Contour-feather moult of Bar-tailed Godwits (*Limosa lapponica baueri*) in New Zealand and the northern hemisphere reveals multiple strategies by sex and breeding region

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Abstract. The extreme long-distance migration of Alaskan breeding Bar-tailed Godwits (*Limosa lapponica baueri*) may present severe constraints on annual moult, and high individual variation in plumage and migration timing suggests that multiple strategies by sex and breeding region may exist. We used digital photography of free-living Bar-tailed Godwits to describe the timing and extent of pre-basic and pre-breeding contour-feather moults in New Zealand, and used plumage of breeding birds in Alaska to infer the proportion of moults occurring in Alaska and Asia. These data demonstrated that: (1) Godwits conducted overlapping pre-alternate and pre-supplemental moults; (2) pre-basic and pre-breeding moults were scheduled differently in relation to southbound and northbound migration respectively; (3) northern and southern Alaskan breeding Godwits of each sex were distinguishable by plumage differences throughout the non-breeding season; and (4) males and northern breeders achieved more extensive breeding plumage by spending longer in pre-breeding moult in New Zealand, rather than through faster moult rates or greater investment in moult during migratory stopover in Asia. The existence of a ventral pre-supplemental moult implies that contemporary selection for red breeding plumage overrides older selection for barred alternate plumage. Our use of individual-based data revealed a continuum of annual moult strategies within the population, which may reflect individual differences in any combination of sex, size, migration distance or breeding location. Even within the highly constrained annual cycle of extreme long-distance migrants, differential selection influences how individuals manage trade-offs among non-breeding activities such as moult, fuelling and migration.

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Introduction

The scheduling of moult is finely tuned by the balancing of direct and indirect costs of feather replacement, the availability of resources and competing energetic requirements of other annual activities (Payne 1972; Murphy and King 1991; Lindström *et al.* 1993). Migratory birds face the particular challenge of conducting moult amid the demands of pre-migratory fuelling, time-critical reproductive efforts on seasonal breeding grounds and migration itself (Alerstam and Lindström 1990), any of which may be to some extent incompatible with moult. Thus, moult schedules in relation to migration may indicate the relative fitness consequences of feather quality and the strength of selection in different segments of the annual cycle (Holmgren and Hedenström 1995; Barta *et al.* 2008).

Bar-tailed Godwits (*Limosa lapponica*) achieve extraordinarily high pre-migratory fuel loads (Piersma and Gill 1998; Battley and Piersma 2005), undertake the most extreme non-stop migratory flights yet recorded (9000–12 000 km; Gill *et al.* 2009; Battley *et al.*, in press) and breed during brief high-latitude summers. Consequently, Godwits may face severe time and energy constraints. In addition, their dramatic seasonal changes in plumage (fig. 1 in Jukema and Piersma 2000) present

potentially significant conflicts between investment in moult and other mandatory annual tasks.

Bar-tailed Godwits moult from non-breeding to breeding plumage in what appear to be overlapping pre-alternate and pre-supplemental contour-feather moults (Piersma and Jukema 1993; Jukema and Piersma 2000). European Bar-tailed Godwits (*L. l. taymyrensis*) appeared to have three generations of ventral plumage: at the population level, plain (basic) feathers were replaced by barred (alternate) feathers, the extent of which then decreased, particularly in males, as the extent of red (supplemental) feathers increased (Piersma and Jukema 1993). Data from individuals are required to confirm that specific feathers are actually replaced twice in the pre-breeding moult(s). However, it has been proposed that barred feathers constitute the ancestral breeding plumage, whereas red feathers reflect more current selection processes (Jukema and Piersma 2000). If true, this presents a conundrum: if moult is costly, why would Godwits retain a redundant and seemingly wasteful moult?

Recently, geographical variation in the Alaskan breeding population of Bar-tailed Godwits (*L. l. baueri*) has been demonstrated: northern breeders of both sexes were smaller, had more extensive breeding plumage and migrated later on both north-

bound and southbound migrations (Conklin *et al.* 2010, 2011; McCaffery *et al.* 2010). It is not yet clear whether the observed variation constitutes discrete evolutionary units or a latitudinal cline within Alaska. However, coupled with dramatic sexual dimorphism in size and breeding plumage (Conklin *et al.* 2011), this population structure suggests multiple strategies for scheduling of moult in relation to migratory flights. For example, how do males manage a more extensive moult in the non-breeding season, when both sexes must accomplish full flight-feather replacement and prepare for equivalent migratory flights? How do northern breeders reconcile a more extensive moult with a longer migration (~1200 km longer each way) between New Zealand and Alaska? If high-quality breeding plumage increases reproductive success, birds should schedule moult as late as possible before breeding (Holmgren and Hedenström 1995). This predicts a significant portion of moult may occur during the Godwits' 4–7 week stopover in Asia before arrival in Alaska (Conklin *et al.* 2010), consistent with observations of continued moult on migration in *L. l. taymyrensis* (Piersma and Jukema 1993). In addition, we expect that moults (both pre-basic and pre-breeding) should be temporally shifted according to breeding phenology, as is migration itself (Conklin *et al.* 2010). However, scheduling of moult in the Alaskan breeding Godwit population has never been described at the individual level (but see McCaffery and Gill 2001).

In this study, we use detailed observations of colour-banded Bar-tailed Godwits to describe plumage and moults throughout the non-breeding season in New Zealand, and compare these with plumage of breeding Godwits in Alaska (Conklin *et al.* 2011) to estimate the duration and proportion of moults occurring outside New Zealand. We use the resulting data to: (1) present the first individual-based evidence for three feather generations in Godwits and describe the temporal overlap of pre-alternate and pre-supplemental moults; (2) assess whether the timing of moults matches intra-population differences in timing of migration; (3) demonstrate the extent to which geographical patterns in Alaskan breeding plumage correspond to differences upon migratory arrival and departure in New Zealand, and in basic plumage; and (4) determine whether differences in the extent of breeding plumage by sex and breeding region are achieved through strategic differences in timing, rate or duration of moult. We then discuss the implications of multiple moult strategies within the population for differential selection for

plumage and potential trade-offs with other non-breeding activities.

