

# Prebreeding moult, plumage and evidence for a presupplemental moult in the Great Knot *Calidris tenuirostris*

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We studied the prebreeding moult and resulting plumage in a long-distance migrant sandpiper (Scolopacidae), the Great Knot *Calidris tenuirostris*, on the non-breeding grounds (northwest Australia), on arrival at the staging grounds after the first migratory flight (eastern China) and on or near the Russian breeding grounds (Russian data from museum specimens). We show that breeding plumage scores and breast blackness were affected not only by the increase in moulted feathers but also in the wearing down of overlaying pale tips of fresh feathers. Birds migrating from Australia and arriving in China had completed or suspended moult, but more moult must occur in Asia as Russian specimens had moulted more of their mantle and scapular feathers. Russian birds had significantly more red feathering on their upperparts than had birds in Australia or those arriving in China. The increase in reddish feathers cannot be accounted for simply by continuation of the prealternate moult. Instead, a third, presupplemental moult must occur, in which red-marked feathers replace some scapular and especially mantle feathers that were acquired in a prealternate moult only 1–3 months earlier. Great Knot sexes show little size and plumage dimorphism, whereas two other sandpipers that have supplemental plumages (Ruff *Philomachus pugnax* and Bar-tailed Godwit *Limosa lapponica*) are thought to be highly sexually selected. Bidirectional sexual selection may therefore be involved in the evolution of a supplemental plumage in Great Knots.

Migrants such as waders (especially the Scolopacidae) typically show seasonal plumage change, with a dull non-breeding plumage being replaced by a distinctive and often colourful plumage before the breeding season. The breeding plumage may have selective importance in mate choice (Owens *et al.* 1994), or, especially in open-ground-nesting birds, for crypsis when nesting (e.g. Byrkjedal & Thompson 1998). The appearance of the plumage is therefore likely to reflect the outcome of competing pressures for conspicuousness and camouflage.

Moulting into a breeding plumage also raises the potential for birds to signal their nutritional or

migratory 'quality'. In the Bar-tailed Godwit *Limosa lapponica*, a long-distance migrant, two groups of birds are discernable upon arrival after a 4000-km flight from West Africa (primarily from Mauritania) to The Netherlands (Piersma & Jukema 1993). One is a heavy, well-moulted group of birds that then resumes moult, further increasing the 'quality' of their breeding plumage. The other is a light, less extensively moulted group of birds that apparently cannot afford to 'upgrade' their plumage further (though there is some overlap in body masses). The more highly moulted individuals are presumably the heaviest at departure (resulting in their higher body masses on arrival), so the appearance of the breeding plumage may reflect migratory quality reliably (Piersma *et al.* 2001).

To understand why (or whether) brighter birds are of higher quality it is important to understand when and where bright plumage develops, and to have a

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plausible theory of how the plumage succession evolved. Detailed studies of the progress of moult in migrants arriving on staging grounds have clarified the nature of the prebreeding moult in Ruffs *Philomachus pugnax* (Jukema & Piersma 2000) and identified a previously unknown feather generation in Bar-tailed Godwits (Piersma & Jukema 1993, Jukema & Piersma 2000). Such detail is important because although moult itself refers to the process of follicle activation and feather replacement, assessment of the resulting plumage may contain little information about the moult process. Terminology systems for moults that are based on external events or states (e.g. annual cycle events, age or season) are therefore unsatisfactory, because they do not define a plumage in relation to the moulting process. A 'breeding plumage' could, for example, contain feathers from one or more moulting periods.

Essentially, identifying specific moults is a problem of identifying how often a follicle is activated during a moulting period. The nomenclatural system of Humphrey and Parkes (1959, 1963), which was designed to allow identification of homologies in the moulting patterns of birds, is by far the most suitable system for naming moults and plumages in this way. Briefly, Humphrey and Parkes (1959) proposed naming a moult in relation to the feather generation that it produces. If a single moult occurs in a year, it is termed the prebasic moult, resulting in the basic plumage. If two moults occur, the second (inserted) moult is the prealternate, generating the alternate plumage. Any further moults are termed presupplemental (with supplemental plumages).

In adult waders, the complete moult that typically occurs after the breeding season is prebasic, and a fairly drab basic plumage is held over the non-breeding season. In the prebreeding moult, the obvious assumption is that the moult is prealternate. However, Ruffs and Bar-tailed Godwits on the breeding grounds may carry three generations of plumage: the non-breeding feather, a striped feather (that is easily overlooked if birds are not in the hand) and an obvious 'breeding plumage' feather. Jukema and Piersma (2000) proposed that the non-breeding feather type is basic, the striped feather is the ancestral breeding plumage type and should therefore be considered alternate, and the more colourful 'breeding plumage' feather is supplemental. Black-tailed Godwits *L. limosa* may also show three feather generations (Roselaar & Gerritsen 1991). Jukema and Piersma (2000) suggested that the presence of a presupplemental moult reflects intense sexual selection pressure.

In northern Australia, one of the commonest waders is the Great Knot *Calidris tenuirostris*, a large sandpiper that breeds in eastern Siberia. During the non-breeding season Great Knots are brownish-grey birds, but in the breeding season they have blackish spotted breasts, and dark brown–black upperparts with extensive red patches or edges on mantle and scapular feathers. Great Knot plumages pose a problem in that birds on the breeding grounds (e.g. photographs in Pringle 1987, Rosair & Cottridge 1995, P.S. Tomkovich unpubl. data) seem to show much more extensively red upperparts than occur in birds in Australia before migration. Can this difference be explained by feather wear (as has been assumed in the past, exposing more of the underlying colour), or is an extra moult responsible?

