

## MOLT OF BRISTLE-THIGHED CURLEWS IN THE NORTHWESTERN HAWAIIAN ISLANDS

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**ABSTRACT.**—I studied molt of Bristle-thighed Curlews (*Numenius tahitiensis*) on Laysan Island in the Northwestern Hawaiian Islands from 1988-1991. Adult curlews underwent a complete prebasic molt between August and December. Duration of primary molt was about 92 days, which is rapid compared with other shorebirds that molt in tropical and southern latitudes. Adults replaced large numbers of primaries and secondaries simultaneously, and about 50% of the birds became flightless during molt. The prealternate molt began in winter and ended in early spring; it involved the body feathers and variable numbers of rectrices but no remiges. Juveniles molted body feathers and some rectrices during their first autumn and winter but did not replace their juvenal primaries until the spring and summer of their second calendar year. Second-year curlews began replacing their new first basic primaries in late summer, in some cases before the outer juvenal primaries had been dropped. The delayed first prebasic primary molt is probably an adaptation allowing inexperienced birds to devote energy expenditure in their first winter to obtaining food rather than to molting remiges. Because second-year birds remain on the wintering grounds throughout the year and do not prepare for migration, there is no selection against replacing new primaries. Unlike most shorebirds, adult Bristle-thighed Curlews gained mass steadily throughout the autumn and winter. Their rapid prebasic molt in autumn may be an adaptation to allow the birds ample time to build up fat reserves during winter. I suggest that the absence of rich intertidal feeding areas and the frequency of winter storms make it difficult for curlews to take on large fat stores in short time periods as do species that winter on continental coasts. The lack of predators and the small size of remote oceanic islands obviate the need for curlews to maintain peak flight efficiency, allowing birds to become flightless during molt in autumn and to carry increasingly large fat stores throughout the winter. *Received 8 October 1992, accepted 15 December 1992.*

SEVERAL GENERAL PATTERNS in the timing and duration of the prebasic molt of shorebirds have been identified. For example, most shorebirds do not overlap molt of flight feathers with either breeding or migration, although molt of body feathers may begin on the breeding grounds (Ferns 1978, Johnson and Johnson 1983). Notable exceptions include some populations of Purple Sandpipers (*Calidris maritima*; Sutton and Parmelee 1955, Bengston 1975) and Dunlins (*C. alpina*; Holmes 1966) that replace their primaries while breeding, and Common Redshanks (*Tringa totanus*; Pienkowski et al. 1976) that molt while migrating. Also, shorebirds wintering in tropical and southern latitudes tend to initiate molt later, and to molt more slowly, than do species that winter farther north (Prater 1981). Despite substantial infor-

mation on the molt of shorebirds (e.g. Boere 1976, Morrison 1976, Pienkowski et al. 1976, Prater 1981), the ecological factors responsible for these general patterns have been difficult to elucidate. Consequently, there remains a need to document molt in additional species.

Bristle-thighed Curlews (*Numenius tahitiensis*) are one of the rarest and least-studied shorebirds in the world. They breed in remote areas of western Alaska and winter on small islands in the tropical and subtropical Pacific Ocean. The only published information on their molt comes from a small sample of subadults collected in the Marshall Islands during summer (Johnson 1977). Bristle-thighed Curlews exhibit several unusual traits that make a study of their molt particularly interesting: (1) they are the only migratory shorebird whose winter range is restricted to oceanic islands, which they reach after nonstop flights of at least 4,000 km (Marks et al. 1990); (2) they have high annual survivorship and extreme longevity (Marks 1992); (3) most subadults remain on the wintering

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grounds until they are at least 34 months old (unpubl. data); and (4) some individuals become flightless during molt (Marks et al. 1990).

I studied molt of Bristle-thighed Curlews on Laysan Island from 1988–1991. In this paper, I document molt of these curlews by age class, including a more thorough treatment of the flightless phenomenon that was first noted in 1988. I also examine how foraging ecology, timing and extent of premigratory fat accumulation, and vulnerability to predation may influence the timing and duration of molt in a migratory shorebird.

#### STUDY AREA AND METHODS

Laysan Island (25°46'N, 171°44'W) is a low coral island within the Northwestern Hawaiian Islands, which extend for 2,000 km WNW of the main Hawaiian Islands and constitute the northern limit for wintering Bristle-thighed Curlews. Laysan has an area of 397 ha, including a 70-ha hypersaline lagoon. It is managed as a wildlife refuge by the U.S. Fish and Wildlife Service and is uninhabited except when researchers are present. Temperatures generally are hot from summer through early autumn (25–32°C) and seldom drop below 15°C in winter. From November through March, wind speeds often range from 35 to 50 km/h for prolonged periods (U.S. Fish and Wildlife Service unpubl. data). About 47% of the island is vegetated (Morin and Conant 1990); the most abundant plant is a bunchgrass (*Eragrostis variabilis*). Ely and Clapp (1973) and Morin and Conant (1990) have provided detailed descriptions of the island, including a complete list of plants.

I visited Laysan Island from: mid-April to mid-May, and late August to mid-November 1988; late June to early September 1989; mid-August to late November 1990; and early February to mid-June 1991. I also captured curlews during brief visits to several other islands in the Northwestern chain: Lisianski Island (225 km WNW of Laysan) in mid-May 1988, Tern Island (604 km ESE of Laysan) in mid-June 1989, and Midway Atoll (621 km WNW of Laysan) in late April 1992.

Curlews were captured at night with a spotlight and hoop net. Of the 420 Bristle-thighed Curlews that I inspected for molt, 349 were captured on Laysan Island, 37 on Midway Atoll, 30 on Lisianski Island, and four on Tern Island. Curlews were banded on their tibiotarsi with a U.S. Fish and Wildlife Service band and a unique combination of four colored plastic bands.

I classified birds in their first, second, and third calendar years as hatching year (HY), second year (SY), and third year (TY), respectively. I considered adults to be after third year (ATY) based on observations of marked, younger birds that did not migrate

north in spring. I followed Humphrey and Parkes (1959) for terminology of molts and plumages. Molt was scored on the right wing using Ginn and Melville's (1983) method. Each remex was given a score of 0 (old feather), 1 (missing or pin feather), 2 (emerging to one-third grown), 3 (one-third to two-thirds grown), 4 (more than two-thirds grown), or 5 (new feather with no sheath). I scored only the first 9 or 10 secondaries during 1988 and 1989, and the first 14 during 1990 and 1991.

Molt duration is typically estimated by regressing primary molt scores of individual birds against date of capture (Pimm 1976, Summers et al. 1983). This method assumes that molt scores increase linearly with time. However, in species that have primaries of unequal length (e.g. shorebirds), molt progresses at different rates over time (Summers 1980). A more accurate estimate of molt duration is obtained by assuming that feather material is grown at a constant rate throughout molt. Accordingly, I converted molt scores of adult curlews to percentage of feather mass grown following the methods of Summers et al. (1983) and Underhill and Zucchini (1988). I collected three adult curlews with broken wings (injuries that likely resulted from midair collisions with seabirds) and fresh primaries on Laysan in 1991. I dried the primaries of each unbroken wing to constant mass in a convection oven (48 h at 60°C) and then weighed them to the nearest 0.1 mg. The percentage mass of each primary relative to all 10 primaries was then averaged for the three collected birds. Molt indices were derived by summing the product of the mid-point interval for the proportion of feather grown and the mean percentage mass for each feather (see Underhill and Zucchini 1988:358–359). The data were of "Type 2" (Underhill and Zucchini 1988). The method assumes that molt scores are derived from a random sample of birds on each sampling date and that no immigration or emigration occurs during the sampling period (Underhill et al. 1990). These assumptions are reasonable because few (if any) curlews arrived at or departed from Laysan during the molting period (unpubl. data). Molt parameters (mean starting date, duration in days, and mean completion date) were calculated using the algorithm of Underhill and Zucchini (1988).

