Ocean-scale variation in migration schedules of a long-distance migratory seabird is fully compensated upon return to the breeding site

Rob SA van Bemmelen, Wageningen Marine Research, Haringkade 1, 1976 CP IJmuiden, the Netherlands. Current address: Waardenburg Ecology, Culemborg, the Netherlands and Wageningen Marine Research, IJmuiden, the Netherlands, rvanbemmelen@gmail.com, ORCID 0000-0002-0688-7058

Børge Moe, Norwegian Institute for Nature Research (NINA), Trondheim, Norway, ORCID 0000-0002-2306-1899

Hans Schekkerman, SOVON Vogelonderzoek Nederland, Nijmegen, the Netherlands, ORCID 0000-0003-3127-4832

Sveinn Are Hansen, Norwegian Institute for Nature Research (NINA), Tromsø, Norway, ORCID 0000-0003-1792-435X

Katherine RS Snell, University of Copenhagen, Copenhagen, Denmark & Max Planck Institute of Animal Behavior, Radolfzell, Germany, ORCID 0000-0003-3720-4579

Elizabeth M Humphreys, British Trust for Ornithology (BTO), Scotland, Stirling University Innovation Park, Stirling, FK9 4NF, United Kingdom, ORCID 0000-0002-2570-400X

Elina Mäntylä, Applied Zoology/Animal Ecology, Institute of Biology, Freie Universität Berlin, Berlin Germany; Institute of Entomology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic; Faculty of Sciences, University of South Bohemia, České Budějovice, Czech Republic & Section of Ecology, Department of Biology, University of Turku, Turku, Finland, ORCID 0000-0002-2267-7114

Gunnar Thor Hallgrimsson, Department of Life and Environmental Sciences, University of Iceland, Reykjavik, Iceland, ORCID 0000-0002-3697-9148

Olivier Gilg, [1] UMR 6249 Chrono□Environnement, CNRS, Université de Bourgogne Franche Comté, 25000

Besançon, France, [2] Groupe de Recherche en Ecologie Arctique, 16 rue de Vernot, 21440 Francheville, France, ORCID 0000-0002-9083-4492

Dorothée Ehrich, UiT The Arctic University of Norway, Tromsø, Norway, ORCID 0000-0002-3028-9488

John Calladine, British Trust for Ornithology (BTO), Scotland, Stirling University Innovation Park. Stirling, FK9 4NF, United Kingdom ORCID 0000-0002-0494-1540

Sjúrður Hammer, [1] Faroese Environment Agency, Traðagøta 38, Argir, FO-165, Faroe Islands, Faroe Islands; [2] Faculty of Science and Technology, University of the Faroe Islands, Vestarabryggja 15, FO-100 Tórshavn, Faroe Islands, ORCID 0000-0002-3986-5074

Sarah Harris, British Trust for Ornithology (BTO), The Nunnery, Thetford, Norfolk IP24 2PU, United Kingdom, ORCID 0000-0002-7732-9758

Johannes Lang, [1] University of Giessen, Giessen, Germany; [2] Groupe de Recherche en Ecologie Arctique, 16 rue de Vernot, 21440 Francheville, France, ORCID 0000-0002-7387-795X

Sölvi Rúnar Vignisson, Sudurnes Science and Learning Center, Suðurnesjabær, Iceland, ORCID 0000-0003-1026-5267

Yann Kolbeinsson, Northeast Iceland Nature Research Centre, Husavik, Iceland, ORCID 0000-0001-6216-1940

Kimmo Nuotio, Pori Ornithological Society, Pori, Finland; Environmental Agency, Pori, Finland

Matti Sillanpää, Pori Ornithological Society, Pori, Finland

Benoît Sittler, [1] University of Freiburg, Freiburg, Germany; [2] Groupe de Recherche en Ecologie Arctique, 16 rue de Vernot, 21440 Francheville, France

Aleksandr Sokolov, Arctic research station of Institute of plant and animal ecology, Ural branch, Russian Academy of Sciences, Labytnangi, Russia, ORCID 0000-0002-1521-3856

Raymond H.G. Klaassen, Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), Groningen University, Groningen, Netherlands, ORCID 0000-0002-9840-506X

Richard A. Phillips, British Antarctic Survey (BAS), Natural Environment Research Council (NERC), Cambridge, United Kingdom, ORCID 0000-0002-0208-1444

Ingrid Tulp, Wageningen Marine Research, IJmuiden, the Netherlands, ORCID 0000-0001-6002-1741

Keywords: Arctic Skua, *Stercorarius parasiticus*, migration, phenology, carry-over effects,

Running title: ocean-scale carry-over effects in timing of migration in a seabird

Abstract

Migratory birds often have tightly scheduled annual cycles, in which a delay in one event can have carry-over effects on the timing of later events, which may ultimately impact reproductive output. We utilize a large-scale study system to investigate carry-over effects in timing: the variation in annual schedules of individual Arctic Skuas *Stercorarius parasiticus* at 12 breeding sites between East Greenland and West Siberia in relation to their use of seven widely divergent wintering areas across the Atlantic Ocean, Mediterranean Sea and Indian Ocean. We studied whether migration schedules differ among breeding populations as a function of their choice of wintering areas, and predicted that migrations over larger distances, with tighter schedules, would provide less room for compensating delays. Breeding at higher latitudes led not only to later timing of reproduction and migration, but also to different allocation of time to different phases, with faster spring migration and shorter time between return to the breeding area and clutch initiation. In contrast, breeding latitude had no effect on the duration of autumn migration and wintering period. Wintering area was consistent within individuals among years and had an additive effect on annual schedules, with more distant areas associated with more time spent on migration and less time spent in the wintering areas. Tracked skuas were able to adjust the period spent in the non-breeding area, regardless of the distance from the colony, which generally buffered the variation in timing of autumn migration. Despite individual variation in migration distances of thousands of km, skuas from the same population arrived largely synchronously at their breeding area. The lack of a consistent effect of migration distance on timing of return to the breeding grounds indicates that individuals synchronize their arrival with others in their population despite extensive individual differences in migration strategies.

Keywords: Parasitic Jaeger, migratory connectivity, phenology, annual cycle, carry-over effects

Introduction

Stages in the annual cycle of animals are intricately linked and the timing of each event can have cascading effects on the timing of subsequent events, usually referred to as carry-over effects [1,2]. Carry-over effects in timing may be particularly pronounced in animals that undertake long and challenging migrations between their breeding and wintering areas, where delays in one phase of the annual cycle can lead to a temporal mismatch with resource availability in subsequent phases, ultimately affecting survival and repro-

ductive success [3,4]. The degree to which delays can be buffered, preventing amplification of carry-over effects across time, may vary as a function of the tightness of scheduling within the annual cycle [5]. Quantifying the geographical variation in timing of annual cycles and carry-over effects is therefore important for our understanding of how phenology drives variation in life-history traits [6]. In addition, considering that daily survival rates may differ between stages of the annual cycle [7–9], variation in annual schedules can drive meta-population dynamics [2,10]. Insight in meta-population dynamics is therefore important to inform location specific conservation efforts.

Population-level differences in the scheduling of the annual cycle may arise as a function of the location of the breeding and wintering areas [11,12] and the conditions experienced there [13]. Annual schedules are generally shifted to later in the season at higher breeding latitudes, where the optimal time for reproduction is associated with a later time of return to the breeding site [18]. In turn, this affects the duration and timing of subsequent phases of the annual cycle, such as migration, given that the degree of seasonality in resources and photoperiod leads to differences in optimal migration speed [19,20]; however, this is little studied. In addition to an effect of the breeding area, the timing of annual cycles may also depend on the choice of wintering area and migration routes, as more distant non-breeding areas require longer travel time. As such, unless departure is earlier or travel speeds higher, arrival will be later [21,22]. In addition, choice of wintering area can lead to delays when fueling conditions in the wintering area itself or along the migration route are sub-optimal. These delays can subsequently carry-over to timing of return to the breeding area and egg laying [13,23–26] and can reduce survival [27]. Thus, carry-over effects in timing are expected to be more pronounced when distances between breeding and non-breeding areas are greater, and there is less leeway in the annual cycle to compensate for delays.

We define the *net* carry-over effect as the timing of an event for an individual or group (for example, with a common migration strategy or non-breeding area) relative to the population mean for a sequence of events (figure 1a). The *strength* of carry-over effects in timing can be conceptualized as the degree to which timing of an event affects the scheduling of a following event (figure 1a-c). If there is full compensation for a delay, each day lost in one phase translates to one less day spent in the next phase, and so the timing of the following event does not change. In the case of complete carry-over of delays, the timing of the next event is delayed by a day, i.e. there is no compensation. Delays may also be amplified at later stages of the annual cycle, i.e. each day of delay translates to more than a day delay in following events.

Geographical variation in the timing of annual cycles and carry-over effects have mainly been studied in single breeding populations [13,26,28], that use a single wintering area or multiple wintering areas at similar latitudes [11,12,15] or in multiple breeding populations that breed at similar latitudes [29]. Ideally however,

quantifying and testing the relative effects of breeding and wintering location on the timing of annual schedules and on carry-over effects requires substantial geographic variation in both breeding and wintering areas and mixing of individuals from different breeding populations within wintering areas and *vice versa* (weak migratory connectivity, [30]). Such studies are rare, because of the challenges of performing large-scale tracking studies and because few species show sufficient variation in both breeding and wintering latitudes. Hence, the extent to which the timing of events and carry-over effects in the annual cycle of migratory birds is driven by both breeding and wintering locations is largely unresolved [31].

We studied carry-over effects on the timing of different phases in the annual cycle of a long-distance migratory seabird, the Arctic Skua *Stercorarius parasiticus*, from multiple breeding populations. Its circumpolar breeding distribution ranges from northern temperate to high arctic zones [[32]; figure 2]. Based on ring recoveries and field sightings, the main wintering areas in the Atlantic are thought to span productive continental shelf and pelagic areas across a large (latitudinal) range, from Iberia to Patagonia and South Africa [32,33]. By tracking the full annual cycle of many individuals over several years from multiple breeding sites ranging from East Greenland to West Siberia (59°N to 79°N in latitude and 24°W to 69°E in longitude), we present for the first time the full extent of the wintering distribution of Arctic Skuas breeding in the Atlantic Ocean, which encompass the Mediterranean Sea and parts of the Indian Ocean. We then explore to what degree different breeding populations mix at wintering areas (migratory connectivity) [30] and whether individuals are consistent from year to year in their migration strategy. We quantify the relative effects of breeding and wintering areas on the timing of key events and duration of intervening periods in the annual cycle. We use the northern hemisphere (breeding area) viewpoint on annual schedules and will refer to non-breeding area as wintering area throughout. Using the variation in annual schedules, we study compensation versus carry-over of variation in timing between subsequent events, and how these depend on breeding and wintering areas. We predict that later timing of events and tighter schedules are associated with more northerly breeding areas [15,16] and that later timing also leads to different allocation of time to phases of the annual cycle. Moreover, we expect less time to be spent in more distant wintering areas due to longer time spent on migration. Among these different annual schedules, we expect carry-over effects to arise particularly among schedules that provide less leeway to compensate for delays and, specifically, that the wintering period generally buffers the variation in timing of autumn migration, but less so when the wintering period is shorter. As such, we predict that migrations to more distant wintering areas are associated with higher risks of delayed spring arrival in the breeding area - a *net* carry-over effect [25,34].

