



Age-specific variation in relationship between moult and pre-migratory fuelling in Wood Sandpipers *Tringa glareola* in southern Africa

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Trans-equatorial avian migrants tend to breed, moult and migrate – the main energy-requiring events in their lifecycle – at different times. Little is known about the relationship between wing moult and pre-migratory fuelling in waders on their non-breeding grounds, where time is less constrained than during their brief high-latitude breeding season. We determined age-related strategies of Wood Sandpipers *Tringa glareola* to balance the energetic demands of primary moult against pre-migratory fuelling in southern Africa by analysing body mass and primary moult at first capture of 1721 birds mist-netted in 1972–96 at waterbodies in Zimbabwe. Adults moulted all their primaries in August–December, but immatures underwent a supplemental moult of varying numbers of outer primaries in December–April, close to departure. We used locally weighted linear regression to estimate trends in Wood Sandpiper body mass from 1 July to 1 May. They maintained low mass from arrival in July–September to February–early March. Adults fuelled from 10 February to 1 May at a mean rate of 0.25 g/day (sd = 0.16). Most adults (98%) began fuelling 10–75 days after completing primary moult. Immatures fuelled from 4 March to 13 April at 0.24 g/day (sd = 0.14). They used varying strategies depending on their condition: a brief gap between moult and fuelling; an overlap of these processes near departure, leading to slower fuelling; or skipping fuelling altogether and staying in southern Africa for a ‘gap year’. Immatures moulting three or five outer primaries fuelled more slowly than post-moult birds. Immatures moulting four outer primaries started fuelling 3 weeks later but at a higher rate than did post-moult birds of this group. In post-moult immatures, the later they ended moult, the later and faster they fuelled. The heaviest adults and immatures using all moult patterns accumulated fuel loads of c. 50% of lean body mass, and could potentially cross 2397–4490 km to reach the Great Rift Valley in one non-stop flight. Immatures were more flexible in the timing and extent of moult and in the timing and rate of fuelling than adults. This flexibility enables inexperienced Wood Sandpipers to cope with inter-annual differences in feeding conditions at Africa’s ephemeral inland waterbodies.

Keywords: eccentric pre-formative moult, pre-migratory fuelling, primary moult, supplemental moult, waders.

Migrant birds tend to breed, moult and migrate at different times, thus separating the most energy-costly stages in their life cycles (Murphy

& King 1992, Lindström *et al.* 1993). Accumulating fuel for migration is another energy-intensive stage that must be fitted in between the other three processes. The timing and rate of moult in migrants is phenotypically flexible and can buffer variation in the timing of other events

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in their life cycles that are linked to changing seasons, such as pre-breeding migration or breeding (Helm & Gwinner 1999, Conklin & Battley 2012). The timing of pre-migratory mass gain (fuelling) is also expected to be flexible, particularly in waders using ephemeral waterbodies typical of their non-breeding grounds in southern Africa (Remisiewicz *et al.* 2009). Relationships between wing moult and fuelling are inadequately known in migrant passerines and waders moulting on their southern non-breeding grounds. Given that they spend about half the year in the southern hemisphere, time pressure on both activities is probably less severe than in the north, with the departure time for northward migration being the key constraint.

Most immature (first-year) Wood Sandpipers *Tringa glareola* moult a few outer primaries shortly before departure from their southern African non-breeding grounds (Remisiewicz *et al.* 2010a), suggesting that moult and pre-migratory fuelling can overlap. Thus, the species provides an opportunity to study the interaction between these two processes. Immatures of medium and large long-distance migrant waders often moult outer primaries on their southern non-breeding grounds. This was first described in waders that migrate between Eurasia and Africa (Pearson 1974, Tree 1974, Ginn & Melville 1983), and has been variously called a 'supplemental first-year partial moult' (Prater 1981), 'first pre-supplemental moult' (Higgins & Davies 1996) or 'eccentric pre-formative moult' (Howell 2010). Adults of these wader species usually moult all 10 primaries on the non-breeding grounds.

Given these differences in primary moult between adult and immature Wood Sandpipers, and the various patterns of supplemental moult used by immatures, we aimed to determine age-related strategies in moult and fuelling in southern Africa by identifying how moult patterns affected their accumulation of fuel for northward migration. We expected that moult and pre-migratory fuelling overlapped in immatures, which moult close to departure time, but not in adults, which complete primary moult a few months before departing north. We also expected the number of primaries that the immatures replaced to be related to their tendency to overlap moult and fuelling. We thereby assess how birds of different ages adapt to different environmental scenarios by flexible moult and fuelling patterns.

METHODS

Study species, study sites and methods of data collection

Wood Sandpiper is a long-distance migrant to southern Africa that breeds in the taiga and boreal zones from Scandinavia to central Siberia (Cramp & Simmons 1983, Lappo *et al.* 2012). Adult Wood Sandpipers arrive in southern Africa in mid-July to September, immatures about a month later; birds of both age groups leave on northward migration in mid-March–April (Fig. 1) (Underhill 1997, Tree 2014). Most immatures depart for the breeding grounds at the end of their first year, but a few stay for a 'gap year' in southern Africa (Underhill 2009). Adult Wood Sandpipers moult all their primaries in southern Africa in August–December; most immatures moult a few outer primaries in December–April (Remisiewicz *et al.* 2009, 2010a; Fig. 1). Supplemental moult of immatures varies from a slow moult of four to six outer primaries started in early December to a quick replacement of two or three outer primaries started in late January (Fig. 1). Regardless of their moult strategy, immatures complete the process on average by 19–23 March, within the period of departures (Remisiewicz *et al.* 2010a, Tree 2014; Fig. 1).

