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Differential migration strategies of the Wood Sandpiper (*Tringa glareola*) – genetic analyses reveal sex differences in morphology and spring migration phenology

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Sex and age differences in spring migration phenology were studied in the Wood Sandpiper – a monomorphic wader of inland wetlands. Birds were sexed by DNA analysis. During the rapid passage through NE Poland in 2003, the first males occurred 4 days before the first females. Thereafter both sexes were represented. Median migration dates were significantly earlier for males than for females among the older age group (2+ birds). A similar tendency was shown for second-year birds (2K). The sex differences can be explained by earlier arrival of males at the breeding grounds. Second-year birds migrated significantly later than older birds. Females were significantly larger than males in total head, tarsus plus toe, wing length and body mass. Total head length allowed for identification of a low proportion of 2+ males and females, but the other measurements did not allow reliable sexing because of size range overlaps between the sexes. Principle Component Analysis (PCA), where the 'body size coefficient' (PC1) combines three linear body measurements, slightly improved the accuracy of the sexing. Thus, genetic sexing of Wood Sandpipers is preferable. We recommend application of molecular sexing in studies of the behaviour of sex, age and population groups in monomorphic species.

1. Introduction

Bird migration is a time consuming and energy demanding activity and different migration strategies have evolved among birds. Many waders are extreme long-distance migrant birds, and thus, migration is an important part of their annual cycle. Migration strategies of waders differ among sex and age groups. Sex differences in migration phenology, moult, and strategy of fat accumulation occur in wader species breeding on the Arctic tundra and migrating to saltwater habitats, such as the Curlew Sandpiper *Calidris ferruginea,* Dunlin *C. alpina* and Bar-tailed Godwit *Limosa lapponica*, (Myers 1981, Gromadzka 1987, Figureola & Bertolero 1996, Chandler & Mulvhill 1990, Piersma & Jukema 1990, 1993, Wennerberg *et al.* 2001). Such dissimilarities are associated with their different breeding activities, and they probably reflect different life strategies (Figureola & Bertolero 1996, Piersma & Jukema 1990, 1993). However, among another ecological group of waders – those breeding in taiga and migrating (usually over inland areas) to freshwater habitats – this phenomenon has rarely been studied, with the notable exception of the Ruff *Philomachus pugnax*, in which migration routes differ between the sexes (Wymenga 1999). Differences between age groups in strategies of fat accumulation and phenology occur in Wood Sandpipers *Tringa glareola* during their autumn migration (Meissner 1997, Wichmann *et al.* 2004). Most of the cited papers consider species with well-pronounced plumage and/or size sexual dimorphism, while studies of differential migration of monomorphic wader species are lacking.

To investigate differential migration strategies in monomorphic waders in freshwater habitats, we chose the Wood Sandpiper as a model species. The Wood Sandpiper is an abundant migrant, widespread in spring and autumn over inland wetlands in most of Europe and Africa. During recent years this species has been the object of intensive investigations conducted by a network of European and African wader scientists and students within the "*Tringa glareola* 2000" project, coordinated by WRG KULING (Remisiewicz 2005). Thanks to the development of laboratory techniques, sex determination in birds, including waders, based on DNA analysis has become possible (e.g. Fridolfsson & Ellegren 1999, Griffiths *et al.* 1998, Wennerberg *et al.* 1999, Nebel *et al.* 2004). In this study, we apply molecular sexing techniques to Wood Sandpiper samples, and thereby reveal differences in spring migration phenology between females and males.

We also analyse biometric characters of genetically sexed birds, and discuss tools for the sexing of this species.

Fig. 1. Location of the study site, Nisko, in NE Poland.

2. Material and methods

2.1. Field work

Wood Sandpipers were caught between 27 April and 14 May 2003 near the village of Nisko in NE Poland (53°50'N, 20°20'E; Fig. 1) by the Waterbird Research Group KULING. The catching period covered the whole, quick and rapid, spring migration of Wood Sandpiper in this region. The study site is a wetland, flooded in spring by the small river Sajna, covered with reedbed, rush and aquatic vegetation. This area is an especially attractive stopover site for waders in spring, providing ideal foraging habitat on a floating layer of old plant material in shallow water (M. Krupa, M. Ściborski, R. Krupa, R. Popis & J. Wołoszyn, in prep.). Wood Sandpipers were caught in walk-in traps (according to Meisnner 1998) or in mist-nets placed over the wetland.