Methods

Fieldwork in New Zealand

We studied plumage and migration timing in a small population of Bar-tailed Godwits (200–280 individuals, ~25% of which were colour-banded) at the Manawatu River estuary, New Zealand (40°28′2″S, 175°13′33″E). During two migratory arrival periods (1 September–20 October 2008–09) we conducted high-tide surveys every 3–4 days to record initial arrival and plumage of marked individuals. During three migratory departure periods (4 March–5 April 2008–10) we conducted daily surveys to record departure date (details in Conklin and Battley 2011) and plumage of marked birds. In the intervening summer months (1 January–3 March 2008, 20 October 2008–3 March 2009, 20 October 2009–3 March 2010) we conducted surveys every 4–8 days. During surveys, we digitally photographed marked Godwits to enable detailed scoring of plumage later. This resulted in ~18 000 identifiable photographs of 78 birds (each individual was photographed on 19–35 days per non-breeding season).

Ageing and sexing

Bar-tailed Godwits <2–3 years old were excluded from the study by considering only migratory individuals (young birds do not migrate). Although plumage at departure from New Zealand may be age-dependent (Battley 2006), we included individuals on their first northbound migration (3 males, 1 female).

Godwits were sexed by culmen length and plumage. Females are larger and have longer bills than males (culmen length >99 mm for females and <90 mm for males), but intermediate birds cannot be sexed by size alone. However, obvious plumage differences at departure (Table 1) allowed unambiguous sexing of all individuals of intermediate size (5 males, 3 females).

Moults and plumage scoring

Bar-tailed Godwits have three types of ventral feathers (Piersma and Jukema 1993; Jukema and Piersma 2000): 'basic' (plain whitish), 'alternate' (dark barring on a pale background) and 'supplemental' (plain pale to rusty red). They have two types of dorsal feathers: non-breeding feathers are plain grey with a dark

Table 1.   Evidence for contour-feather moult by Bar-tailed Godwits outside New Zealand

Breeding data are from Godwits in Alaska (Conklin *et al.* 2011). Non-breeding data are from marked Godwits at the Manawatu River estuary, New Zealand (NZ), with arrival data from 2008–09 and departure data from 2008–10. Barring scores indicate amount of barring on anterior ventral region. BP scores indicate extent (%) of breeding plumage

	NZ departure			Breeding			NZ arrival		
	Mean	Range	*n*	Mean	Range	*n*	Mean	Range	*n*
Male									
Barring (0–3)	1.30	0–3	37	1.00	0–3	99			
Dorsal BP (%)	71.8	30–95	37	92.3	65–100	95	24.3	0–55	30
Ventral BP (%)	56.9	23–96	37	81.0	33–100	105	19.6	0–43	30
Female									
Barring (0–3)	1.59	0–3	41	1.74	1–3	74			
Dorsal BP (%)	20.9	0–80	41	78.8	20–95	70	18.6	0–50	32
Ventral BP (%)	2.5	0–33	41	37.1	0–68	75	5.3	0–27	32

central stripe, whereas breeding feathers are blackish brown with pale or reddish spotting on the edges (McCaffery and Gill 2001). Following the suggestion by Jukema and Piersma (2000) that barred ventral feathers represent a distinct moult, we include red ventral and spotted dorsal feathers in all references to 'breeding plumage' (BP) or 'pre-breeding moult', and consider the barred, alternate plumage separately.

The non-flight-feather component of pre-basic moult begins July–August in Alaska, after breeding, and continues on the non-breeding grounds (McCaffery and Gill 2001). The flight-feather component of pre-basic moult begins after southbound migration, and is not addressed in this study. Hereafter, all references to 'pre-basic moult' consider only non-flight contour feathers.

Using the digital photographs (all scoring done by JRC), we characterised plumage as follows. Barring on the anterior ventral region (belly, flanks and breast): 0 = no barring visible; 1 = barring on flanks only; 2 = barring on flanks and upper breast; 3 = barring on flanks, breast and belly. Ventral supplemental plumage: the proportion (5% increments) of red feathers visible against a pale background of basic or alternate feathers on the vent (posterior ventral plumage from leg to vent), breast (anterior ventral, as above) and throat (ventral plumage above breast to chin) regions. We averaged these to create a summary 'ventral' BP score. 'Dorsal' (mantle and scapulars, not including wing coverts) BP: the proportion represented by dark, spotted feathers (5% increments).

Alaskan data

For comparison with plumage in New Zealand, we summarised population-wide data from Alaskan breeding grounds (60–71°N; details in Conklin *et al.* 2011). These data include breeding Godwits captured or photographed in the field during May–July 2003–09 or collected from breeding sites from 1891 to 2001 and preserved as museum specimens.

Marked birds at the New Zealand site contained similar variation in size (culmen length: males, 71–95 mm; females, 90–125 mm) evident in the entire population (Conklin *et al.* 2011), and used breeding sites encompassing most of the known Alaskan breeding range (Conklin *et al.* 2010). Therefore, we assumed that New Zealand and Alaskan Godwits in this study represent comparable samples.

Analysis

When a marked bird was first observed after arrival, we assigned the midpoint of the period after the previous survey as its arrival date. Consequently, we are confident of individual arrival dates within 2–6 days, and recorded initial BP scores ≤10 days after arrival for nearly all birds; other individuals were omitted from analyses of arrival BP. We are confident of individual departure dates within ±1 day (see Conklin and Battley 2011) and photographed every individual within 1–5 days of departure.

We defined the completion of pre-basic moult as the latest calendar day on which any worn, unmoulted contour feathers were visible; as the pre-breeding moult is partial, these were not necessarily BP. We defined the initiation of pre-breeding moult as the first day on which dorsal or ventral BP was visible. For birds

departing New Zealand with no BP, we used departure date + 8 days (the earliest possible day after arrival in Asia) to represent initiation date of pre-breeding moult. We considered pre-breeding moult suspended when an individual's plumage was first equal to its score at departure. We excluded individuals with >10 days of uncertainty in completion, initiation or suspension of moult from relevant analyses.

