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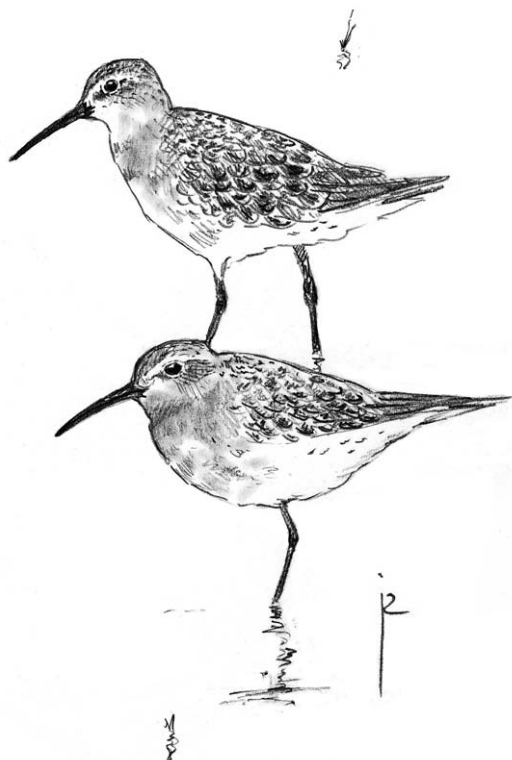
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Conditions on the non-breeding areas affect primary moult strategy of the Curlew Sandpiper *Calidris ferruginea*

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We investigated the adaptations of primary moult to conditions on the non-breeding areas in the Curlew Sandpiper *Calidris ferruginea*, an Arctic breeding, long-distance migratory wader (shorebird). Parameters of moult (start date, duration, and standard deviation) and how they are affected by rainfall patterns were estimated using an extension of the Underhill–Zucchini (1988) moult models which allows the inclusion of covariates. The estimated start date and duration of moult in Kenya was 2 October and 128 days, respectively; start date was negatively correlated with the rainfall in June. In India, the estimated start date of moult was 15 August, duration 107 days and start of moult was positively correlated to the rainfall in August. Circumstantial evidence also suggests that the rate of growth of the primaries was affected by food supply at the non-breeding areas. The timing of moult to coincide with rainfall periods is, perhaps, an adaptation to carry out this energy demanding activity during periods of food abundance. This study shows that in these populations of the Curlew Sandpiper, the timing of moult is a direct response to environmental variation and might be used to measuring the impacts of climate change on life-history traits of migratory birds.

Key words: *Calidris ferruginea*, Underhill–Zucchini model, Kenya, India

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The process of moult in birds is necessary for maintaining feathers in an airworthy condition but the process often comes at a high cost. Moult reduces plumage functionality (Hedenström & Sunada 1999), has energetic requirements (Klaassen 1995), and is considered an inefficient process (Dietz *et al.* 1992, Rohwer *et al.* 2009, Hoyer & Buttemer 2011). Due to energy constraints, most bird species avoid overlapping moult with other energetically demanding activities such as breeding or migration. In many species, moult starts shortly after the breeding season is completed; moult can therefore serve as an indicator for other life-history stages that cannot be quantified directly. For instance, in species that make a single breeding attempt per season, an early onset of moult could indicate breeding failure (e.g. Barshep 2011, Barshep *et al.* 2011) and variance in start date of moult could serve as an indica-

tor for variability in reproductive success (Barshep 2011).

The different moult strategies undertaken by long-distance migratory waders (shorebirds) is an adaptive response to a variety of factors such as seasonal patterns of food abundance (Prater 1981) and the length of the migratory journey to the winter quarters (Morrison 1976). For instance, populations of species such as the Grey Plover *Pluvialis squatarola*, Wood Sandpiper *Tringa glareola*, and Curlew Sandpiper *Calidris ferruginea* at more northern latitudes of Africa start moult earlier than populations farther south (Pienkowski *et al.* 1976, Serra 2000, Remisiewicz *et al.* 2009). Unpredictable food resources and feeding opportunities for shorebirds during the winter months are also reasons for the early start and quick completion of moult observed in the populations moulting at

temperate latitudes compared to species wintering at southern latitudes (Underhill 2003, Summers *et al.* 2004, Summers *et al.* 2010).

