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OF THE HAWAIIAN ISLANDS.

THE LOUISIANA STATE UNIVERSITY AND
AGRICULTURAL AND MECHANICAL COL., PH.D., 1979

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A SYSTEMATIC ANALYSIS OF THE ENDEMIC AVIFAUNA OF THE HAWAIIAN ISLANDS

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Zoology and Physiology

by
Harold Douglas Pratt, Jr.
B. S., Davidson College, 1966
M. S., Louisiana State University, 1973
May, 1979

This paper is dedicated, with deep respect,

to the memory of

GEORGE H. LOWERY, JR.

(1913 - 1978)

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FOREWORD: ABOUT HAWAIIAN WORDS

The Hawaiian language, with its limited 12-letter alphabet and long multi-vowel words can be bewildering to English-speaking readers. Some acquaintance with the rules of pronunciation, as well as the use of standard orthographic conventions, can help to alleviate such problems. Many Hawaiian words appear in the body of this work, usually as names for places, birds, or plants. Although the argument can be made that such terms are now English words and can therefore be orthographically anglicized, I have followed the precedent of the Atlas of Hawaii (Armstrong 1973) in using both the glottal stop (') and the macron (¯) when writing words of Hawaiian origin, with two exceptions: (1) island names used in titles of organizations or publications, when such do not use Hawaiian orthography; and (2) in direct quotations from the literature, where I follow the original author's usage. The use of these orthographic symbols will enable the reader to more accurately pronounce, and therefore more readily remember, Hawaiian names. I have relied on Armstrong (1973) and Pukui et al. (1974) for correct spellings of place names and on Pukui and Elbert (1971) and Pyle (1977) for bird and plant names. The following discussion of Hawaiian pronunciation is based primarily on Pukui and Elbert (1971).

Most Hawaiian consonants (p, k, h, l, m, n) are pronounced essentially as in English. The *w* is sounded as in English when it follows *u* or *o*, as the English *v* after *i* or *e*, and as either *w* or *v* after *a* or initially. The glottal stop (') resembles the stoppage of sound between the syllables of the English "oh-oh." It is a true consonant, not a mark of punctuation. The initial glottal stop functions only when several words are pronounced in sequence. Vowels are pronounced as in Spanish. Dipthongs (ei, eu, oi, ou, ai, ae, ao, au) are stressed on the first vowel, and the two members are not as closely joined in sound as in English.

The stress or accent in Hawaiian words falls on the penultimate syllable and alternating preceding syllables except that five-syllable words are stressed on the first and fourth. Vowels marked with a macron (ā, ē, ī, ō, ū) are always stressed, the macron thus serving as a written irregular accent similar to that used in Spanish.

Some Hawaiian terms are in such widespread use among English-speaking islanders (e. g. "kīpuka") that they can now be considered English words, even though they may yet lack the sanction of standard dictionaries. Such words are not italicized in this work both in recognition of their wide usage and to avoid confusion with scientific nomenclature.

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ABSTRACT

The avifauna of the Hawaiian Islands, the world's most isolated archipelago, provides examples of evolutionary divergence at every level from subspeciation within a single small island to development of endemic taxa at the subfamily level. The relationships of all breeding land and freshwater birds are discussed, and generic and species limits are reassessed on the basis of a wide variety of characters including morphology, behavior, vocalizations, breeding biology, and ecology. Allopatric species are recognized where potential morphological, ethological, or ecological isolating mechanisms exist.

Intra-island geographic variation is demonstrated for *Chasiempis sandwichensis* on Hawai'i, with three subspecies recognized: *C. s. ridgwayi* in the wet windward forests; *C. s. sandwichensis* in Kona and southern Ka'ū; and *C. s. bryani* in the dry leeward uplands of Mauna Kea.

The Hawaiian honeycreepers are shown to be a monophyletic offshoot of cardueline finch stock, and are classified as a subfamily, Drepanidinae, of the Fringillidae. Two characters, a distinctive odor and a truncate base of the tongue, characterize the taxon. Three tribes are recognized: the Psittirostrini comprising five finch-billed genera; the Hemignathini comprising four green-plumaged insectivorous genera; and Drepanidini comprising four genera of red and black-plumaged nectarivores. The genera are redefined on the basis of shared adaptive facies. At the species level, *Loxops caeruleirostris* is shown by vocal playback experiments and ecological differences to be distinct from *L. coccineus*. *Hemignathus stejnegeri* is separated from *H. virens* on the basis of adaptive differences and possible vocal isolating mechanisms. *Hemignathus obscurus* includes the Kaua'i form *procerus*, which represents one extreme of a morphocline. *Telespyza cantans* and *T. ultima* are regarded as separate species. The possibility that *Rhodacanthis flaviceps* actually represents immature specimens of *R. palmeri* is discussed and considered to be likely. A replacement name, *Hemignathus munroi*, is proposed for *H. wilsoni*, preoccupied because of generic shifts in this classification. The complex known as "creepers," formerly considered a single species, is shown to comprise five species belonging to two genera, *Oreomystis* and *Paroreomyza*. The latter genus may not belong to the Drepanidinae.

The Hawaiian thrushes are shown to be inseparable generically from the American solitaires of the genus *Myadestes*, and not to be closely related to the nightingale-thrushes (*Catharus*) as suggested in recent checklists. Playback experiments demonstrate the specific distinctness of three Hawaiian *Myadestes*, and two others are tentatively recognized on the basis of morphology.

Among nonpasserines, the endemic stilt is considered conspecific with *Himantopus mexicanus* of North America, but the Hawaiian Coot is considered an endemic species, *Fulica alai*. Evidence is presented that the Hawaiian Duck, *Anas wyvilliana*, is sympatric with *Anas platyrhynchos* during the pairing phase of the life cycle without interbreeding and is therefore a good species, as is _A_. _laysanensis_.

Taxon cycles in the Hawaiian avifauna are shown to be basically similar to those noted elsewhere, except that immigration plays a minor role. Stage IV species accumulate in Hawaii on the larger and younger islands. Introduced birds may undergo cycles that mimic natural taxon cycles. Distributional anomalies associated with the island of Maui are discussed and possible explanations are offered.

SECTION 1. INTRODUCTION

This study began on a pleasure trip to Hawai'i in 1974 to visit Phillip L. Bruner with whom I was planning a field guide to the birds of the Pacific. That project is still ongoing, but had to be delayed somewhat while this research was completed. I first became dissatisfied with the "accepted" classifications of Hawaiian birds as I began to examine closely the specimens I was using as references for the field guide plates. That the Hawaiian avifauna had not been analyzed adequately in the light of modern ethological and zoogeographical studies became abundantly apparent as I became familiar with the birds in the field. The last significant systematic study had been that of Amadon (1950) on the endemic honeycreepers. The other indigenous taxa had received cursory treatment at best, and all evolutionary studies had been based almost entirely on museum specimens only.

This situation prevailed at a time when research on Hawaiian birds was intensifying rapidly. After years of neglect, scholarly studies of native birds had been resumed in the late 1960s, most of them under the direction of Andrew J. Berger of the University of Hawaii. These included the first modern studies of breeding biology of Hawaiian birds (e. g. Berger 1969a, b; Berger et al. 1969; Eddinger 1970, 1972a, b; van Riper 1973a, 1978; Conant 1977) and the first studies based on captive Hawaiian honeycreepers (Warner 1968; Raikow 1974; MacMillen 1974). Much of this research was summarized by Berger (1972b) in Hawaiian Birdlife.

In the early 1970s the U. S. International Biological Program (IBP) Island Ecosystems Research Program through the University of Hawaii supported the work of many biologists in the islands, many of whom were ornithologists. Several ecological studies conducted under this program have been recently published (Carpenter 1976; Carpenter and MacMillen 1976a, b) and others will be forthcoming. In 1973, a team of University of Hawaii undergraduates participating in the Hana Rain Forest Project of the University's Student Originated Study Program made the spectacular discovery of a new bird species on Maui (Casey and Jacobi 1974).

During the same period, U. S. Government attention began to be focused on Hawaiian birds, particularly the Endangered Species. Early efforts of the U. S. Fish and Wildlife Service (USFWS), such as John L. Sincock's surveys on Kaua'i, were important in establishing the existence of some forms (Banko 1968). By the mid-1970s intensive population surveys had begun under the direction of J. Michael Scott, Sincock, and Eugene Kridler. Eventually, these censuses will cover all remaining native forests in the islands (Scott, pers. comm.) and some limited results have already been published (Scott and Sincock 1977; Scott et al. 1977; van Riper et al. 1978). More recently the U. S. Forest Service has taken an interest in native birds and is conducting, under the direction of C. John Ralph, studies of avian communities in native forests.

In this atmosphere of intensive investigation, I undertook this study in the belief that a sound systematic foundation is essential to proper understanding of community dynamics, ecological relationships, adaptive strategies, and even physiological phenomena. I trust that the result will be of value to researchers in these fields.

Methods and Materials

My field studies were conducted discontinuously over the past five years. I made observations in all seasons and on all the main islands except Lana'i. Primary study areas included Koke'e and Waimea Canyon State Parks, John Sincock's study area near the headwaters of Halehaha Stream in the Alaka'i Swamp, Hanalei National Wildlife Refuge, Moloka'i Forest Reserve (FR), Haleakalā National Park (NP), Ko'olau FR, Polipoli Springs State Park, Kanahā and Waiakea ponds on Maui, Keauhou Ranch, Kilauea FR, Hawaii Volcanoes NP, Hilo FR, Upper Waiakea FR, Mauna Kea FR, Kaohe Game Management Area, Mauna Loa Forest and Game Reserve, and Kaupulehu FR (Hualālai).

An important element of my work has been the recording of vocalizations of native birds, most of which have not been previously so documented. Early recordings were made on a Sony TC-45 cassette recorder with a Sony parabolic reflector, but later I was able to obtain a Uher 4200 recorder and Dan Gibson Parabolic Microphone. I have also obtained recordings from others including J. Michael Scott (cassette recorders and Dan Gibson microphone), Robert J. Shallenberger (Nagra and Nakamichi recorders, Gibson parabola), Richard

Coleman (Shallenberger's equipment), and Colin Huddleston (equipment unspecified). Sonagrams were produced by James L. Gulledge using Spectral Dynamics Model SD301-C Real Time Analyzer with a range of 0-10,000 Hz and a band width of 120 Hz. My entire sound collection is archived in the Library of Natural Sounds, Cornell Laboratory of Ornithology.

In addition to the field data, I re-examined existing specimens of all Hawaiian species, and made some limited additional collections. My specimens are catalogued at the Louisiana State University Museum of Zoology. Most measurements were taken in the manner of Baldwin et al. (1931) with the following differences in terminology: "bill length" is the length of the exposed culmen, measured as the chord; "bill depth" is the same as height of bill at base; and wing length is measured as the chord.

Other methods and techniques are discussed in later sections.

SECTION 2.

SYNOPSIS OF THE HAWAIIAN AVIFAUNA

All the indigenous birds of the Hawaiian Islands arrived by oversea colonization or evolved autochthonously from such an ancestor. Virtually every level of evolutionary divergence is represented in the avifauna, from subspecies undifferentiated from continental forms to groups that have undergone spectacular adaptive radiations from an ancient colonist. The known land and freshwater birds are the products of possibly as few as 14 successful colonizations, and certainly no more than 18. Mayr (1943) discussed the provenance of these ancestral species.

Virtually all the nonpasserines have North American or at least Holarctic affinities. Included are a subspecies of the Black-crowned Night Heron (*Nycticorax nycticorax*) also found in western North America, endemic subspecies of the almost cosmopolitan Short-eared Owl (*Asio flammeus*) and Common Gallinule (*Gallinula chloropus*), and the North American Black-necked Stilt (*Himantopus mexicanus*). Three Hawaiian species are representatives of widespread superspecies. These include a coot (*Fulica alai*) and two endemic ducks, *Anas wyvilliana* and *A. laysanensis*. Endemic species that belong to widespread genera include a goose (*Branta*), a hawk (*Buteo*), and two rails (*Porzana*).

Among passerines, all species are endemic but several belong to continental genera. These include a crow (Corvus), an Old World warbler (Acrocephalus), and a group of thrushes related to the American solitaires (Myadestes). Three endemic genera belong to groups found mainly in the Australian Realm: a monarchine flycatcher (Chasiempis) whose nearest relatives are Monarcha, Mayrornis, and Pomarea; and two distinctive meliphagid genera, Chaetoptila and Moho.

By far the most intriguing Hawaiian passerines are the birds known as honeycreepers. Traditionally considered an endemic family Drepanididae, these birds have close affinities with the cardueline finches. This group comprises the majority of passerine species in the islands and provide the most spectacular example of adaptive radiation known among birds.

To these species may now be added many others recently discovered in fossil deposits on several islands (Ziegler, Olson, pers. comms.). Apparently a varied assemblage of flightless birds, including the aforementioned ibis (Apteribis glenos) and goose (Thambetochen chauliodous), other as yet undescribed geese, and at least two rails in addition to the known species existed in the islands along with large predatory birds such as an eagle and a long-legged owl. Also, passerine remains have been found including an unknown Corvus, Chaetoptila, and representatives of several modern genera of Hawaiian honeycreepers, as well as bizarre new honeycreeper types (Olson, pers. comm.). At this writing, Olson is preparing a complete report on these exciting discoveries. What stories these fossils will tell can only be surmised now, but many questions of phylogeny may well be answered.

Since European contact, these native species have been joined by a vast array of introduced birds (Berger 1972b, 1977; Shallenberger 1978) including numerous popular cage birds such as bulbuls, white-eyes, mynas, and finches as well as francolins, quails, doves, pheasants, and turkeys imported as game birds. These foreigners are now practically the only birds to be seen in the lowlands of the Hawaiian Islands. Though the interactions of the members of this melting-pot avifauna are of considerable scientific interest, even ornithologists find the newcomers a poor substitute for the native birds, the survivors of which are now mostly restricted to high mountain forests.

The following systematic list is provided as a convenience to the reader, and reflects the author's views as discussed in the succeeding pages of this paper. Following as nearly as possible the precepts for such names set forth by the American Ornithologists' Union Check-list Committee (1973), I have recommended English vernacular names for all full species. I have favored the use of native Hawaiian names, where such are available, as English vernaculars for endemic species since these names are in wide use among both professional and amateur field ornithologists in the islands as well as in the literature. In the case of members of cosmopolitan genera, such as _Corvus_ and _Buteo_, I have included alternative names that reflect relationships. Notation for superspecies and megasubspecies follows the recommendations of Amadon (1966) and Amadon and Short (1976). The sequence of families follows that of Morony et al. (1975). For synonymies, see Wilson and Evans (1890-99 [1974]), Bryan and Greenway (1944), and Greenway (1968). Island distributions of native land and freshwater birds are given in Table 1.

Systematic List

Family ARDEIDAE: Herons

Genus Nycticorax

Nycticorax nycticorax (Linnaeus) 1758 - Black-crowned Night Heron

Nycticorax nycticorax hoactli (Gmelin) 1789

Family ANATIDAE: Waterfowl

Genus Branta

Branta sandvicensis (Vigors) 1833 - Nēnē or Hawaiian Goose

Genus Anas

Anas [platyrhynchos] wyvilliana Sclater 1878 - Koloa maoli or Hawaiian Duck

Anas [platyrhynchos] laysanensis Rothschild 1892 - Laysan Duck

Family ACCIPITRIDAE: Eagles and Hawks

Genus Buteo

Buteo solitarius Peale 1848 - 'Io or Hawaiian Hawk

Family RALLIDAE: Rails, Gallinules, and Coots

Genus Porzana

Porzana palmeri (Frohawk) 1892 - Laysan Rail

Porzana sandwichensis (Gmelin) 1789 - Moho or Hawaiian Rail

Genus Gallinula

Gallinula chloropus (Linnaeus) 1758 - Common Gallinule

Gallinula chloropus sandvicensis Streets 1877

Genus Fulica

Fulica [atra] alai Peale 1848 - 'Alae-ke'oke'o or Hawaiian Coot

- Family RECURVIROSTRIDAE: Avocets and Stilts
  - Genus *Himantopus*
    - *Himantopus mexicanus* (Muller) 1776 - Black-necked Stilt
      - *Himantopus mexicanus knudseni* Stejneger 1887
- Family STRIGIDAE: Typical Owls
  - Genus *Asio*
    - *Asio flammeus* (Pontoppidan) 1763 - Short-eared Owl
      - *Asio flammeus sandwichensis* (Bloxam) 1826
- Family MUSCICAPIDAE: Thrushes, Flycatchers, Warblers, etc.
  - Subfamily TURDINAE: Thrushes
    - Genus *Myadestes*
      - *Myadestes myadestinus* (Stejneger) 1887 - Kāma'o
      - *Myadestes* ?*oahensis* (Wilson and Evans) 1899 - O'ahu Thrush
      - *Myadestes lanaiensis* (Wilson) 1891 - Oloma'o
      - *Myadestes obscurus* (Gmelin) 1789 - 'Ōma'o
      - *Myadestes palmeri* (Rothschild) 1893 - Puaiohi
  - Subfamily SYLVIINAE: Old World Warblers
    - Genus *Acrocephalus*
      - *Acrocephalus familiaris* (Rothschild) 1892 - Millerbird
        - *Acrocephalus familiaris familiaris* (Rothschild) 1892
        - *Acrocephalus familiaris kingi* (Wetmore) 1924

Subfamily MONARCHINAE: Monarch Flycatchers

Genus *Chasiempis*

Chasiempis sandwichensis (Gmelin) 1789 - 'Elepaio

Chasiempis sandwichensis sandwichensis (Gmelin) 1789

Chasiempis sandwichensis ridgwayi Stejneger 1887

Chasiempis sandwichensis bryani Pratt 1979

Chasiempis (*sandwichensis*) *gayi* Wilson 1891

Chasiempis (*sandwichensis*) *sclateri* Ridgway 1881

Family MELIPHAGIDAE: Honeyeaters

Genus *Chaetoptila*

Chaetoptila angustipluma (Peale) 1848 - Kioea

Genus *Moho*

Moho [*nobilis*] *nobilis* (Merrem) 1786 - Hawai'i 'Ō'ō

Moho [*nobilis*] *bishopi* (Rothschild) 1893 - Moloka'i 'Ō'ō

Moho [*nobilis*] *apicalis* Gould 1860 - O'ahu 'Ō'ō

Moho braccatus (Cassin) 1855 - 'Ō'ō'a'a

Family FRINGILLIDAE: Finches and Hawaiian Honeycreepers

Subfamily DREPANIDINAE: Hawaiian Honeycreepers and Finches

Tribe *Psittirostrini*

Genus *Telespyza*

Telespyza cantans Wilson 1890 - Laysan Finch

Telespyza ultima Bryan 1917 - Nihoa Finch

Genus *Rhodacanthis*

Rhodacanthis palmeri Rothschild 1892 - Koa Finch

[*Rhodacanthis flaviceps* Rothschild 1892][1]

Genus *Loxioides*

Loxioides bailleui Oustalet 1877 - Palila

Genus *Chloridops*

Chloridops kona Wilson 1888 - Kona Grosbeak

Genus *Psittirostra*

Psittirostra psittacea (Gmelin) 1789 - 'Ō'ū

Tribe Hemignathini

Genus *Pseudonestor*

Pseudonestor xanthophrys Rothschild 1893 - Maui Parrotbill

Genus *Oreomystis*

Oreomystis bairdi (Stejneger) 1887 - 'Akikiki

Oreomystis mana (Wilson) 1891 - Hawai'i Creeper

Genus *Loxops*

Loxops [*coccineus*] *coccineus* (Gmelin) 1789 - 'Ākepa

Loxops coccineus coccineus (Gmelin) 1789

Loxops coccineus ochraceus Rothschild 1893

Loxops coccineus rufus (Bloxam) 1826

Loxops [*coccineus*] *caeruleirostris* (Wilson) 1889 - 'Ō'ū-holowai

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[1] The validity of this species is questionable. See Section 6.

Genus *Hemignathus*

Subgenus *Hemignathus*

Hemignathus obscurus (Gmelin) 1788 - 'Akialoa

Hemignathus obscurus obscurus (Gmelin) 1788

Hemignathus obscurus lanaiensis Rothschild 1893

Hemignathus obscurus ellisianus (Gray) 1860

Hemignathus obscurus procerus Cabanis 1889

Subgenus *Heterorhynchus*

Hemignathus lucidus Lichtenstein 1839 - Nukupu'u

Hemignathus lucidus lucidus Lichtenstein 1839

Hemignathus lucidus hanapepe Wilson 1889

Hemignathus lucidus affinis Rothschild 1893

Hemignathus munroi nom. nov.[1] - 'Akiapola'au

Subgenus *Viridonia*

Hemignathus [*virens*] *virens* (Gmelin) 1788 - Common 'Amakihi

Hemignathus virens virens (Gmelin) 1788

Hemignathus virens wilsoni (Rothschild) 1893

Hemignathus virens chloris (Cabanis) 1850

Hemignathus [*virens*] *stejnegeri* (Wilson) 1889 - Kaua'i 'Amakihi

Hemignathus parvus (Stejneger) 1887 - 'Anianiau

Hemignathus sagittirostris (Rothschild) 1892 - Greater 'Amakihi

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[1] Replacement name for *Hemignathus wilsoni* (Rothschild) 1893, now preoccupied. See page 128.

Tribe Drepanidini

Genus *Ciridops*

Ciridops anna (Dole) 1879 - 'Ula-'ai-hawane

Genus *Drepanis*

Drepanis [pacifica] pacifica (Gmelin) 1788 - Hawai'i Mamo

Drepanis [pacifica] funerea Newton 1893 - Black Mamo

Drepanis coccinea (Forster) 1780 - 'I'iwi

Genus *Palmeria*

Palmeria dolei (Wilson) 1891 - 'Ākohekohe

Genus *Himatione*

Himatione sanguinea (Gmelin) 1788 - 'Apapane

Himatione sanguinea sanguinea (Gmelin) 1788

Himatione sanguinea freethii Rothschild 1892

Genera incertae sedis

Genus *Paroreomyza*

Paroreomyza maculata (Cabanis) 1850 - O'ahu 'Alauahio

Paroreomyza flammea (Wilson) 1889 - Kakawahie

Paroreomyza montana (Wilson) 1889 - Maui 'Alauahio

Paroreomyza montana montana (Wilson) 1889

Paroreomyza montana newtoni (Rothschild) 1893

Genus *Melamprosops*

Melamprosops phaeosoma Casey and Jacobi 1974 - Po'o-uli

Family CORVIDAE: Crows, Ravens, and Jays

Genus Corvus

Corvus tropicus (Gmelin) 1789 - 'Alalā or Hawaiian Crow

TABLE 1.

ISLAND DISTRIBUTION OF NATIVE HAWAIIAN BIRDS

Species and Subspecies	Laysan	Nihoa	Kaua'i	O'ahu	Moloka'i	Lana'i	Maui	Hawai'i
Nycticorax nycticorax			X	X	X	X	X	X
Branta sandvicensis								X
Anas wyvilliana			X	X	(X)[1]		(X)	X
Anas laysanensis	X							
Buteo solitarius								X
Porzana palmeri	(X)							
Porzana sandwichensis					?			(X)
Gallinula chloropus			X	X	X		(X)	(X)
Fulica alai			X	X	X		X	X
Himantopus mexicanus			X	X	X		X	X
Asio flammeus			X	X	X	X	X	X
Corvus tropicus								X
Myadestes myadestina			X					
Myadestes ?oahensis				(X)				
Myadestes lanaiensis					X	(X)		
Myadestes obscurus								X
Myadestes palmeri			X					
Acrocephalus familiaris familiaris	(X)							
Acrocephalus familiaris kingi		X						

TABLE 1. (Contd.)

	Laysan	Nihoa	Kaua'i	O'ahu	Moloka'i	Lana'i	Maui	Hawai'i
Chasiempis s. sandwichensis								X
Chasiempis s. ridgwayi								X
Chasiempis s. bryani								X
Chasiempis s. gayi				X				
Chasiempis s. sclateri			X					
Chaetoptila angustipluma								(X)
Moho nobilis								(X)
Moho bishopi					(X)		?	
Moho apicalis				(X)				
Moho braccatus			X					
Telespyza cantans	X							
Telespyza ultima		X						
Rhodacanthis palmeri								(X)
?Rhodacanthis flaviceps								(X)
Loxioides bailleui								X
Chloridops kona								(X)
Psittirostra psittacea			X	(X)	(X)	(X)	(X)	X
Pseudonestor xanthophrys							X	
Oreomystis bairdi			X					
Oreomystis mana								X

TABLE 1. (Contd.)

