

## Notes on Longevity and Flightlessness in Bristle-thighed Curlews

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Bristle-thighed Curlews (*Numenius tahitiensis*) are among the least-studied shorebirds in the world. They have a highly restricted breeding range in western Alaska and winter exclusively on remote islands in the central and south Pacific (AOU 1983, Kessel 1989). The status of these birds is not known, but they are considered to be rare throughout their range (Johnsgard 1981). We describe two unusual traits of Bristle-thighed Curlews—exceptional longevity and flightlessness during molt—and discuss their significance to the species' migration and nonbreeding ecology.

In spring 1988, we began a study of the nonbreeding ecology of Bristle-thighed Curlews on Laysan Island (25°46'N, 171°44'W) in the Northwestern Hawaiian Islands. Curlews inhabit these tiny, remote islands at the northern edge of their winter range year-round, but are present in greatest numbers from August to May (Ely and Clapp 1973, Clapp and Wirtz 1975, pers. obs.). During April–May and August–November, 1988, and June–September, 1989, we captured and color-banded >300 curlews on Laysan. We used a spotlight and hoop net at night to catch most (>97%) of the birds.

*Longevity records.*—On 4 October 1988 we captured an individual that had been banded on Laysan as a hatching-year bird on 10 September 1967 (USFWS band number 564-02861). It was seen four more times on Laysan in 1988, and again on 25 July 1989. Given that Bristle-thighed Curlews hatch in mid- to late June (Kyllingstad 1948, B. J. McCaffery pers. comm.), this bird would have been approximately 22 years and 1 month old on 25 July 1989. On 24 and 31 August, 1989, we encountered a banded Bristle-thighed Curlew and read the number (564-00019) through a spotting scope. The bird had been banded (age unknown) on Lisianski Island, 225 km NW of Laysan, on 4 September 1967. It was at least 22 years and 2 months old on 31 August 1989.

The previous longevity record for a Bristle-thighed Curlew was a bird that was at least 11 years and 9 months old (Klimkiewicz and Futcher 1989). The previous longevity record for a North American scolopacid was a Least Sandpiper (*Calidris minutilla*) estimated to be 16 years old (Miller and McNeil 1988). The Eurasian Curlew (*Numenius arquata*; 31 years and 7 months), Dunlin (*C. alpina*; 28 years and 8 months), and Red Knot (*C. canutus*; 25 years and 8 months) are

the three oldest known scolopacid species in the world (Mead and Clark 1989, Staav 1989). Therefore, the two Bristle-thighed Curlews that we observed on Laysan are by far the oldest known scolopacids in North America and apparently are among the oldest in the world. When we consider that only 291 Bristle-thighed Curlews were banded before 1988 (Bird Banding Laboratory unpubl. data), these longevity records are remarkable. This finding takes on added significance when considered in light of the species' migration and nonbreeding ecology.

The Northwestern Hawaiian Islands are approximately 4,000 km from the postbreeding staging grounds on the Yukon-Kuskokwim Delta in Alaska (Handel and Dau 1988). Because it is unlikely that Bristle-thighed Curlews rest on the ocean, adults must migrate nonstop at least 4,000 km twice each year. Flights of this length are energetically demanding for shorebirds (see Castro and Myers 1989) and are potentially hazardous (e.g. strong winds could deflect birds off course).

*Flightlessness during molt.*—Bristle-thighed Curlews are unique among migratory shorebirds in that they winter exclusively on remote islands. Historically, most of these islands were free of predators capable of capturing curlews, and many (including Laysan Island) remain predator-free today. One extraordinary and previously undescribed adaptation of Bristle-thighed Curlews to life on predator-free islands is flightlessness during molt.

From late summer through autumn, adult (i.e. after second year) Bristle-thighed Curlews can be distinguished from subadults based on differences in stage of molt (Marks unpubl. data). Adults begin to molt primaries from mid-August to mid-September and finish in November or December. During daytime between 12 October and 7 November, 1988, we captured by hand five adult curlews that were unable to fly. Each bird ran from us before capture and upon release. There was no difference in body condition (log body mass by log tarsus length) between the flightless curlews and all other adults ( $n = 5$ ) known to be capable of flight and captured during the same period (ANCOVA,  $F = 2.59$ ,  $df = 1, 7$ ,  $P = 0.15$ ). Each of the flightless birds was molting large numbers of remiges (Fig. 1). Four were molting 4 middle and outer primaries, and 7–10 secondaries, on each wing;