To answer these questions, we studied the prebreeding moult in Great Knots as they migrated from Australia to Siberia; we had three aims:

- (1) to determine whether birds have completed contour feather moult when they leave Australia,
- (2) to gauge how the appearance of the plumage is affected by the extent of moult and by feather wear, and
- (3) to establish whether the apparent discrepancy between the amount of red feathering on the upperparts of Great Knots on the breeding grounds and those in Australia can be explained by feather wear that reveals greater amounts of coloured feathering along the migration route, or by further moult. If further moult occurs, we aim to determine whether it is a continuation of a suspended prealternate moult or an additional, undescribed, moult.

Although we subscribe to the Humphrey–Parkes scheme here, we will refer to the moult that occurs before and during migration to the breeding grounds as the prebreeding moult, until it is clear whether this moult is simply the prealternate moult or not.

## MATERIALS AND METHODS

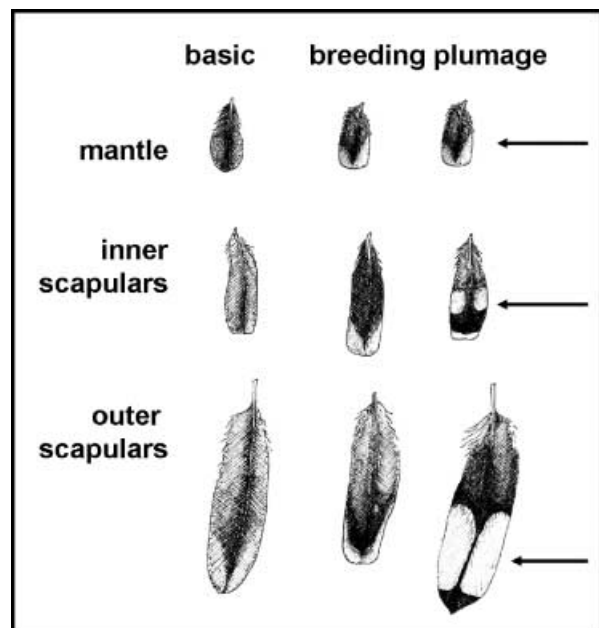
Great Knots are thought to migrate from Australia to Russia in essentially two stages. Birds depart northwestern Australia for eastern Asia from late March to early-mid April (Battley *et al.* 2000). Counts and timing of departures and arrivals indicate that most birds fly directly to eastern China and Korea (5400–6000 km). Numerous band recoveries and leg-flag sightings link northwestern Australian Great Knots to the Yellow Sea (Higgins & Davies 1996, Battley *et al.* 2000, Minton & Jessop 2000, and references therein). Counts indicate that, once in eastern China

or Korea, birds move north to the northern Yellow Sea, where they refuel before leaving for the breeding grounds, approximately 2700–4200 km distant (Wilson & Barter 1998, Barter *et al.* 2000). Most are thought to fly from the Yellow Sea to the breeding grounds without stopping (Tomkovich 1997). Because birds can arrive in Asia in the first half of April, but do not depart for the breeding grounds until late May, there are 4–6 weeks available for refuelling and potentially also for further moult.

Birds were studied before migration from north-western Australia, after migration in China, and from museum specimens collected on the breeding grounds or on eastern Russian staging areas. There is no geographical variation in biometrics or plumage known in Great Knots, and virtually all Great Knots stage in the northern Yellow Sea before migrating to the breeding grounds in Russia. We are therefore confident that no systematic biases exist in our data that would compromise comparisons between sites. Australian birds were caught (primarily by cannon-net) in Roebuck Bay, Broome (17°58'S, 122°15'E). In 1998, 22 adult birds were collected (for body composition analyses; Battley *et al.* 2001): two on 20 February, nine on 6 March, one on 12 March and ten on 21 March (the last group was chosen to represent birds likely to be close to departure, based on plumage and plumpness). In 2000, 92 birds aged as adults (based on wing moult and contour feather appearance) were caught, processed and released between 26 February and 28 March. Samples are grouped in analyses into 10-day time periods: 1998, 1 (20 February), 2 (6 March), 3 (12 March) and 4 (21 March); 2000, 1 (26 and 28 February), 2 (3 and 4 March), 3 (19 March) and 4 (28 March). In China, ten birds were caught by local hunters and collected from 1 to 9 April 1998 at Chongming Island, Yangtze River (30°48'N, 121°27'E); these individuals were believed to have arrived recently (Battley *et al.* 2000). Russian specimens were studied at the Zoological Museum of Moscow State University. Thirty-three adult specimens were examined, primarily from the Chukotka Autonomous region (mostly outside Chukotsky Peninsula, and including the Anadyr region) (14) and Kamchatka Peninsula (13), regions from which the few band recoveries or leg-flag resightings include birds known to spend the non-breeding season in Australia (Tomkovich 1995, Higgins & Davies 1996, Minton & Jessop 2000, and references therein). A few other specimens were used also from Yakutia (one) and Primorye (five). Kamchatka birds were migrating north when collected at what

are believed to be emergency staging sites (Tomkovich 1997) and the Primorye birds were migrating south; other specimens were on or near breeding grounds. Most birds away from Kamchatka were either birds known to have bred or birds with brood patches that indicate attempted breeding. Birds were collected between 21 May and 24 August.

