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Source: Ardea, 97(3) : 271-280

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/078.097.0302

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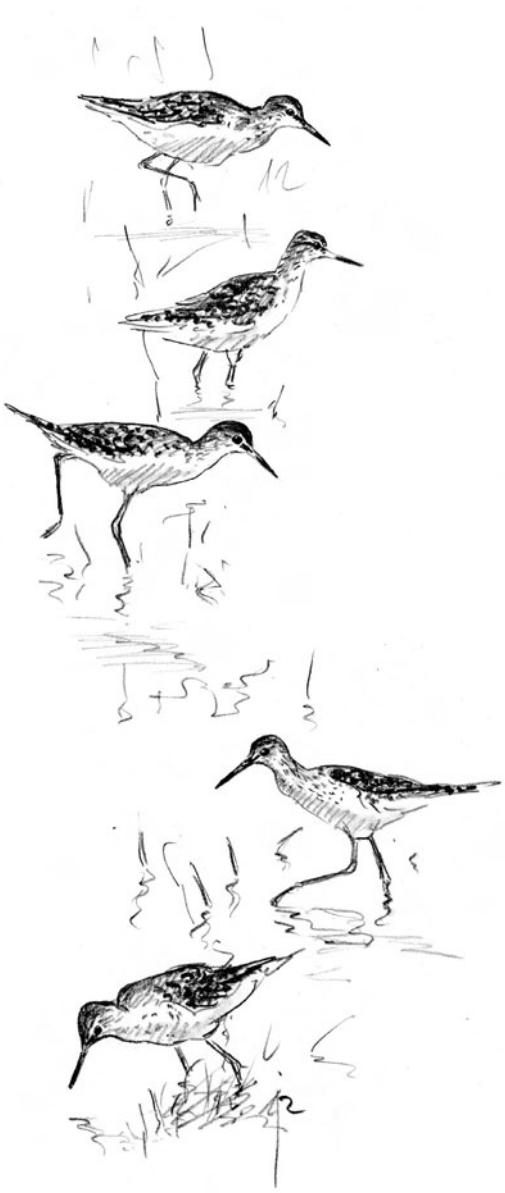
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Extended primary moult as an adaptation of adult Wood Sandpipers *Tringa glareola* to their freshwater habitats in southern Africa

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Remisiewicz M., Tree A.J., Underhill L.G., Gustowska A. & Taylor P.B. 2009. Extended primary moult as an adaptation of adult Wood Sandpipers *Tringa glareola* to their freshwater habitats in southern Africa. Ardea 97(3): 271–280.



Migrant waders using freshwater habitats are hypothesized to have slower primary moult than waders using coastal habitats. We chose the Wood Sandpiper *Tringa glareola* as a representative species using the freshwater habitats and compare its moult pattern with a range of fresh-water and coastal wader species to test the habitat hypothesis. Only fragmentary descriptions of Wood Sandpipers' primary moult in their sub-Saharan non-breeding quarters had existed. We analysed the primary moult formulae of 1496 adult Wood Sandpipers obtained in southern Africa. The Underhill & Zucchini moult model was used to estimate the timing and duration of moult for all 10 primaries combined and for each primary individually. We also estimated the rate of production of feather material during moult. Adult Wood Sandpipers arrive in southern Africa between late July and November, and depart from mid-March to April. Suspension of moult was observed in 56 birds (7.5%) after two to nine primaries had been replaced. The remaining birds performed a continuous complete primary moult, with average start and completion dates of 21 August and 30 December, respectively; estimated duration was 131 days. The overall rate of production of primary feather material was uniform, achieved by growing up to five small inner primaries simultaneously at the beginning of the moult but only one or two simultaneously while the large outer primaries were growing. Primary moult of adult Wood Sandpipers took longer but ended earlier than in similar-sized waders using coastal habitats. Compared with waders using coastal habitats, Wood Sandpipers prolonged moult by shedding their primaries at longer intervals and by extending the growth period of each primary. The longer primary moult and its earlier ending compared with coastal waders are probably adaptations to Wood Sandpipers' use of freshwater habitats, which in southern Africa provide unpredictable food supplies and might require nomadic movements between ephemeral inland wetlands.

Key words: Wood Sandpiper, *Tringa glareola*, primary moult, southern Africa, shorebirds

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INTRODUCTION

Different life histories have been suggested for waders using coastal and freshwater habitats with consequential contrasting attributes such as migration distances, genetic variability and immunocompetence (Piersma 1997, 2003). Moult, being an important part of the life-cycle and migration strategy, might also differ between species that use coastal and inland wetlands. A variety of primary moult strategies has been described for long-distance migrant waders in relation to their breeding success, migration distance, or the latitude they may reach in the non-breeding season (Prater 1981, Ginn & Melville 1983). Most detailed studies of moult patterns have been on tundra-breeding waders that migrate to coastal habitats: Ruddy Turnstone *Arenaria interpres* (Summers *et al.* 1989), Grey Plover *Pluvialis squatarola* (e.g. Serra *et al.* 1999, Serra & Underhill 2006), Sanderling *Calidris alba* (Summers *et al.* 1987, Underhill 2003), Purple Sandpiper *C. maritima* (Morrison 1976, Summers *et al.* 2004), Curlew Sandpiper *C. ferruginea* (Minton *et al.* 2006). This can be attributed to large-scale ringing at coastal localities, combined with the developing methodology of moult studies (Underhill & Zucchini 1988, Underhill *et al.* 1990, Underhill 2003, Underhill *et al.* 2006). In contrast, moult patterns of species that breed in the taiga and use freshwater inland wetlands in the non-breeding season have been poorly studied because of limited material available on these widely dispersed birds. Waders using freshwater wetlands are predicted to need a longer and more flexible strategy because these irregular habitats provide unpredictable food resources (Piersma 2003), in contrast to waders relying on the abundant and predictable food supplies of marine habitats (Velasquez *et al.* 1991, Hockey *et al.* 1992, Underhill 2003, van de Kam *et al.* 2004).

