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Individual migration patterns of Eurasian golden plovers *Pluvialis apricaria* breeding in Swedish Lapland; examples of cold spell-induced winter movements

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Tracking studies normally focus on long-distance migrants, meaning that our understanding about short-distance migration remains limited. In this study, we present the first individual tracks of the Eurasian golden plover *Pluvialis apricaria*, a short-distance migrant, which were tracked from a Scandinavian breeding population using geolocators. In addition, golden plovers are known for their cold spell-induced winter movements, and this study provides some first individual tracking data on this type of movements. In three cases the plovers spent the winter in NW Europe and in four cases they departed during winter from NW Europe to spend the rest of the winter in Iberia or Morocco (one bird that was tracked during two subsequent migration cycles moved to Iberia in the first winter but remained in NW Europe during the second winter). The four winter departures were associated with a cold spell in NW Europe during which maximum temperatures dropped to freezing. Cold spell-induced winter movements were notably long and fast. The birds that remained at their NW European wintering site did not experience such cold spell. However, the plovers did not always move in response to freezing temperatures, as demonstrated by the individual that was tracked for a second season, when it experienced four cold spells at its wintering site in NW France without leaving. Little information was obtained about spring migration, but one bird had a prominent counter-clockwise loop migration pattern through E Europe. Due to their cold spell winter movements, golden plovers exhibit great flexibility in migration patterns, resulting in a notably large spread in final wintering areas.

An intriguing difference between short- and long-distance migrants is that the timing of migration of long-distance migrants is under endogenous control (Berthold 1996, Gwinner 1996), whereas short-distance migrants more often show facultative movements, i.e. only migrate when conditions deteriorate (Newton 2008). Facultative weather-induced escape movements can be rather spectacular in terms of the numbers of birds involved, and mass-migration events in response to cold spells and snowfall are for example known from lapwings *Vanellus vanellus* and Eurasian skylarks *Alauda arvensis* (Kirby and Lack 1993, Del Hoyo et al. 1996, Donald 2004, Newton 2008). Although weather-induced escape movements have been described in detail at the level of the population, little is known about the details of individuals taking part in these mass migration events, possibly as tracking studies normally focus on long-distance migrants (Strandberg et al. 2009b). Consequently, we have a rather limited understanding about the details of weather-induced escape movements such as for example the distances birds travel when pushed out by bad weather and whether and how long birds remain in their secondary wintering sites (Wernham et al. 2002). Here we aim to fill this lacuna by presenting the results of a tracking study of a short-distance migratory wader, known for its cold spell-induced winter movements (Jukema and Hulscher 1988, Yeatman et al. 1991, Kirby 1997), the Eurasian golden plover *Pluvialis apricaria* (hereafter golden plover).

The golden plover is a medium-sized wader that breeds in N Europe on open moorland, montane heaths, and northern tundra, its distribution extending far into Siberia (Byrkjedal and Thompson 1998). They spend the winter mostly in west and southwest Europe, often using agricultural habitats such as grasslands and arable fields (Byrkjedal and Thompson 1998, Gillings et al. 2007, 2012). The Netherlands and S Scandinavia are two examples of prime non-breeding areas where golden plovers stay to

complete their moult from the end of July until September/October (Poot et al. 1996, Jukema et al. 2001, Lindström et al. 2010). Plovers leave these areas when temperatures drop below freezing point, presumably as their main prey, earthworms, becomes unavailable (Jukema et al. 2001, Lindström et al. 2010). Only in very mild winters golden plovers may remain at these northern sites.

The general migration pattern of golden plovers has been inferred from ringing recoveries and observations (Jukema et al. 2001, Wernham et al. 2002, Fransson et al. 2008, Gillings et al. 2012, Saurola et al. 2013). The birds arriving in northwest Europe in autumn seem to have a northern (Scandinavia) and north-eastern (Russia) origin. During autumn and winter, these birds move on, depending on the severity of the winter (Jukema and Hulscher 1988), to sites in the UK, France, Iberian Peninsula and even N Africa. Some British breeders remain in the UK in the winter whereas others travel as far as Morocco (Wernham et al. 2002). Golden plovers originating from Iceland winter mainly in Ireland (Wernham et al. 2002). In spring, part of the birds wintering in S Europe and N Africa seems to follow a more eastern migration route via Italy to return to their northern breeding sites (Del Hoyo et al. 1996, Jukema et al. 2001).

In this paper we describe the migration patterns of seven golden plovers that we tracked using geolocators from a breeding population in Swedish Lapland. In our analyses, we focus explicitly on cold spell-induced winter movements by relating movements to local weather conditions (temperature). This study provides a first description of the migration patterns of a population of golden plovers breeding in N Sweden, and is a first study providing tracking data on cold spell-induced winter movements of golden plovers.

Methods

Study system and fieldwork

Fieldwork was performed in the Vindelfjällen Nature Reserve, Ammarnäs, Sweden (65°59′N, 15°57′E) an area in Swedish Lapland characterized by open mountain heath tundra. Nests were found while walking through the area by locating incubating birds flushed from the nest or by watching adults returning to their nest from a high vantage point using a spotting telescope. For each nest, the fate was followed until eggs hatched, were predated or the nest was abandoned.