Studies of moult in tropical birds indicate that the timing of moult is linked to rainfall pattern. Examples can be found for species such as the weavers and queleas (Oschadleus 2005, Oschadleus & Underhill 2006). However, it is not known if migrant birds that moult in tropical non-breeding areas modify their timing of moult according to weather patterns on these non-breeding areas. If rainfall patterns affect food abundance and food abundance in turn affects the timing and rate of moult, then the weather patterns in the tropics can potentially modify the schedule of moult. To explore the link between rainfall patterns on the non-breeding areas and the schedule of moult in long-distance migratory waders, we examined the moult pattern of populations of Curlew Sandpiper at similar latitudes in Kenya and India, two regions with contrasting weather patterns, especially in the timing of the wet season. The Curlew Sandpiper is a migratory wader that breeds on the tundra of Arctic Siberia. It has a wide wintering distribution spanning Africa, the Indian subcontinent, and Australasia (Cramp & Simmons 1983, del Hoyo *et al.* 1996). Primary moult is carried out almost exclusively on the non-breeding grounds (Cramp & Simmons 1983). We hypothesize that the annual start date of moult and the speed of moult will be affected by the amount of rainfall at these two sites.

METHODS

Curlew Sandpipers were mist-netted in Kenya at various sites around the Rift Valley (00°22'N–03°20'S, 35°02'–39°58'E) from 1970–1988. In India, birds were trapped using mist nets at Mandapam (9°17'N, 79°8'E) and at the Great Vedaranyam Swamp (10°18'N, 79°51'E), in south-eastern India as part of the Bombay Natural History Society's Bird Migration Project between 1980 and 1992 (Balachandran *et al.* 2000). Birds were aged based on feather appearance and wing condition as described in, for instance, Prater *et al.* (1977). The moult of birds aged as adults is explored in this study. Molt scores of the primaries were recorded using the British Trust for Ornithology technique (Ginn & Melville 1983); old feathers were scored 0, new feathers 5, and growing feathers 1–4 depending on their stage of growth. Molt scores were converted into molt indices following the relationship: molt score 0 = 0, 1 = 0.125, 2 = 0.375, 3 = 0.625, 4 = 0.875,

and 5 = 1.000 (Underhill & Summers 1993, Underhill & Joubert 1995), a process which aimed to achieve linearity through time of moult progression (Summers 1980). Molt indices were then transformed into the proportion of feather mass grown (PFMG) using the relative masses of primary feathers (Underhill & Joubert 1995).

The start date and duration of primary moult of all years combined was estimated using the moult models of Underhill and Zucchini (1988). The samples of birds captured in each region were assumed to be part of a population that arrived with old feathers, moulted and remained in the region so that the data were taken as type 2 of the Underhill and Zucchini (1988) model. This method was also used to estimate yearly moult parameters at both sites. The start dates and duration of moult for individual primaries were also estimated following Underhill (2003), Serra and Underhill (2006), and Remisiewicz *et al.* (2009).

An estimate of the gap in the wing during moult was obtained for each individual from the proportion of feather mass missing (PFMM), an extension of the raggedness score (Haukioja 1971) but takes into account the relative sizes of the missing feathers (Remisiewicz *et al.* 2009). To calculate PFMM, the opposite approach to the calculation of PFMG was used. Feathers that had moult scores 1, 2, 3 and 4 were given a corresponding moult indices of 0.875, 0.625, 0.375 and 0.125 respectively to represent the relative mass for the missing feather mass (Remisiewicz *et al.* 2009). Both old and fully grown new feathers were given a moult index of 0. PFMM of the 10 primaries were summed which gave a measure of the relative size of the wing gap for individual birds.

Moult in relation to weather pattern

To relate the onset and duration of moult in Kenya and India with rainfall patterns at the sites where birds were trapped, the averages of four daily rainfall and temperature readings were obtained from the National Oceanic and Atmospheric Administration (NOAA) stations in each of the two countries (<http://www.ncdc.noaa.gov/oa/climate/climatedata.html>). The data from Kenya was from the NOAA station on the coast at Malindi (03°23'S, 40°12'E) and the data from India was from the station in Pamban (09°16'N, 79°18'E), ca. 6 km east of the Mandapam study site. Relationship between the timing of moult and rainfall pattern was obtained using an extension of the maximum likelihood model of Underhill and Zucchini (1988) which allows the inclusion of covariates in the model (Erni *et al.* 2012, <http://cran.r-project.org/package=moult>).

RESULTS

The estimated start date of moult in Kenya using the PFMG of the tract of all primaries combined was 6 October, the duration was 137 days, and end date of moult was 20 February (Figure 1). The estimated standard deviation of the start date of moult was 39.5 days; thus 95% of birds were estimated to start moult between 21 July and 23 December. In India, the estimated start date of moult estimated from the PFMG of the tract of all primaries was 26 July, duration was 145 days, and moult end date was 18 December (Table 1, Figure 1). The estimated standard deviation of start date was 31.5 days; 95% of birds were estimated to start moult between 18 May and 03 October. The annual estimates of the start date of moult in Kenya varied from 24 July to 21 October. In India the annual estimate of the start date of moult ranged from 4 July to 26 September.

