

Migrating Curlews on Schedule: Departure and Arrival Patterns of a Long-distance Migrant Depend on time and Breeding Location Rather than on Wind Conditions

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Research

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Abstract

Background:

Departure decisions in long-distance migratory bird species may depend on favourable weather conditions and beneficial resources at the destination location, overarched by genetic triggers. However, few studies have tried to validate the significance of these three concepts simultaneously, and long-term, high-resolution tagging datasets recording individual movements across consecutive years are scarce. We used such a dataset to explore intraspecific and intra-individual variabilities in departure and arrival decisions from/to wintering grounds in relation to these three different concepts in bird migration.

Methods: We equipped 23 curlews (*Numenius arquata*) wintering in the Wadden Sea with Global Positioning System data loggers to record their spatio-temporal patterns of departure from and arrival at their wintering site, and the first part of their migration. We obtained data for 42 migrations over 6 years, with 12 individuals performing repeat migrations in consecutive years. Departure and arrival dates were related to 73 meteorological and bird-related predictors using the least absolute shrinkage and selection operator (LASSO) to identify drivers of departure and arrival decisions.

Results: Curlews migrated almost exclusively to Arctic and sub-Arctic Russia for breeding. They left their wintering site mainly during the evening from mid- to late April and returned between the end of June and mid-July. There was no difference in departure times between the sexes. Weather parameters did not impact departure decisions; if departure days coincided with headwind conditions, the birds accounted for this by flying at higher altitudes of up to several kilometres. Curlews breeding further away in areas with late snowmelt departed later. Departures dates varied by only <4 days in individual curlews tagged over consecutive years.

Conclusions: These results suggest that the trigger for migration in a long-distance migrant is largely independent of weather conditions but is subject to resource availability in breeding areas. The high intra-individual repeatability of departure days among subsequent years and the lack of relationship to weather parameters suggest the importance of genetic triggers in prompting the start of migration. Further insights into the timing of migration in immatures and closely related birds might help to further unravel the genetic mechanisms triggering migration patterns.

Background

Migration is an essential part of the life cycle of a wide range of species, with potentially important consequences for their fitness [1–5]. Birds show the most extensive and far-ranging migrations [6–8]. Careful timing of migration is crucial, particularly in long-distance migrants, and previous work revealed three general concepts affecting the onset of migration in birds. (1) Departure decisions were significantly related to favourable weather conditions, as consistently demonstrated for different groups of birds [9–12]. (2) The start of migration needs to coincide with beneficial environmental resources in the destination areas, as a prerequisite to ensuring fitness [13–14]. In this respect, particularly Arctic and sub-

Arctic breeders need to time their migration to meet peak food resources at their breeding areas shortly after snowmelt [14–15] (3) Genetic triggers and endogenous programmes also play an overarching role in determining the timing of migration [16–18]. The relevance of this last concept may be difficult to prove; however, one possible approach to investigating this concept would be to assess intra-individual variability by examining repeated migration patterns in the same individuals in different years, though this has rarely been achieved using movement data [19].

The above three concepts have mainly been studied independently using non-individual approaches, such as visual observations, colour-ringing studies [20–21], and radar techniques [22–23]. However, although tagging studies have recently provided some initial insights into individual-based departure decisions with respect to weather conditions [e.g. 12, 24], tagging studies assessing individual repeatability of departure decisions (required to prove the role of genetic triggers for bird migrations) are still lacking [19].

The current study therefore aimed to assess the relevance of each of the three concepts simultaneously, using a high-resolution tagging dataset based on long-term attachment of Global Positioning System (GPS) devices to birds, which allowed individual migration decisions to be analysed in relation to weather, location of breeding sites, and individual repeatability across consecutive years.

We used the Eurasian Curlew (*Numenius arquata*) as a model long-distance migrating shorebird species breeding in Arctic and sub-Arctic regions. We studied departure and arrival patterns at one of its most important wintering sites on the East Atlantic Flyway, the Wadden Sea. Despite strong population decreases in the flyway population as a whole [25], the numbers of curlews wintering in the Wadden Sea have remained stable at around 200,000-260,000 individuals, accounting for around 40% of the total flyway population [26–27]. However, information on the migration patterns of curlews wintering in the Wadden Sea is scarce (but see [28] for a preliminary study). A previous study from south-west England investigated the arrival and departure patterns of curlews based on a dataset of re-sightings of colour-marked individuals [20]. In the current study, we equipped curlews with GPS data loggers that recorded the times of arrival and departure of each individual bird in the Wadden Sea. This allowed individual departure and arrival patterns to be precisely related to meteorological data and location of the breeding area, and allowed the repeatability of temporal patterns across subsequent years to be assessed. We proposed five hypotheses. (1) Given that tailwinds will increase flight and migration speeds [6; 29–30], we expected curlews to time their departure from and arrival at their wintering grounds according to favourable wind and weather conditions, especially in relation to tailwind conditions, lack of precipitation, and air temperature, as found in other bird species [12, 24, 31–32]. (2) In line with this, we expected flight heights (as recorded by GPS tags) to increase during non-tailwind conditions to allow the birds to reach air layers with improved wind conditions [22, 33]. (3) We predicted significant effects of departure date and tailwind component on the distance to and duration of the first stop-over event. Previous studies indicated that headwind conditions could significantly shorten the distance to the first migration stop-over and increase the stop-over duration to allow birds to refuel before continuing [e.g. 34]. (4) We hypothesized that birds breeding further from their wintering site at higher latitudes and more easterly

longitudes would depart later to time their arrival at their Arctic and sub-Arctic breeding grounds according to snowmelt and the underlying availability of food resources [13–15]. In this context, we expected males to arrive at the wintering sites later than females, because, as for other shorebird species, females are known to desert their chicks earlier than males [35]. (5) We expected a certain level of repeatability in curlew departure dates (in accordance with [21]), irrespective of weather conditions, because circadian rhythms and genetic triggers would force the birds to depart if they were already late.

Methods

Study area

Curlews were caught along the eastern Wadden Sea coast of the German federal states of Schleswig-Holstein and north-eastern Lower Saxony between 54°36′N and 53°42′N, and between 7°54′E and 8°54′E (Fig. 1). Meteorological parameters were recorded by the automatic recording station of the Research and Technology Centre, located in Büsum, federal state of Schleswig-Holstein (54°7′ × 55′N; 8°52′ × 37′E; yellow circle in Fig. 1). Flight speeds and altitudes of GPS-tagged individuals were recorded within an area stretching from the Wadden Sea coast to the Baltic Sea and from south Denmark to the northern part of the federal State of Lower Saxony (red box in Fig. 1).

Catching of curlews and deployment of GPS tags

A total of 26 adult curlews were caught at their high-tide roosts using mist nets, between 2014 and 2020. Three of the GPS devices malfunctioned or the birds were predated before departure from their wintering grounds, and data for 23 adult wintering curlews (11 females and 12 males) were therefore available for this study. Some curlews migrated multiple times before the device stopped working, and we were therefore able to record the departures and arrivals of the same individuals in up to 5 subsequent years. We recorded a total of 42 departures from and 33 arrivals at the wintering sites. All individuals were equipped with solar-powered GPS-Global System for Mobile Communications (GSM) data loggers attached by breast harnesses [28, 36]. The devices recorded time, date, geographical position, and flight speed at pre-programmed intervals of 1–15 min. Twelve individuals were equipped with “Skua” data loggers (Ecotone, Poland) weighing 17 g, and the other 11 individuals were equipped with OT-20 (3 individuals), OT-15 (7 individuals), and OT-10 (1 individual) data loggers, weighing 20, 15, and 10 g, respectively (Ornitela, Lithuania). Our study took place over a period of 7 years and we therefore aimed to use progressively lighter data loggers in line with technical developments (particularly logger weight reduction) over this time period. The mean body masses of female and male curlews were 957.7 ± 74.3 g and 827.8 ± 92.1 g, respectively. Even the heaviest data loggers used in this study therefore accounted for only about 2.4% of body mass, which was below the threshold of 3% suggested to avoid confounding effects of the devices [37]. The Skua devices only sent part of the data to a server via a GSM connection, which could then be downloaded directly, and the rest of the data were transmitted to base stations set up next to the high-tide roosts. The full dataset for the Skua devices was thus only obtained after the birds had returned to their wintering sites in the Wadden Sea. The highest temporal resolution achieved

by these devices was 15 min. In contrast, the OT devices transmitted the whole dataset to an online portal, and the recording intervals were programmed according to a flexible schedule, generally ranging from 1–15 min, based on the battery status of the device. We programmed “geofences” (i.e. defined areas in which the devices recorded data constantly in 1-min intervals) for all OT devices. The geofence covered the red box shown in Fig. 1, but excluded high-tide roosts, to save battery power. The high temporal resolution of the GPS fixes allowed flight height measurements to be derived within the red box area shown in Fig. 1, and also further east.