Adult golden plovers were caught on the nests using a walk-in trap (Yalden and Pearce-Higgins 2002) or a bownet-spring trap (Gratto-Trevor 2004). Trapping was mostly performed in the second and third week of incubation, in order to avoid the risk of nest abandonment. Trapped birds were fitted with colour ring combinations to facilitate individual identification in the field. Individuals were sexed on the basis of plumage characteristics (Byrkjedal and Thompson 1998).

In the 2011 breeding season 30 individuals (15 males and 15 females, including 13 pairs) were fitted with light-level geolocators. Geolocators were attached to a 10 mm high plastic colour ring on the leg of the bird with an additional 5 mm high plastic colour ring underneath (Fig. 1). We used geolocator model Mk10 produced by the British Antarctic Survey (BAS), Cambridge, UK (<www.birdtracker.co.uk>). This geolocator weighed 1.1 g and stored light data every 10 min. In the breeding seasons of 2012 and 2013 individuals carrying geolocators were recaptured.

Geolocator data analysis

Archived light-level data was downloaded from loggers and decompressed using BASTrak software 'Communicate' and 'Decompressor' (BAS). TransEdit2 (BAS) was used to inspect raw data and to identify times of sunrise and sunset, using a single light threshold value of 2. False sunrise and sunset events, i.e. caused by shading of the light sensor by for example feathers and vegetation (Lisovski et al. 2012), were removed by hand. Locations were calculated using Locator (BAS), in which estimates for latitude are based on the length of the solar day (or night) and estimates for longitude on the time of local solar noon (or midnight).

The sun angle corresponding to a light-level of 2 was found by Hill–Ekstrom calibration. This procedure is based on the effect that the error in latitude increases with an increasing mismatch between true and used sun angle, in particular near periods of equinox (Ekstrom 2004, Lisovski et al. 2012). Hill–Ekstrom calibration was performed for stationary periods that included an equinox. We chose the sun angle that minimized the difference in the estimate for latitude just before and after equinox. In the case the bird had moved during equinox we picked the sun angle that minimized the variation in latitude. This single sun angle was subsequently used to calculate positions throughout the rest of the year.

Stationary periods were identified by inspecting plots of latitude and longitude over time, alongside with plots of tracks on a map. To identify stopovers we mainly relied on patterns in longitude as the error in longitude is relatively small (Fudickar et al. 2012), and its estimation is not affected by calibration or equinox. Movements between stopover sites can readily be identified from plots of longitude over time (supplementary material), as the plovers' general migration axis has a SSW orientation, i.e. birds only rarely move due south or due north. Furthermore, movements between stopover sites were notably fast, thus it was straightforward to recognize different stationary periods. Mean coordinates were calculated for each stationary period.

Data analysis

Cold spell-induced winter movements were defined as movements from the wintering site in NW Europe (see Results), that were advanced by a notable drop in temperature. For the individuals that made a cold spell-induced winter movement, autumn migration was subdivided in two parts: 'regular' autumn migration and 'cold spell-induced winter movement'. Regular autumn migration includes all movements from the departure from the breeding area until arrival to the NW European wintering site. Cold spell-induced winter movements include all movements from the departure from the NW European wintering site until arrival to the wintering site in S Europe/N Africa (see also Results).

