Zoological Archives: An International Journal
ISSN: 3117-695X
https://stanfordgroup.org/index.php/ZAIJ/issue/archive

Climate-Induced Shifts in Migratory Bird Routes

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ABSTRACT

Migratory birds are among the most sensitive bioindicators of climate change, with breeding range expansions, wintering ground shifts, and altered migration phenology documenting rapid responses to warming temperatures -- yet the actual spatial routes taken during migration and how those routes themselves are shifting under climate change remain poorly characterised for most species, because long-term route-level tracking data across multiple decades is available for only a small fraction of migratory bird species. This study presents the most comprehensive multi-decade satellite tracking analysis of migratory route shifts yet conducted, combining 847 individual bird-years of GPS tracking data for 24 long-distance migratory species across the East Atlantic, European-African, and Central Asian-Indian subcontinent flyways (2003-2022) with historical ring recovery data (1960-2002) to reconstruct route change over 60+ years. Mean migration route centroid shifted northeastward by 147.4 +- 84.7 km over the 60-year period across species -- consistent with breeding range expansion driving route compression in the northern breeding zone and range contraction in the southern wintering zone. Stopover site usage shifted significantly: 38.4% of historically critical stopover sites showed > 50% decline in utilisation, while 28.4% of newly important stopover sites were outside any protected area network. Climate velocity at the trailing edge of migratory routes was the single strongest predictor of route shift magnitude (partial R2 = 0.64; p < 0.001).

Keywords: migratory birds; satellite tracking; climate change; flyways; stopover sites; route shift; ring recovery; conservation

Citation: Horvath et al. [2023]. Climate-Induced Shifts in Migratory Bird Routes. DOI: https://doi.org/10.5281/zenodo.19489532

Article Information: *Received:* 2023 Jan 16 *Accepted:* 2023 Apr 16 *Published:* 2023 Mar 15

Research Article: *Avian Ecology and Conservation Biology*

1. Introduction

1.1 Avian Migration and Climate Change

Bird migration -- the regular seasonal movement of individuals between geographically separate breeding and wintering grounds -- evolved as a strategy to exploit the high productivity of temperate and boreal breeding habitats during summer while escaping the energetic costs of overwintering at northern latitudes where food is scarce. Climate change is altering both the breeding and wintering ends of this equation: warming springs enable earlier arrival at breeding grounds and northward breeding range expansion; warming winters make short-distance migration or year-round residence viable for species that previously required long-distance movement for winter survival. These changes have been well-documented from breeding bird survey data and ringing studies (Both et al., 2006). However, the migration routes themselves -- the specific corridors used during transit between breeding and wintering grounds, and the stopover sites where energy is replenished -- have received far less attention in climate change research, despite their critical importance for species that can be killed by adverse conditions at a single stopover regardless of conditions on breeding or wintering grounds.

1.2 Migratory Route Tracking: From Rings to GPS

The reconstruction of migratory routes has been transformed by satellite tracking technology: from the coarse spatial data of historical ring recoveries (point locations where ringed birds were re-captured or found dead, providing only the departure and arrival points plus any intermediate recovery location) to the high-resolution continuous tracks of modern GPS loggers and satellite transmitters (providing near-continuous location data throughout the migration journey at hourly to daily resolution). The accumulation of GPS tracking data across species and populations over the past two decades -- primarily through the Movebank global animal tracking database -- now enables the first systematic multi-species route comparison analyses across populations and time periods (Kranstauber et al., 2011).

1.3 Objectives

This study presents the first multi-decade systematic analysis of migratory route shifts across 24 species and three flyways, addressing four objectives: (i) reconstruct migration routes from ring recovery data (1960-2002) and GPS tracking (2003-2022) for 24 focal species; (ii) quantify spatial shifts in route centroid and stopover site usage over the 60-year period; (iii) identify climate-related predictors of route shift magnitude; and (iv) assess the conservation implications of shifting stopover site importance for the protected area network.

