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Migration patterns and morphometrics of Common Sandpipers *Actitis hypoleucos* at Ottenby, southeastern Sweden

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Current knowledge of the migration of the Common Sandpiper *Actitis hypoleucos* is still limited. The species has been ringed at Ottenby Bird Observatory, southeast Sweden, since 1947, allowing for analyses of long-term and seasonal trends. We analysed trapping data for 1,942 adults and 3,290 juveniles with respect to patterns in phenology, morphometrics, and fuel load. We used fuel loads to estimate potential flight ranges. The number of adult birds trapped increased significantly over the years, whereas juveniles declined. Median passage date was 27 July and 7 August for adult and juvenile birds respectively, and juveniles showed a significant advancement in median passage date. Mean fuel loads were 28.8% and 27.8% of lean body mass (LBM) for adult and juvenile birds respectively, while maximum fuel load was as high as 98.7% in juveniles and 105.4% in adults. Fuel load increased significantly with date in juveniles but declined in adults. Advancement in passage of juvenile birds over the year is possibly due to climate change. Also, the average adult and juvenile are theoretically capable of a direct flight to central France; a major recovery area. Fuel load patterns suggest that in autumn, the two age classes use different migration strategies.

Migratory shorebirds have been the focus of many migration studies, owing to their propensity to use wetlands and coastal habitats during their breeding, migration and wintering seasons. Some fascinating studies of shorebirds include the great distance and spectacular non-stop flights, of species such as the Red Knot *Calidris canutus*, Great Knot *C. tenuirostris* and the Bar-tailed Godwit *Limosa lapponica* (Battley 1997, Pennycuick & Battley 2003, Battley & Piersma 2005, Gill *et al* 2005, 2009). Nevertheless, for this group of birds there is still a lack of information about migration for many species (Piersma *et al* 1997). The Common Sandpiper *Actitis hypoleucos* is widespread in Europe, across central Asia to Kamchatka, Sakhalin and Japan. It winters from western Europe and Africa through the Middle East and South Asia to Indonesia and Australia (Cramp & Simmons 1983, Urban *et al* 1986, del Hoyo *et al* 1996). The species is mainly a nocturnal migrant flying singly or in small flocks (del Hoyo *et al* 1996, Holland 2009).

Like many bird observatories in Europe, Ottenby Bird Observatory is located at a point where migratory birds concentrate during spring and autumn migration, thus making it possible to catch them in large numbers. Furthermore, trapping and ringing of birds has taken place at this site since 1946 and the result of this is the accumulation of an enormous amount of data for many migratory birds. These data have proven useful in understanding the population trends and migration patterns of several species. Consequently, the migration of waders at Ottenby has been well documented in several studies (*eg* Waldenström & Lindström 2001, Blomqvist *et al* 2002, Hedenström 2004, Helseth *et al* 2005a, b). Although the Common Sandpiper is widespread in Europe, knowledge about its migration pattern and biometrics remains limited (Meissner 1997, Piersma *et al* 1997, Arcas 1999). Data from ring recoveries show that, in autumn, European populations migrate in south-southwesterly to southwesterly directions to wintering areas in West Africa, with birds ringed in Sweden and Finland crossing continental Europe from the Baltic Sea (Cramp & Simmons 1983, del Hoyo *et al* 1996, Fransson *et al* 2008). The long history of ringing at Ottenby makes it possible to study long-term trends in the migration of this species at this site.

Climate change and its effect on the migration phenology of bird species has become a topical issue in recent years. In most of the studies on this topic, advancement in timing of spring migration has been documented (*eg*

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Mason 1995, Sokolov *et al* 1999, Tryjanowski *et al* 2002, Hüppop & Hüppop 2003, Vähätalo *et al* 2004, Stervander *et al* 2005, Jonzén *et al* 2006) while phenological changes during autumn migration have been studied less frequently (Jenni & Kéry 2003, Anthes 2004, Adamík & Pietruszková 2008). Spring temperatures have been shown to influence the nesting date of songbirds and thereby the timing of autumn migration (Ellegren 1990, Sokolov *et al* 1999, Sokolov 2006). Tøttrup *et al* (2006) reported that the effect of climate change on the timing of autumn migration of songbirds does not follow the same trend as that of spring migration. For waders it seems that the relationship between climatic variations and the phenology of autumn migration remains unclear (Adamík & Pietruszková 2008). In this paper, we present results from an analysis of 62 years' trapping and ringing data of autumn-migrating Common Sandpipers at Ottenby Bird Observatory, situated in the southwest Baltic Sea, and from this we describe the patterns in the phenology and morphometrics of adults and juveniles of the species. Also, estimates of potential flight ranges were derived for individuals with the mean and maximum estimated fuel loads.