We analysed the primary moult, body mass and wing length at first capture of 1721 adults and immatures mist-netted by A.J.T. in Zimbabwe in 1972–96 at 35 natural and artificial eutrophic lakes, small dams, ponds and sewage works, mostly around Harare, and on the banks of the Zambezi River (Tree 2014; Fig. 2). We used 1 July to 1 May as the main period when Wood Sandpipers occurred in Zimbabwe (Tree 2014). They were aged by plumage as immatures (during their first year of life), sub-adults (during their second year of life until about 20 months) or adults (older birds) (Tree 1974, Prater *et al.* 1977). The birds were weighed with a Pesola spring balance to 1-g precision. Wing lengths were measured with a ruler to 0.5-mm precision. Too few birds were caught each year to model the annual seasonal trends in the mass of immatures and adults, so masses at first capture were combined across years and ringing locations for each age category. From the tract of 10 primaries of one wing of each bird, numbered P1–P10 from inside of the wing outwards, the moult formula was recorded as a string

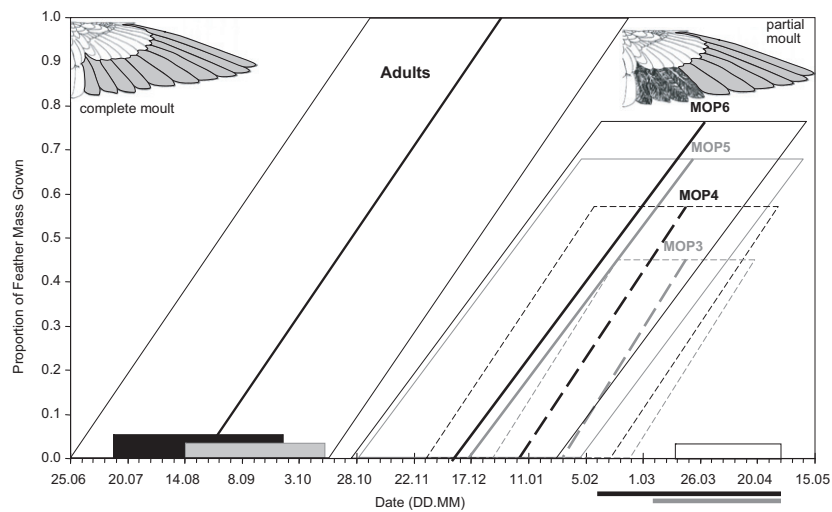


Figure 1. Patterns of primary moult in adult and immature Wood Sandpipers caught in Zimbabwe in 1972–96. Moult progress is reflected by the mean progress of proportion of feather mass grown (PFMG) (thick lines) and 95% confidence interval (CI; thin lines). Groups of immatures: birds that replace three (MOP3), four (MOP4), five (MOP5) and six (MOP6) outer primaries; the top left insert shows MOP6 moult. Horizontal lines under these symbols show the maximum value of PFMG that each group can reach in relation to mass of all primaries (100%) (Remisiewicz *et al.* 2009, 2010a, modified). Bars on the x-axis: black – period of adults' arrival, grey – period of immatures' arrival, white – common period for adults' and immatures' departures (Underhill 1997); lines below the x-axis show estimated fuelling periods: black – for adults, grey – for immatures.

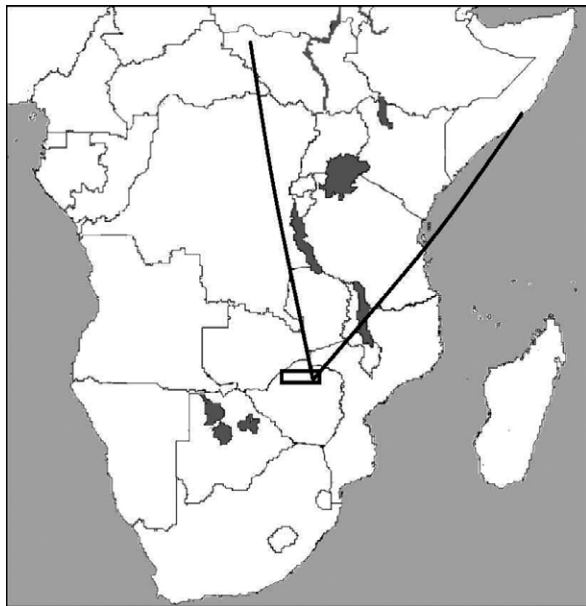


Figure 2. The area where Wood Sandpipers were ringed in Zimbabwe in 1972–96 (black rectangle). The lines show the mean potential flight ranges estimated for the heaviest 20% of adults and immatures combined departing to the north or northeast from the region of Harare, where most birds were ringed.

of 10 digits (moult scores). Scores of 0 and 5 indicated old and new feathers, respectively, and values 1–4 described the stages of feather growth (Ashmole 1962, Ginn & Melville 1983). To assess the relationship between mass and stage of moult, we distinguished three groups of birds using their moult formulae: pre-moulters, which had not yet started moult; moulting birds with growing primaries; and post-moulters, which had completed moult. Among immatures that moulted a few outer primaries we distinguished groups of birds by the number of primaries they were replacing: MOP6 (moult of six outer primaries P5–P10), MOP5 (moult of five outer primaries P6–P10), MOP4 (moult of four outer primaries P7–P10) and MOP3 (moult of three outer primaries P8–P10) (Remisiewicz *et al.* 2010a).

