



Skipping-type migration in a small Arctic wader, the Temminck's stint *Calidris temminckii*

Terje Lislevand and Steffen Hahn

T. Lislevand (terje.lislevand@um.uib.no), Univ. of Bergen, Univ. Museum of Bergen, PO Box 7800, NO-5020 Bergen, Norway. – S. Hahn, Swiss Ornithological Inst., Dept of Bird Migration, Seerose 1, CH-6204 Sempach, Switzerland.

By using morphometric data and geolocator tracking we investigated fuel loads and spatio-temporal patterns of migration and non-breeding in Temminck's stints *Calidris temminckii*. Body masses in stints captured at autumn stopover sites from Scandinavia to northern Africa were generally not much higher than during breeding and did not vary geographically. Thus, we expected migrating stints to make several stopovers and either circumventing the Sahara desert with low fuel loads or fuelling at north African stopover sites before desert crossing. Geolocation revealed that birds ($n = 6$) departed their Norwegian breeding site in the last part of July and all but one migrated south-west over continental western Europe. A single bird headed south-east to the Balkan Peninsula where the geolocator died. As predicted, southbound migration proceeded in a typical skipping manner with 1–4 relatively short stopovers (median 4 d) during 10–27 d of migration before reaching north-west Africa. Here birds spent 11–20 d before crossing the Sahara. The non-breeding sites were located at or near the Niger River in Mali and were occupied continuously for more than 215 d with no indications of itinerancy. Spring migration commenced in late April/early May when birds crossed the desert and used stopover sites in the western Mediterranean basin in a similar manner as during autumn. The lowest body masses were recorded in spring at islands in the central Mediterranean basin, indicating that crossing the Sahara and Mediterranean barriers is exhausting to these birds. Hence, the skipping-type pattern of migration revealed by geolocators is likely to be natural in this species and not an effect of instrumentation.

With their large inter- and intra-specific variation in migration patterns, waders are highly suitable as model organisms in bird migration research (Piersma 2007). Recent studies have demonstrated formidable long-distance flights in some species (Gill et al. 2009, Klaassen et al. 2011, Hooijmeijer et al. 2013) with non-stop migration in a 'jumping' manner powered by high individual fuel loads (Piersma 1987). Other species divide their migratory journeys into several shorter bouts with intermittent fuelling along a chain of stopover sites (i.e. hop or skip migration; Piersma 1987, Colwell 2010, Hedenström et al. 2013) which should result in a different pattern of fuel accumulation (Piersma et al. 2005). During the non-breeding season, migratory birds may either remain in the same area or show some degree of itinerancy, depending on local ecological conditions (Moreau 1972, Curry-Lindahl 1982, Alerstam et al. 2003). Detailed information about such individual movements during migration and non-breeding periods is typically limited or completely lacking for waders. Current knowledge

of specific migration patterns is often derived using auxiliary data like body mass to estimate fuel loads and thus potential flight ranges (Hedenström 2004). However, such indirect evidence for migratory strategies is imprecise and should, if possible, be verified to better understand a species' ecology and for improving our understanding of bird migration in general, e.g. by the means of comparative studies (Piersma 2007). One way to evaluate migration strategies in birds is through direct tracking by using recently developed miniature light-level geolocators (Bridge et al. 2011).

The Temminck's stint *Calidris temminckii* is one of the smallest waders and breeds in Palearctic tundra and alpine regions. It is mainly found from sub-Saharan west-Africa to south-east Asia when not breeding (Cramp and Simmons 1983). The few available ring recoveries indicate that western breeding populations spend the non-breeding season in west-Africa or possibly in the western Mediterranean (Rönka 1996, Bakken et al. 2003, Fransson et al. 2008, Breihagen and Scott 2009, Saurola et al. 2013). However, the species' spatio-temporal occurrence in east-Africa suggests either some form of 'loop migration' (Curry-Lindahl 1982) or itinerancy (sequential changes of nonbreeding sites). From fuel loads of birds migrating southwards through Ottenby in Sweden, Hedenström (2004) estimated that adults are able to fly non-stop to the Mediterranean region, and perhaps

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even to the presumed Sahelian non-breeding sites. However, our understanding of migration and non-breeding in Temminck's stints is largely based on scant or indirect evidence.