We expect that the Wood Sandpiper *Tringa glareola* represents the group using freshwater habitats. Wood Sandpiper populations of the African-Eurasian migration system breed in the taiga from Fennoscandia to western Siberia. Their non-breeding grounds are the wetlands of sub-Saharan Africa, including the mesic northeastern part of southern Africa (Cramp & Simmons 1983, Lebedeva *et al.* 1985, Underhill 1997, Underhill *et al.* 1999). Unlike many wader species in which first-year birds skip their first breeding opportunity, most first-year Wood Sandpipers return to the breeding grounds aged about nine months, a factor which simplifies the analysis (Summers *et al.* 1995, Underhill 1997, 2006). Though the Wood Sandpiper is often abundant at stopover and non-breeding grounds, descriptions of its moult are fragmentary and do not provide a wider overview (Hoffmann 1957, Tree 1974, Pearson 1974, Ginn & Melville 1983, Pinchuk *et al.* 2008).

This paper has two aims. (1) To identify the adult Wood Sandpiper's strategy for primary moult in the southernmost part of its non-breeding range by analysing a large data set of moult records collected in southern Africa since 1900. (2) To verify the hypothesis that the Wood Sandpiper's primary moult has distinctive attributes related to its use of freshwater habitats which contrast with those of waders using coastal habitats in southern Africa.

METHODS

We analysed the primary moult formulae of 1496 adult Wood Sandpipers from three sources: 116 specimens from the National Museum of Zimbabwe in Bulawayo collected in 1900–1975 and examined by AJT; 1277 birds ringed in southern Africa in 1966–1999 by AJT, and 103 birds ringed in 2001–2007 by PBT (with MR and AG in 2007). Most of the museum specimens originated from Zimbabwe, with a few from Botswana. Data on live birds were obtained from irregular mist-netting at wetlands in Zimbabwe and South Africa (Fig. 1). The state of moult in the primaries of one wing was recorded as a moult formula, a string of 10 digits, one for each primary, following the standard approach: scores of 0 and 5 indicate old and replaced feathers, respectively, and intermediate values describe growth stages (Ashmole 1962, Ginn & Melville 1983).

Wood Sandpipers were aged by their plumage as first-year, second-year, or adult birds. First-year and second-year birds (up to c. 18 months) were aged by the retained juvenile-type inner median coverts or by the contrast between two generations of primaries showing partial moult (Prater *et al.* 1977, MR unpubl. data). From about December of their second year immatures become indistinguishable from adults. Birds aged as second-year birds were excluded from this analysis; however, our sample contains a small number of unidentified second-year birds, especially among those captured after December. Most of these birds had completed migrations to and from the breeding grounds, and their moult is likely to have become synchronized with the adults.

Only the moult formula described at the first capture of an individual in a season was used in estimating moult parameters. Moult records were pooled, assuming they were representative of all southern African

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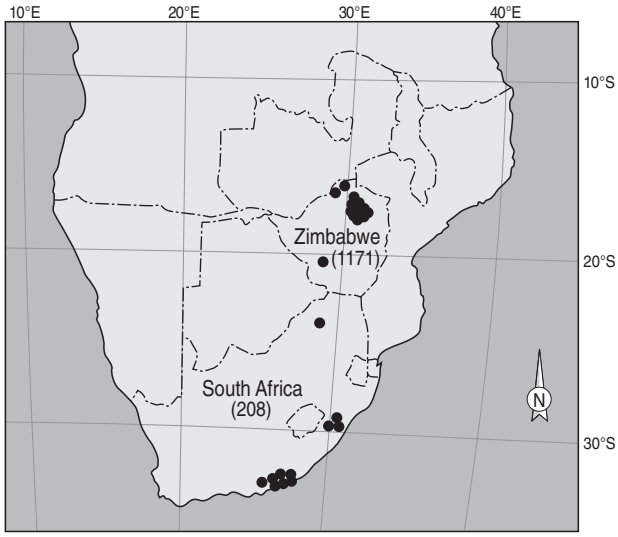


Figure 1. Catching sites of Wood Sandpipers in Zimbabwe and South Africa. The number of birds from each country are shown.

birds. The date of capture or collection was taken as the number of days from 1 June; records from all years were combined because we lacked sufficient data from any year to estimate annual moult parameters. Birds with suspended moult (e.g. a moult formula of 5550000000, with no growing feathers) were distinguished from those in continuous moult (scores of 1, 2, 3 or 4 in the moult formula). Birds that had suspended and then resumed moult could not be identified by the moult formulae.