Modelling seasonal trends in body mass

We plotted the masses of adults and immatures against their date of capture. To estimate the seasonal trends in body mass we used a smoothing algorithm consisting of a locally weighted linear regression method (adapted from Summers *et al.* 1985, 1992 and Mullers *et al.* 2009, see Supporting Information Appendix S1). This method estimates a smoothed

curve of body mass through time. The algorithm is an extension of the concept of moving averages. The smoothed curve is non-parametric, although the individual values for particular dates are derived from a regression model. The extent of smoothing is user-driven; we chose a smoothing parameter so that only masses within 15 days of a particular date have influence on the smoothed mass (and confidence limits) on that date. This non-parametric approach has the advantage of being totally flexible and data-driven. We conducted these calculations in R 3.1.2 (R Foundation for Statistical Computing) applying a script by M.S.B. and L.G.U. (Appendix S1) to the original data (Appendix S2).

We estimated the daily increments of the smoothed body mass curve to find the date on which fuelling for migration started. Daily reductions indicated decreasing body mass, increments reflected increasing mass, and the size of the daily change reflected the estimated daily fuelling rate. To estimate the date pre-migratory fuelling started, we used the date on which these daily changes became positive and stayed above 0.01 g for more than three successive days. We estimated the mean rate of pre-migratory fuelling from this start date either until 1 May, which we assumed was the last departure date from southern Africa, or until an earlier date on which the daily rate became negative. These calculated rates of fuelling are likely to be underestimated because the heaviest birds leave on migration once they attain departure mass, leaving leaner birds to be sampled, which reduces the smoothed mass on a given date.

To determine the effect of age and moult status on the rate of fuelling, we estimated the mean daily mass increments during the period of fuelling for three groups (post-moult adults, post-moult immatures, moulting immatures) and compared means for these groups. We determined the effect of moult pattern on fuelling by comparing the mean daily mass increments of moulting and post-moult birds within groups of immatures that had replaced different numbers of outer primaries (MOP3, MOP4, MOP5, MOP6). The MOP6 group was too small to analyse. To determine whether the mean daily rate of fuelling differed between groups, we used a pairwise permutation test with 1000 permutations to estimate whether the difference in means was statistically different from zero (Manly 2007). For each pair of groups, the test compared the observed difference between the means of the two groups with the difference in means obtained by permuting (i.e.

resampling without replacement) the combined dataset into two groups. The permuted difference was obtained after random sorting, so it was not expected to differ significantly from zero. This comparison was then repeated 1000 times, and the *P*-value was the proportion of times the permuted difference was equal to or greater than the observed difference (Pitman 1937, Howell 2015). We adopted $P < 0.05$ as indicating statistical significance. When comparing three groups, we used an analogous permutation test for ANOVA (Manly 2007, Howell 2009) and *post-hoc* pairwise permutation tests. Permutation tests were conducted in R 3.1.2 (R Foundation for Statistical Computing 2014) using Howell's scripts (2009, 2015).

Estimation of the potential flight range

To assess how different patterns of fuelling affected migration to the breeding grounds, we compared the potential flight ranges of adults and immatures on their departure from Zimbabwe. We assumed that the 5% of post-moult birds with the lowest mass divided by wing length ('ratio index'; Jakob *et al.* 1996) represented birds that had not yet started fuelling. For this, we combined adults and immatures because they had similar wing lengths. We then applied a linear model, body mass against wing length of lean birds, both transformed by logarithms (Summers 1988). The slope coefficient from this regression is the value ('scaling coefficient') to which wing length needs to be raised to make it scale approximately directly with mass (Summers 1988, Summers *et al.* 1992). This adjustment reduces any potential bias introduced by scaling of body mass with wing length. We used the scaling coefficient and wing length to adjust the birds' mass to the equivalent body mass of a bird with the mean post-moult wing length, using the approach of Summers *et al.* (1992). This adjusting enabled us to compare masses of birds of different size. We then estimated the adjusted lean body mass (aLBM) as the mean adjusted body mass of these 5% leanest birds we had used earlier. We calculated individual fuel loads by subtracting aLBM from the adjusted actual body mass (aBM) of each individual.

We used the 20% of adults and immatures with the highest fuel loads to estimate their potential flight range on departure from Zimbabwe, applying the Davidson (1984) formula, which accounts for the loss of mass during flight:

$$R = 95.447 * S * (aBM^{0.302} - aLBM^{0.302}),$$

where R is the estimated flight range (km) and S is the flight speed (km/h). We used a flight speed of $S = 70$ km/h, a representative value between those given in the literature for mid-sized waders (Summers & Waltner 1979, Remisiewicz *et al.* 2014). We used pairwise t -tests to test whether departure fuel loads and the potential flight ranges differed between adults and immatures; these variables had normal distributions and equal variances. We compared the body mass of groups by age and moult status using non-parametric Kruskal–Wallis tests because the distributions of body mass in these groups departed from normality. These calculations and tests were conducted with STATISTICA 12.0 software (StatSoft Inc. 2014).