We applied a dual approach to test the various hypotheses about migratory movements in Temminck's stints. First, we collated body mass data from migrating Temminck's stints since the level of fuel accumulation indirectly reflects a species' migratory strategy. If Temminck's stints migrate in long jumps from breeding to non-breeding sites we expected to find formidable fuel reserves along the flyway, especially before barrier crossing. However, if stints use a skipping strategy accumulated fuel stores can be kept at a lower level, and should be depleted after presumed barrier crossings. Secondly, we tracked the migration and non-breeding movements of individual birds breeding in Norway to confirm our expectations derived from the body mass approach. Direct tracking also allowed us to check for itinerancy during the non-breeding period, which may be expected in waders relying on ephemeral wetlands in dry regions like sub-Saharan Africa (Colwell 2010).

Methods

We collated data on body mass in Temminck's stints both from the literature and by inquiries to bird ringing institutions in Europe (see Supplementary material Appendix 1, Table A1 for details and references). Data were available for a total of 22 sites from southern Sweden to east Africa. For migratory body masses we considered data from July–September and April–May, the main periods of migration in Europe (Hedenström 2004, this study). Measurements from our study population (see below) are included for comparison. For each site we calculated weighted means if raw data were not available. We restricted the statistical analysis to sites with $n > 4$, whereas other sites are only visually presented.

We deployed geolocators to Temminck's stints in an alpine breeding population at Finse, southern Norway (60.6°N, 7.5°E). A detailed description of the study site and field methods is found in Lislevand and Hahn (2013). The geolocators, manufactured by the Swiss Ornithological Inst. (SOI), were attached using a flexible leg loop harness made of silicone. In 2010, a total of 10 stints were equipped with SOI-GDL1 geolocators (mean mass incl. harness = 1.13 ± 0.01 g) and in 2011 we tagged another 20 birds with the model SOI-GDL2 (0.58 ± 0.01 g incl. harness). Apparently, the devices had no severe effects on the birds, as judged from returning rates between years, breeding behaviour, breeding success, body mass, and body condition (Lislevand and Hahn 2013). Of the 30 tagged birds, 12 (40%) returned to Finse in the following year (53% in colour-ringed birds; Breihagen 1989). One returning bird had lost the logger and we failed to trap two other birds, resulting in a total of nine successfully retrieved loggers. Of these, three loggers contained no data, three had stopped working in August in the year of deployment (on autumn migration) and three devices contained data for complete, or near-complete, annual migratory cycles.

We used the threshold method for positioning by light (Hill 1994). Sunset and sunrise times of 1 min interval

interpolated data were determined using GeoLocator software (Swiss Ornithological Inst.). All further data processing were done with the R package GeoLight 1.03 (Lisovski et al. 2012). The two geolocator models differed in light sensor sensitivity (GDL1 more sensitive than GDL2) and light measurement intervals thus necessitated the use of model specific parameter settings in the data analysis. Hence, outlying sunset/sunrise times were removed using Loess filter function with $k = 5$ and $k = 2$ interquartile ranges as thresholds for GDL1 and GDL2, respectively. Stationary periods were separated from non-stationary movement periods using the ChangeLight function with a threshold at the 0.9-quantile of change point probability and a minimum staging time of 2 d. For the incomplete tracks we used a threshold at the 0.8-quantile to account for longer relative migration times compared to staging times. It should be noted that, although geolocation data cannot be used to determine spatial positions at equinox (here equinox ± 8 or 10 d depending on sun elevation angle; see calibration), the timing of migratory steps can still be identified using sunrise/sunset data (Lisovski and Hahn 2012). Each of the six geolocator data sets was calibrated using light data from a period after the logger was deployed when birds were known to reside in the breeding area ('in-habitat calibration'; Lisovski et al. 2012). Finally, we mapped stationary sites, namely (post-)breeding stationary, autumn stopover, non-breeding stationary and spring stopover sites for each individual using medians \pm inter-quartile ranges of longitudes and latitudes. We merged temporarily subsequent sites, if they overlapped considerably. Travel rates were calculated as the sum of distances covered during periods of actual movement only, whereas migration rate also included stopover periods.

The data is available upon request from the MoveBank data repository (project id 54908235).