Two approaches were used to obtain the starting date of primary moult and its duration for birds in continuous moult. Firstly, we followed Summers *et al.* (1989, 2004), Underhill & Summers (1993) and Serra *et al.* (1999) and used the Underhill & Zucchini (1988) model to analyse the entire tract of 10 primaries combined. Moult data were of Type 2 (Underhill & Zucchini 1988) because most adult Wood Sandpipers had not commenced moult on arrival in August to October and they were available for sampling of moult (Fig. 2). The exceptionally early moulters were a few so they hardly influenced the results. From the moult formula we calculated the Proportion of Feather Mass Grown (PFMG) (Underhill & Summers 1993). Assuming primary feather tissue is deposited at a continuous rate, this provided the moult index required by the Underhill & Zucchini (1988) model. The calculation of PFMG from the moult formula (Underhill *et al.* 1993, Underhill & Joubert 1995) requires the mean relative mass of each primary; to obtain this we weighed the dried primary feathers of six dead adult Wood Sandpipers, and averaged the relative masses for each primary (Table 1). Moult parameters (mean starting date, standard deviation of mean starting date, and moult duration) were estimated using the software described in Brandão (1998) and in Underhill *et al.* (2006). The confidence limits for the moult starting date (when 95% of birds had started to moult) were calculated as the estimated mean starting date ± 1.96 × standard deviation.

Secondly, we used the Underhill & Zucchini (1988) model to estimate the moult parameters of individual primaries (as in Underhill 2001, 2003, Serra 2002, Serra & Underhill 2006, Underhill *et al.* 2006). For each primary we created a moult index by transforming its score of 0 to 5 in the moult formula to the values 0, 0.125, 0.375, 0.625, 0.875 and 1 respectively, as described by Serra (2002) and Underhill (2003). The date the first (innermost) primary (P1) started to moult was taken as the date primary moult commenced and the date the outermost primary (P10) ended moult was taken as the date it finished.

The growth rate of the primary feather tract, estimated by the Underhill & Zucchini (1988) model, was compared with the growth rates of primaries calculated from the increase of the PFMG of 16 individuals caught twice in the same season. We computed the weighted average of the difference between the two PFMG values, using the intervals between capture as weights.

The ratio of the relative mass of each primary to its estimated duration of moult provides an estimate of its daily growth rate (units: % PFMG/day). Using these values and the estimated starting and ending dates of moult for each primary, we estimated the daily increments of PFMG for each feather during moult. We summed these increments for each calendar day. This

Table 1. Relative masses of Wood Sandpiper primaries expressed as a percentage of the total mass of primary feathers, based on the weights of primaries of six individuals caught in 2003–06 during northward passage in Poland (W. Meissner, L. Pilacka, P. Gogga in litt.).

Primary	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
Relative mass (%)	4.58	5.34	6.23	7.20	8.81	10.72	12.10	13.61	14.93	16.48

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enabled us to model, for the average bird, the daily production rate of primary feather material and to plot the cumulative growth during moult. If the underlying assumption of the Underhill & Zucchini (1988) moult model is correct, the plot of daily growth values should be constant and the cumulative growth curve should be linear.

We also estimated the Proportion of Feather Mass Missing (PFMM), providing a measure of the size of the gap in the primary feathers during moult that takes into account the relative sizes of the missing feathers. To calculate PFMM we used an approach that is complementary to the calculation of PFMG: feathers with moult scores of 1, 2, 3 and 4 are taken as representing 0.875, 0.625, 0.375 and 0.125 respectively of the missing relative mass of each primary. We used these values for growing feathers as shown by the moult formula, following Ward *et al.* (in press). PFMM is a refinement of the raggedness score of Haukioja (1971) and Bensch & Grahn (1993); raggedness is based only on the moult formula, whereas PFMM takes account of the relative sizes of the feathers.

RESULTS

Pattern and timing of primary moult

The earliest date an adult Wood Sandpiper was caught after arrival was 16 July; four birds had already started to moult by the end of July (Fig. 2). Of the 1496 Wood Sandpipers ringed and examined between July and May, 7% had not yet started to moult, 50% were in moult and 43% had completed their moult (Fig. 2). Of 746 birds in moult, 56 (7.5%) had suspended moult after 2–9 inner primaries had been renewed. 95% of birds with suspended moult were observed between 4 and 23 November; 57% of suspension occurred after seven or eight inner primaries had been replaced (Table 2).

The remaining 690 birds in active moult showed continuous moult of the primaries, starting at P1 and progressing outwards to P10. The PFMG values of four individuals were identified by the model as outliers: formula 0000000000 on 24 October, 5555555554 on 26 October, 4400000000 on 26 November and 5555552100 on 30 January. For Data Type 2 of the Underhill & Zucchini (1988) moult model we included the individuals in active moult (excluding the four outliers), birds that had not started to moult and the birds that had finished moulting, a total sample of 1435 (Fig. 2).

The mean starting date of the primary feather tract moult was estimated to be 21 August; the mean starting date of moult of P1 as an individual primary was 22 August (Table 3). The mean completion dates of primary moult as estimated by the two methods differed by two days: 28 December (completion date of moult of P10) and 30 December (based on the primary feather tract) (Table 3).

