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AGE DETERMINATION OF BREEDING SHOREBIRDS: QUANTIFICATION OF FEATHER WEAR IN THE LEKKING GREAT SNIPE[1]

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Abstract. We develop a method of aging Great Snipe (*Gallinago media*) by quantifying primary feather wear. No reliable method has hitherto existed to separate young (first-summer, second calendar year) and old Great Snipe during the breeding season. We quantified primary wear of cut-off feather tips using a binocular microscope and scored the degree of wear on six variables. We found that primary wear separated well between young and old birds, whereas morphological variation did not. In a sample of 405 Great Snipes from Norway, 98.7% of the males of known age (74 old, 3 young) were correctly classified to age with discriminant analysis using primary feather wear. We review the potential use of primary feather wear to separate first-summer individuals from older individuals in 113 Nearctic and Palearctic shorebird (Charadriiformes) species. We note that in the majority of species, differential primary wear is the only available aging method during the breeding season.

Key words: Aging; primary feather wear; molt; lek mating system; morphology; Gallinago media.

INTRODUCTION

Information about the age of individuals, and thus the ability to age individuals, is of great importance in studies of population dynamics, natural and sexual selection, and the evolution of life histories (Clutton-Brock 1988, Sæther 1990, Stearns 1992). Many methods exist for age determination of living birds (see Prater et al. 1977, Pyle et al. 1987, Svensson 1992). However, due to feather molt and other factors, these methods often cannot be used to age birds beyond their first winter. Most birds replace primary feathers annually (but see Summers 1983), but the timing of replacement may differ between age groups. In most shorebirds (Charadriiformes) breeding in the northern hemisphere, adults molt primary feathers in fall or winter, whereas the juveniles of many species do not renew their primaries until the following summer (Prater et al. 1977, Prater 1981, Cramp and Simmons 1983). Therefore, in many species of shorebirds, differential wear of primary feathers is used as a key to separate first summer and older individuals during the breeding season (Prater et al. 1977) and may, in some species, be the only method available. However, no study has provided estimates of the success of age determining birds according to primary feather wear during the breeding season (but see Schamel and Tracy 1988 who did not succeed in distinguishing yearling and older *Phalaropus lobatus* using primary wear). Therefore, there is a need to evaluate the usefulness of this method. Indeed, few studies have tried to quantify feather wear at all (see attempts for shorebirds in Sheldon et al. 1958, Clausager 1973, Taylor 1979, Holz 1987, Devort 1989; for passerines in e.g., Willoughby 1986, 1991; and references for other groups in Rogers 1990), and these attempts often only use a three or four point scale (see Rogers 1990).

As part of a larger study on the biology of the lekking Great Snipe (*Gallinago media*), we needed information about the age of individuals. In particular, we wanted to separate first summer (2y, alternate 1 plumage) and older (3y+) birds during the breeding season. During the fall, juvenile Great Snipe may be distinguished from adults on the basis of color and pattern of wing-

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coverts and tail-feathers (Prater et al. 1977, Cramp and Simmons 1983). These feathers are molted on the winter grounds and aging is thought to be impossible after all juvenile wing-coverts are replaced in early spring (Cramp and Simmons 1983). However, the juvenile primary feathers are retained to be molted after the first breeding season (Prater et al. 1977). Adult Great Snipes molt their primaries in fall and winter (Jackson 1919, Woodman 1944, Kozlova 1962 [cited by Tuck 1972], Devort and Paloc 1992), and thus have fresher primaries in spring than do first summer (2y) snipes. First summer Great Snipes might therefore be expected to show more primary feather wear and tear. In addition, age-related differences in the durability of feathers, as have been found in other shorebirds (Prater et al. 1977), may also cause more primary wear in young birds.

The purpose of this study was to develop a method of aging Great Snipe during the breeding season. We show that a simple quantification of primary feather wear, using a binocular microscope, separated young and old birds, whereas variation in six morphological traits did not. By simply looking at feathers, and noting wear on a three point scale, a relatively large number of birds were not ageable. We discuss the usefulness of our method for other hard-to-age shorebirds, and present a list of the molt pattern of immature Nearctic and Palearctic shorebirds, indicating in which species primary wear can be used to age birds during the breeding season.

METHODS

STUDY AREA AND FIELD METHODS

We caught Great Snipes with mist nets on their leks in Gåvålia near Kongsvoll (62°17′N, 9°36′E), Dovrefjell, mid-Norway in May–June 1986–1992 (see also Fiske et al. 1994). The 15 km^2 study area is situated in the sub-alpine and low-alpine regions, from 1,000 to about 1,200 m altitude. Further description of the study area can be found in Pedersen et al. (1983) and in Løfaldli et al. (1992). Birds were banded and several morphometric measures taken: length of bill, length of bill plus head (see Fig. 2b in Green 1980), wing length, true tibio tarsus length (Prater et al. 1977) and length of white on tail. Wing length was measured as the maximum length (Svensson 1992) to the nearest 1.0 mm with a ruler. All other measurements were taken with a digital caliper, to the nearest 0.1 mm. Length of white on tail was measured as "... the distance from the distal end of the most distal dark spot on the right outer tail feather to the tip of that feather ..." (Höglund et al. 1990b). In addition, the number of tail feathers with more than 50% white was counted (except in 1986). Measurements were taken by the same person in more than 90% of the cases. Birds known to be old (3y+) are those banded as full grown the year before or earlier whereas birds known to be young (2y) are those banded as downy the year before.

