The path to adult dress: primary moult in second-year Wood Sandpipers *Tringa glareola* in southern Africa

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We know little about the primary moult of waders in their second year of life, especially migrants. Remisiewicz *et al.* (2009a & b) have provided details on the primary moult of immature and adult Wood Sandpipers *Tringa glareola* in southern Africa, but there is no information on the primary moult of second-year birds. Most Wood Sandpipers leave southern Africa for their northern breeding grounds when they are 10–11 months old, so migration separates the subsequent cycles in their primary moult. We chose this species to determine if the pattern of the first complete primary moult of waders during their second year of life differs from that of adults. We analysed the primary moult scores of 97 sub-adult (13- to 20-months-old) Wood Sandpipers obtained in southern Africa by using the Underhill–Zucchini moult model to estimate the timing and duration of moult for all 10 primaries combined and for P1 and P2 individually. Sub-adult Wood Sandpipers were observed in southern Africa between June and December, when, by about 19 months of age, they become indistinguishable from adults. Half of the sub-adults showed two generations of their fully grown primaries after a previous partial moult. All 54 sub-adults in active moult started at P1 and progressed outwards to P10. The starting date of moult for all sub-adults estimated using all 10 primaries was 2 September, 13 days later than for adults. The sub-adults' primary moult was estimated to last on average 134 days, which did not differ significantly from the 131 days in adults. The rate primary feather mass is deposited did not differ between the sub-adults and the adults. Moult of P1 and P2 in sub-adults started 10–11 days later than in adults, but overlapped in the same manner as in adults. The number of primaries grown simultaneously with subsequently moulted primaries and the size of the wing gap in sub-adults resembled the pattern in adults. Sub-adults finished their primary moult on 15 January on average, 15 days later than adults. We suggest that sub-adult Wood Sandpipers catch up with the timing of the adults when they are 19–20 months old, when they finish their first complete moult of primaries, before the pre-migratory fattening period in February–March.

INTRODUCTION

Migrant waders use a variety of moult patterns in their first year, but usually replace all or some of the first set of primaries on their non-breeding grounds. In small species these immatures usually moult all 10 primaries, but many medium-size and most large waders replace a varying number of outer primaries (Ginn & Melville 1983, Pearson 1974, Prater 1981, Prater *et al.* 1977, Pyle 2008, Tree 1974). This moult is usually completed before the birds depart on their first northward migration. Waders that take a "gap year" and spend the austral summer and the following winter on their non-breeding grounds, such as Curlew Sandpiper *Calidris ferruginea*, delay this moult for a few months (Elliott *et al.* 1976, Ginn & Melville 1983, Pyle 2008, Underhill 2006). The first moult of primaries is usually followed by a complete replacement of all 10 primaries during the birds' second year of life, as the adults do (Ginn & Melville 1983, Pearson 1974, Prater 1981, Tree 1974). Fragmentary attempts have been made to describe this second-year moult of birds in several wader species, but these descriptions have been confined to the moult of birds spending a "gap year" in the southern hemisphere, in species such as Curlew Sandpipers *Calidris ferruginea* (Elliott *et al.* 1976, Underhill 2006, Waltner 1976), Ruddy Turnstones *Arenaria interpres* (Summers *et al.* 1989) and Grey Plovers *Pluvialis squatarola* (Serra *et al.* 1999). The course of this second-year complete moult has not been described in detail for any migrant wader species because of the paucity of suitable moult records and inadequate methods to analyse this moult. The development of the Underhill–Zucchini (1988) moult model and the realization that it could be applied to estimate moult parameters for single primaries (Serra 2000, Serra & Underhill 2006, Underhill 2003) has enabled studies of moult to be extended to include the partial moult of