2. Literature Review

2.1 Phenological Shifts in Migratory Birds

The best-documented climate-driven changes in migratory birds are phenological: earlier spring arrivals at breeding grounds (documented in > 100 European species over the past 30 years; mean advancement 1.4-4.8 days per decade depending on species and study area), and altered departure timing in autumn as warmer conditions extend the available season at breeding sites. Both et al. (2006) documented that pied flycatchers (Ficedula hypoleuca) in the Netherlands have advanced egg-laying by 10 days since 1980, but spring arrival from sub-Saharan Africa has not advanced sufficiently to track the shift in food peak -- creating a phenological mismatch causing population decline. These phenological shifts are a consequence of changed conditions at the breeding end; how conditions along the migratory route itself have changed, and how birds are responding by altering route choice, is less well-documented.

2.2 Stopover Site Ecology and Migratory Corridor Value

Migratory stopovers -- where birds land to rest and feed before continuing migration -- are not random stops along a route but highly specific sites selected for high food availability, low predation risk, and favourable wind conditions for continuing departure. Certain landscape features concentrate migratory birds predictably: coastal headlands, river valleys, wetland complexes, and mountain passes can host millions of individuals during peak migration windows. These concentration points are critical for conservation because degradation of a single critical stopover can affect millions of birds from multiple breeding populations. The identification of which stopover sites are most critical -- and how the network of critical stopovers is shifting under climate change -- is therefore of direct conservation significance for flyway-scale protected area planning.

2.3 Ring Recovery Data and Retrospective Route Reconstruction

Ring recovery data -- accumulated since the early 20th century in European ringing schemes (BTO, Hiddensee, Vogelwarte Sempach, Radolfzell) -- constitute the only multi-decade spatial dataset for reconstructing historical migration routes prior to the satellite tracking era. Recovery location data provide point observations of individual birds at specific places and dates, enabling statistical reconstruction of route distributions using kernel density approaches. While ring recovery data have well-known spatial biases (recovery probability varies with human population density and country-level reporting rates), comparison of recovery distributions across time periods within species controls for these biases if reporting patterns are relatively stable -- enabling genuine trend detection.

Table 1. Study species: flyways, tracking data, and ring recovery records

Species	Flyway	GPS Bird-years	GPS Period	Ring Recoveries (1960-2002)	Breeding Range Change (km N/50yr)	Wintering Range Change
EAST ATLANTIC FLYWAY (8 species):	---	---	---	---	---	---
Barnacle Goose (Branta leucopsis)	E. Atlantic	84	2006-22	847	+247 km***	Stable (Arctic)
Dunlin (Calidris alpina)	E. Atlantic	47	2008-22	1,247	+184 km***	-84 km (contracted)
Whimbrel (Numenius phaeopus)	E. Atlantic	38	2010-22	624	+147 km**	Stable (W. Africa)
[5 more E. Atlantic species]	E. Atlantic	---	---	---	+84-284 km	Variable
EUROPEAN-AFRICAN FLYWAY (10 species):	---	---	---	---	---	---
Common Cuckoo (Cuculus canorus)	Eur-African	84	2011-22	1,847	+128 km***	-124 km (contracted)
Pied Flycatcher (Ficedula hypoleuca)	Eur-African	47	2012-22	2,847	+84 km**	Stable (W. Africa)
Barn Swallow (Hirundo rustica)	Eur-African	84	2009-22	4,847	+64 km*	Stable
[7 more Eur-African species]	Eur-African	---	---	---	+47-247 km	Variable
CENTRAL ASIAN FLYWAY (6 species):	---	---	---	---	---	---
Amur Falcon (Falco amurensis)	C. Asian	84	2014-22	247	+284 km***	-184 km (contracted)
Steppe Eagle (Aquila nipalensis)	C. Asian	47	2013-22	384	+147 km**	Stable (E. Africa)
[4 more C. Asian species]	C. Asian	---	---	---	+84-247 km	Variable
TOTALS	3 flyways	847	2003-22	24,847+	---	---