FEATHER WEAR

Wear causes several structural changes in feathers (Burtt 1986). For a detailed quantification of feather wear, we cut off about 1 cm of the left ninth primary feather tip (counted from inside) of most birds caught in 1987–1990 and in 1992. All feathers were coded and randomly sorted before being analyzed by one of us who was unaware of the age and sex of the birds involved, using a binocular microscope (20–60 × magnification). Degree of wear was scored according to a scale from 1 to 3 on three variables (barb wear, barbule wear and hook wear, see Fig. 1 and Table 1). This was done for both the inner and outer web of the feather, giving a total of six wear score variables for each feather. The total score was computed as the sum of the six scores. This sum is hereafter referred to as "total wear score." As wear progressed inwards from the outside, only the edge of the terminal 0.5 cm of the feather tip was examined for wear.

To evaluate the visual impression of feather wear, we also subjectively assigned the age of each feather tip as young (strong wear), intermediate (moderate wear) or old (little wear) simply by looking at individual feather-tips. This was done by the same person who scored feather wear, and after all feathers had been scored.

STATISTICAL ANALYSIS AND MATERIAL

We analyzed age-related feather wear by discriminant analysis, using feathers from birds of known age. We used both a stepwise and a direct, simultaneous method of entering predictor variables in our multivariable discriminant analysis model. The stepwise method of variable entering was based on maximization of the minimum Mahalanobis distance (D^2) between groups. Variables were here entered/removed in the model when their partial F values were greater/less than

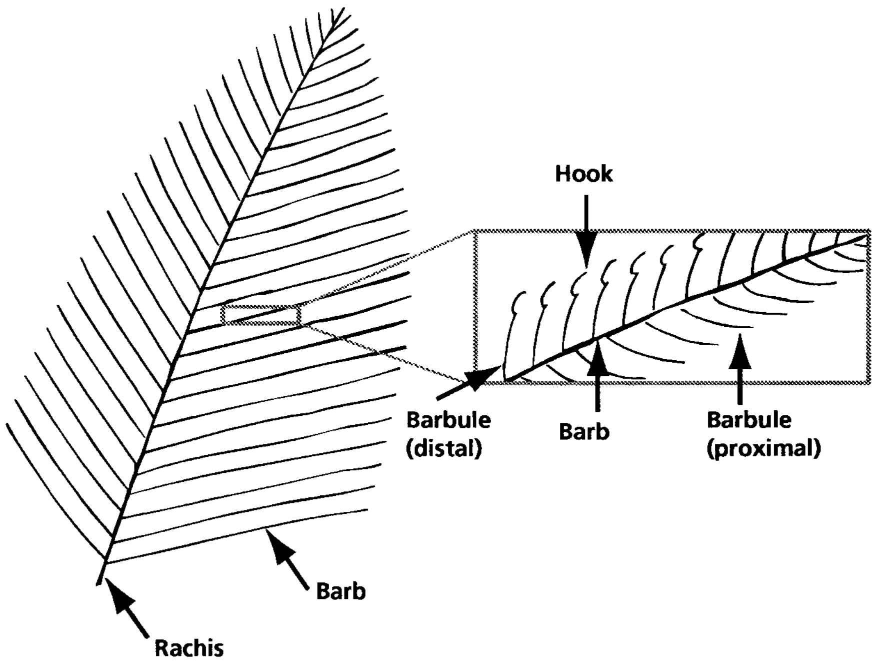

FIGURE 1. Simplified structure of a Great Snipe primary feather tip.

1. We also analyzed age-related morphological differences by stepwise and direct discriminant analysis. To increase statistical power in the discriminant models using morphology, we also made analyses with a larger sample of aged birds. Here we included birds aged according to primary wear using a conservative criterion. Birds with a total wear score of 9 or less were considered old, whereas birds with a total wear score of 14 or more were considered young (see RESULTS). Because there is a slight morphological sexual dimorphism in Great Snipes (Höglund et al. 1990b), we analyzed morphology of males and females separately.

Counting each individual once per year (1986–1992), a total of 806 birds have been measured (578 males, 224 females), involving 591 different individuals. A total of 405 feathers (300 males, 105 females) from 361 different individuals were aged according to feather wear (1987–1990 and 1992). A larger number of feathers was collected, but some of these were excluded from the anal-

TABLE 1. Criteria used to score primary feather wear. Each feather was scored 1 (no wear), 2 (moderate wear) or 3 (strong wear) according to the criteria in the table, for three variables for both the inner and outer web of the feather. Thus, the possible range of the sum of all wear scores (total wear score) was 6–18. Only the edge of the terminal 0.5 cm of the feather tip was examined.

Variable	Scores and criteria 1	2	3
Barb wear inner web (BI) and outer web (BO)	No barb tips missing or broken, often white edge at the very tip	A few barb tips missing or broken	Missing barb tips in most parts of the feather tip
Barbule wear inner web (BUI) and outer web (BUO)	No barbules missing	A few barbules missing	Barbules missing several places
Hook wear inner web (HI) and outer web (HO)	No hooks missing	A few hooks missing	Hooks missing several places, feather often looks transparent

