

A global perspective on the annual cycles of whimbrels

CAMILO CARNEIRO,^{*1,2}  X TÓMAS G. GUNNARSSON,¹ GARY ALLPORT,³ PHILIP W. ATKINSON,⁴ ANNE N. M. A. AUSEMS,^{5,6}  PIERRICK BOCHER,⁷  ROELAND BOM,^{8,9} MALO BRAQUIER,¹⁰ STEPHEN C. BROWN,¹¹ SAYAM U. CHOWDHURY,¹² PAULA CIMPRICH,¹³ DELIP K. DAS,^{8,14,15} CHARLOTTE FRANCESIAZ,¹⁶ ROBERT E. GILL,¹⁷ DIANA J. HAMILTON,¹⁸ MAINA C. HANDMAKER,¹⁹ SHARIFUL ISLAM,¹⁴ AUDREY JAEGER,²⁰  FRÉDÉRIC JIGUET,²¹ CHRYSTYN JONES,⁵ EMMANUEL JOYEUX,²² JEFFREY F. KELLY,¹³ ALAN H. KNEIDEL,¹¹ FENLIANG KUANG,^{23,24} CHRIS LATTY,²⁵ MATHIEU LE CORRE,²⁰  DAVID LI,²⁶ REBECA C. LINHART,²⁷ ÁDÁM LOVAS-KISS,^{28,29}  ZHIJUN MA,³⁰  SCOTT MCWILLIAMS,²⁷  VERÓNICA MÉNDEZ,¹ JASON MOBLEY,³¹ SAMUEL NG,²⁶ JOSHUA NIGHTINGALE,^{1,2} ERICA NOL,⁵ JULIE PAQUET,³² THEUNIS PIERSMA,^{8,9,33}  MARIE PITTS,³⁴ RIVO RABARISOA,³⁵ FLORINAH RAZAFIMANDIMBY,²⁰ DANIEL R. RUTHRAUFF,¹¹ FELICIA SANDERS,³⁶ SHILOH SCHULTE,^{11,†} PHILIPP SCHWEMMER,³⁷ NATHAN R. SENNER,^{19,38}  BÖÐVAR ÞÓRISSON,¹ LEE TIBBITTS,¹⁷ NILS WARNOCK,³⁹ BRYAN WATTS,³⁴ BRAD WINN,¹¹ SAMANTHA J. WOLFE,¹¹ SHUFEN YANG²⁶ & JOSÉ A. ALVES^{1,2}

¹South Iceland Research Centre, University of Iceland, Laugarvatn, Iceland

²Department of Biology & CESAM, University of Aveiro, Campus de Santiago, Aveiro, Portugal

³BirdLife International, The David Attenborough Building, Cambridge, UK

⁴British Trust for Ornithology, Norfolk, UK

⁵Department of Biology, Trent University, Peterborough, Ontario, Canada

⁶Aarhus University Department of Ecoscience, Aarhus C, Denmark

⁷Littoral Environnement et Sociétés UMR LIENSs 7266 CNRS, La Rochelle University, La Rochelle, France

⁸BirdEyes, Centre for Global Ecological Change at the Faculties of Science & Engineering and Campus Fryslân, University of Groningen, Leeuwarden, The Netherlands

⁹Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, Texel, The Netherlands

¹⁰Groupe d'Études et de Protection des Oiseaux de Mayotte (GEPOMAY), Tsingoni, Mayotte

¹¹Manomet Conservation Sciences, Manomet, Massachusetts, USA

¹²Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge, UK

¹³University of Oklahoma School of Biological Sciences, Norman, Oklahoma, USA

¹⁴Department of Zoology, Faculty of Life and Earth Sciences, Jagannath University, Dhaka, Bangladesh

¹⁵Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands

¹⁶OFB – Service Conservation et Gestion Durable des Espèces Exploitées, Direction de la Recherche et de l'Appui Scientifique, Pérols, France

¹⁷Independent Researcher, Anchorage, Alaska, USA

¹⁸Department of Biology, Mount Allison University, Sackville, New Brunswick, Canada

¹⁹Department of Environmental Conservation, University of Massachusetts, Amherst, Massachusetts, USA

²⁰UMR ENTROPIE, Université de La Réunion, IRD, IFREMER, Université de Nouvelle-Calédonie, Saint-Denis Cedex, France

²¹UMR 7204 Centre d'Ecologie et des Sciences de la Conservation, MNHN-CNRS-Sorbonne Université, Paris, France

²²OFB—Service Conservation et Gestion Durable des Espèces Exploitées, Direction de la Recherche et de l'Appui Scientifique, Ile d'Olonne, France

²³Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, National Observations and Research Station for Wetland Ecosystems of the Yangtze Estuary, Institute of Eco-Chongming, School of Life Sciences, Fudan University, Shanghai, China

²⁴School of Resources Environment and Chemistry, Chuxiong Normal University, Chuxiong, Yunnan, China

²⁵Arctic National Wildlife Refuge, U.S. Fish and Wildlife Service, Fairbanks, Alaska, USA

²⁶Sungei Buloh Wetland Reserve, National Parks Board, Singapore, Singapore

²⁷Department of Natural Resources Science, University of Rhode Island, Kingston, Rhode Island, USA

²⁸MTA-HUN-REN Centre for Ecological Research, 'Lendület' Momentum Dispersal Ecology Research Group, Debrecen, Hungary

²⁹Department of Planetary Health, One Health Institute, Faculty of Health Sciences, University of Debrecen, Debrecen, Hungary

³⁰Shanghai Institute of Infectious Disease and Biosecurity, State Key Laboratory of Wetland Conservation and Restoration, National Observations and Research Station for Wetland Ecosystems of the Yangtze Estuary, School of Life Sciences, Fudan University, Shanghai, China

³¹Associação de Pesquisa e Preservação de Ecossistemas Aquáticos – Aquasis, Caucaia, Brazil

³²Canadian Wildlife Service, Environment and Climate Change Canada, Sackville, New Brunswick, Canada

³³Rudi Drent Chair in Global Flyway Ecology, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, The Netherlands

³⁴Center for Conservation Biology, Williamsburg, Virginia, USA

³⁵Asity Madagascar, Antananarivo, Madagascar

³⁶South Carolina Department of Natural Resources, McClellanville, South Carolina, USA

³⁷Research and Technology Centre (FTZ), University of Kiel, Büsum, Germany

³⁸Massachusetts Audubon, Lincoln, Massachusetts, USA

³⁹All Hands Ecology, Marshall, California, USA

Comparative analyses are central to understanding broad-scale patterns in avian ecology, yet their application is often constrained by fragmented and uneven data availability. Recent advances in tracking technology have generated unprecedented insights into shorebird movements, resulting in numerous studies on single populations or flyways. Bringing them together creates the opportunity to assess large-scale knowledge gaps and develop a holistic understanding of migration patterns across a species' entire range. This can be particularly important for globally declining taxa, where population-specific trends and threats may be obscured by coarse global assessments. We gathered most of the whimbrel (*Numenius hudsonicus* and *N. phaeopus*) tracking datasets collected to date to identify spatial gaps in tracking coverage, compare subspecies across the annual cycle to detect broad-scale patterns, and integrate threat assessments to highlight key research fronts. Based on 2 626 843 locations from 251 individuals, we document a bias in tracking coverage with the major gaps in the African continent, Middle East, the Indian sub-continent, and the breeding grounds in northern and central Russia. We also highlight spatial overlap among subspecies and substantial variation in annual-cycle timing, migration distance, speed and stopover behaviour. Knowledge of threats was incomplete across subspecies, but we identified widespread pressures including development, hunting, invasive species, habitat alteration and other climate-driven impacts, with particularly strong effects on Nearctic breeders and poorly understood but potentially escalating risks in several Palaearctic populations. Addressing the identified gaps through expanded and strategically co-ordinated tracking studies, integration with demographic and taxonomic research, and focused analyses of migration ecology is essential to achieve a full annual-cycle perspective and guide effective conservation for migratory species.

Keywords: conservation, migration ecology, *Numenius hudsonicus*, *Numenius phaeopus*, waders.

*Corresponding author.

Email: camilofcarneiro@gmail.com

Twitter: @Camilo_Carneiro

†Deceased.

INTRODUCTION

Comparative approaches in ornithology can reveal emerging patterns, help identify knowledge gaps and provide a foundation for future research. For

example, by comparing species, populations or age–sex cohorts, researchers have explored how ecological factors shape migratory behaviour (Piersma 2007, van Bemmelen *et al.* 2019), influence habitat use (Ribeiro *et al.* 2004), and affect demographic performance (Salgado-Ortiz *et al.* 2008, Grist *et al.* 2017), population sizes (Piersma 2003) and trends (Kwon *et al.* 2021). However, conducting broad comparative studies depends heavily on the availability of data. In this regard, recent advances in tracking technology are revolutionizing the study of avian migration ecology by providing unprecedented spatial coverage and detail (Nathan *et al.* 2022, Michel *et al.* 2026). This surge in tracking efforts is reflected in the growing number of studies on shorebird movements, with most focusing on single populations or flyways (Michel *et al.* 2026). Such volume of studies creates the opportunity to assess large-scale knowledge gaps and develop a holistic understanding of migration patterns across a species' entire range.

Many shorebirds are undergoing global declines (Studds *et al.* 2017, Rosenberg *et al.* 2019, Smith *et al.* 2023, van Roomen *et al.* 2025), some with tragic outcomes. A striking example is the Numeniini, a tribe within the Charadriiformes that includes eight curlews *Numenius*, four godwits *Limosa* and the Upland Sandpiper *Bartramia longicauda* (Pearce-Higgins *et al.* 2017). Of these 13 species, nine currently exhibit declining population trends (BirdLife International 2026), and two – the Eskimo Curlew *Numenius borealis* and Slender-billed Curlew *N. tenuirostris* – are probably extinct (last seen in 1963 and 1995, respectively; Elphick *et al.* 2010, Buchanan *et al.* 2025). However, while global trends provide an overarching view, they can mask variation at the subspecies or population levels (Ceballos *et al.* 2017), which can arise due to ecological and behavioural differences (e.g. habitat use, migratory routes, reliance on specific stopover sites; Lisovski *et al.* 2021, Knight *et al.* 2025) and population-specific threats (e.g. flyway-specific pressures; Pearce-Higgins *et al.* 2017). Tracking data provide the necessary spatio-temporal detail to unmask such variation, for example by uncovering overlapping populations (Chan *et al.* 2022, Conklin *et al.* 2026). Furthermore, tracking data allow researchers to gauge the flexibility of behavioural responses to environmental changes, such as of migration timings (Conklin *et al.* 2013, Carneiro *et al.* 2019a) and

migration speed (Rakhimberdiev *et al.* 2018), and determine the degree of reliance on stopover sites along flyways (Lisovski *et al.* 2021).

There are two recently widely accepted whimbrel species (Hudsonian *N. hudsonicus* and Eurasian *N. phaeopus*, a split based on morphology and deep genomic DNA divergence; Tan *et al.* 2019, McLaughlin *et al.* 2020, AviList Core Team 2025), which separate into seven subspecies: two Nearctic (*N. h. rufiventris* and *N. h. hudsonicus*) and five Palearctic (*N. p. islandicus*, *N. p. phaeopus*, *N. p. alboaxillaris*, *N. p. rogachevae* and *N. p. variegatus*). Both species are still jointly classified as being of Least Concern on the IUCN Red List (BirdLife International 2026). Although their global numbers are decreasing (BirdLife International 2024), different subspecies exhibit different trends (Brown *et al.* 2014, see Table S1). For instance, Nearctic-breeding populations (*N. h. rufiventris* and *N. h. hudsonicus*) are undergoing steep declines (Smith *et al.* 2023, Reiter *et al.* 2026), while wintering counts suggest that Western Palearctic breeders (*N. p. islandicus* and *N. p. phaeopus*) remain stable (van Roomen *et al.* 2025; however, recent surveys in a part of their breeding distribution suggest declines; Lindström *et al.* 2019b, Pálsdóttir *et al.* 2025b). Notably, population trends for *N. p. alboaxillaris* and *N. p. rogachevae* remain unknown (Table S1).

Whimbrels (hereafter referring to *N. hudsonicus* and *N. phaeopus* combined unless otherwise defined) are long-distance migrants with a nearly global distribution, breeding primarily in Arctic and boreal regions of North America, Europe and Asia, and wintering along coastal areas across a wide latitudinal range. They are socially monogamous with high mate fidelity and shared parental care between the sexes, both during incubation and chick rearing (although females tend to stop the latter duties earlier than males). Clutches are usually of four eggs, incubated for ca. 25 days. Chicks can fly at ca. 27 days old but usually stay in the breeding territory for longer. Individuals perform a complete moult during the wintering season and tend to be territorial and faithful to wintering and breeding sites (Skeel *et al.* 2025, Smith *et al.* 2025). Several tracking studies that have provided valuable knowledge into whimbrel migration ecology along various flyways (e.g. Alves *et al.* 2016, Allport *et al.* 2018, Kuang *et al.* 2020, Ruthrauff *et al.* 2021, Watts *et al.* 2021), now

allow for a comprehensive and direct comparison among them, and new insights into whimbrel ecology and conservation.

In this study, we compile most of the whimbrel tracking datasets collected to date to (1) identify spatial gaps in tracking efforts, which may indicate knowledge deficiencies about specific subspecies, and (2) compare subspecies across their annual cycles to detect broad-scale patterns to inform future research. We then (3) assess threats to each subspecies throughout its annual cycle and integrate that information with the patterns detected to outline key research possibilities. Given the unbalanced publication volume among flyways, we expect tracking effort to be unevenly distributed across the globe, resulting in geographical knowledge gaps and unsampled regions. We also expect substantial variation among subspecies' annual-cycle behaviour, such as in migration distance, migration speed and stopover behaviour. By comparing these metrics across subspecies, we can explore whether broad patterns consistent with trade-offs between time, energy and risk emerge (e.g. longer distance migrants show higher migration speed and shorter stopover time; Alerstam & Lindström 1990, Hedenström & Alerstam 1997). Differences in migratory behaviour may then link to differences in exposure to threats throughout the annual cycle.

METHODS

We gathered tracking data from 382 whimbrels, tagged on all of the continents on which the species occur, including in 14 countries across all periods of the annual cycle (Table 1). Data collection spanned from 28 June 2006 to 31 October 2025, and data were compiled with support of the Global Wader initiative (<https://www.globalwader.org/>; Nightingale 2023).

Data filtering

Location data were recorded with trackers using the ARGOS or GNSS satellite systems, of various models and manufacturers, and attached with a leg-loop harness, body harness, glue, sutures or surgical implantation (Table S2). Before further analyses, ARGOS data were filtered to include only fixes of classes 1–3, that is, fixes with accuracy up to 1000 m, and GNSS data to include fixes determined with at least three satellites. While differences in fix accuracy and frequency can influence the calculation of migration metrics, we consider that variation to be negligible for our purpose of exploring general patterns at the global scale.

We calculated the speed between fixes using the function 'track_param()' in the *SDLfilter* R

Table 1. Summary of number of individual whimbrels tagged per country and annual-cycle period, as well as the temporal range across which tagging occurred. Wintering tagging in France refers to individuals tagged in La Reunión and Mayotte.