	Laysan	Nihoa	Kaua'i	O'ahu	Moloka'i	Lana'i	Maui	Hawai'i
Loxops coccineus coccineus								X
Loxops coccineus ochraceus							X	
Loxops coccineus rufus				X[2]				
Loxops caeruleirostris			X					
Hemignathus obscurus obscurus								(X)
Hemignathus obscurus lanaiensis						(X)		
Hemignathus obscurus ellisianus				(X)				
Hemignathus obscurus procerus			X					
Hemignathus lucidus lucidus				(X)				
Hemignathus lucidus hanapepe			X					
Hemignathus lucidus affinis							X	
Hemignathus munroi (=*wilsoni*)								X
Hemignathus virens virens								X
Hemignathus virens wilsoni					X	X	X	
Hemignathus virens chloris				X				
Hemignathus stejnegeri			X					
Hemignathus parvus			X					
Hemignathus sagittirostris								(X)
Ciridops anna								(X)
Drepanis pacifica								(X)

TABLE 1. (Contd.)

	Laysan	Nihoa	Kaua'i	O'ahu	Moloka'i	Lana'i	Maui	Hawai'i
Drepanis funerea					(X)			
Drepanis coccinea			X	X	X	(X)	X	X
Palmeria dolei					(X)		X	
Himatione sanguinea sanguinea			X	X	X	X	X	X
Himatione sanguinea freethi	(X)							
Paroreomyza maculata				X				
Paroreomyza flammea					X			
Paroreomyza montana montana						(X)		
Paroreomyza montana newtoni							X	
Melamprosops phaeosoma							X	

[1] Extinct populations indicated by parentheses.

[2] Last certain record 1893; possibly sighted 1977 (Ralph and Pyle 1977).

SECTION 3.

THE AVIAN ENVIRONMENT IN HAWAI'I

The Hawaiian Islands are the world's most isolated archipelago. Over 3200 km of open ocean separate the islands from the nearest continent (North America) or the nearest large islands (the Marquesas). Entirely volcanic in origin, the islands form a chain lying just inside the northern tropics and stretching approximately 2700 km from northwest to southeast. Most geologists agree that the volcanoes that formed the islands represent successive locations of a "melting spot" in the earth's mantle over which the Pacific plate has moved in a more or less continuous direction since the early Miocene (Dalrymple et al. 1973; Schlanger and Gillett 1976). The youngest and largest island, Hawai'i, at the southeastern end of the archipelago, is the site of the only presently active volcanoes. To the northwest of Hawai'i, the islands become successively older and more eroded with the oldest islands represented today by low atolls.

The Hawaiian Archipelago may be conveniently subdivided into two island groups: the main cluster of eight large islands and a chain of small coral or rocky islands known as the Leeward or Northwest Hawaiian Islands. These latter islands are important breeding grounds for seabirds but they harbor only a few indigenous passerines. Whether these low islands figured in the evolution of the present Hawaiian avifauna can not be determined, but the islands certainly were large enough to support a varied fauna in the Pliocene (Carlquist 1970; Schlanger and Gillett 1976). Today, only the atoll of Laysan and the rocky island of Nihoa have native land birds.

Of the eight main islands, only six are important ornithologically. The two smallest, Ni'ihau at the northwest end of the group and Kaho'olawe in the central cluster of islands, are low and dry, lying in the rain shadows of Kaua'i and Maui, respectively. No native passerines nest on them, although some may have occurred there in the past (Bryan 1931; Fisher 1951). Both islands were joined to the nearby larger islands in fairly recent geological time (Carlquist 1970).

Kaua'i is the oldest and most extensively eroded of the main islands. Wai'ale'ale is the highest point (1598 m). To the northwest of Wai'ale'ale lies the boggy plateau known as the Alaka'i Swamp, actually a dense upland forest. The streams that drain the Alaka'i flow mainly into deeply eroded Waimea Canyon, which cuts across the western part of the island northward from the south coast. On the western rim at the head of the canyon is the ornithologically important region known as Koke'e. A detailed description of Kaua'i from the point of view of bird distribution is that of Richardson and Bowles (1964).

O'ahu, the commercial and political center of the State of Hawai'i, lies approximately 120 km southeast of Kaua'i. Two parallel mountain ranges, the Wai'anae in the west and the Ko'olau to the east, are separated by a broad lowland plain. Pearl Harbor is located at the southern end of this plain and west of the city of Honolulu, where over half the state's people live. The highest elevation (1225 m) is reached by Mt. Ka'ala in the Wai'anae Range. Among the four larger islands, O'ahu has the lowest maximum elevation and the most extensive lowlands.

Approximately 40 km southeast of O'ahu lies Moloka'i, the first of a group of islands that were joined during the last glaciation when sea levels were 100 m lower than at present (Terborgh 1975). The group includes, in order of size, Maui, Moloka'i, Lana'i, and Kaho'olawe. Moloka'i is a more or less rectangular island oriented from east to west. The western portion is low and flat but the eastern half exhibits a high (1402 m) mountainous area with two deep valleys, Pelekunu and Wailau, cutting into the northern windward side. Maui is formed by two volcanoes joined by a low isthmus. West Maui is the older of the two mountains and exhibits deeply cut valleys and steep slopes. Its highest point is Pu'u Kukui (1764 m). Eastern Maui is formed by the massive Haleakalā (3055 m). This mountain features a large erosional crater with two prominent gaps in the rim, Ko'olau Gap to the north and Kaupo Gap to the south. A series of deep valleys dissect the eastern and northeastern slopes. The largest and ornithologically most important is Kīpahulu, which, with the upper reaches of the mountain, is included in Haleakalā National Park. Lana'i, to the west of Maui, has a single low (1027 m) peak and is the smallest of the main islands to possess endemic birds. According to data summarized by Terborgh (1975), the four islands of the Maui complex became separated between about 14,000 and 8000 years ago.

The larger islands mentioned thus far all emerged from the sea in the Pliocene, but the island of Hawai'i is of Pleistocene age. Larger than all the other islands combined, Hawai'i has been built by five volcanoes, two of which are still active. The island's history has been outlined in detail by Macdonald and Abbott (1970) and Stearns (1966). Today the horizon of the Big Island, as it is known locally, is dominated by dormant Mauna Kea, at 4205 m the highest peak in the archipelago, still active Mauna Loa (4169 m), and the smaller dormant volcano Hualālai (2521 m). The leeward slopes of Hualālai and Mauna Loa together form the region known as Kona. The area between the three main peaks is called the Saddle. At the north end of the island a highly eroded area is often referred to as the Kohala Mountains, although it is the remains of a single long-extinct volcano. The summit of Mauna Loa and the crater of Kīlauea on its flank are included in Hawai'i Volcanoes National Park. Lava flows of various ages characterize the landscape of the Big Island. In many areas the flows have produced islands of ancient forest in a sea of lava. Such an isolated forest is called a kīpuka. Approximately 50 km separate Hawai'i from Maui to the northwest.

Except as noted above, none of the larger islands have ever been connected. Deep channels lie between Kaua'i and O'ahu and between Maui and Hawai'i with a somewhat shallower one between O'ahu and Moloka'i. Figure 1 is a map of the archipelago showing the prominent geographical features.

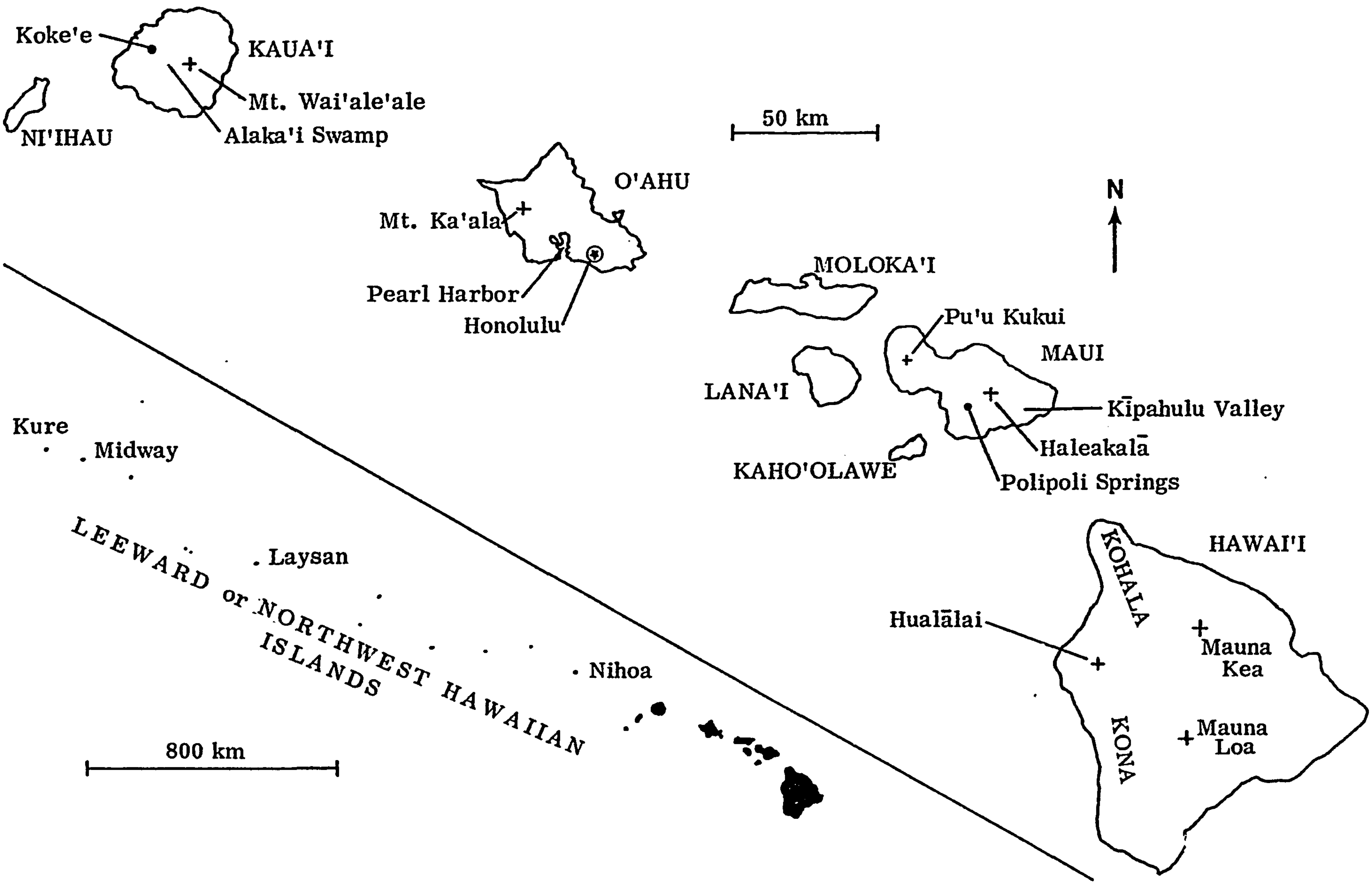


Figure 1. The Hawaiian Islands, showing the major geographical features mentioned in the text.

Climate

The Hawaiian climate has been described in detail by Carlquist (1970) and Price (in Armstrong 1973). The northeast tradewinds are the dominant force in island weather, producing heavy rainfall on the windward slopes of the high islands, usually with a dry rain shadow of the leeward side. Kaua'i receives the heaviest rainfall of all. Wai'ale'ale is often believed to be the world's wettest spot, with over 1000 cm of rain per year. Other significant areas that receive over 700 cm per year include West Maui, the northeast slope of Haleakalā, and the windward slope of Mauna Kea above Hilo. Xeric regions occur on all islands but the most extensive such areas are western Moloka'i, the southern quarter of O'ahu, the isthmus of Maui, and most of Lana'i. The Big Island has extensive dry habitats at the southern extremity and in the region northwest of Mauna Kea. An extensive dry alpine zone is found in the Saddle and on the slopes above. Both Mauna Kea and Mauna Loa are snow capped in some years. These two peaks effectively block the action of the northeast tradewinds in Kona, and there a local weather system based on convection patterns predominates. Thus the leeward side of the Big Island is moderately wet rather than dry as might otherwise be expected. Rainfall is heaviest throughout the archipelago between October and April. Temperatures during that period average somewhat cooler, but the islands experience little seasonal variation in this respect. As can be readily seen, the rugged nature of the Hawaiian Islands produces a wide range of climatic conditions within a generally mild and equable climate.

Vegetation

Vegetation patterns in the islands are determined largely by rainfall, with elevation only indirectly related. Both Carlquist (1970) and Rock (1974) give detailed accounts of Hawaiian plant communities, so I shall discuss here only those of major importance to native birds. Both wet and dry lowland forests once occurred on all the islands but these associations had been greatly altered by the time systematic collections of Hawaiian birds were made in the 1890s. No bird species are known to have been restricted to these forests, but some of those with very small ranges may have had a wider distribution in lowland forests now destroyed.

The most important ecosystem in terms of native bird diversity and abundance is the wet forest. On the windward slopes of the islands heavy rainfall produces luxuriant rainforests and cloud forests. Throughout the islands such forests are dominated by 'ōhi'a-lehua (*Metrosideros collina*), a tree of almost infinitely varied growth form. The brilliant red or yellow flowers of 'ōhi'a provide copious nectar and are the major food source for many nectarivorous birds. Numerous other wet forest plants are of special significance to one or another bird species. The climbing screw-pine called 'ie'ie (*Freycinetia arborea*) is important to *Psittirostra psittacea*, *Corvus tropicus*, and possibly *Hemignathus sagittirostris*. The dense understory of tree ferns (*Cibotium* and *Sadleria*) on Hawai'i provides nest sites for *Myadestes obscurus* (Berger 1969b), and fruits of 'ōlapa (*Cheirodendron*) provide food, The arborescent Lobeliaceae of the genera *Cyanea* and *Clermontia*, with their long, curved, tubular corollas, are favored by honeycreepers of the genus *Drepanis* (Perkins 1903; Bryan 1908;

Spieth 1966). The lo'ulu palm (*Pritchardia*) was visited by these same birds as well as by the little-known *Ciridops anna*, which presumably fed on the fruits (Perkins 1903).

Second in importance to the 'ōhi'a-lehua ecosystem are the somewhat drier forests dominated by koa (*Koa acacia*). Such forests occur both above and below the wet 'ōhi'a forests, and in some areas a mixed 'ōhi'a-koa ecosystem predominates. On Hawai'i, *Rhodacanthis palmeri* was found only in the upper koa forests on Kona. *Hemignathus munroi* feeds primarily in koa, and other birds, such as *Pseudonestor* of Maui and *Oreomystis bairdi* of Kaua'i, are found most frequently in these drier forests.

At their upper limit, the koa forests give way to a low open forest ecosystem dominated by māmane (*Sophora chrysophylla*) and naio (*Myoporum sandwicense*). *Loxioides bailleui* is confined to this habitat (van Riper et al. 1978), and the now extinct *Chloridops*, which fed exclusively on the dry naio fruits, probably was also. *Hemignathus virens* reaches its greatest abundance in the māmane-naio forests (van Riper 1973).

Laysan, largest (405 h) of the Leeward Islands, has a typical atoll vegetation of low shrubs and grasses, but with a few remnants of its former high island flora (Schlanger and Gillett 1976). The ecosystem was diverse enough to support a surprisingly large avifauna including a duck, a rail, and three passerines. Of these probably only the endemic subspecies of *Himatione sanguinea* was primarily vegetarian, feeding on the nectar of a morning-glory (*Ipomoea*) and beach naupaka (*Scaevola*). The only passerine to survive a plague of introduced rabbits on Laysan early in this century was the drepanidine finch Telespyza cantans.

Nihoa's vegetation is dominated by grasses (Eragrostis) and shrubs such as 'ilima (Sida) and 'āweoweo (Chenopodium) (Carlquist 1970). The two native land birds, Telespyza ultima and Acrocephalus familiaris, seem well adapted to this depauperate flora.

Human Influences

Hawai'i was populated first by Polynesians from the southeastern Pacific more than a millenium ago. Several waves of South Pacific visitors arrived in the islands in the ensuing centuries (Suggs 1960; Wyndette 1968) bringing with them their food plants, chickens, and domestic mammals such as dogs and pigs which established feral populations (Tomich 1969). Inadvertently the ancient immigrants also brought a rat (Rattus exulans) (ibid.) and seven species of skinks (Scincidae) and geckos (Gekkonidae) (Oliver and Shaw 1953). Until recently, the assumption that the influence of the early Hawaiians on the indigenous biota was relatively benign was widespread. Even though many birds were killed for feathers, such activities probably did not significantly affect bird populations. On the other hand, the ground-nesting seabirds were almost surely evicted from nesting grounds on the main islands by aboriginal man or his commensals. Furthermore, recently discovered fossils indicate not only that the birds known from historic times represent only part of a much richer avifauna, but that the early Polynesian colonists may have had a drastic influence on the native biota (Olson, pers. comm.). The deposits on Moloka'i that yielded bones of a flightless goose (Thambetochen) are only 25,000 years old (Stearns 1973), and the flightless ibis (Apteribis) found on Maui and Moloka'i may have survived almost until the coming of Europeans to the islands (Olson and Wetmore 1976; Olson, pers. comm.). These birds and others were likely destroyed by the native Hawaiians. Certainly other flightless island birds such as those of Madagascar and New Zealand suffered greatly at the hands of aboriginal man. Nevertheless, Hawaiian ecosystems were apparently stable at the time of Cook's first visit to the islands in 1778.

The history of the Hawaiian biota since European contact has been one of progressive degradation. No other comparable area of the globe has witnessed such tragic destruction of native ecosystems or such widespread extinction of endemic species. Well over half of the endemic forms of birds are either extinct or surviving as Endangered Species (U. S. Fish and Wildlife Service 1975). The exact reasons for such havoc are not, however, readily apparent and the disappearances of many bird species are mysterious, despite considerable investigation and speculation. Greenway (1967), Berger (1972b), and Atkinson (1977) have reviewed the various extinction hypotheses. These ideas fall roughly into three schools of thought: 1) destruction of habitat; 2) effects of introduced predators and competitors (Atkinson 1977); and 3) epizootic disease (Warner 1968). All of these factors, as well as others as yet unknown, may have been important. Those native birds believed to be extinct are so indicated in Table 1. Excellent summaries of Hawaiian destruction at the hands of man are those of Greenway (1967), Wenkam (1967), and Berger (1972a, b).

SECTION 4.

INTRA-ISLAND VARIATION IN THE 'ELEPAIO

Intra-island variation in birds is rare. Only large islands such as New Guinea and Madagascar, which function zoogeographically as continents (Diamond 1975), usually exhibit subspeciation. Two subspecies of the whistler *Pachycephala pectoralis* occur on Vanua Levu in Fiji, but that situation is apparently a case of secondary contact of forms that evolved on separate islands (Mayr 1932). On Jamaica (11,784 sq km), the hummingbird *Trochilus polytmus* exhibits true intra-island subspeciation (Gill et al. 1973). On the Indian Ocean island of Reunion (2590 sq km), the white-eye *Zosterops borbonicus* exhibits a mosaic of color and size variation and was originally divided into four subspecies (Storer and Gill 1966). Gill (1973) later advocated that the various forms of *Z. borbonicus* on Reunion be considered a single variable taxon, making Jamaica again the smallest island with recognized autochthonous subspecies. This study shows that on Hawai'i (10,458 sq km), the 'Elepaio, *Chasiempis sandwichensis*, exhibits striking geographic variation, and that at least three recognizable subspecies are present.

Because of wide variation in plumage, *Chasiempis* has been the source of much confusion. Not only are the birds sexually dimorphic as adults, but immatures also have characteristic plumages. In some early writings (e. g. Stejneger 1887) as many as five species were recognized, but later publications (Wilson and Evans 1890-99; Rothschild 1893-1900; Henshaw 1902a; Perkins 1903; MacCaughey 1919) reduced the number to three: *C. sclateri* of Kaua'i, *C. gayi* of O'ahu, and *C. sandwichensis* of Hawai'i. Bryan and Greenway (1944) were apparently the first to consider the three forms conspecific, and this treatment has been followed in virtually all recent works. As subspecies, the three allopatric populations are strongly differentiated in color, but in habits, ecology, and vocalizations are very similar. Whether the plumage differences alone are potential isolating mechanisms is moot. I consider the Kaua'i and O'ahu forms "megasubspecies" as defined by Amadon and Short (1976). Neither *C.* (*sandwichensis*) *sclateri* nor *C.* (*s.*) *gayi* show any evidence of intra-island variation.

Henshaw (1902a) was the first to analyze variation in *Chasiempis* on the island of Hawai'i. His study suffered from a lack of specimens from many parts of the island but, as I will show, his findings were more or less accurate. He recognized two subspecies on Hawai'i: *C. s. ridgwayi*, a dark form on the wet windward side; and *C. s. sandwichensis* on the rest of the island. The form called *ridgwayi* was earlier named as a full species by Stejneger (1887). Despite Henshaw's (1902a) study, subsequent writers (MacCaughey 1919; Bryan and Greenway 1944; Amadon 1950; Munro 1944; Berger 1972b) ignored *ridgwayi* as a taxon and considered all *Chasiempis* from the Big Island members of the nominate race.

Appearance of the Birds

Adult Chasiempis on Hawai'i are basically brown birds boldly patterned with white wing-bars, rump, and tail tip, a pale breast and belly more or less streaked with rufous-chestnut, and a pale eyebrow that varies from deep rufous-chestnut to pure white. The throat feathers of males are black, more or less tipped with white. The white tips wear away between molts, and thus some very worn specimens appear entirely black throated. In females the throat is often entirely white, and at most only a small area of black in the chin is present. Usually the white throat of females is separated from the rufous-streaked breast by a diffuse dark brown or black band. Immatures of both sexes are plain gray-brown or dull reddish brown above, white below, and lack the white wing-bars, rump, and tail tip of the adults.

The most striking variation occurs in the coloration of the head of adults, with males exhibiting a wider range than females. In some localities, the eyebrow is pure white and quite broad, the white feathers of the throat very extensive, and an almost complete white collar encircles the neck. In most such birds, no trace of rufous can be seen in the head region, and the white is so extensive that the birds appear white-headed in the field. In contrast, other localities are inhabited by birds whose plumage above is a rich, dark chestnut, with the eyebrow a dark rufous like the color of the breast streaks. In such birds the white tips of the throat feathers stand out in sharp contrast to the rest of the head plumage. Other specimens show various stages of intermediacy between these extremes. Henshaw (1902a) discussed the variants and defined Stejneger's (1887) ridgwayi as the dark form. His studies provided the first good evidence that the variation exhibited by *Chasiempis* on Hawai'i is is geographically based. He designated the range of *C. s. ridgwayi* as lying between 'Ō'ōkala and Volcano on the windward side of the island. He had extensive series of specimens from this area that showed great uniformity. At the periphery of the range of *ridgwayi*, intermediates appeared. Henshaw (1902a) also collected extensively at Pu'u Lehua in Kona, where he encountered a form with a white eyebrow. He considered this form to be the nominate *C. s. sandwichensis*, since the specimens upon which the name was based probably came from Kealakekua Bay in Kona (Henshaw 1902a). Henshaw's collection also included a few localities in Ka'ū, but basically represented samples from only two parts of the island. Nevertheless, his collections are now extremely valuable in documenting the distribution of the color variants of the 'Elepaio in areas where the bird no longer exists. The fact that Henshaw's samples did not represent the entire range of *C. sandwichensis* may account for the reluctance of subsequent authors to follow his subspecific designations.

My investigation of this matter began after I observed a particularly pale, almost white-headed 'Elepaio at Pu'u Lā'au on the northwest slope of Mauna Kea. So different was the bird from those I had seen before in the Volcano area that I at first took it to be an albinistic individual. Further observation revealed that all members of this population were similarly colored. I then examined the series of specimens, mostly collected by Henshaw, at the Bishop Museum in Honolulu in search for a bird resembling those I had seen on Mauna Kea. The extensive series from Kona, the *C. s. sandwichensis* of Henshaw (1902a), showed white eyebrows with a slight rufous tinge, but none of these birds appeared as pale as those at Pu'u Lā'au. Further investigations at other museums in the United States revealed that no 'Elepaio specimens had apparently ever been collected from the high leeward slope of Mauna Kea. The Pu'u Lā'au population was so obviously distinctive that, after obtaining a series of specimens, I described it as a new subspecies, C. s. bryani (Pratt in press).

Analysis of Variation

I compared the type series of Chasiempis sandwichensis bryani with other specimens collected on the island in 1976-78 and with older specimens in the Bishop Museum (BM), American Museum of Natural History, National Museum of Natural History, Museum of Vertebrate Zoology, Berkeley (MVZ), and Louisiana State University Museum of Zoology (LSU). The total sample comprised 136 adult males and 118 adult females from 23 localities (Fig. 2). The number of specimens is much smaller than that available to Gill (1973) in his study of Zosterops borbonicus on Reunion, but sufficient, I believe, to provide a general picture of intra-island variation.

Color variation was documented by use of a series of reference specimens for each character state. The specimens were designated 1 to 5 to show a gradation of the character. A description of these character states and the museum numbers of the reference specimens are given in Table 2 (males) and Table 3 (females). More parameters were available for males than for females in the color analysis. Mensural data included length of exposed culmen, width of bill at base, wing chord, and tail length.

TABLE 2. Key to color characters of male *Chasiempis sandwichensis* from the island of Hawai'i. Capitalized color names are from Smithe (1975).