RESULTS

Seasonal trends in body mass by bird age and moult status

The body mass of 1187 adults trapped between 9 July and 1 May ranged from 41 to 94 g. The mass of 534 immatures caught between 18 August and 28 April ranged from 45 to 92 g (Fig. 3). Adults maintained a consistently low average mass from 9 July to 9 February, and immatures from 18 August to 3 March (Fig. 3). Adults increased in mass from 10 February to 1 May at a mean rate of 0.25 g/day ($sd = 0.16$), and immatures from 4 March to 13 April at 0.24 g/day ($sd = 0.14$) (permutation test: $P = 0.81$); these are the estimated fuelling periods. Adult mass increased until 1 May, although the rate slowed after 12 April. Immature mass decreased after 13 April, by which time most of the heavy birds had left the study sites (Fig. 3). If we consider 10 February as the mean start of fuelling in adults, then primary moult and pre-migratory fuelling were separated by 10–75 days in 98% of adults (Fig. 3), and fuelling began on average 35 days before the assumed beginning of departures in mid-March (Fig. 1). Immatures began fuelling on average 12 days before the mid-March start of departures (Fig. 1).

Two per cent of adults and 42% of immatures caught during the fuelling periods were moulting (Fig. 3). Moulting immatures at this time were on average 7 g lighter than post-moult immatures, and 6 g lighter than post-moult adults (Table 1;

Kruskal–Wallis ANOVA: $H_{3,439} = 39.08$, $P < 0.001$). Post-moult immatures and adults did not differ in body mass (Table 1). Pre-moult immatures caught during the fuelling period were on average 8 g lighter than were post-moult immatures (Table 1).

Variation in pre-migratory fuelling among immatures by moult pattern

In immatures grouped by the number of replaced primaries (MOP3, MOP4, MOP5), groups that started fuelling later, fuelled faster (Table 2). The post-moult MOP5s began fuelling on average 15 days later (on 17 March) and fuelled more than twice as fast as MOP4s; MOP3s started fuelling on 19 March, 17 days after the MOP4s at an even higher rate (permutation test for ANOVA: $P < 0.001$, *post-hoc* tests in Table 2, Fig. 4). Immatures during moult showed varied patterns of fuelling. MOP5s during moult did not increase body mass (Table 2, Fig. 4). Moulting MOP4s started fuelling 8 days later and faster than the post-moult MOP4s (Table 2). Moulting MOP3s began fuelling 18 days earlier but almost three times slower than the post-moult MOP3s. The heaviest MOP5s weighed 89 g, the heaviest MOP4s 84 g and the heaviest MOP3s 92 g (Fig. 4).

Potential flight ranges of post-moult adults and immatures

After moult, the wing lengths of adults (mean = 126.5 mm, $sd = 3.4$ mm, $n = 421$) and immatures (mean = 126.0 mm, $sd = 3.3$ mm, $n = 71$) were not significantly different ($t_{481} = 1.06$, $P = 0.29$), so we combined these groups in estimating lean body mass. For the 5% of post-moult adults and immatures with the smallest ratio of mass to wing length ($n = 27$), the regression equation between the natural logarithms of body mass (lnBM, in g) and wing length (lnWL, in mm) was:

$$\ln BM = -1.5323 + 1.1336 * \ln WL$$

$$(F_{1,25} = 44.42, P < 0.001, R^2 = 0.63)$$

We used the slope coefficient $\beta = 1.1336$ ($se = 0.1701$) as the exponent to which wing length has to be raised to rescale it and to make it directly proportional to the mass (Summers *et al.*

