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Migration routes and strategies of Grey Plovers (*Pluvialis squatarola*) on the East Atlantic Flyway as revealed by satellite tracking

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Abstract

Background: While the general migration routes of most waders are known, details concerning connectivity between breeding grounds, stopover sites and wintering grounds are often lacking. Such information is critical from the conservation perspective and necessary for understanding the annual cycle. Studies are especially needed to identify key stopover sites in remote regions. Using satellite transmitters, we traced spring and autumn migration routes and connectivity of Grey Plovers on the East Atlantic Flyway. Our findings also revealed the timing, flight speed, and duration of migrations.

Methods: We used ARGOS satellite transmitters to track migration routes of 11 Grey Plovers that were captured at the German Wadden Sea where they had stopped during migration. Birds were monitored for up to 3 years, 2011–2014.

Results: Monitoring signals indicated breeding grounds in the Taimyr and Yamal regions; important staging sites on the coasts of the southern Pechora Sea and the Kara Sea; and wintering areas that ranged from NW-Ireland to Guinea Bissau. The average distance traveled from wintering grounds to breeding grounds was 5534 km. Migration duration varied between 42 and 152 days; during this period birds spent about 95% of the time at staging sites. In spring most plovers crossed inland Eastern Europe, whereas in autumn most followed the coastline. Almost all of the birds departed during favorable wind conditions within just 4 days (27–30 May) on northward migration from the Wadden Sea. In spring birds migrated significantly faster between the Wadden Sea and the Arctic than on return migration in autumn (12 vs. 37 days), with shorter stopovers during the northward passage.

Conclusions: Our study shows that satellite tags can shed considerable light on migration strategies by revealing the use of different regions during the annual cycle and by providing detailed quantitative data on population connectivity and migration timing.

Keywords: Annual cycle, Long-distance migration, Migration speed, Migration strategy, Migration timing, Satellite transmitters, Shorebirds, Tracking, Stopover

Background

Many shorebird species on the East Atlantic Flyway (EAF) are declining, especially species feeding on benthic invertebrates (van Roomen et al. 2015, 2017). This is particularly evident at the Wadden Sea which is the most important resting site for waders on the EAF. Here, nearly half of wader and waterbird species have declined over the past three decades (Blew et al. 2016). The driving factors are unclear (Ens et al. 2009) because most of the affected species are long-distance migrants that also rely on other stopover sites during their travels. Similar reliance on stopovers occurs among waders elsewhere as on the East Asian-Australasian Flyway (Battley et al. 2012; Conklin et al. 2013; Gill et al. 2014; Lisovski et al. 2016; Johnson et al. 2017); in the Americas (Niles et al. 2012; Page et al. 2014; Senner et al. 2014; Johnson et al. 2016)

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and recently also revealed by studies on the EAF (Rakhimberdiev et al. 2016). Notably, some waders are remarkably able to migrate over vast distances without stopping over (e.g. Gill et al. 2009; Johnson et al. 2011).

The Grey Plover (*Pluvialis squatarola*) provides an excellent example to study migration strategies of waders on the EAF. In Eurasia it inhabits the southern tundra eastwards from the Kanin Peninsula to the Bering Sea (Lappo et al. 2012). While birds of central (and eastern) Siberia follow a flyway across the Black Sea and eastern Mediterranean into East Africa, the Grey Plovers of western Siberia and northwestern Russia follow the EAF across western Europe into western Africa (Branson and Minton 1976; van Dijk et al. 1986; Exo and Stepanova 2000; Engelmoer 2008; van Roomen et al. 2015). This population decreased between the 1990s and 2014 by c. 20% (van Roomen et al. 2015). About 70% of the EAF population uses the Wadden Sea for stopover (Blew et al. 2016) but nothing is known whether and which other sites along their flyway are used. Recent developments in tracking technology (Bridge et al. 2011; Exo et al. 2013) make it possible to study the migration of Grey Plovers.

Therefore, we conducted a pilot study on the spatial and temporal patterns of Grey Plover migration using satellite transmitters. For the first time we determined spring and autumn migration routes of individual Grey Plovers on the EAF, the locations of their breeding, staging and wintering grounds, as well as the timing, speed and duration of the entire migration. Analysing different speed and duration variables for differences between the migration seasons is important to understand ecological constraints (e.g. Schmaljohann 2018). If birds follow a time-minimizing strategy sensu Alerstam (Alerstam and Lindström 1990; Alerstam 2011) we expect faster migration in spring as compared to autumn because spring migrants may be forced to arrive at breeding grounds as early as possible to benefit from higher reproduction opportunity (Kokko 1999). As overall migration speed is basically due to the number of stopovers and their durations rather than flight speed, we expect that spring migrants undertake less and/or shorter stopovers than autumn migrants. Furthermore, we expect that spring migrants do not follow the shortest migration route (great circle route; Alerstam 2001) between the Wadden Sea and their northern Siberian breeding grounds rather follow a more southerly, longer but inland migration route with more predictable stopover sites and better habitat availability as some other wader species do (Green et al. 2002; Green 2004).

Materials and methods

Satellite tracking

In 2011 and 2012, 14 Grey Plovers were captured at a coastal roosting site in the Lower Saxon Wadden Sea, Germany (53.71°N, 7.95°E; cf. Fig. 1). One bird was caught in autumn, all others in spring (Table 1). Birds were caught during night at high-tide roosts using mist-nets in combination with tape playbacks, uniquely colour-ringed and equipped with solar powered satellite transmitters. Each bird was aged and sexed according to plumage characteristics (Byrkjedal and Thompson 1998; Meissner and Cofta 2014). Birds were released between 15 and 30 min after capture.

For tagging we used solar powered 5 g ARGOS PTT (PTT: platform transmitter terminal), measuring 24 × 14 × 7.5 mm (L × W × H; PTT 100 series, Microwave Telemetry Inc., Columbia, MD). In order to minimize the aerodynamic drag (Pennycuick et al. 2012), transmitters were attached to the lower back using a leg-loop harness made from 5 mm wide Teflon® ribbon (Bally Ribbon Mills, PA). To prevent the solar panels from being covered by feathers we designed a particular casserole shaped plastic shield using 0.4 mm thin PET (Polyethylene terephthalate) or Darvic. The shields weighed only 0.5 g and 0.7 g, respectively (for details see Hillig et al. 2012). We glued a shield to the bottom of the transmitter and one small neoprene pad under the shield to raise the construction slightly. In total, the PTTs plus shield, one neoprene pad and the Teflon® ribbon weighed c. 7.3 g. Body mass of the tagged Grey Plovers ranged between 175 g and 300 g (mean ± SD 218.1 ± 31.5 g, $N = 14$). According to Zwarts et al. (1990) the 175 g resemble approximately the fat free mass of Grey Plovers. Thus, we loaded the birds by 4.2% of fat-free mass, and on average by 3.4 ± 0.4% (mean ± SD, $N = 14$) of mass at capture.

