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Migration and morphometrics of Temminck's Stint *Calidris temminckii* at Ottenby, southern Sweden

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Data are reported from 55 years of ringing and observation on the migration of Temminck's Stint *Calidris temminckii* at Ottenby Bird Observatory, Sweden. Numbers ringed have declined since the 1940s due to high numbers caught in 1948 and 1949. Thereafter there is no clear trend. The overall autumn migration direction of 13 recoveries is south-southwest, with a concentration of recoveries in northeast Italy. Median date of spring passage was 20 May, while median date of autumn passage was 28 July for adults and 20 August for juveniles. Hence, the duration of the breeding season is about two months. On autumn migration, adults carry larger fuel (fat) loads (32% of lean body mass, LBM) than juveniles (21.2%), and so adults are capable of a direct flight to the northeast Italian stopover, while the average juvenile cannot do so unless assisted by winds. Over the autumn migration season, fuel loads did not change in adults but late migrant juveniles had higher fuel loads. The maximum rate of fuel accumulation was 7.7% of LBM, which is near the physiological maximum. The maximum migration speed was estimated to be 150 km/day.

The migration of the Temminck's Stint *Calidris temminckii* is little known in spite of its wide breeding range, extending from the Scandinavian mountains across the Siberian tundra belt to the Chukotka Peninsula in the far east (Glutz *et al* 1975, Cramp & Simmons 1983, Lappo 1998). The species winters in sub-Saharan Africa, mainly in the Sahel zone, and to some extent in the Mediterranean region, while more easterly breeding populations migrate to wintering areas in India and eastwards through China, Indochina and Japan. Hence, the Temminck's Stint has a vast distribution but seems never to occur in spectacular numbers.

There are some indications, from Finland, of a population decline during the 20th century (Hildén 1978, Rönkä 1996). Information about Temminck's Stint migration, which potentially could be of value in understanding the dynamics of population numbers, are therefore of interest. On migration, Temminck's Stints usually appear singly, in pairs or small flocks, which probably is the reason why so few birds have been ringed over the years and consequently why so little is known about their migration. Waders have been caught and ringed at Ottenby on the island of Öland in southeast Sweden since Ottenby Bird Observatory was established in 1946. Even though the numbers of Temminck's Stint caught annually are relatively low at this site, the accumulated data over 55 years might shed some new light on migration direction, phenology, fuel stores and population trend. Here I present results from an analysis of these data.

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METHODS

Study site

Observations and ringing of migrating birds have been carried out systematically at Ottenby Bird Observatory (56°12' N 16°24' E) since 1946. The data for this study were collected during 1947-2001. The observatory is situated on the southern point of the island of Öland in the Baltic, off the Swedish mainland southeast coast. In the first few years of operation (1946-49), only autumn seasons were covered, but since 1950 the spring migration season has also been covered. From 1979 onwards, the observatory has been manned from 15 March to 15 November annually.

Ringing

Waders are trapped on the shorelines using walk-in funnel traps (Bub 1991). Traps are placed in combinations so that the shoreline strip of decaying seaweed is cut-off perpendicularly to the coastline, leading foraging waders into the traps. Before 1972 other types of traps were also used, but since 1972 about 80-120 traps have been used each year. Numbers of traps vary due to fluctuations in the amount of seaweed and water levels. Wader catching starts around 1 July and continues until the end of September. The traps are visited and checked

every hour throughout the daylight period, and trapped birds are brought back to the ringing laboratory, 250 m away, for examination, ringing and release.

Observations

Each day observations of birds are noted on special 'tick-cards' and notable sightings are registered in a diary. For data on spring phenology I used these tick-cards from the years 1976-98, where a date is marked if the species have been observed on that day by the observatory staff. These data are therefore not quantitative, but since the data span many years, the accumulated number of days of observed Temminck's Stints should reflect the timing of migration. It should be noted that the bird observatory staff make these observations in a non-systematic way. Previous analyses of similar non-systematic observations indicate that such data nevertheless can give reliable information on migration phenology in waders, provided that a sufficient number of years are included (Hedenström *et al* 1993).

Morphometrics

Since 1977, birds trapped in autumn have been aged on the basis of plumage differences according to Prater *et al* (1977). Since 1990, morphological measurements have been recorded as follows: wing length as maximum flattened chord from the carpal joint to the tip of the longest primary (Svensson 1992), to the nearest mm; and body mass to the nearest 0.1 g, using either a Pesola spring balance or an electronic balance.