To monitor seasonal changes in body mass, I weighed ( $\pm 1$  g) curlews with a Pesola spring balance, usually within 20 min after capture. To measure fat content at the start of spring migration, I collected three adult curlews on Laysan in late April and early May 1991 and three on Midway Atoll in late April 1992. Because the peak of spring migration of curlews from the Northwestern Hawaiian Islands occurs in early May (unpubl. data), the collected birds probably carried maximum fat stores. The whole carcasses were passed through a meat grinder at least five times and a random sample of homogenate removed for analysis. Samples were dried for 12 h at 60°C and water

content determined by subtraction. Lipids were extracted with a Soxhlet apparatus using diethyl ether as a solvent.

## RESULTS

*Feather numbers and plumage mass.*—Bristle-thighed Curlews have 12 rectrices, and on each wing they have 10 functional primaries, 16 or 17 secondaries, and 4 alular feathers. Two adults had 11 functional primaries on one wing. An adult curlew found dead on 18 August 1991 had 6,081 contour feathers with a dry mass of 23.45 g (or about 6.2% of lean body mass estimated at 377 g; see below). The total number of contour feathers was 2.3 times larger than predicted by Kendeigh's (1970) formula:

$$\log F_n = 2.9718 + 0.1779 \log W, \quad (1)$$

where  $F_n$  is the number of feathers and  $W$  is the body mass (g). Using this formula, a curlew weighing 377 g would be expected to have 2,693 contour feathers. The total plumage mass was close to that predicted by Kendeigh's (1970) formula:

$$\log F_w = -1.1677 + 0.9591 \log W, \quad (2)$$

where  $F_w$  is the dry plumage mass. Using this formula, a 377-g curlew would be expected to have a plumage mass of 20.10 g, or 5.3% of the estimated lean mass. The plumage mass was similar to that measured for other species of shorebirds with similar body mass (Kersten and Piersma 1987:fig. 7).

*Molt in hatching-year curlews.*—HYs had fresh plumage and incompletely grown bills when they arrived on Laysan in late August and early September. From that time until mid-October, they were easily identifiable as young of the year. Only three of the 60 HYs captured in September were molting body feathers (the first on 26 September), whereas 21 of 32 HYs caught in October and all 15 HYs caught in November were molting body feathers. The latest non-molting HY was caught on 17 October. Thus, most HYs began body molt in early to mid-October. I found no evidence that curlews replaced their remiges during their first calendar year. Molt of the rectrices was highly variable. Eight HYs captured in October and six captured in November were replacing from 1 to 12 rectrices. The earliest rectrix molt was found on 4 October; no HYs had completely replaced their rectrices when I left the island in mid- to late

November. Apparently, some curlews did not begin their rectrix molt until their second calendar year (i.e. as SY birds).

*Molt in second-year curlews.*—The best evidence for determining molting patterns in SYs came from observations of birds marked as HYs. Twenty-one of 22 curlews marked as HYs on Laysan in autumn 1990 were observed there from February to June 1991. The earliest indication of primary molt was a bird captured on 7 March that had recently dropped primary 1 on each wing. A marked SY captured on 3 May 1991 had a complete set of worn and faded juvenal primaries, whereas another captured on 6 May had replaced primaries 1 through 6 and was growing primaries 7 and 8. Judging from observations of birds in flight, at least 14 of 21 SYs were replacing primaries by the end of May (the remaining seven birds were not observed closely enough to determine whether they were molting). Thus, most Bristle-thighed Curlews began postjuvenal primary replacement sometime between March and June of their second calendar year (Fig. 1).

Completion of the first prebasic primary molt varied among years. In 1988, I captured five birds that had retained juvenal primaries into September or October, whereas in 1990 I did not capture any birds with juvenal primaries after 15 August (Table 1). Most of the SYs examined in July and August 1989 were replacing juvenal primaries (Table 1). The earliest completion of the first prebasic primary molt appears to occur in July (i.e. no. 761; Table 1). Replacement of the juvenal secondaries began in June or July and was completed in August or September.

Most SYs began replacing their first basic primaries in July and August when these feathers were virtually new (Table 1). The replacement of new primaries, which was the second prebasic flight feather molt (K. C. Parkes pers. comm.), apparently was confined to SYs. Individuals that retained outer juvenal primaries at the start of this molt carried three generations of primaries simultaneously (e.g. no. 675 on 10 September 1988, no. 783 on 23 July 1989, no. 847 on 31 July 1989; Table 1). The second prebasic molt typically began with primary 1 and proceeded outward in sequence (e.g. no. 761 on 26 July 1989, no. 835 on 19 August 1989). I was unable to determine how many new primaries were replaced during the second prebasic molt. Owing to the presence of two generations of

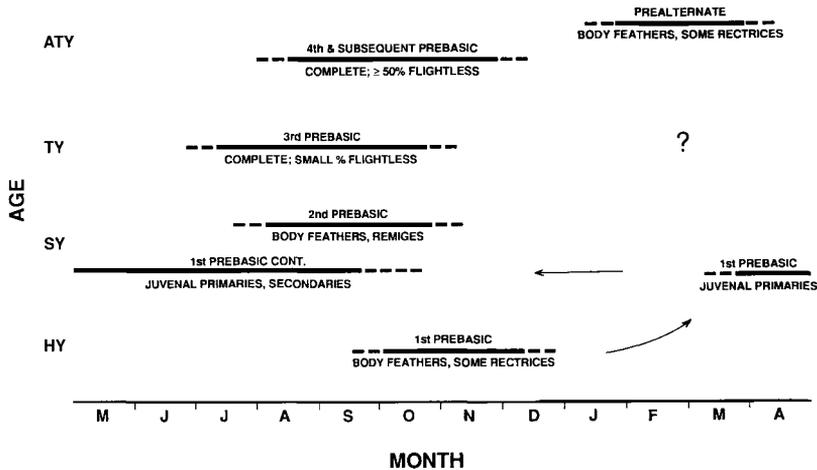


Fig. 1. Molt chronology by age class for Bristle-thighed Curlews on Laysan Island. (HY) hatching year; (SY) second year; (TY) third year; and (ATY) after third year. Data arranged so that ATY molts are shown in proper sequence.

primaries in many TY curlews, however, I suspect that the second prebasic primary molt often was incomplete (see below). Based on a small sample of birds, replacement of the first basic secondaries began about halfway through the primary molt; I was unable to determine whether this molt was complete.

For convenience, I labelled the new first basic primaries that appeared to be in line for replacement with an "N" in Table 1. Within each wing, these primaries would have been older than the ones labelled "5." Based on its occurrence in six birds that had been marked as HYs (Table 1), I suggest that this unusual pattern of primary molt was typical of SYs during late summer and early autumn.