Breeding latitude of New Zealand Bar-tailed Godwits has been strongly linked with migration timing (Conklin *et al.* 2010) and body size (Conklin *et al.* 2011). We assigned the likely Alaskan breeding region ('north' or 'south' of 64°N) to marked Godwits at the Manawatu River estuary (*n* = 78) by the following process. Sixteen Godwits were tracked to breeding sites using geolocators (Conklin *et al.* 2010); among these, all birds departing New Zealand by 24 March bred south of 64°N, and five of six that departed after 24 March bred north of 64°N. We therefore divided the remaining 62 Godwits into 'early' and 'late' by average departure date (cutoff: 24 March). Also, northern breeders of both sexes are smaller than southern breeders (Conklin *et al.* 2011), so we divided the birds into 'small' and 'large' classes using culmen length (cutoffs: males, 82 mm; females, 108 mm). For 46 birds (74%), the two criteria suggested the same breeding region (small and late departure or large and early departure). When the criteria disagreed, we used the criterion more divergent from the cutoff to assign breeding region (e.g. very large + slightly late = 'south'). This method might misclassify a small number of individuals.

To test whether data on the phenology of moult and migration were comparable across years, we first ran analyses of variance (ANOVA) for each parameter (sexes separate), using Alaskan region and year as fixed factors (results not shown); there were no significant region × year interactions. Therefore, we averaged values for each individual across available years (1–3 years, depending upon bird and parameter).

Results

Contour-feather moult in New Zealand

Upon arrival at the Manawatu River estuary (September–early November), all marked Godwits had both worn and new contour feathers (e.g. Fig. 1*a*). Most individuals (95–98%) arrived with visible dorsal or ventral BP, the extent of which then decreased after moult resumed within 1–2 weeks of arrival. The last trace of BP was seen 23 September–22 December (sexes similar). Worn dorsal feathers (basic type, or unknown type owing to extreme wear) were often visible 10–35 days after an individual's last BP disappeared. All birds completed pre-basic moult by late December (Fig. 2).

Basic plumages (Fig. 1*b*) of males and females were similar. All birds were strongly barred on the vent and completely lacked barring on the throat, central breast and belly. All males and most females had some barring on the flanks (score 1); 29% of females had none (score 0).

First increases in ventral barring occurred on all males between 5 January and 9 February (Fig. 3*a*). Most females showed increased barring between 9 January and 4 March; 18% showed no increase before leaving New Zealand.

For males, the first increases in ventral barring, dorsal spotting and red ventral feathers were approximately simulta-

Fig. 1. Plumage of one northern breeding male Bar-tailed Godwit through the non-breeding season in New Zealand. (*a*) 6 October, showing incomplete pre-basic moult; (*b*) 5 January, in basic plumage; (*c*) 29 January, showing increases in ventral barring, dorsal spotted feathers and red ventral feathers; and (*d*) 1 March, showing further increases in dorsal and ventral breeding plumage and a decrease in barring.
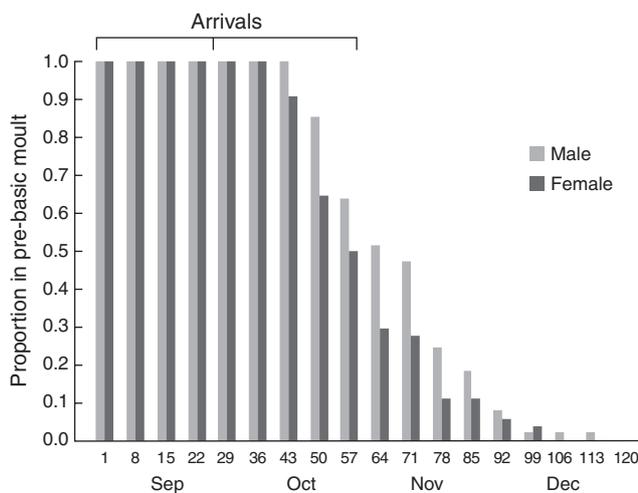
Fig. 2. Timing of pre-basic contour-feather moult of male and female Bar-tailed Godwits in New Zealand, 2008–09; Day 1 = 1 September, Day 120 = 29 December. Values represent mean proportion of individuals with visible, unmoulted feathers. For migratory arrivals, median and span of dates are indicated.

neous (generally within 1–2 weeks; see Fig. 1*c*); first dorsal BP appeared 12 January–28 February (Fig. 3*b*) and ventral BP appeared 7 January–17 February (Fig. 3*c*). After initial increases, 74% of male barring scores subsequently dropped as ventral BP scores increased (e.g. Fig. 1*c–d*). All males appeared to suspend moult before migration: breast-plumage scores stopped increasing 5–40 days (mean = 18.5 days) before departure.

By contrast, female BP appeared later and not universally. A total of 79% of females gained dorsal BP, which first appeared 30 January–23 March (Fig. 3*b*); 41% gained ventral BP, which appeared 23 January–23 March (Fig. 3*c*). No female barring scores dropped after a pre-departure peak. Among moulting females, suspension was not uniformly evident: some appeared to add BP as late as 1–5 days before departure.

Evidence for moult beyond New Zealand

Dorsal and ventral BP scores of both sexes were higher in Alaska than at arrival or departure in New Zealand (Table 1; Mann–Whitney tests, all $P < 0.001$), indicating that portions of both pre-basic and pre-breeding moult occurred outside of New Zealand. Males had lost 75% of total Alaskan BP before southbound migration and females had lost 81% of BP. Upon departure from