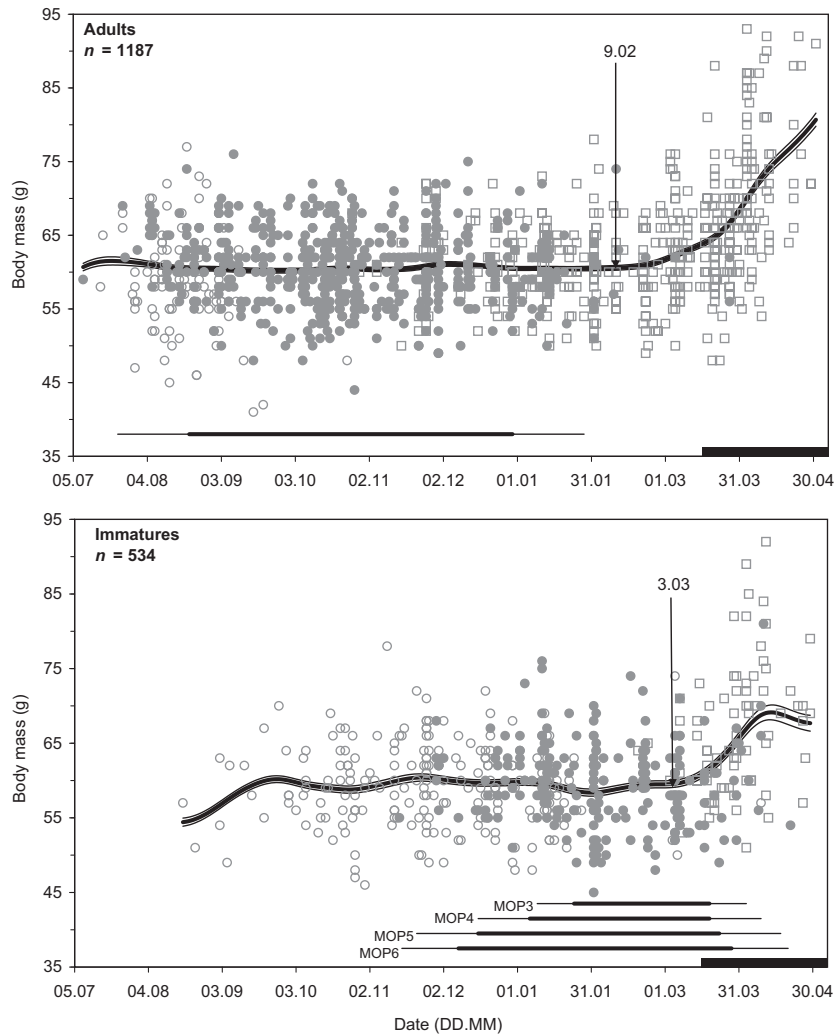


Figure 3. Body mass in relation to the date of capture for Wood Sandpipers caught in Zimbabwe in 1972–96. The body mass trends (thick lines) and 95% CI (thin lines) are based on locally weighted linear regression. Open circles – pre-moult birds; grey circles – moulting birds; open squares – post-moult birds. Arrows and dates indicate beginning of fuelling. Horizontal lines show mean periods (thick lines) and sd (thin lines) of primary moult in southern Africa for adults, and for groups of immatures (symbols of groups as in Fig. 1) (after Remisiewicz *et al.* 2009, 2010a). The black bar on the x-axis shows the departure period.

1992). The mean post-moult wing length was 126.4 mm. Using the rescaled wing length, the standardized and adjusted body mass (aBM) for each bird (Summers *et al.* 1992) was thus:

$$aBM = BM * \frac{126.4^{1.1336}}{WL^{1.1336}}$$

For the 5% leanest birds, the mean standardized and adjusted body mass was 52.3 g. The heaviest

20% of adults and immatures accumulated a fuel load of 52% and 53% on average, respectively, in relation to this lean body mass (Table 3). Using these fuel loads and Davidson’s (1984) formula, we estimated that adults and immatures could fly on average similar distances, about 3000 km in a single flight (Table 3, Fig. 1). Among the heaviest immatures, the MOP4s could cross 2468–3451 km (mean = 2929 km, sd = 346 km, *n* = 11), MOP5s 2397–4091 km (*n* = 3) and the one MOP3 3723 km, in a single flight.

Table 1. Comparison of median body masses of adult and immature Wood Sandpipers at different stages of moult caught in Zimbabwe in 1972–96 during their fuelling period. Differences in masses of each group are examined with respect to post-moult immatures.

| Age | Moult status | Median mass (g) (min–max) | No. of birds | Z | P |
|-----------|--------------|---------------------------|--------------|------|----------|
| Adults | Post-moult | 64.0 (48–93) | 295 | 1.04 | 0.999 |
| Immatures | Pre-moult | 57.0 (50–74) | 7 | 2.58 | 0.059 |
| | Moult | 58.0 (49–81) | 60 | 5.29 | < 0.0001 |
| | Post-moult | 65.0 (51–92) | 77 | | |

Z and P are results of *post-hoc* Mann–Whitney tests.

Table 2. Estimated starting dates and mean rates of fuelling of moulting and post-moult immatures in groups that replaced different numbers of outer primaries: MOP3 – birds that moulted three outer primaries, MOP4 – four outer primaries, MOP5 – five outer primaries. No. of days – number of days of the fuelling periods.

| Group and moult status | No. of days | Estimated start of fuelling | Mean fuelling rate (g/day) | Within-group comparison of rate | Between-group comparison of rate (post-moult only) |
|------------------------|-------------|-----------------------------|----------------------------|---------------------------------|--|
| MOP3 | | | | | |
| Moult | 12 | 1 Mar | 0.17 | $P < 0.001$ | $P < 0.001$ (MOP3/MOP4) $P = 0.75$ (MOP3/MOP5) |
| Post-moult | 25 | 19 Mar | 0.49 | | |
| MOP4 | | | | | |
| Moult | 32 | 10 Mar | 0.33 | $P < 0.01$ | |
| Post-moult | 46 | 2 Mar | 0.22 | | |
| MOP5 | | | | | |
| Moult | 44 | – | –0.08 | $P < 0.001$ | $P < 0.001$ (MOP5/MOP4) |
| Post-moult | 24 | 17 Mar | 0.47 | | |

P values are significance values of pairwise permutation tests comparing mean fuelling rates within groups (comparing moulting with post-moult birds), and between MOP groups (compared groups indicated in parentheses).