The standard deviation of the starting date estimated for the primary tract was 29 days (Table 3), thus the estimated period during which 95% of birds started moult was 112 days between 25 June and 16 October (Fig. 2). Similarly, 95% of adults completed primary moult between 3 November and 24 February. The period between the start of moult of P1 and the end of

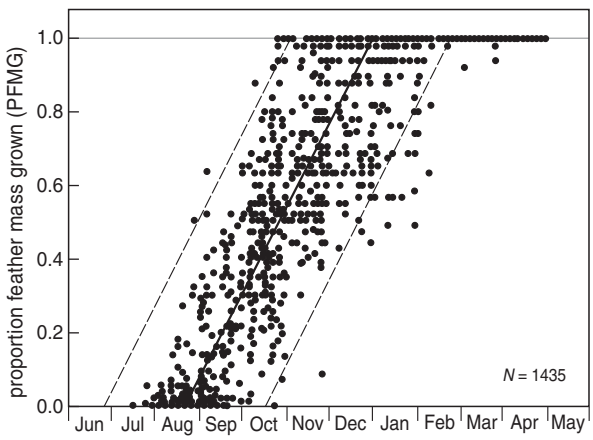


Figure 2. Temporal distribution of the Proportion of Feather Mass Grown (PFMG) of adult Wood Sandpipers in southern Africa. The continuous line shows the timing of moult for an average bird, the dashed lines show estimated confidence intervals between which 95% of birds caught on a particular date ought to fall.

Table 2. Percentages of adult Wood Sandpipers that renewed feathers given below before the suspension of moult in southern Africa (n = 56).

Primaries moulted	P1–P2	P1–P3	P1–P4	P1–P5	P1–P6	P1–P7	P1–P8	P1–P9
Percentage	4	0	2	14	12	25	32	11

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moult of P10 was estimated to be 128 days; based on the primary feather tract the estimated duration of moult was 131 days.

The average moult rate calculated for 16 individuals caught twice in one season was 0.77 PFMG/day (SD = 0.19). This suggested a primary moult duration of 130 days. The average of the estimated moult period for six of these birds trapped more than 30 days apart was 126 days (SD = 31 days). These results confirm the duration of moult obtained by using the moult models.

Moult parameters of individual primaries

The estimated duration of growth for each of the primaries varied from 20 to 31 days (Table 3, Fig. 3). The daily growth rates of the smaller primaries P1 to P4 were about two or three times slower than of the largest P9 and P10 (Table 3, final column). This is shown by the steeper growth lines for the outer primaries than those for the inners (Fig. 3). During the replacement of P1–P4 on average the number of feathers growing simultaneously was larger than three and

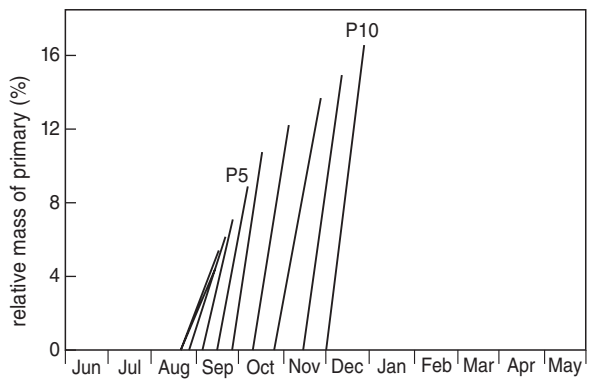


Figure 3. Dates of the start and the end of moult of individual primaries (P1–P10) moulted by adult Wood Sandpipers in southern Africa. The endpoints of lines are at the relative mass of each primary so that the slopes of the lines represent the growth rates of the primary.

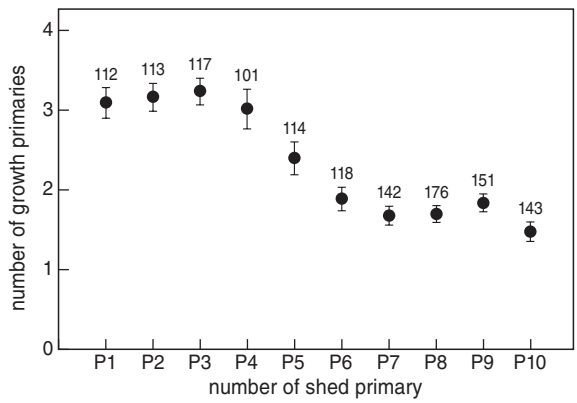


Figure 4. The mean number of simultaneously growing primaries while each of the 10 primaries is in moult. Sample sizes and 95% confidence intervals for the mean are shown.

Table 3. Estimates of moult parameters of each primary and of the 10 primaries as a single tract for adult Wood Sandpipers in southern Africa. The final column provides the estimated daily growth rate of each primary, calculated from the relative feather mass (Table 1) and the estimated moult durations.