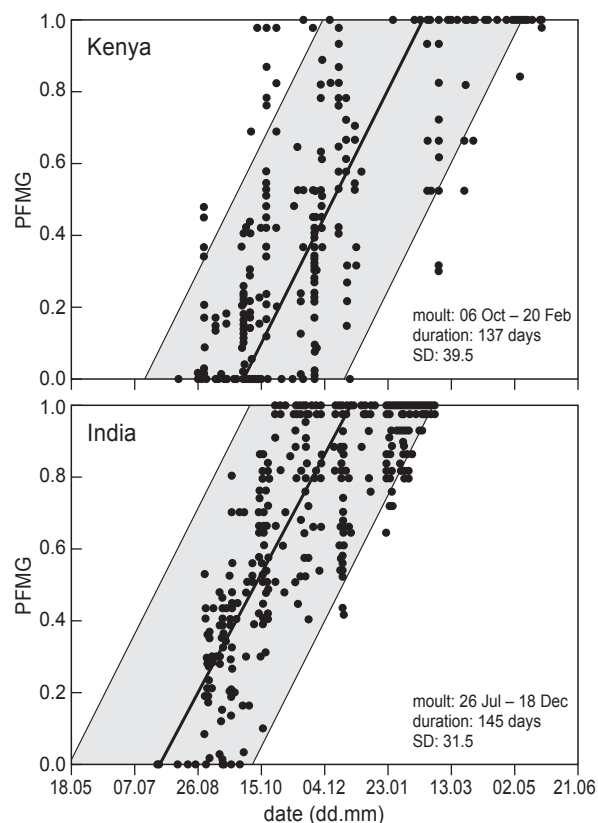


Figure 1. Temporal distribution of the Proportion Feather Mass Grown (PFMG) of adult Curlew Sandpipers moulting in Kenya and India. Thick black line reflects the course of moult from estimated start to end dates; thin lines are 95% confidence intervals.

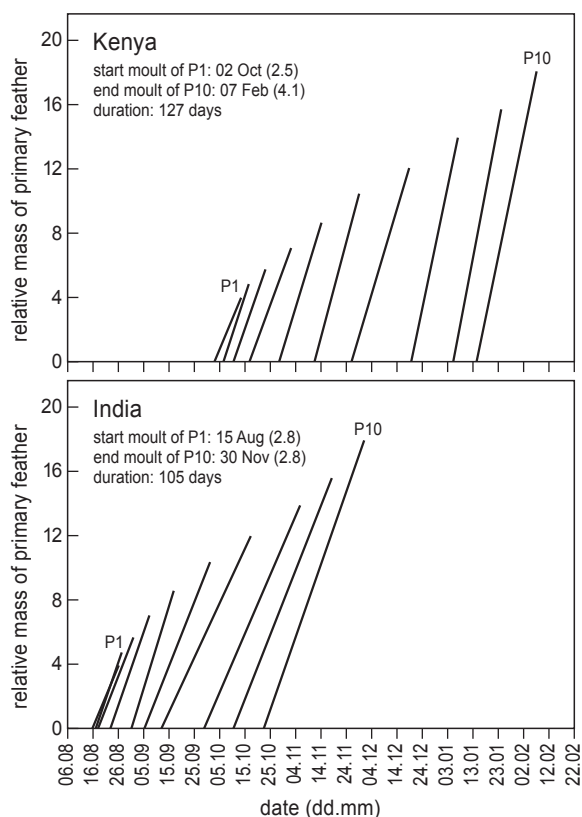


Figure 2. Growth lines of primary feathers P1–P10 of Curlew Sandpipers in Kenya and India, showing the amount of the primary mass produced between start and end date of each primary development. Slopes of the lines reflect the growth rate of each primary.

In Kenya, estimated starting date of P1 and moult end date of P10 were 2 October and 7 February, respectively, suggesting an overall moult duration of 128 days (Table 1; Figure 2). In India, these dates were 15 August and 30 November, suggesting a moult duration of 107 days (Table 1; Figure 2). There was a difference in the estimated start date and duration of moult from the tract of 10 primaries combined and the estimates obtained when considering the moult of individual primary feathers. In Kenya, there was a two-day difference in the moult start date, nine-day difference in the moult duration, and a 13-day difference in the end date of moult between the two methods (Table 1). In India, there was a 21-day difference in the start date of moult, a 38-day difference in the moult duration, and a 16-day difference in the end date of moult from the two methods (Table 1). The temporal distribution of moult scores indicates that the progress of moult in Kenya was faster towards the end of moult compared to the beginning, whereas in India, the progress of moult was

slower towards the end compared to the beginning. Both deviations from the assumed constant progress of moult assumption lead to an overestimation of the duration of moult. Therefore, in discussing the difference in the estimates of moult between Kenya and India, we will refer to estimates obtained from individual primaries.

