

Sexual dimorphism in size and plumage in adult Curlew Sandpipers (*Calidris ferruginea*) migrating in autumn through the Baltic Sea region

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The Curlew Sandpiper (*Calidris ferruginea*) displays sexual dimorphism in size and in breeding plumage. We analysed biometric and plumage characteristics in adult Curlew Sandpipers and proposed a protocol for sexing individuals, with the use of the discriminant function analysis. We measured 222 females and 164 males captured during autumn migration on the southern Baltic coast, among which 92 females and 84 males were photographed for analysis of plumage characteristics. All birds were sexed with molecular methods. Females were larger than males in all body measurements. Bill length was the most dimorphic trait, and the most effective function with bill length as a single predictor correctly identified the sex of 82.1% of birds. A similar function was described by Wymenga *et al.* 1990, yet there is an ambiguity in the description of those methods. The effectiveness of the previously published discriminant function was lower compared to the discriminant functions obtained in this study. Males were more rufous and less barred on breast and underparts than females. Yet the relationship between these two traits was weak as 62.7% of females and 89.5% of males were found in an overlapping zone. Moreover, we found that some individuals showed plumage features that were typical for the opposite sex. This indicates that sexing of adult Curlew Sandpipers based on their plumage characteristics is less reliable than with the use of discriminant functions. Discriminant functions not only allows for sexing birds throughout the annual cycle (including periods when both sexes are indistinguishable based on plumage traits), but also can be applied to archival data of birds measured in the past.



1. Introduction

All distinct differences in appearance between males and females of the same species are termed as sexual dimorphism. It applies both to variation in colour and ornamentation as well as in body size (Bennett & Owens 2002, Berns 2013). Evolution of sexual dimorphism is driven mainly by sexual

selection that maximizes reproductive success (Székely *et al.* 2000, Sandercock 2001, Blonder *et al.* 2002). Both sexes can increase reproductive success by becoming more attractive to the opposite sex or by physically improving access to potential mates (Berns 2013). Alternatively, sexual dimorphism might have evolved from ecological mechanisms such as competition for resources

leading to ecological niche differentiation between sexes (Szekely *et al.* 2000, Sandercock 2001).

Wader species exhibit different levels of sexual dimorphism – from highly dimorphic species like the Ruff (*Calidris pugnax*) and Greater Painted-Snipe (*Rostratula bengalensis*) to monomorphic species like the Kittlitz's Plover (*Charadrius pecuarius*) and the White-fronted Plover (*Charadrius marginatus*) (Hayman *et al.* 1987, Zefania *et al.* 2010, Meissner *et al.* 2011), but the majority of species from the suborder *Charadrii* present distinct reversed sexual size dimorphism in which females are larger than males and weakly pronounced sexual dichromatism in plumage (Glutz von Blotzheim *et al.* 1975, Cramp & Simmons 1983, Meissner & Pilacka 2008, Jiménez *et al.* 2015, Meissner & Krupa 2016, Niemc *et al.* 2018, Zhu *et al.* 2020). While a number of hypotheses aiming to explain the evolution and ecological importance of reversed sexual size dimorphism in waders have been proposed (Jönsson & Alterstam 1990; Figuerola 1999, Szekely *et al.* 2000, Sandercock 2001), sexual dimorphism in plumage in this group seems more complex and understudied (Schroeder *et al.* 2008, Blizzard & Pruett-Jones 2017).

Despite a lack of differences in appearance between males and females in some monomorphic species, ecological, behavioural and physiological disparities between two sexes are often observed. Differences between the sexes include foraging strategy and selection of feeding areas (Puttick 1981, Catry *et al.* 2012), phenology and strategy of migration (Figuerola & Bertolero 1998, Remisiewicz & Wennerberg 2006, Meissner & Krupa 2017), physiological response to stressors (van der Meer & van Oers 2015), or variation in level of hematological parameters (Jakubas *et al.* 2013). Thus, correct assignment to sex of an individual is crucial in both research projects that include sex of individuals as a factor influencing species biology (Lewis *et al.* 2002, Bush *et al.* 2011) as well as in species conservation programmes (Bosé *et al.* 2007, Jensen *et al.* 2012).

Among different methods for sex identification in birds, molecular sexing provides the best accuracy (Dubiec & Zagalska-Neubauer 2006, Morinha *et al.* 2012, but see Casey *et al.* 2009), but requires specialized equipment and collection of

DNA samples. Therefore, the development of non-molecular procedures, that provide reliable sex identification based on morphological characteristics is still necessary. The analysis based on a discriminant function, which allows using a combination of morphological measurements to predict bird's sex with a known probability, is becoming increasingly popular among researchers (e.g., van Franeker & Ter Braak 1993, Sikora & Dubiec 2007, Lislevand *et al.* 2009, Herring *et al.* 2010, Meissner *et al.* 2018, Niemc *et al.* 2018). Although a large sample of birds with known sex is needed for developing such discriminant function, it provides a simple, inexpensive and effective method of sex identification in avian species with sexual dimorphism (Dechaume-Moncharmont *et al.* 2011).