Methods

Device deployments

Adult Arctic Skuas were captured and fitted with geolocators (Global Location Sensor or GLS) loggers at twelve breeding sites in eight countries. Data from sites within countries were combined to avoid very small sample sizes in models and are henceforth referred to as breeding areas, as follows: East Greenland (GRE; Karupelv, 72°30'N 24°00'W, and Hochstetter Forland, 75°09'N, 19°40'W), Iceland (ICE; Hroarstunga, 65°35'N, 14°22'W), Faroe Islands (FAR; Fugloy, 62°20'N, 6°19'W), Scotland (SCO; Fair Isle, 59°54'N, 1°63'W and Rousay, 59°09'N 3°02'W), mainland Norway (NOR; Brensholmen, 69°35'N, 18°01'E and Slettnes, 71°05'N, 28°12'E), Spitsbergen (SVA; Kongsfjorden, Svalbard, 79°57'N, 12°06'E), Finland (FIN; Satakunta, 61°33'N, 21°27'E), and Russia (RUS; Tobseda, 68°36'N, 52°19'E, and Erkuta, 68°14'N, 69°09'E).

Birds were captured either on the nest using bow nets, tent spring traps or walk-in traps, remote release nooses, or away from the nest using net guns. Various models of geolocators were used: C65, C250 (Migrate Technology, Cambridge, UK), Mk9, Mk13, Mk15 and Mk18H (British Antarctic Survey, Cambridge, UK) and Mk3006 (Biotrack, Wareham, UK). Geolocators measured ambient light in lux (Migrate Technology) or arbitrary units (BAS/Biotrack) every 1 minute and saved the maximum value every 5 minutes. Geolocators were attached to a Darvic ring fitted around the bird's tarsus. Upon recapture of the birds in subsequent breeding seasons, geolocators were removed and data downloaded.

Sample size

In total, data for 276 interbreeding periods (i.e. one migration cycle, referred to as a 'track' below) from 155 individuals were obtained in 2009-2021. Sample sizes per breeding area are given in figure 2 and ranged from 103 tracks of 57 individuals in mainland Norway to 8 tracks of 3 individuals in East Greenland. In total, 34, 23 and 12 individuals were tracked for 2, 3 and 4-6 years, respectively. Some of the tracks (n=48) were incomplete due to battery or electronics failure. Of all failures, 46% occurred between 9 November and 30 December.

Geolocator data processing

Sunrises and sunsets were calculated from light measurements using the function `twilightCalc` from the R-package `GeoLight` [35] at a light threshold value of 10 (arbitrary light units, BAS/Biotrack models) and 2 (lux, Migrate Technology models). As Arctic Skuas spend the non-breeding period in open habitat (at

sea), light transitions at twilight were rarely shaded, and so most twilights could be assigned automatically. Remaining outliers (twilights considerably earlier or later than surrounding twilights) were identified visually by plotting date against time of sunset and sunrise and were replaced by interpolated values using a local regression (LOESS) smoother. Locations were calculated for each noon and midnight for a sequence of potential sun angles, in steps of 0.5°. By visual inspection of the resulting tracks, we selected the sun angle resulting in a good fit of locations to the shape of continent land masses and a match in latitude estimates before and after each equinox. On this basis, the most appropriate sun angles for individual tracks were from −1° to −3° for BAS/Biotrack loggers and −4.5° to −6.0° for Migrate Technology loggers. Mean error in position estimates for this method is typically ±185 km for flying seabirds [36], but can be much larger close to the equinoxes, which coincided with autumn and to a lesser extent spring migration in the tracked skuas.

We describe the phenology from the perspective of a breeding bird, i.e. 'autumn migration' is post-breeding, and 'spring migration' is pre-breeding. We define the following key events in the annual cycle: 1) departure from the breeding area; 2) arrival in the wintering area; 3) departure from the wintering area; 4) arrival in the North Atlantic Ocean north of 35°N (mostly around the sub-polar frontal zone where many Arctic Skuas made a stopover before returning to the breeding grounds [37,38]); 5) return to the breeding area; 6) clutch initiation. The duration of the intervening periods (in days) were calculated for the: 1) autumn migration; 2) wintering period; 3) spring migration including the time in the North Atlantic; 4) time in the North Atlantic; 5) pre-laying period; 6) breeding period. As loggers were deployed after birds returned to the colony and retrieved before they departed, a composite index of the length of the breeding period for each bird was calculated as the sum of the periods from 1 July (as all individuals were in the breeding area at this date) to departure from the breeding area in the first year, and from clutch initiation in the second year to 30 June. Timing of movements were identified by inspecting raw position estimates, in particular longitudes, which are more reliable than latitudes estimated close to equinoxes, and clearly signal arrival or departure, especially when the last segment of migration has a strong westerly or easterly component, as was often the case. For birds breeding in areas with continuous daylight (Greenland, Iceland, mainland Norway, Svalbard, Russia), first position estimates (after leaving the zone with continuous daylight) were typically close to the breeding site, but last position estimates in spring (just before entering the zone with continuous daylight) were around 60°N and thus distant from the breeding area. To estimate time of departure from or arrival to the breeding area under continuous daylight, we assumed birds traveled at a speed of ca 850 km d^{-1}, which has been recorded for the closely related Long-tailed Skua *Stercorarius longicaudus* [39], between the breeding site and the first or last position estimate. Rapid movement to or away from the wintering area, roughly entering or leaving the boxes shown in figure 2, was taken as the timing of arrival at and departure

from the wintering area. We recorded the date that birds arrived in the North Atlantic during spring migration as the day birds crossed 40°N, except in birds wintering in the Mediterranean Sea, for which the day after wintering area departure was taken. Clutch initiation dates were inferred from the light data, as incubation stints are apparent as alternating periods of light and darkness each usually lasting more than an hour [40].

Statistical analysis

Wintering centroids were calculated as the geographical mean of position estimates between arrival to and departure from the wintering area. Based on the positions in the wintering areas, tracks were assigned to one of seven discrete wintering areas (abbreviations used in figures and tables between brackets): 1) Caribbean region, Guiyana, Gulf of Mexico and north of Brazil (CAR); 2) Patagonian Shelf (PAT); 3) Benguela region west to Tristan da Cuñha (BEN); 4) Gulf of Guinea and west towards eastern Brazil (GUL); 5) Canary Current and off north-west Africa/Iberia (CAN); 6) Mediterranean Sea (MED); 7) Indian Ocean and adjacent seas (IND) (figure 2). Although skuas moved during the wintering period, sometimes over substantial distances, none had arrival and departure positions in different wintering areas. Tracks from devices that failed but which indicated that the bird was resident beforehand were assigned to the relevant wintering area. Wintering areas assigned from incomplete tracks were always the same as those of the same individual assigned using complete datasets in other years (n=12). Minimum migration distance was calculated as the great-circle distance between the wintering centroid and the breeding site.

As a measure of migratory connectivity, the degree to which individuals from the same breeding site stay together at wintering areas [30], we calculated the Mantel correlation R_{mantel} using the 'MigConnectivity' package in R [41], using the first track of each individual. R_{mantel} gives the correlation between a distance matrix of breeding locations and a distance matrix of mid-winter centroids. Significance of the Mantel correlation coefficient was assessed by 1000 random permutations. R_{mantel} can have negative values but is usually between 0 (no correlation between relative positions of individuals in both seasons) and 1 (same configuration of individuals in both seasons), where higher values thus indicate stronger migratory connectivity.

To quantify individual consistency in choice of wintering area, inter-centroid distances were measured between successive years in a) the same individual and b) different individuals from the same breeding site [42]. To test for greater consistency within than between individuals, a random distribution was generated 10000 times by re-distributing within- and between-individual labels and calculating the within- and between-individual distances between centroids. In addition, we calculated the frequency with which individuals switched between wintering areas.

Relationships between breeding latitude, and timing of key events and periods were assessed by modelling time or duration as a function of breeding latitude, with random intercepts for each combination of breeding and wintering area as well as for individuals, in Bayesian Generalized Linear Mixed-effects Models (GLMMs).

We then assessed whether wintering in certain areas led to earlier or later arrival compared to birds from the same breeding area that wintered elsewhere, by constructing GLMMs with breeding and wintering area as fixed effects and random intercepts for individuals. We selected data with at least three birds for each combination of breeding and wintering areas and so the few migrations to the Mediterranean Sea, Greenland, Iceland and Finland were not included. Similarly, as all birds from the Russian breeding sites wintered in the Indian Ocean, the relative effects of wintering and breeding areas could not be disentangled and so they were also removed from analyses (along with a single bird from Slettnes that also wintered in the Indian Ocean). We performed two analyses to show the effect of wintering area. First, all pairwise comparisons of wintering area effects within breeding areas were made based on the posterior distributions of the contrast between each set of two wintering areas. For visualization, posterior contrast probabilities where 0 was outside the 95% high density interval (HDI) were considered *important*; posterior probabilities can be found in the supplementary material, table S1. Second, to test whether wintering areas led to advances or delays relative to birds from the same breeding area but wintering elsewhere, the 95% HDI of the posterior distributions of each breeding-wintering area combination were compared to the region of practical equivalence (ROPE), defined as the mean timing of birds from the same breeding area but wintering elsewhere, ± 0.1 * sd [43,44]. If the 95% HDI of the posterior distribution fell completely outside the ROPE, the wintering area was taken to have an *important* effect. To show partitioning of variation among breeding and wintering area as well as between and within individuals, variance components were extracted for the fixed effects σ^2_β as well as between σ^2_α and within individuals σ^2_ϵ, and were also used to calculate the marginal repeatability as $R_m = \sigma^2_\alpha/(\sigma^2_\alpha + \sigma^2_\epsilon)$ [45].

Using only data from breeding areas with the largest data sets (FAR, NOR and SVA - see Sample size), we tested whether the duration of periods between events changed according to timing of the onset of each period, by fitting GLMMs with duration as the response variable, the onset of each period as a fixed effect, random intercepts and slopes for breeding-wintering area combinations and random intercepts for individuals. To test whether the duration of periods also changed as a function of timing for each breeding-wintering area combination, GLMMs were constructed with duration as the response variable, slopes with timing per breeding-wintering area as fixed effects and random intercepts for individuals.

GLMMs were fitted using the `brms` package in `R` [46], which provides an interface to `stan` [47], with 6000 iterations, a burn-in of 2000 and a thinning interval of five. We used default uninformative priors. After

running, model results were checked for mixing of and autocorrelation within the chains, and for convergence ($\hat{R}$ ~ 1).

Results

Migratory connectivity and spatial consistency of individuals

For any given colony, there was a range of wintering areas used by individual Arctic Skuas (figure 2). The largest variation was among individuals from Slettnes, mainland Norway (which had the largest sample size, n=46 individuals), which wintered in all seven areas identified in this study. Variation among individuals was smallest in the small samples from Russian sites that all wintered in the Indian Ocean (n=6), and from Greenland, that all wintered in the Caribbean region (n=3). Arctic Skuas breeding in Svalbard (n=42) wintered primarily in the Caribbean region (49%), and none migrated to the southern wintering areas, the Patagonian Shelf and Benguela region. In contrast to the Svalbard population, few individuals from mainland Norway wintered in the Caribbean region (9%, n=57). A considerable proportion of individuals breeding in mainland Norway and Finland wintered on the Patagonian Shelf (42%, n=64). Birds breeding in Iceland, the Faroe Islands and Scotland wintered mainly in the Benguela region (36%), Canary Current (33%) and the Patagonian shelf (21%, n = 33), but none in the Caribbean or Mediterranean Sea.

The considerable degree of mixing of individuals from both the same and from different breeding sites in wintering areas indicated weak overall migratory connectivity, as is expressed in the R_{mantel} of 0.19 (95% HDI: 0.11 – 0.26); excluding the birds from the two Russian sites, which all used the Indian Ocean, resulted in a slightly lower R_{mantel} of 0.14 (95% HDI: 0.07 – 0.22).

