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*Published in:*  
Journal of Avian Biology

*DOI:*  
[10.1111/jav.00807](https://doi.org/10.1111/jav.00807)

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*Document Version*  
Publisher's PDF, also known as Version of record

*Publication date:*  
2016

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

van Bemmelen, R. S. A., Hungar, J., Tulp, I., & Klaassen, R. H. G. (2016). First geolocator tracks of Swedish red-necked phalaropes reveal the Scandinavia-Arabian Sea connection. *Journal of Avian Biology*, 47(3), 295-303. <https://doi.org/10.1111/jav.00807>

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## First geolocator tracks of Swedish red-necked phalaropes reveal the Scandinavia-Arabian Sea connection

Rob S. A. van Bemmelen, Johannes Hungar, Ingrid Tulp and Raymond H. G. Klaassen

R. S. A. van Bemmelen (*rob.vanbemmelen@wur.nl*), Resource Ecology Group, Wageningen Univ. and Research, Droevendaalsesteeg 3a, NL-6708PB Wageningen, the Netherlands. – I. Tulp and RSAvB, Inst. for Marine Resources and Ecosystem Studies (IMARES), Haringkade 1, NL-1976CP IJmuiden, the Netherlands. – J. Hungar, Zoological Research Museum Alexander Koenig (ZFMK), Adenauerallee 160, DE-53113 Bonn, Germany. – R. H. G. Klaassen, Dutch Montagu's Harrier Foundation, Conservation Ecology Group, Groningen Inst. for Evolutionary Life Sciences (GELIFES), Groningen Univ., PO Box 11103, NL-9700 CC, Groningen, the Netherlands.

We studied migration and wintering patterns of a wader with a pelagic lifestyle during the non-breeding period, the red-necked phalarope *Phalaropus lobatus*. Using light-level geolocation, we obtained three full annual tracks and one autumn migration track of male red-necked phalaropes caught during breeding in Scandinavia. These tracks confirmed expectations that individuals from the Scandinavian population winter in the Arabian Sea. Migration was accomplished in two to four migration leaps, staging for a few days in the Gulf of Finland (autumn) or the southern Baltic Sea (spring) and for up to a month in or near the Black and Caspian Sea (autumn and spring). In addition, travel speeds suggested that only the flights between the Baltic and Black/Caspian Sea are non-stop, and thus the birds seem to make additional short stops during the other flights. Stopover time in the Black/Caspian Sea is only 8–10 d in spring but up to 36 d in autumn, which is longer than expected if only used for pre-migratory fattening to cover the ca 2000 km to the Gulf of Oman. After entering the Arabian Sea via the Gulf of Oman, birds dispersed over the entire presumed winter range. Winter movements appear to correspond to the spatio-temporal patterns in primary production linked to seasonally changing monsoon winds. These are not only the first tracks of Scandinavian red-necked phalaropes, but also the first seabird tracks in the Arabian Sea, one of the most productive and dynamic marine areas on the planet.

The red-necked phalarope *Phalaropus lobatus* is a small wader with an unusual lifestyle, spending the winter out on the ocean like a true seabird – a behaviour only shared with grey phalarope *P. fulicarius*. After a short breeding season in (sub)Arctic tundra, red-necked phalaropes migrate to three known main wintering areas: off the Pacific coast of South America, in the Arabian Sea and off the East Indies (Cramp and Simmons 1983). The migration and wintering areas of phalaropes have been much debated in ornithological literature (Meinertzhagen 1925, Höhn 1966, Alerstam 1990, Smith et al. 2014). Ringing efforts have thus far provided a fragmented picture of those parts of the migration routes that run over land (Höhn 1966, Alerstam 1990, Bakken et al. 2003, Fransson et al. 2008) and have failed to unambiguously link wintering areas to circumpolar breeding areas. A spectacular advancement in the study of migration patterns of phalaropes, is a single geolocator track obtained for a Scottish male red-necked phalarope (Smith et al. 2014). This individual crossed the Atlantic and Caribbean to winter in the Pacific. Its westward migration direction contrasts with the assumed migration pattern of the Scandinavian population, for which a small number of ring recoveries in autumn indicates a south-eastern migration direction (Höhn

1966, Schieman 1977, Alerstam 1990, Bakken et al. 2003, Fransson et al. 2008), strongly suggesting that these birds winter in the Arabian Sea. A south-eastern migration direction is rather unusual among European breeding birds (but see Chamberlain et al. 2000, Verkuil et al. 2006, Hedenström et al. 2013) and the idea that Scandinavian red-necked phalaropes winter in the Arabian Sea (Höhn 1966, Alerstam 1990, Bakken et al. 2003, Fransson et al. 2008) has never been confirmed. Even less is known about the behaviour of phalaropes during winter, when they are difficult to study due to their pelagic lifestyle. Phalaropes often occur in notably large concentrations during the winter, congregating at shelf edges or other sites with high primary productivity (Schieman 1986, Brown and Gaskin 1988, Thorne and Read 2013). However, their at-sea winter movements are unknown, i.e. whether they remain at a single site throughout the winter or whether they are itinerant, using several sites (Moreau 1972), as seems to be the more common behaviour among seabirds (Dias et al. 2011, Fijn et al. 2013, Gilg et al. 2013).

Migratory birds have adopted different strategies to trade-off time and energy while bridging long distances (Piersma 1987, Alerstam and Lindström 1990). At the

extremes of a continuum, birds make small hops, requiring small amounts of fuel for each hop, or make a single long non-stop flight, requiring accumulation of a substantial amount of fuel prior to the flight. Birds are expected to opt for longer flights when the availability of habitat suitable for refuelling is limited, or when minimizing time rather than energy (Alerstam and Lindström 1990). It is not completely clear what constitutes 'suitable' fuelling habitat for red-necked phalaropes migrating ca 5500 km overland from Scandinavia to the Gulf of Oman, but large congregations of phalaropes have only been reported from a few specific saline sites (Cramp and Simmons 1983, Delany et al. 2009). Possibly, Scandinavian red-necked phalaropes subdivide their migratory travel in two to three flights, with stopover locations in the Gulf of Bothnia/Gulf of Finland and the Black Sea/Caspian Sea (Schiemann 1977, Cramp and Simmons 1983, Alerstam 1990). Accumulated fat reserves that would enable non-stop flights of about 4300–5100 km have been reported from the Bay of Fundy, Canada (Mercier 1985), indicating that the species might be able to make long flights. Thus, alternatively, (part of) the Scandinavian red-necked phalaropes could also reach the Arabian Sea in a single flight from the breeding area, similar to as for example has been reported for Scandinavian great snipes *Gallinago media* (Klaassen et al. 2011).

