

Phenology of spring migration of Wood Sandpiper *Tringa glareola* through Europe

Grönbenans Tringa glareola fenologi under vårflyttningen genom Europa

MAGDALENA REMISIEWICZ, WŁODZIMIERZ MEISSNER, PAVEL PINCHUK & MATEUSZ ŚCIBORSKI

Abstract

Phenology and dynamics of spring migration of the Wood Sandpiper through Europe was analysed, using both literature and new field data collected at five wetlands in Central Europe (N Poland and S Belarus). The passage through all Europe lasted from mid-March until end of June and at the five Central European sites between mid-April and end of May. Migration was very concentrated (50% of migrants during 6–10 days), and median dates at all Central European sites were between 3 and 15 May. Regression of mean peak dates on latitude of the sites showed that spring migration through Europe was quick, about 97 km/day. In most years passage had one peak, but two peaks in some seasons at eastern sites may reflect passage of migrants using a SE route or be an effect of

adverse weather. Migration intensity varied among seasons. This may have been caused by changes of water levels or other habitat components. Tight timing of spring passage suggests that in Central Europe the Wood Sandpiper adopt a time-minimising migration strategy.

Magdalena Remisiewicz, (corresponding author), Włodzimierz Meissner, and Mateusz Ściborski, Avian Ecophysiology Unit, Dept. of Vertebrate Ecology and Zoology, Univ. of Gdańsk, al. Legionów 9, 80-441 Gdańsk, Poland; e-mail: biomr@univ.gda.pl
Pavel Pinchuk, Institute of Zoology, Belarusian National Academy of Sciences, Akademichnaya Str. 27, 220072 Minsk, Belarus; e-mail: ppinchuk@mail.ru

Received 19 June 2006, Accepted 8 February 2007, Editor: A. Hedenström

Introduction

In spring, Wood Sandpipers *Tringa glareola* are numerous migrants, widespread over the majority of European inland (Glutz von Blotzheim et al. 1977, Cramp & Simmons 1983). Most Wood Sandpipers that pass through these areas spend the winter in sub-Saharan Africa and in spring they return to their breeding grounds in Fenno-Scandia, the Baltic States and northwestern Russia (Myhrberg 1961, Lebedeva et al. 1985, Meissner 1997, Underhill et al. 1999, Remisiewicz 2005). En route they use a wide variety of inland wetlands as stopover places and only low numbers forage at coastal mudflats (Glutz von Blotzheim et al. 1977, Cramp & Simmons 1983, Meltofte 1996).

The existing knowledge of the spring passage of Wood Sandpipers through Europe comes mainly from counts conducted in many wetlands spread over the whole continent (see Appendix 1). However, the data on spring passage of this species in Central Europe, at areas located close to its breeding range, which can be the last stopover places before arrival at nesting grounds, are limited and

dispersed. Some materials on Wood Sandpiper migration have been summarised by Glutz von Blotzheim et al. (1977) and OAG Münster (1994). However, since these publications numerous new data on spring passage have been published, thanks to the interest in the migration of this species, increased by the research project of the International Wader Study Group “*Tringa glareola* 2000” coordinated by WRG KULING (Remisiewicz 2005).

The main aim of this paper is to present an overview of the phenology and the course of spring migration of the Wood Sandpiper through Europe. In particular, we want to test the hypothesis of a very quick and condensed northward passage and explain variation of migration intensity and dynamics in the context of the migration strategy of the species.

Study areas and methods

The analysed data on phenology of Wood Sandpiper spring passage through Europe include dates of the earliest observations, migration peaks and the last records at sites presented in Figure 1. Data from most sites were collected from available literature

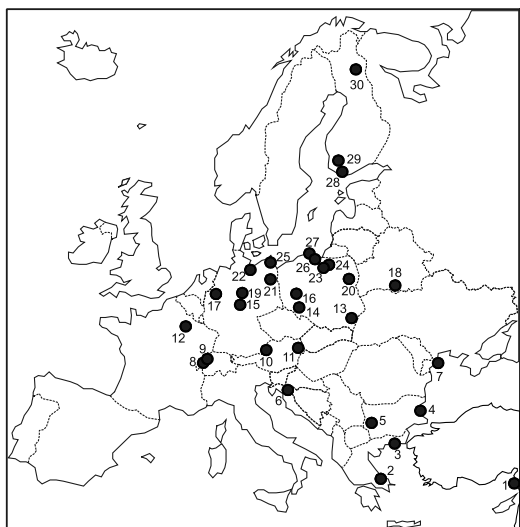


Figure 1. Sites discussed in the study. The site numbers correspond with those in Appendix 1; names and geographical coordinates of sites given in Appendix 1.

Lokaler som diskuteras i denna studie. Lokalernas nummer motsvarar de i Appendix 1, där deras namn och geografiska koordinater ges.

sources (Appendix 1). Spring migration phenology and dynamics in Central and Eastern Europe was analysed in more detail, based on our own counts at five sites located in N and NE Poland and in S Belarus (Figure 1). These surveys were performed from mid-April until mid-May or the end of May, covering the entire migration of the species, in different years within the period 1996–2005. Descriptions of the study sites are presented below, and periods of counts at each site are given in Table 1.