*Molt in third-year curlews.*—I recaptured 23 TY curlews that had been banded in previous years, 10 as HYs and 13 as SYs (Table 2). Most TYs began their third prebasic primary molt in July or August and completed it in October or November (e.g. no. 835 on 18 October 1990; Table 2). Their schedule was about a month ahead of the adult curlews that had migrated to Alaska in spring (Fig. 1). One TY that was replacing an outer primary in February (no. 904 on 15 February 1991) was the only curlew seen molting remiges in winter.

Four TYs captured from February to April 1991 had two generations of fully grown primaries that occurred in blocks of adjacent feathers (nos. 890, 898, 935, and 956; Table 2). Consequently, the second prebasic primary molt was

incomplete. Differences in fading and wear between the two generations were subtle and became difficult to perceive by April and May. Twelve curlews captured on Lisianski Island in mid-May 1988, as well as two at Midway Atoll in late April 1992, also carried two generations of primaries that occurred in blocks. These birds likely were TYs. Two TYs had what appeared to be single generations of primaries in February and March (Table 2), indicating that the second prebasic primary molt was not always incomplete.

*Molt in adults.*—The prebasic molt of adults (i.e. ATYs) appeared to be complete. It began with the body feathers soon after the birds returned from Alaska in July and August (Fig. 1). The first adult that was molting body feathers was captured on 23 July; virtually all adults were molting body feathers by 5 September. Given the sample of adults showing no body molt in late July and August ( $n = 28$ ), it is likely that adults do not molt body feathers before departure from Alaska. Body feather molt continued throughout flight feather molt. Adults typically lost the first two to four primaries rapidly followed by two to three more when the first block was about one-third grown. Up to seven primaries were growing at once on each wing, with an average of nearly four growing primaries during the early and mid-stages of molt (i.e. molt scores 1 to 15 and 16 to 35, respectively) and three growing primaries toward the end of molt (Fig. 2). Adults replaced sig-

TABLE 1. Primary molt scores for second-year Bristle-thighed Curlews captured during summer and autumn on Laysan Island.

Bird	Date	Primary molt score <sup>a</sup>									
<b>1988</b>											
601	6 Sep	5	5	5	5	3	N	N	N	N	N
750	8 Sep	3	4	1	N	N	N	N	N	N	N
755	8 Sep	3	3	3	2	1	N	N	N	N	N
763	9 Sep	5	5	5	5	5	5	4	2	J	J
675	10 Sep	1	5	5	5	5	5	5	1	J	J
766	10 Sep	5	5	5	5	5	5	5	4	2	
782	15 Sep	5	5	5	5	5	5	4	2	J	J
641	1 Oct	5	5	5	5	5	5	4	2	J	J
803	2 Oct	3	2	2	N	N	N	N	5	4	
808	4 Oct	5	5	5	5	5	5	5	J	J	J
601	6 Oct	5	5	5	5	5	3	N	N	N	N
782	9 Oct	2	5	5	5	5	5	5	4	3	2
820	11 Oct	5	5	5	4	3	1	N	N	N	N
823	12 Oct	4	5	5	5	3	N	N	N	N	N
826	13 Oct	5	5	5	5	4	3	1	N	N	N
636	14 Oct	5	5	1	N	4	5	5	5	5	4
766	8 Nov	5	5	5	4	4	N	N	N	N	N
667	12 Nov	5	5	5	5	4	N	N	N	N	N
<b>1989</b>											
813 <sup>b</sup>	1 Jul	5	5	5	5	5	4	4	1	J	J
814 <sup>b</sup>	9 Jul	5	5	5	5	5	5	5	1	J	J
762 <sup>b</sup>	9 Jul	4	4	3	3	2	J	J	J	J	J
850	20 Jul	1	4	4	5	5	5	5	4	3	2
741 <sup>b</sup>	22 Jul	5	5	5	5	5	4	3	J	J	J
722 <sup>b</sup>	22 Jul	5	5	5	5	3	1	5	5	4	3
783 <sup>b</sup>	23 Jul	4	5	5	5	5	4	3	1	J	J
851	23 Jul	5	5	5	5	5	5	4	2	J	J
855	25 Jul	3	2	1	N	N	N	N	4	J	J
856	26 Jul	5	5	5	5	5	4	2	J	J	
761 <sup>b</sup>	26 Jul	5	5	5	3	N	N	N	N	N	N
857	27 Jul	5	4	3	2	N	N	N	N	N	N
847 <sup>b</sup>	31 Jul	1	1	1	N	N	N	N	4	2	J
743 <sup>b</sup>	3 Aug	5	5	5	5	5	5	2	J	J	J
861	3 Aug	5	5	5	3	N	N	4	1	J	J
862	4 Aug	1	5	5	5	5	5	5	3	2	
863	4 Aug	5	5	5	4	1	N	N	J	J	J
835 <sup>b</sup>	19 Aug	5	4	3	1	N	N	N	N	N	N
800 <sup>b</sup>	26 Aug	5	5	4	2	1	N	N	N	4	1
798 <sup>b</sup>	26 Aug	5	5	5	4	N	N	N	N	N	N
793 <sup>b</sup>	27 Aug	5	5	5	5	5	5	5	4	3	1
883	30 Aug	5	5	5	5	4	4	N	N	N	N
889 <sup>b</sup>	2 Sep	2	1	5	5	5	5	5	5	4	4
<b>1990</b>											
901	14 Aug	5	5	5	5	4	3	N	N	N	N
902	14 Aug	5	5	5	5	4	2	N	N	N	N
904	14 Aug	3	3	N	N	N	N	N	N	N	N
905	15 Aug	N	2	N	N	N	N	N	N	4	3
906	15 Aug	5	5	5	5	5	5	5	5	2	J
909	18 Aug	2	1	N	N	N	N	N	N	3	2
898 <sup>b</sup>	18 Aug	5	5	5	5	5	5	5	5	5	4
910	19 Aug	5	5	4	N	N	N	N	N	4	
911	20 Aug	2	1	5	5	5	5	5	4	N	N
914	21 Aug	1	1	N	N	N	N	N	N	3	2
915	21 Aug	5	5	5	5	5	5	5	5	5	4
916	21 Aug	3	1	N	N	N	N	N	N	N	N
917	22 Aug	5	5	5	3	N	N	N	N	4	4
918	23 Aug	1	N	N	N	N	N	N	N	N	4

TABLE 1. Continued.

Bird	Date	Primary molt score <sup>a</sup>									
902	23 Aug	5	5	5	5	4	3	N	N	N	N
920	30 Aug	5	5	5	5	4	2	N	N	N	4
921	2 Sep	5	4	2	N	N	N	N	N	N	N
923	7 Sep	5	5	4	4	N	N	N	N	N	N
931	11 Sep	5	5	5	4	3	1	N	N	4	3
932	12 Sep	5	5	5	5	5	3	N	N	N	N
934	14 Sep	5	5	5	5	4	1	N	N	N	N
935	14 Sep	5	5	5	5	5	5	4	N	N	N
938	15 Sep	5	5	5	5	4	3	N	N	N	N
939	15 Sep	5	5	5	5	2	N	N	N	N	N
943	20 Sep	1	N	N	N	2	N	N	N	N	N
944	20 Sep	5	5	5	5	4	4	1	N	4	4
915	20 Sep	2	N	N	N	N	N	N	N	N	N
910	21 Sep	5	5	5	1	N	N	N	N	N	N
901	22 Sep	5	5	5	5	5	5	2	N	N	N
902	8 Oct	5	5	5	5	5	5	N	N	N	N
956	10 Oct	5	5	5	5	5	N	N	N	N	N
898 <sup>b</sup>	29 Oct	5	5	4	N	N	N	N	N	N	N
964	17 Nov	5	5	5	5	N	N	N	N	N	N
932	21 Nov	5	5	5	2	3	N	N	3	N	N

<sup>a</sup> N = "new" first basic primaries; J = juvenal primaries.