Here, we describe autumn and spring migration patterns of male Scandinavian red-necked phalaropes. Specifically, we test the hypotheses that they 1) winter at the Arabian Sea, 2) reach this destination in two or three non-stop flights, and 3) have staging sites at the Black and Caspian Sea and the Baltic region. Furthermore, we describe the behaviour of red-necked phalaropes during winter, in particular whether they remain at a single site or are more mobile and exploit several sites.

## Methods

Ten breeding male red-necked phalaropes were captured on the nest using walk-in traps between 17–19 June 2013 in the Vindelfjällen Nature Reserve, near Ammarnäs, Sweden (65°59'N–16°01'E) and recaptured on 10–24 June 2014 using walk-in traps on the nest or mist-nets away from the nest. Geolocators (Mk10 model, British Antarctic Survey, Cambridge, UK) were back-mounted using leg-loop harnesses (Rappole and Tipton 1991) constructed from 1 mm wide flat braided shelf-string (British Trust for Ornithology, UK), with a total weight of 1.0 g. In comparison with our dataset of captured males in Ammarnäs ( $n = 74$ ), this extra weight represents 3.7% of the body mass of the lightest individual (27.3 g) and 3.1% of the average weight (32.5 g).

## Data analysis

After retrieving geolocators, data were downloaded from the loggers and processed using BASTrak software (BAS, UK). Further analysis was carried out using the package 'GeoLight' (Lisovski and Hahn 2012) in R 3.1 (R Core Team). Twilight events were identified using the 'threshold method' (Ekstrom 2004) at a light intensity value of 2. For each track, the corresponding sun angle was selected that

resulted in equal latitudes on both sides of equinox periods when birds were stationary (as indicated by longitude, which is not affected by equinox), which was at  $-5^\circ$  for all individuals. Geolocation provides position estimates with an accuracy  $\pm$  SD of about 186 km (Phillips et al. 2004), with lowest accuracy in latitude estimates close to the equinoxes. Therefore, latitude data were deleted from 14 d prior till 18 d after the autumn equinox and 18 d prior till 14 d after the spring equinox. To increase accuracy of positions estimates (Phillips et al. 2004), positions were smoothed twice following the method of Pütz (2002).

Departure and arrival at Ammarnäs could not be recorded as this location experiences permanent daylight from late May to early August. For flight speed calculations (see below), we only used the recorded part of the tracks, but for the overall migration distance and overall migration speed between the breeding site and the wintering area we included the distance from Ammarnäs to the first and last position estimate. First or last points often were located just south of the polar circle (see Results), presumably within one day of travelling off/ to the breeding site based on a ground speed of  $13.3 \text{ m s}^{-1}$  (Alerstam and Gudmundsson 1999). Therefore, one day was added to the migration duration. We take the arrival at and departure from oceanic waters as the endpoint of autumn migration and the start of spring migration, respectively.

With two position estimates per day, each migration step is made up of multiple (more or less 12 h) segments. For the migration steps between main stopover sites, we calculated ground speed and airspeed for each segment and then took the mean, weighted for the duration of each segment. Segment length was calculated as the great-circle distance between two smoothed position estimates (cf. above). Duration of migration flights was calculated as the time difference between midnight or noon at each position. If the initial or final position was at a staging area, the last twilight event (departure) or the first twilight event (arrival) was used as the start- and end-time of the segment, respectively. For each segment, the ground speed of the bird was calculated by dividing the segment length by segment duration. Although there is uncertainty in the departure and arrival timings of up to half a day, this affects the flight speed only marginally as flight speeds are averaged over larger time periods (cf. above), in which the shorter departing and arriving segments have less weight in the weighted mean flight speed. For each position estimate and associated time of local midnight or local noon, wind data at 925, 850, 700 and 500 hPa (corresponding to approximately 750, 1500, 3000 and 5000 m a.s.l.) were obtained from the NCEP/NCAR reanalysis project (Kalnay et al. 1996) using the RNCEP package (Kemp et al. 2012). Subsequently, airspeed of the bird was calculated by subtracting the wind vector from the track vector. We present resulting airspeeds for 850 hPa, considering 1500 m a.s.l. appears a regular flying height for waders (Dick et al. 1987), and for a scenario in which individuals selected the most profitable elevation for each segment, i.e. resulting in the lowest airspeed.

For visualisation of monthly positions throughout the winter period (August–May), 50% home range kernels were calculated using a grid-cell size of 50 km and a smoothing factor of 50 km, which is similar to the longitude error in geocator positions reported for other seabirds (Phillips

et al. 2004), in the package ‘adehabitatHR’ (Calenge 2006), if at least 25 position estimates were available (i.e. not for September and March due to inference by equinoxes). Monthly net ocean primary productivity was obtained from O’Malley (2015) and is based on the Vertically Generalized Production Model (VGPM) algorithm (Behrenfeld and Falkowski 1997).

Geolocator data has been uploaded at <www.movebank.org> (project id 99570338) and is available upon request.

## Results

Four out of ten birds fitted with geolocators in 2013 were resighted and subsequently recaptured in 2014. A return rate of 40% falls within the range of return rates of 17 to 56% reported for adults at various locations in Alaska (Colwell et al. 1988, Schamel and Tracy 1991, Sandercock 1997). In all four recaptured individuals, body mass was 1.6–5.4 g higher at recapture in 2014 compared to initial capture in 2013 ( $t_{\text{paired}} = -3.652$ ;  $DF = 3$ ,  $p = 0.035$ ). This difference could not be attributed to a seasonal effect, as the dates of recaptures in 2014 were both before and after the capture dates of 2013. Body mass measured in 2013 was slightly higher for individuals recaptured in 2014 than for individuals that were not resighted in 2014 ( $t = -2.476$ ,  $DF = 5.9$ ,

$p = 0.048$ ). All four males attempted to breed in 2014 (see below).

Three geolocators contained a full year of data; the fourth contained data up to 3 December 2013. The migration trajectories of all four birds are shown in Fig. 1 and Supplementary material Appendix 1, Fig. A1, and migration schedules are detailed in Supplementary material Appendix 1, Table A1. Labels A–D refer to the four tracked individuals and are consistent between all tables, figures and text.