Tagging country	Temporal range	Annual-cycle period			Total
		Wintering	Breeding	Stopover	
<i>N. hudsonicus</i>					
USA	2006–2025		67	83	150
Canada	2012–2023		25	6	31
Brazil	2024	1			1
<i>N. phaeopus</i>					
Iceland	2017–2025		49		49
Guinea-Bissau	2018–2019	13			13
France	2021–2024	2		74	76
Germany	2022–2025			8	8
Hungary	2022			5	5
Mozambique	2016	1			1
Madagascar	2025	4			4
Bangladesh	2021–2022	4			4
Singapore	2017–2018	7			7
China	2018–2019			15	15
Australia	2017–2018	18			18
Total	2006–2025	50	141	191	382

package (Takahiro 2018), and only those with a speed lower than 45 m/s from the previous and to the subsequent fix were considered, as speeds faster than that probably resulted from incorrectly determined locations (Carneiro *et al.* 2019a, 2019b, Watts *et al.* 2021). Only data from adults were considered, since juveniles were not tracked across all subspecies and their behaviour may differ from that of adults (Carneiro *et al.* 2024). Since there is no reliable way to sex individuals across subspecies, this trait was not considered in the analyses (but see Skeel 1982, Katrínardóttir *et al.* 2013, Ausems *et al.* 2023).

Data segmentation and timing determination

Tracking data were segmented in three steps to determine (1) the wintering site, (2) the breeding site and (3) stopover sites of each individual per annual cycle.

- 1 Wintering site was determined as the minimum convex polygon drawn with all fixes recorded across at least 40 days during December and January – that is, when whimbrels are very probably at their wintering site and remain stationary. Then, arrival and departure dates from the wintering site were determined using the function ‘getRecursionsInPolygon()’ in the *recurse* R package (Bracis *et al.* 2018). To do this, we conservatively considered the period from 1 July of one year to 30 June of the subsequent year, a window that should not only encompass the arrival and departure dates to/from the wintering site, but also help determine potential over-summering events (i.e. staying at the wintering grounds during the breeding season; see below). When multiple entrance and exit times were identified by the function, the earliest entrance was considered the arrival at the wintering site, and the latest exit the departure date. However, if the arrival at the wintering site was earlier than 10 July or the departure later than 20 June, the ‘breeding period’ of the corresponding year was flagged as possible over-summering, and those timings were not included in further analyses.

In the case of seven individuals tagged after January at their wintering grounds in East Africa and West Indian Ocean, we visually

inspected the tracks and manually determined their wintering locations and associated departure dates. These exceptions were conducted to ensure those tracks, which originate from a little sampled region, were included in the analysis.

- 2 The breeding site was considered a 100-km-radius circle centred on the nest location (recorded in the field or estimated), and arrivals and departures to that area were determined using ‘getRecursionsInPolygon()’. For estimated nest locations ($n = 563$), the function ‘find_nests()’ of the *nestR* R package was used to determine their locations (Picardi *et al.* 2024). This function is sensitive to the user-defined buffer size, which is the radius at which revisitations to the potential nests are calculated. Hence, given the differing accuracies of the ARGOS and GNSS tags, we analysed the two groups of trackers separately. GNSS data were thinned to 1 fix/hour to make processing faster, while preserving sufficient temporal detail. Among the potential nest locations identified by the function, the first location flagged as a nest was selected. Given that the function failed to identify some nest locations in certain years, and instead clearly identified biologically incorrect ones, such as at latitudes considerably south of the known distribution, the function was used a second time, with more relaxed parameters, to try to identify the estimated nest locations for those cases. Again, nest locations at implausibly low latitudes were excluded. The parameters used in the function on each run and for each tag type are shown in Table S3.
- 3 Stopover sites were determined for the periods between breeding and wintering departure and arrival, first by annotating the fixes either as ‘stationary’ or ‘in movement’. Stationary fixes were defined as those where the speed from the previous and to the subsequent fix was lower than 3 m/s. This threshold was first determined based on the distribution of speeds, and location data were subsequently visually assessed for accurate classification. Then, we used the *dbscan()* function in the R package *dbscan* to determine clusters of fixes (Hahsler *et al.* 2019), with a minimum of three and an epsilon neighbourhood size of 3000 m. Each cluster was considered a stopover site (*sensu* Warnock 2010), and arrival and departure

dates at each were conservatively assumed as those of the first and last fix, respectively.

Any arrival or departure dates that coincided with the start or end of tracking were excluded from the analyses.

Subspecies attribution

The taxonomy of whimbrels was recently revised to reflect two species, Nearctic *N. hudsonicus* and Palaearctic *N. phaeopus* (AviList Core Team 2025). Our focus was on the subspecies within each and included Nearctic *N. h. rufiventris* and *N. h. hudsonicus* and Palaearctic *N. p. islandicus*, *N. p. phaeopus*, *N. p. alboaxillaris*, *N. p. rogachevae* and *N. p. variegatus*.

Individuals tagged on the breeding grounds were directly assigned a subspecies, plus a single *N. p. alboaxillaris* tagged at a wintering site that was not tracked to the breeding region (Allport 2017, Allport et al. 2018). Although there are some plumage differences among subspecies (Skeel et al. 2025, Smith et al. 2025), for the remaining individuals, a subspecific identity was assigned based on their nesting location (see *Data segmentation 2*) and according to the longitudinal ranges in Table 2, which are based on the known and presumed subspecific breeding ranges (Tan et al. 2019, Kuang et al. 2022, BirdLife International & Handbook of the Birds of the World 2023, Fink et al. 2023). Due to uncertainty in some subspecies' breeding ranges, we have considered two overlapping regions, one for *N. p. phaeopus-rogachevae*, and another for *N. p. rogachevae-variegatus* (Kuang et al. 2022).

Table 2. Longitudinal ranges used to determine whimbrel subspecies based on nesting longitude. Subspecies are grouped by biogeographical realm of the breeding regions.

Subspecies	Longitudinal range (decimal degrees)
Nearctic	
<i>N. h. rufiventris</i>	180°–108°W
<i>N. h. hudsonicus</i>	107.9°W–50°W
Palaearctic	
<i>N. p. islandicus</i>	49.9°W–2°E
<i>N. p. phaeopus</i>	2.1°E–75°E
<i>N. p. phaeopus – rogachevae</i>	75.1°E–80°E
<i>N. p. rogachevae</i>	80.1°E–114°E
<i>N. p. rogachevae – variegatus</i>	114.1°E–132°E
<i>N. p. variegatus</i>	132.1°E–180°

Gaps in tracking

To identify geographical gaps in tracked whimbrels, we visually compared the tracking data with the global distribution of whimbrel. The global distribution was established as the merged distributions from BirdLife International and Handbook of the Birds of the World (2023), Fink et al. (2023) and the breeding ranges from Kuang et al. (2022).

Migration metrics

We calculated the migration distance as the cumulative distance between consecutive fixes along the whole track between first departure and arrival at a bird's final destination – that is, breeding or wintering site. To calculate migration speed, we estimated the first fuelling period by estimating how long individuals would need to store the necessary fuel to cover the first flight, because this period is part of migration and ignoring it could result in highly biased speed estimates (Lindström 2020). We considered a fuel deposition rate (FDR) of 3.55% of the lean body mass (LBM; Lindström 2003) and used a flight model fitted to the *N. p. islandicus* subspecies (the only subspecies where such a model has been parameterized; Carneiro et al. 2021), where $\%LBM = -9 \times 10^{-9} \times FF^2 + 0.0002 \times FF + 0.0129$, FF representing the length of the first flight in km. The first fuelling period was then added to the period between first departure and arrival at the final destination to achieve the total migration period. Migration speed was calculated as the migration distance divided by the total migration period (including the first fuelling period). Although ideally a flight model should be fitted to each population, we believe the advantages of our approximation outweigh ignoring the first fuelling period when investigating migration speed (Lindström et al. 2019a).

Ground speed was calculated as the average speed per individual among fixes classified as in movement, excluding samples with fewer than five fixes. We calculated the total stopover duration as the sum of the time spent at all stopovers and the number of stopovers used per migration.

Statistical analysis

Given that 17% of the individuals were tracked for at least 2 years and could therefore bias the

sample with repeated measurements, only the first record of the variable of interest for each individual was included in the statistical tests (but all tracking is shown in Figure 1; analyses of individual repeatability have been published elsewhere: Carneiro *et al.* 2019a, An *et al.* 2024, Handmaker *et al.* 2024).

To test for differences among subspecies in migration timing and duration of the main stationary annual-cycle periods (i.e. wintering and breeding), we used the Kruskal–Wallis rank sum test (with the function ‘oneway_anova()’ in the *statsExpressions* R package; Patil 2021), since the data were not distributed normally. Post-hoc pairwise comparisons were conducted with Dunn’s test (function ‘pairwise_comparisons()’ in *statsExpressions*; Patil 2021).

To assess whether migration distance, migration speed, ground speed, total stopover time and number of stopovers varied between seasons, among subspecies and within subspecies between seasons, we used generalized linear models with the structure *response* ~ *season* * *subspecies*, where *season* refers to autumn (i.e. post-breeding, southwards) or spring (i.e. prebreeding, northwards) migration. To model migration distance, migration speed and ground speed, a gamma error distribution was used, while a Gaussian distribution was used in the other two models. Model assumptions were visually checked with the *performance* R package (Lüdtke *et al.* 2021). From each model, we used the *emmeans* R package (Lenth & Piaskowski 2024) to extract the contrasts between seasons across subspecies, among subspecies across seasons and between seasons within subspecies. Given that only one individual of *N. p. alboaxillaris* and one of *N. p. phaeopus* – *rogachevae* were tracked, we did not include these subspecies in these analyses. Additionally, we excluded an individual classified as *N. p. phaeopus*, as its track was considered an outlier: it migrated in spring from La Reunion (France) to Bangladesh, where it stayed until the following spring migration (despite visiting Sri Lanka too), and then migrated to the breeding sites. We could not exclude such behaviour as being an individual response to carrying a tag. These three individuals are nevertheless shown in Figure 1.

Results are presented as mean ± se, unless otherwise indicated.

Threat identification and scoring

We based our threat assessment on the IUCN Threats Classification Scheme (Version 3.3), a standardized hierarchical framework. The scheme organizes threats into 12 broad categories (Level 1), which are further subdivided into more specific threat classes (Levels 2 and 3). We classified threats to Level 2, providing a balance between broad threat categories and sufficient detail to distinguish among major types of threats. When possible, threats were assessed separately for each subspecies and period of the annual cycle (i.e. breeding, wintering and migration). However, given the considerable overlap between *N. h. rufiventris* and *N. h. hudsonicus* along the Atlantic Americas Flyway, the two species in this region were considered as a unit, while *N. h. rufiventris* using the Pacific Americas Flyway were treated separately. The individual of *N. p. phaeopus* – *rogachevae* was considered under *N. p. rogachevae*, and those of *N. p. rogachevae* – *variegatus* were considered under *N. p. variegatus*.

We scored Scope (i.e. the proportion of the total population affected) and Severity (i.e. the overall declines caused by the threat) for ongoing threats only. Within Scope, we differentiated between *Unknown* – that is, when we did not know if the threat affects <50% of the population, up to 90% or more – and *Not a threat* – when we knew that something is not a threat (Table S4). Ongoing threats were classified into impact scores, following Garnett *et al.* (2019) and Dias *et al.* (2019). Additionally, we highlighted potential future threats (without scoring Scope or Severity), if it was agreed they were likely to happen.

The assessment was conducted in two steps. First, each author reflected on and scored the threats for the subspecies and annual periods about which they were knowledgeable. Second, collaborators scoring the same subspecies met to discuss their scores and produced a single final score per threat for that subspecies.

RESULTS

A total of 3 703 078 locations remained after filtering to remove low-quality locations, of which 2 626 843 were recorded during individuals’ first tracking year and were retained for analyses. After

data segmentation into stages of the annual cycle and assignment to subspecies, the dataset included 251 individuals attributed to subspecies and 131 individuals of unknown subspecies; the latter were excluded from analyses (Table 3).

The variation in migratory routes among and within taxa is shown in Figure 1. Except for the Pacific Americas Flyway, which is exclusively used by *N. h. rufiventris*, all other major flyways are used by more than one subspecies, and sometimes single subspecies move through more than one flyway. Both Nearctic subspecies migrate along the Atlantic Americas Flyway, but some of the individuals also migrate through the Central Americas Flyway. The Pacific Americas Flyway is exclusively used by *N. h. rufiventris*.

N. p. islandicus and *N. p. phaeopus* migrate mainly along the East Atlantic Flyway, but the latter also use the Black Sea–Mediterranean Flyway to some extent. These subspecies therefore overlap along most of the recorded non-breeding regions. *N. p. alboaxillaris*, *N. p. phaeopus* and *N. p. rogachevae* were tracked through the East Asia–East Africa Flyway, and *N. p. rogachevae* and *N. p. variegatus* along the East Asian–Australasian Flyway.

Four subspecies made long ocean crossings over the Pacific and Atlantic Oceans: *N. h. rufiventris*, *N. h. hudsonicus*, *N. p. islandicus* and *N. p. variegatus*. Large ecological barriers were also crossed on

land, with *N. p. phaeopus* flying over the Sahara Desert, and *N. p. rogachevae* over the Himalayas.

Gaps in tracking

The distribution of breeding, stopover and wintering locations this study recorded in the Americas, Western Europe and West Africa accurately represents the known distribution of whimbrels in these regions, except for gaps in tracking to locations in southern South America and Greenland. Less well covered is the East Asian–Australasian Flyway, where the tropical and southern hemisphere non-breeding distributions have been only partially used by the tracked whimbrels. The largest gap in tracking information comes from most of the African continent, Middle East, the Indian subcontinent, and the breeding grounds in northern and central Russia. The few individuals tracked from East Africa, Bangladesh and Singapore converged in a breeding region where subspecies segregation of Eurasian Whimbrel is more ambiguous (Kuang *et al.* 2022), yet with most individuals overlapping the range of *N. p. rogachevae* (Fig. 1).

Migration metrics

Migration timing varied among subspecies, at spring departure ($\chi^2_{\text{Kruskal-Wallis}}(6) = 30.77$,

Table 3. Total number of fixes, number of individual whimbrels and range of tracking years per subspecies and tracking technology in the dataset after filtering.