<sup>b</sup> Banded as hatching year.

nificantly fewer primaries simultaneously during the final stage of molt (molt scores 36 to 49) than during the early and mid-stages (ANOVA,  $F = 4.64$ ,  $df = 2$  and  $121$ ,  $P = 0.011$ ; Tukey test,  $P < 0.05$ ). Overall, molting adults were growing an average of  $3.6 \pm SD$  of  $1.4$  primaries simultaneously on each wing ( $n = 124$ ).

At least the first six primaries were lost before secondary molt began. After dropping the first one or two outer secondaries, the birds began shedding the innermost secondaries (sometimes referred to as tertials). Thus, there were two waves of molt that converged between secondaries 9 and 12. Because large blocks of secondaries were molted simultaneously (see below), the secondaries were replaced shortly before or at about the same time that primary molt was completed. Rectrices were not dropped until adults were well into secondary molt. As seems to be the case for many shorebirds (e.g. Thomas and Dartnall 1971a, Page 1974, Boere 1976, Morrison 1976, Johnson and Johnson 1983), molt of the rectrices was highly variable and followed no discernible pattern.

During winter, adults underwent a partial prealternate molt that included a variable number of rectrices and most of the body feathers except the median and marginal wing coverts. Although the exact timing of this molt is unknown, 7 of 8 adults caught in February, but only 3 of 26 adults caught in April (the latest

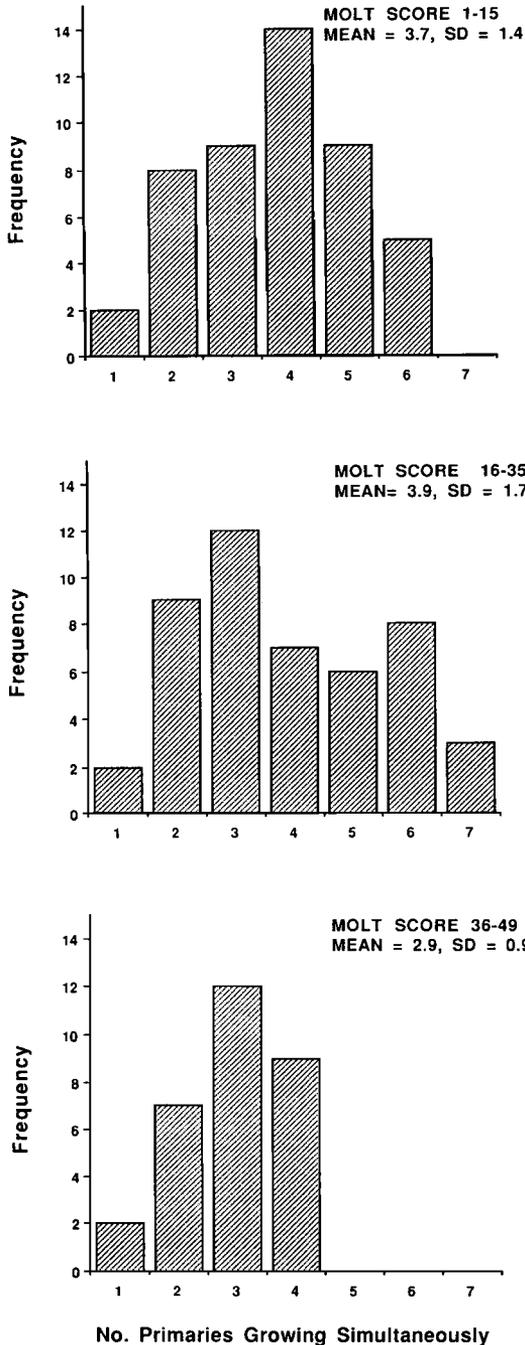


Fig. 2. Number of adult Bristle-thighed Curlews molting a given number of primaries simultaneously on each wing at three stages of molt, Laysan Island, 1988-1990.

TABLE 2. Primary molt scores for third-year Bristle-thighed Curlews previously captured during their first or second calendar year on Laysan Island.

Bird	Date	Primary molt score										Age at banding
<b>1989</b>												
763	3 Jul	2	1	0	0	0	0	0	0	0	0	SY
661	3 Jul	0	0	0	0	0	0	0	0	0	0	SY
829	7 Aug	5	0	0	0	0	0	0	0	0	0	SY
617	12 Aug	5	0	0	0	0	0	0	0	0	0	SY
680	22 Aug	5	5	5	5	5	3	0	0	0	0	SY
658	24 Aug	5	5	1	0	0	0	0	0	0	0	SY
668	25 Aug	0	0	0	0	0	0	0	0	0	0	SY
<b>1990</b>												
727	19 Aug	5	5	5	5	5	4	2	0	0	0	HY
744	26 Aug	5	5	5	4	3	2	1	0	0	0	HY
850	8 Sep	2	2	2	2	1	0	0	0	0	0	SY
718	13 Sep	5	5	5	5	5	5	4	4	3	0	HY
761	15 Sep	5	5	5	5	4	3	0	0	0	0	HY
862	16 Sep	5	5	5	5	4	4	2	1	0	0	SY
718	26 Sep	5	5	5	5	5	5	5	4	4	0	HY
799	8 Oct	5	5	4	2	2	1	0	0	0	0	HY
835	18 Oct	5	5	5	5	5	5	5	4	4	0	HY
<b>1991</b>												
897	10 Feb	5	5	5	5	5	5	5	5	5	5	HY
898	15 Feb	5	5	5	0	0	0	0	0	0	0	HY
904	15 Feb	5	5	5	5	5	5	5	4	0	0	SY
935	15 Feb	5	5	5	5	5	5	5	0	0	0	SY
890	19 Feb	5	5	5	5	5	5	5	0	0	0	HY
903	7 Mar	5	5	5	5	5	5	5	5	5	5	SY
956	15 Apr	5	5	0	0	0	0	0	0	0	0	SY

on 11 April), were molting body feathers. Three adults caught in February were also molting from two to six retrices, and several others caught in February and early April had two generations of retrices with the inner feathers being newer than the outer ones.

The dry mass of primary 10 was 4.1 times that of primary 1, making up more than 16% of the total mass of the primaries (Table 3). Molt parameter estimates were based on 168 captures of 129 adults between late July and late November 1988 to 1990. Molt parameters were similar among years, although sample sizes were too small for statistical comparisons. The raw primary molt scores were positively correlated with date of capture ( $r = 0.88$ ,  $n = 129$ ,  $P < 0.0005$ ; Fig. 3). The duration of primary molt was 92 days, with a mean starting date of 2 September (SE = 1.7 days) and a mean completion date of 3 December (SE = 3.2 days). The starting dates estimated by the Underhill-Zucchini method were comparable to the empirical data. The earliest that I captured a molting adult

TABLE 3. Dry mass (mg), with relative mass (%) in parentheses, of primaries for three adult Bristle-thighed Curlews from Laysan Island.