Individual wintering-site fidelity was very high: out of 69 individuals tracked for 2-6 years (n=190 tracks), only two birds (2.9%) switched area between years. The first individual, a bird breeding in Brensholmen (mainland Norway), went to the Gulf of Guinea in the first two years of tracking, but wintered in the Canary Current in the third year. The second individual, breeding in Svalbard, wintered in the Caribbean region in the first year and in the Gulf of Guinea in the second year. The large overall consistency in wintering area is reflected in the smaller distance between wintering centroid of the same individuals (485 ± 558 km) compared with those of different individuals from the same breeding area (5634 ± 3152 km, p<0.001).

During both autumn and spring migration, most birds wintering in the Atlantic staged in a broad area across the central North Atlantic, roughly between 35°N and 55°N (figure 2). Individuals breeding at Svalbard and wintering in the Canary Current, however, skipped this staging area in spring and followed a more eastern

route along Western Europe (see also [38]).

Annual schedules in relation to migration strategies

Breeding populations showed clear differences in timing of all events in the annual cycle. Birds at more northerly colonies starting breeding (i.e. laid the first egg) later (figure 3, 4) and also all started and finished migration later. The duration of spring migration, the time spent in the North Atlantic and the time between return to the breeding area and clutch initiation all decreased with breeding latitude (figure 4). However, the duration of autumn migration, wintering and breeding periods did not change with breeding latitude (figure 4).

Birds that used different wintering areas also showed differences in timing and duration of migration (figure 5). There was a clear trend of longer migration periods and shorter wintering period when wintering further south for all breeding areas. Birds wintering on the Patagonian Shelf and the Benguela region (the two furthest wintering areas, at 12647-14664 km and 9803-11800 km, respectively, from colonies) generally stayed for shorter periods in the wintering areas and had longer spring migrations than individuals wintering in the Canary Current (the closest wintering area, at 4021-7140 km from colonies), with the Guinean and Caribbean regions showing intermediate duration of migration and wintering periods. The clear relation between duration of the wintering and spring migration periods with wintering area distance was caused by only subtle and non-significant pairwise differences in timing of arrival and departure on the wintering area. In all breeding areas except Norway, the timing of return to the breeding area was similar between birds from different wintering areas. Among Norwegian birds, however, we found weak evidence that return to the breeding grounds was slightly delayed among birds that wintered on the Patagonian Shelf and was slightly advanced among those that wintered in the Canary Current. Although timing of clutch initiation varied among Norwegian birds — birds that wintered in the Caribbean region bred substantially earlier — there was no relation between wintering area and clutch initiation date across breeding areas.

Variation within and between individuals in timing and duration

From wintering area arrival to clutch initiation in the next breeding season, individuals were increasingly consistent in their timing (supplementary material, figure S1a). The variance between individuals was substantially higher than the variance within individuals for timing of arrival to and departure from the wintering area and arrival in the North Atlantic, leading to highest marginal repeatabilities (R_m ~ 0.7). Variance between and within individuals was similar for the timing of return to the breeding area and clutch initiation, with accordingly lower marginal repeatabilities (R_m ~ 0.55 and 0.25, respectively, supplementary material,

figure S1c). With respect to the duration of periods, individuals were most consistent in the time spent in the North Atlantic and least in the duration of the wintering period (supplementary material, figure S1b). Similarly, the repeatability of the duration of periods was *ca.* 0.7 for autumn migration to the time spent in the North Atlantic, after which it dropped to *ca.* 0.4 due to similar variances between and within individuals (supplementary material, figure S1d).

Strength of carry-over effects in timing

Both between and within breeding populations, the duration of each migration phase was strongly linked to the start date: durations were shorter for migrations that started later (figure 6). There was no consistent pattern among breeding areas in the steepness of this relationship, and slope estimates (a measure of the *strength* of the carry-over effect) were not consistently associated with breeding or wintering areas (figure 7). Overall, the decline of duration with time was steepest for the wintering period (figure 7b), when slope estimates around -1 indicate complete compensation of the timing of arrival in the wintering area (figure 1). There were two exceptions to this pattern: slope estimates around -0.5 for the two farthest wintering areas suggested only partial compensation for late arrival in a) Norwegian birds wintering at the Patagonian Shelf (β = -0.5, 95% HDI = -0.83 – -0.15) and b) Faroese birds wintering in the Benguela region (β = -0.48, 95% HDI = -1.2 – 0.24). Note, however, that the estimate for the Faroese birds wintering in the Benguela region was associated with a very wide HDI overlapping with both 0 and 1, and that the slope estimate for birds from mainland Norway wintering in the Benguela region indicates complete compensation. The duration of the spring migration and the time spent in the North Atlantic were tightly related to their timing, with overlapping distributions across breeding and wintering areas (figure 6c-d). The slope estimates between -0.5 and 0 indicated a partial to complete carry-over effect of the arrival in the North Atlantic on return to the breeding area (figure 6d-e). The timing of return partially carried-over to the timing of clutch initiation, with most slope estimates between -1 and -0.5 (figure 7e).

Discussion

Our study demonstrates substantial variation within and between breeding populations in both wintering areas and annual schedules of the Arctic Skua, a long-distance migratory seabird with a huge wintering range. Arctic Skuas showed weak overall migratory connectivity in the Atlantic, with very high variation among individuals, including individuals within breeding sites, in their use of wintering areas separated by thousands of kilometers. Individuals from the colony with the most tracked birds (Slettnes, mainland Norway)

wintered in all productive areas of the Atlantic between 50°S and 30°N, and also in the Mediterranean Sea and the Persian Gulf (figure 2), together representing roughly a tenth of the world's ocean surface area. The lower variability in wintering destinations of birds from other breeding sites may partly reflect smaller sample sizes. The wintering range of Arctic Skuas is as large or larger than most other well-studied long-distance seabirds [48–52] and also far exceeds the variation shown by a congeneric species, the Long-tailed Skua *Stercorarius longicaudus* [53]. Such ocean-scale variation in wintering area selection makes the Arctic Skua exceptionally well-suited for directly testing the relationships between the timing of annual events (breeding and migration) and wintering site selection within and between breeding colonies.

Migration timing of the tracked Arctic Skuas varied principally with breeding latitude, with later-timed schedules of more northern breeders associated with faster spring migrations and shorter periods between spring arrival at the breeding grounds and clutch initiation. Variation in timing of autumn migration was completely compensated during the wintering period, even in the most distant wintering areas. Despite the large variation in migration distances and schedules and the *strong* carry-over effect of timing during spring migration, the timing of return to the breeding area was highly synchronized among individuals from the same site, leaving no substantial *net* carry-over effect.

Annual schedules in relation to breeding and wintering area

In Arctic Skuas, breeding latitude not only shifted the timing of annual schedules, as expected [12,15,16,54–56], but later timing subsequently also affected the duration of key periods within the annual cycle. Most notably, Arctic Skuas breeding at high latitudes had faster spring migrations compared to birds breeding at lower latitudes. The faster spring migration of later-timed spring migration of Arctic Skuas contrasts with little or no geographical variation in the duration of spring migration of two insectivorous songbirds [16,56] and a long-distance migratory seabird, the Arctic Tern *Sterna paradisaea* [57]. Arctic Skuas may be more flexible in adjusting travel speeds by regulating the time spent in the North Atlantic staging area (where Arctic Terns stage for no or only a few days in spring; [58]; [57]) and the amount of foraging *en route*. Considering that a fly-and-forage migration strategy increases travel rates [59], faster migration later in the season may be facilitated by more favourable winds, higher food availability or increasing daylength and therefore time available for foraging in a diurnal species [60–62]. Wind support seems unlikely to explain the faster migrations later during spring; however, as surface wind speeds over the North Atlantic decrease rather than increase during April-June and the prevailing wind directions remain consistent [63]. Travel speeds may also be influenced by food availability, but in less predictable ways; high food abundance may permit efficient refueling *en route* and thus high travel speeds, or individuals with body reserves attained in

the wintering area may select migration routes with no or few stops [60,61]. As Arctic Skuas feed mainly by kleptoparasitizing other seabirds [64], foraging opportunities during migration in the North Atlantic are set by the abundance and foraging success of other seabirds. Although ocean productivity in the North Atlantic increases during spring, late-migrating Arctic Skuas may face deteriorating feeding conditions in the North Atlantic stopovers during April to May, when potential host species for kleptoparasitism, such as Arctic Terns and Sabine's Gull *Xema sabini*, which also stage in this region, return to their breeding areas [57,58,65,66]. This may necessitate fueling up before migration rather than depend on foraging *en route* to fuel the migration flight, which is common among migrating seabirds [67]. Indeed, an analysis of the saltwater immersion data collected by the loggers in this study, revealed that significantly fewer days were spent during spring migration at stopovers by Arctic Skuas from Svalbard compared to birds from more southern breeding areas [38].

The more northern, late-migrating Arctic Skuas also had shorter pre-laying periods (e.g., mean = 17 d in Svalbard, 19 d in mainland Norway, 24 d in the Faroe Islands and 35 d in Scotland, similar to values in Furness 1987, p 219-221), suggesting they may rely more on distantly-acquired resources ('endogenous' reserves) for egg production [68,69]. Although these pre-laying periods are all longer than the 7-8 d needed to produce eggs [33], 16% of the protein in Arctic Skua eggs originated from distantly-acquired resources in a population breeding at 61°N [68], a latitude similar to our most southern study sites and thus presumably with a relatively long pre-laying period. Skuas arrive in the breeding area with large body stores [70], which they may build up at the wintering areas or at stopovers. Late-migrating individuals spent little or no time at the North Atlantic stopover region (figure 6d; [38]) and thus likely acquired nutrient stores in the wintering areas. Carrying large nutrient stores on migration is however costly and hence less beneficial as migratory distance increases. This trade-off potentially explains why Arctic Skuas breeding in the high Arctic (East Greenland and Svalbard), which have the fastest spring migrations and shortest pre-laying periods, do not migrate to the southernmost wintering areas (Patagonian Shelf and Benguela region). However, carrying large nutrient stores on migration can also sometimes be advantageous as it increases flight speed when adopting the 'dynamic soaring' flight technique [71], which skuas utilize at high wind speeds [33]. Furthermore, carrying nutrient stores is relatively less costly in larger-bodied birds [19]. Interestingly, Arctic Skuas from Svalbard were heavier and larger than those from mainland Norway, the Faroe Islands and Scotland (B. Moe, R.S.A. van Bemmelen, K.R.S. Snell, R.A. Phillips *unpublished data*). Selection for larger body size to reduce the relative costs of carrying nutrient stores during migration provides an alternative hypothesis to explain latitudinal clines in body size, for which Bergman's rule is usually invoked [72].

As exemplified by our study of Arctic Skuas, variation in timing of migration schedules is not necessarily

linear across breeding latitudes. Compared to sites at intermediate latitudes, the time spent in the breeding area was longer in one of the southernmost breeding areas, Finland, as well as the northernmost breeding area in our sample, Svalbard. These later onsets of autumn migration are surprising, because the duration of incubation and parental care are expected to be similar across latitudes in a single-brood species such as the Arctic Skua [73]. A later start of autumn migration may be profitable if feeding conditions are better locally than at stopovers or wintering areas. Indeed, the extended period that Arctic Skuas stay around Svalbard coincides with an abundance of Black-legged Kittiwakes – an important host species for kleptoparasitizing Arctic Skuas – concentrating here for Capelin *Mallotus villosus* and other prey species [74]. These findings show how annual schedules can be affected by factors specific to a breeding site as well as by general latitudinal gradients, and highlight the advantages of multi-population studies.

