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ORIGINAL ARTICLE

Rapid or slow moult? The choice of a primary moult strategy by immature Wood Sandpipers *Tringa glareola* in southern Africa

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Abstract Immature migrant waders have more complex patterns of primary moult than adults, but these have been described only fragmentarily. The Wood Sandpiper *Tringa glareola* breeds in the taiga region of the Palearctic and part of the population migrates to southern Africa. We selected this population for a study of the primary moult strategies of an immature wader. After analysing the moult formulae of 674 immatures, we discuss potential factors that influence the choice of moult strategy. All moulters replaced two to six outer primaries; 91% moulted four or five. We used the Underhill–Zucchini model to estimate the timing and duration of moult in immatures replacing different numbers of primaries. A slow moult of five or six primaries, adopted by 29%, lasted on average 98–111 days, beginning on average 8–16 December. Moult of four primaries (63%) began on 6 January and averaged 73 days. A rapid moult of three primaries (7%) began on 24 January and averaged 55 days. All groups ended their moult between 19 and 28 March. GLM models showed that heavier immatures were more likely to start moulting than leaner birds. This tendency was more pronounced in November–January than in later months. The later the moult started, the fewer feathers were replaced and the faster the process. Departure time set the limit for the end of moult. We suggest the ability to choose different strategies allows immature Wood Sandpipers to adjust their moult to the variable conditions they encounter at wetlands in southern Africa.

Keywords Wood Sandpiper · *Tringa glareola* · Moult strategy · Southern Africa

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Introduction

oult is an important event in the life cycle of all birds, and, especially for migrants, its extent and timing are an important aspect of their life strategy. Migration and moult are both energetically costly and the moult of flight feathers impedes flight performance (Ginn and Melville 1983; Hedenström and Sunada 1999; Lindström et al. 1994); migrants therefore avoid overlapping these two activities (Ginn and Melville 1983; Zenatello et al. 2002; Newton 2008). Adult migrant waders replace their primaries annually, most commonly on the non-breeding grounds so that they have fresh flight feathers for the return migration and the breeding season (e.g. Prater et al. 1977; Ginn and Melville 1983; Summers et al. 1989, 2004; Serra et al. 1999; Pearson and Serra 2002; Minton et al. 2006). In

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contrast, juvenile waders use a wide variety of moult patterns. Some retain their first set of primaries and complete the first migration back to their breeding grounds with these feathers (Pearson 1974; Prater et al. 1977). Some moult primaries before the return migration; this moult can either be complete, with all 10 primaries replaced, as for example in Little Stints *Calidris minuta* (Tree 1974; Dean 1977), or partial, replacing a variable number of outer primaries, as for example in Curlew Sandpipers *Calidris ferruginea* and Greenshanks *Tringa nebularia* (Pearson 1974; Tree 1974; Elliott et al. 1976; Prater 1981). Different patterns of moult occur among immatures of the same species (Pearson 1974; Tree 1974; Prater et al. 1977; Ginn and Melville 1983). Prater (1981) suggested that the immatures of shorter-winged species and more southerly migrating populations tend to moult more primaries. Studies describing the partial moult of immature waders have been general and fragmentary, in part because methods which would facilitate detailed analyses of moult patterns were unavailable. The statistical model for primary moult, developed by Underhill and Zucchini (1988), Underhill et al. (1990, 2006) and Underhill (2003), has mostly been used to analyse the moult of adult waders that replace all primaries (e.g. Summers et al. 1989, 2004; Serra et al. 1999; Pearson and Serra 2002; Serra and Underhill 2006). Application of the Underhill and Zucchini (1988) moult model to estimate parameters of moult for single primaries was pioneered by Serra (2000), Underhill (2003) and Serra and Underhill (2006). In this paper, we extend this method to subsets of primary feathers, enabling the analysis of partial moult. This application of the moult model enables us to achieve a detailed description of the moult of an immature wader and to discuss factors that might affect the choice of a moult strategy.

Wood Sandpipers *Tringa glareola* migrate from breeding grounds in the sub-Arctic and the boreal zones between Fennoscandia and the Ural Mountains to non-breeding grounds that, within Africa, extend from the sub-Sahel region to southern Africa (Cramp and Simmons 1983; Piersma et al. 1996; Underhill et al. 1999). These medium-size waders mostly use freshwater inland habitats in the non-breeding season and occur abundantly in these habitats in sub-Saharan Africa (Cramp and Simmons 1983; Underhill 1997; Underhill et al. 1999). Many of the medium-size waders which migrate to spend their first austral summer in southern Africa skip their first possible breeding season and take a "gap year" (Summers et al. 1995; Underhill 2006). In contrast, most immature Wood Sandpipers return to their breeding grounds aged about 10 months, at the first opportunity (Cramp and Simmons 1983; Piersma et al. 1996; Underhill 1997). Immature Wood Sandpipers' tendency to undertake a relatively extensive moult of primaries during their first austral summer has been noted in birds migrating to Kenya and South Africa, but has not been described in detail (Pearson 1974; Tree 1974). We chose the population of Wood Sandpipers in southern Africa to quantify the primary moult of an immature migrant wader. Immature Wood Sandpipers undertake only a partial primary moult a few months after arriving at the non-breeding destination. We would expect this moult to be more variable and flexible than the primary moult of all 10 primaries that the adults perform in southern Africa shortly after their arrival (Remisiewicz et al. 2009). Because of these differences, we present our analyses of the immatures' moult separately. We also discuss the factors that likely influence their choice of a moult strategy and the constraints they encounter.

Methods

Primary moult formulae of Wood Sandpipers were obtained from two sources. Wood Sandpipers formed a small component of the total catch during mist-netting operations for waders at wetlands in Zimbabwe and in South Africa between 1966 and 2008. The cumulative total capture effort in each month was similar. Additionally, Wood Sandpiper specimens in the National Museum of Zimbabwe in Bulawayo were examined. Birds were aged by their plumage (Prater et al. 1977); immatures and subadults could be distinguished from adults until c. 18 months of age by retained juvenile-type inner median coverts or by the contrast between two generations of primaries (Prater et al. 1977; M.R., unpublished data). This study analyses the primary moult of those aged as immatures; the primary moult of adults was described by Remisiewicz et al. (2009).

The state of moult in the primaries of one wing was recorded as a moult formula, a string of 10 digits, following the standard approach of Ashmole (1962) and Ginn and Melville (1983). A moult score of 0 for a primary indicates an old feather, a score of 5 indicates a fully-grown new feather, and intermediate values describe the stage of feather growth. We pooled the data from southern Africa because the types of moult shown across this area were similar. The date of capture or collection was expressed as the number of days from 1 June. Body masses determined for most of the ringed birds were used as an additional dataset.

