

SPECIES LIMITS IN AKEPAS (DREPANIDINAE: *LOXOPS*)¹

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Abstract. The Hawaiian honeycreepers (Drepanidinae) known as akepas (*Loxops sensu stricto*), long regarded as comprising a single polytypic species, are best regarded as two species. The Akepa (*L. coccineus*) has representatives on Hawaii (*L. c. coccineus*), Maui (*L. c. ochraceus*), and Oahu (*L. c. wolstenholmei*). The Akekee (*L. caeruleirostris*) is restricted to Kauai. Potential isolating mechanisms include differences in male coloration (red in Akepa, yellow with black face in Akekee), degree of sexual dichromatism (striking in Akepa, slight in Akekee), bill size, shape, and color (smaller and gray or yellow vs. heavy and blue) nest placement (cavities vs. open branches), and vocalizations. The two respond differentially to playback of each other's songs. The little-known Maui and Oahu forms may also warrant recognition as full species.

Key words: Akekee; Akepa; Drepanidinae; Hawaii; Hawaiian honeycreeper; isolating mechanism; Kauai; *Loxops caeruleirostris*; *Loxops coccineus*.

INTRODUCTION

Akepas are small Hawaiian honeycreepers that have short, finchlike bills with the mandibles slightly crossed at the tip. Crossed mandibles are found elsewhere only in the cardueline finch genus *Loxia* (crossbills). The genus *Loxops* Cabanis 1847 was used only for the akepas until Amadon (1950) merged it with several other genera. Amadon's *Loxops* was a heterogeneous group of short-billed species now distributed among at least four genera (*Loxops*, *Hemignathus*, *Oreomystis*, and *Paroreomyza*). Greenway (1968) again restricted *Loxop* to the akepas, as did Berger (1981), who followed my earlier recommendations (Pratt 1979) at the generic level. The AOU check-list (1983) followed Berger (1981).

Distinct akepa populations are found on the four largest Hawaiian Islands: *coccineus* Gmelin 1789 on Hawaii; *ochraceus* Rothschild 1893 on Maui; *wolstenholmei* Rothschild 1893 on Oahu; and *caeruleirostris* Wilson 1889 on Kauai. The epithet *rufus* Bloxam 1827, used for the Oahu form for the past 160 years, is incorrect on technical grounds (Olson 1986). The Hawaiians used the name 'akepa for the first three populations, and also the name 'akepeu'ie on Maui and Oahu. The Kauai form they called 'akeke'e or 'o'u-hollowai, the latter possibly incorrectly reported by European observers (Perkins 1903). Perkins (1903) regarded the four forms as separate species, but considered the first three more closely related

among themselves than to *caeruleirostris*. Bryan and Greenway (1944) recognized two species, *L. coccineus* (including *ochraceus* and "rufus" as subspecies) and *L. caeruleirostris*. Amadon (1950) lumped the two, and was followed by Berger (1981) and the AOU check-list (1983). Pratt et al. (1987) again recognized the two akepa species proposed by Bryan and Greenway (1944). This paper presents the rationale for such a classification. I use the English names Akepa for *Loxops coccineus* and Akekee for *L. caeruleirostris*. The uncapitalized form "akepa" is a general term for all members of the genus. For a discussion of English names for this complex see Pratt et al. (1987, p. 308-309).

At the time of my main studies (1975-1978), akepas were believed to be uncommon to rare throughout their range, and the Maui and Hawaii populations were considered endangered (Anon. 1974). Subsequent surveys by Scott et al. (1986) found pockets of much higher population density than had previously been known for *L. c. coccineus*, but the population is still regarded as endangered. The surveys delineated four disjunct population centers that I will call Hualalai, Kau, Keauhou-Kulani, and Mauna Kea. Akepas are now extremely rare and seldom observed on Maui, and nearly, if not totally, extinct on Oahu. On Kauai, *L. caeruleirostris* now exists as a single main population centered on the Alakai Plateau, with a tiny noncontiguous population in the Makaleha Mountains (Scott et al. 1986). I found the Akekee to be uncommon in the mid-1970s, as did Scott et al. (1986) later. Suggestions that the species might be declining (Scott et al. 1986)

¹ Received 3 April 1989. Final acceptance 26 July 1989.

may have been overly pessimistic. On several visits to the Kokee area in 1988 and 1989, I found the birds to be possibly more common than in the recent past. Apparently, the Akekee is holding its own in the face of very noticeable and alarming declines of such other species in the Kokee/Alakai area as *Oreomystis bairdi* (pers. observ.).