All data recorded by the GPS devices were finally stored in the online portal Movebank (www.movebank.org).

In addition to equipping each bird with a GPS device, all individuals were ringed and weighed, bill and wing lengths were measured, age was determined, and sex was determined by taking a breast feather for genetic sexing in the lab (Tauros Diagnostics, Berlin).

Data analyses

We visualized the GPS data for each curlew using the Geographical Information System ArcGIS (version 10.3) [38]. The time (UTC) and day of the year at which the birds left their wintering grounds heading north-east towards their breeding sites were determined. This departure was evident from the GPS tracks, and was always associated with a clear increase in flight speed (and flight heights in OT devices). The time and day of year of arrival at the wintering grounds was determined in a similar manner.

Meteorological data were recorded at 1-min intervals by an automatic recording station located at the Research and Technology Centre in Büsum, and weather conditions were related to the curlews’ departure and arrival patterns (see Statistical analysis section below). The recorded parameters were: temperature (°C), wind speed and maximum wind speed (m/s), wind direction (degrees), precipitation (mm), global radiation (W/m²), UVA and UVB (W/m²), photosynthetically active radiation (W/m²), air pressure (mbar), and air humidity (%). For all parameters, we computed the mean values of the 1-min recordings over a period from 90 min before to 90 min after the departure/arrival of each individual curlew. The mean values were then related to the departure/arrival day (see Statistical analysis section below) and used to test for differences in weather conditions between departures and arrivals. To account for the circular nature of the wind direction, means were calculated as the direction of a circular vector using the R-package *circular* [39]. Wind-rose plots of the wind direction during the departure and arrival of curlews were created using the R-package *openair* [40].

To relate the departure and arrival dates to linear distance from the breeding area, it was necessary to determine the location of the breeding area for each curlew. The likely breeding area was identified in GIS (white triangles in Fig. 4). It could be distinguished from stop-over locations by being the most distant point from the wintering location, and at the same time as a location where the birds stayed for several weeks (more than at each stop-over location) with very limited movement behaviour. The approximate coordinate of the nest site was calculated by computing the mean geographical position of all positions

in the potential breeding site. Finally, the linear distance between this position and the wintering site was calculated in GIS.

Departure dates were also related to the linear and flown distances (calculated in GIS) to the first stop (red circles in Fig. 4), the flight time to the first stop, and the duration of the first stop. The same was applied for the arrival dates using the last stop before the wintering site (orange circles in Fig. 4). The mean locations of the nearest stops to the wintering sites were calculated in the same way as for the breeding site. In some cases, birds migrated from their wintering sites in the Wadden Sea to other Wadden Sea areas (always < 30 km distance), probably to join other birds shortly prior to departure. These locations were not regarded as first stop-over events, and the departure from the last site in the Wadden Sea was used for the analyses instead.

Finally, we computed the relative deviation between the flown and linear distances (%) as an indicator of the curvature of the actual flight track. This was expected to increase during headwind conditions, because birds might try to avoid headwinds by choosing different flight angles. Only flight tracks with log-intervals of ≤ 5 min were used for this to keep the flight tracks comparable.

We determined the mean departure direction of each individual across the red box shown in Fig. 1 and related it to the mean recorded wind speed and wind direction to compute the tailwind component (TWC). This is known to have a significant impact on the migration speed of birds [29–30, 41], and was therefore expected to affect the departure and arrival decisions of the curlews in the current study. According to [42], we used the following formula: $TWC = v \times \cos x$, where v is the wind speed in ms^{-1} and x is the angular deviation between the opposite flight direction of the curlew (i.e., tailwind direction) and the wind direction (in degrees). In addition to using TWC as an additional predictor of departure and arrival decisions, we also related it to mean flight speed to demonstrate if the birds were able to increase their speed during tailwind conditions, and to mean flight height within the red box in Fig. 1.

Statistical analysis

All statistical analyses were carried out using the open source software R, version 3.6.3 [43]. Plots were visualized using the R package *ggplot2* [44]. All regressions were performed using generalized additive models (GAMs) [45–46] using the R package *mgcv* [47]. Individual was included as a random intercept in the GAMs to avoid pseudo-replication due to multiple observations of the same individual. For each model, we selected an appropriate probability distribution for the variable of interest; if different probability distributions were reasonable (e.g. in the case of possibly overdispersed count data), we selected the most appropriate distribution based on the Akaike Information Criterion [48].

We related the departure day to meteorological data to see if departure decisions were affected by the weather. We considered the meteorological data under six conditions, including (1) at the moment of departure and (2) the mean conditions 90 min before to 90 min after departure. We also contrasted (3) the moment of departure and (4) the mean conditions 90 min before to 90 min after departure with the same measure on the 4 days before departure, to determine if curlews experienced suboptimal conditions

prior to their departure, which might have delayed their departure decision. Finally, we also contrasted (5) the moment of departure and (6) the mean conditions 90 min before to 90 min after departure with the same measure at the same time of day on the same date for the average of the 4 previous years to determine if the curlews experienced suboptimal meteorological conditions compared with the average conditions on similar dates. In all cases, the meteorological conditions were compared by dividing the weather data at the moment of departure (respectively 90 min before to 90 min after departure) by the average conditions at the same moment (same time interval) for the 4 preceding days/years. If the meteorological variable of interest had a zero value, the difference was calculated instead of the quotient.

In addition to the above meteorological parameters, we also used the following additional predictors to model the departure decision (defined by day of the year): number of migrations for each individual bird, sex of the individual, catching location in the Wadden Sea, year, time of day, breeding latitude, linear distance to breeding area, departure direction, TWC, time to first stop-over, duration of first stop-over, flown distance to first stop, and linear distance to first stop. For TWC, we used the six different combinations of meteorological data given above. All other predictors were kept constant.

We therefore used a total of 73 predictors to model the departure decision (i.e. 55 constant and contrasted meteorological predictors, 6 constant and contrasted combinations of TWC, and 12 constant predictors related to the individual curlews or the first stop-over event). The same predictors were used to model the arrival of the birds in their wintering grounds.

The effects of the 73 predictors on day of the year (outcome variable) were tested using the least absolute shrinkage and selection operator (LASSO) [49–50] technique for predictor selection. This technique is known to handle a large number of possible predictors without being prone to statistical problems e.g. compared with stepwise methods (c.f., below). Notably, LASSO has been combined with cross-validation to select promising predictors based on their predictive capacity [49–51]. In contrast to the common stepwise methods (e.g., forward or backward selection procedures), LASSO-based results are not sensitive to the order of the performed tests [51–52]. However, it is necessary to bear in mind that the chance of detecting a significant relationship between a predictor and the considered outcome variable increases with the number of investigated predictors.

Results

Phenology of departures and arrivals

The first curlew departed from the wintering grounds on April 7 and the last on May 16. Most individuals departed between mid- and late April (Fig. 2). Females tended to depart earlier, but the sex difference was not significant (GAM: $t = 1.23$, $df = 41$, $p = 0.23$). The first curlews arrived at the wintering sites on June 3 and the last on July 24, with most birds arriving between mid-June and the end of July (Fig. 2). There was a clear but not significant tendency for females to arrive earlier than males (GAM: $t = 1.97$, $df = 31$, $p = 0.067$; mean day of year females: 177.9 ± 13.1 , mean day of year males: 189.9 ± 11.7).

Departures mainly occurred during the late evening, shortly before sunset, with no significant difference between the sexes (GAM: $t = -0.29$, $df = 41$, $p = 0.78$; Fig. 3a). The time of day for arrivals differed from that for departures (Table 1, Suppl. 1a), with significantly more arrivals during the nighttime and also occasionally during daytime. As for departing curlews, there was no sex difference in terms of arrivals (GAM: $t = 1.7$, $df = 31$, $p = 0.09$; Fig. 3b).

Table 1

GAMs comparing migration parameters, and wind variables between departing and arriving curlews.

