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Biometric variability and sexual size dimorphism in the Great Knot *Calidris tenuirostris*

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Abstract

The Great Knot is a species from the Scolopacidae family of waders migrating within the East Asian-Australasian Flyway, and studies on this species have contributed greatly to understanding of migration ecophysiology and migration strategies in long-distance migrants. In this paper, we provide the first description of biometric variability and sexual size dimorphism in Great Knots. During the study on the Kamchatka Peninsula, 683 adults and 229 juveniles were measured and sexed molecularly. In adults, the mean measurements of females were larger than in males, except for tarsus length. In juveniles, at the early stage of migration from breeding to wintering grounds, apparently growth was not complete. Sexual dimorphism was small, with only wing length being significantly longer in females than in males. All dimensions of juveniles were smaller than those of adults, especially in bill length. The most sexually dimorphic trait in both adults and juveniles was wing length, and the most effective discriminant function with wing length as a single predictor correctly identified the sex of 76% of birds in both age classes. However, molecular sexing is the method of choice for reliable sexing, especially in juveniles.

Keywords: Waders, sexing, linear measurements, Kamchatka Peninsula, migration

1. Introduction

Many Arctic waders migrate along East Asian-Australasian Flyway covering a thousand kilometres between breeding areas in eastern Siberia and wintering grounds in New Zealand and Australia (Parish et al. 1987; Hansen et al. 2016; Li et al. 2019). The crucial stopover site on their route is localised in the extensive intertidal areas and near-coastal wetlands of the Yellow Sea, which support about 40% of all waders migrating in the East-Asian-Australasian Flyway (Barter 2002). The loss of coastal habitats and environmental degradation results in a population reduction of many migrants using this migratory route (Wilson

et al. 2011; Conklin et al. 2016; Piersma et al. 2016), which necessitates the intensification of ecological research and habitat conservation measures in stop-over sites (Amano et al. 2010; Szabo et al. 2016).

The Great Knot *Calidris tenuirostris* (Scolopacidae) is a long-distance migratory wader, restricted in their distribution to the East Asian-Australasian Flyway. Here, considerable population declines were documented in the past decades (Wetlands International 2023). The declines are explained by the loss and degradation of coastal staging habitat in the Yellow Sea region (Melville et al. 2016; Piersma et al. 2016). Our knowledge on

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breeding biology and breeding behaviour of this species is still very limited (Tomkovich 2011a, 2011b). More studies on this species concern the migration period. During northward migration, the Great Knot makes spectacular migratory flights, flying non-stop for more than 5,000 km from non-breeding areas to the Yellow Sea region and then, after refuelling for 1–2 months, to breeding areas in Siberia (Lisovski et al. 2016; Chan et al. 2019). Recently, the studies on Great Knot have contributed to understanding migration ecophysiology and migration strategies in long-distance migrants (i.e. Battley et al. 2001, 2004; Pennycuik & Battley 2003; Piersma et al. 2008; Peng et al. 2015; Zhang et al. 2019), but our knowledge on biometrics variation is still sparse with only few papers providing data from live birds (Barter 1986; Balachandran 1997; Andreev 2010). Although adult males and females differ only slightly in breeding plumage, with females tending to have less chestnut in the scapulars (Prater et al. 1977; Hayman et al. 1986), sexing is possible only by comparing partners within a mated pair. In juvenile and non-breeding plumages, both sexes look the same and differ only in size, as females are slightly larger than males, which is typical of birds in the genus *Calidris* with only a few exceptions (Cramp & Simmons 1983; Székely et al. 2000). However, existing data on biometric differences between the sexes in the Great Knot are based only on small samples of museum specimens (Kozlova 1962; Prater et al. 1977; Cramp & Simmons 1983) and cannot be used for reliable sex determination, except for exceptionally large or small individuals.

