

MIGRATION OF BRISTLE-THIGHED CURLEWS ON LAYSAN ISLAND: TIMING, BEHAVIOR AND ESTIMATED FLIGHT RANGE¹

JEFFREY S. MARKS²

Division of Biological Sciences, University of Montana, Missoula, MT 59812

ROLAND L. REDMOND

Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812

Abstract. Bristle-thighed Curlews (*Numenius tahitiensis*) fly at least 4,000 km non-stop from staging grounds in western Alaska to the northern edge of the winter range at Laysan Island in the Northwestern Hawaiian Islands. Adults migrate from Laysan in early May and return in July and August. Juveniles, which arrive in late August and early September, largely migrate unaccompanied by adults. Compared with other shorebirds, Bristle-thighed Curlews migrate in small flocks and show no diurnal pattern in timing of departures. Subadults do not fatten adequately for migration but often accompany departing adults briefly and then return to the island. Fat content in adults at the start of spring migration is high, averaging 42%. Our findings indicate that curlews wintering in the Central and South Pacific overfly Hawaii during spring and autumn, undertaking non-stop flights of >6,000 km. In the absence of tailwinds, only two of the four flight range models that we tested (Summers and Waltner 1979, Davidson 1984) provide reasonable estimates of the migratory performance of Bristle-thighed Curlews (i.e., non-stop flights from Alaska to Laysan and beyond). Within the range of altitudes at which they migrate, curlews probably seek out tailwinds that facilitate long-distance, non-stop flights.

Key words: *Bristle-thighed Curlew; flight ranges; Laysan Island; Numenius tahitiensis; transoceanic migration.*

INTRODUCTION

Owing in part to widespread concern for the conservation of shorebirds (Pitelka 1979, Myers 1983, Howe et al. 1989), much recent attention has been devoted to understanding their migration patterns (Morrison 1984, Pienkowski and Evans 1984, Dunn et al. 1988, Wymenga et al. 1990). Because most studies have been conducted along continental coasts, shorebird migrations to oceanic wintering grounds are poorly understood. In particular, little is known about migrations in the tropical Pacific, even though shorebirds are conspicuous components of these insular ecosystems (Johnson et al. 1989). Moreover, the behavior of migrating shorebirds has received surprisingly little attention, even in continental areas (but see Lank 1989, Alerstam et al. 1990, Piersma et al. 1990b).

Many shorebirds undertake long, non-stop mi-

grations between their breeding and wintering grounds (Evans and Davidson 1990, Gudmundsson et al. 1991). These flights are fueled by large stores of fat that may approach 50% of an individual's body mass (Page and Middleton 1972, Davidson 1984). Several models that incorporate data on fat loads have been developed to estimate the flight range of migratory shorebirds (Castro and Myers 1989), but few studies have attempted to assess their validity (Davidson 1984, Harrington et al. 1991). These models are difficult to test because even if the breeding and wintering areas are known, migration between the two areas may not occur in one flight.

Bristle-thighed Curlews (*Numenius tahitiensis*) breed in remote tundra habitats in western Alaska and winter on small islands in the tropical and subtropical Pacific Ocean. No more than 7,000 individuals are thought to breed in Alaska (Gill and Redmond 1992). They are the only migratory shorebirds that winter exclusively on oceanic islands, which they reach by non-stop flights of at least 4,000 km (assuming they do not land on the ocean; see Evans and Davidson 1990). Thus, they are ideal subjects for testing

¹ Received 11 October 1993. Accepted 30 December 1993.

² Present address: Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812.

flight range models because minimum non-stop flight distances are known for some individuals.

Wintering on islands that historically were predator-free, Bristle-thighed Curlews have high annual survivorship and have evolved a rapid prebasic molt during which about 50% of the adults becomes flightless (Marks 1992, 1993). Consequently, disturbance on the wintering grounds (e.g., harvest by humans and losses to introduced predators) could have disastrous effects on their numbers (Marks et al. 1990). A thorough understanding of their migration system and knowledge of major wintering and stop-over areas are essential to conservation efforts for this rare shorebird.

Based on observations of uniquely marked, known-age individuals, we studied timing of migration and migratory behavior of Bristle-thighed Curlews on Laysan Island in the Northwestern Hawaiian Islands. In conjunction with known minimum non-stop flight distance, fat content data from curlews collected at the peak of spring migration enabled us to assess the validity of several flight range estimation models. We also speculate on the existence of staging areas south of Hawaii that are probably important to curlews on their way to and from wintering sites in the South Pacific Ocean.

STUDY AREA AND METHODS

Most of the work occurred on Laysan Island (25°46'N, 171°44'W), which is a small (397 ha) coral island with a maximum elevation of 12 m. Laysan Island is part of the Northwestern Hawaiian Islands, which extend for 2,000 km beyond the main Hawaiian Islands and constitute the northern limit for wintering Bristle-thighed Curlews (Fig. 1). Laysan Island is managed as a National Wildlife Refuge by the United States Fish and Wildlife Service (USFWS) and is uninhabited except when researchers are present. About 47% of the island is vegetated with grasses, forbs, and low shrubs (Morin and Conant 1990). Between 300–350 curlews resided on Laysan during the non-breeding seasons of 1988–1991 (J. S. Marks, unpubl. data). Ely and Clapp (1973) provide a detailed account of the natural history of the island.

We visited Laysan Island from 15 April to 14 May and 30 August to 14 November 1988, 28 June to 8 September 1989, 12 August to 30 November 1990, and 3 February to 14 June 1991. Curlews were dazzled with flashlights at night

and caught in a hoop net. They were marked on their tibiotarsi with a USFWS metal band and a unique combination of four colored plastic bands that were sealed with cyanoacrylate adhesive. Each bird was weighed to the nearest 1 g with a Pesola spring balance, usually within 20 min after capture, and the unflattened wing was measured to the nearest 1 mm with a stopped ruler. Wing span was measured on a sample of 33 adults caught at Midway Atoll (see below) in April 1992. Based on these measurements, wing span (mm) was estimated ($r^2 = 0.80$, $P < 0.0005$) for additional curlews captured on Laysan by the formula:

$$\text{Wing span} = \text{unflattened wing} \cdot (2.713) + 192.033.$$

We also observed and captured curlews during brief visits to several other islands in the Northwestern chain: Lisianski Island (225 km WNW of Laysan) from 16–18 May 1988, Tern Island (604 km ESE of Laysan) from 13–19 June 1989, and Midway Atoll (621 km WNW of Laysan) from 23–30 April 1992. In total, we marked 420 curlews in the Northwestern Hawaiian Islands between 1988 and 1992.

Based on molt and plumage wear, we classified curlews in their first, second, and third calendar years as hatching-year (HY), second-year (SY), and third-year (TY) birds, respectively (Marks 1993). We considered after-third-year (ATY) birds to be adults based on the presence of marked, younger birds that did not migrate north in spring. Upon their arrival on Laysan in late summer, HYs had fresh plumage and incompletely grown bills and were easily identifiable as young of the year. Timing of southward migration of adults was determined by noting the presence of marked individuals during daily surveys of the island in late summer 1989. Spring migration was inferred from changes in flock size and flight behavior in 1988 and by observing actual departures of curlews in 1991. We considered a flock to have departed when it disappeared from our view (using 9× binoculars). Length of stay during southward migration was assessed in 1988 and 1990 by examining resightings of adults marked prior to 10 September (i.e., after the peak of southward migration). Marked adults still present after 1 October (by which time virtually all adults are molting primaries; Marks 1993) were considered to have spent the winter on the island (see below). During spring 1991,