Character	Character States	Specimens
A. Breast Color	1. Chestnut to Amber	BM 3896
	2. Amber	BM 3889
	3. pale Amber	BM 3942
	4. between Amber and Antique Brown	LSU 81726
	5. Antique Brown	LSU 81713
B. Breast Streaks	1. No streaks, uniform color	BM 3896
	2. Breast band broken posteriorly	BM 3932
	3. Complete streaks in center only	BM 3949
	4. Heavily streaked	LSU 81726
	5. Streaks confined to sides, center clear	LSU 81713
C. Auricular Color	1. between Chestnut and Amber	BM 3896
	2. Cinnamon-Rufous	BM 3907
	3. Tawny	BM 3894
	4. Cinnamon-Brown	BM 3905
	5. Olive-Brown	LSU 81713
D. Back Color	1. dark Cinnamon-Brown	BM 3852
	2. Cinnamon-Brown	BM 3924
	3. Antique Brown	BM 3780
	4. grayish Antique Brown	BM 7210
	5. Olive-Brown	LSU 81712
E. Color of Eyestripe and Side of Head	1. Between Chestnut and Amber	BM 3896
	2. Amber	BM 3889
	3. between Tawny and Cinnamon-Rufous	BM 3852
	4. white tinged Cinnamon-Rufous	BM 3808
	5. white	LSU 81725
F. Amount of Black in Lores	1. extensive	BM 3728
	2. less extensive	BM 3848
	3. moderate amount	BM 3845
	4. trace	BM 3849
	5. none	LSU 81713

TABLE 2. (contd.)

G. Crown Color	1. dark reddish Amber	BM 3822
	2. Amber	BM 3734
	3. Cinnamon-Brown	BM 3749
	4. dark Cinnamon-Brown	LSU 81736
	5. Brownish Olive	LSU 81725

TABLE 3. Key to color characters of female Chasiempis sandwichensis from the island of Hawai'i. Capitalized color names are from Smithe (1975).

Character	Character States	Specimens
A. Breast Color	1. Amber	BM 3888
	2. between Tawny and Cinnamon	BM 3919
	3. Tawny	BM 3813
	4. between Tawny and Antique Brown	BM 3778
	5. Antique Brown	LSU 81732
B. Breast Streaks	1. no streaks	BM 3920
	2. breast color broken posteriorly	BM 3909
	3. breast entirely streaked	BM 3794
	4. streaks confined to sides	BM 3811
	5. few streaks, on sides only	LSU 81715
C. Dorsal Color	1. dark Cinnamon-Brown	BM 3899
	2. dark Antique Brown	BM 3910
	3. Antique Brown	BM 3847
	4. between Antique Brown and Cinnamon	BM 3953
	5. between Olive Brown and Cinnamon-Brown	LSU 81723
D. Color of Sides of Head	1. dark Cinnamon-Rufous	BM 3887
	2. Cinnamon	BM 3879
	3. pale Cinnamon	BM 3943
	4. white tinged with Cinnamon	BM 3817
	5. white	LSU 81710

TABLE 4.

MEAN COLOR SCORES OF 'ELEPAIOS FROM FIVE LOCALITY GROUPINGS ON THE ISLAND OF HAWAI'I

Character State[1]	Locality Groupings[2] 1	2	3	4	5
Males					
A	3.0	3.5	2.2	2.3	4.1
B	3.6	4.1	2.7	3.1	3.8
C	3.7	3.4	2.8	3.1	4.7
D	2.5	2.3	1.7	1.4	4.3
E	3.9	3.8	2.5	2.8	4.7
F	4.5	3.3	4.6	4.6	4.7
G	2.2	2.5	1.3	1.4	4.1
Females					
A	2.7	2.8	2.3	2.0	4.2
B	3.4	2.0	2.0	2.5	4.0
C	3.4	3.0	2.6	2.1	4.5
D	3.3	3.3	2.1	2.3	4.9

---

[1] For descriptions of characters and meanings of scores, see Tables 2 and 3.

[2] Locality groupings given on p. 38.

Figure 2 is a map of Hawai'i with numbered localities from which 'Elepaios were examined. Also shown are other geographical features mentioned in this section. Names are given for the numbered localities except for 23, which groups together several unnamed kīpukas along the Saddle Road between 1494 m and 1743 m elevation. Some of the numbered localities undoubtedly represent samples from fairly large areas. For example, most of Henshaw's Kona specimens are labelled "Puluhua" (=Pu'u Lehua) but his written account (Henshaw 1902b) reveals that he ranged far from this base of operations. Thus his series from Kona represents a larger area than his single locality designation would indicate. Other such locality designations that probably refer to large areas are Volcano (8), 'Ōla'a (9), Kaūmana (12), and Waimea (19). The exact location represented by three names could not be determined, but an approximate location could be deduced from the collection dates of surrounding localities. These "approximate" localities are "Dalway's" (5), "Kuaia" (15), and Horner's Ranch (20). The specimens were, of course, collected before the advent of high-speed travel. The 23 localities produce a good coverage of areas where Chasiempis occurs on the island, but a few areas of difficult access remain to be sampled. Two particularly important such areas are the forests of the Kohala region and the wet upper forests of Ka'ū.

The localities fall into five geographical clusters (Fig. 2) as follows: 1) Hualālai-Kona (Localities 1-3); 2) Ka'ū (4-7); 3) Volcano-'Ōla'a (8-10); 4) Hāmākua Coast (11-16); and 5) Mauna Kea (19-22). These groupings were treated as single localities in the computer analysis of the data. Mean scores of these groups for plumage color characters are given in Table 4.

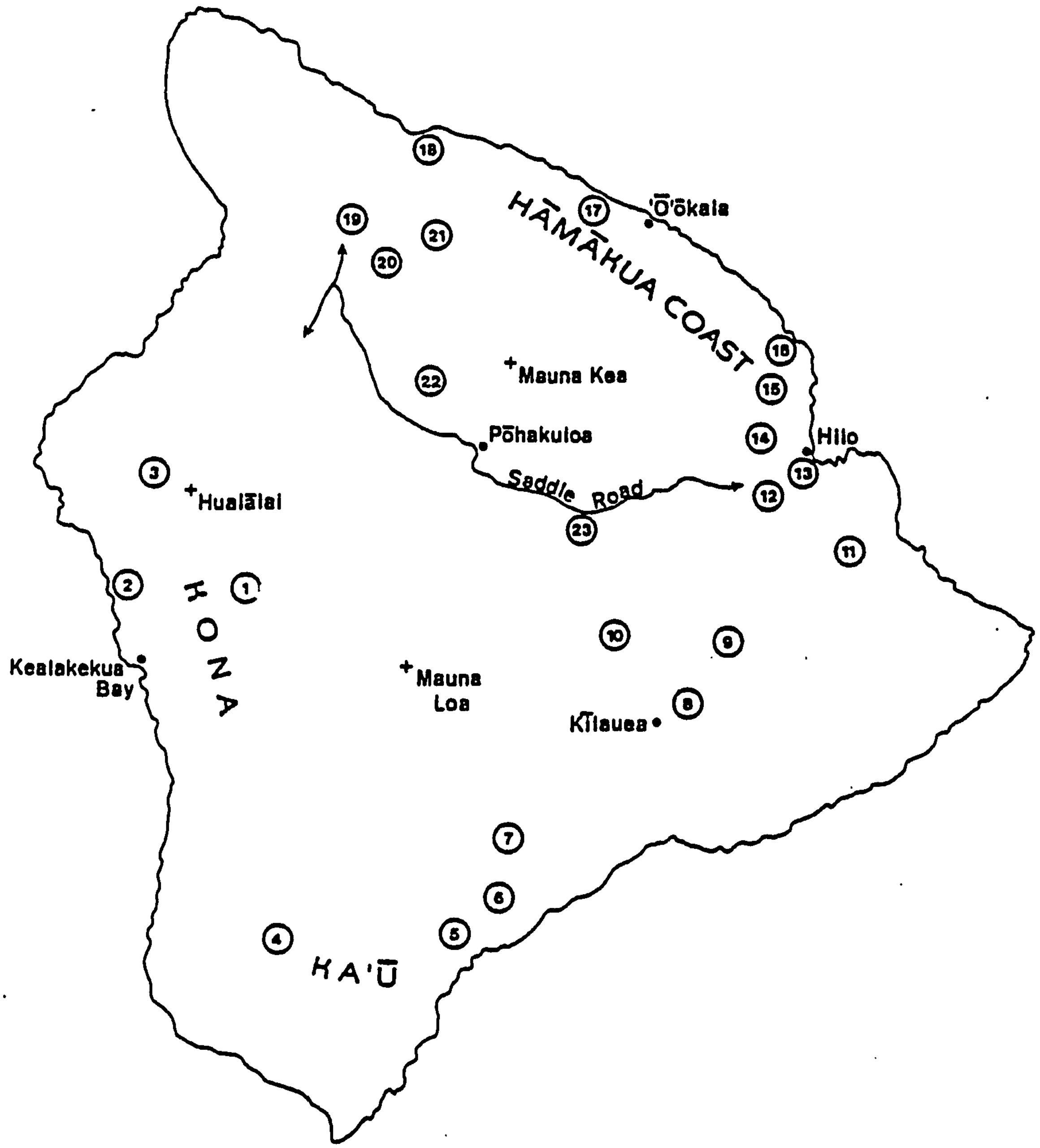


Figure 2. Map of island of Hawai'i showing localities of specimens of Chasiempis sandwichensis and other localities mentioned in the text. Numbered localities listed on the following page.

Figure 2 (contd.)

1	Pu'u Lehua
2	Keauhou (Kona)
3	Kaloko Mauka
4	Ocean View Estates
5	Dalway's
6	Pāhala
7	Kapāpala
8	Volcano/Kīlauea
9	'Ōla'a
10	Keauhou Ranch
11	Kea'au
12	Kaūmana
13	Waiakea
14	Kaiwiki
15	Kuaia
16	Honomū
17	Pa'auilo
18	Kukuihaele
19	Waimea
20	Horner's Ranch
21	Mānā
22	Pu'u Lā'au
23	Saddle Road kipukas

Localities 17, 18, and 23 were not grouped for reasons that will be made apparent below.

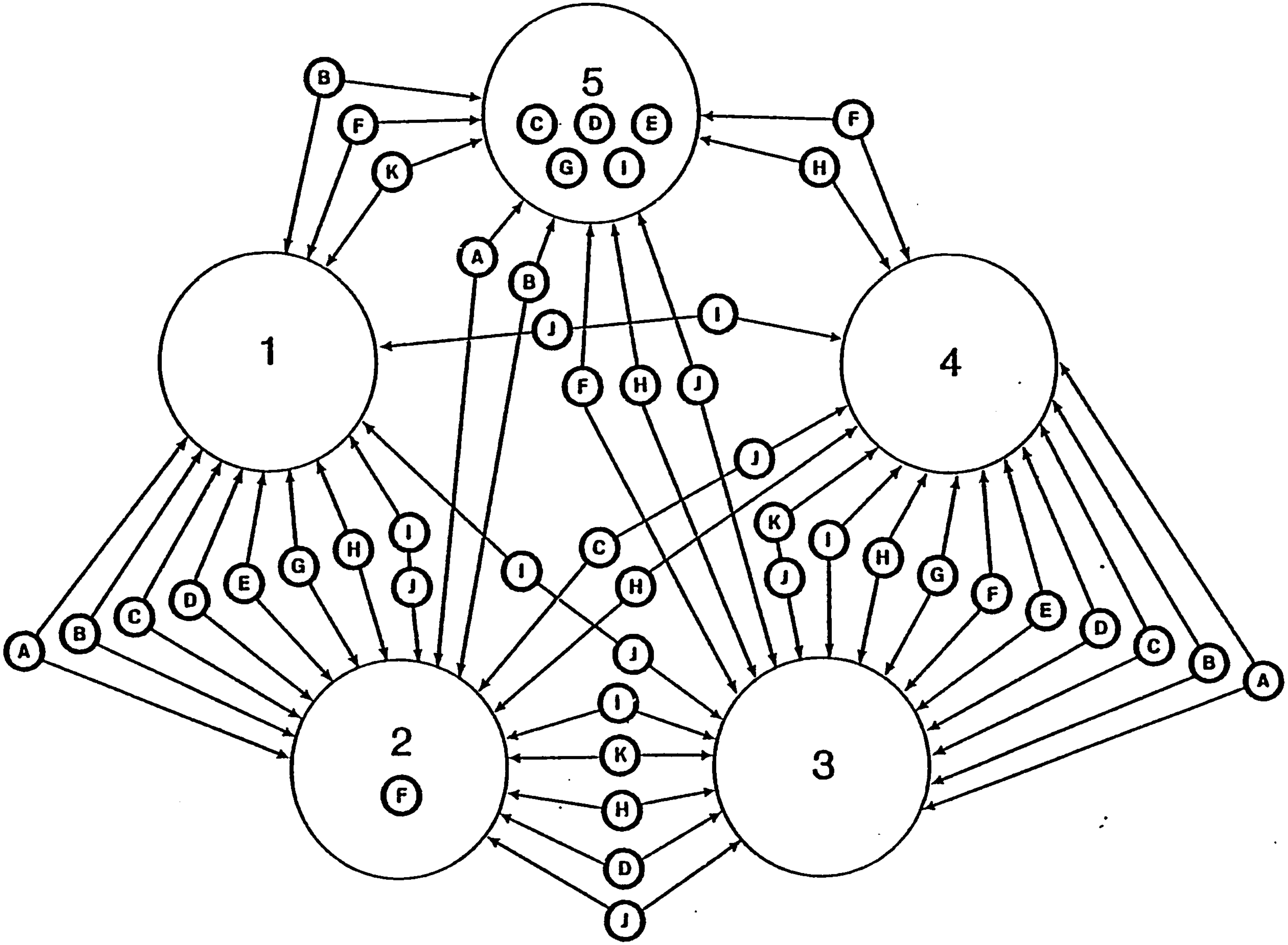
An analysis of variance procedure was conducted using Duncan's Multiple Range Test (Duncan 1955). This test shows which sample means are significantly different ($P<0.05$) and thus allows groupings of populations whose means are not statistically different.

Results of Analysis

Figure 3 shows diagrammatically the pattern of variation among males of the five populations examined. For each character, those populations showing no significant differences are connected by lines. For example, character A (breast color) is not different in populations 3 and 4, but both of these populations differ in this character from the other three. Within the numbered circles, letters are given that designate those characters in which a population differs significantly from all others.

Although some congruence of characters occurs among all populations, the greatest similarities occur between populations 1 and 2 and populations 3 and 4. A much simpler diagram is produced if these groups are combined and only three populations considered (Fig. 4). But this arrangement, while providing a reasonable approximation of geographic variation, obscures some subtleties. For example, in character A, populations 1 and 2 do not differ significantly, nor do populations 2 and 5, but a significant distinction can be made between 1 and 5. This pattern is not discernible in Figure 4. Other characters whose variation is somewhat inaccurately portrayed by the simplified diagram

Figure 3. Diagrammatic representation of character distributions among male Chasiempis on the island of Hawai'i. For plumage characters (A-G) see Table 2. H = bill length, I = bill width, J = wing chord, and K = tail length. Arrows connect those populations that do not differ significantly in a given character. Those characters in which populations differ significantly from all others are enclosed within the numbered circles. See text for localities included in each population.


5
C
D
E
G
I
B
F
K
F
H
1
4
A
B
J
I
F
H
J
J
K
I
C
H
I
H
G
E
D
C
B
A
I
H
G
E
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K
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D
J
3

FIGURE 3.

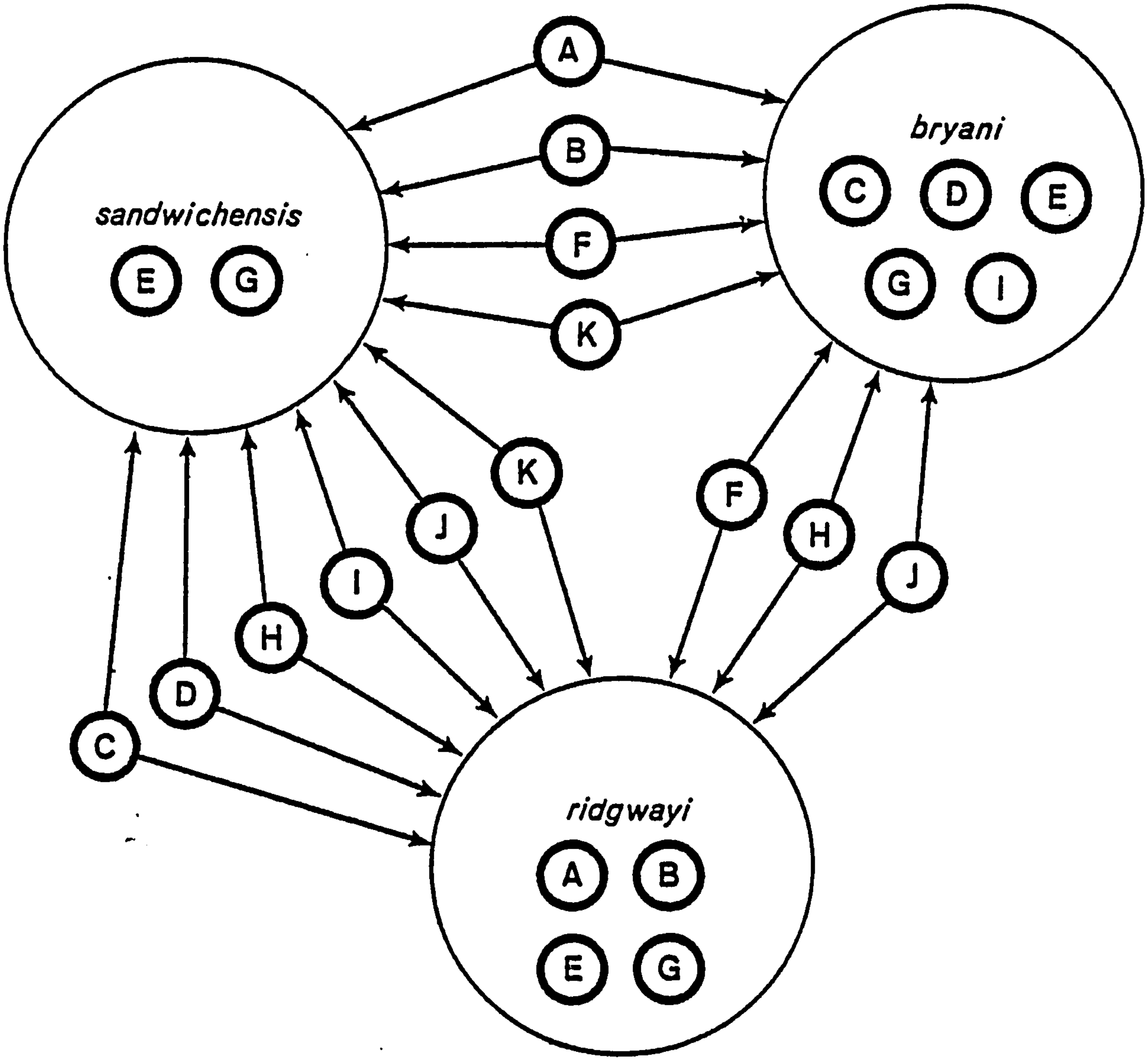


Figure 4. Simplified diagram of character distributions among male Chasiempis sandwichensis on the island of Hawai'i. For explanation of symbols, see Fig. 3.

are auricular color (C), back color (D), amount of black in lores (F), wing chord (J), and tail length (K).

A clearcut pattern of variation for males emerges from this analysis. Groups 3 and 4 appear to represent subdivisions of a single population. No significant differences occur between these areas. Groups 1 and 2 also show little differentiation, although the color of the lores of Ka'ū males sets them apart from all other populations. Between birds from the two regions represented by 1 + 2 and 3 + 4, several differences are obvious and consistent. These differences include color and amount of streaking of the breast (A and B), color of the eyebrow and face (E), and crown color (G). The Mauna Kea population (5) stands clearly apart from the others. Males from that area are distinct from all other C. sandwichensis on the island in five character states.

Females are much less variable than males. Figure 5 shows diagrammatically the relationship among the five geographic groups of the four variable plumage characters. Other characters, such as the extent of the black border of the throat, and dimensions of the bill, wing, and tail exhibit no geographical variation. The pattern shown here is essentially the same as that for males, but is somewhat less obvious because of the small number of characters available. As with males, the Mauna Kea population stands clearly apart from the others. The distinction between populations 1 + 2 and 3 + 4 is less clearcut, however. But the most obvious character, color of the eyebrow and face (D), follows the pattern revealed by the males.

The recognition of the three subspecies C. s. sandwichensis (Gmelin) 1788, C. s. ridgwayi Stejneger 1887, and C. s. bryani Pratt 1979, seems from

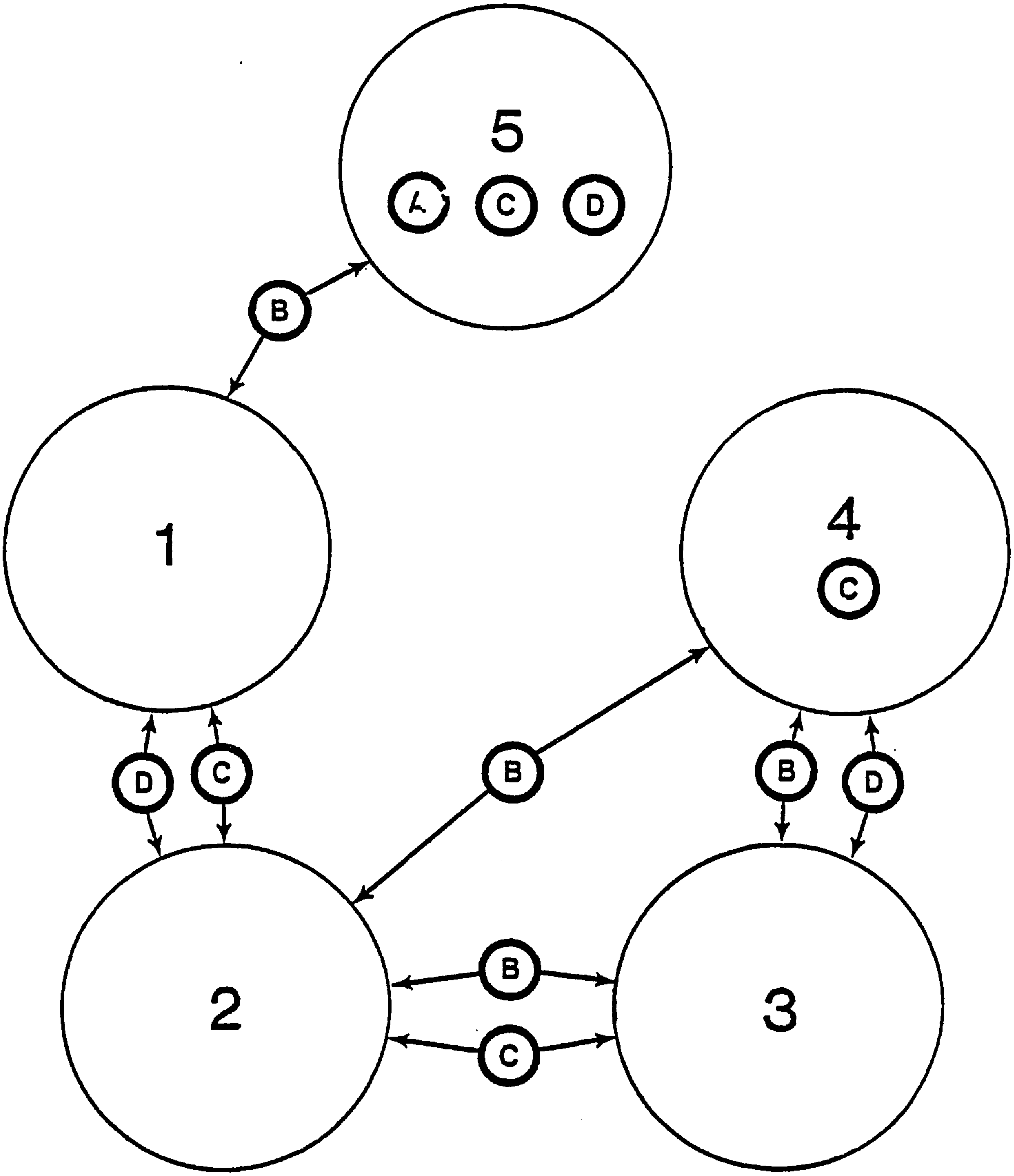


Figure 5. Diagrammatic representation of character distributions among female Chasiempis sandwichensis on the island of Hawai'i. See Table 3 for character code. Symbolism as in Fig. 3.

this analysis to be entirely justified. The range of C. s. bryani is also expanded by the inclusion of older specimens from lower elevations adjacent to the present range of the subspecies (Pratt in press). Because of habitat destruction, 'Elepaios no longer occur in these areas. Hawai'i is thus the smallest single island to exhibit autochthonous subspeciation.