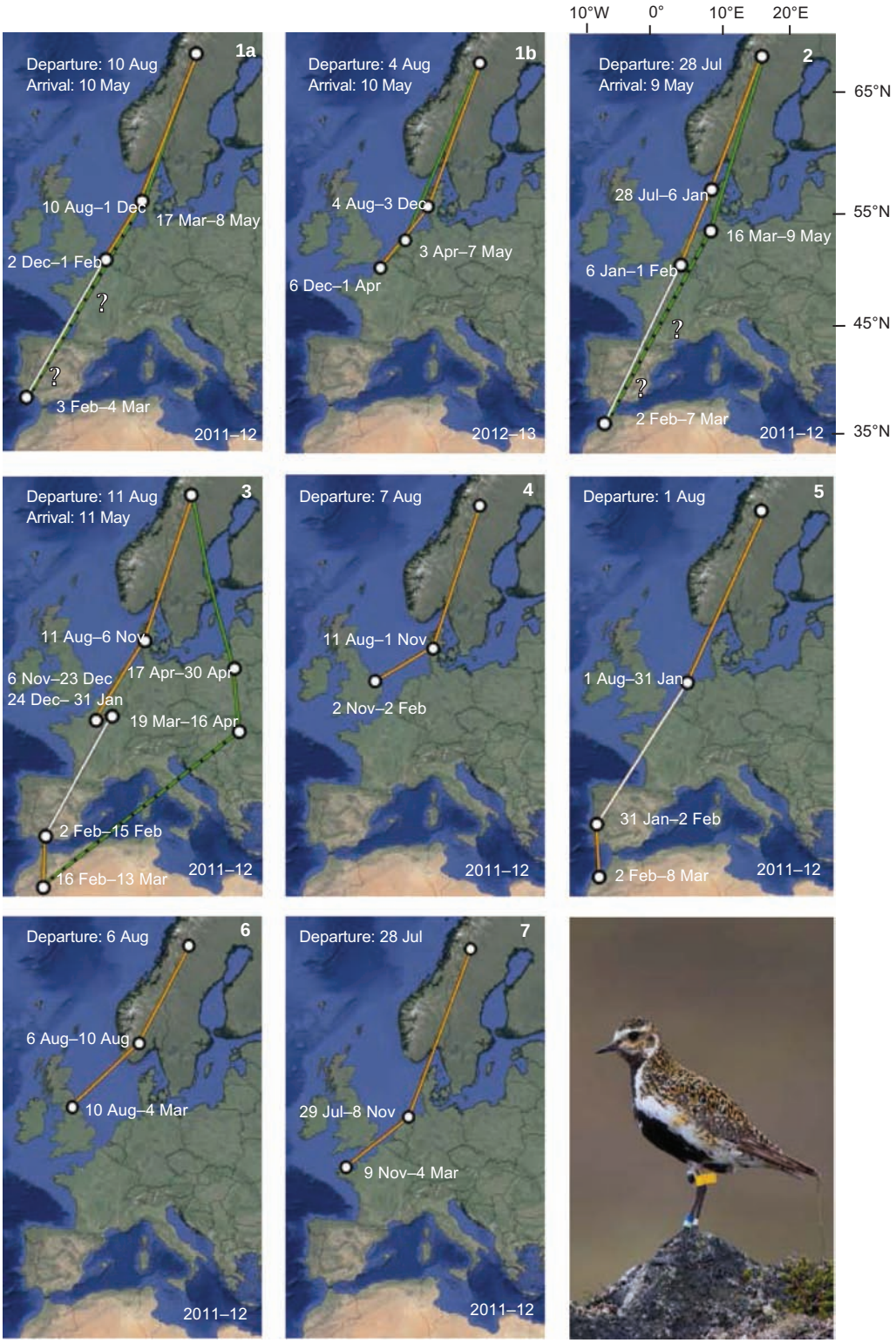

Figure 1. Migration routes of golden plovers deployed with geolocators. Orange lines refer to autumn migration, green lines to spring migration, and white lines to cold spell movements. Circles refer to stopovers and its duration is specified. Dashed lines refer to parts of the migratory movements that were uncertain due to interference by equinox. Question marks along dashed lines indicate that omewhere along this track stopovers were made, but the exact location is unknown (duration is specified). Each map correspond to a different individual except map 1a and 1b, which refers to two subsequent migration of the same individual. Map source: QGIS open plugin Google Satellite.

Travel distances were calculated as loxodrome distances between subsequent stationary sites, i.e. not considering exact flight paths and excluding local movements on stopovers. Duration simply was the time between departure and arrival (e.g. for regular autumn migration the time from the departure from the breeding site to arrival to the NW European wintering site), and migration speed was subsequently calculated by dividing total distance by total duration. Temperature data (daily minimum and maximum temperature) for the different stationary sites were obtained from the nearest weather stations from <www.wunderground.com>. Differences in frequencies (e.g. return rates of plovers carrying geolocators and plovers fitted with colour rings only) were compared using Chi-square tests. Differences in performance (e.g. timing of migration, migration speed, latitude of wintering site) between sexes, seasons and successful versus unsuccessful breeders were explored by t-tests.

Results

Return rates

In 2012, at least 17 out of 30 golden plovers fitted with geolocators were observed in the study area. The return rate of geolocator-birds (57%) was similar (Chi-square = 0.07, DF = 1, p = 0.78) to the return rate of individuals not fitted with geolocators but only carrying colour rings (52%, 10 out of 19 birds). In 2013, there were no extra observations of individuals carrying geolocators different from 2012. Nine out of the seventeen birds seen in 2012 (53%) were seen in the study area and all nested. Although a fairly good sample of birds carrying geolocators returned to the study area we had great difficulties in recapturing these birds as breeding conditions in the two seasons we tried to recapture birds were very unfavourable, and nest predation pressure was very high. In total only seven geolocators could be recovered, four in 2012 and three in 2013.

Three of these geolocators had been placed on males and four on females. Individual #1 and #7 (Fig. 2 and Table 1) were a breeding pair in 2011 but bred with other partners in 2012. Nest fate in 2011 varied between geolocator birds. Four individuals bred successfully, two birds abandoned their nest (pair of the same nest), and one nest was predated. Successful nests hatched between 30 June and 10 July.

Geolocator issues

From the seven geolocators that were retrieved, four contained incomplete data as the batteries had failed prematurely. Loggers had failed on 2 February, 4 March, 4 March and 8 March respectively. Two of the loggers that did not fail prematurely contained data for a full annual cycle and one logger had data of two full annual cycles. In total we obtained partial or complete data for eight migration routes (Fig. 2 and Table 1).