The present distributions of all *Loxops* are probably artifacts of environmental degradation. Akepas are now confined to high elevation areas free of mosquito-borne avian diseases (Scott et al. 1986), but once had wider distributions that extended into lower elevations (Henshaw 1902, Perkins 1903).

METHODS

I studied akepas as part of a broader study of Hawaiian birds (Pratt 1979) that included both field observations and examination of study skins. Fieldwork on Hawaii and Kauai included observations of habitat, foraging behavior, and vocalizations. My primary study areas and dates were: eastern Alakai Plateau, Kauai (July 1975); Keauhou Ranch and Kilauea Forest Reserve, Hawaii (February 1978), and Kokee State Park, Kauai (May 1976, October 1976, March 1977, January 1978). Subsequently I have made incidental observations of akepas at these localities as well as the Kulani Tract and Hakalau Forest National Wildlife Refuge on Hawaii, but have conducted no systematic research. All population centers on Hawaii except Kau are included in my observations. I have searched for but not seen any living examples of the Oahu or Maui populations, both of which are nearly extinct (Scott et al. 1986).

I made tape recordings beginning in 1975 using a variety of equipment and studied recordings made by J. M. Scott at Kahuku Ranch, in Kau, a locality I was unable to visit. All recordings are archived in the Library of Natural Sounds (LNS), Laboratory of Ornithology, Cornell University. I conducted limited song playback experiments at Keauhou Ranch (1977) and Kokee State Park (1978). At the time of these attempts, only four nests of *L. caeruleirostris* (Eddinger 1972) and none of *L. coccineus* has been found, and seasonality of breeding had not been determined. Thus I did not have the opportunity to conduct playbacks with birds known to be breeding. Because of these problems, as well as the birds' general scarcity, I took an opportunistic ap-

proach to the experiments. To any male akepa encountered, I played a recording of the off-island bird's song first, then one from the same island, and noted the response. Occasionally, after repeatedly failing to elicit a response to a song from a different island and without subsequently being able to present the same-island song for comparison (because the subject had wandered too far away), I played conspecific songs first to determine whether birds at the time would respond to their own songs.

I examined study skins of all akepa populations at the Bernice P. Bishop Museum, Honolulu; American Museum of Natural History, New York; National Museum of Natural History, Washington, DC; Academy of Natural Sciences, Philadelphia; Museum of Comparative Zoology, Harvard University, Cambridge; and the Museum of Vertebrate Zoology, University of California, Berkeley. I measured culmen length from insertion, bill width at its maximum dimension, and bill depth at feather insertion above and below.

CHARACTER ANALYSIS

APPEARANCE

Adult akepas from Hawaii, Maui, and Oahu exhibit the greatest sexual dichromatism known in Hawaiian honeycreepers (Freed 1988), with males being much brighter than females (see illustrations in Pratt et al. 1987). Capitalized color names herein are from Smithe (1975). In all three populations, females and juvenile males are rather dull-colored, nondescript Pale Olive-Green birds darker above and paler below. Adult females may have a pale Orange-Yellow wash across the breast. Males of both *L. c. coccineus* and *L. c. ochraceus* are highly variable. Hawaii males vary from Spectrum Orange to Chrome Orange, a few approaching Flame-Scarlet. The degree of brightness may be age related, but definitive data are lacking. Adult Maui males fall mostly into two color groups, Chrome Orange or Spectrum Yellow with a tinge of Olive-Yellow, but a few intermediates are represented in collections. This variation approaches true color dimorphism (ca. 45% orange, 45% yellow, 10% intermediate) and is apparently not age related. The six adult male specimens that I have seen from Oahu are all bright Brick Red, but the sample is too small to be considered representative. The "red" akepas all lack dark feathers in the lores, but the pri-

TABLE 1. Means, ranges, and standard deviations (brackets) for bill measurements of male *Loxops*.