Among waders, there are many species that exhibit no plumage dimorphism between the sexes (Del Hoyo et al. 1996) and studies on their behavioural ecology, ecophysiology, and migration phenology often do not take into account possible differences between sexes (Puttick 1981; Both et al. 2003; Meissner & Krupa 2017; de Zwaan et al. 2019). Molecular sexing is the method of choice for sex determination (Fridolfsson & Ellegren 1999; Morinha et al. 2012), but it requires the collection of DNA samples and specialized laboratory equipment. Moreover, this is a costly procedure, especially when sample sizes are large. Therefore, the development of hardly invasive non-molecular methods based on a discriminant function, which provide reliable sex identification based on morphological characteristics, is still needed and becoming increasingly popular (e.g., Sikora & Dubiec 2007; Lislevand et al. 2009; Meissner & Krupa 2016; Niemi et al. 2018; González et al. 2022). In this paper, we aimed to describe for the first time the

biometrical variability of adult and juvenile males and females of the Great Knot using a large sample of birds sexed molecularly. Additionally, we develop discriminant functions for sexing adult and juvenile Great Knots based on linear body measurements which are commonly used in studies on various aspects of bird behaviour (i.e. Alves et al. 2013; Gwiazda & Ledwoń 2015; Meissner & Krupa 2017; Meissner et al. 2019).

2. Material and methods

2.1. Fieldwork

Field studies were conducted in 2016–2019 in the Khairusova-Belogolovaya estuary on the western coast of Kamchatka (Russia) (Figure 1), which is the first stopover during southbound migration after leaving the breeding grounds, where birds switch from feeding on insects and berries to foraging on invertebrates on mudflats (Dorofeev & Kazansky 2013). Birds were caught during high tide using a modified pull net (Dorofeev et al. 2019) between 15 July and 16 August. This period covers the main part of the migration of the Great Knot through Kamchatka (Lisovski et al. 2016; Gerasimov et al. 2018). Age was determined on the basis of plumage characteristics, distinguishing juveniles (younger than 4 months) and adults (older than one year) (Prater et al. 1977). Wing length was measured with a ruler (1 mm accuracy), while the total head, bill, and tarsus lengths were measured using callipers (0.1 mm accuracy) (Busse & Meissner 2015). Birds were also weighed with an electronic balance with an accuracy of 1 g. However, the body mass was omitted in analyses, because it varies considerably during migration due to accumulation of fat reserves.

2.2. Laboratory work

All birds were sexed molecularly. About 50 µl of blood was taken from the branchial vein and preserved in 96% ethanol (EtOH). In the laboratory, subsamples of 5–10 µl blood cells were dried at 55°C to ensure that ethanol evaporated. For 554 of 912 samples, DNA was extracted with ammonium acetate (AmAc) (Richardson et al. 2001), lysing blood in a soapy buffer with proteinase K, followed by a clean-up with AmAc and ethanol perspiration. For the remaining samples, a rapid alkaline (NaOH) extraction method was used, lysing blood cells with 0.2 M NaOH at 75°C for 20 min and neutralizing the solution with 0.04 M TriSHCl (pH 7.5) (Rudbeck & Dissing 1998).