## Autumn migration

All four nests hatched successfully between 21–27 June (Table 1). First positions outside the breeding area were obtained mid-July. Three birds made short stopovers of 3–6 d at the Gulf of Finland (individuals A and D) or in the eastern Ukraine (individual B) before reaching the Black or Caspian Sea. Individual C apparently arrived directly to the Caspian Sea. Here, birds spent 13–36 d before migrating to the Gulf of Oman or just south of Oman, where they arrived on 11 (B), 13 (C) and 25 August (A) and 6 September (D).

The total autumn migration distance amounted to 5514–6954 km, which was covered in 24–55 d, including 15–35 d spent at stopover sites (Table 1). Overall migration speed (including stopovers) was 140–230 km d<sup>-1</sup>.

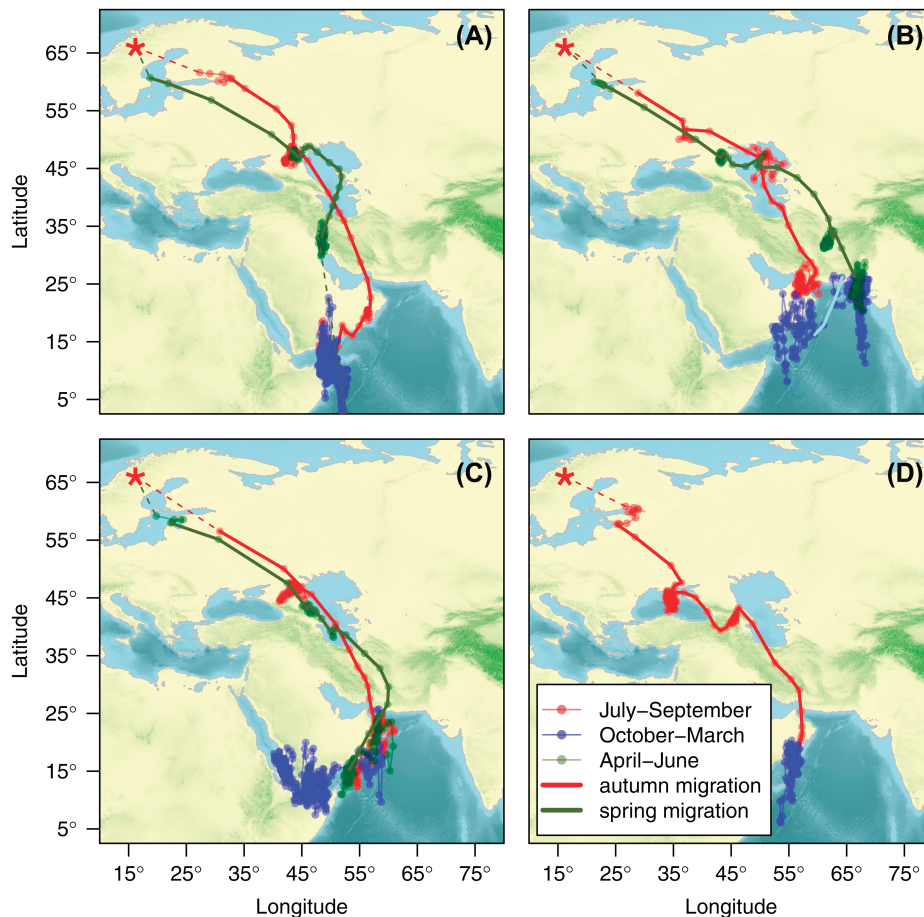


Figure 1. Geolocator tracks of four male red-necked phalaropes from Ammannäs, Swedish Lapland, during 2013–2014. Position estimates are connected by lines; bold lines were used for flight speed calculations and dotted lines from (red) and towards (green) Ammannäs (indicated by a red star) have not been recorded due to continuous daylight.



Table 1. Overview of migration duration, distance and speed of four male red-necked phalaropes from Sweden to and from the Arabian Sea. Note that the last part of spring migration is more synchronised than the onset; see Results for details.

Individual	Autumn migration				Spring migration		
	A	B	C	D	A	B	C
Clutch hatching date in 2013 (autumn migration) and 2014 (spring migration)	22 Jun	27 Jun	21 Jun	23 Jun	2 Jul	NA	4 Jul
<b>Migration to/from sea</b>							
Onset of migration <sup>1</sup>	15 Jul	18 Jul	15 Jul	13 Jul	20 Mar	23 Apr	15 May
End of migration <sup>2</sup>	3 Sep	11 Aug	13 Aug	6 Sep	25 May	3 Jun	4 Jun
Total duration (days)	49	24	29	55	65	40	19
Total cumulative distance (km)	6939	5514	5709	6954	7379 <sup>3</sup>	6345	6908
Total migration speed (km d <sup>-1</sup> )	142	230	197	126	114	159	364
<b>Stopover duration (d)</b>							
Baltic Sea, Gulf of Finland or Ukraine <sup>4</sup>	3	3	–	6	–	2	3
Black Sea and/or Caspian Sea <sup>4</sup>	29	13	23	36	9	10	8
Persian Gulf or west Pakistan <sup>4</sup>	–	–	–	–	46	21	–
Total stopover time	32	16	23	42	55	33	11

<sup>1</sup>In autumn, date at last recorded position minus one day.

<sup>2</sup>In spring, date at last recorded position plus one day.

<sup>3</sup>Including the not-recorded flight from the Gulf of Aden to the Persian Gulf (~ 2400 km).

<sup>4</sup>See Supplementary material Appendix 1, Table A1 for which areas were used by each individual.

## Behaviour during wintering

After arrival in the seas surrounding Oman, birds spread in different directions. After a short stop south of Oman, individual A spent 198 d in the Gulf of Aden before moving to the northern Persian Gulf. Another individual (B) stayed for 27 d in the gulf of Oman before slowly moving south along the Omani coast for 74 d, after which the bird moved east to the seas off Pakistan, where it stayed for 152 d. The third individual (C) stayed for 6 d in the Gulf of Oman before moving south of Oman. After 59 d, the bird moved to the Gulf of Aden for 41 d, spent 33 d in the southern Red Sea, moved back into the Gulf of Aden for 41 d, and finally spent 53 d south of Oman. Winter movements were not recorded for the fourth individual (D): this bird stayed south of Oman until logger failure.