One of the geolocator-birds (ID #4, Table 1) was observed at its wintering site at Cley Marshes NWT Reserve, UK (52°57′N, 1°3′E) from 18 November 2011 to 2 January 2012 and once again on the 4 November 2014 at the same area (David and Pat Wileman pers. comm.). Before arriving at this site, this bird made a stopover in Denmark from 11 August–1 November (Fig. 1). Equinox occurred during this stopover on Denmark, hence the Hill–Ekstrom calibration was conducted for this site. The obtained sun angle (–1.4°) was used to calculate the position of the bird during the rest of the year, which placed the wintering site just 50 km to the north of where the bird was observed.

General migration patterns

Golden plovers left the breeding area between 28 July and 11 August (Table 1). Departure date differed between sexes (t = –3.46, DF = 6, p = 0.01, females departing on average 6 days earlier than males), but not between successful and failed broods (t = 0.35, DF = 6, p = 0.74). From the breeding site, the plovers moved SSW to SW to stopover sites in Norway (n = 1), Denmark (5) and the Netherlands (1) (Fig. 1). The exception is a bird (ID #5) that travelled directly from the breeding site to its NW European wintering site in the Netherlands, without making an additional stopover in Scandinavia. Autumn stopover sites were used for on average 100 d (range 4–161 d). In November–beginning of January the plovers left the stopover sites and made relatively short movements (average 756 km) to wintering sites in NW Europe in the UK (n = 2) and Belgium/NW France (n = 4). In addition, the NW European wintering site of individual #5 was located in the Netherlands. Autumn migration to the wintering sites in NW Europe for the individuals that made a prolonged stopover (i.e. excluding individuals #5 and #6), took on average 113 d. Average migration distance was 1968 km, resulting in an average migration speed of 18.4 km d^{-1} (Table 1).

In four cases, plovers left NW European wintering sites as a response to a sudden decline in temperature (see below). Final wintering sites of the latter individuals were located in Portugal (n = 1) and Morocco (n = 3) (Fig. 1). In two cases the cold spell-induced winter movements consisted of two stages including short additional stopovers in Portugal and S Spain (Fig. 1). Cold spell movements were notably fast, on average 1531 km d^{-1}. Final winter location latitude did not differ between sexes (t = –0.006, DF = 6, p = 0.49).

Only four spring migration tracks were obtained from three different individuals, which included three spring migrations from wintering sites in Iberia/Morocco and one spring migration from a NW European wintering site (Fig. 1). In all cases, the birds made at least one stopover, located in Denmark (1), the Netherlands (1), NW Germany (1), Romania (1) and Poland (1). These stopovers lasted 14 to 54 d (on average 37 d). No reliable information was obtained from the first part of the spring migration journeys as the birds initiated migration very close to the spring equinox, although using longitude data it is known that both individuals #1a and #2 made two stopovers during that period (Fig. 1). In three cases, the spring migration route was very similar to the autumn migration route. In contrast, one individual (ID #3) followed a much more eastern route, reaching a longitude as far east as 23°E. This was the only bird approaching the breeding area from the southeast, possibly crossing the Baltic Sea. Birds returned to the breeding site between 9 and 11 May.

