

## Kona Grosbeak

*Chloridops kona* FRENCH: *Psittirostre à gros bec*

## Greater Koa-Finch

*Rhodacanthis palmeri* FRENCH: *Psittirostre de Palmer*

## Lesser Koa-Finch

*Rhodacanthis flaviceps* FRENCH: *Petit Psittirostre*

**T**hese 3 large Hawaiian finches, among the least known of the Drepanidinae, share remarkably similar and dismal histories. All were known historically mainly or entirely from a limited area on the Kona (western, leeward) side of the island of Hawai'i, although the fossil record shows that the same or closely related species once probably occurred throughout the main Hawaiian islands. All 3 were first discovered by ornithological collectors in the waning years of the nineteenth century, were apparently unknown to native Hawaiians at the time, and disappeared forever in less than a decade following their discovery. There are no credible records of any of the species after the last specimens of each were taken. The only published observations of these birds in life come from Scott Wilson's first and brief exposure to the Kona Grosbeak (Wilson 1888, Wilson and Evans 1890–1899); from Walter Rothschild's collectors Henry Palmer (Rothschild 1892, 1893–1900) and George C. Munro (1944); and from the naturalist R. C. L. Perkins (Perkins 1893, 1903). Although these published sources have been cited time and again, because all the species are extinct there is no recourse but to turn to them once more. The present compilation augments these traditional sources with much original

**The  
Birds of  
North  
America**  
Life Histories for  
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Kona Grosbeak © J. Hume

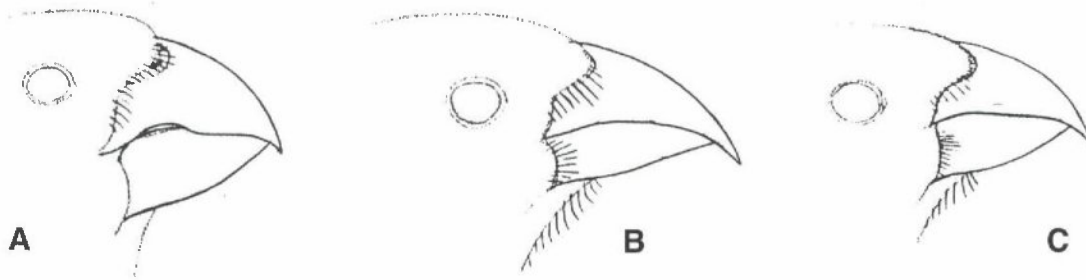


Adult male Greater Koa-Finch © J. Hume



Adult male Lesser Koa-Finch © J. Hume

data from a thorough check of world museum collections for all extant specimens of the 3 species, as well as with original observations from G. C. Munro's unpublished field journal in the B. P. Bishop Museum, Honolulu (cited throughout this account as "Munro journal").



**Figure 1.**  
Bill shapes.  
A. Kona  
Grosbeak.  
B. Greater Koa-  
finch. C. Lesser  
Koa-Finch.  
(From Rothschild  
1893–1900.)

The Kona Grosbeak (also called Kona Finch or Grosbeak Finch) was first obtained on 21 June 1887 by Wilson and last collected in September 1892 by Perkins, the period of its historical existence thus lasting 5 years and 6 months. Munro (1944: 131), who was evidently the source for the last year of observation given by Berger (1972) and Grant (1995), credits Perkins with encountering this species in 1894, but Perkins made no mention of a sighting in 1894, either in publication (1903) or in his field notes (Banko 1986), and no specimens exist with such a date. Thus Banko (1986) is correct that the last evidence of the species is from 1892.

Palmer shot the first Greater Koa-Finch (also called Orange Koa-Finch) on 26 September 1891, and Perkins took the last specimens in March 1896, giving the species a historical existence of only 4 years and 6 months, even though it persisted for three and a half years longer than the Kona Grosbeak.

The Lesser Koa-Finch (also called Yellow-headed Koa-Finch) was obtained only by Palmer and Munro, who collected their first specimen on 30 September 1891 and their last on 16 October of the same year, for a total historical existence of only 17 days.

Historically, these 3 species were confined to mesic forests at middle elevations on the drier, leeward slopes of the island of Hawai'i; only the Greater Koa-Finch was found elsewhere. The Kona Grosbeak was closely associated with the naio, or bastard sandalwood, tree (*Myoporum sandwicense*) growing on relatively recent 'a'a lava; its massive beak, hypertrophied jaw muscles, and "thick tongue like a parrots" (Munro journal: 25 Sep 1891) were adaptations for processing the small, very hard fruits of that plant. The beaks of the koa-finches, as their name implies, were adapted for cutting the green pods of the leguminous koa tree (*Acacia koa*). The stomachs of the koa-finches were very large and thin-walled for processing large masses of vegetable material, in contrast to the much smaller gastrointestinal tract of the Kona Grosbeak (Perkins 1903, Munro 1944). All 3 species had the characteristic drepanidine odor "in a marked degree" (Perkins 1903: 440), and the flesh of the koa-finches

was also reported to have a strong odor (Munro 1944). Although each species varied its diet somewhat, the birds were undeniably specialized feeders and doubtless could not have survived in places where their principal food plant was absent.

There is no evidence that native Hawaiians in the nineteenth century had any knowledge of these species. Perkins (1893), followed by Wilson and Evans (1890–1899), applied the name "palila" to the Kona Grosbeak, but this was merely a lapse intended for *Loxioides bailleui*, to which the name belongs. Of the Greater Koa-Finch, Palmer stated that "natives on Hawaii called the bird 'poupou' and 'Hopue,' but did not seem to be well acquainted with it" (Rothschild 1893–1900: 204), but Perkins (1903: 440) considered the accuracy of this statement to be very doubtful, saying that "natives with a really extensive knowledge of the avifauna, to whom the skins were shown, declined to give them a name, and even suggested that they were 'malihini' (foreign)."

The history of these 3 enigmatic finches, whose discovery was nearly simultaneous with their disappearance, has been the source of considerable wonder. What were the causes of such restricted distributions and almost instantaneous disappearance? In light of the massive loss of species diversity and island populations shown by the fossil record (James and Olson 1991, Olson and James 1991), the extinctions seem less remarkable, a few among many. Perhaps speculation should focus instead on what caused the prolonged survival of these 3 finches in the Kona District of Hawai'i I., when all other populations of their relatives had long since been extinct.

## DISTINGUISHING CHARACTERISTICS

**KONA GROSBEEK.** Medium-sized (15 cm) drepanidine finch with a disproportionately large head and bill (Figs. 1A, 2). Culmen and gonys arched; maxilla and mandible of nearly equal height; maxillar tomium doubly sinuated and overhanging the mandibular tomium; distinct gap between the tomia just anterior to rictus. Nostrils rounded and nearly covered by feathers. Primaries 6–8 equal



and longest, P5 equal to P9. Tail relatively short and weakly notched. Plumage almost entirely dull olive green; little or no sexual dimorphism, and young birds much like adults.

**GREATER KOA-FINCH.** Largest (23 cm total length) of the historically known Drepanidinae. Bill large and conical, with sharp tomtia and strongly angled commissure, maxilla slightly overhanging the mandible (Fig. 1B). Nostrils have a conspicuous dorsal operculum. Wings and tail relatively longer than in Laysan (*Telespiza cantans*) and Nihoa (*T. ultima*) finches; tail slightly notched; primaries 6, 7, and 8 longest and nearly equal in length. Very sexually dichromatic: Fully adult male is lustrous scarlet orange on head, neck, and breast; lighter orange below; olive-brown suffused with orange on back, wings, and tail, with rump more orange. Female is brownish olive, lighter below, and in some older individuals may develop yellowish orange on head, particularly forecrown. Juveniles similar to females, but lighter below; ventral feathers have dark areas, giving blotched or streaked appearance.

**LESSER KOA-FINCH.** Very similar to Greater Koa-Finch, but smaller (19 cm total length). Bill less curved; lower edge of mandible angled upward, versus straight or even decurved in Greater Koa-Finch (Fig. 1C). Adult males bright yellow on head, neck, and breast; females and juveniles generally similar to Greater Koa-Finch counterparts, although juveniles less streaked.

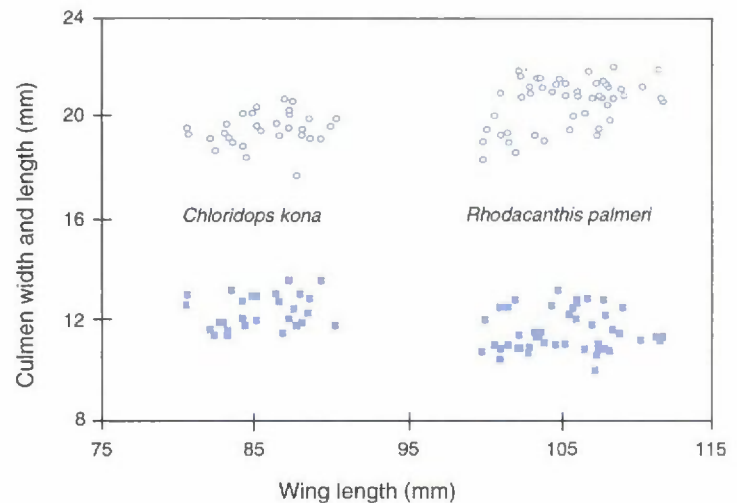
## DISTRIBUTION

### HAWAIIAN ARCHIPELAGO

See Figure 3.