New Zealand, total BP scores of males and females were 74% and 17% of Alaskan scores. Barring scores of males were lower in Alaska than at departure from New Zealand ($U_{99,37} = 2271.5$, $Z = 2.34$, $P = 0.02$), but female scores did not differ ($U_{74,41} = 1379.0$, $Z = -0.87$, $P = 0.39$).
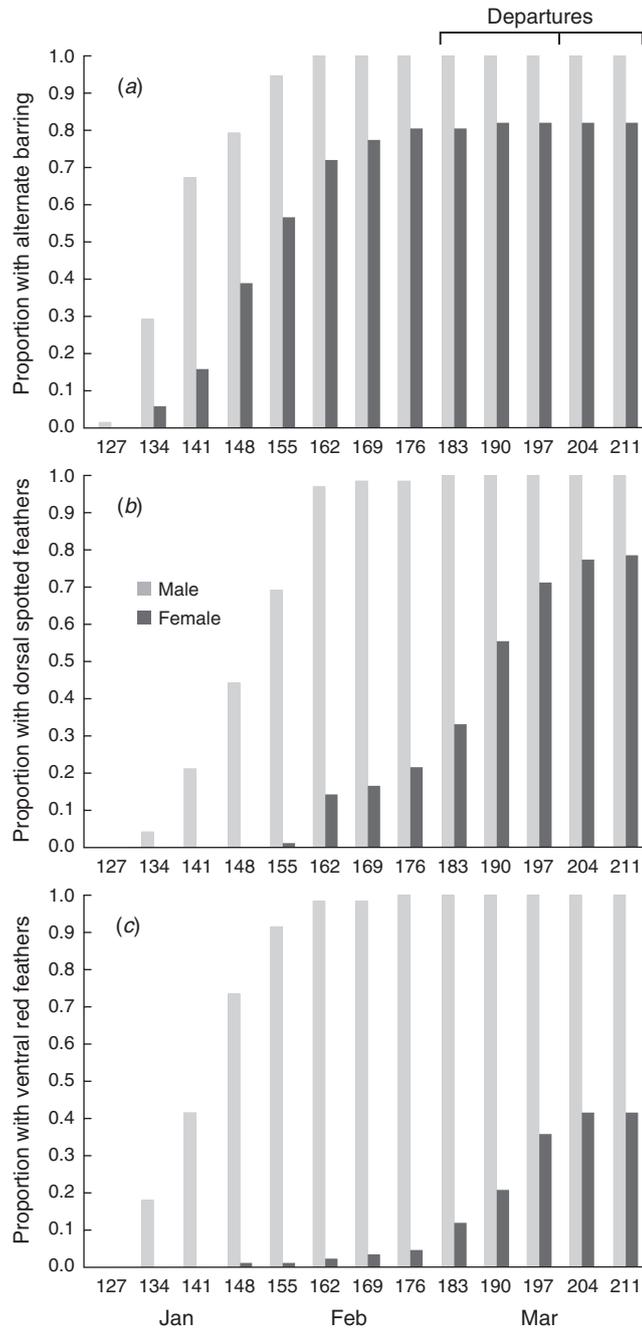

Fig. 3. Timing of pre-alternate and pre-supplemental contour-feather moults of male and female Bar-tailed Godwits in New Zealand, 2008–10; Day 127 = 5 January, Day 211 = 30 March. Values represent mean proportion of individuals with: (*a*) alternate ventral barring; (*b*) dorsal spotted feathers; and (*c*) ventral red feathers. For migratory departures, median and span of dates are indicated.

### Plumage differences by breeding region

Ventral barring scores of northern and southern breeding males were indistinguishable throughout the non-breeding season in New Zealand (Fig. 4*a*; all tests $P > 0.20$). For both groups, the peak barring score in New Zealand was greater than the score at departure (Wilcoxon paired tests, north: $W_{19} = 0.0$, $Z = -3.35$, $P = 0.001$; south: $W_{16} = 0.0$, $Z = -3.30$, $P = 0.001$). In Alaska, northern breeding males had less barring than southern breeding males ($U_{68,31} = 1344.5$, $Z = 2.38$, $P = 0.017$).

Northern breeding females had more barring than southern breeding females at every stage in New Zealand and Alaska (Fig. 4*b*; Basic: $U_{11,23} = 71.5$, $Z = -2.56$, $P = 0.010$; NZ peak and departure: $U_{15,26} = 56.0$, $Z = -4.00$, $P < 0.001$; Breed: $U_{54,20} = 324.0$, $Z = -2.85$, $P = 0.004$). All Godwits with barring scores of 0 in basic plumage were southern breeding females.