Primary	Bird 1	Bird 2	Bird 3	Mean	SD
1	78.0 (4.15)	63.2 (3.70)	82.4 (4.07)	74.5 (3.97)	0.24
2	95.3 (5.08)	83.1 (4.87)	102.2 (5.05)	93.5 (5.00)	0.11
3	118.3 (6.30)	101.0 (5.91)	123.7 (6.11)	114.3 (6.11)	0.20
4	145.4 (7.74)	127.6 (7.47)	156.0 (7.71)	143.0 (7.64)	0.15
5	173.2 (9.23)	154.7 (9.06)	186.5 (9.22)	171.5 (9.17)	0.10
6	207.9 (11.07)	184.0 (10.77)	220.3 (10.89)	204.1 (10.91)	0.15
7	225.1 (11.99)	209.6 (12.27)	248.2 (12.26)	227.6 (12.17)	0.16
8	248.0 (13.21)	236.3 (13.83)	273.7 (13.52)	252.7 (13.52)	0.31
9	279.2 (14.87)	265.8 (15.56)	300.9 (14.87)	282.0 (15.10)	0.40
10	307.1 (16.36)	282.7 (16.55)	329.9 (16.30)	306.6 (16.40)	0.13

was on 20 August, and the latest that I captured an adult that had not started primary molt was on 8 September.

*Molt-induced flightlessness.*—I captured 13 curlews that were unable to fly (1 TY and 12 ATYs), 5 in 1988, and 8 in 1990. I captured 11 by hand during the day, and 2 were netted at night and instrumented with radio transmitters to confirm that they were flightless. One bird was never seen again; the other 12 were seen after they had regained the ability to fly. Flightless birds were encountered from early September to late November (Table 4).

Flightlessness resulted from two states of molt. The first occurred while curlews replaced from four to seven inner and middle primaries and either had not started secondary molt or had dropped only the first one to three outer secondaries (nos. 750, 824, 832, 865, and 922; Table 4). These birds were also missing most of their greater secondary coverts, leaving gaps between the secondary calami. The second occurred during replacement of three to five middle and distal primaries and large blocks of secondaries (Table 4). In some cases, at least 14 secondaries were growing simultaneously (e.g. nos. 760, 773, and 966). I tried to determine the duration of the flightless period by radio-tagging flightless individuals in 1990. Owing to effects of the transmitters, however, the birds lost substantial mass (up to 82 g in three days), which reduced wing loading and shortened the duration of the flightless period. The flightless period probably lasts at least two weeks (Marks et al. 1990) and likely varies with the condition (i.e. body mass) of the individual. Although undocumented, it is possible that some individuals become flightless during both states of molt.

Compared with volant individuals, flightless curlews were extremely secretive during day-

time. They seldom were observed in the open and immediately ran into dense vegetation when disturbed by humans. While flightless, several radio-tagged birds allowed me to approach to less than 0.5 m of where they hid in dense vegetation. Volant radio-tagged birds ( $n = 22$ ) never allowed humans to approach closely. Owing to their furtive behavior, I encountered only a fraction of the curlews that became flightless.

I estimated the proportion of adults that became flightless by examining resighting records of marked birds in 1988 and 1990 (i.e. years that I was present through most of molting period). I did not consider TYs in this analysis because flightlessness is probably very rare in this age class. Any ATY that was seen in August and September and then resighted from late September through November with at least 14 days between sightings was considered to have become flightless. ATYs seen throughout these

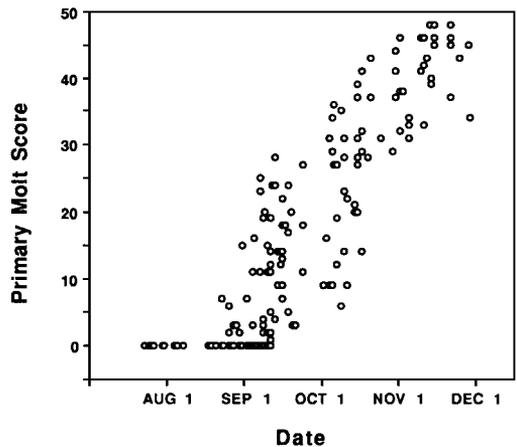


Fig. 3. Primary molt scores of adult Bristle-thighed Curlews captured on Laysan Island, 1988-1990.

TABLE 4. Primary and secondary molt scores for flightless Bristle-thighed Curlews captured on Laysan Island.

Bird	Date	Molt score																									
		Primaries								Secondaries <sup>a</sup>																	
<b>1988</b>																											
824	12 Oct	5	5	5	4	4	3	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
831	21 Oct	5	5	5	5	4	4	2	1	0	0	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
832	26 Oct	5	5	5	4	4	3	2	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
833	27 Oct	5	5	5	5	5	5	4	3	2	2	5	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
842	7 Nov	5	5	5	5	5	5	4	3	3	2	5	4	4	4	4	4	4	4	3	3	3	3	3	3	3	3
<b>1990</b>																											
922	2 Sep	3	3	3	2	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
750	7 Sep	3	3	3	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
862 <sup>b</sup>	16 Sep	5	5	5	5	5	4	4	2	1	0	2	1	1	2	1	1	1	1	1	0	1	1	1	1	1	4
865	16 Sep	4	4	4	3	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
773	14 Oct	5	5	5	5	5	4	3	2	2	2	4	4	3	3	3	2	2	2	2	2	2	2	3	3	3	3
675	17 Nov	5	5	5	5	5	4	2	1	0	3	2	2	1	1	1	1	1	1	0	0	1	2	2	2	2	2
760	21 Nov	5	5	5	5	5	5	4	4	3	2	4	4	3	3	3	2	2	2	2	2	2	2	2	4	4	4
966	25 Nov	5	5	5	5	4	4	3	2	1	0	2	2	1	1	1	1	1	1	1	1	1	1	2	3	4	4

<sup>a</sup> 10 secondaries scored in 1988; 14 secondaries scored in 1990.

<sup>b</sup> 862 was TY; all others were ATY.

months with less than 14 days between sightings were classified as "not flightless," and those seen only a few times were classified as "status unknown." The estimate was conservative because some of the status unknown birds probably had become flightless. All five of the ATYs marked in previous years and known to have become flightless in 1990 were classified correctly using the above criteria. These birds disappeared for an average of  $28.8 \pm 17.6$  days during molt (range 14–58).

Based on resighting records of the 85 marked ATYs seen in 1988, I estimate that 50 (58.8%) became flightless and 10 did not (11.8%); the status was unknown for 25 (29.4%) birds. Of the 92 marked ATYs seen in 1990, 64 (69.6%) were classified as flightless, 22 (23.9%) as not flightless, and 6 (6.5%) as status unknown. Including all three categories, the classification estimates differed significantly between years ( $G = 18.6$ ,  $df = 2$ ,  $P < 0.0005$ ). When the unknown-status birds were eliminated, however, the proportions did not differ significantly between years ( $G = 1.68$ ,  $df = 1$ ,  $P = 0.20$ ). To assess potential errors in classification, I examined resighting records of HYs, which do not molt remiges and thus never become flightless. Seven of 47 HYs (14.9%) in 1988, and 2 of 22 (9.1%) in 1990 were classified as having become flightless. There were significant differences between age classes in both years (1988,  $G = 61.7$ ,  $df = 2$ ,  $P < 0.0001$ ; 1990,  $G = 28.8$ ,  $df = 2$ ,  $P < 0.0001$ ). Overall (including status unknown birds), 64% of the

ATYs were classified as flightless during their prebasic molt. Subtracting the proportion of HYs that were incorrectly classified as flightless (13%) reduced the estimate of flightlessness in ATYs to 51%.