**KONA GROSBEEK.** Restricted to very small area in district of North Kona, just north of border with South Kona, Hawai'i. This area is centered roughly on the volcanic cone of Pu'ulehua (19°33'57"N, 154°48'00"W) and Pu'ulehua Ranch (1.3 km west), near which Palmer and Munro established their camp in 1891. Most of Palmer and Munro's specimens appear to have been taken within about 3 km of this point. The species occurred at middle elevations, usually said to be around 1,200–1,500 m, although Rothschild (1893–1900: 210) gives 1,100–1,700 m. As far as can be gathered from Munro's journal, the elevational range would probably not have extended much below 1,400 m.

Rothschild (1893–1900) reported that Palmer and Munro's camp at Pu'ulehua was very near the mountain house in which Scott Wilson had stayed (probably Pu'ulehua Ranch), so Wilson's observation of 3 birds and collection of the type specimen in 1887 doubtless occurred in this same area. Perkins (1903) thought the total range of the Kona Grosbeak



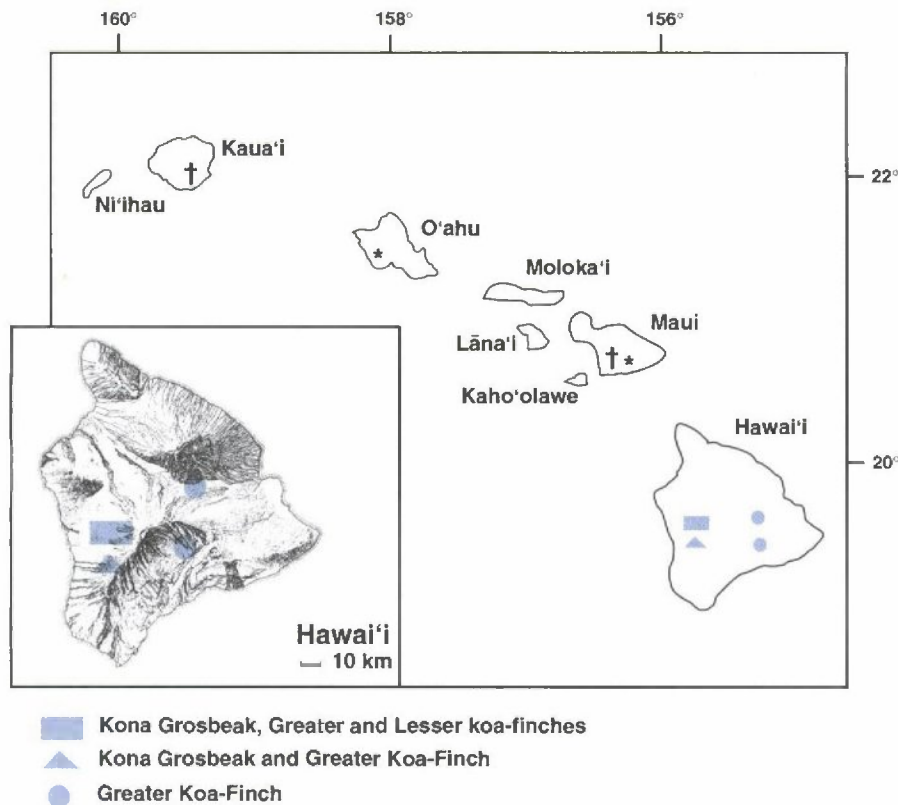
**Figure 2.** Scatterplot of wing length (mm) versus culmen length (open circles) and culmen width (solid squares) in Kona Grosbeak and Greater Koa-Finch, to show the disproportionately large bill of Kona Grosbeak, whose overall body size was considerably smaller than that of Greater Koa-Finch.

would be encompassed in about 10 km<sup>2</sup>, although the species was patchily distributed within this area and was absent from seemingly suitable habitat to the north and the south. This estimate of area corresponds closely with that covered by Palmer and Munro.

The only report of the species away from Pu'ulehua was Palmer's sighting of a pair (not collected) about 16 km to the south, above Hōnaunau (Munro 1944, journal) at about 1,800 m, in the same area in which a Greater Koa-Finch was obtained (see below).

**GREATER KOA-FINCH.** Most specimens came from the same vicinity of Pu'ulehua in which the Kona Grosbeak occurred, usually at elevations of about 990 and 1,200 m. There are 4 recorded exceptions. On 23 Oct 1891, Palmer and Munro left their camp near Pu'ulehua and "went out to Kikiaia [Kīkī'ae'ae, an area about 1.6 km east-southeast of Pu'ulehua] and on up through alternate clears and patches of bush on to the lower slopes of Mauna Loa," obtaining 3 "good" specimens of Greater Koa-Finch on the way up (Munro journal). Palmer obtained another specimen about 16 km farther south of Pu'ulehua, above Hōnaunau on 20 Nov 1891. Because Palmer's diary (Rothschild 1893–1900) indicates that they ascended to about 2,700 m that day, Berger (1972) assumed that the specimen was taken at a high elevation, but Munro's journal indicates that it was obtained about 1.6 km from their camp at "Johnson's dairy," which Palmer thought was at about 1,800 m. Banko (1986: 93) suggested that this was probably now Ka'ohē Ranch at 1,630 m, South Kona, which, however, would be an additional 10 km farther south.

After Munro had left the expedition on 1 Mar 1892, Palmer obtained an additional 4 specimens of Greater Koa-Finch, but because his specimen labels give only the island of origin, the only means of



**Figure 3.** Distribution of Kona Grosbeak and Greater and Lesser Koa-Finches. Fossil *Rhodacauthis* the size of Greater Koa-Finch (daggers); at least the Kaua'i bird is a distinct as yet undescribed species. Fossil *Rhodacauthis* the size of the Lesser Koa-Finch prehistoric (asterisks).

determining more precise localities is through portions of Palmer's diary that were extracted in Rothschild (1893–1900). Palmer's original diary was "wantonly destroyed by the British Museum (Natural History)" (Mearns and Mearns 1992: 353).

Two specimens were labeled 21 Mar 1892 and two 26 Jun 1892. Rothschild (1893–1900) indicated that on the former date, Palmer would have been "at Hanneberg's sheep station on Mauna Kea," which Banko (1984: 23) thought might be incorporated in what is now Pu'u'ō'ō Ranch at the border of the North and South Hilo Districts. There is now no way to know where Palmer's Jun 1892 specimens were obtained, but as Banko (1986: 94) surmised, perhaps these, and certainly the Mar specimens, must have been the source of Rothschild's (1893–1900) inclusion of the "Hilo District" in the range of the Greater Koa-Finch, which Berger (1972) had previously assumed to have been an error.

Perkins (1903: 438) recorded the species in the Ka'ū District "in the Koa woods some miles above Kilauea." According to Banko (1986: 94), this observation was in 1895, and he cites a much later letter of Perkins (19 Sep 1947) indicating that he saw only 1 or 2 "about 6 miles [10 km] from the Volcano House up the slopes of Mauna Loa," which conflicts somewhat with Henshaw (1902: 68), who said that Perkins reported "numbers" of this bird

"in the extensive koa woods above [Kilauea] volcano ... on the very edge of the rainy Olaa District which the bird appears never to enter." Perkins obtained no specimens from this area, however. These additional scattered records indicate that under natural conditions the Greater Koa-Finch probably occurred throughout the island of Hawai'i, wherever there was mesic koa forest.

**LESSER KOA-FINCH.** All 8 specimens were obtained in the general vicinity of Palmer and Munro's camp at Pu'ulehua in the southern part of the North Kona District. Munro's journal indicates specimens taken on a track leading southwest to another dairy (see above) and on the track leading east to the area known as Kīkī'ae'ae (19°33'26"N, 154°46'39"W).

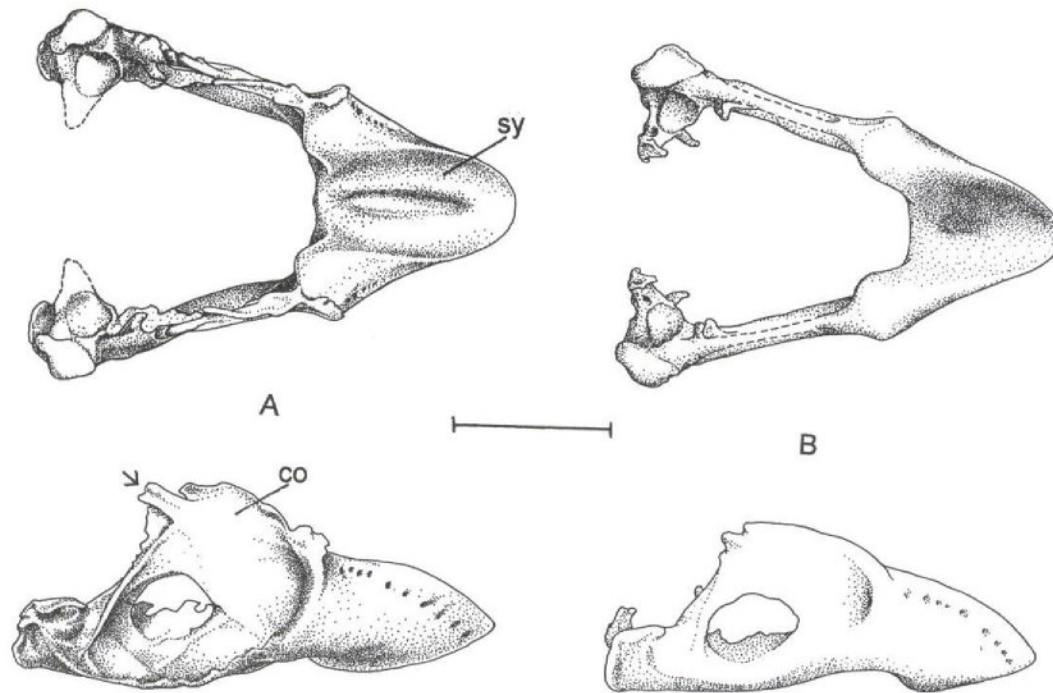
#### ELEVATIONAL MOVEMENT

All 3 species were essentially sedentary, although some elevational movement was reported in Greater Koa-Finch.