Results

In contrast to birds captured in southern Sweden (Hedenström 2004) there were no difference in autumn body mass in adult and juvenile birds captured in eastern Germany, in southern France, northern Italy and in Hungary (t -test, all $p > 0.29$, Supplementary material Appendix 1, Table A1), and thus age specific data were pooled for each site in further analyses. On autumn migration, mean body mass per site did not correlate with longitude ($r_s = 0.62$, $p = 0.09$, $n = 9$) or latitude ($r_s = -0.02$, $p = 0.95$, $n = 9$) along the European continent (Fig. 1). The grand mean of body masses was 25.3 g. Lowest mass was recorded in coastal southern France (23.1 ± 5.9 (SD) g, Glutz von Blotzheim 1999), the highest in eastern Bulgaria (28.3 ± 4.64 (SD) g, Nankinov 2001). Body mass data from northern Africa were not available. During spring migration there was no relation between latitude and body mass ($r_s = 0.65$, $p = 0.11$) or longitude ($r_s = 0.09$, $p = 0.84$; Fig. 1). Birds captured at Corsica, i.e. after crossing the Sahara and the Mediterranean Sea, showed lowest average mass of 18.8 ± 0.9 (SD) g ($n = 6$), presumably very close to lean body mass. The grand mean body mass at European stopover sites in spring was 22.1 g.

All geolocator birds departed from the breeding site in the last half of July (median: 22 July, range: 15–26 July, $n = 6$).

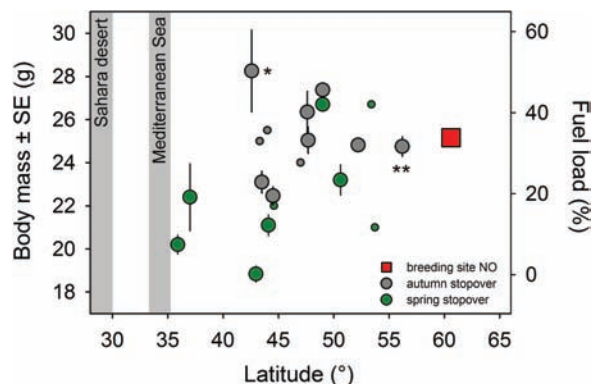


Figure 1. Body mass (g) and fuel loads of migrating Temminck's stints in relation to latitude of the locality where birds were trapped and season. A bird's fuel load is the difference between body mass and the assumed lean body mass (here 18.8 g; see Results) and is plotted as a percentage of the latter. Positions of potential migratory barriers are indicated by grey bars. Values shown are means \pm SE, large circles for sites with $n > 4$, small circles $n < 3$. The symbol '*' marks transient birds in eastern Bulgaria, possibly from Asia, '**' indicates data from Hedenström (2004).

Except a single bird (bird D, Table 1) that followed a more eastern track before the logger died 10 August while the bird apparently was in western Macedonia, all birds headed southwest along a rather narrow migration path across western continental Europe (Fig. 2). Four of the western migrants initially moved from the breeding site to the coast of southwest Norway before heading southwards, whereas one bird staged for the first time in the Wadden Sea area. The five western migrating birds used one to four stopovers between Norway and north-Africa (median = 3) with stopover sites located in the Wadden Sea region and along the Mediterranean coast (southern France, the east coast of Spain). The eastern migrant used 3 stopovers to Macedonia (Fig. 2C). All stopovers in Europe lasted 2–8 d (mean = 4 d, $n = 13$, Fig. 3).

Birds reached north-Africa, i.e. northern coastal parts of Morocco, Tunisia and Algeria (Fig. 2), after a period of 10–27 d (mean = 16 ± 7 SD d, $n = 5$). The three birds with data on further migration (birds A–C, Table 1) has a prolonged stopover in north-Africa for 11, 18 and 20 d before spending about one day crossing the Sahara (Fig. 3). The mean overall travel rate in autumn for these individuals was 583 ± 193 (SD) km d^{-1} ($n = 3$) whereas the average total migration rate was 147 ± 39 (SD) km d^{-1} ($n = 3$; Table 1).