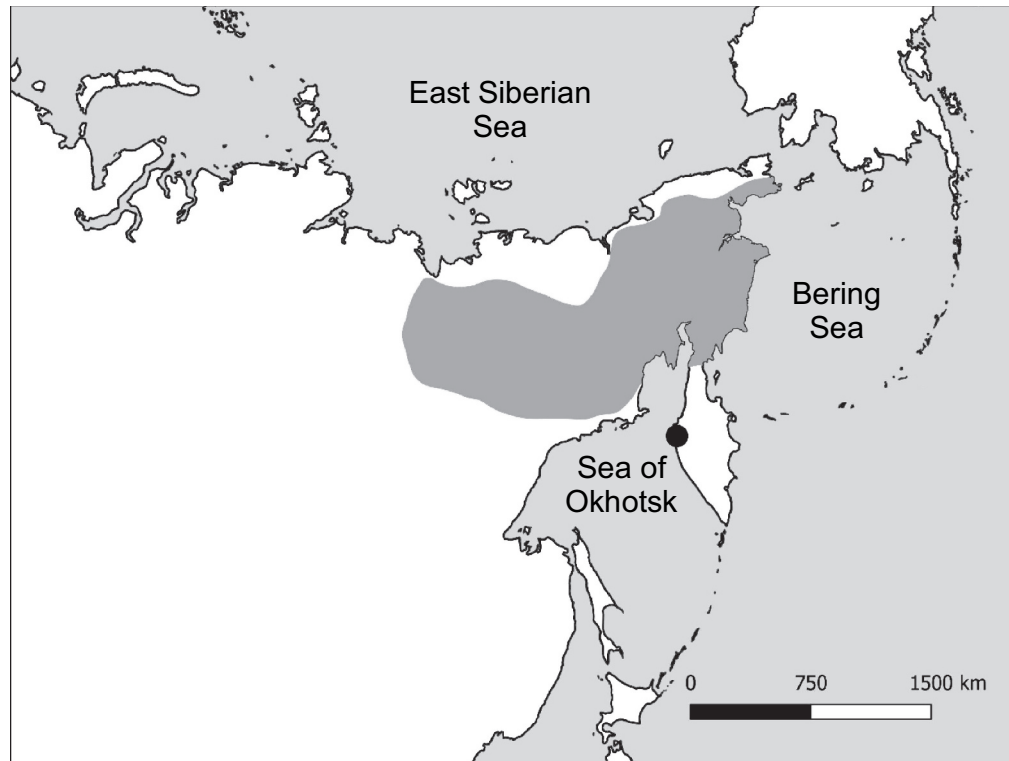


Figure 1. Location of bird ringing site in the Khairusova-Belogolovaya estuary (black dot). Dark grey area indicates the breeding range of the Great Knot (according to Tomkovich 2021).

These two methods were verified in several bird species to give the same results (Y.I. Verkuil, unpublished data). For molecular sexing, the specific wader primers 2602F/2669 R and PCR protocols of van der Velde et al. (2017) were used. PCR products were visualized on a 2% agarose gel. To perform a check for errors in laboratory procedures, of the 912 individual samples, 16 were randomly picked to repeat the DNA extraction and PCR. In all cases, the assigned sexes were 100% consistent. In total, 683 adults and 229 juveniles were measured and molecularly sexed, but not all biometrics had been taken from each individual so sample sizes differed for certain measurements.

2.3. Statistical analyses

The differences in linear body measurements between males and females were determined with the two-sample t-test or Cochran–Cox test for non-homogeneous variances (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. However, we modified the original equation so that positive values indicate a higher mean for a given measurement in females (a larger sex) and negative values in males.

$$\text{SDI} = \left(\frac{\text{mean value of females}}{\text{mean values of males}} \right) - 1$$

The method of calculating the Lovich and Gibbons dimorphism index was also used to assess differences in mean linear measurements between adults and juveniles within the same sex, the age dimorphism index (ADI). All data met the assumptions of the homogeneity of variance (Brown–Forsyth test, $p > 0.228$) and normality (Shapiro–Wilk test, $P > 0.075$), except for wing length in adults (Shapiro–Wilk test, $W = 0.992$, $p = 0.001$). Nevertheless, we did not transform this variable because discriminant analysis (DFA) and ANOVA robustly withstand deviations from normality, especially for large sample sizes (Tabachnick & Fidell 1996; Zar 1999).

A discriminant function analysis (DFA) was carried out to identify the best predictors of sex. We recognise criticisms of automated stepwise selection of variables (Whittingham et al. 2006; Mundry &

Nunn 2009), so we have presented models that include only linear measurements with means significantly different between males and females. Two measurements, bill and head length, in which one included the other, were highly correlated with Pearson's correlation coefficients between them $r = 0.89$ and $r = 0.90$ for adults and juveniles, respectively. Therefore, we did not include both highly correlated variables in the same discriminant function to avoid strong multicollinearity between independent variables. For all other pairs of measurements, the correlation coefficients were low ($r < 0.46$). In DFA, the sexes were coded “-1” for males and “1” for females and equations presented in this paper are based on unstandardized canonical discriminant function coefficients, with discriminant score $D < 0$ indicating a male, and $D > 0$ indicating a female. We validated the success rate of classification of each discriminant function with squared Mahalanobis distances from each sex-group centroid, where the given individual is classified into a sex group for which it has the highest posterior classification probability (Hair et al. 2014). To show the degree of overlap between sexes in two most dimorphic measurements, 95% prediction intervals were presented, a range of values likely to contain the value of any single new observation given the settings of the predictors (Patel 1989).

There was only a slight bias in the sex ratio in caught juveniles (60% of males), whereas among adults, males comprised 83%. This unequal sex ratio in adults does not necessarily reflect an unbalanced sex ratio in the sampled population, but is more a result of the timing of the study, as females leave the breeding grounds before males (Kistchinski 1988; Artyukov 1990; Tomkovich 1997), while the field study began after migration had already begun. Hence, similar to other papers (Ackerman et al. 2008; Meissner & Krupa 2016; Yannic et al. 2016), *a priori* classification probabilities were set as equal for both sexes ($p = 0.50$). The statistical analyses were performed using Statistica 13.3 software (TIBCO Software Inc.).

