Geographical Patterns in Primary Moult and Body Mass of Greenshank Tringa nebularia in Southern Africa

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Geographical patterns in primary moult and body mass of Greenshank *Tringa nebularia* in southern Africa

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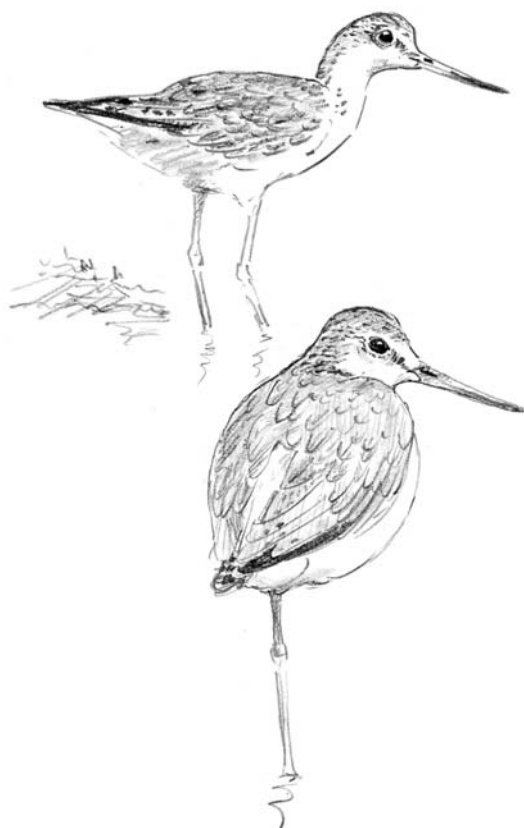
Greenshanks *Tringa nebularia* show various patterns of primary moult in the northern hemisphere, but farther south moult patterns are known only fragmentarily. We identified geographical patterns in primary moult and pre-migratory fattening of Greenshanks on their southernmost African non-breeding grounds. We compared primary moult (using Underhill-Zucchini models) and body mass at a population level based on 356 Greenshanks caught in 1968–1998 at inland wetlands in Zimbabwe, and on the east and west coasts of South Africa. About 20% of immatures replaced one to five outer primaries in December–May, a rare pattern in the north. Sub-adults moulted all primaries on average 40 days earlier than adults, yet at the same rate. Adults started primary moult on average 16–19 days earlier in Zimbabwe and at the east coast than at the west coast (7, 4, 23 September, resp.). These dates correspond with the Greenshanks' broad-front arrival in Zimbabwe and the east coast, and their later arrival at the west coast. Moult took 10–17 days longer on average in Zimbabwe and at the east coast than at the west coast (122, 115, 105 days, resp.), thus the end of moult coincided within six days (31 December–6 January). Pre-migratory fattening began about 13–19 January across all regions. The mean departure fat loads of adults were 76 g in Zimbabwe, 116 g at the west coast and 125 g at the east coast. The heaviest adults from all three regions could reach the Nile Valley or the Red Sea coast in one non-stop flight. We suggest that Greenshanks at inland wetlands of Zimbabwe benefit from a shorter return migration distance and lower competition than at the coasts, and abundant food during the entire austral summer in favourable years, but can move on to the coasts if conditions deteriorate.

Key words: primary moult, body mass, flight range, waders, Greenshank, southern Africa

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The Greenshank *Tringa nebularia* is a common migrant wader across Africa's inland wetland and coastal areas during its non-breeding period (Cramp & Simmons 1983, Urban *et al.* 1986, Scott 2009). Within the Eurasian-African bird migration system, Greenshanks move between their breeding grounds in the taiga zone – ranging from Scotland in the west, through Scandinavia, to the Ural Mountains in the east – and their non-breeding grounds in western Europe, northern Africa, the Nile Valley and Africa south of Sahara (Cramp & Simmons 1983, Urban *et al.* 1986, Underhill 1997, Scott 2009). Most ringing recoveries of the birds that visit southern Africa come from breeding grounds near the White Sea in northwest Russia and from Central Russia (Underhill *et al.* 1999). These populations migrate to southern Africa probably mostly along the eastern coast and across the interior of Central and eastern Africa (Underhill *et al.* 1999, Scott 2009). A

record of a Greenshank ringed in southern Africa and recovered in France (Tree 1979) and of a bird ringed in the south of England and recovered near the White Sea (Robinson & Clark 2012), at the same breeding grounds as the southern African visitors, indicate occasional birds from Western Europe's migratory population.

Greenshanks use inland wetlands as well as coastal mudflats and rocky shores in the non-breeding season (Cramp & Simmons 1983, Piersma *et al.* 1996, Scott 2009). In southern Africa they are common non-breeding waders in both habitats. At inland wetlands Greenshanks are scattered in small groups, but at coastal areas they might join larger mixed flocks of other waders (Tree 1979, 2005, Underhill 1997). As with other medium and large waders, many immature Greenshanks stay for a "gap year" in Africa (Underhill 2006) and return to the breeding grounds when they are almost two years old (Tree 1979, Urban *et al.* 1986, Summers *et al.* 1995, Underhill 1997). On average 30% of Greenshanks arriving in South Africa for the austral summer, and up to 48% of the birds arriving at the Berg River estuary on the west coast, probably mostly first-year individuals, remain for the winter months (Velásquez *et al.* 1991, Summers *et al.* 1995). Adults arrive in southern Africa from late July until September, juveniles from early September to late October. They depart between late March and early May (Tree 1979, 1985, Underhill 1997).

During the non-breeding season Greenshanks are usually dispersed, making them difficult to catch in large numbers (Tree 1979). Several papers provide general information on this species' moult patterns at their migration stopover sites in the Dutch Wadden Sea (Boere 1976) or at their non-breeding grounds in Morocco (Pienkowski *et al.* 1976), Kenya (Pearson 1974) and southern Africa (Tree 1974, 1979, 1985, Summers & Waltner 1979). Cramp & Simmons (1983), Ginn & Melvile (1983) and Meissner (2008) have summarised the available information. These studies conclude that most Greenshanks do not moult their primaries in their first year of life, though birds at the Dutch Wadden Sea and Kenya occasionally replace one or two outer primaries (Boere 1976, Pearson 1974). However, in southern Africa some first-year birds (hereafter referred to as "immatures") moult two to four outer primaries (Tree 1974, 1979, Summers & Waltner 1979). Greenshanks in their second year of life (referred to as "sub-adults") replace all primaries, but their moult timing varies in different areas (Cramp & Simmons 1983). Adult Greenshanks show a variety of strategies for post-breeding primary moult. Most populations begin their primary moult before they reach their non-breeding grounds: some start to moult in June at the breeding grounds, replace at least a few primaries at their migration stopover sites between July and October, suspend their moult for the next stage of movement and complete it at the non-breeding grounds. Others moult their primaries only at their final non-breeding destinations (Pearson 1974, Tree 1974, Boere 1976, Pienkowski *et al.* 1976, Cramp & Simmons 1983, Ginn & Melville 1983).

Since these studies, more data on Greenshanks' moult and body mass in southern Africa have become available and the methods of analysing moult have advanced greatly (e.g. Underhill & Zucchini 1988, Underhill *et al.* 1990, Serra & Underhill 2006, Remisiewicz 2011, Erni *et al.* 2013). We re-evaluated data on primary moult of Greenshanks in southern Africa with the use of moult models (Underhill & Zucchini 1988, Underhill *et al.* 1990) to refine the knowledge of the species' patterns of moult and to relate it with pre-migratory fattening. We aimed to identify geographical patterns in primary moult and pre-migratory fattening of different age classes of Greenshanks within their southernmost African non-breeding grounds.