Mechelinki Meadows

This 120 ha wetland is situated in N Poland, on the coast of Gulf of Gdańsk (Figure 1, site 27). The site consists of open wet meadows and rushes, with water stagnating in spring. At this site studies were conducted in 1994–1998 and 2000. In the periods of pentad counts (Table 1), controls were done two or three times per pentad; during the period of daily counts only single controls were missed.

Drewnica Meadows

This site, located in N Poland about 3–4 km up the Vistula river mouth within its flood embankments, is ca 190 ha temporarily flooded open meadows

(Figure 1, site 28). Wader counts were performed there in 1997–1999. In the periods of pentad counts (Table 1), controls were done two or three times per pentad (Wójcik et al. 1999).

Nisko

This ca 50 ha wetland is located in NE Poland (near Olsztyn), in the Sajna river valley (Figure 1, site 24). It is a mosaic of reedbeds, rushes and aquatic plants, permanently flooded by river water. At this site pentad counts were conducted in 2000, and daily counts in 2003 (see Table 1).

Kwiecewo

This site is located in NE Poland, ca 50 km southwest of Nisko (Figure 1, site 23). It is a natural ca 60 ha shallow lake among farmland. Its shallow littoral zone, with abundant water vegetation and rushes, and surrounding wet meadows, provide favourable foraging and resting conditions for Wood Sandpipers. Daily counts were conducted there in 2004 and 2005 (Table 1).

Turov

This site, located in S Belarus in the floodplain of the Pripyat river (figure 1, site 18), consists of ca 200 ha grazed meadows. Large oscillations of flooded area among years, due to different water level in the Pripyat river, are characteristic of this place. Counts of waders in 2002 were performed twice or more times per pentad and in 2005 on a daily basis (Table 1). In 2004 controls were irregular and only maximum observations are used in this paper.

The periods of counts at each site in most years included the entire period of Wood Sandpiper migration. In the remaining years the counts covered the main peaks and the majority of Wood Sandpiper passage. At most sites daily counts were conducted during the main concentration of migration, as shown in Table 1. Before and after this period, counts were done 2–3 times per five-day period (pentad); these counts will be referred to as “pentad counts”. Based on both daily and pentad counts, migration dynamics at each site was analysed using the standard pentad scheme of Berthold (1973). For each year and site, the mean and maximum number of Wood Sandpipers in a pentad were presented. This pentad migration dynamics was compared with the pentad pattern of spring migration available from the literature data. For years when daily counts were conduct-

ed at studied sites, the reference period when counts were performed in each year was established as 29 April–13 May. For these years, the median migration date and 1st and 3rd quartiles were calculated and compared by the Kruskal-Wallis test and *post-hoc* Dunn's test (Zar 1996). The dates of the first arrival, mean peaks and median dates, obtained from the studied sites were combined with the analogous information collected by the survey of the available literature sources. Based on both literature and our field data, we analysed the timing and speed of the birds' northward movement through the continent. We checked the relation of the first arrival or the peak dates and the geographical latitude of stopover sites from all over Europe by Pearson correlation coefficient. We estimated migration speed according to the slope of regression equation. Statistical analyses were carried out with the software package STATISTICA 6 (Statsoft 2003), significance level of $p < 0.05$ was accepted.

To check whether variation in seasonal migration pattern has a local or wider character, we compared daily migration dynamics between sta-

tions Mechelinki and Drewnica Meadows, which worked contemporaneously in a few seasons, in particular in 1997, and between the more distant stations Kwiecewo and Turov that operated at the same time in 2005. One missing count in each of these seasons was filled with the mean number from the two neighbouring days. To compare migration intensity between years at the same station and between sites, we calculated the mean number of birds per count for each site and season. The total number of birds observed at a site during all counts within the reference period was summed up for each season (years with both pentad and daily counts considered). This total does not reflect the real number of migrant Wood Sandpiper in a given season, due to unknown turn-over rates. However, we assumed that the length of the birds' stay did not differ among seasons to an extent that would substantially influence the observed totals. These totals were divided by the number of counts (7–15 counts evenly distributed within the reference period), providing the measure of migration intensity in a certain season.

Table 1. Periods of pentad counts (one to three counts per five-day period) and daily counts at the studied sites in subsequent years.

Perioder med pentadräkningar (en till tre räkningar per femdagarsperiod) och dagliga räkningar vid de studerade lokalerna.