Procedures were not equally extensive on all birds, partly because of time pressures when working on live birds that formed part of other studies, and partly because some work was performed on museum specimens. To determine how far a bird was through its moult, old, growing and new feathers were counted in three areas of the body, the breast, mantle and right scapulars. Breast and mantle samples (one per region) were counted in a 2 × 2-cm paper quadrat that was wrapped around the torso, and the feathers pulled through with a fine probe. The whole scapular tract was counted feather by feather, though it was sometimes difficult to determine where the inner scapulars finished. New breast feathers could be distinguished by their large black spots and, often, crisp white tips. Mantle and scapular feathers were assigned to three categories: (1) basic plumage, grey with dark shaft-streaks; (2) dull breeding plumage, dark-centred feathers lacking reddish colouring; and (3) colourful breeding plumage, dark feathers with reddish fringes, patches or spots (Fig. 1).



**Figure 1.** Feather types in moulting Great Knots: (1) basic plumage, (2) dull breeding plumage, and (3) coloured breeding plumage. Arrows indicate red parts of the feathers.

As it was impractical to make detailed measurements on large numbers of individual feathers, notes were also made of the following: minimum and maximum white feather tip length on new (non-basic) breast feathers (to 0.5 mm, although a trace was given a 0.1 mm value); minimum and maximum pale tip lengths on non-basic mantle and scapular feathers in specimens from 1998 and Russia; the total number of 'red' feathers on the upperparts (including the scapulars of both wings and the whole mantle, but excluding tertials, as the edges, which may be coloured, wear off making comparisons between Australia/China and Russia unreliable). A standard breeding plumage score was given to each bird (an index of the amount of breeding plumage attained, maximum 100%), taking into account both upperpart and underpart feathering. A body moult index (BMI) score was estimated for the sides of the breast and neck (hereafter 'standard' BMI). BMI scores represent: 0, no moult; 1, light moult; 2, medium moult; 3, heavy moult. Standard breeding plumage and BMI scores were made by D.I.R. for the birds caught in 2000, but by P.F.B. for the others. Both observers are experienced at scoring moult in waders, particularly Great Knots. Although it is possible that small differences may have entered the data through estimates coming from two of us, the breeding plumage scores made by D.I.R. closely matched the more detailed feather data collected by P.F.B.; any scoring differences are probably trivial. Separate breeding plumage and BMI scores were also made for the breast and mantle (by P.F.B.). All detailed feather counts were made by P.F.B. Standard biometric measurements were made on the birds caught in Australia and China: body mass (precision 1 g), bill length (0.1 mm), total head length (0.1 mm), tarsus length (0.1 mm), tarsus + mid-toe length (1 mm), flattened wing length (1 mm). Birds were sexed by dissection (Australia 1998 and China), by genetic sexing (Australia 2000; see Baker *et al.* 1999) or from museum labels (Russian specimens).

The breast feathering was photographed, with a ruler labelled with the individual's code, or a label of known size, visible. The photographs were scanned and analysed using the program Scion Image for Windows (version 4.0.2; Scion Corp., www.scioncorp.com). To determine the proportion of the breast feathering that was dark, a rectangular section of the breast was highlighted and the number of pixels contained in the area counted. A threshold darkness value was selected (from examination of the image with the cursor, which showed the greyscale value for the

selected pixel) and the area of the sample that was equal to or darker than the threshold value was calculated (in pixels). The total area of the sample divided by the area above the threshold value gave the proportion of the area that was dark. The process was repeated using an elliptical selection to ensure that the shape of the selection did not influence the data (e.g. by corners encountering especially dark or light areas). The two darkness values were averaged to give the 'darkness' value in data analyses. Disorderly feather arrangements could influence the amount of underlying white that is exposed, but there was no systematic difference in plumage condition among the groups. We also measured the width of the spots on breast feathers in 18 birds caught in Australia in late March and in 23 Russian specimens. Using Scion Image, a known length (of a ruler in the photograph) was measured on the image. Where the width of a black spot could be delimited, it was measured on the image, and converted into millimetres. Two to five feathers were measured on each bird (the number was limited by how many complete spots were visible), and the average value for each individual was calculated.

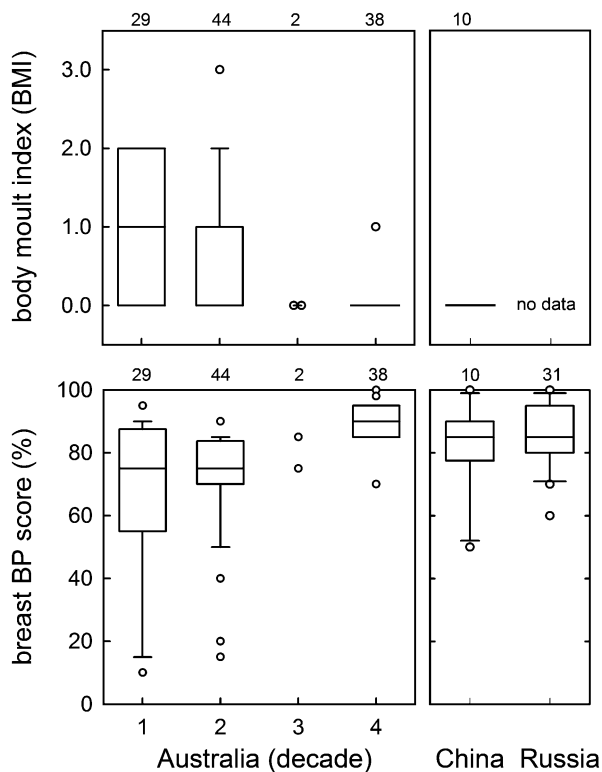
In analyses, all proportions were arcsin-transformed. Comparisons between moult characteristics of different sites were made with ANOVAS with site, sex and site\*sex as factors, or with *t*-tests. Least-squares regression was used to test whether feather tip lengths decreased over time (regressed against day or (log)day). Multiple regressions were used to evaluate how the appearance of the plumage was related to the proportion of feathers moulted, and to the minimum and maximum tip lengths.