The Curlew Sandpiper (*Calidris ferruginea*) is a medium-sized wader showing sexual dimorphism both in size and plumage (Glutz von Blotzheim *et al.* 1975, Cramp & Simmons 1983). This species exhibits reversed sexual size dimorphism, with bill length being the most useful linear body measurement for sexing this species, as females have distinctly longer bill than males (Glutz von Blotzheim *et al.* 1975, Cramp & Simmons 1983). The current method for sexing Curlew Sandpipers using a discrimination function was developed by Wymenga *et al.* (1990) from measurements of museum specimens, and has been widely applied (Figuerola & Bertolero 1995, Melter & Kepp 2006, Barshep *et al.* 2011, Barshep *et al.* 2012). Wymenga *et al.* (1990) do not, however, offer error rates associated with their methodology, nor is there information on the sample size of birds used in their analysis. Discriminant functions calculated on small sample size may lead to biased results (Dechaume-Moncharmont *et al.* 2011). Hence, possible error in applying procedure proposed by Wymenga *et al.* (1990) for determining the sex of adult Curlew Sandpipers remains unknown.

Breeding plumage characteristics may be also used for sexing Curlew Sandpipers. In males, deeply coloured rufous feathers cover body from head to underparts, whereas females tend to have less uniform and not so deep rufous plumage with dark bars formed by darker tips of body feathers and paler heads compared to males (Kozlova 1962, Glutz von Blotzheim *et al.* 1975, Cramp &

Simmons 1983) (Fig. S1). Although within a breeding pair those differences in plumage allow sexing birds with almost certainty (Portenko 1959, Holmes & Pitelka 1964), some individuals captured during autumn and spring migration show intermediate plumage characteristic (Keijl 2006, authors' unpublished data), which impedes sexing of individuals of this species based on plumage traits. Moreover, in this species the moult of body feathers overlaps with migration, birds undergo moult from breeding to winter plumage from July till October (Portenko 1959, Hirschfeld *et al.* 1996, Khomenko & Diadicheva 1999). Therefore, in this period sexing of Curlew Sandpipers according to plumage characteristics may become ambiguous, as the sexes are indistinguishable based on plumage characteristics alone during winter. Moreover, for this reason sexing this species on wintering grounds based on plumage traits is impossible (Glutz von Blotzheim *et al.* 1975, Cramp & Simmons 1983).

The main aim of this study is to develop a non-invasive method for sexing adult Curlew Sandpipers based on linear body measurements and plumage characteristics, which enables to estimate the sex ratio in a studied population with a certain level of accuracy without necessity of using molecular methods. Moreover, we wanted to compare the results of our study to those of Wymenga *et al.* (1990). We also aimed to verify whether plumage characteristics may be used as an alternative method for biometrics analysis in sex determination of adult Curlew Sandpipers during autumn migration.

2. Materials and methods

2.1. Fieldwork

The study was conducted in the Vistula Mouth at the Gulf of Gdańsk (southern Baltic coast), Poland (54°21'N, 18°57'E). Birds were captured in walk-in traps (Busse & Meissner 2015) from the beginning of July to the end of August in 2009–2018. This period covers entire autumn migration of adult Curlew Sandpipers through the study area (Meissner 2006). Only individuals older than two calendar years (Prater *et al.* 1977) were included in the analyses and these comprised 222 females and

164 males. The following measurements were taken: total head length, bill length, tarsus length, all measured with callipers to the nearest 0.1 mm, as well as wing length and tarsus plus toe length, all measured with a ruler to the nearest 1 mm (Busse & Meissner 2015).

For plumage characteristics assessment 92 females and 84 males were photographed on the white background in such position that underparts, breast, neck and side of head were visible. Before the pictures were taken, the bird's feathers were arranged in a way that reflected undisturbed appearance of plumage. The photos were taken with different models of digital cameras always working in AUTO mode. All photos were saved as JPEG files. To sex birds with molecular methods, blood samples of about 50 µl were taken from the brachial vein of each individual. Blood was stored in 70% ethanol till further laboratory analyses. Blood samples were taken in accordance with the permission of the Local Ethics Committee no. 40/2015.

2.2. Laboratory work

Blood samples were placed on tissue-paper for ethanol to evaporate. From the samples prepared in that way, DNA was isolated with Blood Mini DNA kit (A&A Biotechnology, Gdynia, Poland) following the manufacturer's protocol. Extracted DNA was stored in refrigerator till further analyses. The W- and Z- linked sequences of sex chromosomes were amplified with 2602F/2669R primers (van der Velde *et al.* 2017). Each 9.78 µl PCR sample contained: 1.8 µl of DNA, 0.6 µl of 10 µM of each primer, 1.8 µl of sterile-filtered water, 0.5 µl of 25 µM solution of MgCl₂, 4.5 µl of Sigma REDTaq Ready-Mix (Sigma-Aldrich). The PCR protocol included an initial denaturation at 94°C for 2 min, followed by 40 cycles: denaturation at 94°C for 30 seconds, annealing at 62°C for 55 seconds, elongation at 72°C for 2 minutes. A final elongation step was performed at 72°C for 5 minutes. PCR products were separated in 30 minutes long electrophoresis at 80mA and 300V with a 2% agarose gel stained with 5 µl of Midori Green (ABO, Gdańsk, Poland). In the case of two exceptionally small females and three large males, their sex was doublechecked and confirmed with the