Site <i>Lokal</i>	Year <i>År</i>	Pentad counts <i>Pentadräkningar</i>	Daily counts <i>Dagliga räkningar</i>
Mechelinki Meadows	1994	12 Apr–22 Apr 14 May–30 May	23 Apr–13 May
	1995	14 Apr–20 Apr 12 May–30 May	21 Apr–11 May
	1996	12 Apr–22 Apr 20 May–30 May	24 Apr–19 May
	1997	–	30 Apr–12 May
	1998	25 Apr–28 Apr 18 May–29 May	29 Apr–17 May
	2000	–	28 Apr–10 May
Drewnica Meadows	1997	25 Apr – 28 Apr 16 May – 30 May	29 Apr – 15 May
	1998	24 Apr – 2 May 11 May – 19 May	3 May – 10 May
	1999	12 May – 17 May	27 Apr – 11 May
Nisko	2000	8 Apr – 14 May	–
	2003	–	28 Apr – 14 May
Kwiecewo	2004	–	24 Apr – 12 May
	2005	–	28 Apr – 14 May
Turov	2002	27 Feb – 30 May	–
	2005	–	25 Mar – 18 May

Results

Phenology of Wood Sandpiper spring migration through Europe

Spring migration of Wood Sandpipers through Europe lasts from mid March to the beginning of June, as shown by the literature data (see Appendix 1) and our own results. Dates of first arrival showed over two months difference between the southern and northern parts of Europe (Figure 2). The earliest occurrence was recorded on 5 March at Draganic fishponds in Croatia (Radovic et al. 1999) and the latest on 7 May at Yyteri in Finland

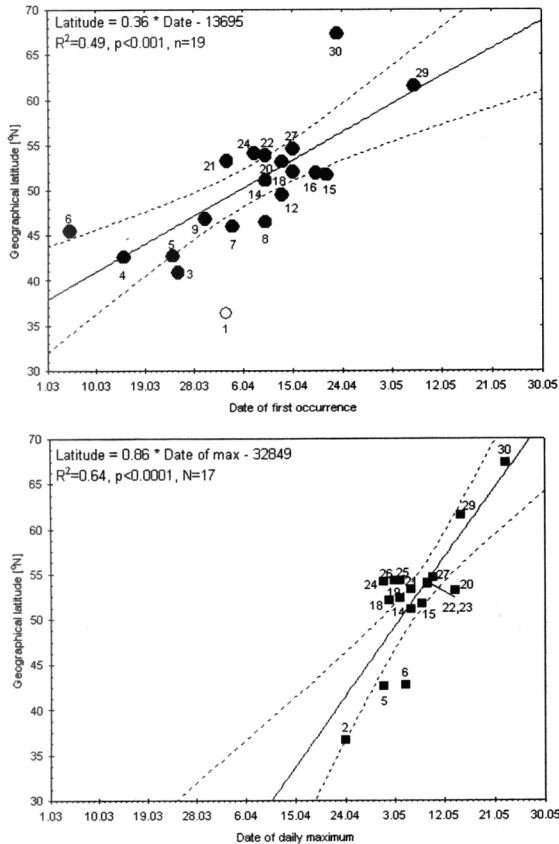


Figure 2. Correlation of dates of first occurrence and daily maximum of Wood Sandpipers and geographical latitude of the site, based on our results and literature data presented in Appendix 1. Open sign – outlier data excluded from regression. Dashed lines – 95% confidence interval around regression line (solid line).

Sambandet mellan första ankomst och dagligt maximum och lokalens geografiska läge, baserat på såväl egna data som litteraturuppgifter enligt Appendix 1. Öppen symbol – avvikande värde som uteslutits från regressionen. Streckade linjer – 95% konfidensintervall runt regressionslinjen (hel-dragen).

(A. Eriksson, pers. comm.). At some sites, particularly in Southern Europe and Asia Minor, Bulgaria, Greece and Israel, the earliest migrants occurred in low numbers already in the end of March (Akriotis 1991, Nankinov et al. 1998, Dalakchieva & Popov 2002, Yosef et al. 2002). At most Central European sites spring passage of Wood Sandpipers fell in the middle of this period – the passage begun between 8 and 22 April. Thus, the site- and season-dependent variation of the first arrival date at these sites was only 14 days (Figure 2). This was also the case at the studied Polish and Belarusian sites, where the first observations came from 8 April 2000 at Nisko and 13 April 2002 at Turov. The relatively late date of first arrival (3 April) at the south-east of Turkey (Çukurova Deltas; Berrevoets et al. 1994) draws attention (Figure 2). This date departs significantly from the pattern of the remaining sites, and was therefore excluded from the analysis of the relation between first occurrence date and geographical location of sites. The dates of first arrival at all remaining European stopover sites were positively correlated with the geographical latitude of the sites ($r=0.72$, $p<0.001$, $n=19$), reflecting the northward progress of spring passage. A significant regression was obtained (Figure 2), with 10 out of 19 data points falling within the 95% confidence interval.

The major wave of migrants moved northwards over Europe during one month, from 24 April in Turkey (Çukurova Deltas; Berrevoets et al. 1994) to 23 May in Finland (Ita-Lapin; Saari et al. 1998), as shown in Figure 2. At all analysed Central European sites the variation between sites and years in the occurrence of the main peak was only two weeks (29 April–15 May, Figure 2). At the studied Polish and Belarusian sites, the peak fell in the first week of May in all years. The maximum numbers of Wood Sandpipers reached during one count at Polish sites were 1371 individuals at Nisko (1 May 2000) and 1000 individuals at Turov (2 May 2004). The movement of this main peak of Wood Sandpiper migration through the continent was positively correlated with the geographical latitude of the stopover sites ($r=0.81$, $p<0.0001$, $n=17$). The slope of the regression (Figure 2) allowed us to estimate the migration speed at 52 minutes/day, i.e. ca 97 km/day. For 11 sites, peak dates were concentrated within 95% confidence interval around the regression line.