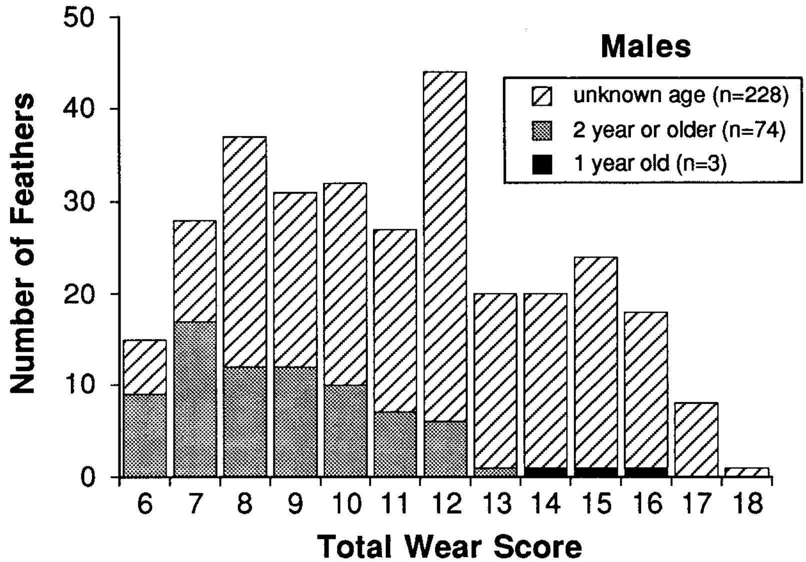

FIGURE 2. Total wear score for Great Snipe males captured during the breeding season in Gåvålia, Norway, 1987–1990 and 1992.

yses due to damage (n = 8) or presence of feather lice (n = 2). Feathers from birds of known age included 74 old males, 10 old females and 3 young males.

Statistical analyses were performed using SuperANOVA 1.11 (Abacus Concepts 1989) and SPSS 4.0.1. (SPSS 1990) for the Macintosh computer. To reduce the probability of falsely rejecting null-hypotheses in comparing the success of the various aging methods, we adjusted the significance level to take account of the number of tests performed. This was done using the sequential Bonferroni technique (Holm 1979, Rice 1989).

RESULTS

AGE DETERMINATION BASED ON FEATHER WEAR

Discriminant analysis using total wear score. There was no overlap in the total wear score for old ($\bar{x}$ = 8.64, SD = 1.88, n = 74) compared to young males ($\bar{x}$ = 15.0, SD = 1.0, n = 3) with younger males showing more wear (see Fig. 2, one-way ANOVA, $F_{1,75}$ = 33.54, P < 0.001). A discriminant analysis using total wear score as the sole predictor variable, classified 90.9% of the males correct (no young birds were misclassified, n = 74 old, 3 young, Wilk's Lambda = 0.691, χ^2 = 27.54, df = 1, P < 0.001). By including known old females (n = 10) the model classified 92.0% correctly (no old females or young males were classified wrongly, Wilk's Lambda = 0.703, χ^2 = 29.84, df = 1, P < 0.001). Females (Fig. 3) showed significantly less wear than did males (ignoring age; males: $\bar{x}$ = 10.98, SD = 3.03, n = 305; females: $\bar{x}$ = 9.35, SD = 3.13, n = 105; one-way ANOVA, $F_{1,408}$ = 22.11, P < 0.001). Considering only known old birds, females still showed less wear than did males, although the difference was not significant (males: $\bar{x}$ = 8.64, SD = 1.88, n = 74; females: $\bar{x}$ = 7.5, SD = 1.35, n = 10; one-way ANOVA, $F_{1,82}$ = 3.38, P = 0.07, ns).

Discriminant analysis using all wear score variables. Discriminant analysis models using all six wear score variables (see Table 1) classified 98.7% of males and 98.9% of both sexes to the correct age group. Again no females or young males were incorrectly classified (standardized canonical discriminant function coefficients for males, direct method: BI = 0.363, BO = 0.526, BUI = 0.101, BUO = 0.227, HI = −0.151, HO = 0.399; Wilk's Lambda = 0.637, χ^2 = 32.5, df = 6, P < 0.001; standardized canonical discriminant function coefficients for both sexes together, direct method: BI = 0.368, BO = 0.526, BUI = 0.071, BUO = 0.216, HI = −0.156, HO = 0.420; Wilk's Lambda = 0.644, χ^2 = 36.06, df = 6, P < 0.001). A stepwise procedure classified correctly the same percentages as above of both males

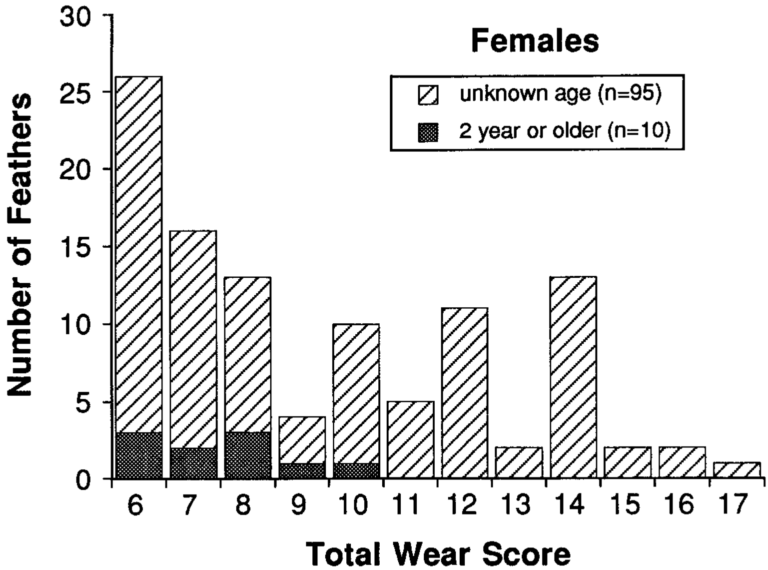

FIGURE 3. Total wear score for Great Snipe females captured during the breeding season in Gåvålia, Norway, 1987–1990 and 1992.

alone and males and females together, but did not include BUI and HI (standardized canonical discriminant function coefficients for males, in the same order as they entered the model according to the stepwise criteria: BO = 0.527, HO = 0.323, BI = 0.354, BUO = 0.237; Wilk's Lambda = 0.64, $\chi^2 = 32.57$, df = 4, $P < 0.001$).