The lean body mass (LBM) was estimated as 19.6 g by taking the average of the five lightest birds in the sample. This value is similar to body mass during breeding and wintering periods (Glutz *et al* 1975, Cramp & Simmons 1983), when fat loads are expected to be at annual minima. The structural size, measured as wing length, of the five lightest birds did not differ from the rest of the birds ($F_{1,93} = 0.022$, $P = 0.88$), indicating that these birds were of representative size. The LBM was used to calculate fuel loads in the captured birds (expressed as percentage of the LBM) as 100 x (BM-LBM)/LBM, where BM is body mass as recorded.

Morphometric data used for flight performance calculations were as follows: wing span = 0.29 m, wing length = 0.10 m, wing area = 0.0110 m^2, and aspect ratio (calculated as wing span squared divided by wing area; Pennycuick 1989) = 7.7 (Hedenström 1995).

Flight range

There are two main approaches for estimating the potential flight range of a bird given a specified fuel load; those based on aerodynamic models or those based on measured fuel consumption of birds flying a known distance. In the aerodynamic approach the main mechanical power components (induced, parasite and profile power) are estimated and summed to give an overall power output (Pennycuick 1989). The mechanical power is produced by the cyclical contraction of the flight muscles, and the total flight cost is estimated by assuming a conversion efficiency for metabolising fat to produce the mechanical power output to the surrounding air by the beating wings. The conversion efficiency is often assumed to be 0.23, but there are uncertainties regarding the correct value. In addition to morphological data of the bird (body mass, wing span, wing area), we also need to assume a value for the body drag coefficient (C_{db})that describes the streamlining of the bird body and affects the parasite power. To calculate potential flight range I used Pennycuick's (1989) model assuming $C_{db} = 0.2$ (Hedenström & Liechti 2001), a flight muscle fraction = 0.2, a constant proportion between flight speed and the speed of minimum power (Pennycuick 1989), and a flight altitude of 1,000 m (Hedenström *et al* 2002).

An alternative physiological approach is based on measured metabolic rate during flight of known distance. According to Castro & Myers (1989) the flight range (Y, in km) is given by the formula:

$$Y = 96.8 \times U \times L^{1.614} \times (m_0^{-0.464} - m_1^{-0.464})$$

where U is flight speed (m/s), L is wing length measured from carpal joint to the longest primary tip (cm), m_0 is body mass at the end of the flight and m_1 is the body mass at flight departure. The flight speed U = 13 m/s was assumed as typical for waders on migration (Hedenström *et al* 2002). Both approaches require assumptions and any estimated flight range must therefore be treated with caution.

Statistics

Directional data ranging between 0° and 360°, such as the directions of ringing recoveries, are called circular variables and must be analysed using different methods than for linear variables (Batschelet 1981). Basically any sums and differences have to be reduced modulo 360°, and we can calculate means, measures of scatter and perform significance tests. Each direction is represented by a unit vector, ie a vector of unit length. To calculate the mean direction we simply calculate the vector sum and, dividing by the sample size n, the mean vector r of the sample is obtained. The length of the mean vector ($0 \leq r \leq 1$) is also a measure of the angular scatter and r = 1 only if all the directions of the sample are the same. Analogous to the standard deviation for linear variables, we can calculate the angular deviation for circular variables as:

$$s(\text{degrees}) = \frac{180°[2(1 - r)]^{1/2}}{\pi}$$

Given a random sample n of angular values and a derived mean vector r, the Rayleigh test determines the probability that the population from which the sample is drawn differs from randomness (Batschelet 1981).

Other statistical tests were performed using STATISTICA 5.5 (StatSoft, Inc).

RESULTS

Numbers ringed

The number of ringed birds, of all age classes, caught in a season varied from 0 to 76, with an average of 11.4 per year (SD = 13.7, n = 55 years). A total of 629 individuals were ringed from 1947 to 2001. Annual ringing totals are shown in Fig 1 with a trend line (three-year moving average). The two major peaks occurred at the beginning of the time series, and hence the data show a significant decline in ringing numbers throughout the period (log-transformed data: linear regression b = -0.015, t = 2.10, P = 0.041). However, on removing the two years 1948 and 1949 the negative trend is no longer significant (b = -0.008, t = 1.11, P = 0.273).