Compensation of timing of autumn migration during the wintering period

Arctic Skuas were able to compensate for the timing of the autumn migration during the wintering period. Thereby, our study adds to a growing number of studies of ducks, waders and passerines reporting the wintering period to be the main period in the annual cycle where delays are compensated [17,28,75–77], although the migration periods may additionally act as time buffer in some species [78,79]. The ability to shorten the wintering period to compensate for later timing of autumn migration has also been shown by experimentally increasing the duration of parental care [80]. The wintering period is usually the longest period in the annual cycle of migratory birds (including Arctic Skuas, see figure 4) and may therefore be less likely to pose a time constraint. We investigated whether birds are less able to compensate for timing of autumn migration if the wintering period is shorter, as observed in more distant wintering areas, and evidence was inconsistent. Indeed, reduced compensation in the wintering period was found among skuas breeding in northern Norway and wintering at the furthest wintering area, the Patagonian Shelf (figure 5), where the wintering period is up to 50 d shorter than in the northernmost wintering area (but still about 50d longer than the 122 d needed to complete the moult of the primary feathers; [81]). However, no conclusive evidence for reduced compensation was found among individuals wintering in the Benguela region, at a similar latitude and migration distance. Therefore, site-specific effects, rather than migration distance alone, may explain the difference in the degree to which birds compensate earlier timing variation during the wintering period, which corresponds to findings for the Sanderling *Calidris alba* [13].

No consistent carry-over effect of wintering area on timing of spring migration or breeding

Our study shows largely synchronized timing of return to the breeding grounds as well as clutch initiation within breeding sites, despite differences between wintering areas in migration distance of thousands of kilometers and in average spring migration duration of up to 19 d (in Scotland). Despite the longer duration of spring migration from more distant wintering areas and the increasing *strength* of the carry-over effect of timing during spring migration, the similar departure dates across wintering areas did not result in substantial *net* carry-over effects on the breeding grounds. This indicates that, rather than departing earlier from the wintering grounds, Arctic Skuas with longer migrations increase travel speeds to ensure a timely return to the breeding grounds, which agrees with empirical data from songbirds [21]. The similarity in timing of departure across wintering areas observed in Arctic Skuas suggests control by endogenous biological 'clocks', which are thought to be fine-tuned by selection [31].

Birds from widely separated wintering areas arrived back in the breeding area, on average, within less than a week. This synchrony underpins the strong selection on timing of spring arrival and breeding when competition for territories is high [82]. In other species, later arrival at the breeding grounds of individuals from more distant wintering areas has been reported for several short- to long-distance migrants, including Blackcap *Sylvia atricapilla*, Great Cormorant *Phalacrocorax carbo*, European Shag *Gulosus aristotelis* and Eurasian Spoonbill *Platalea leucorodia* [83–86], but only in European Shags (a partial migrant) and Eurasian Spoonbills (a long-distance migrant) did the later arrival at the breeding grounds also lead to later reproduction and lower reproductive success. In Arctic Skuas, however, we found partial compensation for later return at the breeding grounds: on average, a 1 d later spring arrival led to 0.6 d later clutch initiation, but with substantial individual variation in the duration of the pre-breeding period. We did not have data on reproductive success, but as wintering area had a minimal influence on timing of return to the breeding area (on average up to 6 d later than birds wintering elsewhere) and laying dates (up to 3 d), a substantial effect of wintering area specifically on reproductive success via timing of breeding seems unlikely. Furthermore, unless an effect of non-breeding strategy on productivity is substantial, demonstrating a carry-over effect on reproduction would be difficult considering the multitude of local effects at the breeding grounds – effects that have been shown to impact reproduction and thus drive population declines in Arctic Skuas, at least in Scotland and mainland Norway [87,88]

By describing the migratory connectivity and ocean-scale geographic variation in annual schedules and carry-over effects of a long-distance migratory seabird, our study contributed to our understanding of potential drivers of meta-population dynamics. Our results indicate that choice of wintering area is unlikely to affect population trends through a carry-over effect on timing of breeding, but do not rule out effects on sur-

vival or reproduction via other mechanisms. For example, as daily survival rate may differ between stages of the annual cycle [7–9], wintering areas may affect annual survival rates and therefore population trends, given their concomitant annual schedules. While the weak migratory connectivity means that conditions in each wintering area can affect multiple breeding populations, each breeding population may be buffered from the effect of conditions at specific wintering areas due the large spread of individuals across wintering areas [30]. Interestingly, the population decline in Svalbard (from where no individuals wintered in the two most distant wintering areas) is less than in the Faroe Islands, Scotland and mainland Norway [87–89] and the longevity record holder of the species, a bird from Finland, wintered in one of the closer wintering areas, the Canary Current [90]. If and how breeding area, wintering area, and the corresponding annual schedules affect seasonal survival rates in Arctic Skuas, and whether these can explain differences in population trends, remains to be investigated.

Ethics

This study was carried out in accordance with guidelines in the use of wild birds for research [91]. Catching and tagging Arctic Skuas was approved for the following countries by the appropriate licensing authority: East Greenland (Government of Greenland, #C11-31, C12-28, C13-4(29), C13-11, C14-4(23), C14-16, C15-4(10), C15-14, C16-4(15), C16-20, C17-3(28), C17-23), Svalbard/Norway (Governor of Svalbard and Norwegian Food Safety Authority, FOTS ID 2086, 3817, 6329, 8538, 15726); Iceland (Icelandic Bird Ringing Scheme); Faroe Islands (Copenhagen Bird Ringing Centre and The National Museum of the Faroe Islands); Scotland (Special Methods Technical Panel of the British Trust for Ornithology Ringing Committee); Finland (Centre for Economic Development, Transport and the Environment, VARELY/418/07.01/2012) and Russia (Federal Law No. 52-FZ of April 24, 1995, Article 44).

Data accessibility

Geolocator data is stored on movebank.org under movebank IDs: 2746281685 (Svalbard, Norway), 968984187 (Slettnes, Norway), 2746341928 (Brensholmen, Norway), 976692287 (Tobseda, Russia), 1260558178 (Greenland), 2746320914 (Iceland), 2746186408 (Faroe Islands), 2743674038 (Scotland) and 2747912295 (Finland). The extracted individual-level data on timing is available at github/dryad.

Author contributions

conceptualization: R.S.A.vB., B.M., H.S., K.R.S.S. & I.T.; methodology: R.S.A.vB.; formal analysis: R.S.A.vB.; fieldwork: R.S.A.vB.; B.M., H.S., S.A.H. K.R.S.S., S.H., E.M., K.N., M.S., D.E., S.R.V., G.T.H., Y.K., S.H., J.C., O.G., J.L., B.S., A.S., I.T. writing original draft: R.S.A.vB. with input from B.M., H.S., I.T., K.R.S.S., E.M.H & R.P.; writing and editing: R.S.A.vB., B.M., H.S., I.T., K.R.S.S., E.M.H, J.C. & R.P.; visualization: R.S.A.vB.; supervision: B.M. & I.T.; funding acquisition: R.S.A.vB., B.M., E.M.H, J.C., E.M. & I.T..

Competing interests

The authors declare no competing interests.

Funding

RvB was funded by the Netherlands Organisation for Scientific Research (project number 866.13.005). BM and SAH and work in Svalbard and North Norway (Brensholmen) were financed by the Fram Center flagship "Climate Change in Fjord and Coast" (grant nr 2019147470 1152018), as well as by the County Governor of Troms and the County Governor of Finnmark. The fieldwork at the Faroe Islands (KS and SH) was financially supported Faroese Research Council and the National Museum of the Faroe Islands. Work at Hochstetter (led by OG and Loïc Bollache) was funded by the French Polar Institute-IPEV (grant "Interactions-1036") and by the Agence Nationale de la Recherche (programs ILETOP ANR-16-CE34-0005 and PACS ANR-21-CE02-0024). DE was financed by the terrestrial flagship of the Fram Center (project Yamal EcoSystem nr 362259). Fieldwork in Scotland was funded by a donor programme managed by David Agombar. The Arctic Skua project in Finland was funded by the Kone Foundation (application number 28-1235), the Finnish Cultural Foundation (grant to EM) and the ERC grant no 669609 (EM). The Arctic Skua project in Iceland was funded by University of Iceland Research Fund (grant to GTH) and financed by the Southwest Iceland Nature Research Centre.

Acknowledgements

This study would not have been possible without the help of the many fieldworkers that invested substantial time and resources. In Slettnes, we were assisted in the field by Geert Aarts, Daniël van Denderen, Jan

van Dijk, Maria van Leeuwe, Daan Liefhebber, Morrison Pot, Marc van Roomen, Janne Schekkerman and Rinse van der Vliet. Other help was provided by Cees and Mimi Tesselaar, Barbara Ganther, Hans-Ulrich Rösner, Karl-Birger Strann, Jeanette Hickman, Torstein Johnsrud, Niels Westpahl and Benedicte Færevåg. In Svalbard and Brensholmen, help was provided by Erlend Lorentzen, Elise Biersma, Fokje Schaafsma, Anouk Goedknegt, Oebele Dijk, Maarten Loonen, Anette Fenstad, Elise Skottene, Liv Monica Trondrud, Nora Bjørnlid, Heidi Kilen, Eline Rypdal, Emilly Hill, Melissa Fontenille and Thomas Oudman. Expeditions to Tobseda in 2014-2015 were organized by Thomas Lameris and in 2018 by Götz Eichorn (NIOO-KNAW), and joined by Kees Schreven, Stefan Sand, Jasper Koster and Chiel Boom. In the Faroe Islands, help was provided by Jón Aldará, Leivur Janus Hansen and Anthony Weatherhill; we kindly acknowledge the landowners on Fugloy for permission to work on their property. In Greenland, Adrian Aebischer, Vadim Heuacker, Eric Buchel, Brigitte Sabard and Vladimir Gilg helped at Hochstetter, and Anita Lang, Mark Nitze and Felix Norman at Karupelv Valley. In Erkuta, help was provided by Natalia Sokolova, Ivan Fufachev and Stijn Hofhuis. In Finland, Kari Mäntylä and Jukka Nuotio assisted during fieldwork. Support in the field in Scotland was provided by Helen and David Aiton on Rousay and the Fair Isle Bird Observatory. James Fox (Migrate Technology Ltd) and Glen Fowler (Biotrack Ltd) kindly retrieved data from loggers that failed to download.

Literature

1. Piersma T. 1987 Hink, stap of sprong? Reisbeperkingen van arctische steltlopers door voedselzoeken, vetopbouw en vliegsnelheid. *Limosa* **60**, 185–194.
2. Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S. 2011 Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* **80**, 4–18. (doi:10.1111/j.1365-2656.2010.01740.x)
3. Alerstam T. 1990 *Bird migration*. Cambridge University Press.
4. Norris DR, Taylor CM. 2006 Predicting the consequences of carry-over effects for migratory populations. *Biology Letters* **2**, 148–151. (doi:10.1098/rsbl.2005.0397)
5. Wingfield JC. 2008 Organization of vertebrate annual cycles: Implications for control mechanisms. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**, 425–441. (doi:10.1098/rstb.2007.2149)
6. Marra PP, Cohen EB, Loss SR, Rutter JE, Tonra CM. 2015 A call for full annual cycle research in animal ecology. *Biology letters* **11**, 2015.0552. (doi:10.1098/rsbl.2015.0552)

7. Klaassen RHG, Hake M, Strandberg R, Koks BJ, Trierweiler C, Exo K-M, Bairlein F, Alerstam T. 2014 When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal Ecology* **83**, 176–184. (doi:10.1111/1365-2656.12135)

8. Lok T, Overdijk O, Piersma T. 2015 The cost of migration: Spoonbills suffer higher mortality during trans-Saharan spring migrations only. *Biology Letters* **11**, 20140944. (doi:10.1098/rsbl.2014.0944)

9. Buechley ER *et al.* 2021 Differential survival throughout the full annual cycle of a migratory bird presents a life-history trade-off. *Journal of Animal Ecology* **90**, 1228–1238. (doi:10.1111/1365-2656.13449)

10. Norris DR, Marra PP. 2007 Seasonal interactions, habitat quality, and population dynamics in migratory birds. *The Condor* **109**, 535–547.