Subspecies	Tracking technology	Number of fixes	Number of individuals	Temporal range
<i>N. h. rufiventris</i>	ARGOS	34 757	46	2006–2019
	GNSS	377 505	37	2020–2025
<i>N. h. hudsonicus</i>	ARGOS	12 649	11	2010–2024
	GNSS	412 300	25	2021–2025
<i>N. p. islandicus</i>	ARGOS	25 376	6	2018–2025
	GNSS	382 205	55	2017–2025
<i>N. p. phaeopus</i>	ARGOS	4465	2	2021–2022
	GNSS	1 519 194	35	2021–2025
<i>N. p. alboaxillaris</i>	ARGOS	77	1	2016–2017
	GNSS	9561	1	2025–2025
<i>N. p. phaeopus – rogachevae</i>	ARGOS	5903	3	2017–2020
	GNSS	58 321	5	2018–2025
<i>N. p. rogachevae – variegatus</i>	ARGOS	7903	3	2017–2021
	GNSS	15 898	7	2018–2020
<i>N. p. variegatus</i>	ARGOS	15 406	6	2017–2022
	GNSS	13 089	8	2018–2021
Undetermined	ARGOS	22 232	50	2009–2025
	GNSS	786 237	81	2018–2025
Total		3 703 078	382	2006–2025

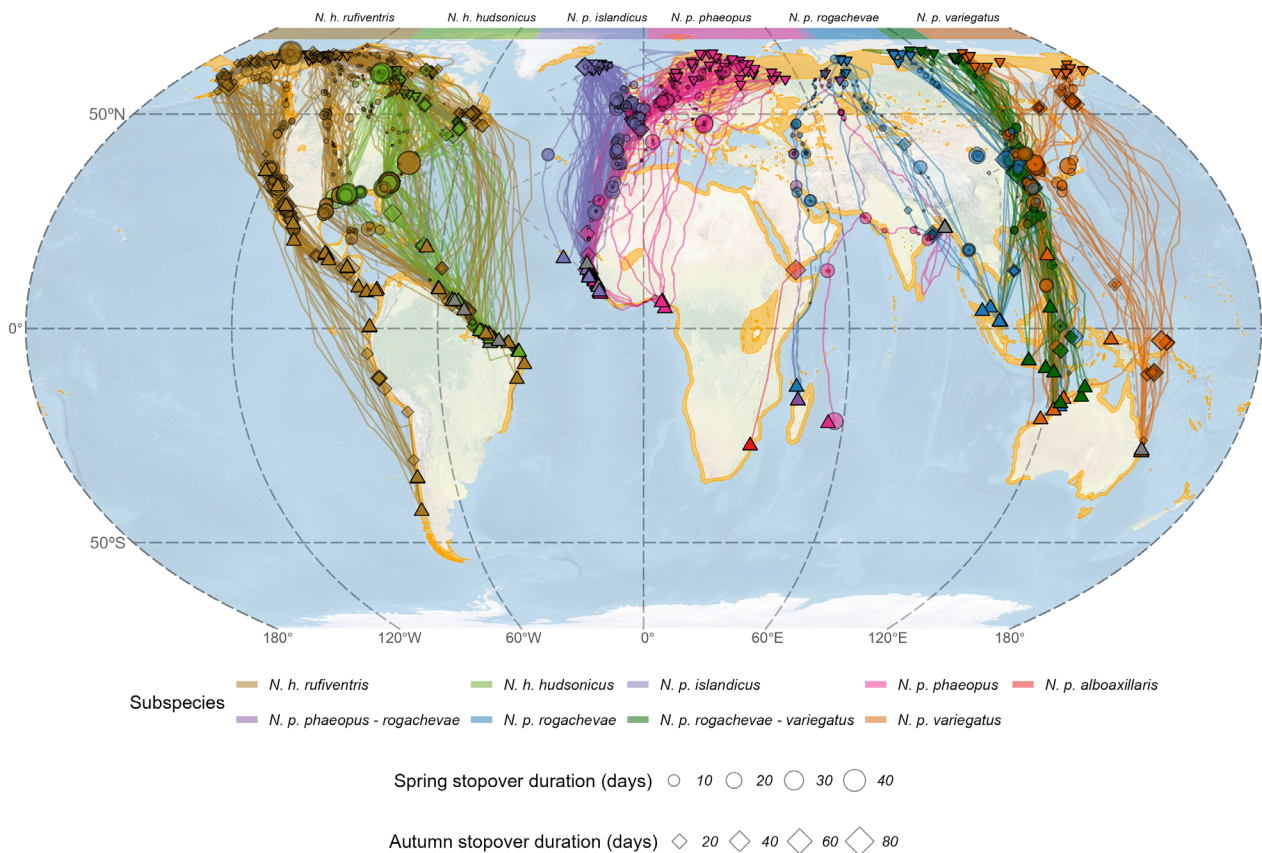


Figure 1. Migratory routes of tracked whimbrels with the breeding (triangles pointing downwards), wintering (triangles pointing upwards) and stopover sites (spring: circles; autumn: diamonds). Stopover symbol sizes represent duration in days. Each subspecies is represented by a distinct colour, with undetermined by grey symbols and dashed tracks. The coloured polygons at high northern latitudes illustrate the longitudinal ranges considered to assign subspecies with exception of *N. p. alboaxillaris* (see Table 2; note that presumed overlapping subspecies *N. p. phaeopus* – *rogachevae* and *N. p. rogachevae* – *variegatus* are not labelled). Repeated individual tracks are shown but not included in statistical analysis. The map is presented in an equal area projection, which retains the relative size of areas.

$P < 0.001$, $n = 94$), spring arrival ($\chi^2_{\text{Kruskal-Wallis}}(6) = 63.72$, $P < 0.001$, $n = 156$), autumn departure ($\chi^2_{\text{Kruskal-Wallis}}(6) = 86.27$, $P < 0.001$, $n = 199$) and autumn arrival ($\chi^2_{\text{Kruskal-Wallis}}(6) = 47.55$, $P < 0.001$, $n = 96$; Fig. 2, Table 4).

At spring migration departure, *N. h. rufiventris* and *N. h. hudsonicus* did not show differential timing, nor did their timing differ from that of *N. p. phaeopus*, *N. p. rogachevae* and *N. p. rogachevae* – *variegatus*. However, both Nearctic subspecies departed significantly earlier than *N. p. islandicus* and *N. p. variegatus* (Table 4; Table S5). Spring arrival timings were earliest for *N. p. islandicus* and *N. p. phaeopus* (both 19 May ± 2 days), while the remaining subspecies did not differ significantly in their arrival dates (Table 4; Table S5).

In autumn, *N. h. rufiventris* departed earlier than other subspecies (8 July ± 2 days), except *N. p. phaeopus*, while the latter departed significantly earlier than *N. p. islandicus* (Table 4; Table S5). Arrival during autumn migration was earliest for *N. p. islandicus* (12 August ± 1 day), with arrival of the remaining subspecies not differing significantly, but with considerable variation among subspecies (Table 4; Table S5).

The duration spent at the wintering and breeding sites varied among subspecies (wintering: $\chi^2_{\text{Kruskal-Wallis}}(6) = 39.11$, $P < 0.001$, $n = 90$; breeding: $\chi^2_{\text{Kruskal-Wallis}}(6) = 51.29$, $P < 0.001$, $n = 144$). *N. p. islandicus* spent the longest period at the wintering sites (253 ± 3 days), significantly longer than all other subspecies (Table 5; Table S6). The period at the breeding grounds for

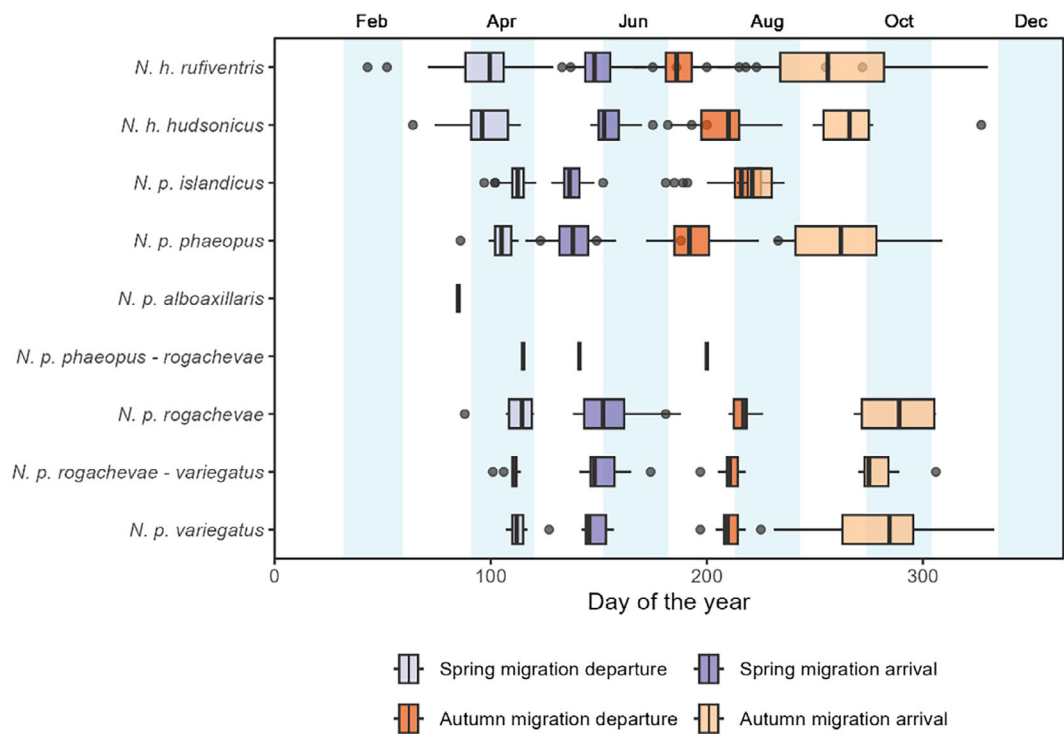


Figure 2. Main migratory timings of whimbrels by subspecies. Boxplots are slightly transparent to help visualize overlaps. Note that for *N. p. alboaxillaris* and *N. p. phaeopus – rogachevae*, there is only one data point for each stage. Months are marked by white and pale blue bars. Boxes show the median and 25% and 75% quartiles, whiskers extend up to 1.5 times the interquartile range from the median and points beyond that are individually marked. Sample sizes are shown in Table 4.

Table 4. Mean ($\pm$ se) migration departure and arrival dates, during spring and autumn migrations, for each of the whimbrel subspecies.

Subspecies	Spring migration				Autumn migration			
	Departure	<i>n</i>	Arrival	<i>n</i>	Departure	<i>n</i>	Arrival	<i>n</i>
<i>N. h. rufiventris</i>	6 April $\pm$ 4 days	28	1 June $\pm$ 2 days	40	8 July $\pm$ 2 days	81	16 September $\pm$ 5 days	32
<i>N. h. hudsonicus</i>	6 April $\pm$ 4 days	13	8 June $\pm$ 3 days	24	27 July $\pm$ 3 days	23	25 September $\pm$ 6 days	13
<i>N. p. islandicus</i>	23 April $\pm$ 2 days	20	19 May $\pm$ 2 days	24	3 August $\pm$ 2 days	29	12 August $\pm$ 1 day	21
<i>N. p. phaeopus</i>	15 April $\pm$ 4 days	7	19 May $\pm$ 2 days	36	14 July $\pm$ 3 days	35	20 September $\pm$ 11 days	7
<i>N. p. alboaxillaris</i>	26 March	1		0		0		0
<i>N. p. phaeopus – rogachevae</i>	25 April	1	21 May	1	19 July	1		0
<i>N. p. rogachevae</i>	21 April $\pm$ 5 days	6	5 June $\pm$ 6 days	8	31 July $\pm$ 6 days	7	15 October $\pm$ 10 days	4
<i>N. p. rogachevae – variegatus</i>	20 April $\pm$ 1 day	9	1 June $\pm$ 3 days	10	29 July $\pm$ 2 days	10	7 October $\pm$ 4 days	9
<i>N. p. variegatus</i>	23 April $\pm$ 2 days	11	28 May $\pm$ 1 day	14	30 July $\pm$ 2 days	14	7 October $\pm$ 9 days	10

N. p. islandicus (75 ± 4 days) was significantly longer than for *N. h. rufiventris* (37 ± 3 days) and *N. h. hudsonicus* (50 ± 4 days), but not longer than for *N. p. phaeopus*, *N. p. rogachevae*, *N. p. rogachevae – variegatus* or *N. p. variegatus* (Table 5; Table S6).

On average, *N. h. rufiventris* made the longest migrations ($10\,831 \pm 388$ km), followed by *N. h. variegatus*, *N. h. hudsonicus*, *N. p. phaeopus*, *N. p. rogachevae* and *N. p. rogachevae – variegatus*. *N. p. islandicus* made significantly shorter migrations than the average (6592 ± 162 km; Tables 6

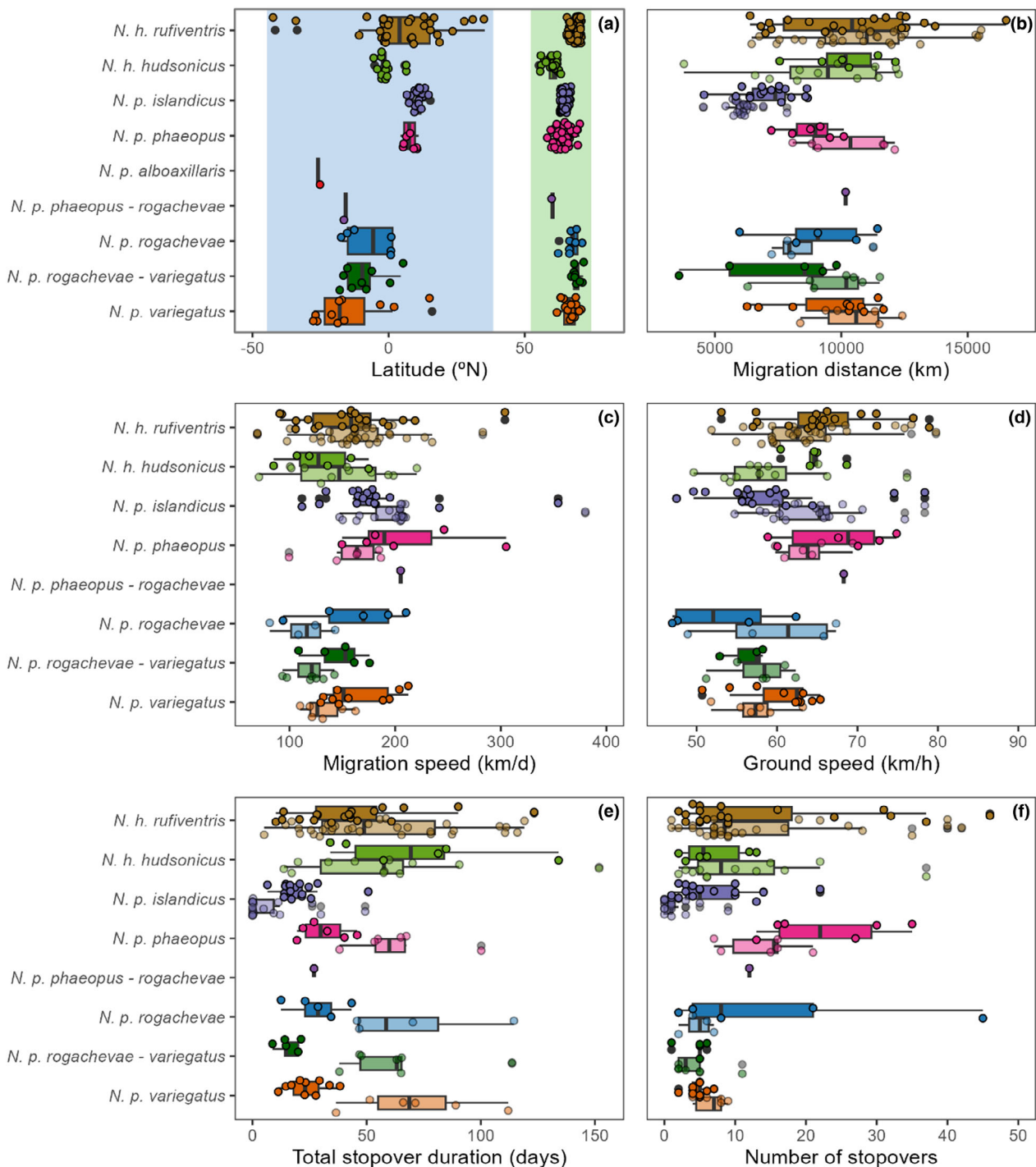


Figure 3. (a) Wintering (blue shade) and breeding (green shade) latitudes across whimbrel subspecies. On (b)–(f), spring is shown by the top boxplot with darker tones within each pair, and autumn by the bottom boxplot with paler tones. Sample sizes are given in Table S9. (b) Distance travelled between first migration departure and arrival at final destination. (c) Migration speed. (d) Ground speed. (e) Total stopover duration, between first migration departure and arrival at final destination. (f) Number of stopovers recorded per migration. Boxes show the median and 25% and 75% quartiles, whiskers extend up to 1.5 times the interquartile range from the median and points beyond that are individually marked aligned with the whiskers. Individual data points overlap the box plots. Metrics were not calculated for *N. p. alboaxillaris* because there were no complete migration tracks for this subspecies. Sample sizes are shown in Table 6.