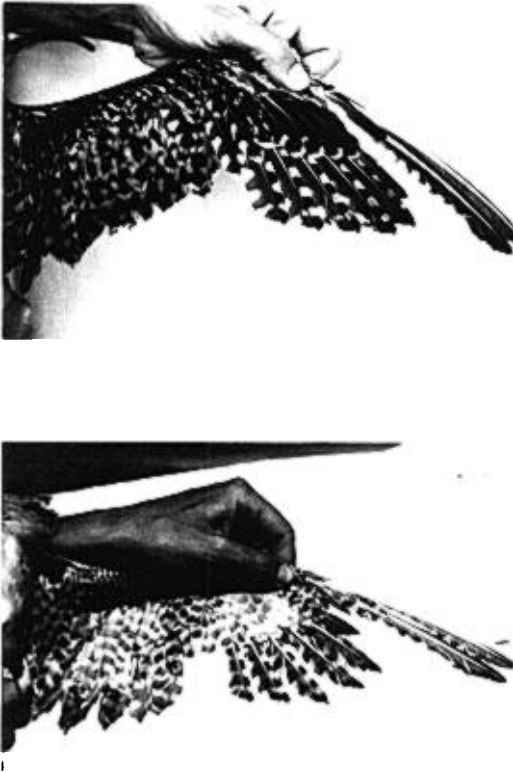


Fig. 1. Two flightless Bristle-thighed Curlews during prebasic molt on Laysan Island. Top: Primaries 1-4 are new, 5 and 6 are nearly full-grown, 7 and 8 are gone, 9 and 10 are old. Secondary 1 has just broken sheath, secondaries 2-10 are gone (band no. 794-28831, 21 October 1988). Bottom: Primaries 1-3 are new, 4 and 5 are nearly full-grown, 6 and 7 are less than half-grown, 8 is gone, 9 and 10 are old. Secondary 1 has not broken sheath, 2 and 3 are gone, the rest are old (band no. 794-28832, 26 October 1988).

another was molting 5 middle and outer primaries, and 3 outer secondaries. Curlews did not drop more than 3 adjacent primaries at once. Secondaries, however, were shed nearly simultaneously in blocks of 4-10 feathers. Adults did not drop secondaries until they had replaced at least the first 3 primaries, and secondaries were not dropped in large blocks until after the first 1 or 2 had been shed singly. Based on a flightless bird that was captured twice, the flightless period lasts at least 2 weeks.

Flightless curlews were very secretive during daytime, residing in dense stands of bunchgrass (*Eragrostis variabilis*) in the interior of the island. We came upon them by chance and surely detected only a fraction of those present. Between 6 October and 11 November (our last trapping night in 1988), we captured

13 adult curlews that we suspected were flightless (12 had dropped 7-10 secondaries, and one had dropped 6 primaries). We did not confirm flightlessness in these birds, however, because they were caught and released at night when curlews are reluctant to fly. Sixteen other adults were captured during this same period. Molt in these birds had not reached the stage at which large blocks of secondaries are dropped. Accordingly, we estimate that at least 45% (13/29) of the adult curlews on Laysan become flightless during the prebasic molt in autumn.

Our findings from Laysan corroborate a statement made by an elderly native of Rangiroa Atoll, Tuamotu Archipelago (15°05'S, 147°45'W) in April 1988 (interview by Redmond and Gill). His recollection was that some curlews were unable to fly in October. This information indicates that a flightless period probably occurs in many adult Bristle-thighed Curlews during their prebasic molt in autumn.

Because Bristle-thighed Curlews can be long-lived despite the potential hazards of migrating long distances over open ocean twice each year, we infer that the costs of such a migration are outweighed by the benefits of wintering in a predator-free environment (see Amadon 1953). Clearly, flightlessness during molt would be maladaptive in the presence of predators. Since human settlement of Oceania, first by Polynesians and more recently by Europeans, exotic mammals able to prey on curlews have been introduced to many Pacific islands (Holyoak 1973, King 1973, Loope et al. 1988). These introductions, coupled with harvest by humans (Bruner 1972), very likely have reduced Bristle-thighed Curlew numbers and altered the species' winter distribution. Thus, conservation of Bristle-thighed Curlews may depend on the maintenance of predator-free islands within the species' winter range.

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## Possible Causes of Territory Takeovers in a North-temperate Population of House Wrens

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In most animal species, residents defeat nonresident challengers in a high proportion of contests over territories and other resources (summary in Leimar and Enquist 1984; see also Krebs 1982, Walton and Nolan 1986, Jakobsson 1988). Three explanations are generally suggested for this observation. First, residents may be stronger or larger, or have larger weapons, greater energy reserves, more experience in fighting, etc., which gives them greater "resource holding potential" (Parker 1974). Second, residents may assign a greater value to the disputed resource than do challengers, and may therefore fight harder or longer for that resource. The relative value of a territory should increase as the resident gains knowledge of its resources (i.e. food sources, areas of cover, and potential nest sites). Challengers are presumably less familiar with the resident's territory and thus should not value it more than any other territory.

Third, under certain conditions, the simple convention of "owner wins" may be used to settle contests (Maynard Smith and Parker 1976). Conflicts should be settled in this manner only if the cost of an escalated contest is high relative to the value of the resource, if individuals have little control over the risk of injury in escalated contests, or if resources are readily available elsewhere (Krebs 1982).

Recent reports have indicated that, in populations of several species of birds, challengers regularly evict residents from territories (Freed 1986, Ueda 1986, Eckert and Weatherhead 1987, Arcese 1989). Because such results run counter to the frequently observed outcome of resident-challenger contests, they may provide unique insights into the nature and evolution of animal conflict behavior. We report observations of territory takeover attempts in a north-temperate population of House Wrens (*Troglodytes aedon*). We outline several hypotheses to explain the occurrence of territory takeover attempts in birds, and we discuss the success of some challengers in evicting residents in a game-theoretical framework.

Observations were conducted from 1985 to 1989 on

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