All transmitters were programmed to a standard duty cycle of 10 h ON followed by 48 h OFF to recharge the batteries. This duty-cycle enabled tracking of up to 3 years, but the long OFF periods (48 h) hampered some of the analyses, e.g. of the number of stopovers (see below). Location data were obtained from Collecte Localisation Satellites (CLS; for details see CLS 2012). The Argos data were stored in the free online database Movebank (https://www.movebank.org; Douglas et al. 2012).

Data analysis

Locations were estimated using Doppler geolocations. Thus location errors can range from a few tens of metres up to hundreds of kilometres (CLS 2012; Douglas et al. 2012). To exclude implausible locations and to improve location accuracy the Douglas Argos-filter algorithm (DAF) was used, with the filtering method of distance, angle and rate (DAR) as implemented in Movebank (Douglas et al. 2012).

Plausibility of auxiliary positions was assessed based on movement rates, turning angles and spatial redundancy. To analyse long-distance migration we used the following user-defined thresholds (for a detailed description of the parameters see Douglas et al. 2012):

- keep_lc = 1: Each location was assigned to one of seven accuracy classes by CLS (CLS 2012). All locations belonging to the most accurate standard classes (LC ≥ 1) were retained, i.e. positions with an accuracy of < 1500 m (LCs 3, 2, 1 have a nominal error of up to 1.5 km),
- maxredun = 25 km: consecutive locations within a distance of < 25 km were retained,
- minrate = 120 km/h: locations with a maximum movement rate of 120 km/h (including potential assistance by winds) were retained,
- ratecoef = 15: this parameter evaluates the angle among three consecutive locations.

For home range analysis we considered more accurate positions, therefore we used the following thresholds: keep_lc = 3 (LC 3 accuracy < 250 m), maxredun = 10 km, minrate = 80 km/h and ratecoef = 15.

To depict the migration routes and stopover sites the 'best of duty cycle' option was used, i.e. the most accurate available position per 10 h transmission period. Stopovers were defined as times when a bird showed non-directional movements of < 20 km. Accordingly, travel days were defined if a bird moved more than 20 km towards the migration goal. Migration routes as well as stopover sites were visualized by using ArcMap 10.0 (https://www.esri.de/).

All distances were calculated as great circle routes (orthodrome = shortest distance) (Imboden and Imboden 1972) using the best of duty cycle locations. Total migration distances were estimated as the sum of the distances between consecutive best of duty cycle positions. The great circle approach implies that the calculated flight distances underestimate the actual distances flown.

To analyse the seasonal scheduling we used the last dates on which individual Grey Plovers were recorded at their breeding, wintering or staging sites for departure from the respective site, and the first fix from the breeding, wintering or staging grounds for arrival. Accordingly, staging duration in different areas was calculated as the number of days between the first and last record at one site. Given the transmission periods of the PTTs, especially the comparatively long OFF-cycle periods (48 h), most dates are accurate within ± 2–3 days. Where it was not possible to determine departure and/or arrival dates, the data were excluded from further analyses.

Total speed of migration (km/day) was calculated as the total migration distance divided by the total migration duration, including stopover times. Travel speed is the average distance covered on travel days only. Although PTT transmission phases were short (10 h ON), we could calculate some flight speeds. Flight speed (speed above ground) was calculated based on the distance and the time interval between three consecutive bearings during phases of flight. Migration speed, travel speed and flight speed, respectively, are minimum estimates, since we assumed a direct flight path between the fixes. The same applies to the total number of stopovers per migration period and the number of stopover days. Because of the long intervals between transmission periods (48 h) short interruptions (< 2 days) could not be identified. Thus the number of stops could be slightly underestimated, in turn the number of migration days slightly overestimated. Checking all routes visually indicates that the number of missed stopovers was probably low.

Statistical analyses

Because of the relatively low sample sizes, we give median values, unless otherwise stated. Calculating median values, the data of the 2nd calendar year birds were excluded. For between season and route comparisons, we applied the non-parametric Mann–Whitney *U*-test. Spearman's rho correlation analyses were performed to check for relationships between arrival dates on Arctic breeding grounds and different migration variables. All analyses were run in IBM SPSS Statistics 24.

Results

Three of the 14 transmitters failed to work within the first four weeks after mounting. These birds were excluded from all further analyses. Eight of the remaining 11 birds were tagged as adults; three as 2nd calendar year birds (Table 1). One PTT transmitted locations for more than 35 months (PTT # 104701; last satellite transmission 14.01.2014, last observation 27.01.2015, still carrying the transmitter; Yves La Ball pers. comm.). In total, they provided 12,732 Argos Doppler locations (31.03.2011–14.01.2014) of which 9389 (73.7%) remained after filtering.

Breeding and winter locations

Most adult Grey Plovers arrived at Russian breeding grounds in the first half of June and departed around mid-July (Additional file 5: Table S2). During the breeding season, four of the seven spring tagged adult Grey Plovers stayed on Taimyr two birds in two consecutive

