

Sex and age differences in the development of breeding plumage in the Wood Sandpiper *Tringa glareola* during spring migration in north-eastern Poland

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We investigated the effects of sex and age on the progression of breeding plumage moult in the Wood Sandpiper, a migrant wader that shows weak sexual size dimorphism and no dichromatism. We sexed the birds by DNA and examined the plumage of 416 Wood Sandpipers caught at a spring stopover site in north-eastern Poland. We scored the proportion of new breeding-type feathers on the head, back and scapulars in 20%-wide stages, and summed these scores as a body moult index, and on the lesser and median wing coverts summed as a wing covert moult index. Only 10% of all these birds fully developed breeding plumage on the upper body and 8% had only 21–40% of new feathers there. About 90% of the birds had moulted less than half of their wing coverts. No Wood Sandpiper showed a complete breeding plumage. We investigated whether moult indices were related to the date of the bird's capture and its body mass adjusted for size, age and sex, using generalised linear models. The best model indicated that the body-moult index was significantly affected by age, sex and year. Immatures had a more advanced body moult than adults, and females were more advanced than males. None of the predictors had a significant effect on the wing-covert moult index.



1. Introduction

Sandpipers of the genus *Tringa* show no clear sexual dichromatism. Their breeding plumages are plain and inconspicuous, predominantly grey, black and brown (Hayman *et al.* 1987). As with most other waders, *Tringa* sandpipers undergo a partial pre-breeding moult between January and May, which begins at their wintering grounds (Ginn & Melville 1983). Wood Sandpipers *Tringa glareola*, which occur abundantly in spring at Polish wetlands, are migrants returning from their non-breeding grounds in African wetlands south

of Sahara to their breeding grounds in the boreal zones between Fennoscandia and the Ural Mountains (Lebedeva *et al.* 1985, Meissner 1997, Underhill *et al.* 1999). Wood Sandpipers wintering in western Africa return northwards over south-western and western Europe, those wintering in eastern Africa head back over the Middle East and the Balkans. Ringing recoveries suggest that the migration routes of these groups cross in Central and Eastern Europe, including Poland (Glutz von Blotzheim *et al.* 1977, Lebedeva *et al.* 1985, Meissner 1997, Scott 2009). Wood Sandpipers ringed at stopover sites in Poland have been



Fig. 1. Location of the ringing site at Kwiecewo, north-eastern Poland (black dot). Grey area indicates the breeding range of the Wood Sandpiper according to Scott (2009).

recovered in Finland and Sweden, which indicates their breeding origin (Meissner 1997, Remisiewicz 2005). This species breeds in May and June, migrates southwards in July and August, stays on the non-breeding grounds between September and March, and migrates north to the breeding grounds between mid-March and mid-May (Glutz von Blotzheim *et al.* 1977, Cramp & Simmons 1983). Most Wood Sandpipers undertake their first migration from the non-breeding grounds towards the breeding grounds aged about 9–10 months, but a few immatures defer their return until their second year of life (Remisiewicz *et al.* 2010a, 2010b). Spring migration of Wood Sandpipers north through Europe is rapid and quicker than their autumn passage south (Remisiewicz *et al.* 2007). Wood Sandpipers replace their flight feathers and begin their pre-breeding moult at the non-breeding grounds, but the advancement of this moult at their departure and during spring migration has not yet been studied (Ginn & Melville 1983, Remisiewicz *et al.* 2009, 2010a).

While ringing Wood Sandpipers at a spring

stopover site in north-eastern Poland, close to their breeding grounds, we noted that the proportions of two generations of body feathers on the upperparts of individuals varied considerably. These two types of feathers were identified as dull brown worn feathers of the non-breeding plumage and as fresh glossy-blackish feathers of the breeding plumage. In north-eastern Poland, adult male Wood Sandpipers occur on spring passage a few days ahead of adult females, but immature males are, on average, the latest of all age and sex groups (Remisiewicz & Wennerberg 2006). This migration pattern suggests that the sexes and age groups potentially use different strategies for energy investment in spring migration and for the development of breeding plumage. Sexual differences in the development of the breeding plumage and a relationship with the individuals' condition at a spring stopover site have been shown in the Bartailed Godwit *Limosa lapponica*, a wader with clear sexual dimorphism in size and plumage coloration (Piersma & Jukema 1993, Piersma *et al.* 2001).