An autocorrelation analysis, after removing the linear trend, did not reveal any significant periodicity; neither did a spectral analysis of the frequency domain. Hence, the variation in ringing numbers did not show any indication of cyclic population fluctuations.

Migration route, breeding and wintering area

The ringing at Ottenby has generated 13 recoveries during autumn migration (Fig 2). The recoveries south of Ottenby are concentrated in southern Europe with a mean direction of 201.8° vector length r = 0.98, mean angular deviation s = 11.5°, P < 0.001, Rayleigh test), ie towards the south-southwest. Also, the only recovery north of Ottenby comes from autumn migration and falls near the overall migration axis (Fig 2). Including all recoveries yields an axis (the direction of a bimodal sample) of 21.9°-201.9° (r = 0.94, mean angular deviation s = 19.8°, P < 0.001). Extrapolating the overall migration direction to the sub-Saharan winter range suggests that Temminck's Stints migrating through Ottenby spend the winter in West Africa. Likewise, extrapolating the migration direction to the breeding range suggests the passage of mainly Fennoscandian birds through Ottenby. There is a cluster of recoveries in northern Italy (Fig 2), suggesting that this area might be an important stopover area for Temminck's Stints. Out of the 13 recoveries, 11 were shot or probably shot by hunters, while one was 'found dead' and for one the recovery cause was unknown.

Spring migration

The main passage during spring is in May, with a median date of 20 May (Fig 3, n = 100 days with recordings). The last spring migrating birds occur in the first week of June.

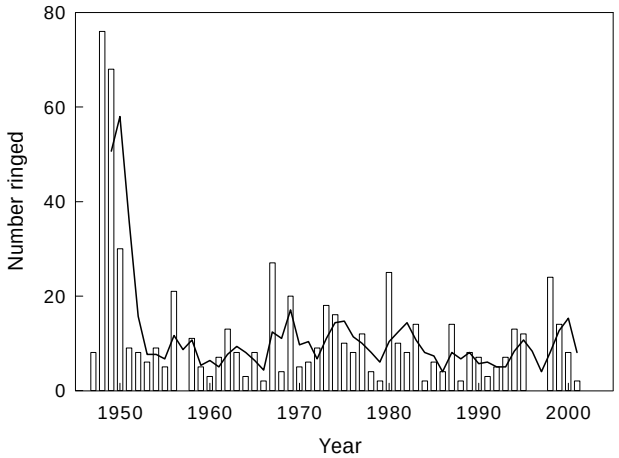

Figure 1. Annual ringing numbers of the Temminck's Stint at Ottenby Bird Observatory during 1947-2001. The line indicates the three-year moving average.

Figure 2. Recoveries of Temminck's Stint (•) ringed at Ottenby Bird Observatory (■). The overall axial direction from Ottenby is 21.9º - 201.9º (r = 0.94, n = 13, P < 0.001; Rayleigh test, Batschelet 1981). The map is a Mercator projection.

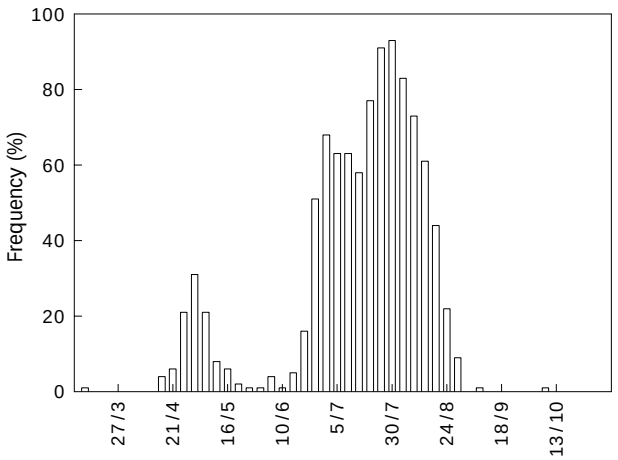

Figure 3. Migration phenology of Temminck's Stint at Ottenby Bird Observatory based on records of sightings during 1976-98. For display, the data have been lumped into 5 day periods.

