Seasonally differential migration strategies, detour, and bottleneck in Common Crane *Grus grus* wintering in western India

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Abstract

Background: Understanding migratory route selection and seasonal migration strategies helps better plan transboundary conservation. We investigated the seasonal dynamics of migration behavior in Common Cranes *Grus grus*, a potential sentinel species for understanding and conserving the Central Asian Flyway. We tracked five individuals from Gujarat, western India, to breeding sites in south-western Siberia using solar-powered GPS-GSM transmitters. We analysed 18 migration trajectories to investigate the seasonally-explicit migration behaviour, to quantify the migratory detour and bottleneck, and to identify high-use areas along the migration route.

Results: The results highlighted seasonally differential migration strategies in Common Crane. GLM analyses confirmed significant seasonal differences: Outward migration covered greater distances, lasted longer, and was slower, with increased stopover duration and reduced straightness. Detours, likely undertaken to avoid the Hindukush Himalaya and capitalize resources, increased migration distances by 23.3% (inward) and 36.8% (outward). Cranes followed distinct seasonal migration routes that converged in Turkmenistan, creating a migratory bottleneck between 33°N and 35°N.

Conclusion: These findings reveal the adaptive strategies of Common Cranes in response to seasonal and topographical challenges, emphasizing the urgency of protecting key stopover sites and migratory corridors.

Keywords: Central Asian Flyway, Movement Ecology, GPS telemetry, Flyway connectivity, Stop-over site

Background

Avian migration is a periodic, repetitive, and large-scale movement, taking place at the same season each year, with individuals commuting between breeding and non-breeding areas (Rappole and Jones 2002; Newton 2011; Åkesson and Helm 2020). Migratory species are exposed to the highest risk during their migratory journeys (Sillett and Holmes 2002; Rockwell et al. 2017) encountering a

spectrum of natural and anthropogenic challenges during migration. These challenges include extreme weather changes, habitat alterations, hunting and poisoning along with many other (Kirby et al. 2008; Gallo-Cajiao et al. 2020; Newth et al. 2022). Certain avian migratory species allocate more than half of their annual life cycle to traversing between breeding and wintering habitats (Newton 2011). Adversities encountered during these transitions significantly contribute to a considerable proportion of annual mortality across various species(Sillett and Holmes 2002; Klaassen et al. 2014). Considering these, extensive studies have been undertaken to understand the patterns, drivers, and consequences of migratory movements (Vansteelant et al. 2017; Norevik et al. 2020; Gregory et al. 2023), including the evolution of partial migration (B. B. Chapman et al. 2011), stop-over site ecology (Cai, Huettmann, and Guo 2014; Kölzsch et al. 2016; Arizaga et al. 2018; Elmore et al. 2024), and the influence of environmental changes on the shifting migratory timings and movements (Brisson-Curadeau, Elliott, and Côté 2019; Haig et al. 2019; Remisiewicz and Underhill 2020; Davies et al. 2023; Ozsanlav-Harris et al. 2023).

A flyway concept provides a spatial framework for the management and conservation of migratory avian species across political boundaries as it encompasses the multiple migratory routes spanning countries along the entire geographic range (Boere 2006). One such flyway is the Central Asian Flyway spread across a large continental area of Eurasia between the Arctic and Indian Oceans and the associated island chains (cms.int). This flyway falls in the Asia-Pacific region where the highest number of threatened soaring bird species have been reported (Kirby et al. 2008). However, this is also the flyway that is the least known among all the flyways (Mundkur et al. 2023). The Asian Flyways are experiencing large-scale threats, including hunting migrant birds (Ahmad et al. 2021; Hussain and Khan 2021; Mundkur et all. 2023), habitat loss, and urbanization, which will likely have population-scale impacts on birds (Clark et al. 2013; Malakoff et al. 2016). Understanding a species' movements and migratory connectivity can help understand the species-specific and route-specific threats including the spread of infectious diseases that may have population-level consequences (Webster et al. 2002; Takekawa et al. 2023).

Among the numerous migratory species that travel along the Central Asian Flyway, Common Crane *Grus grus* is one of the widespread species that winters in tens of thousands in India. Across the world, four subspecies of the Common Crane have been recognized: the Western common Crane *G. g. Grus* in Europe; the Transcaucasian subspecies *G. g. archibaldi* in the Inner Caucasus/borderland of Turkey, Georgia, and Iran (V. Y. Ilyashenko et al. 2007; V. Yu Ilyashenko 2008); the Tibetan subspecies *G. g. korelovi* in Tibet, Kyrgyzstan, and Kazakhstan (V. Yu Ilyashenko and Belyalov 2011); and the Eastern Common Crane *G. g. lilfordi* in Asia from the Ural Mountains

eastward to Northeastern Siberia (Haase and Ilyashenko 2012; Ilyashenko, V.Y. 2013). The Western and Eastern Common cranes are separated by the Ural Mountains (Mudrik et al. 2015). The population size of the eastern subspecies is estimated at 125,000–130,000 individuals (Prange 2015), of which more than 100,000 migrate from Western Siberia and Kazakhstan to the wintering grounds in India (Higuchi et al. 1994 & 2008; Ram et al. 2023) and Central Asia in the Amudarya River Valley (Bulyuk and Shamuradov 1995; Rustamov et al. 2011; Sorokin et al. 2011).

The arid plains in the States of Gujarat and Rajasthan in western India support large populations of the Common Crane that arrive from different parts of their breeding range (Higuchi et al. 1994 & 2008; Ram et al. 2023). Few of the wintering sites witness huge congregations of the cranes and these are often species-specific flocks numbering in thousands (HB unpublished count data). Previous studies on the migratory behaviour of the Common Crane have provided important, yet fragmented, insights into their movement patterns along the Central Asian Flyway. The first attempt to document Common Crane migration routes was made by Higuchi et al. (1994), who tracked two individuals from Rajasthan, western India, to southwestern Siberia. A subsequent study by Higuchi et al. (2008) expanded on this by tracking three additional cranes from Gujarat, western India, to Siberia. However, both studies were constrained to outward (spring) migration data only, limited by the technology available at the time, thus offering an incomplete picture of the species' annual migratory dynamics. Ram et al. (2023) later employed improved tracking technology to follow two Common cranes from the Saurashtra region of Gujarat, documenting detailed migratory routes during both inward and outward migrations, as well as movement on wintering grounds. Nevertheless, these prior studies were limited by single season or single year data, restricting their ability to characterize migration patterns comprehensively across seasons or to delineate primary migration corridors and critical stopover sites. Further, these studies did not quantify migratory detours and bottleneck, crucial parameters to understand the migration ecology and conservation priorities.

To address these limitations, our study applied state-of-the-art solar-powered GPS-GSM transmitters to track five Common Cranes from Gujarat across multiple years, capturing fine-scale, seasonal migratory movements from western India to the Siberian steppes in Russia and Kazakhstan. This dataset enabled an in-depth characterization of migration parameters, allowing us to analyze and compare inward and outward migrations, and thus identify any significant seasonal variation in migratory strategies. Additionally, we investigated migratory detours and bottlenecks along the migratory path, and mapped high-use areas critical for the conservation of this species along the Central Asian Flyway. By expanding both the scope and resolution of tracking

data, this study addresses key gaps in our understanding of Common Crane migration ecology and provides foundational data for prioritizing conservation efforts in high-use regions.