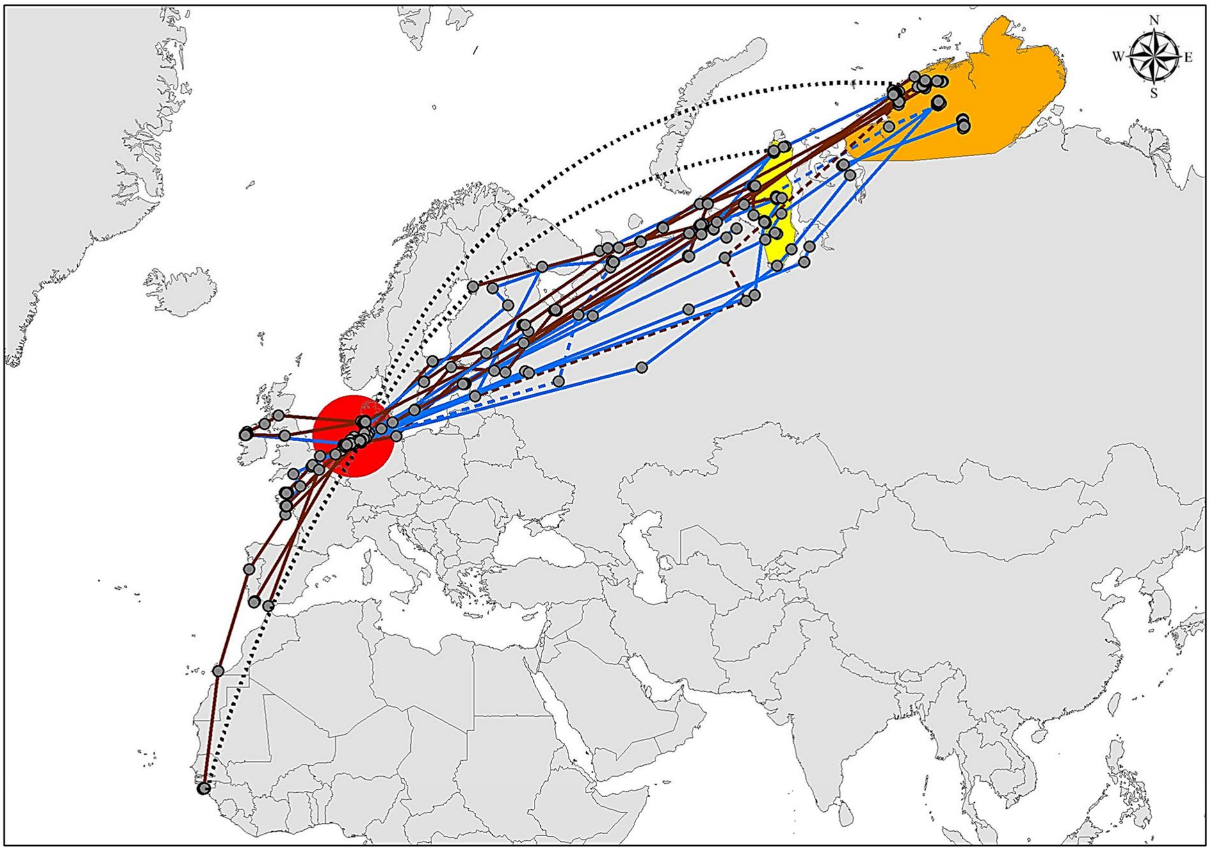

Fig. 1 Spring (blue) and autumn (brown) migration routes of satellite-tagged Grey Plovers marked on migration in the Lower Saxon Wadden Sea, Germany. The location of the Wadden Sea is highlighted by a large red dot. Grey dots represent Argos 'best of duty cycle' positions, and lines connect subsequent fixes. Dashed lines denote the spring and autumn migration routes of a 2nd calendar year bird; curved black dotted lines represent great circle routes between the Wadden Sea and breeding sites on Yamal (c. 3400 km, yellow highlighted) and Taimyr (c. 4000 km, orange highlighted) as well as between the Wadden Sea and a wintering site in Guinea Bissau (c. 5000 km; map: Mercator projection)

years, the other three on Yamal (Fig. 1, Table 1; Additional file 3: Fig. S3).

Of the three 2nd calendar year birds two oversummered in the Wadden Sea, and the other migrated to Taimyr (PTT # 104699, Table 1). Compared to adults this bird arrived late, on June 30, 2011 (Additional file 5: Table S2). It stayed on Taimyr for about three weeks at two different locations, about 400 km apart. In the following year, it visited these areas again, but arrived 26 days earlier than the previous year.

Wintering grounds could be determined in six Grey Plovers (Table 1). They ranged from NW-Ireland to Guinea Bissau (Fig. 1; Additional file 3: Fig. S3): one female Grey Plover wintered at Donagal Bay, NW-Ireland in two consecutive years; one male stayed in the Wadden Sea; two birds wintered in two and four, respectively, years at the coast of Brittany, France; one adult male moved to S-Portugal (data transmission stopped on 27.11.2012 indicating it's presumed wintering ground); and one adult female migrated to Guinea Bissau. The birds stayed at the wintering grounds between three and seven months (Additional file 5: Table S2). During the winter all birds used rather confined areas, usually of less than c. 5×5 km (Additional file 1: Fig. S1). Relocations were not recorded.

Migration routes

In total, seven complete autumn migration routes of five birds and four complete spring migration routes of three birds were obtained (Table 1, Fig. 1; Additional file 2: Fig. S2). Seven birds provided nine tracks from the Wadden Sea to the Arctic breeding grounds, five birds seven tracks from the Arctic to the Wadden Sea. On average, adult Grey Plovers covered a distance of 5534 km (median, range 4586–6626 km, $n = 10$ birds respectively tracks, Table 2; Additional file 4: Table S1a) between their breeding and wintering areas. Total duration of migration varied between 42 days and 152 days.

Table 1 Overview of the records obtained by satellite telemetry of Grey Plovers caught in the Lower Saxon Wadden Sea (WS), Germany

ID	Age	Sex	Tracking period		Spring	Location breeding season	Autumn		Location winter season	Spring
			Start	End	WS-Arctic		Arctic-WS	WS-winter		Winter-WS
104699	2nd		05.04.2011		x	Taimyr	x	x	Brittany	x
				31.03.2013	x	Taimyr	x	x	Brittany	
104701	2nd		05.04.2011			Wadden Sea		x	Brittany	x
					x	Taimyr	x	x	Brittany	x
				14.01.2014	x	Taimyr	x	x	Brittany	
104704	2nd	f	05.04.2011			Wadden Sea		x	NW-Ireland	x
				02.12.2012	x	Jamal	x	x	NW-Ireland	
104703	ad	f	02.04.2011	09.06.2011	(Petchora)					
113996	ad	f	22.05.2012	13.08.2012	x	Jamal	(Sweden)			
113997	ad	m	19.04.2012	27.06.2012	(Petersburg)					
113998	ad	m	19.04.2012	09.09.2012	x	Jamal	(Bothnian Bay)			
113999	ad	m	24.04.2012	21.01.2013	x	Taimyr	x	x	Wadden Sea	
114001	ad	m	22.05.2012	27.11.2012	x	Taimyr	x	x	Portugal	
114002	ad		20.05.2012	08.07.2012	(Karelia)					
104700	ad	f	01.08.2011	11.03.2012				x	Guinea-Bissau	

For the tracking period, the first and last date after applying the Douglas Argos-filter (DAF) are given; for the 2nd year birds (2nd) the oversummering locations are specified. If transmitters failed on migration the last locations are given in parenthesis

Wadden Sea to and from wintering grounds

Migration routes between the wintering grounds and the Wadden Sea concentrated usually on a narrow corridor along the West African and West European Atlantic coast, respectively (Fig. 1). One adult female (PTT # 104700) wintering near Ilha de Boloma, Guinea-Bissau, crossed the Bay of Biscay, stopped over for about a week at the Spanish and Portuguese Atlantic coast before continuing in a presumed non-stop flight of about 3400 km over the open sea and along the African Atlantic coast into its wintering ground. The two birds that wintered on the French Atlantic coast (PTT # 104699, PTT # 104701) migrated either directly from the Wadden Sea into their wintering grounds, or made a detour with a stopover of 3–8 days at the east coast of England (Additional file 2: Fig. S2).