Taxon	<i>n</i>	Width	<i>n</i>	Culmen	<i>n</i>	Depth
<i>caeruleirostris</i>	23	5.3 {0.25} A ^a (4.8–5.8)	23	11.1 {0.37} A (10.5–12.0)	24	5.4 {0.33} A (4.4–6.0)
<i>wolstenholmei</i>	6	4.6 {0.19} C (4.3–4.9)	6	10.0 {0.45} B (9.6–10.8)	4	4.8 {0.26} BC (4.5–5.1)
<i>ochraceus</i>	12	4.9 {0.14} B (4.7–5.2)	16	10.8 {0.67} A (9.4–11.8)	11	5.0 {0.36} B (4.4–4.5)
<i>coccineus</i>	41	4.9 {0.28} B (4.5–5.8)	39	10.8 {0.41} A (9.9–11.6)	35	4.7 {0.28} C (4.2–5.5)

^a Data sets with the same letter are not significantly different ($P < 0.05$) as analyzed using Duncan's (1955) multiple range test.

maries, secondaries, and rectrices are mostly Sepia with edgings the color of the contour feathers. The bill is Pearl Gray in all specimens from Maui and Oahu, but on Hawaii the bill of adult males varies from Pearl Gray to between Straw Yellow and Spectrum Yellow, possibly related to age.

Color and pattern are both strikingly different in *L. caeruleirostris*, and sexual color dimorphism is much less pronounced. Adult males are Yellowish Olive-Green on the back, wing coverts, and edges of dark flight feathers. The underparts, rump, and cheeks are between Spectrum Yellow and Sulfur Yellow, as is a distinctive cap that extends from the forehead to the crown. A black mask completely encircles the base of the bill and extends backward to a point behind the eye. Females resemble males in pattern, but have duller yellows (near Sulfur Yellow) with olive tinges below and a smaller pale cap. The female's mask is Blackish Neutral Gray and usually does not encircle the bill below. The bill in both sexes is Light Sky Blue, grayer in females and sometimes with a blue-black tip in males.

BILL SHAPE

The heavier bill of *L. caeruleirostris* as compared to any form of *L. coccineus* is obvious at a glance. Amadon (1950) obscured the difference by measuring only culmen length. My data (Table 1) show that although *coccineus*, *ochraceus*, and *caeruleirostris* do not differ significantly in culmen length, the latter has a significantly wider and deeper and thus differently shaped bill. The opposite extreme appears to be shown in the geographically adjacent *wolstenholmei*, whose bill is significantly shorter and narrower than those of all other akepas in a small sample.

NESTS

Loxops c. coccineus may be an obligate cavity-nester (Freed 1988). Sincock and Scott (1980),

Collins (1984), and Freed et al. (1987) documented the first seven nests discovered, all of which were in tree cavities in the Kau sector of the Akepa's range on Hawaii. Recently, five nests have been found in the Mauna Kea sector of the range, again all in cavities (L. Freed and J. Lepson, in litt.). Hawaii Akepas nest in both koa (*Acacia koa*) and ohia (*Metrosideros polymorpha*) trees, with an apparent preference for the latter (Collins 1984; Freed et al. 1987; J. Lepson, pers. comm.). In contrast, the Akekee builds upright open cup nests in the terminal crowns of ohia trees. Eddinger (1972) found four such nests and I discovered another at the intersection of the Alakai Swamp and Pihea trails on 4 May 1989. The latter was about 10 m from the ground in the dense leafy crown of an ohia tree, a few centimeters within the uppermost leaves. It was similar in all respects to the nests reported by Eddinger (1972). I saw the female sit in the nest briefly, then depart to meet her mate in an adjacent tree. She shivered her wings and crouched in an apparently submissive posture and was then mounted by the male, who sang loudly following copulation. My other duties precluded lengthy study of this nest. As Freed et al. (1987) noted, no other Hawaiian honeycreeper exhibits such a degree of interisland variation in nest construction, an indication, in my opinion, that the two differing forms of akepa are not conspecific. The Kauai Creeper (*Oreomystis bairdi*) and the Hawaii Creeper (*O. mana*), which also differ (but less sharply) in nest placement, were formerly considered conspecific but are now widely regarded as separate species (Pratt 1979, Berger 1981, Olson and James 1982, AOU 1983). The only report of nest construction by a member of any other akepa population is that of Perkins (1903), who saw a pair of the Maui form apparently building a nest near the end of a high horizontal branch of an ohia tree. He did not

actually see the nest, however, and we know nothing further about the nesting of akepas on Maui or Oahu.