All three birds spent the non-breeding period in Mali, most likely in the Niger River Basin or surrounding areas (range of individual median positions: 13.17°N – 16.14°N and 0.75°W – 6.57°W). Two of the birds staged for 11 and 3 d at a sub-Saharan locality different from the main non-breeding site (Fig 2B and C) but all three birds arrived at their final non-breeding sites by 1 September after on average 47 d on migration. They remained there without any apparent movements until late-April/early May in the following year (Table 1, Fig. 3). The total orthodromic distance between breeding and non-breeding sites were on average 5207 km ($n = 3$) and the estimated mean total migration distance was 6003 km ($n = 3$), resulting in a

Table 1. Migration and non-breeding data in six individual Temminck's stints breeding in southern Norway, estimated from one year geolocator tracks. Loggers B and C were deployed in 2011, the rest in 2010. Stopovers are defined as periods when birds were stationary for more than two days. Data are incomplete, only covering parts of the autumn migration (birds D–F), lacking the last parts of spring (bird B), or lasting until just after the spring crossing of Sahara (bird C).

	Individual birds					
	A	B	C	D	E	F
Autumn migration						
Departure date	17-Jul	15-Jul	19-Jul	25-Jul	25-Jul	26-Jul
breeding site						
Travel time (d)	9	15	9	7	3	6
Number of stopovers	4	7	5	3	2	3
Sum stopover time (d)	27	35	31	7	12	16
Total duration (d)	36	50	40	14	15	22
Migration distance (km)	6840	5650	5520	2330	2590	2950
Direct distance (km)	5020	5200	5400	2330	2580	2820
Detour (%)	36	9	2	0	<1	5
Travel rate (km d^{-1})	760	377	613	333	863	492
Migration rate (km d^{-1})	190	113	138	166	173	134
Non-breeding period						
Arrival	21-Aug	1-Sep	27-Aug	–	–	–
Departure	19-Apr	> 4-Apr	5-May	–	–	–
Duration (d)	241	>216	252	–	–	–
Spring migration						
Arrival date	5-Jun	–	–	–	–	–
breeding site						
Travel time (d)	17	–	3	–	–	–
Number of stopovers	3	–	–	–	–	–
Sum stopover time (d)	30	–	–	–	–	–
Total duration (d)	47	–	–	–	–	–
Migration distance (km)	5070	–	2230	–	–	–
Direct distance (km)	5020	–	–	–	–	–
Detour (%)	1	–	–	–	–	–
Travel rate (km d^{-1})	298	–	743	–	–	–
Migration rate (km d^{-1})	108	–	–	–	–	–

mean detour of about 15%. Both birds (A and C; Table 1) which provided data on spring migration departed in late April–early May and stopped over in coastal Algeria after 1 and 3 d. Here the logger of bird C stopped functioning after 3 d (11 May). Bird A moved on after 21 d (11 May) and reached Denmark after 10 d were it staged for 5 d. It eventually reached the breeding site on 5 June. The distances travelled between stationary periods, excluding desert crossing, ranged from 110 to 2390 km (mean = 789 ± 669 km, $n = 27$; autumn and spring combined). Length of the Sahara crossing ranged between 1960 to 3190 km (mean = 2550 ± 561 km, $n = 5$).