The total distances travelled between wintering grounds and the Wadden Sea varied between 792 km (PTT # 104699) and 5375 km (PTT #104700) (Table 2; Additional file 4: Table S1c), which is, on average, c. 5% longer than the respective great circle route (shortest distance) of 787 km and 5118 km.

Wadden Sea to and from breeding grounds

During northward migration from the Wadden Sea to Arctic breeding grounds in spring five of seven adult Grey Plovers migrated over land south of the Gulf of Finland, south of Lake Ladoga and Lake Onega to the Ob river estuary on Yamal and from there further to Taimyr (Table 1, Fig. 1; Additional file 2: Fig. S2). The southernmost route proceeded at a distance of up to 800 km from the coast of the Barents Sea (PTT # 113999, Additional file 2: Fig. S2b). In contrast to spring, during autumn migration most birds followed the coastline, except one adult female (PTT # 104704, Additional file 2: Fig. S2a) which migrated further inland.

The migration distance between the Wadden Sea and the Arctic breeding grounds of adult birds was on average 4467 km ($n = 8$ tracks) during spring and 4491 km ($n = 8$ tracks, Table 2; Additional file 4: Table S1b) in autumn, respectively, being, on average about 10% longer than the shortest possible route.

One Grey Plover migrated to Taimyr in its 2nd calendar year (PTT # 104699, Fig. 1; Additional file 2: Fig. S2c). It flew northbound alongside the coast, southbound across the interior of Northern Russia and Eastern Europe. In contrast, a year later on northbound migration the bird migrated across the European continent. During subsequent autumn migration from Taimyr to the Wadden Sea the bird followed the coastline, thus using different routes on northbound and southbound migration as well as in two consecutive years.

Stopovers

All Grey Plovers marked with PTTs in the Lower Saxon Wadden Sea re-visited the Wadden Sea during all subsequent migration periods (Additional file 3: Fig. S3). During spring migration the birds stayed there for 46–82 days, on autumn migration between 2 days and

Table 2 Distance and duration of major migratory movements for 11 satellite-tracked Grey Plovers, 2011–2014

	Total migration distance (km)	Max. nonstop flight (km)	Number of stopover sites	Number of travel days	Number of stopover days	Migration speed (km/day)	Travel speed (km/day)
(a) Entire route wintering—breeding sites							
Spring							
Median	5533	2147	6	4	77	70	1309
Min	5013	1171	3	4	72	50	903
Max	5640	3611	7	6	97	71	1425
Autumn							
Median	5453	2977	5	6	46	111	891
Min	4586	1964	4	4	20	35	575
Max	6626	3510	6	10	145	244	1380
(b) Wadden Sea—breeding sites							
Spring							
Median	4467	3346	2	4	7	480	1358
Min	3827	1171	1	2	0	186	836
Max	5232	3978	5	6	18	1550	1752
Autumn							
Median	4491	3011	3	4	31	120	1181
Min	3598	1964	2	3	8	105	513
Max	4727	3510	6	9	39	373	1373
(c) Wadden Sea—wintering sites							
Spring							
Median	970	566	1	1	6	188	1312
Min	792	409	0	1	0	80	1284
Max	1041	1041	1	1	11	1041	1370
Autumn							
Median	1167	947	1	1	0	912	1400
Min	900	778	0	1	0	199	1052
Max	5375	3408	2	4	9	1937	1937

Distance and duration between (a) wintering and breeding sites, (b) the Wadden Sea and Arctic breeding sites, and (c) the Wadden Sea and the wintering sites. Migration speed (km/day) is the overall migration speed, including stopover times; travel speed (km/day) is the average distance covered on travel days only. Given are the median, minimum and maximum values; for individual datasets and sample sizes see Additional file 5: Table S2

106 days (Additional file 5: Table S2). One male wintered in the Wadden Sea (PTT # 113999), staying there at least from beginning of September till mid-January, before the PTT failed due to low battery charge.

No Grey Plover flew non-stop between the Wadden Sea and the Arctic breeding grounds. Adults made at first a non-stop flight of on average 3346 km (median, range 1171–3978 km, $n=8$ tracks; Additional file 4: Table S1b) into a first stopover area. Subsequent flights to the next stopover site or to the breeding site were much shorter (Fig. 1; Additional file 2: Fig. S2). Before leaving the Arctic, most Grey Plovers made several rests alongside the Russian coast (Additional file 3: Fig. S3), on average for 21 days (median, range 15–31 days, $n=7$) before embarking to a non-stop flight to the Wadden Sea. During autumn migration non-stop flight distances varied between 1964 km and 3510 km (median 3011 km, $n=6$ tracks).

During migration between the Wadden Sea and the Arctic adult Grey Plovers visited on average two ($n=8$ tracks; Additional file 4: Table S1b) stopover sites during spring migration and three ($n=6$ tracks) during autumn migration (Table 2, Mann–Whitney U-test, $U_{8,6}=32.5$, $p=0.282$). During autumn migration birds rested significantly longer than during spring migration (31 vs. 7 days, $U_{8,6}=44$, $p<0.008$). Birds following the Russian coast on spring migration used slightly more stopover sites than birds migrating across the continent (median 5 vs. 1 stopover site, $U_{5,3}=1.5$, $p<0.07$; Fig. 2).