## Spring migration

Departure from the Arabian Sea commenced in late March to mid-May. Two birds first moved to an intermediate stopover site. The first individual (A) flew approximately 2400 km from the Gulf of Aden to the northern Persian Gulf, where it stayed for 46 d. Due to the equinox, latitude estimates were unreliable during this period, but the narrow range of longitude estimates (47°–53°E) show that this migration must have been overland. The second individual (B) moved from offshore Pakistan to inland western Pakistan where it stayed for 21 d, before joining the other two individuals at the Caspian Sea in mid-May, where they stayed 8–10 d. All three birds then moved to the Baltic Sea, using a trajectory just south of the autumn route. Two individuals (B and C) stayed here for 2–3 d, but for individual A only two positions were obtained from this region, suggesting that it more or less directly moved on towards the breeding area that already experiences permanent daylight at this time of the year.

The total spring migration distance amounted to 6345–7379 km (Table 1), which was covered in 19–65 d, including total stopover time of 11–55 d. The corresponding overall

migration speed (including stopovers) was 114–364 km d<sup>-1</sup>. Variation in the total distance covered, stopover time and migration speed was lower in the last part of the migration (from staging areas the Persian Gulf, from inland western Pakistan and from offshore Oman): a total distance of 4472–6908 km, a duration of 19 d in all three birds, including total stopover time of 8–10 d, and migration speed of 262–364 km d<sup>-1</sup>.

For three individuals (A–C) the nest was found in the 2014 breeding season. Individual D probably was incubating as well, as suggested by consistent bearings when arriving and departing from regular visits to a specific pond for feeding. Two nests hatched successfully on 2 (A) and 4 July (C). Assuming an incubation period of 18 d (Cramp and Simmons 1983), these clutches had been laid at 14 and 16 June, respectively. The nest of individual B was found on 13 June but was depredated soon after this date.

## Flight speed

For most migration steps (75%,  $n = 20$ ) mean ground speed (Fig. 2) was lower than the single measurement of airspeed of 13.3 m s<sup>-1</sup> for red-necked phalarope by Alerstam and Gudmundsson (1999). Ground speeds exceeding 13.3 m s<sup>-1</sup> were observed only for migration steps shorter than 50 h. Derived airspeeds at 850 hPa were on average 10.2 m s<sup>-1</sup> ( $n = 20$ ,  $SD = 3.9$ , range = 4.2–21.9). If birds would select the elevation resulting in the lowest airspeed, the average airspeed would be 8.6 m s<sup>-1</sup> ( $n = 20$ ,  $SD = 4.1$ , range = 3.7–21.2). Airspeeds were both lower (14/20) and higher (6/20) than ground speeds, suggesting that phalaropes experienced tailwinds as well as headwinds, respectively. Only for some migration steps, mostly between the Baltic region and the Caspian Sea region, derived mean airspeeds were equal to the measured airspeed of 13.3 m s<sup>-1</sup>, suggesting non-stop flights. In most cases the derived airspeed was lower than the measured airspeed, suggesting that the phalaropes did not fly continuously. Assuming a constant airspeed of 13.3 m s<sup>-1</sup>, birds flew on average for 77%

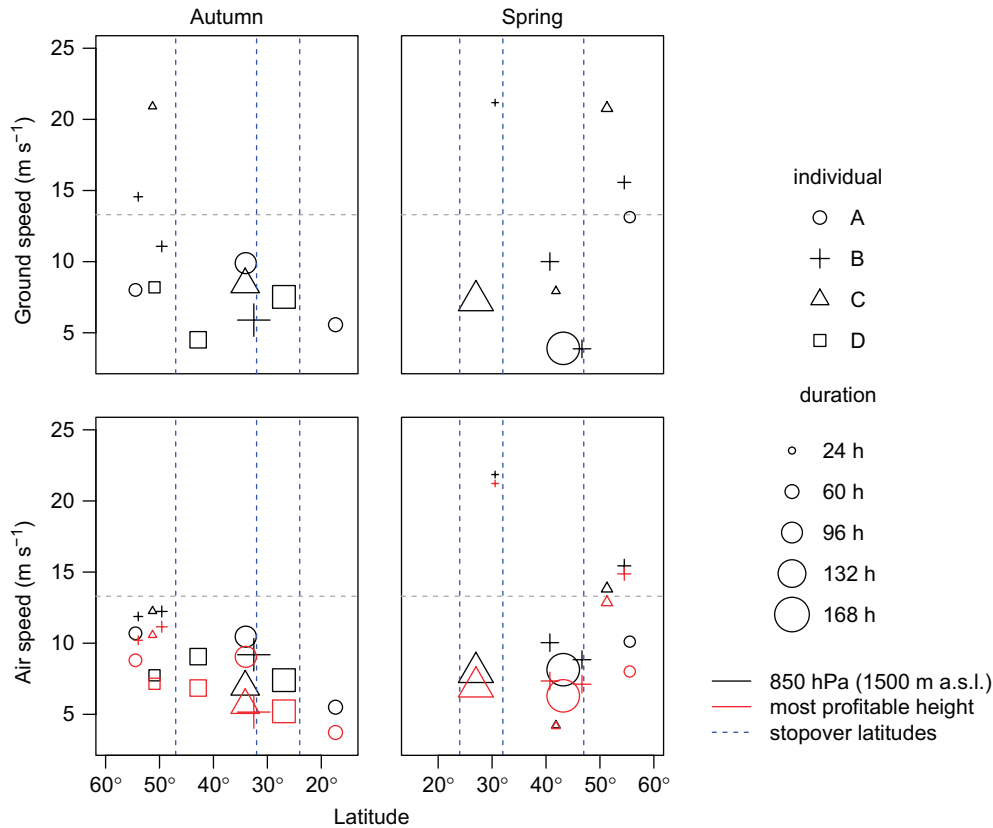


Figure 2. Mean ground (upper figures) and airspeed (lower figures) per migration step of four red-necked phalaropes. Symbol shape relates to the individual and symbol size is proportional to the duration of the migration leg. Airspeeds in case the bird always flies at the most profitable elevation are shown in red. Blue dotted lines roughly indicate the latitude of main stopover areas: Caspian Sea region (47°NB), western Pakistan and northern Persian Gulf (32°NB) and the Gulf of Oman (24°NB). The grey dotted horizontal lines indicate the measured airspeed of 13.3 m s<sup>-1</sup> based on Alerstam and Gudmundsson (1999).

(n = 20) of the time if flying at 850 hPa or 65% (n = 20) if always flying at the most profitable elevation.