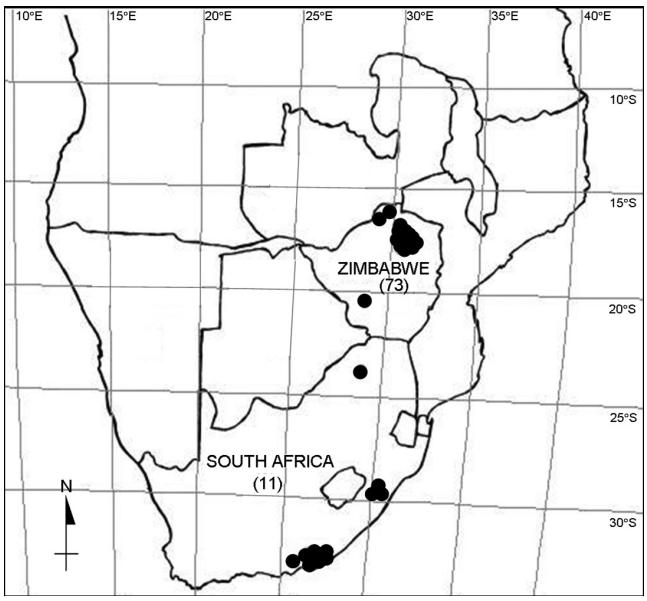

Fig. 1. Location of catching sites of Wood Sandpipers in southern Africa (black dots). Numbers in brackets indicate the number of birds trapped in Zimbabwe and in South Africa.

immature waders (Remisiewicz *et al.* 2010). It has also enabled other patterns of moult to be investigated quantitatively.

Wood Sandpipers *Tringa glareola* are migrants which breed from Fennoscandia to the Ural Mountains and have non-breeding grounds that in Africa extend from the sub-Sahel region to southern Africa (Cramp & Simmons 1983, Piersma *et al.*1996, Scott 2009, Underhill *et al.* 1999). Eggs are laid from the end of April and in May, and are hatched in June and July (Cramp & Simmons 1983, Dementev & Gladkov 1951). So, we use June as the reference month for hatching and use the term immatures for Wood Sandpipers during their first year of life, sub-adults – for birds during their second year of life, and adults – for unidentified sub-adults or older birds. In contrast to other medium and larger waders that defer their first northward migration until they are almost two years old and spend their first austral winter in southern Africa (Summers *et al.* 1995; Underhill 2006), most Wood Sandpipers undertake their first northward migration when they are about 10 months old (Cramp & Simmons 1983, Piersma *et al.* 1996, Remisiewicz *et al.* 2010, Underhill 1997). Earlier studies of the moult of Wood Sandpipers in their African non-breeding grounds provided general descriptions of the moult of immature and adult birds (Pearson 1974, Remisiewicz *et al.* 2010, Tree 1974). These studies showed that most immatures in southern Africa undertake a partial moult of two to six outer primaries and have a choice of strategies for this moult. Adults in southern Africa generally moult all ten primaries before migrating north (Remisiewicz *et al.* 2009). The moult of sub-adults remained a gap in our knowledge of the moult patterns of most migrant waders. We chose Wood Sandpipers for an analysis of this primary moult in migrant waders because in this species the northward migration by most immatures separates subsequent cycles of primary moult. This is in contrast with the pattern adopted by waders that take a "gap year", among which the partial moult and the following complete moult of primaries might overlap (Underhill 2006).

This paper aims to present the pattern of primary moult of sub-adult Wood Sandpipers in southern Africa and to compare this pattern with that of immature and adult birds to provide the full picture of the consecutive primary moult cycles in this species in their southernmost African non-breeding grounds. In particular we aim to determine if sub-adult birds' first complete primary moult differs in timing and duration from the following sequences of complete primary moult by adults.

MATERIAL AND METHODS

We analysed the primary moult scores of 97 sub-adult Wood Sandpipers from two sources: 13 specimens from the National Museum of Zimbabwe in Bulawayo collected in 1900–1975 from Zimbabwe and Botswana, and 84 birds ringed in southern Africa in 1966–2008 during irregular mist-netting at wetlands in Zimbabwe and South Africa (Fig. 1). Wood Sandpipers were aged by their plumage (Prater *et al.* 1977) as immatures (birds 3–12 months old, from their arrival in August till 31 May of the following year), sub-adults (birds 13–20 months old, from 1 June of their second year of life to the end of their primary moult in the following December–January) and adults (unidentified sub-adults and birds older than 20 months). Sub-adults, analysed in this paper, could be identified either by the juvenile-type inner median coverts, which they might retain up to about 14 months (MR, unpubl. data) or by the different generations of primaries (Prater *et al.* 1977). Individuals analysed in this paper were identified as sub-adults by the presence of one or both of these diagnostic features. The contrasting tones and wear between two generations of primaries can indicate completed partial moult of a few outer primaries, typical of immatures (Remisiewicz *et al.* 2010, Tree 1974). Some sub-adults replace the diagnostic coverts and all primaries earlier and then become indistinguishable from adults. All available moult records of sub-adults from all years and locations were combined, assuming them to be representative of the whole of southern Africa. The date of capture or collection was taken as the number of days from 1 June.