All caught birds (N=389) were aged according to criteria given by Prater *et al.* (1977). Second-year birds (age: 2K) were identified by the presence of juvenile-type inner median coverts, or by the pattern of their primary wear. However, not all second-year birds can be identified according to these features, so the older age category (age: 2+) may also include some non-identified 2K birds.

From each bird, a standard set of measurements was taken, including total head length (measured with 0.1 mm accuracy; Green 1980), length of tarsus+toe (to 1 mm; Piersma 1984), wing length (to 1 mm, Evans 1986); and body mass (to 1 g). The three ringers that measured the birds (including MR) were calibrated in previous years and changed randomly during the study season. Blood samples were taken from randomly selected birds throughout the spring migration season (120 individuals in total), 50–100 µl of blood was taken from the underwing vein, added to TE buffer (10 mM TRIS HCL, 0.1 mM EDTA), frozen to –5°C, and stored at –70°C until laboratory analyses.

2.2. Laboratory methods

DNA was extracted using the Blood Mini Kit (A&A Biotechnology). Specific amplification of the chromo-helicase-DNA-binding (CHD) gene was performed using primers P2 and P8 according to Griffiths *et al*. (1998). Polymerase chain reactions (PCR) were run with 2–4 µl of DNA template in 15 µl volumes according to the procedure described by Wennerberg *et al*. (2002). The thermic profile included an initial denaturation step of 94°C for 2 min, 40 cycles of [94°C for 30 sec, 50°C for 30 sec, 72°C for 45 sec] and a final elongation step of 72°C for 5 min. $MgCl_2$ concentration was optimised to 2.5 mM. AmpliTaq Polymerase, 0.4 mM dNTP and PCR Buffer II (Applied Biosystems) were used for half of the samples. Then, costs were reduced by shifting to Jump Start Red Taq Ready Mix (Sigma-Aldrich), which gave identical results. PCR products were run on 2–3.5% agarose gels where sex-specific patterns of electropohoretic bands were obtained: two bands for females (Z and W chromosomes) and one band for males (ZZ).

2.3. Data analysis

Field data of all ringed birds (sexed and non-sexed) were analysed and used for comparing migration phenology and biometric measurements between sex and age groups. Comparisons of spring migration phenology between age categories were performed in two ways: for genetically sexed birds (analysing males and females separately), and for all 389 ringed birds (sexes pooled). In analyses of migration dates, non-parametric tests were used (Mann-Whitney U-test and Spearman rank correlation), while in comparisons of body measurements t-tests were applied. Analysis of biometric characters by Principle Component Analysis (PCA; Zar 1999) was performed for 2+ birds only. Three individuals of this age class were excluded because standardised residuals of their linear measurements exceeded 3δ, which indicated possible measurement errors in the field (Stanisz 2001) which cause bias in PCA analysis. The two age classes were not jointly treated in PCA, because 2K females had a smaller total head and tarsus + toe length (t-test: $t = 2.14$, $P < 0.05$) than 2+ females. There were too few 2K females to allow a separate PCA for this age class. All statistic analyses were performed using the Statistica 6.0 software package.

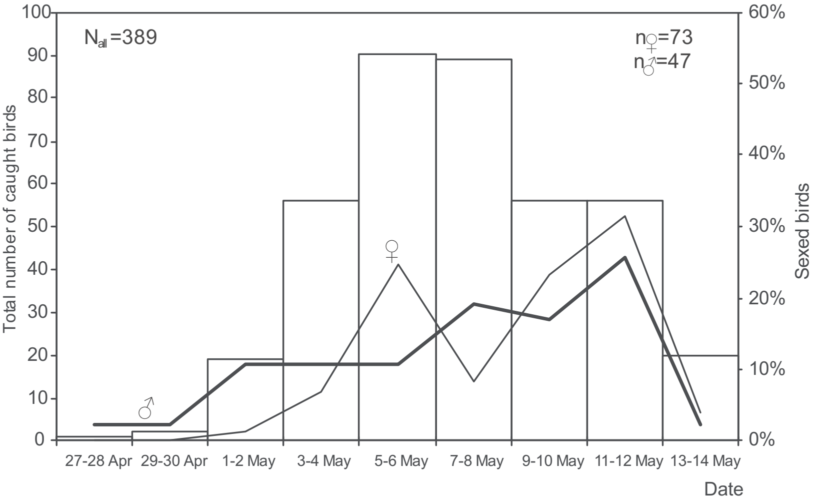

Fig. 2. Spring migration dynamics and percent of females and males among Wood Sandpipers at Nisko (Poland) in 2003. Data grouped in two-day periods. Bars – all ringed birds; thick line – females and thin line – males, respectively.