DISCUSSION

Different moult patterns in adult and immature Wood Sandpipers

Adult Wood Sandpipers arrive in Zimbabwe from mid-July and immatures about a month later (Fig. 1; Tree 2014), which corresponds with the 1-month-delayed departure of immatures from the breeding grounds (Cramp & Simmons 1983). Adults arriving in southern Africa have flight feathers 6–8 months old, which are worn after migration to and from the breeding grounds. This wear is probably why they start moulting their primaries soon after arrival and replace all 10 primaries in 131 days on average (Fig. 1; Remisiewicz *et al.* 2009). On arrival in southern Africa, immatures have 2- or 3-month-old primaries that grew on the breeding grounds and were used for their first migration south (Remisiewicz *et al.* 2010a). Thus, immatures replace only a few primaries in a pre-

supplemental moult in southern Africa, probably because they arrive with newer feathers compared with adults. The fewer primaries an immature replaces, the less time it spends moulting, between 55 days for MOP3s and 111 days for MOP6s on average (Fig. 1; Remisiewicz *et al.* 2010a). Because immatures replace fewer primaries in less time than adults take for a complete moult, they can delay primary moult by 4–5 months relative to adults (Fig. 1; Remisiewicz *et al.* 2009, 2010a).

Supplemental partial wing moult is common among immature long-distance migrant sandpipers (Scolopacidae), including Wood Sandpiper, in coastal and freshwater regions in the tropics and sub-tropics of Africa, South America and Australia, and has also been observed in New Zealand (Prater 1981, Higgins & Davies 1996, Howell 2010). However, this type of moult is uncommon in waders spending the non-breeding season in the northern hemisphere, such as Dunlin *Calidris alpina* (Prater *et al.* 1977) and Purple Sandpiper

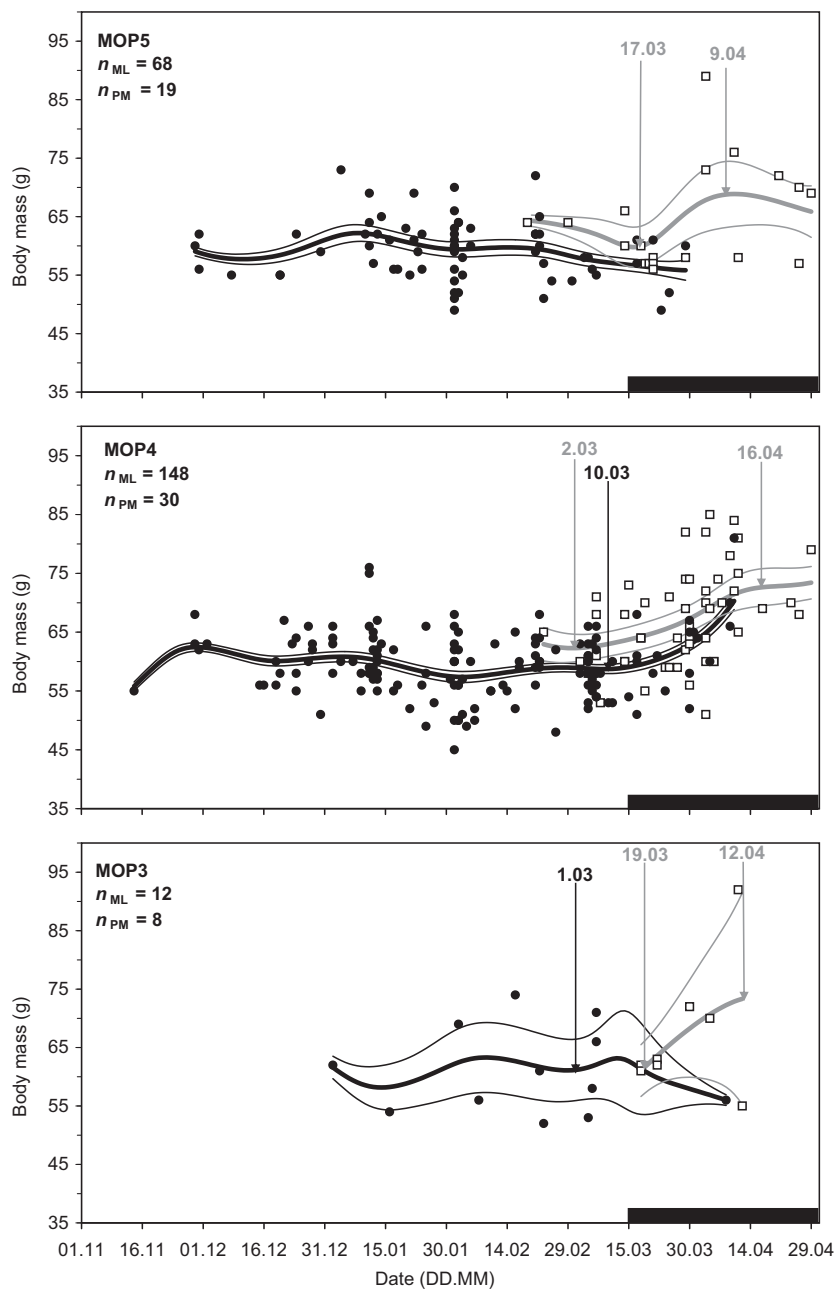


Figure 4. Body mass in relation to the date of capture for immature Wood Sandpipers caught in Zimbabwe in 1972–96. The body mass trends (thick lines) and 95% CI (thin lines), based on locally weighted linear regression, were drawn separately for groups of immatures (symbols as in Fig. 1), moulting (ML, black circles, black lines and dates) or post-moulting (PM, open squares, grey lines and dates). Arrows and dates indicate mean start and end dates of fuelling periods. The black bar on the x-axis shows the departure period.