Intergradation

Approximate distributions of the three races of the 'Elepaio on the Big Island are shown in Figure 6. These distributions include lowland areas where the birds occurred historically but which are now largely planted in sugar cane or converted to pastureland. The gaps shown in the central saddle area of the island probably reflect natural patterns of distribution. Areas of intergradation are indicated by cross-hatching. Question marks indicate areas where 'Elepaios are known to occur, but which have not been sampled by collectors.

Henshaw (1902a) described zones of intergradation between C. s. ridgwayi and C. s. sandwichensis (then including bryani) north of 'Ō'ōkala on the Hāmākua Coast, and west of Kīlauea Volcano. Specimens from these areas are few but revealing. One male (MVZ 21445) from Pa'auilo about 10 km north along the coast from 'Ō'ōkala is clearly intermediate in several characters. It generally resembles C. s. ridgwayi, but has a slightly rusty-tinged white eyebrow that forms an almost complete collar around the back of the head as in C. s. bryani. Another male (MVZ 7028), taken the same day at the same locality shows much less influence of bryani in the color of the eyebrow but does have

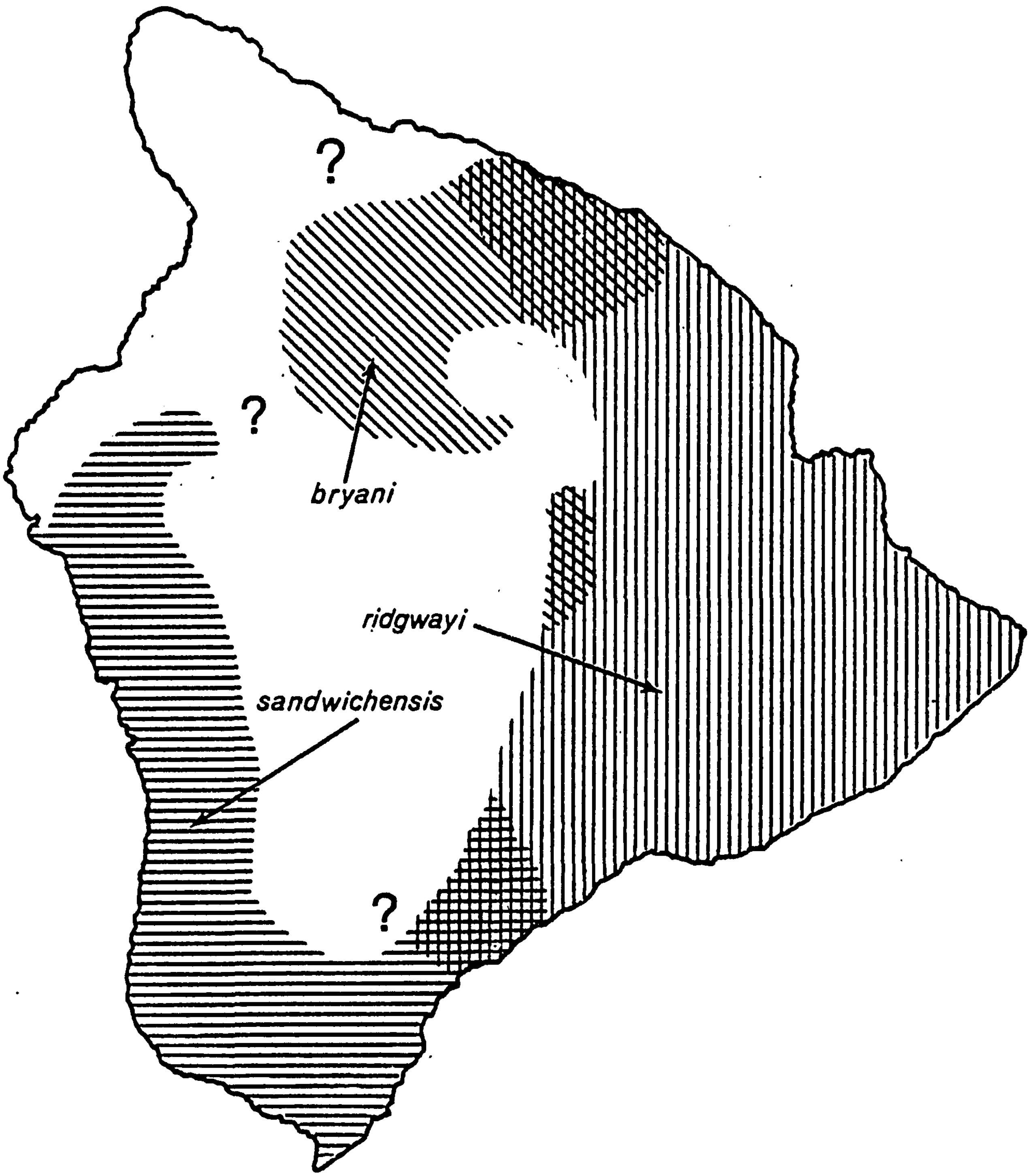


Figure 6. Approximate distributions of the three subspecies of Chasiempis sandwichensis on the island of Hawai'i. Areas where Chasiempis occurs but which are not represented by specimens are indicated by question marks. Cross-hatching indicates intergradation.

a few white feathers scattered among the rufous ones, and has a trace of a pale collar.

Henshaw (1902a) apparently considered his specimens from localities in Ka'ū to represent intergrades, and indeed the small series of specimens from Pāhala (4 males, 3 females) and Kapāpala (3 males, 2 females) show intermediacy in various characters. Since these specimens were included in the computer analysis, they may account for the greater degree of similarity between *sandwichensis* and *ridgwayi* than between either of these and *bryani* (Figs. 3, 4, and 5).

A particularly interesting zone of intergradation occurs in the saddle between Mauna Kea and Mauna Loa. Here a gap of approximately 10 km occurs in the distribution of *Chasiempis*. Apparently the present range of the race *C. s. bryani* corresponds closely to that of the Palila *Loxioides bailleui* on leeward Mauna Kea (van Riper et al. 1978). 'Elepaios do not occur, or are very scarce, in the seemingly suitable scrub forest of the flat region known as Pōhakuloa. From the southeast, the range of *C. s. ridgwayi* extends to the upper limit of wet forests. At the upper forest fringe, lava flows have dissected the wooded areas and produced numerous kīpukas. 'Elepaios are relatively uncommon in this area. I was able to obtain at most only two specimens in any single kīpuka. By chance, the specimens include only one male, and it is a typical specimen of *ridgwayi*. The six females, however, show varying degrees of intergradation in the color of the eyebrow. Female *ridgwayi* only rarely show appreciable amounts of white over the eye, but one specimen (LSU 81443) from a kipuka at 1494 m has only a slight tinge of rufous in an otherwise white eyebrow. But another bird from the same elevation (LSU 81728) shows no evidence of intergradation. At the uppermost elevation (1743 m) before the distributional hiatus, three specimens (LSU 81731, 81732, 81733) all possess eyebrows of mingled rufous and white feathers, but in a small kipuka at 1597 m I obtained a bird (LSU 81730) that represents the dark extreme for every plumage character! Apparently these forest islands function in a manner similar to actual islands, receiving chance immigrants from the nearby "mainland" forests. Some kīpukas are populated by pure ridgwayi, but some have apparently received genetic input from bryani or perhaps even sandwichensis. These kīpukas can therefore be considered zones of secondary contact, whereas most intergradation between populations of C. sandwichensis is probably primary.

Adaptive Significance of Color Variation

The variation in Chasiempis on Hawai'i appears to be related to rainfall. The range of C. s. ridgwayi corresponds almost exactly to the windward parts of the island that receive over 190 cm of annual rainfall. This area at its heart receives over 762 cm of rain, and in such very wet areas the darkest plumage variants occur. Local populations are not uniform, however, and no smooth clines associated with rainfall can be discerned. Similar variation in local populations can be seen in C. s. sandwichensis, with the pale extremes occurring in the drier areas of southern Ka'ū. Some specimens from this area possess plumage characters similar to those of C. s. bryani. The latter race is apparently adapted to xeric habitats that receive annual rainfall of less than 76 cm.

Chasiempis sandwichensis on the island of Hawai'i provides the only clear expression of Gloger's Rule among Hawaiian birds. That such ecogeographic rules exist is well established (Mayr 1956) but the selective forces involved are a matter of controversy. Gloger's Rule predicts an increase in melanins in more humid regions, with red pigments increasing in drier localities. In most cases, these patterns produce darker individuals in humid regions, and to that extent Chasiempis reflects the model. However, the darker plumage of C. s. ridgwayi appears to be caused not only by an increase in melanins but also by an increase in red pigments. Indeed, C. s. ridgwayi is the reddest of the three subspecies. This observation is probably not a serious exception to the rule.

The expression of Gloger's Rule in Chasiempis provides insight into the selective basis of the rule. Concealment has often been regarded as the main adaptive advantage of dark pigmentation in humid habitats (Cott 1957). The island of Hawai'i has two potential bird predators, the hawk Buteo solitarius and the diurnal owl Asio flammeus. Thus predation may have been a factor in selection for concealing coloration on the island. O'ahu and Kaua'i 'Elepaios show no variation within their respective islands where only the owl occurs. However, the effectiveness of Buteo solitarius as a predator of small birds such as Chasiempis is probably not great. Certainly the hawk must have fed on birds before rats were introduced by aboriginal Hawaiians, but in historic times has fed mainly on introduced rodents and arthropods (Henshaw 1902b; Munro 1960; Tomich 1971; Berger 1972b). Henshaw (1902b: 81) found 'Apapane and 'Amakihi remains in the stomachs of two hawks, and he and Munro (1960), Baldwin (1969), and Tomich (1971) report limited predation on exotic bird species. No instance of predation on *Chasiempis* by *Buteo solitarius* is known and because 'Elepaios are sedentary birds of the understory, such predation seems particularly unlikely.

Another possible basis for the observed color variation may be that proposed by Hamilton and Heppner (1967), who hypothesized that selection would favor dark pigmentation as a heat-absorbing mechanism in areas of reduced sunlight. Heppner (1970) presented experimental evidence of differential heat absorption by dark and light-colored individuals of the same species. Paler coloration would presumably be selected for in open, brightly sunlit areas such as the high leeward slopes of Mauna Kea where *C. s. bryani* occurs. A similar expression of Gloger's Rule has been documented for the Wrentit, *Chamaea fasciata* (Bowers 1960), a bird somewhat similar in habits to the 'Elepaio and probably also an infrequent victim of predation. Bowers (1960) concluded in that instance that the variation was due to "natural selection" but did not specify the forces that may have been involved. Perhaps further studies of the intra-island variation of *Chasiempis* will reveal more precise correlations of color pattern with environmental factors. At present, the selective forces involved in the variation are obscure.

SECTION 5.

PHYLOGENY AND ADAPTIVE RADIATION OF THE HAWAIIAN HONEYCREEPERS

The majority of bird species in the Hawaiian Islands belong to a group known as honeycreepers, a rather misleading epithet since not all of them eat honey (nectar) and those that creep eat mostly insects! But probably no single name would suffice for such a diverse assemblage. With adaptations that span almost the entire range of variation exhibited by passerines, these birds are the pre-eminent avian example of adaptive radiation (Carlquist 1965, 1974). Early naturalists at first divided these species among several families and such a classification might have prevailed except for the admonitions of R. C. L. Perkins (Gadow 1899). No author in the 20th Century has seriously questioned the idea that the Hawaiian honeycreepers are monophyletic, but the origins of the group and the phylogeny of its diverse members have remained controversial. Most authors have classified the complex as an endemic family, Drepanididae.

Taxonomic History

Virtually every subspecies of Hawaiian honeycreeper was originally described as a full species, and these "species" were grouped into genera that corresponded roughly to the currently recognized species. Such a classification revealed nothing about evolutionary history, but was probably better than an arbitrary grouping in the absence of data. Perkins (1901) began the process of taxonomic consolidation. Some relationships were obvious a priori, such as that between *Chrysomitridops* and *Loxops*. Perkins combined these "genera," and Amadon (1950) even regarded them as conspecific. The first revision of the honeycreeper group after the development in the 1930s of the biological species concept (Mayr 1942) was that of Bryan and Greenway (1944) who reduced Perkins' 18 genera to 16 and his 36 species to 22. Amadon (1950) carried the generic consolidation much further and recognized only nine genera for his 22 species. Although the number of species is the same, Amadon's alpha taxa do not correspond exactly to those of Bryan and Greenway (1944). Greenway (1968) listed 21 species in Peters' Checklist of the Birds of the World, but redivided several of Amadon's large genera to yield a total of 12. Nevertheless, Amadon's classification is the one most widely followed in both technical and popular works today (e. g. Berger 1972b; Morony et al. 1975; Pyle 1977a; Shallenberger 1978). Recently Banks and Laybourne (1977) challenged Amadon's genus *Psittirostra* and advocated that the five genera he consolidated be resurrected. Raikow (1977b) followed Amadon at the generic level except for the removal of *Paroreomyza* from *Loxops*. Figure 7 is a graphic presentation of the history of generic classification of the Hawaiian honeycreepers.

Perkins (1903: 408) was the first to illustrate the relationships of the genera by means of a dendrogram. His system showed a tree with two main

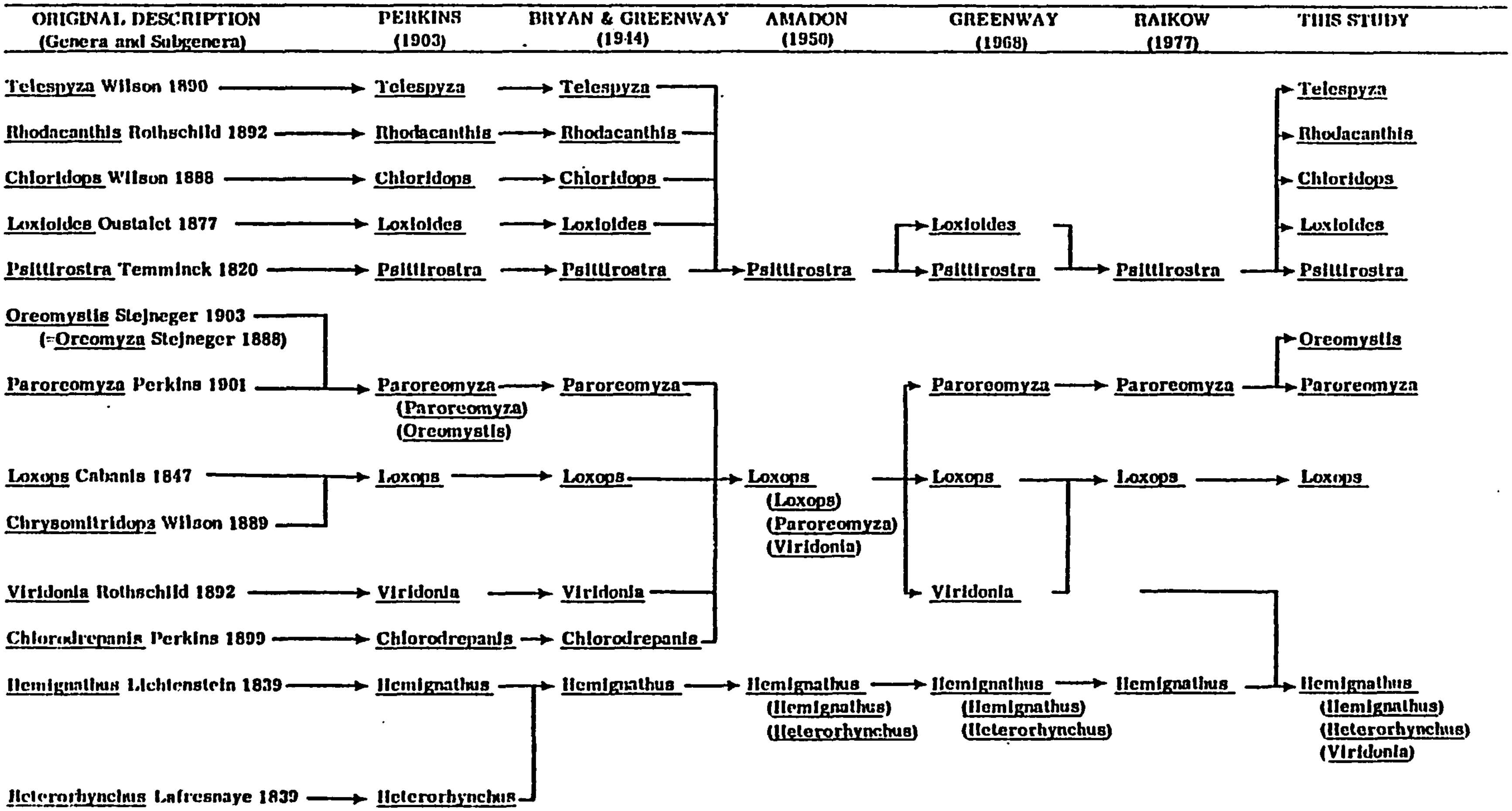


Figure 7. Flow chart of generic classifications of the Hawaiian Honeycreepers (Drepanidinae), Part I.

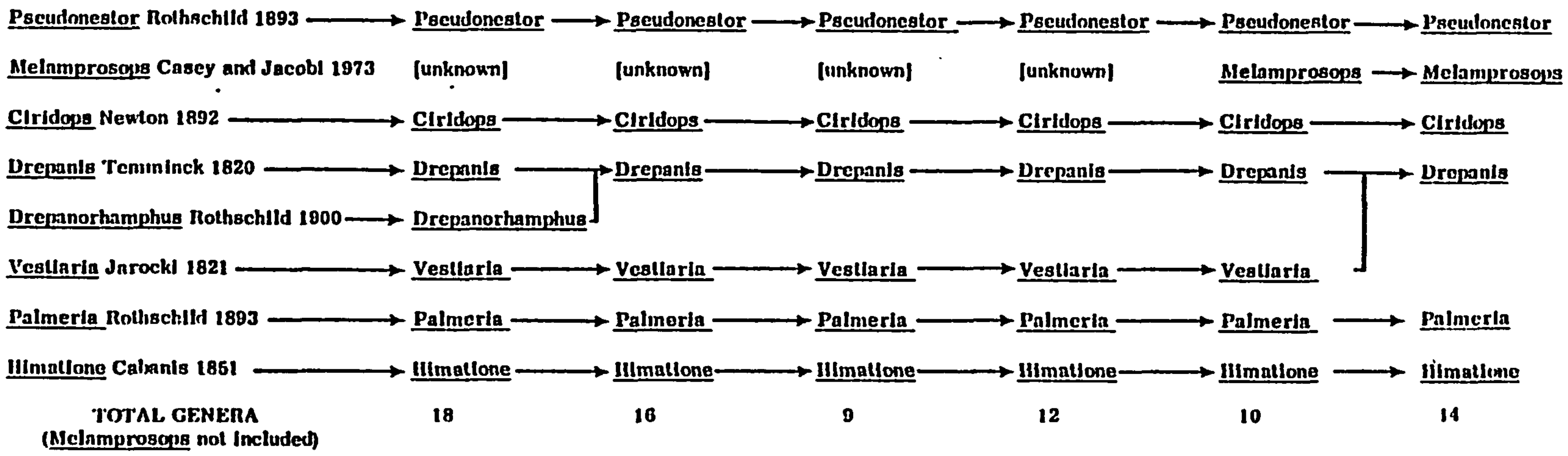


Figure 7. Part II

branches, the birds at the base of each having short straight bills. One branch terminated in nectar-feeders with long sickle-shaped bills, the other in birds with stout finch-like bills. Greenway (1944) was critical of Perkins' dendrogram, particularly this basic dichotomy. Amadon (1950: 230) pruned the tree rather severely, recognizing two subfamilies, Psittirostrinae and Drepanidinae, that correspond to Perkins' two divisions. Raikow (1977b) proposed an entirely different pattern that de-emphasized Amadon's subfamilies and placed the finch-billed birds at the base of the tree.

The Nature of the Genus

Amadon (1950: 163) stated the belief that genera in an adaptively radiating taxon should be more broadly defined than in a conservative one. Why such should be the case is not apparent to me. Should genera reflect recency of divergence or the degree of that divergence? Among mainland birds, genera seem to reflect similarities and differences and are usually definable in such terms; recency of divergence is seldom used as a criterion. The discussions in the following pages reflect my belief that generic limits within a family or subfamily should be based on clearcut morphological, behavioral, or ecological similarities. When no such resemblances can be cited, I believe the best course is to keep the taxa in question separate generically. Banks and Laybourne (1977) have recently expressed a similar philosophy. These authors objected to Amadon's lumping of all finch-billed honeycreepers into the single genus Psittirostra on the grounds that such taxonomy "implies not only that the species had a common origin but also that the relationships of one to another are known" (Banks and Laybourne 1977: 348). The alternative recognizes that the birds differ "to degrees usually recognized by generic rank in other groups" and that their phylogeny is not clearly discernible.

The generic limits outlined herein are based on a wide variety of morphological, ecological, zoogeographical, and behavioral considerations. This classification is a true revision, whereas that of Greenway (1968) simply reflected his philosophical differences with Amadon (1950) without revealing any new information. Greenway (1968) simply raised some of Amadon's subgenera to full generic status and demoted one species to subspecies. A similar case was discussed by Bock (1963) in evaluating differences between Lack (1947) and Bowman (1961) in the delimitation of genera in the Galapagos finches. Lack (1969a) later agreed with Bowman (1961) that the original consolidation of 14 genera to four had "gone too far." Still, none of Bowman's or Lack's geospizine genera are nearly so adaptively broad as Amadon's (1950) Loxops or Psittirostra. Bowman (1961) grouped species in genera on the basis of shared adaptive facies as determined by the shape of the bill. Inger (1958) advocated that genera be be defined adaptively, and I have followed that philosophy. That Amadon (1950) was overly impressed with bill length as a generic character is clearly shown by his generic separation of the 'amakihis and the 'Akialoa, which can be diagnosed externally on virtually no other grounds than the shorter bill of the former. Amadon's Loxops comprises, in addition to the several 'amakihis, the bizarre cross-billed 'ākepas and the straight-billed "creepers." That these three groups represent three fundamentally different adaptive facies was demonstrated by Richards and Bock (1973). On a continent, such divergent forms would usually not be considered congeneric. Amadon tried to make diagnoses for his genera, but where several older taxa were lumped, he was forced to resort to vague generalities to find any character that could be applied to all members of the genus. His characterization of Loxops is an example (Amadon 1950: 164):

> Bill pointed (its tips slightly crossed sidewise in one species), moderately decurved or almost straight, little if any longer than head, and neither attenuated and greatly decurved nor heavy and grosbeak- or parrot-like. Color ranging from grayish to scarlet, often olive green. Color pattern simple.

Or, in essence, all psittirostrine honeycreepers with short bills. Baldwin (1952) expressed misgivings about both Loxops and Psittirostra as delimited by Amadon, but nevertheless considered such broad genera "convenient." Richards and Bock (1973: 5) followed Amadon because of "ease of style in dealing with one, not three genera." Raikow (1977b), because of details of limb musculature, removed the "creepers" (Paroreomyza sensu Greenway 1968) from Amadon's Loxops. He then cited a number of other differences to corroborate the separation, but I doubt that such other factors would have been considered important were it not for what seems like a minor myological difference. Raikow (1977b) retained the 'amakihis (subgenus Viridonia) in Loxops despite their equally distinctive characters, but unfortunately did not dissect an 'ākepa (Loxops sensu stricto) for comparison.

My classification has been developed in the light of considerable field experience with the birds. I have observed in life 15 of the 21 extant species, and all but one of the living genera. I do not make this point boastfully, but rather because, as any field ornithologist can attest, such observations provide insights unavailable to those who work only from specimens. Of the many systematists who have studied Hawaiian honeycreepers previously, only R. C. L. Perkins had more extensive field experience. My studies in the islands over a six-year period have revealed many points missed by previous workers that I believe to be of taxonomic significance. In some instances, field observations suggested new avenues of morphological investigation. Also, recordings of vocalizations have not only helped to elucidate species limits, but have revealed evolutionary trends that were obscure on morphological grounds alone.

Amadon (1950) was troubled by the large number of monotypic genera in the Hawaiian honeycreepers. I believe a larger number of genera is desirable because it calls attention to the extent of the adaptive radiation of the group. Otherwise, simple perusal of a taxonomic list would not reveal that the drepanidines were any more diverse than any other passerine group of comparable size. However, because Amadon (1950) considered many strongly differentiated allopatric forms conspecific that my research has shown are better considered species, our genus/species ratios are almost identical and my classification actually has a slightly lower proportion of monotypic genera (64%) than Amadon's (70%).