METHODS

Trapping and ringing

Ottenby Bird Observatory (56°12′N 16°24′E) is situated on the southern point of Öland, an island *c* 10 km off the coast in southeastern Sweden. Bergström & Svärdson (1938) conducted a pilot study at this site in 1937–38, when waders were ringed. The Bird Observatory was founded in 1946. Since then waders have been trapped mostly in the autumn from early July to late September and sometimes later. Every year, between 80 and 120 of the 'Ottenby model' of walk-in funnel traps (Bub 1991) were used, depending on water level and the amount of decaying seaweed. Traps were checked every hour from dawn to dusk. Trapped birds were brought to the ringing laboratory where they were processed and subsequently released. A total of 5,232 fully grown Common Sandpipers ringed within the period 1947–2008 were available for analysis.

Morphometrics and phenology

During autumn passage, Common Sandpipers were aged either as juveniles (first-calendar-year birds) or as adult birds (second calendar year or older) using the features described by Prater *et al* (1977). Since 1990, the following morphometrics data were also recorded for all birds trapped: wing length to the nearest 1 mm, using the maximum-chord method (Svensson 1992), body mass to the nearest 0.1 g using a Pesola spring balance or an electronic balance, and total head length (bill + head) to the nearest 1 mm (Green 1980). In this study the lean body mass (LBM) was estimated at 38.7 g and 39.6 g for juvenile and adult birds respectively, by taking the average of the ten lightest birds with the mean wing length (113 mm) in each age group, while assuming that these birds represent a lean (fat-free) state. The LBM was used to estimate fuel load in the birds captured (expressed as percent of the LBM) as 100 x (BM − LBM)/LBM, where BM is body mass as recorded. We acknowledge that individual values of fuel load may be less precise than population averages (Helseth *et al* 2005a). In order to have a representative measure for analysis of trends in median dates, we excluded years in which fewer than five adults or juvenile birds were trapped. We also tested for the effect of climate change on migration phenology by correlating three different phases of migration, namely the 5^{th}, median and 95^{th} percentiles of each age class, with mean air temperature for the month of May at three weather stations – Norrköping 58°36′N 16°12′E, Örebro 59°16′N 15°13′E and Växjö 56°53′N 14°47′E – in south/central Sweden. The climate data were obtained from the Swedish Meteorological and Hydrological Institute (SMHI) for the period 1947–2008. For the purpose of understanding age-related patterns in morphometrics and also to enable comparison with similar studies on the Common Sandpiper and other species, separate analyses were conducted for adult and juvenile birds in all cases.

Morphometric data used for flight performance calculations were as follows: wing span = 0.32 m, wing area = 0.0147 m^2, and aspect ratio = 7.1 (calculated as the square of wing span divided by wing area; Pennycuick 1989). The potential flight range was calculated using Pennycuick's Flight program version 1.21 (Pennycuick 1989), assuming a flight muscle fraction of 0.2 and a flight altitude of 1,000 m.

Normality of data and homogeneity of variances were tested using Levene and Kolmogorov–Smirnov tests respectively. In the statistical analyses we used Pearson's correlation, General Linear Models (GLM) and Analysis of Variance (ANOVA) where a plot of the residuals gave a good fit and assumptions of normality were met. A Mann–Whitney U non-parametric test was used where data violated the assumptions of normality. All tests were conducted using SPSS Statistics 17.0 (SPSS Inc, 2008) and differences were considered significant at $P < 0.05$.

RESULTS

Numbers ringed

In total 5,232 Common Sandpipers were ringed during 1947–2008, with an annual average of 85 birds (standard deviation [sd] = 47.01, range 2–204) and an average of 53 juvenile (sd = 32.2, n = 3,290) and 31 adult birds (sd = 24.6, n = 1,942, ANOVA, $P < 0.001$) ringed yearly. There was no significant trend in the annual total number of Common Sandpipers trapped and ringed (GLM, $F_{1,60} = 1.583$, $P = 0.213$). The number of adults ringed each year was positively correlated with number of juveniles (Pearson $R = 0.270$, $P = 0.034$, n = 62). The interaction of age and year had a significant effect on the number of Common Sandpipers ringed (ANCOVA, $F_{1,122} = 8.703$, $P = 0.004$), *ie* the slopes of the relationship differs between the two age classes. The number of juvenile Common Sandpipers did not show any long-term trend (GLM, $F_{1,60} = 1.693$, $P = 0.198$, $B = -0.295$, n = 62 trapping years; Fig 1). There was however a long-term positive trend in the number of adult birds trapped and ringed (GLM, $F_{1,60} = 21.385$, $P < 0.001$, $B = 0.700$, n = 62 trapping years; Fig 1). However when we tested three-year running averages of number of adults and juveniles trapped, there was a significant negative trend in the number of juveniles trapped over the years (GLM, $F_{1,58} = 5.444$, $P = 0.023$, $B = -0.379$, $R^2 = 0.086$), while the positive trend in number of adults was maintained (GLM, $F_{1,58} = 41.520$, $P < 0.001$, $B = 0.666$, $R^2 = 0.417$). Further, we tested for a lagged relationship between number of adults and juveniles using a correlation of lagged average number of