Here, we aimed at determining the effects of sex and age on the development stage of the breeding plumage at a spring stopover site in north-eastern Poland in the Wood Sandpiper, a wader with a weak sexual dimorphism in size and no sexual dichromatism apparent to human eye (Remisiewicz & Wennerberg 2006).

2. Material and methods

We collected our data on the development of breeding plumage at a wader ringing station on banks of a shallow lake at a farmland area near Kwieciewo, a village in north-eastern Poland (53°56.30' N, 20°18.97' E). This site is located 100–200 km southwest of the closest breeding grounds of the Wood Sandpiper located in the Kaliningrad region, Lithuania, Estonia, Latvia and Belarus (Fig. 1). We caught waders using walk-in traps (Meissner 1998) and mist nets during the spring-migration period (end of April until mid-May) of Wood Sandpipers passing through this site in 2005–2007.

We ringed and aged the Wood Sandpipers by their plumage as immatures (birds during their first year of life, about 10–11 months old at capture) or as adults (unidentified immatures and older birds). Most immatures can be identified up to the age of about 18 months by the retained juvenile-type inner median coverts or by the contrast between two generations of primaries showing partial moult (Prater *et al.* 1977, Remisiewicz *et al.* 2010a, 2010b, Waterbird Research Group KULING, unpublished data). A small proportion of immatures might lose these features earlier, so our sample of adults might contain a few immatures. We measured each ringed Wood Sandpiper's total head length, bill length, wing length, tarsus length and tarsus-plus-toe length. The birds were weighed, and about 30 µl of blood was collected from brachial wing vein and conserved in TE buffer or 70–96% ethyl alcohol for sexing in the laboratory (Permit of the Local Ethics Committee 4/KEiZK/2005).

We sexed the Wood Sandpipers by analysing DNA obtained from the collected blood samples, following Remisiewicz and Wennerberg (2006). We used the P2/P8 primers for 85% of the samples (Griffiths *et al.* 1998) and the 1237L/1272H prim-

ers (Kahn *et al.* 1998) for the remaining 15% of the samples that did not give a PCR product with the P2/P8 primers. Samples from 20 birds were sexed with both pairs of primers to cross-check their validity, and both yielded identical results. We had earlier compared the results of sexing with the P2/P8 primers and with the 2550F/2718R pair of primers, which amplify different introns (Fridolfsson & Ellegren 1999), and for 30 Wood Sandpipers caught in Poland during 2002–2003 we obtained identical results (analysis not shown). PCR reactions using the P2/P8 primers allowed us to sex more Wood Sandpipers successfully than with the 2550F/2718R primers, so we chose the former method for individuals caught in later seasons because it was more efficient.

We developed our PCR products on a dense 3.5% agarose gel and identified by a two-bar pattern on the gel and by comparing the size of both bars with the molecular marker (Dubiec & Zagalska-Naubauer 2006). Cross-checking our results with three different pairs of primers and examining the pattern of our PCR products on the gel minimised the risk of incorrectly sexing Wood Sandpipers by the use of P2/P8 primers, as had happened with other waders (Casey *et al.* 2009).