## RESULTS

### Are birds fully moulted before leaving Australia?

Most birds caught in the first half of the study in Australia showed active body moult, whereas those caught late in the Australian study and in China showed very little or no visible moult (Fig. 2). At the same time, breeding plumage scores (a visual assessment of the extent of the breeding plumage) levelled off (Fig. 2), so birds had evidently completed or suspended moult before departure on migration.

Figure 3 shows the increase in the proportion of feathers moulted in focal feather tracts during fuelling and migration. Birds in the late March catches in Australia had moulted virtually all of their breast



**Figure 2.** Decrease in body moult intensity scores (BMI) and increase in breeding plumage scores in Great Knots during fuelling in Australia, immediately after migration to China, and on or near the breeding grounds in Russia. Decades in Australia refer to (1) end February, (2) first decade in March, (3) middle decade in March, and (4) last decade in March. Boxes enclose the median, with 25th–75th percentiles, and whiskers show the 10th and 90th percentiles. Sample sizes are given above the plots.

feathers (proportion moulted =  $0.979 \pm \text{se } 0.005$ ,  $n = 38$ ) but somewhat less in the mantle and scapulars (mantle, proportion moulted =  $0.920 \pm 0.018$ ,  $n = 38$ ; scapulars, proportion moulted =  $0.836 \pm 0.021$ ,  $n = 35$ ). The proportions moulted in birds having arrived in China were similar (breast,  $0.985 \pm 0.010$ ; mantle,  $0.917 \pm 0.037$ ; scapulars,  $0.807 \pm 0.034$ ;  $n = 10$ ; all differences with Australia non-significant). We there-

fore combined data from late March with data from China in order to compare the moult status of birds around departure from Australia and on or near the breeding grounds. Birds in Russia had moulted significantly more of their mantle quadrat and scapular tract than had birds in Australia and China (Table 1).

### Does wear affect the feathers?

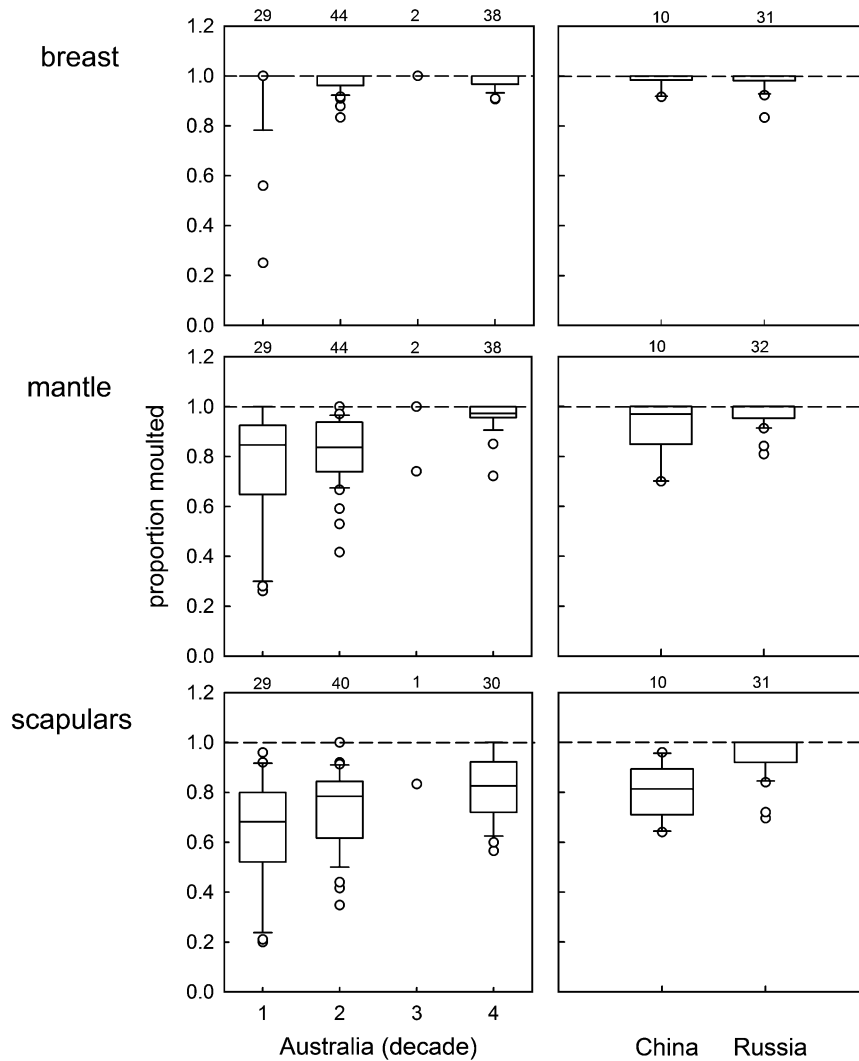
Freshly moulted breast feathers have a distinct white tip that overlays lower dark feathering (Fig. 4). The maximum and minimum tip lengths on the breast feathering were negatively related to day of capture, showing that feather wear reduces the tip lengths (Table 2). The same was true for maximum and minimum tip lengths on the mantle and scapular tracts (Table 2). Hence, feathers on the breast and upperparts showed discernible wear that could affect the appearance of the plumage independently of changes resulting from further moult.