Subjective estimation of age. A subjective assignment of age (young, intermediate, old) by simply looking at the feathers correlated well with wear score ($n = 410$, $r_s = -0.85$, $P < 0.001$), but there was some overlap in wear score between the age groups (Fig. 4, only males shown). Ninety of 410 feathers (22.0%) were judged intermedi-

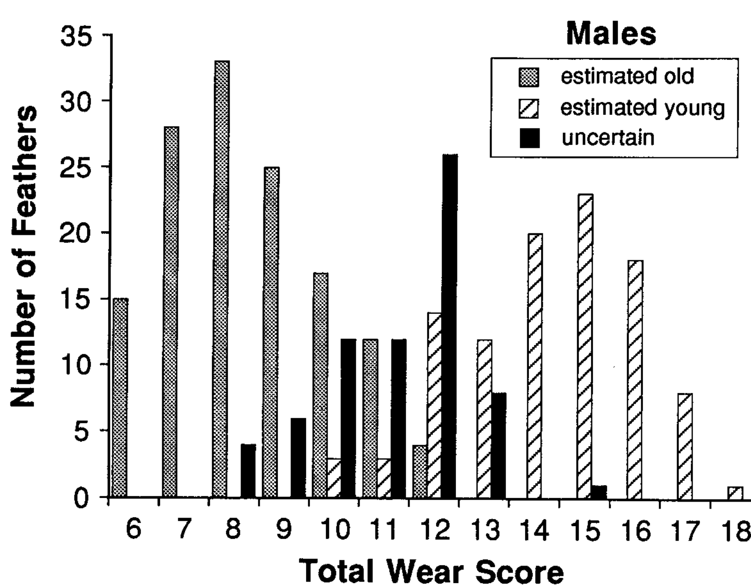

FIGURE 4. Subjective assignment of age in relation to total wear score in Great Snipe males captured during the breeding season in Gåvålia, Norway, 1987–1990 and 1992.

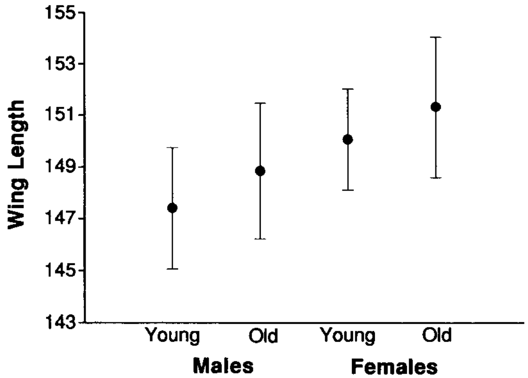

FIGURE 5. Mean (±SD) wing length during the breeding season for young (second year) and old (three years plus) males and females, 1986–1992. Young birds are those banded as downy the year before, or had a total wear score of 14 or more. Old birds are those banded as adult the year before or earlier, or had a total wear score of 9 or less. The difference in wing length between young (n = 71) and old (n = 273) males was significant (one-way ANOVA, $F_{1,342}$ = 17.87, P < 0.0001). The difference in wing length between young (n = 17) and old (n = 116) females was not significant (one-way ANOVA, $F_{1,131}$ = 3.37, P = 0.069, ns).

ate. Of those feathers with known age (n = 84 old, 3 young), 78.2% were correctly aged by the subjective estimate, 4.6% wrongly aged and 17.2% not aged. All young feathers (n = 3) and all female feathers (n = 10) were correctly aged.

Increase in feather wear over season for old birds. Among males known to be old there was a significant increase in total wear score during the breeding season (pooled data from 1987–1990; n = 71, y = 6.505 + 0.084 x, R^2 = 0.163, F = 13.45, P < 0.001). There was a tendency that the relationship between total wear score and date differed between years (ANCOVA, date-year interaction, $F_{2,65}$ = 3.07, P = 0.053, ns).

AGE DETERMINATION USING MORPHOLOGY

Discriminant analysis based on known age. A stepwise discriminant model using morphology classified only 57.0% of the males correctly (n = 3 young, 211 old; only number of white tail feathers passed the criteria for variable entering; Wilk's Lambda = 0.985, χ^2 = 3.18, df = 1, P = 0.075, ns). By forcing all variables into the model simultaneously (direct method), 72.4% of males were classified correctly (the standardized canonical discriminant function coefficients were: bill length = −0.097, number of white tail feathers = 0.723, bill plus head = 0.564, tarsus length = −0.524, wing length = 0.199, length of white on tail = −0.001; Wilk's Lambda = 0.975, χ^2 = 5.30, df = 6, P = 0.505, ns).