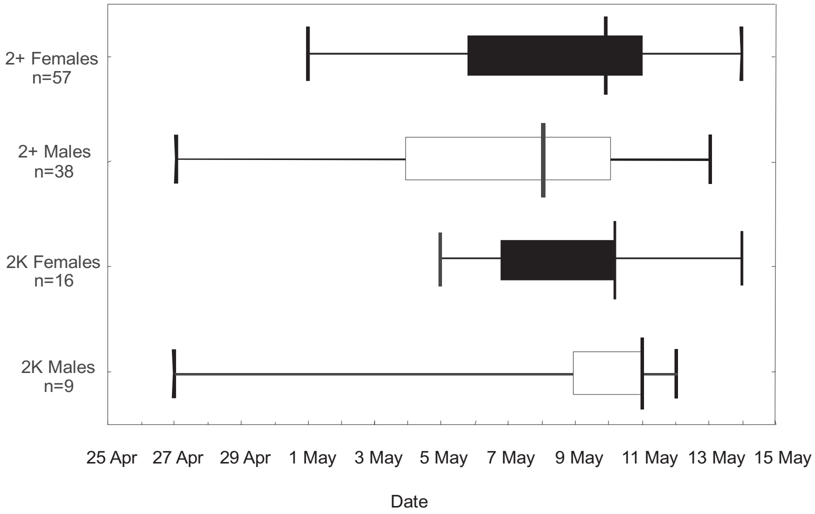

Fig. 3. Spring migration phenology of females and males, separated by age categories. Vertical lines – median date of migration, boxes – 25–75% of all birds, horizontal line – first to last occurrence. 2K – birds in second year of life, 2+ – birds of older age category (see the text), sample sizes are shown to the left of bars.

3. Results

3.1. Migration phenology

The very first migrants, which appeared in the study area already at the end of April, were males while the first females occurred 4 days later, at the beginning of May. The detailed course of migration dynamics of Wood Sandpipers shows that males predominate among migrants in the beginning of the spring season (Fig. 2). The migration peak in early May was formed by both sexes, with a slight prevalence of females. Passage of both sexes lasted until the end of the migration season in mid-May (Fig. 2).