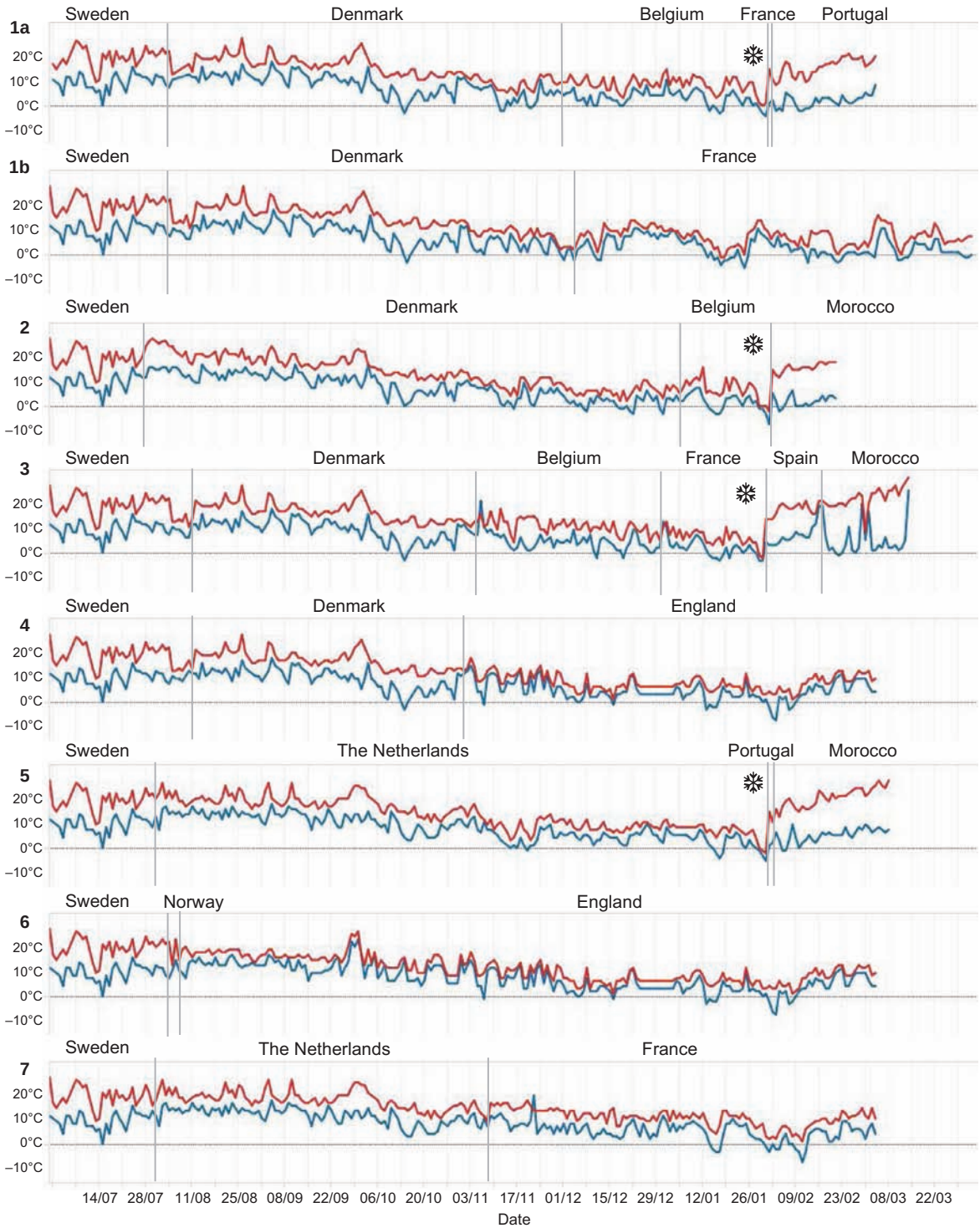

Figure 2. Minimum (blue) and maximum (red) temperatures as experienced by different individual golden plovers throughout their annual cycle, for autumn and winter. Vertical lines indicate the movement to the subsequent stationary site. Snow crystals mark the movements we considered to be cold spell-induced winter movements (see main text).

Spring migration for the three travels from Iberia/Morocco took 59–67 d, which was longer than the travel from the wintering site in NW Europe (39 d), but this individual travelled a considerably shorter distance (1918 vs 4190 km). Subsequently, spring migration speeds were similar for the birds travelling from Iberia/Morocco (67.2 km d^{-1}) and the bird travelling from NW Europe (49.2 km d^{-1}). Migration speeds were higher during spring compared to autumn ($t = -5.6$, $DF = 8$, $p < 0.001$).

The individual male tracked during two subsequent years (Fig. 1, individual 1a and 1b) varied in its migration pattern between years. It used the same initial stopover site in autumn, but only in 2011/2012 it was pushed out by a cold spell, and wintered, in the end, in Portugal. In 2012–2013

Table 1. Summary of migration parameters for each individual. See main text for details about how different parameters were calculated. Values in italic were not included in the calculation of averages.