	Estimate Std.	Error	t-value	p-value
Time of day	-3.08	1.32	-2.33	0.023
Rel. diff. between flown and linear distance to nearest stop	-2.06	1.75	-1.8	0.244
Linear distance to nearest stop	-432.4	106.2	-4.07	< 0.001
Time to nearest stop	-189.47	118.16	-1.6	0.114
Duration of nearest stop	258.7	433.5	0.6	0.553
Mean flight speed	-18.53	4.12	-4.49	< 0.001
Tail wind component	-0.33	0.67	-0.5	0.618
Mean flight altitude	-930.2	164.9	-5.64	< 0.001
Mean wind speed	-1.29	0.45	-2.89	0.005
Mean wind direction	-2.2	27.43	-0.08	0.936
Estimate Std = estimated standard deviation. GAM outputs are illustrated in Suppl. 1.				

GPS tracks of curlews and relationships with nearest stop-over sites

After their departure from the wintering grounds in the Wadden Sea, all curlews headed towards their breeding sites, which were located exclusively in north-western Russia (except for one individual that was breeding in Finland; see white triangles in Fig. 4). The most distant breeding site was 3,840 km from the wintering site, east of the Ural Mountains. The mean linear distance of all flight tracks was $2,339 \pm 612$ km. The relative differences between the flown and linear distances to the breeding sites were similar for arriving and departing curlews (Table 1; Suppl. 1b).

The mean linear distance between the nearest stop-over site and the wintering site for departing curlews was 775.8 ± 376 km, which represents 33.2% of the linear distance to their breeding sites (i.e. birds

performed about 1/3 of their overall migration during their first migration bout). Curlews selected a straight flight path to reach their first stop-over site, with the distance flown on average only 45.7 km longer than the linear distance (5.6%).

Many curlews crossed the Baltic Sea directly, while others stopped over on the Danish islands or the southern Baltic Sea coast (see red circles in Fig. 4). The nearest stop-over site for arriving curlews was significantly closer to the wintering site than that for departing curlews (mean: 342.4 km; Table 1; Suppl. 1c), but the distance was highly variable (± 503.1 km). In contrast, both time to the nearest stop-over site and duration of the nearest stop were similar for departing and arriving curlews (Table 1; Suppl. 1d, e).

Finally, there was no significant relationship between flight time to the nearest stop-over and stop-over duration, suggesting that curlews did not take longer to recover after longer migration bouts.

Flight speed and flight height in relation to TWC

The flight speeds of both departing (GAM: $t = 8.42$, $df = 32$, $p < 0.001$) and arriving curlews (GAM: $t = 5.07$, $df = 27$, $p < 0.001$) were positively and highly significantly related to TWC (Fig. 5), suggesting that birds were able to increase their migration speeds with wind assistance. Interestingly, flight speeds during departure were significantly higher (mean: 73.8 ± 18.5 km/h, range: 41.9–115.6 km/h) than speeds during arrival (mean: 55.3 ± 11.9 km/h, range: 40.8–84.0 km/h), as indicated by the small overlap of confidence intervals in Fig. 5 (see also Table 1; Suppl. 1f). There was no difference in the TWC relationships between departing and arriving curlews (Table 1; Suppl. 1g).

Curlews departed at significantly higher altitudes during headwind compared with tailwind conditions (GAM: $t = -9.52$, $df = 19$, $p < 0.001$), but there was no significant relationship between TWC and flight altitude in arriving curlews (Fig. 6; GAM: $t = -1.25$, $df = 13$, $p = 0.25$). As for flight speeds, flight altitudes were significantly higher and more variable during departure (mean: $1,113.3 \pm 592.0$ m, range: 175.2–2337.7 m) compared with during arrival (mean: 182.3 ± 164.4 m, range: 37.0–639.2 m) (Table 1; Suppl. 1h).

There was no significant relationship between TWC and the relative difference between the flown and linear distances, indicating that the straightness of the flight pass was not impacted by wind conditions. Finally, there was also no correlation between TWC and migration distance to the first stop or stop-over duration, suggesting that headwind conditions had no effect on flight distances and length of the first stop-over.

Departure/arrival decisions

The LASSO model showed that only one of the 73 predictors significantly influenced the departure day of curlews: curlews departed significantly later with increasing linear distance to their breeding sites (Fig. 7; GAM: $t = 2.63$, $df = 37$, $p < 0.05$). Wind direction at the time of departure contrasted with the mean wind direction at the same time of day, and day of year 4 years prior to departure remained a predictor in the final LASSO model, but had no significant impact on departure day (GAM: $t = -0.77$, $df = 37$, $p = 0.45$).

Interestingly, LASSO did not select any other meteorological predictors, bird-related variables, or variables associated with the nearest stop-over event. Mean wind direction and wind force in the period from 90 min before to 90 min after departure were highly variable (Fig. 8a), which explains the absence of any significant relationships with day of departure.

According to LASSO, none of the 73 predictors was related to arrival day. As for departures, wind direction and force were highly variable (Fig. 8b). Wind force (but not wind direction) differed significantly between departure and arrival flights (Table 1; Suppl. 1i, j). During arrival, most of the higher wind forces were associated with north-easterly winds (Fig. 8b), which might have assisted some returning curlews, but eventually had no significant impact. This also led to a lack of any significant difference in tailwind conditions between departing and arriving curlews (Suppl. 1 g).

In addition, there was no significant relationship between departure/arrival date and stop-over duration, indicating that curlews that migrated later did not have shorter stop-overs.

Repeatability:

Among the 42 curlews with departure information, we recorded multiple departures in subsequent years for 12 individual birds (2–5 consecutive years). It was therefore possible to assess the repeatability of the departure day in the same individuals in different years. The mean absolute difference in departure days in subsequent years was only 3.68 ± 2.97 days ($n = 19$). However, the variability in arrival days of returning curlews was more than twice as high (7.17 ± 4.83 , $n = 12$). The departure days recorded in each individual's first year were significantly related to the departure days in subsequent year(s) (Fig. 9; GAM: $t = 5.29$, $df = 18$, $p < 0.001$), while there was no significant relationship for arrival dates (GAM: $t = -0.5$, $df = 11$, $p = 0.62$).

There was also high site fidelity in terms of the locations of breeding and wintering sites, but less fidelity for the location of the nearest stop-over sites (Fig. 4). The repeatability of flight directions was also high, with a mean variability of only $9.7 \pm 8.2^\circ$ for departures and $13.3 \pm 10.2^\circ$ for arrivals among subsequent years for the same individuals.

Discussion

Low impact of weather effects

Surprisingly, our findings provided no evidence for weather as a migration trigger in curlews, in contrast to various other bird species [12, 24, 31–32]. However, our data confirmed that flight speed increased with increasing TWC, in accordance with previous studies [6, 29]. Based on the clear benefit of faster flight speeds during tailwind conditions, this suggested that curlews would mainly select days with suitable tailwind conditions for their departure from (and arrival at) their wintering grounds in the Wadden Sea. However, in contrast to our assumption, the current results revealed virtually no effect of wind or other weather parameters on the departure/arrival day, even when the actual weather during departure was

compared with the mean weather conditions 4 days and/or 4 years prior to departure. Although curlews rarely departed during hours with precipitation (in accordance with other bird species), this predictor had no significant influence in our final model. The current findings were therefore not in agreement with previous studies, which found that the probability of departure of curlews from a pre-breeding staging site was reduced during precipitation [53]. However, our findings were in accord with observations of departing curlews in China [53], and of the closely related whimbrel (*Numenius phaeopus islandicus*), which also demonstrated no significant influence of wind force or wind direction [53–54].

Although weather parameters had no impact on departure/arrival decisions, we found a significant negative correlation between TWC and flight altitude. Unfortunately, there were no available data for wind speed (and direction) for different air layers for this study; nevertheless, the pattern clearly suggested that curlews tried to find more favourable wind conditions at higher altitudes if they encountered headwinds at lower altitudes. In temperate latitudes, the prevailing westerly wind conditions in the higher air layers suggest wind assistance when ascending [55]. This behaviour has previously been recorded for nocturnal songbird migrants [22, 33], as well as for diurnal long-distance migrants using radar techniques [23]. [56] found intensive songbird migration in air layers up to 3 km altitude in temperate regions, when the birds encountered headwind conditions close to the surface. The authors demonstrated that migrating birds benefited from the wind conditions in higher air layers by ascending, exclusively during their spring migration. This might explain why there was no significant relationship between flight altitude and TWC in arriving curlews during their autumn migration. The current results clearly suggest that curlews depart (and stay) at lower altitudes when wind conditions close to the surface are beneficial, and use higher air layers during spring migration when they encounter headwinds.