Northern breeders of both sexes always had more extensive BP than southern breeders (Fig. 5). On departure from New Zealand, northern and southern breeding males differed in ventral BP
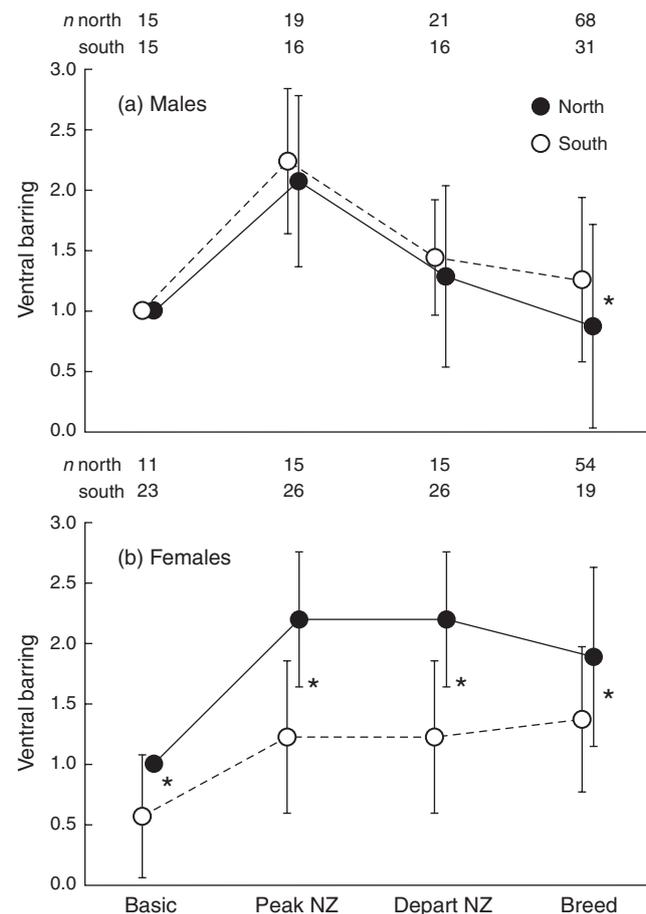
Fig. 4. Change in ventral barring (score 0–3; data are mean score ± 1 s.d.) of (*a*) male and (*b*) female Bar-tailed Godwits from northern and southern Alaskan breeding regions (north or south of 64°N). On *x*-axis, Basic indicates full basic plumage in mid-December; Peak NZ indicates highest score achieved before departure from New Zealand; Depart NZ indicates plumage at departure; and Breed indicates full breeding plumage in Alaska. Cohorts are offset horizontally for clarity. Asterisks indicate significant north–south differences.
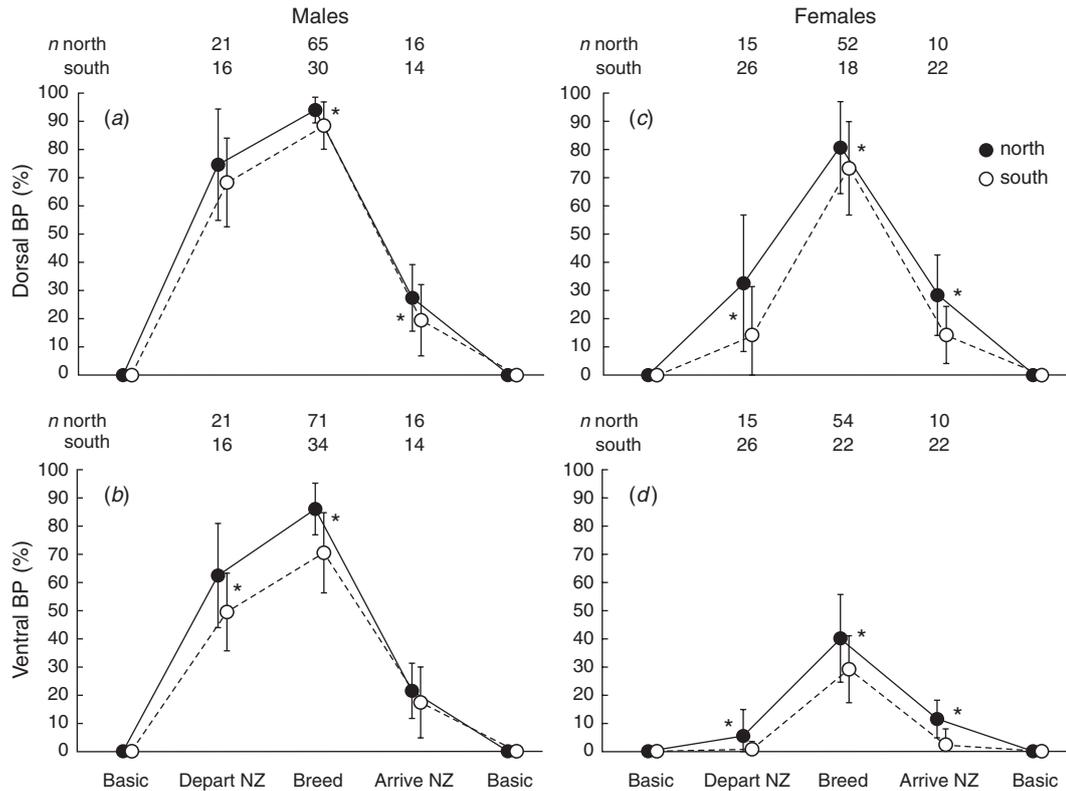
Fig. 5. Change in breeding plumage (BP): (*a*) male dorsal, (*b*) male ventral, (*c*) female dorsal and (*d*) female ventral breeding plumage of Bar-tailed Godwits from northern and southern Alaskan breeding regions (north or south of 64°N). Data are mean % ± 1 s.d. See Fig. 4 for explanation of *x*-axis categories. Cohorts are offset horizontally for clarity. Asterisks indicate significant north–south differences.

($U_{21,16} = 87.0$, $Z = -2.48$, $P = 0.012$) but not dorsal BP ($U_{21,16} = 113.5$, $Z = -1.67$, $P = 0.10$). In Alaska, male cohorts differed in both dorsal BP ($U_{65,30} = 566.5$, $Z = -3.42$, $P = 0.001$) and ventral BP ($U_{71,34} = 388.5$, $Z = -5.61$, $P < 0.001$). On arrival in New Zealand, males differed in dorsal BP ($U_{16,14} = 64.5$, $Z = -1.99$, $P = 0.047$) but not ventral BP ($U_{16,14} = 85.0$, $Z = -1.13$, $P = 0.28$).

Northern and southern breeding females were always distinguishable by both dorsal BP (NZ departure: $U_{15,26} = 93.0$, $Z = -2.77$, $P = 0.006$; breeding: $U_{52,18} = 306.5$, $Z = -2.21$, $P = 0.027$; NZ arrival: $U_{10,22} = 47.0$, $Z = -2.57$, $P = 0.010$) and ventral BP (NZ departure: $U_{15,26} = 90.0$, $Z = -3.17$, $P = 0.002$; breeding: $U_{54,21} = 319.5$, $Z = -2.92$, $P = 0.003$; NZ arrival: $U_{10,22} = 18.0$, $Z = -3.78$, $P < 0.001$).

Moult schedules by breeding region

Northern breeding Godwits of both sexes arrived in New Zealand later than southern breeders (Table 2). On average, northern breeding females and all males completed pre-basic moult 40–45 days after arrival, compared with 33.5 days for southern breeding females.

Both male cohorts initiated pre-breeding moult *c.* 21 January and suspended moult ~18 days before departure; thus, northern breeding males spent longer in moult owing to their later departure (Table 2). Northern breeding males moulted 68.6% of their contour feathers (dorsal and ventral BP combined; Fig. 5*a–b*) in 45.9 days, for a mean moult rate of 1.49% per day. Southern breeding males moulted 58.9% of their contour feathers in 36.1 days, a rate of 1.63% per day. These moult rates did not differ ($t_{18,16} = 1.52$, d.f. = 32, $P = 0.07$); the overall mean rate for males was $1.57 \pm 0.42\%$ (s.d.) per day.

Southern breeding females initiated pre-breeding moult *c.* 8 March, just 9 days before departure (Table 2). Northern breeding females began moult *c.* 2 March, 25 days before departure. For females, the brief time in moult and uncertainty regarding suspension of moult precluded the calculation of useful moult rates. Assuming the moult rate observed in males (1.6% per day), northern breeding females spent on average 12 days in moult to reach departure BP and southern breeding females spent just 5 days (Table 2).

