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# The primary moult of Curlew Sandpipers *Calidris ferruginea* in North-western Australia shifts according to breeding success

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The population moult parameters, yearly onset of moult and sex-specific schedule of moult in relation to breeding success, and pattern of feather mass growth were examined in a population of Curlew Sandpipers *Calidris ferruginea* that migrate to northwest Australia. The mean start date of moult was 18 September, and it lasted on average 129 days. No significant variation in duration of moult was detected and feather mass was deposited at a constant rate. The yearly onset of moult was positively correlated with the proportion of first year (juvenile) birds: the mean start date of moult in good breeding years was 25 September, ten days later than mean start date of moult in poor breeding years, being 15 September. Males generally started moult five days earlier than females. The mean moult start date of males was five days earlier in poor breeding years compared to good breeding years, while the moult of females was 11 days earlier in poor breeding years compared to good breeding years. In Curlew Sandpipers the timing of post-breeding migration is advanced in bad breeding seasons, which explains the observed correlation between breeding success and the timing of moult in non-breeding areas.

Key words: *Calidris ferruginea*, Curlew Sandpiper, breeding success, moult onset, carry-over effect

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Moult is one of the indispensable aspects of the annual cycle of birds, as the maintenance of feathers in an 'airworthy' condition is critical to flight performance (Barrowclough & Sibley 1980). Long-distance migrants have to fit breeding, migration, moult and other activities into a one-year calendar and, therefore, the timing of the commencement of any of these activities is crucial. Waders (Charadrii) have developed different moult strategies to fit into their tight schedule (Ginn & Melville 1983). Species like the Little Stint *Calidris minuta* and the Red Knot *Calidris canutus* moult most body and flight feathers almost exclusively on the wintering ground (Middlemiss 1961, Pearson 1984, Summers *et al.* 2010), others like the Dunlin *C. alpina* and the Golden Plover *Pluvialis apricaria* start moult on or near the breeding grounds (Holmes 1966, Byrkjedal

1978, Kania 1990), and yet others like the Wood Sandpiper *Tringa glareola*, Redshank *Tringa totanus*, and Wilson's Phalarope *Phalaropus tricolor* start moult at stop-over sites during southward migration which is then suspended and continued on the wintering ground (Pienkowski *et al.* 1976, Jehl 1987, Pinchuk *et al.* 2008, Remisiewicz *et al.* 2009). Whichever way it is done, the timing and duration of moult can usually be linked to the availability of food, breeding season and/or winter conditions (Prater 1981).

Here, we demonstrate the connection between breeding success and the timing of primary moult in a population of Curlew Sandpipers *Calidris ferruginea* that migrate to north-western Australia. The Curlew Sandpiper breeds in Arctic Siberia between 80°E and 155°E (Lappo & Tomkovich 2006), although a few

breeding records have been reported in Alaska (Holmes & Pitelka 1964). They winter in Africa south of the Sahara, around the Indian Ocean and in South-East Asia, and Australia (Wilson *et al.* 1980). Breeding productivity (number of fledged chicks) in Curlew Sandpipers can be largely explained by predation pressure on the breeding grounds (Underhill *et al.* 1993, Summers *et al.* 1998). Predators that prey primarily on lemmings (*Lemmus sibiricus* and *Dicrostonyx torquatus*) broaden their diet to include the eggs and chicks of waders (prey-switching) in years of low lemming abundance (Underhill 1987, Summers *et al.* 1998). In poor breeding years, Curlew Sandpipers were found to migrate earlier than in years when breeding was successful (Blomqvist *et al.* 2002, Figuerola 2006). Arrival on the non-breeding grounds should then be earlier in poor breeding years compared to good breeding years, and this could affect the timing of moult. Studies by Schekkerman *et al.* (1998) have also shown a relationship between breeding productivity of the Curlew Sandpiper and June temperature on the Arctic breeding grounds.

Curlew Sandpipers moult flight feathers almost exclusively on the non-breeding areas (Cramp & Simmons 1983, but see Figuerola 1995). In adult birds, moult typically starts from the innermost primary and progresses outward (Minton *et al.* 2006). With the development of statistical methods specifically for the analysis of moult data (Underhill & Zucchini 1988), it became possible to not only estimate moult parameters at the population level (e.g. Minton & Serra 2001 for Grey Plovers *Pluvialis squatarola*, Remisiewicz *et al.* 2009 for Wood Sandpiper *Tringa glareola*, and Summers *et al.* 2004 for Purple Sandpiper *Calidris maritima*), but also growth parameters (start date, duration and standard deviation) of the individual feathers (e.g. Underhill 2003, Serra & Underhill 2006, Remisiewicz *et al.* 2009). In this paper we explore yearly variations in the onset of moult and the factors which underlie this yearly variation in the timing and duration of moult.

This study had three aims. (1) Describe the growth pattern of individual primary feathers using the Underhill & Zucchini (1988) model, exploring how the estimate of start date and duration of moult using the growth of individual primaries compares with the method which uses the combined moult scores of all ten primaries. The first method only requires the conversion of moult scores into moult indices, while the second converts moult scores into Proportion Feather Mass Growth using the relative mass of each primary feather (see methods); the latter method can only be used if the

mass of the primaries are known. (2) Estimate the moult parameters annually for years with large enough sample sizes, as well as for adult males and females, examining the link between the onset of moult on the wintering ground and breeding success. Curlew Sandpipers have a sex-biased parental care system where males leave the breeding grounds as soon as the clutch is completed and only the females care for the brood (Holmes & Pitelka 1964, Tomkovich 1988). We predict therefore, that the moult of males will be earlier than that of females and that the onset of moult will differ with respect to breeding success only in females. (3) Test the underlying assumption of the Underhill & Zucchini (1988) moult model that the rate of feather production is constant throughout the moult period.