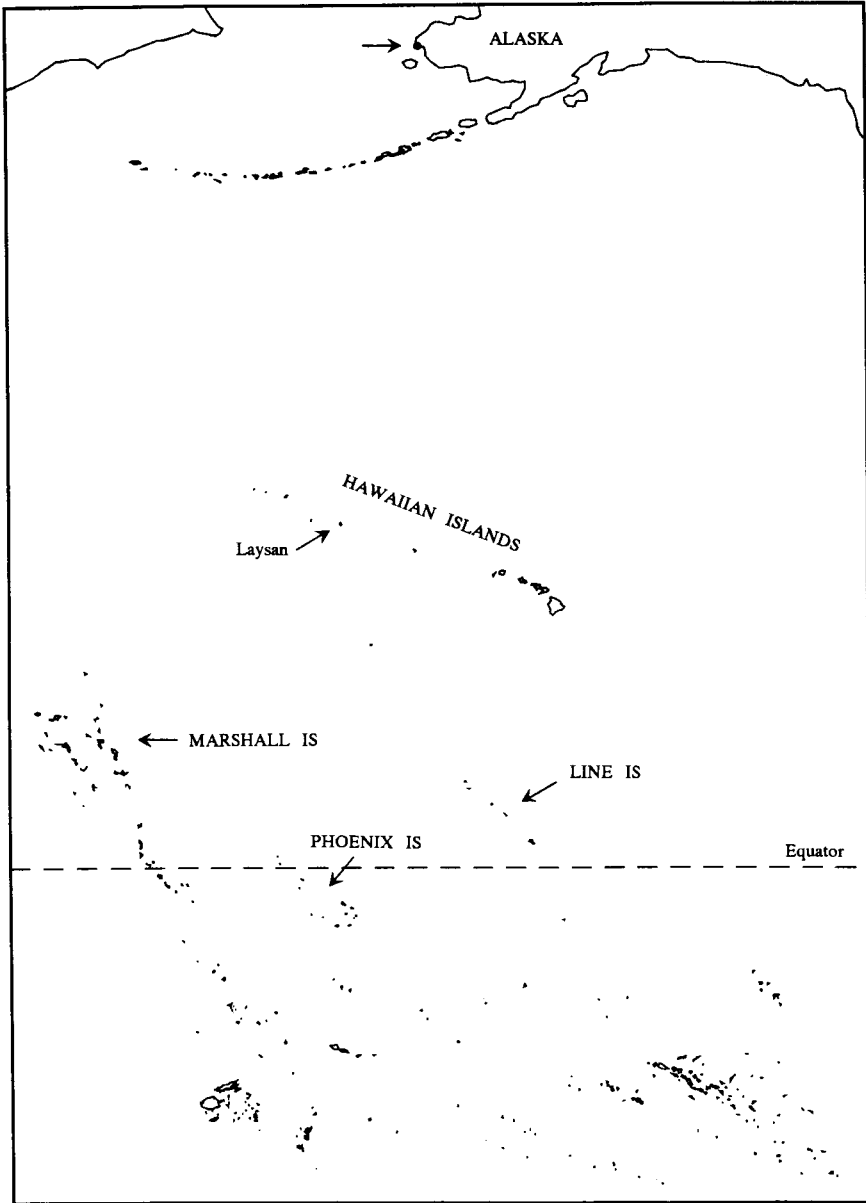


FIGURE 1. Winter range of Bristle-thighed Curlews including Laysan Island and potential stopover areas for curlews that overfly the Hawaiian Islands. Likely stopover sites are the northern Line Islands (about 6,190 km south of the staging grounds in Alaska), the Marshall Islands (6,180 km), and the Phoenix Islands (7,160 km). The main staging ground in Alaska is denoted by a dot and an arrow.

we determined whether birds that wintered farther south were stopping on Laysan by comparing ratios of marked to unmarked birds before and during the peak of northward migration. We also used shorebird census data obtained at Tern Island from 1989–1992 to further evaluate turn-

over during migration in the Northwestern Hawaiian Islands.

We collected three adult curlews on Laysan in late April and early May 1991 and three on Midway Atoll in late April 1992. The birds were collected at or very near the peak of spring mi-

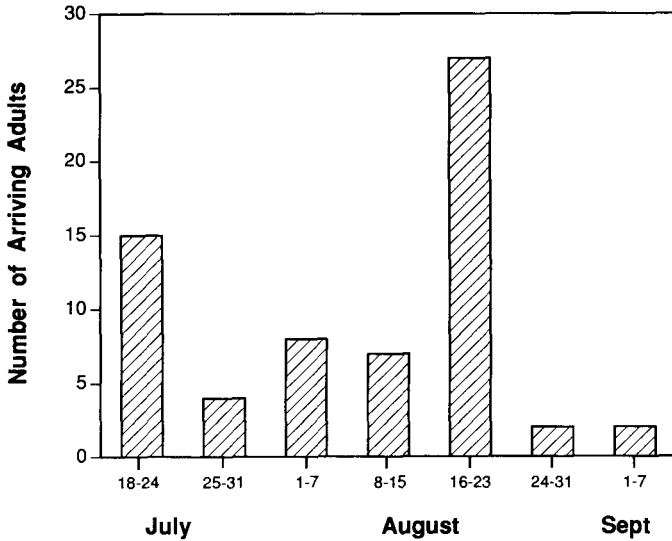


FIGURE 2. Timing of arrival of adult Bristle-thighed Curlews on Laysan Island during southward migration, 1989.

gration and probably carried maximum fat stores. The whole carcasses were passed through a meat grinder at least five times, and a random sample of homogenate was removed for analysis. Samples were dried for 12 hr at 60°C; lipids were extracted with a Soxhlet apparatus using diethyl ether as a solvent.

Using data on body mass, fat content, and wing length, and assuming a constant flight speed of 75 km hr⁻¹ (Castro and Myers 1989), we estimated migratory flight ranges for the six collected curlews based on the methods of Summers and Waltner (1979), Davidson (1984), and Castro and Myers (1989; see Appendix for formulae). We also used Pennycuik's (1989) computer program to estimate flight ranges from wing span and body mass data and assuming still air conditions and a flight altitude of 2,000 m (Richardson 1979). Great-circle distances between locales were calculated following Zar (1989).

RESULTS

SEASONAL TIMING OF SOUTHWARD MIGRATION

When we arrived on Laysan on 28 June 1989, only one of the 83 ATY curlews marked in 1988 was present on the island. This bird had been observed since May by other researchers and thus did not migrate north in the previous spring. There was an influx of adults on 18 July, in-

cluding five marked ATYs. Altogether, 15 marked ATYs arrived between 18–24 July, and another four arrived during the last week of July (Fig. 2). At least 15 marked ATYs arrived during the first two weeks of August, and 27 more were seen between 16–23 August. The last two marked ATYs were found on 3 and 4 September, although they may have arrived earlier. Thus, the two major pulses of adult arrivals occurred in mid-July and mid- to late August (Fig. 2). No adults were known to have arrived after the first week of September. Based on the timing of events in Alaska, the first adults to arrive at Laysan were probably failed breeders, with the successful breeders arriving after mid-August (Handel and Dau 1988, McCaffery and Gill 1992).

With respect to migration of HYs at Laysan, we were unable to chronicle the first arrivals in 1988 because several were already there when we landed on 30 August. In 1989, the first HY was seen on 29 August. At least 31 were present on 2 September, including flocks of six and 14 individuals that arrived that day. In 1990, the first HY was seen on 19 August and the next on 24 August; we did not see groups of HYs until 5 September. Thus, most HYs arrived at Laysan between late August and early September. Given that at least 95% (63 of 66) of the marked ATYs seen on Laysan in 1989 were present before the arrival of the first HY, most Bristle-thighed Cur-

TABLE 1. Details of the departure of 16 Bristle-thighed Curlew flocks from Laysan Island, Spring 1991.

Date in May	Time present ^a	Time of departure	Original flock size	Number departing
1	12:15–12:45	12:30	25	20
2	08:55–10:00	— ^b	—	—
	13:40–15:10	—	—	—
	16:00–17:35	—	—	—
3	09:20–11:35	10:11	29	22
		10:49	17	15
4	16:35–18:30	—	—	—
	10:05–12:45	12:01	30	22
5	15:30–19:40	16:00	11	5
	13:45–15:00	14:01	20	19
6	16:35–18:05	—	—	—
	08:30–17:45	17:29	7	4
7	07:50–17:55	09:09	14	14
		10:35	5	5
		15:30	12	8
8	08:30–19:00	—	—	—
	9	08:25–16:50	14:13	31
15:33			2	2
10	09:00–09:30	—	—	—
	12:10–13:00	—	—	—
	14:35–17:00	—	—	—
11	08:35–13:25	—	—	—
	15:00–17:05	15:50	4	2
12	07:50–18:10	15:39	13	5
13	08:15–19:00	10:47	1	1
		11:04	8	7

^a Time during which staging site was observed.