ID	1a	1b	2	3	4	5	6	7	Average
General information									
Ring number	–434	–434	–408	–419	–420	–430	–432	–433	
Sex	male	male	female	Male	male	female	female	female	
Breeding success before migration	fail	–	success	success	fail	success	success	fail	
Date nest failed or hatched	2 Jul	–	1 Jul	30 Jun	27 Jun	10 Jul	10 Jul	2 Jul	
Tracking season	2011–2012	2012–2013	2011–2012	2011–2012	2011–2012	2011–2012	2011–2012	2011–2012	
Date logger failure	–	–	–	–	2 Feb	8 Mar	4 Mar	4 Mar	
Autumn migration (breeding ground until wintering site NW Europe, i.e. excluding cold spell movement)									
Departure from breeding area	10 Aug	4 Aug	28 Jul	11 Aug	7 Aug	1 Aug	6 Aug	28 Jul	4 Aug
Distance movement 1 (km)	1229	1265	1004	1180	1171	1519	813	1483	1208
Stopover Scandinavia	10 Aug–1 Dec (113 d)	5 Aug–3 Dec (121 d)	28 Jul–6 Jan (161 d)	11 Aug–6 Nov (86 d)	11 Aug–1 Nov (82 d)	–	6 Aug–10 Aug (4 d)	29 Jul–8 Nov (101 d)	100 d
Distance movement 2 (km)	532	658	826	1067	617	–	822	773	756
Wintering site NW Europe	2 Dec–1 Feb (61 d)	6 Dec–1 Apr (117 d)	6 Jan–1 Feb (26 d)	6 Nov–31 Jan (84 d)[1]	2 Nov–*2 Feb* (–)[2]	1 Aug–31 Jan (183 d)	10 Aug–*4 Mar* (–)[2]	9 Nov–*4 Mar* (–)[2]	94 d
Total duration (d)	114	124	162	87	87	(1)	(4)	104	85[3]/113[4]
Total distance (km)	1761	1923	1830	2247	1788	(1519)	(1635)	2256	1870[3]/1968[4]
Migration speed (km d)	15.4	15.5	11.3	25.8	20.5	(1519)	(408.7)	21.7	255[3]/18.4[4]
Cold spell movement									
Departure date	1 Feb		1 Feb	31 Jan		31 Jan			31 Jan
Distance (km)	1834	–	2023	1569	–	2555	–	–	1995
Wintering site S Europe/N Africa	3 Feb–4 Mar (30 d)	–	2 Feb–21 Feb (19 d)	2 Feb–13 Mar (39 d)[5]	–	2 Feb–*8 Mar* (–)[6,2]	–	–	29
Duration (d)	2	–	1	2.5	–	1	–	–	1.3
Travel speed (km d^{-1})	917.3	–	2023	628.1	–	2555	–	–	1531
Spring migration									
Departure from wintering area	4 Mar	1 Apr	7 Mar	13 Mar	–	–	–	–	3 Mar[8]/1 Apr[9]
Arrival at breeding area	10 May	10 May	9 May	11 May	–	–	–	–	10 May[8]/10 May[9]
Total duration (d)	67	39[7]	63	59	–	–	–	–	67.7[8]/39[9]
Total distance (km)	3597	1918[7]	3885	5087	–	–	–	–	4190[8]/1918[9]
Migration speed (km d^{-1})	53.7	49.2[7]	61.66	86.2	–	–	–	–	67.2[8]/49.2[9]

Notes:
[1]Actually two very nearby stationary periods: 6 Nov–23 Dec and 24 Dec–31 Jan.
[2]Logger failed.
[3]Average including two autumn migrations without longer stopover (i.e. including ind. 5 and 6), n = 8.
[4]Average excluding two autumn migrations without longer stopover (i.e. excluding ind. 5 and 6), n = 6.
[5]Consists of two parts: after cold spell movement the bird arrived in S Spain, where it stays from 2 Feb–15 Feb (13 d). Final wintering area is in Morocco (16 Feb–13 Mar).
[6]Consists of two parts: after cold spell movement the bird arrived in Portugal, where it stays from 31 Jan–2 Feb (2 d). Final wintering area is in Morocco (2 Feb–8 Mar).
[7]This individual did not make a cold spell movement, so spring migration started from NW France.
[8]Average for individuals migrating from wintering site in S Europe/N Africa, n = 3.
[9]Average for individual migrating from wintering site in NW Europe, n = 1.

the bird left the stopover area before temperatures dropped (see below), and moved to a much closer wintering site in NW France. Data from latitude and longitude during all migration overtime is detailed shown in Supplementary material Appendix 1, Fig. A1.

Timing of movements in relation to temperature

When the birds left the breeding area in late summer, temperatures were still relatively high, not reaching zero degrees. During the prolonged stopovers in Scandinavia (n = 5) and the Netherlands (n = 1, individual 7), minimum temperatures occasionally dropped below freezing point, but not maximum temperatures (Fig. 2), and these stopover sites were left before maximum temperatures went down. At the NW European wintering sites temperatures were very similar to the temperatures experienced at the stopover sites. At the first occasion of a cold spell, occurring at 30 January–1 February 2012, when maximum temperatures dropped rapidly to freezing point, the birds wintering in the Netherlands

(n = 1), Belgium (n = 2) and NW France (n = 1), left the wintering site and made a long and fast cold spell movement (Fig. 1, 2). The birds wintering in England (n = 2) and W France (n = 1) experienced milder conditions during this period, in which maximum temperatures did not drop below zero degrees (Fig. 2), and these individuals remained at their NW European wintering sites. For these individuals, temperatures remained relatively mild throughout the winter, i.e. never really dropping below freezing point. For 2013, data from only one individual was obtained (1b). During its stay at its NW European wintering site in NW France the individual experienced at least four cold spells in which maximum temperatures dropped to freezing. In two cases this appeared before the beginning of February, i.e. before the period the cold spell movements occurred in 2012. Despite these cold spells, the bird did not leave this wintering area.

Discussion

General migration patterns

The annual movements of the seven golden plovers we successfully tracked using geolocators confirmed ideas about general migration patterns of Scandinavian golden plovers as had been inferred from observations and ring recoveries (Jukema et al. 2001, Gillings et al. 2012). After the breeding season, the plovers fitted with geolocators moved to sites in NW-Europe for a stopover. Lindström et al. (2010) intensively studied golden plovers during their autumn stopover in S Sweden, which revealed that a main function of these stopovers is to moult flight feathers, suggesting that these are key high-quality stopover sites for plovers. Based on observations on individuals fitted with radio transmitters, they estimated that the plovers would stay for at least 80 d (i.e. mean for birds fitted with transmitters in August), which is slightly less than the average of 100 d as observed in this study. Importantly, Lindström et al. (2010) suggest that the plovers leave the stopover site in S Sweden in October–November in response to the first prolonged period of ground frost. Our results indicate that these stopover sites instead are left before the occurrence of cold spells. However, this might simply be an effect of the particular year as in winter 2011–2012 a real cold spell did not occur in NW Europe until the end of January (see below).