11. Bogdanova MI *et al.* 2017 Multi-colony tracking reveals spatio-temporal variation in carry-over effects between breeding success and winter movements in a pelagic seabird. *Marine Ecology Progress Series* **578**, 167–181. (doi:doi.org/10.3354/meps12096)

12. Gow EA *et al.* 2018 A range-wide domino effect and resetting of the annual cycle in a migratory songbird. *Proceedings of the Royal Society B: Biological Sciences* **286**, 20181916.

13. Reneerkens J *et al.* 2019 Low fitness at low latitudes: Wintering in the tropics increases migratory delays and mortality rates in an Arctic breeding shorebird. *Journal of Animal Ecology* **89**, 671–932. (doi:10.1111/1365-2656.13118)

14. van der Jeugd HP, Eichhorn G, Litvin KE, Stahl J, Larsson K, van der Graaf AJ, Drent RH. 2009 Keeping up with early springs: Rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply. *Global Change Biology* **15**, 1057–1071. (doi:10.1111/j.1365-2486.2008.01804.x)

15. Conklin JR, Battley PF, Potter MA, Fox JW. 2010 Breeding latitude drives individual schedules in a trans-hemispheric migrant bird. *Nature communications* **1**, 67. (doi:10.1038/ncomms1072)

16. Briedis M, Hahn S, Gustafsson L, Henshaw I, Träff J, Král M, Adamík P. 2016 Breeding latitude leads to different temporal but not spatial organization of the annual cycle in a long-distance migrant. *Journal of Avian Biology* **47**, 743–748. (doi:10.1111/jav.01002)

17. Gow EA *et al.* 2019 Effects of Spring Migration Distance on Tree Swallow Reproductive Success Within and Among Flyways. *Frontiers in Ecology and Evolution* **7**, 380. (doi:10.3389/fevo.2019.00380)

18. Pedersen L, Jackson K, Thorup K, Tøttrup AP. 2018 Full-year tracking suggests endogenous control of migration timing in a long-distance migratory songbird. *Behavioral Ecology and Sociobiology* **72**, 139. (doi:10.1007/s00265-018-2553-z)

19. Alerstam T, Lindström Å. 1990 Optimal bird migration: The relative importance of time, energy and safety. In *Bird migration: The physiology and ecophysiology* (ed E Gwinner), pp. 331–351. Springer Berlin Heidelberg.

20. Lisovski S, Ramenofsky M, Wingfield JC. 2017 Defining the Degree of Seasonality and its Significance for Future Research. *Integrative and Comparative Biology* **57**, 934–942.

21. Morbey YE, Hedenström A. 2020 Leave earlier or travel faster - optimal mechanisms for managing arrival time in migratory songbirds. *Frontiers in Ecology and Evolution* **7**, 492. (doi:10.3389/fevo.2019.00492)

22. Sorte FAL, Fink D, Hochachka WM, DeLong JP, Kelling S. 2013 Population-level scaling of avian migration speed with body size and migration distance for powered fliers. *Ecology* **94**, 1839–1847. (doi:10.1890/12-1768.1)

23. Marra PP, Hobson KA, Holmes RT. 1998 Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* **282**, 1884–1886. (doi:10.1126/science.282.5395.1884)

24. Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM. 2004 Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences* **271**, 59–64. (doi:10.1098/rspb.2003.2569)

25. Tøttrup AP, Klaassen RHG, Kristensen MW, Strandberg R, Vardanis Y, Lindström Å, Rahbek C, Alerstam T, Thorup K. 2012 Drought in Africa caused delayed arrival of European songbirds. *Science (New York, N.Y.)* **338**, 1307. (doi:10.1126/science.1227548)

26. Kentie R *et al.* 2017 Does wintering north or south of the Sahara correlate with timing and breeding performance in black-tailed godwits? *Ecology and Evolution* **7**, 2812–2820. (doi:10.1002/ece3.2879)

27. Dossman BC, Rodewald AD, Studds CE, Marra PP. 2023 Migratory birds with delayed spring departure migrate faster but pay the costs. *Ecology* **104**, e3938. (doi:10.1002/ecy.3938)

28. Senner NR, Hochachka WM, Fox JW, Afanasyev V. 2014 An exception to the rule: Carry-over effects do not accumulate in a long-distance migratory bird. *PloS one* **9**, e86588. (doi:10.1371/journal.pone.0086588)

29. Renfrew R, Kim D, Perlut N, Cadman MD. 2019 Migration tactics of a long-distance migratory songbird from across a continental breeding range. *The Wilson Journal of Ornithology* **131**, 735–749. (doi:10.1676/1559-4491-131.4.735)

30. Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT. 2002 Links between worlds: Unraveling migratory connectivity. *Trends in Ecology and Evolution* **17**, 76–83. (doi:10.1016/S0169-5347(01)02380-1)

31. Åkesson S, Ilieva M, Karagicheva J, Rakhimberdiev E, Tomotani B, Helm B. 2017 Timing avian long-distance migration: From internal clock mechanisms to global flights. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**, 20160252. (doi:10.1098/rstb.2016.0252)

32. Furness RW. 1987 *The Skuas*. London: T. & A.D. Poyser.

33. Olsen KM, Larsson H. 1997 *Skuas and jaegers. A guide to the skuas and jaegers of the world.* East Sussex: Pica Press.

34. Briedis M, Hahn S, Adamík P. 2017 Cold spell en route delays spring arrival and decreases apparent survival in a long-distance migratory songbird. *BMC Ecology* **17**, 11. (doi:10.1186/s12898-017-0121-4)

35. Lisovski S, Hahn S. 2012 GeoLight - processing and analysing light-based geolocator data in R. *Methods in Ecology and Evolution* **3**, 1055–1059. (doi:10.1111/j.2041-210X.2012.00248.x)

36. Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Briggs DR. 2004 Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series* **266**, 265–272. (doi:10.3354/meps266265)

37. Davies TE *et al.* 2021 Multispecies tracking reveals a major seabird hotspot in the North Atlantic. *Conservation Letters* **14**, e12824. (doi:10.1111/conl.12824)

38. O'Hanlon NJ *et al.* 2023 Cross population comparison of complex migration strategies in a declining oceanic seabird.

39. Sittler B, Aebischer A, Gilg O. 2011 Post-breeding migration of four Long-tailed Skuas (Stercorarius longicaudus) from North and East Greenland to West Africa. *Journal of Ornithology* **152**, 375–381. (doi:10.1007/s10336-010-0597-6)

40. Verhoeven MA *et al.* 2020 Geolocators lead to better measures of timing and renesting in black-tailed godwits and reveal the bias of traditional observational methods. *Journal of Avian Biology* **51**, jav.02259. (doi:10.1111/jav.02259)

41. Cohen EB, Hostetler JA, Hallworth MT, Rushing CS, Sillett TS, Marra PP. 2018 Quantifying the strength of migratory connectivity. *Methods in Ecology and Evolution* **9**, 513–524. (doi:10.1111/2041-210X.12916)

42. McFarlane Tranquilla LA, Montevecchi WA, Fifield DA, Hedd A, Gaston AJ, Robertson GJ, Phillips RA. 2014 Individual winter movement strategies in two species of murre (Uria spp.) In the Northwest Atlantic. *PloS one* **9**, e90583. (doi:10.1371/journal.pone.0090583)

43. Kruschke JK. 2014 *Doing Bayesian data analysis: A tutorial with R, JAGS, and Stan*.

44. Kruschke JK. 2018 Rejecting or accepting parameter values in Bayesian estimation. *Advances in Methods and Practices in Psychological Science* **1**, 270–280. (doi:10.1177/2515245918771304)

45. Nakagawa S, Schielzeth H. 2010 Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews* **85**, 935–956. (doi:10.1111/j.1469-185X.2010.00141.x)

46. Bürkner P-C. 2017 Brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software* **80**, 1–28. (doi:10.18637/jss.v080.i01)

47. Team SD. 2021 Stan Modeling Language Users Guide and Reference Manual.

48. Dias MP, Granadeiro JP, Phillips RA, Alonso H, Catry P. 2011 Breaking the routine: Individual Cory's shearwaters shift winter destinations between hemispheres and across ocean basins. *Proceedings. Biological sciences / The Royal Society* **278**, 1786–1793. (doi:10.1098/rspb.2010.2114)

49. Frederiksen M *et al.* 2012 Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. *Diversity and Distributions* **18**, 530–542. (doi:10.1111/j.1472-4642.2011.00864.x)

50. Phillips RA, Catry P, Silk JRD, Bearhop S, McGill R, Afanasyev V, Strange IJ. 2007 Movements, winter distribution and activity patterns of Falkland and brown skuas: Insights from loggers and isotopes. *Marine Ecology Progress Series* **345**, 281–291. (doi:10.3354/meps06991)

51. Delord K, Cherel Y, Barbraud C, Chastel O, Weimerskirch H. 2017 High variability in migration and wintering strategies of brown skuas (Catharacta antarctica lonnbergi) in the Indian Ocean. *Polar Biology* **41**, 59–70. (doi:10.1007/s00300-017-2169-1)

52. Weimerskirch H, Tarroux A, Chastel O, Delord K, Cherel Y, Descamps S. 2015 Population-specific wintering distributions of adult south polar skuas over three oceans. *Marine Ecology Progress Series* **538**, 229–237. (doi:10.3354/meps11465)

53. van Bemmelen R *et al.* 2017 Flexibility in otherwise consistent non-breeding movements of a long-distance migratory seabird, the long-tailed skua. *Marine Ecology Progress Series* **578**, 197–211. (doi:10.3354/meps12010)

54. Burr ZM *et al.* 2016 Later at higher latitudes: Large-scale variability in seabird breeding timing and synchronicity. *Ecosphere* **7**, 1–12.

55. Fraser KC, Silverio C, Kramer P, Mickle N, Aeppli R, Stutchbury BJM. 2013 A Trans-Hemispheric Migratory Songbird Does Not Advance Spring Schedules or Increase Migration Rate in Response to Record-Setting Temperatures at Breeding Sites. *PLoS ONE* **8**, 1–5. (doi:10.1371/journal.pone.0064587)

56. Neufeld LR, Muthukumarana S, Fischer JD, Ray JD, Siegrist J, Fraser KC. 2021 Breeding latitude is associated with the timing of nesting and migration around the annual calendar among Purple Martin (Progne subis) populations. *Journal of Ornithology* **162**, 1009–1024. (doi:10.1007/s10336-021-01894-w)

57. Wong JB *et al.* 2022 Variation in migration behaviors used by Arctic Terns (Sterna paradisaea) breeding across a wide latitudinal gradient. *Polar Biology*, 14.

58. Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JRD. 2010 Tracking of Arctic terns Sterna paradisaea reveals longest animal migration. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 2078–2081. (doi:10.1073/pnas.0909493107)

59. Strandberg R, Alerstam T. 2007 The strategy of fly-and-forage migration, illustrated for the osprey (Pandion haliaetus). *Behavioral Ecology and Sociobiology* **61**, 1865–1875. (doi:10.1007/s00265-007-0426-y)

60. Alerstam T. 2003 Bird migration speed. In *Avian Migration* (eds P Berthold, E Gwinner, E Sonnenschein), pp. 253–268. Springer.