Discriminant models based on known and estimated age. In these analyses, we grouped birds known to be old and those with a total wear score of 9 or less as "old," and birds known to be young and those with a total wear score of 14 or greater as "young." This permitted us to analyze males and females separately. A stepwise model for males classified 64.6% correctly (n = 220 old, 65 young; standardized canonical discriminant function coefficients, in order of entering the model: wing length = 0.778, number of white tail feathers = 0.377, bill plus head = −0.449, length of white on tail = 0.284, Wilk's Lambda = 0.919, χ^2 = 23.82, df = 4, P < 0.001). By forcing all variables into the model simultaneously, 65.3% of the males were correctly classified (standardized canonical discriminant function coefficients: bill length = −0.162, number of white tail feathers = 0.365, tarsus length = −0.043, length of white on tail = 0.282, bill plus head = −0.336, wing length = 0.779, Wilk's Lambda = 0.917, χ^2 = 24.19, df = 6, P < 0.001). The two variables that best separated young and old males were thus wing length (Fig. 5) and number of white tail feathers (Fig. 6). For comparison, Figures 5 and 6 also show wing length and number of white tail feathers, respectively, according to age for females.

A stepwise model for females classified 60.6% of the cases correctly, and only wing length passed the variable selection criteria (n = 96 old, 13 young; Wilk's Lambda = 0.969, χ^2 = 3.37, df = 1, P = 0.066, ns). A direct model classified 65.1% correctly (standardized canonical discriminant function coefficients: bill length = −0.806, number of white tail feathers = −0.301, tarsus length = −0.343, length of white on tail = 0.147, bill plus head = 1.131, wing length = 0.678, Wilk's Lambda = 0.941, χ^2 = 6.30, df = 6, P = 0.391, ns).

COMPARISON OF THE METHODS

Although some discriminant models using morphology were not significant (i.e., there was more than a 5% probability that the mean of the discriminant scores was the same in young and old birds, based on Wilk's Lambda), we compared the effectiveness of the various models. The discriminant analysis model using all feather wear scores separated significantly more males than any of the models using morphology, as did the model using only total wear score. The fraction of males correctly classified by the subjective guessing of age was lower than both the discriminant model using all wear scores and the model using only total wear score. The subjective guessing classified more males than the stepwise model using morphology, but not more males than the other models using morphology (χ^2 tests; 15 comparisons, significance adjusted by sequential Bonferroni technique). Further, there was a tendency that the model using all wear scores separated more males than the model using only total wear score (98.7% vs. 90.0%, two-tailed Fisher exact test, $P = 0.063$, ns).

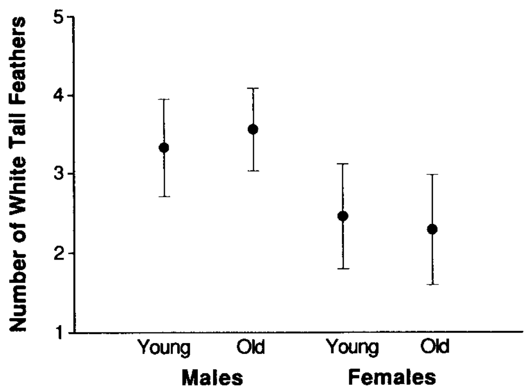

FIGURE 6. Mean (±SD) number of white tail feathers (NWTF, tail feathers with more than 50% white) during the breeding season for young and old males and females, 1987–1992. Birds grouped to age as in Figure 5. The difference in NWTF between young ($n = 66$) and old ($n = 223$) males was significant (Kruskal-Wallis one-way ANOVA, corrected for ties, $\chi^2 = 6.63$, $P = 0.01$). The difference in NWTF between young ($n = 13$) and old ($n = 99$) females was not significant (Kruskal-Wallis one-way ANOVA, corrected for ties, $\chi^2 = 0.93$, $P = 0.33$, ns).

DISCUSSION

Our results demonstrate that one year old (first summer) Great Snipe showed more primary feather wear than older birds during the breeding season, and that the extent of wear can be used to age individuals. By including all wear scores in a discriminant model instead of the sum of wear scores (total wear score), the percentage of males correctly classified to age increased. This might be because the difference in wear between young and old birds differed between the wear variables. Differential wear on the outer web variables seemed to be more important in discriminating ages than wear on the inner web variables. This is probably a consequence of the outer web being more exposed than the inner web. Likewise, barb wear was more important than hook wear, which was more important than barbule wear (based on the standardized canonical discriminant function coefficients). Therefore, total wear score might include unnecessary "noise." However, there was no overlap between the age groups in total wear score.

Females showed less wear than males when ignoring age, but no female known to be young was available to us. Sex-related differences in feather wear in this species might partly be due to males being more exposed to contact with vegetation during their lekking behavior. Among old males we found an increase in total wear score during the breeding season. Unfortunately, too few old females were available for comparison. However, the difference in wear between the two sexes will probably also be influenced by the timing of molt the preceding fall, as Devort and Paloc (1992) found that females complete primary molt later than males. The only previous report, known to us, of a sex-related difference in feather wear is the finding by Francis and Wood (1989) that female primaries wear faster in some species of wood-warblers (Parulinae) than male primaries.

Discriminant analysis based on feather wear was a better predictor of age than analysis using morphological variation. However, several morphological variables contributed significantly to discriminate between young and old males. Age-related difference in wing length is a common phenomenon in birds (see references in Alatalo et al. 1984, Francis and Wood 1989, Nakamura 1990). In Great Snipe, this might simply be because of more primary feather wear in young birds. In addition, the length of new primary feathers may increase with age, as has been found in other shorebirds (see e.g., Pienkowski and Minton 1973). The amount of white on the tail of Great Snipe males is previously known to be age-related (Höglund et al. 1990a), but also to fluctuate between years (Höglund et al. 1992). Elsewhere, we will explore the effects of age, year and cohort on morphological variation in this species.