**KONA GROSBEEK.** No information.

**GREATER KOA-FINCH.** In his field journals, Perkins (as extracted in Banko 1986) recorded some elevational movement of the species, finding the birds in Aug 1894 at about 900 m, whereas in 1892 they had occurred some 300 m higher. In Mar 1896, the birds were found to be quite numerous at 900 m and were absent from areas at 1,200 m, where they





**Figure 4.** Mandibles. A. Kona Grosbeak. B. Prehistorically extinct species *Chloridops wahi* in dorsal (top) and lateral (bottom) views. Note the narrower trough of the mandibular symphysis (sy), much deeper and more heavily sculpted ramus in the area of the coronoid process (co), and greater development of the area of attachment of the mandibular adductor muscle (arrow) in Kona Grosbeak (*C. kona*) than in *C. wahi*, indicating that Kona Grosbeak had a more powerful seed-cracking mechanism. *C. wahi* appears to have ranged from Kaua'i to Maui (the specimen illustrated is from Kaua'i) and probably fed on seeds less difficult to open than those of naio, on which Kona Grosbeak fed.

had been observed in 1892. This movement does not seem to have been a seasonal descent because the birds were found at the lower elevation in both Aug and Mar, so the shift in elevation may reflect local changes in availability of food sources.

*LESSER KOA-FINCH.* No information.

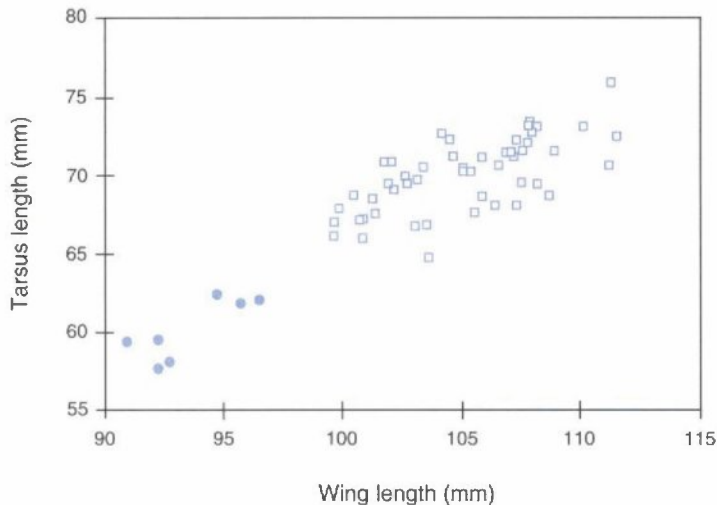
#### HISTORICAL CHANGES

The only changes were simply the complete disappearance of each species from its limited historic range within a very short span of time, too fast even for any contractions to be noted (see Introduction, above, and Demography and populations, below).

#### FOSSIL HISTORY

Fossils relevant to both of these groups of finches have been found widely in the Hawaiian Archipelago on islands other than Hawai'i (James and Olson 1991). Most of these are late Holocene in age and the birds would have been contemporaneous with Polynesians in the prehistoric period, indicating that these island populations and species went extinct within the past 1,500 yr.

No fossils of the Kona Grosbeak proper have yet been recovered, although several populations of other members of the genus *Chloridops* have been found. The most similar in size to the Kona Grosbeak is *C. wahi* (James and Olson 1991), known from O'ahu and Maui Is. New fossils of the bird from Kaua'i listed only as *Chloridops* sp. (James and Olson 1991) indicates that this population should probably also be referred to *C. wahi* (H. F. James and S. L. Olson unpubl.). This species had less massive development of the cracking mechanism of the jaws than did Kona Grosbeak and probably fed on seeds that were less difficult to open than those of naio (Fig. 4). A second undescribed species of *Chloridops* from Maui is very similar to *C. wahi*, but considerably smaller (James and Olson 1991). A much larger species, *C. regiskongi* James and Olson (1991), known so far only from O'ahu, had a substantially different bill morphology and was probably less closely related to Kona Grosbeak and *C. wahi* than those 2 are to each other. Grosbeak-like drepanidines related to Kona Grosbeak once probably occurred on all the main Hawaiian islands.



**Figure 5.** Scatterplot of wing length versus tarsus length in Greater Koa-Finch (open squares) and Lesser Koa-Finch (solid circles) to show lack of overlap.

Fossils tentatively referred to as *Rhodacanthis palmeri* were reported from Maui (James and Olson 1991). Exquisitely preserved new material from a deposit at sea level on Kaua'i I. is the size of Greater Koa-Finch but indicates a distinct, as yet undescribed species. (H. F. James and S. L. Olson unpubl.). Thus the Greater Koa-Finch or close relatives likely occurred throughout the main islands on which there were stands of koa. The same may well have been true of the Lesser Koa-Finch, to which fossils from Maui and O'ahu have been tentatively referred (James and Olson 1991).

Although the Kona Grosbeak appears to have been truly endemic to Hawai'i I., the historical restriction of the 2 species of *Rhodacanthis* to that island appears to be the result of contraction from a formerly greater range.

## SYSTEMATICS

### GEOGRAPHIC VARIATION; SUBSPECIES

Historically, all 3 species of these finches had very restricted distributions; consequently, no geographic variation has been noted, nor have any subspecies been proposed (see Fossil history, above and Related species, below).

### RELATED SPECIES

Apart from Amadon (1950) and those who followed him in lumping all finch-billed drepanidines in genus *Psittirostra*, or Greenway (1968), who kept *Psittirostra* for the 'O'ū (*P. psittacea*) and placed all others in the genus *Loxioides*, most authors have recognized the distinctiveness of *Chloridops*. However, as Rothschild (1893–1900: 199) noted,

*Rhodacanthis* is very close to *Telespiza*, and if those 2 genera were combined it would be inconsistent to keep *Loxioides* apart, because these "form a continuous series." All of these genera have come back into use (e.g., James and Olson 1991, Am. Ornithol. Union 1998) and are convenient for recognition of the various groups, particularly because most have been expanded in diversity by the fossil record. Should intermediate fossil species be found, however, it may prove necessary to combine *Telespiza* and *Rhodacanthis* under the oldest name, *Loxioides*.

Although most authors, including Rothschild (1893–1900), Wilson and Evans (1890–1899), James and Olson (1991), Grant (1994), and even Amadon (1950), who otherwise reduced many species of drepanidines to subspecies, have considered Lesser Koa-Finch to be a valid species, others have questioned whether it is really distinct from Greater Koa-Finch. The original collectors had no idea that 2 species were involved at the time of collection (Perkins 1903, Munro 1944), and were surprised by Rothschild's description of Lesser Koa-Finch.

Pratt (1979: 133–134) suggested that the specimens assigned to Lesser Koa-Finch were variational extremes of Greater Koa-Finch, with most differences perhaps being due to wear, but later (Pratt et al. 1987) he agreed that 2 species were involved.

There is no overlap in wing and tail measurements, nor in the length measurements taken in the flesh by Munro (see Fig. 5, Tables 1, 2) between Greater and Lesser koa-finches. That the bill measurements do overlap could be taken as evidence for a difference in proportion between the species, the Lesser having a larger bill in relation to body size than the Greater, rather than as evidence for similarity. In addition, the bills differ in shape (see Distinguishing characteristics, above). The 8 specimens of Lesser Koa-Finch include obviously adult males, adult females, and juveniles, the last of which are not at all worn. Furthermore, Greater Koa-Finch males appear to molt into orange adult plumage while retaining juvenile rectrices (see Appearance: molts and plumages, below). No specimens of Lesser Koa-Finch have pointed rectrices except the 2 obvious juveniles, so the 2 yellow male specimens are all the more unlikely to be younger birds. Lesser Koa-Finch is a valid species that will have to be acknowledged and accommodated despite the paucity of specimens.

## HABITAT

General habitat of all 3 finches was mesic forest dominated by tall koa trees, with an understory of



**Table 1.** Linear measurements (mm) from skins of Kona Grosbeak and koa-finches. Data shown as mean  $\pm$  SD (range, *n*).