Primary	Moult parameters				Sample sizes			% PFMG / day
	Mean start date (SD)	Duration (SD)	Standard deviation of start date (SD)	End date (SD)	Not yet moulted	In moult	Moult complete	
P1	22 Aug (1.6)	25 (1.9)	19 (1.1)	16 Sep (1.5)	108	109	1218	0.18
P2	23 Aug (1.5)	25 (1.9)	19 (1.1)	17 Sep (1.1)	114	108	1213	0.21
P3	28 Aug (1.6)	25 (1.9)	20 (1.1)	22 Sep (1.5)	136	108	1191	0.25
P4	7 Sep (1.5)	20 (1.7)	21 (1.1)	27 Sep (1.5)	183	89	1163	0.36
P5	17 Sep (1.5)	21 (1.7)	20 (1.0)	8 Oct (1.4)	224	105	1106	0.42
P6	27 Sep (1.5)	21 (1.7)	21 (1.0)	18 Oct (1.4)	273	113	1049	0.51
P7	11 Oct (1.6)	25 (1.8)	26 (1.2)	5 Nov (1.5)	350	140	945	0.48
P8	27 Oct (1.7)	31 (1.9)	30 (1.2)	27 Nov (1.7)	440	178	817	0.44
P9	16 Nov (1.7)	27 (1.9)	32 (1.3)	13 Dec (1.7)	556	152	727	0.55
P10	2 Dec (1.8)	26 (1.9)	34 (1.3)	28 Dec (1.8)	650	145	640	0.63
P1–P10	21 Aug (1.7)	131 (2.5)	29 (0.8)	30 Dec (1.4)	108	687	640	0.76

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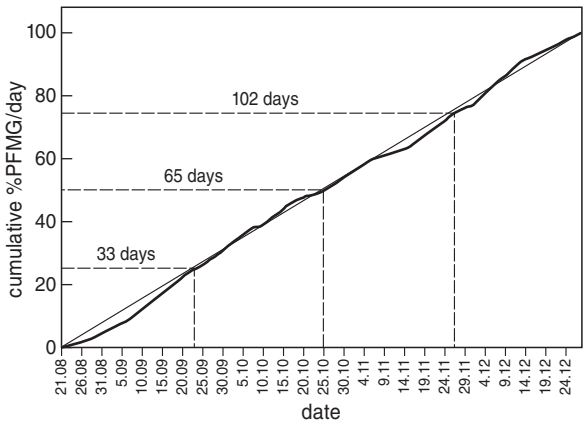


Figure 5. The cumulative Proportion of Feather Mass Grown (PFMG) during moult. The straight line shows a uniform growth rate. The dashed lines represent the dates on which the quartiles of PFMG are reached; the number of days from the start of moult taken to reach each quartile is given.

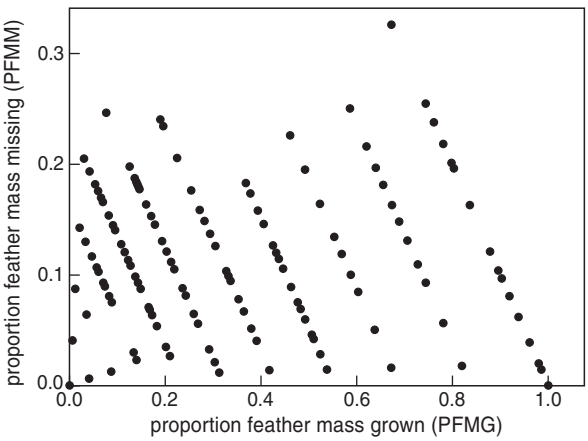


Figure 6. The relationship between the size of the gap in the primaries during moult, expressed as a Proportion of Feather Mass Missing (PFMM) and Proportion of Feather Mass Grown (PFMG). The pattern of parallel lines is a consequence of the recording of moult scores for individual feathers to integer values.

during the replacement of P6–P10, the average was less than two (Fig. 4). For P1–P5, the estimated intervals between shedding successive primaries were 1–10 days (mean 7 days), and for P6–P10 they were 10–20 days (mean 15 days) (Table 3, Fig. 3).

Rate of primary feather mass production

Using daily production rates of primary feather material for each individual primary (Table 3, final column) and considering the overlapping growth of neighbouring primaries, the plot of the cumulative feather mass growth during moult was nearly linear (Fig. 5). The intervals between which the quartiles of PFMG were achieved were similar (Fig. 5). This indicates that PFMG increased at an almost constant rate.

Size of the wing gap during primary moult

The mean size of the wing gap described by PFMM was 0.10 (SD = 0.056, range 0.01–0.03), so that, on average, birds were missing 10% of their primary flight feathers' mass during moult (Fig. 6). The two largest values were 0.33: one bird was replacing its three outer primaries (formula 5555555311 on 11 January), and an exceptional bird was recorded with seven actively growing primaries (formula 5554443322 on 13 November). In birds with active moult, the Proportion of Feather Mass Missing (PFMM) was negatively correlated with PFMG ($r = –0.19$, $P < 0.001$) so that gaps tended to be larger at the start of moult than at the end.