^b Indicates that no departures occurred.

lews undertake their first southward migration unaccompanied by adults.

SEASONAL TIMING OF NORTHWARD MIGRATION

Even though we did not actually observe curlews departing Laysan during spring 1988, marked changes in flocking behavior, and the presence of curlews at what eventually proved to be a staging site at the north end of the island, enabled us to determine when migration was occurring. Beginning on 27 April 1988, flock sizes increased substantially at a rock ledge roosting area ("South Ledge") at the south end of the island (Fig. 3). The maximum daily count was 84 birds on 28 April and peaked at 85 and 86 birds on 5 and 6 May, respectively. Roost counts dropped significantly at the South Ledge after 7 May, ranging from 8–17 birds (Fig. 3; Mann-Whitney $U = 60$, $P = 0.001$, $n_1 = 10$, $n_2 = 6$). Concomitant with

increased flock sizes at the South Ledge, curlews began congregating on a sand flat at the north end of the island, where maximum daily counts of 12–43 birds were recorded between 2–7 May (Fig. 3). (During spring 1991 this flat was confirmed as the staging site for curlew flocks departing Laysan for Alaska [see below].) We also noticed a marked increase in flight activity during the first week of May 1988, with vocal flocks of 5–20+ curlews flying back and forth between the south and north ends of the island and occasionally flying out to sea and back.

In addition to behavioral changes, pre-migratory fattening was very evident. Twenty-four curlews caught on Laysan from 1–9 May 1988 weighed substantially more (mean = 621.4 g, SD = 82.8, range = 419–736 g) than 28 after-second-year birds that we caught on Lisianski Island from 16–18 May 1988 (mean = 432.1 g, SD = 56.2, range = 335–538 g; $t = 9.8$, $P < 0.0001$, $df = 50$). We infer that the Laysan sample contained many adults that had fattened for migration, whereas the Lisianski sample was composed of subadults that were going to overwinter on the island. Presumably, there were no adults in the Lisianski sample because they had already migrated by the time we arrived there on 16 May.

Curlew departures from Laysan were monitored closely during 1991. As in 1988, flock sizes at the South Ledge increased markedly during the last week of April (Fig. 3). At the same time, curlews began flying about in small, vocal flocks. Maximum daily counts exceeded 75 curlews between 28 April and 3 May, with a peak count of 156 birds on 2 May. Curlew numbers declined significantly at the South Ledge after 5 May, with daily counts ranging from 9–33 birds (Fig. 3; Mann-Whitney $U = 156$, $P < 0.0005$, $n_1 = 12$, $n_2 = 13$). Curlews first used the staging site at the north end of the island on 28 April. Maximum daily counts there ranged from 18–48 birds between 30 April and 9 May and declined to zero after 13 May (Fig. 3).

We observed 16 migratory departures of 171 curlews between 1–13 May, with most (75% of departures and 91% of individuals) occurring during the first nine days of May (Table 1). Although we undoubtedly missed some departures, it is unlikely that any curlews left the island before 28 April or after 15 May. Thus, in 1988 and 1991, migratory behavior began in the last week of April, with most northward departures occurring during the first week of May.

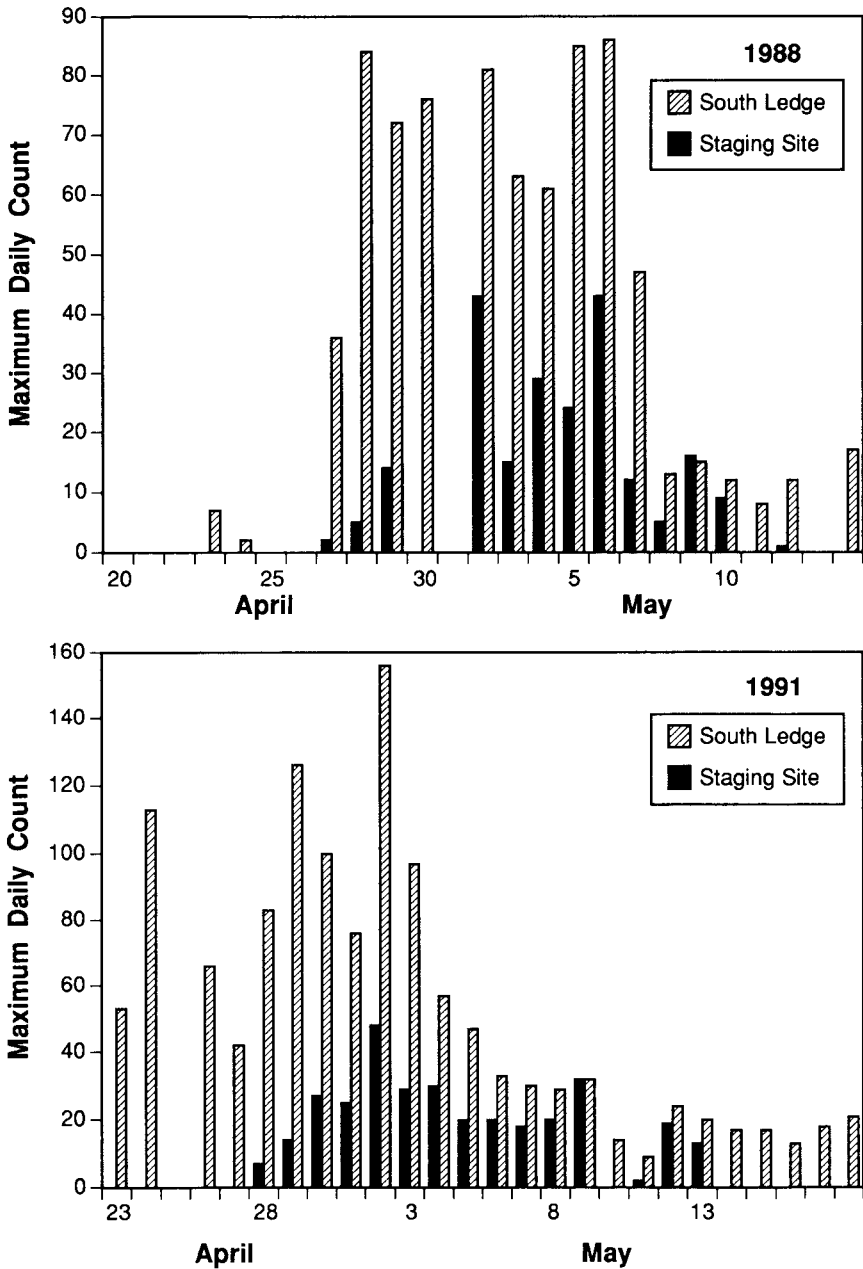


FIGURE 3. Maximum daily counts of Bristle-thighed Curlews at the South Ledge (hatched bars) and Staging Site (filled bars) on Laysan Island, Spring 1988 (upper) and 1991 (lower).

DAILY TIMING OF NORTHWARD DEPARTURES

There was no pattern in the daily timing of departures; half of the flocks left before 14:00 Hawaii Standard Time and half after, with the ear-

liest flock departing at 09:09 and the latest at 17:29 (Table 1). Moreover, there was no relationship between daily timing and date of departure ($r_s = 0.123$, $P > 0.50$, $n = 16$). We observed departing curlews for 4–28 min after they

left the island (mean = 9.9, SD = 6.2 min). All flocks took a N or NNW heading. The birds initially formed loose clusters that became vees or echelons (see Piersma et al. 1990b:166). Although we do not know the altitude at which curlews migrated, they appeared to be climbing when we lost sight of them.

BEHAVIOR DURING NORTHWARD DEPARTURES

Only four of the 16 departing flocks failed to stop at the staging site. These four flocks were among the last to depart the island, leaving between 9–13 May. The other flocks attended the staging site for 7–75 min (mean = 36.2, SD = 25.5 min). Larger flocks tended to remain at the staging site longer than did smaller flocks ($r_s = 0.711$, $P = 0.006$, $n = 14$). Staging curlews typically roosted quietly in a loose flock, facing north towards the ocean. Occasionally the birds walked about and vocalized, but they did not forage or drink.