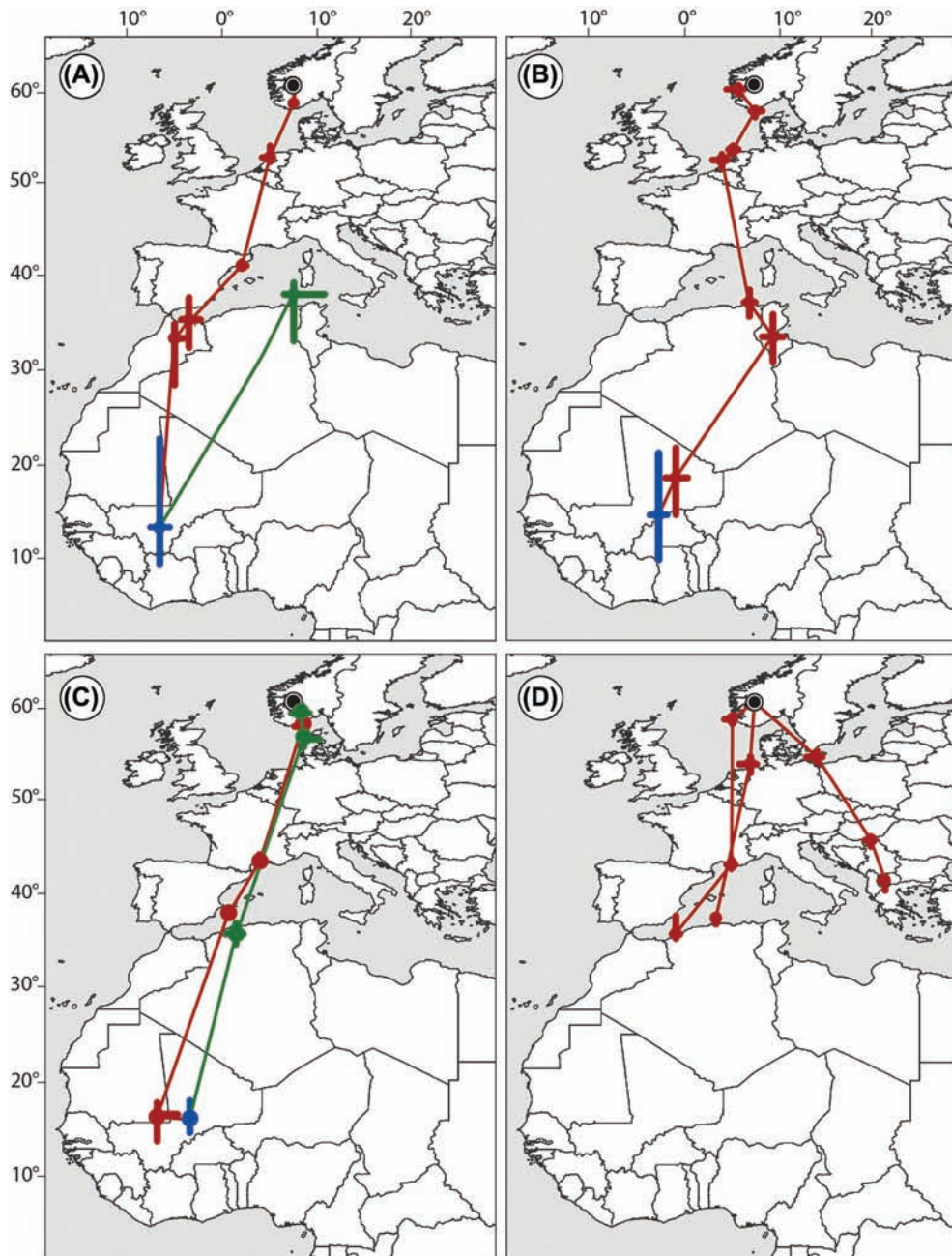


Figure 2. Maps showing the migration of six individual Temminck's stints tracked by light-level geolocators. (A–C) Show individual tracks, whereas (D) shows the incomplete tracks of three different birds where geolocators failed en route due to technical problems. Lines connect the tracks of individual birds in all cases but do not necessarily reflect actual paths of migration. The breeding site in southern Norway is shown by a black dot. The tracks are divided into autumn (red), winter (blue) and spring (green) positions, all of which are stopovers lasting for more than two days (median latitude and longitude with inter-quartile ranges).

Discussion

We found that Temminck's stints breeding in southern Norway flew a distance of more than 5000 km across continental western Europe and spent the boreal winter in the west-African Sahel region. Hence, the geolocator data confirmed former speculation about migration direction and non-breeding areas in these birds (Bakken et al. 2003, Hedenström 2004, Fransson et al. 2008, Breiehagen and Scott 2009, Saurola et al. 2013). However, Temminck's stints divided their migratory journeys in a skipping manner

(cf. Piersma 1987) both in autumn and spring, staging several times en route for two days to three weeks (Fig. 3). This result is compatible with Hedenström's (2004) most conservative estimates of flight range in birds trapped at Ottenby.