In Kenya, the duration of moult of individual primaries increased from 10 days (P1) to 23 days (P10) (Table 1), while in India duration of moult of P1 was also 10 days increasing to 40 days for P10 (Table 1). In Kenya the interval between the shedding of neighbouring primaries increased from nine days between P1 and P2 to a maximum of 23 days between P8 and P9 while the interval between the shedding of neighbouring primaries in India ranged from one day between P1 and P2 to a maximum of 12 days between P9 and P10. The shorter interval between the moult of primaries

coupled with the longer duration of moult of individual primaries in India compared to Kenya resulted in greater overlap in the growth of successive primaries (Figure 3). Consequently, the average number of primaries growing simultaneously in India was larger (average: 2.3, range: 1.4–3.2) than the average number in Kenya (average: 1.6; range: 1.1–2.4) and this difference was statistically significant (t -test: $t = -2.27$, $P = 0.03$, $df = 18$; Figure 3).

Rate of moult

By dividing the relative mass of each primary by its moult duration, the PFMG/day of each primary was estimated (Table 1). By summing up the PFMG/day for all feathers growing simultaneously on any given day, the daily rate of feather material production for the entire moult period could be modelled, a method demonstrated by Remisiewicz *et al.* (2009). The daily

Table 1. Primary moult estimates of individual primaries of the Curlew Sandpipers in Kenya and India and overall population estimate of the start date and duration of moult estimated from the Proportion of feather mass grown (PFMG) of all 10 primaries combined.

Site	Primaries	Moult parameters				Sample sizes			PFMG/day (%)
		Mean start date (SD)	Duration (SD)	Standard start deviation of date (SD)	End date (SD)	Not in moult	In moult	Moult complete	
Kenya	P1	2 Oct (2.5)	10.8 (4.3)	51.3 (5.6)	13 Oct (4.0)	115	20	366	0.37
	P2	6 Oct (2.3)	10.1 (4.1)	50.0 (5.4)	16 Oct (3.9)	121	19	361	0.48
	P3	10 Oct (2.3)	12.7 (3.8)	47.4 (4.9)	23 Oct (3.7)	134	19	348	0.45
	P4	17 Oct (3.3)	16.2 (3.6)	45.2 (4.2)	2 Nov (3.8)	138	41	322	0.33
	P5	28 Oct (2.8)	16.4 (3.4)	42.8 (3.9)	14 Nov (3.8)	163	32	306	0.52
	P6	12 Nov (3.1)	17.3 (4.0)	49.9 (4.1)	29 Nov (4.4)	188	30	283	0.6
	P7	26 Nov (3.5)	22.6 (3.9)	46.4 (3.4)	19 Dec (4.5)	217	35	249	0.53
	P8	19 Dec (3.4)	18.4 (4.2)	46.3 (3.1)	7 Jan (4.7)	252	24	225	0.76
	P9	5 Jan (3.6)	18.4 (4.4)	47.7 (3.0)	24 Jan (4.7)	275	22	204	0.85
	P10	15 Jan (4.4)	23.4 (4.5)	47.8 (2.9)	7 Feb (4.7)	287	25	189	0.77
	Combined PFMG	6 Oct (3.0)	137 (5.3)	39.5 (1.7)	20 Feb (4.0)	115	193	185	0.88
India	P1	15 Aug (2.8)	10.1 (5.6)	20.8 (3.8)	23 Aug (3.3)	15	10	1736	0.40
	P2	16 Aug (3.0)	10.7 (5.9)	23.1 (4.0)	27 Aug (3.5)	17	11	1733	0.45
	P3	18 Aug (5.2)	14.3 (3.5)	22.0 (2.2)	2 Sep (3.4)	18	20	1723	0.40
	P4	22 Aug (4.2)	15.2 (3.1)	20.6 (2.8)	7 Sep (2.7)	22	25	1714	0.46
	P5	30 Aug (2.9)	16.7 (2.7)	18.0 (2.0)	16 Sep (2.1)	38	35	1697	0.51
	P6	4 Sep (2.8)	26.2 (2.7)	20.5 (1.7)	1 Oct (2.0)	51	54	1663	0.40
	P7	14 Sep (3.6)	35.3 (3.4)	35.4 (2.0)	20 Oct (2.7)	82	70	1613	0.34
	P8	28 Sep (3.6)	38.1 (3.1)	44.7 (1.9)	5 Nov (2.7)	133	105	1525	0.36
	P9	10 Oct (3.5)	38.7 (2.9)	45.7 (1.9)	17 Nov (2.7)	161	110	1480	0.40
	P10	22 Oct (3.2)	39.7 (2.8)	43.9 (1.7)	30 Nov (2.4)	196	129	1405	0.45
	Combined PFMG	26 Jul (4.0)	145 (4.4)	31.5 (1.2)	18 Dec (3.7)	22	377	778	0.96