Comparison of migration phenology for each

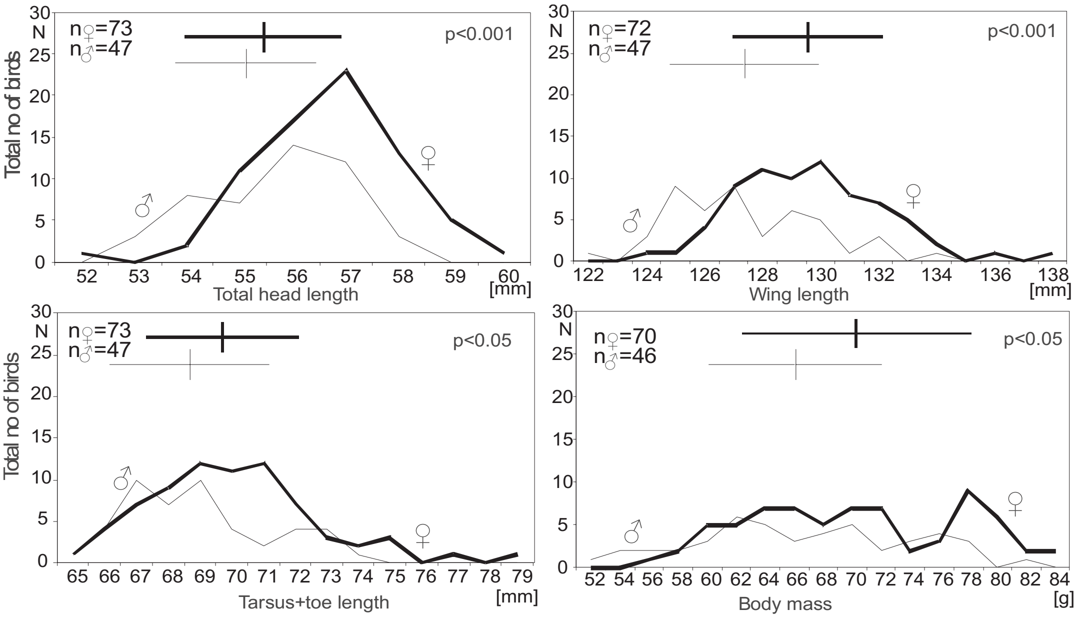

Fig. 4. Distributions and mean values of total head length, tarsus+toe length, wing length and body mass for female (thick lines) and male (thin lines) Wood Sandpipers. Vertical lines – mean values, horizontal lines – + SD.

age class separately showed that among 2+ birds, males migrated on average 2 days earlier than females (median dates, Fig. 3), and the difference was significant (Mann-Whitney U-test: U = 800, P < 0.05). Among the 2K birds, although the first males came 5 days before the females, their median dates of migration were not significantly different (Mann-Whitney U-test: U = 62, P – n.s.).

In males, a tendency for differences in timing of migration between age groups was observed (Mann-Whitney U-test: U = 106, P = 0.08), with the median arrival date of 2K males being 3 days later than that of 2+ males (Fig. 3). For females, the median dates of the two age classes were identical. Comparison of migration phenology based on all caught birds showed a significant difference between age classes: 2K birds migrated on average 2 days later (median date – 9 May) than 2+ birds (median date – 7 May, Mann-Whitney U-test: U = 7703, P < 0.0001).

3.2. Biometric differences between sexes

Females proved to be larger than males, although ranges of all body measurements overlapped between the sexes (Fig. 4). This shift in distributions of measurements between sexes is shown by statistically highly significant differences in mean values. The females had wings over 2 mm longer than males (t-test: t = 4.69, P < 0.001) and total head length almost 1 mm greater than males (t-test: t = 3.55, P < 0.001). The length of tarsus + toe also differed significantly (t-test: t = 2.28, P < 0.05). Females had on an average nearly 1 mm longer tarsus + toe. Females were also significantly heavier than males (t-test: t = 2.52, P < 0.05).

For 2K birds, none of the body measurements allowed for sex identification – ranges overlapped completely. However, in the 2+ age category, the distributions of all three morphological measurements of females and males were shifted to some extent. Among the three parameters, this was most pronounced in the total head length, where the

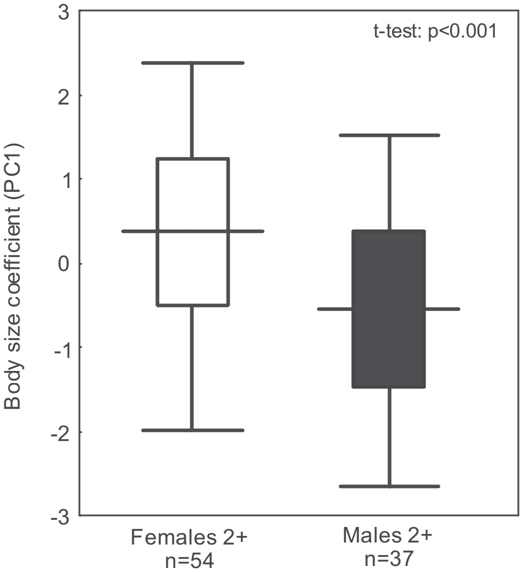

Fig. 5. Comparison of body size factor (PC1) between females and males of Wood Sandpipers aged as 2+. Horizontal lines – mean values, boxes – + SD, vertical line – range.

Table 1. Comparison of the efficiency of different morphological parameters for sexing of Wood Sandpipers, age 2+, caught at Nisko (Poland) during spring migration. Birds are assigned to two theoretical sex groups as distinguished by dividing the overall distribution of each body size parameter by its median, and assuming birds greater than this value to be females and smaller to be males. Then, the proportion of birds accurately sexed is verified by DNA analysis, and results for the efficiency of each morphological parameter for sexing shown in the table.