The time spans between the first observations and the main wave of migrants are worth attention. In Bulgaria (on Atanasovsko Lake and near Sofia) the first migrants occurred over 40 days earlier than

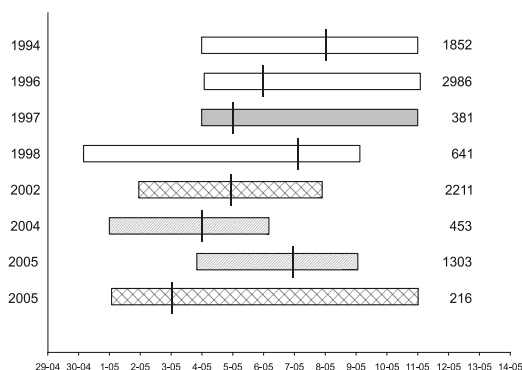


Figure 3. Comparison of phenology of spring migration of Wood Sandpipers at the studied sites. Bars – interquartile increments (25–75% of birds), vertical lines – medians; white bars – Mechelinki Meadows, grey bar – Drewnica Meadows, hatched bars – Turov, lined bars – Kwiecewo; numbers at sides of bars give the number of birds in the reference period. *Jämförelse av vårfenologin för grönbena på de olika lokalerna. Horisontella staplar – 25–75% av fåglarna, vertikala linjer – medianer, vita staplar – Mechelinki, grå staplar – Drewnica, korsade staplar – Turov, linjerade staplar – Kwiecewo. Värden vid staplarna anger antal fåglar under referensperioden.*

the main wave (Nankinov et al. 1998, Dalakchieva & Popov 2002), while at the wetlands of Central Europe (Germany, Poland, Belarus), the difference was 15–33 days (Kube 1988, Lontkowski et al. 1988, Dierschke & Dierschke 1990, Górski & Nowakowski 1999, our data).

Spring passage of Wood Sandpipers at the studied Polish and Belarusian sites was concentrated within the first half of May (Figure 3). In seasons when daily counts were available, 50% of the birds migrated during 6 to 10 days (interquartile increment) of an intensive passage. All median dates of migration for the Polish and Belarusian sites in different years fell between 3 and 8 May. Median dates of passage at stopover sites in the whole of Europe in different seasons were also very concentrated in a short period between 5 and 13 May, and a similar, condensed passage was observed in Austria and Germany (Winkler & Herzig-Straschil 1981, Dierschke & Dierschke 1990, Pannach 1992, Sauvage 2000, Anthes et al. 2002). The last migrants were observed in Central Europe until the end of May with the latest record from 30 May (Mechelinki in 1996 and Turov in 2002).

Table 2. Total number of birds observed, number of counts, and mean number of birds per count (‘migration intensity’) during the reference period (30 April–13 May) at the studied sites and seasons. *Totlat antal observerade individer (ind.), antal räkningar (räkn.) samt medeltal individer per räkning (flyttintensiteten) under referensperioden 30 april–13 maj.*

Site	Year	Birds	Counts	Mean
Lokal	År	ind.	räkn.	medel
Mechelinki	1994	1852	15	123.5
Meadows	1995	2443	13	187.9
	1996	2839	14	202.8
	1997	632	11	57.5
	1998	641	15	42.7
	2000	799	12	66.6
Drewnica	1997	381	15	25.4
Meadows	1999	797	13	61.3
Nisko	2003	2211	15	147.4
Kwiecewo	2004	453	14	32.4
	2005	1303	15	86.9
Turov	2002	734	7	104.9
	2005	200	14	14.0

Migration pattern

Despite similar median dates of passage, migration dynamics of Wood Sandpipers differed significantly among the studied Polish and Belarusian stations and seasons (Figure 3; Kruskal-Wallis test: $H_{4,8071}=358.08$, $p<0.0001$). Differences in the course of passage between all the stations and even between consecutive seasons at the same station (Figure 3), were highly statistically significant (*post-hoc* Dunn test: for all pairwise comparisons – $p<0.0001$). In addition, the total numbers of counted birds fluctuated strongly from year to year. We did not find any common trends of changes in numbers for the stations that operated in the same years (Table 2). The highest mean number of Wood Sandpipers per count was over 200 birds (in 1996 at Mechelinki Meadows), and the lowest was 14 birds (in 2005 at Turov). At Mechelinki Meadows, the numbers of birds observed in 1994–1996 were high, but they were much lower in 1997–1998 and 2000. At Drewnica Meadows, located only 50 km away, the mean number of Wood Sandpipers during a count was lowest in 1997 but twice as high in 1999 (Table 2). At Turov in 2002 and at Nisko in 2003 Wood Sandpipers were particularly

abundant. In contrast, at Turov in 2005 very low numbers of birds were observed, while in the same season at Kwiecewo migration intensity was more than twice that in the previous year (Table 2).