For each individual we scored the proportion covered by new fully grown breeding plumage feathers in five regions on the upper parts of the body: head, back, scapulars, lesser upper wing coverts and median upper wing coverts. We derived body-moult scores for each part of the body by grouping the assessed percentage of new feathers into 20%-wide intervals: 0 = no new feathers, 1 = 1–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = 81–100%. This transformed the percentage scale into an ordinal scale of six scores that served as a moult index. The feathers of the non-breeding plumage were old and worn, bleached blackish-brown, with whitish spots. The newer feathers of the breeding plumage had a glossy black background with clear white spots and fresh edges. We did the scoring by daylight or by the light of an electric lamp. Light conditions had a small effect on the accuracy of scoring because the assessment was based on the contrast in the gloss and on the wear of the feathers, which was not as noticeable in artificial light as in daylight. Distinguishing these two generations and estimating their proportions required practice, so descriptions of the body

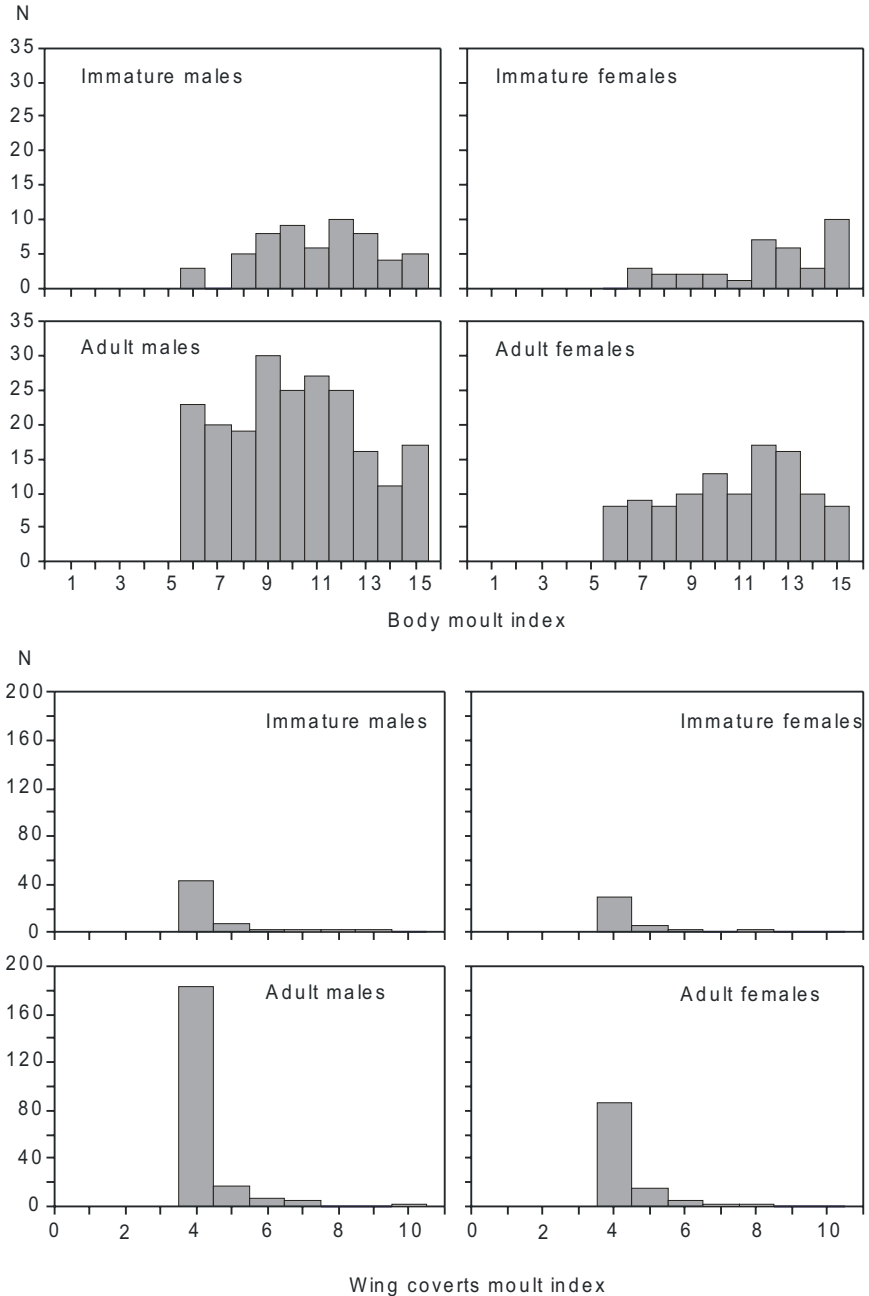


Fig. 2. Variation in the body-moult index according to age and sex of Wood Sandpipers caught during spring migration in north-eastern Poland in 2005-2007.