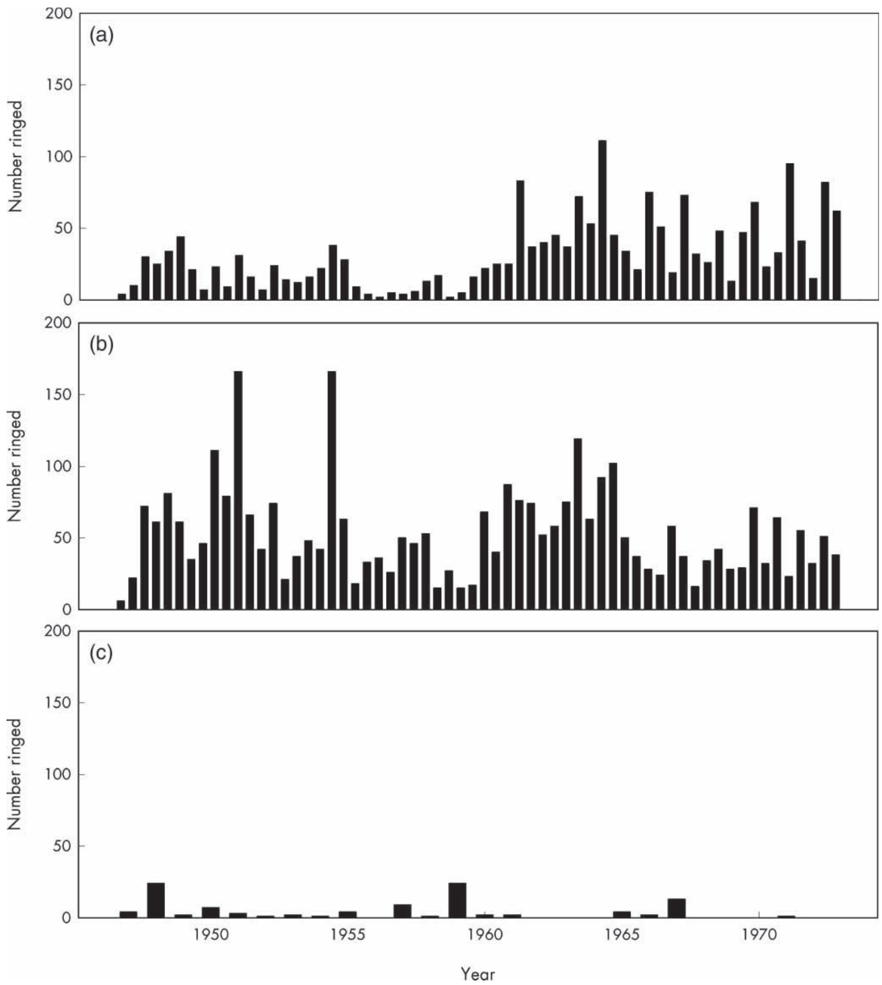

Figure 1. Annual ringing totals of a) adult b) juvenile and c) unaged Common Sandpipers on autumn migration at Ottenby, southeast Sweden during 1947–2008.

adult with the average number of juveniles from the preceding three years (as a way of determining whether juveniles translate to adults in subsequent years). However, we did not find any significant correlation (Pearson R = −0.088, $P = 0.720$).

Migration phenology

Median date was 21 July for adults (n = 103; Fig 2) and 7 August for juveniles (n = 110; Fig 2), *ie* there was a 17-day difference between adults and juveniles in the timing of passage. Median passage dates of juveniles showed a significant negative trend over the years, while the trend was not significant in adults (GLM, juveniles: $F_{1,60} = 5.469$, $P = 0.023$, B = −0.089, adults: $F_{1,55} = 1.851$, $P = 0.179$, B = −0.059; Fig 3). However, the slopes of the relationship did not differ significantly between the two age classes (ANCOVA, $F_{1,115} = 0.277$, $P = 0.600$). Spearman's correlation analysis of 5th, median and 95th percentiles of migration with mean May temperature at three weather stations in Central Sweden gave varying results (Table 1), but mean temperature did not differ significantly between the three weather stations (square-root-transformed values, Norrköping mean 3.3°C, sd = 0.20, Örebro mean 3.3°C, sd = 0.17, and Växjö mean 3.3°C sd = 0.19, ANOVA, $F_{2,185} = 0.093$, $P = 0.911$). Also, there was no significant change in the mean temperatures at these sites over the years (Spearman's correlation, Norrköping $r_s = 0.175$, $P = 0.175$, Örebro $r_s = 0.118$, $P = 0.362$, Växjö $r_s = -0.085$, $P = 0.511$, n = 62 years).