METHODS

We analysed the primary moult formulae and the body mass of 356 Greenshanks collected during irregular mist-netting at wetlands in three regions: in Zimbabwe by AJT in 1972–1994, at the east coast of South Africa by AJT in 1968–1998 and at the west coast by the Western Cape Wader Study Group in 1970–1988 (Figure 1). We used original data on Greenshank moult and body mass collected until 1978 (Tree 1974, 1979, 1985, Summers & Waltner 1979), but augmented it with later material. The ringing sites in Zimbabwe (Figure 1) were inland eutrophic lakes, small dams, ponds and sewage works around Harare (Tree 1979, 1985). On the east coast, Greenshanks were caught at coastal tidal lagoons, mudflats and estuaries between Port Alfred and Port Elizabeth (Figure 1). On the west coast they were trapped at tidal coastal lagoons, at estuaries between the Berg River and Betty's Bay, and at coastal lakes and pans (Figure 1). The catching sites in Zimbabwe and on the east coast lie in the summer rainfall area, with rains between September and March, but on the west coast these months, when most waders occur, are the dry season (Allan *et al.* 1997). Descriptions of these ringing sites and the capture methods are provided by Tree (1979, 1985) and Summers & Waltner (1979).
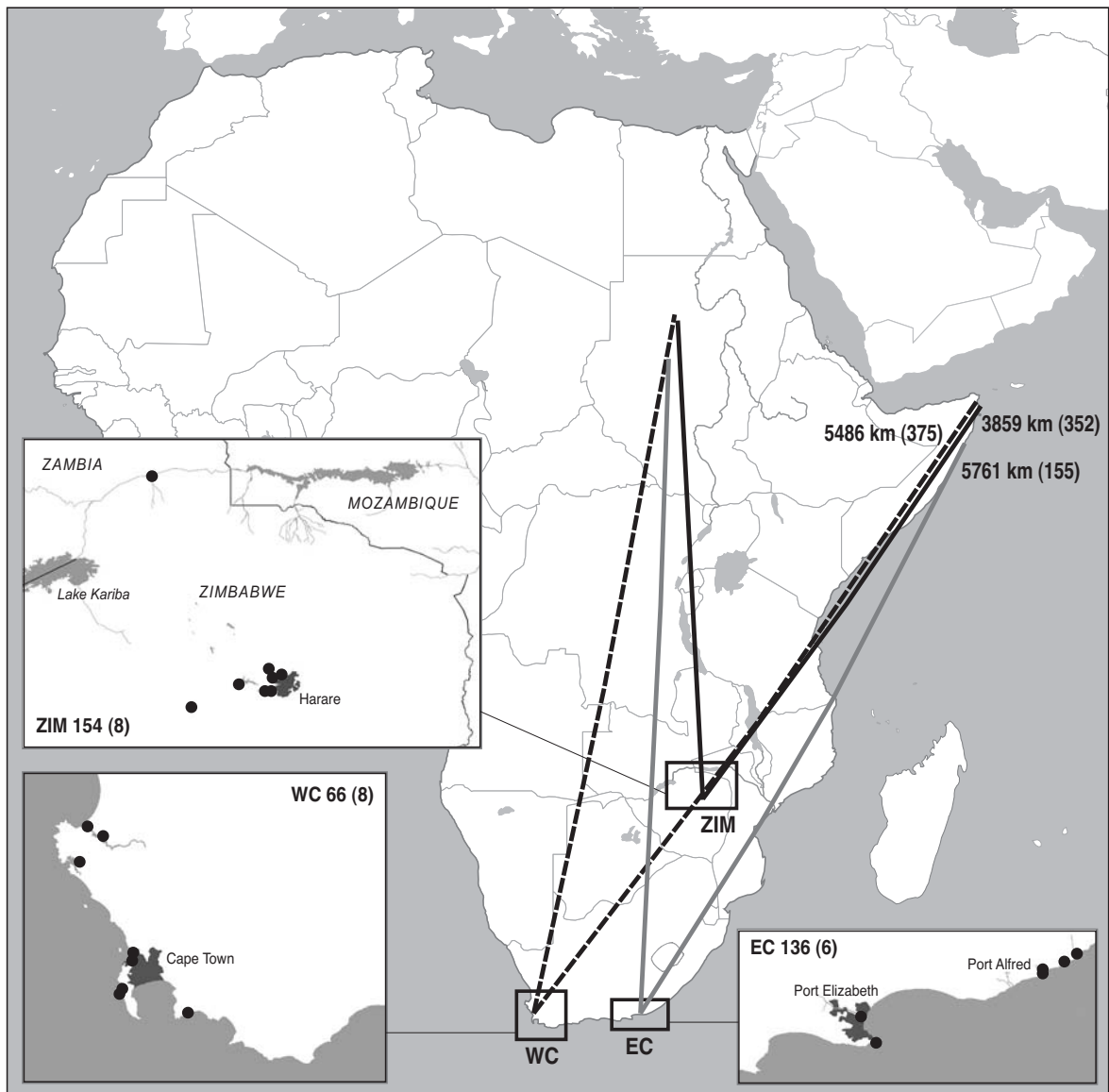
Figure 1. Greenshank capture sites in southern Africa in 1968–1998 grouped in geographical regions: ZIM = Zimbabwe, EC = east coast, WC = west coast. Numbers of ringed Greenshanks and of ringing sites (in brackets) shown in each region. Lines and values in km show mean (SD) potential flight ranges estimated cautiously according to Davidson (1984) for the heaviest 20% adults departing to the north-east from each region.

Greenshanks were aged by their plumage (Tree 1974, 1979, Prater *et al.* 1977) as immatures (birds in their first year of life, 2–12 months old, between arrival in September–October until 31 May of the following year), sub-adults (birds 13–18 months old, from 1 June to the end of their primary moult in December of their second year of life), and adults (birds older than 18 months and unidentified sub-adults). Immatures and sub-adults could be identified by the juvenile-type

upper wing coverts and tertials, which they might retain until 12 months, or by the contrast between two generations of primaries: the new outer primaries replaced in a partial moult and the old inner primaries (Prater *et al.* 1977).

At capture, wing length was measured to 1 mm with a ruler. The birds were weighed with a Pesola spring balance to 0.5 g accuracy in Zimbabwe and at the east coast, and to 1 g at the west coast, so we

rounded the body mass to 1 g in analyses. We presented the seasonal trends in body mass using a Lowess-regression curve, following Serra *et al.* (1999). To compare body mass between the regions, we standardised body mass for a bird's size with ANCOVA as in e.g. Battley & Piersma (2005). We used the length of the "worn" wing (the longest primary P10 old) before primary moult, and of the "fresh" wing (the longest primary P10 new) for birds after moult.

We used the standard moult formulae, where the moult stage of each of ten primaries was recorded as a score between 0 and 5 (Ashmole 1962, Ginn & Melville 1983). We used the records at an individual's first capture to estimate the Greenshanks' moult timing and trends in the body mass. The date of capture was calculated as the number of days from 1 June. Data from all years were combined because of the small samples from separate years, which did not allow us to account for year-to-year variation in moult timing. In each region 0–30 birds were caught per season from 1 June to 31 May of the following year. Catches overlapped in 23 seasons (1972/73–1993/94) in Zimbabwe and the east coast, and in 19 seasons (1970/71–1987/88) in all three regions. To check how different catching years might affect moult timing, we compared the estimates of adults' moult in three regions in 1970/71–1987/88 with those for all available seasons.

We calculated the Proportion of Feather Mass Grown (PFMG; Underhill & Summers 1993), which served as a moult index, from each bird's moult formula using the mean relative mass of each primary for Greenshank from Underhill & Joubert (1995). We used this index in the model for the Type-2 moult data (Underhill & Zucchini 1988) to estimate timing of adults' and sub-adults' continuous moult of the entire primary tract, and of each primary P5–P10 separately in adults from Zimbabwe and the west coast. We compared the mean daily growth rates (PFMG/day) of P5–P10 (samples of P1–P4 and for the east coast were too small) between Zimbabwe and the west coast using a Z-test. The application of these methods is presented in Remisiewicz *et al.* (2009, 2010a, 2010b). To estimate the primary moult timing we used the "moult"-package (Erni *et al.* 2013) for software R (version 2.11.1; R Development Core Team 2009).