3. Results

3.1. Sexual and age dimorphism in size

In adults, females were larger than males in all linear body measurements, except tarsus length. The most sexually dimorphic trait in adults and juveniles was wing length with SDI of about 3%. However, the overlap in wing length distributions between the sexes in adults and juveniles is large (Figure 2). When taking into account wing and bill length simultaneously, 75% and 71% of males, and 85% and 70% of females were

found within the overlapping zone of two ellipses showing a 95% confidence interval for wing length and bill length in adults and juveniles, respectively (Figure 3).

In adults, the total length of the head and bill showed less than half the index of sexual dimorphism than the length of the wing, whereas differences between sexes in mean tarsus length were statistically insignificant (Table I). In juveniles, there were no statistically significant differences in bill and total head lengths and only wing length was significantly larger in females. As in adults, the tarsus length was similar in males and females (Table I).

Adult males and females were larger than juveniles in all linear measurements (t-test, $p < 0.001$ in all cases) with bill length and total head length being the most dimorphic, whereas wing and tarsus length was the less dimorphic traits (Table II).

3.2. Sexing

In adults, individuals with wings shorter than 185 mm were males, and 20% of males in the sample may be sexed correctly according to this criterion. Adults with wings longer than 197 mm are females, but only 9% of females may be correctly sexed using this cut-off value. There is less overlap in juveniles and, using the cut-off values of 172 and 192 mm, correct sex determination applies to 26% of males and 10% of females (Figure 2).

In adults, males and females differed significantly in wing, bill, and total head length (Table I). Wing length contributes the most to the model, as the three equations with this measurement have very similar efficiencies of 74–76% of correctly sexed birds, higher than equations with only the bill and total head length (Table III). Furthermore, the inclusion of the bill and total head length in the model did not increase the proportions of birds sexed correctly. In juveniles, only wing length was significantly different between the sexes. The overall performance of the discriminant function with the wing length only (76%) is similar to that of adults, with the same proportion of correctly classified females and males (Table III).

4. Discussion

As in the majority of shorebird species from the Scolopacidae family, the Great Knots reveals distinct reversed sexual size dimorphism in which females are larger than males (see Cramp & Simmons 1983). In *Calidris* sandpipers, this dimorphism is usually well pronounced, allowing to sex individuals according to linear measurements with high effectiveness (i.e. Meissner & Pilacka 2008; Hallgrímsson et al. 2008;