Figure 4. Summary of the threat assessment across whimbrel subspecies and for each of the main annual-cycle periods. Impact scores were assigned following Garnett *et al.* (2019) and Dias *et al.* (2019). We also show what we do not consider an existing threat (Not a threat), threats that we believe will arise in the future, the periods not assessed, Unknown threats and the cases where we could only assign scope or severity (see also Fig. S1). Due to considerable overlap of *N. h. rufiventris* and *N. h. hudsonicus* along the Atlantic American Flyway, these subspecies were treated as a unit (except during breeding), while excluding *N. h. rufiventris* individuals using the Pacific Americas Flyway. The dots next to the subspecies names mark the current population trends (red = decrease; grey = unknown; Table S1). Additionally, we collated a list of relevant references that support some of the assessments (Table S7).

and 7). While there were no overall significant differences in migration distance between seasons, *N. p. islandicus* showed significantly shorter distances in autumn, while *N. p. rogachevae* – *variegatus* showed significantly shorter migration distances in spring (Tables 6 and 7, Fig. 3). Such variation between seasons is partially explained by different migratory routes.

Migration speed varied among subspecies, with *N. p. islandicus* migrating faster than all others (192 ± 8 km/d), and *N. p. rogachevae* – *variegatus* migrating the slowest (130 ± 7 km/d; Tables 6 and 7). Overall migration speed was significantly different between spring and autumn (Table 7), but not between seasons within subspecies (Table 7, Fig. 3).

Ground speed was significantly higher for *N. p. phaeopus* (65.6 ± 1.5 km/h) and *N. h. rufiventris* (64.4 ± 0.9 km/h), and significantly lower for *N. p. rogachevae* (56.6 ± 2.9 km/h; Tables 6 and 7). Although not different between seasons across most subspecies, ground speed was higher in autumn than in spring for *N. p. islandicus* (Table 6).

Overall, the total time spent at stopover sites varied considerably among subspecies (Tables 6 and 7), particularly with *N. p. islandicus* spending a significantly shorter amount of time at stopovers compared to the average (12.9 ± 2.0 days), while *N. h. hudsonicus* spent significantly longer time at stopover sites (61.9 ± 8.8 days; Tables 6 and 7). In general, whimbrels spent a shorter total time at stopover sites in spring than in autumn (Table 7), and these durations differed significantly for *N. p. phaeopus*, *N. p. rogachevae*, *N. p. rogachevae* – *variegatus* and *N. p. variegatus* (Tables 6 and 7; Fig. 3).

N. p. islandicus stopped less than the average, while *N. h. rufiventris* and *N. p. phaeopus* stopped more. Overall, whimbrels did not differ in the number of stops between seasons, but seasonal differences were significant for *N. p. islandicus* (7.3 ± 1.4 vs 1.4 ± 0.5 times per migration in spring vs autumn; Tables 6 and 7, Fig. 3).

Threats assessment

The threats faced by whimbrels were more comprehensively assessed throughout the annual cycle for the Nearctic and *N. p. islandicus* subspecies. For *N. p. phaeopus*, threats at the breeding sites were not assessed, and for *N. p. rogachevae*, we

were only confident in assessing threats for the stopover and wintering sites. Threats at the breeding sites remain mostly unknown for both *N. p. alboaxillaris* and *N. p. variegatus* (Fig. 4).

Threats from *residential and commercial development* were identified at some period of the annual cycle for all subspecies. While these were not a threat on the breeding grounds for the Nearctic subspecies, *N. p. islandicus* were thought to face a medium impact from *housing and urban development* on the breeding grounds, mainly due to the expansion of summer houses that are built on whimbrel breeding habitat, reducing its availability but potentially also via disturbance from people and pets (Pálsdóttir *et al.* 2024).

Similarly, breeding *N. p. islandicus* were also considered to have a medium impact from *agriculture and aquaculture*, mainly due to increased afforestation (Pálsdóttir *et al.* 2022). The area of planted trees on open-habitat landscapes in Iceland has increased, removing suitable breeding habitat but also creating a buffer effect with whimbrels avoiding areas near plantations (Pálsdóttir *et al.* 2022). Wintering *N. p. rogachevae* were considered to be threatened from coastal afforestation through mangrove plantation in the feeding areas, although mangroves are important roosting habitats too (Johnston-González & Abril 2019).

Hunting and collecting terrestrial animals was classified with a medium impact on migrating and wintering whimbrels along the Atlantic Americas Flyway (i.e. all *N. h. hudsonicus* and some *N. h. rufiventris*), where evidence suggests that mortality is higher during autumn than spring migration (Watts *et al.* 2019), with unsustainable harvest levels (Watts *et al.* 2015). Whimbrels migrating along the Atlantic Americas Flyway and wintering *N. p. rogachevae* were considered to have a medium impact from *recreational activities*.

Invasive species were considered to have a medium impact on breeding *N. p. islandicus*, due to the expansion of Nootka lupin *Lupinus nootkensis* in key breeding habitats (Katrínardóttir *et al.* 2015). This invasive plant in Iceland spreads relatively fast and grows tall and dense, reducing the available breeding habitat for whimbrel. Migrating *N. p. rogachevae* and *N. p. variegatus* are threatened by the rapid expansion of smooth cordgrass *Spartina alterniflora* along China's coasts, which reduces foraging and roosting habitats (Jackson *et al.* 2021).

Table 5. Mean ($\pm$ se) durations at the wintering and breeding sites, for each of the whimbrel subspecies.

Subspecies	Wintering	n	Breeding	n
<i>N. p. rufiventris</i>	201 $\pm$ 7 days	28	37 $\pm$ 3 days	40
<i>N. p. hudsonicus</i>	193 $\pm$ 9 days	13	50 $\pm$ 4 days	23
<i>N. p. islandicus</i>	253 $\pm$ 3 days	20	75 $\pm$ 4 days	15
<i>N. p. phaeopus</i>	207 $\pm$ 12 days	7	56 $\pm$ 3 days	35
<i>N. p. phaeopus</i> – <i>rogachevae</i>		0	59 days	1
<i>N. p. rogachevae</i>	192 $\pm$ 10 days	4	57 $\pm$ 6 days	7
<i>N. p. rogachevae</i> – <i>variegatus</i>	195 $\pm$ 4 days	9	58 $\pm$ 4 days	10
<i>N. p. variegatus</i>	197 $\pm$ 11 days	9	63 $\pm$ 2 days	14

Pollution only had a complete score for wintering *N. p. rogachevae*, due to the use of agrochemicals, oil spills, ship-breaking activities and

untreated urban effluents along the rivers and coasts, which impacts intertidal mudflats and possibly biomagnification of heavy metals.

Climate change and severe weather threats are unknown in most cases, but were considered to have a very high impact on *N. h. hudsonicus* due to rapid climate change during breeding, in the form of trophic mismatches with their food resources, when chicks may experience food shortages with development implications (Senner *et al.* 2017, Kwon *et al.* 2019; but see Chagnon-Lafortune *et al.* 2024). *Habitat shifting and alteration* was considered to have a high impact on breeding *N. h. rufiventris* and *N. h. hudsonicus*, and a medium impact on *N. p. islandicus*, due to shrub encroachment that reduces suitable breeding habitat (Ballantyne & Nol 2015, Thompson *et al.* 2016, Alfredsson 2018). Along the Atlantic American Flyway, we scored a medium

Table 6. Mean ($\pm$ se) of the wintering and breeding latitudes, migration distance and speed, ground speed, total stopover duration and number of stopovers. Positive latitudes represent decimal degrees north of the equator, and negative latitudes represent decimal degrees south of the equator. Sample size of each variable is the first one to the right of it. For migration metrics, sample sizes are shown as autumn/spring.

Subspecies	Wintering latitude	n	Breeding latitude	n	Migration distance (km)		Migration speed (km/day)		n
					Autumn	Spring	Autumn	Spring	
<i>N. h. rufiventris</i>	4.8 $\pm$ 2.8	32	68.8 $\pm$ 0.2	81	11 116 $\pm$ 496	10 375 $\pm$ 625	163 $\pm$ 8	158 $\pm$ 11	32/20
<i>N. h. hudsonicus</i>	–1.1 $\pm$ 0.9	13	60.1 $\pm$ 0.4	24	9245 $\pm$ 741	10 121 $\pm$ 664	147 $\pm$ 13	130 $\pm$ 14	12/6
<i>N. p. islandicus</i>	11 $\pm$ 0.4	21	64.4 $\pm$ 0.1	61	6088 $\pm$ 134	7180 $\pm$ 253	202 $\pm$ 10	180 $\pm$ 12	21/18
<i>N. p. phaeopus</i>	7.7 $\pm$ 1	7	64.3 $\pm$ 0.5	36	10 241 $\pm$ 723	8813 $\pm$ 424	157 $\pm$ 13	209 $\pm$ 23	6/6
<i>N. p. alboaxillaris</i>	–25.9	1		0					0
<i>N. p. phaeopus</i> – <i>rogachevae</i>	–15.8	1	60.2	1		10 169		205	0/1
<i>N. p. rogachevae</i>	–6.9 $\pm$ 3.8	6	67.6 $\pm$ 0.9	8	8599 $\pm$ 903	9055 $\pm$ 954	114 $\pm$ 13	161 $\pm$ 21	4/5
<i>N. p. rogachevae</i> – <i>variegatus</i>	–9.1 $\pm$ 2.6	9	69 $\pm$ 0.4	10	9574 $\pm$ 663	7356 $\pm$ 1194	119 $\pm$ 7	146 $\pm$ 12	7/5
<i>N. p. variegatus</i>	–14.2 $\pm$ 4.1	11	66.3 $\pm$ 0.7	14	10 474 $\pm$ 620	9674 $\pm$ 613	132 $\pm$ 8	165 $\pm$ 10	6/10

Subspecies	Ground speed (km/h)		n	Total stopover duration (days)		Number of stopovers		n
	Autumn	Spring		Autumn	Spring	Autumn	Spring	
<i>N. h. rufiventris</i>	63.6 $\pm$ 1.2	65.5 $\pm$ 1.5	30/19	56.4 $\pm$ 5.9	44.2 $\pm$ 6.1	13.3 $\pm$ 2.1	13.3 $\pm$ 2.9	32/20
<i>N. h. hudsonicus</i>	59.2 $\pm$ 2	64.6 $\pm$ 1.3	12/6	56.7 $\pm$ 11	72.1 $\pm$ 15	11.7 $\pm$ 2.9	6.8 $\pm$ 1.9	12/6
<i>N. p. islandicus</i>	64.7 $\pm$ 1.3	58.8 $\pm$ 1.8	21/18	6.9 $\pm$ 2.8	19.9 $\pm$ 2.2	1.4 $\pm$ 0.5	7.3 $\pm$ 1.3	21/18
<i>N. p. phaeopus</i>	63.9 $\pm$ 1.4	67.4 $\pm$ 2.7	6/6	63.2 $\pm$ 8.5	31.2 $\pm$ 4.2	13.8 $\pm$ 2.2	23 $\pm$ 3.6	6/6
<i>N. p. alboaxillaris</i>			0					0
<i>N. p. phaeopus</i> – <i>rogachevae</i>		68.3	0/1		26.9		12	0/1
<i>N. p. rogachevae</i>	59.8 $\pm$ 4.3	53.4 $\pm$ 3.7	4/4	69.3 $\pm$ 16.1	28.4 $\pm$ 5.2	4.8 $\pm$ 1.1	16 $\pm$ 8	4/5
<i>N. p. rogachevae</i> – <i>variegatus</i>	57.7 $\pm$ 1.7	56.2 $\pm$ 1.7	6/3	62.8 $\pm$ 9.4	15.8 $\pm$ 2.2	4.3 $\pm$ 1.2	4.4 $\pm$ 0.9	7/5
<i>N. p. variegatus</i>	57.4 $\pm$ 1.6	60.4 $\pm$ 1.5	6/10	71 $\pm$ 11	23.9 $\pm$ 2.7	6.5 $\pm$ 0.9	4.7 $\pm$ 0.4	6/10

Table 7. Contrasts of comparisons between explanatory variable levels, for several models. Among seasons, the estimate is the difference to the overall estimated mean between seasons; for Subspecies, estimates are the difference to the overall estimated mean across subspecies; for the interaction of Season * Subspecies, estimates are the difference between autumn and spring means within subspecies. Sample sizes are shown in Table 6.

Response variables	Explanatory variables	Level	Estimate	se	df	t ratio	P value
Migration distance	Season	Spring	-121.19	184.75	144	-0.66	0.513
		<i>N. h. rufiventris</i>	1639.12	339.61	144	4.83	<0.001
	Subspecies	<i>N. h. hudsonicus</i>	569.27	473.85	144	1.20	0.324
		<i>N. p. islandicus</i>	-2504.71	270.79	144	-9.25	<0.001
		<i>N. p. phaeopus</i>	379.18	534.64	144	0.71	0.559
		<i>N. p. rogachevae</i>	-272.71	573.25	144	-0.48	0.635
		<i>N. p. rogachevae</i> – <i>variegatus</i>	-774.29	495.10	144	-1.56	0.210
		<i>N. p. variegatus</i>	964.14	505.97	144	1.91	0.137
	Season * Subspecies	Autumn–spring <i>N. p. rufiventris</i>	740.98	655.17	144	1.13	0.260
		Autumn–spring <i>N. p. hudsonicus</i>	-875.71	1059.95	144	-0.83	0.410
		Autumn–spring <i>N. p. islandicus</i>	-1091.80	463.64	144	-2.36	0.020
		Autumn–spring <i>N. p. phaeopus</i>	1428.10	1188.56	144	1.20	0.232
		Autumn–spring <i>N. p. rogachevae</i>	-455.95	1272.76	144	-0.36	0.721
		Autumn–spring <i>N. p. rogachevae</i> – <i>variegatus</i>	2217.33	1053.79	144	2.10	0.037
		Autumn–spring <i>N. p. variegatus</i>	800.20	1132.97	144	0.71	0.481
Migration speed	Season	Spring	9.07	4.06	144	2.24	0.027
		<i>N. h. rufiventris</i>	5.98	6.35	144	0.94	0.406
	Subspecies	<i>N. h. hudsonicus</i>	-16.44	8.67	144	-1.90	0.088
		<i>N. p. islandicus</i>	36.02	7.80	144	4.62	<0.001
		<i>N. p. phaeopus</i>	25.24	12.18	144	2.07	0.088
		<i>N. p. rogachevae</i>	-20.47	10.93	144	-1.87	0.088
		<i>N. p. rogachevae</i> – <i>variegatus</i>	-23.05	9.22	144	-2.50	0.047
		<i>N. p. variegatus</i>	-7.29	9.47	144	-0.77	0.443
	Season * Subspecies	Autumn–spring <i>N. p. rufiventris</i>	4.88	11.90	144	0.41	0.683
		Autumn–spring <i>N. p. hudsonicus</i>	16.54	17.74	144	0.93	0.353
		Autumn–spring <i>N. p. islandicus</i>	22.23	15.98	144	1.39	0.166
		Autumn–spring <i>N. p. phaeopus</i>	-51.72	27.91	144	-1.85	0.066
		Autumn–spring <i>N. p. rogachevae</i>	-46.72	24.04	144	-1.94	0.054
		Autumn–spring <i>N. p. rogachevae</i> – <i>variegatus</i>	-27.60	20.75	144	-1.33	0.186
		Autumn–spring <i>N. p. variegatus</i>	-32.57	19.64	144	-1.66	0.099
Ground speed	Season	Spring	-0.13	0.65	136	-0.20	0.839
		<i>N. h. rufiventris</i>	3.74	1.02	136	3.66	0.002
	Subspecies	<i>N. h. hudsonicus</i>	0.95	1.52	136	0.63	0.531
		<i>N. p. islandicus</i>	0.81	1.06	136	0.76	0.521
		<i>N. p. phaeopus</i>	4.76	1.74	136	2.74	0.024
		<i>N. p. rogachevae</i>	-4.44	1.82	136	-2.44	0.037
		<i>N. p. rogachevae</i> – <i>variegatus</i>	-3.86	1.84	136	-2.10	0.066
		<i>N. p. variegatus</i>	-1.96	1.45	136	-1.35	0.250
	Season * Subspecies	Autumn–spring <i>N. p. rufiventris</i>	-1.86	1.93	136	-0.97	0.336
		Autumn–spring <i>N. p. hudsonicus</i>	-5.36	3.40	136	-1.58	0.118
		Autumn–spring <i>N. p. islandicus</i>	5.91	2.01	136	2.95	0.004
		Autumn–spring <i>N. p. phaeopus</i>	-3.50	3.84	136	-0.91	0.365
		Autumn–spring <i>N. p. rogachevae</i>	6.38	4.06	136	1.57	0.118
		Autumn–spring <i>N. p. rogachevae</i> – <i>variegatus</i>	1.54	4.07	136	0.38	0.706
		Autumn–spring <i>N. p. variegatus</i>	-3.02	3.06	136	-0.99	0.326