moult were done by the authors MR or PG, two experienced observers who cross-checked the accuracy of scoring between themselves at the beginning of the first season until they achieved identical scores.

We sexed and recorded moult scores for 416 birds: 58 immature males and 36 immature fe-

males, 213 adult males and 109 adult females. As a supporting dataset to adjust the birds' body mass for their size we used measurements of all 540 Wood Sandpipers ringed during spring fieldwork in 2005–2007, including the 416 sexed birds. We used only the moult scores and the measurements taken at an individuals' first capture. We com-

bined the data from all seasons and in analyses we used the number of the day in the year, as the date of measurement.

For our analyses we derived two moult indices from the original scores: the body moult index, which was the sum of the scores for the head, back and scapulars; and the wing covert moult index, which was the sum of scores for the lesser upper wing coverts and the median upper wing coverts. The maximum possible value for the body moult index was therefore 15 and was 10 for the wing covert index.

We used a generalised linear model (GLM) with a logarithmic link function (McCullagh & Nelder 1983) and normal error distribution in the module provided by Statistica 9.1 (StatSoft 2010) to account simultaneously for the effects of all independent variables. Each of the moult indices was related to date and body mass as the continuous variables, and to sex, age and year as discrete factors. We considered all the possible combinations of predictors and all their two-way interactions. In Wood Sandpipers females are slightly larger than males (Remisiewicz & Wennerberg 2006), thus as a proxy for the body condition we adjusted the body mass of Wood Sandpipers from Poland for their size using the measurements of all 540 birds caught in Kwiecewo. We chose the total head length as the correction factor, because it correlated best with the body mass (Pearson $r = 0.30$, $P < 0.001$) of all linear measurements. The standardisation of body mass was done according to the equation:

$$\text{Adjusted Body Mass} = \text{Body Mass} + 1.44(56.11 - \text{Total Head Length}), \quad (1)$$

where 56.11 is the mean total head length, irrespective of the birds' age and sex, and the coefficient of 1.44 comes from the linear regression equation of the body mass against the total head length:

$$\text{Body mass} = 1.44 \times \text{Total Head Length} - 8.36 \quad (2)$$

We used Akaike's Information Criterion (AIC) to evaluate which of the models best explained the variance and was best supported by the data (Burnham & Anderson 2002, Burnham *et al.* 2011). We calculated differences in AIC (ΔAIC)

values by subtracting the minimum AIC for the best-fitted model from the AIC of all subsequent candidate models. We used these differences to determine which model provided the best description of the data on the basis of the fewest model parameters (k). We presented only models with $\text{AIC} < 3$, because they are considered to be fairly similar in their ability to describe the data (Burnham *et al.* 2011: Fig. 2), while models with $\text{AIC} > 3$ receive considerably less support (Burnham & Anderson 2002). We reported the Akaike weight (AICw), which gives the relative support of the data for each model to determine the relative likelihood of each (Burnham & Anderson 2002, Burnham *et al.* 2011).

3. Results

The body-moult index varied between 6 and 15 with no clear peak in any sex or age group (Fig. 2). Ten percent of all examined birds had fully-developed breeding plumage on the head, back and scapulars, and 8% had the lowest body-moult index recorded in this study, with 21–40% of new feathers in these parts of plumage combined.