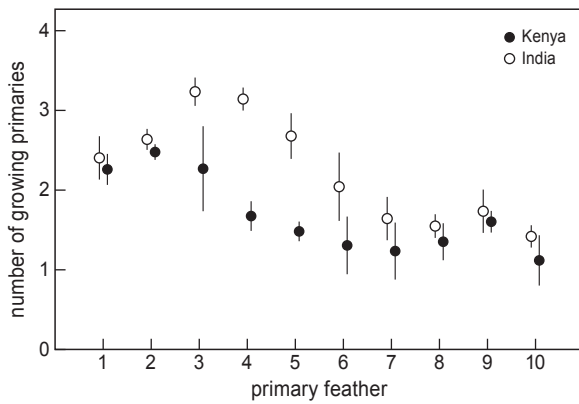


Figure 3. Average number of primary feathers growing simultaneously during the moult of individual primaries (P1–P10). Whiskers represent 95% confidence intervals.

rate of feather material growth in Kenya was estimated at an average of 0.88%/day (Table 1), less than the estimated rate of PFMG/day in India of 0.93%/day (Kolmogorov–Smirnov test: $D = 0.39$, $P = 0.019$). The daily rate of feather material grown was relatively uniform at the beginning and middle of moult in Kenya; this is demonstrated by the almost linear cumulative curve of PFMG until a value of c. 76% is reached; thereafter, towards the end of moult in Kenya, rate of feather material growth accelerated (Figure 4).

In contrast, in India, the opposite pattern was observed; moult progress slowed down in India towards the end of moult (Figure 4). Consequently, in Kenya the 25th percentile of primary feather mass production was achieved after 33 days (average 0.82 PFMG/day), 50th percentile in 41 days (average of 0.65 PFMG/day), 75th percentile in 33 days (average of 0.87 PFMG/day), and 100th percentile in 22 days (average of 1.10 PFMG/day). In India, the 25th percentile of primary feather mass production was achieved after 21 days (average 1.21 PFMG/day), 50th percentile in 28 days (average 0.97 PFMG/day), 75th percentile in 27 days (average 0.97 PFMG/day), and 100th percentile in 34 days (average 0.80 PFMG/day). These are close to the values obtained by assuming constant rate of feather material deposition despite the fluctuation of feather material growth above and below the overall average.

Proportion of feather mass missing

The average proportion of feather missing (PFMM) per day in Kenya was estimated at 0.028, the average of the daily minima was 0.01 and the average of the daily maxima was 0.05 (Figure 5). This means that, on aver-

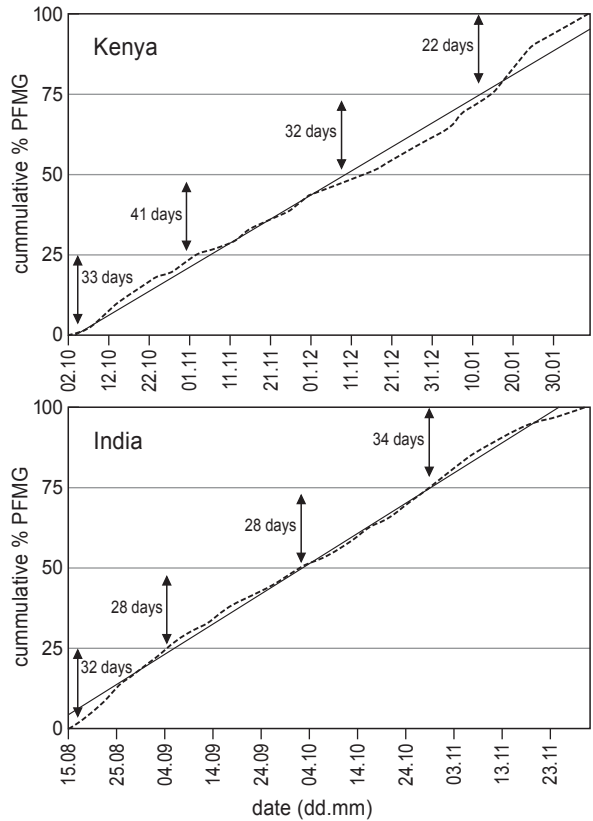


Figure 4. Modelled cumulative rate of percentage feather mass grown (dotted lines) in Kenya and India estimated from daily values of the moult parameters of individual primary feathers (Table 1). Thin lines are the linear regression lines fitted through the daily values of PFMG. Vertical arrows and day numbers indicate the interval in days between quartiles.

age, 2.8% of the mass of primary feathers was missing during moult at any one time. The average PFMG/day in India was 0.020 (average range: 0.011–0.013); 2.0% of the mass of primary flight feathers was missing during moult at any one time. The average PFMG/day was negatively correlated with average PFMG/day in both Kenya ($r = -0.24$, $P = 0.01$) and India ($r = -0.54$, $P < 0.001$). PFMM in Kenya was not correlated with the average number of primaries in moult ($r = -0.12$, $P = 0.08$) whereas in India there was a negative correlation between PFMM and the average number of primaries in moult ($r = -0.647$, $P < 0.001$).