Interestingly, curlews arrived at significantly slower flight speeds and lower altitudes compared with departing birds. Meteorological reasons for this can be excluded, given that the wind conditions and TWC were similar for departing and arriving individuals. One likely reason is that the linear distance to the nearest stop-over in arriving curlews was far smaller than for departing individuals, which might explain why departing curlews ascended to higher altitudes and had faster flight speeds compared with arriving birds.

Timing of migration according to resource availability

Our data clearly supported the concept that the onset of migration respected resource availability in the breeding grounds, given that distance to the breeding site was the single (highly significant) predictor affecting the day of departure in our LASSO analyses. Although no field data on food resources within the breeding sites were available for this study, previous studies demonstrated that arthropod densities in Arctic and sub-Arctic breeding grounds peaked shortly after snowmelt, resulting in higher chick growth rates if birds started nesting early [14–15]. This suggests that curlews should aim to arrive at their breeding sites as soon as the areas are free from snow and ice. This could in turn explain why curlews that breed further from their wintering grounds (e.g. in the eastern parts of Russia in this study) might

delay their migration to allow the snow and ice in their Arctic and sub-Arctic breeding grounds to melt, and/or to ensure that they encounter optimal arthropod densities. Similarly, a previous study [20] showed that colour-ringed curlews breeding in Fennoscandia departed later than birds breeding further west. Although this study dealt with a different sub-population, the results were in agreement with the patterns found in the current study.

We found that curlews wintering in the Wadden Sea departed within a very short time window (i.e. mostly between mid-April and mid-May). This contrasted with birds wintering in south-west Britain, which had already started to depart during February and March [20]. However, in contrast to British curlews that breed in north-western Europe [20], all but one of the curlews in the present study bred in Russia, i.e. much further east. The more condensed departure window in our study might thus reflect the relatively late availability of breeding sites due to snow and ice melt. This emphasises the involvement of an internal clock to ensure their timely departure (see discussion on repeatability and genetic trigger below).

Temporal patterns of migration start

The main window of arrival of birds in the Wadden Sea was late June to mid-July, which is about 2 weeks later than reported for birds breeding in central or northern Europe [20]. Although desertion of offspring by females is common in shorebirds and has been shown for curlews [35], we found no sex differences in departure patterns, and only a non-significant tendency for females to arrive earlier (in contrast to our hypothesis). The reason for this is unclear. It is possible that some birds failed to rear chicks successfully, leading to the earlier arrival of at least some males.

Departures of songbirds usually occur at night and around sunset [17, 25] and the same is true for many long-distance migratory wader species, given that birds are thought to take advantage of favourable atmospheric factors during the night and to calibrate their orientation systems before they start in the evening hours [57–58]. Our results support these patterns, with more curlews departing during the early evening or early nighttime. However, an earlier study of curlews departing from a final pre-breeding stop-over site in China showed high variability in terms of the time of day for departures [53]. The reason for these different findings remains unclear. Given the higher number of individuals arriving during morning and afternoon, our results suggest the existence of a strong temporal trigger regulating departure decisions, but a weaker such trigger for arrivals.

Correlations with first and last stop-overs

We expected that the departure day and TWC would be significantly related to the distance to the nearest stop-over site and the stop-over duration; however, no such correlation was found. Curlews did not stage for shorter periods if they departed later, nor did they stage for longer if they encountered headwind conditions during the first part of their migration to allow more time for re-fuelling. This finding is in accordance with studies of songbirds, which likewise showed no or only weak relationships [59–60].

Similar results were also found for whimbrels, with no impact of wind conditions on stop-over patterns; however, in contrast to our study, they tended to skip a potential stop-over when they departed later [54].

High repeatability in departure patterns suggest genetic triggers

Studies on repeated individual-based migration patterns across consecutive years are scarce. To the best of our knowledge, the current study is among the first to record high-resolution GPS-movement data in birds across consecutive years (see [19] for a study on black-tailed godwits (*Limosa limosa limosa*) equipped with geolocators). We found a high degree of repeatability in curlew departure and arrival dates for the same individuals across subsequent years. Given the absence of clear relationships between departure decision and wind/weather parameters, this supports the concept of an internal genetic trigger [see also reviews in 16–18], which seemed to play the most important role in departure and arrival decisions in our model species

A recent review [18] presented evidence for genetic control of the timing of bird migration. However, the authors also found considerable individual variation in this genetic programme, as a result of interactions with environmental and social factors, and individual learning. Given the highly repeatable, conservative time pattern and lack of any relationships between departure date and weather parameters for our model species, the current results suggested that such intraspecific variation in the genetic programme may be very low. Our results thus provide robust support for the concept of an internal clock, responsible for timing bird migration [16–17]. In contrast to these results however, black-tailed godwits tracked across subsequent years exhibited a much broader window of inter- and intra-individual timing of migration [19]. The authors suggest that this broad window of repeatability indicated weak selective forces with respect to migration timing. This assumption would suggest that such forces are strong for curlews, although for the specific mechanisms affecting the high inter- and intra-individual repeatability of migration timing evidence is currently lacking. In contrast, [8] hypothesized a conservative annual-cycle strategy in long-distance migrants that was thought to minimise risks and reduce carry-over effects. Our study may support this hypothesis, given that curlews clearly showed constant, conservative patterns in terms of their departure decisions, independent of the weather conditions at their wintering sites. These findings are in line with other Arctic breeding birds, such as bar-tailed godwits (*Limosa limosa baueri*) from New Zealand, which also showed high repeatability [21].

Conclusions

We used data from long-term attachment of high-resolution GPS devices across multiple years to simultaneously explore the relative impacts of weather-related, resource-driven, and genetically-induced migration decisions. In contrast to previous studies in different groups of bird species [9–12, 24], our results suggest that weather has only a minor effect on migration in curlews; if their individual departure day happens to coincide with headwind conditions, the birds simply account for this by flying at higher

altitudes. However, further studies are needed to determine if curlews have knowledge of the wind conditions at higher altitudes when they encounter headwinds on the ground. Intraspecific variability in departure decisions was mainly driven by differences in the locations of the breeding sites, which underpins the importance of synchronising their departure with resource availability after the snowmelt in Arctic and sub-Arctic breeding sites. The low intra-individual variability in departure decisions in subsequent years, however, clearly suggests a strong genetic trigger regulating the timing of migration. Based on our results, we postulated that genetic triggers controlling the timing of migration are so pronounced in some bird species that extrinsic factors, such as weather, play only a minor role. Follow-up studies on closely related bird species as well as migration studies on immature curlews, ideally by tagging birds from the same clutch and their parents, will further help us to understand the genetic mechanisms triggering temporal migration patterns.

Abbreviations

GPS: Global Positioning System

GSM: Global System for Mobile Communications

TWC: tailwind component

Declarations

Ethics approval and consent to participate

Permission to attach GPS tags was issued by the Ministerium für Energiewende, Landwirtschaft, Umwelt, Natur und Digitalisierung of the federal state of Schleswig-Holstein (file numbers V 312-7224.121-37(42-3/13) and V 241-35852/2017(88-7/17)) as well as by the Niedersächsisches Landesamt für Verbraucherschutz und Lebensmittelsicherheit of the federal state of Lower Saxony (file number 33-19-42502-04-17/2699). Catching and treatment of birds complied with current EU and German laws. All authors consent to participate in this study.

Consent for publication

Not applicable.

Availability of data and materials

The tracking data of curlews are available in www.movebank.org.

Competing interests

The authors declare that they have no competing interests.

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Author’s contributions

PS designed the study, conducted the fieldwork, performed the data analyses and wrote most parts of the manuscript. MM designed and performed the statistical tests and wrote parts of the method section. KHV recorded and analysed the meteorological data. PB wrote parts of the manuscript. SG designed the study and compiled the movement data. All authors read and approved the final manuscript.