Departures were always preceded by increased vocalizations. Watching the flocks on the staging site, we had the impression that the birds were “restless” immediately before departure. Several times one to a few birds made false starts by flying up and calling, and then settling down if others did not follow. We triggered two departures while approaching flocks to identify color-banded individuals. Two other departures were prompted by Black-footed Albatrosses (*Diomedea nigripes*) landing among curlews. Flocks departing from the staging site always circled above the island as they gained altitude. Circling flocks were extremely vocal, with birds uttering “*chiueet*” and “*klee*” calls that are characteristic of Bristle-thighed Curlews during the non-breeding season. On at least three occasions, departing birds gave “sexual display calls” that are commonly heard on the breeding grounds. Outside migration periods, display calls are given on the non-breeding grounds only during agonistic encounters (J. S. Marks, pers. observ.).

ABORTED DEPARTURES AND POSSIBLE EFFECTS OF WEATHER

We observed eight aborted departures between 2–13 May; each of the flocks contained a mixture of adults and subadults. In all but one case, the birds returned to the island within 10 min and never flew out of view. One flock disappeared from view for five min before returning to the staging site. Unfavorable surface winds were as-

sociated with five of the eight aborted attempts. In four cases there were steady E winds of about 50 km hr⁻¹, and in the other there were NE winds of 40 km hr⁻¹.

Only three of 16 departures occurred when there was no sun visible (cloud cover nearly 100%), whereas five of eight aborted departures occurred during nearly complete cloud cover (Fisher exact test, $P = 0.065$). Because the cloudy days on which aborted departures occurred were also windy, it was difficult to assess possible effects of cloud cover on departures.

FLOCK SIZES DURING DEPARTURES

Some members of departing flocks (5–62%) returned to the island in 12 of 16 instances (Table 1). The mean size of departing flocks was 14.1 (SD = 9.8) at the initial departure and 10.7 (SD = 7.9) for birds actually disappearing from view. The mean flock size experienced by the average bird ($\Sigma g^2/\Sigma g$ where g = flock size; see Jarman 1982) was 20.5 (SD = 8.6) and 16.2 (SD = 6.4) for departing and disappearing birds, respectively. These latter means, which are probably more biologically relevant (Clutton-Brock and Harvey 1984, Piersma et al. 1990b), were about 1.5 times larger than their respective arithmetic means.

In four cases, departing curlews were associated with Pacific Golden-Plovers (*Pluvialis fulva*). On 3 May, two plovers joined a flock of 15 departing curlews as they circled over the island. Small flocks of curlews (2–5 individuals) joined flocks of about 80 plovers on 6, 11, and 12 May; surface winds exceeded 35 km hr⁻¹ on all three days. In each of the latter cases, the curlews positioned themselves at the rear of the string of plovers after trailing behind them for >1 km. The only single curlew that we observed departing Laysan appeared to follow a flock of 26 plovers but had not caught up with the plovers by the time we lost them from view. Because several thousand plovers and Ruddy Turnstones (*Arrenaria interpres*) were migrating on the same dates as the curlews, it is possible that other mixed-species flocks formed outside of our view.

AGE OF MIGRATING CURLEWS

We had sufficient time to scrutinize all of the individuals in nine of the 12 departing flocks that landed at the staging site (Table 2). The singleton was an unmarked adult. In the other eight flocks, 58–100% of the curlews were individually marked (mean = 79.2, SD = 14.4%). Each of these flocks

TABLE 2. Age composition of departing Bristle-thighed Curlew flocks from the migration staging site on Laysan Island, Spring 1991.

Date in May	Flock size	Number marked	% marked	Age composition of marked birds ^a
3	17	13	76.5	8 ATY, 5 TY
4	30	24	80.0	19 ATY, 5 TY
4	11	11	100.0	6 ATY, 5 TY
5	20	≥ 14	≥ 70.0	9 ATY, 5 TY
6	7	5	71.4	3 ATY, 2 TY
7	14	14	100.0	12 ATY, 2 TY
7	12	≥ 7	≥ 58.3	3 ATY, 4 TY
9	31	24	77.4	11 ATY, 12 TY, 1 SY
13	1	0	0.0	

^a ATY = after-third-year, TY = third-year, SY = second-year; TYs and SYs are considered subadults.

contained subadults (TYs and an SY) that were noticeably thinner than adults and clearly had not taken on fat stores adequate for migration. Subadults made up a large proportion of the birds observed breaking off from migrating flocks and returning to the island. Indeed, some of the marked TYs "left" the island in at least four different flocks over a six-day period. All 21 marked subadults seen in migrating flocks were present on Laysan when we left in mid-June and probably oversummered on the island. In contrast, only one adult reappeared on the island after disappearing from view in a migrating flock; it succeeded in leaving the following day. Most of the subadults returned within minutes after departing the island. Rather than suggest an adaptive explanation for these migration attempts, we suspect that subadults joined migrating flocks simply out of a propensity to be social.

LENGTH OF STAY DURING SOUTHWARD MIGRATION

Observations of adults marked during southward migration indicated that very little turnover was occurring. In 1988 and 1990, 93 of 96 adults marked between mid-August and 10 September remained on Laysan throughout the autumn. Moreover, 97% of the 213 marked individuals seen on Laysan during autumn 1990 were still there between February and May 1991, confirming that curlews that molt on the island also spend the winter there.

Shorebird counts conducted twice each month at Tern Island from 1989–1992 indicated that curlews arriving during southward migration remained on the island throughout the winter (USFWS, unpubl. data). During these years, 6–

12 curlews wintered on the island, with numbers increasing slightly when birds arrived in late summer and then remaining the same throughout the winter. There was no evidence of an influx of individuals using the island as a migratory stopover. Data from Laysan and Tern islands thus provide strong evidence that a large proportion of the curlews arriving in the Northwestern Hawaiian Islands during southward migration remain there until the following spring.

STOPOVERS DURING NORTHWARD MIGRATION

If curlews wintering south of Hawaii stop at Laysan during northward migration, it should be evident from one or more of the following. (1) Curlews marked elsewhere are sighted on Laysan during migration. (2) Curlews marked on Laysan in previous years but wintering elsewhere in the present year reappear during migration. (3) Large numbers of unmarked adults appear during migration. (4) More curlews are seen leaving the island than were thought to be present before migration.

Although Bristle-thighed Curlews have not been color-marked south of Hawaii, none of the curlews marked in Alaska before 1991 ($n = 90$) was seen on Laysan during spring 1991 (except for an adult that regularly winters there). Also, of the 40 adult curlews marked on Laysan in 1988 or 1989 but not resighted there in 1990 or early 1991, none was seen during spring 1991. During 21 systematic censuses conducted on Laysan in 1991 (through 23 April), 73% of the curlews were individually marked. This figure is a reasonable estimate of the proportion of marked curlews on the island at the start of northward migration. Scrutiny of curlew flocks at the South

TABLE 3. Estimated proportions of marked Bristle-thighed Curlews at the South Ledge, Laysan Island, Spring 1991.^a

Date	Flock size	Number scrutinized	Number marked	% marked
April				
28	83	40	32	80
29	126	113	83	73
30	100	90	65	72
May				
1	76	27	19	70
2	156	83	62	75
3	97	82	64	78
4	57	47	37	79
5	47	45	36	80
6	33	28	25	89
7	30	27	24	89
8	29	23	19	83
9	32	31	24	77

^a Based on number of birds known to be either uniquely marked or unmarked. Oftentimes birds flushed before being scrutinized, or birds were in places where their legs were not visible.

Ledge around the peak of migration (i.e., 28 April to 9 May) indicated that 79% (SD = 6.1, range = 70–89%) of the birds were marked (Table 3). Moreover, 79% of the individuals in flocks stopping at the staging site were marked (Table 2). We observed a total of 171 curlews departing the island. Given that about 300 curlews wintered on Laysan, and that approximately 30% of these birds were non-migratory subadults, the number of birds that we observed leaving the island was lower than the estimated number of adults wintering on the island (i.e., 210).

Counts conducted at Tern Island (USFWS, unpubl. data) showed that curlew numbers remained stable throughout the spring until adults departed in early May. Thus, data from Laysan and Tern islands indicate that curlews wintering in the Central and South Pacific do not stop in the Northwestern Hawaiian Islands during spring migration. Combined with the lack of turnover that we documented during autumn, we suggest that most of the curlews wintering in the Central and South Pacific overfly the Northwestern Hawaiian Islands, thus migrating large distances ($\geq 6,000$ km) non-stop between their wintering and breeding grounds twice each year.