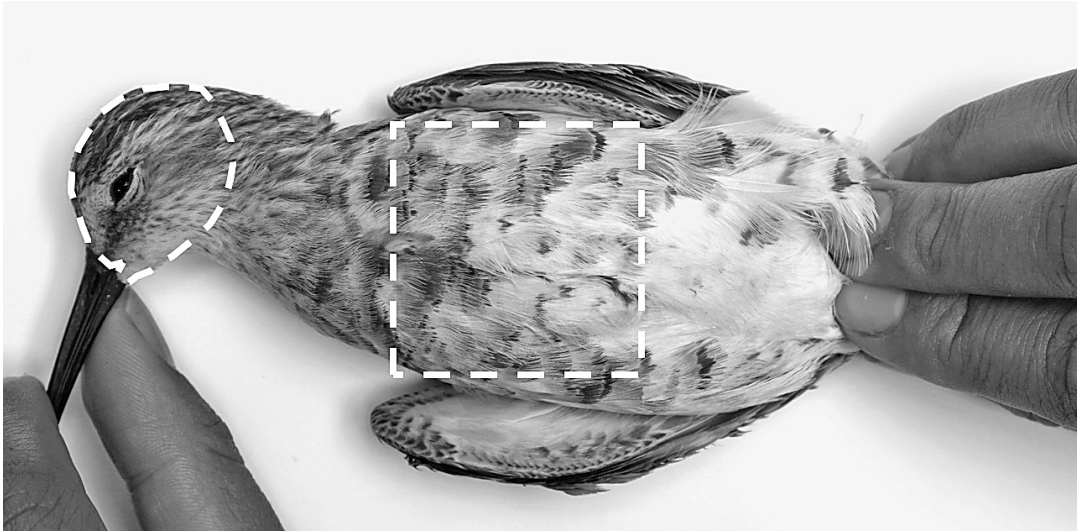


Fig. 1. Exemplary photo of adult Curlew Sandpiper used in the analysis of plumage characteristics. The areas of head and breast plumage analysed in the present study were marked with a dashed line.

use of different set of primers – 2987F/3112R (Fridolfsson & Ellegren 1999).

2.3. Photo analysis

In the Curlew Sandpiper, adult males precede females during autumn migration (Barshep *et al.* 2012). For studying the differences in plumage characteristics between males and females we established a period of joint presence of both sexes in the study area (12th July – 1st August) and only data collected in that time were included in the analysis. The analyses were conducted with the GIMP 2.8.10 software (GIMP-Team). As different light conditions during photo shooting may influence colours of the picture, colours in each photo were standardized by RGB histogram alignment. RGB values for the brightness section of picture (white background) were set as RGB values for white colour (R = 255, G = 255, B = 255). As a result, the white background served as a reference for other colours of the photo. From the pictures prepared in this way three plumage characteristics were obtained: 1) intensity of rufous colour on breast, 2) amount of white colour on head and 3) total number of bars on breast.

The photos were taken with different cameras having different image resolutions, with no established distance between a camera and photographed bird. We were not able to define the exact

diameters of the analysed breast area that could be applied for every photo. Hence, intensity of rufous colour on breast and total number of bars on breast were measured on the region, which was defined as in Blizard & Pruett-Jones (2017) as a square situated on the centre of breast with the top edge in line with the top of *furculum* and wrists joints (Fig. 1).

From the defined square, RGB values of 30 randomly selected pixels were obtained. RGB is an additive colour coding system and the actual value in a given channel is descriptive only in relation to the values in other channels. In order to describe intensity of rufous colour on breast we used the ratio of mean value of red channel to mean value of green channel (Bergman & Beehner 2008) obtained from previously selected pixels (further referred to as R/G ratio). In the same area we counted a total number of bars on breast. If a part of a bar was included in the area, then only bars with more than a half of their length visible in the defined square were counted.

The amount of white colour on head was described as the ratio of the number of rufous pixels to the number of white pixels (further referred to as R/W ratio) on the side of the bird's head. The limits of this area were established by base of bill, crown line, top of ear covers, cheek and base of head (Fig. 1). Pixels were included as rufous or white with “select by colour” tool.

Table 1. Differences in mean linear body measurements of males ($n = 164$) and females ($n = 222$) of adult Curlew Sandpipers. Lovich and Gibbons' (1992) Sexual Dimorphism Index (SDI) is given.

Measurement [mm]	Males		Females		t-test		
	Mean \pm SD	Range	Mean \pm SD	Range	t or t'	P	SDI
Bill length	36.35 \pm 1.74	32.8–42.6	39.55 \pm 1.89	33.7–45.1	$t = 16.91$	< 0.001	0.088
Total head length	60.49 \pm 1.77	56.3–66.1	63.74 \pm 2.04	57.9–69.8	$t = 16.27$	< 0.001	0.054
Tarsus length	30.55 \pm 1.01	28.3–33.3	31.63 \pm 1.25	28.0–35.0	$t' = 9.32$	< 0.001	0.034
Tarsus plus toe length	53.5 \pm 1.62	49–57	55.1 \pm 1.82	51–61	$t = 8.98$	< 0.001	0.030
Wing length	132.2 \pm 2.59	127–140	133.5 \pm 2.63	127–140	$t = 5.02$	< 0.001	0.010

2.4. Statistical analysis

All statistical analyses were conducted in Statistica 13.1 software (Dell Inc.) with additional Statistica Macro File (SVB) for the Jackknife procedure downloaded from <http://sdn.statsoft.com>. The data distribution of the ratio of rufous pixels to white pixels on head (R/W ratio) varied from normal distribution. The analysis of this parameter was preceded by the Box-Cox data transformation (Sakia 1992). The differences in linear body measurements between males and females were determined with the two-sample t-test or in the case of unequal variances with the Cochran-Cox test (t' statistic) (Zar 1999).

The degree of sexual dimorphism of a given trait was determined by Lovich and Gibbons' sexual dimorphism index (SDI) (Lovich & Gibbons 1992), in which mean values of linear body measurements of both sexes are taken into account. SDI value is positive when a given trait is larger in females and negative when it is larger in males. To show the degree of overlap between sexes in their measurements a 95% prediction intervals were presented, that is a range of values that is likely to contain the value of a single new observation given specified settings of the predictors (Patel 1989). Discriminant analysis was applied to assess which variables were the most reliable in identifying sex of a given individual and to develop a discriminant function for sexing adult Curlew Sandpipers.