When we simply looked at feathers without using a microscope, we were unable to age all feathers correctly, and about 20% were judged intermediate. Although this visual impression correlated well with total wear score, there was

TABLE 2. Summary of the juvenile molt pattern and methods for aging Nearctic and Palearctic shorebirds during the breeding season (see Appendix 1 for data). Numbers refer to number of species. We have here counted *Pluvialis dominica dominica* and *P. dominica fulva* as two separate species.

Molt pattern	All can be aged by other characters	Not all can be aged by other characters
All 2y individuals have older primaries than adults or show contrast between old and new (all individuals can potentially be aged by primary wear).	13	64
Some, but not all 2y individuals, have older primaries than adults or show contrast between old and new (some individuals can potentially be aged by primary wear).	1	29
All 2y individuals have molted the juvenile primaries (no individuals can be aged by primary wear).	2	4

some overlap. This method may be of a higher value in the field where it is possible to look at more feathers on the same bird. This eliminates the need for cutting off feather tips. Our experience is, however, that some birds must be left unaged also in the field as wear will be judged as intermediate. For other species of shorebirds, there may be more distinct differences in wear between young and old birds. Then there should be no need for cutting off feather tips, but one should always compare the effectiveness of the aging method for a sample of birds with known age, and also consider the inclusion of a group of birds with "intermediate wear." If one needs to cut off feather tips, this should be done for the feathers most exposed to wear (one of the outermost primaries). Our experience with Great Snipe is that only the terminal 0.5 cm of the feather need to be examined, and thus cut off. This minimizes one possible harmful effect of the method: that the tips of feathers nearby the one cut off tend to be damaged (pers. observ.), probably because they become more exposed to wear and tear.

MOLT PATTERN AND THE SCOPE FOR AGING OF SHOREBIRDS BY PRIMARY WEAR

For the majority of Nearctic and Palearctic shorebirds (68.1%, see Table 2 and Appendix 1), differential primary feather wear of some sort is an available aging method during the breeding season, and the only method to age all individuals in 56.6% of the species. For some species this involves comparing the outer primaries with the inner, as young birds will have replaced only the outer primaries. Such young birds show contrasting degree of wear between the inner and outer primaries, whereas old birds show evenly new primaries. In such cases it is relatively easy to age most individuals during the breeding season. However, in most species no young birds or only some will molt the outer primaries in spring. In this case one could either examine cut-off feather tips the way we have described or, if the difference in wear is more pronounced, test the reliability of age determination in the field on a sample of birds with known age. In addition, one should always check whether there is any contrast in wear between the inner and the outer primaries. We have never noticed such partial postjuvenile primary molt in Great Snipe.

In other species, it is probably impossible to age all individuals according to feather wear as some young birds molt all primaries before the breeding season (26.5% of the species, Table 2 and Appendix 1). In 5.3% of the species it is probably impossible to age any individuals according to primary feather wear as all young birds molt all primaries before the breeding season. Beware that variation in molt pattern among young birds is poorly known in most shorebirds, and is generally in need of more study. Note that in some species there is geographical variation in the molt pattern of young birds. Note also that in some species many 2y birds (as well as some older) do not migrate to the breeding grounds in their first spring, but instead spend this summer in the south (McNeil 1970, van Dijk et al. 1990). These 2y individuals might molt differently from those who migrate, but this is largely unexplored. We have not been able to indicate such variation in Appendix 1, and we present information on the molt of 2y birds ignoring their migratory status. Melville (1981) examined migrating *Calidris ferruginea* in spring in Hong Kong, and found birds with fresh primaries (adults), all primaries worn, only inner primaries worn or with ongoing primary molt. This suggests (*contra* Melville 1981) that some 2y birds of this species migrate to breeding areas, and also that both 2y birds that do not molt and those who molt their outer primaries may migrate. Melville (1981) also examined some *C. ruficollis* with abraded primaries. This suggests that 2y birds of this species also might migrate to the breeding areas, although many do not (Paton and Wykes 1978).

In several species of shorebirds, 2y individuals molt their primaries earlier in the fall than do older birds (e.g., *Haematopus ostralegus,* Boere 1976, Wilson and Morrison 1981; *Pluvialis squatarola,* Boere 1976, Prater et al. 1977; *Calidris canutus,* Boere and Smit 1981a, Barter 1992; *C. alpina,* Gromadzka 1986; *Limosa lapponica,* Boere 1976; *Numenius arquata,* Cramp and Simmons 1983; *Arenaria interpres,* Boere 1976, Branson et al. 1979). Thus, in some species it might be possible to separate both first summer, second summer and older individuals using primary wear (see Johnson and Johnson 1983 on *Pluvialis dominica fulva*).

We have not included information on adult primary molt in Appendix 1, but beware that the timing of adult molt varies among species. In the genus *Calidris* (see Holmes 1966, 1971, 1972; Bengtson 1975), some species molt all primaries on the breeding grounds before migration in fall (*C. maritima,* some populations of *C. alpina*), others molt only some primaries (i.e., suspended or "arrested" molt, see Ginn and Melville 1983 for terminology) before migration (*C. mauri*) and some migrate before molting primaries on the wintering grounds (*C. melanotus, C. bairdii, C. pusilla*). This will probably influence the degree of difference in primary wear between first-summer and older individuals. Another potential problem is that the strategy and timing of adult primary molt may vary within a species (e.g., in *C. alpina,* see references in Holmgren et al. 1993) leading to variation in the degree of primary wear among adult birds the following breeding season. Although the completion of primary molt in adult Great Snipe varies by several months (Devort and Paloc 1992), we have here demonstrated that adults consistently showed less wear than young birds during the breeding season.