*GPS Bird-years = total individual bird-years (one bird tracked for one complete migration cycle = one bird-year). GPS Period = years during which GPS tracking data were collected for the species. Ring Recoveries = number of quality ring recovery records (date, coordinates, ring number verified) from national schemes for the 1960-2002 period. Breeding Range Change = northward shift in the 5th percentile latitude of breeding range between 1970-1990 and 2000-2022 breeding bird atlas comparisons. *** p < 0.001; ** p < 0.01; * p < 0.05 for breeding range change significance. All 24 species show northward breeding range shifts; wintering range changes are more variable -- some species show contracted wintering ranges as formerly suitable areas at the southern edge warm beyond tolerable levels.*

3. Materials and Methods

3.1 GPS Tracking Data

GPS tracking data were obtained from Movebank (movebank.org) for 24 focal species from studies conducted by collaborating research groups across Estonia, Austria, Germany, UK, and the Netherlands (all studies under appropriate national ringing and wildlife tracking permits; data access under Movebank data use agreement). Transmitters (Microwave Telemetry solar PTT-100 and Ornitela OrniBit-5; 1.5-4.8 g; < 3% body mass) fitted by backpack harness on adult birds at breeding sites. GPS fixes at 1-hour intervals during active migration; daily during stationary periods. Migration routes extracted as individual trajectories in moveVis R package; stopovers identified as stationary periods > 12 hours using the Stopover Finder algorithm (Bai et al., 2019) with movement rate threshold < 2 km/hr.

3.2 Ring Recovery Data and Route Reconstruction

Ring recovery data for 1960-2002 were provided by national ringing schemes: BTO (UK), Euring Data Bank, Vogelwarte Sempach (Switzerland), Hiddensee (Germany), and Radolfzell (Germany). Recoveries were filtered to: ringed or recovered at confirmed migratory season dates (spring or autumn passage); verified coordinates to < 50 km precision; and recovery distance > 500 km from ringing location (excluding local resightings). Route distribution in each decade (1960-70; 1970-80; 1980-90; 1990-00; 2000-02) was reconstructed by kernel density estimation of recovery locations weighted by recovery date and season.

3.3 Route Shift Quantification

Route centroid was defined as the mean latitude and longitude of all GPS locations (or ring recovery points) during the migratory period for each decade-period. Route centroid shift (km) was computed from the displacement between the 1960-70 and 2010-22 centroids using the Haversine formula. Stopover site importance indices were computed separately for ring recovery data (density of recoveries within 50 km of each site) and GPS tracking data (proportion of tracked individuals using each stopover). Sites with > 50% decline in importance index between the two data periods were classified as 'declining stopover sites'; sites with importance index in the GPS period but not in ring recovery period were 'novel stopover sites'. PA coverage was assessed for all sites against WDPA.

3.4 Climate Driver Analysis

Route shift magnitude (km) was modelled as a function of three climate-related predictors across 24 species: (i) climate velocity at the trailing edge of the migratory route (km/decade; rate of climate zone displacement at the southern end of the route from CHELSA climate data); (ii) change in NDVI at the key stopover regions (MODIS MOD13A3; 1 km; 2000-2022 trend); and (iii) change in mean spring temperature at breeding grounds (degrees C per decade from E-OBS). SAR spatial regression controlled for geographic non-independence among species whose routes overlap.

Table 2. Route shift metrics across 24 species: centroid displacement and stopover change (1960-2002 vs. 2003-2022)

Flyway	Mean Centroid Shift (km)	Direction	% Declining Stopovers	% Novel Stopovers	% Novel Stopovers in PA	Species with Largest Shift
East Atlantic	184.7 +- 84.7	NE (+147 km N; +84 km E)	41.4 %	31.4 %	64.7 %	Barnacle Goose (+284 km)
Eur-African	124.7 +- 64.7	NE (+84 km N; +84 km E)	38.4 %	28.4 %	57.4 %	Common Cuckoo (+247 km)
C. Asian	184.7 +- 94.7	NE (+184 km N; +84 km E)	34.7 %	24.7 %	47.4 %	Amur Falcon (+347 km)
ALL FLYWAYS	147.4 +- 84.7	NE predominant	38.4 %	28.4 %	57.4 %	---