Two main patterns of Wood Sandpiper migration dynamics were identified at the studied Polish and Belarusian sites (Figure 4) and in the literature data. The typical passage at the Polish stations had one peak between the first (3 May) and the third (13 May) pentad of May. In most years this main migration peak lasted for two of these pentads, e.g. in 1994 at Mechelinki Meadows and in 2005 at Kwiecewo, but in some seasons intensive migration lasted even for over 4 pentads, as in 1996 at Mechelinki Meadows. This pattern was common in many places of Europe and at several other sites in Poland (Kuźniak & Lorek 1993, Meissner & Sikora 1995, Górski & Nowakowski 1998, 1999), in Denmark (Melfotte 1993), Germany (Bruch & Löschau 1973, Harenger et al. 1973, Kowalski 1985), Switzerland (Leuzinger & Jenni 1993), Romania (Sandor & Virginas 1998), Italy (Scebba & Moschetti 1996) and Greece (Akriotis 1991). The dates of this main peak were very similar at the studied sites and in other Central European wet-

lands with all peaks within the period 1–10 May (Figure 2). In some years and sites, e.g. at Turov in 2002 and 2005 and at Mechelinki Meadows in 1998, the passage had two migration peaks (Figure 4). In these cases the first migration peak occurred in the end of April and the second peak was observed in the second pentad of May, as the main peak in other years and stations.

In 1997 counts were done simultaneously at two sites in N Poland, Mechelinki Meadows and Drewnica Meadows (Figure 5). The daily spring migration pattern was generally similar, with two migration waves (Figure 5). The first wave at Mechelinki Meadows occurred 3–7 May, and at Drewnica Meadows 4–6 May. The second migration wave occurred 9–11 May at Mechelinki Meadows and two days later at Drewnica Meadows (11–12 May). However, the number of birds observed at Drewnica Meadows was slightly higher during the first than during the second peak, while at Mechelinki Meadows numbers during the second peak were about 2.5 times higher than during the first one. In 2005, when daily counts were conducted simultaneously at Kwiecewo and Turov, the migration pattern at these stations was very different (Figure 5). At

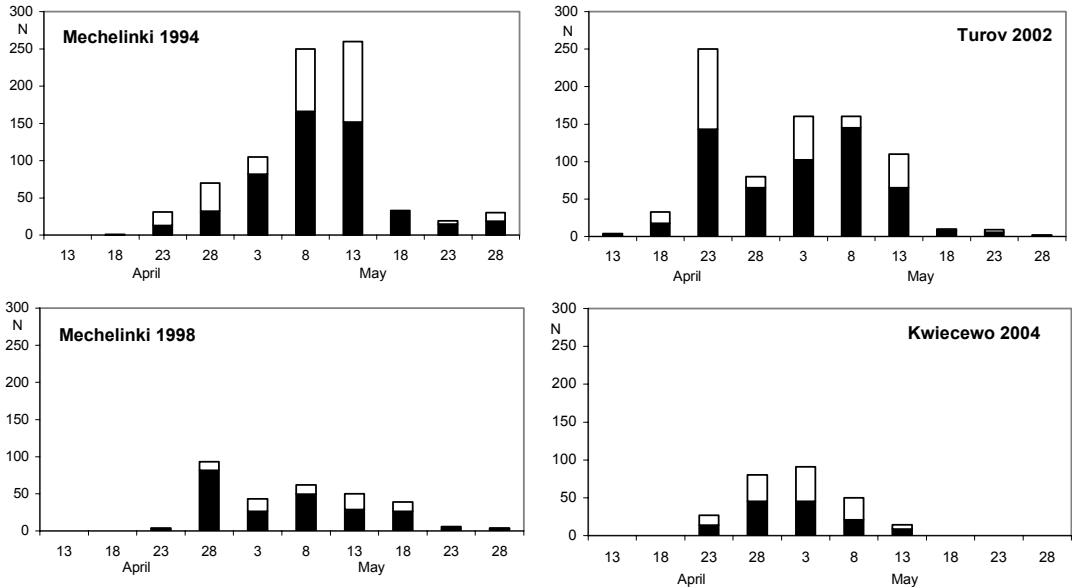


Figure 4. Pentad spring migration dynamics of Wood Sandpipers at selected sites and seasons in reference period (29 April–13 May). Black bars – mean number of birds observed in a pentad, white bars – maximum count in a pentad; pentads described by their middle dates.

Flyttningmönster under pentader på valda plaster och år under referensperioden (29 april–13 maj). Svarta staplar – medeltal fåglar i pentaden, vita staplar – maximalt antal under pentaden. Pentadn ange med dess medelddatum.