The immatures were divided into three groups: those which had not yet begun to moult when caught, birds in active moult, and those which had finished moulting when caught. The primary feather at which moult would commence could not be identified for those immatures which had not yet begun primary moult when examined, so these birds were used only in some analyses. We therefore analysed the moult pattern of immatures which were in active moult or had finished moult. For birds that had finished

moult, the primary at which moult had started was identified by the contrast between old and new feathers. In all these individuals, moult had started from an inner primary and had continued outwards to P10. Thus, the primary at which moult started indicated the number of feathers the bird would moult. We divided these birds into groups according to the number of primaries replaced and estimated three moult parameters for each group: mean starting date, duration and the standard deviation of starting date. We will refer to these groups as MOPn where n refers to the number of outer primaries moulted, so, for example, MOP6 refers to the group of birds undertaking a moult of six outer primaries.

We computed each bird's stage of moult by transforming its moult formula into the proportion of feather mass grown (PFMG), as described by Underhill and Summers (1993). This transformation requires the relative masses of primary feathers to be known; we used the masses determined by Remisiewicz et al. (2009), calculated as described by Summers (1980), Summers et al. (1983) and Underhill and Joubert (1995). Assuming that primary feather tissue is deposited at a continuous rate, this provided the moult index required by the Underhill–Zucchini (Underhill and Zucchini 1988) model. Because immatures which performed a partial moult replaced a limited number of outer primaries, the maximum PFMG relative to the mass of all 10 primaries was less than 1. For example, a bird which replaced six outer primaries attained a PFMG value of 0.77 when moult was complete. For each group of moulters, we divided the PFMG value of each bird by the PFMG value at moult completion for birds from this group. In each group, the transformed values of PFMG thus lay in the range 0–1 as required by the Underhill–Zucchini model (1988), where 0 indicates that moult has not started and 1 indicates that moult has been completed. For each group, we used the software described in Brandão (1998) and in Underhill et al. (2006) to estimate the three moult parameters. The data were assumed to be of Type 4 as defined by Underhill et al. (1990), because only birds which were in active moult or had finished moult could be included; records of birds that had not yet started moult could not be used because we could not determine how many primaries they would moult and thus assign them to any of MOP groups. The 95% confidence limits around the moult starting date (the period during which 95% of the birds commenced moult) were calculated as the estimated mean starting date ± 1.96 standard deviation of starting date. The 95% confidence limits were calculated similarly for the moult ending dates.

Secondly, we estimated the three moult parameters separately for each individual primary using the approach described in Serra (2000) and Underhill (2003); we transformed the moult score from 0 to 5 for each primary into the values 0, 0.125, 0.375, 0.625, 0.875, 1, respectively. These estimates were obtained separately for each group of moulters distinguished by the number of primary feathers they were replacing. Moult parameters for the first primary of the group to moult were estimated using data Type 4. Data for the remaining primaries were of Type 2 (Underhill and Zucchini 1988); the samples included birds which had not yet started to moult this primary (but were moulting the previous ones), birds which were actively moulting the focal primary, and birds which had finished moulting this feather. If sample sizes were small, the algorithm either did not converge or the standard errors of the estimates of the moult parameters were too large to be biologically meaningful. In such cases, results are not reported. In each group, the estimated date of moult completion for the outermost primary (P10) is compared with the moult completion date obtained for the group as a whole, as described above.

The ratio of the relative mass of each primary to its estimated duration of moult provided an estimate of its daily growth rate (proportion of total primary mass/day). This enabled us to compare the average daily growth rates of corresponding primaries in each group of moulters. For each group, we also calculated the overall average daily rate of primary feather mass production by dividing the sum of the relative masses of the primaries in the group by the estimated moult duration for this group. We compared this rate among the groups. We also estimated the proportion of feather mass missing (PFMM) for each individual, providing a measure of the gap in the primary feathers during moult, which takes into account the relative sizes of the missing feathers, following Ward et al. (2009) and Remisiewicz et al. (2009). To calculate PFMM, we used a complementary approach to the calculation of PFMG; feathers that in a moult formula had moult scores 1, 2, 3 and 4 were taken as representing 0.875, 0.625, 0.375 and 0.125, respectively, of the relative mass for the missing feathers.

To evaluate factors that might influence the selection of a moult strategy, we selected immatures actively moulting their first replaced primary and birds that were not in moult on the dates when these moulting birds were observed; we excluded the exceptionally late non-moulters. We used the generalised linear model with a binomial distribution and a logit link function (McCullagh and Nelder 1983) to model moult status (commenced moult vs not yet in moult) using body mass and date of capture as explanatory variables. We also used ANOVA and regression analysis to test whether the number of feathers moulted depended on the body mass at the start of moult or the date when the bird was caught.

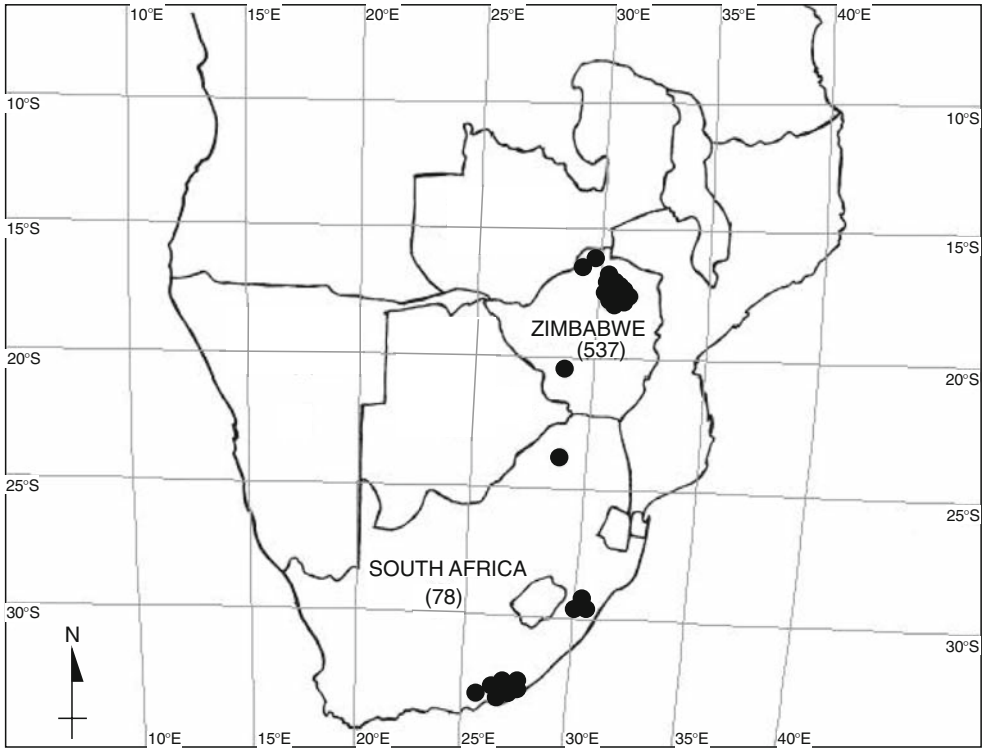

Fig. 1 Location of catching sites of Wood Sandpipers *Tringa glareola* in southern Africa. *Numbers in brackets* indicate the numbers of birds trapped in Zimbabwe or South Africa