The state of moult in the primaries of one wing was recorded as a moult formula, a string of 10 scores, one for each primary, following the standard approach of Ashmole (1962) and Ginn & Melville (1983). The sub-adults were divided into two main groups by these moult scores: birds in which contrasting patterns indicated an earlier partial moult of outer primaries and those that showed no traces of partial moult.

In sub-adults that showed previous partial primary moult we treated both generations of fully grown primaries (the oldest juvenile primaries and the newer ones acquired in the partial moult) as the "old generation" feathers because both were grown before the complete moult started. We assigned both generations of the old primaries scores of 0. Primaries being grown in the complete moult were given scores of 1–5. Further calculations followed the methods used to analyse the primary moult of adult Wood Sandpipers (Remisiewicz *et al.* 2009). Based on the moult scores, and using the entire tract of all 10 primaries combined (minute outermost 11th primary ignored), we calculated for each individual the Proportion of Feather Mass Grown (PFMG) recommended by Underhill & Zucchini (1988). Assuming that primary feather tissue is deposited at a continuous rate, this provides the moult index required by the Underhill–Zucchini (1988) model. For this calculation we followed Underhill & Summers (1993) and used the mean relative masses of each primary for Wood Sandpipers given by Remisiewicz *et al.* (2009). We estimated three parameters of moult (mean starting date, its standard

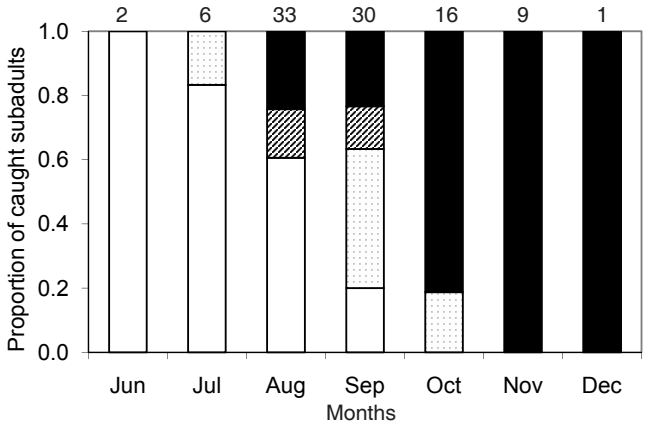

Fig. 2. Percentages of sub-adult Wood Sandpipers caught in southern Africa with different moult status of primaries: white bars – birds showing partial moult of outer primaries and complete moult from P1 not yet started; dotted bars – birds showing partial moult and complete moult in progress; bars with diagonal lines – birds showing no partial moult and complete moult not yet started; black bars – birds showing no partial moult and complete moult in progress; numbers above bars show monthly sample sizes.

deviation, and moult duration) using the Underhill–Zucchini moult models (Underhill & Zucchini 1988, Underhill *et al.* 1990) and applied the software designed to run these models (Brandão 1998, Underhill *et al.* 2006). We used the moult model for data of Type 5 of Underhill *et al.* (1990) because the sample contained only birds which had not yet started moult and birds in active moult; no birds which had completed moult were considered because they become indistinguishable from adults when they are close to completion of moult. The confidence limits for the moult starting date (during which 95% of birds are estimated to start moult) were calculated as the estimated mean starting date +1.96×standard deviation.

Additionally we estimated the three moult parameters separately for individual primaries (Serra 2000, Underhill 2003), forming a moult index by transforming moult scores from 0 to 5 to the values 0, 0.125, 0.375, 0.625, 0.875 and 1 respectively. We applied the standard Underhill–Zucchini moult model using data Type 2 because the sample contained birds that had not yet started moult, birds in active moult and birds which had completed moult of the analysed primary.

We estimated the size of the gap in the primary feathers during moult, accounting for the relative sizes of the missing feathers, by calculating Proportion of Feather Mass Missing (PFMM) for each individual (Remisiewicz *et al.* 2009, 2010, Ward *et al.* in press). Feathers that had moult scores 1, 2, 3 and 4 were estimated to be missing 0.875, 0.625, 0.375 and 0.125 respectively of the relative mass of the feathers.