(continued)

Table 7. (continued)

Response variables	Explanatory variables	Level	Estimate	se	df	t ratio	P value
Total stopover duration	Season	Spring	-10.78	2.41	144	-4.47	<0.001
		<i>N. h. rufiventris</i>	5.88	3.86	144	1.52	0.302
	Subspecies	<i>N. h. hudsonicus</i>	20.01	5.81	144	3.44	0.003
		<i>N. p. islandicus</i>	-31.03	4.17	144	-7.45	<0.001
		<i>N. p. phaeopus</i>	2.77	6.56	144	0.42	0.674
		<i>N. p. rogachevae</i>	4.45	7.49	144	0.59	0.674
		<i>N. p. rogachevae</i> – <i>variegatus</i>	-5.12	6.64	144	-0.77	0.674
		<i>N. p. variegatus</i>	3.04	5.97	144	0.51	0.674
	Season *	Autumn–spring <i>N. p. rufiventris</i>	12.23	7.13	144	1.72	0.088
		Autumn–spring <i>N. p. hudsonicus</i>	-15.35	12.50	144	-1.23	0.222
		Autumn–spring <i>N. p. islandicus</i>	-13.03	8.03	144	-1.62	0.107
		Autumn–spring <i>N. p. phaeopus</i>	31.95	14.44	144	2.21	0.028
		Autumn–spring <i>N. p. rogachevae</i>	40.91	16.77	144	2.44	0.016
		Autumn–spring <i>N. p. rogachevae</i> – <i>variegatus</i>	47.07	14.64	144	3.22	0.002
		Autumn–spring <i>N. p. variegatus</i>	47.17	12.91	144	3.65	<0.001
Number of stopovers	Season	Spring	1.41	0.86	144	1.64	0.104
		<i>N. h. rufiventris</i>	3.96	1.38	144	2.88	0.011
	Subspecies	<i>N. h. hudsonicus</i>	-0.13	2.07	144	-0.06	0.949
		<i>N. p. islandicus</i>	-5.03	1.49	144	-3.38	0.003
		<i>N. p. phaeopus</i>	9.03	2.34	144	3.86	0.001
		<i>N. p. rogachevae</i>	0.99	2.67	144	0.37	0.830
		<i>N. p. rogachevae</i> – <i>variegatus</i>	-5.04	2.37	144	-2.13	0.062
		<i>N. p. variegatus</i>	-3.78	2.13	144	-1.78	0.109
	Season *	Autumn–spring <i>N. p. rufiventris</i>	-0.01	2.54	144	0.00	0.998
		Autumn–spring <i>N. p. hudsonicus</i>	4.83	4.46	144	1.08	0.281
		Autumn–spring <i>N. p. islandicus</i>	-5.85	2.87	144	-2.04	0.043
		Autumn–spring <i>N. p. phaeopus</i>	-9.17	5.15	144	-1.78	0.077
		Autumn–spring <i>N. p. rogachevae</i>	-11.25	5.99	144	-1.88	0.062
		Autumn–spring <i>N. p. rogachevae</i> – <i>variegatus</i>	-0.11	5.23	144	-0.02	0.983
		Autumn–spring <i>N. p. variegatus</i>	1.80	4.61	144	0.39	0.697

impact from *storms and flooding*, which can influence migrating whimbrels in active flight, but also their stopover sites.

Renewable energy developments were considered to become a threat for breeding *N. p. rufiventris* and *N. p. islandicus*. *Diseases of unknown cause* (e.g. avian cholera, avian flu) may become a threat to all whimbrels in the Nearctic along the annual cycle. Wintering *N. p. rogachevae* may face numerous new threats in the future, across most threat categories, while migrating *N. p. rogachevae* and *N. p. variegatus* are expected to face new threats due to *climate change and severe weather*.

DISCUSSION

By collating whimbrel tracking data from across the globe, we identified major coverage gaps,

compared annual-cycle movement patterns among subspecies and assessed the threats whimbrels encounter throughout the year. Together, the tracking and threat information reveal species facing multiple conservation challenges across all stages of the annual cycle, while simultaneously exposing substantial geographical and taxonomic biases in our estimation of those challenges. Notably, despite improvements in knowledge since previous global assessments, population trends remain unfavourable for most subspecies, suggesting that existing conservation measures have been insufficient to halt declines.

Breeding

We found substantial subspecific variation in the period of the annual cycle spent at breeding areas.

N. p. islandicus represents one extreme, being at breeding sites for 75 days on average, whereas *N. h. rufiventris* and *N. h. hudsonicus* occupy the opposite end of the spectrum (37 and 50 days, respectively). These differences may be partly attributable to differences in behaviour and variation in breeding success. On the one hand, Nearctic breeders tend to leave the breeding site soon after the breeding attempt and fuel for the first autumn migratory flight elsewhere (Ruthrauff *et al.* 2021), while *N. p. islandicus* usually fuels at or very near the breeding site (C. Carneiro, T. G. Gunnarsson, J. A. Alves, unpubl. data). Hence, the latter is expected to spend longer periods of time at the breeding area. On the other hand, it has been shown that for *N. p. islandicus*, but also *N. h. hudsonicus*, successful breeders typically depart later and therefore remain longer at the breeding grounds than unsuccessful individuals (Carneiro *et al.* 2023, Ausems *et al.* 2025). The short durations recorded for the Nearctic subspecies nevertheless imply generally low breeding success, as at least ca. 56 days are required for a successful nesting attempt (i.e. ca. 29 days for laying and incubation + ca. 27 days to fledging; Smith *et al.* 2025). Additionally, variation in breeding success could be related to variation in tag types and attachments used (Table S2), since these may influence reproduction (Hooijmeijer *et al.* 2014).

Breeding-ground threats that constrain the window of suitable conditions will influence subspecies differently, depending on their degree of temporal flexibility. In our threat assessment, *climate change and severe-weather* impacts were classified as largely unknown for most breeding whimbrel populations; however, *N. h. hudsonicus* was identified as strongly affected, particularly through probable trophic mismatches, as these have been documented for other sympatric breeding shorebirds (Senner *et al.* 2017, Kwon *et al.* 2019). These patterns suggest that timing constraints at high-latitude breeding grounds may be particularly severe for some subspecies.

Despite these pressures, the breeding regions for multiple subspecies remain poorly understood, especially those of *N. p. phaeopus*, *N. p. rogachevae* and *N. p. variegatus*, as highlighted by the converging wintering populations from each side of the Indian Ocean into central Northern Russia. Many of these breeding areas are remote and difficult to access, limiting our ability to identify local threats or evaluate habitat change. As a result, a

large proportion of threats at northern breeding sites remain classified as unknown.

In contrast to these under-studied regions, the breeding grounds of *N. p. islandicus* are among the best monitored. Here, *residential and commercial development* has emerged as a notable threat. Given the high densities of breeding whimbrels in Iceland (Katrínardóttir *et al.* 2015, Cerezo-Araujo *et al.* 2025), even localized increases in housing and infrastructure can have disproportionate population effects. Surveys from the southern Icelandic lowlands, where development is most intense (Pálsdóttir *et al.* 2024, 2025a), have documented annual declines in whimbrel numbers of 5% per year (Pálsdóttir *et al.* 2025b), highlighting the sensitivity of Icelandic breeding sites to habitat alteration.

Investigating habitat requirements and monitoring change during the breeding season across subspecies would narrow a currently wide knowledge gap, while informing conservation actions on habitat restoration and protection (RF1; Table 8).

Wintering

Whimbrels spend most of their year at the wintering sites, and we show a clear overlap in the wintering distribution of different subspecies. Particularly for *N. p. islandicus* and *N. p. phaeopus*, such overlap complicates population assessments, as highlighted by the contrast between stable long-term trends found through wintering counts (van Roomen *et al.* 2025), and declining trends based on breeding surveys (Lindström *et al.* 2019b, Pálsdóttir *et al.* 2025b). Based on molecular analyses and tracking data, Conklin *et al.* (2026) recently showed that the assumption of total segregation of Bar-tailed Godwit *Limosa lapponica* subspecies wintering in Europe, and on which population size estimates stood, was wrong. Utilizing tracking data to disentangle the distinct taxonomic groups of overlapping wintering whimbrel populations can improve population size estimates (RF2; Table 8). This, in turn, would enable conservation actions to be targeted towards the populations experiencing the greatest declines.

Migration

Migration distance

Subspecies exhibited substantial differences in migration distance, with *N. p. islandicus*

Table 8. Research fronts (RF) emerging from the synthesis of knowledge gaps, annual-cycle behaviour and threats across whimbrel subspecies. Conservation relevance reflects the potential contribution of each research front to improving conservation decisions and outcomes.

Research front	Description	Conservation relevance
1	Identify habitat requirements and monitor habitat changes at the breeding sites remotely, by combining tracking of individuals with remote-sensing techniques and assess how environmental alterations may affect breeding success and population dynamics. As a complement, where breeding sites are accessible, a detailed examination of trophic interactions for both adults and chicks would clarify the specific trophic relationships involved and improve predictions of how environmental change may propagate through population dynamics.	Medium
2	Comprehensive analysis of tracking data at overlapping distributions, including the temporal axis. Existing datasets, coupled with targeted tracking from unsampled areas along the wintering distribution, should help clarify which subspecies use each site, as well as when and, therefore, whether any segregation exists that can lead to more accurate population size monitoring.	High
3	Determine the drivers of migration distance among subspecies. Differences may emerge during juvenile settlement, with some individuals encountering suitable wintering habitat earlier along the route and establishing fidelity to these sites. Tracking juveniles across subspecies, documenting their first migrations, exploratory movements and initial winter site choices, could clarify the mechanisms shaping subspecific migration strategies (overlaps with RF8).	Low
4	Comparative analysis across subspecies to quantify the pressures shaping arrival timing at both breeding and wintering sites. By integrating remote-sensing information and weather models and/or locally recorded conditions such as snow cover, temperature and wind, with individual tracking data, it should be possible to link environmental cues to arrival dates, breeding phenology and reproductive success. In parallel, migration-related metrics such as migration speed should be incorporated to understand the mechanisms birds use to adjust their timing.	Low
5	Explore the factors explaining the variation in the number and duration of stopover events within and among subspecies. By integrating stopover habitat information (derived from land-cover data and remote sensing), weather conditions, migration metrics and local movement patterns, it should be possible to infer the specific functions and drivers of individual stopover events.	Medium
6	Determine the most important stopover sites along each flyway. Advances in network analyses provide powerful tools for quantifying site connectivity and assessing the relative importance of individual stopover sites within broader migratory networks, offering promising applications for targeted conservation (e.g. site protection, habitat restoration).	High
7	Assess the balance between individual site fidelity and stopover site importance, by conducting detailed behavioural studies during overlapping stopover periods and regions. Investigating spatiotemporal patterns of stopover site use at the individual level, ideally across multiple years, will help understand whether certain sites are used differently depending on subspecies. Links with RFs 5 and 6.	Medium
8	Conduct sex- and age-specific analyses of whimbrel migration to assess spatial and temporal segregation. Differences in behaviour between cohorts may result in differential vulnerability to threats, and in turn influence population dynamics.	Medium
9	Expand tracking efforts to under-sampled regions and subspecies. By increasing the geographical and taxonomic breadth of tracking, it will be possible to map the full range of areas used by whimbrels, clarify migration routes, and improve our understanding of connectivity and population structures.	High
10	Incorporate tracking data and migratory connectivity information into taxonomic classification. Particularly building on RF9, establishing a clearer map of connectivity between annual-cycle periods should provide valuable context for taxonomic distinctions. This approach will also help identify where and when to target further studies on vocalizations, morphology and molecular markers, which are likewise needed for more informed taxonomic decisions.	Medium

migrating roughly 5000 km less than *N. h. rufiventris*, a pattern mirrored by clear variation in wintering latitudes. Such differences probably entail ecological and energetic consequences, as shorter and longer distance migrants may experience different levels of energy expenditure, exposure to en route hazards, and potential carry over effects on body condition and subsequent breeding performance (Fayet *et al.* 2017, Soriano-Redondo *et al.* 2023), although within *N. p. islandicus* no such carry over effects were observed (Carneiro *et al.* 2021). Moreover, the relationship of migration distance, and associated wintering latitude, with individual fitness consequences may not vary linearly, as shown in another globally distributed shorebird species—the Sanderling *Calidris alba*—where survival is lower for individuals wintering at the tropics but higher at higher latitudes in both hemispheres (Reneerkens *et al.* 2020). Since whimbrels are faithful to the wintering sites and because the wintering location and habitat can influence individual fitness, understanding where an individual settles during its first migration may provide crucial insight into population limitations (RF3, Table 8). Furthermore, it would help identify whether certain sites are more likely to be used by juveniles, where protection may be particularly important during this life period.

Migration and ground speed

Overall, whimbrels tended to migrate faster in spring, possibly reflecting a greater time pressure to reach the breeding grounds compared to the wintering sites. In general, there is pressure to arrive early at the breeding sites because early arrival confers several advantages (Drent *et al.* 2003, 2006, Smith & Moore 2005). Individuals that reach the breeding grounds early are more likely to maintain their mate (Gunnarsson *et al.* 2004) and increase the likelihood of successful breeding (Morrison *et al.* 2019, Carneiro *et al.* 2021). However, comparable pressures probably operate at the wintering grounds as well. Whimbrels defend winter territories and show strong site fidelity (Mallory 1982, Zwarts 1990) and spend a substantial proportion of the annual cycle in the wintering sites; hence, arriving at these sites at the appropriate time is also likely to be relevant for individual fitness.

Although we did not find significant differences between seasons within subspecies, it has been

previously shown that *N. p. islandicus* migrate more rapidly in autumn than in spring (Carneiro *et al.* 2019b). That study also showed higher ground speeds in autumn, in line with our results, where only *N. p. islandicus* had significantly different ground speeds between seasons. Opposite patterns in migration and ground speeds between seasons among subspecies may indicate differences in migration strategy (Alerstam & Lindström 1990) and a different relative importance of timely arrival between seasons, but it could equally arise from different environmental conditions encountered en route, such as wind assistance or variation in refuelling opportunities (Alves *et al.* 2016, Carneiro *et al.* 2020). Investigating the factors shaping arrival and migration speeds between seasons will inform on the mechanisms underlying annual-cycle timing and improve predictions of how environmental change may affect migratory performance and population dynamics (RF4, Table 8).