*Body mass during nonbreeding season and pre-migratory fat accumulation.*—Upon their arrival in the Northwestern Hawaiian Islands in July and August, mean body mass of adults was less than 450 g (Table 5). It increased steadily throughout the molting period, exceeding 500 g by November. Although I did not weigh curlews in December and January, the February data suggest that curlews continued to gain mass throughout the winter. They completed pre-migratory fattening in late April and early May, at which time body mass averaged 656 g, with the heaviest individual weighing nearly 800 g (Table 5). Mean body mass was 430 g in mid-May, reflecting the presence of nonmigrants.

Six curlews collected on Laysan and Midway at the start of spring migration in 1991 and 1992, respectively, had a mean lipid index (percent body fat relative to total body mass) of  $42.5 \pm 4.2\%$  (range 36.3–47.0). Based on this figure, the estimated lean mass of 70 adults caught in late April and early May was 377.4 g.

## DISCUSSION

Because molt parameters may vary geographically within species (Holmes 1971, Spaans 1976, Myers et al. 1985, Summers et al. 1989), the

timing, duration, and age-specific patterns of molt that I observed apply only to Bristle-thighed Curlews that winter in the Northwestern Hawaiian Islands. Aside from evidence that some birds become flightless at Rangiroa Atoll (Marks et al. 1990, Gill and Redmond 1992), nothing is known about molt of Bristle-thighed Curlews in the Southern Hemisphere.

*Replacement of juvenal primaries and timing of second prebasic molt.*—Differences in the timing and extent of molt of the juvenal primaries of migratory shorebirds seem to be related to the age of first breeding and to wintering latitude. In Hawaii, Pacific Golden-Plovers (*Pluvialis fulva*) that breed as yearlings do not molt their juvenal primaries until August of their second year, whereas those that oversummer on the wintering grounds begin primary molt in June (Johnson and Johnson 1983). Semipalmated Sandpipers (*Calidris pusilla*) that breed as yearlings replace some outer juvenal primaries during their first autumn, whereas birds that oversummer on the wintering grounds molt their juvenal primaries during their second autumn (Spaans 1979, Gratto and Morrison 1981). Sanderlings (*C. alba*) wintering in California do not molt their juvenal primaries during their first winter, and those wintering in South America molt their juvenal primaries between December and March (Myers et al. 1985).

Bristle-thighed Curlews delay molt of their juvenal primaries until the spring and summer of their second calendar year. The small, predator-free islands inhabited by curlews obviate the need to have fresh primaries during winter and spring (i.e. the birds do not need to maintain peak flight efficiency for access to foraging areas or to escape predators). Thus, if stressed energetically, inexperienced curlews could devote most of their energy expenditure in their first winter to foraging and establishing home ranges among those of adults rather than to molting remiges.

In Bristle-thighed Curlews, molt of the first basic primaries often begins before the outer juvenal primaries have been dropped, resulting in the replacement of primaries that are no more than a few months old. Replacement of these new primaries would seem energetically inefficient. Because second-year curlews remain on the wintering grounds throughout the year, however, they do not prepare for migration. Thus, selection has not been strong enough to delay the start of the second molt, which pre-

TABLE 5. Body mass (g;  $\bar{x} \pm SD$ , with range in parentheses) of adult Bristle-thighed Curlews captured in Northwestern Hawaiian Islands, 1988–1992.

Time period	n	Body mass
July	9	439.8 $\pm$ 39.3 (368–485)
August	33	449.9 $\pm$ 57.6 (343–558)
September	66	482.9 $\pm$ 39.8 (398–577)
October	44	490.2 $\pm$ 49.1 (393–584)
November	21	506.2 $\pm$ 48.7 (410–622)
February	9	594.1 $\pm$ 69.0 (501–684)
Early to mid-April	14	583.9 $\pm$ 69.5 (434–690)
Late April/early May	70	656.3 $\pm$ 77.4 (419–796)
Mid- to late May	39	430.4 $\pm$ 80.4 (335–546)

sumably entails little cost during the mild summer months. In southern Africa, second-year Ruddy Turnstones (*Arenaria interpres*) also replace new primaries during their second prebasic molt (Summers et al. 1989). In some cases the second molt is completed in late April and, like Bristle-thighed Curlews, these turnstones oversummer on their wintering grounds.

*Molt-induced flightlessness.*—As an adaptation in shorebirds, flightlessness apparently is unique to Bristle-thighed Curlews. Middlemiss (1961) caught a flightless Little Stint (*Calidris minuta*) that had dropped all of its primaries and secondaries on both wings. Because it was the only bird out of nearly 3,000 captured to display such a molt, it was dismissed as an aberration. Owen and Krohn (1973) caught several American Woodcocks (*Scolopax minor*) that had molted all of their secondaries simultaneously, but they did not comment on the ability of these birds to fly. Sach (1968) reported that Eurasian Curlews (*Numenius arquata*) increased their wing-beat frequency during primary molt, suggesting that the birds were flight-impaired during molt. Similarly, Boere (1976:231) noted that Sanderlings were nearly flightless during primary molt.

I estimated that at least 50% of the adult curlews on Laysan became flightless during their prebasic molt. Flightlessness resulted from the replacement of large numbers of remiges at the same time, thereby decreasing the duration of molt (see below). The evolution of molt-induced flightlessness in Bristle-thighed Curlews surely is related to the historic absence of predators throughout their wintering range. Boere (1976) and Prater (1981) also remarked on the importance of predator- and disturbance-free molting areas for shorebirds whose flight ca-

pabilities are impaired during primary replacement.

*Latitudinal trends in primary molt of shorebirds.*—Holmes (1971, 1972) identified three distinct prebasic molt schedules in New World *Calidris* sandpipers: (1) molting entirely on breeding grounds (e.g. some Dunlins and Purple Sandpipers); (2) starting molt on breeding grounds, but completing it on wintering grounds (e.g. Western Sandpiper [*C. mauri*]); and (3) molting entirely on wintering grounds (e.g. Semipalmated Sandpiper, Baird's Sandpiper [*C. bairdii*], Pectoral Sandpiper [*C. melanotus*], and many other species). These patterns reflect latitudinal differences in wintering areas (i.e. differences in energetic requirements for migration and food availability on the wintering grounds). Dunlins and Purple Sandpipers winter in northern latitudes comparatively close to their breeding grounds, Western Sandpipers winter in both North Temperate and tropical latitudes north of the equator, and species that molt on their wintering grounds tend to migrate long distances to the Southern Hemisphere. Prater (1981) provided a detailed review of primary molt in Palearctic migratory shorebirds. He suggested several latitudinal patterns of molt that were similar to those of New World species. First, the farther a species migrates, the later it begins to molt. This pattern was reflected in completion dates of molt at different latitudes. Most of the species that winter in northern latitudes finish molting in September or October, most of the species wintering in tropical latitudes finish from November to January, and most of the species wintering south of the Tropic of Capricorn finish molting in March (Prater 1981:table 2). Second, the duration of molt is shorter, and the timing more synchronous, in species wintering in northern latitudes than in species wintering farther south. Presumably, there are strong selective pressures for shorebirds in northern latitudes to complete the prebasic molt before cold winter temperatures cause food availability to decline and energetic demands to increase. And finally, molt duration is more clearly related to body size in northern species than in southern species. Specifically, Prater found a positive correlation ( $P < 0.05$ ) between wing length and primary-molt duration for species molting in western Europe but no clear relationship for those molting in Africa and Australia.