Results

Timing of primary moult

Primary moult formulae were obtained for 674 immature Wood Sandpipers: 59 specimens from the National Museum of Zimbabwe in Bulawayo, collected in 1900–1975 and examined by A.J.T., 588 live birds ringed in southern Africa in 1966–1999 by A.J.T., and 27 birds ringed in 2001–2008 by P.B.T. (with M.R. in 2007 and 2008) (Fig. 1). Twenty birds were recaptured while still immatures and their moult formulae were recorded a second time. The records from both occasions were used in this study. The earliest date after arrival on which an immature was examined was 18 August; numbers of immatures increased during September and particularly October; none were in moult (Fig. 2). The first bird in active moult was recorded on 14 November (Fig. 3). The proportion of birds in active moult increased from November until February, when the moulters were 95% of all collected birds, and then decreased until April (Fig. 2). Only two immatures were caught in May: one exceptionally late bird in active moult (formula 0000055553 caught on 31 May 1986), and one that had completed moult (Fig. 3). Of the 674 immature Wood Sandpipers for which moult formulae were available, 274 had not begun to moult when collected. These non-moulters were observed

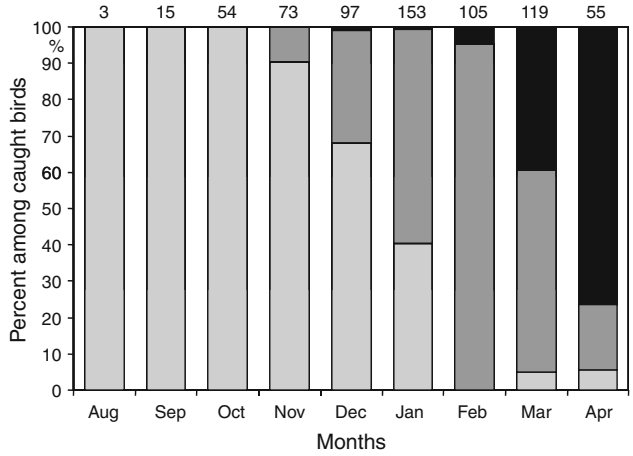

Fig. 2 Monthly percentages of immature Wood Sandpipers in southern Africa in three moult categories: not yet started moult (*light grey bars*), in active moult (*dark grey bars*) and finished moult (*black bars*). The *numbers* above the *bars* are the sample sizes

between mid-August and April, but 97% were prior to 30 January (Figs. 2 and 3). The nine remaining non-moulters were caught between 4 March and 9 April, they comprised 6% of all immatures caught in this period.

The moult group was identified for 400 immatures in active moult or which had completed moult. These birds undertook a partial moult of outer primaries, with between two (group MOP2) and six (group MOP6) primaries

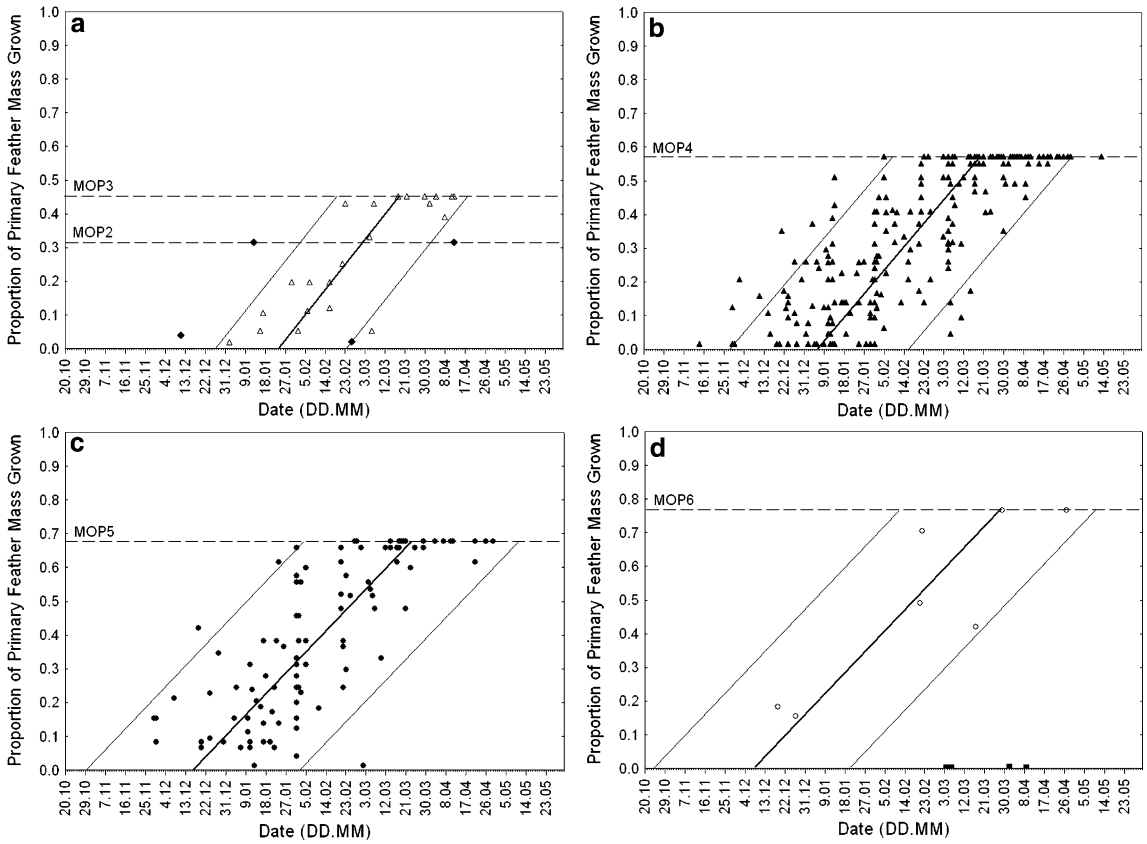

Fig. 3 Temporal distribution of the proportion of feather mass grown (PFMG) of immature Wood Sandpipers that moulted different numbers of outer primaries in southern Africa; birds that had not yet started to moult and thus were not analysed were not included. *Thick lines* show the timing of moult for an average bird of each group, *thin lines* show the estimated 95% confidence intervals into which moult scores on any given date ought to fall, *dashed lines* described by *symbols* show the maximum value of PFMG that can be reached by birds moulting different numbers of outer primaries (cf. Table 1); **a** *MOP2* birds that moulted two primaries (*black rhombuses*, $n = 5$) and *MOP3* three primaries (*open triangles*, $n = 26$), the 95% confidence intervals are drawn only for this group; **b** *MOP4* four primaries ($n = 254$); **c** *MOP5* five primaries ($n = 108$); **d** *MOP6* six primaries ($n = 7$) and late non-moulters (*black squares*, $n = 9$)

