to shift the focus of the article from conservation to migration patterns. Accordingly, we have rewritten both the Introduction and Discussion sections to focus on migration behavior rather than conservation.

However, we respectfully disagree with the suggestion that the migration patterns we describe are synonymous with itinerancy. We acknowledge that our original presentation may have been unclear and may have hindered full understanding. In the revised version, we provide a detailed analysis of migratory behavior in the Introduction that describes how our pattern differs from itinerancy. We also revisit this distinction in the Discussion section. We have also carefully revised Figure 1 to improve clarity and avoid potential misunderstandings.

Regarding the applicability of the described migration pattern, we acknowledge that the Rough-legged Buzzard is not listed as an endangered species. However, we believe that our findings have practical implications. We have moved our discussion of this issue to the end of the Discussion section and have completely revised Figure 5. While the overall population of Rough-legged Buzzards is not declining, certain regions within its range are experiencing declines. We show that this decline does not warrant listing the species as endangered. Instead, it may represent a redistribution within the non-breeding range - a shift in range dynamics. We use the example of the Rough-legged Buzzard to illustrate this concept and emphasize the importance of considering such dynamics when assessing the conservation status of species in the future.

We also acknowledge that the hypothesis of this form of behavior has been proposed previously for Montagu's Harrier, and we have included this information in the revised manuscript. In addition, we agree that the focus on the Anthropocene is unnecessary in this context and have therefore removed it.

We believe that these revisions significantly improve the clarity and robustness of the manuscript, and we are grateful for your insightful comments and suggestions.

> *As a general comment, please note that including line numbers (as it is the standard in any manuscript submission) would facilitate reviewers providing more detailed comments on the text.*

We apologize for this oversight and have added line numbers to our revised manuscript.

> *Dataset: unclear what is the frequency of GPS transmissions. Furthermore, information on relative tag mass for the tracked individuals should be reported.*

We have included this information in our manuscript (L 157-163). We also refer to the study in which this dataset was first used and described in detail (L 164).

> *Data pre-processing: more details are needed here. What data have been removed if the bird died? The entire track of the individual? Only the data classified in the last section of the track? The section also reports on an 'iterative procedure' for annotating tracks, which is only vaguely described. A piecewise regression is mentioned, but no details are provided, not even on what is the dependent variable (I assume it should be latitude?).*

Regarding the deaths. We only removed the data when the bird was already dead. We have corrected the text to make this clear (L 170).

Regarding the iterative procedure. We have added a detailed description on lines 175-188.

> *Data analysis: several potential issues here:*
>
> *(1) Unclear why sex was not included in all mixed models. I think it should be included.*

Our dataset contains 35 females and eight males. This ratio does not allow us to include sex in all models and adequately assess the influence of this factor. At the same time, because adult females disperse farther than males in some raptor species, we conducted a separate analysis of the dependence of migration distance on sex (Table S8) and found no evidence for this in our species. We have written a separate paragraph about this. This paragraph can be found on lines 356-360 of the new manuscript.

> *(2) Unclear what is the rationale of describing habitat use during migration; is it only to show that it is a largely unsuitable habitat for the species? But is a formal analysis required then? Wouldn't be enough to simply describe this?*

Habitat use and snow cover determine the two main phases (quick and slow) of the pattern we describe. We believe that habitat analysis is appropriate in this case and that a simple description would be uninformative and would not support our conclusions.

> *(3) Analysis of snow cover: such a 'what if' analysis is fine but it seems to be a rather indirect assessment of the effect of snow cover on movement patterns. Can a more direct test be envisaged relating e.g. daily movement patterns to concomitant snow cover? This should be rather straightforward. The effectiveness of this method rests on among-year differences in snow cover and timing of snowfall. A further possibility would be to demonstrate habitat selection within the entire non-breeding home range of an individual in relation snow cover. Such an analysis would imply associating presence-absence of snow to every location within the non-breeding range and testing whether the proportion of locations with snow is lower than the proportion of snow of random locations within the entire non-breeding home range (95% KDE) for every individual (e.g. by setting a 1/10 ratio presence to random locations).*

The proposed analysis will provide an opportunity to assess whether the Rough-legged Buzzard selects areas with the lowest snow cover, but will not provide an opportunity to follow the dynamics and will therefore give a misleading overall picture. This is especially true in the spring months. In March-April, Rough-legged Buzzards move northeast and are in an area that is not the most open to snow. At this time, areas to the southwest are more open to snow (this can be seen in Figure 4b). If we perform the proposed analysis, the control points for this period would be both to the north (where there is more snow) and to the south (where there is less snow) from the real locations, and the result would be that there is no difference in snow cover.