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APPENDIX 1. Molt of juvenile primary feathers, and age determination of Palearctic and Nearctic shorebirds during the breeding season. Information in footnotes refers to young birds unless otherwise stated, and molt refers to primary molt. Beware geographical variation and that young birds not migrating to the breeding grounds might molt differently from migrating birds, and that in some species a minority might molt all or some primaries without it being discovered. We have excluded some species only marginally breeding in the Palearctic (*Haematopus moquini, Burhinus capensis, Esacus recurvirostris, Glareola lactea*).

Shorebird species	Molt[a]	Other characters[b]	Source[c]
Rostratula benghalensis	A?	–	14
Haematopus ostralegus	N	+	8, 16, 26, 31, 50
H. palliatus	N	?	54
H. bachmani	N	–	54, 70
Ibidorhyncha struthersii	N	(+?)	54
Himantopus himantopus	N	+	14, 27, 54
H. mexicanus	N	?	54
Recurvirostra avosetta	N	(+)	14, 54
R. americana	N	–	54
Dromas ardeola	N	(+?)	14, 54
Burhinus oedicnemus	N, (A)	–	14, 54
B. senegalensis	N*[d]	(+)	14, 54
Pluvianus aegyptius	N*[d]	–	54
Cursorius cursor	A, O, I?[e]	–	14, 54
Glareola pratincola	A	(+)	14, 54
G. maldivarum	A	?	54, 75
G. nordmanni	A	+	14, 54
Charadrius dubius	N, (A?)	(+)	14, 25, 54
C. hiaticula	N, I, A*	+	7, 24, 25, 30
C. semipalmatus	N	?	14, 54
C. placidus	N	–	54
C. wilsonia	N	+	54
C. vociferus	N	–	14, 54
C. melodus	N	–	54
C. pecuarius	N, (A?)	(+)	14, 54, 62
C. alexandrinus	N	(+)	6, 14, 25
C. mongolus	N, I, A*	–	14, 54, 74
C. leschenaultii	N, O, (I), (A?)*	–	1, 14, 54

APPENDIX 1. Continued.

Shorebird species	Molt[a]	Other characters[b]	Source[c]
C. asiaticus	N	–	14, 54
C. veredus	N	(+)	54
C. montanus	N	+	54
Eudromias morinellus	N?	+	14, 54
Pluvialis dominica dominica	A	+	35
P. dominica fulva	N	(+)	2, 13, 36
P. apricaria	N	+	14, 54
P. squatarola	N	+	9, 14
Hoplopterus spinosus	N	(+)	14, 54
Vanellus cinereus	N	(+)	54
V. indicus	N	–	14, 54
V. vanellus	N	+?	14, 26, 54
Chettusia gregaria	N	–?	14, 54
C. leucura	N	(+)	14, 54
Aphriza virgata	N	–	54
Calidris tenuirostris	N, A, (O), (I)	–	4, 14, 54, 72
C. canutus	N, (I?), (O), (A)*	(+)	5, 14, 54, 68
C. alba	N, A, (O)*[f]	(+)	14, 17, 40, 67
C. pusilla	N, O, (A)	–	14, 28, 59
C. mauri	N	–	14, 54
C. ruficollis	N, (O)	(+)	14, 20, 37, 43, 54, 71
C. minuta	O, A, (N)*	(+)	14, 45, 48, 54, 63, 64
C. temminckii	O	(+)	14, 54
C. subminuta	N	–	14, 54
C. minutilla	N, O, (A)*	–	14, 42, 54, 58, 59
C. fuscicollis	N, (O), (A)	(+)	14, 54
C. bairdii	N, (O), (A)	(+)	14, 32, 54
C. melanotus	N, (A?)	–	14, 54
C. acuminata	N, A, O	–	4, 14, 54
C. ferruginea	O, (A), (N)*	(+)	4, 14, 19, 37, 44, 45, 49, 54, 64, 68
C. maritima	N	+	14, 54
C. ptilocnemis	N	(+)	54
C. alpina	N	+	14, 54
Eurynorhynchus pygmeus	N	+	54
Limicola falcinellus	O	(+)	14, 22, 54
Micropalama himantopus	O, (N)	?	14, 54, 59
Tryngites subruficollis	A, (N?)	(+?)	14, 54
Philomachus pugnax	N, O[g]	(+)	14, 39, 45, 47, 54, 56, 64
Lymnocryptes minimus	N?	–	14, 54
Gallinago gallinago	N	?*	14, 38, 54, 66
G. media	N	–	14, 18, 54, 61
G. stenura	N	–	14, 54
G. megala	N	–	54
G. hardwickii	A[h]	–	21, 54
G. solitaria	N?	–	54
G. nemoricola	N	(+)	54
Limnodromus griseus	N, (O)	–	14, 54
L. scolopaceus	N	–	14, 54
L. semipalmatus	N	–	54
Scolopax rusticola	N	–	12, 14, 54
Philohela minor	N	–	41, 54, 57
Limosa limosa	N	(+)	14, 54
L. haemastica	N	+	54
L. lapponica	N, A*	(+)	3, 4, 14, 15, 29, 54
L. fedoa	N	–	54
Numenius minutus	N, (O), (A?)	–	14, 54
N. borealis	N	–	54

APPENDIX 1. Continued.