Methods

Study population and GPS tracking

During the winter seasons of 2019-20 and 2021-22, efforts to tag Common cranes were concentrated in Nal Sarovar Bird Sanctuary (22.8183 N; 72.0439 E, area: 12,000 ha) and Thol Lake Wildlife Sanctuary (23.1339 N; 72.4001 E, area: 699 ha) in the western Indian state of Gujarat. Both sanctuaries are designated as Ramsar Sites under the Ramsar Convention and harbor a substantial population of Common Cranes, estimated to be as high as 30,000 (based on unpublished data from regular, systematic roost counts by the first author).

We tagged five adult Common cranes with solar-powered GPS-GSM leg-mount transmitters (OrniTela Inc., Lithuania). The cranes were captured during their arrival at the roosting wetland and while foraging during daylight hours. In the roosting wetland, mist nets were strategically deployed at the appropriate angle to the direction of Crane arrival during dusk, and in foraging fields, Cranes were captured using slip-knot leg nooses. Upon capture, each Crane was immediately extracted and blindfolded to minimize stress. Subsequently, a 40 g L-40 transmitter was fitted to the tibia of each Crane, adding approximately 0.93% to the average weight of the tagged cranes. The deployment of transmitters was completed within a minute, morphological measurements were taken and the tagged cranes were released within 17–30 minutes after capture. All transmitters were programmed to record GPS locations at 10-minute intervals, which were then transmitted via a 2G GSM network.

Data processing, migration parameters, and high-use areas

The transmitter data was downloaded in CSV format and was subsequently visualized in QGIS 3.34.5 to look for any errors in GPS locations during which duplicate and unusually deviated data points were removed. Trajectories between the breeding and wintering grounds were extracted in QGIS. The breeding and wintering areas were identified through visual inspection, observing when the cranes began their characteristic routine movements between the roosting wetlands and foraging fields within their respective breeding and wintering ranges. In this study, various parameters were defined and calculated to precisely characterize the migration patterns. The "departure date" was defined as the date of the first recorded position when a Crane left its wintering or breeding sites and stopped showing regular movements between the foraging fields

and roosting wetland. Conversely, the "arrival date" was identified as the date when a bird was determined to have reached its wintering or breeding sites and started showing the regular movements between the foraging patches and roosting wetland.

The "migration duration" was calculated as the total time a Crane took to travel, including any stopovers, between the last breeding site and the first wintering site for inward migration, or between the last wintering site and the first breeding site for outward migration. The "migration distance" was measured as the cumulative travel distance in km between all consecutive GPS locations during migration. The "migration speed" was defined as the total migration distance divided by the total duration of the migration, expressed in km/day. The "travel speed" was calculated as the daily distance traveled during the travel days, where the total migration distance was divided by the total travel duration and expressed as km/day. The "travel duration" was defined as the total number of travel days during migration, subtracting any days spent at stopover sites.

The "stopover duration" was the aggregate of all days spent at various stopover sites during each migration season. Further, the "straightness index" was calculated to measure orientation efficiency, defined as the ratio of the straight-line distance 'D' from the migration starting point to the ending point to the actual path length 'L' traveled by the bird. For this, the straight lines were simulated for each migration trajectory and the ratio D/L was calculated to determine an empirical measure of the directness of the migration path.

To assess the extent of longitudinal detours adopted by each individual, we computed the linear distance of each location along the actual migration path from the simulated straight line (D. Liu et al. 2018). The mean longitudinal detours were calculated for each latitude to pinpoint the latitudes exhibiting the highest degree of detour. We identified the migratory bottleneck, characterized by the convergence of all migratory trajectories through a very narrow passage. To determine this, we aggregated all trajectories and calculated the distance between the easternmost and westernmost GPS locations (Supplementary Information) for each latitude. It was anticipated that at the bottleneck, the distance between these points would be minimal. The latitude with the shortest distance was designated as the migratory bottleneck.

Additionally, we utilized Kernel Density Estimates (KDE) (Worton 1989) via ArcGIS Pro to map utilization distribution and identify high-occurrence areas along the migratory flyway. This method allowed us to delineate regions of high utilization during both stopovers and migratory corridors. The final maps were produced using QGIS 3.34.5, while the graphs were generated using R and Microsoft Excel.

Statistical analysis

To assess the impact of migration direction on key migration parameters, a General Linear Model (GLM) was utilized, employing ordinary least squares (OLS) regression with robust methodology. Bootstrapped confidence intervals were generated using 1000 samples and the bias-corrected and accelerated (BCa) method to ensure accurate parameter estimates and address potential deviations from normality in the residuals. Heteroscedasticity-consistent standard errors (HC3) were applied to account for potential violations of homoscedasticity. The model fit was evaluated using R^2. The summary statistics for each migration parameter were calculated and data is presented as mean ± SE and range. The visual comparison of different parameters between outbound and inbound migrations were presented using dot whisker plots where whiskers show 95% CI.

Results

A total of 40,336 GPS fixes were collected attributed to the migratory journeys of five Common Crane individuals across three years (Supplementary table S1). One of the individuals tagged in 2020 completed a full migration cycle (defined as complete inward and outward migration) before data transmission ceased, while the other four individuals tagged in 2022 completed two full migration cycles each, resulting in a total nine complete migration cycles containing 18 trajectories.

Migration timing, routes and stop-over sites

During their outward migration, the birds left India for their breeding grounds between March 18 and April 11, with an average departure date of March 29. They arrived at the breeding sites between April 9 and April 26, averaging an arrival date of April 19. For their return journey, the birds began migrating back to India from southwestern Siberia (55°N - 58°N) between September 28 and October 12, with an average departure date of October 5. They reached Gujarat, in western India (22°N - 23°N), between October 6 and October 25, with an average arrival date of October 16.

The migration route of all tagged Common cranes passed through Pakistan, Afghanistan, northwest Iran, Turkmenistan, Uzbekistan, and Kazakhstan, ending in southwestern Siberia and northern Kazakhstan (Figure 1 and 2). During both migrations, the cranes never crossed the Hindukush Himalayas. Along the route, they also traversed the vast Registan, Margo, and Karakum deserts. On the outward journey, the cranes initially flew in a northwest direction towards the Aral Sea at 45°N latitude. From there, they turned northeast to reach their breeding grounds. However, on two occasions, the cranes maintained a northwest direction until reaching 50°N before heading northeast. Notably, the cranes never crossed 56°E, the western limit of the Ural Mountains of Russia.

During their return migration, the cranes generally avoided flying over the Aral Sea, except on two occasions, and took a more eastern route, still steering clear of the Hindukush Himalayas. The tracking data revealed two migration corridors: the outward corridor, which is relatively more western and crosses the Aral Sea, and the inward corridor, which is more eastern and largely avoids the Aral Sea. Both corridors converge in Turkmenistan and then merge into a single major corridor through Afghanistan and Pakistan, leading to western India.