Projected pre-breeding moult in Asia

During staging in Asia, northern males must increase BP from 69% (New Zealand departure) to 90% (breeding; Fig. 5). At the observed New Zealand moult rate (1.6% per day), this would require ~13 days. Southern breeding males similarly require 13 days to increase from 59 to 79%. Assuming the male moult rate, northern breeding females require 26 days (from 19 to 61%), compared with 27 days for southern breeding females (from 8 to 51%). Thus, total investment in pre-breeding moult is 59 days for

Table 2. Moult and migration schedules of Bar-tailed Godwits during the non-breeding season in New Zealand

Data on arrival in New Zealand (NZ) and pre-basic moult are from 2008–09; data on pre-breeding moult and departure from New Zealand are from 2008–10. For dates, Day 1 = 1 September, Day 211 = 30 March. North and South are assumed Alaskan breeding regions (north or south of 64°N). Asterisks indicate significant north–south differences

| | Unit | South | | | North | | | | | |
		Mean	s.d.	n	Mean	s.d.	n	t	d.f.	P
Males										
NZ arrival	date	22.6	4.2	15	29.9	4.4	17	4.80	30	<0.001*
End pre-basic moult	date	67.4	14.6	14	70.8	13.8	16	0.64	26	0.53
NZ pre-basic moult	days	44.8	15.2	14	41.6	13.1	14	0.59	26	0.56
Start pre-breeding moult	date	141.8	7.9	16	144.1	7.3	18	0.88	32	0.39
Suspend pre-breeding moult	date	178.1	7.9	16	190.4	8.0	19	4.56	33	<0.001*
NZ departure	date	197.1	4.1	16	208.3	3.1	19	9.07	33	<0.001*
NZ pre-breeding moult	days	36.1	8.1	16	45.9	7.9	18	3.56	32	0.001*
Females										
NZ arrival	date	21.0	11.2	22	33.4	12.2	10	2.81	30	0.009*
End pre-basic moult	date	52.6	9.5	20	73.4	16.3	9	4.35	27	<0.001*
NZ pre-basic moult	days	33.5	8.2	20	40.1	6.5	9	2.12	27	0.043*
Start pre-breeding moult	date	188.5	15.8	26	182.1	12.5	12	1.24	36	0.22
NZ departure	date	197.8	4.4	26	207.9	2.9	15	8.03	39	<0.001*
NZ pre-breeding moult[A]	days	4.7	5.9	26	11.9	9.2	15	3.07	39	0.004*

[A]Calculated using male moult rate of 1.6% per day.

northern breeding males, 49 days for southern breeding males, 38 days for northern breeding females and 32 days for southern breeding females (Fig. 6).

Discussion

Evidence for pre-supplemental moult

Our study provides the first direct evidence that individual Godwits replace some ventral feathers twice during pre-breeding moult, confirming that the barred and plain-red feathers represent distinct plumages (alternate and supplemental respectively; Humphrey and Parkes 1959). This was strongly suggested by a population-level decline of (recently grown) barred feathers of male European Bar-tailed Godwits (*L. l. taymyrensis*) during northbound stopover in the Netherlands (Piersma and Jukema 1993), but population turnover during the study precluded strong inferences regarding individual moult. Furthermore, hormonal changes during moult potentially produce colour differences between feathers grown at different stages of the same moult (Howell 2010). Our photographic monitoring of individuals throughout moult provided many specific examples of red feathers replacing barred feathers that were just 3–5 weeks old (e.g. Fig. 1b–d).

This rapid replacement of alternate feathers resulted in pre-departure decreases in barring of most males, and lower scores in Alaska testify to additional loss of alternate feathers in Asia. In females, the extent of pre-supplemental moult was insufficient to cause significant decreases in barring before departure from New Zealand or arrival in Alaska. However, some females may conduct additional pre-alternate moult in Asia: 7% of females departed New Zealand with a barring score of 0, whereas all females in Alaska had some degree of barring.
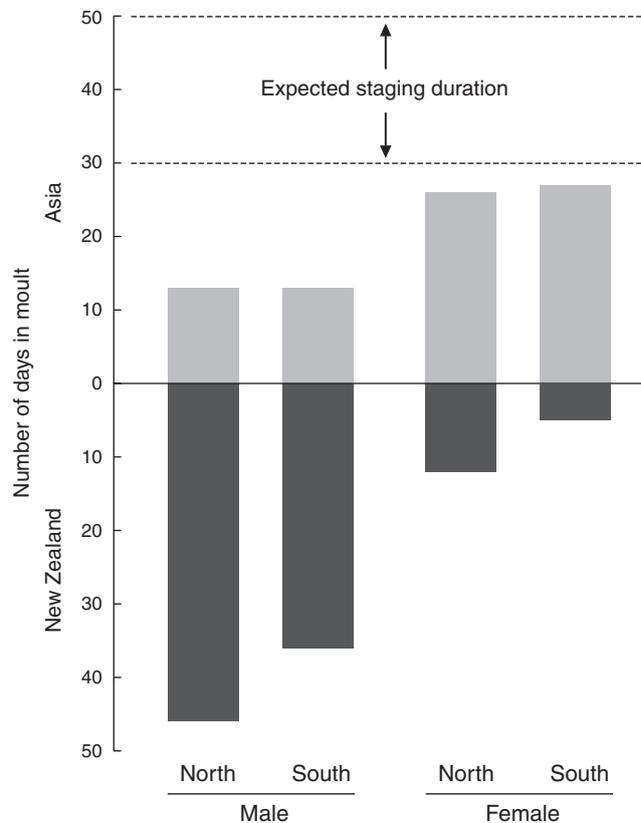
Fig. 6. Estimated average duration of Bar-tailed Godwit pre-breeding moult occurring in New Zealand and Asia by sex and Alaskan breeding region (north or south of 64°N). For reference, expected staging duration in Asia (30–50 days; Conklin *et al.* 2010) is indicated.