61. Lindström Å, Alerstam T, Hedenström A. 2019 Faster fuelling is the key to faster migration. *Nature Climate Change* **9**, 288–289.

62. Felicísimo ÁM, Muñoz J, González-Solis J. 2008 Ocean surface winds drive dynamics of transoceanic aerial movements. *PLoS ONE* **3**, 1–7. (doi:10.1371/journal.pone.0002928)

63. Laurila TK, Sinclair VA, Gregow H. 2021 Climatology, variability, and trends in near-surface wind speeds over the North Atlantic and Europe during 1979–2018 based on ERA5. *International Journal of Climatology* **41**, 2253–2278. (doi:10.1002/joc.6957)

64. Furness BL. 1983 The feeding behaviour of Arctic Skuas Stercorarius parasiticus wintering off South Africa. *Ibis* **125**, 245–251. (doi:10.1111/j.1474-919X.1983.tb03107.x)

65. Stenhouse IJ, Egevang C, Phillips RA. 2012 Trans-equatorial migration, staging sites and wintering area of Sabine's Gulls Larus sabini in the Atlantic Ocean. *Ibis* **154**, 42–51. (doi:10.1111/j.1474-919X.2011.01180.x)

66. Hromádková T, Pavel V, Flousek J, Briedis M. 2020 Seasonally specific responses to wind patterns and ocean productivity facilitate the longest animal migration on Earth. *Marine Ecology Progress Series* **638**, 1–12. (doi:10.3354/meps13274)

67. Bonnet-Lebrun A-S *et al.* 2021 Seabird Migration Strategies: Flight Budgets, Diel Activity Patterns, and Lunar Influence. *Frontiers in Marine Science* **8**, 683071. (doi:10.3389/fmars.2021.683071)

68. Hobson KA, Sirois J, Gloutney ML. 2000 Tracing Nutrient Allocation to Reproduction with Stable Isotopes: A Preliminary Investigation Using Colonial Waterbirds of Great Slave Lake. *The Auk* **117**, 760–774. (doi:10.2307/4089600)

69. Drent R, Daan S. 1980 The prudent parent: Energetic adjustments in avian breeding. *Ardea* **68**, 225–252. (doi:10.5253/arde.v68.p225)

70. Belopol'skii LO. 1961 *Ecology of sea colony birds of the Barents Sea.* Jerusalem: Israel Programme for Scientific Translations.

71. Pennycuick CJ. 2008 *Modelling the flying bird*. London: Academic Press.

72. Bergmann C. 1847 Ober die Verhaltnisse der Warmeokonomie der Thiere zu ihrer Grosse. *Gottinger Studien* **3**, 595–708.

73. Cramp S, Simmons KEL. 1983 *Handbook of the Birds of Europe, the Middle East and North Africa, The Birds of the Western Palearctic, Volume III: Waders to Gulls*. Oxford: Oxford University Press.

74. Reiertsen TK *et al.* 2014 Prey density in non-breeding areas affects adult survival of black-legged kittiwakes Rissa tridactyla. *Marine Ecology Progress Series* **509**, 289–302. (doi:10.3354/meps10825)

75. Oppel S, Powell AN, Dickson DL. 2008 Timing and distance of King Eider migration and winter movements. *The Condor* **110**, 296–305. (doi:10.1525/cond.2008.8502)

76. Briedis M, Krist M, Král M, Voigt CC, Adamík P. 2018 Linking events throughout the annual cycle in a migratory bird — non-breeding period buffers accumulation of carry-over effects. *Behavioral Ecology and Sociobiology* **72**, 93. (doi:10.1007/s00265-018-2509-3)

77. Carneiro C, Gunnarsson TG, Alves JA. 2023 Annual Schedule Adjustment by a Long-Distance Migratory Bird. *The American Naturalist* **201**, 353–362. (doi:10.1086/722566)

78. Stutchbury BJM, Gow EA, Done T, MacPherson M, Fox JW, Afanasyev V. 2011 Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. *Proceedings of the Royal Society B: Biological Sciences* **278**, 131–137. (doi:10.1098/rspb.2010.1220)

79. van Wijk RE, Schaub M, Bauer S. 2017 Dependencies in the timing of activities weaken over the annual cycle in a long-distance migratory bird. *Behavioral Ecology and Sociobiology* **71**. (doi:10.1007/s00265-017-2305-5)

80. Fayet AL, Freeman R, Shoji A, Kirk HL, Padget O, Perrins CM, Guilford T. 2016 Carry-over effects on the annual cycle of a migratory seabird: An experimental study. *Journal of Animal Ecology* **85**, 1516–1527. (doi:10.1111/1365-2656.12580)

81. van Bemmelen RSA, Clarke RH, Pyle P, Camphuysen CJ. 2018 Timing and duration of primary molt in Northern Hemisphere skuas and jaegers. *The Auk* **135**, 1043–1054. (doi:10.1642/AUK-17-232.1)

82. Kokko H. 1999 Competition for early arrival in migratory birds. *Journal of Animal Ecology* **68**, 940–950.

83. Bearhop S, Fiedler W, Furness RW, Votier SC, Waldron S, Newton J, Bowen GJ, Berthold P, Farnsworth K. 2005 Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science* **310**, 502–504. (doi:10.1126/science.1115661)

84. Bregnballe T, Frederiksen M, Gregersen J. 2006 Effects of distance to wintering area on arrival date and breeding performance in Great Cormorants. *Ardea* **94**, 619–630.

85. Grist H, Daunt F, Wanless S, Burthe SJ, Newell MA, Harris MP, Reid JM. 2017 Reproductive performance of resident and migrant males, females and pairs in a partially migratory bird. *Journal of Animal Ecology* **86**, 1010–1021. (doi:10.1111/1365-2656.12691)

86. Lok T, Veldhoen L, Overdijk O, Tinbergen JM, Piersma T. 2017 An age-dependent fitness cost of migration? Old trans-Saharan migrating spoonbills breed later than those staying in Europe, and late breeders have lower recruitment. *Journal of Animal Ecology* **86**, 998–1009. (doi:10.1111/1365-2656.12706)

87. Perkins A, Ratcliffe N, Suddaby D, Ribbands B, Smith C, Ellis P, Meek E, Bolton M. 2018 Combined bottom-up and top-down pressures drive catastrophic population declines of Arctic skuas in Scotland. *Journal of Animal Ecology* **87**, 1497–1748. (doi:10.1111/1365-2656.12890)

88. van Bemmelen RSA, Schekkerman H, Hin V, Pot M, Janssen K, Ganter B, Rösner H-U, Tulp I. 2021 Heavy decline of the largest European Arctic Skua Stercorarius parasiticus colony: Interacting effects of food shortage and predation. *Bird Study*, 13. (doi:10.1080/00063657.2021.1969334)

89. Santos I. 2018 Survival and breeding success of the declining Arctic Skua population of the Faroe Islands. University of Copenhagen, Denmark. {{MSc}} Thesis, University of Copenhagen, Copenhagen, Denmark.

90. Mäntylä E, Mäntylä K, Nuotio J, Nuotio K, Sillanpää M. 2020 Longevity record of arctic skua (*Stercorarius Parasiticus*). *Ecology and Evolution*, ece3.6875. (doi:10.1002/ece3.6875)

91. Fair JM, Jones J. 2010 *Guidelines to the use of wild birds in research*. Ornithological council.

Figures

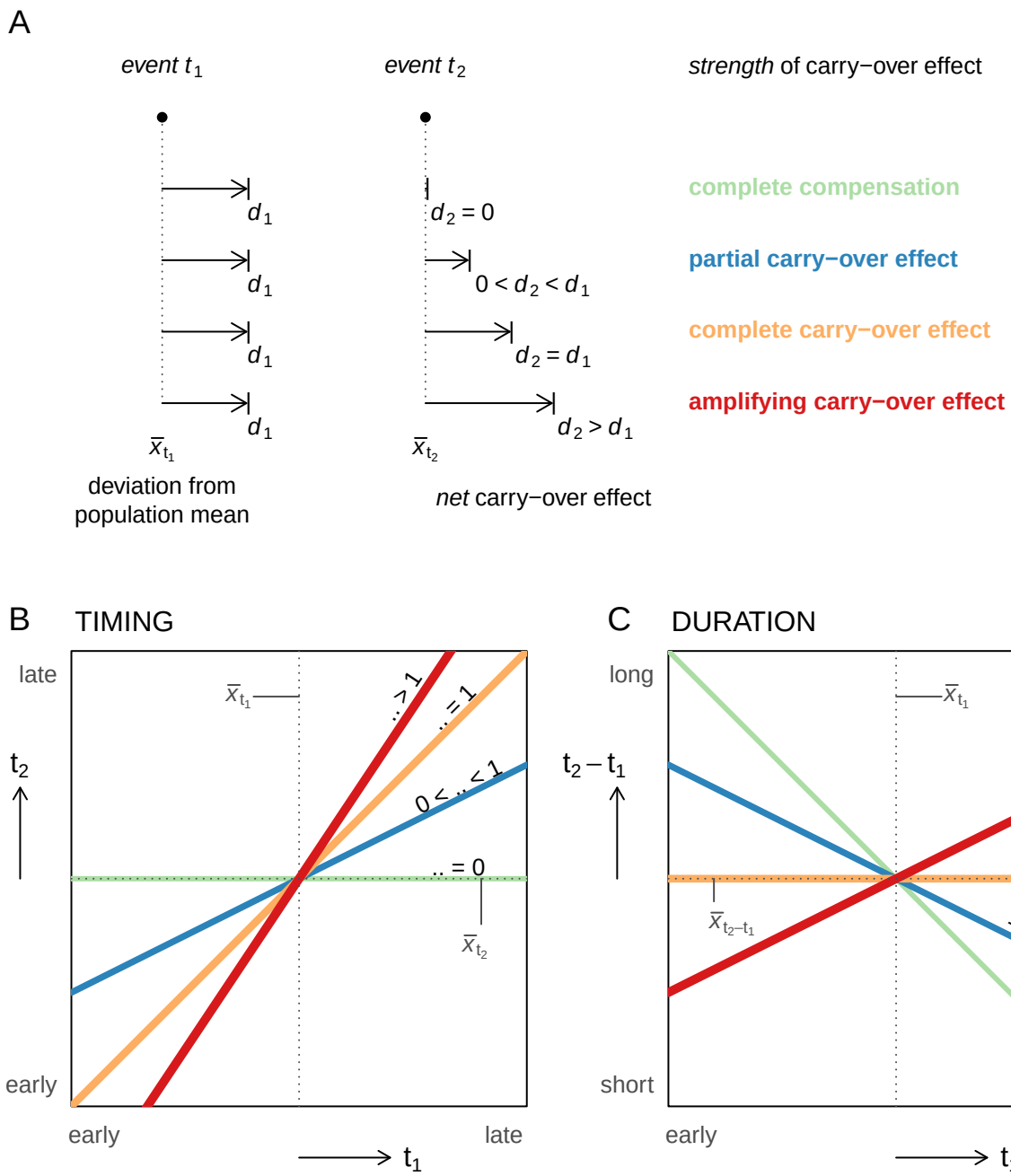

Figure 1: Conceptual framework of the two interrelated measures of carry-over effects between events in the annual cycle. The framework assumes the population mean represents the overall optimal timing, while throughout the range of timings different advantages and disadvantages can be attributed. (A) Here an example delay (d_1) relative to the population mean timing ($\overline{x}_{t_1}$) of event 1 affects the timing of a subsequent event t_2 relative to the population mean $\overline{x}_{t_2}$ to different degrees. The resulting degree of advancement or delay in event (t_2) is the *net* of carry-over effects and is described by its *strength* as partial, complete, or amplified carry-over effect, or a complete compensation. The *strength* of the carry-over effect can be quantified as the slope between t_1 and t_2 (B), or, between t_1 and the duration of the period between t_1 and t_2 (C).