Previously unknown staging sites between the Wadden Sea and the Arctic were (Additional file 3: Fig. S3): (1) the coast of the Pechora Sea (southeastern Barents Sea) for spring and autumn, (2) the coasts of the southern Kara Sea and of the Yamal Peninsula during both migration

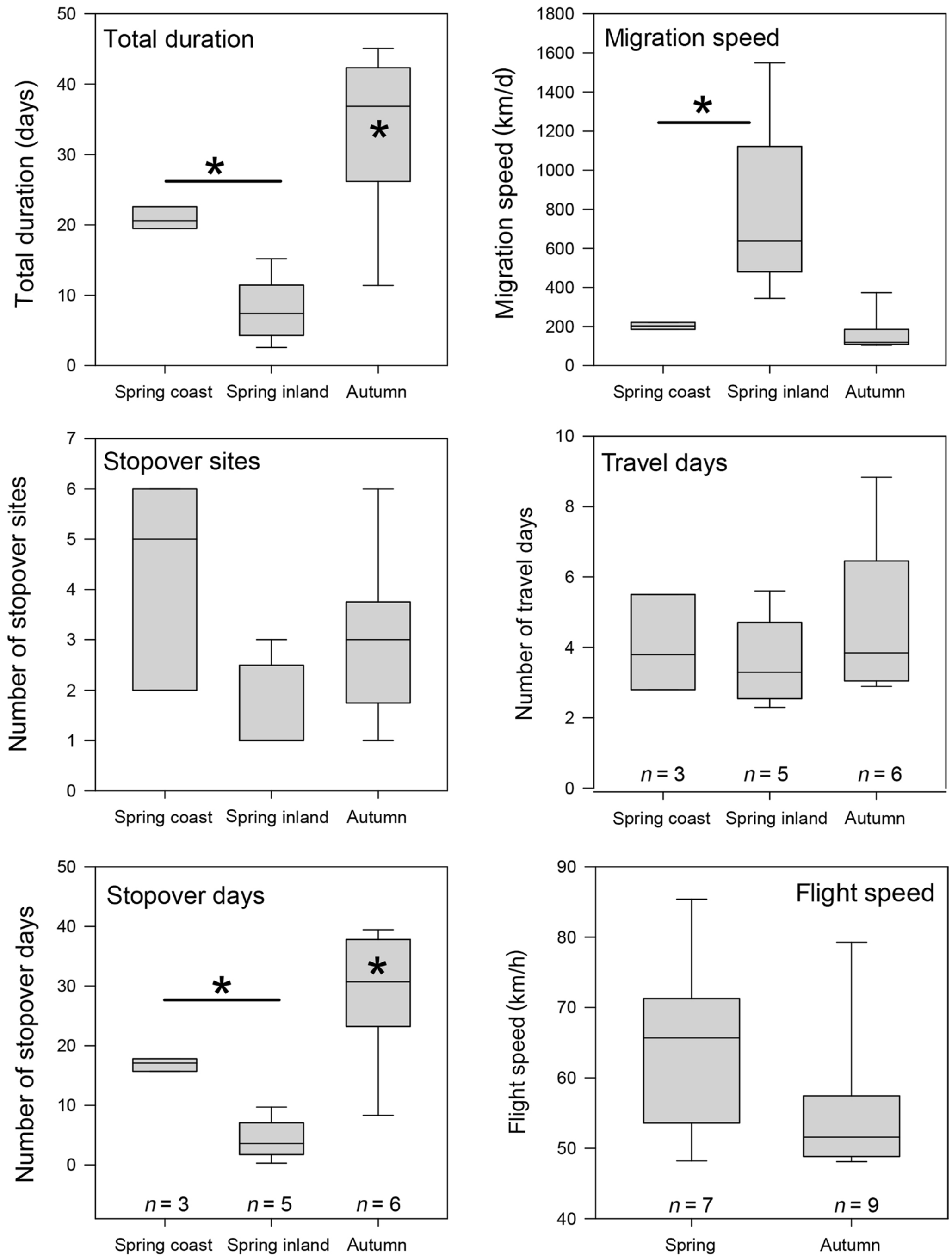

Fig. 2 Boxplots summarizing migration parameters for satellite-tagged Grey Plovers migrating between the Wadden Sea and Arctic breeding sites. Data for spring migration are split according to the route, inland versus coastal migration (cf. Fig. 1, Additional file 2: Fig. S2). Stars indicate significant differences between the inland and coastal route on spring migration; stars within the 'autumn box' indicate significant differences between spring and autumn migration (for details see text). The boxplots show the median as horizontal line in boxes, the 1st and 3rd quartiles and the minimum and maximum values

periods, and (3) the coasts of the White Sea in spring and of the Baltic Sea in autumn.

Flight speed, migration speed

Flight speed varied between 48.1 km/h and 85.4 km/h ($n=16$ records, 8 birds; Fig. 2). Flight speed for spring migration averaged 65.7 km/h ($n=7$ records, 6 birds) and was 27.3% higher than during autumn migration (51.6 km/h, $n=9$ records, 7 birds; $U_{7,9}=15$, $p<0.09$).

Total spring migration from wintering grounds to breeding areas, including stopover times in the Wadden Sea, took 81 days (range 78–101 days, $n=4$; cf. Additional file 5: Table S2). Autumn migration from Arctic breeding areas to wintering grounds lasted 51 days (range 42–152 days, $n=5$; $U_{5,4}=8$, $p=0.730$). Grey Plovers spent 95% (79–96%; $n=9$) of the total migration time at staging sites, without seasonal differences (spring 95%, $n=4$, autumn 91%, $n=5$). For about 70% of the total migration time Grey Plovers spent in the Wadden Sea. Total migration duration did not correlate with the distance between breeding and wintering grounds (Spearman's rho correlation, $R_S=-0.117$, $n=9$).

In spring Grey Plovers migrated significantly faster between the Wadden Sea and the Arctic breeding areas than on return migration in autumn, 12 days ($n=8$) versus 37 days ($n=6$; $U_{8,6}=44$, $p<0.008$; Fig. 2). While there was hardly any difference in the number of travel days (spring vs. autumn: 3.6 vs. 3.8 days, $U_{8,6}=32$, $p=0.345$, Table 2), on northward migration adult plovers rested on average for 7 days, on southward migration 31 days ($U_{8,6}=44$, $p<0.008$). Grey Plovers migrating alongside the Russian coast during spring migration stopped over more frequently (see above) and for longer times than birds using an intra-continental route (17 vs. 4 stopover days, $n=3$ vs. $n=5$, $U_{3,5}=15$, $p<0.03$). Hence, birds crossing the mainland migrated faster, 638 km/day and 203 km/day, respectively ($U_{5,3}=0$, $p<0.036$). The maximum recorded migration speed added up to about 1550 km/day (PTT # 113998), on spring migration from the Wadden Sea to Yamal (Additional file 4: Table S1b).

Time schedule

Adult Grey Plovers arrived in their potential breeding areas between June 1 (PTT # 113998) and June 21 (PTT # 104704, Fig. 3; Additional file 5: Table S2). Departure dates scattered over a wider period than arrival times: First birds left Yamal already end of June (June 27, PTT # 113998), others not before beginning of August (August 2, PTT # 104701). In 2012, the majority of birds departed already around mid-July (median July 14, $n=8$). Adult Grey Plovers spent on average 35 days (range 16–46 days, $n=8$) at their potential breeding sites.