The red ventral feathers of males are generally darker than those of females (Piersma and Jukema 1993; J. R. Conklin, pers. obs.), and males perform an earlier and more extensive pre-supplemental moult than females. By contrast, the barred feathers of males and females are indistinguishable, and the extent and timing of pre-alternate moult were also similar. This supports the view that historical selection for alternate plumage was similar for the sexes (promoting equivalent crypsis during shared parental duties), whereas pre-supplemental plumage reflects current sexual selection acting more strongly upon males, as in Ruffs (*Philomachus pugnax*; Jukema and Piersma 2000). As the ventral breeding 'aspect' of female Bar-tailed Godwits contains significant contributions from two moults, both may be under current selection. However, breeding males retain little alternate barring, and so this moult may be an evolutionary artefact which is insufficiently costly to be maladaptive. If barred feathers represent the ancestral breeding plumage within the Scolopacidae, other species with both barred and red ventral feathers (e.g. Curlew Sandpiper *Calidris ferruginea*, dowitchers *Limnodromus* spp.) may undergo pre-supplemental moults that have yet to be described.

It is intriguing that increases in the extent of ventral barred, dorsal spotted and ventral red feathers occurred approximately synchronously in males, whereas the three types were staggered in females (Fig. 3). This means that initiation of dorsal and ventral pre-alternate moults are temporally decoupled, by ~3–5 weeks, in females but not in males. Another consequence is that temporal overlap of pre-alternate and pre-supplemental moults differs substantially between the sexes. As most male Godwits begin the two moults simultaneously, it appears that ventral pre-supplemental moult replaces some basic feathers and some alternate feathers. Presumably, selection for early timing of pre-supplemental moult in males has led to the effective loss of pre-alternate moult in some follicles, which 'skip' directly from plain to red feathers without an intervening barred feather. As discussed by Battley *et al*. (2006) with regard to dorsal pre-supplemental moult in Great Knots (*Calidris tenuirostris*), this creates an inconsistency within the Humphrey and Parkes (1959) nomenclature, in which follicles undergoing just two moults in the definitive cycle can only produce 'basic' and 'alternate' plumage. As pre-alternate moult appears partial in both sexes, certain follicles may skip directly from basic to supplemental plumage in females as well, but we have no conclusive evidence of this. Regardless, it seems sensible to refer to the red ventral feathering of Godwits as supplemental plumage, irrespective of the number of moults undertaken by individual follicles. Thus far, there is no evidence that Godwits perform a dorsal pre-supplemental moult.

Are timing of moult and migration linked?

As the timing of both northbound and southbound migration were 2–4 weeks later in northern breeding Bar-tailed Godwits tracked with geolocators (Conklin *et al*. 2010), we hypothesised that other annual events may be shifted temporally to accommodate individually optimised migration schedules (e.g. Buehler and Piersma 2008). This predicts that northern breeders should complete pre-basic moult and initiate pre-breeding moult later than southern breeders. However, evidence here

does not uniformly support this. On average, northern breeding males completed pre-basic moult and initiated pre-breeding moult later than southern breeding males by ~3 days, which was less than differences in migration timing and not statistically significant. For females, the prediction was upheld for completion of pre-basic moult, but not for initiation of pre-breeding moult.

Achieving breeding plumage has an effective deadline (arrival on breeding grounds) and, therefore, timing of pre-breeding moult should be closely linked to timing of migration (Holmgren and Hedenström 1995). However, geographical breeding cohorts of Godwits differed substantially in extent of BP and, consequently, in the duration of pre-breeding moult, obscuring any simple relationship between moult initiation and migratory departure.

As pre-basic is a complete moult for all Godwits, we do not expect systematic differences in moult duration by sex or breeding region. Therefore, variation in completion of pre-basic moult is likely to mirror variation in onset of moult, which may be triggered by hormonal changes associated with cessation of breeding activity (Hahn *et al*. 1992; Dawson 2006). Accordingly, we found no evidence of active moult on the breeding grounds in Alaska (May–early August; $n = 77$ captures or specimens); Godwits appear to initiate pre-basic moult on post-breeding staging grounds (McCaffery and Gill 2001). Earlier thawing of southern Alaskan breeding sites allows clutch initiation 2–4 weeks earlier than northern breeding sites (Conklin *et al*. 2010), and Godwits caring for young through fledging may spend 3–6 weeks longer on breeding sites than those that fail during incubation. Thus, the timing of pre-basic moult reflects both breeding-site phenology, which may vary little annually, and duration of breeding investment, which should vary substantially among individuals and years. This explains why completion of pre-basic moult varied by 10–11 weeks between individuals in our study.

Bar-tailed Godwits tracked with geolocators moved from breeding sites to staging sites 40–88 days before departing Alaska (J. R. Conklin and P. F. Battley, unpubl. data). Birds in this study had completed ~50–90% of pre-basic moult upon arrival in New Zealand, and finished moulting 33–45 days after arrival. Godwits suspend moult for several days before migratory flights, perhaps to prioritise fuel accumulation and preparation of flight muscles and internal organs for migratory condition (Piersma *et al*. 1999; Landys-Ciannelli *et al*. 2003). Upon arrival, they may invest primarily in recovery from long-distance flights before resuming moult (Piersma and Jukema 1993). Accounting for these periods of suspension, the estimated total duration of pre-basic moult is ~70–90 days.

Are breeding cohorts distinguishable in New Zealand?

The plumage of Bar-tailed Godwits varies across the latitude of the Alaskan breeding range (59–71°N): the extent of male breeding plumage increases with latitude, whereas the reddest females occur ~66°N (Conklin *et al*. 2011). This population structure is not maintained in the non-breeding season, as Godwits from all Alaskan regions mix freely at New Zealand sites. By assigning individuals to probable breeding region based on size and migration timing (which also vary geographically), we asked

whether cohorts were distinguishable by plumage in the non-breeding season. In New Zealand, northern breeders of both sexes had more dorsal and ventral breeding plumage than southern breeders at both arrival and departure. As investment in moult in Asia was similar for cohorts within each sex, plumage differences upon departure from New Zealand were similar to those found in Alaska.

In Alaska, alternate barring of females increases with latitude (Conklin *et al*. 2011). Males, however, do not show this pattern, probably owing to their more extensive replacement of barred feathers during pre-supplemental moult. We hypothesised that the ancestral alternate plumage occurred in a north–south cline, before the evolution of the pre-supplemental moult. Thus, the extent of barring at the onset of pre-supplemental moult in present-day Godwits may indicate breeding region. This could not be adequately tested for males, because pre-alternate and pre-supplemental moults were nearly simultaneous rather than sequential. However, the prediction held for females: north–south differences in barring were greatest in New Zealand, before substantial pre-supplemental moult in Asia.