Timing of moult in relation to rainfall pattern

The start dates of moult of the Curlew Sandpiper in Kenya and India corresponded well with rainfall seasons in these areas. The onset of primary moult for individual birds in Kenya was negatively related to average rainfall in June ($F_{1,494} = 20.25$, slope = -0.49 ,

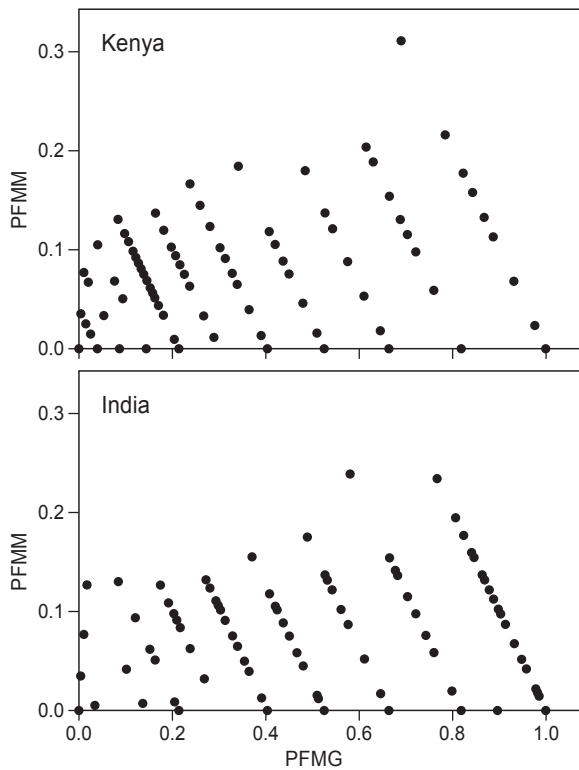


Figure 5. The relationship between the size of the wing gap during moult expressed as a Proportion of Feather Mass Missing (PFMM) and Proportion of Feather Mass Grown (PFMG). The pattern of parallel lines is a consequence of the recording of moult scores for individual feathers to integer values.

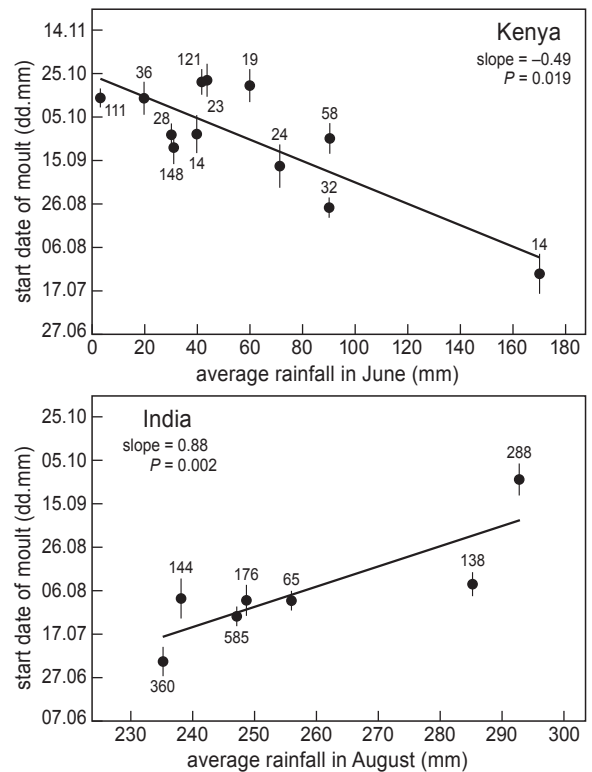


Figure 6. Relationship between the start date of moult and rainfall pattern in Kenya and India. Each dot represents one year, numbers above and below error bars are sample sizes.

$P = 0.019$; Figure 6). The average rainfall in August was a significant predictor of the start of moult in India with moult starting relatively later for individual birds facing high August rainfall ($F_{1,1767} = 9.09$, slope = 0.88, $P = 0.002$; Figure 6). Curlew Sandpipers in India thus commence moult as soon as they arrive, coinciding with the Monsoon rains which extend from mid-August through December (Guhathakurta & Rajeevan 2006, Indian Meteorological Department 2010).