The stepwise method of variable selection was not used as it produces a bias in parameter estimation and inflates the probability of incorrectly rejecting the null hypothesis of no effect (Whittingham *et al.* 2006). Hence, stepwise methods may

fail to include all variables that have an actual influence on the dependent variable, while frequently include variables that do not influence the dependent variable (Derksen *et al.* 1992, Mundry & Nunn 2009). Therefore in this paper, a model that included all independent variables was presented as well as the models with combination of measurements with high SDI value.

In our study, more females were measured than males (58% and 42% of all individuals, respectively). Similar to other papers (Włodarczyk *et al.* 2011, Meissner & Krupa 2016), a priori classification probabilities were set as equal for both sexes ($P = 0.50$), because biased sex ratios were not recorded in the Curlew Sandpiper. Lower numbers of males is caused by irregular sampling at the beginning of July when the majority of males migrate through the study area (Meissner 2006, Barshep *et al.* 2012). The sexes were coded “-1” for male and “1” for female and discriminant functions were calculated based on unstandardized discriminant function coefficients, with $D < 0$ indicating a male, and $D > 0$ indicating a female. For each variable the standardised coefficients of discriminant analysis were calculated to assess the contribution of one predictor in the context of the other predictors in the model. Effectiveness of each discriminant function was calculated with the Jackknife cross-validation procedure (Miller 1964).

We did not have access to the data set used to calculate discriminant function by Wymenga *et al.*'s (1990), therefore to compare the results of the previously published method and those developed in our study, another validation method called the resubstitution was used. Validation of both Wymenga *et al.*'s (1990) and ours discriminant func-

tions were conducted using the resubstitution method. In resubstitution sex of each individual is predicted using the functions calculated from the complete data set (Manly 1994). This technique usually overestimates the proportion of correctly classified males and females (Dechaume-Moncharmont *et al.* 2011), but is appropriate for comparison of the results of two discriminant functions. In order to assess the differences between both sexes in three plumage characteristics, i.e., intensity of rufous colour on breast (R/G ratio), amount of white colour on head (R/W ratio) and the total number of bars, three Generalized Linear Models (GLM) (McCullagh & Nelder 1983) with log link function and normal error distribution were used, with date of the capture (date number in the season; continuous factor) and sex of an individual (categorical factor) as explanatory variables.

3. Results

Females were on average larger than males in all linear body measurements. The most dimorphic trait was bill length and the least was wing length and the difference in SDI between these two measurements was 8.3% (Table 1). Tarsus length was highly correlated with tarsus plus toe length ($r = 0.86, P < 0.001$) as well as bill length with total head length ($r = 0.96, P < 0.001$), because in both cases the latter measurement includes the former. Hence, only tarsus length and bill length, which

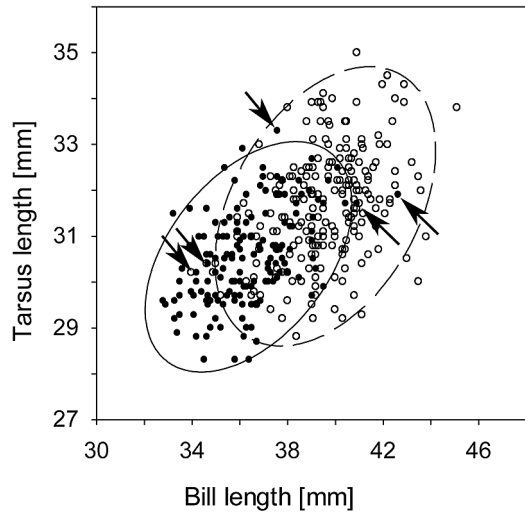


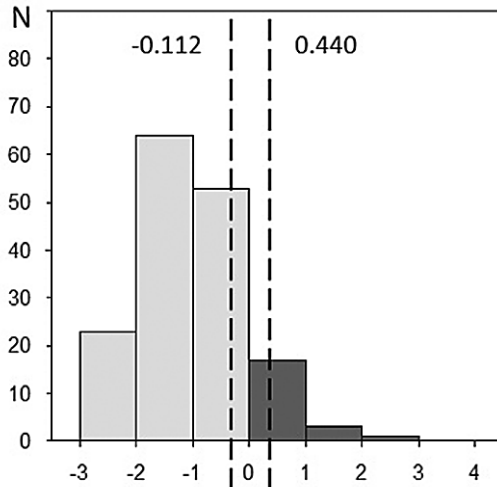
Fig. 2. Relationship between bill length and tarsus length in males (black dots) and females (black circles) of adult Curlew Sandpipers. The ellipses show the 95% prediction interval for a single new observation for males (solid line) and females (dashed line). The arrows indicate exceptionally small females and large males whose sex was doublechecked with a different set of primers.

both showed higher sexual dimorphism index, were used in discriminant analyses, especially that inclusion of both measurements would have violated the multicollinearity assumption of independent variables in discriminant function (Tabachnick & Fidell 1996). There was a large overlap in two most dimorphic body measurements (bill length and tarsus length) between females and

Table 2. Discriminant functions for sex determination in adult Curlew Sandpipers. Effectiveness of given functions was calculated with the Jackknife method. B – bill length, T – tarsus length, W – wing length. Maximum difference in effectiveness among presented functions is given.