FAT CONTENT AND FLIGHT RANGE ESTIMATES

Most shorebirds accumulate fat rapidly in the month before migration (Pienkowski et al. 1979,

TABLE 4. Total mass, fat content, and lipid index of six Bristle-thighed Curlews collected in the Northwestern Hawaiian Islands. Bird numbers A91 to C91 were collected on Laysan Island from 30 April to 3 May 1991; bird numbers A92 to C92 were collected on Midway Atoll from 24 to 26 April 1992.

Bird number	Sex	Total mass (g)	Fat mass	Fat-free mass	Lipid index ^a
A91	F	773	363.3	409.7	47.0
B91	F	796	369.3	426.7	46.4
C91	M	465	190.6	274.4	41.0
A92	M	632	281.9	350.1	44.6
B92	F	743	269.7	473.3	36.3
C92	M	638	252.0	386.0	39.5

^a Mass of fat as % of total mass.

Johnson et al. 1989, Zwarts et al. 1990, Summers et al. 1992). In contrast, Bristle-thighed Curlews take on fat stores gradually beginning in autumn (Marks 1993). Lipid indices for the six adults collected at Laysan and Midway ranged from 36.3–47.0% (mean = 42.5%, SD = 4.2; Table 4). Fat as a proportion of lean mass ranged from 57.0–88.7% (mean = 74.6%, SD = 12.6). The slightly higher fat content of Laysan curlews (Table 4) probably resulted from the birds being collected at the staging site on the day they would have migrated. The Midway birds, which were collected about a week before migration, may not have completed premigratory fattening.

The four methods used to estimate migratory flight ranges gave widely different results ($F_{3,20} = 33.2$, $P < 0.0001$; Table 5). Distances estimated using Summers and Waltner (1979) and Davidson (1984) were statistically equal and greater (Tukey test, $P < 0.025$) than those obtained using Castro and Myers (1989) and Pennycuik (1989). With Pennycuik's method, only the three fattest curlews could have made the 4,000-km flight from Laysan to Alaska unless the others were aided by tailwinds of > 20 km hr⁻¹ (Pennycuik 1975). Using the other three methods, all of the birds had more than enough fat reserves to fly between Laysan and Alaska (Table 5). However, the Castro and Myers method would not allow birds to overfly the Northwestern Hawaiian Islands unless flight speeds were increased to about 100 km hr⁻¹. Even at flight speeds of 75 km hr⁻¹, the Summers and Waltner and Davidson methods predicted that curlews could fly non-stop between Alaska and the Marshall Islands (6,180 km) or the northern Line islands (6,190 km) with reserves to spare (Fig. 1, Table 5). Indeed, Sum-

mers and Waltner's formula indicated that curlews could fly non-stop from Alaska to the central Phoenix Islands (7,160 km).

DISCUSSION

Baker (1951) proposed the "Nearctic-Hawaiian Flyway" as the route taken by Bristle-thighed Curlews and several other shorebird species migrating between arctic breeding grounds and insular wintering grounds. This sound concept has been accepted by various investigators (e.g., Johnson 1979, Williams and Williams 1988, Johnson et al. 1989), but it sheds no light on migratory flight ranges or on the location of potential stopover sites.

Prior to the late 1980s, information on Bristle-thighed Curlew migration was largely anecdotal. Kirby (1925) and Gallagher (1960) noted migratory influxes in the Line Islands during September. Stickney (1943) suggested that southward migration occurs from late July to early August throughout Oceania. Amadon (1953) speculated that most curlews stopping in the main Hawaiian Islands eventually fly on to wintering areas farther south. Based on high counts of roosting birds during August–September and April–May, this view was also suggested for curlews in the Northwestern Hawaiian Islands (Amerson 1971, Woodward 1972, Ely and Clapp 1973, Amerson et al. 1974, Clapp and Wirtz 1975). More recently, Handel and Dau (1988) stated that after stopping in the Northwestern Hawaiian Islands, most Bristle-thighed Curlews "move south to other islands in the central and south Pacific by early October."

Based on our observations at Laysan and Tern islands, we contend that the Northwestern Hawaiian Islands are a migratory terminus for wintering Bristle-thighed Curlews rather than a stopover for transients. The high counts recorded in the Northwestern Hawaiian Islands during migratory periods result from increased flocking behavior of local curlews at traditional roosting areas (like the South Ledge at Laysan) rather than from influxes of transients. Thus, most of the curlews that winter farther south overfly the Hawaiian Islands during both northward and southward migration.

SEASONAL TIMING OF MIGRATION

During both years that we visited Laysan in spring, most curlews left the island during a nar-

TABLE 5. Estimated flight ranges (km) for six Bristle-thighed Curlews collected in the Northwestern Hawaiian Islands. Bird numbers are the same as in Table 4.

Bird number	Flight range ^a			
	S&W	DAV	C&M	PEN
A91	10,067	9,296	5,649	4,240
B91	9,976	9,227	5,853	4,260
C91	7,470	6,754	4,902	3,600
A92	8,958	8,204	5,390	4,000
B92	7,261	6,720	4,023	3,010
C92	7,721	7,087	4,288	3,260

^a S&W = Summers and Waltner (1979); DAV = Davidson (1984); C&M = Castro and Myers (1989); and PEN = Pennycuik (1989). Calculations based on still air conditions using an average flight speed of 75 km hr⁻¹ and a cruising altitude of 2,000 m.

row window of about one week in early May. This conforms with their arrival on the breeding grounds in early to mid-May (Gill et al. 1991, McCaffery and Gill 1992). Similarly, most Red Knots (*Calidris canutus*) and Ruddy Turnstones departed from Iceland during a week in late May (Alerstam et al. 1990). In Mauritania, northward departures of shorebirds were significantly correlated with breeding latitude, and most species had a unimodal pattern of departure (Piersma et al. 1990a). The fact that some departures occurred during cloudy weather (Alerstam et al. 1990, this study) and with unfavorable surface winds (Piersma et al. 1990a, this study) indicates that shorebirds respond more strongly to their reproductive schedule than to local weather. Most likely, the timing of spring migration in these species is under endogenous circannual control (Gwinner 1986, Berthold and Terrill 1991).

As might be expected, autumn arrivals at Laysan were much more protracted, extending from mid-July to late August for adults and from mid-August to early September for juveniles. These dates agree closely with observations on Alaskan staging grounds. Failed breeders begin arriving there in late June and successful breeders and juveniles in early August; most curlews are gone by mid-August (Handel and Dau 1988). Depending on the outcome of their breeding attempt, most adult Bristle-thighed Curlews reside in Alaska for only two to three months each year. Given the variety of predators that they face on the breeding grounds (McCaffery and Gill 1992), we suggest that Bristle-thighed Curlews minimize their exposure to predation by returning to the wintering grounds as soon as they are physiologically capable.

DAILY TIMING OF MIGRATION

Migratory departures of shorebirds tend to occur during rising tides and in the few hours before sunset (Dick et al. 1987, Lank 1989, Alerstam et al. 1990, Piersma et al. 1990b). Evening departures may confer several advantages. For example, polarized light at sunset (Moore 1987) and stars after sunset (Emlen 1975) could aid in orientation and navigation. Cooler, less turbulent atmospheric conditions that prevail at night could reduce water loss and energy consumption (Berthold 1975, Kerlinger and Moore 1989). Evening departures would also enable birds to forage during the most productive daylight hours prior to departure (Lank 1989).

Distinguishing among these alternatives, which are by no means mutually exclusive, is difficult. Piersma et al. (1990b) noted that cues provided by polarized light and stars could also be used when departing at dawn, yet shorebirds typically do not depart in the morning. Also, shorebirds departing during mid-day have no trouble orienting correctly (Lank 1989). Evening departures of shorebirds have also been documented at inland sites that are unaffected by tides, and the proposed energetic advantages of nocturnal migration do not predict tidally induced departures (Lank 1989). Therefore, maximization of foraging opportunities may be the main selective force favoring nocturnal migration in shorebirds (Lank 1989).