Stopovers

We documented considerable variation in the time spent at stopovers and number of stopovers used across subspecies. Stopovers typically enable migrants to accumulate the energy required for subsequent flight segments, but they may also serve additional functions such as resting, recovering or gathering information (Linscott & Serner 2021). Consequently, understanding where, when, for how long and how often migrants stop, as well as the reasons underlying these behaviours, is crucial for evaluating the ecological relevance of stopover locations. Variation in stopover behaviour, including the number and duration of stops, also mediates exposure to threats encountered en route.

Furthermore, the importance of stopover sites in a flyway can vary. For example, along the Atlantic American Flyway nearly half of the whimbrel population is estimated to stop at a specific site in South Carolina, USA—Deveau Bank (a Site of International Importance in the Western Hemisphere Shorebird Reserve Network; Sanders *et al.* 2021)—with individuals repeatedly using the same foraging and roosting patches in the area across years (Handmaker *et al.* 2024). Threats to such sites, where a large proportion of the population stop, can have severe consequences. This has been shown for shorebirds that stopover on the Yellow Sea, where species declines were positively correlated with the degree of dependence on the

site (Studds *et al.* 2017). Determining the reason for stopover events (RF5; Table 8) and identifying the most important sites along flyways (RF6; Table 8; Lamb *et al.* 2019, Beal *et al.* 2025) will support informed site protection and habitat restoration actions.

Some subspecies show significant overlap in certain regions and times during the annual cycle, such as migrating *N. h. rufiventris* and *N. h. hudsonicus* along the Atlantic American Flyway, or *N. p. islandicus* and *N. p. phaeopus* along the East Atlantic Flyway. This overlap implies that different subspecies may share vulnerability to threats during overlapping periods, while differences in life-history traits, like migration speed and stopover duration, can lead to varying impacts. For example, *N. p. islandicus* tends to migrate faster with fewer and shorter stopovers than *N. p. phaeopus*, potentially making it more sensitive to changes at specific stopover sites. A recent comparative study between Eurasian Whimbrel (*N. p. islandicus*) and Bar-tailed Godwits along the East Atlantic Flyway (R. A. Bom, T. Piersma, A. D. Rocha, C. Carneiro, A. Coelho, A. Regalla de Barros, J. A. Alves, pers. comm.) showed that individual whimbrels are relatively more flexible in the sites used among years, so despite using relatively few sites, individual flexibility in site use across years may benefit this subspecies. However, site fidelity and flexibility may vary across whimbrel subspecies or flyways, as along both the Atlantic American and East Asian–Australasian Flyway individuals show high fidelity to stopover sites between years (An *et al.* 2024, Handmaker *et al.* 2024). Further research to understand the balance between individual site fidelity and stopover site importance, particularly for overlapping whimbrel subspecies, will inform how site-specific conditions (both threats and conservation actions) would affect different subspecies (RF7; Table 8).

Age and sex differences

We did not account for the sex of individuals, but some of the variation we found could be related to different sex ratios between groups. Beyond subspecific variation, there is evidence that males and females differ in several aspects during the annual cycle. Some studies have documented sexual differences in migration timings in whimbrels (Carneiro *et al.* 2019b, Ruthrauff *et al.* 2021, Aulsems *et al.* 2025), raising the possibility that spatial segregation may occur as well. Likewise, variation

between ages has been documented, with juveniles migrating at a different timing than adults and varying slightly in their routes (Hines *et al.* 2023, Carneiro *et al.* 2024). If different sex or age groups differ in space and time use across the annual cycle, they may also encounter different environmental conditions, stopover opportunities or threats. Conducting sex- and age-specific analyses of whimbrel migration to assess spatial and temporal segregation may help identify details relevant for population dynamics and enable more targeted conservation actions (RF8; Table 8).

Uneven research

Not surprisingly, in light of the variation in distribution of researchers, we show heterogeneous tracking efforts among flyways and, consequently, subspecies. These gaps are particularly pronounced in regions such as the Indian Ocean non-breeding areas and breeding grounds in northern central Russia, where limited tracking may obscure the identification of important breeding, stopover or wintering sites. For example, there are no tracking data from a large portion of the wintering regions along most of Southern Africa. Individuals wintering there would probably belong to the nominate subspecies and their tracking would reveal, at least, wider migration distances than what we amassed here, but could also vary in other metrics.

The most detailed ecological and threat data originate from a few well-studied flyways—such as the Pacific Americas, Atlantic American and East Atlantic—potentially biasing conservation priorities towards these regions and underestimating threats in under-sampled areas (Scarpignato *et al.* 2023). This bias in data collection can lead to the oversight of critical habitats along poorly studied migration corridors in international conservation planning (Chan *et al.* 2019). In fact, three out of the four most extensively tracked subspecies (i.e. *N. h. rufiventris*, *N. h. hudsonicus* and *N. p. islandicus*) tend to have fewer unknown threats, underscoring how data gaps translate directly into knowledge gaps and potentially missed conservation needs. It is important to recognize that our threat assessment has inherent limitations and biases that mirror those in the tracking data, as a greater number of experts contributed to evaluating threats in flyways with more available data, but nevertheless the threats we identified largely coincide with those highlighted several years ago

by Brown *et al.* (2014) and Pearce-Higgins *et al.* (2017). Although some of the research recommendations by Brown *et al.* (2014) and Pearce-Higgins *et al.* (2017) have been addressed and our understanding of potential population bottlenecks has improved, population trends remain unfavourable for most subspecies (Table S1), indicating that conservation efforts have been insufficient. Expanding tracking efforts to under-sampled regions and subspecies (particularly of the wintering individuals around the Indian Ocean) will allow for a better understanding of connectivity and population structures across the globe (RF9; Table 8).

A fragmented understanding of global migration routes and migratory connectivity also hinders a robust taxonomic classification of whimbrel species and subspecies. We have considered the seven subspecies that fall under Hudsonian and Eurasian Whimbrels (AviList Core Team 2025), plus two other groups due to unclear distinction at the breeding range (*N. p. phaeopus* – *rogachevae* and *N. p. rogachevae* – *variegatus*; Kuang *et al.* 2022). However, taxonomic classification, while grounded in empirical data, has an associated subjectivity since taxonomists must interpret the relevance and weight of multiple lines of evidence, and these decisions are further complicated by uneven data availability across taxa. Tracking data may provide an important source of information for taxonomists, since they expose the degree of migratory connectivity among populations (Knight *et al.* 2025), and may contribute to conservation decision-making by allowing practitioners to target the group in need. For instance, although the breeding ranges of the Nearctic subspecies (*N. h. rufiventris* and *N. h. hudsonicus*) are presumed to be geographically separate, their non-breeding distributions overlap significantly along the America–Atlantic Flyway. Therefore, the extensive tracking data available across the Americas may support revising the (breeding) boundaries of these subspecies. Incorporating tracking data and migratory connectivity information into taxonomic classification would help clarify management units and guide conservation efforts (RF10, Table 8).

CONCLUSION

Our tracking data compilation shows that our current understanding of whimbrel ecology remains

fragmentary, with under-sampled regions and subspecies possibly having crucial but still unrecognized conservation needs. At the same time, we highlight consistent pressures that are likely to intensify under ongoing environmental change. The set of research fronts we outline provides guidance for future work, by emphasizing the need for expanded tracking and other work, such as on molecular and demographic aspects, into poorly sampled regions, incorporation of movement data into taxonomic and population assessments, and deeper investigation of stopover and timing mechanisms. Addressing these will not only fill the many knowledge gaps but also deliver the integrated understanding of connectivity, behaviour and demography required to guide effective conservation for wide-ranging whimbrels across their full annual cycle. But how can this be achieved efficiently?

Current research coverage in shorebird ecology tends to reflect funding structures, geographical inequalities and topic-driven incentives, rather than conservation priorities, resulting in a systematic bias towards certain regions and themes. The uneven tracking coverage we identify could then also be interpreted as a structural issue requiring action from international conservation and scientific organizations. Migratory shorebirds have international, often trans-hemispheric lives, yet research investment remains fragmented and disproportionately distributed. Large-scale initiatives such as Global Wader (www.globalwader.org) are crucial to helping identify gaps, but that alone is insufficient. International bodies and funding mechanisms must take co-ordinated responsibility for strategically supporting under-represented regions and species. A globally co-ordinated, gap-driven funding strategy is therefore essential to ensure that conservation decisions are based on representative knowledge rather than convenience.

We are truly thankful to everyone who helped in collecting and maintaining the datasets used in this paper, as well as all the landowners who allowed us to work on their properties. We thank BirdLife International and Handbook of the Birds of the World, and eBird, for the whimbrel distribution maps. We thank Maria Dias for guidance on the threat assessment methodology, and the editors and anonymous reviewers who provided valuable feedback on an early version of the manuscript.

AUTHOR CONTRIBUTIONS

Camilo Carneiro: Data curation; formal analysis; project administration; supervision; validation; writing – original draft; writing – review and editing; methodology; investigation; conceptualization. **Gary Allport:** Writing – review and editing; data curation; validation; investigation. **Tómas G. Gunnarsson:** Data curation; investigation; project administration; methodology; funding acquisition; resources; supervision; validation; writing – review and editing. **Delip K. Das:** Data curation; investigation; validation; writing – review and editing. **Philip W. Atkinson:** Investigation; validation; data curation. **Charlotte Francesiaz:** Data curation; investigation; validation; writing – review and editing. **Anne N. M. A. Ausems:** Investigation; validation; writing – review and editing; data curation. **Pierrick Bocher:** Investigation; validation; writing – review and editing; data curation. **Roeland Bom:** Investigation; validation; writing – review and editing; data curation. **Robert E. Gill:** Data curation; investigation; validation; writing – review and editing. **Malo Braquier:** Investigation; validation; data curation. **Diana J. Hamilton:** Data curation; validation; investigation; writing – review and editing. **Sayam U. Chowdhury:** Data curation; investigation; validation; writing – review and editing. **Stephen C. Brown:** Investigation; validation; data curation. **Paula Cimprich:** Data curation; investigation; validation. **Maina C. Handmaker:** Data curation; investigation; validation; writing – review and editing. **Shariful Islam:** Data curation; investigation; validation; writing – review and editing. **Frédéric Jiguet:** Data curation; investigation; validation; writing – review and editing. **Audrey Jaeger:** Data curation; investigation; validation. **Chrystyn Jones:** Data curation; investigation; validation. **Emmanuel Joyeux:** Data curation; investigation; validation; writing – review and editing. **Alan H. Kneidel:** Data curation; investigation; validation. **Jeffrey F. Kelly:** Data curation; investigation; validation. **Fenliang Kuang:** Data curation; investigation; validation; writing – review and editing. **Chris Latty:** Data curation; investigation; validation. **Mathieu Le Corre:** Data curation; investigation; validation; writing – review and editing. **David Li:** Data curation; investigation; validation; writing – review and editing. **Rebeca C. Linhart:** Data curation; investigation; validation; writing – review and editing. **Adám Lovas-Kiss:** Data curation; investigation; validation; writing –

review and editing. **Zhijun Ma:** Data curation; investigation; validation; writing – review and editing. **Scott McWilliams:** Data curation; investigation; validation. **Verónica Méndez:** Data curation; investigation; validation; writing – review and editing. **Jason Mobley:** Data curation; investigation; validation. **Samuel NG:** Data curation; investigation; validation. **Joshua Nightingale:** Data curation; investigation; validation. **Erica Nol:** Data curation; investigation; validation; writing – review and editing. **Marie Pitts:** Data curation; investigation; validation. **Julie Paquet:** Data curation; investigation; validation; writing – review and editing. **Theunis Piersma:** Data curation; investigation; validation; writing – review and editing. **Rivo Rabarisoa:** Data curation; investigation; validation. **Florinah Razafimandimby:** Data curation; investigation; validation. **Daniel R. Ruthrauff:** Data curation; investigation; validation; writing – review and editing. **Felicia Sanders:** Data curation; investigation; validation. **Shiloh Schulte:** Data curation; investigation; validation. **Böðvar Þórisson:** Data curation; investigation; validation; writing – review and editing. **Philipp Schwemmer:** Data curation; investigation; validation; writing – review and editing. **Lee Tibbitts:** Data curation; investigation; validation. **Bryan Watts:** Data curation; investigation; validation. **Nathan R. Senner:** Data curation; investigation; validation; writing – review and editing. **Nils Warnock:** Data curation; investigation; validation; writing – review and editing. **Brad Winn:** Data curation; investigation; validation. **Samantha J. Wolfe:** Data curation; investigation; validation. **Shufen Yang:** Data curation; investigation; validation. **José A. Alves:** Conceptualization; data curation; funding acquisition; project administration; resources; writing – review and editing; supervision; validation; investigation; methodology.

FUNDING

This work was supported by multiple funds: Icelandic Research Fund (IRF:228625, IRF:228937–051, IRF:217587 and IRF:2511504); national funds through FCT – Fundação para a Ciência e a Tecnologia I.P., under the project CESAM-Centro de Estudos do Ambiente e do Mar, references UID/50017/2025 ([10.54499/UID/50017/2025](https://doi.org/10.54499/UID/50017/2025)) and LA/P/0094/2020 ([10.54499/LA/P/0094/2020](https://doi.org/10.54499/LA/P/0094/2020)); ProPolar; African Bird Club and A. D. Leventis; National Fish and Wildlife Foundation, Donors to Manomet, Knobloch

Family Foundation; National Science Foundation RAISE; The embassy of France in Dhaka and Jagannath University, Bangladesh; Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant, Mount Allison University, NMBCA; Carolina Bird Club, Georgia Ornithological Society; LIM-OIO project (French Office for Biodiversity (Grant number: OFB 22–1084)); Migratlane project (OFB); FEDER 'Marais d'Olonne'; The International Direction of University of Réunion Island and the Research Fédération OMNCG (WITS project). INTERREG 2021–2027; Regional Council from Réunion Island; National Parks Board Singapore; USFWS; Fundamental and Interdisciplinary Disciplines Breakthrough Plan of the Ministry of Education of China (JYB2025XDXM911); Programa Petrobras Socioambiental; Environment and Climate Change Canada; David and Lucile Packard Foundation, USGS Ecosystems Mission Area; German Federal Agency for Nature Conservation within the project OWP Vogelzug (FKZ 352315100A) with funds from the German Federal Ministry for the Environment, Climate Action, Nature Conservation and Nuclear Safety (BMUKN); National park Administration Schleswig-Holstein Wadden Sea within the project INAR with funds from the Federal Ministry for Energy Transition, Climate Protection, Environment and Nature of the federal state of Schleswig-Holstein; National Fish and Wildlife Foundation Atlantic Flyway Shorebird Initiative grant numbers 67006, 74101; The Nature Conservancy, Center for Conservation Biology William & Mary; National Parks Board Singapore.

CONFLICT OF INTEREST

We declare that we have no conflict of interests.

ETHICAL NOTE

Catching, handling and tagging were conducted in accordance with the local legislation and ethical guidelines for research on wild birds under natural conditions.

DECLARATION OF GENERATIVE AI IN THE WRITING PROCESS

The authors used ChatGPT 5.2 (<https://chatgpt.com/>) to revise and smooth some text sections. The authors critically reviewed and edited the

generated material as needed and accept full responsibility for the content of the publication.

DATA AVAILABILITY STATEMENT

Movement data are available via Global Wader (www.globalwader.org).