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Figures

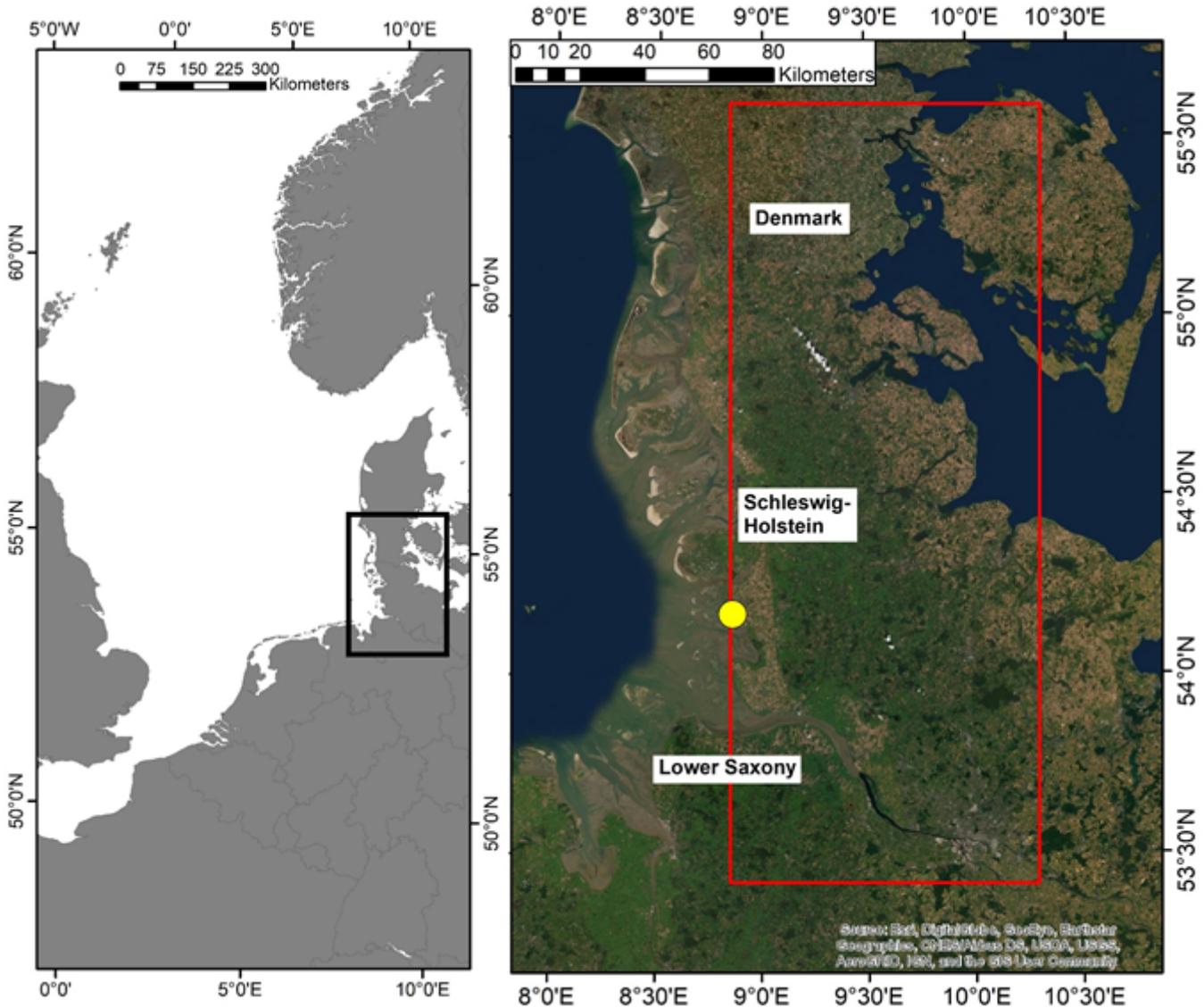


Figure 1

Left: location of study area in the southern part of the German Wadden Sea, south-eastern North Sea coast, indicated by black box. Right: study area for analyses of tailwind component flight speeds and flight altitudes (red box) and location of weather recording station (yellow dot). Satellite image: ESRI, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community.

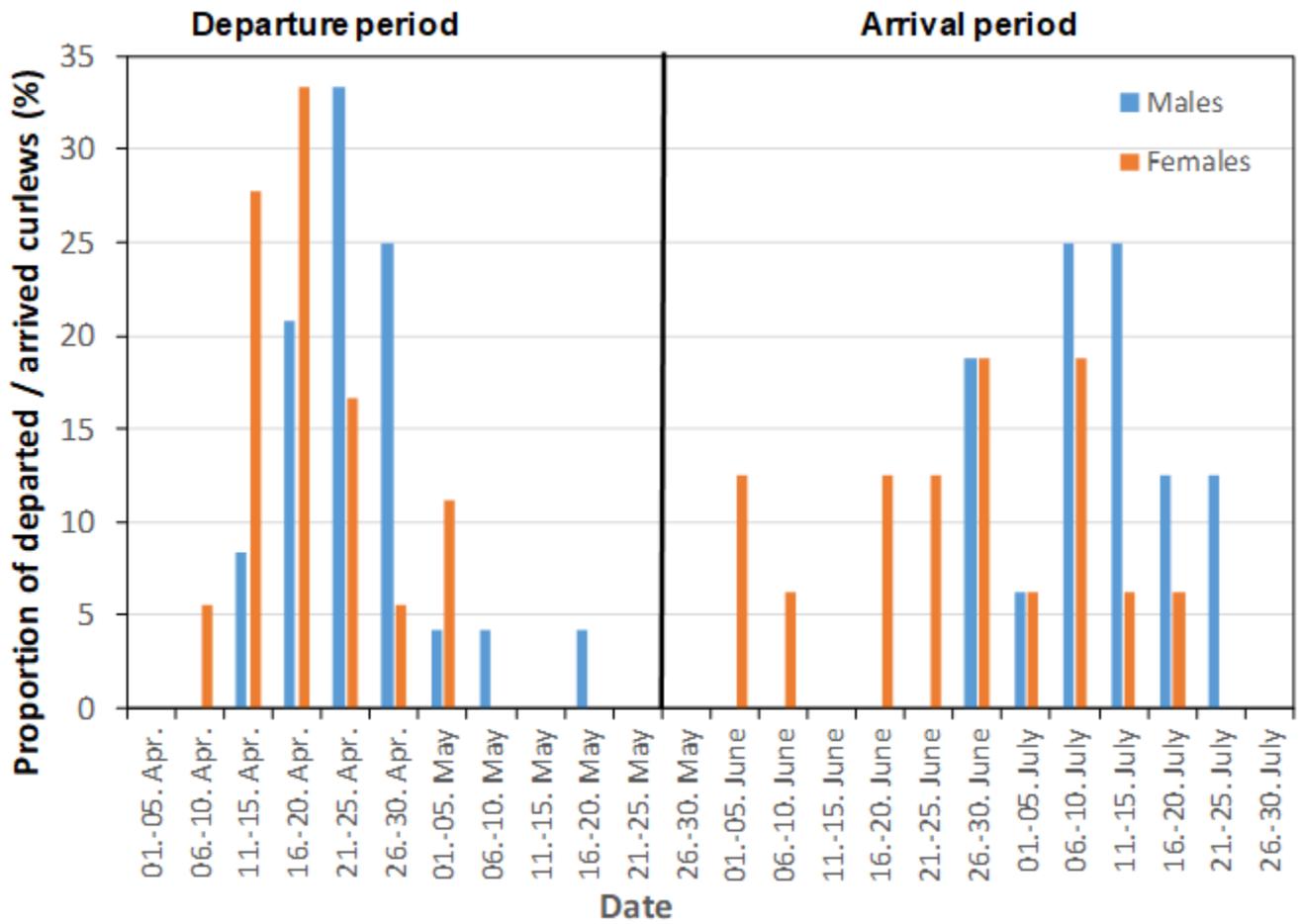


Figure 2

Proportion of curlews that departed from (left) and arrived at the wintering site (right) in relation to date.