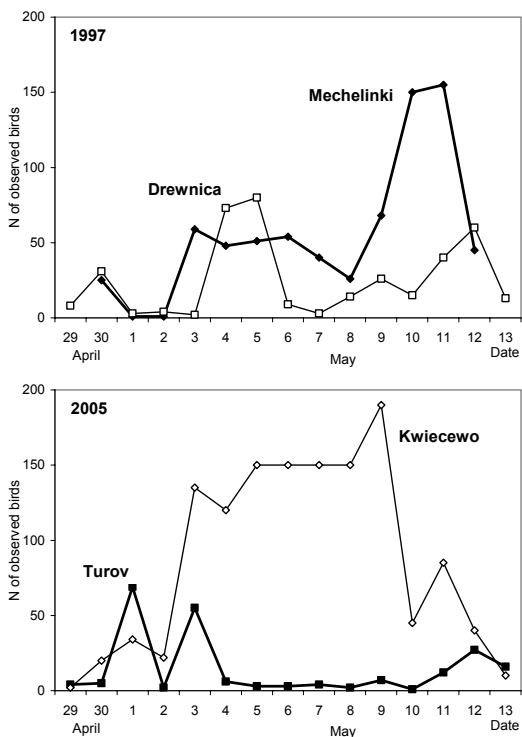


Figure 5. Comparison of daily migration dynamics at two sites working parallelly in 1997 (Mechelinki and Drewnica Meadows) and in 2005 (Kwiecewo and Turov).

Jämförelse mellan dagligt antal grönbenor på lokaler som bevakats samtidigt 1997 (Mechelinki och Drewnica) och 2005 (Kwiecewo och Turov).

Turov, the majority of migrants occurred between 29 April and 4 May and later migration intensity was very low; the second, small wave of migrants appeared between 11 and 14 May. At Kwiecewo, located ca 700 km to the west (Figure 1), the first migration started on 30 April and peaked between 3 and 9 May; the last small wave of migrants occurred on 11–13 May, as well as at Turov.

Discussion

Wood Sandpipers observed in spring throughout Europe are on their northwards passage from wintering grounds in the Mediterranean region and Africa south of the Sahara, towards breeding grounds in Fennoscandia, the Baltic countries and Western Russia (Myhrberg 1961, Glutz von Blotzheim et al. 1977, Lebedeva et al. 1985, Meissner 1997, Rem-

isiewicz 2005). Analysis of geographical location of the analysed European sites in relation to breeding grounds and distribution of ringing recoveries presented by Lebedeva et al. (1985), suggests that a higher proportion of Wood Sandpipers breeding in western Russia may be expected at the more eastern locations.

At most European wetlands, the passage had one main peak. Thus, this seems to be the most common pattern of Wood Sandpiper migration. Two peaks, similar to those noted at some Belarusian and Polish sites (Figure 4), have been observed only at few sites in Germany (Beitz 1985, Dierschke & Dierschke 1990, Pannach 1992), in Czech Republic (Fiala 1991) and Switzerland (Maumary et al. 1997). At these latter sites, data was pooled from many years. Occurrence of two peaks in such cases should be treated cautiously, because if timing of single peaks differs between seasons, pooled data may produce two peaks. However, in our data, analysed in separate seasons, the earlier April peak was evident in Turov and in one season at Mechelinki Meadows (Figure 4). These two migration peaks are too distant in time to reflect subsequent passage of males and females (Remisiewicz & Wennerberg 2006). Ringing recoveries show that through Western Europe Wood Sandpipers migrate almost exclusively to wintering areas in the Western Africa, while in Central and Eastern Europe migration routes are more to the east (Myhrberg 1961, Glutz von Blotzheim et al. 1977, Lebedeva et al. 1985, Meissner 1997, Bakken et al. 2003). Thus, the April peak, observed only at more eastern sites, might be formed by birds moving northward along the Eastern African migration flyway (Kam et al. 2004), and therefore not being represented in Western Europe. However, occurrence of two peaks in some seasons might also be an effect of weather, e.g. a delay caused by adverse conditions at earlier stages of migration.

The relatively late date of first arrival at SE Turkey (Figure 2) may indicate later passage of populations wintering in Asia Minor and East Africa, following the south-eastern migration route, suggested by ringing recoveries (Lebedeva et al. 1985). The time span between dates of the first arrival and the main migration peak in the south of Europe (in Bulgaria) was much greater than in the central part of the continent. The first broods of the Wood Sandpiper were observed in Belarus near Grodno already on 25 April (Nikiforov et al. 1989), while in other parts of the breeding range they occurred two to four weeks later. For example, in Karelia and near Ural, first broods were observed on 20–28

May (Kozlova 1961, Glutz von Blotzheim et al. 1977). Thus, it is possible that the very early migrants observed only in southern Europe may be the earliest breeders from the southern edge of the breeding range (Belarus or Ukraine), which do not occur on passage further north. The monthly span in the occurrence of earliest migrants in different regions of southern Europe would correspond with the monthly difference in dates of first broods between the western and the eastern part of the European breeding range of the Wood Sandpiper. However, analyses of dates of the earliest occurrence should be treated cautiously, as they can be biased by overlooking the first, usually single migrants, especially at stopover sites with irregular counts. Thus, such dates were not used here to estimate the migration speed.

Generally, spring migration of Wood Sandpipers through Europe lasts for ca 2.5 months and dates of first arrival show over two months difference between southern and northern Europe (Figure 2). Single birds (probably not breeding) remain for summer at stopover places outside the breeding range (e.g. Harengerdt et al. 1973, Nankinov et al. 1998). These individuals might be second-year birds that have abandoned breeding or were delayed on migration, as suggested for other wader species (Glutz von Blotzheim et al. 1977). The major wave of migrants, however, moves over Europe during only one month, and the calculated migration speed indicates a very quick northward migration at about 100 km/day. This value, however, should be treated only as a rough estimate because the wave of birds moves to the NE. The migration speed would be even higher if the true distance rather than latitude was considered in the calculation. Also the fact that the dates used came from different years would tend to make the estimated speed too low.