The Genera of Hawaiian Honeycreepers

The finch-billed honeycreepers (Amadon's *Psittirostra*) are difficult to classify simply because so little is known about some of them (Banks and Laybourne 1977). Within the group, *P. psittacea* clearly stands apart from the others; Greenway (1968) placed it in its own monotypic genus and retained the other finch-bills in *Loxioides*. That arrangement would be an acceptable alternative to the classification offered here. However, if generic limits in this complex are set so that they are comparable to those of other finches (Fig. 8), the recognition of five genera, as advocated by Banks and Laybourne (1977), is clearly justified. The fact that all but one of these genera are monotypic may be an artifact. Finch-billed birds are well represented in recently discovered fossil and subfossil deposits in Hawai'i (Olson, pers. comm.), and many of these species may have survived until after the arrival of man in the islands. Thus their extinctions may not have been "natural" and some may belong to the following historical genera.

Genus *Telespyza*: Hawaiian Finches

Medium-sized Hawaiian honeycreepers with heavy finch-like bills, slightly hooked at the tip, adapted for generalized feeding on seeds, buds, and seabird eggs. Tongue thick, fleshy, nontubular, with the ventral surface cornified and curving upward at the sides (Raikow 1977b). Nasal opercula lacking (Raikow 1977b). Sexually dimorphic in plumage, males brightly colored in yellows and grays, females and immatures streaked with dark brown. Bill grayish white. Highly vocal with complex canarylike songs and finchlike calls. Two species, *T. cantans* on Laysan and *T. ultima* on Nihoa.

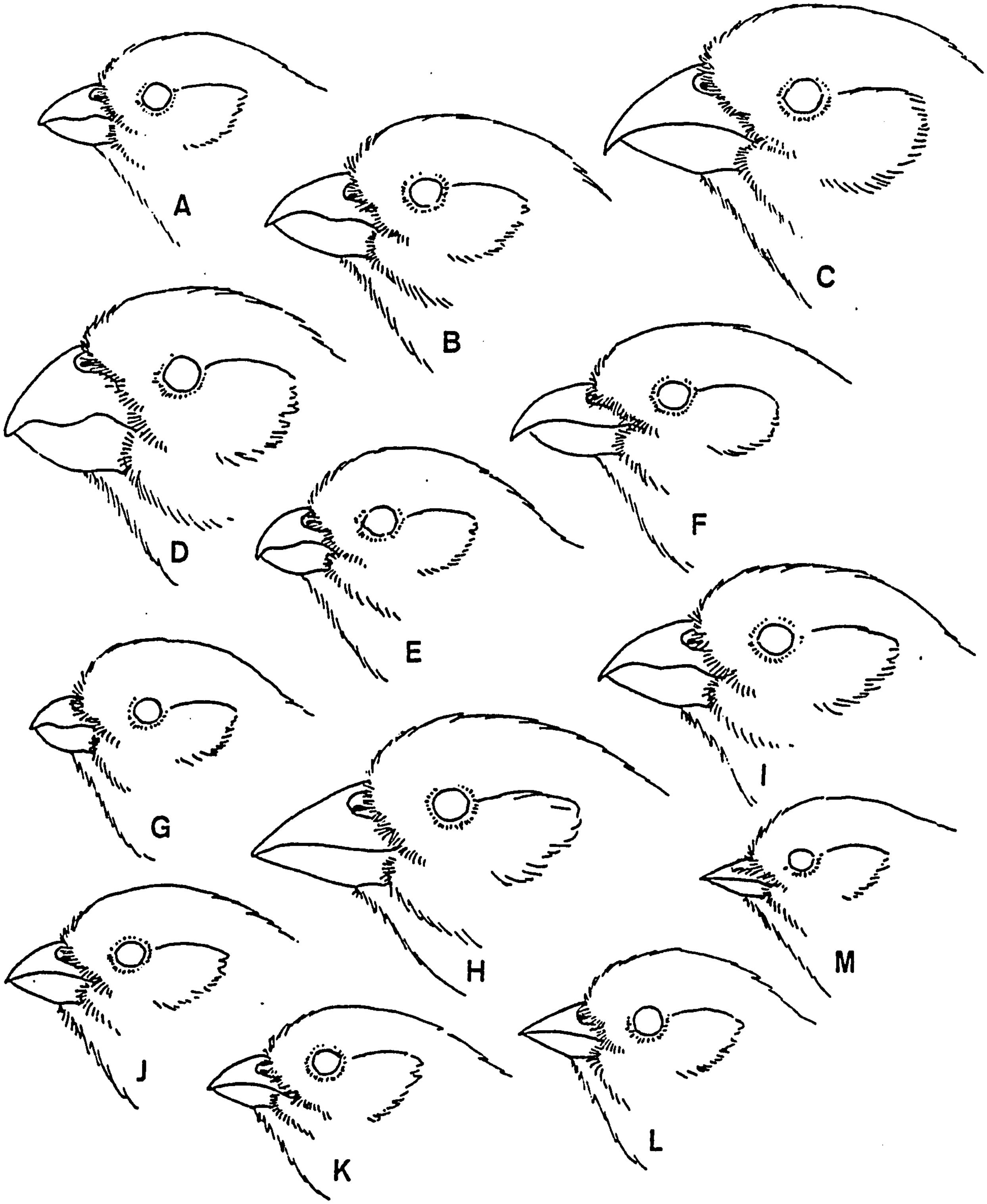


Figure 8: Bills of Hawaiian finches and representatives of various cardueline genera. A, <u>Telespyza ultima</u>; B, <u>T. cantans</u>; C, <u>Rhodacanthis palmeri</u>; D, <u>Chloridops kona</u>; E, <u>Loxioides bailleui</u>; F, <u>Psittirostra psittacea</u>; G, <u>Pyrrhula pyrrhula</u>; H, <u>Coccothraustes coccothraustes</u>; I, <u>Pinicola enucleator</u>; J, <u>Serinus sulphuratus</u>; K, <u>Carpodacus mexicanus</u>; L, <u>Carduelis sinica</u>; M, <u>Acanthis flammea</u>.

Genus Rhodacanthis: Koa Finches

Large, heavy-billed Hawaiian honeycreepers adapted to feeding on fruit of Koa acacia (Perkins 1903). Tongue nontubular, compact, scooped out dorsally, the cornified ventral surface curving upward laterally (Gadow 1899). Nasal opercula lacking (ibid.). Sexually dimorphic with red-, orange-, or yellow-headed males and dull green females. Bill dull blue. Song loud, whistled, unlike those of other drepanidine genera (Perkins 1903). One, or perhaps two, species confined to the upper Kona district of Hawai'i. Now extinct.

Genus Loxioides: Palila

Large Hawaiian honeycreepers with bill short and heavy, culmen arched and gonys convex, adapted for feeding on fruits of Sophora chrysophylla. Tongue similar to that of Rhodacanthis, nasal opercula lacking (Gadow 1899). Sexual dimorphism slight, males brighter than females. Head yellow, back gray, underparts white. Bill dark brown or black. Song canarylike, calls whistled. The single species L. bailleui confined to upland māmane-naio forests of Hawai'i.

Genus Chloridops: Kona Grosbeak

Large Hawaiian honeycreepers with massive arched bills (almost as large as rest of head) adapted for crushing hard fruits of Myoporum sandwicense. Tongue as in previous genera, nasal opercula lacking (Gadow 1899). Sexual dimorphism virtually nonexistent, plumage dull green throughout except for black lores. Bill yellowish pink. Song complex, quiet, rarely uttered, call notes whistled (Munro 1960). A single known species C. kona confined to a small area in the upper Kona region of Hawai'i. Probably extinct.

Genus Psittirostra: 'Ō'ū

Large, stocky Hawaiian honeycreepers with unique, thick, hooked bills adapted for generalized feeding on small fruits and nectar. Moderate nasal operculum (Raikow 1977b). Tongue as in *Telespyza*. Sexually dimorphic with plumage basically gray-green but male with bright yellow head. Bill orange-pink. Song complex and canarylike, call notes loud whistles. The single species *P. psittacea* known from all forested islands but now extinct except on Kaua'i and Hawai'i.

The remaining genera of Hawaiian honeycreepers comprise the most spectacular array of adaptation of any monophyletic passerine group. Many of these adaptations, such as the bizarre bill of *Hemignathus munroi* (=*H. wilsoni* of previous authors, see p. 128) are unique, but others are convergent with such varied unrelated forms as honeyeaters, wood warblers, woodcreepers, parrots, tanagers, and nuthatches. Four genera are of uncertain position, but because they can be seen as intermediate in some respects between the finchlike genera and the others, they will be treated first. The first two are clearly part of the Hawaiian honeycreeper complex, but the relationships of *Paroreomyza* and *Melamprosops* are by no means known, and the two are only tentatively considered here to be drepanidine. The genera *Oreomystis* and *Paroreomyza* have been merged in all previous works. Their relationships are discussed in detail in Section 7.

Genus *Pseudonestor*: Maui Parrotbill

Medium-sized Hawaiian honeycreepers with heavy, laterally compressed, parrotlike bills used to tear away bark of trees and to crush twigs in search of insects, the sole known food. Tongue nontubular, slightly curled longitudinally and with lateral and terminal laciniae (Rothschild 1893-1900). Plumage green and yellow, dimorphism slight except in dimensions. Song a simple, descending trill or warble. Call note an explosive chip. The single species *P. xanthophrys* endemic to Maui.

Genus *Oreomystis*: Hawaiian Creepers

Small, short-tailed Hawaiian honeycreepers with short, slightly downcurved bills. Gonys concave in profile. Tongue nontubular, parulidlike but with proximal end truncate (Richards and Bock 1973; Gadow 1899). Primarily insectivorous, foraging almost exclusively by creeping over trunks and branches of trees. Plumage dull gray-browns and greens, sexes alike. Song simple descending trills, call a quiet chip. Two species, *O. bairdi* of Kaua'i and *O. mana* of Hawai'i.

Genus *Paroreomyza*: 'Alauahios

Small, warblerlike birds with short straight bills. Gonys straight or convex in profile. Tongue nontubular, parulidlike, with posterior margin deeply cleft (Richards and Bock 1973). Foods include insects and nectar, obtained by a variety of means including picking among branches and twigs, foliage gleaning, and flycatching. Adults color dimorphic, males green and yellow or uniformly red, females yellowish gray or dull brown. Immatures and some females with pale wing-bars. Song (known for only one species) a lively but choppy whistled phrase. Call a loud, explosive chip. Three species, P. maculata on O'ahu, P. flammea on Moloka'i, and P. montana with subspecies on Maui and Lana'i.

Genus Melamprosops: Po'o-uli

Medium-sized, stocky, short-tailed birds with short, heavy, slightly finchlike bills. Tongue nontubular, with rounded tip and upcurved lateral margins elaborated into short laciniae, and deeply notched at the proximal end (Bock 1978). Feeds on insects and terrestrial mollusks (ibid.), forages over trunks and branches of trees. Plumage brown above, light tan below with face black. Song unknown, call notes short, sharp chips. Monotypic, M. phaeosoma being endemic to Maui.

The remaining genera all share the drepanidine tubular tongue and most feed at least partly on nectar. They represent two different lineages, one with a trend toward insectivory, the other specializing on nectar. The insectivores will be considered first.

Genus Loxops: 'Ākepas

Small Hawaiian honeycreepers with short conical bills, the tips of which are crossed, apparently as an adaptation for opening imbricated buds of Metrosideros and seed pods of Koa (Richards and Bock 1973). Partly nectarivorous, with typical tubular tongue. Sexual dimorphism slight to marked. Colors green, yellow, and red. Tail long, notched at the tip. Song of varied trills, with short upslurred calls. Two species, L. coccineus with subspecies on Hawai'i, Maui, and O'ahu, and L. caeruleirostris on Kaua'i.

Genus Hemignathus: 'Akialoas, Nukupu'us, and 'Amakihis

Small to large Hawaiian honeycreepers with downcurved bills. Bill length varies, but culmen always arched and gonys (with one exception) concave. Tongue tubular. All species take both insects and nectar but percentage of each varies (Perkins 1903). Plumage typically plain gray-green or yellow-green with black lores. Bill color typically black with a bluish gray base of the lower mandible. Immatures duller than adults, often with pale wing-bars. Males often brighter than females. Songs simple trills and warbles. Call notes short, often explosive, chirps or upslurred whistles. Three subgenera can be recognized:

Subgenus Hemignathus.--Bill very long, lower mandible more than half the length of the upper; one species H. obscurus with well-differentiated subspecies on Kaua'i, O'ahu, Lana'i, and Hawai'i.

Subgenus Heterorhynchus.--Bill very long, lower mandible less than half the length of the upper; two species, Hemignathus munroi on Hawai'i and H. lucidus with subspecies on Maui, O'ahu, and Kaua'i.

Subgenus Viridonia.--Bill relatively short; four species, H. virens with subspecies on O'ahu, Moloka'i-Maui-Lana'i, and Hawai'i forming a superspecies with H. stejnegeri of Kauai, H. parvus endemic to Kaua'i, and H. sagittirostris endemic to Hawai'i.

The remaining mostly nectarivorous genera are rather strikingly convergent with Australasian members of the Meliphagidae in color, habits, and even vocalizations. My classification of these genera differs from that of Amadon

(1950) in only one respect. I have merged the genus Vestiaria in Drepanis because I can find no basis other than plumage color to diagnose Vestiaria, and I do not consider that difference sufficient to warrant generic distinction.

Genus Ciridops: 'Ula-'ai-hāwane

Small Hawaiian honeycreepers with short, somewhat finchlike bills. Said to feed on fruits of Pritchardia palms, and probably also nectar (Bock 197). Tongue of the tubular drepanidine type (ibid.). Sexes alike in plumage, adults patterned in bold red, black, white, and gray, immatures olive green and buff. Some feathers stiffened or lanceolate. Voice unknown. The single species C. anna once widespread in forests of the island of Hawai'i.

Genus Drepanis: Mamos and I'iwi

Medium to large Hawaiian honeycreepers with down-curved sickle-shaped bills supported by bone through most of their length (Baldwin 1953). Nostrils fully operculate. Tongue long, tubular, and brush tipped. Primarily nectarivorous, all species favoring flowers of arborescent Lobeliaceae (Perkins 1903; Spieth 1966), to which their bills are well adapted, as well as other flowers. Adults clad in bold patterns of red, yellow, black, and white. Sexes similar. Vocalizations loud and far carrying, convergent with songs of certain Meliphagidae. Three species: the mamos D. funerea of Moloka'i and D. pacifica of Hawai'i; and the I'iwi, D. coccinea, found on all forested islands.

Genus Palmeria: 'Akohekohe

Large Hawaiian honeycreepers with thin, pointed, slightly down-curved bills. Tongue as in previous genus, adapted for nectarivory. Full nasal opercula. Plumage primarily black with red-orange spots and nape patch, white tips to primaries and rectrices. A stiff, recurved, yellowish white crest at base of bill, some contour feathers also stiffened and often lanceolate. Adult sexes similar, immatures lacking bright spots and crest. Vocalizations include a low-pitched gurgling song and loud whistles. Insertion of *flexor digitorum longus* of hind limb shows unusual derived condition (Raikow 1977b). The single species *P. dolei* known from Maui and Moloka'i.

Genus *Himatione*: 'Apapane

Small Hawaiian honeycreepers similar to *Palmeria* in bill shape, body proportions, tongue, and nasal opercula, but differing in plumage and in insertion of *flexor digitorum longus* (Raikow 1977b). Adults crimson with black wings and tail, immatures dark brown. One species, *H. sanguinea*, occurring undifferentiated on all main islands, with a well-marked subspecies, now extinct, on Laysan.

Origin of the Hawaiian Honeycreepers

Gadow (1899) considered the drepanidines an offshoot of the mainly Neotropical tanager-honeycreeper assemblage. Perkins (1903) expressed skepticism with this hypothesis but was unable to offer an alternative. Amadon (1950) presented several arguments favoring a "coerebid" ancestor. His thesis was that evolution had proceeded from more generalized types such as *Hemignathus virens* to the more specialized forms such as *Pseudonestor*, *Ciridops*, and *Chloridops*. This hypothesis requires that the finchlike adaptations of several species have evolved by convergence. Amadon considered heavy seed-crushing bills an evolutionary dead end, but had difficulty reconciling that belief with the spectacular radiation of the Galapagos finches (Lack 1947). Morphological evidence cited by Amadon (1950) included an analysis of tongue structure from which he concluded that the group evolved from a nectar-feeding, tubular-tongued ancestor. Nasal opercula were also interpreted as indicating a nectarivorous ancestor. In the light of Beecher's (1951) then unpublished finding that the Coerebidae were a polyphyletic assemblage of convergently evolved nectar-feeders, Amadon (1950) suggested the Thraupidae, Parulidae, Icteridae, and Vireonidae as other potentially ancestral groups and gave only brief consideration to the possibility of descent from the cardueline finches. Baldwin (1953) agreed with Amadon's and Beecher's (1953) hypothesized thraupidlike ancestor, but proposed a different sequence of events, with Himatione considered the most primitive drepanidine genus.

Sushkin (1929), after studying skeletons of a varied selection of Hawaiian honeycreepers, concluded that the group's affinities lay with the carduelines. He considered Telespyza to be the most primitive genus and the thin-billed forms to be specialized derivatives--just the reverse of Perkins' (1903) phylogeny. Sushkin's conclusions were generally disregarded until recently, when new anatomical studies by Bock (1960, 1972, 1978), Richards and Bock (1973), and Raikow (1976, 1977a and b) have borne out his findings. Analysis of egg-white proteins (Sibley 1970) also demonstrated a cardueline affinity, and van Riper's (1978) studies of breeding biology added further support to the idea.

Beecher (1951, 1953) presented an enigmatic twist to the cardueline-coerebid controversy. After pointing out the nearly identical jaw muscle configurations of Telespyza and the cardueline Carpodacus, he states (Beecher 1953:

312): "The striking similarity of the Hawaiian finches to the cardueline finches in all but plumage suggests parallel development from isolated segments of thraupine stock." However, Beecher's (1953) classification considers both the carduelines and the coerebids to be of "thraupine stock." Thus his data can be interpreted as supporting a cardueline ancestry, at least indirectly.

Acceptance of a cardueline ancestry for the drepanidines would seem to dictate a reversal of the evolutionary sequence proposed by Amadon (1950). In his study of the Fringillidae, Tordoff (1954) took exception to the belief that heavy seed-crushing bills are evolutionary dead ends by stating (Ibid.: 31):

> If heavy bills are indeed evolutionary dead ends, then for a hypothetical ancestor of the fringillids, one must visualize some kind of bird with a bill at least as thin as the most needle-beaked living fringilline...If one grants that bills of seed-eating birds can become a little thinner, then it is fruitless to argue that they cannot become much thinner. I see no justification for considering a heavy, seed-crushing bill an evolutionary dead end.

Raikow's (1977b) phylogeny, with a sequence of change from a finch-billed type to extreme sickle-billed types reflects such reasoning. However, Bock (1970, 1978), while advocating a cardueline ancestry, enigmatically proposes a sequence in which the drepanidine finch-bills are derived from the thin-billed <u>Hemignathus</u>.

The tanager-cardueline controversy has been reviewed recently by Eddinger (1970), Raikow (1977b), and van Riper (1978). The following discussions cover much of the same ground, but because my research has not concentrated on any single character complex, and has considered all the species of Hawaiian honeycreepers, my synthesis is perhaps the broadest to date.

Character Analysis

Tongue.-- Many Hawaiian honeycreepers possess a uniquely derived tubular tongue. Although somewhat variable, the basic structure exhibits a tube formed by a curling upward of the distal lateral margins of the tongue. These edges are elaborated into laciniae that overlap dorsally to close the tube. Often the tip of the tongue is frayed to form a brushlike tip. Illustrations of such tongues are given by Gadow (1899), Gardner (1925), Amadon (1950), Richards and Bock (1973), and Raikow (1977b). This type of tongue probably first arose as an adaptation for nectarivory, but it is also present in several genera that feed extensively on insects as well as nectar (Perkins 1903). Amadon (1950) believed this tongue to be the ancestral type for the honeycreeper group, but no mainland counterpart for it exists. The drepanidine tongue resembles only vaguely the tongues of the Coerebidae (Amadon 1950). This derived tongue is present in Hemignathus, Loxops, Ciridops, Drepanis, Himatione, and Palmeria.

An entirely different tongue morphology is present in the five finch-billed genera of honeycreepers. The suggestion of partial tubularity in some of these tongues (Gardner 1925; Amadon 1950) has been clearly refuted by Raikow (1977b). Indeed the latter author has demonstrated the very striking similarity of these tongues to those of cardueline finches. In other genera, the tongues are seemingly intermediate in structure. That of Pseudonestor is non-tubular, but possesses lateral laciniae and a frayed tip, with the lateral edges apparently somewhat curled upward (Rothschild 1893-1900). Amadon (1950) considered this tongue "partially tubular." In Oreomystis and Paroreomyza the tongue is simple and resembles those of many wood warblers (Parulidae) (Richards and Bock 1973; Gardner 1925), except that in Oreomystis the proximal end is truncate. Melamprosops exhibits a unique nontubular tongue with an entire, spoonlike distal end and a few supposedly vestigial lateral laciniae (Bock 1978). At the proximal end, the tongue of Melamprosops, like that of Paroreomyza, is deeply cleft (Richards and Bock 1973; Bock 1978).

This latter characteristic may be of considerable phylogenetic significance. Gardner (1925) illustrated and discussed the tongues of a wide variety of birds. Among passerines, a V-shaped proximal end, as shown by P. newtoni, is the rule. Gardner's figures of 118 passerine tongues show only three with truncate proximal ends, those of a sunbird (Nectariniidae) and two drepanidines, Psittirostra psittacea and Hemignathus obscurus procerus. Raikow (1977b) has shown Gardner's (1925) illustration of the tongue of Telespyza cantans, showing a V-shaped proximal end, to be erroneous; that tongue also has a truncate rear margin. Although Raikow did not mention the distinction, his illustrations show that the tongues of the several carduelines he studied are deeply cleft at the proximal end. Published illustrations show proximally truncate tongues in Pseudonestor (Rothschild 1893-1900); Himatione (Gadow 1899); Drepanis coccinea (Raikow 1977b); Ciridops (Bock 1972); Loxops coccineus, Hemignathus virens, H. sagittirostris (Richards and Bock 1973); Oreomystis bairdi (Gadow 1899); and O. mana (Richards and Bock 1973). Only

Melamprosops and *Paroreomyza* exhibit the typical passerine configuration. These observations could mean that the latter two genera branched early from the main line of drepanidine evolution, that their proximally cleft tongues are secondarily derived from a truncate ancestor, or even that these two genera are not Hawaiian honeycreepers.

Whatever the derivation of the two aberrant forms, tongue structure in Hawaiian honeycreepers clearly supports a cardueline affinity. The only difference that can be demonstrated between the tongues of carduelines and Hawaiian finches is the truncate base of the latter. Evolutionary parsimony suggests, therefore, that such a finch-like tongue is primitive within the drepanidine complex. The derivation of the tubular tongue of some Hawaiian honeycreepers, which has no mainland counterpart, from such an ancestor is relatively easy to envision.

Nasal opercula.-- Many Hawaiian honeycreepers possess a dorsal operculum that partly covers the nostril. Such an operculum is found in many nectarivorous birds (Amadon 1950). Amadon interpreted the presence of a moderate operculum in *Psittirostra psittacea* as indicating that the finch-billed drepanidines evolved from nectar-feeding ancestors. But Raikow (1977b) found the nonoperculate nares of *Telespyza cantans* identical to those of cardueline finches and attributed the operculum of *P. psittacea* to secondary adaptation to its diet of fruit and nectar. Since operculate nostrils have evolved in such diverse families as Parulidae and Nectariniidae (Amadon 1950), the feature cannot assume much phylogenetic significance.

Musculature.--Myological studies of drepanidines have involved primarily the muscles of the jaw and tongue (Beecher 1951, 1953; Bock 1972, 1978; Richards and Bock 1973) and the limbs (Raikow 1976, 1977a). Beecher's (1953) interpretation of the jaw musculature has already been discussed. Bock (1972) found the tongue musculature of drepanidines to differ from that of coerebids and to resemble that of cardueline. The appendicular myology also resembles that of cardueline in a number of particulars, while differing from that of the Coerebidae and some other passerine groups (Raikow 1977b).

Osteology.--The drepanidine skull has received considerable attention from anatomists. The first suggestion of cardueline affinities for the group (Sushkin 1929) was based largely on comparisons of cranial morphology. Amadon (1950) reviewed the pertinent literature at the time, and concluded that cranial osteology held little phylogenetic information. His tabular summary (ibid.: 218) however, shows many points of similarity between Hawaiian honeycreepers and cardueline and many contrasting conditions among tanagers and coerebids. Bock (1960) based his suggestion that drepanidines are cardueline derivatives on their shared lack (or fusion) of the palatine process of the premaxilla as well as some behavioral considerations (see beyond).

Lucas (1894) examined the hypotarsi of several drepanidines in an attempt to elucidate affinities, but Amadon (1950) has shown that this feature is so uniform among passerines as to be useless in delimiting higher categories.