	Kona Grosbeak	Greater Koa-Finch	Lesser Koa-Finch
Wing length <sup>1</sup>			
Male	87.0 $\pm$ 2.0 (83.4–90.2, 18)	105.2 $\pm$ 3.2 (99.7–111.5, 47)	95.7 (94.8–96.6, 3)
Female	83.4 $\pm$ 2.0 (80.4–87.4, 15)	103.1 $\pm$ 2.4 (99.9–107.3, 8)	93.5 $\pm$ 3.1 (91.0–98.9, 5)
Tail length			
Male	57.1 $\pm$ 1.2 (54.6–58.7, 17)	70.3 $\pm$ 2.3 (66.0–76.0, 43)	62.1 (61.9–62.4, 3)
Female	54.5 $\pm$ 1.7 (52.7–56.4, 15)	68.7 $\pm$ 2.3 (64.8–72.3, 8)	58.9 $\pm$ 1.1 (57.6–60.2, 5)
Tarsus length			
Male	22.9 $\pm$ 0.6 (22.0–23.9, 17)	27.4 $\pm$ 0.9 (25.6–29.5, 46)	24.7 (24.0–25.9, 3)
Female	22.8 $\pm$ 1.0 (21.0–25.1, 15)	27.6 $\pm$ 0.7 (26.7–28.5, 8)	23.8 $\pm$ 0.7 (23.2–25.0, 5)
Culmen length			
Male	19.6 $\pm$ 0.8 (17.7–20.8, 18)	20.8 $\pm$ 0.9 (18.4–22.2, 46)	19.1 (18.9–19.4, 3)
Female	19.4 $\pm$ 0.5 (18.7–20.7, 12)	20.3 $\pm$ 1.0 (19.2–22.0, 8)	17.7 (16.3–19.6, 4)
Culmen width <sup>2</sup>			
Male	12.5 $\pm$ 0.7 (11.4–13.5, 17)	11.5 $\pm$ 0.8 (10.0–13.2, 45)	9.8 (9.1–10.6, 2)
Female	12.0 $\pm$ 0.6 (11.3–12.9, 12)	11.3 $\pm$ 0.5 (10.8–12.2, 8)	9.9 (9.2–10.5, 4)
Culmen depth <sup>2</sup>			
Male	18.7 $\pm$ 0.4 (18.3–19.6, 8)	14.3 $\pm$ 0.7 (13.1–15.9, 13)	13.4 ( <i>n</i> = 1)
Female	18.3 (18.2–18.5, 4)	14.3 (13.2–15.4, 2)	13.5 (13.3–13.7, 3)
Mandibular symphysis length			
Male	14.3 $\pm$ 0.4 (14.0–14.7, 9)	12.3 $\pm$ 0.4 (11.3–12.8, 13)	11.4 ( <i>n</i> = 1)
Female	14.4 (13.8–14.8, 4)	12.4 (11.9–13.0, 2)	10.7 (10.0–11.8, 4)

<sup>1</sup>Measurement of flattened wing.

<sup>2</sup>Measurement taken at level of nostrils.

naio, māmane (*Sophora chrysophylla*), 'a'ali'i (*Dodonaea viscosa*), and 'iliahi, or sandalwood (*Santalum*). Perkins (1893) noted a decided change in the fauna and flora between 914 and 1,220 m, at which point koa increased in numbers; naio, māmane, and 'a'ali'i grew profusely; and sandalwood was less abundant. Kona Grosbeak and the koa-finches inhabited the upper zone.

**KONA GROSBEEK.** Occupied a more restricted habitat than the koa-finches did; found only on "the more recent aa ['a'ā] or clinker flows. These areas were covered with medium-sized trees and little undergrowth" (Munro 1944: 131). In his journal (9 Oct 1891), Munro added an interesting refinement to these observations: "We have only in one case found it off [the clinkers], & we have travelled over a deal of ground where the aaka [naio] was growing plentifully & with lots of seeds, perhaps the seeds of those on the clinkers are richer or sweeter, as all vegetation is more luxuriant there."

Perkins' (1903: 440) experience was similar; he found the Kona Grosbeak to have "a predilection for such Naeo [naio] trees as grow on the roughest lava-flows, but it also visits those which grow in and about the more open spaces in the forest." Both Perkins and Palmer (in Rothschild 1893–1900) remarked on the patchiness of the birds' occurrence; they were absent from much apparently suitable habitat. On one day Palmer found them abundant on one lava flow and secured a dozen specimens, half of them within 5 min and within 50 m of one another, yet on a similar lava flow some 60 m farther down he found none, even though the naio trees were as plentiful and had as abundant fruit. Such numbers of the grosbeaks may have represented aggregations of family groups rather than true flocking behavior.

**GREATER KOA-FINCH.** Mainly resorted to tops of tallest and leafiest koa trees, whether growing on rough lava flows or in open grassy forest; most

**Table 2.** Total body-length measurements (mm) of fresh specimens of Kona Grosbeak and koa-finches taken from specimen labels and Munro's journal. These measurements were made "by contour" according to a system of Palmer's—"in the flesh including all curves" as explained by Munro (1944: 10, 128). Although not useful in comparison with any measurements made by others, they were carefully taken by Munro during the preparation of specimens and are valuable mainly for contrasting the sizes of Greater and Lesser koa-finches, in which there is no overlap. Data given as mean (range, *n*).

Species	Kona Grosbeak	Greater Koa-Finch	Lesser Koa-Finch
Male	189 (181–194, 6)	221 (206–229, 13)	195 (194–197, 2)
Female	182 (168–190, 5)	219 (206–222, 4)	187 (181–190, 6)
Sexes combined	—	220 (206–229, 17)	189 (181–197, 8)

frequent at about 1,200 m (Perkins 1893: 103). Habitat of this species in Ka'ū was also reported to be koa woods (Perkins 1903).

*LESSER KOA-FINCH.* The little that is known suggests habitat choice similar to that of Greater Koa-Finch, because all specimens were collected in the same forests where Greater Koa-Finch occurred.

## FOOD HABITS

### FEEDING

*Main foods taken.* *KONA GROSBEEK.* Almost entirely seeds of naio.

*GREATER KOA-FINCH.* Green pods and seeds of koa, augmented at least by caterpillars.

*LESSER KOA-FINCH.* Koa pods.

*Food capture and consumption.* *KONA GROSBEEK.* When breaking the hard endocarp of naio fruits, produced a loud cracking noise, almost always said to be "incessant." Munro reported that the birds cut each fruit into several pieces, and the manner in which the fruit may have been processed in the bill is suggested by an entry in his journal (10 Oct 1891): "Two shot today had a piece of aaka [naio] seed clenched in the bill & we left them there after skinning, in each it was held in the left side between the edges of the mandibles just above the tooth of the lower mandible." As reported by Perkins (1893), and still evident in skins today, the bills of these finches were often caked with exudate of the naio fruits. Munro (journal 12 Oct 1891) noted that this species "seems to feed pretty nearly all day."

*GREATER KOA-FINCH.* Perkins (1893) found that the birds swallowed the pods in "very large pieces," the blue bills becoming stained green from the juice. Similar large pieces of green pod, "unmasticated," were fed by male and female adults to the young. On the other hand, Munro (journal: 12 Oct 91) observed that "while extracting the koa seeds

(which are eaten green) the bird clings on to the pod hanging in a starting position with tail and back downwards, they tear a hole in the large flat pods over each seed to get it (from pods I have seen on the ground)." Perhaps the degree of maturity of the pods determined whether they were eaten entire in large pieces or whether only the seeds were extracted.

*LESSER KOA-FINCH.* Presumably similar to food habits of Greater Koa-Finch.

### DIET

*KONA GROSBEEK.* By all accounts, practically the only food of this species was the "drupaceous" fruit of the naio, which has an extremely hard, "bony" endocarp containing 4–10 cells with 1 seed per cell (Wagner et al. 1990: 928). The stomachs of feeding birds would be crammed with hundreds of the tiny "maggot-like" seeds. Munro (1944, journal) occasionally found cut-up portions of green naio fruits and bits of green leaves in the throat and stomach of specimens, and both he and Perkins (1903) mentioned occasional caterpillars. The last may have figured more prominently in feeding of young. Wilson (1888), who really knew nothing of the habits of the Kona Grosbeak, thought that it might feed on māmane seeds, as does the Palila, and Perkins (1893) speculated that it might at times eat the seeds of sandalwood, but no evidence exists for either conjecture. The skull and mandible and associated musculature are so much more massively developed in Kona Grosbeak, compared with other fossil species of genus *Chloridops* (see Fig. 3), including even the much larger species *C. regiskongi*, that the species was undoubtedly specialized for feeding on the hard fruits of naio.

*Myoporum sandwicense* (naio) exhibits geographic variation; one of the 3 recognized subspecies, *st.-johnii*, is confined to "dry woodland of North and South Kona" (Wagner et al. 1990: 929). Characteristic of this subspecies is smaller fruit with more cells



(seeds) per fruit. Number of seeds per fruit is probably not as important as the smaller size. Endocarp size in the species as a whole varies from 2 to 9 mm (Wagner et al. 1990), and the larger fruits may have been impossible for birds to crack. Kona Grosbeak may thus have been a species that evolved extremely rapidly to exploit a food source that physically could not be processed outside the Kona District of Hawai'i.

**GREATER KOA-FINCH.** This species was largely specialized for a single plant, the koa, the green pods of which were its principal food. Munro (1944) reported birds feeding on seeds of 'a'ali'i, making considerable rustling noise in the process. He also noted a juvenile specimen containing koa seeds and "some small seeds like the Cape Gooseberry" (Munro journal: 29 Sep 1891). The cape gooseberry, or pohā (*Physalis peruviana*), is an alien species, established in the islands before 1825 (Wagner et al. 1990), that Munro (journal: 21 Sep 1891) and Perkins (1893) indicated was abundant in the area at the time. Munro found its seeds in the stomachs of Palila, so the koa-finches may have fed opportunistically on it as well.