Only one Grey Plover (PTT # 104701 in 2013) departed directly from Arctic breeding sites to the Wadden Sea. The majority of birds left their breeding sites and remained for about three weeks (mean ± SD: 21 ± 6 days, $n=7$), usually about 200 km (median, range 40–400 km, $n=6$ tracks) apart at the adjacent coast before departure from the Arctic ultimately (Additional file 3: Fig. S3). Grey Plovers left the Arctic between July 25 and August 13 (median: 31.07./01.08., $n=8$).

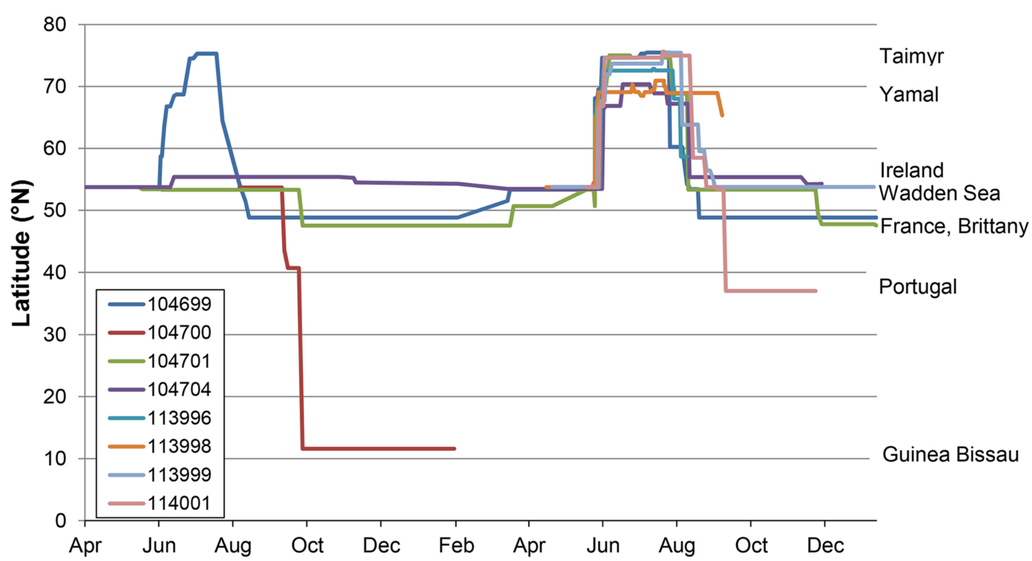

Fig. 3 Seasonal movements of eight satellite-tracked Grey Plovers by latitude, April 2011 to December 2012. The main whereabouts are named on the right-hand side

The majority of birds arrived at the Wadden Sea around mid-August (median 14.08., August 07 to September 05, $n=6$; Additional file 5: Table S2), and left the Wadden Sea around mid-September. One female (PTT # 104704) wintering in two consecutive years in Northern Ireland left the Wadden Sea in both years not before mid/end of November. First birds completed autumn migration already by mid-August (PTT # 104699), others not before end of November/beginning of December.

Grey Plovers left their wintering grounds between mid and end of March (March 10–30; Additional file 5: Table S2). In both years the majority of tracked Grey Plovers (7 out 9 birds, 78%) departed from the Wadden Sea within just four days, 27–30 May (median 28.05., range 23.05.–01.06., $n=10$).

In 2012 eight Grey Plovers were tracked during departure from the Wadden Sea. Until May 27 constant headwinds of 14–25 km/h at sea level prevailed in the Wadden Sea, on May 28 wind directions changed from northeastern directions to western directions, both at the ground as well as at 1500 m a.s.l. (weather data were obtained from the Env-DATA tool by Movebank; https://www.movebank.org). Most plovers (75%, 6 out of 8) departed from the Wadden Sea after the change in wind direction, i.e. when wind favoured migration to the Arctic. The birds departed getting assistance from westerly winds of about 14–36 km/h at sea level and 25–50 km/h at 1500 m a.s.l. Only two birds started earlier when headwinds prevailed.

Even though the birds departed in a narrow time slot from the Wadden Sea arrival dates on Arctic grounds differed considerably, adults reached their breeding sites between June 01 and June 21 (median 09.06., $n=8$; Fig. 3; Additional file 5: Table S2). Correlation analyses showed a significant positive relationship between the arrival dates and the number of stopover days ($R_S=0.922$, $n=8$, $p<0.0001$) and a weak negative relationship between arrival dates and travel speed ($R_S=-0.635$, $N=8$, $p=0.072$). Departure dates ($R_S=0.382$, $p=0.321$), total migration distance ($R_S=0.024$, $p=0.931$) and the number of travel days ($R_S=0.479$, $p=0.230$) did not show significant relationships with arrival dates.

Discussion

Migration routes, migration patterns

This tracking study confirms former evidence about the general migration routes as well as about the locations of the breeding and wintering grounds of Grey Plovers on the EAF (Branson and Minton 1976; Smit and Piersma 1989; Exo and Wahls 1996; Byrkjedal and Thompson 1998; Exo and Stepanova 2000; Engelmoer 2008; Delany et al. 2009; Bairlein et al. 2014). However, using satellite transmitters we could map spring and autumn migration routes of individual birds for the first time. As expected, Grey Plovers resting in the German Wadden Sea stayed during the breeding season either on Yamal or on Taimyr, eastwards to c. 100°E. Wintering grounds stretched from Northern Ireland over the Wadden Sea all the way to Guinea Bissau in West Africa. Three male Grey Plovers deployed with geolocators on Kolguev Island (c. 69°05′N, 49°55′E, Barents Sea, RU; Klaus-Michael Exo unpubl. data) spent the winter at the West African coast, in the Western Sahara, Sierra Leone respectively Guinea; another colour-ringed bird was observed in Mauritania (25.11.2011, Harry te Horn pers. comm.). Throughout the annual cycle these birds travelled between 14,000 km and 17,000 km. As shown by mid-winter counts, all identified wintering grounds hold particularly large numbers of Grey Plovers (Delany et al. 2009; van Roomen et al. 2017).