Table 1. Percentages of outer primary feathers renewed in the partial moult during the first year in sub-adult Wood Sandpipers in southern Africa, determined for immatures (n = 400, Remisiewicz *et al.* 2010) and sub-adults (n = 50). Calculations are restricted to birds which moulted outer primaries.

No. of primaries replaced	Primary feathers moulted	% among immatures	% among sub-adults
2	P9–P10	1.3	0.0
3	P8–P10	6.5	2.0
4	P7–P10	63.3	55.1
5	P6–P10	27.3	38.8
6	P5–P10	1.8	4.1

We compared the moult of sub-adult Wood Sandpipers with the results obtained for adults (Remisiewicz *et al.* 2009) and immatures (Remisiewicz *et al.* 2010) and made use of the data from those papers. We applied the G-test (Zar 1999) to compare proportions of immature and sub-adult birds showing different patterns of partial moult. We used the likelihood ratio test (Burnham & Anderson 1998) to test the null hypotheses that the starting dates of primary moult and of the moult of individual primaries for sub-adults were the same as for adults.

RESULTS

We classified 97 Wood Sandpipers as sub-adults (Fig. 2). We recorded two in June and six in July, then 33 in August and 30 in September and fewer in subsequent months (Fig. 2). Three to six outer primaries had been replaced during the partial moult in 50 birds and 16 of these had already initiated a full moult from the innermost P1 (Fig. 2). Of the 50 sub-adults birds with partial moult, 94% had replaced either four or five outer primaries (Table 2). Of the 47 sub-adults without partial moult, 38 were actively moulting, having started at P1 (Fig. 2).

The earliest date for a sub-adult in active moult was 30 July. The 54 sub-adults in active moult had all started at P1 and were progressing without suspending to P10. From September the proportion in active moult gradually increased (Fig. 2). After December no Wood Sandpipers were identified as sub-adults because they were indistinguishable from adults.

To estimate the timing of moult of sub-adult Wood Sandpipers, we combined the samples showing a previous partial moult with those that had not moulted. This assumed that there were no biological reasons for these two groups to differ in the timing of their first complete primary moult; the sample

Table 2. Estimates of moult parameters of primaries P1 and P2 and of the 10 primaries as a single tract for sub-adults and adults (Remisiewicz *et al.* 2010) in Wood Sandpipers moulting in southern Africa.

Primary and age group	Moult parameters				Sample sizes			Moult model used
	Mean start date (SD)	Duration (SD)	Standard deviation of start date (SD)	End date (SD)	Not yet moulted	In moult	Moult complete	
P1 adults	22 Aug (1.6)	25 (1.9)	19 (1.1)	16 Sep (1.5)	108	109	1218	Type 2
P1 sub-adults	1 Sep (3.1)	27 (4.6)	19 (2.5)	27 Sep (4.2)	42	23	30	Type 2
P2 adults	23 Aug (1.5)	25 (1.9)	19 (1.1)	17 Sep (1.1)	114	108	1213	Type 2
P2 sub-adults	2 Sep (3.0)	27 (4.6)	18 (2.4)	29 Sep (4.2)	44	22	29	Type 2
P1–P10 adults	21 Aug (1.7)	131 (2.5)	29 (0.8)	30 Dec (1.4)	108	687	640	Type 2
P1–P10 sub-adults	2 Sep (3.0)	134 (9.9)	20 (2.1)	14 Jan (8.6)	53	42	0	Type 5