### Does feather wear affect the appearance of the plumage?

On the breast feathering, the decrease in the length of the pale tips increased the apparent darkness of the plumage. Across all the birds, the breeding plumage score of the breast increased with the proportion of feathers moulted and as the minimum and maximum pale tip lengths decreased (multiple regression, breeding plumage score vs. minimum tip length, std coeff. =  $-0.322$ ,  $t = -4.204$ ,  $P < 0.001$ ; vs. maximum tip length, std coeff. =  $-0.316$ ,  $t = -4.235$ ,  $P < 0.001$ ; vs. proportion feathers moulted, std coeff. =  $0.341$ ,  $t = 5.779$ ,  $P < 0.001$ ;  $n = 154$ , overall  $R^2 = 0.511$ ). Removal of three birds with low breeding plumage scores (possibly second-year birds or behind-schedule adults that had high leverage on the analysis; breeding plumage scores of 10, 10 and 0% with proportions moulted of 0.56, 0.88 and 0.25, respectively, compared with average values for other birds of

**Table 1.** The mean proportion of feathers in the quadrat or tract that were moulted (alternate vs. basic). Proportions were arcsin transformed before analysis. Significance values are from ANOVAs relating the proportion of feathers moulted to site, sex and sex\*site. Sex and sex\*site were not significant.

	Australia/China				Russia				df	F	P	R <sup>2</sup>
	mean	se	n	range	mean	se	n	range				
Breast	0.981	0.004	48	0.906–1	0.990	0.004	28	0.923–1	1,71	2.035	0.158	0.029
Mantle	0.919	0.016	48	0.636–1	0.972	0.009	28	0.810–1	1,71	5.371	0.023	0.072
Scapulars	0.830	0.018	45	0.565–1	0.946	0.016	27	0.696–1	1,67	30.343	< 0.001	0.324



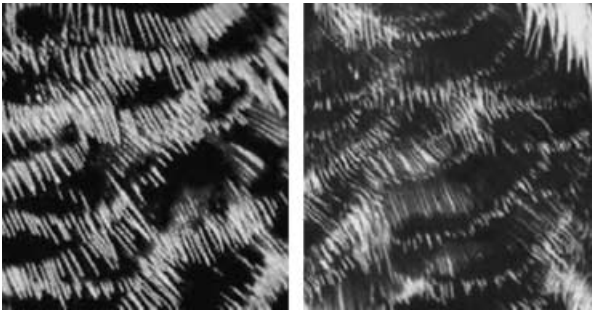
**Figure 3.** Progression of moult in three feather regions in Great Knots during fuelling and migration. Conventions are as in Figure 2.

**Table 2.** Results of simple linear regression analyses showing that the lengths of pale tips on breeding plumage feathers in Great Knots decrease over time. Feather tip measurements were log(+1) transformed before analysis.

Tract	Tip measurement	Independent	std coeff.	df	F	P	R <sup>2</sup>
Breast	maximum	log(day)	-0.347	1152	20.765	< 0.001	0.120
	minimum	log(day)	-0.534	1152	60.510	< 0.001	0.285
Mantle	maximum	log(day)	-0.750	1143	183.521	< 0.001	0.562
	minimum	log(day)	-0.682	1143	124.292	< 0.001	0.465
Scapulars	maximum	log(day)	-0.545	1,52	21.933	< 0.001	0.297
	minimum	day	-0.673	1,52	43.159	< 0.001	0.454

86.3% breeding plumage and proportion moulted of 0.98) did not change the results. Results are similar for the breast darkness values: overall there was a positive relationship between breast darkness and the proportion of feathers moulted, and negative relationships

with tip lengths (minimum tip  $P = 0.005$ , maximum tip  $P = 0.024$ , proportion moulted  $P = 0.001$ ;  $n = 142$ ,  $R^2 = 0.320$ ). Removal of the three 'pale' birds from the analysis resulted in only maximum tip length being significant (std coeff. =  $-0.259$ ,  $t = -2.457$ ,  $n = 139$ ,



**Figure 4.** White tips on fresh breast feathers overlay the dark feathering (left). The tips wear off with time, darkening the appearance of the plumage (right). Images are based on birds caught on 28 February 2000 (left: before migration in Broome), and on 3 April 1998 (right: after migration in China).

$P = 0.015$ ). If only data from the Australian and Chinese birds were analysed, decreasing maximum tip length increased breast darkness (whether or not the three pale birds were included,  $P < 0.01$ ), while the proportion of feathers moulted was significant for the full dataset ( $P = 0.003$ ).

The mean width of the black spots on breast feathers was marginally smaller for Russian birds ( $6.8 \pm 0.3$  mm) than for Australian birds ( $7.0 \pm 0.1$  mm), as might be expected through feather wear ( $t_{39} = 0.938$ ,  $P = 0.354$ ). This also suggests that breast feathers had not been replaced in Asia by feathers with larger back spots. However, Russian birds had on average slightly longer maximum pale tips on the breast feathers than did late Australian and Chinese birds ( $1.34 \pm 0.15$  mm in Russia vs.  $0.77 \pm 0.08$  mm in Australia and China;  $t_{74} = 3.542$ ,  $P = 0.001$ ). Minimum tip lengths were shorter in Russia ( $0.06 \pm 0.02$  mm in Russia vs.  $0.15 \pm 0.04$  mm in Australia/China;  $t_{67.6} = 2.186$ ,  $P = 0.032$ ).

### Red feathering in Australia, China and Russia

Russian birds had significantly more red feathers on their upperparts than did birds in the final catches

in Australia or in China (Table 3). Although males tended to have slightly more red feathering on their upperparts than did females, differences were small and generally non-significant (Table 4).