DISCUSSION

Pattern and timing of moult

More than 90% of adult Wood Sandpipers that migrate to southern Africa performed a continuous complete moult of their primaries. This confirms previous studies which indicate most adult Wood Sandpipers moult only after reaching the non-breeding grounds (Tree 1974, Ginn & Melville 1983). The estimated mean date for the start of moult, 21 August, and the upper limit of the 95% confidence interval, 16 October (Fig. 2), correspond with the stated arrival period of Wood Sandpipers in southern Africa, from late-July but mostly August-September (Underhill 1997, Oschadleus 2002). The lower limit of the confidence interval for the starting date of moult was 25 June (Fig. 2), earlier than the accepted date of arrival in southern Africa. Reconsideration of the modelled reporting rates for Wood Sandpipers in Zimbabwe (Zone 5 in Underhill 1997) shows that reporting rates increase from July and became stable in early October, with arrivals progressively later farther south and east in southern Africa. Given that most birds in this study were captured in Zimbabwe, the lower confidence interval of the starting date of moult is consistent with the early arrival of failed breeders. Overall, the pattern suggests that most migrants commence primary moult shortly after arriving in southern Africa. Thus the 112-day 95% confidence interval for the start of moult probably reflects a genuine lack of synchronisation of moult. Wood Sandpipers migrate to southern Africa from breeding grounds stretching from Scandinavia to west-

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ern Siberia (Underhill *et al.* 1999), so they migrate between c. 8 000 km and 12 000 km. This is probably another reason for the extended period of arrival (Underhill 1997); and consequently the prolonged period over which they begin their moult.

The end of primary moult was estimated, on average, to be late December; departure on northward migration does not take place until mid-March or April (Underhill 1997, Hockey *et al.* 2005). Waders which use mainly coastal habitats, such as Knot, Sanderling, Ruddy Turnstone and Grey Plover, finish moulting their primaries in southern Africa in January or February (Serra *et al.* 1999, Underhill 2003) and depart for their breeding grounds one to two months later, in March and April (Hockey *et al.* 2005). Coastal birds can rely on a fairly constant food supply at tidal mudflats while accumulating reserves before migration (Velasquez *et al.* 1991, Hockey *et al.* 1992, Underhill 2003, van de Kam *et al.* 2004). Wood Sandpipers have two to three months between the completion of primary moult and their departure. During this period the Wood Sandpipers continue replacing other feather tracts, such as secondaries, tertials and rectrices, accumulate reserves and acquire breeding plumage before migration (Ginn & Mellville 1983, AJT, MR unpubl. data). The longer period for these activities compared with coastal waders is probably an adaptation to their use of unpredictable food resources at freshwater habitats (Piersma 2003) and their possible need to move between suitable wetlands. In northeastern southern Africa, where Wood Sandpipers mostly occur, the end of moult coincides with the wettest part of the rainy season. As wetlands fill they become unsuitable for waders, necessitating movements to regions with less rainfall, mainly to the more arid western and southern parts of the region (Underhill *et al.* 1999). Ringing recoveries of Wood Sandpipers confirm these nomadic movements between inland wetlands while staging in southern Africa before their return migration (Underhill *et al.* 1999, SAFRING unpubl. data)

A small proportion of adult Wood Sandpipers caught in southern Africa showed suspended moult. The moult starting dates estimated from the sample of all primaries combined (which might include birds that resumed moult after its suspension before they arrived in southern Africa) and on the moult data for P1 (which did not include such birds) were almost identical, which shows that cases of undetected suspended moult were so few that they did not bias the estimates obtained from the first method. Most of the birds with moult suspension were observed in southern Africa in November, three months after the start of moult, at a time when birds undergoing continuous moult were replacing their outer three primaries (Table 3). It is likely that they suspended moult on the non-breeding grounds, perhaps in response to a need to move to a suitable wetland. Wood Sandpipers moulting or with suspended moult were observed rarely in August or September in eastern, central and southern Europe (Hoffmann 1957, Pinchuk *et al.* 2008) and more frequently in Kenya (Pearson 1974). Thus, the literature and our own data show that a few adult Wood Sandpipers might begin primary moult before migration or at a stopover area, and suspend or interrupt their moult after arrival to move between wetlands, but in southern Africa this is an infrequently used strategy.

Control of the rate of moult

One of the assumptions that underpins the Underhill & Zucchini (1988) moult model is that the moult index increases uniformly. The rate of primary feather mass production in Wood Sandpipers was constant (Fig. 5), confirming that this assumption held true for Wood Sandpipers, as has been found in waders such as Turnstone (Summers *et al.* 1989) and Purple Sandpiper (Summers *et al.* 2004), but not in Redshank *Tringa totanus* (Underhill *et al.* 1990) and Grey Plover (Serra & Underhill 2006). The rate of primary feather growth in the Grey Plover is regulated by the number of primaries grown at a time and their inter-shedding intervals (Serra & Underhill 2006). We found a similar mechanism in the Wood Sandpiper. The relative masses of the three smallest primaries (P1–P3) that are grown almost simultaneously (Table 3, Fig. 3) equal the mass of the largest primary (P10) (Table 1). The larger the primary being replaced, the fewer feathers were grown simultaneously (Fig. 4) and the longer the intervals between shedding consecutive feathers (Fig. 3). As a result, Wood Sandpipers maintained a constant rate of primary feather mass production throughout moult (Fig. 5).