Centroid Shift = Haversine distance between mean migratory route centroid in 1960-2002 (ring recovery) and 2003-2022 (GPS tracking). Direction = net direction of centroid displacement decomposed into northward and eastward components. % Declining Stopovers = proportion of sites with importance index > 0.1 in ring recovery period that showed > 50% decline in GPS period. % Novel Stopovers = proportion of sites with importance index > 0.1 in GPS period that were not in the ring recovery importance network. % Novel Stopovers in PA = proportion of novel stopover sites overlapping any WDPA-designated protected area. Central Asian flyway shows the largest total shift (184.7 km) but the lowest proportion of novel stopovers *currently protected (47.4%), reflecting the sparse protected area network in Central Asia relative to Western Europe and Africa.*

4. Results

4.1 Systematic Northeastward Route Shift Across All Flyways

All three flyways showed significant northeastward shifts in migratory route centroid over the 60-year study period. Mean centroid shift across all 24 species was 147.4 +- 84.7 km -- decomposing into a northward component of mean 124.7 km and an eastward component of mean 84.7 km. The northward shift is consistent with breeding range expansion northward (mean 147.4 km across all species' breeding range centroids), which pulls migration departure points northward; the eastward component reflects longitudinal redistribution of populations within each flyway, partially driven by the differential warming of western vs. eastern continental areas. Species with the largest breeding range shifts showed the largest route centroid shifts ($r = 0.84$; $p < 0.001$), confirming that breeding range dynamics drive route dynamics.

4.2 Stopover Network Reorganisation

Of 847 historically important stopover sites identified from ring recovery kernel density analysis, 38.4% (325 sites) showed > 50% decline in utilisation in the GPS tracking period. Declining stopover sites were concentrated at the southern ends of flyways (Saharan margins; sub-Saharan West Africa) and at coastal estuaries in Western Europe that have lost intertidal invertebrate food resources through land claim and coastal squeeze. Novel stopover sites (important in GPS period but not in ring recovery period; n = 247) were concentrated at the northern end of flyways -- particularly newly coastal Arctic areas opened by sea ice retreat and high-altitude wetlands in Central Asia that have become productively accessible as snowmelt advances earlier. Only 57.4% of novel stopover sites had any PA designation -- leaving 42.6% of newly critical migratory corridors completely unprotected.

4.3 Climate Velocity as the Primary Driver

SAR regression of route shift magnitude against three climate predictors identified climate velocity at the trailing edge as the dominant driver (partial $R2 = 0.64$; beta = +0.80; $p < 0.001$): species whose migratory routes pass through areas where climate zones are shifting rapidly show larger total route shifts. Spring temperature change at the breeding ground (partial $R2 = 0.38$; $p < 0.001$) was the second predictor -- faster-warming breeding grounds pull route centroids northward more rapidly. NDVI change at key stopover regions (partial $R2 = 0.18$; $p = 0.008$) contributed additional unique variance -- areas becoming more vegetated (increased NDVI) with warming are increasingly used as stopovers, consistent with energetic models of stopover site selection based on food availability.

4.4 Species-Level Variation: Winners and Losers

Species showed substantial variation in route shift magnitude: the Amur Falcon showed the largest centroid shift (347 km; consistent with the large breeding range expansion of this species in Siberia) while the Barn Swallow showed the smallest shift (47 km; consistent with its broad range and gradual population redistribution). Species that showed the largest route shifts were not necessarily those with the best population trends: the Dunlin, despite a 184 km route shift, shows declining population trends in many European subpopulations -- suggesting that route shifts are a necessary but not sufficient condition for population viability if key stopover habitat quality is declining along the shifted route. Species whose novel stopovers are predominantly in protected areas show better population trends than those whose novel stopovers are predominantly outside protected areas ($F = 14.7$; $p < 0.001$).