### Do the higher counts of red feathers in Russian birds reflect the completion of prealternate moult?

Table 5 summarizes calculations of whether continued prealternate moult can account for the higher numbers of red feathers in Russian birds. Of the total difference of 19.6 feathers, 59% were in the scapulars and 41% in the mantle region. If the Australian and Chinese birds had simply continued moulting until the proportion of feathers moulted in the scapulars and mantle quadrat was the same as in the Russian birds, only small increases in red feathering would have occurred. The scapulars would still be 48% short of the Russian total, and the mantle feathering 76% short. This calculation assumes that the ratio of red to dull feathers remains the same.

If birds had switched to moulting solely red feathering in Asia, the discrepancy would still have existed. In the scapulars, there were, on average, 5.7 more feathers moulted in Russia than in Australia/China. If these were all red feathers, the predicted total of coloured scapulars is 15.7, still 27% short of the 21.6 observed.

Because the mantle quadrat is only a sample, we cannot predict how many basic feathers remained in the total mantle region. However, feather counts in the  $2 \times 2$ -cm mantle quadrat of the Russian birds imply that only 1.4 basic feathers would have been additionally replaced in this area. To achieve the required increase to 10.4 coloured feathers would require an area 5.9 times that of the quadrat, which is physically impossible.

Finally, looking at the most colourful Australian/Chinese birds (seven birds with more than 20 red upperpart feathers; mean =  $25.7 \pm 2.2$ , range 20–37) showed that whereas the Australian/Chinese

**Table 3.** Results from one-way ANOVAs comparing samples from soon before, and just after, migration from Australia with birds collected on or near the breeding grounds in Russia. Sex and sex\*site were not significant.

	Australia/China				Russia				df	F	P
	mean	se	n	range	mean	se	n	range			
Mantle quadrat	0.8	0.3	48	0–8	6.5	0.5	32	0–12	1,75	115.545	< 0.001
Right scapulars	5.0	0.5	45	0–14	10.8	0.6	31	3–18	1,71	61.291	< 0.001
Total coloured	12.4	1.3	46	0–37	31.9	1.7	30	19–60	1,71	92.165	< 0.001

**Table 4.** Results of *t*-tests comparing the sexes in samples from soon before and just after migration from Australia, and in birds collected on or near the breeding grounds in Russia.

	Male				Female				<i>t</i>	<i>P</i>
	mean	se	<i>n</i>	range	mean	se	<i>n</i>	range		
Australia/China										
mantle quadrat	0.9	0.3	27	0–6	0.7	0.4	21	0–8	0.275	0.785
right scapulars	5.8	0.6	26	0–14	3.9	0.7	19	0–8	0.2021	0.050
total coloured	14.1	1.7	25	1–37	10.2	1.8	21	0–27	1.614	0.114
Russia										
mantle quadrat	6.5	0.7	19	0–10	6.9	0.9	12	0–12	–0.375	0.712
right scapulars	11.3	0.7	18	7–18	10.4	1.0	12	3–14	0.709	0.486
total coloured	33.0	2.4	18	19–60	31.4	2.9	11	21–42	0.508	0.615

**Table 5.** Calculations of the observed and potential increases in coloured feathering in the upperparts of Great Knots in Australia and China compared with Russia.

	Australia	Russia	Difference
Total coloured	12.4	32	19.6
Scapulars <sup>1</sup>	10.0	21.6	11.6
Mantle total <sup>2</sup>	2.4	10.4	8.0
Mantle quadrat <sup>3</sup>	0.8	6.6	5.8
Proportion scapulars moulted (%)	83.0	94.6	11.6
Proportion mantle moulted (%)	91.9	97.2	5.3

increased total if moult continued with same coloured/plain ratio

= feather count Australia \* (proportion moulted Russia/proportion moulted Australia)

	Australia	Russia	Difference	% unexplained
Scapulars	11.4	(21.6)	10.2	47.3
Mantle	2.5	(10.4)	7.9	75.6

increased total if only red feathers grown

= feather count Australia \* (1 + proportion moulted Russia – proportion moulted Australia) \* 2

	Australia	Russia	Difference	% unexplained
Scapulars	15.7	(21.6)	5.9	27.3

minimum percentage of basic and plain alternate feathers replaced in Russia if only red feathers are grown<sup>4</sup>

= (feather count Australia – feather count Russia)/feather count Australia \* 100

	Australia	Russia	Difference	% replaced
Scapulars – basic	4.2	1.3	2.9	68.3
Scapulars – plain alternate	15.4	12.5	2.9	19.1
Scapulars – coloured alternate	5	10.8	5.8	
Mantle quadrat – basic	2.1	0.7	1.4	65.4
Mantle quadrat – plain alternate	22.7	17.1	5.6	24.7
Mantle quadrat – coloured alternate	0.8	7.8	7.0	

<sup>1</sup>Count of right scapulars \* 2.

<sup>2</sup>Equals total coloured minus the scapular count.

<sup>3</sup>Observed in 2 × 2-cm quadrat.

<sup>4</sup>Assuming equal feather numbers counted in Australia/China and Russia.

birds had similar numbers of red scapulars to the average Russian bird (20.3 vs. 21.6), the number of reddish mantle feathers was only half that (5.4 vs. 10.8). The proportions of feathers moulted were similar in the two groups (scapulars, 93.3% vs. 94.6%; mantle, 98.0% vs. 97.2%) so there was little scope for further moult in these Australian/Chinese birds. Compared with the seven most-highly coloured Russian birds (total red feathers, mean =  $43.1 \pm 3.0$ , range 37–60), the Australian/Chinese birds had much lower red feather counts, despite having moulted similar proportions of their feathers (scapulars, 20.3 vs. 27.4 with 93.3% vs. 93.6% moulted; mantle, 5.4 vs. 15.7 with 98.0% vs. 98.8% moulted).