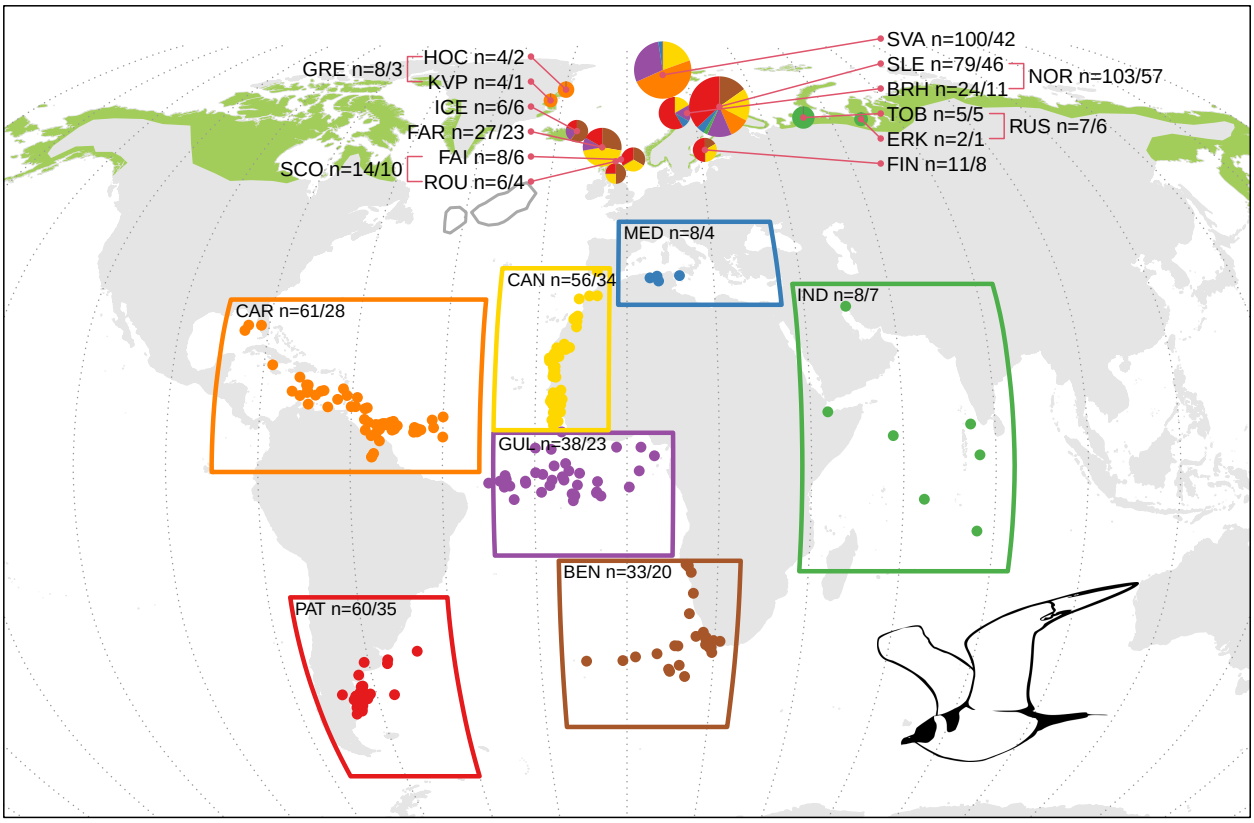

Figure 2: Wintering areas used by Arctic Skuas tracked from breeding areas between East Greenland and West Siberia. Dots represent centroids of January positions for each track, coloured per wintering area (boxes). Pie charts at breeding sites represent the proportion of individuals wintering in each of the seven wintering areas, with the size corresponding to the total number of individuals tracked. Sample sizes are shown as the number of tracks / number of individuals. Green shaded areas reflect the breeding range. The main stopover in the North Atlantic is outlined in dark grey. Abbreviations for breeding sites are SVA = Svalbard, KVP = Karupelv, HOC = Hochstetter Forland, ICE = Iceland, FAR = Faroe Islands, FAI = Fair Isle, ROU = Rousay, SVA = Svalbard, SLE = Slettnes, BRH = Brensholmen, TOB = Tobseda, ERK = Erkuta and FIN = Finland, and for breeding areas are GRE = Greenland, SCO = Scotland, NOR = mainland Norway and RUS = Russia. Abbreviations for wintering areas are PAT = Patagonian Shelf, BEN = Benguela region, GUL = Gulf of Guinea, CAR = Caribbean region, CAN = Canary Current, MED = Mediterranean Sea and IND = Indian Ocean. SLE and BRH were merged into NOR for statistical analyses.

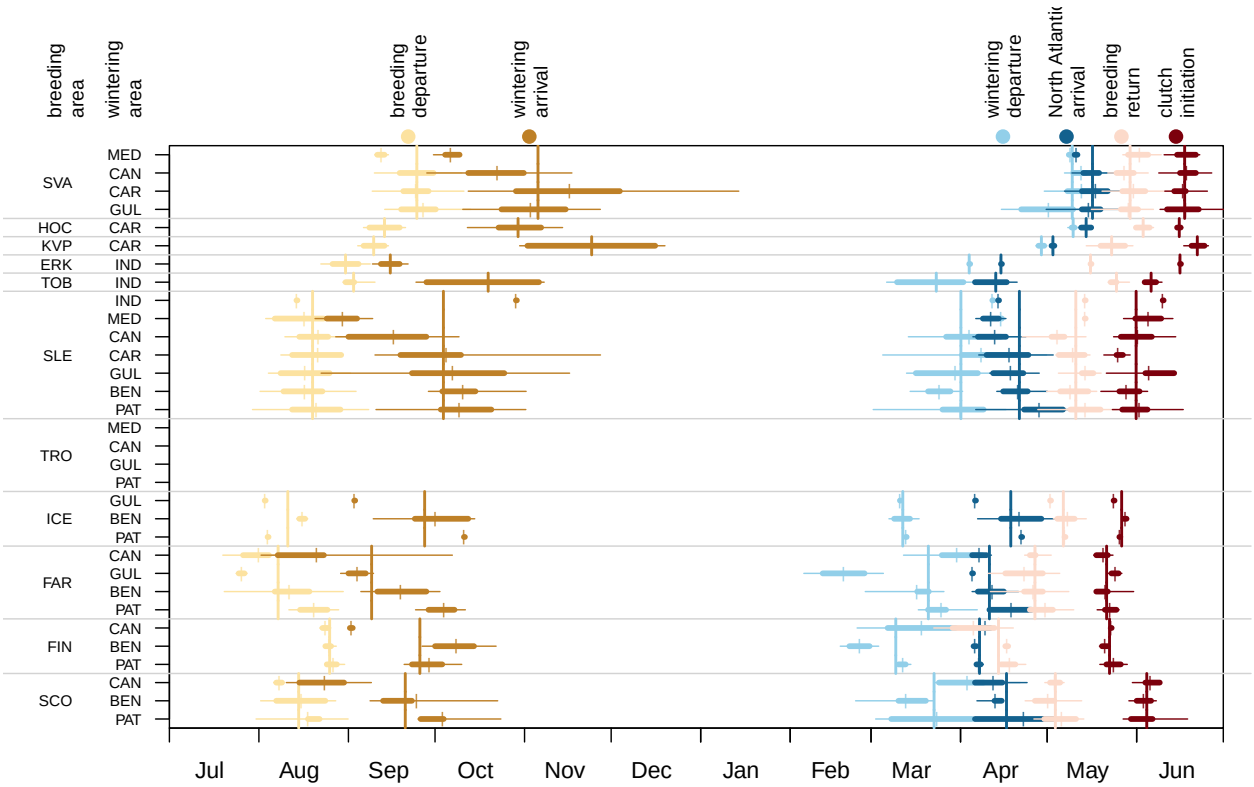

Figure 3: Summary of timing data per breeding and wintering area, not corrected for repeated tracks, of Arctic Skuas tracked from breeding areas between East Greenland and West Siberia to wintering areas in the Atlantic. Vertical lines show the mean, thick horizontal lines show the 25-75 interpercentile range and thin horizontal lines extend to the 5-95 interpercentile range. Breeding areas on the y-axis are ordered from high (SVA) to low (SCO) latitude. For birds breeding in Russia (Tobseda and Erkuta), 'arrival to the North Atlantic' refers to arrival to areas north of 35°N. For abbreviations of breeding and wintering areas, see figure 2.

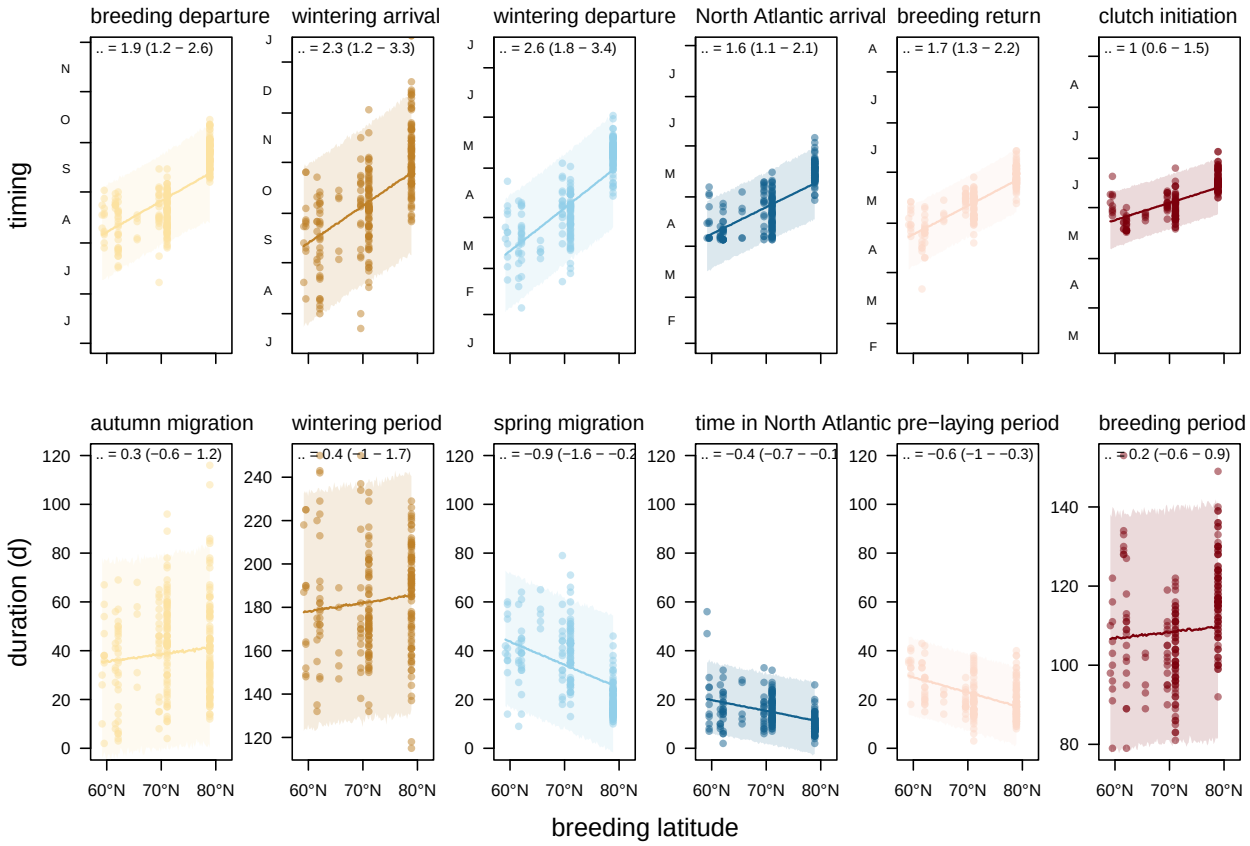

Figure 4: Relation between breeding latitude and timing (upper panels) or duration (lower panels) in Arctic Skuas tracked from breeding areas between East Greenland and West Siberia to wintering areas in the Atlantic. Regression lines are accompanied by 95% HDIs.