replaced. The largest groups were MOP4 and MOP5, which comprised 91% of moulters (Table 1). The PFMG relative to the mass of all 10 primaries at the completion of moult varied between 0.31 in birds replacing two primaries to 0.77 in birds replacing six (Table 1; Fig. 3). The mean starting date of moult was 8 December in immatures which moulted the six outer primaries (group MOP6), and became progressively later for groups which moulted fewer primaries, with 24 January being the latest starting date estimated for birds which moulted three (MOP3), a difference in starting dates between the groups MOP6 and MOP3 of 47 days (Table 2). The estimated 95% confidence intervals around the mean moult starting dates ranged from 59 days for the MOP3 group (26 December–23 February) to 96 days (29 October–2 February) for the MOP5 group (Fig. 3). The average duration of moult was estimated to range from 55 days for group MOP3 to 111 days for group MOP6 (Table 2). The estimated moult completion dates for the four groups fell 9 days apart, between 19 and 28 March (Table 2). The estimated completion dates for the moult of P10, estimated for this individual primary in the MOP3, MOP4 and MOP5 groups, were within 6 days of each other, 20–26 March (Table 3; Fig. 4). The estimates obtained from both all primaries combined and from separate primaries showed that all groups of moulters ended their moult almost synchronously (Tables 2 and 3). For all groups, the lower limits of the 95% confidence intervals for the completion of moult fell within 4–19 February and the upper limits within 18 April–11 May (Fig. 3).

Strategies for moult in immatures

Immatures which replaced five or six primaries (groups MOP5 and MOP6) on average began their moult in December and the estimated moult durations were 98 and 111 days, respectively (Table 2). This strategy was used by 29% of the moulters (Table 1). Birds that replaced four

Table 1 Number of primary feathers renewed in the partial moult of immature Wood Sandpipers *Tringa glareola* in southern Africa ($n = 400$), PFMG—proportion of feather mass grown

Group	Primary feathers moulted	Number (%) in group	PFMG at completion of moult
MOP2	P9–P10	5 (1.3)	0.31
MOP3	P8–P10	26 (6.5)	0.45
MOP4	P7–P10	253 (63.3)	0.57
MOP5	P6–P10	109 (27.3)	0.68
MOP6	P5–P10	7 (1.8)	0.77

Groups of moulters distinguished by the number of primaries replaced (see text)

primaries (MOP4) on average began their moult 22 days later than immatures moulting five primaries and 29 days later than birds moulting six, and the mean moult duration was 73 days (Table 2). This was the most common moult strategy, used by more than 60% of the immature Wood Sandpipers (Table 1). Birds which replaced three primaries (MOP3) on average commenced moult on 24 January and completed it in 55 days (Table 2). This strategy was used by 6.5% of moulters (Table 1). The mean daily rate of primary feather mass production was 0.69%/day in groups MOP5 and MOP6, increased to 0.78%/day in group MOP4, and was 0.82%/day in group MOP3; the differences between these groups were significant (Z test results in Table 2).

During the moult of primaries P8, P9 and P10, immatures that replaced more primaries grew fewer feathers simultaneously than those that replaced fewer primaries (Fig. 5). This difference was largest when P9 was replaced (ANOVA: $F_{2,95} = 4.66$, $P = 0.0117$). The number of primaries grown simultaneously with P9 by the MOP3 group was 2.4, while for the MOP4 and the MOP5 groups it was 1.8 and 1.7, respectively (Fig. 5), which did not differ significantly (post-hoc Newman–Keuls test: $P = 0.49$). In the MOP3 group, 48% of the birds were moulting all three feathers simultaneously. In the MOP4 and MOP5 groups, this pattern was found only in 6% of the birds in each group; the most common pattern (59 and 66% of moulters, respectively) was growing two primaries simultaneously.

In the MOP3 group, the interval between shedding primaries P9 and P10 was on average 11 days (Table 3). In the MOP4 and MOP5 groups, the mean intervals between shedding consecutive primaries were 22 days (range 15–38 days) and 23 days (range 18–26 days), respectively. These mean inter-shedding intervals did not differ between groups MOP4 and MOP5 (Z test for comparison of means: $P = 0.15$), but differed between the group MOP3 and the groups MOP4 or MOP5 (Z test: $P < 0.0001$ for both pairwise comparisons; Bonferroni correction applied). In the MOP3 group, the estimated overlap in the growth of P9 and P10 was 28 days (Table 3; Fig. 4). This differed from the mean lengths of overlap of every pair of neighbouring primaries we considered in group MOP4 (mean 14 days) and MOP5 (mean 11 days) (Z test: $P < 0.001$ for both comparisons; Bonferroni correction applied).

The size of the gap in the wing

The size of the wing gap, expressed as PFMM, in four groups of moulters averaged between 0.08 and 0.11 (Table 4). This means that on average the immatures were missing 8–11% of the mass of their primary flight feathers during moult at any one stage. The size of the wing gap did not differ significantly among the groups of moulters (Kruskal–Wallis test: $H_{4,296} = 1.15$, $P = 0.89$). The maximum wing gaps were 0.41 in a bird from the MOP4 group that was growing all four primaries simultaneously, and 0.31 in a bird from the MOP5 group that was growing P6,

Table 2 Estimates of moult parameters for groups of immature Wood Sandpipers replacing different numbers of primaries in southern Africa, based on all moulted primaries as a single tract

Group of moulters	Moult parameters				Sample sizes			% PFMG/day (SD)
	Mean start date (SD)	Duration (SD) in days	Standard deviation of start date (SD) in days	End date (SD)	Not yet moulted	In moult	Moult complete	
MOP3	24 Jan (10.1)	55 (12.4)	15 (2.9)	19 Mar (4.9)	0	17	7	0.82 (0.24)
MOP4	6 Jan (4.3)	73 (5.5)	21 (1.2)	19 Mar (2.3)	0	185	63	0.78 (0.06)*
MOP5	16 Dec (7.0)	98 (9.6)	25 (2.4)	23 Mar (4.2)	0	85	21	0.69 (0.08)**
MOP6	8 Dec (29.3)	111 (39.7)	23 (7.8)	28 Mar (16.0)	0	5	2	0.69 (0.39)

Groups of moulters distinguished by the number of primaries replaced. The final column provides the estimated daily rate of primary mass production, calculated from completion PFMG (Table 1) divided by the estimated moult duration for each group

* $P < 0.05$, ** $P < 0.001$ indicating significant differences in estimated daily rate of primary mass production from the previous group: (Z test for comparison of means, Bonferroni correction applied)

Table 3 Estimates of moult parameters and daily growth rates (expressed as a proportion of feather mass grown per day) of individual primaries for three groups of immature Wood Sandpipers replacing different numbers of primaries in southern Africa