## Discussion

We have presented the first data on movements of individual Scandinavian red-necked phalaropes during the non-breeding season, confirming expectations based on ring recoveries (Höhn 1966, Schiemann 1977, Alerstam 1990, Bakken et al. 2003, Fransson et al. 2008) that individuals from this population winter in the Arabian Sea. In agreement with field observation on staging birds, the phalaropes divided the ca 5514–6954 km migrations into two to four leaps, staging for a few days in the Gulf of Finland (autumn) or the southern Baltic Sea (spring) and for up to a month at one or two locations in or near the Black and Caspian Sea (autumn and spring). These results thus confirm the role and importance of these areas as staging sites for Scandinavian red-necked phalaropes (Delany et al. 2009).

Previously, overland migration of red-necked phalaropes was assumed to be performed ‘largely’ non-stop (Cramp and Simmons 1983). However, airspeeds from the four individuals tracked in this study were mostly below 13.3 m s<sup>-1</sup>, the single measurement of airspeed for red-necked phalarope measured by Alerstam and Gudmundsson (1999). This

suggests that they did not fly continuously, but for about 65 or 77% of the time, depending on which flight altitude they selected. Although the majority of migration leaps thus likely included short stops, several flights shorter than two days covering up to approximately 2400 km had calculated airspeeds close to or above 13.3 m s<sup>-1</sup>, indicating these were true non-stop flights. These non-stop flights were mostly in the first or last recorded stage of spring migration, between the stopover in the Caspian Sea region and the Baltic.

Spring staging times in the Caspian Sea region were 8–10 d, which is comparable to estimated staging times for broad-billed sandpipers *Limicola falcinellus* in the Ukraine prior to a presumably non-stop flight to the Scandinavian breeding grounds (Verkuil et al. 2006). Autumn staging duration in the Caspian Sea region was however substantially longer compared to spring in three out of four birds and similar to those reported for red-necked phalaropes staging in the Bay of Fundy, Canada. Here, red-necked phalaropes accumulate fat loads to ca 40–45% of lean body mass, which would enable a non-stop flight of up to 5100 km (Mercier 1985). In autumn, red-necked phalaropes staging in the Caspian Sea region would need to ‘only’ cover approximately 2000 km to the Gulf of Oman, and would thus need smaller fat reserves compared to their conspecifics staging in eastern Canada. Indeed, both mean and maximum body mass of large numbers of red-necked phalaropes captured

at inland lakes in Kazakhstan (Gavrilov et al. 1983), were ca 14 g lower than phalaropes staging in the Bay of Fundy (Mercier 1985). Why then do they stop for such long time in the Caspian Sea region on southward migration? Stopover times longer than what seems required for refuelling have also been reported in other studies (McKinnon et al. 2013), and several potential explanations can be proposed. For example, a longer stopover time might simply be the result of suboptimal feeding conditions, resulting in a lower fattening rate. Alternatively, the birds may postpone departure if feeding conditions are better in the Caspian Sea region than in the Arabian Sea. In addition, birds may stay longer at the Caspian Sea stopover in order to moult, an energetically demanding process. Whereas active primary moult has been reported from Mono Lake, California, USA, a key stopover site for red-necked phalaropes following the Pacific Americas flyway (Jehl 1986), only 1% of individuals captured in July–September at inland lakes in Kazakhstan showed active moult (Gavrilov et al. 1983). Active moult of body feathers, which is commenced at the breeding grounds, is however reported from all autumn staging sites (Cramp and Simmons 1983, Gavrilov et al. 1983, Jehl 1986, Eichhorn 2001). Hence moult of body feathers, but probably

not primary feathers, may be another function of the stopover in the Caspian Sea region. Clearly, field observations from the Caspian Sea region and the Arabian Sea are needed to verify these ideas.

All individuals entered the Arabian Sea via the Gulf of Oman and then moved into the seas south of Oman, as was hypothesized on the basis of field observations in this region (Mörzer-Bruyns and Mörzer-Bruyns 1957, Bailey 1966). The four individuals we tracked covered the entire proposed wintering range in the Arabian Sea, spanning from the Gulf of Aden in the west all along the Somalian coast east to offshore Pakistan (Cramp and Simmons 1983, Alerstam 1990, Delany et al. 2009). This large wintering range is largely the result of the high mobility of individual birds that used different sites.

Tracking studies have shown variation in the extent to which birds are stationary (using only a single site) or mobile ('itinerant', using multiple sites) in winter (Moreau 1972, Guilford et al. 2009, Kristensen et al. 2013, McKinnon et al. 2013, Trierweiler et al. 2013). Itinerancy may be expected when resources are highly variable in space and time, especially when this occurs in a predictable pattern (Newton 2008). In the Arabian Sea, seasonally shifting