To compare the moult timing of Greenshanks in the three regions of southern Africa (Figure 1) and to determine the differences between adults and sub-adults, our models used region and age as covariates for each of three moult parameters (moult starting date, its SD and moult duration), or for one or two of these parameters, while the remaining parameters were assumed constant for the whole sample combined. We compared these moult models including covariates with the constant models where no covariates were used, using the Akaike Information Criterion (AIC). The best-fitted model had the lowest AIC of all models, and the highest AIC weight (wAIC; Burnham & Anderson 1998). Additionally, we used the likelihood ratio test (Burnham & Anderson 1998) to test the null hypothesis that moult parameters were the same for all birds combined against the best moult model with covariates.

For 25% of the birds with the lowest body mass and "fresh" wings from all three regions combined ($n = 26$) we calculated the regression equation between body mass and wing length:

$$LBM = -47.78 + 1.09 \times WL,$$
$$(F_{1,24} = 4.84, P = 0.038, n = 26, r^2 = 0.13),$$

where LBM is lean body mass (g) and WL is wing length (mm) of these lean individuals. We used this equation to predict a lean body mass of a bird with a specific wing length to calculate the individual potential flight ranges of Greenshanks departing from the three regions of southern Africa based on their body mass. For that we used the formula by Davidson (1984):

$$R = 95.447 \times S \times (BM^{0.302} - LBM^{0.302}),$$

where R is the estimated flight range (km), S is the flight speed (km/h), BM is the birds' actual body mass (g), and LBM is the lean body mass (g) predicted for the birds' wing length. We used Davidson's (1984) formula because it accounts for the loss of the birds' body mass during flight. This formula usually gives an intermediate estimate of flight range compared with formulae proposed by other authors (Pennycuick 1975, Summers & Waltner 1979, Castro & Myers 1989). We used a flight speed of $S = 70$ km/h, an intermediate value of those given for mid- and large-sized waders (Summers & Waltner 1979, Klaassen *et al.* 2011, Gill *et al.* 2012, Johnson *et al.* 2012). We calculated individual fat loads by subtracting the bird's predicted lean body mass from its actual body mass. We estimated the mean flight ranges for the 20% of adults with the highest fat load in each region.

RESULTS

Moult patterns of Greenshanks in three regions of southern Africa

PRIMARY MOULT OF ADULTS

The earliest adult Greenshank was caught after arrival in southern Africa on 29 July. The numbers of adults caught at the study sites increased in September–October and decreased in late March–April (Figure 2). The earliest adult with moulting primaries was caught on 31 July 1978 at the east coast (Figure 2). Of the 226 adults that we examined, two with moult suspended after one or two inner primaries had been replaced were caught at the east coast on 17 September 1983 and 31 August 1985 (Table 1, Figure 2). Two adults caught in Zimbabwe, on 18 October 1975 and 1 December 1975, had suspended moult after five and eight inner primaries had been renewed. One adult caught at the west coast on 7 January 1972 had suspended moult after eight primaries had been

replaced (Table 1, Figure 2). Two birds with atypical moult patterns, suggesting unidentified sub-adults, we excluded as outliers when modelling continuous moult. The first, caught on 11 January 1986 at the east coast, had a moult formula of 5555543554, which indicated the moult of primaries from P1 outwards before the previous moult sequence had been completed. The second had a moult formula of 5555555554 on 14 April 1989 at the west coast, which showed an outstandingly late moult (Figure 2). Birds with suspended moult at capture constituted 5% of all caught adults. Thus we assumed a small potential bias in our estimates of moult timing caused by undetected birds that had suspended moult, then resumed or completed it, thereby becoming indistinguishable from those that underwent continuous moult.

Most (95%) adults caught while moulting showed a continuous moult of all primaries (Table 1) from P1 outwards to P10. To estimate their moult timing we combined these adults with those that had not started
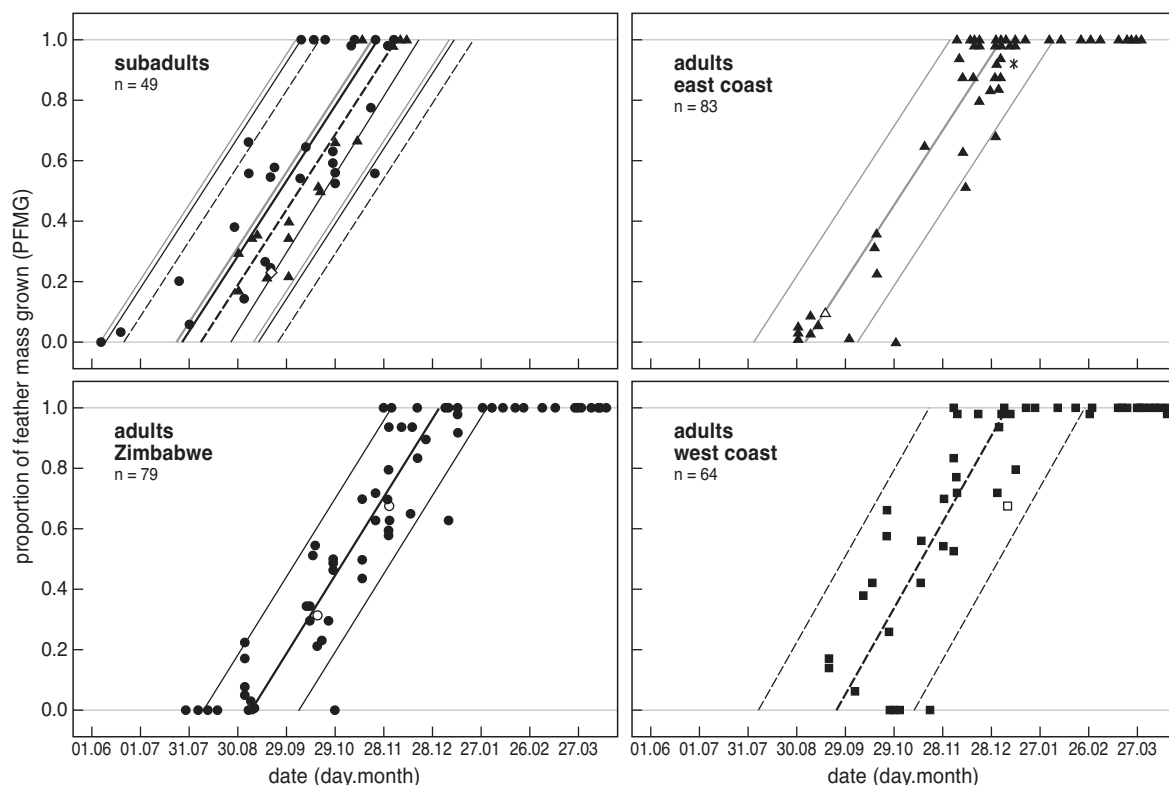
Figure 2. Temporal distribution of the Proportion of Feather Mass Grown (PFMG) of sub-adult and adult Greenshanks caught in three regions of southern Africa (Figure 1) in 1968–1998. Birds caught in Zimbabwe = circles; at east coast = triangles; at west coast = squares; birds in continuous complete moult = black symbols; in suspended moult = white symbols; with partial moult = white rhombus, a bird with "other" sequence of moult = an asterisk. Thick lines = the mean course of the complete primary moult, thin lines = 95% PI (Table 3); Zimbabwe = continuous black lines, east coast = continuous grey lines, west coast = dashed lines.