The key stop-over sites identified by KDE include arid deserts, river floodplains, and steppe habitats. Notable desert stop-over locations include the Karakum Desert near Ashgabat, Mary, and Kerpichli (Turkmenistan), as well as Tejen and the Hanhowuz Reservoir. Floodplain habitats, particularly the Amu Darya floodplains was also used by multiple individuals. In the northern steppe regions, cranes utilize stop-over areas in the northern Aktobe and Kostanay regions of Kazakhstan, as well as in North Kazakhstan. Additional stop-over sites are situated in the Adamovsky district, Orenburg Oblast (Russia), and near Taybad (Iran) (Figure 3).

Seasonal differences in migration parameters

The results of the General Linear Model (GLM) analyses highlight significant seasonal differences in migration parameters between inward and outward migration directions. The model for migration distance exhibited a strong fit (R^2 = 0.78, $\hat{\beta}$ = 652.67; SE = 90.91, 95% CI = 490.30 - 817.78, p = <0.0001), indicating that outward migration covers significantly longer distances. Similarly, the model for migration duration revealed a robust fit (R^2 = 0.68, $\hat{\beta}$ = 10.11; SE = 1.86, 95% CI = 7.05 - 13.72, p = <0.0001), reflecting a notable increase in migration duration for outward migration.

For migration speed, the analysis indicated a strong fit and a significant difference (R^2 = 0.64, $\hat{\beta}$ = -147.75, SE = 29.47, 95% CI = -97.13 - -5.01, p = 0.00013) where the outward migration was associated with a marked decrease in speed. The stopover duration also demonstrated a strong model fit (R^2 = 0.61, $\hat{\beta}$ = 6.33, SE = 1.34, 95% CI = 3.91 – 8.65, p = 0.00024), indicating increased resting periods during outward migration. Furthermore, the analysis of the straightness index (SI) revealed a low model fit (R^2 = 0.48, $\hat{\beta}$ = -0.05, SE = 0.01 95% CI = -0.07 - -0.02, p = 0.00231), suggesting that outward migration exhibited a slight reduction in straightness, indicating less direct routes. The travel speed showed the weakest model fit and no significant difference between the inward and outward migration (R^2 = 0.20, $\hat{\beta}$ = -60.61, SE = 31.73, 95% CI = -124.03 – 2.81, p = 0.07). The summary statistics of the key migration parameters are given in Table 1 and supplementary table S2, and are graphically compared in Figure 4.

Migratory detour and bottleneck

During inward migration, detours commence from the highest latitude of 55°N, where minimal detour distances (11.44) are observed, and progressively increase as latitude decreases toward the southern latitudes and peaks at 34°N with the detour of 829.56 km. Beyond this peak, detour distances decrease at lower latitudes, as the trajectories approach wintering ground. During the outward migration, the detour distances initially increase gradually, showing moderate detours from 22°N to 29°N. A more pronounced increase in detour distances is observed between latitudes 29°N and 35°N, with the highest detour distance of 969.32 recorded at 35°N. Post-peak, outward detours decline toward higher latitudes, as the trajectories approach the breeding ground (Figure 5). The detour resulted in 23.3 % (SE = 1.29, 95% CI = 25.3 – 31.2) and 36.8 % (SE = 1.85, 95% CI = 32.5 – 41.0) increase in the actual distance traveled by the cranes during inward and outward migrations respectively.

The spatial spread of crane migration trajectories showed a distinct migratory bottleneck between latitudes 33°N and 35°N, where the longitudinal spread narrows to its lowest values (3.60° at 34°N). Beyond 35°N, the spread increases, indicating a divergence of migratory paths at higher latitudes (Figure 6).

Discussion

Migration timing, routes and stop-over sites

The migration timings and routes observed in our study, based on multi-year tracking of five tagged Common cranes, offer a more comprehensive understanding compared to previous studies, which tracked fewer cranes over a single season or year. The outward migration timing aligns with prior research by Higuchi et al. (1994, 2008) and Ram et al. (2023), where cranes departed western India in March and early April. The inward departure date is consistent with one of the two individuals tracked in Ram et al. 2023 where the Crane departed from Russia in the last week of September. However, the second individual from Ram et al. 2023 study departed on 14th August, which is 52 days earlier than the mean departure date recorded in our study, suggesting the individual variability in departure decision. The multi-year data in our study reveals more consistent patterns in departure and arrival dates, suggesting stable temporal patterns across years. Further, the migration timings recorded in our study establish a crucial baseline for Common cranes along the Central Asian Flyway, providing a foundation for detecting climate-driven phenological shifts. Long-term studies in Europe and Russia have demonstrated significant advances in Common Crane

migration timing in response to rising temperatures (Filippi-Codaccioni et al. 2011; Kondrakova et al., 2025), suggesting the role of climate change in altering avian movement patterns. Given the accelerating impacts of global warming, continued monitoring of migration phenology is essential for understanding species-level responses and informing conservation strategies.

The broad migration route along crossing Pakistan, Afghanistan, northern Iran, Turkmenistan, Uzbekistan and finally reaching the breeding ground in south-western Siberia is consistent with Higuchi et al. 2008 and Ram et al. 2023. While the breeding region of the cranes is also consistent with Higuchi et al. (1994), the outward migration route differs slightly, as their cranes did not go all the way to northern Iran and the Aral Sea, flying through northern Afghanistan instead of southern Afghanistan. This variation stems from the northern Indian origin of their Crane population. The dual migration corridors observed in our study—western during outward migration and eastern during return migration—offer new insights into seasonal route flexibility. These differences, likely arising from the broader temporal and spatial dataset, emphasize the dynamic nature of Common Crane migrations and the need for long-term tracking to understand these patterns. The migration distances recorded in our study are consistent with those reported by Higuchi et al. (2008) and one individual tracked by Ram et al. (2023). However, another individual in Ram et al. (2023) was recorded traveling 12,982 km during outward migration and 14,873 km during the inward journey. These distances are 2.5 times (outward) and 3.3 times (inward) greater than those recorded in our multi-year study. Given the similarity in breeding and wintering sites between studies, this discrepancy is likely due to differences in analytical approaches.

The identification of key stop-over sites along the Central Asian Flyway highlights the ecological significance of arid deserts, river floodplains, and steppe habitats in sustaining migratory populations of Common cranes. The spatial distribution of these stop-over locations suggests a strong dependence on landscape heterogeneity, wherein cranes utilize resource-rich environments that provide both foraging opportunities and safe roosting sites. The Karakum Desert, including sites near Ashgabat, Mary, Kerpichli, and Tejen, serves as a crucial staging area despite its arid conditions, emphasizing the species' ability to exploit ephemeral water sources and localized productivity within desert ecosystems (Meine and Archibald 1996). Similarly, the Amu Darya floodplains function as essential stop-over sites, offering stable wetland as well as food resources in form of food crops in an otherwise arid landscape, reinforcing the well-documented importance of riparian corridors in Crane migration (Harris and Mirande 2013). Steppe habitats in northern Kazakhstan, including the Aktobe and Kostanay regions, as well as in North Kazakhstan, represent key staging areas that likely support extensive refuelling due to the availability of agricultural fields

and natural grasslands. The prolonged use of these sites aligns with previous studies demonstrating that Common cranes frequently exploit anthropogenically modified landscapes during migration (Alonso, Alonso, and Nowald 2008; Li et al. 2013; Erdenechimeg et al. 2023). Furthermore, the inclusion of Adamovsky district, Orenburg Oblast (Russia), and Taybad (Iran) as stop-over locations indicates the species' reliance on a broad network of habitat patches to mitigate the energetic demands of long-distance migration.