Shorebird species	Molt[a]	Other characters[b]	Source[c]
N. phaeopus	N, (A)*[i]	–	14, 34, 54
N. tahitiensis	N, (A)[i]	?	34, 54
N. tenuirostris	N	–	14, 54
N. arquata	N	–	14, 52, 54
N. americanus	N	–	54
N. madagascariensis	N, (I)	(+)	4, 54, 73
Bartramia longicauda	N	–	14, 54
Tringa erythropus	N	+	14, 54
T. totanus	N	(+)	8, 14, 54
T. stagnatilis	N, O*	–	14, 45, 54, 64
T. nebularia	N, O*	–	8, 14, 45, 54, 64, 65
T. guttifer	N	–	54
T. melanoleuca	N	–	14, 54, 59
T. flavipes	O, (N)	–	14, 54, 59
T. solitaria	O, (A?)	–	14, 54, 59
T. ochropus	N, (O)	–	14, 54
T. glareola	N, O*	(+)	14, 45, 54, 64
Xenus cinereus	N, O*	–	14, 23, 54, 69
Actitis hypoleucos	A, O*	(+?)	8, 10, 14, 45, 46, 51, 54, 64
A. macularia	A, (O)	(+?)	14, 54
Heteroscelus brevipes	O, (A), (I)	–	4, 53, 54
H. incanus	O, (A)[j]	–	34, 53, 54
Catoptrophorus semipalmatus	N	+	54
Arenaria interpres	N, (I)*	(+)	4, 14, 24, 34, 54
A. melanocephala	N	–	54
Phalaropus tricolor	N, (A?)	–	11, 14, 33, 54
P. lobatus	N, A?[k]	–	14, 54, 55, 60
P. fulicarius	N, (O?)[l]	–	14, 54

[a] N = No juvenile primary molt before the first breeding season, O = Juvenile birds molt outer primaries before the first breeding season, I = Juvenile birds molt inner primaries before the first breeding season, A = Juvenile birds molt all primaries before the first breeding season, ( ) = Only a minority of birds molt in this way, ? = Uncertainty, * = Geographical variation.

[b] + = Ageable by other characters during the breeding season, (+) = Only some birds ageable by other characters, – = Not ageable by other characters.

[c] Sources: 1) Barter 1988a, 2) Barter 1988b, 3) Barter 1989, 4) Barter and Davidson 1990, 5) Barter et al. 1988, 6) Becker 1981a, 7) Becker 1981b, 8) Boere 1976, 9) Branson and Minton 1976, 10) Brown 1974, 11) Burger and Howe 1975, 12) Clausager 1973, 13) Connors 1983, 14) Cramp and Simmons 1983, 15) Cronau et al. 1986, 16) Dare and Mercer 1974, 17) Davies 1982, 18) Devort and Paloc 1992, 19) Elliot et al. 1976, 20) Evans 1975, 21) Frith et al. 1977, 22) Fry 1989, 23) Fry 1990, 24) Ginn and Melville 1983, 25) Glutz von Blotzheim 1972, 26) Glutz von Blotzheim et al. 1975, 27) Glutz von Blotzheim et al. 1977, 28) Gratto and Morrison 1981, 29) Greene 1973, 30) Holz 1987, 31) Hulscher 1981, 32) Jehl 1979, 33) Jehl 1987, 34) Johnson 1977, 35) Johnson 1985, 36) Johnson and Johnson 1983, 37) Melville 1981, 38) Münster 1975, 39) Münster 1991, 40) Myers et al. 1985, 41) Owen and Krohn 1973, 42) Page 1974, 43) Paton and Wykes 1978, 44) Paton et al. 1982, 45) Pearson 1974, 46) Pearson 1977, 47) Pearson 1981, 48) Pearson 1984, 49) Pfister 1972, 50) Pienkowski and Knight 1975, 51) Pienkowski et al. 1976, 52) Poslawski 1969, 53) Prater and Marchant 1975, 54) Prater et al. 1977, 55) Schamel and Tracy 1988, 56) Schmitt and Whitehouse 1976, 57) Sheldon et al. 1958, 58) Spaans 1976, 59) Spaans 1979, 60) Stresemann and Stresemann 1966, 61) this study, 62) Tree 1973, 63) Tree 1974a, 64) Tree 1974b, 65) Tree 1979, 66) Tuck 1972, 67) Underhill and Whitelaw 1977 cited by Boere and Smit 1981b, 68) Waltner 1976, 69) Waltner and Sinclair 1981 cited by Urban et al. 1986, 70) Webster 1942, 71) Woehler 1983, 72) Barter 1987, 73) Barter 1990, 74) Barter 1991, 75) Johnson et al. 1991.

[d] Variable timing of breeding season and molt.

[e] Complex and variable molt in winter in both young and adult, possibly more wear in young nevertheless.

[f] Birds wintering in the southern hemisphere often molt all or outer primaries during the winter, those wintering in the north do not.

[g] Münster (1991) found that both males and females replace outer primaries, *contra* suggestions (Cramp and Simmons 1983) that only some females molt outer primaries.

[h] Young molt all primaries in spring, probably less wear than adults during the breeding season.

[i] Most of those who replace all primaries will be in moult until June.

[j] Some molt also one or more inner primaries.

[k] Schamel and Tracy (1988) found primary wear not to be useful. This might be in accordance with Stresemann and Stresemann (1966) who reported primary molt in spring, as opposed to the findings of Prater et al. (1977). Both strategies may occur; perhaps only birds migrating to breeding areas molt (Cramp and Simmons 1983).

[l] Perhaps some females molt outer primaries (Prater et al. 1977).

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