REFERENCES

- Alerstad, T. & Lindström, Å. 1990. Optimal bird migration: The relative importance of time, energy, and safety. In Gwinner, E. (ed) *Bird Migration: Physiology and Ecophysiology*. 331–351. Berlin: Springer.
- Alfredsson, S.B. 2018. The effects of shrub encroachment on avian communities in lowland Iceland. Master's thesis, Faculty of Life and Environmental studies, Reykjavik, Iceland: University of Iceland, 56.
- Allport, G. 2017. Steppe whimbrels *Numenius phaeopus alboaxillaris* at Maputo, Mozambique, in February–March 2016, with a review of the status of the taxon. *Bull. Afr. Bird Club* 24: 27–37.
- Allport, G.A., Atkinson, P.W., Carvalho, M., Clark, N.A. & Green, R.E. 2018. Local site use and first northbound migration track of non-breeding steppe whimbrel *Numenius phaeopus alboaxillaris* (Lowe 1921). *Wader Study* 125: 219–227.
- Alves, J.A., Dias, M.P., Méndez, V., Katrínardóttir, B. & Gunnarsson, T.G. 2016. Very rapid long-distance sea crossing by a migratory bird. *Sci. Rep.* 6: 38154.
- An, S., Kuang, F., Wu, W., Hassell, C.J., Coleman, J.T., Gao, Z., Sun, X., Yuan, Y., Maglio, G., Leung, K.-S.K., Feng, X. & Ma, Z. 2024. Individual consistency in spatiotemporal characteristics of migratory whimbrels in the east Asian–Australasian flyway. *Avian Res.* 15: 100191.
- Ausems, A.N.M.A., MacKellar, H., Brown, G.S. & Nol, E. 2025. Sex-specific variation in breeding-ground departure decisions and detection rates during southbound migration in West Atlantic flyway whimbrels (*Numenius phaeopus*). *Sci. Rep.* 15: 6735.
- Ausems, A.N.M.A., Skeel, M. & Nol, E. 2023. Sex differentiation in whimbrels from Churchill, Manitoba, Canada. *Wader Study* 130: 161–167.
- AviList Core Team. 2025. AviList: The Global Avian Checklist, v2025. <https://doi.org/10.2173/avilist.v2025>
- Ballantyne, K. & Nol, E. 2015. Localized habitat change near Churchill, Manitoba and the decline of nesting whimbrels (*Numenius phaeopus*). *Polar Biol.* 38: 529–537.
- Beal, M., Nightingale, J., Belo, J.R., Batey, C., Belting, H., Bocher, P., Burgess, M., Craft, T.B., Crockford, N., Delaporte, P., Donaldson, L., Gélinaud, G., Gill, J.A., Gunnarsson, T.G., Pórisson, B., Gutiérrez, J.S., Hooijmeijer, J.C.E.W., Howison, R.A., Hunke, P., Jomat, L., Lemke, H., Ludwig, J., Majoor, F.A., Marlow, C., Masero, J.A., Melter, J., Nicholson, I., Parejo, M., O'Mahony, B., Pasanen, E., Pessa, J., Piersma, T., Rocha, A.D., Robin, F., Roodbergen, M., Rousseau, P., Salewski, V., Schmidt, L., Smart, J., Staneva, A., Tibbitts, T.L., Timonen, S., Alves, J.A. & Dias, M.P. 2025. Site-level connectivity identified from multiple sources of movement

- data to inform conservation of a migratory bird. *J. Appl. Ecol.* **62**: 303–316.
- BirdLife International.** 2024. Whimbrel *Numenius phaeopus* Species Factsheet.
- BirdLife International.** 2026. IUCN Red List for birds.
- BirdLife International & Handbook of the Birds of the World.** 2023. Bird species distribution maps of the world. Version 2023.1. <http://datazone.birdlife.org/species/requestdis>
- Bracis, C., Bildstein, K.L. & Mueller, T.** 2018. Revisitation analysis uncovers spatio-temporal patterns in animal movement data. *Ecography* **41**: 1801–1811.
- Brown, D., Crockford, N. & Sheldon, R.** 2014. Drivers of population change and conservation priorities for the Numeniini populations of the world. Conservation statements for the 13 species and 38 biogeographic populations of curlews, godwits and the upland sandpiper. UNEP/CMS/COP11/Inf.33.
- Buchanan, G.M., Chapple, B., Berryman, A.J., Crockford, N., Jansen, J.J.F.J. & Bond, A.L.** 2025. Global extinction of slender-billed curlew (*Numenius tenuirostris*). *Ibis* **167**: 357–370.
- Carneiro, C., Gunnarsson, T.G. & Alves, J.A.** 2019a. Why are whimbrels not advancing their arrival dates into Iceland? Exploring seasonal and sex-specific variation in consistency of individual timing during the annual cycle. *Front. Ecol. Evol.* **7**: 1–8.
- Carneiro, C., Gunnarsson, T.G. & Alves, J.A.** 2019b. Faster migration in autumn than in spring: Seasonal migration patterns and non-breeding distribution of Icelandic whimbrels *Numenius phaeopus islandicus*. *J. Avian Biol.* **50**: 1–8.
- Carneiro, C., Gunnarsson, T.G. & Alves, J.A.** 2020. Linking weather and phenology to stopover dynamics of a long-distance migrant. *Front. Ecol. Evol.* **8**: 1–10.
- Carneiro, C., Gunnarsson, T.G. & Alves, J.A.** 2023. Annual schedule adjustment by a long-distance migratory bird. *Am. Nat.* **201**: 353–362.
- Carneiro, C., Gunnarsson, T.G., Kaasiku, T., Piersma, T. & Alves, J.A.** 2024. Icelandic whimbrel first migration: Non-stop until West Africa, yet later departure and slower travel than adults. *Ibis* **166**: 715–722.
- Carneiro, C., Gunnarsson, T.G., Méndez, V., Soares, A.M.V.M. & Alves, J.A.** 2021. Linking range wide energetic tradeoffs to breeding performance in a long-distance migrant. *Ecography* **44**: 512–524.
- Ceballos, G., Ehrlich, P.R. & Dirzo, R.** 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl. Acad. Sci. U. S. A.* **114**: E6089–E6096.
- Cerezo-Araujo, M., Augusto Alves, J., Thor Hallgrímsson, G., Thórisson, B., Gunnarsson, T.G. & Méndez, V.** 2025. Serenade of a whimbrel: Understanding the function of display behaviour in a sub-Arctic territorial wader. *J. Avian Biol.* 2025: e03324.
- Chagnon-Lafortune, A., Duchesne, É., Legagneux, P., McKinnon, L., Reneerkens, J., Casajus, N., Abraham, K.F., Bolduc, É., Brown, G.S., Brown, S.C., Gates, H.R., Gilg, O., Giroux, M.-A., Gurney, K., Kendall, S., Kwon, E., Lanctot, R.B., Lank, D.B., Lecomte, N., Leung, M., Liebezeit, J.R., Morrison, R.I.G., Nol, E., Payer, D.C., Reid, D., Ruthrauff, D., Saalfeld, S.T., Sandercock, B.K., Smith, P.A., Schmidt, N.M., Tulp, I., Ward, D.H., Høye, T.T., Berteaux, D. & Bêty, J.** 2024. A circumpolar study unveils a positive non-linear effect of temperature on arctic arthropod availability that may reduce the risk of warming-induced trophic mismatch for breeding shorebirds. *Glob. Chang. Biol.* **30**: e17356.
- Chan, Y.-C., Tibbitts, T.L., Dorofeev, D., Hassell, C.J. & Piersma, T.** 2022. Hidden in plain sight: Migration routes of the elusive Anadyr bar-tailed godwit revealed by satellite tracking. *J. Avian Biol.* 2022: e02988.
- Chan, Y.-C., Tibbitts, T.L., Lok, T., Hassell, C.J., Peng, H.-B., Ma, Z., Zhang, Z. & Piersma, T.** 2019. Filling knowledge gaps in a threatened shorebird flyway through satellite tracking. *J. Appl. Ecol.* **56**: 2305–2315.
- Conklin, J.R., Battley, P.F. & Potter, M.A.** 2013. Absolute consistency: Individual versus population variation in annual-cycle schedules of a long-distance migrant bird. *PLoS One* **8**: e54535.
- Conklin, J.R., Bom, R.A., Lindström, Å., Bocher, P. & Piersma, T.** 2026. Challenges in population monitoring: Bar-tailed godwits (*Limosa lapponica*) on the East Atlantic flyway defy assumed population structure. *Ibis* **168**: 824–832.
- Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., Yates, O., Lascelles, B., Borboroglu, P.G. & Croxall, J.P.** 2019. Threats to seabirds: A global assessment. *Biol. Conserv.* **237**: 525–537.
- Drent, R., Both, C., Green, M., Madsen, J. & Piersma, T.** 2003. Pay-offs and penalties of competing migratory schedules. *Oikos* **103**: 274–292.
- Drent, R.H., Fox, A.D. & Stahl, J.** 2006. Travelling to breed. *J. Ornithol.* **147**: 122–134.
- Elphick, C.S., Roberts, D.L. & Michael Reed, J.** 2010. Estimated dates of recent extinctions for north American and Hawaiian birds. *Biol. Conserv.* **143**: 617–624.
- Fayet, A.L., Freeman, R., Anker-Nilssen, T., Diamond, A., Erikstad, K.E., Fifield, D., Fitzsimmons, M.G., Hansen, E.S., Harris, M.P., Jessopp, M., Kouwenberg, A.-L., Kress, S., Mowat, S., Perrins, C.M., Petersen, A., Petersen, I.K., Reiertsen, T.K., Robertson, G.J., Shannon, P., Sigurðsson, I.A., Shoji, A., Wanless, S. & Guilford, T.** 2017. Ocean-wide drivers of migration strategies and their influence on population breeding performance in a declining seabird. *Curr. Biol.* **27**: 3871–3878.e3.
- Fink, D., Auer, T., Johnston, A., Strimas-Mackey, M., Ligocki, S., Robinson, O., Hochachka, W., Jaromczyk, L., Crowley, C., Dunham, K., Stillman, A., Davies, I., Rodewald, A., Ruiz-Gutierrez, V. & Wood, C.** 2023. *eBird Status and Trends*. Data Version: 2022; Released: 2023. Ithaca, NY: Cornell Lab of Ornithology. <https://doi.org/10.2173/ebirdst.2022>
- Garnett, S.T., Butchart, S.H.M., Baker, G.B., Bayraktarov, E., Buchanan, K.L., Burbidge, A.A., Chauvenet, A.L.M., Christidis, L., Ehmk, G., Grace, M., Hocom, D.G., Legge, S.M., Leiper, I., Lindenmayer, D.B., Loyn, R.H., Maron, M., McDonald, P., Menkhorst, P., Possingham, H.P., Radford, J., Reside, A.E., Watson, D.M., Watson, J.E.M., Wintle, B., Woinarski, J.C.Z. & Geyle, H.M.** 2019. Metrics of progress in the understanding and management of threats to Australian birds. *Conserv. Biol.* **33**: 456–468.

- Grist, H., Daunt, F., Wanless, S., Burthe, S.J., Newell, M.A., Harris, M.P. & Reid, J.M. 2017. Reproductive performance of resident and migrant males, females and pairs in a partially migratory bird. *J. Anim. Ecol.* **86**: 1010–1021.
- Gunnarsson, T.G., Gill, J.A., Sigurbjörnsson, T. & Sutherland, W.J. 2004. Arrival synchrony in migratory birds. *Nature* **431**: 646.
- Hahsler, M., Piekenbrock, M. & Doran, D. 2019. Dbscan: Fast density-based clustering with R. *J. Stat. Softw.* **91**: 1–30.
- Handmaker, M.C., Sanders, F.J., Smith, A.D., Shealy, E.P., Fontaine, N., Kaplin, M.B., Thibault, J.M., Martin, M.C., Duquet, C., Sterling, A.V. & Senner, N.R. 2024. Individual foraging site fidelity persists within and across stopover seasons in a migratory shorebird, *Numenius phaeopus* (whimbrel). *Ornithology* **141**: ukae021.
- Hedenström, A. & Alerstam, T. 1997. Optimum fuel loads in migratory birds: Distinguishing between time and energy minimization. *J. Theor. Biol.* **189**: 227–234.
- Hines, C., Duval, L., Watts, B.D., Van Horn, G. & Miller, E. 2023. Citizen science photographs indicate different timing and location use of migrating adult and juvenile whimbrels. *Ornithol. Appl.* **125**: duad011.
- Hooijmeijer, J.C.E.W., Gill, R.E., Mulcahy, D.M., Tibbitts, T.L., Kentie, R., Gerritsen, G.J., Bruinzeel, L.W., Tijssen, D.C., Harwood, C.M. & Piersma, T. 2014. Abdominally implanted satellite transmitters affect reproduction and survival rather than migration of large shorebirds. *J. Ornithol.* **155**: 447–457.
- Jackson, M.V., Fuller, R.A., Gan, X., Li, J., Mao, D., Melville, D.S., Murray, N.J., Wang, Z. & Choi, C.-Y. 2021. Dual threat of tidal flat loss and invasive *Spartina alterniflora* endanger important shorebird habitat in coastal mainland China. *J. Environ. Manage.* **278**: 111549.
- Johnston-González, R. & Abril, E. 2019. Predation risk and resource availability explain roost locations of whimbrel *Numenius phaeopus* in a tropical mangrove delta. *Ibis* **161**: 839–853.
- Katrínardóttir, B., Alves, J.A., Sigurjónsdóttir, H., Hersteinsson, P. & Gunnarsson, T.G. 2015. The effects of habitat type and volcanic eruptions on the breeding demography of Icelandic whimbrels *Numenius phaeopus*. *PLoS One* **10**: e0131395.
- Katrínardóttir, B., Pálsson, S., Gunnarsson, T.G. & Sigurjónsdóttir, H. 2013. Sexing Icelandic whimbrels *Numenius phaeopus islandicus* with DNA and biometrics. *Ring. Migr.* **28**: 43–46.
- Knight, E.C., Carlisle, J., Boyce, A.J., Bradley, D., Cimprich, P., Coates, S., Dinsmore, S.J., Gregory, C.J., Jorgensen, J.G., Kelly, J.F., Newstead, D., Olalla, A., Powell, L.A., Scarpignato, A.L., Tibbitts, T.L., Warnock, N., Wehtje, W., Marra, P.P. & Harrison, A.-L. 2025. Delineating ecologically distinct groups for annual cycle management of a declining shorebird. *J. Appl. Ecol.* **62**: 1152–1165.
- Kuang, F., Coleman, J.T., Hassell, C.J., Leung, K.S.K., Maglio, G., Ke, W., Cheng, C., Zhao, J., Zhang, Z. & Ma, Z. 2020. Seasonal and population differences in migration of whimbrels in the east Asian-Australasian flyway. *Avian Res.* **11**: 1–12.
- Kuang, F., Wu, W., Li, D., Hassell, C.J., Maglio, G., Leung, K.-S.K., Coleman, J.T., Cheng, C., Tomkovich, P.S. & Ma, Z. 2022. Detecting the non-breeding region and migration route of whimbrels (*Numenius phaeopus rogatevayae*) in the east Asian-Australasian flyway. *Avian Res.* **13**: 100011.
- Kwon, E., Robinson, S., Weithman, C.E., Catlin, D.H., Karpanty, S.M., Altman, J., Simons, T.R. & Fraser, J.D. 2021. Contrasting long-term population trends of beach-nesting shorebirds under shared environmental pressures. *Biol. Conserv.* **260**: 109178.
- Kwon, E., Weiser, E.L., Lancot, R.B., Brown, S.C., Gates, H.R., Gilchrist, G., Kendall, S.J., Lank, D.B., Liebezeit, J.R., McKinnon, L., Nol, E., Payer, D.C., Rausch, J., Rinella, D.J., Saalfeld, S.T., Senner, N.R., Smith, P.A., Ward, D., Wisseman, R.W. & Sandercock, B.K. 2019. Geographic variation in the intensity of warming and phenological mismatch between Arctic shorebirds and invertebrates. *Ecol. Monogr.* **89**: e01383.
- Lamb, J.S., Paton, P.W.C., Osenkowski, J.E., Badzinski, S.S., Berlin, A.M., Bowman, T., Dwyer, C., Fara, L.J., Gilliland, S.G., Kenow, K., Lepage, C., Mallory, M.L., Olsen, G.H., Perry, M.C., Petrie, S.A., Savard, J.-P.L., Savoy, L., Schummer, M., Spiegel, C.S. & McWilliams, S.R. 2019. Spatially explicit network analysis reveals multi-species annual cycle movement patterns of sea ducks. *Ecol. Appl.* **29**: e01919.
- Lenth, R.V. & Piaskowski, J. 2024. emmeans: Estimated Marginal Means, aka Least-Squares Means.
- Lindström, Å. 2003. Fuel deposition rates in migrating birds: Causes, constraints and consequences. In Berthold, P., Gwinner, E. & Sonnenschein, E. (eds) *Avian Migration*: 307–320. Berlin: Springer-Verlag.
- Lindström, Å. 2020. Migration tracks of waders: Avoiding the pitfalls of speed estimates and inferred strategies. *Wader Study* **127**: 2–3.
- Lindström, Å., Alerstam, T. & Hedenström, A. 2019a. Faster fuelling is the key to faster migration. *Nat. Clim. Change* **9**: 288–289.
- Lindström, Å., Green, M., Husby, M., Kålås, J.A., Lehtikainen, A. & Stjernman, M. 2019b. Population trends of waders on their boreal and arctic breeding grounds in northern Europe. *Wader Study* **126**: 200–216.
- Linscott, J.A. & Senner, N.R. 2021. Beyond refueling: Investigating the diversity of functions of migratory stopover events. *Ornithol. Appl.* **123**: 1–14.
- Lisovski, S., Gosbell, K., Minton, C. & Klaassen, M. 2021. Migration strategy as an indicator of resilience to change in two shorebird species with contrasting population trajectories. *J. Anim. Ecol.* **90**: 2005–2014.
- Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P. & Makowski, D. 2021. Performance: An R package for assessment, comparison and testing of statistical models. *J. Open Source Softw.* **6**: 3139.
- Mallory, E.P. 1982. Territoriality of whimbrels *Numenius phaeopus hudsonicus* wintering in Panama. *Wader Study Group Bull.* **34**: 37–39.
- McLaughlin, J.F., Faircloth, B.C., Glenn, T.C. & Winker, K. 2020. Divergence, gene flow, and speciation in eight lineages of trans-Beringian birds. *Mol. Ecol.* **29**: 3526–3542.
- Michel, G., Nightingale, J., Beal, M., Bernard, A., Dias, M.P. & Alves, J.A. 2026. Global review of shorebird tracking data to identify research gaps and conservation priorities. *Conserv. Biol.* **40**: e70211.