Greater Koa-Finch also fed to a considerable degree at times on larval butterflies and moths (Lepidoptera)—i.e., caterpillars—for which it usually descended into the naio trees. Perkins (1893: 104, 1903: 437) found specimens containing not only brown and green "looper" caterpillars, but also "gaudily coloured" larvae with conspicuous "warning" colors.

**LESSER KOA-FINCH.** With its similar bill morphology and because of its association with koa, this species appears to have had food habits similar to those of Greater Koa-Finch. The only direct information concerns a male (the holotype) killed in a koa tree, the stomach of which contained mostly koa seeds but also some smaller seeds (Munro journal: 1 Oct 1891). Munro reminded Perkins (1903: 436) that he had obtained a few specimens of *Rhodacanthis* in 'a'ali'i trees and suggested that Lesser Koa-Finch may have been obtained in this way. However, when Perkins went specifically to search for Lesser Koa-Finch in 1896, all the birds he encountered that had "strayed down" to 'a'ali'i or other smaller trees, such as māmane or naio, were Greater Koa-Finches.

#### FOOD SELECTION AND STORAGE

None of the 3 species is reported to have stored food. No information on food selection.

#### NUTRITION AND ENERGETICS

No information.

#### METABOLISM AND TEMPERATURE REGULATION

No information.

DRINKING, PELLETT-CASTING, AND DEFECATION  
No information.

## SOUNDS

### VOCALIZATIONS

**Development.** **KONA GROSBEEK.** No information.

**GREATER KOA-FINCH.** "The young male soon acquires the peculiar whistle, for I have shot one in almost perfect song in quite immature plumage and with the skull still cartilaginous" (Perkins 1893: 104).

**LESSER KOA-FINCH.** No information.

**Vocal array.** All 3 species are long extinct, and in the absence of recordings or sonograms we have only individual impressions of the vocalizations from the few persons who heard them. Because these are not amenable to paraphrase or reinterpretation, they are best repeated verbatim.

**KONA GROSBEEK.** Perkins (1903: 440) said he never heard the Kona Grosbeak sing, apart from "a squeaking cry" when the sexes were in pursuit of one another, although a native assistant told him he had heard it once and the song was not like that of the Greater Koa-Finch.

Palmer and Munro had more experience with vocalizations of this species. "Its call note, Palmer says, or at least the one which is more often heard than any other note, is a low prolonged 'cheep,' not at all loud, and apparently not to be heard at any greater distance than the cracking of the berries. Besides this a low chirping noise was heard when the bird was on the wing, and a real kind of song was heard on October the 19th, consisting of several whistling notes, not very loud but clear. Another time Palmer mentioned a 'plaintive whistling sound of a few notes'" (Rothschild 1900: 210).

"A small squeak and a light sweet song are the only call notes recorded. A low cheep repeated at intervals. The song is sometimes long with a variety of notes. It sang more vigorously when excited, on one occasion when it lost its mate" (Munro 1944: 131). The last statement is a reference to a male that "kept coming round chirping and singing, he sang quite a long song with a variety of notes" after his mate was shot (Munro journal: 19 Oct 1891).

**GREATER KOA-FINCH.** "Its peculiar whistle, though not very loud, is very clear, and can be heard for a considerable distance. If imitated closely it will readily answer, and sometimes, after fruitless hunting for hours without even hearing a sound from this bird, a whistle has been immediately responded to. At other times a distant bird has been drawn close by the imitation of its whistle and easily secured" (Perkins 1893: 103).

"The female I have heard to utter a rather deep single note when alarmed. On one occasion when I had shot a male I heard his mate repeatedly utter this note, and she continued to do so for some five minutes, but seemingly possessed some ventriloquial power—the sound seeming now in front, now behind, now near, now far, yet it was utterly impossible that the bird could have flown without my being aware of it. At last the bird became silent, and I never caught sight of it at all" (Perkins 1893: 104).

"The song, if such it can be called, for apparently it serves also as a mere call, is entirely different from that of any other native bird. It consists of four, five, or even six whistled notes, of which the latter ones are much prolonged. It frequently differs somewhat as whistled by different individuals, and also is sometimes distinctly varied, when repeated by the same bird. Although the notes are not loud, they are very clear, and are very easily imitated, and the bird responds most freely to an imitation. . . . In misty weather they are particularly ready to answer, and I have called as many as seven adult males and two females into one large tree at the same time. . . . When thoroughly scared the female sometimes gives utterance to a deep single note, which is repeated at frequent intervals with varying intensity, so as to have a ventriloquial effect, and make it extremely difficult to locate the bird" (Perkins 1903: 438).

"The call-note is described by Palmer as a low whistle, sounding somewhat like a prolonged 'week.' It generally consists of two or three notes, beginning high and descending towards the end: it sounds melancholy. By imitating the cry Palmer succeeded in luring them very closely towards himself" (Rothschild 1893–1900: 203–204).

Munro (journal: 30 Oct 1891) remarked that the first notes of the song of the 'Ō'ū were "very like that of the big finch [Greater Koa-Finch], but not so strong, (the note of the big finch seems to flood the whole surrounding bush & is difficult to locate)".

*LESSER KOA-FINCH.* Nothing was noted of the vocalizations of this species by Palmer or Munro, who did not discern it as a different species.

*Phenology.* Little known. All observations of Kona Grosbeaks pertain to the fall. Greater Koa-Finches gave their calls and responded to imitations both in fall (Sep–Nov) and in spring (Mar).

#### NONVOCAL SOUNDS

*KONA GROSBEEK.* Although not deliberately produced for any purpose of itself, the incessant cracking noise, audible at "some distance," that Kona Grosbeak made when opening naio fruits was a characteristic sound of this species. It led collectors to the birds and therefore could have led

predators to them as well. Likewise it might have had a social function in leading lone birds to feeding groups of conspecifics. Perkins (1903) likened the sound to the bill snap of the 'Elepaio (*Chasiempis sandwichensis*), although the 2 sounds could be distinguished as different.

*GREATER AND LESSER KOA-FINCHES.* No information.

## BEHAVIOR

### LOCOMOTION

*KONA GROSBEEK.* All observers remarked on the tameness of these birds, which sometimes would not take notice even of a gunshot. To Perkins (1893: 105) the Kona Grosbeak was "singularly uninteresting . . . in habits . . . a dull, sluggish, solitary bird, and very silent—its whole existence may be summed up in the word 'to eat.'" His only observation of other activity occurred "when a male and female were in active pursuit of one another." Munro credited the species with much more vivacity, however, finding that "these birds are active in their movements hopping about the aaka [naio] bushes with alacrity, they do not shew a short neck, the head being held away from the shoulders the weight of the bill does not seem to inconvenience them at all" (journal: 10 Oct 1891). The same impression was conveyed with less poignancy in Munro's published (1944) account.

*GREATER KOA-FINCH.* These birds were also described as "rather fearless and easy to approach" (Rothschild 1893–1900: 203), usually resorting to the tops of the highest koa trees, however, where females and young were especially difficult to observe. They were more active and agile than Kona Grosbeaks, hanging upside down to feed on koa pods.

*LESSER KOA-FINCH.* No information.

### SELF-MAINTENANCE

No information.

### AGONISTIC BEHAVIOR

No information.

### SPACING

*KONA GROSBEEK.* No information.

*GREATER KOA-FINCH.* Males may have had considerable tolerance for presence of conspecifics, even during presumptive breeding season because Perkins (in Banko 1986: 95) called "nine fully adult males" into a single tree in Mar 1896, although this instance may be the same as described under Sounds: vocalizations, above, in which 7 males and 2 females were called into a tree.

*LESSER KOA-FINCH.* No information.



## SEXUAL BEHAVIOR

**Mating system and sex ratio.** Collecting biases appear to have greatly influenced the observed sex ratios of koa-finches.

Kona Grosbeak was located mainly through the sound of its cracking naio seeds, an activity in which both sexes would have engaged. Of the sexed specimens, 30 are male and 19 female (ratio 1.6:1). Koa-finches, however, were located by call of male, which could be imitated to draw the birds, including females, nearer, although females were still difficult to see.

Of sexed adult specimens of Greater Koa-Finch, 46 are male and 7 female (ratio 6.6:1).

The 8 specimens of Lesser Koa-Finches were collected incidentally in the process of obtaining Greater Koa-Finches and consist of 2 adult males, 4 adult females, and 1 each of male and female juveniles.

**Pair bond.** KONA GROSBEAK. Munro's journal indicates a possible strong pair bond in this species following breeding season. He reported at least 3 instances in which one bird of a pair stopped and chirped when its presumed mate had been shot or returned to spot where its mate had been, acting agitated, with much chirping and singing. At least 1 of these singers was determined to be male, so even if these observations reflect attachment of adults for young birds rather than attachment of one member of a pair for its mate, it would still imply that both members of pair were together in attendance well after fledging, as was the case in the koa-finches.

GREATER KOA-FINCH. Perkins (1893) mentioned a female calling for her mate for about 5 min after male had been collected (see Sounds: vocalizations, above), suggesting strong degree of attachment of pairs similar to that of Kona Grosbeak.

LESSER KOA-FINCH. No information.