## METHODS

We used the moult records of 5685 Curlew Sandpipers *Calidris ferruginea* captured mainly by cannon-netting on the shores of Roebuck Bay, Broome and Eighty Mile Beach in northwest Australia from 1981–2006. Nearly all birds were aged based on wing condition (Rogers *et al.* 1990, Higgins & Davies 1996) and were allocated to one of three age categories: birds in their first year of life (juveniles), birds known to be in their second year, and birds in their second year or older, defined to be adults. In this paper, we consider only the moult of adult birds.

Primaries were numbered P1 for the innermost primary to P10 for the outermost feather. Primary moult scores were recorded using the British Trust for Ornithology technique (Ginn & Melville 1983); the stage of moult of individual feathers was scored from 0 (for old feathers) to 5 (for new feathers), and intermediate values for growing feathers. Eight birds that were aged as adults but with evidence of suspended moult (e.g. 5555500000, with no growing feathers) were removed from the analysis.

### Individual primary growth estimate and population estimates

Primary moult scores were transformed into moult indices following the relationship given by the Underhill & Zucchini model (1988); i.e. moult score 0 = 0, 1 = 0.125, 2 = 0.375, 3 = 0.625, 4 = 0.875, and 5 = 1. The start date, duration and standard deviation of moult for each primary feather was estimated using the software described in Brandao (1998), and Underhill *et al.* (2006); data were assumed to be Type 2, which uses observations of birds that have not yet start-

ed moult, birds in moult, and those that have completed moult. The mean start date of moult of the innermost primary (P1) was taken as the date of primary moult commencement, and the date of the completion of moult of the outermost primary (P10) was taken as the date of moult completion. This approach was described in Serra (2000) and Underhill (2003), and applied successfully by Remisiewicz *et al.* (2009).

To estimate the parameters of moult (start date, duration and standard deviation) of the tract of 10 primary feathers as a whole, the moult scores were converted into Proportion Feather Mass Grown (PFMG) using the relative masses of primary feathers (Underhill & Joubert 1995). This process has been demonstrated by Summers (1980) and Underhill *et al.* (1990). This approach was applied to estimate the parameters of moult for the entire population and was applied to estimate moult parameters of male and female adult Curlew Sandpipers. Adult birds were sexed using SHEBA, a set of programmes designed for univariate analysis of measurements of sexually size dimorphic birds: the proportion of each sex was estimated on the basis of bimodally distributed data (Rogers 1995). All the birds were sexed using bill length, as it has been shown to be a reliable sexing criterion in the Curlew Sandpiper (Elliott *et al.* 1976). The Underhill & Zucchini model (1988) was also applied to estimate the start date of moult for individual years.

### Moult and breeding success

The relationship between the mean start date of moult and breeding success was explored using General Linear Models (GLM), with yearly start dates of moult as the dependent variable, breeding success (good/poor) as fixed factors, and proportion of juveniles, predation index, and average June temperature as covariates. A separate model was used to examine the overall difference in the timing of moult of males and females in good and poor breeding years. The proportion of juvenile birds caught in relation to adults was used as an indication of breeding success (Minton *et al.* 2005). A year was classed as a good breeding year when the proportion of juvenile birds was greater than 0.20 and a poor breeding year when less than 0.10. The index of predation pressure was provided by Blomqvist *et al.* (2002). This is the likelihood that wader nests and chicks will be depredated depending on the abundance of lemmings. Scores go from 0 (low predation pressure) to 3 (high predation pressure). Data on the average June temperature were obtained from the National Oceanic and Atmospheric Administration (NOAA).

### Rate of feather production

The underlying principle of the Underhill & Zucchini (1988) moult model is that the rate of feather production is constant throughout the moult period. To obtain the average amount of feather mass grown per day for each primary, we followed the method of Remisiewicz *et al.* (2009). We divided the relative mass of each primary by its corresponding duration of growth (i.e. 4.0 divided by 16 for P1; Table 1). This was summed for all feathers growing simultaneously on any given day and this enabled us to estimate the daily rate of feather material production. If the underlying assumption of the Underhill & Zucchini (1988) moult model is correct, the cumulative growth plot should be a straight line.