- Morrison, C.A., Alves, J.A., Gunnarsson, T.G., Þórisson, B. & Gill, J.A. 2019. Why do earlier-arriving migratory birds have better breeding success? *Ecol. Evol.* **9**: 8856–8864.
- Nathan, R., Monk, C.T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., Baktoft, H., Beardsworth, C.E., Bertram, M.G., Bijleveld, A.I., Brodin, T., Brooks, J.L., Campos-Candela, A., Cooke, S.J., Gjelland, K.O., Gupte, P.R., Harel, R., Hellström, G., Jeltsch, F., Killen, S.S., Klefoth, T., Langrock, R., Lennox, R.J., Lourie, E., Madden, J.R., Orchan, Y., Pauwels, I.S., Riha, M., Roeleke, M., Schlägel, U.E., Shohami, D., Signer, J., Toledo, S., Vilck, O., Westrelin, S., Whiteside, M.A. & Jarić, I. 2022. Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science* **375**: eabg1780.
- Nightingale, J. 2023. Conserving wader tracking data for the future: Introducing the global wader project. *Wader Study* **130**: 183–185.
- Pálsdóttir, A.E., Alves, J.A., Gill, J.A., Pálsson, S., Méndez, V. & Gunnarsson, T.G. 2024. Introduction of summer houses into semi-natural habitats: Impacts on ground-nesting birds. *Anim. Conserv.* **27**: 648–658.
- Pálsdóttir, A.E., Gill, J.A., Alves, J.A., Pálsson, S., Méndez, V., Ewing, H. & Gunnarsson, T.G. 2022. Subarctic afforestation: Effects of forest plantations on ground-nesting birds in lowland Iceland. *J. Appl. Ecol.* **59**: 2456–2467.
- Pálsdóttir, A.E., Gill, J.A., Alves, J.A., Pálsson, S., Méndez, V., Þórisson, B. & Gunnarsson, T.G. 2025a. Effect of low-traffic roads on abundance of ground-nesting birds in sub-Arctic habitats. *J. Avian Biol.* 2025: e03572.
- Pálsdóttir, A.E., Þórisson, B. & Gunnarsson, T.G. 2025b. Recent population changes of common waders and passerines in Iceland's largest lowland region. *Bird Study* **72**: 204–216.
- Patil, I. 2021. statsExpressions: R package for tidy Dataframes and expressions with statistical details. *J. Open Source Softw.* **6**: 3236.
- Pearce-Higgins, J.W., Brown, D.J., Douglas, D.J.T., Alves, J.A., Bellio, M., Bocher, P., Buchanan, G.M., Clay, R.P., Conklin, J.R., Crockford, N., Dann, P., Elts, J., Friis, C., Fuller, R.A., Gill, J.A., Gosbell, K., Johnson, J.A., Marquez-Ferrando, R., Masero, J.A., Melville, D.S., Millington, S., Minton, C., Mundkur, T., Nol, E., Pehlak, H., Piersma, T., Robin, F., Rogers, D.I., Ruthrauff, D.R., Senner, N.R., Shah, J.N., Sheldon, R.D., Soloviev, S.A., Tomkovich, P.S. & Verkuil, Y.I. 2017. A global threats overview for Numeniini populations: Synthesising expert knowledge for a group of declining migratory birds. *Bird Conserv. Int.* **27**: 6–34.
- Picardi, S., Smith, B., Boone, M. & Basille, M. 2024. nestR: Estimation of Bird Nesting from Tracking Data. <https://github.com/picardis/nestR>
- Piersma, T. 2003. 'Coastal' versus 'inland' shorebird species: Interlinked fundamental dichotomies between their life- and demographic histories? *Wader Study Group Bull.* **100**: 5–9.
- Piersma, T. 2007. Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *J. Ornithol.* **148**: 45–59.
- Rakhimberdiev, E., Duijns, S., Karagicheva, J., Camphuysen, C.J., Dekinga, A., Dekker, R., Gavrilov, A., ten Horn, J., Jukema, J., Saveliev, A., Soloviev, M., Tibbitts, T.L., van Gils, J.A. & Piersma, T. 2018. Fuelling conditions at staging sites can mitigate Arctic warming effects in a migratory bird. *Nat. Commun.* **9**: 4263.
- Reiter, M.E., Hickey, C.M., Eusse-González, D., Palacios, E., Barbaree, B.A., Bradley, D.W., Angulo, F., Van Dort, J., Fernández, G., Clay, R., Agreda, A., Morales, S., Reyes, E., Miró, R., Díaz, Y., Kaufman, K., Galán, V., Johnston González, R. & Chu, J. 2026. Trends in nonbreeding shorebirds along the Pacific Americas flyway. *Ornithol. Appl.* **128**: 1–13.
- Reneerkens, J., Versluijs, T.S.L., Piersma, T., Alves, J.A., Boorman, M., Corse, C., Gilg, O., Hallgrimsson, G.T., Lang, J., Loos, B., Ntiamoa-Baidu, Y., Nuoh, A.A., Potts, P.M., Horn, J. & Lok, T. 2020. Low fitness at low latitudes: Wintering in the tropics increases migratory delays and mortality rates in an Arctic breeding shorebird. *J. Anim. Ecol.* **89**: 691–703.
- Ribeiro, P.D., Iribarne, O.O., Navarro, D. & Jaureguy, L. 2004. Environmental heterogeneity, spatial segregation of prey, and the utilization of southwest Atlantic mudflats by migratory shorebirds. *Ibis* **146**: 672–682.
- Rosenberg, K.V., Dokter, A.M., Blancher, P.J., Sauer, J.R., Smith, A.C., Smith, P.A., Stanton, J.C., Panjabi, A., Helft, L., Parr, M. & Marra, P.P. 2019. Decline of the north American avifauna. *Science* **366**: 120–124.
- Ruthrauff, D.R., Harwood, C.M., Tibbitts, T.L., Warnock, N. & Gill, R.E. 2021. Diverse patterns of migratory timing, site use, and site fidelity by Alaska-breeding whimbrels. *J. Field Ornithol.* **92**: 156–172.
- Salgado-Ortiz, J., Marra, P.P., Sillett, T.S. & Robertson, R.J. 2008. Breeding ecology of the mangrove warbler (*Dendroica petechia bryanti*) and comparative life history of the yellow warbler subspecies complex. *The Auk* **125**: 402–410.
- Sanders, F.J., Handmaker, M.C., Johnson, A.S. & Senner, N.R. 2021. Nocturnal roost on South Carolina coast supports nearly half of Atlantic coast population of Hudsonian whimbrel *Numenius hudsonicus* during northward migration. *Wader Study* **128**: 117–124.
- Scarpignato, A.L., Huysman, A.E., Jimenez, M.F., Witko, C.J., Harrison, A.-L., Seavy, N.E., Smith, M.A., Deppe, J.L., Wilsey, C.B. & Marra, P.P. 2023. Shortfalls in tracking data available to inform north American migratory bird conservation. *Biol. Conserv.* **286**: 110224.
- Senner, N.R., Stager, M. & Sandercock, B.K. 2017. Ecological mismatches are moderated by local conditions for two populations of a long-distance migratory bird. *Oikos* **126**: 61–72.
- Skeel, M.A. 1982. Sex determination of adult whimbrels. *J. Field Ornithol.* **53**: 414–416.
- Skeel, M.A., Mallory, E.P. & Pyle, P. 2025. Hudsonian Whimbrel (*Numenius hudsonicus*), Version 1.0. In Billerman, S.M. & Smith, M.G. (eds) *Birds of the World*. Ithaca, NY: Cornell Lab of Ornithology. <https://doi.org/10.2173/bow.whimbr3.01>
- Smith, M.G., Skeel, M.A., Mallory, E.P. & Pyle, P. 2025. Eurasian Whimbrel (*Numenius phaeopus*), Version 1.0. In Billerman, S.M. (ed) *Birds of the World*. Ithaca, NY: Cornell Lab of Ornithology. <https://doi.org/10.2173/bow.whimbr5.01>
- Smith, P.A., Smith, A.C., Andres, B., Francis, C.M., Harrington, B., Friis, C., Morrison, R.I.G., Paquet, J., Winn, B. & Brown, S. 2023. Accelerating declines of North

- America's shorebirds signal the need for urgent conservation action. *Ornithol. Appl.* **125**: duad003.
- Smith, R.J. & Moore, F.R. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. *Behav. Ecol. Sociobiol.* **57**: 231–239.
- Soriano-Redondo, A., Franco, A.M.A., Acácio, M., Payo-Payo, A., Martins, B.H., Moreira, F. & Catry, I. 2023. Fitness, behavioral, and energetic trade-offs of different migratory strategies in a partially migratory species. *Ecology* **104**: e4151.
- Studds, C.E., Kendall, B.E., Murray, N.J., Wilson, H.B., Rogers, D.I., Clemens, R.S., Gosbell, K., Hassell, C.J., Jessop, R., Melville, D.S., Milton, D.A., Minton, C.D.T., Possingham, H.P., Riegen, A.C., Straw, P., Woehler, E.J. & Fuller, R.A. 2017. Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. *Nat. Commun.* **8**: 1–7.
- Takahiro, S. 2018. SDLfilter: filtering and assessing the sample size of tracking data. <https://github.com/TakahiroShimada/SDLfilter>
- Tan, H.Z., Ng, E.Y.X., Tang, Q., Allport, G.A., Jansen, J.J.F.J., Tomkovich, P.S. & Rheindt, F.E. 2019. Population genomics of two congeneric Palaearctic shorebirds reveals differential impacts of quaternary climate oscillations across habitats types. *Sci. Rep.* **9**: 18172.
- Thompson, S.J., Handel, C.M., Richardson, R.M. & McNew, L.B. 2016. When winners become losers: Predicted nonlinear responses of Arctic birds to increasing Woody vegetation. *PLoS One* **11**: e0164755.
- van Bemmelen, R.S.A., Kolbeinsson, Y., Ramos, R., Gilg, O., Alves, J.A., Smith, M., Schekkerman, H., Lehtikainen, A., Petersen, I.K., Pörsson, B., Sokolov, A.A., Välimäki, K., van der Meer, T., Okill, J.D., Bolton, M., Moe, B., Hanssen, S.A., Bollache, L., Petersen, A., Thorstensen, S., González-Solís, J., Klaassen, R.H.G. & Tulp, I. 2019. A migratory divide among red-necked phalaropes in the Western Palearctic reveals contrasting migration and wintering movement strategies. *Front. Ecol. Evol.* **7**: 86.
- van Roomen, M., Reneerkens, J., Citegetse, G., Crowe, O., Gueye, K., Langendoen, T., Dodman, T., Meise, K. & Schekkerman, H. 2025. *East Atlantic flyway assessment 2023. The status of coastal waterbird populations and their sites*. Wilhelmshaven, Germany; Wageningen, The Netherlands; Cambridge, UK: Wadden Sea Flyway Initiative p/a CWSS; Wetlands International; BirdLife International.
- Warnock, N. 2010. Stopping vs. staging: The difference between a hop and a jump. *J. Avian Biol.* **41**: 621–626.
- Watts, B., Reed, E. & Turrin, C. 2015. Estimating sustainable mortality limits for shorebirds using the Western Atlantic flyway. *Wader Study* **122**: 37–53.
- Watts, B.D., Smith, F.M., Hamilton, D.J., Keyes, T., Paquet, J., Pirie-Dominix, L., Rausch, J., Truitt, B., Winn, B. & Woodard, P. 2019. Seasonal variation in mortality rates for whimbrels (*Numenius phaeopus*) using the Western Atlantic flyway. *Condor* **121**: 1–13.
- Watts, B.D., Smith, F.M., Hines, C., Duval, L., Hamilton, D.J., Keyes, T., Paquet, J., Pirie-Dominix, L., Rausch, J., Truitt, B., Winn, B. & Woodard, P. 2021. Whimbrel populations differ in trans-atlantic pathways and cyclone encounters. *Sci. Rep.* **11**: 12919.
- Zwarts, L. 1990. Increased prey availability drives pre-migration hyperphagia in whimbrels and allows them to leave the banc d'Arguin, Mauritania, in time. *Ardea* **78**: 279–300.

Received 2 March 2026;

Revision 5 August 2026;

revision accepted 7 August 2026.

Associate Editor: Philip Battley.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Complementary threat assessment information to Figure 4 in the main text, showing the combinations of scope and severity.

Table S1. Compilation of recent population trends across subspecies, with indication of the period of the annual cycle when data were collected. Given the geographical overlap between some subspecies, trends are shown for both involved.

Table S2. Mounting method, tag brand and model and their mean masses ($\pm$ se) used across subspecies.

Table S3. Parameters used in the 'find_nests()' function of the *nestR* R package. Parameters that were modified between runs are highlighted in bold.

Table S4. Scores considered for Timing, Scope and Severity. Whimbrel generation was considered as 7.23 years, according to Birdlife International (2024).

Table S5. Post-hoc pairwise comparisons of migration timings between subspecies. Statistically significant differences are highlighted in bold.

Table S6. Post-hoc pairwise comparisons of durations of annual-cycle periods between subspecies. Comparisons were made between groups with at least five data points. Statistically significant differences are highlighted in bold.

Table S7. List of references supporting the assessment of existing threats.