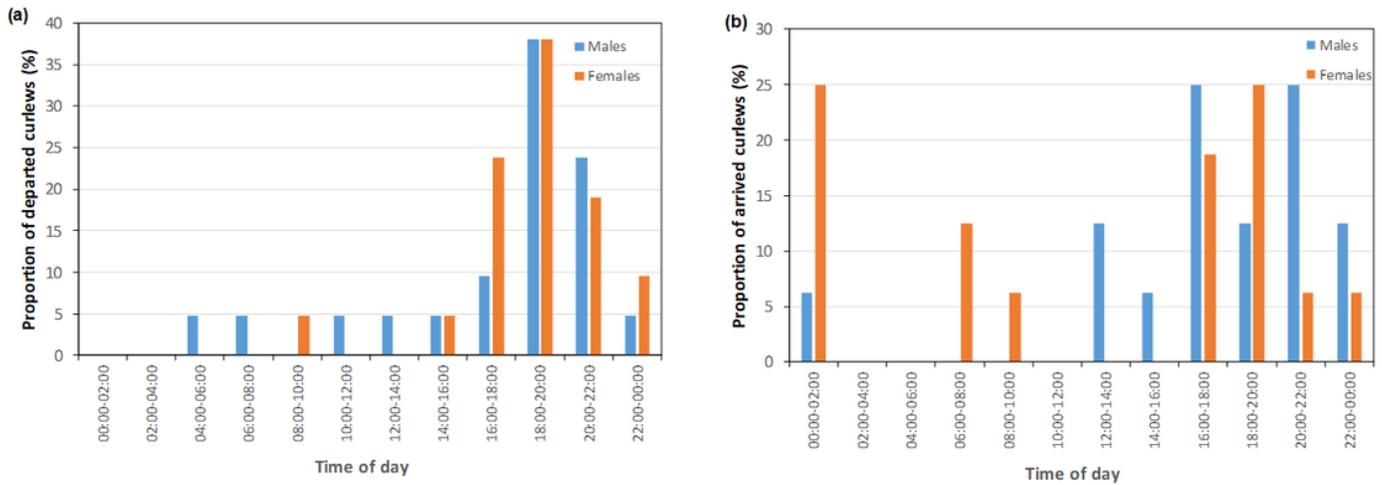


Figure 3

Proportion of curlews that departed from (a) and arrived at the wintering site (b) in relation to time of day (UTC).

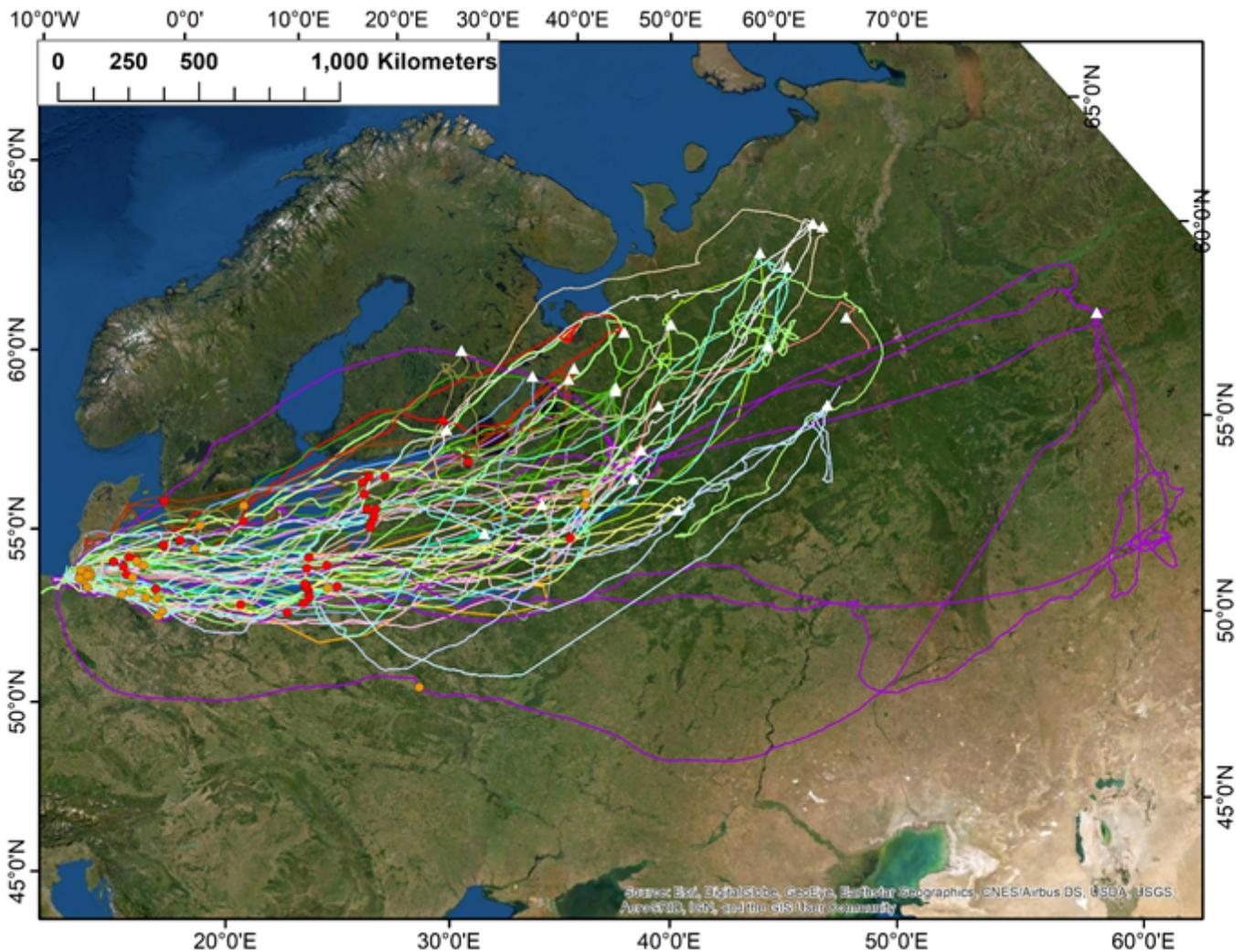


Figure 4

Flight tracks (n=41) of 23 curlews between their wintering sites in the Wadden Sea and their breeding sites (white triangles). Red and orange dots indicate location of the first and last stop-over sites, respectively. Satellite image: see Fig. 1.