Autumn migration

An observation on 13 June could refer to either north or southward migration. The first unequivocal southbound migrants occur from about 20 June (Fig 3), which coincides with the first birds caught (Fig 4a). The first birds are adults that migrate mainly during July and beginning of August, with a median date of passage of 28 July (Fig 4a, n = 227). The first juvenile bird was caught on 29 July, but the main passage of juveniles occurs during August and early September, with a median date of passage of 20 August (Fig 4b, n = 305). The difference between adult and juvenile passage was 23 days. Note that the migration waves representing adult and juvenile birds are clearly seen as two peaks in Fig 3, which is evident also if Figs 4a and 4b are combined into one plot (not shown). The overall median date of passage for all ringed birds was 13 August, while the tick-card recordings gave a median date of 11 August.

Migration speed

Based on the ringing recoveries, the overall migration speed of the three fastest birds was 150, 97 and 59 km/day during 15, 15 and 21 days, respectively.

Wing length

There was no significant difference in structural size between adults and juveniles as measured by wing length (adult mean = 99.7 mm, SD = - 2.3 mm, n = 53; juvenile mean = 100.0 mm, SD = 2.3 mm, n = 42; $F_{1,93}$= 0.42, *P* = 0.52). It should be kept in mind that the adult birds have old feathers and the juvenile birds have relatively new and fresh feathers when passing Ottenby, and so natural feather wear could have reduced the wing length somewhat in adults.

Body mass

There was no relationship between body mass and time of day of capture (linear regression of body mass against hour: slope b = -0.10, t = 1.61, *P* = 0.11, n = 95), and so the body mass data were not corrected for time of day in the analyses. Both wing length and age had an effect on body mass (ANCOVA, wing length: $F_{1,92}$ = 14.5, *P* < 0.001; age: $F_{1,92}$ = 14.4, *P* < 0.001). In juveniles the body mass increases by 0.63 g per mm wing length (t = 3.1, *P* = 0.0036, n = 42), while in adults the increase is 0.38 g per mm wing length (t = 2.29, *P* = 0.026, n = *53)*. The mean body mass in adults was 25.8 g (SD = 2.9, range: 20.2 - 34.3 g) and in juveniles it was 23.7 g (SD = 3.3, range: 18.7 - 36 g).

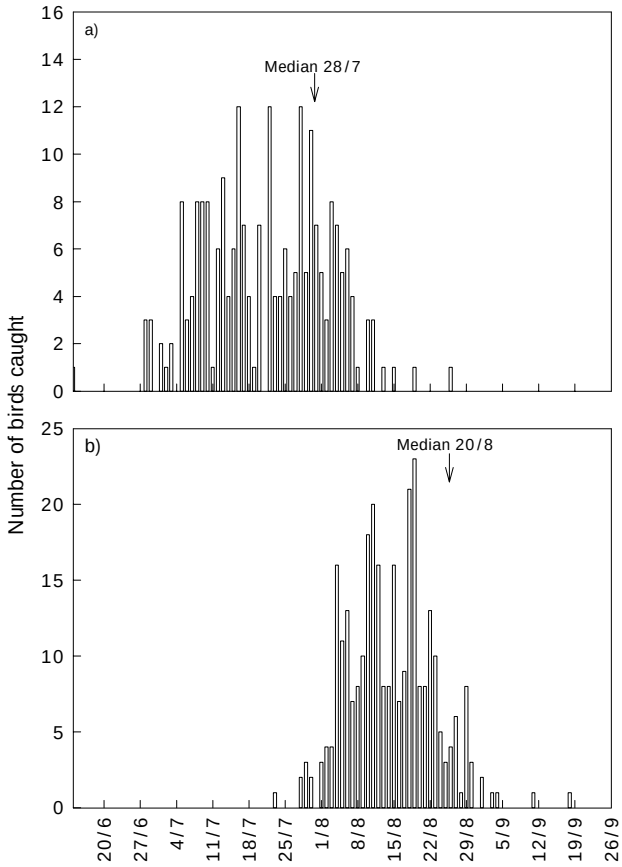

Figure 4. Autumn migration phenology of a) adult and b) juvenile Temminck's Stints that were caught, ringed and aged at Ottenby Bird Observatory between 1947 and 2001.