DISCUSSION

Pattern of primary moult

Two contrasting moult strategies were employed by Curlew Sandpipers in Kenya and India: a rapid moult of a single feather at a time in Kenya *versus* a slow moult of several feathers simultaneously in India. This difference in moult strategies between Kenya and India suggest that either different sub-species are involved or conditions on the non-breeding areas are influencing

the moult patterns. Since no geographic variation or sub-species have been found in the Curlew Sandpiper (Wennerberg & Burke 2001), these moult strategies are likely an adaptation by different populations to climatic conditions at these two locales. Despite this difference, both strategies are aimed at maintaining a uniform rate of feather material growth and, possibly, minimizing wing gap during moult. In Kenya, for instance, the constant daily rate of feather material growth was possible because of the overlap in the growth of the smaller inner primaries and little overlap in the growth of the larger outer primaries. The seven days overlap in the growth of P1 and P2 resulted in a combined PFMG/day of 0.85, a value similar to the amount of feather material deposited per day during the moult of P9 and P10 (0.89). This value is also close to the overall average daily feather material deposition throughout the moult period (0.88%/day).

On the other hand, the larger number of primaries moulted simultaneously in India would normally imply that the amount of feather material deposited daily

would increase progressively during moult especially towards the end of moult when the larger primaries are growing simultaneously. But the lower daily rate of feather material grown during the replacement of the outer five primaries (compared to Kenya) ensured a fairly constant rate of daily feather material growth.

On average, the amount of feather material missing was estimated at 3% in Kenya and 2% in India. This is smaller than the PFMM reported for adult and sub-adult (10% and 11% respectively) Wood Sandpipers (Remisiewicz *et al.* 2009). The average number of primaries growing simultaneously in the Wood Sandpiper was estimated at 2.4 (Remisiewicz *et al.* 2009), similar to the 2.3 found in the Curlew Sandpiper in India, although larger than the number in Kenya, 1.6. The size of wing gap could either be due to the number of primaries moulted simultaneously and/or the wing area (Hedenström 1998). In this instance, the difference in the amount of feather material missing might be a result of the Wood Sandpiper having a longer wing span (40–42 cm) thus larger wing area compared to the Curlew Sandpiper (50–56 cm), despite both species being of similar size at 19–22 cm (Cramp & Simmons 1983).

The overall pattern of moult of Curlew Sandpipers in Kenya and India is similar to the pattern described in Curlew Sandpipers in southern Africa (Elliott *et al.* 1976), north-western and south-eastern Australia (Minton *et al.* 2006), Tasmania (Thomas & Dartnall 1971) and Morocco (Pienkowski *et al.* 1976). The three inner primaries are moulted in quick succession, while only two or even one feather are moulted at a time towards the end (Figure 3). This pattern has also been observed in similar-sized waders such as Sanderling *Calidris alba* (Underhill 2003), and Wood Sandpiper *Tringa glareola* (Remisiewicz *et al.* 2009). It is likely to be an adaptation by these species to minimize the size of wing gap during moult because gaps in the wing compromise flight efficiency (Tucker 1991, Swaddle & Witter 1997, Hedenström & Sunada 1999).

Timing of moult

Based on the estimated start date of moult of P1, moult on average started about two months earlier in India (15 August) compared to Kenya (2 October). Our estimated start date of moult in Kenya was similar to the preliminary result presented by Pearson (1984) of adult Curlew Sandpipers at Lake Magadi. To the best of our knowledge, there are no prior estimates of moult start dates for Curlew Sandpipers in India to which we can compare our results, but in relation to the estimate start date of moult in the Grey Plover on 1 September

(Balachandran *et al.* 2000), Curlew Sandpipers started moult about two weeks earlier.

Also, based on the start date of moult of P1 and moult end date of P10, moult duration of 107 days in India was shorter than moult duration in Kenya of 128 days (Table 1). In India, the short duration of moult was achieved by shortening the interval between shedding of individual primaries, resulting in the growth of several feathers simultaneously; a tactic used by Grey Plovers (Serra 2000, Serra & Underhill 2006) and Ruddy Turnstone *Arenaria interpres* (Underhill 2003) to increase the rate of feather material growth. Birds in Kenya compensate for the late start of moult by increasing the rate of feather material growth, achieved through the increased growth rate of individual feathers rather than the number of feathers moulted simultaneously (Table 1). Overall, birds in Kenya and India completed moult in February and December, respectively, giving them sufficient time to prepare for northward migration to the breeding grounds.

The cost of an early moult start, especially within the tropics, is that strong sunlight coupled with a highly saline or alkaline environment causes new flight feathers to wear out within a few months (Evans 1976). Birds moulting early will likely migrate to their breeding grounds with fairly worn feathers. For Curlew Sandpipers in India, the early moult start might incur negligible fitness cost because of the short migratory distance to the breeding grounds compared to the population in, say, Australia. Also, the slow moult of individual primaries would result in the production of high quality feathers (Serra 2001). Conversely, by delaying start of moult, Curlew Sandpipers in Kenya could potentially increase the likelihood of migrating to the breeding grounds with fairly new feathers but the rapid moult of individual primaries would result in lower quality of feathers (Serra 2001) than would be otherwise.