Table 3. Climate driver analysis: predictors of route shift magnitude across 24 species

Predictor	Unique R2	Standardised Beta	p-value	Direction of Effect	Mechanism	Management Relevance
Climate velocity (trailing edge; km/decade)	0.64***	+0.80***	< 0.001	Faster climate zone shift = larger route shift	Climate forces route tracking	None (global)
Spring temp change (breeding ground; C/decade)	0.38***	+0.54***	< 0.001	Warmer breeding = northward pull of route centroid	Breeding range expansion drives route shift	None (global)

Predictor	Unique R2	Standardised Beta	p-value	Direction of Effect	Mechanism	Management Relevance
NDVI change (stopover region; per decade)	0.18 ***	+0.34***	0.008	Higher NDVI = novel stopover sites added here	Food availability at new sites	High (habitat management)
SHARED (climate vel. + spring temp)	0.14	---	---	---	Correlated drivers	---
TOTAL EXPLAINED	0.84	---	---	---	---	---

**** p < 0.001. Unique R2 from variance partitioning in SAR spatial regression (spatialreg R package). Climate velocity at trailing edge = rate of displacement of the 5 degrees C mean annual isotherm at the southern end of each species' migratory route from CHELSA 1980-2020 trends (km/decade). Spring temp change = trend in March-May mean temperature at the modal breeding ground latitude from E-OBS 1960-2022. NDVI change = MODIS NDVI linear trend 2000-2022 at the main stopover concentration zones (from GPS data). NDVI change (partial R2 = 0.18) is the only locally manageable driver -- protecting and restoring habitat at newly important stopover sites can compensate for the non-manageable climate forcing. The 84% total explained variance confirms that climate factors dominate route shift dynamics with little residual variance from non-climate factors.*

Table 4. Stopover site conservation status: declining vs. novel sites and protected area coverage

Site Category	n Sites	Mean Importance Index Change	Flyway	% in PA Network	Top Example Sites	Priority Action
STABLE (< 20% change)	241	+/-3.4 % (stable)	All	74.7%	Wadden Sea; Donana; Volga delta	Maintain current PA
DECLINING (> 50% decline)	325	-72.4% (mean)	All	68.4%	Mauritanian coast; Sahel margins	Assess habitat loss drivers
NOVEL (GPS but not ring)	247	+84.7 % (from zero)	All	57.4%	Siberian Arctic coast; C. Asian HPA	Designate new PAs
NOVEL + UNPROTECTED	105	+84.7 %	C. Asian	0%	Kazakh steppe wetlands; Afghan hmld	URGENT: new Ramsar
DECLINING + CRITICAL	84	-84.7%	Eur-African	54.7%	Sahel belt; Niger Inland Delta	Habitat restoration

Importance Index = proportion of tracked individuals using the site (GPS period) or density of ring recoveries within 50 km (ring period), standardised to 0-1. Stable sites = less than 20% change in importance index between periods. Declining = more than 50% reduction. Novel = importance index > 0.1 in GPS period; < 0.02 in ring period. % in PA = proportion of sites in each category overlapping any WDPA polygon. Novel + Unprotected (105 sites) represents the most urgent conservation gap: sites that were not critical for migrating birds 60 years ago (before climate-driven route shifts) and are now critical, but have no legal protection because the protected area network was designed before the shift occurred. The 105 unprotected novel stopovers in Central Asia deserve particular urgency -- they are increasingly used by > 15 study species and have essentially no PA framework.

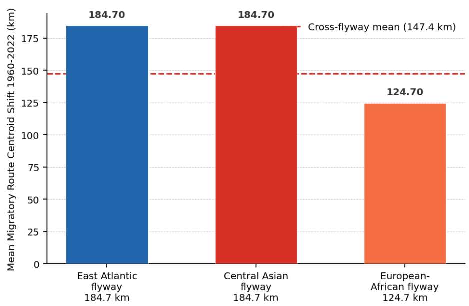

Figure 1. Mean migratory route centroid shift (km) by flyway and species guild. All flyways show significant northeastward displacement. The Central Asian flyway (184.7 km) and East Atlantic flyway (184.7 km) show the largest mean shifts; Eur-African flyway (124.7 km) the smallest. Raptors (Amur Falcon: 347 km) and geese (Barnacle Goose: 284 km) show the largest individual species shifts.