Measurement	N	Median	Prop. of females among large birds	Prop. of males among small birds	Total % of correctly sexed birds
Tarsus + toe length (mm)	92	77	70%	43%	49%
Total head length (mm)	92	56	72%	60%	67%
Wing length (mm)	91	128	76%	58%	67%
PC1	91	–0.14	81%	69%	76%

measurements for 16% (9 individuals) of 2+ females were longer than the greatest male (> 58.0 mm) and 8% (3 individuals) of males were shorter than the smallest female (< 53.7 mm).

We checked whether combining the measurements into one parameter could give higher resolution. Thus, the three body measurements of all 2+ birds were combined by Principle Component Analysis (PCA). One significant factor (PC1), reflecting the body size of the birds, was obtained with the loadings for each variable as follows: total head length (THL) = 0.72, tarsus + toe length (T+T) = 0.83, wing length (WL) = 0.64. Based on these three measurements, the 'body size coefficient' (PC1) was calculated according to the equation $PC1_{THL,T+T,WL} = (0.44 * THL) + (0.51 * T+T) + (0.39 * WL)$.

The coefficient of determination (R^2) for this equation was 0.54, which indicates that it describes body size satisfactorily. Comparison of PC1 between the sexes again showed that females were on an average larger than males (Fig. 5), and the difference in their body size was highly significant (t-test; $t = 4.83$, $P < 0.001$).

To compare the applicability of body measurements and PC1 for sexing Wood Sandpipers (age 2+), we divided the overall distribution of each parameter into two parts by its middle value and calculated the percentage of females among birds larger than and of males smaller than this value (Table 1). This shows that the PC1 is more effective in sexing Wood Sandpipers than any single measurement, with an accuracy of 76%. The best single parameters are total head length and wing length, with an overall accuracy of 67% in each case.

3.3. Relationship between body size and migration phenology

We checked for passage of morphologically different populations by testing if there was any relationship between the date of migration and the size of the birds, as described by the principle component calculated for three body measurements (PC1). This analysis was performed only for 2+ birds and for each sex separately. Correlation coefficients were negligible, and no correlation between body size and timing of migration was found (females: $r_S = 0.16$, P – n.s.; males: $r_S = -0.06$, P – n.s.).

Body mass was positively correlated with the date of migration in females ($r_S = 0.48$, $P < 0.05$). In males, such correlation was not found ($r_S = 0.13$, P – n.s.). However, the body mass and body size factor PC1 were not correlated in either females ($r_S = 0.09$, P – n.s.) or males ($r_S = 0.17$, P – n.s.). Regression analysis of the body mass of females against their date of migration provided the regression equation BODY MASS = 1.08 × DATE – 40744.9 ($R^2 = 0.24$, $P < 0.001$), which showed that the weight of females increased on average 1.1 g per day. The weight of the earliest arriving females (1 May), estimated according to this equation, was 62.4 g, while the last arrivals (14 May) weighed approximately 76.4 g.

4. Discussion

4.1. Migration phenology

The spring migration course of Wood Sandpipers found in this study (Fig. 2) was very similar to other stopover sites in Central Europe (e.g. Ściborski 2000, Anthes *et al.* 2002, G. Wichmann – unpubl. data). However, in the study site, both in 2003 and previous years, the proportion of retraps was high (ca 4% of all caught Wood Sandpipers) in comparison with other spring ringing sites in Poland and Belarus (M. Remisiewicz, W. Meissner, P. Pinchuk & M. Ściborski, in prep.). This indicates that this place is not an "emergency refuelling site" (Meissner 2001), but a traditional stopover site, providing reliable feeding conditions from year to year.

The differences revealed in timing of migration between males and females (Figs 2 and 3) can be explained by the mating system of the Wood Sandpiper. This species is seasonally monogamous and males arrive first at breeding grounds and hold territories. Females come later and select a mate among territorial males (Kozlova 1961, Cramp & Simmons 1983, Piersma *et al.* 1996). The observed pattern of spring migration of the sexes, with males as the earliest migrants, has been observed in other wader species where males are territorial and display to attract females, e.g. the Ruff (Wymenga 1999) and Bar-tailed Godwit

(Piersma & Jukema 1990). In our results, the uneven sex ratio is well-pronounced only at the beginning of the spring season (Fig. 2). This could be explained by the fact that northern Poland is crossed by Wood Sandpiper populations migrating to different breeding regions, including Sweden, Finland, the Baltic States and Russia, as shown by ringing recoveries and resightings of colour-ringed birds (Myhrberg 1961, Lebedeva *et al.* 1985, Meissner 1997, Remisiewicz 2005). Possibly, the earliest males that occurred at the study site belong to the earliest breeding populations, for example Fennoscandian, where egg laying begins on average in mid-May (Glutz *et al.* 1977). The latest migrants encountered at the study site could still reach more distant breeding grounds in western Russia, where the displays start at the turn of May and June (Kozlova 1961), on time.