Body mass

Body mass was significantly related to wing length (ANCOVA, $F_{1,1,573} = 98.972$, $P < 0.001$, B = 0.531) and time of day (hour) of capture ($F_{1,1,573} = 36.402$, $P < 0.001$, B = 0.197), but this relationship did not differ between the two age classes ($F_{1,1,572} = 2.894$, $P = 0.089$). This made it possible to correct for body mass using the equation:

$$\text{Bodymass} = -12.36 + 0.53 \times \text{Wing} + 0.20 \times \text{Hour}$$

The mean corrected body mass of juvenile birds (mean = 49.8 g, sd = 1.92, n = 743) was slightly higher than that of adult birds (mean = 49.7, sd = 1.85, n = 843), but the difference was not significant (ANOVA, $F_{1,1,584} = 1.954$, $P = 0.162$). The interaction of age and date of capture had a significant effect on corrected body mass (ANCOVA, $F_{1,1,582} = 4.838$, $P = 0.028$); there was no significant trend in the corrected body mass of juveniles over the season (GLM, $F_{1,742} = 0.109$, $P = 0.742$, B = 0.002), whereas adults showed a significant decline in

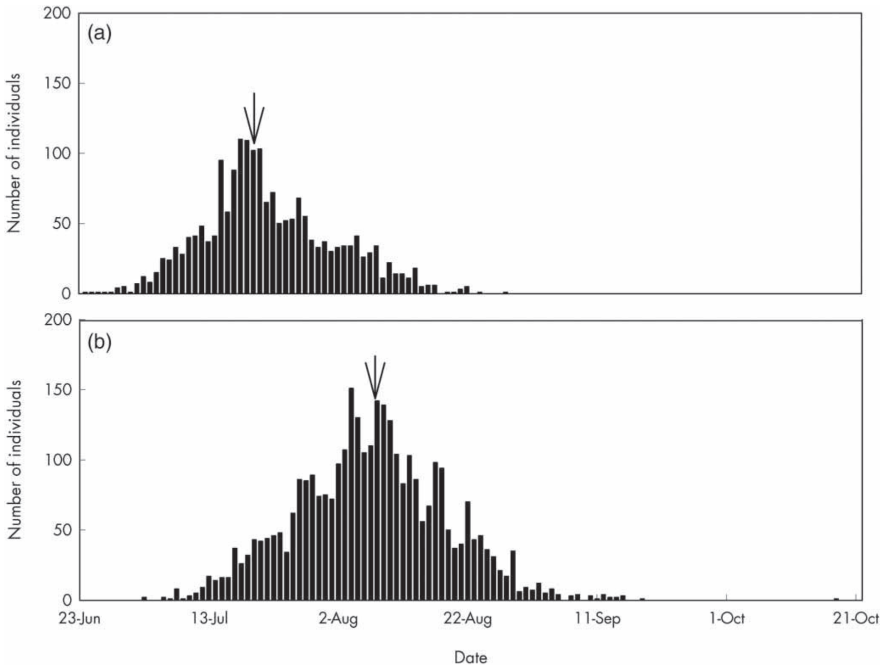

Figure 2. Autumn migration phenology of a) adult and b) juvenile Common Sandpipers trapped, aged and ringed at Ottenby, southeast Sweden.

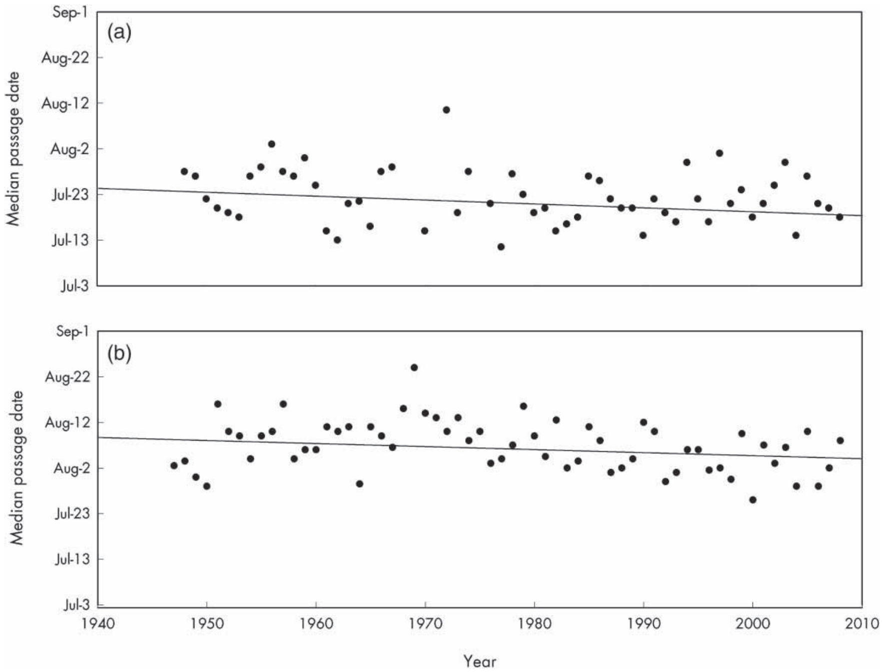

Figure 3. Trend in autumn median passage date of a) adult and b) juvenile Common Sandpipers trapped, aged and ringed at Ottenby, southeast Sweden during 1947–2008.

body mass over the season (GLM, $F_{1,841} = 6.909$, $P < 0.001$, $B = -0.019$).