**Extra-pair copulations.** No information.

## SOCIAL AND INTERSPECIFIC BEHAVIOR

**Degree of sociality.** See Breeding: parental care, below.

**Play.** No information

**Nonpredatory interspecific interaction.** No information.

## PREDATION

**Kinds of predators.** No historic record even of attempted predation on any of these finches. Under natural conditions, island of Hawai'i may have had fewer avian predators than other islands in the Hawaiian Archipelago, where there were representatives of a now extinct endemic owl (*Grallistrix*) and of a harrier (*Circus*) (Olson and James 1991). Several productive fossil sites lacking the owl suggest that its absence on the island of Hawai'i

is not an artifact of collection. The remains of the harrier are so rare, however, even on islands where it occurred, that its former absence on Hawai'i I. cannot be assumed. Short-eared Owl (*Asio flammeus*) is a post-Polynesian arrival (Olson and James 1991) whose colonization may have been made possible by introduction of Pacific rat (*Rattus exulans*), so it would have had at most a limited effect on the large native finches.

Crows (*Corvus*) may have preyed on eggs or nestlings of the large finches. Hawaiian Crow, or 'Alala (*Corvus hawaiiensis*), is known historically only from Hawai'i I. Fossil record adds 2 more species of crow to that island (H. F. James and S. L. Olson unpubl.), and additional species are known from Maui, Moloka'i, and O'ahu (James and Olson 1991). Strangely, no evidence of crows has yet been found on Kaua'i, despite intensive recent paleontological effort.

Hawaiian Hawk, or 'Io (*Buteo solitarius*), also known historically only from Hawai'i I., was known elsewhere only from a few bones of 1 individual from Moloka'i (Olson and James 1991) until a single Pleistocene bone was found on Kaua'i (Olson and James 1997). Subsequently, remains of Hawaiian Hawk were found abundantly in a Holocene lake deposit on southern coast of Kaua'i. In the same deposits were found several intact skulls of *Chloridops* and *Rhodacanthis* with the cranium bitten open to remove the brain (H. F. James and S. L. Olson unpubl.), a behavior typical of many bird-eating hawks. The endemic owl *Grallistrix auceps* is also abundant in the same deposits, but no previous evidence suggests that species of *Grallistrix* processed prey in this manner, and it is assumed that the opened skulls of the large finches constitute direct evidence of predation on these birds by the Hawaiian Hawk.

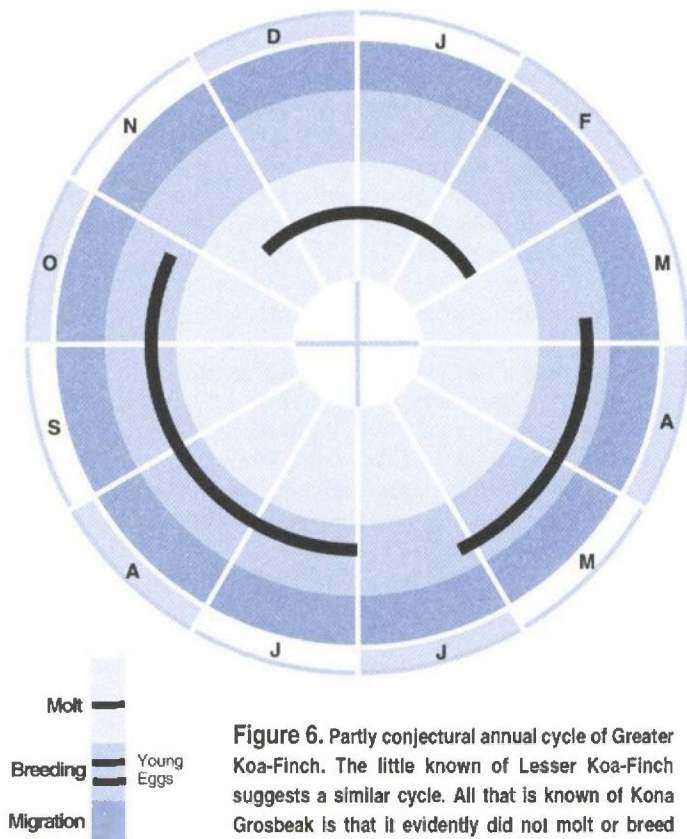
**Manner of predation.** No information.

**Response to predators.** No information.

## BREEDING

## PHENOLOGY

KONA GROSBEAK. With the exception of 2 taken in Jun, all specimens of this species were obtained from Jul through Oct. This series and the few observations of the species in life indicate that breeding and molt took place during the remainder of the year, because from Jul to Oct there were no obvious fledglings seen or taken, no notes of enlarged gonads in Munro's journal, no observations of birds feeding young or of possible courtship or singing by males. These negative indications are all that is known concerning any aspect of breeding in this species.



**Figure 6.** Partly conjectural annual cycle of Greater Koa-Finch. The little known of Lesser Koa-Finch suggests a similar cycle. All that is known of Kona Grosbeak is that it evidently did not molt or breed from about mid-Jun through Oct.

*GREATER KOA-FINCH.* Specimen representation during the year is skewed in much the same way as for Kona Grosbeak, most (26) being derived from the period Jul through Oct (plus 3 from Jun and 1 in Nov), with the exception of an additional 20 taken in Mar. The little available evidence suggests either a lengthy nesting season or prolonged parental attendance of young—probably the latter (Fig. 6). All juvenile specimens are fully feathered and of adult size, ranging in date from 1 Jul to 20 Oct. Parents were observed by Perkins (as noted in his specimen labels) feeding such young in Sep. A similar pattern occurs in Palila, in which young were observed with parents up to at least 30 d after fledging (van Riper 1980), and in Laysan Finches, in which both parents may feed fledged young for at least 30–45 d (Morin 1992).

An adult female Greater Koa-Finch taken 15 Oct was noted (Munro journal) as having enlarged ovaries. Perkins (1903) described seeing a male of the species coming to the ground for nesting material, and although he did not identify the time of year, he did not mention this observation in his earlier account (Perkins 1893), so it was probably made at the time he collected a large series in Mar 1896. Thus if nest-building was under way in Mar

and juveniles had fledged by 1 Jul, eggs probably were laid in the period from Apr through Jun.

*LESSER KOA-FINCH.* An adult female was still with full-grown juveniles on 5 Oct, suggesting a similar breeding schedule to that of Greater Koa-Finch.

#### NEST SITE AND NEST

*KONA GROSBEEK.* No information.

*GREATER KOA-FINCH.* All that is known comes from Perkins' (1903: 438) observation that he had seen "a male bird come down to the ground for building material and carry this to the top of one of the tallest Koa trees, and in this situation, in the locality frequented by the bird, certain largish nests which became visible later, when the trees were stripped by caterpillars" he assumed to be of this species. Both sexes cooperate in nest-building in all Drepanidinae for which there is information, with the exception of Hawai'i 'Ākepa (*Loxops coccineus coccineus*) and Laysan Finch (Morin 1992:665), so Morin's tentative inclusion of Greater Koa-Finch with the last 2 may have been based on faulty recollection of Perkins' observation just quoted.

*LESSER KOA-FINCH.* No information.

#### EGGS

No eggs are known for any of the species.

*Clutch size.* *KONA GROSBEEK.* No information.

*GREATER KOA-FINCH.* There is only indirect evidence of clutch size. Three specimens taken by Perkins were labeled as consisting of a family group, 2 being juvenile males and the third a female (University Museum of Zoology, Cambridge, specimen no. 27/Dre/5/e/4) that Perkins regarded as the mother of the others. However, this third bird could not have been the mother because it has streaked underparts, pointed rectrices, and apiculate secondaries of the Juvenal plumage (see Appearance: molts and plumages, below); thus all 3 are juveniles of a single brood, so the clutch size may be assumed to have been at least as high as 3 at times.

*LESSER KOA-FINCH.* Munro's journal indicates that of 4 birds seen together on 5 Oct 1891, 3 were collected (an adult female and 2 juveniles—1 male and 1 female). Had the fourth been a more desirable adult male, it would presumably have been collected first, or at least Munro would have remarked on it in his journal, so it was probably an additional juvenile, suggesting that the clutch size in this species was at times 3 and at least 2.

In the closest living relatives of koa-finches, mean clutch size in Laysan Finch ( $n = 166$ ) was 3.19 (mode 3; Morin 1992), whereas in Palila ( $n = 12$ ) mode was 2 (van Riper 1980).



## INCUBATION

No information.

## HATCHING

No information.

## YOUNG BIRDS

Youngest birds known for any of the species are all of fully adult size (see Parental care, and Appearance, below).

## PARENTAL CARE

*KONA GROSBEAK.* An immature specimen collected 24 Sep does not have the usual plant residue caked on the bill, which may be an indication of prolonged parental feeding, as was true of the Greater Koa-Finch. Perkins was under the impression that the groups encountered by Palmer and Munro consisted of parents leading young, and that larger assemblages were several broods combined.

*GREATER AND LESSER KOA-FINCHES.* Male Greater Koa-Finch assisted in nest-building (see Nest site and nest, above), and both sexes were observed feeding fully grown young as late as Sep. The same presumably applied to Lesser Koa-Finch because adults were apparently accompanying young in Oct (see Phenology, above; Munro journal). Perkins (1903: 438) said that young of Greater Koa-Finch were fed partly on large fragments of koa pods, such as their parents ate, and that both sexes were steadily attentive in feeding them.

## COOPERATIVE BREEDING

No information.

## BROOD PARASITISM

No information.

## FLEDGLING STAGE

No information.

## IMMATURE STAGE

See Parental care, above, and Appearance: molts and plumages, below.

## DEMOGRAPHY AND POPULATIONS

## MEASURES OF BREEDING ACTIVITY

See Breeding: phenology; Breeding: eggs, above.

## LIFE SPAN AND SURVIVORSHIP

No information.