The best model indicated significant effects of date, age, sex and year on the body-moult index, with no significant interactions among these variables (Table 1, model 1). This model was supported by the data more than twice as well as the second-best model, which included the adjusted body mass (Table 1, model 2), or models with interactions age \times sex and age \times year (Table 1, models 3–4). The subsequent two models (Table 1, models 5–6) were less supported by the data.

All variables included in model 1 had a significant effect on the body-moult index (Table 2). The adjusted body mass (BMA) in model 2 had no significant effect on the body-moult index (GLM; Wald statistic = 0.364, $P = 0.546$). The interactions age \times sex in model 3 (GLM; Wald statistic = 0.190, $P = 0.663$) and age \times sex in model 4 (GLM; Wald statistic = 1.987, $P = 0.370$) were not significant. This confirmed model 1 – which excluded these variables – to be the best model. This model showed that immature Wood Sandpipers were more advanced in their body moult into breeding plumage than adults, and that males had a lower body-moult index than females (Table 2, Fig. 3).

Table 1. Model selection using Akaike's Information Criteria (AIC) to determine the effect of age, sex, date (day since the beginning of year), year and adjusted body mass (BMA) on the body-moult index of Wood Sandpipers caught at a spring stopover site in north-eastern Poland in 2005–2007. AIC gives the difference in the AIC between a given model and the best model; Akaike weights (AIC_w) show the relative support each model has from the data, k is the number of parameters in a model.

Model #	Variables	k	AIC	ΔAIC	AIC_w
1	Date + Age + Sex + Year	4	2006.13	0.00	0.0014
2	BMA + Date + Age + Sex + Year	5	2007.77	-1.64	0.0031
3	Date + Age + Sex + Year + Age*Sex	5	2007.94	-1.81	0.0034
4	Date + Age + Sex + Year + Age*Year	5	2008.16	-2.02	0.0038
5	Date + Age + Year	3	2008.51	-2.38	0.0045
6	Date + Age + Sex + Year + 1*2*3	5	2009.04	-2.91	0.0058

Table 2. Effects of age, sex and year on the body-moult index of Wood Sandpipers, according to the best GLM model (see Table 1). All three variables are categorical, with baseline categories, for which the estimated regression coefficients are set to zero.

Explanatory variable	Coefficient	SE	df	Wald	P
Constant	1.061	0.541	1	3.851	0.0497
Age (adult)	0	0	1	0	–
Age (immature)	0.046	0.018	1	6.511	0.0107
Sex (female)	0	0	1	0	–
Sex (male)	-0.033	0.016	1	4.316	0.0378
Year (2005)	-0.027	0.026	2	1.150	0.2836
Year (2006)	-0.074	0.031	2	17.944	0.0001
Year (2007)	0	0	2	0	–

Year had a significant effect on the body-moult index, and birds in 2007 were more advanced in moult than in 2006 (Table 2).

Body- and wing-covert moult indices showed a small but significant correlation when birds of different ages or sexes combined from all years (Pearson $r = 0.15$, $P = 0.002$, $N = 416$). However, no GLM model indicated significant influence by any factor or covariate on the wing-covert moult index. Most Wood Sandpipers (82%) had a wing-covert moult index of 4, which was the lowest score recorded at the study site (Fig. 2), suggesting that these birds had only 21–40% of the breeding-type wing coverts. Only one adult male of all the 416 Wood Sandpipers had all new wing coverts. The wing-covert moult index showed no significant relationship with any of the analysed factors or covariates, which might result from the small variation of this index. The most parsimonious model considered only the effect of age on the moult index, which was, however, not significant (AIC = 1432.90; effect of age: Wald statistic =

0.454, $P = 0.074$). Immatures were more advanced in the moult of wing coverts than adults, which is consistent with the effect of age on body moult.