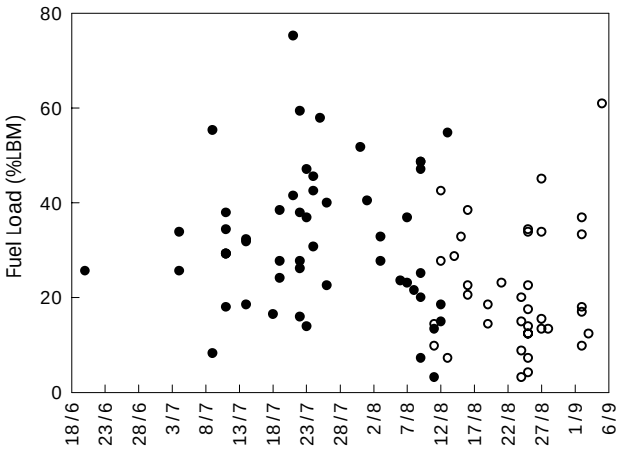

Figure 5. Fuel load expressed as percentage of lean body mass (19.6 g) in adult (filled circles) and juvenile (open circles) Temminck's Stints at Ottenby Bird Observatory. There was a significant increase of fuel load with time of season in juveniles but not in adults.

Fuel load

The mean fuel load was significantly higher in adults than in juveniles (adults 32.0 % of LBM, juveniles 21.2%; $F_{1,93} = 11.0$, $P = 0.0013$), while the maximum fuel load was 84% in a juvenile and 75% in an adult bird. Over the season, fuel load did not change significantly in adults (Spearman rank correlation $r_s = 0.06$, $P = 0.67$) or in juveniles ($r_s = 0.15$, $P = 0.33$), although in juveniles there were some very high fuel loads in birds migrating late (Fig 5). The rate of fuelling in two recaptured birds was 7.7% (of LBM) over three days and 3.8% over four days, respectively, while a third bird lost mass over one day (-4.6%).

DISCUSSION

Population trend

The ringing data did not show any clear trend over the years, although a negative trend is indicated if including the years 1948 and 1949 when very high numbers were caught. These high numbers could however have been due to favourable trapping conditions in these years, and so we should not draw any definite conclusions concerning a population change. The breeding population in Finland has declined since about 1950. Mainly the coastal populations around the Gulf of Bothnia have reduced. The reasons for this decline are probably manifold (Rönkä 1996), but changes to the breeding habitat are probably an important factor (Hildén 1978).

Wing length

Adult and juvenile birds had an almost identical wing length of 100 mm. At the time of autumn migration, adult birds possess old primaries that, due to natural feather wear, should be about 2% shorter than just after moult (Serra 2001). If compensating for this the wing length of adults should be slightly longer than in juveniles when fresh, a difference of the same magnitude as found between adult and juvenile in many passerine species (Alatalo *et al* 1984).

Migration route

The general migration direction of ringing recoveries showed an overall north-northeast to south-southwest migration axis, which suggests birds of Fennoscandian breeding origin that are destined to winter somewhere in West Africa. Temminck's Stints are found in the Sahel region in sub-Saharan Africa during the winter, and so wintering areas might not necessarily be on the coast. There are also a few recoveries from France and Spain (Fig 2), indicating that some birds might go to the extreme western part of the winter range, which is perhaps not so surprising for birds belonging to the most western breeding population of its range (except for the very small population in Scotland). There is one recovery from Greece of a bird ringed as a nestling in Swedish Lapland (Glutz *et al* 1975), while the majority of Ottenby recoveries suggests a parallel migration pattern (*sensu* Salomonsen 1955). Although the data available are not enough to suggest or reject more complicated migration patterns involving, for example, leap-frogging (Palmén 1874, Salomonsen 1955), such patterns might be less likely in a species such as the Temminck's Stint with a latitudinally rather narrow breeding range.

The concentration of recoveries in Italy strongly suggests a migration across continental Europe rather than along the coasts of Europe, which is further supported by observations of birds in central Europe (Glutz *et al* 1975). However, the majority of the recovered birds were shot by hunters, and so the concentration in Italy could reflect the distribution of hunters in the Mediterranean region.