to moult and with those that had finished, a sample of 220 birds (Table 1). We estimated moult timing of all 10 primaries for adult Greenshanks caught in Zimbabwe, the east coast and the west coast (Figure 1) using moult models with region as a covariate. The best model, where region was a covariate that had an effect on moult starting date, its SD, and moult duration (model 1 in Table 2), was significantly better fitted to the data than the model where data from all three regions were combined (model 5 in Table 2; log-likelihood ratio test: $\chi^2_{(6)} = 19.05$, $P < 0.01$). This confirmed that the differences in moult timing between the three regions were significant. On average, moult started earliest at the east coast (4 September), three days later in Zimbabwe, and 19 days later at the west coast (Table 3). The 95% prediction interval when adults ought to start moult was 72–143 days, from early July or August to late November, depending on the region (Table 3, Figure 2). The mean duration of primary moult was between 122 days (east coast) and 105 days (west coast; Table 3). Moult was completed on average between 31 December and 6 January (Table 3, Figure 2). In 1970/71–1987/88 moult started in Zimbabwe (1 September, SD = 19, n = 62) and at the east coast (4 September, SD = 16, n = 50) on average 11–14 days earlier than at the west coast (15 September, SD = 36, n = 61; $\chi^2_{(6)} = 22.36$, $P = 0.001$), a pattern

similar to all seasons combined. However, because of small samples for 1970/71–1987/88, at the edge of the moult model's performance, we use hereafter moult timing estimated for all available seasons as the most reliable proxy of the Greenshank's general moult pattern. Adults moulted simultaneously two primaries (median; range 1–4), and it was the same in each region when each of primaries P1–P5 were growing (K-W ANOVA: for each primary $P > 0.46$; for P6–P10 small samples). Daily growth rates of P5–P7 were slower in Zimbabwe than at the west coast, but P8–P10 were grown at a similar rate (Table 4).

MOULT PATTERNS OF SUB-ADULTS
Few sub-adults were caught between June and August, but their numbers increased from the beginning of September up to December, when they become indistinguishable from adults (Figure 2). The earlier immature-type partial moult could still be recognised in six of 49 sub-adults caught between June and December. Three of these birds had replaced two outer primaries and three had replaced three outer primaries. Ten sub-adults caught in June–November in Zimbabwe and at the east coast (Table 1) showed a complete moult of primaries from P1 outwards after the previous partial moult. We combined scores showing the new moult sequence of these 10 birds, with the scores for 27 sub-

Table 1. Numbers of Greenshanks of different ages caught at different stages of moult in 1968–1998 in three regions of southern Africa (see Figure 1). The numbers of sub-adults in parentheses show the birds in which complete moult followed an earlier partial moult.

| Age/Region | Moult not started | Moult in progress | | | | Moult completed | Total |
		Partial	Complete (after partial)	Suspended	Other		
Immatures							
Zimbabwe	36	6	1			2	45
East coast	30	4		1		1	36
Total	**66**	**10**	**1**	**1**		**3**	**81**
Subadults							
Zimbabwe		1	22 (8)	1		6	30
East coast			13 (3)			4	17
West coast			2 (0)				2
Total		**1**	**37 (10)**	**1**		**10**	**49**
Adults							
Zimbabwe	8		40	2		29	79
East coast	1		38	2	1	41	83
West coast	5		26	1		32	64
Total	**14**		**104**	**5**	**1**	**102**	**226**
Grand total	**80**	**11**	**142 (10)**	**7**	**1**	**115**	**356**

adults caught during complete moult that did not show earlier partial moult, and 10 birds that had finished a complete moult, therefore using 47 birds to estimate the timing of the complete primary moult in sub-adults (Table 1). Two sub-adults caught in Zimbabwe, one that showed only partial moult and another that had suspended moult after it had replaced four inner primaries, were excluded from these analyses (Table 1, Figure 2). These outliers constituted 2% of all sub-adults, so we assumed a negligible bias in our estimates of continuous moult caused by undetected birds that had suspended moult.

Of the moult models that combined the effect of age (adults *vs* sub-adults) and region (Zimbabwe, east coast and west coast), the best fitted model (wAIC = 0.55) showed the effect of age and region on moult starting date when moult duration and SD of moult starting date were assumed to be constant. This model was significantly better than the model with no covariates (wAIC = 0) where all data were treated as one uniform sample (log-likelihood ratio test: $\chi^2_{(3)}$ = 72.35, $P < 0.0001$). The complete moult of sub-adults started on average 40 days earlier than adults in all three regions (Table 3, Figure 2). This moult started on

Table 2. Moult models used to determine the effect of geographical region (see Figure 1) on moult parameters estimated for all ten primaries in adult Greenshanks caught in southern Africa 1968–1998. The model ranking by Akaike's Information Criteria (AIC), *df* is the number of parameters in a model, ΔAIC gives the difference in AIC from the best model, the Akaike weights (wAIC) assess the relative support that a given model has from the data compared with the other models. Best fitted model in bold face.

Model no	Covariate	Parameters affected by the covariate	Parameters assumed constant	*df*	AIC	_AIC	wAIC
1	**region**	**moult start date SD of start date moult duration**	**none**	**9**	**35.3**	**0.0**	**0.7454**
2	region	moult start date moult duration	SD of start date	7	38.3	3.0	0.1693
3	region	moult start date	SD of start date moult duration	5	40.4	5.1	0.0590
4	region	none	moult start date SD of start date moult duration	3	42.4	7.0	0.0220
5	none	moult duration	moult start date SD	5	45.6	10.3	0.0044

Table 3. Moult parameters estimated for all ten primaries for adult Greenshanks in 1968–1998 in three regions of southern Africa (see Figure 1). 95% PI = 95% prediction interval for the moult start date (mean starting date + 1.96 × SD of start date). For sub-adults common moult duration and SD of moult start date were assumed to reduce the number of estimated parameters. PFMG/day = the estimated daily rate of the primary feather material growth (PFMG), calculated from the moult durations.

Region	Moult parameters					Sample sizes			
	Mean start date (SE)	Duration in days (SE)	SD of start date (SE)	95% PI	End date (SE)	Not in moult	In moult	Moult ended	PFMG /day (%)
Adults									
Zimbabwe	7 Sep (6.9)	115 (6.9)	18.4 (6.5)	2 Aug–13 Oct	31 Dec (4.7)	8	40	29	0.87
East coast	4 Sep (7.6)	122 (10.5)	20.0 (6.8)	27 Jul–13 Oct	3 Jan (3.3)	1	38	41	0.82
West coast	23 Sep (12.1)	105 (15.1)	29.8 (11.8)	5 Jul–25 Oct	6 Jan (6.9)	5	25	32	0.95
Sub-adults									
Zimbabwe	29 Jul (4.5)			23 Jun–3 Sep	23 Nov (9.5)	1	19	6	
East coast	25 Jul (4.5)	117 (5.1)	24.3 (6.3)	19 Jun–30 Aug	19 Nov (9.5)	0	13	4	0.86
West coast	7 Aug (4.5)			2 Jul–12 Sep	2 Dec (9.5)	0	2	0	

average from 25 July (east coast) to 7 August (west coast), with a common moult duration for all groups estimated at 117 days. Moult ended between 19 November (east coast) and 2 December (west coast) on average, 13 days apart between the regions (Table 3, Figure 2).