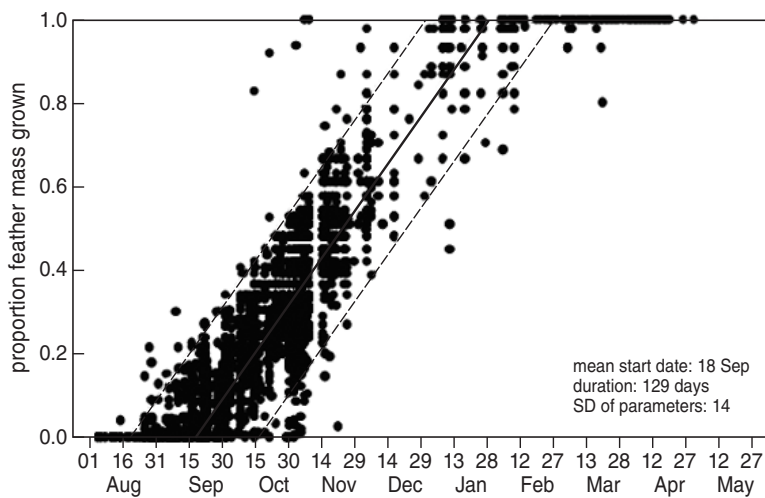
## RESULTS

### Timing and pattern of primary moult

Using moult data from all years pooled (1981–2006), the estimated mean start date of moult using the PFMG of the tract of 10 primary feathers as a whole was 18 September (SD 0.4), the mean duration was 129 days and the mean end date of moult was 25 January (SD 0.8). 95% of adult birds start moult between 21 August and 15 October (Fig. 1). The onset of moult estimated from individual feather growth was 17 September and the end date was 23 January (duration of 128 days, Fig. 2). On average, the first primary was shed on 17 September, and the second two days later, so that they grew almost simultaneously. There was little overlap in the growth of primaries 5–10 (Fig. 2). The estimated duration of growth for each of the primaries varied between 16 (P1) and 28 days (P10); the time taken for each primary to grow was correlated with its mass ( $r = 0.91$ ,  $P < 0.001$ ) indicating that the duration of each primary moult was size dependent. Variation in the masses of individual primaries resulted in differences in the rates at which feather material was deposited; this rate was three times larger for P9 and P10 than for P1 and P2 (Table 1), and this is shown in their much steeper growth lines (Fig. 2).

### Yearly variation in moult

19 years had a large enough sample size to obtain moult parameters (Appendix 1). The onset of moult of adult Curlew Sandpipers ranged from 10 September to 14 October. The mean start date of moult was significantly related to the proportion of juvenile birds (GLM:  $F_{1,47} = 16.31$ ,  $P < 0.001$ , slope = 15.81) and the index of predation ( $F_{1,47} = 15.03$ ,  $P = 0.002$ , slope = -3.05), but not to the average June temperature ( $F_{1,47} = 0.80$ ,



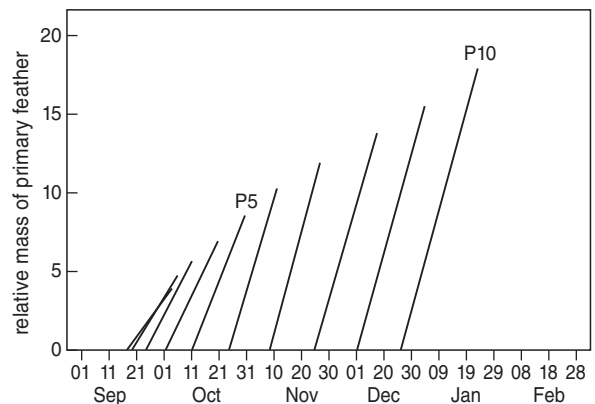
**Figure 1.** Temporal distribution of the Proportion Feather Mass Grown (PFMG) of adult Curlew Sandpipers. The continuous line reflects the course of moult from estimated start to end dates; dashed lines indicate 95%-confidence intervals.

$P < 0.751$ , slope =  $-0.18$ ). The mean start date of moult in good breeding years was 25 September (SD 14.0), significantly later ( $F_{1,47} = 19.01$ ,  $P < 0.001$ , slope = 4.98) than the mean start date of moult in poor breeding years, which was 15 September (SD 14.0; Fig. 3). We found no statistically significant relationship between the duration and the onset of moult ( $F_{1,18} = 0.26$ ,  $P = 0.615$ , slope =  $-0.03$ ). This implies that in years when moult started early, the completion of moult was also early and *vice versa*.

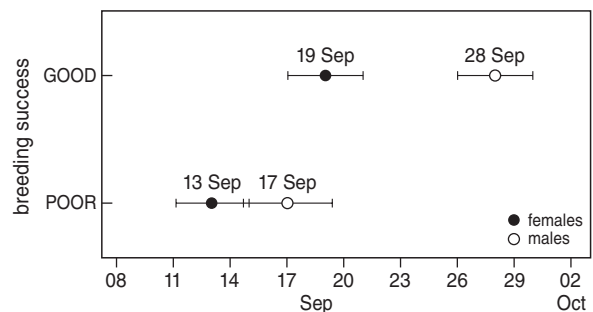
### Moult of males and females

The mean start date of the primary moult of males was 16 September (SD 0.86), duration 132 days, end date 26 January (SD 2.1). This was significantly earlier ( $F_{1,20} = 6.09$ ,  $P = 0.022$ ) than the estimated mean start date of female moult on 20 September (SD 0.9), duration 130 days, end date 28 January (SD 2.1). The interaction term between sex and breeding success was significant ( $F_{1,20} = 4.12$ ,  $P = 0.042$ ) indicating that the start of moult with respect to breeding success differed between the sexes.