VOICE

Both call notes and songs (Fig. 1) differ noticeably in *L. c. coccineus* and *L. caeruleirostris*. Vocalizations of *L. c. wolstenholmei* have not been described but songs and calls of *L. c. ochraceus* reportedly resemble those of *L. c. coccineus* (Engilis, unpubl.). The call notes of the Akepa on Hawaii are short, frequency-modulated, double-voiced whistles that give the impression of more than one "syllable" (three examples given in Fig. 1). Less often the birds utter an upslurred whistle similar to some calls of other Hawaiian honeycreepers (e.g., *Hemignathus virens*, *H. munroi*) on Hawaii. Calls of the Akeke usually seem monosyllabic to human ears, although sonograms reveal them to be more complex. The complexity is obscured by the shorter duration of the calls as compared to typical calls of the Akepa. Higher pitched overtones give the Kauai bird's calls a ringing or piercing quality.

Songs of *L. c. coccineus* are quite variable, with the individual singer rarely reiterating a song in identical form during a performance, but all can be described as long, loose, often lackadaisical trills. Some trills are shorter and louder with a "sweet" finchlike quality (second example in Fig. 1). The trills characteristically alter speed or note quality in mid-strophe, and the placement of this shift in the source of much of the observed variation. I have noticed no geographical variation in song among three widely separated Akepa populations (Kau, Keauhou/Kulani, and Mauna Kea). The song of *L. caeruleirostris* is much less variable. Its trills are always much more energetic and usually faster (6–11 pulses/sec) than those of *L. c. coccineus* (5–7 pulses/sec). The notes have the same piercing or ringing quality noted in the calls of this species. Although the songs of the two species overlap in speed of pulses and range of pitch, they are virtually always identifiable to species by skilled human observers. Thus they probably differ in parameters (i.e., amplitude) not revealed by sonograms, or the two parameters of speed and pitch may combine in species-specific ways. A more detailed analysis of akepa songs will be the subject of future studies. Apparently only male akepas sing the loud trilled (territorial?) songs, but both sexes utter lengthy whisper songs, similar to whisper songs

of other Hawaiian honeycreepers (e.g., various *Hemignathus*, *O. bairdi*), either while foraging in the canopy or from concealment in low shrubbery (Perkins 1903; Eddinger 1972; pers. observ.).

To determine whether the birds differentiate between their songs, I conducted some exploratory playback experiments. On Hawaii during 1–5 May 1977 (during what now appears to be the height of the breeding season), I found Akepas generally unresponsive to playback even of songs from their own population. Four individuals that had ignored the taped song of a Kauai bird did respond vocally (no approach) to a Hawaii tape, and four others responded to the Hawaii tape by approach after showing no response to the Kauai song. Two individuals, however, did respond to the Kauai song, one by vocal reply and one by approach. On Kauai during 27–30 January 1978, I again noted low responsiveness to recorded songs. Two Akeke, after ignoring the Akepa tape from Hawaii, responded vigorously to a Kauai tape by both approach and song. In one instance, I played the Hawaii tape close to a Kauai male that was calling and actively foraging. The bird did not alter its behavior in any way. After playing about 10 repetitions of the Akepa song, I switched to the Akeke (Kauai) tape. Almost with the first note of the song, the bird ceased foraging, approached the sound source, and behaved in a very agitated manner. I could induce no response by any *L. caeruleirostris* to the voice of *L. coccineus*, and often the subjects left the area before hearing a tape of their own population's song. When Kauai songs were presented first, response was the rule. Although these results suggest a differential response to each other's songs by the two species, interpretation must be made with extreme caution (see Discussion).