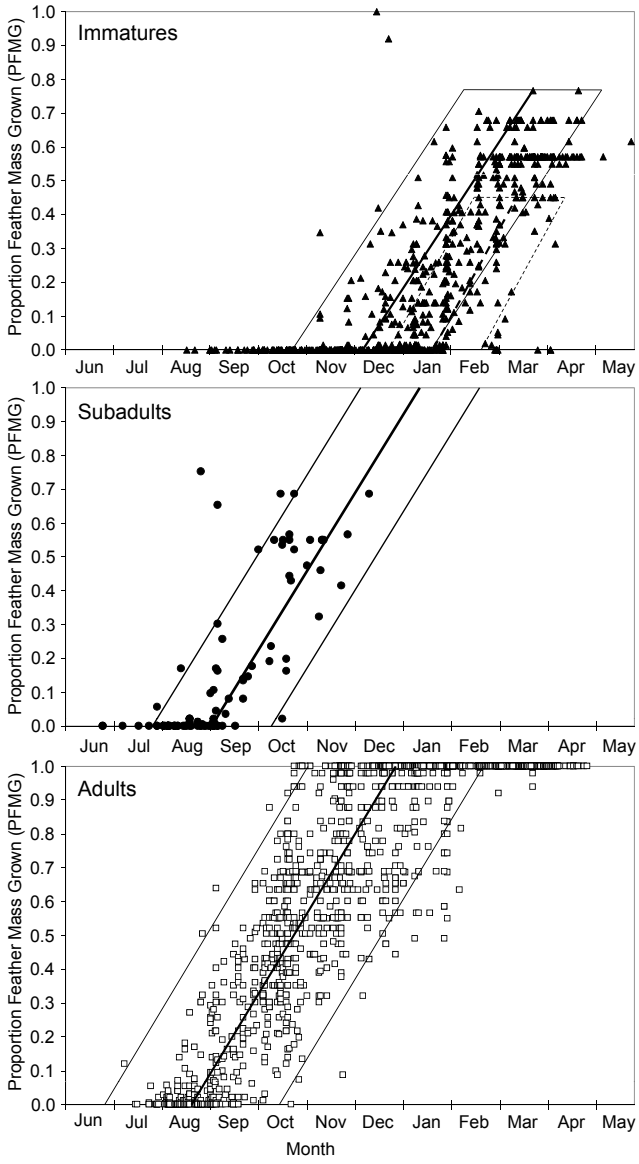

Fig. 3. Distribution through time of the Proportion of Feather Mass Grown (PFMG) of Wood Sandpipers of three age categories, corresponding with birds' years of life: top figure – immatures (birds during their first year of life, n = 674) (Remisiewicz *et al.* 2010); middle figure – sub-adults (birds during their second year of life, n = 97), bottom graph – adults (n = 1495) (Remisiewicz *et al.* 2009). The parallelograms show the temporal limits of moult for 95% of birds; the thick lines through the centre of the parallelograms show the estimated timing of moult; in the top figure: solid lines – immatures that moult six primaries in partial moult, dashed lines – immatures that moult three primaries in partial moult.

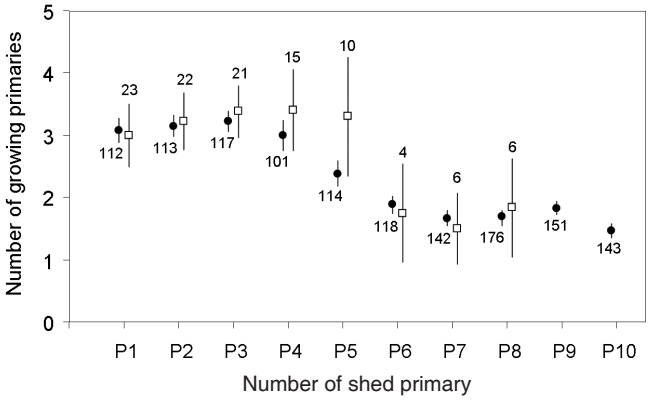

Fig. 4. Simultaneously growing primaries of Wood Sandpipers in southern Africa: open squares – sub-adults; black circles – adults (Remisiewicz *et al.* 2009). Values shown are the means and 95% confidence intervals of the number of primaries growing while each primary is being replaced. Sample sizes for adults and sub-adults are shown below and above the lines representing the confidence intervals respectively.

sizes were too small to verify this statistically. The PFMG values of two individuals were identified by the moult model as outliers: formula 5555555322 on 27 July and 5555555315 on 7 September. For the remaining 95 sub-adults the mean starting date of the primary moult, estimated using the whole primary feather tract, was 2 September (Table 1, Fig. 3) with the standard deviation of the starting date estimated to be 20 days (Table 2), so that 95% were estimated to begin moult during the 77-day period 26 July–11 October (Fig. 3). The estimated duration of the primary moult was 134 days so that the mean completion date was 14 January and 95% of sub-adults completed primary moult in the period 7 December–21 February (Table 2, Fig. 3). From the duration of moult (134 days) we estimated that the rate of production of the primary feather material, if uniform, was 0.75% PFMG per day. For individual primaries, the mean starting date of moult of P1 was estimated to be 1 September and that of P2 was one day later; the moult duration for both primaries was 27 days (Table 2). The numbers of birds in active moult of other primaries was too small to obtain estimates of those moult parameters.