In good breeding years, the mean start date of moult in males was 17 September (SD 1.1) which was not significantly later ( $F_{1,20} = 0.26$ ,  $P = 0.615$ ) than the start of moult in poor breeding years on 13 September (SD 0.9; Fig. 3). Females started moult on the 28 September (SD 1.4) in good breeding years and this was significantly later ( $F_{1,20} = 13.22$ ,  $P = 0.002$ ) than the onset of moult on 19 September in poor breeding years (SD 1.4; Fig. 3). Although the duration of moult was longer in males than in females, this was not statistically significant ( $F_{1,20} = 0.13$ ,  $P = 0.737$ ).



**Figure 2.** Growth lines of primaries P1-P10, showing the amount of primary mass produced between the start and end date of the development of each primary. Slopes of the lines reflect the growth rate of each primary.



**Figure 3.** Mean start date of moult of adult male and female Curlew Sandpipers in good and poor breeding years. Based on moult data of adult birds in north-west Australia 1981–2006.

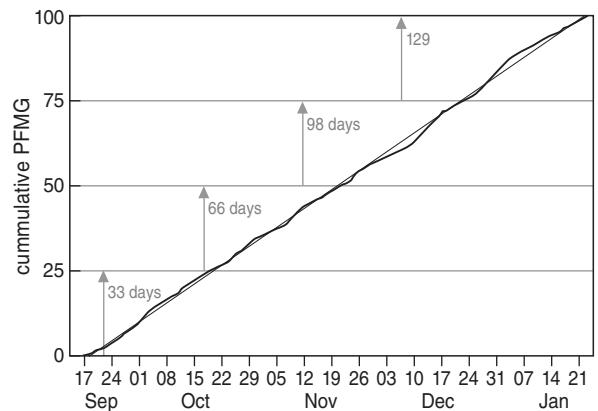


### Rate of primary feather mass production

The average rate of primary feather material grown per day was estimated at 0.78% (SD 0.16). Although the rate of feather material grown per day would have fluctuated above and below this average depending on the number of feathers growing simultaneously, the overall rate of production of feather material was relatively stable throughout the whole season, as demonstrated by the almost linear cumulative curve of PFMG (Fig. 4). The 25th percentile of primary feather mass production was achieved after 33 days, Median in 66 days and 75th percentile in 98 days, which are close to the values obtained by assuming a constant rate of feather material deposition.

## DISCUSSION

Our estimated start date of moult on 18 September (SD 0.4) and duration of 129 days for adult Curlew Sandpipers when using PFMG of all ten feather tracts combined, was very similar to the estimates obtained by Minton *et al.* (2006) who estimated the start date of moult to be 18 September, duration 131 days. Based on the growth of individual feathers, the mean start date (17 September) and end date (23 January) of moult estimated from PFMG was also similar to the estimated start date of 18 September and end date of 25 January estimate from the combined PFMG. Similar starting



**Figure 4.** Cumulative production of feather mass (Proportion Feather Mass Grown, PFMG) in consecutive days of the season. The thick line is the cumulative curve; the thin line is the fitted regression line; horizontal grey lines indicate the percentiles of feather mass produced and their durations.

dates were given for Curlew Sandpipers in Tasmania by Thomas & Dartnall (1971). The start of moult of adult birds in Tasmania was between 8 August and 6 November, with most starting in September and October and finishing between 13 December and 12 March (estimated duration of moult 125 to 130 days). Elliott *et al.* (1976) estimated the start of moult of adult birds in South Africa to be in September (exact dates not given), with a duration of 140 days.

**Table 1.** Estimates of moult parameters of each primary and of all 10 tracts of primaries pooled and their growth rate (expressed as percent Proportion Feather Mass Grown (PFMG) per day), for adult Curlew Sandpipers that perform continuous primary moult in North-west Australia.

Primary	Feather mass %	Moult parameters				Sample sizes			PFMG/day %
		Mean start date (SD)	Duration (SD)	Standard deviation of start date (SD)	End date (SD)	Not yet moulted	In moult	Moult complete	
P1	4.0	17 Sep (0.5)	16.5 (0.6)	13.7 (0.3)	04 Oct (0.5)	1210	443	4032	0.24
P2	4.8	19 Sep (0.5)	16.7 (0.6)	13.7 (0.3)	05 Oct (0.5)	1260	442	3983	0.29
P3	5.7	24 Sep (0.5)	17.0 (0.6)	13.4 (0.3)	11 Oct (0.5)	1401	434	3850	0.34
P4	7.0	01 Oct (0.5)	18.9 (0.6)	13.9 (0.3)	20 Oct (0.5)	1600	471	3614	0.37
P5	8.6	11 Oct (0.5)	19.4 (0.7)	14.1 (0.4)	30 Oct (0.5)	1820	520	3345	0.44
P6	10.4	24 Oct (0.5)	17.7 (0.7)	13.4 (0.4)	11 Nov (0.6)	2185	478	3022	0.59
P7	12.0	08 Nov (0.5)	18.3 (0.8)	12.5 (0.4)	26 Nov (0.8)	2583	382	2720	0.66
P8	13.9	25 Nov (0.8)	23.0 (1.2)	14.8 (0.6)	17 Dec (1.2)	2909	226	2550	0.60
P9	15.6	10 Dec (1.1)	24.3 (1.6)	17.7 (0.7)	03 Jan (1.5)	3063	123	2499	0.64
P10	18.0	26 Dec (1.4)	28.0 (1.8)	21.2 (0.7)	23 Jan (1.8)	3151	124	2410	0.64
PFMG combined		18 Sep (0.4)	129 (1.0)	14 (0.2)	25 Jan (0.8)	1210	2068	2407	2.74