The presence of cranes at artificial reservoirs, such as Hanhowuz Reservoir, highlights the potential role of human-managed water bodies in supplementing natural wetlands, a trend observed in other migratory waterbirds (Li et al. 2013). Given the increasing anthropogenic pressures on natural habitats within the Central Asian Flyway (Mundkur et al. 2023), the conservation of these critical stop-over sites requires a multi-scalar approach integrating habitat protection, sustainable land-use practices, and transboundary conservation initiatives. Future research should focus on quantifying habitat selection at these stop-over locations using high-resolution tracking data and remote sensing to refine conservation strategies and predict the potential impacts of environmental change on migratory connectivity. Further, the identified stopover sites likely host high densities of migratory birds, creating potential hotspots for disease transmission. Recent outbreaks of highly pathogenic avian influenza (H5N1) have caused mass mortality in Common cranes (Braverman 2024; Djurdjević et al. 2024), highlighting the vulnerability of migratory populations to emerging infectious diseases. Given the risks associated with high-density aggregations, regular disease monitoring and screening at key stopover sites are essential for early detection and mitigation. Integrating such measures into transboundary flyway conservation and management plans will be critical for safeguarding both migratory bird populations and ecosystem health.

Seasonally explicit migration duration

The analysis of migration parameters revealed that outward migration in Common cranes was significantly slower than inward migration, with longer stopovers contributing to the extended duration. This contrasts with findings from the Eastern Mongolian Common Crane population (Erdenechimeg et al. 2023), where outward (spring) migration was faster. Outward migration found to be faster in the case of many other long-distance migratory species (Nilsson, Klaassen, and Alerstam 2013), however, these species are predominantly small in size. Faster outward migration is typically linked to securing better territories, enhanced reproductive success, and improved readiness for subsequent migrations (Van Noordwijk, McCleery, and Perrins 1995; Kokko 1999; R 2005). Like in our case, the slower outward migration is also reported in many other long-distance

317 migrants with large body seizes such as White Stork (Shamoun-Baranes et al. 2003), Common Eider
318 (Mosbech et al. 2006), Black-backed Gull (Bustnes et al. 2013), Bewick's swan (Nuijten et al. 2014),
319 Booted Eagle (Mellone et al. 2014), Egyptian Vulture (López-López, García-Ripollés, and Urios 2014)
320 and White-fronted Goose (Kölzsch et al. 2016; Deng et al. 2019). This suggests that the seasonally
321 differential migration duration is a function of body size and environmental factors.

322 Given the cranes are long-lived capital-income breeders, the slower outward migration observed in
323 our cranes may reflect the females' need to accumulate energy reserves for reproduction, a strategy
324 documented in geese species which is also a large grazing species like cranes (Prop, Black, and
325 Shimmings 2003; Deng et al. 2019). Additionally, the Cranes may delay migration to coincide with
326 snowmelt at their northern breeding grounds ensuring that breeding areas are accessible and
327 favorable upon arrival (Nuijten et al. 2014). This behavior helps cranes optimize their reproductive
328 success, as arriving too early could mean facing harsh conditions on breeding grounds. The
329 proximate factors governing stopover duration during outward migration in Central Asian Flyway
330 Common Crane warrant further investigation.

331 *Migratory detour and bottleneck*

332 This study presents the first quantitative assessment of detours undertaken by Common cranes
333 along the Central Asian Flyway (CAF), revealing a substantial deviation from the shortest possible
334 migration route. Earlier, migratory detour has been examined in White-naped Crane *Grus vipio*
335 where the cranes took detours to capitalise on high-quality habitat (Fujita et al. 2004). Conversely,
336 Black-necked Crane, an Asian Crane species did not exhibit detour while migrating within the
337 Tibetan Plateau (Q. Liu et al. 2012). While long-distance migration is inherently constrained by the
338 energetic demands of sustained flight (Alerstam 2011), migratory birds frequently exhibit route
339 adjustments to optimize refuelling opportunities and minimize physiological stress and the risk of
340 predation (Ydenberg, Butler, and Lank 2007; Aharon-Rotman et al. 2016; Norevik et al. 2020) . Our
341 findings demonstrate that detours increased the total migration distance by up to 41% compared
342 to the shortest route. The significant increase in migration length observed across latitudes during
343 both spring and autumn migrations suggests that environmental and topographical factors
344 strongly influence route selection.

345 A shortest straight migratory trajectory would necessitate crossing the Hindukush and Kashmir
346 Himalaya. The complex topography of these high-altitude regions is characterized by turbulent
347 wind regimes, low atmospheric pressure, and unpredictable thermal availability (Ohlmann 2017;
348 Galtbalt et al. 2022), conditions that are largely unsuitable for facultative soaring species like

Common Crane. Given that Common cranes also rely on thermal uplift to sustain long-distance flights with minimal energy expenditure, the scarcity of stable thermals in this region likely renders the shortest route energetically expensive. Consequently, the observed detours reflect a strategic avoidance of suboptimal flight conditions, favoring alternative routes that facilitate soaring flight and reduce reliance on energetically costly flapping flight.

The westward deviation observed in both spring and autumn migrations directs the cranes through the arid landscapes of Pakistan, Afghanistan, and Turkmenistan, where extensive desert expanses generate strong and consistent thermal uplift and also provide wind assistance (Galtbalt et al. 2022; Mi et al. 2022). The availability of such atmospheric conditions likely enables Common cranes to employ mixed flying strategy, mitigating the energetic costs associated with increased detour distances. Beyond the benefits conferred by thermal availability, the presence of critical stopover habitats along this route appears to further justify the observed deviations from the shortest path. The agricultural landscapes near the Iran-Afghanistan border, wetland complexes and desert oases in Turkmenistan, and the highly productive agricultural fields of the Amu Darya River delta provide key restring and foraging opportunities, enabling cranes to replenish energy reserves at strategically spaced intervals. The pronounced detours and prolonged stop-over period observed during outward migration further highlight the role of habitat quality in influencing route selection, as cranes must accumulate substantial energy reserves before continuing into breeding grounds. By integrating thermal soaring opportunities with access to high-quality stopover habitats, the observed flyway effectively offsets the energetic costs associated with increased travel distance.

The identified migratory bottleneck along the Iran-Afghanistan border, particularly between latitudes 33°N and 35°N, highlights a critical conservation priority for the Common Crane. This bottleneck possibly results from geographic constraints such as the Aladagh, Binalud and East Iranian Mountain ranges in the West and the high reaches of the Hindukush Himalaya of Afghanistan in the East, forcing cranes to funnel through a narrow corridor. Such natural barriers shape migratory routes by limiting alternative flight paths, concentrating individuals into specific regions (La Sorte et al. 2016). However, this convergence makes the species highly vulnerable to habitat degradation, land-use changes, and direct threats such as hunting even if the birds are not resting or foraging in these areas (Mostafawi, Naseri, and Ostrowski 2017). The consequences of migratory bottlenecks extend beyond localized threats. Because such areas channel a significant portion of a species' population, disturbances can have disproportionate impacts on overall population dynamics (Iwamura et al. 2013). Recognizing bottlenecks as ecological priorities can help integrate their protection into broader conservation strategies, benefiting not only cranes but

also other migratory species that rely on these corridors. By addressing threats at these critical junctures, conservationists can enhance the resilience of migratory populations and maintain the ecological integrity of these essential flyways.