The effect of the wing gap

In Wood Sandpipers, the size of the gap in the wing caused by moulting feathers, as described by PFMM, decreased during the season as the PFMG increased. This contrasts with the relationship described in Kelp Gulls *Larus dominicanus vetula* moulting in South Africa (Ward *et al.* in press), though both species have similar relative masses for consecutive primaries, typical of waders and gulls (Underhill & Summers 1993, Underhill & Joubert 1995). In the Wood Sandpiper, the decrease in PFMM over the season is a consequence of the initial intensive moult of up to five primaries, followed by a reduction in the number of larger feathers

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that grow simultaneously (Fig. 4). The Kelp Gull moults up to three primaries at all stages of its moult (Ward *et al.* in press). The wing gap caused by shedding primaries increases the energetic costs of flight and impedes bird's ability to escape predators, but this can partly be compensated for by the moulting birds keeping a lower body mass (Slagsvold & Dale 1996, Hedenström & Sunada 1999). The wing gap in the Wood Sandpiper was on average only 10% of the mass of all primaries, and adults maintain a low body mass between August and February (authors' unpubl. data), thus they retain adequate flight ability to move between wetlands during moult.

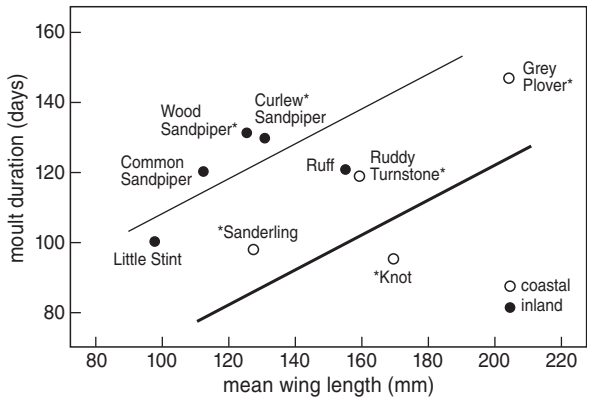


Figure 7. Relationship between wing length and moult duration in waders at coastal and inland habitats of southern Africa, located at similar geographical latitudes as the studied Wood Sandpipers (see Fig. 1). Asterisks indicate that moult durations were estimated using the Underhill & Zucchini (1988) model; the remaining durations were obtained using 'fitting-by-eye' methods specified in original papers. Data sources for each species are in the text. Unless specified in original study, wing lengths are from Hockey et al. (2005). See text for explanation of the regression lines for inland and coastal waders.

Moult patterns among wader species

The duration of primary moult in the Wood Sandpiper, estimated at 131 days, is longer than that estimated with the Underhill & Zucchini (1988) model for populations of Knot, Sanderling and Ruddy Turnstone moulting in southern Africa, which complete moult in 95–119 days (Underhill 2003). It is similar to those of the Curlew Sandpiper *Calidris ferruginea* and the larger Grey Plover (Fig. 7), which complete moult in 129 and 131 days respectively (Serra 2002, Y. Barshep pers. comm.).

Prater (1981) suggested that at similar geographical latitudes waders with longer wings have longer primary moult durations. We therefore assembled from the literature wing length and moult duration data for southern Africa (Fig. 7). The durations of moult of Wood Sandpiper, Knot, Sanderling, Curlew Sandpiper, Ruddy Turnstone and Grey Plover were estimated using the Underhill & Zucchini (1988) method. We also included data on moult duration obtained from moult curves 'fitted-by-eye' for Little Stint *Calidris minuta* (Dean 1977) and Common Sandpiper *Actitis hypoleucos* (Tree 2008). We estimated the moult duration of female Ruffs *Philomachus pugnax* (Schmitt & Whitehouse 1976, their Table 4). For these nine species, the correlation between wing length and primary moult duration, i.e. Prater's hypothesis, was not significant ($r = 0.43$, $n = 9$, $P = 0.13$). We then split these species into two groups: those exclusively using coastal habitats and those using inland habitats, allocating Curlew Sandpiper to the inland group (Fig. 7). We fitted a model with two parallel lines for the inland and coastal groups (Fig. 7). This model explained 37.7% of the variance in the duration of primary moult. The model suggested that moult duration (days) for inland waders was estimated from wing length w (mm) as $58.0 + 0.501w$ and for coastal waders $22.1 + 0.501w$. The model indicates that moult duration for inland waders was 25.9 (SD = 12.2, $t_6 = 2.12$, $P = 0.039$, one-sided test) days longer than for coastal waders. Prater's (1981) hypothesis was confirmed, in that the slope coefficient of 0.501 (SD = 0.197, $t_6 = 2.55$, $P = 0.022$, one-sided test) indicates that, for each additional millimetre of wing length, the duration of primary moult was extended by half a day. However, this modelling was performed on small samples and needs further confirmation. This is probably caused by the unpredictable and varied food resources and irregular nature of inland habitats (Piersma 2003) that require species using them to minimize gaps in primary feathers, so that they are continuously prepared to undertake nomadic movements. The Wood Sandpiper's prolonged moult is thus likely to be an adaptation to its almost exclusive use of inland wetlands on migration and at staging destinations (Cramp & Simmons 1983, Underhill *et al.* 1997).