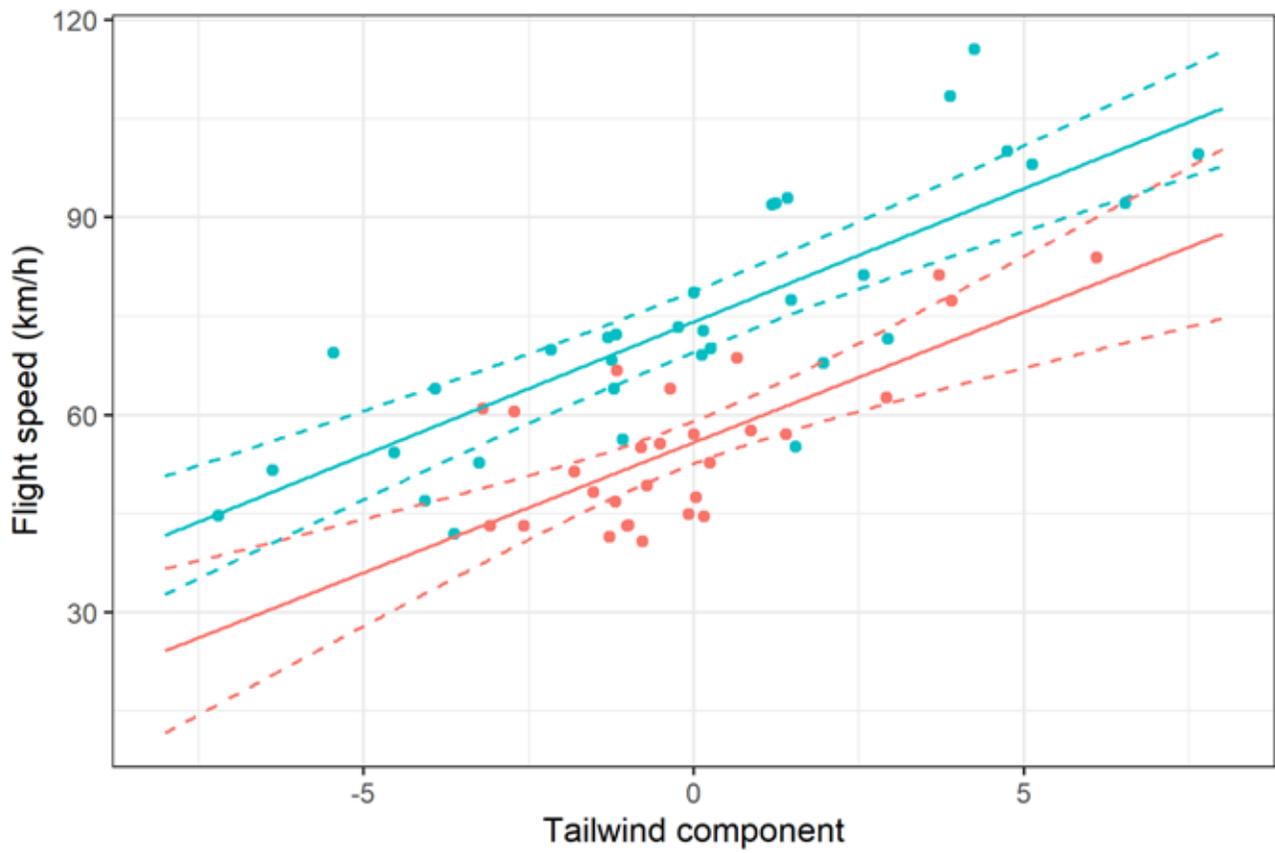


Figure 5

Flight speed of departing (blue) and arriving curlews (red) in relation to tailwind component. Solid line: model curve; dashed lines: 95% confidence intervals.

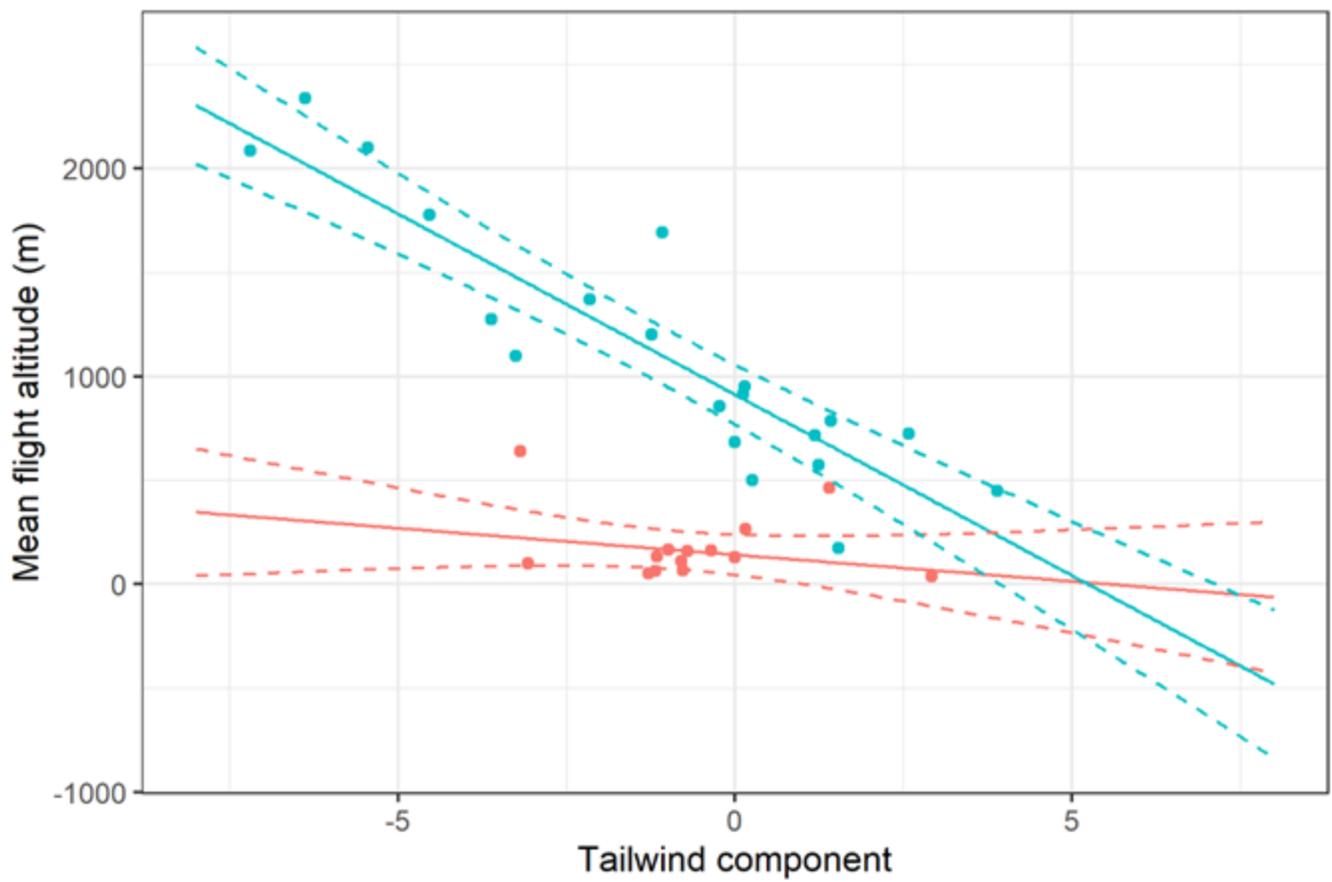


Figure 6

Flight altitudes of departing (blue) and arriving curlews (red) in relation to tailwind component. Solid line: model curve; dashed lines: 95% confidence intervals.

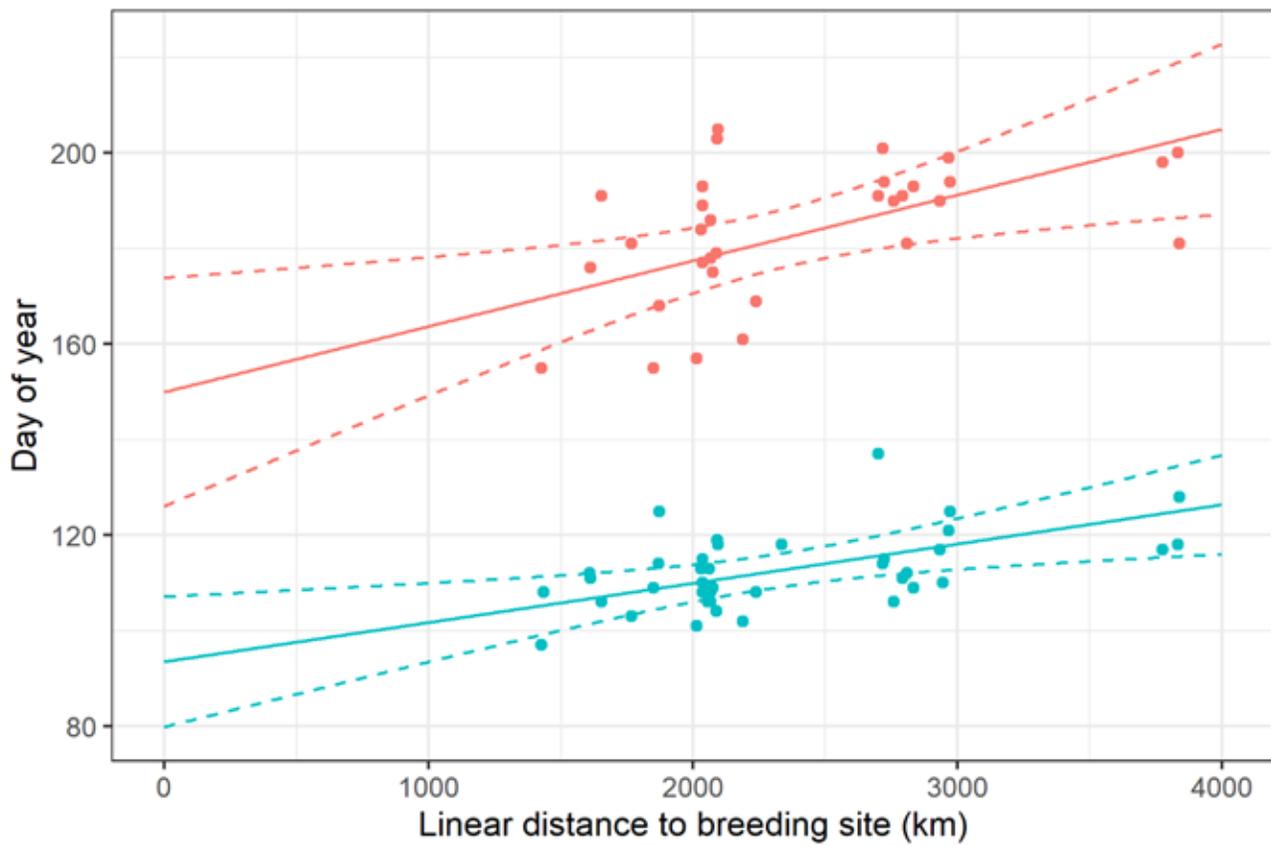


Figure 7

Day of year of departure (blue) and arrival (red) in relation to linear distance to the breeding site. Solid line: model curve; dashed lines: 95% confidence intervals.