Wing length

Wing length did not differ significantly between the two age classes (juvenile mean = 113.2 mm, sd = 3.07, n = 743, adult mean = 113.3, sd = 2.94, n = 852; ANOVA, $F_{1,1,584} = 0.646$, $P = 0.422$). The trend in wing length over the season differed between the age classes (ANCOVA, $F_{1,1,582} = 6.512$, $P = 0.011$). The wing length of juvenile birds did not change significantly over the season (GLM, $F_{1,741} = 2.385$, $P = 0.123$, $B = -0.015$; Fig 4) while, in adult birds, there was a significant decline in wing length as the season progressed (GLM, $F_{1,841} = 22.653$, $P < 0.001$, $B = -0.054$; Fig 4). Over the years there has been a significant increase in wing length of both juvenile (GLM, $F_{1,741} = 11.204$, $P = 0.001$, $B = 0.067$) and adult birds ($F_{1,841} = 11.601$, $P = 0.001$, $B = 0.061$).

Table 1. Spearman's correlation coefficient values (r_s) between three different parts of the populations of adult and juvenile Common Sandpipers with mean May air temperature in three regions in Sweden. Negative values indicate earlier autumn migration.

			Mean May temperature (°C)		
Age	Years (n)	Migration phase (percentile)	Norrköping	Örebro	Växjö
Adult	57	5^{th}	−0.082	0.085	0.025
	57	median	−0.11	0.098	−0.016
	57	95^{th}	**– 0.277***	0.042	0.105
Juveniles	62	5^{th}	−0.191	0.075	−0.177
	62	median	**– 0.448***	−0.218	−0.007
	62	95^{th}	**– 0.321***	−0.048	−0.151

* values in bold indicate significance ($P < 0.05$)

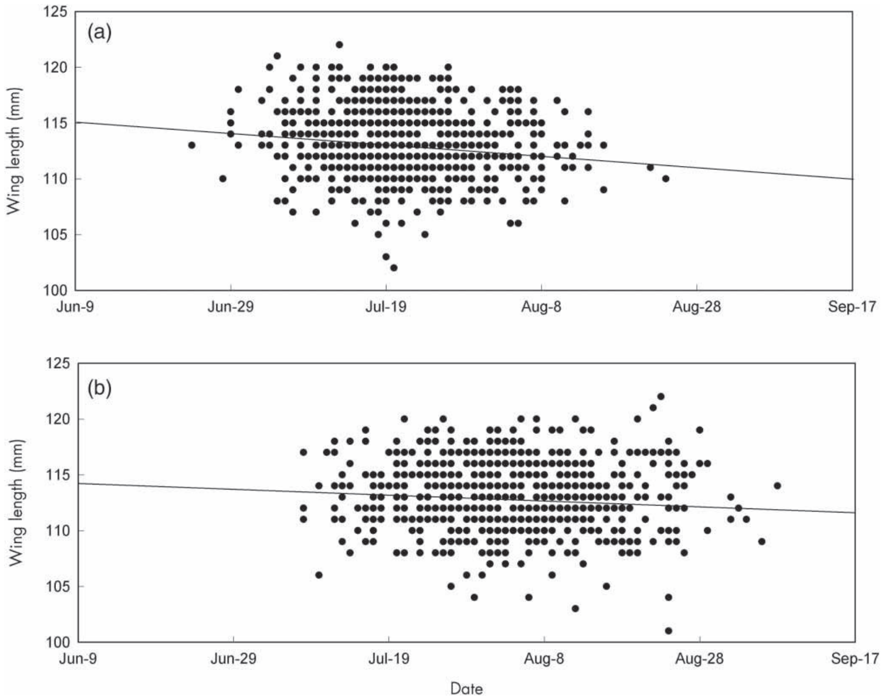

Figure 4. Trend in wing length (mm) of a) adult and b) juvenile Common Sandpipers trapped, aged and ringed in autumn at Ottenby, southeast Sweden. One late juvenile bird with wing length 110 mm trapped on 18 October was excluded from this figure.