4. Discussion

Our results showed an advanced pre-breeding moult in the first half of May in the Wood Sandpiper, suggesting that – at the last stage of their spring migration – this species' pre-breeding moult of contour feathers occurs between January and May and begins at the non-breeding grounds (Ginn & Melville 1983, Cramp & Simmons 1983). However, due to the Wood Sandpipers' short stay and high turnover rate at the spring stopover in Kwieciewo (Remisiewicz *et al.* 2007, Waterbird Research Group KULING, unpublished data), we were unable to determine if these birds continued with their pre-breeding moult during the last stage of migration, or if they held back their body moult during spring migration, as do other waders leav-

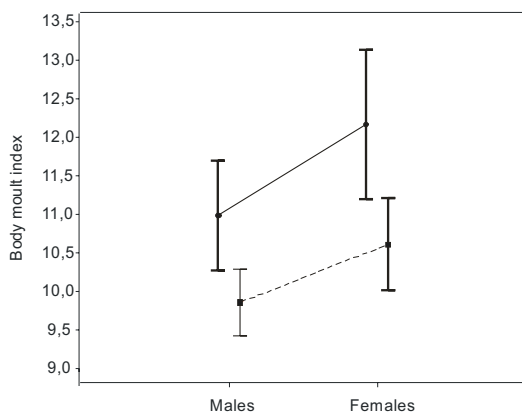


Fig. 3. Advancement of body moult in males and females of immature (circles, thin line) and adult (squares, dashed line) Wood Sandpipers caught during spring migration in north-eastern Poland in 2005-2007. Symbols show the mean moult index, and whiskers show 95% confidence intervals.

ing their wintering area in Mauritania (Zwarts *et al.* 1990, Piersma & Jukema 1993).

Our finding that immature Wood Sandpipers in Poland showed more advanced breeding plumage of their body than adults was an unexpected finding: many waders do not develop full breeding plumage in their first year of life (Prater *et al.* 1977). Of the Wood Sandpipers we caught, 24% of immatures and 39% of adults had a body-moult index in the lower half of the range (below 9; Fig. 2). This higher proportion of adults than immatures in the early stages of moult could explain why adults had on average lower body-moult index. Immatures whose moult of primary and body feathers is retarded at the time of their northwards departure usually stay on their wintering grounds for another year, but adults generally migrate to the breeding grounds whatever their stage of moult (Cramp & Simmons 1983, Remisiewicz *et al.* 2010a, 2010b). Immature Wood Sandpipers appear later than adults on spring migration and probably arrive at breeding grounds after adults (Remisiewicz & Wennerberg 2006). They might therefore improve their competitive ability at breeding grounds by having darker and more advanced breeding plumage than adults.

The wing-covert moult index did not vary much, which impeded finding significant effects of age, sex, date or body mass on the stage of moult

for this part of plumage. The moult of wing coverts was less than half-advanced in between 88% and 94% of the birds in each age and sex class (wing-covert moult index <5). Though the body-moult and wing-covert moult indices were positively correlated, none of the Wood Sandpipers we caught had developed a complete breeding plumage (Fig. 2). The lack of a full breeding plumage in Wood Sandpipers caught in the last stage of their spring migration would result in a mixture of brownish and blackish feathers with white spots, which might provide good camouflage at the fine-scale-mosaic breeding sites at swamps, taiga and tundra (Pulliainen & Saari 1991). Displaying Wood Sandpipers on their Siberian breeding grounds may still have a mixture of fresh newly moulted and older non-breeding worn wing coverts in late June (W. Meissner, unpublished data). A few Wood Sandpipers caught on post-breeding migration through Poland in early July had a similar mixed plumage (Remisiewicz *et al.* 2010b). These findings suggest that Wood Sandpipers may not complete their pre-breeding moult, as was found in Bar-tailed Godwits (Piersma & Jukema 1993).