If the "foraging maximization" hypothesis is correct, then shorebirds that do not feed in the hours before migration should exhibit no diurnal pattern in departure times. On the day of migration, curlews roosted for hours without feeding and did not feed at the staging site. Stomachs of birds collected at the staging site were virtually empty. Curlews exhibited no distinct pattern in the timing of departures from Laysan, and they never left during the evening. Thus, data for Bristle-thighed Curlews provide indirect support for the foraging maximization hypothesis. We conclude that daytime departures impose no constraints on orientation or navigation for Bristle-thighed Curlews departing from the Northwestern Hawaiian Islands.

BEHAVIOR DURING DEPARTURES

The migratory behaviors that we observed were similar to those reported by others. Departing curlews were always vocal, occasionally giving sexual display calls (Lank 1989, Alerstam et al.

1990, Piersma et al. 1990b). The birds often jumped up and settled back down as if "restless," at which time humans could induce departures (Piersma et al. 1990b, Gudmundsson and Lindström 1992). The birds circled as they ascended (Alerstam et al. 1990; but see Piersma et al. 1990b) and tended to leave in fluid groups that eventually became vees or echelons (Alerstam et al. 1990, Piersma et al. 1990b). In contrast to the other species that have been studied, 25% of curlew departures occurred as mixed flocks. Mixed flocks of departing shorebirds were rare in Iceland (5.5%; Alerstam et al. 1990, Gudmundsson and Lindström 1992), Mauritania (3.9%; Piersma et al. 1990b), and the Netherlands (4.0%; Piersma et al. 1990b). As with Red Knots and Ruddy Turnstones in Iceland, Bristle-thighed Curlews remained segregated within mixed flocks. Given our small sample size, it is difficult to say if the high proportion of mixed-species flocks that we observed is typical of departing Bristle-thighed Curlews.

An unusual aspect of curlew migration was that departing flocks often contained subadults that returned immediately to the island. Departing shorebirds were not observed to return to the departure point in Mauritania (Piersma et al. 1990b), perhaps because those flocks did not contain subadults destined to overwinter on the wintering grounds.

FLOCK SIZES

In theory, group migration confers energetic and navigational benefits to individual flock members. Thus, one might expect flocks to be "maximally large" at departure (Piersma et al. 1990b). Departing flocks of curlews were substantially smaller than those reported for other shorebird species (Alerstam et al. 1990, Blomert et al. 1990, Piersma et al. 1990b, Gudmundsson and Lindström 1992). Indeed, the unusual circumstances under which Bristle-thighed Curlews winter suggest that small flocks are typical during migration. Throughout much of their winter range, Bristle-thighed Curlews inhabit tiny islands that support fewer than 50 individuals (e.g., Gallagher 1960; Thompson and Hackman 1968; Amerson 1969, 1971; Woodward 1972; Amerson et al. 1974; Child 1981). If some of them are subadults (which do not migrate), then flocks of curlews migrating from these islands must always be small (unless flocks from different islands coalesce en route). Yet, they make spec-

tacular long-distance flights over open ocean and have high survivorship (Marks 1992). Clearly, then, large flocks are not requisite for long-distance migration in Bristle-thighed Curlews.

Factors determining flock sizes in migrating birds are not well understood. Piersma et al. (1990b) posited that the size of migrating shorebird flocks might be limited by "organizational constraints." Regardless of what determines maximum flock size, however, the wide variability in shorebird flock sizes (Piersma et al. 1990b) suggests that shorebirds often migrate in flocks that are larger than necessary in terms of energetic and navigational benefits. There is probably some minimum number of birds necessary for efficient long-distance migration, but there is no reason to expect that flock sizes above this minimum would decrease migration efficiency. Thus, one might expect flock sizes to be at or above some "minimally small" number. The comparatively small flock sizes that we observed probably resulted from the fact that there were fewer than 300 adult curlews on Laysan versus thousands of individuals per species in the other studies.

FAT CONTENT

The Bristle-thighed Curlews that we collected had some of the highest lipid indices (fat as % of total mass) ever measured for shorebirds (mean = 42.5%, range = 36.3–47.0%). Average lipid indices for other migrating shorebirds include 32.4% for Pacific Golden-Plovers on Oahu, Hawaii (maximum = 36.8%; Johnson et al. 1989), 34% for Semipalmated Sandpipers (*Calidris pusilla*) in Ontario, Canada (maximum = 42.1%; Page and Middleton 1972), and 33.5% to 41.7% for seven species in South Africa (Summers and Waltner 1979). In the latter study, only the Sanderling (*Calidris alba*) had a mean lipid index >40% (mean = 41.7%, maximum = 51.2%).

Owing to their long, non-stop migration, Bristle-thighed Curlews might be expected to accumulate large amounts of fat relative to other shorebirds. In general, however, lipid indices are largest in small birds (King and Farner 1965). This tendency probably results from the fact that the power needed to fly increases more rapidly with body size than does the power available from the flight muscles. Therefore, the capacity to carry fat generally decreases with increasing body mass (Hedenström and Alerstam 1992). Considering the relatively large size of Bristle-

thighed Curlews, the high fat stores that we measured are especially noteworthy.

Because the curlews we collected were about to depart on migration, their fat stores were at or near maximum levels. Other studies have been less precise with regard to sampling at the time of departure (Davidson 1984, Johnson et al. 1989). Thus, the lower lipid indices measured in other shorebirds may be due to collecting individuals that were not fully prepared for migration. Nonetheless, in each species except the Sanderling, the maximum lipid index was below that of the Bristle-thighed Curlew. Again, this suggests that Bristle-thighed Curlews take on large fat stores relative to most other shorebirds.

FLIGHT RANGE ESTIMATES

Because it is impossible to account for all of the variables influencing flight energetics (Gudmundsson et al. 1991), flight range calculations are at best only crude estimates of actual performance. Ideally, a test of the models should be conducted with individuals whose migration distances are known (Davidson 1984). Bristle-thighed Curlews fly 4,000 km non-stop to winter on Laysan, and curlews that overfly Hawaii must fly at least 2,000 km farther. Pennycuick's (1975, 1989) model clearly underestimates the flight range of Bristle-thighed Curlews, allowing the three fattest individuals to reach Laysan with little or no reserves (Table 5). Empirical data that would improve the accuracy of Pennycuick's model (e.g., flight altitude and wind speed and direction) are not available for long-distance migrants (see Davidson 1984).

Estimates derived from the Castro and Myers (1989) model gave results that were consistent with a Laysan-to-Alaska flight. However, the calculations did not account for curlews that overfly Hawaii. Although it could be argued that birds preparing for a 4,000-km flight should not take on fat stores for longer flights (Gudmundsson et al. 1991), it is difficult to imagine curlews taking on fat stores that, according to the Castro and Myers model, would be necessary for a flight of >6,000 km (viz., lipid index of about 55%). Consequently, one must assume flight speeds of >100 km hr⁻¹ to account for curlews that overfly the Northwestern Hawaiian Islands.

Only the Summers and Waltner (1979) and Davidson (1984) models predicted that Bristle-thighed Curlews could fly to island groups south of Laysan. Both of these models rely on flight

metabolism values for nonpasserines (Summers and Waltner combine passerine and nonpasserine flight metabolism). Because shorebirds are now thought to have high, passerine-like metabolism (Castro 1987, Kersten and Piersma 1987, Mathiu et al. 1989), these two models probably overestimate flight ranges.

On balance, it is difficult to evaluate flight range models without information on how shorebirds use winds aloft (Davidson 1984, Summers et al. 1987, Gudmundsson et al. 1991). Piersma and van de Sant (1992) used synoptic weather data to evaluate wind conditions between West Africa and Siberia during spring. Over a 13-year period, tailwinds of 5–35 km hr⁻¹ were usually available within altitudes of 1–5 km. Piersma and van de Sant (1992) suggested that migrating shorebirds sample a range of altitudes to seek out favorable winds. Although synoptic wind data were not available for the Northwestern Hawaiian Islands, it is likely that favorable winds do exist within the range of altitudes at which Bristle-thighed Curlews migrate. These tailwinds probably enable curlews (and other shorebirds) to migrate large distances (>6,000 km) non-stop over open ocean.