## DISCUSSION

Birds departing on migration from the non-breeding grounds have finished or suspended moult, judging by the BMI scores of birds in the late catches in Australia and in China and by the proportion of feathers moulted in the feather tracts studied (including some fully moulted birds). Resightings of colour-banded birds in northwestern Australia have also shown that some individuals reach a high breeding-plumage score, which stays constant for some weeks before migration (Battley *et al.* 2004), implying that moult is suspended well before migration starts. However, this cannot be the entire moult of Great Knots migrating to Russia. As suspected beforehand, birds from the Russian breeding grounds have far more red feathering in their upperparts. Although a reduction in feather fringe length may play a role in exposing underlying red coloration, the difference in appearance is primarily because Russian birds have more red feathering, particularly on the mantle. We therefore propose that at least some Great Knots, when refuelling in the northern Yellow Sea, undergo a separate partial moult of upperpart feathering, particularly on the mantle. We do not know whether a similar moult occurs on the underparts, although this might explain why slightly broader pale feather tips were found on breast feathers in Russia than were found in China. The upperpart moult would require replacement of feathers that are only 1–3 months old. Thus, the prebreeding moult of Great Knots from Australia consists of:

- (1) an extensive (though not necessarily complete) prealternate moult in Australia,
- (2) further moult replacing most remaining basic feathers in northern Asia, and

- (3) partial moult in northern Asia replacing alternate feathers; this moult is primarily responsible for generating the difference in red feathering seen in birds in Australia and the breeding grounds.

We are left with the scenario that body moult is completed or suspended before departure on migration from Australia, with further moult, replacing potentially both basic and alternate feathering, occurring during the final staging period in the northern Yellow Sea. Under strict Humphrey–Parkes principles, only feathers grown in follicles activated three times in a year can be supplemental, so any replacement of basic feathers in Asia ought to be considered prealternate (see Discussion below). Replacement of alternate feathers must be pre-supplemental moult.

The moult in Australia produces predominantly ‘dull’ (i.e. brown–grey) alternate plumage, with some reddish feathering. Moult in Asia seems predominantly to produce feathers with red patches or fringes that may replace dull newly moulted feathers. So how should we view the red feathering grown in Australia and the equivalent feathering grown in Asia? One option would be to treat the ‘dull’ breeding plumage feathering as alternate (the ancestral breeding plumage) and to regard the coloured feathers as supplemental, with the two moults occurring simultaneously. However, this interpretation would contravene the basis of the Humphrey–Parkes scheme by supposing that most Great Knots moult many feathers directly from basic to supplemental feathering (although Reeves [female Ruffs] in captivity have been observed ‘skipping’ the alternate feather generation; D.B. Lank in Jukema & Piersma 2000). An alternative interpretation is that while the prealternate moult on the non-breeding grounds introduces a combination of plain and coloured feathers, any further moult on the staging grounds, be it prealternate or presupplemental, introduces predominantly or exclusively coloured feathering. All feather replacement in Asia is likely to be stimulated by the same hormonal controls, whether or not follicles have been activated once or twice in the annual cycle, and it is feasible that a ‘switch’ to coloured feathering could result.

This interpretation conundrum highlights a problem in the Humphrey–Parkes system: how to treat the possible ‘loss’ of a moult in some follicles. If a bird or species shows partial or complete loss of a moult, do the remaining moults retain their ‘identity’? If a prealternate moult were succeeded by a presupplemental moult, but there was subsequent

partial loss of the prealternate moult, can the presupplemental moult still be classified as such, even if some of the feathers replaced are basic rather than alternate? To retain evolutionary information and to aid in identifying homologies among species, the logical answer would be that partial loss of one moult does not directly influence a succeeding one. Therefore, a presupplemental moult in Great Knots on the northern staging grounds in Asia might replace some remaining basic feathers, while predominantly replacing alternate feathers. Calculations of the minimum proportion of the basic and dull alternate feathering that would be replaced if only red feathers were grown (Table 5) suggest that the few remaining basic feathers were 2–2.5 times more likely to be replaced in Asia than were plain alternate feathers. However, we cannot rule out a far more extensive moult of the upperparts, involving replacement of basic, dull alternate and red alternate feathers. When the presupplemental moult is stimulated in Asia, unless feather follicles retain some 'memory' of their moult status and/or feather type, general replacement of any existing feathers with new coloured feathers would result. We have not assessed how extensive coloured areas on the feathering were in Great Knots, and it is possible that supplemental feathers on average show more coloured areas than reddish feathers grown in Australia.

A third moult in the definitive moult cycle has been reported in two other species of the Scolopacidae, the Ruff and Bar-tailed Godwit (Jukema & Piersma 2000). As in Great Knot, one of these moults must be presupplemental. The presupplemental moult should be the most recently evolved one, as all other species of scolopacid are thought only to have two moults per definitive cycle and this is presumably the ancestral condition. The prealternate moult in those species with three moults per cycle would be expected to be the one most similar phenotypically to the prealternate moult in those scolopacids with only two moults per cycle. This is in keeping with the widely followed principle that moult homologies should be determined by comparing 'the timing, extent, and colour change in each moult with that of closely related species that have already been described' (Rohwer *et al.* 1992). Howell *et al.* (2003) have recently argued that colour changes should be used particularly cautiously as feather pigmentation is not necessarily linked directly to the processes that govern timing and extent of moult. We consider the identification of the presupplemental moults of Ruffs, Bar-tailed Godwits and Great Knots to be consistent

with these principles; in all three species, the presupplemental moult occurs on staging areas, while the prealternate moult, like that of other species of scolopacid (cf. Higgins & Davies 1996), occurs mainly on the non-breeding grounds before the onset of northwards migration. In the Ruff, the alternate plumage is a relatively unobtrusive striped feather, with the obvious 'breeding plumage' being the supplemental plumage. In the Bar-tailed Godwit, the 'striped feather' component of the prebreeding moult (Piersma & Jukema 1993) is thought to be the alternate plumage, with the bright red plumage typical of the species being the supplemental plumage. Texts that equate only alternate plumage with breeding plumage in birds are therefore misleading, because some wader species breed in supplemental plumage.