Group	Primary	Moult parameters				Sample sizes			PFMG/day (SD)
		Mean start date (SD)	Duration (SD)	Standard deviation of start date (SD)	End date (SD)	Not yet moulted	In moult	Moult complete	
MOP3	P9	18 Jan (10.5)	39 (12.0)	31 (8.4)	27 Feb (8.5)	6	9	16	0.38 (0.130)
	P10	30 Jan (10.0)	51 (13.7)	35 (8.9)	20 Mar (9.8)	9	12	10	0.33 (0.095)
MOP4	P8	5 Jan (3.6)	34 (3.9)	28 (2.5)	9 Feb (2.8)	46	63	145	0.39 (0.045)
	P9	31 Jan (2.6)	33 (3.3)	25 (1.9)	4 Mar (2.6)	92	64	98	0.45 (0.055)**
	P10	17 Feb (2.3)	34 (3.1)	22 (1.7)	22 Mar (2.6)	125	66	63	0.49 (0.045)**
MOP5	P7	9 Dec (10.0)	35 (8.2)	35 (6.6)	12 Jan (6.1)	8	20	80	0.35 (0.087)
	P8	15 Jan (4.4)	23 (4.7)	24 (3.5)	7 Feb (3.8)	26	22	60	0.59 (0.123)**
	P9	1 Feb (3.4)	29 (4.6)	22 (2.7)	1 Mar (3.8)	42	27	39	0.52 (0.086)**
	P10	12 Feb (3.8)	38 (5.5)	24 (2.9)	26 Mar (4.6)	57	30	21	0.43 (0.064)**

*** $P < 0.001$ indicating significant differences in the daily growth rate for the corresponding primary in the previous group of moulters: (Z test for comparison of means, Bonferroni correction applied)

P7 and P9 (P8 was fully grown) simultaneously (Table 4). The values of PFMM for all the remaining birds in all groups were less than 0.27. The correlations between the size of the wing gap and the date in the season was not significant in the MOP4 group ($r = -0.11$, $P = 0.15$, $n = 183$) and the MOP5 group ($r = -0.03$; $P = 0.82$, $n = 87$). However, in birds that replaced only two or three primaries (groups MOP2 and MOP3) the size of the wing gap decreased over the season ($r = -0.52$; $P = 0.015$, $n = 21$).

Moult parameters of primaries

Comparing the moult parameters of individual primaries revealed that immatures replacing fewer primaries tended to grow each corresponding feather slower than birds replacing more feathers (Table 3). For example, P10, the last primary to grow, had a significantly slower daily growth rate in the MOP3 group than in the MOP4 and MOP5 groups (Z test results in Table 3). Thus, the daily growth rate for corresponding primaries was the slowest in birds that had the fastest overall rate of primary mass production. Rapid primary mass production in the MOP3 group was achieved by the simultaneous growth of two or three feathers. Thus, in spite of the slow daily growth rates of these individual primaries (Table 3), the MOP3 group achieved a faster overall rate of production of feather material than the other groups of moulters (Table 2).

In two groups of slow moulters, MOP5 and MOP4, the second primary to be moulted (P7 and P8 respectively) had slower daily growth rates than the following primary in the moult sequence (Fig. 4; Table 3). This was not the case in birds of the MOP3 group, in which P9 had a faster daily growth rate than P10 (Table 3; Fig. 4). The estimated

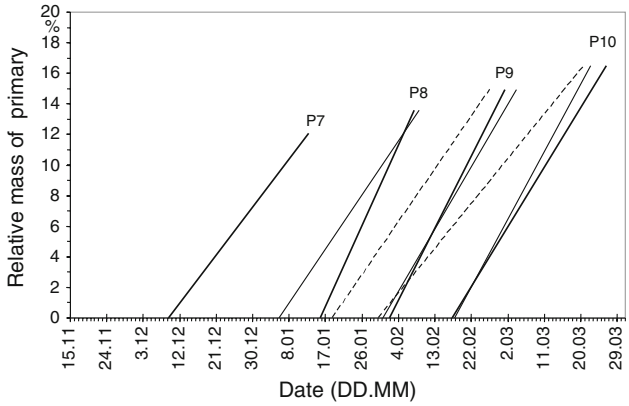

Fig. 4 Dates of the start and the end of moult for individual primaries (P7–P10) moulted by immature Wood Sandpipers in southern Africa. The *endpoints of lines* are at the relative mass of each primary so that the *slopes of the lines* represent the growth rates of the primary. *Dashed lines* MOP3, birds which moulted the three outermost primaries; *thin lines* MOP4, four primaries; *thick lines* MOP5, five primaries

starting dates of moult of corresponding primaries differed among the three groups of moulters (MOP3, MOP4 and MOP5) from 10 days for P8 to 18 days for P10 (Table 3; Fig. 4). The estimated completion dates for P8 were 2 days apart for the MOP4 and MOP5 groups; for P9 the moult completion dates were 5 days apart for the MOP3, MOP4 and MOP5 groups, and for P10 they were 6 days apart (Table 3; Fig. 4).

Factors that influence the pattern of moult

In a subsample of 238 birds captured between 14 November and 11 March, when immatures actively moulting their first primary were observed, 82 had

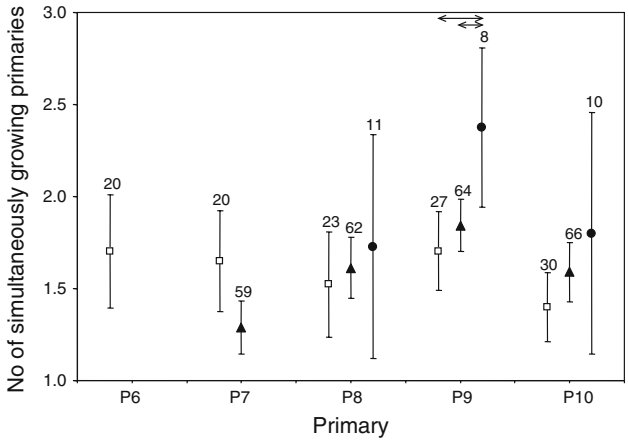

Fig. 5 Means, 95% confidence intervals and sample sizes of the number of simultaneously growing primaries in immature Wood Sandpipers in southern Africa while the primary marked at the *X* axis is in moult. Statistics are shown for birds that were moulting three primaries MOP3 (*black circles*), four primaries MOP4 (*black triangles*) or five primaries MOP5 (*open squares*). The *numbers above whiskers* are the sample sizes, *arrows* mark statistically significant differences (ANOVA, post-hoc Newman–Keuls test, $P < 0.05$)

Table 4 Average proportions of feather mass missing (PFMM) for groups of immature Wood Sandpipers in southern Africa replacing different numbers of primaries (see text)