MOULT PATTERNS OF IMMATURES

The earliest immature Greenshanks were caught on 3 October in Zimbabwe and on 26 October at the east coast (Figure 3). At the west coast small numbers of immatures were caught in mid-December–April. Numbers decreased in April and May, and a few remained through the austral winter (Figure 3), when they entered their second year of life and were classified as sub-adults (Figure 2). Sixty-six (81%) of 81 immatures caught in Zimbabwe and at the east coast did not show any primary moult between 3 October and 21 April (Table 1, Figure 3). Thirteen birds (19%) showed partial moult of one to five outer primaries between December and May (Figure 3). The most common patterns were the replacement of three outer primaries (54% of moulters), starting from P8 outwards, or of four primaries (23%), starting from P7. Four immatures began moult of four or five primaries in December and January. One immature in March was growing the first (P8) of three primaries to be replaced, another was growing only P10 in May. Three imma-
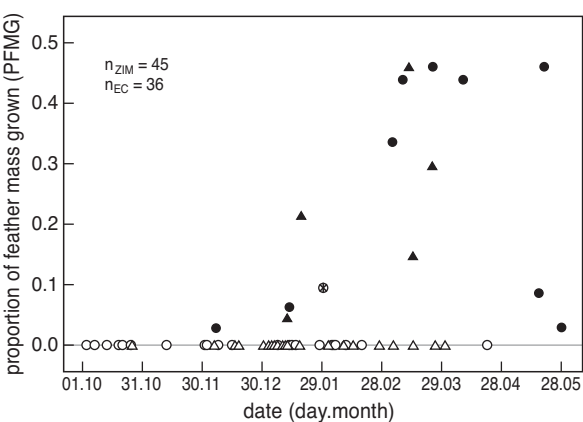

Figure 3. Temporal distribution of the Proportion Feather Mass Grown (PFMG) of immature Greenshanks caught in Zimbabwe (circles) and at the east coast (triangles) in 1968–1998. Birds with no moult at capture = white symbols; birds showing partial moult of a few outer primaries = black symbols; bird with suspended moult = asterisk.

tures that had finished a partial moult were caught in March–May (Figure 3). One bird caught at the east coast on 30 January 1994 had suspended its moult after replacing two inner primaries (Figure 3). Another immature on 29 May 1973 in Zimbabwe was growing P1, suggesting the beginning of a complete primary moult of the sub-adult type.

Table 4. Moult parameters of separate primaries for adult Greenshanks caught in 1968–1998 in Zimbabwe and at the west coast. *P*-level of significance in *Z*-test for comparison of mean daily growth rates (PFMG/day) between the two regions. Remaining table headings as in Table 3.

| Primary | Region | Moult parameters | | | | | % PFMG /day (SD) | *P* |
		Mean start date (SE)	Duration in days (SE)	SD of start date (SE)	End date (SE)	*n*		
P5	Zimbabwe	29 Sep (5.5)	24 (6.8)	16 (7.2)	22 Oct (5.7)	77	0.37 (0.08)	<0.0001
	West coast	16 Oct (10.1)	9 (6.4)	29 (16.6)	25 Oct (12.4)	61	0.96 (0.39)	
P6	Zimbabwe	13 Oct (5.3)	14 (6.0)	13 (7.3)	26 Oct (4.7)	77	0.72 (0.21)	<0.0001
	West coast	27 Oct (6.8)	10 (5.8)	20 (10.7)	7 Nov (9.3)	61	1.00 (0.36)	
P7	Zimbabwe	22 Oct (7.6)	24 (8.7)	16 (5.6)	14 Nov (7.5)	77	0.51 (0.14)	<0.0001
	West coast	1 Nov (6.0)	18 (6.5)	18 (8.9)	19 Nov (5.5)	61	0.60 (0.19)	
P8	Zimbabwe	7 Nov (5.6)	28 (6.9)	20 (8.6)	3 Dec (5.1)	77	0.50 (0.10)	0.11
	West coast	11 Nov (6.1)	26 (7.3)	20 (9.2)	7 Dec (5.7)	61	0.53 (0.12)	
P9	Zimbabwe	27 Nov (5.9)	23 (6.8)	23 (10.3)	19 Dec (5.8)	77	0.67 (0.15)	0.46
	West coast	28 Nov (5.6)	22 (7.0)	17 (8.1)	20 Dec (5.5)	61	0.69 (0.17)	
P10	Zimbabwe	8 Dec (5.7)	26 (7.3)	22 (9.8)	2 Jan (6.2)	77	0.66 (0.15)	0.35
	West coast	9 Dec (8.7)	42 (10.0)	34 (13.6)	20 Jan (6.7)	61	0.41 (0.08)	

Trends in Greenshank body mass in relation to primary moult

BODY SIZE, BODY MASS, AND MOULT IN ADULTS

Adults' body mass in all regions showed a constant trend during moult and increased from about 13–19 January, after the first birds completed moult (Figure 4). In each region a few adults that had completed moult were lighter than 170 g between February and April (Figure 4). Adults caught in Zimbabwe were smaller than at both coastal regions (Table 5). Thus, we standardised the body mass for the mean "worn" or "fresh" wing length, depending on the birds' moult status, to enable comparisons between the regions. During the period of the constant body mass trend (before 13–19 January, Figure 4) birds in Zimbabwe (mean = 174.5 g, SE = 3.7 g, n = 32) were on average 4 g lighter than at the east coast (mean = 178.6 g, SE = 4.8 g, n = 14) and 14 g lighter than at the west coast (mean = 188.4 g, SE = 4.1 g, n = 21), comparing the body mass standardised for the mean "worn" wing (ANCOVA, model of different slopes: region: $F_{2,61}$ = 5.00, P = 0.01, region × wing: $F_{2,61}$ = 3.42, P = 0.02). During the period of the body mass increase, birds in Zimbabwe (mean = 214.5 g, SE = 8.4 g, n =16) were on average 44 g lighter than at the east coast (mean = 260.0 g, SE = 6.7 g, n = 23) and 20 g lighter than at the west coast (mean = 232.7 g, SE = 6.6 g, n = 23), comparing the body mass standardised for the mean "fresh" wing (ANCOVA, model of similar slopes: region: $F_{2,72}$ = 5.05, P = 0.009, wing: $F_{1,71}$ = 8.31, P = 0.05).

Figure 4. Body mass of adult Greenshanks caught in three regions of southern Africa in 1968–1998. Crosses = birds that had not yet started moult, black symbols = birds during continuous moult; open symbols = birds that completed moult; asterisks = adults that suspended moult. The lines represent Lowess smoothed curves, continuous lines show trends for most birds, excluding individuals with a body mass below the median after 1 February, for which the trend is shown by dashed lines. Arrows indicate approximate dates when the body mass increase began.
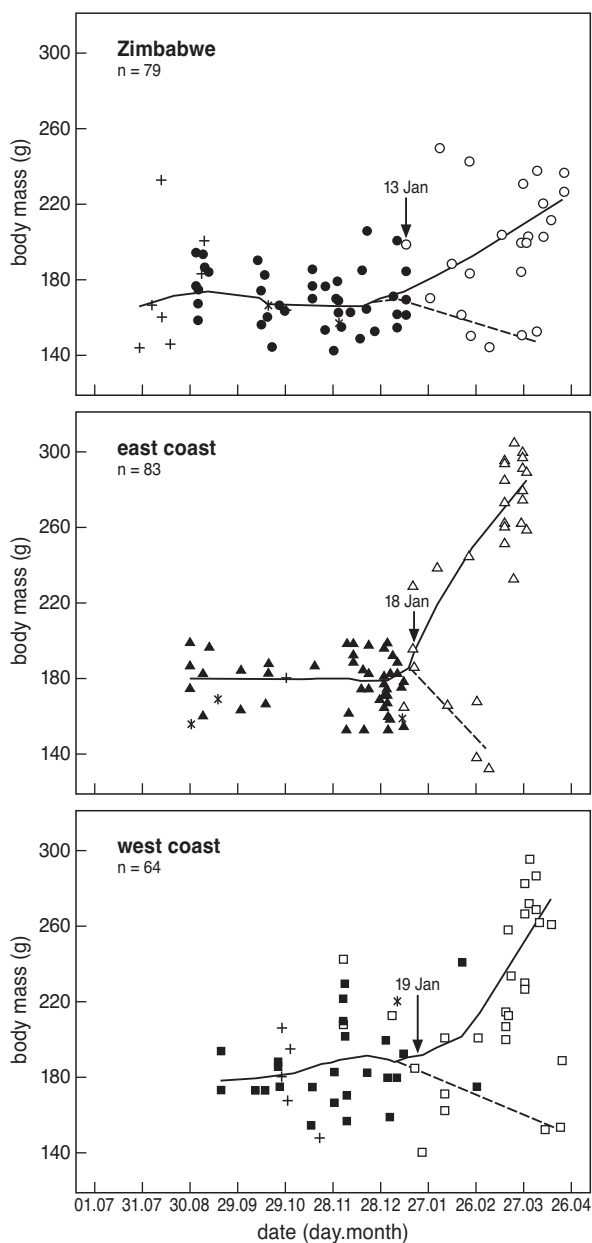
Table 5. Comparison of wing length among adult Greenshanks caught in 1968–1998 in the three regions of southern Africa. *F*-results of ANOVA, *P*-level of significance.