Total head length

Total head lengths of adult birds were significantly longer than that of juvenile birds (ANOVA, $F_{1,1,589} = 7.431$, $P = 0.006$, adult mean: 49.7 mm, sd = 1.43, juvenile mean: 49.5, sd = 1.41). Over the season, the total head length of juvenile birds did not show any significant trend (GLM, $F_{1,742} = 3.313$, $P = 0.069$, $B = -0.008$; Fig 5), but in adult birds there was a significant negative trend over the season (GLM, $F_{1,845} = 6.628$, $P = 0.010$, $B = -0.014$; Fig 5). These slopes were not significantly different, however (ANCOVA, $F_{1,1,587} = 0.706$, $P = 0.401$). Total head length did not show any long-term trend in either of the age classes (GLM, juveniles: $F_{1,742} = 0.815$, $P = 0.367$, adults: $F_{1,845} = 0.080$, $P = 0.777$).

Fuel load

Mean fuel load was significantly higher in adults than juveniles (Mann–Whitney $U = 292165.5$, $P = 0.021$, adult mean = 28.8% of LBM, sd = 15.7, n = 842, juvenile mean = 27.8% of LBM, sd = 18.6, n = 744,). Fuel load in juveniles showed a significant increase over the season (GLM, $F_{1,742} = 11.207$, $P = 0.001$, $B = 0.201$; Fig 6), while in adult birds there was a significant decline over the season (GLM, $F_{1,840} = 12.733$, $P < 0.001$, $B = -0.218$; Fig 6), and the slopes of the relationships were significantly different (ANCOVA, $F_{1,1,582} = 23.425$, $P < 0.001$). The maximum fuel loads were 98.7% and 105.4% in a juvenile and an adult bird respectively.

DISCUSSION

The yearly totals of adult Common Sandpipers ringed at Ottenby were positively correlated with the number of juveniles, yet when we tested the age-specific trapping trends independently, the observed positive trend in number of adults was accompanied by a non-significant negative trend in juvenile numbers. We therefore used three-year running averages of age-specific yearly totals. This revealed that, over the years, the numbers of adults trapped have increased significantly, while juveniles have decreased. We suggest two alternative explanations for this trend. First, more individuals may have been aged correctly after the wader identification and ageing guide was published by Prater *et al* (1977). However, only about 2% of all birds ringed were individuals whose age had not been determined and these were ringed between 1947 and 1971. Thus, the publishing of the Prater *et al* (1977) guide may not have influenced this trend, though it has been very useful. Secondly, more adults other than those of the Swedish and Finnish populations may have crossed the Baltic from Ottenby in recent years, and so

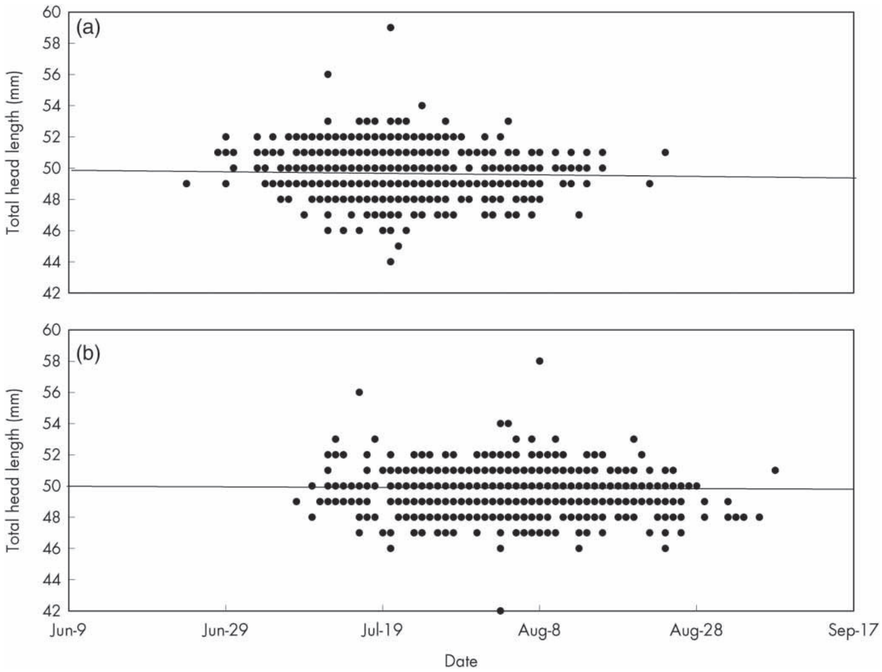

Figure 5. Trend in total head length (mm) of a) adult and b) juvenile Common Sandpipers trapped, aged and ringed in autumn at Ottenby, southeast Sweden. One late juvenile bird with total head length 49 mm trapped on 18 October was excluded from this figure.