CONSERVATION IMPLICATIONS

We provide strong evidence (albeit indirect) that most of the Bristle-thighed Curlews wintering on Central and South Pacific islands overfly the Northwestern Hawaiian Islands during migration. Assuming that curlews cannot fly to the southern end of their winter range non-stop (>8,500 km), migratory stopover sites must exist in the Central Pacific. Possible locations include the Marshall Islands (6,180 km from the staging grounds in Alaska), the northern Line Islands (6,190 km), and the Phoenix Islands (7,160 km) (see Fig. 1). Such non-stop flights would rank among the longest known or postulated for any shorebird (e.g., Barter and Wang Tianhou 1990).

Traditional staging sites are essential for the successful migration of many shorebirds that winter along continental coasts (Myers 1983). We suggest that Bristle-thighed Curlews that overfly Hawaii also use traditional staging sites, and that these sites are critical for the migration of large numbers of curlews that winter in the South Pacific. Considering the devastating effects that humans have had on the biota of oceanic islands (Wodzicki 1981, Loope et al. 1989), the identification and protection of these staging sites would

be imperative for the conservation of Bristle-thighed Curlew populations.

ACKNOWLEDGMENTS

D. K. McDermond, L. Honigman, R. E. Gill, Jr., and I. J. Ball helped ensure the success of our work on the remote islands. We also thank K. P. Dial, R. L. Hutto, A.E.H. Perkins, and especially O. W. Johnson and T. Piersma for helpful suggestions on the manuscript; M. G. Burcham, D. L. Evans, D. P. Hendricks, and S. M. Leasure for assistance in the field; B. J. McCaffery for information on curlews in Alaska; L. H. Fredrickson for arranging for the fat analysis; R. A. Petty and J. V. Schumacher for preparing the figures; and U.S. Fish and Wildlife Service personnel for census data from Tern Island. The research was supported by the U.S. Fish and Wildlife Service (Alaska Fish and Wildlife Research Center, Hawaiian Islands National Wildlife Refuge, Montana Cooperative Wildlife Research Unit), the National Geographic Society, the World Wildlife Fund, University of Montana Bertha Morton Fellowships, the Hawaii Audubon Society, Sigma Xi, a Curby-Pavelsky-Harris award, and a Paul A. Stewart award. Logistical support was provided by the National Marine Fisheries Service, the U.S. Coast Guard, and the NOAA research vessel 'Townsend Cromwell.'

LITERATURE CITED

- ALERSTAM, T., G. A. GUDMUNDSSON, P. E. JÖNSSON, J. KARLSSON, AND Å. LINDSTRÖM. 1990. Orientation, migration routes and flight behaviour of knots, turnstones and Brant Geese departing from Iceland in spring. *Arctic* 43:201–214.
- AMADON, D. 1953. Migratory birds of relict distribution: some inferences. *Auk* 70:461–469.
- AMERSON, A. B., JR. 1969. Ornithology of the Marshall and Gilbert islands. *Atoll Res. Bull.* 127.
- AMERSON, A. B., JR. 1971. The natural history of French Frigate Shoals, Northwestern Hawaiian Islands. *Atoll Res. Bull.* 150.
- AMERSON, A. B., JR., R. B. CLAPP, AND W. O. WIRTZ, II. 1974. The natural history of Pearl and Hermes Reef, Northwestern Hawaiian Islands. *Atoll Res. Bull.* 174.
- BAKER, R. H. 1951. The avifauna of Micronesia, its origin, evolution, and distribution. *Univ. Kansas Publ., Mus. Nat. Hist.* 3:1–359.
- BARTER, M., AND WANG TIANHOU. 1990. Can waders fly non-stop from Australia to China? *Stilt* 17:36–39.
- BERTHOLD, P. 1975. Migration: control and metabolic physiology, p. 77–128. *In* D. S. Farner and J. R. King [eds.], *Avian biology*. Vol. 5. Academic Press, New York.
- BERTHOLD, P., AND S. B. TERRILL. 1991. Recent advances in studies of bird migration. *Ann. Rev. Ecol. Syst.* 22:357–378.
- BLOMERT, A.-M., M. ENGELMOER, AND Y. NTIAM-OA-BAIDU. 1990. The Banc D'Arguin, Mauritania, as a meeting point for Avocets during spring migration. *Ardea* 78:185–192.
- CASTRO, G. 1987. High basal metabolic rate in Sand-erlings (*Calidris alba*). *Wilson Bull.* 99:267–268.

- CASTRO, G., AND J. P. MYERS. 1989. Flight range estimates for shorebirds. *Auk* 106:474-476.
- CHILD, P. 1981. Birdlife of Aitutaki, Cook Islands. *Notornis* 28:29-34.
- CLAPP, R. B., AND W. O. WIRTZ, II. 1975. The natural history of Lisianski Island, Northwestern Hawaiian Islands. *Atoll Res. Bull.* 186.
- CLUTTON-BROCK, T. H., AND P. H. HARVEY. 1984. Comparative approaches to investigating adaptation, p. 7-29. *In* J. R. Krebs and N. B. Davies [eds.], *Behavioural ecology: an evolutionary approach*. Blackwell Scientific Publications, Oxford, England.
- DAVIDSON, N. C. 1984. How valid are flight range estimates for waders? *Ring and Migration* 5:49-64.
- DICK, W. J. A., T. PIERSMA, AND P. PROKOSCH. 1987. Spring migration of the Siberian Knots *Calidris canutus canutus*: results of a co-operative Wader Study Group project. *Ornis Scand.* 18:5-16.
- DUNN, P. O., T. A. MAY, M. A. MCCOLLOUGH, AND M. A. HOWE. 1988. Length of stay and fat content of migrant Semipalmated Sandpipers in eastern Maine. *Condor* 90:824-835.
- ELY, C. A., AND R. B. CLAPP. 1973. The natural history of Laysan Island, Northwestern Hawaiian Islands. *Atoll Res. Bull.* 171.
- EMLEN, S. T. 1975. Migration: orientation and navigation, p. 129-219. *In* D. S. Farner and J. R. King [eds.], *Avian biology*. Vol. 5. Academic Press, New York.
- EVANS, P. R., AND N. C. DAVIDSON. 1990. Migration strategies and tactics of waders breeding in arctic and north temperate latitudes, p. 387-398. *In* E. Gwinner [ed.], *Bird migration: physiology and ecophysiology*. Springer-Verlag, Berlin.
- GALLAGHER, M. D. 1960. Bird notes from Christmas Island, Pacific Ocean. *Ibis* 102:489-502.
- GILL, R. E., JR., AND R. L. REDMOND. 1992. Distribution, numbers, and habitat of Bristle-thighed Curlews (*Numenius tahitiensis*) on Rangiroa Atoll. *Notornis* 39:17-26.
- GILL, R. E., JR., R. B. LANCTOT, J. B. MASON, AND C. M. HANDEL. 1991. Observations on habitat use, breeding chronology and parental care in Bristle-thighed Curlews on the Seward Peninsula, Alaska. *Wader Study Group Bull.* 61:28-36.
- GUDMUNDSSON, G. A., AND Å. LINDSTRÖM. 1992. Spring migration of Sanderlings *Calidris alba* through SW Iceland: wherefrom and whereto? *Ardea* 80:315-326.
- GUDMUNDSSON, G. A., Å. LINDSTRÖM, AND T. ALERSTAM. 1991. Optimal fat loads and long-distance flights by migrating knots *Calidris canutus*, Sanderlings *C. alba* and turnstones *Arenaria interpres*. *Ibis* 133:140-152.
- GWINNER, E. 1986. Circannual rhythms in the control of avian migrations. *Adv. Study Behav.* 16:191-228.
- HANDEL, C. M., AND C. P. DAU. 1988. Seasonal occurrence of migrant Whimbrels and Bristle-thighed Curlews on the Yukon-Kuskokwim Delta, Alaska. *Condor* 90:782-790.
- HARRINGTON, B. A., F. J. LEEUWENBERG, S. L. RESENDE, R. MCNEIL, B. T. THOMAS, J. S. GREAR, AND E. F. MARTINEZ. 1991. Migration and mass change of White-rumped Sandpipers in North and South America. *Wilson Bull.* 103:621-636.
- HENDENSTRÖM, A., AND T. ALERSTAM. 1992. Climbing performance of migrating birds as a basis for estimating limits for fuel-carrying capacity and muscle work. *J. Exp. Biol.* 164:19-38.
- HOWE, M. A., P. H. GEISSLER, AND B. A. HARRINGTON. 1989. Population trends of North American shorebirds based on the International Shorebird Survey. *Biol. Conserv.* 49:185-199.
- JARMAN, P. J. 1982. Prospects for interspecific comparison in sociobiology, p. 323-342. *In* King's College Sociobiology Group [eds.], *Current problems in sociobiology*. Cambridge Univ. Press, Cambridge, England.
- JOHNSON, O. W. 1979. Biology of shorebirds summering on Enewetak Atoll. *Stud. Avian Biol.* 2:193-205.
- JOHNSON, O. W., M. L. MORTON, P. L. BRUNER, AND P. M. JOHNSON. 1989. Fat cyclicity, predicted migratory flight ranges, and features of wintering behavior in Pacific Golden-Plovers. *Condor* 91:156-177.
- KERLINGER, P., AND F. R. MOORE. 1989. Atmospheric structure and avian migration. *Curr. Ornithol.* 6:109-142.
- KERSTEN, M., AND T. PIERSMA. 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. *Ardea* 75:175-187.
- KING, J. R., AND D. S. FARNER. 1965. Studies of fat deposition in migratory birds. *Ann. New York Acad. Sci.* 131:422-440.
- KIRBY, H., JR. 1925. The birds of Fanning Island, Central Pacific Ocean. *Condor* 27:185-196.
- LANK, D. B. 1989. Why fly by night? Inferences from tidally-induced migratory departures of sandpipers. *J. Field Ornithol.* 60:154-161.
- LOOPE, L. L., O. HAMANN, AND C. P. STONE. 1988. Comparative conservation biology of oceanic archipelagoes. *BioScience* 38:272-282.
- MARKS, J. S. 1992. Longevity record for the Bristle-thighed Curlew: an extension. *J. Field Ornithol.* 63:309-310.
- MARKS, J. S. 1993. Molt of Bristle-thighed Curlews in the Northwestern Hawaiian Islands. *Auk* 110:573-587.
- MARKS, J. S., R. L. REDMOND, P. HENDRICKS, R. B. CLAPP, AND R. E. GILL, JR. 1990. Notes on longevity and flightlessness in Bristle-thighed Curlews. *Auk* 107:779-781.
- MATHIU, P. M., O. W. JOHNSON, P. M. JOHNSON, AND G. C. WHITTOW. 1989. Basal metabolic rate of Pacific Golden-Plovers. *Wilson Bull.* 101:652-654.
- MCCAFFERY, B. J., AND R. E. GILL, JR. 1992. Anti-predator strategies in breeding Bristle-thighed Curlews. *Am. Birds* 46:378-383.
- MOORE, F. R. 1987. Sunset and the orientation behaviour of migrating birds. *Biol. Rev. Camb. Phil. Soc.* 62:65-86.
- MORIN, M. P., AND S. CONANT. 1990. Nest substrate variation between native and introduced popu-