ECOLOGY

Whether the two akepas differ in habitat choice is problematical. Present distributions are almost certainly artificial (Scott et al. 1986), and historical accounts are sometimes conflicting. The Hawaii Akepa is today found mainly in mixed koa/ohia forests, but in the Kau Forest Reserve reaches its highest density in forests dominated by ohia only (Scott et al. 1986). Henshaw (1902), however, found the birds extremely rare in localities where koa was absent, and Perkins (1903) considered them "extremely partial to koa forests,"

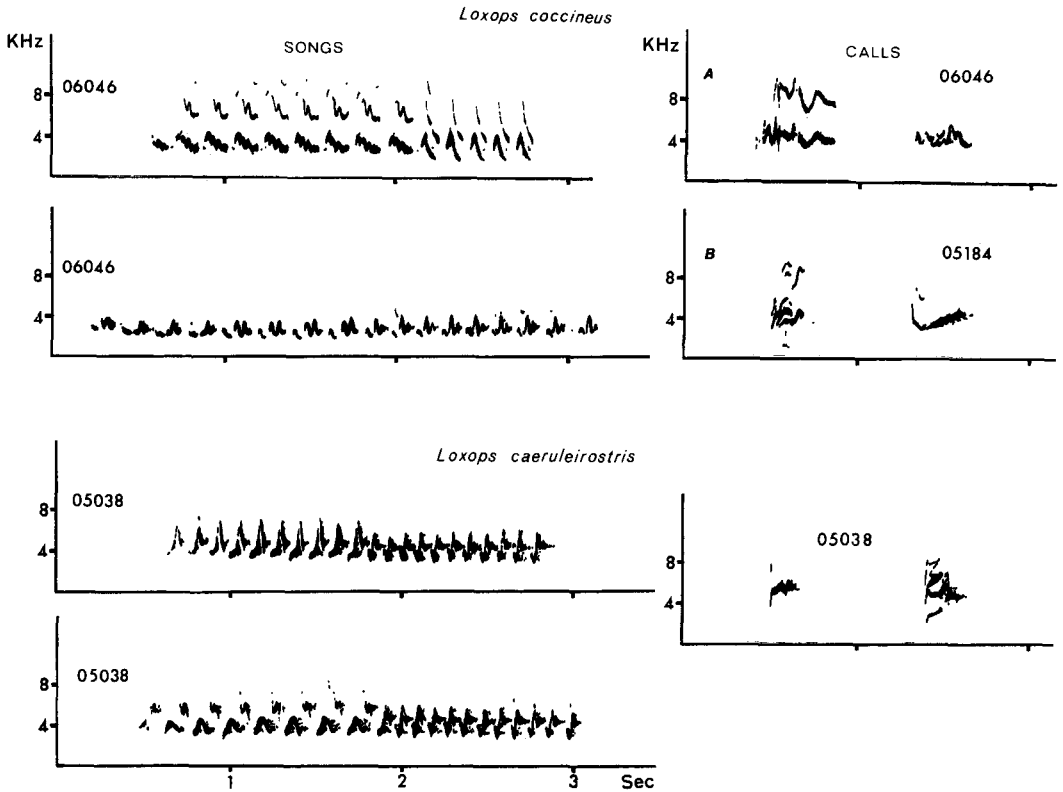


FIGURE 1. Vocalizations of the two species of *Loxops*. *Loxops coccineus* songs and calls (A) recorded by J. M. Scott, July 1976, Kahuku Ranch, Kau District, Hawaii; calls (B) recorded by the author August 1975, Keauhou Ranch, Kau District, Hawaii. *Loxops caeruleirostris* recorded by the author at Kokee State Park, Kauai, May 1976. Numbers indicate cuts in LNS Catalog from which these examples are taken.

but found them in low numbers in forests devoid of koa. Both C. J. Ralph (pers. comm.) and I have noted that, in mixed koa/ohia forests, Hawaii Akepas feed preferentially among ohia leaves, whereas earlier observers stated that they fed "almost entirely" (Henshaw 1902) or "largely" (Perkins 1903) on caterpillars gleaned from koa phyllodes. Henshaw (1902) and Perkins (1903) also reported feeding in understory trees such as naio (*Myoporum sandwicense*), mamane (*Sophora chrysophylla*), and aalii (*Dodonaea* spp.). Conant (1981) found that Hawaii Akepas in Kilauea Rainforest fed mostly in ohia (71%), but also foraged frequently in koa (26%), and occasionally (3%) in shrubs such as naio and pilo (*Coprosma rhynchocarpa*). Whether Akepas on Hawaii now feed less often than formerly in koa may never be known, but even today they are far from being ohia specialists.