Timing of moult in relation to rainfall patterns

The contrasting rainfall patterns between Kenya and India explain the differences in the onset of moult in these areas. Most regions in Kenya experience two rainy seasons: the “long rains” extends roughly from March to June, and the “short rains” from approximately October to December (Kenyan Meteorological Department 2010). Adult Curlew Sandpipers arrive in Kenya in August (Pearson 1974), during the dry period between the two rainy seasons. If the amount of rain in June was high, then moult started early and *vice versa* (Figure 6).

While there is no specific information about the timing of arrival of the Curlew Sandpiper in India,

personal observations (S. Balachandran unpubl. data) indicate that birds arrive from mid-August. It would appear then that adult Curlew Sandpipers commence moult almost immediately after arriving so the timing of moult coincides with the monsoon (rainfall) season which extends from September through December (Indian Meteorological Department 2010).

Studies show that the diet of the Curlew Sandpipers consists mostly of the larvae and imagos of Coleoptera, *Brachicera* sp., *Daphnia* sp., and *Bolboschoenus* sp. (Puttick 1979, Barker & Vestjens 1989). In India, Curlew Sandpipers have also been observed feeding on *Artemia* sp, which are abundant during the dry season in salt pans of Point Calimere (S. Balachandran, unpubl. data). At both high and low temperatures, the hatchability of eggs and larval development of these insect species is affected (Howe 1959, Lee & Denlinger 1991). Also, high temperatures coupled with low precipitation results in high evapotranspiration which leads to the hardening of the substrate from which prey has to be extracted. This might explain why Curlew Sandpipers in Kenya delayed moult until the second rain season in October. Although Curlew Sandpipers in India mostly depend on the intertidal sand flats where the food resources are renewable on daily basis, the onset of northeast monsoon (retreating monsoon) in November, a period characterized by the rapid decline in rain, high daily temperatures and dry northeast winds (Indian Meteorological Department 2010), might reduce food availability, accounting for the early completion of moult in India. It might also explain why the moult of the outer five primaries was slower in India compared to the rate observed in Kenya. Empirical findings have demonstrated that food shortage slows moult in certain species. Riddle (1908) found that the linear growth rate of the feathers of Ring Doves *Streptopelia risoria* became much slower after three days of starvation. Ashmole (1962) found that in a population of the Black Noddy *Anous tenuirostris* primary moult was slower when food was inferred to be scarce than when it was more plentiful.

However, there is also the possibility that the early start of moult in India is due to the distance between the breeding and non-breeding areas. Studies of moult in other waders indicate that birds wintering in the northern Hemisphere start early and complete early than the southern Hemisphere (Serra 2000, Summers *et al.* 2010). The slowing down of moult observed in India could be that an early moult start afforded the birds plenty of time to complete moult. Johnson and Minton (1980) found that Dunlins initiating moult relatively early, moulted at a slower rate such that moult

was completed more or less simultaneously with birds that started at a later date.

In conclusion, our study shows that the speed of moult in the Curlew Sandpiper is governed by the rate of moult of individual feathers as well as the number of primaries moulted simultaneously. There is circumstantial evidence to suggest that food availability at the non-breeding areas in Kenya and India, which is related to rainfall patterns in these regions, affected the rate of feather material growth. If, indeed, the timing of moult is sensitive to rainfall patterns, it suggests that moult is a potential variable at measuring the impacts of climate change on life-history traits within the annual cycle of migratory birds.

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SAMENVATTING

De meeste steltlopers ruïen hun slagpennen buiten het broedgebied. Dit onderzoek gaat in op de vraag hoe de ruï van de grote slagpennen aansluit bij de plaatselijke voedselomstandigheden. De onderzochte soort betrof de Krombekstrandloper *Calidris ferruginea*, een noordelijk broedende steltloper die grote afstanden aflegt tussen broedgebied en overwinteringsgebied. Relevante maten van de ruï (begin, duur en spreiding) werden geschat met behulp van een model ontwikkeld door Underhill en Zucchini (1988). Het voordeel van dit model is dat ook de invloed van covariabelen geschat kan worden. Bij dit onderzoek was dat het neerslagpatroon. Het onderzoek werd uitgevoerd in Kenia en India. In Kenia begon de ruï van de grote slagpennen

op 2 oktober en duurde 128 dagen. Het begin viel eerder in de tijd naarmate er meer regen in juni was gevallen. In India begon de ruï op 15 augustus en duurde 107 dagen. Hoe meer regen er in augustus viel, des te later begon de ruï. Er waren bovendien aanwijzingen dat de groeisnelheid van de grote slagpennen afhing van het voedselaanbod in het ruïgebied. De auteurs veronderstellen dat het verschuiven van de ruïperiode met de hoeveelheid neerslag een aanpassing is om te ruïen op een moment dat het voedselaanbod het grootst is. Dit betekent dat de Krombekstrandloper zich goed leent om de invloed van klimaatverandering op de biologie van trekvogels te bestuderen. (JP)

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