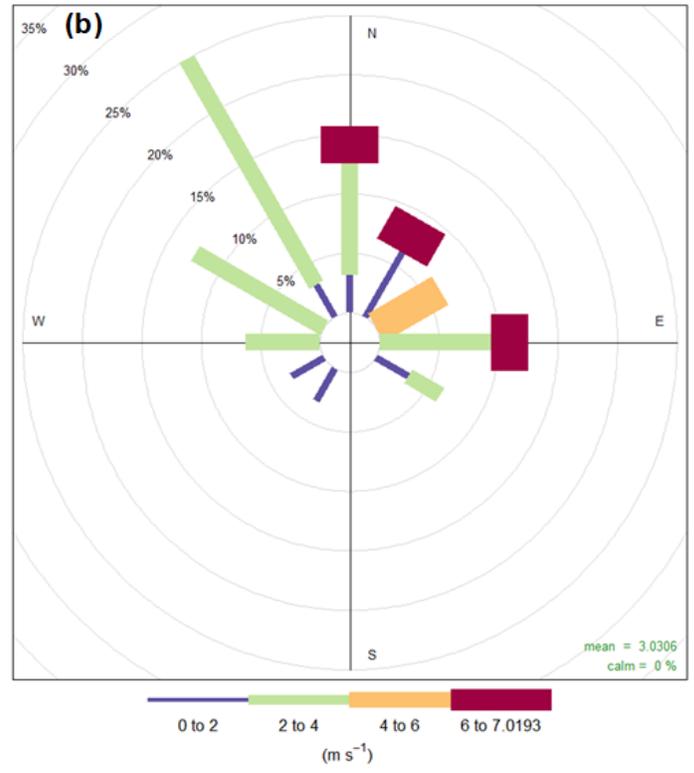
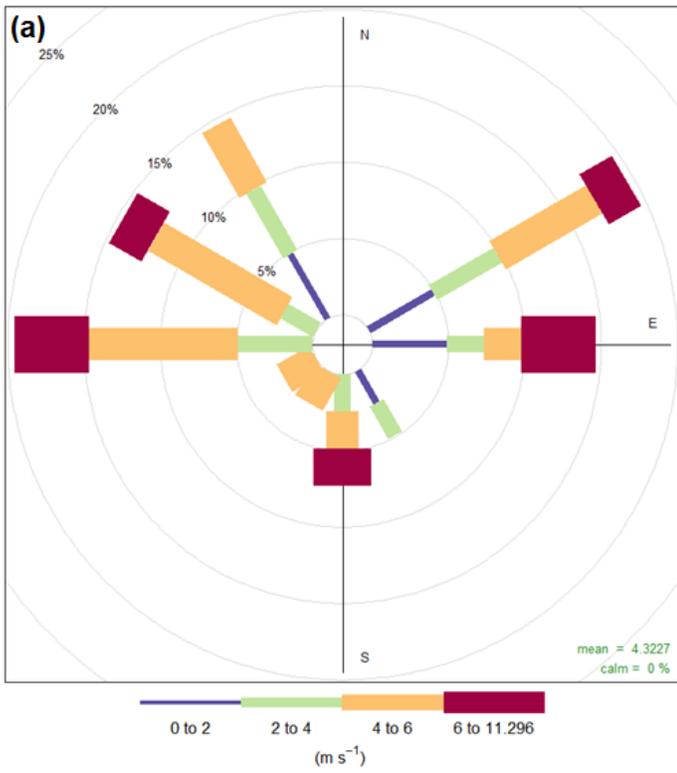


Figure 8

Frequency distribution of mean wind directions and wind forces (ms⁻¹) in the period 90 min before to 90 min after curlew departure (a) and arrival (b).

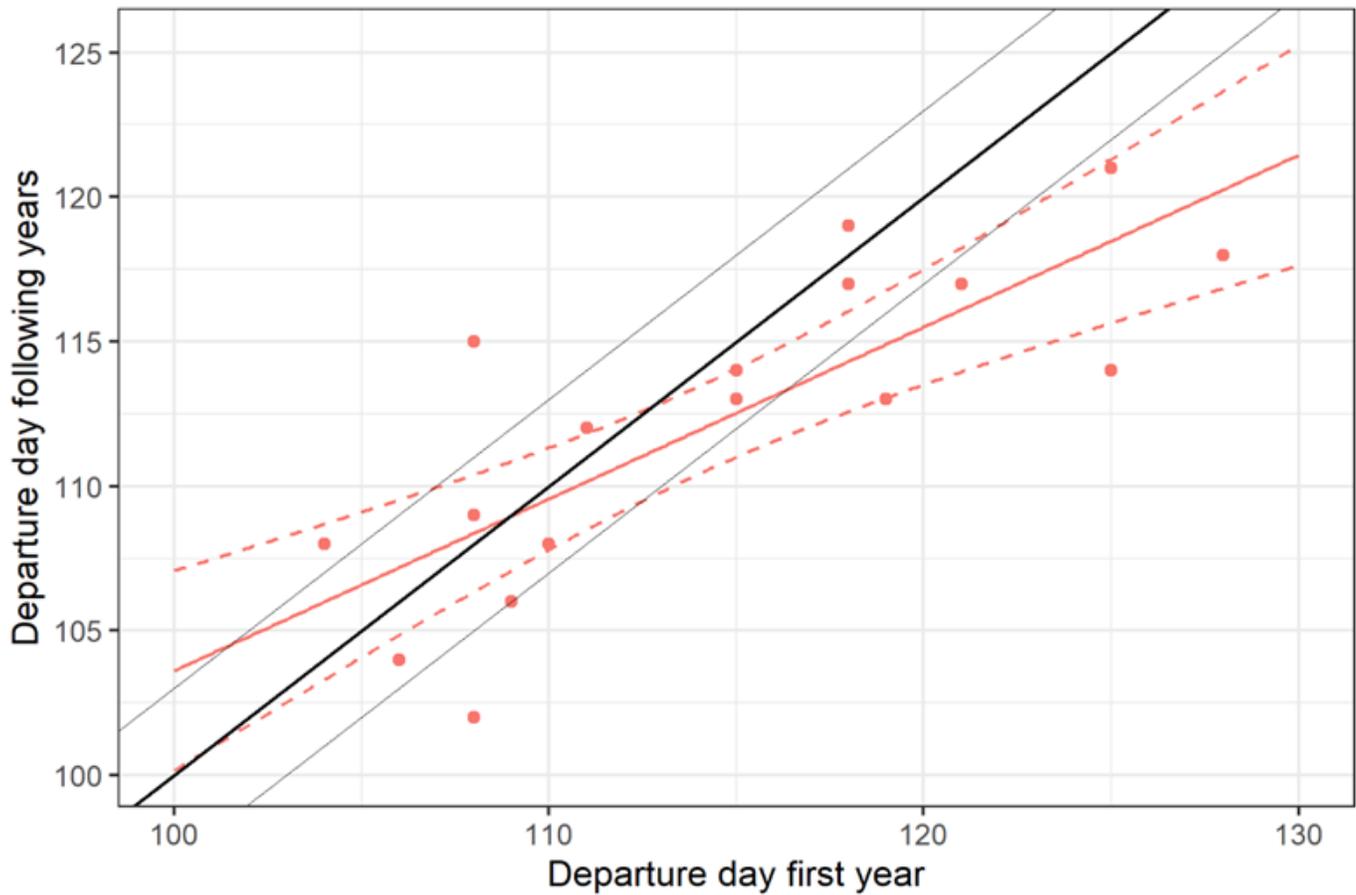


Figure 9

Departure days in successive years. Red solid line: model curve; dashed lines: 95% confidence intervals, bold black line indicates 1:1 relationship, thin black lines depict departure days 3 days before or after this.

Supplementary Files

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