Among the Hawaiian honeycreepers, some osteological variations occur that may be helpful in determining the direction of evolution within the group. The aforementioned palatine process of the premaxilla is fused to the palatine and elaborated as a lateral flange virtually identical to that of carduelines in the finch-billed genera (Bock 1960). In the thin-billed taxa, the flange is much reduced. The most parsimonious explanation of this trend is that the latter condition is derived from the former. Many nectar-feeding birds also possess long, thin transpalatine processes, and the nectarivorous drepanidines are no exception (Amadon 1950). Since this feature has evolved convergently in many passerine taxa, it can be considered a derived condition in Hawaiian honeycreepers.

Plumage.--Hawaiian honeycreepers are a relatively conservative group in coloration, the brilliant plumages of several species notwithstanding. In the group as a whole, only black (melanin), red, and yellow pigments occur. The chemical nature of these pigments has not been investigated. These colors in various combinations produce the greens, browns, grays, and other tints seen in the various species. No Hawaiian honeycreepers exhibit structural colors such as blue, violet, or iridescent green, nor are metallic or opalescent qualities present in the plumage.

I have examined specimens of 56 species of cardueline finches, 186 tanagers, and 35 coerebids in an attempt to find parallels to drepanidine plumage coloration. Tanagers and American honeycreepers run the gamut of the plumage spectrum, except that red is rare among the Coerebidae. Structural colors, particularly blue, are very frequent, and iridescent or opalescent effects are the rule rather than the exception. Among carduelines, only reds, yellows, and melanins occur, and no species exhibit iridescence or opalescence. Blue does not occur, and indeed, no cardueline exhibits any plumage color not represented also among Hawaiian honeycreepers. Some parallels of pattern, such as that between Leucosticte atrata and Ciridops anna, are rather impressive. Amadon (1950) did not consider plumage color to be of much value in revealing phylogeny, but I find such consistent parallels as those cited above highly suggestive.

In details of plumage pattern, carduelines also parallel drepanidines. White wing-bars are present in many species of both groups, but are relatively rare among tanagers and coerebids. Contrasting black feathers in the face are found in many Hawaiian honeycreepers and are also seen in such carduelines as redpolls (Acanthis), serins (Serinus), goldfinches and siskins (Carduelis), and the hawfinches (Coccothraustes). Among tanagers and coerebids, black facial feathers occur in many species, but usually as part of a bright variegated color pattern, and seldom as the only dark feathers in the plumage.

The females and immature males of both species of Telespyza exhibit a plumage with sparrowlike streaks (Banks and Laybourne 1977) highly reminiscent of plumages of carduelines of the genus Serinus. No such streaking is exhibited by any tanager or coerebid. Amadon (1950) attempted to explain the streaking as convergence resulting from adaptation to the low grassy habitats on Laysan and Nihoa, but I find this argument unconvincing since neither island has any avian predators to exert selection pressure for concealing coloration. Besides, the resemblance to Serinus is too close, in my opinion, to be attributable to convergence, particularly when considered in the light of other morphological and behavioral traits.

Phylogenetic shifts from yellow to red and red to yellow have apparently occurred several times among Hawaiian honeycreepers, and one form (Loxops coccineus ochraceus) is even polymorphic in this respect (Amadon 1950). Such red-yellow pigmentation shifts are also frequent within species and between closely related species of cardueline finches. The development of yellow and orange variations in House Finches (Carpodacus mexicanus) introduced to Hawai'i is well known (Grinnell 1911; Peterson 1961). Brush and Power (1976) have shown it to be genetically based but influenced by diet. The South American siskins Carduelis magellanica and C. cucullata differ only in that the former is yellow where the latter is red (De Schauensee and Phelps 1978). No such red-yellow species pairs occur among coerebids but at least one such case is known among tanagers (Brush 1970). These observations suggest that carduelines and drepanidines share similar genetic and physiological bases for pigmentation.

Another plumage character can be mentioned here as an interesting, but probably coincidental, parallel. Several species of nectarivorous drepanidines possess modified tips of the primaries that produce an audible whirr in flight. No such modified feathers occur among tanagers or coerebids, but a striking modification of the inner primaries occurs in the cardueline hawfinch Coccothraustes (Newton 1973).

Breeding Biology.--Relatively few detailed studies of the breeding biology of Hawaiian honeycreepers have been done. Sincock et al. (ms) summarized the published records of nests, eggs, and nestlings of Hawaiian native birds. Among the honeycreepers, nests of only 16 of the 28 species have been discovered and still fewer eggs and nestlings are known. However, the nests found to date represent a variety of morphological types, and all branches of the complex are represented. Enough is known that valid comparisons of drepanidines with possible mainland relatives can now be made.

Most Hawaiian honeycreepers build compact, open, cup-shaped nests in trees. Such nests have been described, for example, for the nectar-feeding Himatione and Drepanis (Berger 1972b), the insectivorous Oreomystis (Eddinger 1972b), the omnivorous Hemignathus (Berger 1969a; van Riper 1973b, 1978), and the seed-eating Loxioides (van Riper 1978). Similar nests are built by cardueline finches and some tanagers, and van Riper (1978) has pointed out that that the carduelines are relatively homogeneous in this respect. Exceptions to the general pattern include nesting in grass tussocks by Telespyza cantans (Ely and Clapp 1973); in rock cavities by T. cantans (Bailey 1956), T. ultima (Richardson 1954; Clapp et al. 1977), and Himatione sanguinea (van Riper 1973a); and in tree cavities by Loxops coccineus (Sincock and Scott, in press) and Oreomystis mana (Sincock et al. ms). A few cardueline species also deviate from the normal nesting behavior in similar ways (Newton 1973).

Baldwin (1953) studied the breeding biology of Himatione sanguinea, Drepanis coccinea, and Hemignathus virens on Hawai'i; Eddinger (1970) observed it in Hemignathus stejnegeri, H. parvus, D. coccinea, and Himatione sanguinea on Kaua'i; and van Riper (1978) investigated Hemignathus virens and Loxioides bailleui on Hawai'i. No other species' nesting habits have been studied in depth in the wild, but breeding in captivity has been observed in Telespyza cantans (Throp 1970) and T. ultima (Berger 1972b).

Eddinger (1970) made a comparison of ten aspects of breeding biology in the four drepanidines he studied with published data on the American members of all possibly ancestral taxa. The results appear to me to be inconclusive, but Eddinger nevertheless interpreted them as indicating a coerebine-thraupine ancestry rather than a cardueline one. For the ten points of comparison, he could report only two differences among the Drepanididae, Thraupinae, Coerebidae, and Carduelinae: Coerebidae lack courtship feeding, present in the other three taxa, and Thraupinae frequently have helpers at the nest, a rare or unknown phenomenon in the others. The four taxa showed no significant differences in the other traits analyzed. Polygamy is unknown in all. Both sexes may participate in nest construction and feed nestlings, but only females incubate or brood. Injury feigning has not been observed in any of these groups. They also exhibit wide and overlapping ranges of incubation and nestling periods.

Eddinger (1970) eliminated the Carduelinae from consideration as ancestors primarily on two bases. First, most cardueline nests are built by the female alone whereas in the drepanidines he studied, both sexes participate. Second, the lack of nest sanitation characteristic of carduelines (Newton 1973) stands "in strong contrast to the fastidiousness of the honeycreepers" (Eddinger 1970: 189). Van Riper (1978) found that only the female built the nest in <u>Hemignathus</u> <u>v</u>. <u>virens</u>. A more important finding, however, was that both <u>Loxioides</u> and <u>Telespyza</u> lack nest sanitation. This trait is rare in passerines generally and among the New World nine-primaried Oscines is found only among cardueline finches and Hawaiian honeycreepers. Nest sanitation has evolved secondarily in several carduelines (Newton 1973), so the presence of sanitation in many drepanidines does not negate a cardueline ancestry. Thus, by eliminating both of Eddinger's (1970) contrary indications, van Riper (1978) has shown the carduelines and drepanidines to be very similar in breeding biology, while differing from American honeycreepers and tanagers. Other comparisons made by van Riper (1978) include characteristics of nestlings and use of regurgitation in feeding. He found no significant differences among tanagers, cardueline finches, and Hawaiian honeycreepers in these two traits.

Also noteworthy are van Riper's (1978) data on territoriality. In *Loxioides bailleui*, the territory is centered on the female initially, but later in the breeding cycle defense shifts to the nest site. The territory does not include foraging areas. Very similar territorial behavior has been reported among cardueline finches (Bent 1968; Lack 1968; Newton 1973). In *Hemignathus virens*, the territory is used for feeding, mating, and rearing of young (van Riper 1978). Eddinger (1970) found somewhat different territorial behavior in the closely related *H. stejnegeri* on Kaua'i with birds defending only a small area around the nest. Baldwin (1953) reported "loosely held" territories in *H. v. virens* in a different habitat from that studied by van Riper (1978). Other species that appear to hold small, weakly defended territories include *Himatione sanguinea* (Baldwin 1953; Eddinger 1970) and *Hemignathus parvus* (Eddinger 1970).

Territories appear to be held by Hawaiian honeycreepers only during the nesting period. At other times many species, especially the nectarivorous ones but also the seed-eating *Loxioides*, associate in single-species flocks that roam widely (Baldwin 1953; Pratt et al. 1977; van Riper 1978; pers. obs.). Such flocks are usually small, with fewer than ten members. In many species such small flocks fly high over forested ridges for considerable distances and thus strongly resemble flocks of carduelines such as goldfinches, siskins, and crossbills (Loxia). Such behavior is in contrast to the flocking behavior of most tanagers, wherein the flock moves slowly through the forest without covering great distances on long flights (Skutch 1954; T. A. Parker III, J. V. Remsen, pers. comms.). I have often seen such long flights by small flocks of Himatione sanguinea, Hemignathus virens, Loxioides bailleui, and Loxops coccineus, and less frequently by several other drepanidines.

Vocalizations.--Hawaiian honeycreepers are as varied vocally as they are in feeding adaptations. Still, enough similarities exist that some reasonable inferences about vocal phylogeny of the group can be made. Recordings are now available of all extant species except Hemignathus lucidus, H. obscurus, Paroreomyza flammea, and P. maculata, although some (e. g. Melamprosops) are poorly represented in sound collections. The song types fall basically into three groups. The finch-billed birds possess songs very reminiscent of those of cardueline finches. Voices in three of these genera (Telespyza, Loxioides, and Psittirostra) have been recorded, and those of others have been described. The song of T. cantans is "loud, melodious, and canarylike, even to the inclusion of trills" (Berger 1972b: 155) and the call notes are "melodious, some resembling those of the canary" (ibid.). Fisher (1906) described them as low, mellow, and linnetlike. Telespyza ultima also has a loud melodious song with a "distinct canarylike quality, containing trills, whistles and warbles" and several call notes including an upslurred whistle (Berger 1972b: 159). Both the canary (Serinus) and linnets (Acanthis or Carpodacus) are typical cardueline finches. The term "canarylike" has also been used to describe the song of Psittirostra psittacea (Henshaw 1902b; Perkins 1903; Gauthey et al. 1968), and the song of Loxioides bailleui resembles it but is less powerful (Perkins 1903; pers. obs.). Call notes of Psittirostra are plaintive upslurred whistles (Perkins 1903; Munro 1960; pers. obs.) but those of Loxioides are a short warble (pers. obs.). The extinct Chloridops had a "light sweet song...long with a variety of notes" (Munro 1960: 131) that may well have been of the same canarylike type. Rhodacanthis possessed a song "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" (Perkins 1903: 438). Munro (1960: 127) described these notes as flutelike.

The insectivorous honeycreepers, the mostly green birds that Amadon (1950) grouped with the finch-bills, have much simpler primary songs. Virtually all of them are simple trills, i. e. a similar note or sound figure rapidly reiterated. A typical example is the song of Hemignathus virens (Fig. 9), which varies geographically but is easily recognizable at all localities. It always sounds like a single short note, or a slightly doubled note, repeated quickly. Hemignathus sagittirostris sang such a similar song that "it would be difficult to distinguish between them were it not that [H. sagittirostris] whistles two or three distinct additional notes after completing the...trill" (Perkins 1903: 413). On Kaua'i, H. parvus sings a trill (Fig. 10) of doubled or tripled notes so that instead of singing chi-chi-chi-chi-chi, it sings cheedy-cheedy-cheedy...

or *cheedledee*-*cheedledee*-*cheedledee* etc. Perkins (1903: 424) described the song of *H. obscurus* as a "short, vigorous trill, recalling that of [*H. virens* and *H. wilsoni*] but distinct from either." The song of *H. munroi* is simple, but is more of a quick warble than a trill (Fig. 13) and the song of *H. lucidus* is apparently quieter but very similar (Perkins 1903: 430). The Maui form of the latter species is said to have a variation of the song that resembles closely the song of the introduced cardueline *Carpodacus mexicanus*. (*ibid*.). *Pseudonestor* likewise sings a short vigorous trill that in this case descends in pitch (Perkins 1903; pers. obs.). A descending trill is also sung by the two *Oreomystis* (Shallenberger and Pratt 1978; pers. obs.). That of *O. bairdi* is essentially identical to one variant of the song of *H. stejnegeri* (Fig. 11), which otherwise resembles the song of *H. virens*. The trills of the two species of *Loxops* are more varied and less stereotyped than those of *Hemignathus*, but are of the same general type (Fig. 12). No primary song has yet been described for *Melamprosops* or for *Paroreomyza flammea* or *P. maculata*, but that of *P. montana* is quite unlike the others described here (Shallenberger and Pratt 1978). The vocalizations of *Paroreomyza* will be discussed in detail in Section 7.

Many, and perhaps all, members of the insectivorous assemblage sing, in addition to their simple primary songs, complex and even canarylike subsongs or whisper songs. The function of such songs is not known. They have been described by Baldwin (1953) and van Riper (1978) for *H. virens* and by Eddinger (1970) for *H. parvus*. I have noted the phenomenon in these species and also in *H. stejnegeri*, both species of *Loxops*, and *Oreomystis bairdi*.

Figure 9. Songs of <u>Hemignathus virens</u>. A and C recorded at 1800 m on northwest slope of Hualālai, Hawai'i, 3 May 1977; B at Keauhou Ranch, Hawai'i, 1 May 1977; D, F at Polipoli Springs, Maui, 26 April 1977; F, same locality, 25 April 1977.

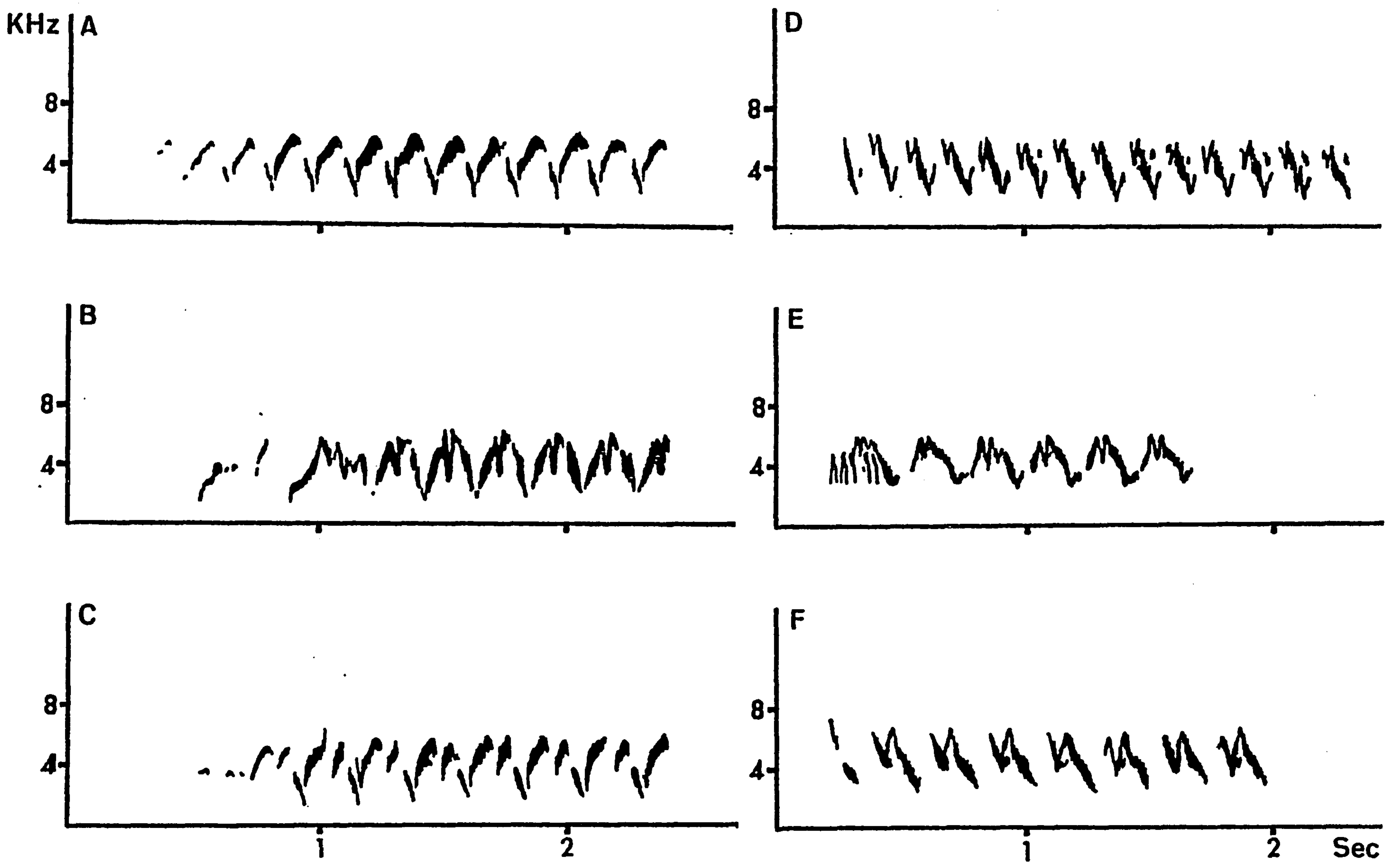


FIGURE 9

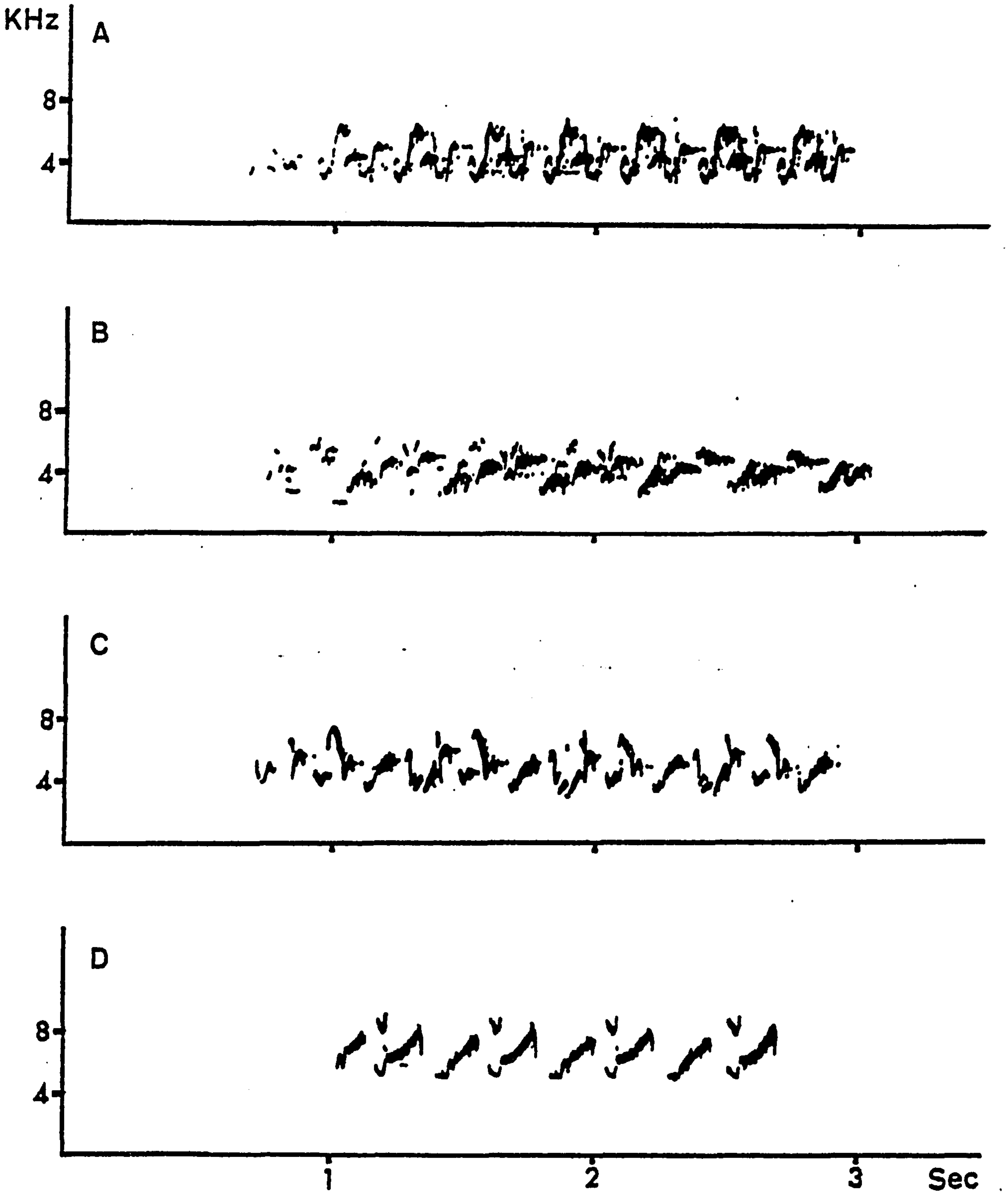


Figure 10. Four songs of Hemignathus parvus recorded by H. D. Pratt at Koke'e, Kaua'i on 2 June 1977 (A), 13 May 1976 (B), and 15 May 1976 (C and D).

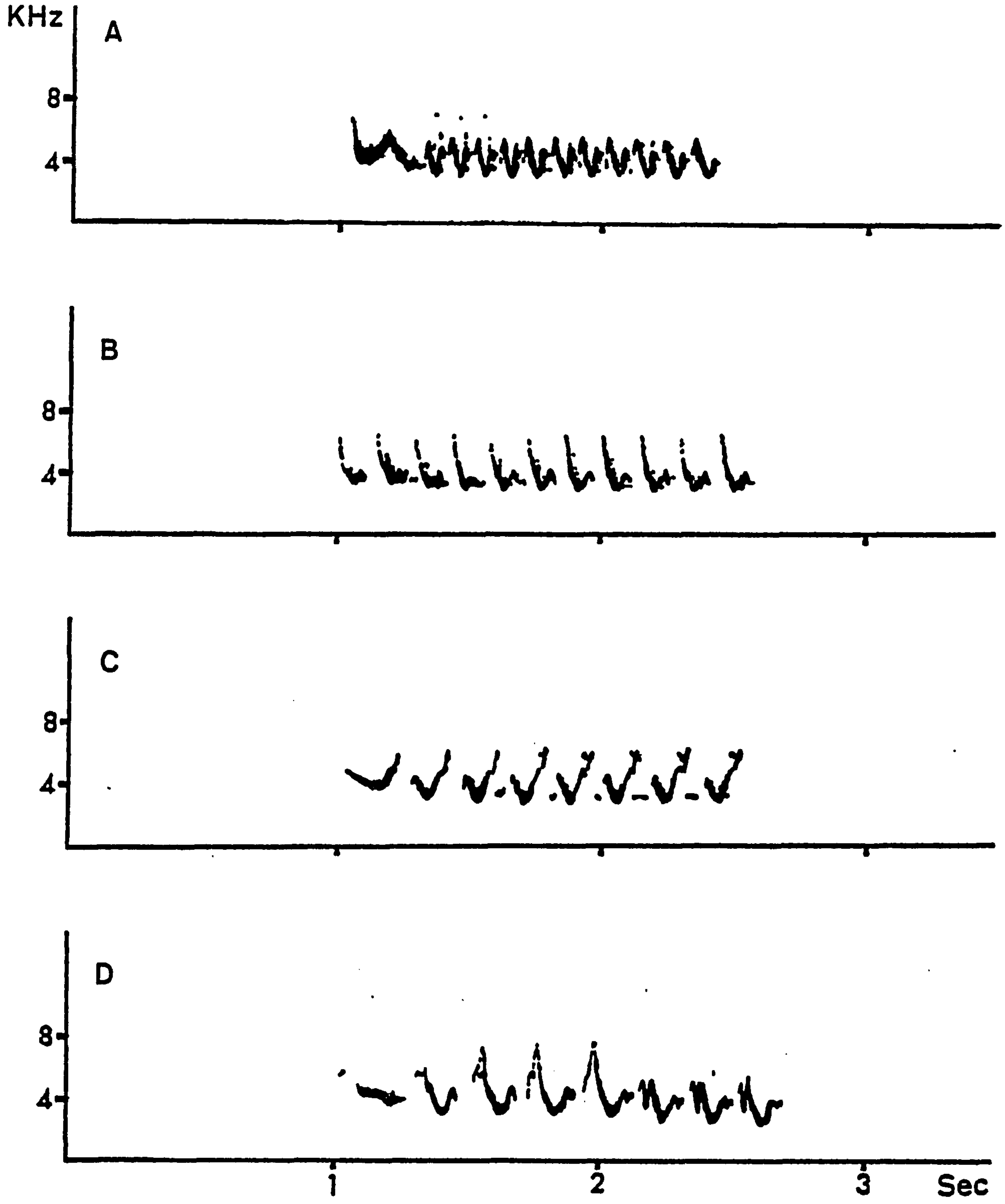


Figure 11. Four songs of Hemignathus stejnegeri recorded by H. D. Pratt at Koke'e, Kaua'i on 2 June 1977 (A), 14 May 1976 (B), 21 May 1977 (C), and 12 May 1976 (D).