I repeated Prater's analysis of the relationship

between molt duration and wing length, adding data from more recent studies and from the New World (Table 6). I also confined the analysis to scolopacids, eliminating several taxa considered by Prater (viz. oystercatchers [*Haematopus*], lapwings [*Vanellus*], and plovers [*Pluvialis* and *Charadrius*]). I placed Bristle-thighed Curlews in the tropical-Southern Hemisphere group because almost all of their winter range occurs south of the Tropic of Cancer. One unavoidable problem with the analysis is that most of the studies did not use the Underhill-Zucchini method to calculate molt duration. However, using the Underhill-Zucchini method, Summers et al. (1989) found that Ruddy Turnstones wintering in Scotland molted 45 days faster than those wintering in South Africa (Table 6). This suggests that the latitudinal differences in shorebird molt duration are real. Moreover, I have assumed that any methodological bias in estimating molt duration is independent of the latitude at which the birds molt.

In general, the results were similar to those of Prater (1981). The correlation between wing length and molt duration was positive and nearly significant for species wintering in North Temperate latitudes ( $r_s = 0.46$ ,  $n = 14$ ,  $P = 0.10$ ; Fig. 4), but there was no clear relationship among species wintering south of the Tropic of Cancer ( $r_s = -0.23$ ,  $n = 14$ ,  $P = 0.45$ ; Fig. 4). One striking result was that primary molt durations of the largest species from northern latitudes (Eurasian Curlew and Bar-tailed Godwit [*Limosa lapponica*]) were very similar to those of the smallest species from tropical and southern latitudes (Rufous-necked Stint [*Calidris ruficollis*], Little Stint, and Least Sandpiper [*C. minutilla*]; Table 6). Controlling for wing length (log wing length as a covariate of log duration), molt duration was significantly shorter in scolopacids wintering in North Temperate latitudes than in those wintering south of the Tropic of Cancer (ANCOVA,  $F = 19.10$ ,  $df = 1$  and  $25$ ,  $P < 0.0005$ ).

*Ecological factors influencing molt timing and duration.*—Molting entirely on the wintering grounds, Bristle-thighed Curlews in the Northwestern Hawaiian Islands fit the pattern of molt typical of many tundra-nesting scolopacids that winter in tropical or southern latitudes. Despite being the largest member of this group for which data are available, they have the shortest molt duration (Fig. 4). Morrison (1976) and Prater (1981) have suggested that the number of primaries growing concurrently is an important

TABLE 6. Duration of primary molt in scolopacid shorebirds.

Species	Locality	Duration (days) <sup>a</sup>	Source
Common Redshank ( <i>Tringa totanus</i> )	Netherlands	130	Boere 1976
	Scotland	72	Underhill et al. 1990
Bristle-thighed Curlew ( <i>Numenius tahitiensis</i> )	Hawaii	92	This study
Eurasian Curlew ( <i>N. arquata</i> )	Germany	100	Sach 1970
Black-tailed Godwit ( <i>Limosa limosa</i> )	Morocco	100	Ginn and Melville 1983
Bar-tailed Godwit ( <i>L. lapponica</i> )	Netherlands	104	Boere 1976
Ruddy Turnstone ( <i>Arenaria interpres</i> )	Netherlands	72	Boere 1976
	South Africa	119	Summers et al. 1989
	Scotland	74	Summers et al. 1989
Red Knot ( <i>Calidris canutus</i> )	Netherlands	95	Boere 1976
Sanderling ( <i>C. alba</i> )	South Africa	98	Underhill 1985
Semipalmated Sandpiper ( <i>C. pusilla</i> )	Suriname	105	Spaans 1979
Western Sandpiper ( <i>C. mauri</i> )	Alaska	70	Holmes 1972
Rufous-necked Stint ( <i>C. ruficollis</i> )	Australia	112	Thomas and Dartnall 1971a
	Australia	130	Paton and Wykes 1978
Little Stint ( <i>C. minuta</i> )	Kenya	115	Pearson 1984
	South Africa	108	Dean 1977
Least Sandpiper ( <i>C. minutilla</i> )	California	96	Page 1974
	Suriname	120	Spaans 1976
	Iceland	50	Morrison 1976
Purple Sandpiper ( <i>C. maritima</i> )	Morocco	100	Ginn and Melville 1983
Dunlin ( <i>C. alpina</i> )	N. Alaska	70	Holmes 1971
	W. Alaska	97	Holmes 1971
	England	60	Boyd and Olgilvie 1966
	Tasmania	127	Thomas and Dartnall 1971b
Curlew Sandpiper ( <i>C. ferruginea</i> )	South Africa	140	Elliott et al. 1976
	Netherlands	72	Koopman 1986
Ruff ( <i>Philomachus pugnax</i> )	Netherlands	72	Koopman 1986
	Kenya	115	Pearson 1981

<sup>a</sup> Midpoint value if range was given.

proximate factor affecting molt duration in shorebirds. In support of this view, Bristle-thighed Curlews replace large numbers of primaries simultaneously. Indeed, the only scolopacids known to replace more primaries simultaneously are the high-arctic populations of Purple Sandpipers and Dunlins that molt extremely rapidly (Morrison 1976:table 2).

Clearly, in both the timing and duration of their primary molt, Bristle-thighed Curlews are more similar to species that molt in North Temperate latitudes than to species that molt in tropical and southern latitudes. I suggest that Bristle-thighed Curlews face conditions on their wintering grounds that make it advantageous for them to complete their prebasic molt as rapidly as possible during autumn. Specifically, the ecological attributes of oceanic islands, and the need to accumulate large fat stores for long-distance migration, have exerted strong selection pressures on Bristle-thighed Curlews to molt more quickly than do shorebird species that winter on tropical continental coasts.