On Maui, Perkins (1903) reported that Akepas were "often seen in the Koa trees but more often

in the Ohia" but Henshaw (1902) found that they fed "almost wholly . . . among the leaves of the koa, although occasionally . . . in the ohia trees." Possibly both observers were already witnessing an artificial pattern of distribution with inherent anomalies. Present populations are far too low (Scott et al. 1986) to yield meaningful observations that would allow us to reconcile the conflicting reports.

On Kauai, the present distribution of the Akeke (Scott et al. 1986) is apparently much closer to that reported historically (Perkins 1903) than is the case with the other akepas, and present habitat preference has apparently not been so strongly influenced by ecological disturbances. The Kauai bird appears to be an ohia specialist, gathering insect prey among the terminal leaf buds (Perkins 1903, Benkman 1989, pers. observ.). Although koa forests are present at upper elevations adjacent to ohia forests inhabited by *L. caeruleirostris*, the birds avoid them (pers. ob-

serv.), and in mixed forests I have rarely seen an Akekee even perched briefly in a koa tree. Richardson and Bowles (1964) and J. L. Sincock (in Scott et al. 1986) also report the birds in mixed koa/ohia forest in the Kokee area, but no observer has reported the Akekee foraging in any tree species other than ohia. The two akepas thus appear to have real ecological differences despite the fact that both are found mainly in ohia trees today. At least occasional foraging in koa has been documented for both *L. coccineus coccineus* and *L. c. ochraceus*.

DISCUSSION AND CONCLUSIONS

The determination of species limits among allopatric island birds is a vexing problem for the systematist. Mayr (1969) suggested that the degree of morphological differentiation between allopatric populations necessary to qualify them as separate species could be inferred by a comparison with closely related sympatric species pairs. Many such species pairs of Hawaiian honeycreepers (i.e., *Hemignathus virens* and *H. parvus* on Kauai, *H. virens* and *H. sagittirostris* on Hawaii, *Rhodacanthis palmeri* and *R. flaviceps* on Hawaii, and possibly *H. munroi* and *H. lucidus* on Hawaii) are much less divergent in plumage color and pattern than *L. coccineus* and *L. caeruleirostris*. In fact, Wilson (1889) considered the plumage of the latter sufficiently distinct to warrant its placement in a separate genus *Chrysomitridops*, but considered the other pairs congeneric. Likewise, the difference in bill shape appears to be about the same as exists in the other species pairs. Indeed, the differences between the two akepas in both plumage color and bill size are highly reminiscent of the differences between the two syntopic koa-finches (*Rhodacanthis*) now extinct. In that case, the two differ in average bill measurements, with some overlap (Pratt 1979), and their plumages are very similar with females nearly identical in color and males yellow to orange in one species (*R. palmeri*) and yellow in the other (*R. flaviceps*). So closely do the two approach in these characters that both the original collectors (Munro 1960) and Pratt (1979) questioned the validity of the smaller species, but recent discoveries by Olson and James (1982) have confirmed that two sympatric species did, in fact, exist.

Seemingly subtle differences in bill size and call notes apparently serve as isolating mechanisms in the cardueline crossbills (Nethersole-

Thompson 1975). Thus, by Mayr's (1969) criterion, the two akepas should be regarded as species on morphological grounds alone. This conclusion is bolstered by potential reproductive isolating mechanisms. The strikingly different nest-building behavior of the two suggests that a mixed pair would have difficulty selecting a nest site and constructing a nest. Possible differences in habitat selection could also work against mixed matings in sympatry, and the different vocal repertoires might restrict communication between the sexes.

Playback experiments have been widely used as experimental tests of sympatry in allopatric island populations (for a review, see Payne 1986), including Hawaiian thrushes, *Myadestes* (Pratt 1982). However, for a variety of reasons, playback experiments with Hawaiian honeycreepers are inherently difficult to interpret. First, the function of primary song is poorly understood in most species. Many of them, including akepas, often sing while foraging in small conspecific flocks that may include more than one adult male (pers. observ.). Birds in such situations seldom exhibit hostility toward their companions (pers. observ.), so one would not expect any response to an additional song being presented by the observer. Also the relationship of song frequency to the breeding cycle has not been determined for akepas. The Common Amakihi (*Hemignathus virens*) on Mauna Kea sings year-round but exhibits peaks of song frequency at two points in the 9-month breeding cycle (van Riper 1987). Other Hawaiian honeycreepers also have protracted breeding seasons (Baldwin 1953, van Riper 1980, Berger 1981). Thus, as Berger (1969) noted, the researcher has "only a vague idea" of the best time to find breeding birds. A further complication is that the nature of territoriality in akepas, and for that matter in most Hawaiian honeycreepers, has not been determined. Freed's (1988) observations suggest that male Akepas on Hawaii defend mate-centered rather than nest-centered territories. Such nonstationary territoriality has been found early in the breeding cycle of the Palila, *Loxioides bailleui* (van Riper 1980), a drepanidine finch, and is characteristic of many cardueline finches (Newton 1973). If the territory moves with a foraging pair, and does not necessarily include the nest site, then the opportunistic approach I used may actually be the best way to proceed with playback experiments on Hawaiian honeycreepers including akepas. The