Conclusion

Our multi-year tracking study of Common cranes along the Central Asian Flyway (CAF) provides critical insights into the species' migration timing, routes, and stop-over areas. Notably, this study is the first quantitative assessment of migratory detours and the identification of a migratory bottleneck of Common Crane along the CAF. The findings reveal that Common cranes deviate substantially from the shortest possible migration route, increasing their travel distance by up to 41% to optimize energy expenditure and access high-quality stop-over habitats. This detour behavior is driven by the avoidance of physiologically demanding ecological barriers, the Hindukush and Kashmir Himalaya, and the strategic use of thermal soaring conditions in arid landscapes. Additionally, a migratory bottleneck recorded at the Iran-Afghanistan border, where geographic constraints funnel all the Crane migration routes, highlights a critical vulnerability in the migratory flyway of Common Crane. Given the

The study also reinforces the importance of long-term, multi-individual tracking in capturing the full spectrum of migratory behaviors. The observed temporal consistency in migration schedules, coupled with individual variability in departure decisions, underlines the dynamic nature of Common Crane migrations. The identification of dual migration corridors—western during outward migration and eastern during return migration—further demonstrates seasonal flexibility in route selection, likely driven by environmental and topographical constraints and breeding location. Furthermore, the reliance on arid landscapes, river floodplains, and steppe habitats for stop-over sites highlights the ecological importance of these regions in sustaining migratory populations.

Conservation implications

Key stopover habitats and a migratory bottleneck along the Iran-Afghanistan border has crucial conservation implications for Common cranes and other species using the Central Asian Flyway. Stopover sites such as the Karakum Desert, Amu Darya floodplains, and northern Kazakhstan's steppe habitats provide essential resources for refueling and resting. Anthropogenic modifications in the habitats in these areas could have cascading effects on migratory population of not only

Common Crane but other species using the same flyway, necessitating habitat protection and integration into transboundary conservation initiatives.

Beyond habitat threats, disease outbreaks pose an increasing risk to migratory birds. The recent mass mortality of Common cranes due to highly pathogenic avian influenza (H5N1) highlights the vulnerability of birds congregating in large numbers. Given that the stopover sites identified in this study likely host a high abundance of migratory birds, they could serve as hotspots for disease transmission. Regular monitoring and screening at these key locations are essential for early detection and mitigation of emerging infectious diseases. Integrating disease surveillance into conservation strategies will be crucial for maintaining population health and ensuring the stability of the broader migratory network.

Importantly, the Common Crane can serve as a sentinel species for monitoring the Central Asian Flyway, particularly along the desert route passing through Pakistan, Afghanistan, Turkmenistan, Uzbekistan, and Kazakhstan. Its dependence on diverse habitats—arid deserts, river floodplains, agricultural fields, steppe grasslands, and human-managed reservoirs—demonstrates its adaptability to both natural and modified landscapes. The identification of key stopover sites, alongside the quantification of detours and a critical bottleneck, underscores its sensitivity to environmental and topographical constraints. These traits, combined with its wide distribution and long-distance migrations, make the Common Crane an ideal indicator for assessing flyway health and the impacts of environmental change. By prioritizing its conservation, we can safeguard not only this species but also the broader ecological network dependent on this vital corridor.

Acknowledgments

We thank the Director and Dean of the Wildlife Institute of India for their support during the study. We thank the Mr. Shwetank Pandit (Rtd. IFS) and and Mr. V.J. Rana (Rtd. IFS), Sh. P. Purushothama (IFS), Dr. Chaudhary (IFS), Mr. Dipak Solanki (GFS), Mr. Swapnil Patel (GFS) of Gujarat State Forest Department for their support in conducting fieldwork. We thank Mr. Gani Sama and late Mr. Karshan Padhar the frontline staff of the Nal Sarovar Ramsar Site, for their expert help in trapping birds. We thank interns and field support staff for their support in field work. We thank the people of Vadla village for providing logistics while field work. Mention of trade names or commercial products in this publication is solely to provide specific information and does not imply recommendation or endorsement by the authors or the affiliated institution.

Author contributions

HLB, RSK, and AB conceived the study. RSK and AB secured funding. HLB, RSK and GS arranged fieldwork logistics. HLB, GS and RSK participated in fieldwork. HLB conducted data analyses. HLB

wrote the original draft of the manuscript. All authors reviewed, edited and approved the final manuscript.

Funding

This research was funded by the PowerGrid Corporation of India Ltd. under its Corporate Social Responsibility initiative. The funding agency had no role in study design, data collection, analysis, interpretation, or conclusions.

Conflict of interest

The authors declare no conflict of interest.

Availability of data and materials

The datasets used and/or analyzed during the current study are uploaded in Move Bank and are kept unavailable for download. The data may be made available from the corresponding author on reasonable written request.

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Figures:

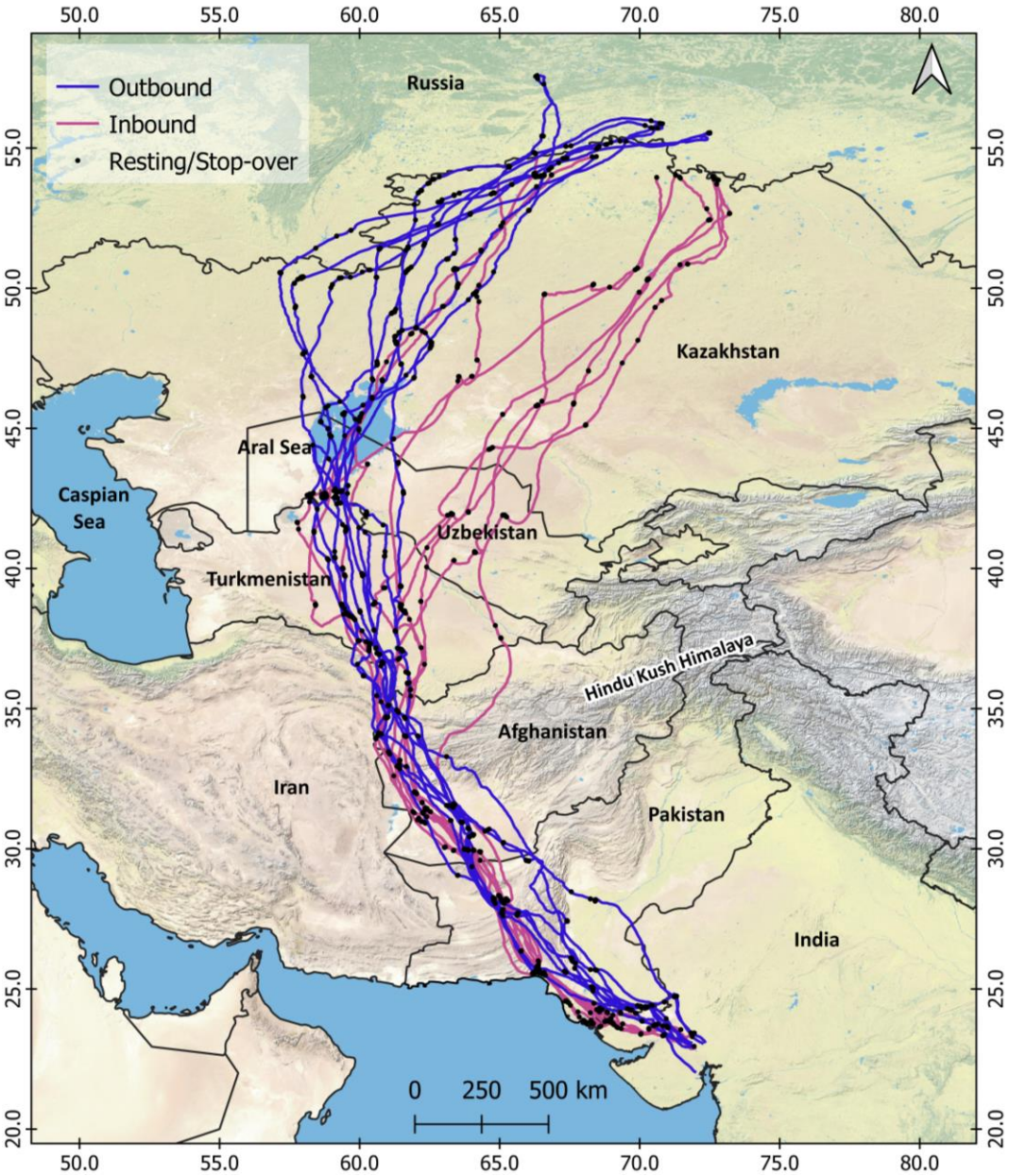

Figure 1. A map showing migration trajectories of five tagged Common Cranes between 2020 – 2023. (Base map: ESRI Physical)

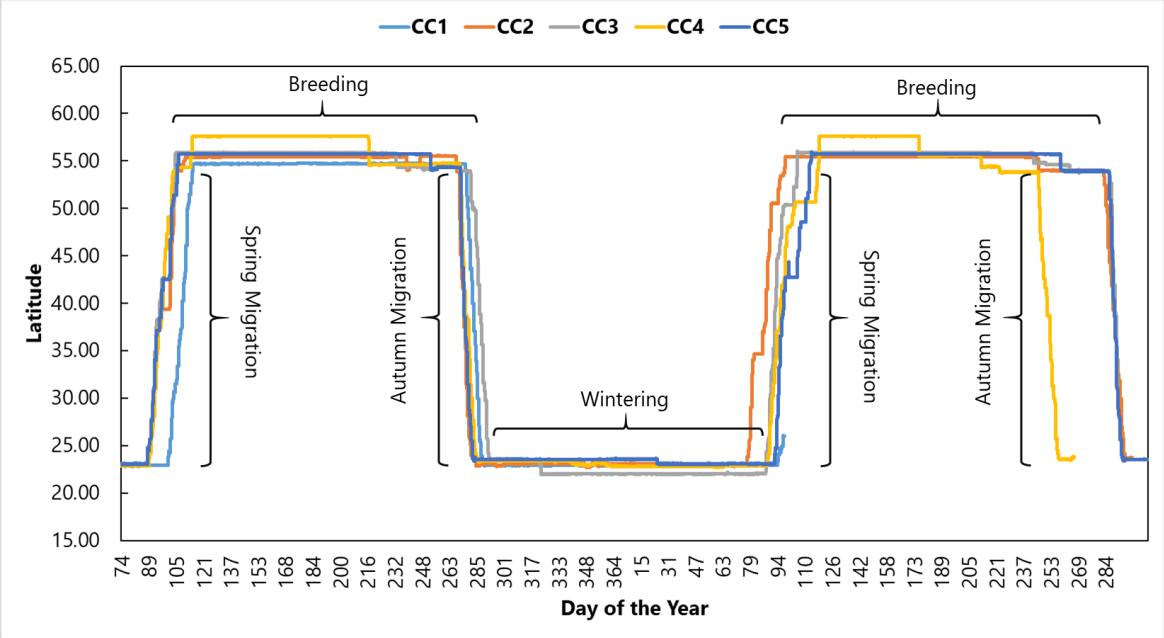

Figure 2. A line graph showing the latitudinal distribution of Common Crane movement trajectories. The different colour shows different tagged individuals.