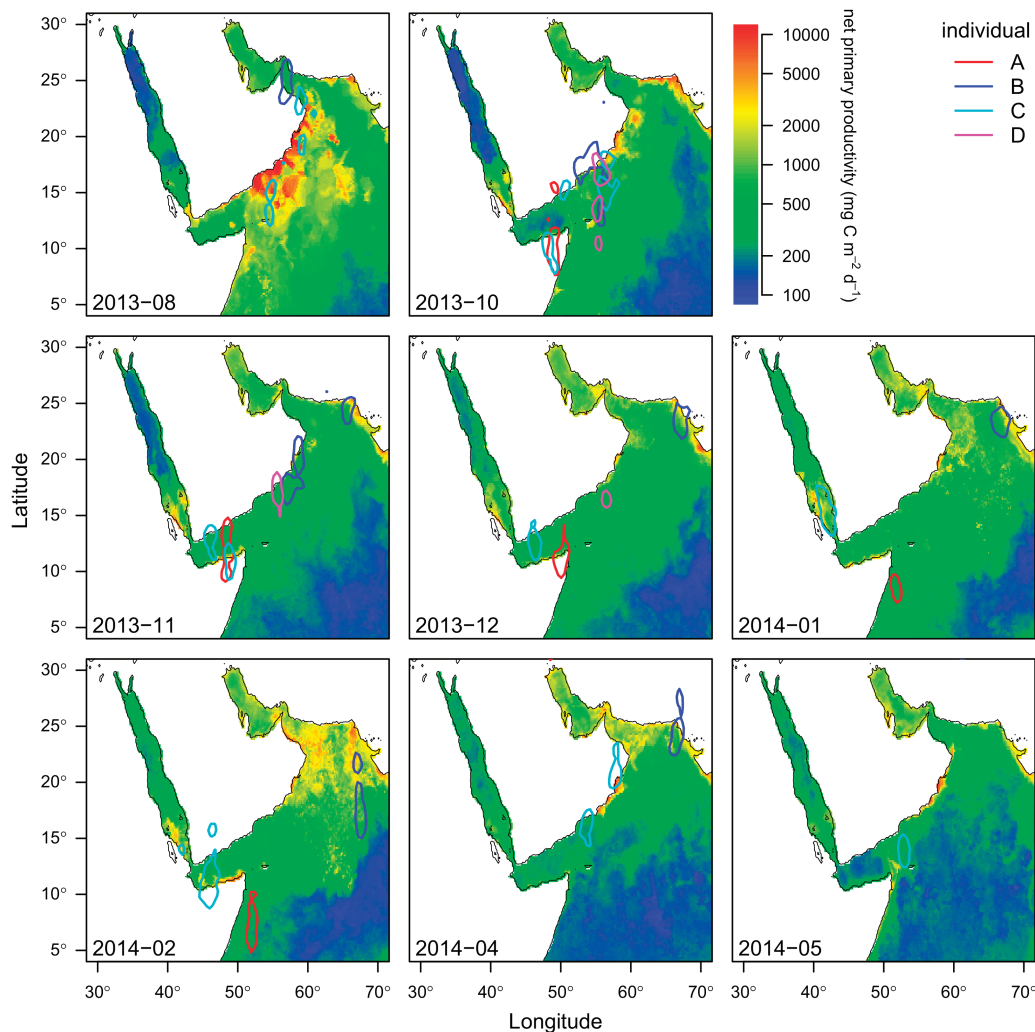


Figure 3. Net primary productivity in the Arabian Sea (background) and the outlines of the 50% home range kernels of four red-necked phalaropes. September and March are left out as the number of position estimates was too low for robust home range kernel estimation.

monsoon winds drive huge upwelling systems with marked spatio-temporal variation in primary production (Marra and Barber 2005). High primary production occurs in particular at shelf edges, which is where high densities of phalaropes have been reported feeding on zooplankton (Schiemann 1986, Bourne 1991, 1997, Thorne and Read 2013). Location shifts of the three red-necked phalaropes tracked over the entire winter coincide with changes in productivity (Fig. 3). For example, individual B switched from the Omani coast to offshore Pakistan after productivity declined in the former area. Similarly, individual C may have tracked high productivity events at the Omani coast, via the northern Somali coast to the southern Red Sea and back again. It returned to the Omani coast in April, when local primary productivity increased here again. These movements match field observations in winter, the largest numbers being present in the Gulf of Aden north to Salalah, Oman, and in the Gulf of Oman, with only small numbers off the Omani east coast (Mörzer-Bruyns and Mörzer-Bruyns 1957, Bailey 1966). These winter movements of red-necked phalaropes may be related to spatio-temporal patterns in primary productivity in a manner similar to the itinerancy reported for migrants wintering in Africa (Moreau 1972, Stach et al. 2012, Trierweiler et al. 2013). In fact, the prolonged stop-over times in autumn (see above) and in early spring (at the Persian Gulf and in western Pakistan) obscure the distinction between ‘migration’ and ‘wintering’ and may also best be regarded as part an optimal timing of movements relative to optimal local conditions. A formal test of the relationship between the birds’ movements and primary production is however problematic given the small sample size, the low spatial resolution of the birds’ position estimates and the high spatial heterogeneity in primary production.

To what extent inter-individual differences in winter movements arise due to the individuals’ direct responses to current local circumstances or to learned routes in earlier years is yet unclear. Seabirds show an overall tendency for large inter-individual variation but small intra-individual variation in route and site fidelity between years (Phillips et al. 2005, Quillfeldt et al. 2010, Guilford et al. 2011, Dias et al. 2013, but see Dias et al. 2011). Such dispersive movement patterns may be best explained by the recently proposed ‘exploration-refinement hypothesis’ (Guilford et al. 2011), in which individuals explore large areas and refine their subsequent movements according to prior experiences. Similar processes may shape the winter movements in red-necked phalaropes in the Arabian Sea and repeated tracks from the same individuals, preferably including their first migration cycle, are needed to shed light on this.

Although our sample size is small (four individuals only), the relative consistency in behaviour (destination, stopover use, flight speeds and mobility during winter) suggests the results are representative for the larger population. Still, future studies should test the robustness of our conclusions.

Tracking studies across a wider range in the Arctic are needed to investigate potential differences in migration strategies among populations using the other two main wintering areas (off the Pacific coast of South America and off the East Indies), but we can now already compare our results to a single male tracked from Scotland to the Pacific and back (Smith et al. 2014). The total migration distance

of ca 22 000 km of this individual is 1.5–1.9 times the ca 12 000–14 000 km covered by the Scandinavian birds. Despite the larger migration distance of the Scottish bird, individuals from both populations may have similar migration speeds: Smith et al. (2014) noted that the ‘slow southward progress’ suggested regular stops – which, although not substantiated by flight speed calculations – is in line with our findings for Scandinavian red-necked phalaropes.

In the current study only males were tracked. It would be interesting to also track females as phalaropes have reversed sex-roles, and thus phalaropes form a good case to test ideas related to sex-specific migration patterns. For example, geolocator tracks could be used to quantify the contribution of three not mutually exclusive proximate causes to the observed earlier arrival of females at the breeding grounds in phalaropes (Reynolds et al. 1986): 1) earlier spring departure from the wintering grounds by females, 2) faster spring migration by females and/or 3) females wintering closer to the breeding grounds.

The Arabian Sea is one of the most productive marine areas on Earth and supports a distinctive but poorly studied avifauna, including several taxa endemic to the area (Bailey 1966). The red-necked phalarope is the only seabird abundant in the Arabian Sea that breeds in the Arctic (Bailey 1966) and our study is the first to establish a definitive link with the Scandinavian breeding population. In addition, our study is – to the best of our knowledge – the first to document movement data of individual seabirds in the Arabian Sea and this and future studies are required to understand how red-necked phalaropes and other seabirds utilize this rich and dynamic area.