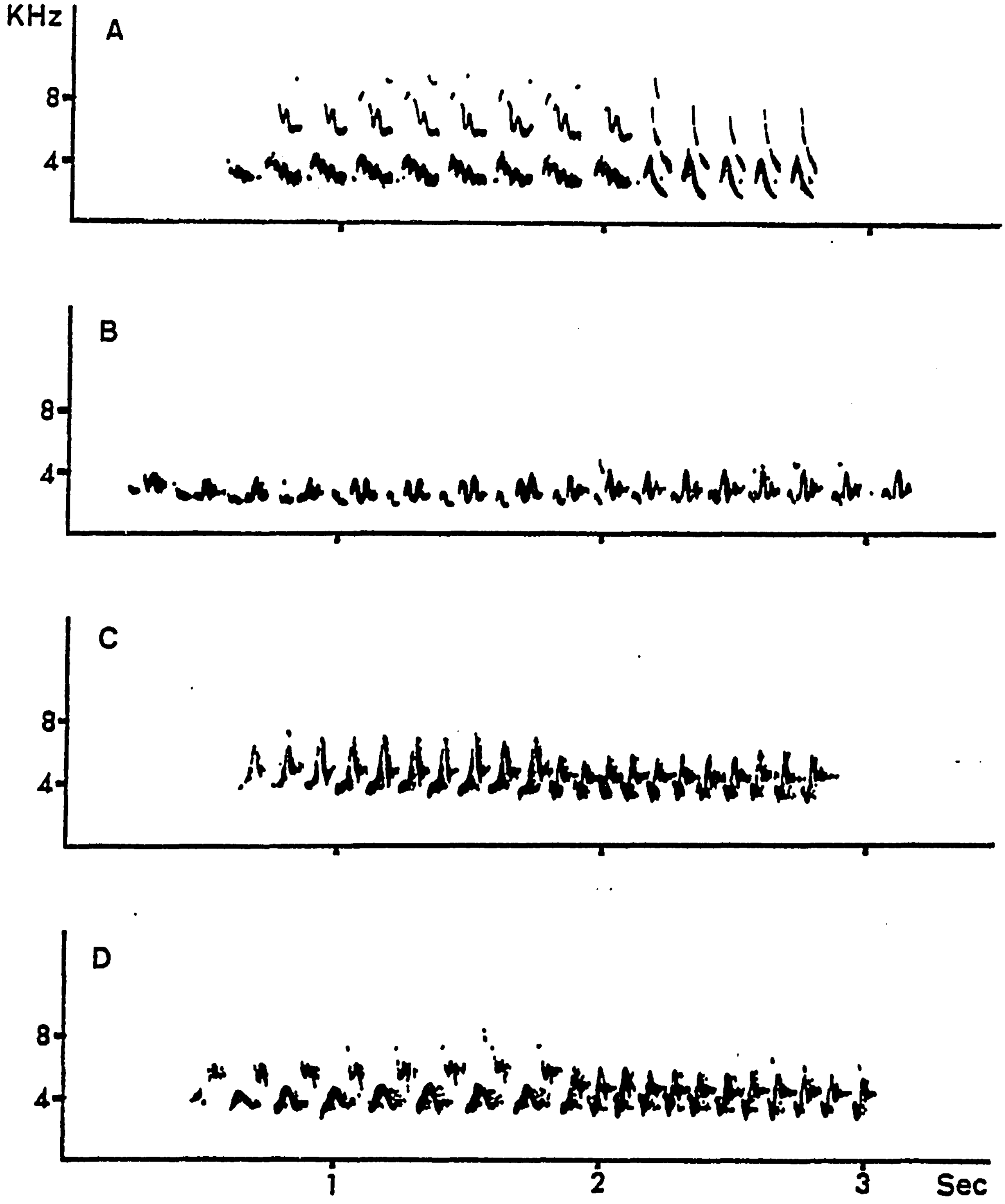


Figure 12. Songs of the two species of Loxops. A and B (L. coccineus) recorded by J. M. Scott at Kahuku Ranch, Ka'ū District, Hawai'i. C and D (L. caeruleirostris) recorded by H. D. Pratt at Koke'e, Kaua'i, 12 May 1976.

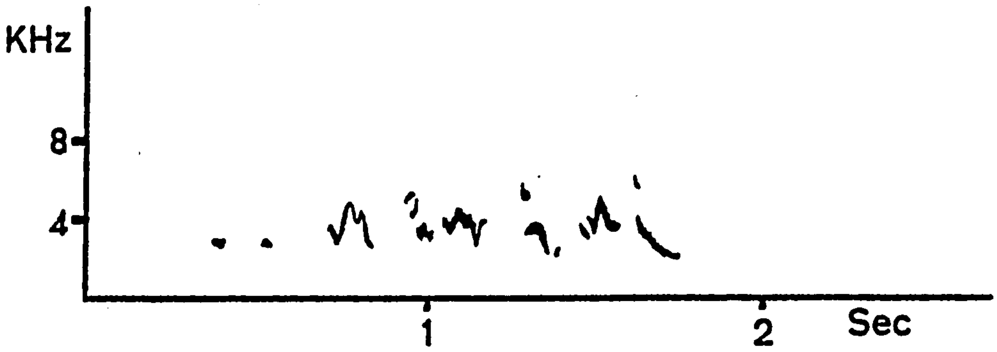


Figure 13. Song of Hemignathus munroi recorded 20 August 1975 at Keauhou Ranch, Ka'ū District, Hawai'i.

These quiet concerts are often lengthy and involve apparent mimicry of other native and introduced birds, a matter that requires further investigation. Van Riper (1978) reported whisper songs in the finch-billed *Loxioides bailleui.*

Call notes among the insectivorous hineycreepers are species-specific (pers. obs.) but, like the songs, can be grouped. Several species (both *Loxops*, *Hemignathus virens*, *H. munroi*) possess short upslurred whistles like those described for some of the finch-bills. Shorter whistled calls are given by all *Hemignathus* and by *Pseudonestor* (Perkins 1903; pers. obs.). Short chips or squeaky notes are produced by *Pseudonestor*, both *Oreomystis*, all *Paroreomyza*, and most *Hemignathus*. Such chips are the only vocalizations yet recorded for *Melamprosops*. Figure 14 shows a variety of honeycreeper calls.

Perkins (1903) was greatly impressed by the vocal divergence from other Hawaiian honeycreepers shown by the red and black nectar-feeders. Baldwin (1944) also remarked about this rather striking vocal dichotomy. Virtually all field ornithologists working in the islands, including the present writer, agree. This vocal difference provided one of the main bases for Amadon's (1950) subfamilies. While little uniformity is present among the five species whose voices are known, every author has considered them to resemble each other in a general way. *Himatione sanguinea* is the best singer of the lot, and its complex series of whistles, trills, bell-like notes, and mechanical-sounding clicks and buzzes seem almost infinitely variable (Ward 1964; pers. obs.). The songs of *Palmeria dolei* are similar, but much lower pitched, sounding as if recordings of songs of *H. sanguinea* are being played back at a lower speed.

Figure 14. Call notes of various Hawaiian honeycreepers. Recording data as follows: A, B, C, 16 August 1976; Pu'u Lā'au, Hawai'i; D, 9 October 1976, Koke'e, Kaua'i; E, 2 June 1977, Koke'e, Kaua'i; F, 3 July 1975, Alaka'i Swamp, Kaua'i; G, H, I, 17-18 August 1975, Keauhou Ranch, Hawai'i; J, K, L, 29 April 1977, Keauhou Ranch, Hawai'i; M, 9 October 1976, Koke'e, Kaua'i; N, 26 April 1977, Polipoli Springs, Maui; O, P, July 1976, Kahuku Ranch, Hawai'i; Q, R, 20 August 1975, Keauhou Ranch, Hawai'i; S, T, 13 May 1976, Koke'e, Kaua'i; All recordings by the author except F (R. J. Shallenberger), O, and P (J. M. Scott).

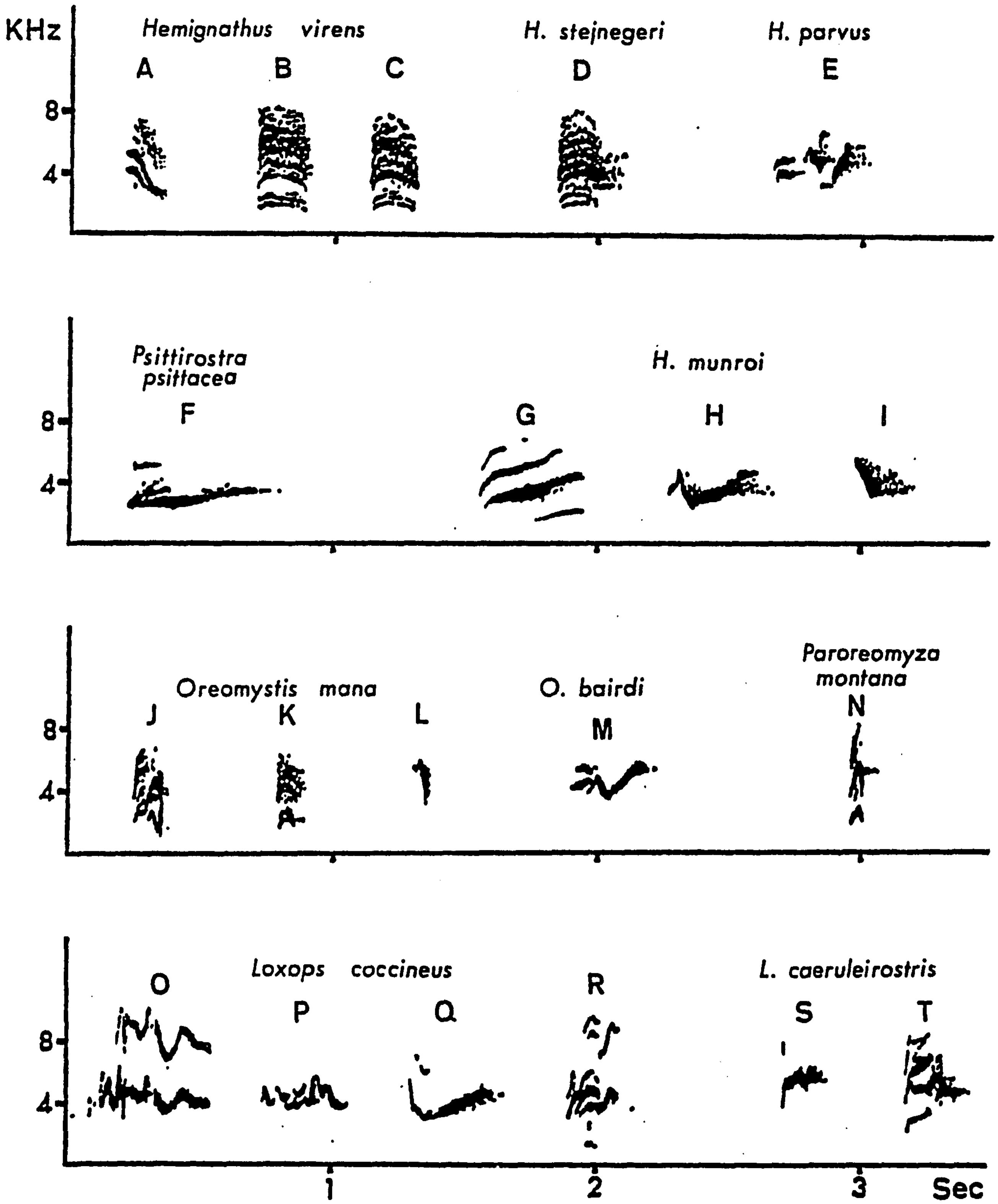

KHz
Hemignathus virens
H. stejnegeri
H. parvus
A
B
C
D
E
8
4
Psittirostra psittacea
H. munroi
F
G
H
I
8
4
Oreomystis mana
O. bairdi
Paroreomyza montana
J
K
L
M
N
8
4
Loxops coccineus
L. caeruleirostris
O
P
Q
R
S
T
8
4
1
2
3
Sec

FIGURE 14.

Palmeria also utters several humanlike whistles. The vocalizations of *Drepanis coccinea* are equally varied and include bizarre wheezy, croaking, and whistled notes as well as twangy mechanical-sounding ones. The extinct *D. pacifica* and *D. funerea* are reported to have produced loud penetrating whistles (Perkins 1903; Bryan 1908). The voice of *Ciridops* is unknown.

The vocalizations of this group of honeycreepers, strange as they are, remarkably resemble those of certain honeyeaters (Meliphagidae) of the Australian Realm. The songs of the Tui (*Prosthemadera novaeseelandiae*) of New Zealand contain passages virtually identical to some of those uttered by *Drepanis coccinea* and *Himatione*. (A recording of the Tui is presented by Gunn and Gulledge 1977.) So similar are they, in fact, that an excellent imitation of the Tui's song could be produced by combining selected passages from the repertoires of *Himatione* and *D. coccinea* with the song of the Hawaiian meliphagid *Moho braccatus*. As striking as these resemblances are, I do not believe they indicate a relationship between the nectarivorous honeycreepers and the Meliphagidae. Olson (pers. comm.) has assured me that anatomically these birds can in no way be associated. I believe rather that the incredible vocal resemblance is the result of convergence, possibly initiated by vocal mimicry among birds sharing the same food resource. I have often heard *D. coccinea* give notes resembling those of *Moho braccatus*, and have also noticed considerable interspecific rivalry between the two. In fact, the calls of *Himatione* and *D. coccinea* may contain "natural recordings" of the voices of long-extinct Hawaiian meliphagids such as the other species of *Moho* and *Chaetoptila angustipluma*.

Flight songs are widespread among Hawaiian honeycreepers in all three of the aforementioned groups. Such behavior occurs in Loxioides (van Riper 1978), Psittirostra (Perkins 1903), Hemignathus (Baldwin 1953; Eddinger 1970; van Riper 1978; pers. obs.), Himatione (Baldwin 1953; pers. obs.), Paroreomyza (Wilson and Evans 1890-99; pers. obs.), and Drepanis (pers. obs.). Flight songs are also common among cardueline finches (Bent 1968; Newton 1973) but are unknown among tanagers or "coerebids" (Skutch 1954).

Vocalizations and their accompanying behavior lend substantial support to the cardueline ancestry hypothesis. Vocal resemblances to carduelines, particularly among the finch-billed genera are striking, even to the upslurred call notes. The reduction of the complex, canarylike songs to subsongs in the insectivorous group may indicate an evolutionary trend. Also, the complex songs and calls of the nectarivorous assemblage can be seen as modifications of an ancestral canarylike song. Noteworthy here is the fact that neither tanagers nor coerebids are at all distinguished as vocalists (Skutch 1954).

Migration and Geographical Considerations.--Bock (1960) pointed out that cardueline finches exhibit migratory behavior that makes them much more likely to have produced island colonizers than either the tanagers or American honeycreepers. Many cardueline species undergo periodic population increases (Newton 1973) and at such times huge flocks may wander great distances and appear in totally unexpected places. More importantly, these wanderers may remain in the new localities to breed. Such colonies can become more or less permanent. Particularly noteworthy in this regard are the crossbills (Loxia), largely boreal birds that have colonized such unlikely areas as Indochina, Luzon, and Hispaniola.

In contrast, only four tanagers (North American Piranga) and no coerebids are long-distance migrants, and most are sedentary tropical birds. Whereas cardueline finches occur in all northern source areas for Hawaiian colonists, the tanagers and American honeycreepers occur primarily in the Neotropics far removed from the islands, and have not succeeded in colonizing either Cocos Island (Slud 1967) or the Galapagos (Harris 1974) located much closer (ca. 523 and 966 km respectively) to the source area.

Relationships

The foregoing review shows that an overwhelming preponderance of evidence has accumulated to indicate that the closest affinities of the Hawaiian honeycreepers are with the Carduelinae of the family Fringillidae. Indeed, the finch-billed honeycreepers would undoubtedly be classified as carduelines if the more divergent forms were unknown. The two Telespyza are as "good" cardueline finches as any member of the genus Serinus. In fact, I believe they may not only resemble the ancestral honeycreeper closely, but may even represent a direct line of descent from it, divergent only to the extent necessary for survival in the Leeward Islands environment. This somewhat heretical belief envisions a relatively recent colonization, not of a single island, but of all the islands more or less simultaneously during a spectacular irruption of a Telespyza-like cardueline. The adaptive radiation that followed occurred by repeated cycles of speciation, double invasion, and character displacement, as envisioned by Amadon (1950) and Bock (1970) among the main islands only.

The descendants of the ancestral stock isolated on far-flung Laysan and Nihoa had no such opportunity. These birds adapted to local conditions, but experienced no selection for divergent species recognition characters, and thus may retain a color pattern not far removed from that of the ancestral species. On the main islands, *Telespyza* was replaced by more advanced forms adapted to high, forested islands. The adaptive success and dispersal abilities of *Himatione sanguinea* enabled it to colonize Laysan at a much later date (the Laysan population was only subspecifically distinct), but possibly no other main-island birds were ever able to reach the Leewards successfully. This hypothesis requires that the initial drepanidine colonization occurred after the reduction of the Leeward Islands to low atolls, and is in fundamental disagreement with the findings of Schlanger and Gillett (1976) who considered both *Telespyza* and *Himatione* to be ancient relicts on Laysan.

The Higher Taxa

The conclusion that the Hawaiian honeycreepers are related to the cardueliness has far-reaching implications for taxonomy. Since the late 19th Century, the group has been considered an endemic family. But if these birds and the carduelines are of equivalent taxonomic rank, as they appear to be, then the Hawaiian group must be considered a third subfamily of the Fringillidae, along with the Carduelinae and Fringillinae, despite the fact that some of them are no longer very finchlike.

This decision also means that the former subfamilies of Drepanididae must be reduced to the level of tribes if they are maintained at all. Raikow

(1977b) considered the subfamilies to be weakly established and interpreted Amadon's (1950) dichotomy as being based mainly on plumage. He cited the uniformity of appendicular myology as arguing for a de-emphasis of the subfamilies. However, I believe that taxonomic subdivision of the subfamily is useful. Amadon (1950) may well have been influenced primarily by plumage, but parallel patterns of divergence can be seen in feeding adaptations, breeding biology, and vocalizations. I believe Amadon (1950) erred in grouping the thin-billed insectivores with the finch-bills. Van Riper (1978) made a strong case for splitting the former Psittirostrinae into two taxa, finch-billed vegetarians and non-finch-billed insectivores. Such a division is warranted on many grounds including breeding biology, tongue morphology, and vocalizations. Thus I restrict the tribe Psittirostrini to the five finch-billed genera. But do the excluded genera of Amadon's Psittirostrinae form a third tribe, or should they be united with the Drepanidini? This issue is clouded by several factors.

The first problem is that four of these genera lack the drepanidine tubular tongue. This tongue is a complex structure that could hardly have evolved twice. Since some of the thin-billed insectivores share this uniquely derived tongue with the nectarivorous birds, the two groups much share a more recent common ancestor than either does with the genera that lack it, unless it has been lost secondarily in those taxa. If only the tubular-tongued genera are considered, a clear dichotomy emerges. A "red" group (Himatione, Drepanis, Palmeria, Ciridops) comprises red and black, hard-plumaged nectarivores with complex meliphagid-like vocalizations. A "green" group (Loxops, Hemignathus) includes soft-plumaged mostly green birds adapted for feeding on insects as well as nectar, and with simple trilled vocalizations. In the green group most species exhibit sexual color dimorphism, with immatures resembling adult females, while among the red birds adults lack dimorphism but have distinctive immature plumages. In the latter group the flight feathers produce an audible whirring sound in flight (Perkins 1903; pers. obs.). In some species (e. g. D. coccinea, Himatione sanguinea) the primaries are obliquely truncate, but in others the whirring sound is produced without any such feather modification. Unlike the tongue, the sickle-shaped bill, which occurs in both the red and the green group, is uniquely derived in each. In the red group the bones of the skull extend virtually to the tip of the bill, but in the green sickle-bills the lengthening is accomplished mainly by an elaboration of the ramphotheca (Baldwin 1953). These distinctions appear to be sufficient to warrant taxonomic recognition, and in fact Amadon (1950) made his major division along these lines. But what about the "green" genera that lack drepanidine tongues?

Two of these genera, Melamprosops and Paroreomyza, may not be Hawaiian honeycreepers at all. In the case of the former, only a very limited amount of anatomical material has been available for study (Bock 1978) and very little is yet known about the bird's natural history (Casey and Jacobi 1973). Bock (1978) believed that the unique tongue showed a drepanidine affinity, but he was apparently unaware of the widespread occurrence of proximal truncation of the tongue in Hawaiian honeycreepers. The tongue of Melamprosops is deeply notched at the proximal end (Casey and Jacobi 1973; Bock 1978). Thus no character can be cited to tie Melamprosops to the honeycreeper radiation.

Zoogeographic considerations make a drepanidine origin of *Melamprosops* likely, but until additional data are available the genus must be considered *incertae sedis*.

Paroreomyza is likewise enigmatic, and will be discussed in detail in Section 7. For the present I believe both of these genera are best classified as members of the Hawaiian honeycreeper complex with uncertain systematic position within it. I have not included either of them in the phylogenetic model which follows.

Pseudonestor is clearly intermediate between the Hawaiian finches and the "green" group of thin-billed honeycreepers. Ecologically, it is very similar to *Hemignathus munroi* and despite its parrotlike movements retains a general resemblance to the green birds. The Maui Parrotbill's song is hemignathine, rather than resembling the canarylike songs of the finches. The nontubular tongue is unique in the complex, but can be seen as intermediate between the tongue of, say, *Psittirostra* and the drepanidine tubular type. Except for the latter feature, *Pseudonestor* could be considered unequivocally a member of the green group. The tongue could be secondarily nontubular, but that would require that the bill be secondarily thickened as well. A more parsimonious hypothesis is that *Pseudonestor* is an early, pre-drepanidine-tongue offshoot of the honeycreeper line leading away from the finches.

A secondary derivation of a nontubular tongue is more plausible in the case of *Oreomystis*. Behaviorally, the creepers are much more similar to *Hemignathus* than is *Pseudonestor*. *Oreomystis mana* shares many anatomical features with both *Loxops* and *H. virens* (Richards and Bock 1973). The tongue of Oreomystis, except for being truncate at the proximal end, resembles the simple tongues that have evolved convergently in a wide variety of unrelated insectivorous passerines (Gardner 1925), and thus can be parsimoniously considered a secondary derivation from a tubular ancestor. I thus place Oreomystis in the green complex.

The branching sequence shown in Figure 15 reflects a basically cladistic approach (Hennig 1966) to phylogenetic analysis. My classification, however, is evolutionary in the sense of Mayr (1969). I believe a strictly cladistic classification of this complex would be unnecessarily cumbersome, with a multiplicity of levels and sublevels, and that the most useful course is to recognize the red and green groups as tribes equivalent to the Psittirostrini, with Pseudonestor included with the green birds. The tribes are thus Psittirostrini, Hemignathini (Hemignathus, Loxops, Oreomystis, Pseudonestor), and Drepanidini. This classification, based on ecological, morphological, and behavioral groupings, reflects the three main bursts of adaptive radiation within the subfamily, if not adhering strictly to genealogy of the taxa.

Are the Drepanidinae Monophyletic?

The Psittirostrini are so strikingly similar to cardueline finches as to suggest two other possibilities: 1) that the honeycreeper assemblage is polyphyletic; or 2) that the group should be merged with the Carduelinae and no longer considered a separate taxon. Two characters, however, argue against such alternative hypotheses.

The first is the aforementioned posterior truncation characteristic of the tongues of all but two aberrant genera of Drepanidinae. The feature occurs in all three tribes and in various types of tongues found in the subfamily. It is the single morphological character that distinguishes the tongues of drepanidine finches from those of cardueline finches. Thus it probably was present in the founder species, or evolved very early in the radiation of the group and was present in the species ancestral to most modern species. Since a proximal truncation of the tongue has been demonstrated in only one other passerine group (Nectariniidae), the feature can be said to be virtually diagnostic for Drepanidinae. Interestingly, the two genera that lack this feature are also aberrant in other morphological and behavioral characters.