One of the novelties of the current study is that we mapped migration patterns of golden plovers at the level of the individual bird. This enabled us to get more reliable estimates of for example stopover durations (cf. above) and migration speeds, which is difficult if not impossible on the basis of observations of (colour) ringed birds (Strandberg et al. 2009a). Overall migration speed in spring and especially autumn was notably low, as expected for a short-distance migrant (Strandberg et al. 2009b). In addition, tracks of individual birds provide an unbiased picture of migration patterns, in contrast to ring recoveries which are strongly biased due to variation in reporting probability (Strandberg et al. 2009a). This is especially true for golden plovers, which are studied extraordinary intensively in the Netherlands (Jukema et al. 2001), meaning that the probability that a plover is reported from the Netherlands is relatively high. Thus, from ringing recoveries it appears that the Netherlands is the single most important non-breeding area for golden plovers, and although the Netherlands in fact is very important for plovers, its relative importance certainly is overestimated on the basis of ring recoveries. For example, 'only' three out of the seven plovers we tracked with geolocators actually visited the Netherlands, which is less than one might had expected on the basis of ring recoveries (Jukema et al. 2001). The unbiased picture of migration patterns of the golden plovers fitted with geolocators also revealed that some of the Scandinavian breeding birds use an eastern migration route in spring. This is new information as it hitherto was believed that birds returning via the eastern route were Russian breeding birds (Jukema et al. 2001). The downside of geolocator studies is that sample sizes typically are small, as in this study, making it difficult to judge how representative observed patterns really are for the whole population.

Weather-induced movements

In four out of eight cases, the plovers left their NW European wintering site in response to a notable sudden drop in temperature, in which also maximum temperatures dropped to freezing. These movements we considered to be 'cold spell escape movements'. Thus part of the plovers seems to stay in northern continental Europe until they are pushed out by harsh winter weather, possibly because food availability is reduced when the soil freezes (Kirby and Lack 1993). Contrary to the suggestion by Fuller and Youngman (1979), i.e. that birds would return to the northern sites as soon as conditions improved again, plovers remained at southern sites throughout the rest of the winter. Individuals that stayed in locations with a milder winter climate (e.g. England), did not experience severe cold spells and remained in these relatively northern areas throughout the whole winter.

The interesting character of cold spell escape movements was that they were long. Final wintering sites of the individuals that made cold spell escape movements were located in Iberia and Morocco. Other movements, not induced by dropping temperatures, were much shorter, bringing the birds to more northern final wintering sites in England and N France. This difference is nicely illustrated by individual 1, for which we obtained tracks for two subsequent years. In 2011 the bird was pushed out by cold weather and it finally wintered in Morocco. In the subsequent year, it did not make a cold spell escape movement and wintered in NW France.

We want to stress that most of the movements between staging sites were not related to a drop in temperature. In other words, golden plovers frequently move for other reasons than escaping winter weather, and possible factors involved are for example competition, predation risk, and local changes in food availability (Alerstam and Lindström 1990, Newton 2008). Moreover, we would like to highlight that plovers did not always move when a cold spell occurred. For example individual #1 did not leave its wintering site in NW France in winter 2012/2013, despite the fact that four cold spells occurred during this period. It is unclear why the bird did not make a cold spell movement, but a possible explanation could be that local temperatures dropped

too little to induce a movement. Alternatively, plovers might only respond to cold spells within a certain time window of the annual cycle, but this is an unlikely explanation in this particular case as the cold spells occurred around the time this individual made a cold spell movement in the previous winter.

Due to the fact that some individuals made long cold spell-induced escape movements whereas other did not, the spread in final wintering areas is remarkable. Clearly, the potential wintering range for this breeding population is large, leaving little room for strong migratory connectivity between breeding and wintering populations (Webster et al. 2002), thus we might expect that the winter distribution of breeding birds from the UK, Scandinavia and Russia strongly overlaps.

The fact that the plovers responded instantly to a cold spell suggest that they are fully prepared to leave, i.e. carrying around sufficient fat stores during the winter to make these notably long and fast movements. Jukema et al. (2001) provided data on the body weights of golden plovers throughout the winter in the Netherlands and indeed showed that golden plovers are heavier in November–January (230–240 g) compared to August–September (190 g). Piersma et al. (2003) noted that mid-winter weights of plovers have decreased over time (maximum weights decreased about 30 g), which were attributed to an increase in avian predators. This suggests that it possibly has become more difficult for golden plovers to make the long cold spell-induced winter movements.