Migration phenology

The median date of spring passage (20 May) is somewhat earlier than in some other arctic breeding wader species passing Ottenby: Little Stint *Calidris minuta* (24 May), Curlew Sandpiper *C ferruginea* (25 May), Sanderling *C alba* (29 May) (Blomqvist & Lindström 1995), Knot *C canutus* (8 June; Blomqvist & Lindström 1992), and Broad-billed Sandpiper *Limicola falcinellus* (29 May; Waldenström & Lindström 2001). The Knot and Sanderling, with the latest spring passage, are destined for the breeding areas furthest away from Ottenby, situated on the Taymyr Peninsula and further east (Lappo 1998). Hence, it seems that distance to the breeding

area is positively correlated with date of passage at Ottenby. If true, this suggests that the majority of Temminck's Stints passing Ottenby in spring belong to breeding populations that are closer than those of the other arctic species mentioned, presumably in northern Fennoscandia.

The autumn median passage of adult Temminck's Stints (28 July) was only a day earlier than that of adult Curlew Sandpipers (29 July), while the median passage of Knots is 9 August (cf Blomqvist *et al* 2002). The juvenile passage was, however, 11 days earlier in the Temminck's Stint than in the Curlew Sandpiper and the Knot (both species median date 31 August, Blomqvist *et al* 2002). This difference in timing probably reflects longer distances between their breeding ranges and Ottenby of the Curlew Sandpiper and particularly the Knot.

The time between median date of spring passage (20 May) and return autumn migration (28 July) is only a little more than two months. In this time birds should migrate to and from the breeding area, find a suitable territory, display to find a mate, lay clutches, incubate and raise the young. Typically, Temminck's Stint females lay two clutches in rapid succession. The male incubates the first clutch and the female incubates the second (Hildén 1975). The laying of two successive clutches takes a minimum of 10 days, incubation is about 21 days (Hildén 1965), and adults leave the young about 14-21 days after hatching (Hildén 1965). Hence, breeding will take about 52 days (assuming a duration of parental care of 21 days), leaving only two weeks for territory establishment, mate finding and migration between Ottenby and the breeding area. This time budget outline shows that the summer schedule is indeed very tight for birds breeding at high latitudes (Piersma 2002). As typical in such species, moult is not undertaken on the breeding grounds but postponed until later on autumn staging areas or the wintering site (Holmgren & Hedenström 1995).

The juveniles migrate on average 23 days later than the adults, which is about 40 days after hatching. This is a similar difference as in the Knot (22 days), but shorter than in the Curlew Sandpiper (33 days; Blomqvist *et al* 2002). The time difference means that juveniles are usually not accompanied by adults from their own breeding population, and they probably have to rely on an innate migration program to direct them to the population-specific wintering grounds. The angular deviation around the overall migration direction is usually larger in juveniles than in adults (Hedenström & Pettersson 1987, Alerstam 1990), which could explain the recovery of a Swedish-ringed chick from Greece (Glutz *et al* 1975).

Table 1. Estimated flight ranges (km) of Temminck's Stints of different departure fuel load, using two commonly used methods.

	Departure mass (g)	Fat (g)	Fuel load (% LBM)	Pennycuick[a]	Castro & Myers[b]
Adult mean	25.8	6.2	32	1,976	1,557
Adult max	34.3	14.7	75	4,414	2,974
Juvenile mean	23.7	4.1	20	1,335	1,097
Juvenile max	36.0	16.4	84	4,886	3,196

[a]Pennycuick (1989) using assumptions presented in Methods
[b]Castro & Myers (1989), assuming U = 13 m/s and L = 10 cm.

Migration strategy

Despite the limited data available for these analyses, some interesting observations have emerged. Adult birds carried significantly larger fuel loads than did juveniles, which might allow longer flights to the next stopover site. To estimate potential flight distances for a bird given a certain fuel load there are two main approaches (see Methods). I estimated flight ranges for Temminck's Stints with the average fuel loads of adult and juvenile birds, as well as for birds carrying the maximum fuel load recorded. The results are presented in Table 1. The calculated distances differ between the methods of estimation and the reasons for this are beyond the scope of this paper (for discussion see Davidson 1984, Pennycuick & Battley 2003). The distance to the area in northern Italy with a concentration of Ottenby recoveries is about 1,500 km (Fig 2). Hence, it seems that the average adult bird could reach this area on a direct flight from Ottenby, while juvenile birds probably do not have sufficient fuel for such a flight (Table 1). Temminck's Stints are observed throughout continental Europe during migration (Glutz *et al* 1975), and the flight range estimates suggest that birds seen refuelling here are more likely to be juveniles. This proposition however has not been tested. The birds with maximum fuel loads would possibly be capable of a direct flight to the sub-Saharan wintering quarters, especially if assisted by tail winds.