The fact that the majority of migrants pass through most Central European sites within just 10 days indicated that a very concentrated spring passage is typical of the Wood Sandpiper. Very similar median migration dates in Western, Central and Eastern Europe (Winkler & Herzig-Straschil 1981, Dierschke & Dierschke 1990, Pannach 1992, Sauvage 2000, Anthes et al. 2002, this study) and very close dates of occurrence of the main migration peak at all Central European sites (Figure 2) suggest that Wood Sandpipers migrate as a synchronised broad-front wave. Direct comparison of migration dates was difficult because in the majority of the cited papers only many-year averages were presented (e.g. Kowalski 1985, Harengerdt et al. 1973). However, similar dynamics and very close

dates of occurrence of main waves of migrants, observed at two sites in N Poland located ca 50 km apart (Figure 5), seem to confirm this synchronisation.

In spite of this concentration and regularity of migration timing, migration intensity (Table 2) and pentad course of migration dynamics varied greatly among seasons at the studied sites (Figures 3–5). This variability probably reflects the response of migrants to different conditions at given stopover sites and also during earlier stages of migration. Farmer & Wiens (1998) showed that in the Pectoral Sandpiper *Calidris melanotos*, a species also using inland stopover sites, spacing and quality of stopover sites can strongly influence the pattern of spring migration. Generally, numbers of waders using certain stopovers, strongly depend on actual environmental conditions offered by these sites (Piersma & Lindström 2004).

One of the most important factors that influence availability and quality of foraging places to migrant waders is water level at stopover sites, as indicated by changes in abundance, species diversity and migration phenology of waders at different water levels on e.g. the Lake Constance (Maumary et al. 1997) and the river Inn valley (Reichholf 1972). Among the sites we studied, daily migration dynamics of the Wood Sandpiper at Drewnica Meadows and changes of the water level in the Vistula river valley were clearly correlated in 1998, when the majority of passage occurred in the period of a medium water level (Ściborski 2000).

However, at this site in 1997 and 1999, no relation between water levels and migration course or intensity was found (Ściborski 2000), which suggests that other factors may also affect migration pattern observed at a certain site. Waders can be flexible in their selection of stopover sites, and their choice depends on the conditions that the site offers, such as predation pressure and food availability (Ydenberg et al. 2002, Gudmundsson et al. 1991). They also react quickly to changes in habitat quality (Wójcik et al. 1999), which has been described also in the Wood Sandpiper (Meissner 1997). This could be the case at Mechelinki Meadows where a remarkable decrease in the numbers of Wood Sandpipers was observed between 1994–1996 and 1997–2000. This decrease could have been an effect not only of a change of the water levels, but also of another habitat change. At this site, due both to low water levels and decrease of cattle grazing over the years, the wet meadows used by migrant waders gradually turned into reed beds (Meissner et al. 2004).

We show here that spring migration of the Wood

Sandpiper through Central Europe is very quick and condensed, yet characterised by great year-to-year variation in numbers of migrants observed at subsequent stopover sites. In general, spring migrants seem to be time selected, due to high costs of being late in breeding grounds (Myers 1981, Lyons & Haig 1995). For example, in Barnacle Geese reproductive success was correlated with the timing of spring migration and individuals departing from the final stopover site at intermediate dates achieved the highest success (Prop et al. 2003). Time minimized migration was suggested for many long-distance migrating waders (e.g. Farmer & Wiens 1999, Gudmundsson et al. 1991).

Waders migrating in spring from Africa across the European inland are not forced to use fixed refuelling sites like coastal waders, which depend strongly on intertidal habitats. In years when abundant food resources appear in many inland sites, some stopover sites may be skipped (Gudmundsson et al. 1991). Such flexibility could result in great differences of the number of migrants and migration pattern in a given site in subsequent seasons, as observed in the present study (Table 2, Figure 4).

It is also possible that, as found in the Bar-tailed Godwit *Limosa lapponica* (Scheiffarth et al. 2002) and Redshank *Tringa totanus* (Meissner 2000), Wood Sandpipers from southern and northern breeding populations have different migration routes and migration strategies due to different distances to cover between wintering and breeding grounds. However, ringing recoveries of Wood Sandpipers from wintering and breeding grounds and data on stopover ecology are too few to allow either confirmation or rejection of this hypothesis (Lebedeva et al. 1985, Underhill et al. 1999). Thus, further studies on migration strategies of this common, yet not very well known species are needed to solve this problem.

Acknowledgements

The paper was prepared thanks to the fellowship of the Józef Mianowski Fund – a Foundation for the Promotion of Science to Pavel Pinchuk. We are grateful to all colleagues who helped in the field-works at the WRG KULING and Turov ringing stations. We thank an anonymous reviewer whose comments helped to improve this paper. This is the paper no. 118 of the Waterbird Research Group KULING.