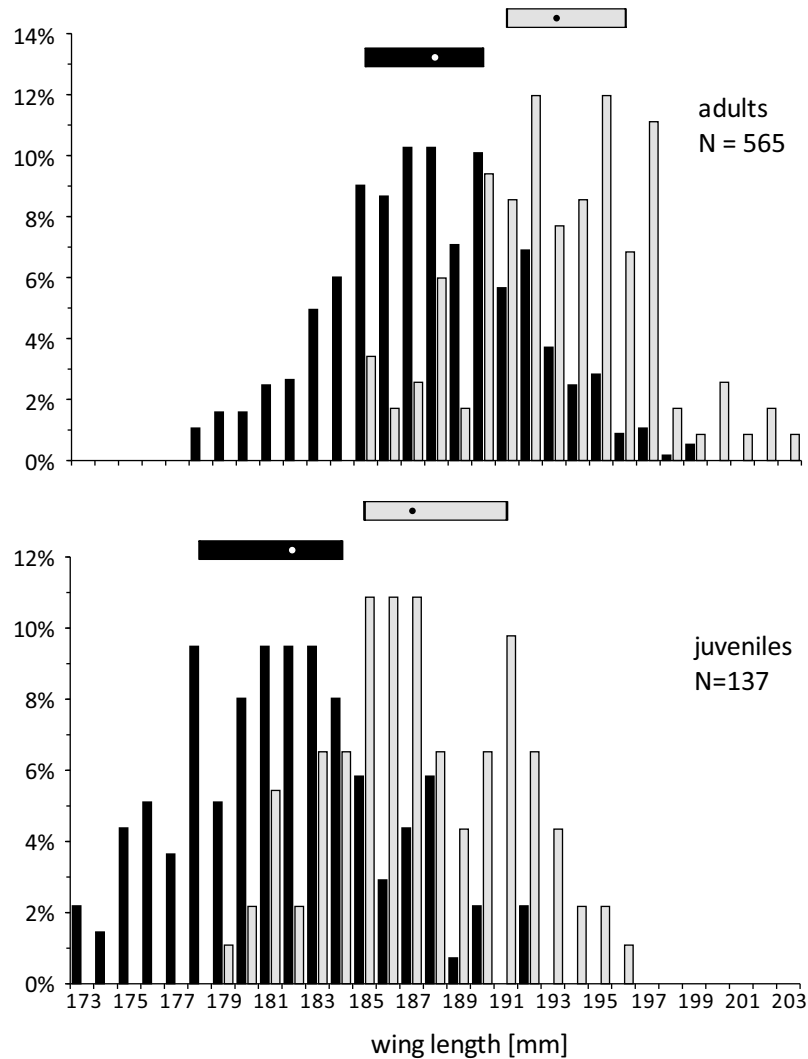


Figure 2. Distribution of the most dimorphic trait, the wing length, of males (black bars) and females (grey bars) of adult and juvenile Great Knots. The median (dot) and interquartile range (rectangle) are given above.

Jiménez et al. 2015). In the Great Knot, the misclassification rate of provided equations is within the limits reported for other *Calidris* species (Table S1). As has been shown for other species with a large overlap in the linear dimensions of both sexes, individuals with a discriminant score close to 0 should be omitted (Meissner & Krupa 2017). Such a procedure will reduce the sample size by not including large males and small females in the analyses but will also reduce the number of incorrect sex identifications.

Intraspecific variation in different linear dimensions reflects the evolutionary responses to selection pressures that commonly differ between males and females (Badyaev & Martin 2000; Badyaev et al. 2000; Zhu et al. 2020). Knot characteristics related to resource use (bill length) were more sexually dimorphic than those related to locomotion (tarsus length). The

differences in bill length, similar to other wader species, may lead to differences in the foraging niche and spatial segregation of males and females during foraging in the non-breeding season (Nebel et al. 2000; Nebel 2005; Hall et al. 2021).

All linear dimensions in juveniles were smaller than in adults, which is especially well pronounced in bill length. Shorter bills in juveniles at stopover sites during autumn migration were also found in some other Scolopacidae species (Hirschfeld et al. 1996; Meissner 1997, 1999). Our study was conducted in close proximity (about 600 km) to Great Knot breeding grounds and the captured birds were just starting their autumn migration. This indicates that the growth of juveniles does not end before they leave the breeding grounds *en route* to the south, as