While our estimates of the start dates of moult are well within the limits given by Thomas & Dartnall (1971) and Elliott *et al.* (1976), the duration of moult of Curlew Sandpipers wintering in South Africa is longer than the duration of moult in the Australian and Tasmanian population, and the population wintering in Morocco (Pienkowski *et al.* 1976). We cannot rule out the possibility that these differences might simply be due to methods used in analysing moult data. However, Summers *et al.* (2004) showed that Purple Sandpipers wintering at different latitudes in Britain, Iceland and Norway had different start dates and duration of moult, and several studies show that the start and duration of moult differed between the subspecies of Dunlins wintering at different latitudes and different continents (Holmes 1971, Boere 1976, Greenwood 1983, Gromadzka 1989, Holmgren *et al.* 1993).

The wide confidence interval of the start date of moult (21 August – 15 October; Fig. 1) indicates high variation in the commencement of moult among individuals and between years. Studies on the Baltic coast of Poland show inter-annual variation in the timing of the southward passage of the Curlew Sandpiper (Meissner 2006). This would result in a varied timing of arrival at the wintering grounds and hence affect the commencement of moult.

### Moult and breeding success

While moult in the Curlew Sandpiper has been investigated in some localities (e.g. Thomas & Dartnall 1971, Dean 1977, Minton *et al.* 2006, Elliott *et al.* 1976), to the best of our knowledge, this is the first time inter-annual variation in the timing of moult has been investigated in the Curlew Sandpiper. As a result, little is known of the factors that underlie variation in the timing of moult in this species. Our results show that birds moulted ten days earlier in years of poor breeding success compared with years of good breeding success. There are several studies which have demonstrated that breeding phenology influences onset of moult in some bird species such as the Greater Snow Geese *Anser caerulescens atlantica* (Reed *et al.* 2003), Lazuli Bunting *Passerina amoena* (Young 1991), Great Tit *Parus major* and Willow Tit *P. montanus* (Orell & Ojanen 1980), Yellow Warbler *Dendroica petechia* (Rimmer 1988), and White-crowned Sparrow *Zonotrichia leucophrys* (Morton & Morton 1990). In the Curlew Sandpiper, the cyclical pattern in reproductive output is strongly linked with predation pressure in the Arctic (Underhill *et al.* 1993, Summers *et al.* 1998). This happens when predators that traditionally feed on rodents broaden their diet to include the eggs and chicks of shorebirds in years of

low rodent abundance. In years when predation pressure is high, clutches are lost early in the season and since there is hardly a chance to lay a second clutch, the timing of post-breeding migration is advanced (Blomqvist *et al.* 2002, Figuerola 2006, Meissner 2006); this could result in an overall early onset of moult at the non-breeding grounds.

### Sex differences in moult

The onset of moult in both males and females was affected by breeding success. In both sexes, moult generally started earlier in poor breeding years compared to good breeding years, although this difference was not statistically significant in males. On average, moult started five days earlier in males compared to females and this is because males, who play no part in parental care, leave the breeding grounds soon after females start the incubation of eggs (Holmes & Pitelka 1964, Tomkovich 1988), and should arrive at the non-breeding grounds before females. The largest difference in the onset of moult between males and females was in good breeding years when males started moult about 12 days earlier (17 September) than females (28 September). While males are usually not involved in parental care, there has been evidence that in localities where male territories formed dense clusters in the best habitats, territory defence and courtship of females by males continued sometimes up to southward departure of the males (Tomkovich & Soloviev 2006, Tulp & Schekkerman 2001). These territorial males provided some protection to their incubating females against constant chasing by other males during the females' feeding bouts (Tomkovich & Soloviev 2006). The earlier moult of females in poor breeding years can be the result of early loss of clutches because of predation.

### Rate of feather production

The almost linear curve of the cumulative percentage feather mass growth indicates that the assumption of the Underhill & Zucchini (1998) model – that feather material is deposited at a constant rate – is met in the Curlew Sandpiper. This is possible because of the overlap in the growth of the first three primaries, while there was little overlap in the growth of the last seven primaries. For instance, the relative feather mass of P1 is about a quarter of P10 (4.0 compared with 18.0), yet the combined daily feather material deposition of P1 and P2 is 0.53% per day, which is close to the daily feather material deposition rate of P10 (0.64). A similar constant rate of primary mass production has been shown in e.g. Turnstone (Summers *et al.* 1989), Purple Sandpiper (Summers *et al.* 2004) and in Wood Sand-

pipper (Remisiewicz *et al.* 2009), achieved also by overlapped growth of the smaller inner primaries.

In conclusion, this study shows that the start of moult in the Curlew Sandpiper shifts according to the breeding success for that year. This paper demonstrates the carry-over effect of events happening during breeding on the onset of moult in a long-distance migrant wader, and of the differences in the moult schedules of the sexes at the non-breeding grounds as related to the different investment of the sexes in parental care. Another important finding of this study is that the use of individual feather moult parameters to estimate the start date and duration of moult is comparable to the estimates obtained from using the combined percentage feather mass growth. This is particularly useful when estimating the start date and duration of moult using the Underhill–Zuchinni model for species whose individual feather masses are not known.