There was no significant change in fuel load with time of season, but the highest fuel loads were found in very late migrating juveniles, which is consistent with the pattern that has previously been observed among passerine species (Alerstam & Lindström 1990). The reason for this could be the need for late migrants to make one long flight away from the Baltic and across continental Europe, where feeding conditions might deteriorate rapidly due to increasing risk of bad weather with the progression of the season.

Unfortunately there were only three within-season retraps recorded. Although this might be because retraps

have, to a large extent, only been recorded in species of special focus over the years, it might also reflect a rapid turnover of Temminck's Stints at Ottenby, suggesting that Ottenby is not an important refuelling site. However, the maximum fuel deposition rate recorded was close to the physiological maximum of about 8% for a wader the size of Temminck's Stint (Lindström 2003). Also, the decline in body mass after one day is typical for birds shortly after arrival at a new site (Mascher 1966, Rappole & Warner 1976, Waldenström & Lindström 2001).

The migration speed of recovered birds was similar to other species of this size (Hildén & Saurola 1982), with the maximum of 150 km/day being close to the theoretical maximum (Hedenström & Alerstam 1998). Overall migration speed includes time for both transport (actual flight) and for refuelling energy at stopovers. Assuming a maximum fuelling rate, Hedenström & Alerstam (1997) estimated that time during migration will be divided between flight and stopover in a ratio of 1:7 in small birds. Therefore, when measured over a relatively short period of time the migration speed will often be overestimated because, when captured, the bird has stored some energy for the next flight already. The shortest duration between capture and recovery was 15 days, which is probably sufficient time to give a reasonable estimate of the overall speed. By way of example, with a fuelling rate of 5% of LBM per day, 15 days will generate a fuel load of 75%, which is near the maximum loads recorded in this study.

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REFERENCES

Alatalo, R.V., Gustafsson, L. & Lundberg, A. (1984) Why do young passerine birds have shorter wings than older birds? *Ibis* **126**, 410-415.

Alerstam, T. (1990) Ecological causes and consequences of bird orientation. *Experientia* **46**, 405-415.

Alerstam, T. & Lindström, Å. (1990) Optimal bird migration: the relative importance of time, energy, and safety. In: Gwinner, E. (ed) *Bird Migration: Physiology and Ecophysiology*, pp. 331-351. Springer-Verlag, Berlin.

Batschelet, E. (1981) *Circular Statistics in Biology.* Academic Press, London.

Blomqvist, S., Holmgren, N., Åkesson, S., Hedenström, A. & Pettersson, J. (2002) Indirect effects of lemming cycles on sandpiper dynamics: 50 years of counts from southern Sweden. *Oecologia* **133**, 146-158.

Blomqvist, S. & Lindström, Å. (1992) Routes of spring migrant Siberian and Nearctic Knots *Calidris canutus* diverge over Sweden. *Wader Study Group Bulletin* **64**, Suppl, 91-94.

Blomqvist, S. & Lindström, Å. (1995) The spring migration of Sanderling *Calidris alba,* Little Stint *C minuta* and Curlew Sandpiper *C ferruginea* in Sweden. *Ornis Sveccia* **5** 55-67.

Bub, H. (1991) *Bird Trapping & Bird Banding*. Cornell University Press, New York.

Castro, G. & Myers, J.P. (1989) Flight range estimates for shorebirds. *Auk* **106**, 474-476.

Cramp, S. & Simmons, K.E.L. (1983) T*he Birds of the Western Palearctic.* Vol III. Oxford University Press, Oxford.

Davidson, N.C. (1984) How valid are flight range estimates for waders? *Ringing & Migration* **5**, 49-64.

Edelstam, C. (1972) Visible Migration of Birds at Ottenby, Sweden. *Vår Fågelvärld*, Suppl 7.

Glutz, U.N., Bauer, K.M. & Bezzel, E. (eds) (1975) *Handbuch der Vögel Mitteleuropas Vol VI, Charadriiformes.* Akademische Verlagsgesellshaft, Wiesbaden.

Hedenström, A. (1995) Flight strategies in arctic birds. In: Grönlund, E. & Mellander, O. (eds) *Swedish-Russian Tundra Ecology-Expedition -94*. A Cruise Report, pp. 271-278. Swedish Polar Research Secretariat, Stockholm.