Calidris maritima (Summers *et al.* 2004). Pre-supplemental moult is probably a strategy related to migration distance (Prater 1981, Howell 2010, Remisiewicz 2011), as demonstrated by immature Red Knots *Calidris canutus*, which do not moult

primaries in Scotland but often moult several outer primaries in South Africa (Summers *et al.* 2010). Supplemental moult also occurs in immature waders migrating between the Americas, such as Lesser Yellowlegs *Tringa flavipes* and

Table 3. Departure fuel loads (adjusted for mean wing length 126.4 mm) and potential flight ranges by age for the heaviest 20% of Wood Sandpipers caught in Zimbabwe in 1972–96.

| Parameter | Adults | | | | Immatures | | | | <i>t</i> | <i>P</i> |
|-----------------------------|------------|------|------|----------|------------|------|------|----------|----------|----------|
| | Mean (sd) | Min | Max | <i>n</i> | Mean (sd) | Min | Max | <i>n</i> | | |
| Departure fuel load (g) | 28.7 (6.0) | 21.3 | 44.3 | 49 | 27.7 (5.2) | 21.3 | 39.5 | 14 | 0.56 | 0.58 |
| Potential flight range (km) | 3106 (560) | 2400 | 4490 | 49 | 3015 (485) | 2397 | 4091 | 14 | 0.55 | 0.59 |

t, *P* are results of *t*-tests.

Semipalmated Sandpiper *Calidris pusilla*, and between Siberia or Alaska and Australia or New Zealand, such as Sharp-tailed Sandpiper *Calidris acuminata*, Curlew Sandpiper *Calidris ferruginea* and Red Knot (Higgins & Davies 1996, Minton *et al.* 2006, Howell 2010, Tavera *et al.* 2016). Juvenile feathers, which are of poorer quality than adults', abrade faster under harsh tropical sun and thus might need to be replaced in the supplemental moult (Pearson 1974, Prater 1981, Howell 2010). The tendency for the supplemental moult is probably not associated with the habitat preferences of immatures. For instance, Terek Sandpipers *Xenus cinereus* conduct supplemental moult at the coast, Curlew Sandpipers *C. ferruginea* at inland and coastal habitats, and Ruffs *Philomachus pugnax* and Wood Sandpipers at inland wetlands, in Africa and Australia (Schmitt & Whitehouse 1976, Barshep *et al.* 2013, C. Jackson unpubl. data).

Age-specific patterns of primary moult and pre-migratory fuelling

We found that adult and immature Wood Sandpipers maintained low masses from arrival until early February or March, a pattern similar to that found in other migrant waders in southern Africa, e.g. Grey Plover *Pluvialis squatarola* (Serra *et al.* 1999), Turnstone *Arenaria interpres* (Summers *et al.* 1989) and Greenshank *Tringa nebularia* (Remisiewicz *et al.* 2014). The decrease in fuelling rates after 12–13 April in both age groups suggests that the heaviest adults and immatures had departed by these dates. In most adults, primary moult and pre-migratory fuelling were separated in time, and fuelling began on average 2 months before the first departures. In contrast, immatures presented at least four patterns of fuelling in relation to primary moult and departure:

- 1 In about 60% of immatures, primary moult and fuelling were separated, but the gap was shorter than in adults.
- 2 In about 40% of immatures, primary moult and fuelling overlapped. These were mostly the MOP4 immatures and many were still moulting in late March or April, although they began fuelling around 10 March.
- 3 Some immatures moulted outer primaries but skipped fuelling, as indicated by several late-moulting lean immatures in each MOP group observed just before departure time. They probably stayed for a 'gap year' in southern Africa, as suggested by the occurrence at the study sites between May and July of sub-adults with low mass in active or completed moult (Remisiewicz *et al.* 2010b).
- 4 Some immatures skipped primary moult and fuelling, and stayed for a 'gap year', as suggested by a few lean (< 60 g) pre-moult immatures present during the fuelling period.

Varied strategies of moult and fuelling in immature Wood Sandpipers

There was no clear relationship in immature Wood Sandpipers between the number of primaries they replaced and the tendency to overlap moult and fuelling, contrary to what we had expected. MOP3 and MOP5 birds started fuelling mostly after they finished moult. However, some MOP4s started fuelling while moulting, at an even higher rate than the post-moult birds, although 3 weeks later. The later the immatures ended moult, the later and faster they fuelled. But this pattern was unrelated to the number of feathers they replaced, as the post-moult MOP4s started fuelling earlier than MOP5s and MOP3s. The number of primaries the immatures replaced was not related to their start of fuelling, probably because all groups of moulters (MOP3, MOP4, MOP5) on average finished moult at a similar time (19–23 March; Remisiewicz *et al.* 2010a).