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## REFERENCES

- Barrowclough G.F. & Sibley F.C. 1980. Feather pigmentation and abrasion: test of a hypothesis. *Auk* 97: 881–883.
- Blomqvist S., Holmgren N., Åkesson S., Hedenström A. & Pettersson J. 2002. Indirect effects of lemming cycles on sandpiper dynamics: 50 years of counts from southern Sweden. *Oecologia* 133: 146–158.
- Boere, G.C. 1976. The significance of the Dutch Waddenzee in the annual life cycle of arctic, subarctic and boreal waders. Part I. The function as a moulting area. *Ardea* 64: 210–291.
- Brandao A. 1998. A comparative study of stochastic models in biology. Unpubl. PhD thesis, University of Cape Town, Cape Town.
- Byrkjedal I. 1978. Altitudinal differences in breeding schedules of Golden Plovers *Pluvialis apricaria* (L.) in South Norway. *Sterna* 17: 1–20.
- Cramp S. & Simmons K.E.L. (eds) 1983. *The Birds of the Western Palearctic*, 3. Oxford University Press, Oxford.
- Dean W.R.J. 1977. Moult of the Curlew Sandpiper at Barberspan. *Ostrich Suppl.* 12: 97–101.
- Elliott C.C.H., Waltner M., Underhill L.G., Pringle J.S. & Dick W.J.A. 1976. The migration system of the Curlew Sandpiper *Calidris ferruginea* in Africa. *Ostrich* 47: 191–213.
- Figuerola J. 1995. The primary moult of the Curlew Sandpiper in the Ebro Delta, North-East Spain. *Ring. Migr.* 16: 168–171.
- Figuerola J. 2006. The role of breeding success and parental care in determining sexual differences in the timing of southward migration of the Curlew Sandpiper *Calidris ferruginea* through Tunisia. *Int. Wader Studies* 19: 148–150.
- Ginn H.B. & Melville D.S. 1983. *Moult in birds*. BTO Guide, 19. British Trust for Ornithology, Tring, England.
- Greenwood J.G. 1983. Post-nuptial primary moult in Dunlin *Calidris alpina*. *Ibis* 125: 223–228.
- Gromadzka J. 1989. Breeding and wintering areas of Dunlin migrating through southern Baltic. *Ornis Scand.* 20: 132–144.
- Higgins P.J. & Davies S.J.J.F. (eds) 1996. *Handbook of Australian, New Zealand & Antarctic Birds*, 3. Oxford University Press, Melbourne.
- Holmes R.T. 1966. Moult cycle of the Red-Backed Sandpiper (*Calidris alpina*) in western North America. *Auk* 83: 517–533.
- Holmes R.T. 1971. Latitudinal differences in the breeding and moult schedules of Alaskan Red-backed Sandpipers (*Calidris alpina*). *Condor* 73: 93–99.
- Holmes R.T. & Pitelka F.A. 1964. Breeding behavior and taxonomic relationships of the Curlew Sandpiper. *Auk* 81: 362–379.
- Holmgren, N., Ellegren H. & Patterson J. 1993. The adaptation of moult pattern in migratory Dunlins *Calidris alpina*. *Ornis Scand.* 24: 21–27.
- Jehl J.R. Jr. 1987. Moult and moult migration in a transequatorially migrating shorebird: Wilson's Phalarope. *Ornis Scand.* 18: 173–178.
- Kania W. 1990. The primary moult of breeding Dunlins *Calidris alpina* in the central Taymyr in 1989. *Wader Study Group Bull.* 60: 17–19.
- Lappo L.G. & Tomkovich P.S. 2006. Limits and structure of the breeding range of the Curlew Sandpiper *Calidris ferruginea*. *Int. Wader Studies* 19: 9–18.
- Meissner W. 2006. Timing and phenology of Curlew Sandpiper *Calidris ferruginea* on southward migration through Puck Bay, Poland. *Int. Wader Studies* 19: 121–124.
- Middlemiss E. 1961. Biological aspects of *Calidris minuta* while wintering in South-west Cape. *Ostrich* 32: 107–121.
- Minton C.D.T. & Serra L. 2001. Biometrics and moult of Grey Plovers *Pluvialis squatarola* wintering in Australia. *Emu* 101: 13–18.
- Minton C., Jessop R., Collins P. & Gosbell K. 2005. Monitoring shorebird breeding productivity by the percentage of first year birds in populations in S.E. Australian nonbreeding areas. *Int. Wader Studies* 17: 73–85.
- Minton C.D.T., Rogers K.G., Jessop R.E., Graham D.M. & Lowther A.D. 2006. Biometrics and moult of the Curlew Sandpiper *Calidris ferruginea* in Australia. *Int. Wader Studies* 19: 195–204.
- Morton, G.A. & Morton M.L. 1990. Dynamics of post-nuptial moult in free-living mountain White-crowned Sparrows. *Condor* 92: 813–828.
- Orell, M. & Ojanen M. 1980. Overlap between breeding and moulting in the Great Tit *Parus major* and Willow Tit *P. montanus* in northern Finland. *Ornis Scand.* 11: 43–49.