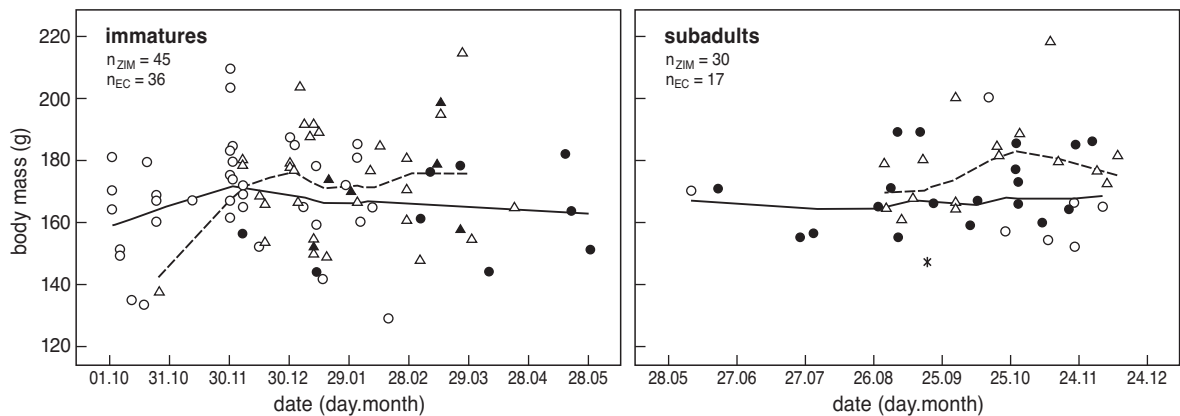| Measurement	Region	n	Mean (SD)	Range	Result of ANOVA
"Worn" wing length (mm)	Zimbabwe	32	190.1 (4.1)	178 – 197	$F_{2,66}$ = 5.78
(P10 scored as 0)	East coast	15	193.8 (5.2)	187 – 204	P = 0.005
	West coast	22	194.0 (5.1)	185 – 205	
"Fresh" wing length (mm)	Zimbabwe	28	191.8 (5.4)	180 – 201	$F_{2,94}$ = 2.67
(P10 scored as 1)	East coast	39	195.1 (6.2)	181 – 207	P = 0.075
	West coast	30	194.5 (6.3)	178 – 206	

Figure 5. Body mass of immature and sub-adult Greenshanks in Zimbabwe (circles) and at the east coast (triangles) in 1968–1998. Open symbols = birds with no signs of moult at capture; black symbols = birds in moult; asterisk = birds with suspended moult. Lowess smoothed curves fitted to show the body mass trends: continuous line = Zimbabwe; dotted line = east coast.

POTENTIAL FLIGHT RANGES IN ADULTS

We estimated mean flight ranges for the 20% of adults with the highest fat load caught in each region. The mean departure fat loads of these birds were 76 g (SD = 8.1 g, n = 6) in Zimbabwe, 116 g (SD = 8.7 g, n = 6) at the west coast and 125 g (SD = 1.5 g, n = 6) at the east coast. The mean potential flight ranges estimated using these fat loads were from 3859 km (Zimbabwe) to 5761 km (east coast; Figure 1).

BODY MASS AND MOULT OF IMMATURES AND SUB-ADULTS

Body mass of immature Greenshanks in Zimbabwe increased slightly between October and November, then remained stable for the rest of their stay. The trends were similar at the east coast (Figure 5). Body mass of immatures before and during moult did not differ, in Zimbabwe (Mann-Whitney test: Z = 1.11, P = 0.27) and at the east coast (Z = 0.27, P = 0.78). A few immatures caught at the end of March at the east coast had a body mass of 195–215 g, 19–30 g higher than the trend for this period (Figure 5). Immatures did not differ in the length of "worn" wing length between Zimbabwe (mean = 187.9 mm, SD = 4.5, n = 40) and the east coast (mean = 188.6 mm, SD = 3.5, n = 28; t-test: t_{61} = 0.66, P = 0.51), so we compared their actual body mass. In Zimbabwe immatures' median body mass was on average 9 g lower than at the east coast (Figure 5), but this difference was not significant (M-W test: Z = 1.81, P = 0.07).

Sub-adults showed a nearly constant trend in body mass between June and December in Zimbabwe and at the east coast (Figure 5). In Zimbabwe the body mass of sub-adults did not differ between birds in or out of moult (M-W test: Z = 0.87, P = 0.38; Figure 5). Sub-adults did not differ significantly in the length of "worn" wing between Zimbabwe (mean = 186.6 mm, SD = 4.6, n = 17) and the east coast (mean = 191.3 mm, SD = 6.6, n = 6; M-W test: Z = –1.61, P = 0.11), so we compared their actual body mass. Sub-adults were on average 12 g lighter in Zimbabwe than at the east coast (Z = 2.66, P = 0.008; Figure 5). Sub-adults and adults did not differ in body mass when they co-occurred (29 July–11 December), in Zimbabwe (M-W test: Z = 0.17, P = 0.86) and at the east coast (Z = 0.64, P = 0.52).

DISCUSSION

Moult patterns of Greenshank at their southernmost non-breeding grounds

PATTERNS OF MOULT IN ADULTS

We analyse patterns of moult in the southern part of the Greenshank's non-breeding range (Cramp & Simmons 1983, Scott 2009). These birds migrate 9000–12,500 km from their breeding grounds to southern Africa, three times farther than to the species' closest non-breeding grounds in western Europe and the north African coast. This probably explains why the moult patterns of Greenshanks in southern Africa differ from those at these northern areas. At the Wadden Sea, a stopover site 800–2300 km from the breeding grounds, adult Greenshanks that arrived in July had an advanced but suspended primary moult; then resumed moult at the site (Boere 1976). At a stopover and final

staging site in Morocco (4500–6500 km from the breeding grounds), a minority of adults arriving in July had suspended moult and then resumed it; most commenced moult and replaced all primaries after arrival (Pienkowski *et al.* 1976). In Kenya (5500–8000 km from the breeding grounds) most adults arrived with primary moult suspended in August and resumed it there in September–January (Pearson 1974). In southern Africa the first adult Greenshanks arrive in late July and their numbers build up until September (Tree 1979, 1985, Underhill 1997). Moult starts from August onwards (Table 3), soon after their arrival. This implies that the migrants to southern Africa commence primary moult only after migration. This corresponds with observations of Greenshanks from southern non-breeding grounds in India and Indonesia, where adults moult their primaries after arrival, early August–early January (Cramp & Simmons 1983).

Adults in Morocco moult over 109 days in July–late September (M. Remisiewicz unpubl. data, based on Pienkowski *et al.* 1976), in southern Africa over 105–122 days in September–January (Table 3). The earlier moult at northern locations might be caused by these Greenshanks' need to finish moulting before they continue their southwards migration (Boere 1976). Greenshanks at the Wadden Sea and in Morocco use the East Atlantic Flyway, hence they might time their moult differently to the populations that visit eastern and southern Africa, which use a more south-easterly migratory route (Summers & Waltner 1979, Scott 2009). The primary moult of adults caught in Kenya takes two–three months (Pearson 1974), as in southern Africa, though most Greenshanks arrive in Kenya with advanced primary moult.