Body mass data collated from several European stopover sites are largely in the same range as the Ottenby data and did not show a significant latitudinal or longitudinal variation. This indicates that migratory fuelling, and thus flight strategies, is similar throughout Europe in this species. From the generally low fuel accumulation in continental

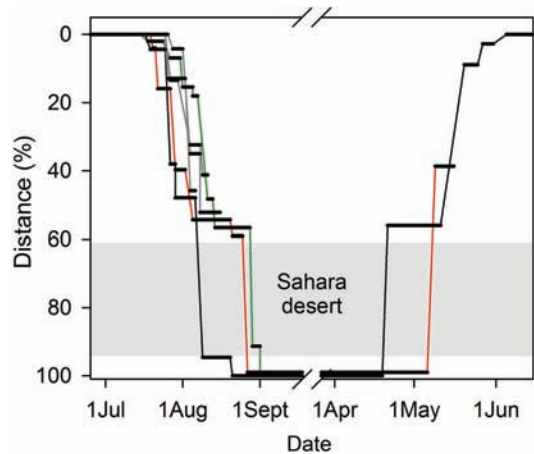


Figure 3. Skip migration in Temminck's stints from a Norwegian breeding site to west-African nonbreeding sites. Movements of each bird are shown by continuous thin lines, whereas residence and stopover periods are indicated by thicker horizontal lines. The y axis gives the relative distance between the breeding site (0%) and known non-breeding sites in Africa (100%, $n = 3$). In the three birds with incomplete data, distances are relative to the median value of the three known migration distances, assuming that they were comparable. Stints frequently stop during the first part of their journey in northern latitudes and extensively before crossing the Sahara desert.

Europe we expected the stints to make prolonged stopovers in northern Africa to fuel-up before Sahara crossing or a detour to circumvent the desert. Our geolocator data confirmed such extended autumnal stopovers in front of the barrier and straight Sahara crossing in autumn and spring. The stopover duration of 9 to 21 d would allow for a maximum fuel accumulation of 8 to 18 g based on a maximum daily fuel deposition rate of 4.7% of lean body mass (Lindström 2003) provided that food availability is not restricted at North African stopover sites. The lowest body masses were recorded in spring at islands in the central Mediterranean basin, indicating that crossing the Sahara and Mediterranean barriers is exhausting to these non-experimental birds. This suggests that the skipping-type pattern of migration (Fig. 3) revealed by geolocators is natural in Temminck's stints rather than an effect of instrumentation.

We could not directly test for migratory differences between adults and juveniles as we were unable to track the latter group with geolocators. However, in contrast to Hedenström (2004) we did not find any age related difference in body mass, suggesting that also juveniles should migrate in a skipping manner. Nevertheless, this conclusion needs to be verified in future studies.

In three birds with annual tracking data we found no indications of itinerant behavior during the non-breeding season. In some waders wintering at relatively high latitudes severe weather conditions may cause movements towards the south (e.g. golden plovers *Pluvialis apricaria*; Piersma and Lindström 2004). In Africa, itinerancy is well documented in many migratory birds during the non-breeding season, especially among passerines (Tøttrup et al. 2012, Lemke et al. 2013, Rappole 2013), but seems to be rarely documented as a strategy in waders on this continent (but see Hedenström

et al. 2013). Waders may largely stay in habitats with more stable and predictable ecological conditions compared with passerines, making the need to move less critical. However, compared with coastal mudflats, ephemeral inland wetlands are more heavily influenced by the temporal changes in precipitation (Zwarts et al. 2009, Colwell 2010). The vast inner Niger delta attracts a wide range of Palearctic migratory birds during their non-breeding periods (Curry and Sayer 1979, Morel and Morel 1992) and the lack of itinerancy during the non-breeding season in Temminck's stints might indicate that this area provides relatively stable environmental conditions at least for this species.

Several temporal patterns of movement in the Temminck's stints seemed consistent across individuals. First, all birds in this study left the breeding area in late July and the one bird which was tracked back to the breeding site in the following year returned in early June. These findings concur with previous field observations that adults in southern Scandinavian populations return in late May/early June and leave in late July resulting in only 2 month presence at their breeding sites (Breihagen 1989). Second, the birds spent 1–3 weeks staging in north-Africa in August before continuing southwards. This staging in the western Mediterranean region indicates a need for recouping fuel stores for the final long flight across the Sahara desert, a behaviour which is typical in migrants about to cross large geographical barriers (Piersma et al. 2005). Third, birds arrived in their non-breeding areas by September and left in late April or early May, spending a seven month long period at the non-breeding site. Our restricted sample is not sufficient to analyze adaptations of migratory behavior in the Temminck's stints in relation to current environmental conditions, especially precipitation and local food availability. These issues therefore need further investigation.