Our data cannot confirm whether breast feathering is involved in the presupplemental moult in Asia. There is certainly no great change between Australia and Russia in the size of the black spots on breast feathers, but partial moult of breast feathering in Asia could result in birds in Russia having a mixture of some retained alternate breast feathers (with narrow white tips) and some fresher supplemental feathers (with longer tips). The extent of the presupplemental moult in Asia needs confirmation.

If restricted to the mantle and scapulars, the proposed presupplemental moult in Great Knots would differ from the more complete plumage replacement found in Ruffs and Bar-tailed Godwits. Supplemental plumages, being more recently evolved than alternate plumage, should be considered evolutionary novelties and need not reflect the same selection pressures. In Ruffs and Bar-tailed Godwits, the sexes show substantial size and plumage dimorphism (Ruffs [male] are larger than Reeves [female], while in Bar-tailed Godwits females are larger than males, which is more usual in the Scolopacidae), and it has been suggested that the existence of supplemental plumages results from intense sexual selection (Jukema & Piersma 2000). The evolution of supplemental plumages may be related to the strength of sexual selection, but such selection can vary in direction between species. In lekking Ruffs, sexual selection is probably related to competition among males for females, and the existence of a supplemental plumage in females could be the result of a lack of complete sex-linked control in the moult process (Jukema & Piersma 2000). In Bar-tailed Godwits migrating north along the East Atlantic Flyway, variation in the (comparatively dull) female plumage indicates parasite resistance, but no relationship

between male plumage and parasite infestation was found (Piersma *et al.* 2001). Male ornaments may reflect other qualities involved in migration (such as fuel storage, moult and flight). There is no reason why only one sex should be able to assess the quality of potential mates, and also no expectation that the sexes experience identical selection pressures during moult and migration. Mutual sexual selection based on plumage has been demonstrated in an auklet (Jones & Hunter 1993) and a tern (Bridge & Nisbet 2004). Bi-directional sexual selection may apply in Great Knots, a species in which there is little difference in the plumage of male and female on or near the breeding grounds.

So why do Great Knots have two prebreeding moults? The alternate plumage attained on the non-breeding grounds provides the basis of the breeding season plumage, and time and energy constraints presumably dictate that this plumage is mostly grown in Australia. But if part of this is replaced only 4–8 weeks later, it would seem energetically cheaper to perform an incomplete prealternate moult on the non-breeding grounds and simply continue it on the staging site. Three possible explanations for the extensive prealternate moult are: (1) that the presence and extent of the prealternate moult are 'hard-wired' into sandpipers and have not been selected against, even in the presence of an additional pre-supplemental moult (Jukema & Piersma 2000); (2) that there is a risk to not moulting extensively enough on the non-breeding grounds, in case poor body condition on arrival or poor feeding conditions during final fuelling do not allow nutrients to be invested in plumage upgrading; (3) that the alternate plumage has some adaptive function during northwards migration of which we are unaware – perhaps in terms of insulation, as the appearance of true alternate plumage of Great Knots appears not to confer obvious advantages in terms of mate choice or crypsis before reaching the breeding grounds.

The evolution of a presupplemental moult on the staging grounds must reflect the benefits to having a fresh and colourful plumage on the breeding grounds. Plausible benefits include crypsis on the lichen-rich breeding tundra, mutual sexual selection, or joint territory defence (although if Great Knots are similar to Red Knots, most of this will be done by the male: Whitfield & Brade 1991). Moulting after a long migration, under tight time constraints, could give rise to condition-dependence in the supplemental plumage. Only birds with good initial condition (that left well-fuelled or were economical migrants)

might be able to upgrade their plumage extensively. Given that red parts of the scapulars and mantle feathers in Great Knots are more susceptible to fading than are dark parts (our pers. obs.) 'cheating' by moulting all the reddish plumage in Australia might result in lower quality plumage appearance.

It is interesting that all the waders in which presupplemental moults have been claimed are long-distance migrants with, at least in Afro-Siberian Bar-tailed Godwits and in Great Knots, only one major staging site en route to the breeding grounds. Does this mean that such plumages have not been studied in short-hop waders to the same extent, or is it possible that presupplemental moults have only evolved in long-flight migrants? An instructive species could be the Surf-bird *Aphriza virgata*, which is closely related to the Great Knot and has a similar breeding season plumage. (Note that the Surf-bird should probably be considered part of the genus *Calidris*; Jehl 1968, Piersma 1994). Some Surf-birds spend the non-breeding season along the west coast of North America to southern Mexico, but there is then a large gap in the distribution down to the west coast of South America, where birds winter from southern Ecuador to southern Chile (R.E. Gill and S.N.G. Howell pers. comm.). Birds from South America stage in the Gulf of California on their way north. Short-hop and long-haul migrating Surf-birds could experience different selection pressures. Such contrasts may give insights into the evolution of both moult and migration strategies.

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