An interesting result was found regarding a difference in timing of migration of Wood Sandpipers on their first spring migration (2K birds) and adults (2+ birds), presented in Fig. 3. A delayed passage of 2K birds in relation to 2+ ones was also found in the larger non-sexed sample. One of the main reasons causing delay of spring migration in2K birds can be that young birds are less experienced and therefore migrate slower or with lower fat stores than adults and, in effect, arrive later at stopover sites and breeding areas, as suggested by Hockey *et al.* (1988). Lower feeding efficiency of immature Wood Sandpipers in comparison with adults during autumn migration, demonstrated by their lower body mass and higher proportion among retraps, was described by Wichmann *et al.* (2004). Thus, less experience in foraging and perhaps in choice of favourable stopover sites during spring migration could explain the later migration through the study site of 2K birds than of older individuals. There may be other additional causes of these age and sex differences in the timing of migration, as described in other waders, for example differences between second-year birds and older birds in their tendency to defer spring migration (Myers 1981, Summers *et al.* 1995, Hockey *et al.* 1998).

The lack of correlation between the body size coefficient (PC1) and date of migration indicated that during spring migration no sequential passage of morphologically different breeding populations took place. This could be caused by mixing of birds from different breeding populations, mentioned above, during quick spring passage at the study site. It could also result from a lack of clear biometric differences between the western and the eastern populations claimed by Cramp & Simmons (1983). The increase in body mass with the progress of the season stated in females, along with the lack of a corresponding tendency in the body size factor PC1 in either of the sexes, suggests that this reflects higher fat loads of females that arrive at the study area later in spring. This increase amounts to as much as ca 20% of the body mass of an average female in the study site (70.7 g). The difference in the pattern of body mass increase between females and males may indicate sex differences in the strategy of fat accumulation. As described for Bar-tailed Godwits (Piersma & Jukema 1993), Wood Sandpiper males might rather invest their energy reserves in quick migration and development of breeding plumage, while females might increase fat deposits as the season progresses in order to be ready for egg laying. It is also likely that high body mass in females caught at the stopover site at the end of migration period, close to egg laying, may be due to the advanced development of their egg follicles.

4.2. Biometric differences between the sexes

Several literature sources provide evidence for differences in body measurements between male and female Wood Sandpipers, showing reversed sexual dimorphism with females being the bigger sex (Dementev *et al.* 1951, Hoffmann 1957, Kozlova 1961, Prater *et al.* 1977, Cramp & Simmons 1983, Glutz *et al.* 1997). However, all the available data on the biometry of sexed individuals come from measurements of museum skins. For each of the body characters – wing, tail, bill, tarsus, toe length (op. cit.) – extensive overlaps of measurement ranges for males and females occur, not allowing for sex determination based on any single linear measurement, although in some cases the differences in mean values between the sexes proved significant (Cramp & Simmons 1983). The results of the present study are in accordance with the literature data, and in addition, we avoid the problems associated with museum specimens (shrinkage etc) by using field data.

Table 2. Comparison of wing length of females and males between literature data and our study. Measurements of live birds are marked with an asterisk, the remaining data come from museum skins; *ad* denotes adult birds (2+, i.e. second year or older) caught on autumn migration, in other sources ages are not specified.

Sex	Mean (mm)	SD	Range (mm)	n	Difference in mean (mm)	Source
F	124	–	120–129	57	2	Dementev *et al*. (1951)
M	122	–	119–129	87		
F	–	–	119.0–130.2	–	–	Kozlova (1961)
M	–	–	117.0–126.0	–		
F *ad*	127.2	–	123–131	12	1.6	Prater *et al*. (1977)
M *ad*	125.6	–	120–131	23		
F	128.5	3.8	123.5–133.5	12	2.8	Glutz *et al*. (1977)
M	125.7	2.6	117.5–129	26		
F *ad*	129	2.82	125–137	63	3	Cramp & Simmons (1983)
M *ad*	126	2.68	121–130	52		
F	129.6	2.55	124–134	72	2.2	Our study*
M	127.4	2.55	122–134	47		

Direct comparison of the biometric results obtained for sexed birds with the literature data is possible only for wing length (Table 2). It should be borne in mind that wing length measurements taken from museum skins can depart from those taken from live birds by 1 mm (Prater *et al*. 1977) to 4 mm (Hoffmann 1957). The methods of measurement could also be different, especially for data given in older sources. Despite differences in ranges and mean values provided by the literature, the relative differences in wing length between the sexes remain at the level of 2–3 mm, with females having longer wings on average in all studies.