Group of moulters	Mean PFMM (SD)	Min–max	*n*
MOP3	0.11 (0.087)	0.02–0.26	18
MOP4	0.10 (0.060)	0.02–0.41	183
MOP5	0.10 (0.058)	0.01–0.31	87
MOP6	0.08 (0.066)	0.01–0.18	5

commenced the moult of an outer primary, and 156 birds had not yet started moult. The generalised linear model showed that body mass and date of capture were statistically significant explanatory variables. Letting P be the probability of having started moult, m the mass (g) and d the number of days since 1 June, the fitted model was $\text{logit}(P) = -15.64 + 0.0716\,m + 0.0499d$, where the standard deviations, t values and associated P values of the three terms in the model, were SD = 2.89, $t = -5.41$, $P < 0.001$, SD = 0.0319, $t = 2.25$, $P = 0.024$ and SD = 0.0080, $t = 6.23$, $P < 0.0001$, respectively. The interaction term md was not significant ($P = 0.21$). The probability of being in moult was thus larger for heavier birds and larger later on in the season; the key characteristics of the fitted model are represented in Fig. 7. Mean body mass at the start of moult varied neither with the number of feathers moulted (MOP3: mean – 60.6 g, $n = 10$; MOP4: 60.0 g, $n = 55$; MOP5: 60.8 g, $n = 15$; ANOVA: $F_{2,77} = 0.22$, $P = 0.80$), nor with the date of capture (modelled mass decrease of 0.0214 g/day was not significant, $t_{1,80} = -0.88$, $P = 0.38$).

Discussion

General pattern of moult in immature Wood Sandpipers

Our results showed that the first immature Wood Sandpipers arrive in southern Africa in the second half of August, but numbers remain low in September and increase in October (Fig. 2). This is only partly in agreement with the statement by Hockey et al. (2005) that immature Wood Sandpipers arrive in southern Africa between mid-September and mid-October. Our results showed that most immatures started to moult between November and January (Figs 2 and 3; Table 2), delaying this process for 2–4 months after arrival. This indicates that, unlike adults, the beginning of moult for immatures was not determined by their date of arrival (Remisiewicz et al. 2009). The duration of moult varied by a factor of two, depending on the number of primaries replaced, from 55 days to 111 days. We attribute this wide period in which they start moulting to the varying conditions provided by the freshwater habitats that this species uses in southern Africa and will discuss this issue later.

A few immatures showed no signs of primary moult by March and April, and one individual was still moulting at the end of May (Fig. 3). These birds would not complete moult in time for the northward migration. But a small proportion of Wood Sandpipers defer their return migration until their second year of life (authors, unpublished data) and single birds are regularly observed in the wetlands of southern Africa during the austral winter (Cramp and Simmons 1983; Underhill 1997; Hockey et al. 2005). The delayed moult of non-migrants is supported by observations in southern Africa of Wood Sandpipers in advanced moult at the beginning of July, before the main arrival of migrants (Remisiewicz et al. 2009).

The extent of the moult in immature waders

A partial moult of two to seven outer primaries is the common strategy in the immatures of medium-sized and larger waders spending the northern winter in the southern hemisphere (Prater et al. 1977; Ginn and Melville 1983; Prater 1981). Prater (1981) showed that larger waders tend to replace fewer primaries in this moult than do smaller species. In southern Africa, immature Greenshanks, Marsh Sandpipers *T. stagnatilis*, Ruffs *Philomachus pugnax* and Curlew Sandpipers moult varying numbers of outer primaries; in contrast with the smaller Common Sandpipers *Actitis hypoleucos* and Little Stints which usually replace all primaries (Tree 1974, 2009; Elliott et al. 1976; Schmitt and Whitehouse 1976). Immature Wood Sandpipers that overwintered in Kenya were frequently found to be moulting two to six primaries (Pearson 1974), a similar

pattern to the birds described in this paper. The number of replaced primaries might vary with the distance the birds must migrate (Prater 1981). Wood Sandpipers spending the austral summer in southern Africa come from breeding grounds extending from Scandinavia to Western Siberia, and their migration distance might thus vary from about 8,000 to 12,000 km (Underhill et al. 1999). In this species, populations from different breeding grounds show no obvious distinguishing characteristics (Cramp and Simmons 1983) so we had no way to link the moult strategies with the birds' breeding origin.

Immature Wood Sandpipers fledge in June or July with their first set of primaries (Dementiev and Gladkov 1951; Prater et al. 1977). These feathers are usually of inferior quality to those of adults (Ginn and Melville 1983). By March or April of the following year, i.e. by the time the birds depart from the southern hemisphere, these primaries are about 10 months old. The outer primaries are the most exposed and would be the most abraded; the inner ones might remain in a relatively good condition (Prater et al. 1977; Ginn and Melville 1983). Pearson (1974) described the unmoulted primaries of immature Wood Sandpipers caught in Kenya in March as being relatively fresh. The most crucial feathers for flight are the six outer primaries (Videler 2005). Most immature Wood Sandpipers replaced four to six outer primaries (Table 1), which is also the most common patterns of moult in other immature waders in southern Africa (Tree 1974; Elliott et al. 1976; Schmitt and Whitehouse 1976; Ginn and Melville 1983). Immature Wood Sandpipers arrive in southern Africa about 2 months later than the adults (compare Underhill 1997 with Fig. 2) and so have less time available for moult before departure in March–April. Replacing the outermost primaries, those most abraded but crucial for flight, allows the immatures prepare for return migration, with heavier birds tending to moult earlier than lighter birds (Fig. 7), and meet the time constraint imposed by the need to complete moult before departure, suggested by the synchronised ending to moult, regardless of the number of outer primaries they moult (Tables 2 and 3).

Control of the rate of primary feather mass production

Immature Wood Sandpipers that moulted five or six primaries (groups MOP5 and MOP6) conducted their moult over a period 1 month shorter than the duration of 131 days for a complete moult by adults (Remisiewicz et al. 2009). The average rate of feather mass production in these immatures was slower than the rate in adults, in which it was 0.76% PFMG/day (Remisiewicz et al. 2009). Similarly, immature Curlew Sandpipers in South Africa grow primaries at about 2/3 of the adult rate (Elliott et al. 1976). In the immatures that replaced three primaries (MOP3), the rate of primary feather mass production over the season was faster than that of adults (Table 2). A slower daily rate of primary feather mass production might allow immature "slow moulters" to produce better-quality feathers than "rapid moulters" or adults. In the Grey Plover *Pluvialis squatarola* (Serra et al. 2001) and the Common Starling *Sturnus vulgaris* (Dawson et al. 2000), primaries grown slowly were more resistant to abrasion than rapidly-grown feathers.