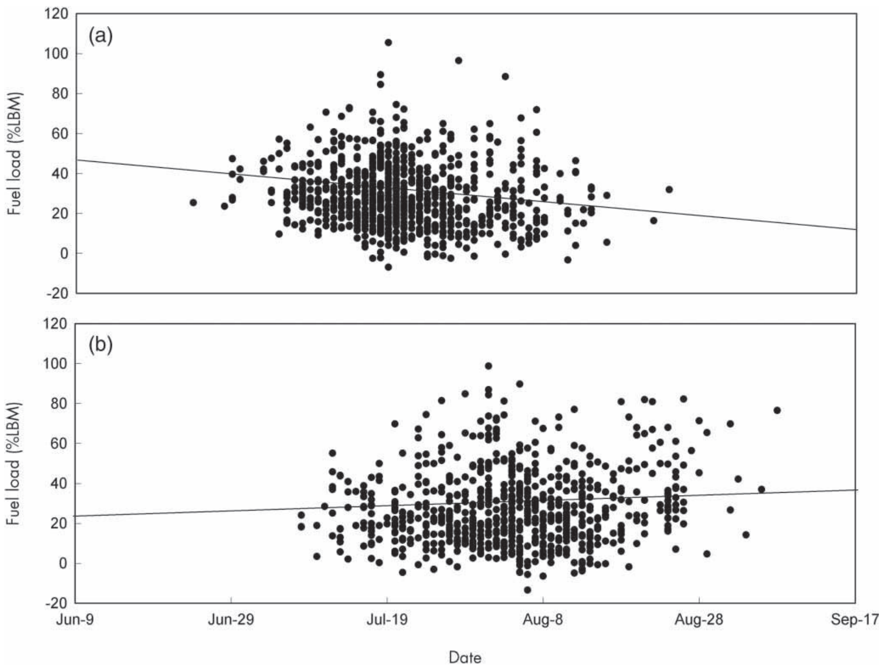

Figure 6. Trend in fuel load (% of LBM) of a) adult and b) juvenile Common Sandpipers trapped, aged and ringed in autumn at Ottenby, southeast Sweden. One late juvenile bird with fuel load 45.6% trapped on 18 October was excluded from this figure.

accounting for the increase since about 1980. The decline in number of juveniles coincides with a recent decline in the population of this species around the edge of its range (Dougall *et al* 2004), suggesting a decline in breeding success and/or juvenile survival in Swedish and Finnish populations. That juveniles were not translated into more adults in subsequent years also raises concern about the conservation status of Fennoscandian populations. The absence of any significant trend in the annual totals (when both age classes were pooled) masks this decline in juvenile numbers as well as the possibility that adults of other populations may pass through Ottenby. Hence, population trends derived from age-specific data could provide insight into subtle changes in numbers.

Timing of passage

The difference between median passage date of adults and juveniles was 17 days, which is somewhat higher than the 10 days reported for Ruddy Turnstones *Arenaria interpres* (Helseth *et al* 2005b). The median dates for adults and juveniles were similar to those of Ruddy Turnstones (27 July for adults and 6 August for juveniles; Helseth *et al* 2005b), but it was earlier than that of the Red Knot (5 August for adults and 31 August for juveniles; Helseth *et al* 2005a), the Temminck's Stint *Calidris temminckii* (28 July for adults and 20 August for juveniles; Hedenström 2004) and the Curlew Sandpiper *C. ferruginea* (adults 29 July and juveniles 31 August; Blomqvist *et al* 2002). Taken together, it seems that the species with the most northerly breeding latitudes migrate through the Baltic at later dates. The median dates reported here were also earlier than those of Common Sandpipers caught in the Czech Republic and Slovakia (28 July for adults and 11 August for juveniles; Adamík & Pietruszková 2008). On balance, it appears that the species breeding in the Arctic have a longer period between passage of adults and juveniles than species with a temperate breeding distribution.

Although adult passage at Ottenby began earlier (24 June) than that of juvenile birds (3 July), there is an overlap in the migration period of the age classes, since juvenile birds were being trapped from early July. This may be due to a short fledging period of about 18 – 20 days (Holland *et al* 1982). Here we show that the passage of adult birds occurred in July and August, whereas juveniles passed through mainly from July to September, although one late individual was trapped on 18 October. This timing of migration is similar to that described for this species in the Münster area of Germany (Harengerd *et al* 1973).