A step-selection analysis could be used, as we did in our previous work (Curk et al 2020 Sci Rep) with the same Rough-legged Buzzard (but during migration, not winter). But this would only give us a qualitative idea, not a quantitative one - that Rough-legged Buzzards move from snow (in the fall) and follow snowmelt progression (in the spring).

At the same time, our analysis gives a complete picture of snow cover dynamics in different parts of the non-breeding range. This allows us to see 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%). 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%). 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.

We write about this in the new manuscript on lines 385-394.

> *Results: it is unclear whether the reported dispersion measures are SDs or SEs. Please provide details.*

For the date and coordinates of the start and end of the different phases of migration, we specified the mean, sd, and sample size. We wrote this in line 277. For the values of the parameters of the different phases of the migration (duration, distance, speed, and direction), we used the mean, the standard error of the mean, and the confidence interval (obtained using the 'emmeans' package). We have indicated this in lines 302-303 and the caption of Table 1 (L 315) and Figure 2 (L 293-294). For the values of habitat and snow cover experienced by the Rough-legged Buzzards, we used the mean and the error of the mean. We reported this on lines 322 and 337 and in Figures 3 (L 332-333) and 4 (L 355-356).

> *Discussion: in general, it should be reshaped taking into account the comments. It is overlong, speculative and quite naive in several passages. Entire sections can be safely removed (I think it can be reduced by half without any loss of information). I provide some examples of the issues I have spotted below. For instance, the entire paragraph starting with 'Understanding....' is not clear to me. What do you mean by 'prohibited management' options? Without examples, this seems a rather general text, based on unclear premises when related to the specific of this study. Some statements are vague, derive from unsubstantiated claims, and unclear. E.g. "Despite their scarcity in these habitats, forests appear to hold significant importance for Rough-legged buzzards for nocturnal safety". I could not find any day-night analysis showing that they actually roost in forests during nighttime. Being a tundra species, it may well be possible that rough-legged buzzards perceive forests as very dangerous habitats and that they prefer instead to roost in open habitats. Analysing habitat use during day and night during the non-breeding period may be of help to clarify this. Furthermore, considering the fast migration periods, what is the flight speed during day and night above forests? Do these birds also migrate at night or do they roost during the night? Perhaps a figure visualizing day and night track segments could be of help (or an analysis of day vs. night flight speed) (there are several R packages to annotate tracks in relation to day and night). This is an example of another problematic statement: "The progression of snow cover in the wintering range of Rough-legged buzzards plays a significant role in their winter migration pattern." The manuscript does not contain any clear demonstration of this, as I wrote in my previous comments. Without such evidence, you must considerably tone down such assertions. But since providing a direct link is certainly possible, I think that additional analyses would clearly strengthen your take-home message.*
>
> *The paragraph starting with "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." is quite odd. Take the following statement "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.". It is based on the assumption that minor vegetation elements play a key role in the ecology of the species, without any evidence supporting this. Does it have any sense?*

> *I could safely say exactly the opposite and I would believe it might even be more substantiated.*

We agree with these comments.

We have completely rewritten this section. As suggested, we have shortened it by removing statements that were not supported by the research. We have completely removed the statements about "prohibited management". We have also removed the statement that "forests appear to be of significant importance to Rough-legged buzzards for nocturnal safety" and everything associated with that statement, e.g. the statement about "small elements of vegetation cover", etc. We do believe that this statement is true in substance, but we also agree that it is not supported by the results and requires separate analysis. At the same time, we believe that this is a topic for a separate study and would be redundant here. Therefore, we leave it for a separate publication.

> *Conclusion paragraph: I believe this severely overstates the conservation importance of this study. That the results have "crucial implications for conservation efforts in the Anthropocene, where rapidly changing environmental factors can severely impact bird migration" seems completely untenable to me. What is the evidence for such crucial implications? For instance, these results may suggest that climate change, because global warming is predicted to reduce snow cover in the non-breeding areas, might well be beneficial for populations of this species, by reducing non-breeding energy expenditure and improving non-breeding survival. I think statements like these are simply not necessary, and that the study should be more focused on the actual results and evidence provided.*

We have completely rewritten this section. We removed the reference to the Anthropocene and focused on migratory behavior and migration patterns.