- Pearson D.J. 1984. The moult of the Little Stint *Calidris minuta* in the Kenyan rift valley. *Ibis* 126: 1–15.
- Pienkowski M.W., Knight P.J., Stanyard D.J. & Argyle F.B. 1976. The primary moult of waders on the Atlantic coast of Morocco. *Ibis* 118: 347–365.
- Pinchuk P., Remisiewicz M., Włodarczyk R. & Karlionova N. 2008. Observations of primary moult in adult Wood Sandpipers *Tringa glareola* on southward migration in east and central Europe. *Wader Study Group Bull.* 115: 24–28.
- Prater A.J. 1981. A review of the patterns of primary moult in Palearctic waders (*Charadrii*). In: Cooper J. (ed.) *Proceedings of the symposium on Birds of the Sea and Shore, 1979*. African Seabird Group, Cape Town, pp 393–409.
- Reed E.T., Bêty J., Mainguy J., Gauthier G. & Giroux J.-F. 2003. Molt migration in relation to breeding success in Greater Snow Geese. *Arctic* 56: 1–109.
- Remisiewicz M., Tree A.J., Underhill L.G., Gustowska A. & Taylor P.B. 2009. Extended primary moult as an adaptation of adult Wood Sandpipers *Tringa glareola* to their use of freshwater habitats of southern Africa. *Ardea* 97: 271–280.
- Rimmer C.C. 1988. Timing of the definitive pre-basic moult in Yellow Warblers at James Bay, Ontario. *Condor* 90: 141–156.
- Rogers K.G. 1995. SHEBA: computer programs sexing birds on measurements using univariate data. *Corella* 19(1): 25–34.
- Rogers K.G., Rogers A. & Rogers D.I. 1990. Bander's Aid. Supplement Number One. Royal Australasian Ornithologists' Union Report No. 67, Melbourne.
- Serra L. & Underhill L.G. 2006. The regulation of primary moult speed in the Grey Plover, *Pluvialis squatarola*. *Acta Zool. Sin.* 52 (Suppl.): 451–455.
- Serra L. 2000. How do Palearctic Grey Plovers adapt primary moult to time constraints? An overview across four continents. *Wader Study Group Bull.* 93: 11–12.
- Schekkerman H., van Roomen M.W.J. & Underhill L.G. 1998. Growth, behaviour of broods and weather-related variation in breeding productivity of Curlew Sandpipers *Calidris ferruginea*. *Ardea* 86: 153–168.
- Summers R.W. 1980. On the rate of change of moult scores in waders. *Wader Study Group Bull.* 28: 24.
- Summers R.W., Underhill L.G., Clinning C.F. & Nicoll M. 1989. Populations, migrations, biometrics and moult of the Turnstone *Arenaria i. interpres* on the East Atlantic coastline, with special reference to the Siberian population. *Ardea* 77: 145–168.
- Summers R.W., Underhill L.G. & Syroechkovski E.E. Jr. 1998. The breeding productivity of dark-bellied Brent Geese and Curlew Sandpipers in relation to changes in the numbers of arctic foxes and lemmings on the Taimyr Peninsula, Siberia. *Ecography* 21: 573–580.
- Summers R.W., Underhill L.G., Nicoll M., Strann K.-B. & Nilsen S.Ø. 2004. Timing and duration of moult in three populations of Purple Sandpipers *Calidris maritima* with different moult/migration patterns. *Ibis* 146: 394–403.
- Summers R.W., Underhill L.G., Waltner M. & Swann R.L. 2010. Differences in biometrics and moult of non-breeding Red Knots *Calidris canutus* in southern Africa and Scotland reflect contrasting climatic conditions. *Ibis* 152: 127–135.
- Thomas D.G. & Dartnall A.J. 1971. Moult of the Curlew Sandpiper in relation to its annual cycle. *Emu* 71: 153–158.
- Tomkovich P.S. 1988. Mating system and parental care in Curlew Sandpiper at the Taimyr. In: Andreev A.V. & Kondratyev A.Ya. (eds) *Studies and Protection of Birds in Northern Ecosystems*. Academy of Science, USSR, pp. 180–184. (In Russian)
- Tomkovich P.S. & Soloviev M.Y. 2006. Curlew Sandpipers *Calidris ferruginea* on their breeding grounds: schedule and geographic distribution in the light of their breeding system. *Int. Wader Studies* 19: 19–26.
- Tulp I. & Schekkerman H. 2001. Studies on breeding shorebirds at Medusa Bay, Taimyr, in summer 2001. *Alterra Report*, 451. Alterra Green World Research, Wageningen.
- Underhill L.G. 1987. Changes in the age structure of Curlew Sandpiper populations at the Langebaan Lagoon, South Africa, in relation to lemming cycles in Siberia. *Trans. R. Soc. South Afr.* 46: 209–214.
- Underhill L.G. 2003. Within Ten Feathers: Primary Molt Strategies of Migratory Waders (*Charadrii*). In: Berthold P., Gwinner E. & Sonnenschein E. (eds) *Avian Migration*. Springer-Verlag, Berlin, pp. 187–197.
- Underhill L.G. & Zucchini W. 1988. A model for avian primary moult. *Ibis* 130: 358–372.
- Underhill L.G. & Summers R.W. 1993. Relative masses of primary feathers in waders. *Wader Study Group Bull.* 71: 29–31.
- Underhill L.G. & Joubert A. 1995. Relative masses of primary feathers. *Ring. Migr.* 16: 109–116.
- Underhill L.G., Zucchini W. & Summers R.W. 1990. A model for avian primary moult – data types based on migration strategies and an example using the Redshank *Tringa totanus*. *Ibis* 132: 118–123.
- Underhill L.G., Serra L. & Brandao A. 2006. Progress with the statistical analysis of primary molt. *Acta Zool. Sin.* 52(Suppl.): 440–443.
- Underhill L.G., Prýs-Jones R.P., Syroechkovski E.E. Jr., Groen N.M., Karpov V., Lappo H.G., van Roomen M.W.J., Rybkin A., Schekkerman H., Spiekman H. & Summers R.W. 1993. Breeding of waders (*Charadrii*) and brent geese *Branta bernicla bernicla* at Pronchishcheva Lake, northeastern Taimyr, Russia, in a peak and a decreasing lemming year. *Ibis* 135: 277–292.
- Wilson J.R., Czajkowski M.A. & Pienkowski M.W. 1980. The migration through Europe and wintering in West Africa of Curlew Sandpipers. *Wildfowl* 31: 107–122.
- Young B. E. 1991. Annual molts and interruption of the fall migration for molting in Lazuli Buntings. *Condor* 93: 236–250.