COMPARISON OF ADULT AND SUB-ADULT MOULT TIMING
Sub-adult Greenshanks moulted their primaries on average 40 days before adults (Table 3), in contrast to sub-adult Wood Sandpipers *Tringa glareola* that moult two weeks earlier than adults in southern Africa (Remisiewicz *et al.* 2010b). However, many Greenshanks remain in southern Africa until they are two years old (Velásquez *et al.* 1991, Summers *et al.* 1995, Underhill 1997), a rare pattern in Wood Sandpipers (Remisiewicz *et al.* 2010a, 2010b), so the sub-adult Greenshanks are able to start their primary moult before the adults. This is supported by immatures and sub-adults undergoing a complete adult-type moult between May and early July (Figures 2 and 3). In Morocco a small group of Greenshanks that had finished primary moult in August, ahead of most adults, was believed to be sub-adults that had over-

stayed in North Africa (Pienkowski *et al.* 1976). In southern Africa, sub-adults moulted at the same rate as adults and thus finished earlier, as in Wood Sandpipers (Remisiewicz *et al.* 2010b). Earlier primary moult might allow sub-adults to avoid competition for food with adults during this energy-demanding process, as Serra *et al.* (1999) suggested in Grey Plovers *Pluvialis squatarola*. There might also be benefits to moulting earlier, e.g. better feeding conditions, which adults cannot exploit because they are able to moult only after arrival. Sub-adults have more time after moult than adults to accumulate fat reserves before departure, which might improve the sub-adults' chances of completing their first return migration.

IMMATURES' MOULT PATTERNS
About 20% of immature Greenshanks in southern Africa replaced one to five outer primaries, usually three or four. In Kenya immatures occasionally moult only one or two outer primaries (Pearson 1974), as do Greenshanks at the Dutch Wadden Sea (Boere 1976). Most immatures in Indonesia replace three to six outer primaries (Cramp & Simmons 1983). This, combined with our results, suggests that the farther south the higher the proportion of immature Greenshanks that undertake a partial moult and the more primaries they replace. Immatures that replaced four or five outer primaries in southern Africa had begun their moult in December–January, but those that replaced one to three primaries started in March–May, close to departure. Similarly, in Indonesia immatures undertake a partial moult in early April–late May (Cramp & Simmons 1983). In Kenya immatures replace one or two outer primaries in February–March, also close to departure (Pearson 1974). These birds might be the part of the population that returns to the breeding grounds in their first year of life. Both tendencies – the higher proportion of immatures undertaking partial moult the farther south and the fewer primaries replaced by birds that start moult later – have been shown in immature Wood Sandpipers in southern Africa (Remisiewicz *et al.* 2010a, Remisiewicz 2011). Heavy Wood Sandpipers start early and moult five or six primaries, but close to the departure time the remaining immatures replace at least 2–3 outer primaries, irrespective of their body mass (Remisiewicz *et al.* 2010a). In both species a looming departure might be a constraint on the end of moult, but the start of partial moult and the number of primaries to be replaced might reflect strategies related to an individual's condition (Remisiewicz *et al.* 2010a).

MOULT TIMING RELATED TO ARRIVAL AND DEPARTURE IN SOUTHERN AFRICA

Most Greenshanks that visit southern Africa probably originate from similar breeding grounds and migrate along the East African Flyway, as suggested by ringing recoveries (Tree 1985, Underhill *et al.* 1999, Scott 2009). But the smaller average size of adult Greenshanks in Zimbabwe than at the coast might reflect different proportions of birds from different breeding areas, given that birds breeding in Scandinavia and eastern Russia are smaller than those from Central Russia (Prater *et al.* 1977). The presence of early non-moulters in Zimbabwe, but few non-moulters and birds in early moult in August and September at the west coast (Figure 2), suggest that some adults at the west coast begin their moult inland. However, in October and November pre-moult adults arrived in both coastal regions (Figure 2). Ringing recoveries show that some Greenshanks move between inland and coastal sites (Tree 1979, Underhill *et al.* 1999). We combined data from coastal and inland regions to compensate for any potential bias in our results caused by the small sample of early non-moulters at the coastal regions (Table 2, Figure 2).

The numbers of Greenshanks increase in July and August across southern Africa, and adults arrive until late September (Tree 1979, 1985, Underhill 1997). The 19-day later average onset of adult moult at the west coast than in Zimbabwe might reflect this sequence of Greenshank arrivals. Similar moult onsets in Zimbabwe and at the east coast might reflect the simultaneous arrival of Greenshanks across a broad front from the northeast, suggested by Tree (1979) and Scott (2009). The numbers of Greenshanks decrease in all three regions from February and March, which might reflect local movements (Tree 1979). Most Greenshanks depart the east coast between the end of March and the beginning of April, in Zimbabwe a few weeks later in April (Tree 1979, 1985; Martin & Baird 1987, Underhill 1997).

Adults at the west coast moulted up to 17 days faster than in the other regions, meaning Greenshanks synchronised the end of moult across all three regions within a week at the turn of the year(Table 3). This left adult Greenshanks three to four months, and sub-adults up to five months, between the end of primary moult and their departure, a time when they replace secondaries, tertials, tail and body feathers (at least partly) into breeding plumage and fatten up before migration. Greenshanks moulted faster at the west coast than in Zimbabwe by growing at least P5–P7 at a faster rate (Table 4), but not by growing more primaries simultaneously. In contrast, Curlew Sandpipers Calidris ferrug-

inea grew more primaries simultaneously, and some faster, to achieve a shorter moult in Kenya than in India (Barshep *et al.* 2013). However, growing feathers fast comes at the cost of their durability and resistance to abrasion (e.g. Swaddle *et al.* 1996, Dawson *et al.* 2000, Serra 2001). So Greenshanks moulting at the west coast might produce lower-quality inner primaries than birds in Zimbabwe. However, P8–P10 grew at a similar rate in both regions (Table 4) and Greenshanks possibly do not compromise on the quality of these outermost primaries, which are crucial for flight (Videler 2005).

The moult flexibility we have shown in Greenshanks at the population level allows those in the extreme south of their range to compensate for a delayed start by moulting faster. Similar mechanisms have been shown in the intra-population level in Curlew Sandpipers (Barshep *et al.* 2011), and at the individual level in e.g. Starling *Sturnus vulgaris* (Dawson 2004) and Bar-tailed Godwit *Limosa lapponica* (Conklin & Battley 2012), in which a delayed and fast wing moult shows no obvious effect on the next stages of life. Such individual flexibility would enable Greenshanks to adjust their moult to feeding conditions that vary in different years, especially at inland sites, without a carry-over effect on their breeding plumage or departure timing.

RELATION BETWEEN BODY MASS AND MOULT

Most immatures had low body mass and some were moulting in April–May (Figures 3 and 5), which suggested that these lean birds did not migrate north. The few immatures that had high body mass in February–April might be the fraction that does leave southern Africa heading north. If this is so, then these migrants accumulated smaller fat reserves than adults before departure (Figure 4 and 5). This suggested that the migrating immatures would cover shorter distances to the next stopover sites than the adults (Pienkowski *et al.* 1976, Tree 2000). Greenshanks of all age classes in Zimbabwe had a lower average body mass during the pre-moult, moult and post-moult stages than those caught at both coastal regions (Figures 4 and 5). This suggested that feeding conditions differ at inland and coastal habitats in southern Africa, that the birds staying inland have a different migration strategy to those at the coast, or both. Greenshanks staying inland might carry smaller fat loads and migrate using shorter flights than those from the coast, who might cross the migration distance in a few long non-stop flights carrying high fat loads, using a time-minimising strategy (Piersma 1987). Coastal sites are thought to provide waders with rich and predictable feeding conditions, in

contrast to inland wetlands, which offer temporarily abundant invertebrate food, depending on rainfall (Allan *et al.* 1997; Piersma 2003, 2007, Kraaijeveld 2008, Colwell 2010, Remisiewicz 2011). Tree (1979, 1985) reports that around Harare, Greenshank numbers fall after the first summer rain in November–December, but rise at the east coast in December–January. Two ringing recoveries between Zimbabwe and Zambia and the Port Alfred area in South Africa show that Greenshanks undertake nomadic movements within the non-breeding range (Tree 1979, Underhill 1997, Underhill *et al.* 1999). Tree (1979, 1985) suggests that in wet years, lakes and dams fill up in the south-east African interior and flood Greenshank feeding habitats along the shores after the rains start in November, including in Zimbabwe. So the birds might move to coastal areas or to newly inundated inland wetlands in search of better conditions (Tree 1979). The end or suspension of primary moult in adult and sub-adult Greenshanks in November–January occurs during these floods, allowing for short-distance movements. Temporary suspension of primary moult to facilitate nomadic movements between wetlands in the interior of southern Africa has been suggested for Wood Sandpipers and Little Stints *Calidris minuta* (Remisiewicz *et al.* 2009, 2010a, Remisiewicz 2011).