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Sammanfattning

Grönbenans vårflyttningsfenologi analyserades med hjälp av räkning av rastande grönbenor vid ett antal lokaler i Polen och Vitryssland. Även publicerad information analyserades. Totala antalet lokaler som analysen baseras på visas i Figur 1. Det var ett signifikant samband mellan latitude och datum för passage av vårsträcket (Figur 2), vilket tyder på att sträckfronten rör sig norr ut som en vågrörelse. Den genomsnittliga hastigheten på vårflyttningen var ca 100 km/dag. Normalt var sträckperioden vid en given lokal kort, med ca 50% av antalet grönbenor inom loppet av 6–10 dagar. Vissa år förekom en tvåtoppighet i passagen (Figur 4), vilket kan bero på olika tidsmässig passage mellan år, inslag av olika populationer eller väderfaktorer som fått sträcket att stanna upp. Mediandatum vid centraleuropeiska lokaler inföll mellan 3–15 maj (Figur 5). Flyttningsintensiteten varierade med en factor 2–3 mellan olika år. Faktorer som kan påverka antalet rastande grönbenor diskuteras. Även grönbenans generella flyttningsstrategi på våren diskuteras, och vi föreslår att grönbenan är en tidsminimerare.

Appendix 1. Locations of described Wood Sandpiper stopover sites and phenological records from these sites, used in analyses of relation of migration timing and geographical location of a site, and literature sources of the data used. Numbers of sites are the same as in Figures 1 and 2.

Läget för de beskrivna rastplatserna för grönbena och fenologiska observationer på dessa plaster, vilka använts i analyserna av flyttningens tidsschema i förhållande till platsens läge. Antalet lokaler är detsamma som i Figur 1 och 2.

No	Site, country	Latitude	Longitude	First arrival	Daily max.	Median date	Reference
	<i>Lokal, land</i>			<i>Första ankomst</i>	<i>Dagligt max.</i>	<i>Median-datum</i>	
1.	Çukurova deltas, TR	36°40'N	35°26'E	3 Apr	24 Apr		Berrevoets et al. 1994
2.	Valtos Psachnon, GR	38°30'N	23°40'E				Akriotis 1991
3.	Porto Lagos, GR	40°58'N	25°10'E	25 Mar			Nobel de et al. 1990
4.	Atanasovsko Lake, BU	42°35'N	27°30'E	15 Mar	1 May		Dalakchieva & Popov 2002
5.	Sofia, BU	42°45'N	23°15'E	24 Mar	5 May		Nankinov et al. 1998
6.	Draganic fishpond, CR	45°30'N	15°31'E	05 Mar			Radovic et al. 1999
7.	S-W Ukraine coast, UA	46°00'N	30°30'E	4 Apr			Chernichko et al. 1992
8.	Venoge River mouth, SU	46°30'N	06°32'E	10 Apr			Maumary et al. 1997
9.	Yverdon, SU	46°48'N	06°38'E	30 Mar			Baula & Sermet 1975
10.	Seewinkel, AT	48°35'N	13°40'E			9 May	Winkler & Herzig-Straschil 1981
11.	Hohenau-Ringelsdorf, AT	48°40'N	16°54'E				G. Wichmann, pers. com.
12.	Attigny, FR	49°28'N	04°35'E	13 Apr		6 May	Sauvage 2000
13.	Middle San, PL	50°00'N	23°14'E				Kunysz & Hordowski 1992
14.	Wroclaw, PL	51°05'N	17°00'E	10 Apr	6 May		Lonkowski et al. 1988
15.	Nörten-Hardenberg, DE	51°39'N	09°56'E	21 Apr	8 May	13 May	Dierschke & Dierschke 1990
16.	Zbiornik Wonieść, PL	51°55'N	16°42'E	19 Apr			Kuźniak & Lorek 1993
17.	Münster, DE	52°02'N	07°39'E			9 May	Anthes et al. 2002
18.	Turov, BY	52°04'N	27°44'E	15 Apr	2 May		our data våra data
19.	Braunshweig, DE	52°15'N	10°34'E		4 May	6 May	Pannach 1992
20.	Wizna, PL	53°12'N	22°24'E	13 Apr	14 May		Górski & Nowakowski 1999
21.	Schwedt, DE	53°15'N	14°00'E	3 Apr	6 May		Kube 1988
22.	Lübeck, DE	53°54'N	10°46'E	10 Apr	9 May		Kowalski 1985
23.	Kwieciewo, PL	53°57'N	20°19'E		9 May	1 May	our data våra data
24.	Nisko, PL	54°04'N	21°02'E	8 Apr	1 May	6 May	our data våra data
25.	Greifswalder Boden, DE	54°12'N	13°26'E		4 May		Teichmann & Conrad 1984
26.	Drewnica, PL	54°17'N	18°58'E		3 May	9 May	our data våra data
27.	Mechelinki, PL	54°37'N	18°31'E	15 Apr	10 May	8 May	our data våra data
28.	Aasla, FI	60°30'N	21°95'E				Asko Eriksson, pers. com.
29.	Yyteri, FI	61°30'N	21°30'E	7 May	15 May		Asko Eriksson, pers. com.
30.	Itä-Lapin, FI	67°20'N	28°12'E	23 Apr	23 May		Saari et al. 1998