The number of primaries growing simultaneously varied from one to four (Fig. 4). During the replacement of P1–P5 the mean number of feathers growing simultaneously was larger than three and it decreased to less than two during the replacement of P6–P8; for P9 and P10 the samples were inadequate for analysis.

The average size of the wing gap, expressed as the Proportion of Feather Mass Missing (PFMM), in sub-adults in active moult was 0.11 (SD = 0.052, n = 44, range 0.01–0.25) (Fig. 5). On average 11% of the mass of primary flight feathers was missing during moult. In all except two sub-adults less than 19% was missing; the largest values were 25% in a bird replacing its three outer primaries simultaneously (formula 5555555322 on 27 July) 24% in a bird replacing five inner feathers simultaneously (formula 2221100000 on 23 September). In sub-adults in active moult, the PFMM was not significantly correlated with PFMG (Fig. 5; r = –0.23, n = 52, p = 0.13).

DISCUSSION

Timing of moult of sub-adult Wood Sandpipers in southern Africa

The small numbers of sub-adult Wood Sandpipers recorded in June and July in southern Africa were most likely the birds that did not migrate northwards at the end of their first year of life. This is in agreement with observations of a few immature Wood Sandpipers in southern Africa in May, after the species' main departure time between mid-March and mid-April (Herremans 1994, Irwin 1981, Remisiewicz *et al.* 2010, Tarboton *et al.* 1987, Taylor 1979, Underhill *et al.* 1997); in June–July these birds enter their second year of life i.e. become sub-adults. The increasing numbers trapped

in August and September reflect the arrival of migrant sub-adults, at the same time as adults arrive in southern Africa (Underhill 1997).

Comparison of moult between sub-adults and immatures

The most frequent pattern of partial moult in immatures is the replacement of the outer four or five primaries; 94% of immature moulters adopt this strategy (Remisiewicz *et al.* 2010). We observed the same pattern in sub-adults (Table 1). The proportions of immatures and sub-adults moulting various numbers of primaries were not significantly different (Table 1, G-test: $G_3 = 5.97$, $p = 0.11$). This is what we would expect, considering that in July the immatures that stayed in southern Africa turn into sub-adults. The small sample of sub-adults caught in June and July did not allow us to check if any particular strategy of partial moult is preferred by birds of this age group staying in southern Africa.

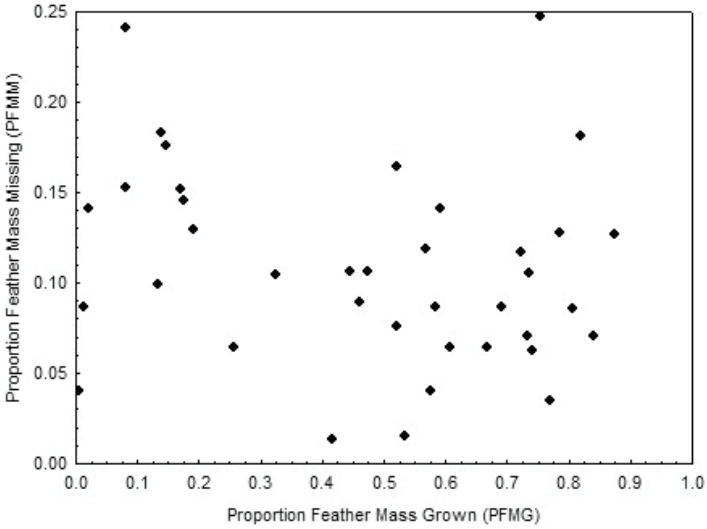

Fig. 5. The relationship between the size of the gap in the primaries during moult, expressed as Proportion of Feather Mass Missing (PFMM) and Proportion of Feather Mass Grown (PFMG) for sub-adult Wood Sandpipers in active moult in southern Africa.