The satellite tracking provided novel information on the migration routes, especially on migration across the Russian tundra and on previously unknown stopover sites along the Russian Arctic coast. In addition, we were able to prove that Grey Plovers used different routes during spring and autumn migration. On northward migration from the Wadden Sea to Arctic breeding grounds most Grey Plovers crossed inland Eastern Europe and Western Russia to reach their breeding grounds, in contrast on southward migration from the Arctic to the Wadden Sea most birds followed the coastline (Fig. 1). Therefore, in spring Grey Plovers migrated on a much wider front than on autumn migration. This is in contrast to previous observations that Grey Plovers on the EAF follow a narrower corridor in spring than in autumn and that they are far less common over inland Europe in spring than in autumn (Byrkjedal and Thompson 1998). On the EAF similar differences were observed in White-fronted Geese (*Anser albifrons*) (e.g. Kölzsch et al. 2016).

Migrating from the Wadden Sea to southern wintering grounds Grey Plovers followed approximately the great circle route, but crossing the European continent on northward migration from the Wadden Sea to Arctic breeding grounds means, Grey Plovers did not minimize the migration distance. In spring the migration route was on average about 10% (400 km) longer than the great circle route. A detour of c. 10% is in the same order of magnitude as for other species (e.g. Alerstam 2001), including Pacific Golden Plovers crossing the Pacific Ocean from Hawaii to Alaska (Johnson et al. 2011) and Dark-bellied Brent Geese (*Branta bernicla bernicla*) migrating from wintering grounds in The Netherlands to breeding sites on Taimyr (Green et al. 2002). Even if the birds make a deviation of c. 400 km, according to Prokosch (1988) Grey Plovers might reach their breeding grounds on Taimyr in one non-stop flight (cf. Serra et al. 2006). Assuming an average body mass of about 330 g end of May, Grey Plovers are able to fly c. 5200 km non-stop. The heaviest birds, birds of about 380 g, are predicted to be able to fly over 6500 km, and these birds may reach sites east of Taimyr without refueling (Prokosch 1988). But, none of our tracked Grey Plovers flew non-stop from Wadden Sea staging sites to Arctic breeding grounds. The longest non-stop flights from the Wadden Sea were performed by two male Grey Plovers flying non-stop c. 4000 km towards the breeding sites (PTT # 114001, PTT # 113999, Additional file 4: Table S1b). The recorded non-stop distances are in the lower range of the values recorded for waders (see review by Conklin et al. 2017). On transoceanic flights Pacific Golden Plovers covered distances of up to 9370 km within one non-stop flight (Johnson et al. 2015) and American Golden Plovers (*P. dominica*) of > 6000 km (Conklin et al. 2017). On the EAAF some satellite-tagged Grey Plovers flew over 7000 km non-stop on northward migration from Australia (Flaherty 2017). Thus, the capability of Grey Plovers for non-stop flights might be much greater than recorded on the EAF.

Why do Grey Plovers migrate along a route about 10% longer than the shortest possible route? Apart from navigational difficulties following the great circle route (Alerstam and Gudmundsson 1999; Alerstam et al. 2008; Schmaljohann et al. 2012), we guess that Grey Plovers made detours (1) for safety reasons but (2) in particular to adjust their arrival dates to the annual weather conditions. Following the great circle route from the Wadden Sea to breeding sites on Taimyr the birds have to cross the Arctic Ocean from northern Scandinavia to Taimyr, thus crossing an ecological barrier of about 2000–2500 km (Alerstam 2001). Migrating along the Arctic coast might also be no viable option on northward migration. To feed on invertebrates waders are dependent on open mud flats and/or open vegetation. But, during the main migration period, end of May/beginning of June vast areas of the Arctic coast are covered by sea ice and snow, respectively, whereas inland areas seem to offer at least some snow-free (appropriate feeding?) sites (for ice/snow data see: http://www.esri.noaa.gov/psd/cgi-bin/db_search/SearchMenus.pl) i.e., ice/snow cover may constrain Grey Plovers to migrate via the inland. Even if Grey Plovers can reach their breeding sites within one non-stop flight from the Wadden Sea, resting possibilities in inland areas may serve as an insurance and may outweigh the longer distances. For Bewick's Swans (*Cygnus columbianus*) (Nolet 2006; Nuijten et al. 2014) as well as for White-fronted Geese (van Wijk et al. 2012; Kölzsch et al. 2015) it has been shown that they follow the retreating ice front closely, their arrival dates on breeding grounds correspond with the disappearance of the ice cover respectively the onset of spring. Such a strategy enables the birds much better to predict weather conditions on the breeding grounds of the specific year and to adjust the speed of migration respectively the arrival on the breeding grounds to the annual and local environmental conditions than a non-stop flight strategy. Cues for the annual variations of environmental conditions are unavailable on the wintering grounds as well as in the Wadden Sea. Appropriate staging sites near the breeding area may be of particular importance for timely arrival, and birds may extend or shorten their stopovers (Aharon-Rotman et al. 2015). As shown, arrival times of Grey Plovers were determined primarily by stopover duration.

Three birds were tracked for ≥ 2 years. These birds showed strong site fidelity to both, breeding sites as well as wintering grounds. Long-term site fidelity to the breeding sites has been reported for many wader species, especially males that are site faithful (Tomkovich and Soloviev 1994; Ryabitsev and Alekseeva 1998). The same applies for the wintering grounds. During the non-breeding season our tracked Grey Plovers returned not only to a specific area, but to almost the same spot (Additional file 1: Fig. S1). This corresponds with observations of colour-ringed birds by Townshend (1985) at the Teesmouth estuary in northeastern England, where the birds returned every year to the same territory. According to Townshend (1985) the lifetime behaviour of Grey Plovers is already determined during the first autumn migration. Site fidelity can be advantageous because the individuals are familiar with the local conditions, e.g. the food resources and the potential predators. Movements within the non-breeding area are typically explained by changing food conditions (Trierweiler et al. 2013). On the other hand, strong site fidelity and the lack of wandering around to explore other areas may limit the ability to abandon degrading sites and to move elsewhere. The site-faithfulness might indicate that the areas provide appropriate conditions for wintering plovers nowadays. But, it may also indicate the absence of suitable alternatives (Battley et al. 2012).