For the remaining two body features analysed in the present paper, it is only possible to make the comparison with literature data based on both sexes combined (Table 3). For total head length, the mean values are very close and the ranges are similar in all compared locations. For tarsus+toe length measurements, the mean values are almost identical for birds caught in Israel and in the two regions of Poland. Among the spring migrants, a higher proportion of eastern-breeding birds can be expected in Israel than in Poland, as suggested by ringing recoveries (Lebedeva *et al.* 1985). Thus, the correspondence of these measurements would

Table 3. Comparison of total head length and tarsus + toe measurements for Wood Sandpipers (both sexes pooled) caught during spring migration in 2003 (our study) and described in literature.

Site	Mean (mm) ± SD	Range (mm)	N	Source
Total head length (mm)				
Eilat, Israel	55.4 ± 2.6	49–61	32	Yosef *et al*. (2002)
Gulf of Gdańsk, N Poland	55.8 ± 1.4	50.6–60.2	955	Ściborski (2000)
Löddesnäs, SW Sweden	55.9 ± 1.3	52.6–58.5	43	Persson (1998)
Nisko, NE Poland	56.3 ± 1.5	52.4–59.6	120	our study
Tarsus + toe (mm)				
Eilat, Israel	69.2 ± 4.9	53–77	33	Yosef *et al*. (2002)
Gulf of Gdańsk, N Poland	69.5 ± 2.7	63–79	144	Ściborski (2000)
Nisko, NE Poland	69.8 ± 2.6	66–79	120	our study

be in accordance with Cramp and Simmons' (1983) statement of no biometrical differences between western and eastern breeding populations of Wood Sandpipers.

The literature data, as well as the results presented here, show that the wing length or body size coefficient (PC1) could have application in sex identification in this species – a proportion of individuals at the extremes of the distributions can be sexed in this way. Significant differences between sexes in all analysed body measurement values suggest that their combination may enable us to provide a discriminant function to improve morphometric sex identification of live birds caught on migration. However, molecular genetic sexing of blood samples (or feathers) is still preferable and works nicely in this species.

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Liron (*Tringa glareola*) muuttostrategiat – sukupuolten välisiä eroja morfologiassa ja kevätmuuton fenologiassa

Kosteikoilla pesivän liron sukupuolen ja iän vaikutusta kevätmuuton fenologiaan tutkittiin Koillis-Puolassa 2003 alueilla, joilla liro on läpimuuttaja. Sukupuoli määritettiin DNA-analyysin avulla. Ensimmäiset koiraat saapuivat 4 päivää ennen ensimmäisiä naaraita. Tämän jälkeen alueella tavattiin molempia sukupuolia. Kaksivuotiailla tai vanhemmilla (+2kv) linnuilla koiraat muuttivat aiemmin kuin naaraat. Samanlainen suuntaus oli myös vuoden (2kv) ikäisillä linnuilla. Sukupuolten väliset erot fenologiassa selittyvät koiraiden aikaisemmalla saapumisella pesimisalueille. Vuoden ikäiset linnut muuttivat myöhemmin kuin vanhemmat linnut. Naaraat olivat koiraita suurempia (pään pituus, tarsuksen ja varpaan pituus, siiven pituus ja massa). Pään pituuden perusteella saatiin selville pieni osuus +2kv linnuista, mutta muut ruumiin mitat eivät kelvanneet sukupuolten määrittämiseen. Peruskomponenttianalyysi (PCA, eng. Principle Component Analysis), jossa yhdistettiin kolme pituusmittaa, paransi hieman sukupuolen määrittämisen tarkkuutta. Tästä huolimatta DNA-tekniikkaan perustuva sukupuolenmääritys on suositeltavaa liron kaltaisilla lajeilla, joilla sukupuolten välillä ei ole suuria eroja.

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