## DISEASE AND BODY PARASITES

*Disease.* Although diseases, such as avian malaria and avian pox, have been implicated in the

sudden disappearance of all these finches, the only relevant evidence is Perkins' (1893: 112) inclusion of Greater Koa-Finch among the birds he obtained in Kona in 1892 that showed swellings of legs and feet. This condition may have been attributable to avian pox, although few, if any, specimens of any of the 3 extinct finches show obviously advanced cases of "bumblefoot." Perkins also remarked that the afflicted birds all came from lower elevations, so he attributed their condition to damp.

*Body parasites.* No information.

## CAUSES OF MORTALITY

No direct evidence apart from the activity of collectors and what is surmised under Behavior: predation, above. Perkins (1903) noted that Hawaiian bird catchers would have had little interest in the somber Kona Grosbeak, and he thought they would have had limited means of capturing koa-finches with the well-known techniques developed for trapping nectarivorous birds.

## POPULATION STATUS

*Former numbers.* Little measure of former population size and abundance of any of these species can be derived other than from the success of collectors relative to the amount of effort expended. In addition, there are a few subjective impressions.

*KONA GROSBEAK.* As determined from Munro's journal, Munro and Palmer spent 21 d, or parts thereof, actively collecting in habitat for Kona Grosbeak, during which time they obtained at least 31 birds. Discounting the single extraordinary day (12 Oct 1891), on which they obtained 12 individuals, their average would have been 1 specimen of Kona Grosbeak per day of collecting, although on 12 d of hunting in appropriate habitat they obtained no specimens. It is more difficult to assess Perkins' efforts because we do not know how many days he devoted to bird collecting (he was also occupied with collecting insects), and in many cases he put only month and year on his labels. From 3 Jul to 10 Aug 1892 he obtained 18 specimens, the most in one day being 4, with another 4 specimens, the last ones known, taken on unspecified dates in Sep. Perkins collected extensively in the same area in Mar 1896 without encountering this species.

*GREATER AND LESSER KOA-FINCHES.* During 23 d of collecting in koa-finch habitat at their Pu'ulehua camp, Palmer and Munro obtained at least 24 Greater Koa-Finches and 8 Lesser, failing to obtain either on 7 d, although for the first 4 d in the field they did not know of the existence of such finches, and after the first discovery only missed them on 3 d of effort, once they had learned the vocalizations. The 8 known specimens of Lesser Koa-Finch were collected on only 5 of the 23 collecting days. Perkins

(1903: 437) reported that "in 1892 in a longer stay in exactly the same locality, I saw several score of the larger bird [Greater Koa-Finch], and in two subsequent visits, the latter of which was made for the special purpose of investigating [the status of the Lesser Koa-Finch], certainly some hundreds were examined with the naked eye or glasses, as the case required" without ever encountering the smaller species. Perkins' last visit, according to specimen labels, was in Mar 1896, when the Greater Koa-Finch was abundant and perhaps much more evident at the start of breeding season, as he obtained at least 16 specimens, all but 2 of which were males. Perkins speculated that the Lesser Koa-Finches obtained in 1891 by Palmer and Munro were strays from another locality.

**Trends (extinction).** Kona Grosbeak disappeared from its limited range between Sep 1892, when Perkins last obtained specimens, and his visit to the same area in Mar 1896. Greater Koa-Finch, so abundant at that time, also disappeared shortly thereafter. In 1901, only 5 yr after Perkins found Greater Koa-Finch so abundant near Pu'ulehua, H. W. Henshaw, who was one of the most thorough and diligent of collectors of birds on the island of Hawai'i, is said to have found the same area to be one of the poorest over which he had hunted (Munro 1944), and he encountered neither Kona Grosbeak nor koa-finches (Banko 1986). Thus, what in 1891 Munro (1944: 131) considered to be a "wonderful collecting area, which we thought a collector's paradise," was depleted of many of its most interesting birds in less than a decade.

Grant (1995) summarized several factors that may have contributed to the extinction of Kona Grosbeak in particular, including deforestation for logging, coffee, and other agriculture; browsing and trampling by cattle; loss of trees to introduced insect pests; and effects of introduced predators and disease vectors, as well as diseases themselves; followed perhaps by inbreeding because of reduced population sizes. Sorting out the effects of combinations of such factors on extinction is difficult at best, even when the process is ongoing, and all but impossible long after the fact.

Because forms of *Rhodacanthis* and *Chloridops* probably occurred throughout the main Hawaiian islands, where they were exterminated after arrival of Polynesians (James and Olson 1991), but before ever being discovered by Western naturalists, how were these large finches able to persist at all into the historic period on Hawai'i I., and why mainly in the Kona District? The large size of Hawai'i I. diluted some of the adverse effects of human impact, so certain species persisted only there while being exterminated elsewhere; the Nene (*Branta sandvicensis*), which once may have occurred on all the

main islands (Olson and James 1991), is a prime example. Lessened human impact may have been a factor in the persistence of the great finches, although at the time of first European contact the Kona District was the most intensely cultivated area of Hawai'i I. (Cuddihy and Stone 1990: 20).

Another possible consideration, however, is the effect that European diseases had on native human populations of the islands. The introduction of venereal disease, tuberculosis, and influenza by members of Cook's voyage in 1778 and 1779, as well as diseases brought by subsequent voyages, caused horrifying mortality among native Hawaiians within a very few years; survivorship was no better than about 1 in 20 (Stannard 1989). Because Kealahou Bay was the place where Cook's expedition spent most of its time at anchor in the islands, disease would have affected human populations of the Kona coast earlier than elsewhere in the islands, which may have caused a significant reduction in the effects of burning and other human perturbation at middle elevations in Kona by the end of the eighteenth century. Thus the forests where *Rhodacanthis* and *Chloridops* were found, which in 1891 were also filled with other native birds that are now extinct or nearly so, may have experienced nearly a century of recovery before the negative effects of a new wave of human immigrants took full effect.

## CONSERVATION AND MANAGEMENT

In extensive surveys of Hawai'i I. in the 1970s (Scott et al. 1986), 80 yr after the last individual of any of these 3 species had been seen, no individuals were detected, so all are considered extinct. Thus no conservation measures have been proposed.

## APPEARANCE

Drepanid finches typically have one complete (Definitive Prebasic) molt per year as adults, thus each plumage described below as "adult" is assumed to represent Definitive Basic plumage. Because so few specimens of these species exist, it has been difficult to determine which plumages (besides Juvenal) may have preceded Definitive Basic. Although other plumages may have existed, only plumages represented by existing specimens are described below.

### MOLTS AND PLUMAGES: KONA GROSBEAK

**Hatchlings.** No information.

**Juvenal plumage.** Some existing specimens exhibit probable signs of immaturity, such as different bill color, or are noted as being young by Munro



(journal). In these birds the underparts are paler, more yellowish, and mixed with whitish on belly, and some of these have an orangish cast on breast and flanks. This paler coloration is irrespective of sex, although many specimens are females, which led Rothschild (1893–1900) to believe that the paler coloration could be characteristic of females and young males. Because some female specimens are not pale below, this conclusion appears unlikely. At least 2 of these paler birds have faint whitish wing-bars. Some birds that Munro (journal: 13 Oct 1891) thought were young had "thin dark bars across some of the tail-feathers at intervals along their length." Since none of these "immature" birds had obviously recently left the nest, it is uncertain whether these manifestations were part of the true Juvenal plumage or belonged to the succeeding First Basic, or were a mixture of the two. Regardless, the differences from adults are not pronounced.

**Adult.** Body almost entirely bright olive green, paler and buffier on lower belly; lores blackish; wings and tail blackish brown, margined with green. In preparing specimens in the field, Munro (journal: 13 Oct 1891) thought females "were duller colored than the finest males," but such a distinction would probably be difficult to appreciate in existing skins after more than a century. Crown may be variously streaked with dusky, which sometimes extends inconspicuously to nape and upper back. Sexes similar.

**Phenology of molts.** All existing specimens are fall birds (Jul–Nov) and, in contrast to specimens of koa-finch from this time of year, are in fresh, unworn plumage. A few specimens from Jul and Aug have various inner primaries in sheath. Tail molt may have been prolonged because some specimens collected in Sep and Oct retain very worn outer rectrices.

#### MOLTS AND PLUMAGES: GREATER KOA-FINCH

**Hatchlings.** No information.

**Juvenal plumage.** Similar to adult female plumage (see below). Upperparts uniform brownish green; throat and upper breast darker; belly more yellowish than pale whitish yellow; lower breast and belly-feathers have dusky tips, giving blotched or streaked appearance, thus differing from adult female. Rectrices decidedly pointed; secondaries strongly apiculate. Of 2 specimens marked as males from same brood, throat of one is much yellower than in the other.

**Changing male.** Following description based on single specimen collected in Sep (British Museum [Natural History] specimen no. 95.7.20.35). Compared to fully adult male specimens, much less orange; throat and upper breast duller, more yellow-

ish orange; belly yellowish, suffused with green; more whitish on lower belly; above only forecrown and slight supercilium are colored and are yellowish, only faintly tinted with orange; rump only faintly yellower than back, not at all orangish; and no orangish in margins of wing- and tail-feathers.