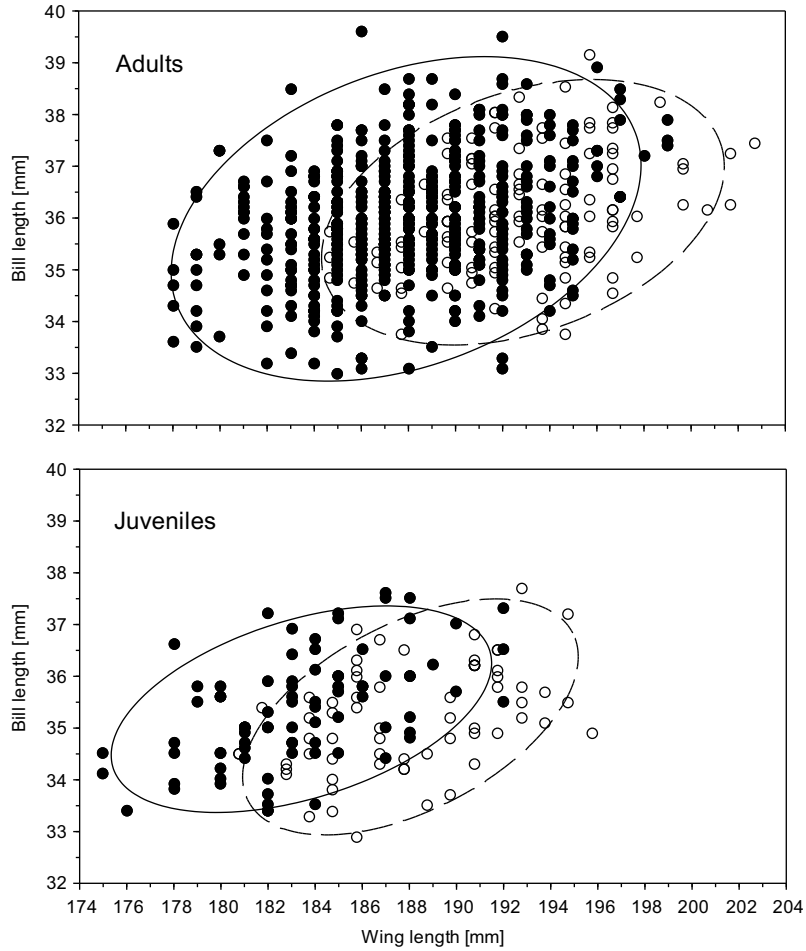


Figure 3. Relationship between the two most dimorphic traits, the wing length, against the bill length in male (black dots) and female (white dots) Great Knots. The ellipses show the 95% prediction intervals for a single observation, given the parameter estimates for the bivariate distribution computed from the data for males (solid line) and females (dashed line).

Table I. Differences in mean linear measurements between male and female Great Knots, with the sexual dimorphism index (SDI) expressed in per cent according to the modified Lovich and Gibbons (1992) equation.

Measurement [mm]	Males			Females			t-test		SDI
	Mean	SD	N	Mean	SD	N	t	p	
Adults									
Wing length	187.7	4.06	565	193.1	3.86	117	13.10	<0.001*	2.9%
Tarsus length	35.99	1.15	537	36.07	1.13	116	0.69	0.491	0.2%
Bill length	42.00	1.71	566	42.48	1.80	117	2.76	0.006	1.1%
Head length	74.06	1.85	566	74.90	2.03	117	4.39	<0.001	1.1%
Juveniles									
Wing length	181.7	4.31	137	187.3	3.93	92	10.03	<0.001	3.1%
Tarsus length	35.35	1.07	84	35.22	1.02	65	0.77	0.443	-0.4%
Bill length	36.10	1.98	137	36.11	2.06	92	0.02	0.988	<0.0%
Head length	67.68	2.28	137	67.59	2.44	92	0.28	0.780	-0.1%

* Cochran-Cox test results instead of t-test.

Table II. Age dimorphism index (ADI) in males and females of the Great Knot.

Measurement	Males	Females
Wing length	3.2%	3.0%
Tarsus length	1.8%	2.4%
Bill length	14.0%	15.0%
Head length	8.6%	9.8%

previously demonstrated for the Bar-tailed Godwit *Limosa lapponica* (Battley & Conklin 2010). The lack of expected differences in bill length in young males and females may be due to the same beak growth rate during postembryonic development in both sexes, which was found in other species (Bancroft 1984; Velando et al. 2000; Jordi & Arizaga 2016). Hence, in females, it probably takes longer to reach the final bill size than in males, as the final bill in females is larger. The length of the bill is the most striking difference between adults and juveniles, which, on the one hand, may have a consequence for juveniles in the temporarily limited availability of food extracted from the substrate (van Gils et al. 2016) and, on the other hand, may limit competition with adults for food resources (Goss-Custard & Durell 1981; Marchetti & Price 1989). It seems that food availability does not appear to be a limiting factor for juveniles in the early stages of southward migration. Shorter bills may be an advantage when foraging on intertidal biofilm, which consists of a thin yet dense layer of microbes, organic detritus, and sediment in a mucilaginous matrix of extracellular polymeric substances and non-carbohydrate components secreted by microphytobenthos (Elner et al. 2005; Kuwae et al. 2012). Biofilm grazing has not yet been found in the Great Knot, but has been confirmed in other waders, including

a closely related species, the Red Knot *Calidris canutus* (Lourenço et al. 2017). In juveniles, shorter wings (flight feathers) than adults have been found in many bird species (Marchetti & Price 1989; Alatalo et al. 2008). Such difference has indeed been observed before in the family Scolopacidae during autumn migration, despite the high degree of primary wear in adults after the breeding season (Atkinson et al. 1981; Meissner 1997; Yousef & Meissner 2006; Fernández et al. 2007). It was suggested that shorter wings in first-year inexperienced birds are a result of strong selection for take-off performance and increased manoeuvrability as an anti-predator adaptation (Fernández et al. 2007), while adults can fly faster and may compensate for reduced manoeuvrability with experience (Alatalo et al. 2008). Wing length is the most dimorphic sexual trait in both adults and juveniles. In adults, the small size of the male may be explained by a female preference for high agility during aerial displays, which also improves male efficiency in parental care (Jönsson 1987; Figuerola 1999; Sandercock 2001). Moreover, the sex difference in wing length in adult and juvenile birds may reflect the overall difference in body size between males and females, as larger and heavier females need larger wing area for long-distance flight.