We were surprised to find differences among females in *basic* plumage: all birds with barring scores of 0 were southern females. The drab basic plumage of Godwits may provide crypsis in tidal estuaries (Ferns 2003), with barring on the flanks and vent serving to enhance countershading (Rowland 2009). However, because the population is not geographically structured year-round, plumage differences among breeding cohorts are unlikely to have functional significance in New Zealand. It is possible that variation in basic plumage barring simply represents a non-adaptive carry-over from alternate plumage.

Moult strategies by sex and breeding region

The more extensive BP of northern breeders was not the result of faster moult rates in New Zealand or greater investment in moult in Asia. Rather, northern birds of both sexes achieved greater BP than southern birds by spending ~7–10 days longer in pre-breeding moult in New Zealand. All cohorts required moult in Asia to reach expected Alaskan plumage, but the extent of this additional moult was nearly identical for cohorts within each sex, despite evidence that the duration of stopovers in Asia increases with breeding latitude (Conklin *et al*. 2010).

Our findings confirm previous indications of distinct strategies of moult and migration in New Zealand Godwits (Battley and Piersma 2005). In early March, non-moulting males were larger and fatter, and had lower BP scores and larger testes than those in active moult. Godwits were collected between the average dates of moult suspension for southern (25 February) and northern (9 March) breeding males in our study. Thus, the inference by Battley and Piersma (2005) that non-moulting birds were preparing for earlier migration was correct: these were clearly southern males, which are larger (Conklin *et al*. 2011) and migrate earlier and with less BP than northern males.

As we calculated moult in Asia from cohort means, the proportion of individuals conducting additional moult after New Zealand departure is unclear. In the Netherlands, moulting male Godwits were redder and heavier than non-moulting males,

suggesting that only 'high-quality' birds could afford to invest in moult during migration (Piersma and Jukema 1993). This predicts greater plumage variation in Alaska than at New Zealand departure, because differential moult in Asia should magnify individual differences. Our data contradict this: variation at departure from New Zealand was generally greater than in Alaska. The lowest BP scores in Alaska were greater than the lowest scores at New Zealand departure, indicating that the palest birds moulted in Asia. Conversely, some males departed New Zealand with BP scores very close to the greatest observed in Alaska, and thus could add little to their plumage in Asia.

If plumage quality influences reproductive success, Godwits should complete pre-breeding moult at the latest opportunity (Asia) to ensure that not all breeding feathers must endure flights of 16 000–18 000 km and 2 months of migration wear before serving their ultimate function (Holmgren and Hedenström 1995). Consistent with this, 75% of female pre-breeding moult occurred in Asia, and some southern females did not moult in New Zealand at all. Godwits spend 30–50 days staging in Asia (mean = 40 days, sexes similar; Conklin *et al*. 2010), and presumably suspend moult at both ends of their stay. Thus, 26–27 days of moult in Asia, as we have projected, may approach the maximum achievable by females, without adopting faster moult rates than observed in New Zealand.

Time spent in Asia is insufficient for a male's entire pre-breeding moult (Fig. 3), which explains why all males initiated moult in New Zealand. However, males performed only half as much moult in Asia as females, and so apparently did not moult as late as possible. This may suggest that females are better suited to moult during migration, owing to greater flight or fuelling efficiency. Alternatively, if moulting conditions were more reliable in New Zealand than in Asia, males may simply follow a more conservative moult strategy; that is, males are unwilling to 'risk' leaving a large proportion of moult until the latest opportunity, whereas females face lower costs of this risk. This assumes that Godwits respond to poor conditions during the northbound flight or at staging sites by increasing investment in thermoregulation and fuelling at the expense of moult. A consequence would be annual variation in plumage in Alaska, potentially population-wide and more extreme in females; there are currently no data to address this.

The existence of a pre-supplemental moult strongly implies contemporary sexual or natural selection for plumage in Alaska. Presumably, sexual differences in plumage reflect the greater role of males in competition for mates and territories (McCaffery and Gill 2001), and north–south differences result from geographical variation in habitat or competition for mates. It is significant that females invested disproportionately in dorsal BP over ventral BP in both New Zealand and Asia; shared incubation requires both sexes to be cryptic, and so selection for male and female plumage should be more similar for dorsal than ventral plumage. Hypothetically, relaxed selection for ventral BP may 'free' females and southern breeders to conduct slower, higher quality flight-feather moults (Dawson *et al*. 2000; Serra 2001) or migrate with greater fuel stores, at the expense of pre-breeding moult. Conversely, prioritisation of ventral BP by males and northern breeders may constrain their investment in wing moult or fuelling.

An alternative view is that plumage differences among Godwits arise from energetic constraints on moult imposed by body size (Hedenström 2006). This simple, but not mutually exclusive, hypothesis requires no differential selection for plumage in Alaska. Ranked smallest to largest (northern males, southern males, northern females, southern females), the cohorts showed decreases in both duration and proportion of pre-breeding moult in New Zealand. As pre-migratory fuel stores scale proportionally with body size (Battley and Piersma 2005), larger birds must accumulate a greater absolute fuel mass, while maintaining a greater non-breeding mass. In addition, they must grow a greater mass of both contour and flight feathers (Hedenström 2006; Rohwer *et al*. 2009). If larger birds were consequently limited in time or energy available for pre-breeding moult in New Zealand, it would predict the relative departure plumages that we observed. This hypothesis may be tested by comparing rates of pre-migratory mass gain or duration of primary-feather moults by sex and body size, and by examining the extent of overlap in the timing of moults and fuelling.

Most current knowledge of moult strategies derives from population-level studies, in which individuals contribute but one data point, owing to the difficulty of capturing or otherwise sampling free-living birds multiple times during a season. Although adequate to describe general patterns of moult, this approach can mask considerable variation of ecological interest. Our use of repeatedly sampled individuals revealed a continuum of annual moult strategies within the New Zealand population of Bar-tailed Godwits, which may reflect individual differences in sex, size, migration distance, or breeding location, or some combination of these. As successive life-history stages of long-distance migrants may be inextricably linked, and differential selection may occur at any stage of the annual cycle, true understanding of how individuals manage trade-offs between moult and other non-breeding activities may require a year-round individual approach.

Acknowledgements

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