*Acknowledgements* – Vital assistance in the field was provided by Vincent Hin in 2013 and by Tim van der Meer, Guido Keijl and Fons de Meijer in 2014. Martin Green and Åke Lindström (Lund Univ., Lund, Sweden) provided essential logistical support and the required permits. Geolocators were provided by Thomas Alerstam (Lund Univ.). James Fox (Migrate Technologies, Cambridge, UK) kindly downloaded the data from the dead logger. Peter Becker, Götz Eichhorn, Jens Eriksen, Jim de Fouw and Pavel Tomkovich helped with obtaining references. Thanks also to Ron Ydenberg (Wageningen Univ., the Netherlands). Special thanks go out to Paula Machin and Juan Fernández-Elipse for support during the fieldwork! This work is financed by the Netherlands Organisation for Scientific Research (project number 866.13.005) and supported by the LUVRE project (< www.luvre.org >).

## References

- Alerstam, T. 1990. Bird migration. – Cambridge Univ. Press.
- Alerstam, T. and Lindström, Å. 1990. Optimal bird migration: the relative importance of time, energy and safety. – In: Gwinner, E. (ed.), Bird migration: the physiology and ecophysiology. Springer, pp. 331–351.
- Alerstam, T. and Gudmundsson, G. A. 1999. Migration patterns of tundra birds: tracking radar observations along the Northeast Passage. – *Arctic* 52: 346–371.
- Bailey, R. 1966. The seabirds of the southeast coast of Arabia. – *Ibis* 108: 224–264.
- Bakken, V., Runde, O. and Tjørve, E. 2003. Norsk ringmerkningsatlas. Volum 1. Lommer – alkefugler. – Ringmerkningscentralen, Stavanger Museum.



- Behrenfeld, M. J. and Falkowski, P. G. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. – *Limnol. Oceanogr.* 42: 1–20.
- Bourne, W. R. P. 1991. The seabirds of Arabia. – *Sea Swallow* 40: 4–12.
- Bourne, W. R. P. 1997. Phalaropes in the Arabian Sea & Gulf of Oman. – *Oman Bird News* 20: 5–6.
- Brown, R. G. B. and Gaskin, D. E. 1988. The pelagic ecology of the grey and red-necked phalaropes *Phalaropus fulicarius* and *P. lobatus* in the Bay of Fundy, eastern Canada. – *Ibis* 130: 234–250.
- Calenge, C. 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. – *Ecol. Model.* 197: 516–519.
- Chamberlain, C. P., Bensch, S., Feng, X., Åkesson, S. and Andersson, T. 2000. Stable isotopes examined across a migratory divide in Scandinavian willow warblers (*Phylloscopus trochilus trochilus* and *Phylloscopus trochilus acredula*) reflect their African winter quarters. – *Proc. Biol. Sci.* 267: 43–48.
- Colwell, M. A., Reynolds, J. D., Gratto, C. L., Schamel, D. and Tracy, D. M. 1988. Phalarope philopatry. – *Proc. Int. Ornithol. Congr.* 19: 585–593.
- Crappe, S. and Simmons, K. E. L. 1983. Handbook of the birds of Europe, the Middle East and north Africa: the birds of the Western Palearctic, Volume III waders to gulls. – Oxford Univ. Press.
- Delany, S., Dodman, T., Stroud, D. and Scott, D. 2009. An atlas of wader populations in Africa and western Eurasia. – Wetlands International.
- Dias, M. P., Granadeiro, J. P., Phillips, R. A., Alonso, H. and Catry, P. 2011. Breaking the routine: individual Cory’s shearwaters shift winter destinations between hemispheres and across ocean basins. – *Proc. Biol. Sci.* 278: 1786–1793.
- Dias, M. P., Granadeiro, J. P. and Catry, P. 2013. Individual variability in the migratory path and stopovers of a long-distance pelagic migrant. – *Anim. Behav.* 86: 359–364.
- Dick, W. J. A., Piersma, T. and Prokosch, P. 1987. Migration of the Siberian knots *Calidris canutus canutus*: results of a co-operative Wader Study Group Project. – *Ornis Scand.* 18: 5–16.
- Eichhorn, G. 2001. Zur Bedeutung der Steppenseen Zentral-Kasachstans als Rastplatz arktischer Watvögel Charadrii, insbesondere zur Rastplatzökologie von Zwergstrandläufer *Calidris minuta* und Odinshühnchen *Phalaropus lobatus*. – Diploma thesis.
- Ekstrom, P. A. 2004. An advance in geolocation by light. – *Mem. Natl. Inst. Polar Res* 58: 210–226.
- Fijn, R. C., Hiemstra, D., Phillips, R. A. and Winden, J. Van Der 2013. Arctic terns *Sterna paradisaea* from the Netherlands migrate record distances across three oceans to Wilkes Land, east Antarctica. – *Ardea* 101: 3–12.
- Fransson, T., Österblom, H. and Hall-Karlsson, S. 2008. Svensk ringmärkningsatlas. Vol. 2. – Naturhistoriska riksmuseet and Sveriges Ornitologiska Förening.
- Gavrilov, E. I., Jerochov, S. N., Gavrilov, A. E. and Chrokov, V. V. 1983. Über den Herbstzug des Odinswassertreters (*Phalaropus lobatus*) in Kasachstan. – *Die Vogelwarte* 32: 103–116.
- Gilg, O., Moe, B., Hanssen, S. A., Schmidt, N. M., Sittler, B., Hansen, J., Reneerkens, J., Sabard, B., Chastel, O., Moreau, J., Phillips, R. A., Oudman, T., Biersma, E. M., Fenstad, A. A., Lang, J. and Bollache, L. 2013. Trans-equatorial migration routes, staging sites and wintering areas of a high-Arctic avian predator: the long-tailed skua (*Stercorarius longicaudus*). – *PLoS One* 8: e64614.
- Guilford, T., Meade, J., Willis, J., Phillips, R. A., Boyle, D., Roberts, S., Collett, M., Freeman, R. and Perrins, C. M. 2009. Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. – *Proc. Biol. Sci.* 276: 1215–1223.
- Guilford, T., Freeman, R., Boyle, D., Dean, B., Kirk, H., Phillips, R. A. and Perrins, C. M. 2011. A dispersive migration in the Atlantic Puffin and its implications for migratory navigation. – *PLoS One* 6: e21336.
- Hedenström, A., Klaassen, R. H. G. and Åkesson, S. 2013. Migration of the little ringed plover *Charadrius dubius* breeding in south Sweden tracked by geolocators. – *Bird Study* 60: 466–474.
- Höhn, E. O. 1966. Ringing (banding) and recoveries of phalaropes: a summary of presently available information. – *Bird-Banding* 37: 197–200.
- Jehl, J. R. Jr 1986. Biology of red-necked phalarope (*Phalaropus lobatus*) at the western edge of the Great Basin in fall migration. – *Great Basin Nat.* 46: 185–197.
- Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S., White, G., Woollen, J., Zhu, Y., Chelliah, M., Ebisuzaki, W., Higgins, W., Janowiak, J., Mo, K. C., Ropelewski, C., Wang, J., Leetmaa, A., Reynolds, R., Jenne, R. and Joseph, D. 1996. The NCEP/NCAR 40-year reanalysis project. – *Bull. Am. Meteorol. Soc.* 77: 437–471.
- Kemp, M. U., van Loon, E., Shamoun-Baranes, J. and Bouten, W. 2012. RNCEP: global weather and climate data at your fingertips. – *Methods Ecol. Evol.* 3: 65–70.
- Klaassen, R. H. G., Alerstam, T., Carlsson, P., Fox, J. W. and Lindström, A. 2011. Great flights by great snipes: long and fast non-stop migration over benign habitats. – *Biol. Lett.* 7: 833–835.
- Kristensen, M. W., Tøttrup, A. P. and Thorup, K. 2013. Migration of the common redstart (*Phoenicurus phoenicurus*). – *Auk* 130: 258–264.
- Lisovski, S. and Hahn, S. 2012. GeoLight – processing and analysing light-based geocator data in R. – *Methods Ecol. Evol.* 3: 1055–1059.
- Marra, J. and Barber, R. T. 2005. Primary productivity in the Arabian Sea: a synthesis of JGOFS data. – *Prog. Oceanogr.* 65: 159–175.
- McKinnon, E. A., Fraser, K. C. and Stutchbury, B. J. M. 2013. New discoveries in landbird migration using geolocators, and a flight plan for the future. – *Auk* 130: 211–222.
- Meinertzhagen, R. 1925. The distribution of the phalaropes. – *Ibis* 67: 325–344.
- Mercier, F. M. 1985. Fat reserves and migration of red-necked Phalaropes (*Phalaropus lobatus*) in the Quoddy region, New Brunswick, Canada. – *Can. J. Zool.* 63: 2810–2816.
- Moreau, R. E. 1972. The Palearctic-African bird migration system. – Academic Press.
- Mörzer-Bruyns, W. F. J. and Mörzer-Bruyns, M. F. 1957. Waarnemingen van de Grauwe Franjepoot, *Phalaropus lobatus* (L.), in de Indische Oceaan. – *Ardea* 45: 72–84.
- Newton, I. 2008. The migration ecology of birds. – Academic Press.
- O’Malley, R. 2015. Ocean productivity. – <www.science.oregonstate.edu/ocean.productivity/>.
- Phillips, R. A., Silk, J. R. D., Croxall, J. P., Afanasyev, V. and Briggs, D. R. 2004. Accuracy of geolocation estimates for flying seabirds. – *Mar. Ecol. Prog. Ser.* 266: 265–272.
- Phillips, R. A., Silk, J. R. D., Croxall, J. P., Afanasyev, V. and Bennett, V. J. 2005. Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. – *Ecology* 86: 2386–2396.
- Piersma, T. 1987. Hink, stap of sprong? Reisbepervingen van arctische steltlopers door voedselzoeken, vetopbouw en vliegsnelheid. – *Limosa* 60: 185–194.
- Pütz, K. 2002. Spatial and temporal variability in the foraging areas of breeding king penguins. – *Condor* 104: 528–538.
- Quillfeldt, P., Voigt, C. C. and Masello, J. F. 2010. Plasticity versus repeatability in seabird migratory behaviour. – *Behav. Ecol. Sociobiol.* 64: 1157–1164.