Discriminant function	Correctly sexed individuals			Standardized coefficients of discriminant function		
	All	Females	Males	Bill length	Tarsus length	Wing length
D1 = 0.505·B – 0.113·T – 0.034·W – 27.374	81.4%	83.9%	78.9%	0.916	0.129	0.089
D2 = 0.513·B + 0.129·T – 23.596	81.3%	84.3%	78.3%	0.930	0.147	–
D3 = 0.537·B + 0.043·W – 26.173	82.0%	85.7%	78.3%	0.973	–	0.111
D4 = 0.552·B – 21.077	82.1%	85.3%	78.9%	1	–	–
Maximum difference in effectiveness between functions	0.8%	1.8%	0.6%			

MALES



FEMALES

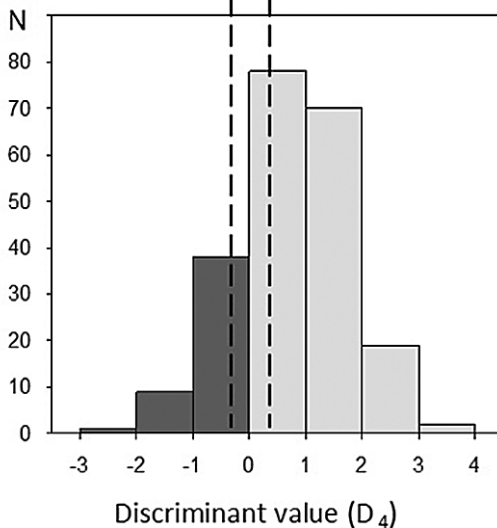


Fig. 3. Distribution of discriminant scores for D_4 discriminant function in A) males and B) females. Grey bars – individuals sexed correctly, black bars – individuals sexed incorrectly. Dashed line shows discriminant values that allow for correct sex determination of 95% males and females.

males (Fig. 2). In the overlapping zone of two ellipses showing 95% confidence interval for bill length and tarsus length in each sex, 80.2% of females and 52.5% of males were found.

We developed three discriminant functions which included bill length, tarsus length and wing

length. In all these equations bill length was characterized with the highest standardised coefficients of discriminant function (> 0.90), thus additionally we proposed discriminant function with bill length as the only predictor (Table 2). Difference in effectiveness between discriminant functions was small; it did not exceed 2% and was higher in females than in males (Table 2). Hence, we recommended function D_4 with bill length as a single predictor, because this measurement is a standard in the protocol of wader ringing station (Gratto-Trevor 2004, Busse & Meissner 2015).

Effectiveness of discriminant function may be increased by defining the limits of discriminant values which overlap least between sexes and then excluding individuals with discriminant score fitting between the range established by these limits (Herring *et al.* 2010, de Marchi *et al.* 2012, Meissner & Krupa 2016). Identifying birds with $D_4 < -0.112$ as males and those with $D_4 > 0.440$ as females led to incorrect sex determination of only 5% of males and 5% of females (Fig. 3). This approach resulted in 10.6% of individuals in which sex was not determined.

According to the resubstitution method, discriminant function by Wymenga *et al.* (1990) allowed correct sex identification in 81.7% of birds sexed molecularly in this study. This effectiveness was very similar to the one obtained by the Jackknife procedure of D_3 function based on the same measurements and D_4 with bill length as a single predictor (Table 2). Effectiveness established by resubstitution of equations D_3 and D_4 developed in the present study allowed correct sex determination in 97.4% and 95.5% of Curlew Sandpipers, respectively. This is a higher effectiveness compared to the discriminant function by Wymenga *et al.* (1990).

Females had significantly more bars on breast than males (GLM, Wald statistic = 74.60, $P < 0.001$). This trait was the most dimorphic plumage characteristics (SDI = -1.922), that did not change in the period of joint presence of both sexes (GLM, Wald statistic = 1.64, $P = 0.200$) (Fig. 4). R/G ratio also did not change over the time of autumn migration of the studied species (GLM, Wald statistic = 1.39, $P = 0.237$) and was higher in males compared to females (SDI = 0.107) (GLM, Wald statistic = 7.38, $P = 0.007$). There was no significant difference between sexes in R/W ratio (SDI =