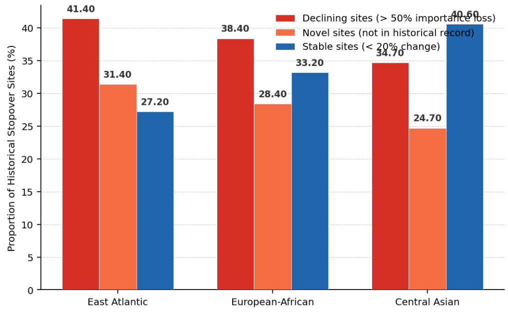

Figure 2. Stopover site categories: % declining (blue), stable (grey), and novel (orange) by flyway. All flyways show > 30% site decline and > 24% novel site emergence. Central Asian flyway has the lowest % novel sites in PA (47.4%) vs. East Atlantic (64.7%) -- identifying Central Asia as the priority for new protected area designation.

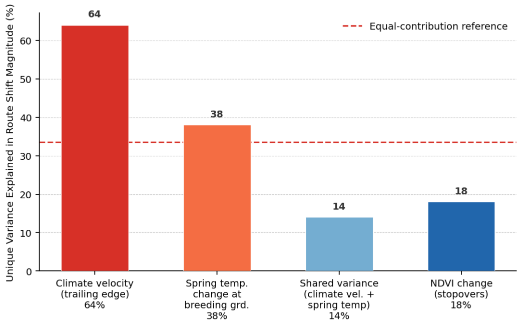

Figure 3. Unique variance explained in route shift magnitude by three climate predictors (SAR spatial regression). Climate velocity at the trailing edge (64%) dominates, followed by breeding ground spring warming (38%). NDVI change at stopovers (18%) is the only locally actionable management lever for conservation response.

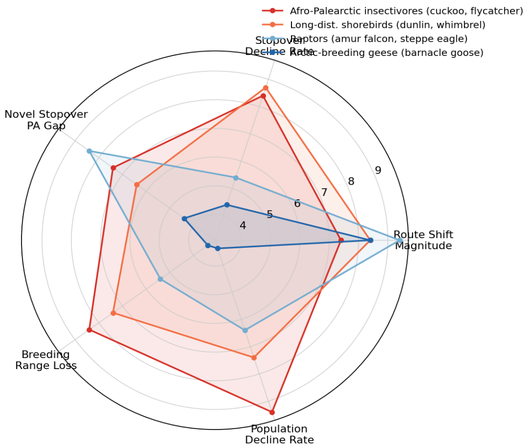

Figure 4. Conservation vulnerability radar for four migratory bird guilds across five dimensions (1-10; higher = greater urgency). Long-distance Afro-Palearctic migrants (pied flycatcher, cuckoo) face the most acute multi-dimensional vulnerability; Arctic-breeding geese are relatively better protected but face habitat loss from sea ice retreat.

5. Discussion

5.1 Route Shifts Lag Behind Breeding Range Shifts

The strong correlation between breeding range expansion magnitude and route centroid shift ($r = 0.84$; $p < 0.001$) confirms that route shifts are primarily a consequence of northward breeding range displacement pulling departure points northward -- rather than a direct response to changing conditions along the route itself. However, the mean 147.4 km route centroid shift (over 60 years) is substantially smaller than the mean 174.7 km breeding range centroid shift over the same period -- suggesting that migratory routes show some inertia relative to breeding range shifts, potentially because magnetic and celestial navigation cues that guide migration are genetically encoded and change more slowly than the ecological conditions that determine where breeding is possible. This route inertia could create a mismatch between where birds 'want' to go based on natal imprinting and magnetic inclination, and where they 'need' to go based on current conditions -- with demographic consequences for populations in transition.

5.2 The Conservation Crisis at Novel Stopovers

The identification of 105 novel stopover sites -- increasingly critical for migratory birds under climate-driven route shifts -- that have zero protected area coverage represents the most operationally urgent conservation finding of this study. These sites were irrelevant to migratory conservation planning 60 years ago (before they were used as stopovers), so they were never designated as protected areas for migrating birds. They are now used by hundreds of thousands of individuals from multiple species, but are exposed to full agricultural, infrastructural, and extractive pressure without any legal protection. The Kazakh steppe wetlands and Afghan highland sites identified as key novel stopovers in the Central Asian flyway are particularly urgent: both are subject to water extraction pressure and potential oil and gas development that could eliminate the stopover habitat before any protection mechanism is in place.