- Rappole, J. H. and Tipton, A. R. 1991. New harness design for attachment of radio transmitters to small passerines. – *J. Ornithol.* 62: 335–337.
- Reynolds, J. D., Colwell, M. A. and Cooke, F. 1986. Sexual selection and spring arrival times of red-necked and Wilson's phalaropes. – *Behav. Ecol. Sociobiol.* 18: 303–310.
- Sandercock, B. K. 1997. The breeding biology of red-necked phalaropes *Phalaropus lobatus* at Nome, Alaska. – *Wader Study Group Bull.* 83: 50–54.
- Schamel, D. and Tracy, D. M. 1991. Breeding site fidelity and natal philopatry in the sex role-reversed red and red-necked phalaropes. – *J. Ornithol.* 62: 390–398.
- Schiemann, H. 1977. Beringungsergebnisse Nordeuropäischer Odinshünchen. – *Sterna* 16: 73–80.
- Schiemann, H. 1986. Red-necked phalaropes *Phalaropus lobatus* off the coast of Somalia and Kenya. – *Scopus* 10: 42–44.
- Smith, M., Bolton, M., Okill, D. J., Summers, R. W., Ellis, P., Liechti, F. and Wilson, J. D. 2014. Geolocator tagging reveals Pacific migration of red-necked phalarope *Phalaropus lobatus* breeding in Scotland. – *Ibis* 156: 870–873.
- Stach, R., Jakobsson, S., Kullberg, C. and Fransson, T. 2012. Geolocators reveal three consecutive wintering areas in the thrush nightingale. – *Anim. Migr.* 1: 1–7.
- Thorne, L. H. and Read, A. J. 2013. Fine-scale biophysical interactions drive prey availability at a migratory stopover site for *Phalaropus* spp. in the Bay of Fundy, Canada. – *Mar. Ecol. Prog. Ser.* 487: 261–273.
- Trierweiler, C., Mullié, W. C., Drent, R. H., Exo, K. M., Komdeur, J., Bairlein, F., Harouna, A., De Bakker, M. and Koks, B. J. 2013. A Palearctic migratory raptor species tracks shifting prey availability within its wintering range in the Sahel. – *J. Anim. Ecol.* 82: 107–120.
- Verkuil, Y., Van Der Have, T. M., Van Der Winden, J., Keijl, G. O., Ruiters, P. S., Koolhaas, A., Dekinga, A. and Chernichko, I. I. 2006. Fast fuelling but light flight in broad-billed sandpipers *Limicola falcinellus*: stopover ecology at a final take-off site in spring (Sivash, Ukraine). – *Ibis* 148: 211–220.

Supplementary material (Appendix JAV-00807 at <[www.avianbiology.org/appendix/jav-00807](http://www.avianbiology.org/appendix/jav-00807)>). Appendix 1.