Conclusions

Using geolocators, we successfully tracked a sample of golden plovers breeding in Swedish Lapland, providing some first data of the migration pattern of this short-distance migrant and on its cold spell-induced winter movements. Because of these long winter movements, the migration system of Scandinavian golden plovers includes both stopover and wintering sites in NW Europe, as well as wintering sites in S Europe and N Africa. These southern wintering areas must be important for this population, especially or even exclusively so in years when temperatures in NW Europe drop below freezing. This flexibility in the migratory behaviour of golden plovers and the apparent ease of the species to perform rapid movements to southern staging areas in relation to cold spells are important aspects of their migration strategy, and possibly of the migration strategy of short-distance migratory waders in general.

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Supplementary material (Appendix JAV-00768 at <www.avianbiology.org/readers/appendix>). Appendix 1.

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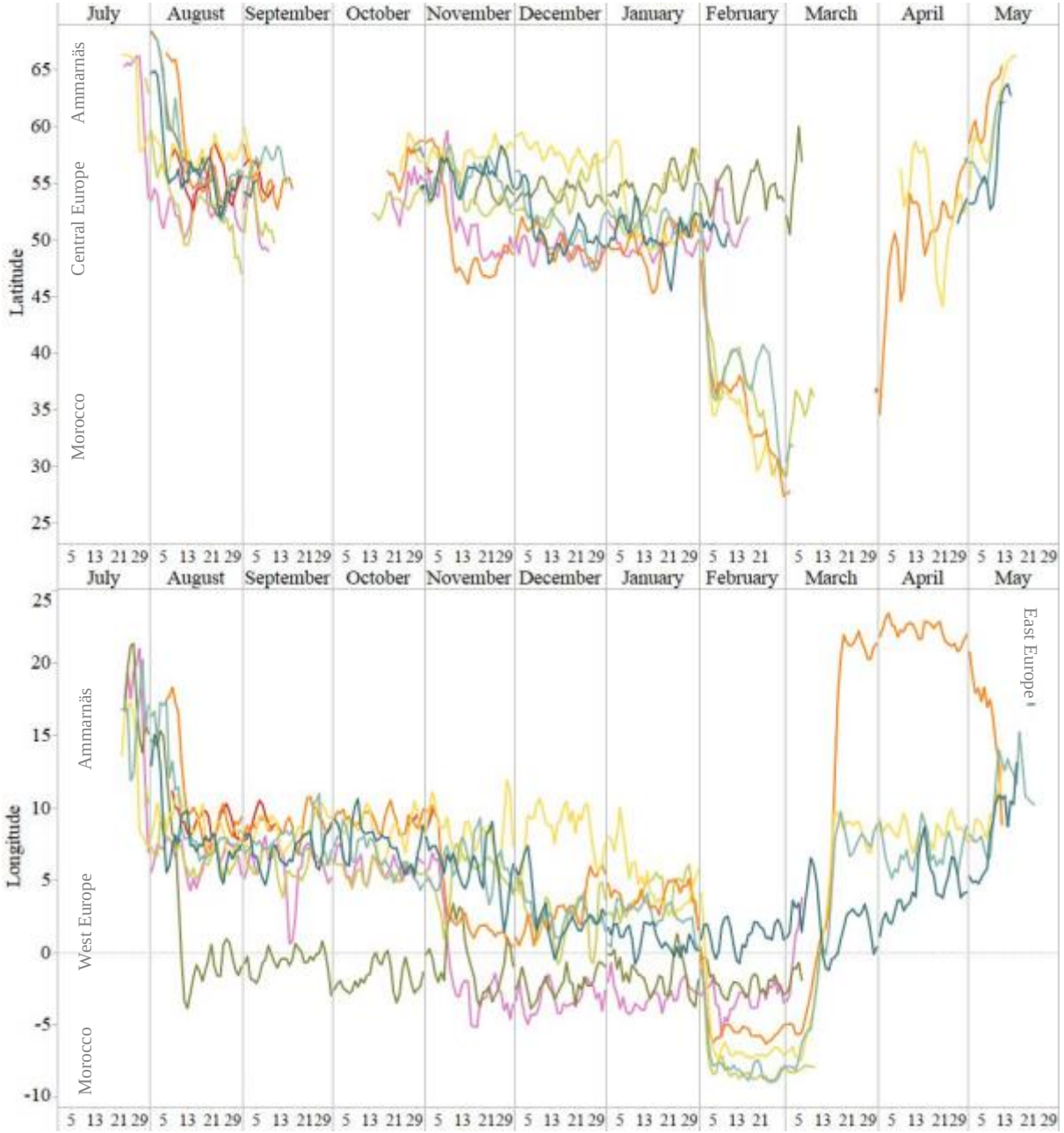
Supplementary material

Appendix 1

Figure A1. Latitude and longitude of each migration route over time. Dark blue 5145434 (1b), light blue 5145434 (1a), yellow 5145408 (2), orange 5145419 (3), red 5145420 (4), light green 5245430 (5), dark green 5245432 (6), pink 514543 (7).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