Date had no significant effect on the body-moult index, which may be a result of our short, three-week study period. Wood Sandpipers migrate rapidly through Central Europe in spring and stay at our Polish stopover site for only a few days (Remisiewicz *et al.* 2007, Waterbird Research Group KULING, unpublished data), which may be too short a period for them to resume their moult. The short stay and high turnover rate of Wood Sandpipers at Kwieciewo prevented us from obtaining data on the progression of body moult. Additionally, the stage of pre-breeding moult might vary each year, depending on local conditions (O'Hara *et al.* 2002), which was confirmed in our study. Thus it remains unknown if Wood Sandpipers hold back their body moult during spring migration, or if individuals arriving in the beginning and in the end of the migration season at our stopover site.

We were unable to relate the progression of breeding plumage with body condition, as determined by our index of body mass adjusted for the bird's size. This contrasts with the clear relationship between pre-breeding moult, body mass and individual condition in the Bar-tailed Godwit at a

spring stopover site (Piersma & Jukema 1993). The body mass of birds shows large fluctuations during long-distance migration, and the Wood Sandpipers we caught stayed at the stopover site for only a short time, which might blur relationships between body mass and stage of pre-breeding moult.

Our main findings were that (1) immatures were in a more advanced stage of body moult than adults, and (2) females were more advanced than males. Black plumage contrasts against the sky (Walsberg 1982), and Bókonyi *et al.* (2010) showed that male waders of species with aerial displays featured a more melanistic plumage than related species with ground displays. Wood Sandpipers perform conspicuous aerial displays, in which both sexes take part (Kozlova 1961, Cramp & Simmons 1983). This might explain why males were not more advanced in moult into the breeding plumage than females, which would have been expected if only the males performed display flights. The advancement of breeding plumage seems to be a reliable indicator of the quality of potential mates (Piersma & Jukema 1993, Lendvai *et al.* 2004).

Thus, inexperienced immatures of both sexes might benefit during displays from a more advanced breeding plumage than would experienced adults. The observed incomplete breeding plumages in all age and sex groups of Wood Sandpipers near their breeding grounds suggest that this species may undergo an incomplete pre-breeding moult, which provides a beneficially cryptic plumage at local breeding grounds.

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Sukupuolten ja ikäluokkien väliset erot liron pesimäpuvun kehityksessä kevätkuuton aikana Koillis-Puolassa

Tutkimme sukupuolen ja iän vaikutusta liron (*Tringa glareola*) pesimäpuvun sulkasatoon. Laji on muuttolintu, jolla on pieni sukupuolten välinen koko- muttei värieroa. Käytimme DNA:ta sukupuolen määrittämiseen ja tutkimme 416 höyhenpukua yksilöillä, jotka pyydystettiin keväisellä muutonaikaisella levähdyspaikalla Koillis-Puolassa. Arvioimme uudet pesimäpuvun höyhenet pään, selän ja hartiahyhenten alueilla 20 % välein vaihtuvalla luokituksella ja summasimme arvot ruumiinhöyhenyksen sulkimisindeksiksi, sekä pienten ja keskimmäisten siiven peitinhöyhenen alueella peitinhöyhenen sulkimisindeksiksi. Vain 10 %:lla yksilöistä oli kehittynyt ruumiin yläpuolen pesimäpuku, ja 8 %:lla oli vain 21–40 % höyhenistä vaihtuneita. Noin 90 %:lla yksilöistä alle puolet peitinhöyhenistä oli vaihdettu. Yhdelläkään ei ollut täydellistä pesimäpukua. Tutkimme myös, riippuivatko sulkimisindeksien arvot pyyntipäivämäärästä tai ruumiinpainosta (suhteutettuna kokoon, ikään ja sukupuoleen) yleistyillä lineaarisilla malleilla. Parhaan mallin mukaan ikä, sukupuoli ja näytteenottovuosi vaikuttivat merkittävästi ruumiinhöyhenysindeksiin. Esiakuisilla oli aikuisia ja naarailla koiraita edistyneempi ruumiinhöyhenyksen sulkasato. Mallien muuttajat eivät merkittävästi selittäneet peitinhöyhenindeksin arvoja.

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