**Adult. MALE.** Plumage dominated by brilliant satiny orange; much of the luster of crown was lost soon after death (Perkins 1903). Head and throat bright scarlet orange, duller on upper breast and becoming more yellowish on abdomen; undertail-coverts pale yellow. Upperparts olivaceous, appearing almost brownish from suffusion of orange, which is more intense on rump and uppertail-coverts. Wings and tail fuscous, with orange margins. Underwing-coverts and axillaries dark grayish, with orange wash. More or less fully plumaged birds vary in degree of posterior extent of orange in crown and of orange suffusion in belly, which may be yellowish or yellow-green without much orange overcast. This variation may be due to age.

**FEMALE.** One specimen (American Museum of Natural History [AMNH] no. 453636) appears as follows: Olive green above; rump lighter, pale greenish compared to mantle but hardly yellow; no orangish cast anywhere; forecrown, throat, and upper breast yellowish; belly yellowish white; wings and tail fuscous, with greenish yellow margins. Another specimen (AMNH 453627), interpreted on label as "young" (i.e., changing) male, appears instead to be an old female because the rectrices are those of an adult bird; it has orange-yellow forecrown and throat but no orange wash on belly, as in males passing into Definitive plumage (e.g., AMNH 453636, with pointed rectrices). The great scarcity of adult females in collections has doubtless led to misunderstanding of the full degree of color development in this plumage; furthermore, yellower cast of the old adult female may have contributed to the impression in the field of intermediates between Greater and Lesser koa-finches (Munro 1944, journal).

**Phenology of molts.** Most specimens in collections are fall birds (Jul–Nov, mainly Oct), with feathers of mantle and primaries obviously worn. A female specimen collected in Jul has very worn head-feathers and primaries. Perkins (1903: 437) reckoned the birds to be in their best plumage in "winter," his only such specimens having been taken in Mar. These specimens, as well as birds collected by Palmer in Mar, have fresh, unworn plumage. A Jun specimen is in an intermediate stage of wear. Almost none of the existing specimens shows signs of molt, which must therefore have taken place about Dec–Feb because no specimens are available for that period (see Fig. 6). At least males presumably underwent a partial molt

from Juvenal plumage into a femalelike First Basic plumage, in which at least Juvenal rectrices were retained because some specimens with orange coming into forecrown and throat, and gaining orange wash below, still have pointed rectrices but lack blotched underparts of Juvenal plumage. One specimen of changing male (Sep) has primary 4 in sheath.

#### MOLTS AND PLUMAGES: LESSER KOA-FINCH

*Hatchlings.* No information.

*Juvenal plumage.* Similar to Juvenal plumage of Greater Koa-Finch, with paler, more whitish belly than in adults; also has scattered dark-tipped feathers, but not nearly so conspicuously streaked or blotched as in Greater Koa-Finch. Rectrices and secondary tips likewise pointed.

*Adult. MALE.* Pattern similar to that of adult male Greater Koa-Finch, but orange of head and breast replaced by yellow; dorsum more greenish than brownish, owing to lack of orange suffusion; and no yellow in wings where there is orange in Greater Koa-Finch. Head and neck golden yellow; chin, throat, and upper breast duller yellow; lower breast, belly, and undertail-coverts yellowish green; dorsum greenish olive, lighter on rump and upper-tail-coverts; tail- and wing-feathers dark brownish, with dull greenish margins.

*FEMALE.* Olive drab above, with paler green rump and trace of yellow behind nostrils. Uniform dingy yellow-green below; slightly more yellowish on throat and upper breast.

*Phenology of molts.* Molt pattern presumably like that of Greater Koa-Finch. All specimens taken in Oct, when adults were moderately worn and juveniles were in fresh plumage. One adult female specimen (collected 5 Oct) is in wing molt with secondaries new, and primaries 9–5 old, 4 new, and 3 in sheath.

#### BARE PARTS

*KONA GROSBEEK.* "Iris dark hazel. Maxilla horn-grey; mandible grey, much lighter at base. Legs and toes dark brown, almost blackish" (Rothschild 1893–1900: 209). "Legs almost black and bill grey the upper mandible being darkest" (Munro journal: 24 Sep 1891). A specimen that Munro thought young because the bill was "quite brown" (Munro journal: 13 Oct 1891) also has immature plumage characters. Wilson's (1888) description of the bill in his only specimen, the holotype, as "dull flesh-colour," along with his description of the plumage, suggests that this too was a young bird. Thus the bill in immature birds appears to have been lighter in color, brown rather than dark gray.

*GREATER KOA-FINCH.* "Adult male with bill bluish-gray, tip brownish; feet bluish-gray, soles pale

yellow" (Rothschild 1893–1900: 203). Munro (journal: 26, 28 Sep 1891) described bill and legs of an adult female as bluish gray, and bill of juvenile as darker, the maxilla brown, and sides of gape (rectal flanges) yellow.

*LESSER KOA-FINCH.* In 2 adult females, tips of bills lighter, probably having been yellowish in life, in contrast to fuscous remainder of bill.

## MEASUREMENTS

### LINEAR

See Figures 3 and 5, and Tables 1 and 2. Although females in all 3 species average slightly smaller than males in some measurements, there is nearly complete overlap and all may be regarded as essentially monomorphic in size.

### MASS

No information.

## NUMBER, LOCATION, AND PRESERVATION OF SPECIMENS

Study of Munro's journal shows that the dates that Palmer put on labels of his specimens were usually not the dates of collection, but rather the dates the specimens were prepared, or more likely, the dates the labels were written. The discrepancy usually amounts to a day, but can be more, as with the last 2 specimens of Lesser Koa-Finch, which were taken 16 Oct but were labeled 19 Oct. Dates of Palmer specimens cited in this account are from Munro's journal rather than from labels, when traceable in the former.

Total number of specimens collected of each species is small. A thorough check of world museum collections yields 56 specimens of Kona Grosbeak (those given in Banko 1979, plus 1 each at Edinburgh, Liverpool, Manchester, and Stockholm, 2 in Berlin, and 2 fluid-preserved specimens at Moscow and the British Museum); 65 specimens of Greater Koa-Finch (those given in Banko 1979, plus 1 each at Stockholm and Liverpool, 1 specimen in fluid in Moscow, 1 uncataloged head at the University Museum of Zoology in Cambridge, and an additional specimen at the American Museum of Natural History in New York); and 8 specimens of Lesser Koa-Finch (per Banko 1979). A few specimens of Kona Grosbeak or Greater Koa-Finch on public exhibit or in smaller collections may have been overlooked, but the number would be small. None of the existing specimens was prepared as a skeleton, although bones have been removed from a skin of each of the 3 species using techniques outlined by



Olson et al. (1987). There are 2 fluid-preserved specimens of Kona Grosbeak and 1 of Greater Koa-Finch (Knox and Walters 1994, Koblik 1994), which, although lacking data, were almost certainly taken by the Rothschild expedition because Munro (journal: 21 Oct 1891) specifically mentions preserving 2 Kona Grosbeaks in this manner.

One of 3 specimens of Greater Koa-Finch collected 23 Oct 1891 by Palmer and Munro (Munro journal) cannot be accounted for and may be either an undated skin at Toronto or the pickled specimen in Moscow.

From Banko 1986: 130, it might be inferred that 2 specimens of Kona Grosbeak, preserved in spirits, were taken after the last known specimens were collected in 1892. This is attributable to statements in a letter by Perkins (1945: 33): "The only reason why I did not send back a spirit specimen of *Chloridops* for Gadow was because in 1896 Henry Greenwell had 2 whole birds in spirit, having shot these for Scott Wilson and I presumed that he would turn these over to Gadow, but I heard afterwards that Wilson had these made into skins without doing so!" Either Perkins accidentally wrote *Chloridops* in place of *Rhodacanthis*, or his memory was at fault, because no specimens of Kona Grosbeak, other than the holotype, have any connection with Wilson. Two skins of Greater Koa-Finch once seemed rather enigmatic because they bear Wilson's labels, even though he never encountered the species. These are the sole specimens of the species in the museums at Paris and Liverpool and are labeled with dates of Nov 1892 and Jan 1893, respectively. These must certainly be the specimens originally preserved in spirit by Greenwell. Because there is now only 1 known fluid-preserved specimen of Greater Koa-Finch in existence, and there are no skeletons, it is an even greater shame that these specimens were skinned.

### PRIORITIES FOR FUTURE RESEARCH

With the current emphasis in ornithology on areas such as ecology, behavior, and conservation, little potential for future research on 3 species that are totally extinct might be expected. However, the fossil record still needs to be expanded to elucidate the former diversity and distribution of both *Chloridops* and *Rhodacanthis*. If the Kona Grosbeak was a recently evolved specialist on naio growing on recent lava flows, were there other forms of *Chloridops* in other habitats on the island of Hawai'i? This issue begs the questions of the nutritional value of naio seeds from plants growing in different habitats, the consistency of geographic variation in seed size, and the genetic variability of naio in the

archipelago in relation to its potential as a food source.

The recent discovery of a fluid-preserved specimen of the Greater Koa-Finch and an additional one of the Kona Grosbeak (Koblik 1994) raise the possibility of a comparative anatomical study of the digestive tract and jaw muscles, which could be particularly informative if combined with similar studies of *Psittirostra*, *Loxioides*, *Telespiza*, and continental cardueline finches showing convergent adaptations.

There also remains the possibility of using "ancient" DNA from study skins to determine the phylogenetic position of *Rhodacanthis* and *Chloridops* within a phylogeny of the Drepanidinae developed from DNA sequences (for example, Fleischer et al. in press). Although their voices have been stilled, there is yet much to be learned about these most interesting finches.

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