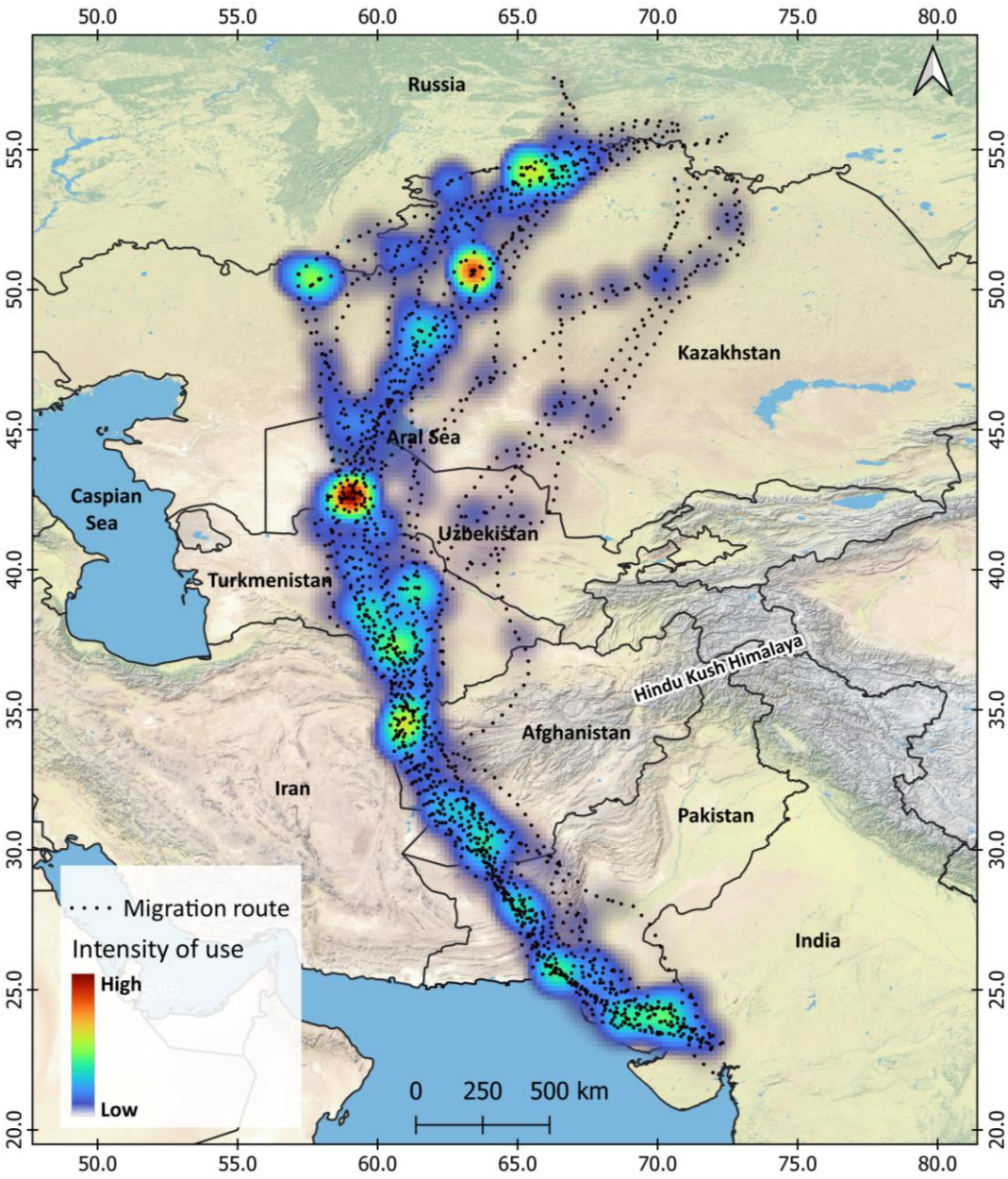

Figure 3. A map showing high occurrence areas of Common Cranes derived through Kernel Density Estimation. (Base map: ESRI Physical)

Table 1. A table showing the summary statistics of key migration parameters of the five tagged Cranes during inward and outward migration journeys

Parameter	**Migration Direction**	**Mean**	**Median**	**SE**	**Range**
Migration Distance (km)	Inward	4378.78	4340.00	51.04	4165.00 - 4593.00
	Outward	5031.44	5046.00	68.86	4638.00 - 5278.00
Migration Duration (days)	Inward	11.56	12.00	0.65	9.00 - 14.00
	Outward	21.67	22.00	1.62	15.00 - 31.00
Straightness Index	Inward	0.78	0.78	0.01	0.74 - 0.81
	Outward	0.73	0.73	0.01	0.69 - 0.78
Stop-over Duration (days)	Inward	0.22	0.00	0.15	0.00 - 1.00
	Outward	6.56	8.00	1.26	0.00 - 12.00
Migration Speed (km/day)	Inward	388.93	381.17	23.15	310.00 - 500.78
	Outward	241.19	239.91	15.37	169.00 - 320.53
Travel Days	Inward	11.33	12.00	0.67	8.00 - 14.00
	Outward	15.11	15.00	0.70	12.00 - 19.00
Travel Speed (km/day)	Inward	398.39	381.17	26.55	324.15 - 551.38
	Outward	337.78	330.87	13.80	275.79 - 394.69

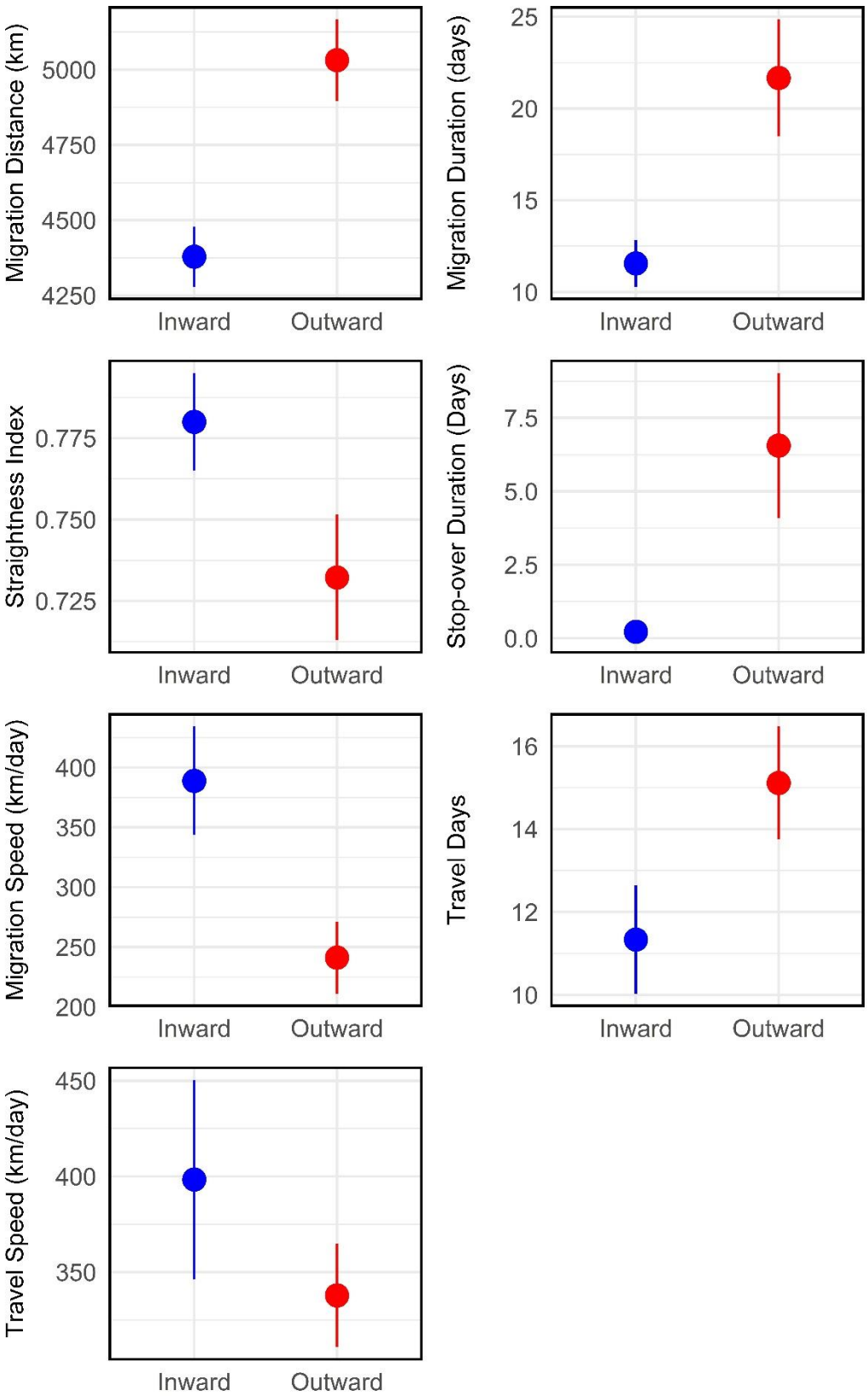

Figure 4. Dot-whisker plots comparing the key migration parameters of the five tagged Common Cranes. The whiskers show 95% confidence interval.