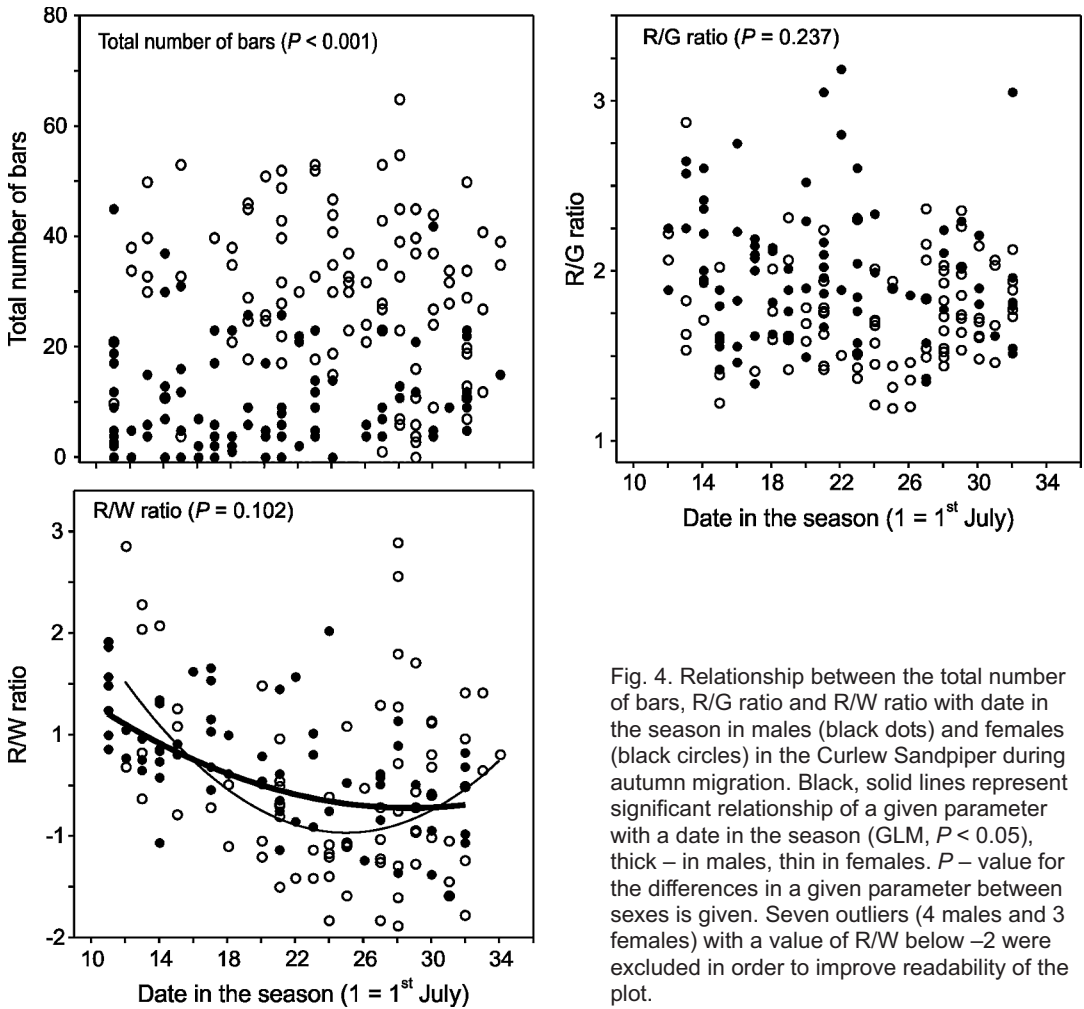


Fig. 4. Relationship between the total number of bars, R/G ratio and R/W ratio with date in the season in males (black dots) and females (black circles) in the Curlew Sandpiper during autumn migration. Black, solid lines represent significant relationship of a given parameter with a date in the season (GLM, $P < 0.05$), thick – in males, thin in females. P – value for the differences in a given parameter between sexes is given. Seven outliers (4 males and 3 females) with a value of R/W below -2 were excluded in order to improve readability of the plot.

0.033) (GLM, Wald statistic = 2.67, $P = 0.102$), but only this parameter decreased significantly over time (GLM, Wald statistic = 19.38, $P < 0.001$) (Fig. 4). Additionally, the absolute value of SDI for the total number of bars was almost 22 times higher than the values of SDI for any other biometric parameter, while R/G ratio showed a comparable level of sexual dimorphism to biometric parameters (Table 1).

The overlap in two most dimorphic parameters of plumage characteristics was considerable, as 62.7% females and 89.5% males were found in the overlapping zone for total number of bars and R/G ratio (Fig. 5A). Similarly, we observed high overlap between sexes in the total number of stripes and D_4 discriminant score used as an indicator of

sexual size dimorphism, with 60.0% of females and 97.1% of males found in the overlapping zone (Fig. 5B).

There was a negative relationship between the total number of bars and R/G ratio ($r = -0.30$, $P < 0.001$) and between the total number of bars and R/W ratio ($r = -0.20$, $P = 0.016$). This indicates some typical pattern in plumage in which individuals with intense rufous plumage and small amount of white feathers on head were less barred. R/G ratio and R/W ratio were positively correlated ($r = 0.25$, $P = 0.003$). However, the strength of all these relationships was very weak (Zar 1999). Moreover, none of the plumage characteristics correlated with D_4 discriminant value ($P > 0.116$ in all cases).

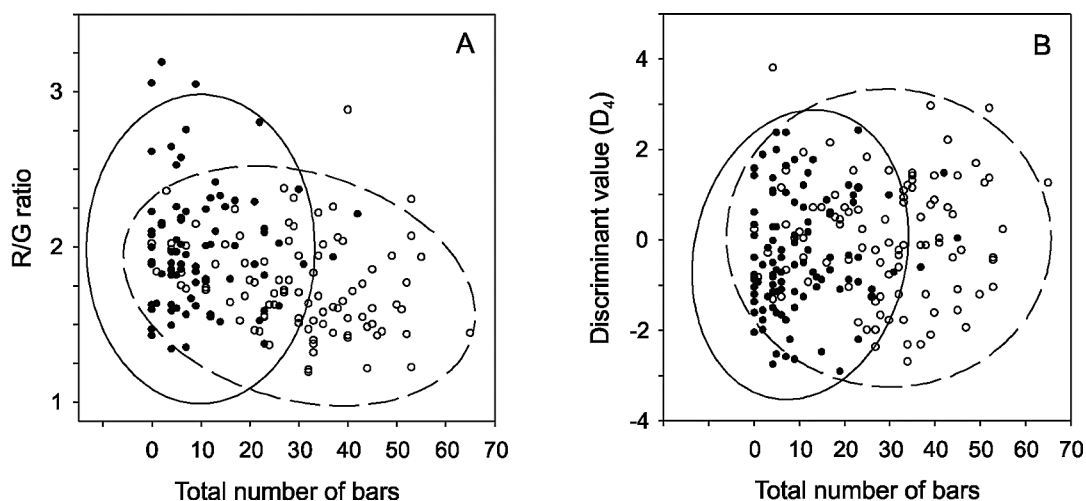


Fig. 5. Relationship between A) R/G ratio and total number of bars and B) discriminant value (D_4) and total number of bars in males (black dots) and females (black circles) of adult Curlew Sandpipers. The ellipses show the 95% prediction interval for a single new observation for males (solid line) and females (dashed line).