In Grey Plovers, Black Terns *Chlidonias niger* and adult Wood Sandpipers, the rate of primary feather mass production is controlled by the number of feathers grown simultaneously and by the shedding intervals between successive primaries (Zenatello et al. 2002; Serra and Underhill 2006; Remisiewicz et al. 2009). We found the same mechanism in immature Wood Sandpipers, which varied the number of feathers grown simultaneously as well as the duration of growth of each primary. This resulted in different rates of primary feather mass production for birds replacing different numbers of primaries (Table 2). Black Terns which undertook a "heavier moult" grew more primaries simultaneously, but with a slower growth rate of each feather, than birds in "weaker moult" (Zenatello et al. 2002). We found a similar relationship between the number of primaries moulted at the same time and their growth rate, comparing the moult pattern of the "rapid moulting" Wood Sandpipers of group MOP3 and the "slow moulting" groups MOP4 and MOP5 (Table 2; Fig. 5).

The gap in immature birds' wings caused by shedding primaries was on average the same size as in adults at about 10% of the mass of primaries (Remisiewicz et al. 2009). A wing gap increases the energetic costs of flight, but a gap in the outer primaries is less costly than a gap closer to the body because of the lift force close to the optimal when the gap is at the wing tip (Hedenström and Sunada 1999). Thus, considering the relatively small size of the gap and its outer position in the wing, it should not substantially impede the immature Wood Sandpipers' flight ability and would not prevent them from moving among wetlands during moult.

Synchronisation of end of moult among immatures

Although the mean starting dates of moult for the groups MOP3 to MOP6 took place over a 7-week period (8 December–24 January), the mean completion dates ranged over 9 days (19–28 March) (Table 2). Wood Sandpipers leave southern Africa from mid-March to early May (Underhill 1997; Hockey et al. 2005); our results suggest that immature Wood Sandpipers complete moult shortly before departure. This synchronised ending of moult among all groups of moulters was already apparent by the

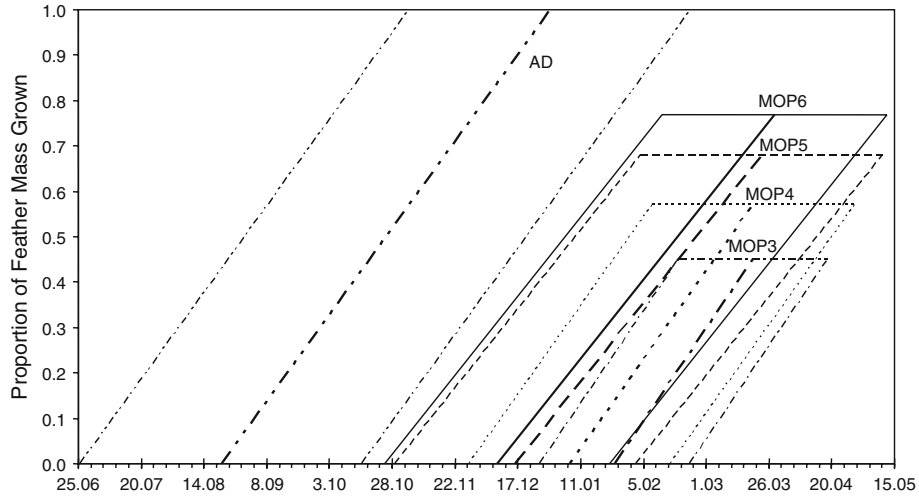

Fig. 6 *Lines* showing estimated timing of moult and 95% confidence intervals into which moult scores on any given date ought to fall for the immatures moulting different numbers of outer primaries (*MOP3, MOP4, MOP5, MOP6*; explanations of *symbols* as in Fig. 2) and for the adults (*AD*) of Wood Sandpipers (after Remisiewicz et al. 2009) in southern Africa

end of the moult of P9 and correlated even better by the end of the growth of P10 (Table 3; Fig. 4). The tight synchronisation to the end of moult in immature Wood Sandpipers is probably required by their departure. Moult and migration are considered to be mutually exclusive activities (Ginn and Melville 1983; Lindström et al. 1994; Zenatello et al. 2002; Newton 2008). In songbirds, for example in the Willow Warbler *Phylloscopus trochilus* (Underhill et al. 1992), Lesser Whitethroat *Sylvia curruca* (Hall and Fransson 2000) and Blackcap *Sylvia atricapilla* (Pulido and Coppack 2004), migration departure has been described as a constraint that enforces rapid moult and sets a limit by which moult must end.

A similar, but less tight, synchronisation of the end of moult was observed in Curlew Sandpipers in Australia, where moult of between three and six outer primaries commenced between January and April, but the estimated moult ending dates of all groups of moulters fell within 30 days in May and June (Minton et al. 2006). That departure date is a constraint to the moult of immature Wood Sandpipers is supported by comparing its pattern of moult with that of immature Curlew Sandpipers in southern Africa. Immature Curlew Sandpipers are a similar size to Wood Sandpipers (mean wing lengths 130.5 and 124.6 mm, respectively) and they replace three to six outer primaries, usually four or five, as do Wood Sandpipers (Elliott et al. 1976; Y. Barshep, personal communication). But Curlew Sandpipers start their moult on average only at the beginning of April, 2–5 months later than Wood Sandpipers, and finish by the end of June (Elliott et al. 1976; Y. Barshep, personal communication). Most immature Curlew Sandpipers do not migrate to the breeding grounds in their second year of life (Elliott et al. 1976; Underhill 2006), which probably explains their delayed moult. This is in contrast with immature Wood Sandpipers, most of which migrate northward in their second year (Underhill 1997; Hockey et al. 2005). Thus, they should avoid extending their moult beyond the optimum date of departure because the delay would decrease their chances of successful mating and breeding in their first breeding season (Myers 1981; Summers et al. 1995; Hockey et al. 1998).

The starting dates of primary moult in juvenile Wood Sandpipers, as a whole, were asynchronised; the lower value of the 95% confidence interval for group MOP6 was 122 days earlier than the upper limit for MOP3 (Fig. 6, calculations based on Table 2). In contrast, the length of the 95% confidence limits of the start of adult primary moult was 114 days (Fig. 6; Remisiewicz et al. 2009). However, the estimated standard deviation parameters for each group of immatures ranged from 15 to 23 days (Table 2); for adults, it was 29 days (Fig. 6) (Remisiewicz et al. 2009). This suggests that, although the overall timing of the start of moult was less synchronised in juveniles than in adults, the timing of moult within each juvenile moult group was more synchronised than in adults (Fig. 6).