The distribution of Bristle-thighed Curlews in winter extends from 23° to 28°N in the North-

western Hawaiian Islands to about 25°S in the Pitcairn Islands (Stickney 1943). Although many species of shorebirds migrate longer distances (e.g. Myers et al. 1985, Boland 1991), the migration of Bristle-thighed Curlews is extraordinary because the birds fly 4,000 km or more nonstop over open ocean. The islands and atolls on which these curlews winter are small and predator-free. They may also be relatively poor foraging areas for shorebirds because they lack the extensive mudflats and rich intertidal habitats common on continental coasts (R. B. Clapp pers. comm.; also see Johnson 1985). Perhaps for this reason, Bristle-thighed Curlews in the Northwestern Hawaiian Islands virtually never feed in the intertidal zone. Instead, they feed on a wide variety of terrestrial foods such as insects, spiders, land crabs, seabird eggs, lizards, and carrion (Marks and Hall 1992; unpubl. data). Moreover, the Northwestern Hawaiian Islands are frequently beset by storms and high winds during winter (pers. observ.). As reported for shorebirds elsewhere (Dugan et al. 1981, Burger 1984), foraging opportunities in the Northwestern Hawaiian Islands are probably

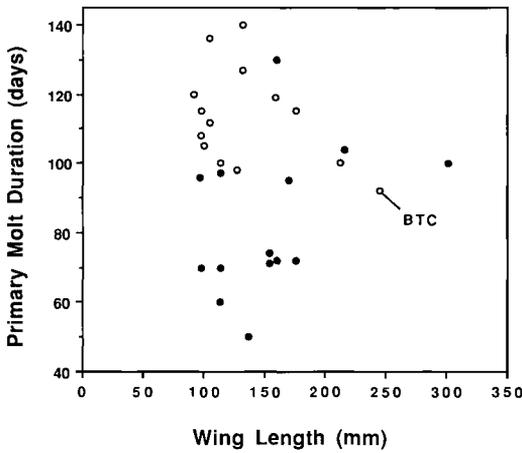


Fig. 4. Relationship between primary-molt duration and wing length in scolopacid shorebirds that molt in North Temperate latitudes (closed circles), and tropical and southern latitudes (open circles). BTC = Bristle-thighed Curlew. Wing-length data from Cramp and Simmons (1983) for all species but Bristle-thighed Curlew (unpubl. data).

reduced when high winds persist for days at a time.

The absence of rich intertidal habitats and the frequency of winter storms presumably make it difficult for curlews to take on large fat stores rapidly as do shorebirds that winter on continental coasts (e.g. Pearson et al. 1970, Pienkowski et al. 1979, Summers and Waltner 1979, Pearson 1981, Zwarts et al. 1990). Pacific Golden-Plovers on the main Hawaiian Islands accumulate most of their fat during the month preceding migration (Johnson et al. 1989), but these birds forage in man-made habitats that provide an unnaturally high availability of insects (Johnson 1985). Large numbers of Pacific Golden-Plovers, Ruddy Turnstones, and Wandering Tattlers (*Heteroscelus incanus*) winter on Laysan (unpubl. data). During spring, all three of these species fatten up on brine flies (*Neosca-tella sexnotata*) and brine shrimp (*Artemia salina*) that are extremely abundant along the shoreline of Laysan's lagoon (Caspers 1981; unpubl. data). Curlews differ markedly from these other species in that they do not feed on brine flies or brine shrimp at Laysan.

In North Temperate latitudes, most shorebirds maintain low fat stores during autumn and winter with a peak in mass (i.e. fat content) during the coldest months in midwinter (Evans and Smith 1975, Pienkowski et al. 1979, Davidson 1981, 1982, Dugan et al. 1981; but see Sum-

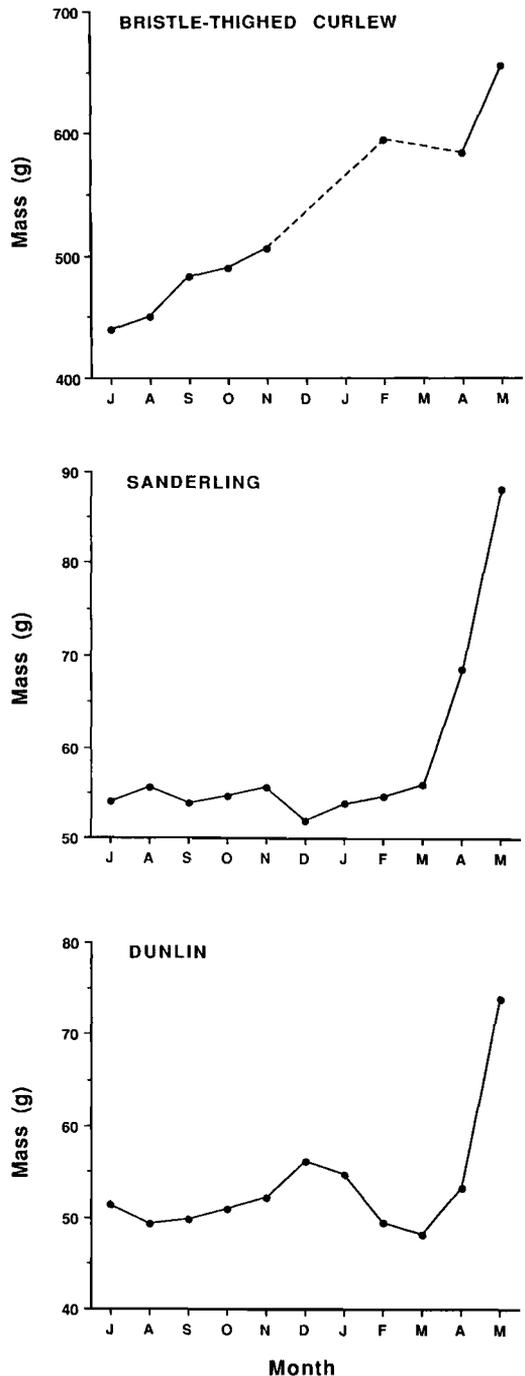


Fig. 5. Seasonal trends in body mass for representative shorebirds wintering in North Temperate latitudes (Dunlin; Pienkowski et al. 1979), and tropical and southern latitudes (Sanderling; Summers and Waltner 1979). Bristle-thighed Curlews are unique among migratory shorebirds in that they gain mass steadily throughout autumn and winter. Dotted lines span months for which data not available.

mers et al. 1992). Body mass then drops in late winter before increasing sharply in the month before northward migration (Fig. 5). This relationship is modified in the tropics and in the Southern Hemisphere, where shorebirds typically maintain low levels of fat throughout the autumn and winter with no midwinter peak (Fig. 5; Middlemiss 1961, Pearson et al. 1970, Thomas and Dartnall 1971b, Pienkowski and Dick 1975, Summers and Waltner 1979, Pearson 1981, Johnson et al. 1989). In contrast, body mass in Bristle-thighed Curlews increases steadily throughout autumn and winter (Fig. 5). Given the relatively low food availability on oceanic islands, I suggest that it is difficult (if not impossible) for curlews to fatten rapidly just before spring migration. Consequently, they must take on fat stores gradually throughout the winter. Moreover, the lack of predators on oceanic islands, and the short distances that birds fly to feeding sites, enable curlews to carry comparatively large stores of fat during winter without the added costs associated with reduced maneuverability (i.e. increased vulnerability to predation) and higher wing loading (i.e. increased flight costs). The lack of predators also allows Bristle-thighed Curlews to drop large numbers of remiges simultaneously (in some cases becoming flightless), enabling molt to be completed in autumn while foraging conditions are relatively good. Thus, freedom from predation, low food availability and suboptimal foraging conditions during winter, and the need to accumulate large quantities of fat for migration act in concert to shape the timing and duration of molt in Bristle-thighed Curlews.

In conclusion, Bristle-thighed Curlews and shorebirds that molt at higher latitudes appear to have a common need to complete molt before a period of major energetic demand. For northern species, this demand is brought about by severe winter weather, whereas for Bristle-thighed Curlews, it is the accumulation of fat during winter in preparation for spring migration. For a more complete understanding of the factors that influence molt in migratory shorebirds, studies of other species that inhabit small oceanic islands (viz. Pacific Golden-Plovers, Ruddy Turnstones, and Wandering Tattlers) would be especially valuable.

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