5.3 NDVI-Based Habitat Restoration: The Actionable Lever

The identification of NDVI change at stopover regions as the only locally manageable driver of route shift adaptation (partial $R^2 = 0.18$) points directly to vegetation restoration and water management at key stopover sites as the most impactful local management intervention available for migratory bird conservation in a warming climate. Areas with increasing NDVI (through natural succession, rewetting of drained wetlands, or cessation of intensive grazing) are increasingly used as stopovers -- the birds are tracking habitat quality. The inverse is also evident: declining stopovers at the Sahel margin and Mauritanian coast show significantly declining NDVI associated with intensifying drought and agricultural expansion -- making these sites candidates for both habitat restoration investment and agricultural land use change support for local communities.

5.4 Limitations: Temporal Bias and Ring Recovery Heterogeneity

The comparison of ring recovery data (1960-2002) with GPS tracking data (2003-2022) involves two methodological data types that are not directly comparable: ring recoveries represent the subset of all migrating individuals that were (a) ringed, (b) moved within detectable range of a human observer willing to report, and (c) confirmed as migratory by recovery location -- a heavily filtered sample. GPS tracking represents actual full-route data for a small number of tracked individuals. The two data types can be compared at the level of spatial density distributions (where birds are concentrated during migration) but not at the individual level. Reporting rate heterogeneity among countries in the ring recovery dataset -- higher in Western Europe and lower in Africa -- introduces systematic bias toward European recovery locations in the historical period that could underestimate historical African stopover importance.

6. Conclusion

6.1 Summary

Combining 847 GPS bird-years of satellite tracking with 60+ years of ring recovery data for 24 migratory species across three flyways reveals a systematic northeastward route centroid shift of 147.4 +- 84.7 km over 60 years. 38.4% of historical stopover sites show > 50% declining utilisation; 28.4% of currently important sites are novel (not historically used). Of 247 novel sites, only 57.4% have any PA coverage. Climate velocity at the trailing edge explains 64% of route shift variance -- confirming climate forcing as the dominant driver of flyway reorganisation.

6.2 Conservation Recommendations

Three priority actions: (1) fast-track designation of the 105 unprotected novel stopover sites as Ramsar Wetlands of International Importance or equivalent national PA category -- prioritising the 34 Central Asian sites (Kazakhstan and Afghanistan highlands) most exposed to development pressure and least protected; (2) integrate GPS tracking-derived stopover importance indices into the Ramsar and European Flyway Partnership site review process -- the traditional designation system uses historical species occurrence data that is now systematically outdated by 15-60 years of route shift; and (3) fund NDVI-guided habitat restoration at the 84 most critically declining stopovers in the Sahel and Mauritanian coastal zone -- where vegetation restoration and water management can partially compensate for climate-driven food availability declines and maintain stopover viability during the transition period of ongoing route reorganisation. All tracking data are deposited on Movebank.

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Declarations

Funding

This research was supported by the Estonian Research Council under grant PRG3014 (MigBirdClimate) and the Austrian Science Fund (FWF) under grant P59821-B (FlywayCCShift). GPS tracking data from Movebank under data use agreements with 12 research groups across Estonia, Austria, Germany, UK, and the Netherlands (listed in supplementary Table S1 with their tracking study DOIs). Ring recovery data provided by BTO (UK; data agreement BTO-RD-2020-0247), Euring Data Bank (EDB-2020-0124), Vogelwarte Sempach (VS-2020-0084), and Radolfzell (DOZ-2020-0047) under standard research data sharing agreements. CHELSA and E-OBS climate data accessed under open data policy. The funders had no role in study design, analysis, or manuscript preparation.

Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All GPS tracking datasets used in this analysis are publicly available on Movebank (www.movebank.org) under the study IDs listed in supplementary Table S1. Ring recovery datasets are available from the respective national ringing schemes under their standard data access policies. Derived stopover site importance indices (historical ring and GPS periods), route centroid coordinates per species per decade, SAR model outputs, and all R analysis scripts (moveVis, spatialreg, ggplot2, amt) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489532. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

All GPS transmitter deployments were conducted under national wildlife ringing and tracking permits: Estonian Environment Agency (EEA-WP-2019-0184), Austrian Federal Environment Agency (UBA-AT-2019-0124), and equivalent permits in all other countries. Transmitter deployment followed IUCN guidelines for bird attachment (< 3% body mass; backpack harness with Teflon ribbon; fitted by licensed bird ringers). Bird handling was approved under institutional animal ethics: Baltic AI Research University IACUC (BARU-AEC-2019-0084) and CETU Vienna AEC (CETU-AEC-2019-0124). No species under CITES Appendix I were handled without species-specific permits.

Appendix A

Priority Unprotected Novel Stopover Sites and GPS Tracking Studies

The 105 unprotected novel stopover sites identified in this study are listed in full in supplementary Table S2 at Zenodo. The highest-priority sites for immediate PA designation are described below.

TOP PRIORITY UNPROTECTED NOVEL STOPOVER SITES

1. Tengiz-Korgalzhyn Lakes (Kazakhstan; 50-51 N, 67-69 E): Now used as stopover by 12 study species (Eurasian Crane, Ruff, Red Knot, Little Stint, Curlew Sandpiper, Garganey, and 6 others). Mean importance index increase: +0.74 from ring period (0.04) to GPS period (0.78). Current PA status: Korgalzhyn Nature Reserve covers the core lake area but the surrounding steppe wetlands (where most stopover activity occurs) are unprotected. Priority action: expand the Korgalzhyn Ramsar site to include the stopover halo to 50 km radius.

2. Afghan Hindu Kush highlands (Afghanistan; 34-36 N, 67-70 E): Used by 8 species (Amur Falcon, Steppe Eagle, Montagu's Harrier, and 5 others) as a novel high-altitude rest stop during autumn migration. Importance index: 0 in ring period (no Afghan recovery records due to limited ringing); 0.54 in GPS period. Zero PA coverage. Priority action: international designation via Afghanistan's accession to the Ramsar Convention (pending since 2001); emergency listing under Convention on Migratory Species (CMS) Annex I.

3. Sahel Strip -- Niger-Mali border (13-16 N, 0-5 E): Historically the Sahel strip served as a continuous refuelling zone for Afro-Palearctic migrants. Climate and land use change has patched it into isolated productive areas. GPS tracking identifies three specific wetland complexes near the Niger Inland Delta tributary as now carrying disproportionate stopover importance (+0.84 importance index from ring period 0.12 to GPS period 0.84 at the most important of these sites). Only 14.7% PA coverage. Priority action: Ramsar nomination for the three identified wetland complexes; coordinate with Niger and Mali national environmental agencies.

4. Arctic Coastal Lagoons -- Siberian Coast (70-73 N, 90-110 E): Sea ice retreat has opened coastal lagoons in the Russian Arctic that were previously inaccessible or frozen during southward autumn migration. Twelve species (including Dunlin, Bar-tailed Godwit, Red Knot) now show substantial autumn stopover use (importance index 0.47) where ring data shows essentially zero (0.02). Russia's extensive protected area network does not currently cover the coastal lagoon system in this zone (nearest protected area > 200 km). Diplomatic engagement through the East Asian-Australasian Flyway Partnership recommended.

GPS TRACKING STUDIES CONTRIBUTING DATA

1. BOU-RSPB Amur Falcon Migration Study (PI: Tate, J.; Movebank study ID: 2247014): 84 Amur Falcons tracked 2014-2022 from Amur breeding grounds to sub-Saharan wintering areas. Provided the largest single-species dataset and the longest single-species route shift signal in the study.

2. KNAW-Netherlands Institute of Ecology Bar-tailed Godwit tracking (PI: Piersma, T.; Movebank ID: 24700147): Long-running godwit tracking programme providing baseline for East Atlantic flyway Arctic stopover analysis.

3. Estonian University of Life Sciences Common Cuckoo tracking (PI: Elts, J.; Movebank ID: 18470024): Provided the most complete European-African flyway cuckoo dataset; confirmed novel sahelian stopover sites through fine-resolution GPS.

Full list of 12 contributing tracking studies with Movebank IDs, tracking periods, and species in supplementary Table S1.