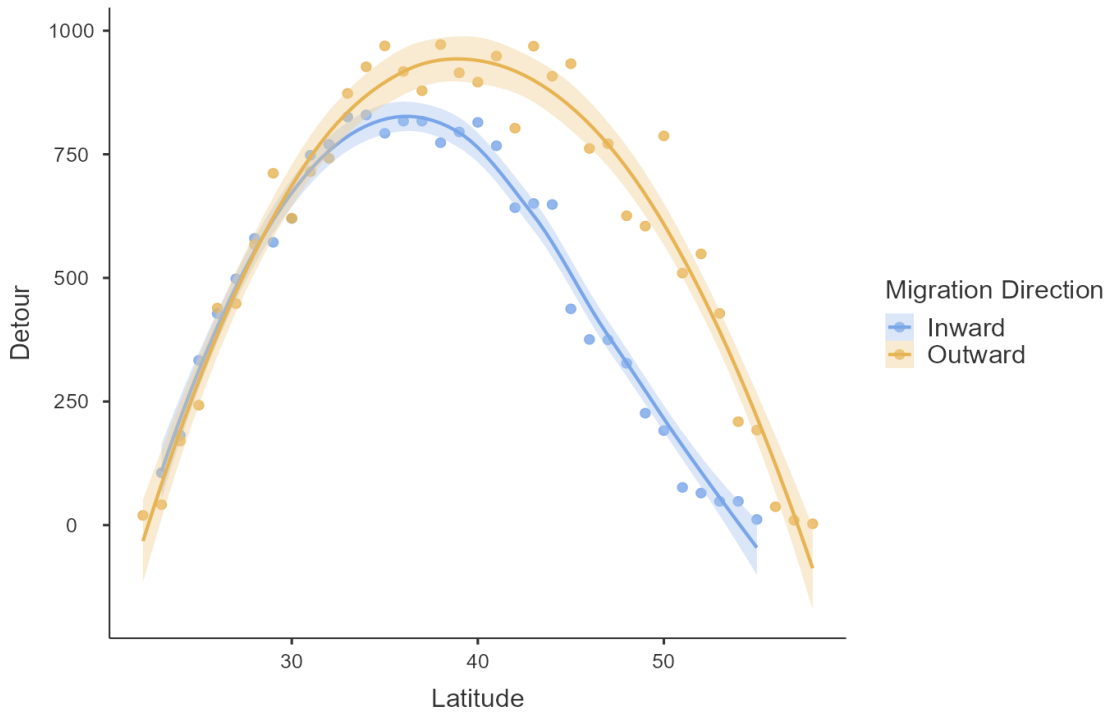

Figure 5. A graph showing the seasonally explicit spatial patterns in the migratory detour, visualised by fitting smoothed LOESS lines. The values of detour are in km.

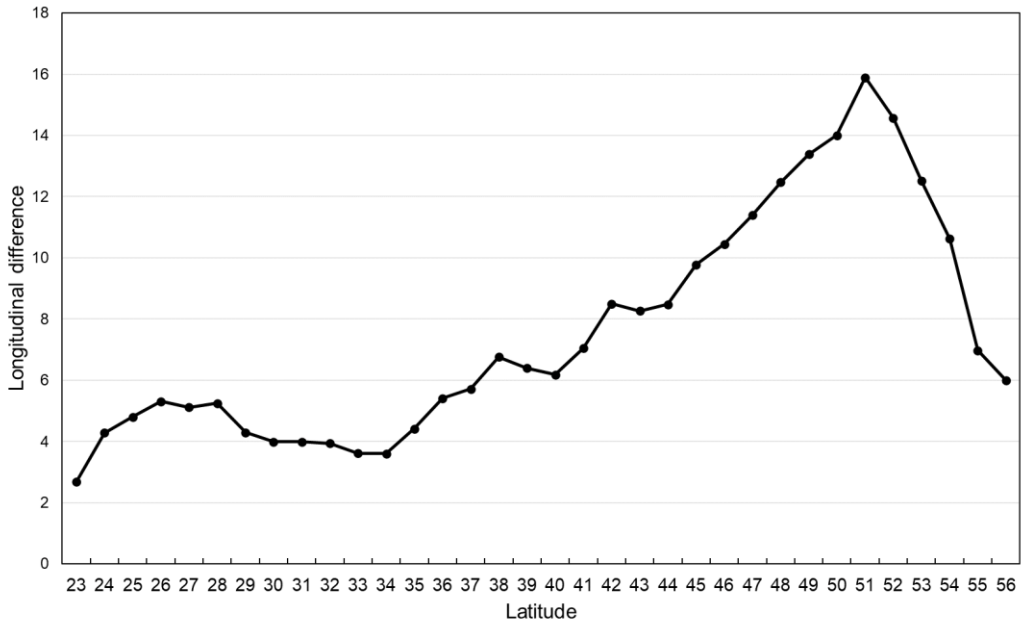

Figure 6. A figure showing spatial spread (depicted as a longitudinal difference (in km) between the west-most and the east-most location in each latitude) in Common Crane migration trajectories. The lowest spread is observed at 34°N, making it a migratory bottleneck.

Supplementary material

Table S1: A table showing basic information of tagged Common cranes

Sr. No.	Name of the individual	Date of tagging	Capture and Tagging location	Weight (kg)	No. of locations used in the study
1	Vadla	12-03-2020	Vadla Wetland (22.922671 N; 71.958432 E)	4.7	3649
2	Gani	10-02-2022	Thol Ramsar Site (23.139794 N; 72.405048 E)	4.3	8283
3	Sanand	22-02-2022	Thol Ramsar Site (23.135603 N; 72.401336 E)	4.5	7759
4	Nal	04-03-2022	Vadla Wetland (22.918991 N; 71.96749 E)	4.7	9289
5	Bhal	05-03-2022	Vadla Wetland (22.910345 N; 71.984059 E)	4.6	11356

Table S2: A table showing the migration parameters of the tagged Common cranes

Migration Direction	Individual	Migration Distance (km)	Migration Duration (days)	Straightness Index	Stop-over Duration (Days)	Migration Speed (km/day)	Travel Days	Travel Speed (km/day)
Inward	Bhal_1	4593.00	14.00	0.81	0.00	328.07	14.00	328.07
	Bhal_2	4340.00	14.00	0.80	1.00	310.00	13.00	333.85
	Gani_1	4295.00	11.00	0.80	0.00	390.45	11.00	390.45
	Gani_2	4165.00	10.00	0.78	0.00	416.50	10.00	416.50
	Nal_1	4507.00	9.00	0.78	0.00	500.78	9.00	500.78
	Nal_2	4214.00	13.00	0.79	0.00	324.15	13.00	324.15
	Sanand_1	4574.00	12.00	0.76	0.00	381.17	12.00	381.17
	Sanand_2	4411.00	9.00	0.76	1.00	490.11	8.00	551.38
	Vadla	4310.00	12.00	0.74	0.00	359.17	12.00	359.17
Outward	Bhal_1	5046.00	26.00	0.78	10.00	194.08	16.00	315.38
	Bhal_2	5240.00	31.00	0.77	12.00	169.03	19.00	275.79
	Gani_1	5016.00	19.00	0.74	2.00	264.00	17.00	295.06
	Gani_2	5278.00	22.00	0.74	8.00	239.91	14.00	377.00
	Nal_1	4963.00	23.00	0.73	8.00	215.78	15.00	330.87
	Nal_2	5163.00	23.00	0.72	8.00	224.48	15.00	344.20
	Sanand_1	4638.00	17.00	0.72	5.00	272.82	12.00	386.50
	Sanand_2	5131.00	19.00	0.70	6.00	270.05	13.00	394.69
	Vadla	4808.00	15.00	0.69	0.00	320.53	15.00	320.53