The age difference in tarsus length was the lowest among all linear measurements. Wader chicks forage for themselves from the first or second day onwards and this requires a well-developed locomotive ability, which is reflected in the large size of the legs at hatching (Schekkerman et al. 1998). Consequently, just after fledging their tarsus has the same length as in adults, which was found also in other Scolopacidae species (Hirschfeld et al. 1996; Meissner 2005; Meissner & Koss 2009). Moreover, the tarsus length does not differ significantly

Table III. Equations for calculating discriminant scores. The percentage of birds correctly sexed is given according to squared mahalanobis distances from each sex-group centroid. WL – wing length, BL – bill length, THL – total head length.

Equation	Correctly sexed		
	Males	Females	All
Adults			
$D_1 = 0.265 \text{ WL} - 0.237 \text{ BL} - 41.397$	75%	71%	74%
$D_2 = 0.244 \text{ WL} - 0.026 \text{ THL} - 48.037$	75%	75%	75%
$D_3 = 0.248 \text{ WL} - 46.824$	76%	75%	76%
$D_4 = 0.869 \text{ BL} - 31.281$	54%	46%	53%
$D_5 = 0.531 \text{ THL} - 39.406$	58%	60%	58%
Juveniles			
$D_6 = 0.240 \text{ WL} - 44.195$	76%	76%	76%

between sexes, and this was found also in other wader species (Ottval & Gunnarsson 2007; Sikora & Dubiec 2007; Scherer et al. 2014; Aradis et al. 2015).

Equations with wing length as a single predictor (D_3 and D_6) seem to be better for sexing Great Knots, as the inclusion of the bill length or total head length did not improve the classification (Table III). The wing length is a standard measurement in the protocol for Scolopacidae species in bird ringing stations (Engelmoer et al. 1987; Gratto-Trevor 2004; Busse & Meissner 2015). Moreover, using equations to sex Great Knots does not produce a biased sex ratio, like in some other shorebird species (Lislevand et al. 2009; Meissner & Krupa 2016; Witkowska & Meissner 2020), because the proportions of correctly sexed males and females are similar or the same. However, the misclassification rate during sex determination of the Great Knot is one of the highest among the species of the genus *Calidris* studied (Table S1). Obtained discriminant functions may offer sufficiently high classification accuracy when individuals with a D value close to 0 would be left unsexed, as in other species with a large overlap of linear measurements between sexes (Meissner & Krupa 2017; Meissner et al. 2021). The equations provided may be sufficient for use not only in the future research but importantly also to sex birds already measured during previous studies. However, including wing length in discriminant analysis may cause potential biases resulting from feather wear and moult, and birds with worn or moulting outermost primaries should be excluded from the analysis.

Biometric variation among the Great Knot populations originating from different parts of the breeding area has not been reported (Kozlova 1962; Cramp & Simmons 1983). The breeding area of the Great Knot is vast (Lappo et al. 2012; Tomkovich 2021), but flagged individuals from all known wintering grounds from the Australian coastline to the coastline of the Persian Gulf were observed in the Khairusova–Belogolovaya estuary (authors' unpublished data). Hence, it seems that the equations provided in this study may be used not only for Great Knots migrating through the Kamchatka Peninsula. However, in the case of adults provided discriminant function is applicable throughout the annual cycle, while in juveniles it should be used with caution because the equation was derived from data collected in the early part of autumn migration when their growth was not finished. Hence, molecular sexing remains the method of choice for reliable sexing, especially in juveniles.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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Availability of data and material

Data analysed in this study are available from the corresponding author upon reasonable request.

Authors' contributions

Design and methodology: D.D., A.I., W.M., Fundraising: D.D., T.P. Data collection: D.D., A. I. E.K. Laboratory analysis: Y.V. Data analysis: W. M. Writing original draft: W.M. Writing review and editing: all authors.

Compliance with ethical standards

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Ethics approval consent to participate

Bird ringing and data collection were conducted by experienced, professional ringers having valid licenses and permissions of the national ringing centre. All fieldwork was done according to the ethical standards recommended by those institutions.

Geolocation information

Eastern Asia.

Supplementary material

Supplemental data for this article can be accessed online at <https://doi.org/10.1080/24750263.2023.2293120>.

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