MOP3s fuelled slowly during moult but rapidly after completing primary moult, which might be a strategy immatures use when good feeding conditions occur late in the season. Late fuelling by MOP3s corresponds with their moulting later and faster than MOP4–MOP6s (Remisiewicz *et al.* 2010a). Most (63%) immature Wood Sandpipers moulted four primaries (MOP4) (Remisiewicz *et al.* 2010a). Our results showed that this was also the most flexible strategy, enabling them to finish moult early and then accumulate fuel, or to moult and fuel simultaneously, probably depending on environmental conditions. Availability of waders' food at inland waterbodies in southern Africa is erratic and unpredictable, varying from swarms of insects after the first rains, to hardly any invertebrates when ephemeral ponds dry up (Allan *et al.* 1997). The plethora of combinations in the timing and extent of partial moult with the varied timing and rates of fuelling probably enables immatures to balance their energy use between growing new primaries and fuelling, while adjusting to environmental conditions such as food availability.

Costs of overlapping primary moult and pre-migratory fuelling

Most studies on the interaction of moult and pre-migratory fuelling have focused on passerines during post-nuptial wing moult on the northern breeding grounds, where the short time available before departure southwards compels these migrants to moult and to deposit fuel simultaneously. Some migrant passerines which moult wing feathers at the northern breeding grounds, such as Robin *Erithacus rubecula* and Blackcap *Sylvia atricapilla*, do not overlap moult and pre-migratory fuelling. Others, such as Garden Warbler *Sylvia borin* and Bluethroat *Luscinia svecica*, sometimes overlap their late moult of flight feathers with fuelling (Lindström *et al.* 1994, Jenni-Eiermann & Jenni 1996). Given that long-distance migrants spend about 6 months at the southern non-breeding grounds, with less severe time constraints on moult and fuelling than at the north, we did not expect these two activities to overlap in the south.

This proved true for most adult and immature Wood Sandpipers, in which the energetically demanding primary moult and fuelling were separated. This is a typical pattern in adults of other waders, such as Curlew Sandpipers, Red Knots,

Turnstones and Greenshanks, which begin fuelling after primary moult and 2–6 weeks before leaving southern Africa or Mauritania (Elliott *et al.* 1976, Summers *et al.* 1989, 2010, Zwarts *et al.* 1990, Remisiewicz *et al.* 2014). Relative to conspecifics in southern Africa, adult Curlew Sandpipers in north-west and southeast Australia have a shorter gap between the mean end of primary moult and the start of fuelling (Elliott *et al.* 1976, Minton *et al.* 2006), suggesting that these processes overlap in late-moulting adults. Adult Wilson's Phalaropes *Phalaropus tricolor* present a rare example of simultaneous moult and fuelling during their short stay at Mono Lake in California, enormously rich in invertebrates, before continuing their migration to South America (Jehl 1987). Thus, waders are able to moult and deposit fuel at the same time when food is abundant. Southern African Wood Sandpipers that moulted and fuelled simultaneously probably took advantage of erratic favourable feeding conditions. But overlapping moult and fuelling suggest that departure poses an approaching constraint. The changing photoperiod of austral autumn might signal the proximity of departure from the non-breeding grounds and act as a trigger for pre-migratory fuelling, as it does in passerines at the breeding grounds (e.g. Helm & Gwinner 1999).

Using different strategies of moult and fuelling, the heaviest immature Wood Sandpiper on average attained similar departure mass to adults. But in some immatures (MOP3) fuelling during moult came at the cost of lower efficiency in adding mass, which might be an effect of the competing demands of late moult and pre-migratory fuelling. Similarly, White-crowned Sparrows *Zonotrichia leucophrys* increased mass slowly during primary moult, and at a much faster rate afterwards (Morton & Welton 1973). Inefficient fuelling during moult is probably an effect of splitting energy resources between physiologically different processes, pre-migratory lipogenesis for fat deposition and protein conversion into new feathers (Jenni-Eiermann & Jenni 1996).

Carry-over effects of the moult and fuelling strategy on subsequent life stages

Wood Sandpipers increased their mass by *c.* 50% before leaving southern Africa. With such fuel loads, the heaviest adult and immature Wood Sandpipers could cover *c.* 2397–4490 km in one

non-stop flight, reaching Lake Victoria or the Kenyan coast (Fig. 2). This would be a medium-distance flight in comparison with that of Greenshanks, which increased their mass by up to 87% before leaving southern Africa, potentially enough fuel to reach the Nile Valley in one non-stop flight (Remisiewicz *et al.* 2014). The heaviest immatures in all moult groups attained similar departure weights and were able to cross similar distances in a non-stop flight. Thus, different combinations of the various patterns of primary moult and fuelling provide adequate preparation for departure. However, Wood Sandpipers that accumulated smaller fuel loads than those of the heaviest birds probably migrated north in short-distance hops (Piersma 1987) using wetlands en route as stopover sites. More flexible patterns of primary moult and pre-migratory fuelling in immatures than in adults might enable immatures to maximize their survival during the critical first year of life. The flexibility we observed in Wood Sandpipers of all age groups enables them to adjust best to the varied and unpredictable conditions at the waterbodies they use in Africa.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Application of the locally weighted linear regression in modelling seasonal trends in body mass.

Appendix S2. Data on moult, body mass and wing length of Wood Sandpipers ringed in Zimbabwe in 1972–96.