4. Discussion

Similar to other *Calidris* species (Wood 1987, Hallgrímsson *et al.* 2008, Meissner & Pilacka 2008, Jiménez *et al.* 2015, Niemi *et al.* 2018) the most dimorphic trait in adult Curlew Sandpipers is bill length, followed by tarsus length (Barter 1985, Wymenga *et al.* 1990, Engelmoer & Roselaar 1998, this study). Niche segregation between males and females of Curlew Sandpipers during foraging was observed in the wintering grounds and it was suggested these two biometric traits reduce intraspecific competition in this species (Puttick 1981). Females with longer legs and bills are able to feed in the deeper parts of flooded wetlands or to extract prey from deeper parts of mud in comparison to males, which was also documented in other waders like Bar-tailed Godwits (*Limosa lapponica*) (Both *et al.* 2003), Black-tailed Godwits (*Limosa limosa*) (Catry *et al.* 2012) and in the Western Sandpiper (*Calidris mauri*) (Nebel 2005).

Large overlap of linear body measurements of males and females might be also caused by biometric variability of populations occurring in different geographical regions (Gates *et al.* 2013). Yet Curlew Sandpiper is considered a monomorphic species with a relatively small breeding range (del Hoyo *et al.* 1996, Lappo *et al.* 2012).

Although some data indicate that individuals from the eastern part of breeding range may have shorter wings and longer bills than European migrants (Cramp & Simmons 1983), more recent analyses of a large sample of museum skins and comparison of the measurements taken in the East Atlantic and East Asian flyways showed that geographical variation in this species was negligible (Engelmoer & Roselaar 1998, Tomkovich & Soloviev 2006).

Discriminant functions for sexing adult Curlew Sandpipers presented in this study had lower effectiveness compared to discriminant functions calculated for some other species from the genus *Calidris*, that oscillates around 95% of correctly sexed individuals (Meissner & Pilacka 2008, Jiménez *et al.* 2015). This is caused by high overlap even in the most dimorphic body measurements of males and females, i.e., bill length and tarsus length. Similar lower efficiency of the discriminant function of about 79% of correctly sexed individuals was obtained for the White-rumped Sandpiper *Calidris fuscicollis* (Scherer *et al.* 2014), a species that exhibits the same parental care system, where females exclusively incubate eggs and care for young (Borowik & McLennan 1999).

Therefore, it seems plausible that the existence of selective pressure on the small size of males that

perform aerial display during the courtship with the lack of male parental care may reduce the magnitude of sexual dimorphism among *Calidris* species.

A sexing protocol of the Curlew Sandpiper proposed by Wymenga *et al.* (1990) based on bill and wing length was in accordance with the results of molecular sex determination. Therefore, despite some shortcomings in the description of discriminant function developed by these authors, the results obtained using it are not affected by any significant error. This may be due to small differences in effectiveness of proposed discriminant functions that are related to extremely high contribution of bill length in each model. Hence, the influence of other measurements on the results of sex determination was negligible and any discriminant function based on bill length would show similar effectiveness.

In the Curlew Sandpiper, adult females were on average larger than males in all linear body measurements (Glutz von Blotzheim *et al.* 1975, Cramp & Simmons 1983, this study). In waders it is assumed that sexual selection has the strongest impact on evolution of reversed sexual size dimorphism (Figuerola 1999, Székely *et al.* 2000). It has been theorized, that great agility, favoured by females, during aerial display of a male is a consequence of its small size, which also improves its performance in parental care (Peters 1983, Figuerola 1999, Sandercock 2001). Smaller body size of males results in smaller energetic expenditure during chick rearing, additionally shorter bill allows males to feed in areas suitable for chicks to forage. Hence, reversed sexual size dimorphism is commonly observed in the *Scolopacidae* family (Jönsson & Alterstam 1990, Figuerola 1999). In contrast to the majority of *Calidris* species (Borowik & McLennan 1999), male Curlew Sandpipers do not take part in parental care (Portenko 1959, Pietka *et al.* 1974, Tomkovich & Soloviev 2006).

Sexual selection mechanisms favouring smaller males as better suited for rearing chicks are invalid in this species. The Curlew Sandpiper is a polygynous wader species, however its reproductive system is considered to evolve recently from social monogamy, being the most common reproductive system among waders (Tomkovich & Soloviev 2006). Hence, it is possible that reversed

sexual size dimorphism in this species is a remnant from its previous reproductive system. Males of the Curlew Sandpiper present aerial courtship display with vocalization, based on which females select their partner (Portenko 1959, Holmes & Pitelka 1964, Cramp & Simmons 1983). Small body size facilitates males with greater manoeuvrability, which may be the factor allowing males for more effective courtship display. Then it may be the reason for reversed sexual size dimorphism lasting in the Curlew Sandpiper, despite lack of link between its breeding behaviour with parental skills. Moreover, the lack of mechanism selecting small-bodied males as better adapted to parental care may be one of the reasons of substantial overlap between sexes in their most dimorphic measurements.