Comparison of moult between sub-adults and adults

Based on the whole primary feather tract, sub-adults started moult 13 days later on average than adults (Table 2, Fig. 2). This difference was significant; we performed a likelihood ratio test by first pooling the two data sets and estimating a single set of parameters and then allowing the sub-adults and adults to have different starting dates, and assuming a common duration and SD of starting date ($\chi^2_1 = 21.73$; $p < 0.001$). The mean moult starting date estimated for P1 was 10 days later in sub-adults than in adults (Table 2); and the similar likelihood ratio test showed that this difference was also significant ($\chi^2_1 = 13.01$; $p < 0.001$). The moult starting date estimated for P2 in sub-adults was 11 days later than for adults (Table 2); this difference was again significant ($\chi^2_1 = 14.39$; $p < 0.001$). The duration of moult for all primaries combined was estimated at 134 days in sub-adults and at 131 days in adults, but this difference was not significant ($z = 1.00$; $p = 0.16$). The estimated date of completion of moult by sub-adults was 14 January, 15 days later than the adults (Table 2, Fig. 2). But the two-week delay in completing the primary moult in southern Africa should not affect sub-adults' ability to catch up with adults as they prepare for their next departure to the breeding grounds. Adult Wood Sandpipers begin fattening in mid-February (authors' unpubl. data) before leaving between mid-March and mid-April. Thus the sub-adults would still have at least a month from the end of their primary moult to the beginning of the fattening period; during this time they could also finish moulting their secondaries, tertials, rectrices and advance with body moult into breeding plumage (authors' unpubl. data). But the northwards passage of sub-adults through stopover sites close to the breeding grounds was on average three days later than of adults (Remisiewicz & Wennerberg 2006). This might reflect slightly later departures of sub-adults than adults for the breeding grounds, but also slower migration of less experienced sub-adult birds, similar to that described during their first southward migration (Wichmann *et al.* 2004).

Sub-adults and adults showed a similar pattern in the number of primaries grown simultaneously during the replacement of each primary (Fig. 4). The mean values during the replacement of each of the primaries P1–P5 did not differ significantly between sub-adults and adults (t-test, for each primary: $p > 0.05$); the samples for the remaining primaries in sub-adults were too small to compare. The gap in sub-adults' wings caused by shedding primaries averaged 11% of the mass of primaries, similar to that of adults (10%) (Remisiewicz *et al.* 2009) and of immatures (8–11% in different groups of moulters) (Remisiewicz *et al.* 2010). These values did not differ significantly between the three age groups (Kruskal–Wallis test: $H_{2, 1031} = 1.28$, $p = 0.53$). In adult Wood Sandpipers PFMM was significantly correlated with PFMG ($r = -0.19$, $p < 0.001$), but there was no similar relationship in sub-adults. But in both age classes the trend shown by the correlation coefficient was negative, so that gaps tended to be smaller at the start of moult than at the end. These relatively small wing gaps should not substantially impede the immature Wood Sandpipers' flight ability and would allow them to move between ephemeral wetlands during their moult in southern Africa (Remisiewicz *et al.* 2009).

Comparison with the moult patterns in sub-adults of other wader species

Migrant waders that spend a "gap year" in the southern hemisphere usually moult all their primaries in their second year soon after undertaking a partial moult of their primaries. These two moult sequences sometimes overlap (Pyle 2008). The overlap of two consecutive cycles of moult has been described in sub-adult Curlew Sandpipers *Calidris ferruginea* (Elliott *et al.* 1976, Underhill 2006, Waltner 1976), Ruddy Turnstones *Arenaria interpres* (Summers *et al.* 1989) and Grey Plovers *Pluvialis squatarola* (Serra *et al.* 1999). These waders spend their first austral winter in southern Africa (Summers *et al.* 1995). Overlapping moult has never been observed in Wood Sandpipers in southern Africa, probably because these first two moults of primaries are separated by migration to and from the breeding grounds in most birds (Remisiewicz *et al.* 2010).

In Curlew Sandpipers, which do spend a "gap year" in southern Africa or Australia, the question of whether the duration and timing of the complete moult of primaries in sub-adults differs from that of adults remains unanswered (Elliott

et al. 1976, Minton *et al.* 2006, Underhill 2006). Summers *et al.* (1989) described the second cycle of primary moult in Ruddy Turnstones in southern Africa as so slow that some second-year birds had not finished this moult by the time of their northwards departure. This was not the case in Wood Sandpipers, in which the rate of the second moult of primaries in sub-adults was the same as in adults, and this moult was completed about two months before the departure period.

CONCLUSIONS

Our results showed that the complete moult of primaries of sub-adult Wood Sandpipers is similar to that of adults in duration, rate of primary feather mass deposition, the number of primaries grown simultaneously and the size of the gap in the wing. But the moult of sub-adults starts and ends about two weeks later than in the adults. We suggest that the sub-adult Wood Sandpipers catch up with the timing of the adults after they complete this primary moult, when they are 19–20 months old, during the pre-migratory fattening period in February–March, before they depart from southern Africa between mid-March and mid-April.

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