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LATERAL ASYMMETRY OF THE BILL OF *LOXOPS COCCINEUS* (DREPANIDINAE)

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Unlike the claws of crustaceans, the shells of snails, or flatfish that lie on one side, few bird species show lateral asymmetry in external morphology. Asymmetries have been described in ears, legs, and bills: (1) several species of owls have asymmetric, feather-covered external ears (Newton 1896, p. 178 and 675; Norberg 1977); (2) asymmetry of leg and foot bones associated with predominant use of a given limb has been reviewed by McNeil et al. (1971); (3) lateral bending of the bill has been noted in Charadriiformes: the bill of the Wry-billed Plover (*Anarhynchus frontalis*) of New Zealand bends to the right (Johnsgard 1981, p. 204–206), and in at least four species of oystercatchers (*Haematopus* spp.), a minority of individuals have bent bills, most of which are bent to the left (Hockey 1981); (4) crossbills (*Loxia* spp.) have crossed mandibles; and, (5) the Akepa (*Loxops coccineus*), a small, endangered species of the Drepanidinae (Hawaiian finches, formerly honeycreepers) has crossed mandibles that resemble those of crossbills. The Akepa is small (wing 59–69 mm, culmen 9–11.5 mm; Amadon 1950) and is found on the islands of Hawaii, Kauai, Maui, and formerly Oahu. The island populations differ considerably in color and morphology but all show the characteristic bill-asymmetry. The populations were formerly more numerous but are now rare and of limited distribution. Most of the museum specimens were collected in the period 1890 to 1900.

The Akepa's bill-crossing, although slight and inconspicuous, is likely to be related to the feeding habit of the species. Richards and Bock (1973) reported (from four specimens) that the asymmetry is confined to the horny rhamphotheca and does not involve the underlying skeleton. They suggested how the asymmetry functions in prying apart closely imbricated structures. Preliminary evidence suggested to me that the sexes might differ in the direction of laterality and, perhaps, present a novel form of sexual niche-diversification (Selander 1966). The acquisition of these specialized foraging skills is presumably contingent upon development of the appropriate structures. Thus, it is valuable to compare the bill-crossing between Akepas of different ages.

Here, I report the direction of bill-crossing in Akepas from different islands in relation to age and sex, and the magnitude of lateral asymmetry in relation to age for males from one population.

I examined all available, undamaged skins in the following collections: American Museum of Natural History, New York (105); Bernice P. Bishop Museum, Honolulu (87); British Museum, Tring (57); Museum of Comparative Zoology, Harvard University (20). These comprise 71% of all specimens reported to exist in collections (Banko 1979).

For each specimen, I recorded from the label(s) age, sex, and details of collection, and from the skin, the direction of asymmetry (position of lower mandible with reference to sagittal plane), and plumage color. For the majority of specimens, I measured (under a microscope) the lateral separation of the tips of the mandibles (i.e., extent of asymmetry). Some of the Akepa skins had been damaged or distorted during collection or preparation, but the direction of laterality was rarely obscured. Some severely distorted skins were rejected for measurements of tip separation.

All females (and males from Kauai) cannot conveniently be aged by plumage color. Other males were classified into three age-classes by the extent of orange (or red) plumage: (a) juveniles (without any orange), (b) sub-adults (orange incomplete), (c) adults (fully orange). The timing of these transitions in plumage is not yet known, but they are believed to represent an increasing age sequence. Males are significantly more numerous than females in the collections ($\chi^2 = 18.6$, $P < 0.005$).

Right-billed birds predominated, especially in adult males (58%), and the only groups with a majority of left-billed birds were females from Maui and the six males

TABLE 1. Direction of lateral asymmetry[a] in populations of *Loxops coccineus* sorted by age and sex.

	Age				Sex			
	Imm. males[b]		Adult males		All males		All females	
Island, race	L	R	L	R	L	R	L	R
Hawaii, *coccineus*	16	18	33	45	49	63	21	23
Kauai, *caerulirostris*					14	20	10	12
Maui, *ochraceus*	5	7	6	9	11	16	8	5
Oahu, *rufus*					4	2	1	0
Totals	21	25	39	54	78	101	40	40

[a] Side to which the lower mandible is twisted.
[b] Less than completely orange plumage.

from Oahu (Table 1). The differences, however, were not statistically significant (chi-square test). I therefore concluded from these samples that the direction of the asymmetry differs neither between young and old males ($P > 0.5$), nor between males and females ($P > 0.1$), and further, that the overall frequencies of left and right do not differ from 50/50 ($\chi^2 = 1.34$, $0.1 < P < 0.5$).

To examine more closely the possible effect of age, I compared the extent of asymmetry (separation of bill-tips) in 76 males from Hawaii that were classified by plumage into three presumed age-classes. Juveniles had slight asymmetry (0.10 ± 0.06 mm) that was significantly less than that of older birds, but I found no difference between partly-orange males (0.40 ± 0.06) and fully orange individuals (0.42 ± 0.04).

Recent intensive observations on Hawaii by a team from the U.S. Forest Service (Ralph, pers. comm.) have confirmed and extended Perkins' (1903) findings that the Akepa's favored feeding sites are in the terminal buds and foliage of ohia (*Metrosideros collina*) and the young phyllodes of koa (*Acacia koa*), from which they appear to extract spiders and other invertebrate prey.

The feeding sites of the Akepas suggest that the asymmetry of the bill functions in the prying apart of closely paired structures, as has been proposed for crossbills (Newton 1972, Richards and Bock 1973). In crossbills, both directions of bill-crossing occur approximately equally (Neville 1976), but the direction of crossing is associated with a foot preference for holding the cone (Newton 1972), which apparently guides the approach to the spirally-organized cone. It would be interesting to know how Akepas approach their feeding sites. Although my initial hypothesis of sex-differences in laterality was not supported, niche diversification could still occur if Akepas mate assortatively.

Concerning the ontogeny of the laterality, nothing is known of early development of Akepas, but the increased tip separation evident in older birds suggests a similar pattern to crossbills, which have straight bills at hatching and whose mandibles do not start to cross for 10 days after fledging (Nethersole-Thompson 1975, p. 114). Crossbills have a lengthy period of post-fledging care compared to that of related finches; this might be associated with the development of bill-crossing and the acquisition of specialized foraging skills. Newton (1972, p. 181), however, pointed out that "every stage of body growth is extended, both in the nest and out. The slow growth might instead be linked with the fact that most young are raised at seasons when days are short and cold." It would be interesting to compare the development of Akepas with that of other drepanids and to learn if the young birds feed in a different way than do adults.

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