Factors that trigger moult and flexible strategies of moult

A bird's condition, reflected by its body mass, is the key factor for Black Terns in the Gulf of Venice to begin moult and to select a moulting strategy (Zenatello et al. 2002). Black Terns with a higher body mass undertook a "heavier moult" and grew more primaries simultaneously, but with a slower growth rate of each feather, than birds in "weaker moult"; birds that lost body mass switched from a "heavy" to a "weak" moult. In immature Wood Sandpipers, both body mass and the date in the season were important factors in triggering moult (Fig. 7). Despite the extended period over which Wood Sandpipers started their moult, we found that the later in the season, the more likely an immature would begin to moult, and also the heavier the bird, the more likely it was to start moulting. This shows

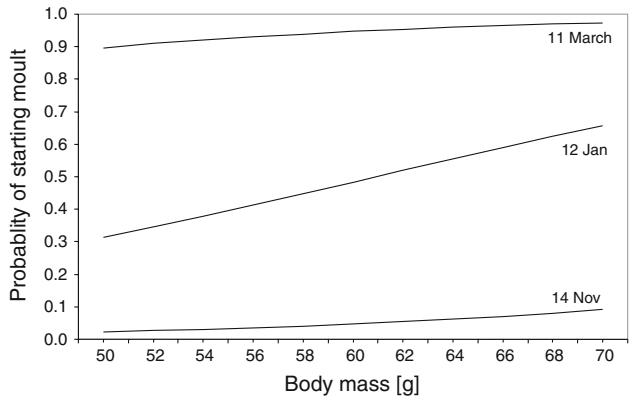

Fig. 7 Results of a generalised linear model relating the start of moult by immature Wood Sandpipers in southern Africa to body mass. The *lines* show, for three representative dates, the modelled probabilities of a bird with a particular body mass having started moult. The chosen dates represent earliest (14 November), mean (12 January) and the latest (11 March) dates on which birds were observed to start primary moult. The range of masses covers the 95% confidence interval of observed masses; the overall range was 48–74 g

that Wood Sandpipers, like Black Terns, tend to accumulate reserves before commencing moult. But the importance of body mass in triggering moult was greater in the middle of the moulting period than later in the season, when the probability of birds being in moult was more than 80% for all birds, irrespective of their body mass (Fig. 7). Unlike the Black Tern (Zenatello et al. 2002), the moult strategy of immature Wood Sandpipers, and the number of feathers replaced, were not influenced by body mass. We found that late-starting moulters were more likely to adopt a strategy of moulting fewer feathers together with a higher rate of primary mass production than those starting earlier in the season. We suggest the following explanation for these results. Early in the season, immature Wood Sandpipers would begin moult once they had reached a threshold level of accumulated reserves, and moult five or six primaries at a pace that ensured completion at departure. Later in the season, moult commenced even if mass reserves had not reached the required threshold (Fig. 7), and fewer feathers were moulted, but tended to be moulted simultaneously with large energy demands. Presumably, there are fitness and survival advantages of moulting as many primaries as possible, and to moulting them slowly. In some migrants, for example in Common Starlings (Dawson 2004) and Red Knots *Calidris canutus* (Zwarts et al. 1990), it was shown that the timing of moult and migration were controlled by hormonal mechanisms that were tied to the birds' internal clock, in turn adjusted to the photoperiod. Other hormonal mechanisms have been suggested that allow migrant waders to assess their level of fat reserves at stopover sites (Meissner 2001; Kochan et al. 2006); these are likely also to operate at the non-breeding grounds.

Our results point to immature Wood Sandpipers being flexible in their choice of a moult strategy in a response to the variable environmental conditions they encounter at the non-breeding grounds, but we cannot exclude that these different strategies related to birds' differences in breeding origin. Immatures adjusting their moult to environmental conditions were described in Semipalmated Sandpipers *Calidris pusilla* at their breeding grounds in Alaska (Gratto and Morrison 1981). In that species, different proportions of immatures began a partial moult of primaries and varied the extent of this moult in relation to environmental conditions that varied between years. The flexibility of moult strategies within a species in response to both the birds' internal condition and environmental conditions has been observed in Cory's Shearwaters *Calonectris diomedea* (Alonso et al. 2009). Wood Sandpipers during the non-breeding period use freshwater wetlands almost exclusively (Cramp and Simmons 1983; Underhill 1995, 1997). In the north-eastern and north-central parts of southern Africa, where Wood Sandpipers mostly occur, the summer rainy season usually starts in October or November and the wettest months are usually December and January (Milstein 1972; Allan et al. 1997). Rain-fed inland wetlands provide these waders with suitable conditions for feeding and moulting in these months, but the timing and intensity of the rainfall varies between years and locations. Thus, these wetlands are often irregular or ephemeral and provide unpredictable food resources (Milstein 1972; Underhill 1995; Taylor et al. 1999), and Wood Sandpipers probably need to move between these wetlands in search of optimum feeding conditions. Such nomadic movements between wetlands in southern Africa are shown by ring recoveries of Wood Sandpipers (Underhill et al. 1999). The varying conditions in different years and at different wetlands mean the birds probably reach a body mass that allows them to start moulting at different times in the season. Wood Sandpipers might assess the level of their reserves and the time left before departure, and then apply the most efficient moult strategy for their circumstances. Thus, in conclusion, we suggest that immature Wood Sandpipers adopt a variety of moult strategies that provide them with the flexibility to adjust to the unpredictable and variable conditions they encounter at inland wetlands during their first season in southern Africa.

Zusammenfassung

Junge ziehende Watvögel haben komplexere Mausermuster als Adultvögel, die bisher jedoch nur bruchstückhaft beschrieben worden sind. Der Bruchwasserläufer *Tringa*

glareola brütet in der Taigaregion der Paläarktis, und ein Teil der Population zieht ins südliche Afrika. Wir wählten diese Population für eine Untersuchung der Handschwingen-Mauserstrategien eines jungen Watvogels aus. Nach einer Analyse der Mauserformeln von 674 Jungtieren diskutieren wir potentielle Faktoren, welche die Wahl der Mauserstrategie beeinflussen. Alle mausernden Tiere ersetzten zwei bis sechs äußere Handschwingen; 91% mauserten vier oder fünf. Wir haben das Underhill-Zucchini-Modell verwendet, um das Timing und die Dauer der Mauser bei Jungtieren, die unterschiedliche Anzahlen von Handschwingen ersetzen, abzuschätzen. Eine langsame Mauser von fünf oder sechs Handschwingen, beobachtet bei 29%, dauerte im Durchschnitt 98 bis 111 Tage und begann im Durchschnitt vom 8. bis zum 16. Dezember. Eine Mauser von vier Handschwingen (63%) begann am 6. Januar und dauerte im Durchschnitt 73 Tage. Eine schnelle Mauser von drei Handschwingen (7%) begann am 24. Januar und dauerte im Durchschnitt 55 Tage. Alle Gruppen beendeten ihre Mauser zwischen dem 19. und 28. März. GLM-Modelle zeigten, dass schwerere Jungvögel mit höherer Wahrscheinlichkeit später mit der Mauser begonnen als schlankere Vögel. Diese Tendenz war im November bis Januar stärker ausgeprägt als in späteren Monaten. Je später die Mauser begann, desto weniger Federn wurden ersetzt und desto schneller war der Prozess. Die Abflugzeit setzte die Grenze für das Ende der Mauser. Wir schlagen vor, dass die Fähigkeit, unterschiedliche Mauserstrategien zu wählen, es jungen Bruchwasserläufern erlaubt, ihre Mauser an die variablen Bedingungen anzupassen, die sie in Feuchtgebieten im südlichen Afrika vorfinden.

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