In summary, the following picture emerges: On northward migration from the Wadden Sea to Arctic breeding grounds initially Grey Plovers made a non-stop flight of about 3000 km, subsequently birds stopped over several times before reaching their final destination. Making shorter flights approaching the breeding sites offers the possibility to refuel nutrient stores as well as to adjust arrival dates precisely to the local and annual conditions (e.g. Aharon-Rotman et al. 2016), and it prevents the birds to arrive too early if snow still covers Arctic breeding sites. Birds arriving at the breeding sites just in time should be in a better starting position to breed successfully. In accordance with earlier studies on waders

(Klaassen et al. 2001; Klaassen 2003; Morrison and Hobson 2004; Yohannes et al. 2010) our results could suggest that Grey Plovers are not strict income breeders and that at least early arriving females use a mixed income-capital strategy as documented for Ruddy Turnstones (*Arenaria interpres*), Red Knots (Morrison and Hobson 2004), Pectoral Sandpipers (*Calidris melanotos*) (Yohannes et al. 2010) and Whimbrels (Johnson et al. 2016). In contrast to spring on autumn migration Grey Plovers flew along the coastline, i.e. the birds used different routes during spring and autumn migration. Before take-off for another non-stop flight of about 3000 km, back to the main staging site on the EAF, to the Wadden Sea, the birds rested alongside the Russian coast. Probably Grey Plovers filled up their nutrient stores close to the breeding grounds in coastal areas. In addition, they could have been waiting for favourable wind conditions. The observed pattern is similar to that of Pacific Golden Plovers breeding in Chukotka. Before leaving Arctic breeding grounds finally, Pacific Golden Plovers also made one or two pre-migratory stopovers (Johnson et al. 2017).

Migration speed and time schedule

Migration between wintering grounds and breeding sites, took between 40 and 150 days, without seasonal differences. Adults spent about 95% of the total migration time at stopover sites. That means, the estimated flight fraction of c. 5% was slightly lower as the theoretically predicted value of about 15% for flights (Hedenström and Alerstam 1997). For about 70% of the total migration time Grey Plovers stayed in the Wadden Sea, which as well as the fact that about 70% of the EAF population (Blew et al. 2016) are resting in the Wadden Sea on migration emphasizes the outstanding importance of the Wadden Sea for waders on the EAF.

Despite longer detours between the Wadden Sea and the Arctic in spring, Grey Plovers migrated significantly faster during spring than during autumn migration (Fig. 2; Additional file 4: Table S1b). Birds using the inland route in spring migrated significantly faster than birds travelling along the Arctic coast (7 vs. 21 migration days, $U_{5,\,3}=0$, $p<0.036$). In both cases, the differences are mainly caused by prolonged stopovers. On spring migration between the Wadden Sea and the Arctic, Grey Plovers stopped over less frequently and for shorter times than in autumn. Moreover, flight speed and thus also travel speed was about 20% higher for spring migration than for autumn migration. These data coincide with those from most other tracking studies on related species (see review by Nilsson et al. 2013).

Our estimates of flight speeds (48–85 km/h) are similar to measurements of other wader species (see review by Nilsson et al. 2013), including Pacific Golden Plovers (Johnson et al. 2012). However, studies on Pacific Golden Plovers have shown that under favourable weather conditions plovers may fly long distances at much higher speeds, at speeds of about 100–110 km/h (Johnson et al. 2011, 2012). Higher flight speeds in spring compared to autumn can be a result of higher air speed in spring (Schmaljohann and Liechti 2009). At least on the first migration leg in western Europe wind conditions are more supportive in spring than in autumn (Kemp et al. 2010). As shown by Green (2004) most waders crossing southern Sweden on spring migration from the Wadden Sea towards Arctic Russia migrated with strong tailwinds. These data are supported by our observations. One of the most striking results was that all birds departed from the Wadden Sea to Arctic breeding grounds more or less synchronously (Fig. 3) under favourable tailwind conditions. These observations are unsurprising, and several studies have shown that migratory activity (activity, departure, flight height etc.) is strongly related with favorable (tail) wind conditions (e.g. Piersma and van de Sant 1992; Gudmundsson 1994; Åkesson and Hedenström 2000; Conklin and Battley 2011; Conklin et al. 2013; Eikenaar and Schmaljohann 2015). Our data might indicate that after fuel accumulation in the Wadden Sea (Prokosch 1988) the birds may have waited for improved wind conditions. The synchronous departure from the Wadden Sea end of May and that Grey Plovers migrated significantly faster in spring than in autumn is in accordance with the time minimizing hypothesis. In general, spring migration is more time selected than autumn migration (Nilsson et al. 2013).

Conclusions

By applying satellite tagging we were able to reveal the migration of Grey Plovers along the EAF in so far unprecedented details, in particular the migration patterns between the Wadden Sea as the major stopover site and the Arctic breeding grounds. However, due to small sample sizes we still miss details for the migration to and from the African wintering area. In contrast to previous evidence, Grey Plovers during spring migration between the Wadden Sea and the Arctic used inland routes, likely because of ice and snow cover along the northern coasts. However, this hypothesis needs further consideration by additional high resolution GPS tagging and tracking over multiple seasons. Moreover, more work is needed to localize the key staging sites in remote areas. Given the importance of stopover sites within the annual cycle of migratory species, it is not only vital to identify key staging sites, but to study stop-over ecology in detail. Furthermore, for a better understanding of the entire global migration system of Grey Plovers more work is needed on the other suggested flyways as well.

Additional files

Additional file 1: Fig. S1. Fixes of four satellite-tagged Grey Plovers during wintering.

Additional file 2: Fig. S2. Representative migratory tracks of satellite-tagged Grey Plovers.

Additional file 3: Fig. S3. Locations and durations of stopovers of satellite-tagged Grey Plovers during spring and autumn migration.

Additional file 4: Table S1. Distance and duration of major migratory movements.

Additional file 5: Table S2. Temporal schedule of the annual cycle for 11 satellite-tagged Grey Plovers, 2011–2014.

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Supplementary material
Supplementary material can be found at https://academic.oup.com/cz.

Authors' contributions
KME designed the study. FH carried out field work and processed tracking data. KME performed statistical analyses and wrote the manuscript with advice from FB and FH. All authors read and approved the final manuscript.

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Availability of data and materials
The data used in this study are available on Movebank (https://www.movebank.org, study name: 'Wader migration German Wadden Sea: grey plovers') and are published in the Movebank Data Repository (Exo et al. 2019).

Ethics approval and consent to participate
The tracking study was approved by the animal care and ethical committee at the Niedersächsisches Landesamt für Verbraucherschutz und Lebensmittelsicherheit (LAVES), Oldenburg, Germany (# 33-42502-04-10/0307). Catching and ringing were carried out under the license of the Institute of Avian Research, Wilhelmshaven, Germany. The national park administration of Lower Saxony, Wilhelmshaven, Germany, gave the permission to catch birds at high-tide roosts within the National Park.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests. The funders had no influence on the study design, data collection and analysis, decision to publish, or preparation of the manuscript.

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