Hedenström, A. & Alerstam, T. (1997) Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. *Journal of Theoretical Biology* **189**, 227-234.

Hedenström, A. & Alerstam, T. (1998) How fast can birds migrate? *Journal of Avian Biology* **29**, 424-432.

Hedenström, A., Alerstam, T., Green, M. & Gudmundsson, G.A. (2002) Adaptive variation of airspeed in relation to wind, altitude and climb rate by migrating birds in the Arctic. *Behavioral Ecology and Sociobiology* **52**, 308-317.

Hedenström, A., Hedenström, L. & Åkesson, S. (1993) Autumn passage of migrating waders in the archipelago of Östergötland, Sweden. *Vingspegeln* **12**, 134-140. (English summary)

Hedenström, A. & Liechti, F. (2001) Field estimates of body drag coefficient on the basis of dives in passerine birds. *Journal of Experimental Biology.* **204**, 1,167-1,175.

Hedenström, A. & Pettersson, J. (1987) Migration routes and wintering areas of Willow Warblers *Phylloscopus trochilus* (L.) ringed in Fennoscandia. *Ornis Fennica* **64**, 137-143.

Hildén, O. (1965) Zur Brutbiologie des Temminckstrandläufers, *Calidris temminckii* (Leisl.). *Ornis Fennica* **42**, 1-5.

Hildén, O. (1975) Breeding system of Temminck's stint *Calidris temminckii. Ornis Fennica* **52**, 117-146.

Hildén, O. (1978) Population dynamics in Temminck's stint *Calidris temminckii. Oikos* **30**, 17-28.

Hildén, O. & Saurola, P. (1982) Speed and autumn migration of birds ringed in Finland. *Ornis Fennica* **59**, 140-143.

Holmgren, N. & Hedenström, A. (1995) The scheduling of molt in migratory birds. *Evolutionary Ecology* **9**, 354-368.

Lappo, E.G. (1998) Mapping breeding range structure of tundra waders in Russia. *International Wader Studies* **10**, 145-151.

Lindström, Å. (2003) Fuel deposition rates in migrating birds: causes, constraints and consequences. In: Berthold, P., Gwinner, E. & Sonnenschein, E. (eds) *Avian Migration*, pp. 307-320. Spinger-Verlag, Berlin.

Mascher, J.W. (1966) Weight variations in resting Dunlins (*Calidris a. alpina*) on autumn migration in Sweden. *Bird Banding* **37**, 1-34.

Palmén, J.A. (1874) *Om foglarnas flyttningsvägar*. J.O. Frenckell & Son, Helsingfors. (In Swedish)

Pennycuick, C.J. (1989) *Bird flight performance: a practical calculation manual*. Oxford University Press, Oxford.

Pennycuick, C.J. & Battley, P.F. (2003) Burning the engine: a time-marching computation of fat and protein consumption in a 5420-km non-stop flight by Great Knots, *Calidris tenuirostris*. *Oikos* **103**, 323-332.

Piersma, T. (2002) Energetic bottlenecks and other design constraints in avian annual cycles. *Integrative and Comparative Biology* **42**, 51-67.

Prater, A.J., Marchant, J.H. & Vuorinen, J. (1977) *Guide to the Identification and Ageing of Holarctic Waders.* BTO Guide 17. BTO, Tring.

Rappole, J.H. & Warner, D.W. (1976) Relationships between behavior, physiology and weather in avian transients at a migration stopover site. *Oecologia* **26**, 193-212.

Rönkä, A. (1996) Distribution, status and population trends in the Temminck's Stint *Calidris temminckii* in the Finnish Bothnian Bay. *Ornis Fennica* **73**, 1-11.

Salomonsen, F. (1955) The evolutionary significance of bird-migration. *Danske Biologiske Meddelser* **22**, 1-62.

Serra, L. (2001) Duration of primary moult affects primary quality in Grey Plovers *Pluvialis squatarola*. *Journal of Avian Biology* **32**, 377-380.

Svensson, L. (1992) *Identification Guide to European Passerines.* 4th edn. Svensson, Stockholm.

Waldenström, J. & Lindström, Å. (2001) Migration and morphometrics of the Broad-billed Sandpiper *Limicola falcinellus* at Ottenby, southern Sweden, 1950-2000. *Ornis Fennica* **78**, 184-192.

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