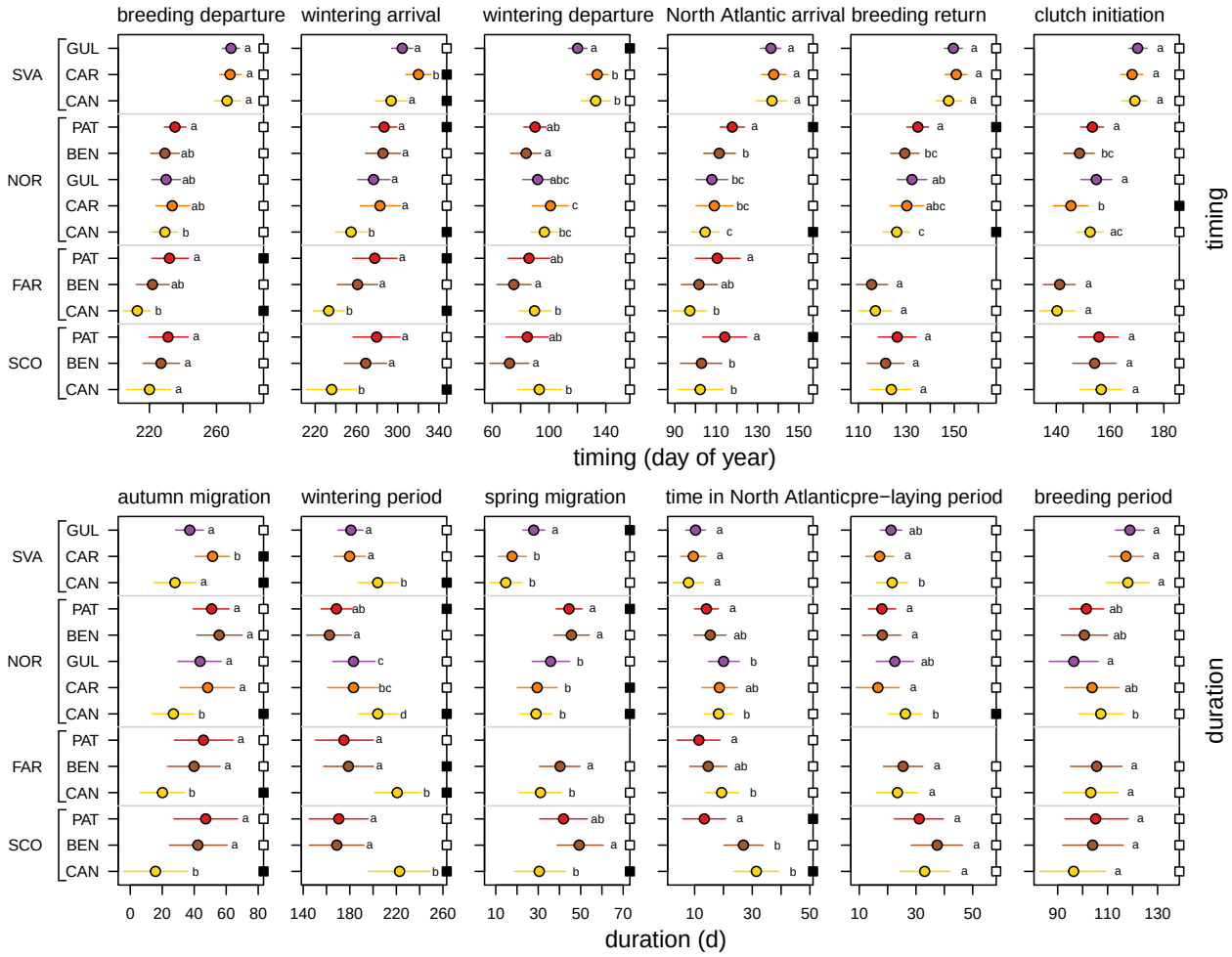

Figure 5: Model parameter estimates of the timing of events (upper panels) or duration of phases (lower panels) per combination of breeding and wintering area for Arctic Skuas tracked from breeding areas in the North Atlantic to wintering areas in the Atlantic. Along the left y-axis, outer labels show breeding areas ordered from South (SCO) to North (SVA) and inner labels show wintering areas ordered from North (CAN) to South (PAT). Error bars show 95% HDIs. Within breeding areas, estimates accompanied a common letter are equivalent based on whether 0 was included in the 95% HDI of their contrast posterior distribution. Filled squares on the right y-axes indicate that the 95% HDI was outside the ROPE of birds from the same colony wintering elsewhere. Colours correspond to the wintering areas.

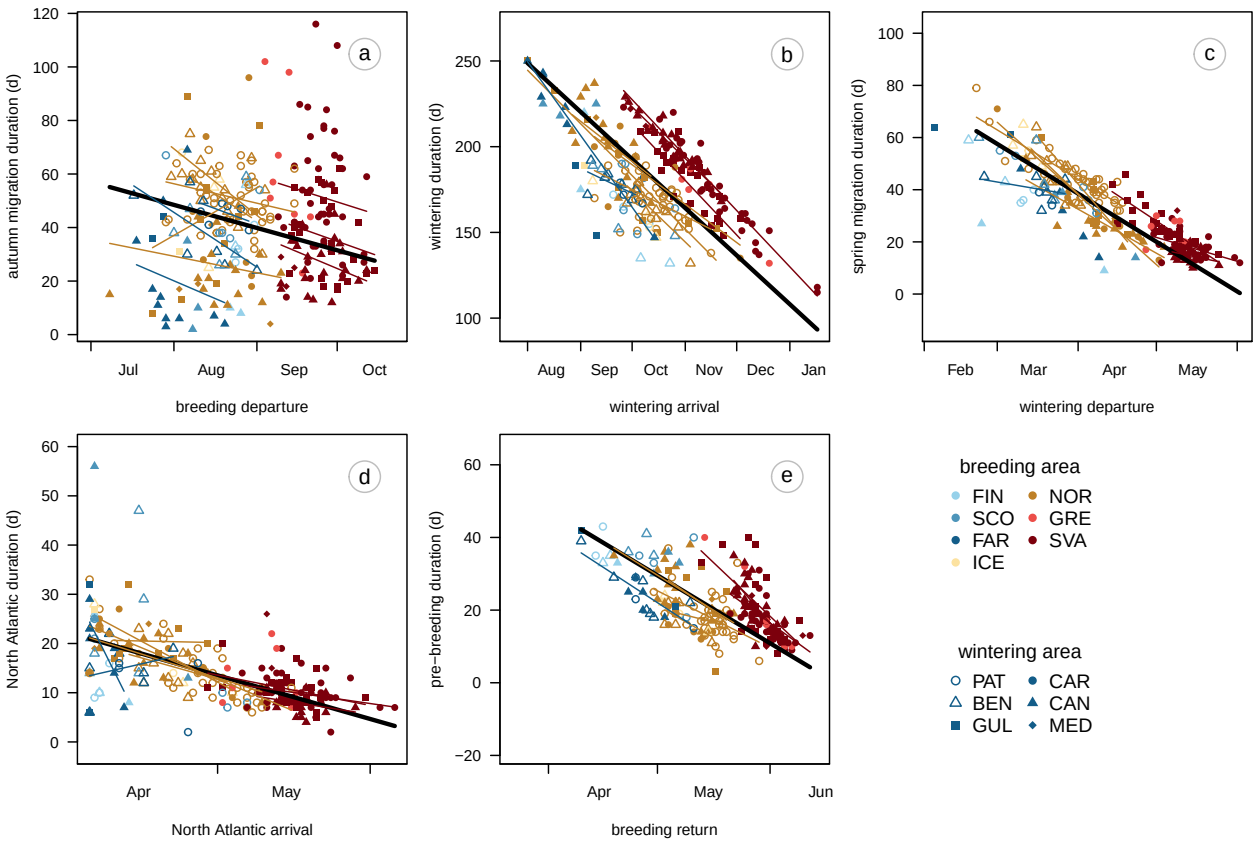

Figure 6: The relationship between duration of each period and the timing of its start in Arctic Skuas tracked from breeding areas in the North Atlantic to wintering areas in the Atlantic. Thick lines show overall slope estimates, thin lines show regression lines per combination of breeding and wintering area. Note that the aspect ratio of all plots is 1, but the axis scales differ between plots.

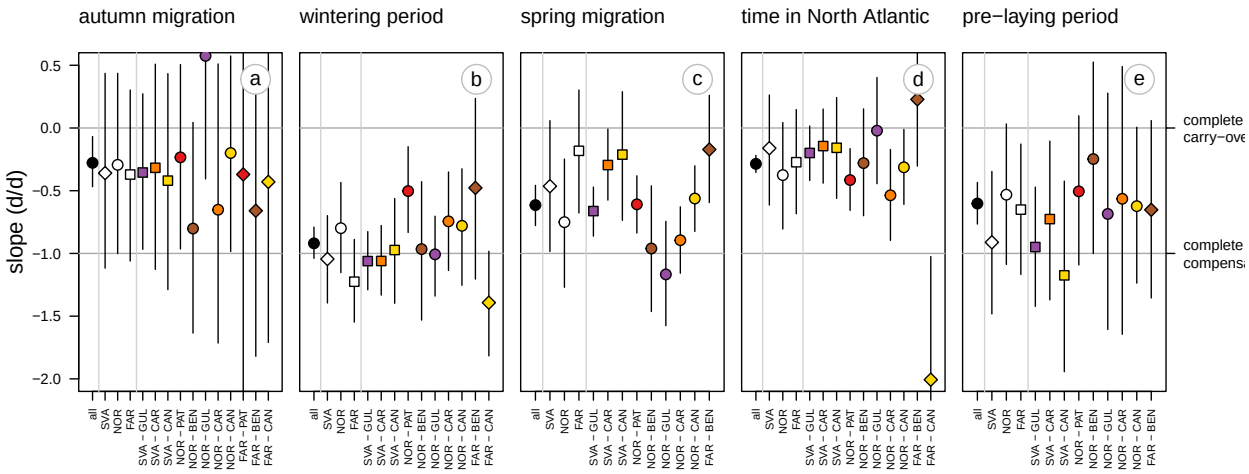

Figure 7: Slope estimates of the duration of periods as a function of the timing of their start in Arctic Skuas tracked from breeding areas in the North Atlantic to wintering areas in the Atlantic. Steepness of the slopes indicates the strength of carry-over effects: they show to what extent advances or delays at the start translate in the timing of the end of each period. For example, a slope of 0 indicates that every day delay at the start of a period translates in a day delay at the end of the period, and a slope of -1 indicates that every day delay is compensated so that the duration of the period gets one day shorter. Estimates are given at three levels, which are separated by grey vertical lines: 1. across all breeding and wintering areas, 2. for each of the three breeding areas and 3. for each combination of breeding and wintering area. Error bars are 95% HDIs.