Morphometrics

Average body masses of adults (49.7 g) and juveniles (49.8 g), corrected for size and time of day of capture, were 2 g higher than reported for Common Sandpipers caught during autumn migration at the Gulf of Gdańsk, Poland (47.8 g; Meissner 1997), suggesting a difference in migration strategy of birds at these two locations, with birds at Ottenby probably anticipating a longer next flight than the Gdańsk birds. Alternatively, the birds at Gdańsk may have consumed more fat during their preceding flight than Ottenby birds. An average wing length of 113 mm in adults and juveniles was also higher compared to the 112 mm reported by Meissner (1997) at the Gulf of Gdańsk. That average wing length was similar in the two age classes can be attributed to adult birds having old and worn primaries, while juveniles have fresh and new feathers when passing through Ottenby in autumn. A similar pattern was reported by Meissner (1997) for Common Sandpipers, for the Temminck's Stint (Hedenström 2004), and for the Red Knot (Helseth *et al* 2005a). Adult birds had significantly longer total head length than juveniles, and both wing length and total head length of adult birds showed a negative trend over time. Female Common Sandpipers have been reported to be significantly larger than males (Lofaldi 1980, Holland *et al* 1982) and that the females often leave the nest after about two weeks of brood care, so that males carry on with parental care (Yalden & Holland 1992). The observed trend in adults is therefore likely because the larger females migrate early in the season while the smaller males migrate later on. Also, the average wing length of adults and juveniles showed a long-term increase. This probably reflects measurement errors, so that wing lengths have been systematically measured longer than they really are, since measurements of total head lengths (a measurement less susceptible to errors) did not change during the same period.

Fuel load, migration speed and flight range

At Ottenby, adult Common Sandpipers seem to carry marginally larger fuel loads (mean 28.8%) than juveniles (mean 27.8%). These average fuel loads were similar to values reported for the Temminck's Stint (adults 32% and juveniles 20%; Hedenström 2004), but the maximum values were higher in Common Sandpipers (105% in adults and 99% in a juvenile) than the Temminck's Stint (75% in adults and 84% in juveniles) and Red Knot (77% in a juvenile; Helseth *et al* 2005a). These maximum values might reflect that maximum daily energy assimilation in Common Sandpipers is very high (Kvist & Lindström 2003), and also that the feeding opportunities at Ottenby may be very good for this species. Whereas fuel load in juvenile birds increased significantly over the season, adults showed a significant decline. A similar trend of weight gain by late migrating waders has been reported in previous studies (Pienkowski *et al* 1979, Meissner 1997, Helseth *et al* 2005a). We suggest that the differing patterns observed may reflect differences in migration strategy between the two age classes. We speculate that juvenile birds passing Ottenby later in the season have deposited more fuel before the crossing of the Baltic as insurance against unfavourable conditions along the migratory route and probably intend a longer next flight (Pienkowski *et al* 1979). Migration speeds of Swedish-ringed Common Sandpipers based on data from ring recoveries was estimated at 97.4 km d^{-1} (Fransson *et al* 2008).

Many Common Sandpipers ringed in Sweden move through France and Iberia into their wintering grounds in sub-Saharan Africa (Cramp & Simmons 1983, Fransson *et al* 2008). The distance to the area near central France with the highest number of recoveries from Ottenby is about 1,400 km. That many individuals have been recovered in France does not necessarily imply that the area is a favorable stopover, and may perhaps reflect the activity of bird hunters in the region. Nonetheless, it seems that the average juvenile and adult individual can cover this distance in a single flight (Table 2). The average adult bird may even reach the Iberian Peninsula (distance of about 2,284 km from Ottenby) in a single flight, whereas the fuel load of the average juvenile may not carry them that far except with the assistance of tail winds (Table 2). If conditions along the migratory route remain favourable, birds with the maximum fuel loads may be capable of a direct flight to the sub-Saharan winter quarters (Table 2).

Climate change and migration phenology

The effect of climate change on the spring migration phenology of bird species has captured the interest of ornithologists. In recent years however, more studies are beginning to focus on the response of autumn migration to recent global climate change. According to Jenni & Kéry (2003), many long-distance passerine migrants in western Europe have responded to recent climatic variations by adjusting towards an earlier autumn passage over the past four decades. Further, Adamík & Pietruszková (2008) reported advancement in the autumn median passage of both adult and juvenile Common Sandpipers at several inland sites in central Europe. In this study we found a similar trend of advancement in autumn median passage date for juvenile Common Sandpipers passing through Ottenby. However, for adults there was no significant change over the years. We tested whether the weather in May, measured as mean temperatures in May at three stations in south/central Sweden was related to autumn migration phenology, but found a significant correlation with May temperatures only at one station. However, given that the mean May temperatures at the three weather stations have not changed significantly over the years, we cannot conclude that the advancements are driven by recent warming in the region. Perhaps there are other more subtle climatic variables responsible for the trend. Generally, this result supports already existing submissions that the impact of climate change on autumn migration phenology does not necessarily follow the same pattern as spring migration, and possibly there are also differing age-related responses within this species.

Table 2. Estimated flight ranges for Common Sandpipers of different departure fuel loads, calculated using Pennycuick's (1989) method, version 1.21, with the assumption of a body drag coefficient of 0.01.

	Departure mass (g)	Fuel load (% LBM)	Fat fraction (%)	Flight range (km)
Juvenile mean	49.4	27.8	0.19	2,182
Juvenile max	76.9	98.7	0.41	5,902
Adult mean	49.8	28.8	0.20	2,324
Adult max	79.5	105.4	0.42	6,102

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