The moult of Wood Sandpipers has a different pattern to that of smaller and similar-sized coastal waders moulting in southern Africa at similar geographical latitudes (Underhill 2003, Fig. 7). Knots, Sanderlings and Ruddy Turnstones moult the inner primaries P1–P5 rapidly, up to four feathers simultaneously, with short inter-shedding intervals (mean four days in all three species) (Underhill 2003). Wood Sandpipers also grow up to five inner primaries simultaneously, but with longer inter-shedding intervals (mean seven days). During the moult of P6–P10 the shedding intervals in

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Wood Sandpiper were on average longer (mean 15 days) than in these three species (means 11–14 days; Underhill 2003). The duration of the moult of corresponding primaries in Wood Sandpipers was longer than for Sanderlings, Knots and Ruddy Turnstones, but similar or shorter than those of Grey Plover (Underhill 2003, Table 3, Fig. 3).

The habitats that migrant waders choose in the non-breeding season affect various population attributes, in consequence of their different life histories. This paper supports the hypothesis that moult, which is an important component of the migration strategy, is another feature that differs between waders which use coastal habitats and those that use inland wetlands. We suggest that Wood Sandpipers have several adaptations in consequence of their exclusive use of irregular and ephemeral inland wetlands that provide variable and unpredictable food resources: the small wing gap during moult, the prolonged moult duration achieved by the slow growth of primaries, the long inter-shedding intervals, and the extended period between the end of primary moult and their departure to the breeding grounds. Whether these adaptations are common to other inland wader species needs confirmation.

ACKNOWLEDGEMENTS

This study was made possible through research grants to MR, AG and LGU from the National Research Foundation (NRF), South Africa, and the University of Gdańsk, Poland, within the Poland-South Africa Agreement in Science and Technology. MR was supported by a fellowship from the Claude Leon Foundation. LGU acknowledges support from the SeaChange Programme of the NRF. Lorenzo Serra, Danny Rogers, Ken Rogers, Phil Battley, Guy Morrison, Peter Pyle and Joel Avni commented on earlier versions of the manuscript; Joel Avni assisted with language correction and editing.

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SAMENVATTING

In dit artikel worden de resultaten beschreven van een onderzoek naar de rui van de grote slagpennen van in zuidelijk Afrika overwinterende Bosruiters *Tringa glareola*. Om de gevonden patronen in een breder kader te plaatsen, zijn ook de ruipatronen van andere in zuidelijk Afrika overwinterende steltlopers bij het onderzoek betrokken. De onderzoekers verwachtten dat Bosruiters als steltlopers van het zoete water een ruipatroon hebben dat lijkt op dat van andere steltlopers van het zoete water en dat dit ruipatroon verschilt van dat van kustgebonden steltlopersoorten. Hiermee testten ze een onderdeel van de hypothese van Piersma (2003) over contrasten tussen vogelsoorten die in zoete en zoute habitats voorkomen. Om de rui te beschrijven werden de ruiscores van de grote slagpennen van 1496 volwassen Bosruiters gebruikt die in Zimbabwe en Zuid-Afrika waren gevangen. Een deel van de ruiscores werd bepaald aan museumexemplaren die waren verzameld in Zimbabwe en Botswana. Start en duur van de rui werd zowel voor de slagpennen afzonderlijk als voor alle tien slagpennen gezamenlijk bepaald. Ook werd de ruisnelheid berekend van 16 Bosruiters die binnen hetzelfde seizoen waren teruggevangen. Daarnaast werd geschat hoeveel veermateriaal er steeds werd aangelegd. Volwassen Bosruiters arriveren in zuidelijk Afrika tussen eind juli en november en vertrekken tussen half maart en april naar de noordelijke broedgebieden. Bijna alle Bosruiters ruiden alle grote slagpennen in zuidelijk Afrika. Slechts bij 56 vogels (7,5%) werd een onderbroken rui vastgesteld. De gemiddelde startdatum van de rui was 21 augustus, de gemiddelde einddatum 30 december. Daarmee komt de totale ruiperiode op 131 dagen. Voor de terugvangsten was de gemiddelde periode 130 dagen. De hoeveelheid aangelegd veermateriaal was uniform gedurende de ruiperiode, een gevolg van het feit dat aan het begin de vijf binnenste, kortere, slagpennen gelijktijdig groeien en aan het eind van de buitenste, langere, slagpennen er maar een of twee tegelijk worden vervangen. De rui van de grote slagpennen van volwassen Bosruiters (en andere binnenlandse steltlopersoorten) duurt langer dan de rui van steltlopersoorten van vergelijkbare grootte die in de kustgebieden overwinteren. Maar doordat Bosruiters vroeg beginnen te ruien zijn ze eerder klaar met de rui. Bosruiters hebben een tragere rui omdat de tijdsperiode tussen het verliezen van de opeenvolgende slagpennen groter is en omdat de groei van de afzonderlijk pennen langer duurde. De auteurs veronderstellen dat de langere duur van de slagpenrui en het ruim voor de terugtrek beëindigen ervan aanpassingen zijn aan het gebruik van zoetwatergebieden. Het voedselaanbod van zoetwatergebieden in zuidelijke Afrika is erg onvoorspelbaar en vereist dat de vogels zich vaak moeten verplaatsen tussen snel veranderende binnenlandse 'wetlands'. (YIV)

Corresponding editor: Yvonne I. Verkuil
Received 21 February 2009; accepted 19 June 2009

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Layout by Dick Visser, Haren, The Netherlands

Printed by Van Denderen, Groningen, The Netherlands, October 2009

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