We found a clear tendency that birds with a high intensity of rufous colour on a breast had low number of dark bars on underparts and little white colour on their heads, whereas birds with low intensity of rufous colour on their breasts had high numbers of dark bars and relatively more white colour on head. This was expected from previously described differences in plumage characteristics in both sexes (Kozlova 1962, Glutz von Blotzheim *et al.* 1975, Cramp & Simmons 1983) (Fig. S1). However, the relationship between these traits was weak as many individuals were found in an overlapping zone.

Moreover, the lack of significant relationship between any of plumage characteristics and discriminant score indicates that plumage traits are not significantly related to body size. It may also result from the occurrence of individuals with untypical, mixed set of plumage characteristics (e.g., birds with high intensity of rufous plumage and high number of dark bars) and individuals with plumage characteristics typical for opposite sex. The analysis of museum specimens showed that some females are indistinguishable from males according to breeding plumage (Kozlova 1962), as a result that was also supported by the present study (Fig. S2a).

Moreover, we found that some males with deep rufous colour of the underpart have quite intensive dark barring (Fig. S2b) or they have almost no bars, but the intensity of rufous colour resembles that of females (Fig. S3b). During spring migration through the Black Sea 35% of females had

dark rufous breast feathers and 43% of males had bars on their breast feathers (Keijl 2006). In that study 6% among 118 captured Curlew Sandpipers had completely opposite plumage characteristics to their sex. Although only 10 feathers were randomly taken from the central part of breast for this assessment, this is in accordance with the results of our study, in which some individuals had plumage features that were totally or partially characteristic of opposite sex (Fig. S2, Fig. S3).

Despite the active moult of body feathers during autumn migration neither intensity of rufous colour nor amount of dark bars changed in time of the Curlew Sandpiper occurrence in Central Europe. The post-breeding body moult in this species starts with replacement of feathers on head and neck (Kozlova 1962) in the breeding grounds or during migration, while feathers from belly remain unmoulted for much longer (Glutz von Blotzheim *et al.* 1975). Therefore, both males and females in this study showed declining amount of white colour on the head with date, while the changes in plumage of underparts were not so clearly pronounced. Hence, we do not recommend using amount of white colour on head in sex identification in this species during autumn migration. Total number of bars was the most dimorphic plumage trait and therefore it seems to be more useful in sexing adult Curlew Sandpipers than intensity of rufous colour. It should be noted however that females from the eastern part of the breeding range have less dark bars on the underparts than those migrating through Europe to Africa (Cramp & Simmons 1983), but their occurrence in Europe is unlikely (Gromadzka 1985, Minton 1998).

Therefore, sex determination of Curlew Sandpipers based on the number of dark bars and on intensity of rufous colour on breast is advised only in those cases when sexing based on linear body measurements is impossible (e.g., during field observations). Nevertheless, due to the presence of untypically coloured individuals in this species, sexing according to plumage characteristics is relevant only if an individual has dark rufous underparts with no or very low number of bars (male) or light rufous underparts with a lot of bars (female). In some, though uncommon cases, sexing according to these plumage characteristics may lead to wrong results.

Summing up, sex determination in adult Curlew Sandpipers based on bill length is more reliable than based on plumage characteristics. Discriminant functions are applicable throughout the annual cycle, particularly during the wintering period when males and females of this species cannot be distinguished according to plumage characteristics. Moreover, this method enables the analyses of archival data and sex determination in birds already measured in the past.

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Muuttavien kuovisirrien sukupuolierot koossa ja höyhenpuvussa

Kuovisirrin sukupuolet eroavat kooltaan ja pesimäpuvultaan. Analysoimme aikuisten kuovisirrien morfologisia ja höyhenpuvun eroja ja kehitimme diskriminanttianalyysin sukupuolten tunnistamiseksi. 222 naaraista ja 164 koiraslintua mitattiin syysmuuton aikana Itämerellä. Lisäksi 92 naaraan ja 84 koiraan höyhenpuvut valokuvattiin, ja kaikkien lintujen sukupuoli määritettiin molekyyli-menetelmin.

Naaraat olivat koiraita kookkaampia kaikkien mittojen osalta. Nokan pituus oli eniten eroava ominaisuus, ja se ennusti sukupuolen oikein 82.1 %:ssa tapauksista. Wymenga *et al.* (1990) havaitsivat saman tuloksen, vaikkakin tutkimuksen menetelmät oli puutteellisesti kuvattu, ja tämän aiemman tutkimuksen ennustearvo oli huonompi.

Koiraat olivat väriltään enemmän punertavia ja rinnasta ja alapuolelta vähemmän raidallisia. Näissä piirteissä 67.2 % naaraista ja 89.4 % koirasta sijoittuivat kuitenkin päällekkäin, ja joidenkin yksilöiden höyhenpuku oli selvästi vastakkaiselle sukupuolelle tyypillinen. Tämä viittaa siihen, että kuovisirrin sukupuolenmäärittäminen on epäluotettavampaa höyhenpuvun kuin diskriminanttianalyysin perusteella. Diskriminanttifunktioita voidaan lisäksi hyödyntää ympäri vuoden (riippumatta pesimäpuvusta) sekä historiallisista aineistoista.

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Online supplementary material

The supplementary material provided with this paper contain exemplary photos in colour of adult Curlew Sandpipers exhibiting different plumage traits. We included photos of individuals displaying plumage characteristics typical for their own sex, typical for the opposite sex as well as with mixed set of plumage characteristic.