TABLE 2. Distribution and potential reproductive isolating mechanisms of akepas.

	<i>Loxops c. coccineus</i>	<i>L. c. ochraceus</i>	<i>L. c. wolstenholmei</i>	<i>L. caeruleirostris</i>
Distribution	Hawaii	Maui	Oahu	Kauai
Degree of sexual dichromatism	extreme	extreme	extreme	slight
Adult male color	scarlet orange	orange or mustard	brick red	lemon yellow
Bill color	yellow or gray	gray	gray	pale blue
Facial contrast	none	none	none	extreme
Bill shape	medium	medium	shorter, narrower	wider, deeper
Trees used for foraging	koa, ohia, and others	koa and ohia	{no data}	ohia
Call note	multisyllabic	multisyllabic	{no data}	monosyllabic
Song	slow, loose	slow, loose	{no data}	fast, energetic
Nest site	tree cavity	{no data}*	{no data}	terminal tree crown

* Perkins (1903) did not actually see a nest (see text).

limited number of playback experiments that I conducted with akepas can provide inferences about potential vocal isolating mechanisms, but cannot be regarded as experimental tests of sympatry. Clearly, they suggest that two "languages" exist. My experiments do not by themselves "prove" that *L. coccineus* and *L. caeruleirostris* are biological species, but they help to shift the burden of proof to the hypothesis that the two are conspecific.

With their striking differences (Table 2) in plumage, bill shape, and nest building, possible ecological differences, and potential vocal isolating mechanisms, the conclusion that *L. caeruleirostris* of Kauai and *L. c. coccineus* of Hawaii are good biological species is very compelling. Problematical, however, is the position of the two lesser known "red" akepas of Maui and Oahu. If *L. c. ochraceus* of Maui is not a cavity-nester, then one of the points of distinction between *L. caeruleirostris* and *L. coccineus* is blurred. The possible nesting behavior difference of *ochraceus* does not, however, weaken the case for recognition of two akepa species, but rather suggests that more than two species may warrant recognition. Because they resemble *coccineus* rather than *caeruleirostris* in most respects, I suggest that *ochraceus* of Maui and *wolstenholmei* of Oahu be regarded as subspecies of *L. coccineus* until new data indicate otherwise.

ACKNOWLEDGMENTS

Numerous individuals assisted me in the field. I am grateful for logistical and moral support from Rob and Annarie Shallenberger, Carol and C. John Ralph, J. Michael Scott, John L. Sincock, Phillip and Andrea

Bruner, and Sheila Conant. I was assisted at their respective institutions by the following individuals: John Farrand and Francois Vuilleumier (American Museum of Natural History); A. C. Ziegler, F. J. Radovsky, R. L. Pyle, and A. Engilis (Bernice P. Bishop Museum); J. L. Gullede and A. Priori (Library of Natural Sounds); R. A. Paynter (Museum of Comparative Zoology); S. L. Olson, R. L. Zusi, and R. B. Clapp (National Museum of Natural History); Ned K. Johnson (Museum of Vertebrate Zoology); and F. B. Gill (Academy of Natural Sciences, Philadelphia). Recording equipment was loaned by the Laboratory of Ornithology and The Museum of Natural Science, Louisiana State University. J. M. Scott permitted me the use of his tape recordings. Sonograms were prepared by J. L. Gullede assisted by A. Franklin. J. V. Remsen, Jr., A. Engilis, Jr., and S. L. Mountspring provided helpful comments on the manuscript. Some of the fieldwork was supported by funds provided by J. S. McIlhenny to Louisiana State University.

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