lations of Laysan Finches. *Wilson Bull.* 102:591-604.

MORRISON, R.I.G. 1984. Migration systems of some New World shorebirds, p. 125-202. *In* J. Burger and B. L. Olla [eds.], *Shorebirds: migration and foraging behavior*. Plenum Press, New York.

MYERS, J. P. 1983. Conservation of migrating shorebirds: staging areas, geographic bottlenecks, and regional movements. *Am. Birds* 37:23-25.

PAGE, G., AND A.L.A. MIDDLETON. 1972. Fat deposition during autumn migration in the Semipalmated Sandpiper. *Bird-Banding* 43:85-96.

PENNYCUICK, C. J. 1975. Mechanics of flight, p. 1-75. *In* D. S. Farner and J. R. King [eds.], *Avian biology*. Vol. 5. Academic Press, New York.

PENNYCUICK, C. J. 1989. *Bird flight performance. A practical calculation manual*. Oxford Univ. Press, Oxford, England.

PIENKOWSKI, M. W., AND P. R. EVANS. 1984. Migratory behavior of shorebirds in the western Palearctic, p. 73-123. *In* J. Burger and B. L. Olla [eds.], *Shorebirds: migration and foraging behavior*. Plenum Press, New York.

PIENKOWSKI, M. W., C. S. LLOYD, AND C.D.T. MINTON. 1979. Seasonal and migrational weight changes in Dunlins. *Bird Study* 26:134-148.

PIERSMA, T., M. KLAASSEN, J. H. BRUGGEMANN, A.-M. BLOMERT, A. GUEYE, Y. NTIAMOA-BAIDU, AND N. E. VAN BREDERODE. 1990a. Seasonal timing of the spring departure of waders from the Banc D'Arguin, Mauritania. *Ardea* 78:123-134.

PIERSMA, T., AND S. VAN DE SANT. 1992. Pattern and predictability of potential wind assistance for waders and geese migrating from West Africa and the Wadden Sea to Siberia. *Ornis Svecica* 2:55-66.

PIERSMA, T., L. ZWARTS, AND J. H. BRUGGEMANN. 1990b. Behavioural aspects of the departure of waders before long-distance flights: flocking, vocalizations, flight paths and diurnal timing. *Ardea* 78:157-184.

PITELKA, F. A. [ED.]. 1979. *Shorebirds in marine environments*. Stud. Avian Biol., No. 2.

RICHARDSON, W. J. 1979. Southeastward shorebird migration over Nova Scotia and New Brunswick in autumn: a radar study. *Can J. Zool.* 57:107-124.

STICKNEY, E. H. 1943. Birds collected during the Whitney South Sea Expedition. *Northern shorebirds in the Pacific*. *Amer. Mus. Novit.* 1248:1-9.

SUMMERS, R. W., L. G. UNDERHILL, M. NICOLL, R.

RAE, AND T. PIERSMA. 1992. Seasonal, size- and age-related patterns in body-mass and composition of Purple Sandpipers *Calidris maritima* in Britain. *Ibis* 134:346-354.

SUMMERS, R. W., L. G. UNDERHILL, M. WALTNER, AND D. A. WHITELAW. 1987. Population, biometrics and movements of the Sanderling *Calidris alba* in southern Africa. *Ostrich* 58:24-39.

SUMMERS, R. W., AND M. WALTNER. 1979. Seasonal variations in the mass of waders in southern Africa, with special reference to migration. *Ostrich* 50:21-37.

THOMPSON, M. C., AND C. D. HACKMAN. 1968. Birds of the Tokelau Islands. *Notornis* 15:109-117.

WILLIAMS, T. C., AND J. M. WILLIAMS. 1988. Radar and visual observations of autumnal (southward) shorebird migration on Guam. *Auk* 105:460-466.

WODZICKI, K. 1981. Some nature conservation problems in the South Pacific. *Biol. Conserv.* 21:5-18.

WOODWARD, P. W. 1972. The natural history of Kure Atoll, Northwestern Hawaiian Islands. *Atoll Res. Bull.* 164.

WYMENGA, E., M. ENGELMOER, C. J. SMIT, T. M. VAN SPANJE. 1990. Geographical breeding origin and migration of waders wintering in West Africa. *Ardea* 78:83-112.

ZAR, J. H. 1989. Microcomputer calculation of distance and initial direction along great-circle routes. *J. Field Ornithol.* 60:520-522.

ZWARTS, L., B. J. ENS, M. KERSTEN, AND T. PIERSMA. 1990. Moults, mass and flight range of waders ready to take off for long-distance migrations. *Ardea* 78:339-364.

APPENDIX. Formulae used to estimate migratory flight ranges.

Summers and Waltner (1979)
 $R = 163.24 \cdot S \cdot (M_2^{0.256} - M_1^{0.256})$

Davidson (1984)
 $R = 95.447 \cdot S \cdot (M_2^{0.302} - M_1^{0.302})$

Castro and Myers (1989)
 $R = 26.88 \cdot S \cdot L^{1.614} \cdot (M_1^{-0.464} - M_2^{-0.464})$

R = flight range (km); S = flight speed (km hr⁻¹); L = wing length (cm); M₁ = lean mass (g); M₂ = total mass (g).