Acknowledgements – We are grateful to Oddvar Heggøy and Fred Marius Svendsen for their dedicated help with the field work. Unpublished data on stint morphometry were kindly provided by U. Köppen, Hiddensee Bird Ringing Centre, Greifswald, Germany, F. Jiquet, CRBPO, Paris, France, L. Serra, Italian Ringing Centre, ISPRA, Ozzano Emilia, D. Cikovic, Inst. of Ornithology, Zagreb, Croatia, K. Oosterbeek, Dutch *Calidris* shorebird catching group, Schiermonnikoog, the Netherlands, O. Geiter, Inst. of Avian Research, Wilhelmshaven, Germany, as well as A. Pelling, Fertő-Hanság National Park, Sarród, Hungary. The study was supported by grants from the Meltzer Research Fund and the Fund for Natural Sciences, Univ. of Bergen. Permission to carry out the study was granted by the Norwegian Animal Research Authority (protocol ID 3392) and the Norwegian Environment Agency.

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Supplementary material (Appendix JAV-00653 at <www.avianbiology.org/readers/appendix>). Appendix 1.

Supplementary material

Appendix 1

Table A1. Seasonal variation of body mass in Temminck's stints (mean \pm SE). The age category 'all' encompassed weighted means from adults, juveniles, and indet for birds with unknown age.

Season	Site	Area	°N	°E	All/indet		Adult		Juvenile		Source	
					Mass (g)	Range	n	mass (g)	n	mass (g)		n
breeding	southern Norway	inland	60.6	7.5	25.2 \pm 0.3	21.6 - 29.5	42				1	
autumn	southern Sweden	coastal	56.2	16.4	24.8 \pm 0.5	18.7 - 36.0	95	25.8 \pm 0.4	53	23.7 \pm 0.5	42	2
	eastern Germany	inland	52.2	12.1	24.8 \pm 0.3	19.5 - 32.0	96	25.3 \pm 0.7	29	24.6 \pm 0.4	46	3
	Czech Republic	inland	49.0	15.0	27.4	20.8 - 34.0	10	26.6	3	27.7	7	4
	Hungary	inland	47.7	16.8	25.0 \pm 0.6	18.4 - 35.6	62	24.8 \pm 1.1	12	24.3 \pm 0.8	30	5
	Switzerland	inland	47.6	9.0	26.4 \pm 1.0	23.0 - 35.0	17	24.5	2	28.2 \pm 1.0	15	6
	central France	inland	47.0	4.0	24.0		2					7
	northern Italy	inland	44.5	12.2	22.5 \pm 0.4	17.2 - 29.9	47	22.4 \pm 0.4	33	22.7 \pm 1.0	14	8
	Dalmatia	coastal	44.0	15.0	25.5	21.0 - 30.0	2					9
	southern France	coastal	43.5	4.3	23.1 \pm 0.5	17.2 - 36.0	139	23.1 \pm 0.4	111	23.2 \pm 0.8	28	6

	southern France	coastal	43.3	3.0	25.0		1	7
	eastern Bulgaria	coastal	42.6	27.5	28.3 ± 1.9	22.0 - 33.0	6	10
non-breeding	Tabalakh /sw Niger	inland	15.1	5.7	24.0	23.0 - 25.0	2	7
	Kenya	inland	0.0	38.0	20.5	17.0 - 26.0	39	11
spring	Malta	coastal	35.9	14.4	20.2 ± 0.4	18.2 - 27.0	9	12
	southern Italy	coastal	37.0	15.3	22.4 ± 1.6	18.6 - 28.5	6	8
	Corsica	coastal	43.0	9.4	18.8 ± 0.4	18.0 - 20.0	6	7
	northern Italy	inland	44.1	11.6	21.1 ± 0.5	18.1 - 23.1	9	8
	northern Italy (*)	inland	44.6	10.9	22.0		1	1
	Czech Republic	inland	49.0	15.0	26.7	25.4 - 29.0	5	4
	eastern Germany	inland	50.6	11.7	23.2 ± 0.7	20.8 - 27.6	9	3
	Wadden Sea	coastal	53.5	6.1	26.7		1	13
	northern Germany	inland	53.7	8.0	21.0		1	14

Sources

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