The lower body mass of Greenshanks during the pre-departure period (February–April) in Zimbabwe than at the coasts suggests that food was less abundant inland or that they used a different strategy to accumulate fat reserves. At inland wetlands Greenshanks feed mostly on fish fry, arthropods, including dipterans, and tadpoles collected in shallow water; thus high water levels might impede their feeding (Tree 1979). At the west coast's Berg River estuary between November and March Greenshanks feed mainly feed on small crabs *Hymenosoma orbiculare* supplemented by small fish, nereids and other small invertebrates (Kalejta 1992, 1993). In November and the following months the proportion of nereids in Greenshanks' diet in this area increases to about 30%, probably following the nereids' reproduction and high availability (Kalejta 1992, 1993). In the Swartkops estuary on the east coast, Greenshanks feed mostly on estuarine mud prawns *Upogebia africana* and sand prawns *Callianassa kraussi*, especially in summer, when they are abundant close to the sand's surface (Tree 1979, Martin & Baird 1987). The seasonal differences in prey abundance, its caloric value and the time available for feeding at the west and the east coasts might explain the differences in Greenshanks' body mass at these areas, especially during the pre-migratory fattening period (Figure 4).

POTENTIAL FLIGHT RANGES AFTER DEPARTURE FROM SOUTHERN AFRICA

The lightest birds were caught in southern Africa on arrival (133–155 g) and were probably emaciated after their long-distance movement. The heaviest adults caught at the west and the east coasts had the highest body masses reported for the species (Cramp & Simmons 1983, Tree 2005), and at about 300 g they had almost doubled their lean body mass. Hence they could potentially cover about 4000–6000 km in one non-stop flight as we cautiously estimated (Figure 1), or even longer distances if they had wind assistance as in Bar-tailed Godwits (Gill *et al.* 2012) and Great Snipes *Gallinago media* (Klaassen *et al.* 2011), a factor we did not calculate. The ca. 2000 km shorter potential flight ranges of the heaviest adults departing from Zimbabwe than from both coastal regions (Figure 1) corresponds with about 1100–1800 km distance between these areas. Though the average Zimbabwean Greenshanks departed with lower fat reserves, the heaviest birds from all three regions could reach at least the northern Nile Valley or the Red Sea coast in one non-stop flight (Figure 1). This corresponds with the suggestion by Summers & Waltner (1979) that Greenshanks leaving South Africa migrate to the breeding grounds in several long-distance flights, instead of many small hops. But some adults, especially from Zimbabwe, and immatures migrating with lower fat reserves, might cover the distance in smaller hops and use closer stopover sites (Summers & Waltner 1979, Scott 2009), such as lakes in the Great Rift Valley or the eastern coasts of Africa, though no direct evidence for this has yet been found (Tree 1985).

Conclusions

Greenshanks using the southernmost non-breeding grounds in Africa demonstrated different moult strategies from those that migrate shorter distances. About 20% of immatures replaced one to five outer primaries in December–May, a rare pattern in the north. Sub-adults, which mostly stay in southern Africa for a "gap year", moulted all primaries about 1.5 months earlier but at the same rate as adults arriving from the breeding grounds. Most adults only moulted their primaries in southern Africa, in contrast to northern sites where adults often arrive with primary moult advanced and suspended. Mean dates of adult moult onset were up to 19 days apart across southern Africa, probably reflecting the birds' arrival sequence. However, the end of moult was synchronised within six days across all three regions, as was the beginning of their pre-migratory fattening. We suggest that adults fitted their primary

moult to the time available between arrival and about three weeks before the onset of the pre-migratory fattening. Greenshanks had a higher average body mass at the east and the west coasts than in Zimbabwe, which suggests that the coastal areas provide them with a richer food supply than the inland wetlands or that they used different return strategies. However, Greenshanks moulted at a similar rate inland and at the coasts, and accumulated sufficient fat reserves for a long-distance return flight. We suggest that the inland Greenshanks benefit from abundant food over the entire austral summer in some years, shorter migration distance and lower intra- and inter-specific competition than at the coasts, which are more crowded with waders. In bad years the inland birds can fall back on foraging through nomadic movements and can move to the coasts if conditions deteriorate inland.

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SAMENVATTING

Groenpootruiters *Tringa nebularia* ruien hun grote slagpennen
op het noordelijke halfrond niet steeds volgens hetzelfde
patroon. Over de vogels die verder naar het zuiden ruien, is
weinig over deze rui bekend. De auteurs beschrijven hier de rui
van de grote slagpennen en de veranderingen in lichaamsge-
wicht in de meest zuidelijke Afrikaanse overwinteringsgebie-
den. Zij vergeleken de slagpenrui (met Underhill-Zucchini
modellen) en het lichaamsgewicht op populatieniveau van 356
Groenpootruiters die tussen 1968 en 1998 in binnenlandse
wetlands in Zimbabwe en aan de oost- en westkust van Zuid-
Afrika waren gevangen. Ongeveer 20% van de eerstejaars
vogels verving in december-mei een tot vijf van de buitenste
grote slagpennen (in het noorden worden de buitenste grote
slagpennen bij eerstejaars vogels veel minder vaak en boven-
dien in kleiner aantal geruid). De één jaar oude vogels ruien
hun slagpennen gemiddeld 40 dagen vroeger in het seizoen dan
de volwassen vogels. De ruisnelheid was in beide leeftijds-
categorieën echter gelijk. Bij de volwassen vogels begon de slag-
penrui in Zimbabwe en aan de oostkust van Zuid-Afrika
gemiddeld 16–19 dagen vroeger dan aan de westkust van Zuid-
Afrika (start respectievelijk 7, 4 en 23 september), overeenko-
mend met een verschil in aankomst van de vogels in de drie
gebieden. Er was ook een verschil in de periode dat de vogels in
slagpenrui waren (Zimbabwe gemiddeld 122 dagen, oostkust
Zuid-Afrika 115 dagen, westkust Zuid-Afrika 105 dagen), een
verschil van 10-17 dagen. Als gevolg hiervan was de rui in alle
drie gebieden tussen 31 december en 6 januari voltooid. In
alle drie regio's begonnen de vogels ongeveer tussen 13 en 19
januari met opvetten. De gemiddelde gewichtstoename aan vet
was voor volwassen vogels in Zimbabwe 76 g, aan de westkust
van Zuid-Afrika 116 g en aan de oostkust ervan 125 g. Uit bere-
keningen blijkt dat de zwaarste Groenpootruiters vanuit alle
drie gebieden in één non-stopvlucht de vallei van de Nijl of de
kust van de Rode Zee zouden moeten kunnen bereiken. De
auteurs denken dat Groenpootruiters die in de binnenlandse
wetlands van Zimbabwe overwinteren, profiteren van een korte-
re terugvlucht naar het broedgebied en een geringere intra- en
interspecifieke voedselconcurrentie dan vogels die aan de Zuid-
Afrikaanse kusten overwinteren. In goede jaren is er tijdens de
hele noordelijke winter in de binnenlandse wetlands een over-
vloed aan voedsel, terwijl in andere jaren de vogels een noma-
disch gedrag kunnen vertonen of kunnen uitwijken naar de kust
als de omstandigheden in het binnenland verslechteren.   (PW)