## SAMENVATTING

Krombekstrandlopers *Calidris ferruginea* ruien hun vleugelpennen na aankomst in de overwinteringsgebieden. Dit zou kunnen inhouden dat deze rui niet wordt beïnvloed door de situatie in de broedgebieden. Om dit te onderzoeken volgden de auteurs de jaarlijkse en geslachtgebonden variatie in de start en de duur van de rui van Krombekstrandlopers tijdens hun overwintering in het noordwesten van Australië en vergeleken vervolgens deze parameters met het aandeel eerstejaars vogels in de populatie. Gemiddeld begon de rui op 18 september en duurde 129 dagen. Er werd tussen jaren geen variatie gevonden in de duur van de rui. Binnen het jaar was de veergroei lineair. De start van de rui

correleerde met het percentage eerstejaars vogels in de populatie. De gemiddelde startdatum was in jaren met een goed broedsucces 25 september en in jaren met een slecht broedsucces 15 september. Voor mannen was het verschil tussen goede en slechte jaren gemiddeld vijf dagen, terwijl vrouwen na een slecht broedseizoen elf dagen eerder ruiden dan na een goed broedseizoen. Na een slecht broedseizoen vertrekken Krombekstrandlopers eerder uit de broedgebieden. Dit zou de gevonden relatie tussen broedsucces en de timing van vleugelrui in het overwinteringsgebied kunnen verklaren. (YIV)

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**Appendix 1.** Annual estimates of primary moult parameters for adult Curlew Sandpipers that performed continuous primary moult in north-west Australia. Results are for the 19 years where there was a large enough sample size.

Year	Moult parameters				Sample size		
	Mean start date (SD)	Duration (SD)	Standard deviation of start date (SD)	End date (SD)	No moult	In moult	Moult completed
1981	16 Sep (2.6)	126.9 (1.5)	14.1 (0.2)	21 Jan (3.1)	67	8	0
1982	23 Sep (1.2)	119.6 (1.5)	13.1 (1.8)	21 Jan (2.1)	513	41	0
1983	24 Sep (0.7)	123.9 (1.5)	13.8 (1.3)	26 Jan (1.2)	2	539	4
1986	30 Sep (2.3)	118.1 (1.5)	11.0 (0.9)	26 Jan (2.9)	71	12	0
1988	14 Oct (1.4)	130.0 (1.5)	11.9 (1.5)	21 Feb (1.5)	10	45	658
1990	17 Sep (2.1)	129.3 (1.5)	14.4 (1.5)	24 Jan (2.2)	6	33	21
1992	18 Sep (0.6)	126.9 (2.5)	8.2 (1.8)	23 Jan (4.8)	125	385	0
1993	06 Oct (4.6)	126.9 (1.5)	14.8 (1.5)	10 Feb (3.3)	4	6	18
1994	21 Sep (2.1)	128.9 (1.4)	13.8 (1.5)	27 Jan (1.6)	53	18	376
1996	08 Oct (3.8)	126.9 (1.6)	14.6 (1.5)	12 Feb (1.5)	0	5	343
1998	16 Sep (0.7)	127.8 (0.9)	9.1 (1.1)	22 Jan (1.6)	312	253	6
1999	18 Oct (1.5)	130.0 (1.5)	13.4 (1.5)	25 Feb (5.9)	0	14	99
2000	22 Sep (2.9)	126.8 (1.5)	13.8 (1.5)	27 Jan (1.5)	5	23	21
2001	13 Sep (0.9)	127.2 (1.5)	13.8 (1.4)	18 Jan (1.8)	9	372	27
2002	10 Sep (1.5)	130.6 (1.3)	11.4 (1.5)	18 Jan (1.5)	0	147	0
2003	20 Sep (5.9)	131.6 (1.5)	13.8 (1.5)	30 Jan (2.8)	45	3	2
2004	29 Sep (2.2)	126.9 (1.5)	10.7 (1.2)	03 Feb (1.2)	2	49	37
2005	17 Sep (1.9)	129.7 (2.5)	12.3 (1.5)	25 Jan (1.5)	1	55	114
2006	10 Sep (1.5)	131.3 (1.5)	13.8 (1.5)	20 Jan (1.5)	0	107	2