The second character that argues for monophyly of the Hawaiian honeycreepers is the occurrence of a characteristic "drepanidine odor" in many species. Perkins (1893: 108-9) wrote:

> And here it will be appropriate to notice the scent emitted by so many and so different species of Hawaian [sic] birds. I cannot liken this scent to any other that I know; but I should certainly call it disagreeable. In [Hemignathus virens] it is strongest of all, so much so that when a small company of these birds was overhead in the trees the whole air was often full of it; both my native assistant and myself noticed it again and again. Certain nests I could readily recognize as belonging to [Hemignathus virens] by the overpowering scent that still clung to them after

> the young had flown. It may also be noticed in [*H. obscurus*], *Loxioides*, [*Psittirostra*], *Chloridops*, and *Rhodacanthis*; in some specimens much more strongly than in others, in some perhaps not at all. Whether the red birds *Loxops*, [*Drepanis coccinea*], and *Himatione sanguinea* possess it I have not noticed. It is absent from the birds related to the Australian forms--the Oo, *Chasiempis*, and *Phaeornis*. How this scent, exactly the same in quality, comes to be attached to the insect-eating Drepanididae, and to such species as *Chloridops kona*, which appears to live entirely on the seeds of the fruit of the sandal-trees, I cannot imagine.

At that time the Hawaiian finches had not yet been classified with the honeycreeper complex. Perkins (1901: 571-2) later commented:

> It is still my belief that the biological reasons on the strength of which I first concluded that all these birds belonged to one family are of utmost importance, chief amongst which is the peculiar odour to be noticed in both groups, in the thin-billed and thick-billed forms alike. So far as Hawaiian birds are concerned, this odour is *absolutely restricted* to the Drepanines. Mr. Rothschild in his work on Laysan makes the astonishing statement that the Meliphagine Moho has a similar and even more powerful odour; but this is only one of those errors which, for want of due care, the museum naturalist is liable to make in opposing facts ascertained and proven in the

> field. The explanation is very simple: the Moho. . .freshly killed or alive has no such odour. The specimens supposed to possess it had no doubt been enclosed in boxes with Drepanines, or when collected in the field had been placed in a bag with them, and had thus become impregnated with their odour.

In addition to the genera mentioned above, Perkins (1903) also reported the odor in Pseudonestor and Palmeria, and I have noticed it in Oreomystis bairdi. Not surprisingly, Paroreomyza lacks the scent (Wilson and Evans 1890-99; pers. obs.). This odor is still noticeable in specimen cases that house 80-year-old drepanidine skins at the Bishop Museum in Honolulu, and I agree fully with Perkins that it is peculiar to the honeycreeper subfamily. The biochemical basis for this odor, as well as its biological significance, is unknown and deserves close scrutiny with modern techniques. If indeed the drepanidine odor is not found in any other taxa, then the group must surely be monophyletic, with the odor present in the founder species or evolved soon after colonization.

Phylogeny

The Psittirostrini represent little divergence from the ancestral cardueline, and can therefore be considered primitive in the Drepanidinae. Phylogenetic details among the Hawaiian finches are difficult to determine, however (Banks and Laybourne 1977). All genera show relict distributions except Psittirostra, and thus we might expect it to be the most recently evolved, most highly derived form, and indeed it appears to be. Further, the widespread occurrence of P. psittacea without subspeciation shows it to be in an earlier stage of its "taxon cycle" (see Section 11) than the other genera. Earlier authors (Perkins 1903; Amadon 1950; Baldwin 1953) attributed the lack of differentiation of this species to frequency of interisland dispersal. Certainly, this bird does make long flights over the forest, but I doubt that any significant amount of interisland gene flow occurs (or could occur if the birds were still as numerous as formerly). I believe rather that Psittirostra is a recently evolved successful species that has simply had insufficient time to exhibit divergence. The Hemignathus [virens] superspecies appears to be as dispersable as Psittirostra, but is well differentiated into species and subspecies.

Telespyza, as discussed previously, is clearly the most primitive genus of the Psittirostrini. Its streaked plumages can be regarded as the primitive type from which the unstreaked ones are derived. Laysan and Nihoa Finches also possess the primitive song type, and a relatively unspecialized finch bill. The more specialized bills of Loxioides, Chloridops, and Psittirostra are derived from the simpler type, each being an adaptation to a particular food. A tentative phylogenetic sequence based on vocalizations and bill shape can be suggested. The song of Rhodacanthis palmeri may be derived, but its bill resembles those of Telespyza. A trend toward reduction in both the amount of singing and the complexity of the song is seen in Loxioides and Chloridops and in general shape, the bills of these two more closely resemble each other than either does that of any other Hawaiian finch. Thus I tentatively consider them to be sister groups. A possible branching sequence is shown in Figure 15.

Disagreement has occurred as to which of the two other tribes represents the older radiation. Amadon (1950) considered Hemignathus virens the most primitive species in the subfamily, but Baldwin (1953) argued that Himatione sanguinea represented a closer approximation of the ancestral type. Both authors considered generalized species more primitive than specialized ones, but such need not always be the case. Several facts suggest that both species are recently evolved and not at all primitive. The first is the zoogeographical consideration that both species are in relatively early stages of their taxon cycles. As in the case of Psittirostra, Himatione is undifferentiated at the subspecies level on the main islands. Again, this fact might be attributable to frequent interisland dispersal, but I do not believe sufficient dispersal occurs to prevent subspeciation. A consideration of the subgenus Viridonia supports this supposition. These birds appear to be easily dispersable as shown by the occurrence of two examples of double invasion in the subgenus. The differentiation shown by Hemignathus (Viridonia) [virens] indicates that this complex may be an older taxon than Himatione, but not particularly so. The Hemignathini comprise several such apparently young taxa, and thus appear to be a rapidly evolving group. That many "intermediate" types survive in this lineage (Bock 1970) also suggests a relatively recent radiation.

The Drepanidini include two apparently young species, both of which are allied with older species with restricted distributions. This fact can be readily explained by a consideration of the islands' floral history. The Lobeliaceae apparently represent a very ancient colonization and have undergone an adaptive radiation in the islands comparable to that of the Drepanidinae. But *Metrosideros collina*, which now dominates the Hawaiian native forests, is a recent arrival and is considered by most botanists to be conspecific with a Tahitian form (Carlquist 1970). The genus is widespread in Polynesia. Perkins (1903) recognized the recency of the arrival of *Metrosideros*, and believed the honeycreepers evolved primarily before its arrival. If such were the case, we could expect those species that were able to take advantage of this new food resource to have begun a new phase of expansion and thus to be at the start of new taxon cycles, while those ancient forms adapted to the Lobeliaceae would be old taxa with relict distributions. That is precisely what is reflected by the Drepanidini and Hemignathini today. The relationship between the curved corollas of lobelioid flowers and the curved bills of many honeycreepers has been cited many times (Perkins 1903; Spieth 1966; Carlquist 1970), but *Metrosideros* requires no such close "fit." Thus the sickle-shaped bill of *Drepanis coccinea* probably evolved before the arrival of *Metrosideros*, and was preadapted to feeding on that plant. This adaptation may have allowed a former relict to begin a new expansive cycle. The Drepanidini can thus be viewed as a collection of relict types that reflect a very early radiation following the development of the tubular drepanidine tongue.

Ciridops is probably the most primitive genus of the Drepanidini. Its bill is closest to the finchlike ancestral type, its immatures retain green coloration lost in other members of the tribe, and its partly frugivorous feeding habits resemble those of the primitive Psittirostrini. *Drepanis* probably evolved more or less directly from such a short-billed ancestor. For the reasons given above, I consider it a more primitive genus than Himatione. This latter genus is closely allied with Palmeria and might well be united with it. The two are very close in bill morphology, postures, and vocalizations (Perkins 1903; pers. obs.) but Palmeria exhibits at least one myological difference that Raikow (1977b) considered important, and has the most bizarre plumage of the entire subfamily.

Characters that may be regarded as primitive in the Hemignathini include the tubular tongue and the occurrence of nest sanitation, both shared with the Drepanidini but not with the Psittirostrini. Derived characters include the short call notes and adaptations to insectivory, both occurring in varying degrees in all hemignathine genera but not in the other tribes. Pseudonestor, as discussed previously, is an early offshoot that belongs to the same evolutionary "grade" as the other Hemignathini, but which cannot be united with them genealogically. The "main line" of hemignathine phylogeny can be seen as that leading to the genus Hemignathus. Loxops may be primitive, since the bills, songs, and general appearance of its two species are finchlike, but these characteristics may be superficial. Oreomystis probably diverged from the main line fairly early, abandoning nectarivory entirely. Hemignathus itself is in an early stage of a rather complex radiation. Other authors (Amadon 1950; Bock 1970) have envisioned a trend toward lengthening of the down-curved bill, but I believe the trend may well have been first for lengthening of a straight bill followed by down-curving. This idea would help to explain why the short-billed subgenus Viridonia seems to be the most recent and most rapidly expanding group. Also, I do not believe that the subgenera Heterorhynchus and Hemignathus (sensu stricto) can be united. The latter is more closely related to the short-billed group than to Heterorhynchus as shown by many vocal, plumage, and ecological characters. Thus I see Heterorhynchus as an earlier offshoot within the genus. The degree of species-level differentiation shown by that subgenus bears out this observation.

Figure 15 summarizes the phylogeny presented here, with the branching points clearly indicated.

Figure 15. Phylogeny of the Drepanidinae to the level of the subgenus. This diagram should not be interpreted strictly as either a cladogram or a phenogram. Numbered characters are as follows:

1. Drepanidine odor; truncate proximal end of tongue.
2. Broad-spectrum feeding habits.
3. Increasing insectivory.
4. Adaptations to feeding on soft fruits (hooked bill, partial nasal opercula).
5. Seed-eating specializations.
6. Loss of streaked plumage.
7. High, arched, thick bill; loss of streaked plumage.
8. Enlargement and lengthening of bill.
9. Adaptations for egg-eating.
10. Adaptations for feeding on *Koa*; loss of streaked plumage.
11. Extreme enlargement of bill, adaptations for feeding on *Myoporum*.
12. Small, blunt bill adapted to feeding on *Sophora*.
13. Parrotlike bill; bark-shredding and twig-crushing adaptations.
14. Smaller, longer bill; tubular tongue; full nasal opercula.
15. Increased insectivory; soft, green plumage; simple trilled song.
16. Increased nectarivory; hard, red and black plumage; Meliphagid-like songs; loss of plantaris muscle.
17. Bark-foraging adaptations: secondary simplification of tongue, loss of nasal opercula.
18. Leaf and flower-foraging specializations.
19. Short bill with mandibles crossed at tip.

Figure 15. (Contd.)

20. Down-curved bill; green plumage with black lores.

21. Lower mandible much shorter than upper.

22. Lower mandible only slightly shorter than upper.

23. Bill very long.

24. Bill short; plantaris muscle lost.

25. Tanager-like bill.

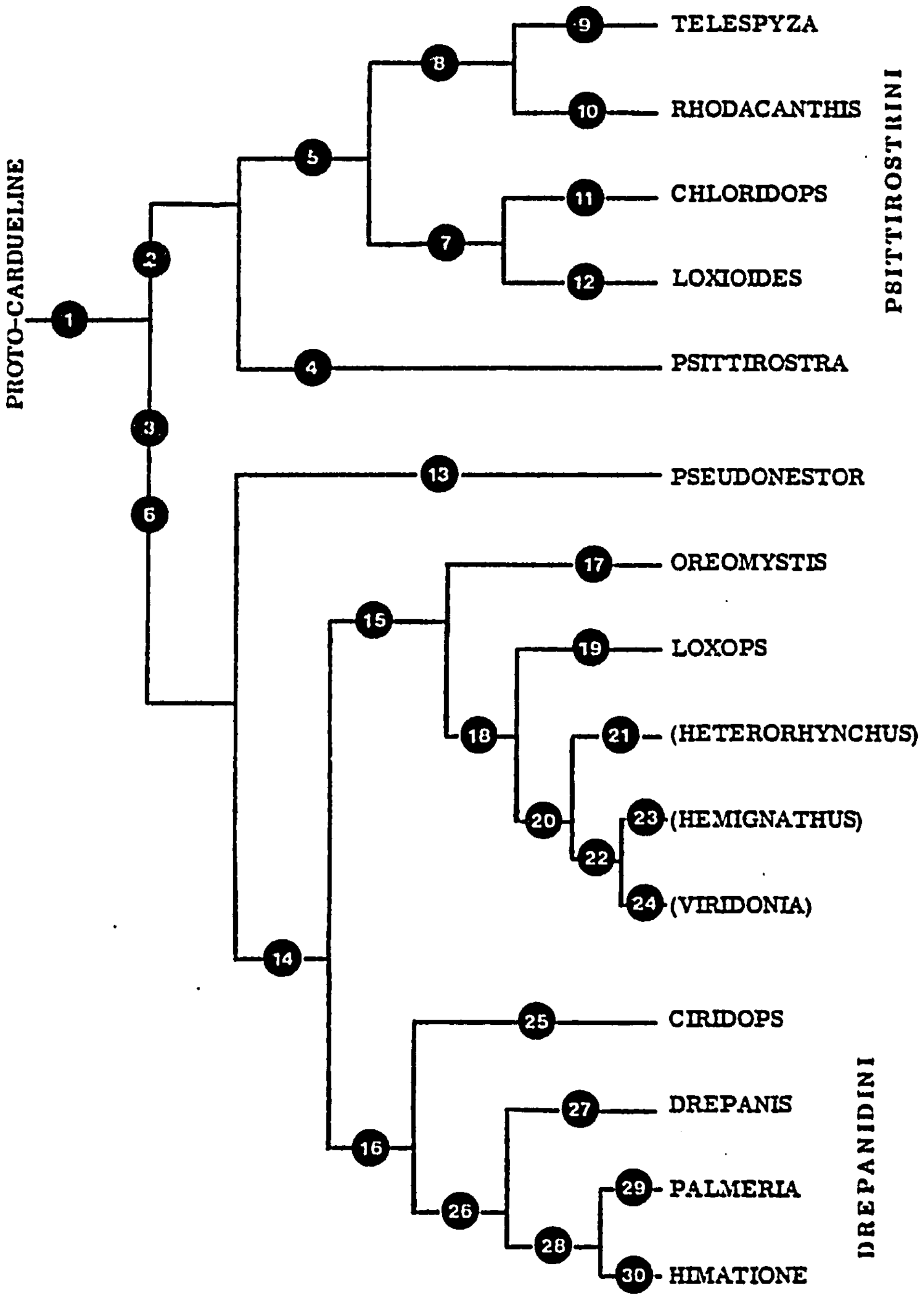
26. Thin, down-curved bill supported by bone throughout its length.

27. Bill very long, adapted to the Lobeliaceae.

28. Bill short, almost straight; feeding adaptations for Metrosideros.

29. Variegated plumage with crest; derived condition of flexor digitorum longus. Low-pitched songs.

30. Simple plumage pattern; high-pitched songs.


PROTO-CARDUELINE
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TELESPYZA
RHODACANTHIS
CHLORIDOPS
LOXIOIDES
PSITTIROSTRA
PSITTIROSTRINI
PSEUDONESTOR
OREOMYSTIS
LOXOPS
(HETERORHYNCHUS)
(HEMIGNATHUS)
(VIRIDONIA)
HEMIGNATHINI
CIRIDOPS
DREPANIS
PALMERIA
HIMATIONE
DREPANIDINI

FIGURE 15.

SECTION 6: SPECIES LIMITS AMONG THE DREPANIDINAE

The determination of species limits within closely related groups of allopatric populations is one of the taxonomist's most vexing problems. Allopatry precludes the operation of reproductive isolating mechanisms, and forces decisions at the species level to be based on inference (Mayr 1969: 196). Within an isolated archipelago such as Hawai'i, the problem is particularly acute. Mayr (1969: 197) lists three criteria that can indicate the degree of difference to be expected between species in a given taxon: 1) degree of difference between sympatric species; 2) degree of difference between intergrading subspecies within widespread species; and 3) degree of difference between hybridizing populations in related species. Only the first of these criteria is of any value within an archipelagic endemic taxon such as the Drepanidinae.

Mayr (*ibid.*) takes to task those taxonomists who consider all morphologically distinct isolated populations full species unless proven otherwise on the grounds that such classification is "impractical, because it is impossible in most of these cases ever to obtain clear-cut proof one way or the other." He further states that the "opposite extreme--considering all related allopatric forms to be conspecific--is equally wrong" but on the next page he enigmatically states: "*It is preferable for various reasons to treat allopatric populations* of doubtful rank as subspecies. The use of trinomials conveys two important pieces of information: (1) closest relationship and (2) allopatry." However, as Amadon (1966) has indicated, precisely the same information is conveyed by classifying such forms as allospecies of a superspecies, with the additional requirement that the forms in question be as distinct as other species in the same genus or related genera.

I can see no justification for adopting, as Mayr (1969) has apparently done, either philosophical extreme for classifying closely related allopatric forms. Surely an educated guess as to status is more likely to be accurate than automatically lumping such populations at the species level. While Mayr (1969: 196) is correct that no proof of species status can be obtained from consideration of potential isolating mechanisms, I do not believe that such considerations "cannot be used (except experimentally, and even then only with reservations)" (Mayr, ibid.). On the contrary, such considerations are the best source of the inferences upon which taxonomy of allopatric forms is necessarily based. In the case of vocal isolating mechanisms, playback experiments have proven very useful in determining species limits among morphologically similar allopatric forms (Lanyon 1967). Such experimental results do not, of course, prove that two forms are species, but they clearly place the burden of proof on the taxonomist who, in the face of contrary inferential information, would consider the forms conspecific.

The following analyses reflect my belief that species should be delimited among allopatric forms by reference to potential isolating mechanisms. These mechanisms can be grouped broadly into three categories: (1) morphological,

(2) ethological, and (3) ecological. Morphological characters include those features that are important in visual recognition, such as color and pattern of plumage. These factors often include such subtle things as size and shape of the bill (Lack 1947). Usually, morphological differences, particularly plumage color, are the ones most likely to be obvious to humans. Ethological isolating mechanisms include differences in vocalizations, particularly territorial songs, and displays. These mechanisms, as mentioned previously, sometimes lend themselves to experimental analysis. Ecological mechanisms are such things as differences in foraging behavior and food choices that could either prevent the two forms from meeting if they became sympatric, or could make intermediately adapted hybrids less able to compete with the parent forms. An important point here is that differences among allopatric forms need not be as well defined as differences between sympatric forms to be potential isolating mechanisms. For example, if two forms have reached species level in allopatry through the development of ethological or morphological isolating mechamisms, they need not show any ecological divergence, even though such divergence is certain to occur if the two should become permanently sympatric. By the same token, two forms that are ecologically so different that their hybrids could not survive as well as the parental types would, in sympatry, soon develop other isolating mechanisms to reinforce the ecological ones.

If clearcut morphological, ethological, and ecological differences occur between two allopatric forms, I believe the two are virtually always best considered species. But if differences occur in only one of the three categories, then the forms should be regarded as subspecies unless the differences can be shown experimentally to be effective isolating mechanisms. When no experimental evidence is available or where it is equivocal, and when no difference is apparent in one of the three types of isolating mechanisms, the decision is more subjective. In the following accounts I have followed the rule that allopatric forms showing clearcut potential isolating mechanisms in two of the three categories are species unless proven otherwise. I believe this procedure will result in a classification that is closer to the truth than one produced by wholesale uncritical lumping or splitting.

I have made extensive use of the superspecies concept (Amadon 1966) in these discussions. The Hawaiian avifauna exhibits many superspecies, as might be expected in an archipelago, but no previous author, including Amadon (1950) who later became the chief proponent of the concept, has formally designated them. Less important is the recently introduced concept of the megasubspecies (Amadon and Short 1976). Among Hawaiian birds, only Chasiempis sandwichensis exhibits megasubspecies (see Section 4). In the Drepanidinae, all forms that might have qualified as megasubspecies under Amadon's (1950) taxonomy I have found to be best treated as allospecies by the criteria outlined above.

All drepanidine genera that present alpha-level taxonomic problems are analyzed in this section with the exception of Oreomystis and Paroreomyza, whose systematic problems are so complex as to warrant separate discussion in Section 7. Alpha taxonomy of members of other families of Hawaiian birds are also discussed later.

The 'Amakihi Complex

The subgenus Viridonia comprises a group of forms that have all been called 'amakihis. They are small olive-green birds with black lores and short, down-curved bills. Those whose diets are well known are omnivores, taking insects, nectar, and other foods. The complex included three basic kinds of birds--the typical 'amakihi plus a smaller straighter-billed "lesser 'amakihi" or 'Anianiau, Hemignathus parvus, and a larger straighter-billed Greater 'Amakihi, H. sagittirostris. Some form of the "typical" 'amakihi occurs on all six main islands, while the 'Anianiau is endemic to Kaua'i and the Greater 'Amakihi (now extinct) was confined to the Big Island. Typical 'amakihis vary from island to island in plumage color and measurements, and endemic forms were described for all six islands. As I will show, however, the forms described from Moloka'i and Lana'i are not distinguishable from Maui birds. Perkins (1903) considered all typical 'amakihis, except the form stejnegeri of Kaua'i, to be conspecific. This opinion has been followed throughout the literature except that Bryan and Greenway (1944) and subsequent writers also included stejnegeri in the single species.

My analysis of variation in 'amakihis involved plumage color and measurements of wing, tail, and bill. For color, four variables were considered for males and three for females. A series of reference specimens arranged to exhibit morphoclines was used to score other specimens for each character state. The reference specimens and the character states they represent are listed in Table 5 (males) and Table 6 (females). The sample from the Big Island was assorted as to collecting locality in order to reveal any intra-island

TABLE 5.
PLUMAGE CHARACTERS AND REFERENCE SPECIMENS OF MALE 'AMAKIHIS

Character	Character State	Specimen
Color of underparts	1 (light)	202[1]
	2	3630
	3	3653
	4	3625
	5 (dark)	3686
Color of dorsum	1 (light)	4486
	3	4046
	5 (dark)	3636
Extent of black lores	1 (almost none)	1509
	2	300
	3	1532
	4	3691
	5 (extensive)	3641
Extent of yellow over the eye	1 (very little)	1498
	2	1490
	3	4575
	4	3659
	5 (very much)	3676

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[1] Bernice P. Bishop Museum catalog number.

TABLE 6.
PLUMAGE CHARACTERS AND REFERENCE SPECIMENS OF FEMALE 'AMAKIHIS

Character		Character State	Specimen
Color of breast	1	yellowish white	1501[1]
	2	a few yellow streaks	3637
	3	yellow throat and upper breast	5009
	4	yellow-green below	3687
	5	yellow-green below, darker	3654
Presence and character of wing-bars	1	two bars, broad, white	1503
	2	two bars, narrow, white	1504
	3	one bar, greenish white	4568
	4	one narrow bar, greenish white	5087
	5	no wing-bar	3650
Color and extent of eyebrow	1	small white loral spot	1496
	2	larger white loral spot	297
	3	spot extending posteriorly as narrow eyebrow	1521
	4	narrow yellow eyebrow	3697
	5	broad yellow eyebrow	3633

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[1] Bernice P. Bishop Museum catalog number.

geographic variation. The localities are the same, with some gaps, as those shown for Chasiempis (Fig. 2). The smaller islands were considered as single localities. Duncan's (1955) Multiple Range Test was used to analyze these data and to group those populations that were not significantly different ($P > 0.05$).

I found no geographically based variation in color or measurements within the island of Hawai'i despite the occurrence of 'amakihis in a wide variety of habitats on that island. I attribute this uniformity to the fact that these birds are much less sedentary than Chasiempis (see Section 4). The different islands, however, exhibit some significant differences. Males from Hawai'i are significantly darker, have more black in the lores, and have broader yellow eyebrows than 'amakihis of other islands. Females lack wingbars and are greener than others. The males also exhibit significantly shorter bills than all others, and tails that are shorter than those of the Maui, Lana'i, Moloka'i, and O'ahu populations but significantly longer than those of Kaua'i birds. The Hawai'i population thus represents a good subspecies, Hemignathus virens virens.

The populations on Maui, Moloka'i, and Lana'i show virtually no differentiation. Maui birds have longer bills than those of Lana'i and Moloka'i, but no color differences are present. Very few (n = 8) Maui specimens were available for comparison, however, so I do not consider this one difference to be of taxonomic significance. Thus the subspecies described from these three islands are poorly based and are best synonymized. The Moloka'i-Maui-Lana'i population is significantly different from all others only in the extent of the black lores, but differs from at least one other island population in every character, and thus is a recognizable taxon, Hemignathus virens wilsoni.

The O'ahu population also merits nomenclatural recognition. Males stand apart from all others in breast color (yellowest of all) and amount of yellow over the eye (least of all) and have less black in the lores than all other 'amakihis except those of Kaua'i. Females differ from Hawai'i females in breast color and wing-bars, but cannot be distinguished in this respect from Maui-Moloka'i-Lana'i birds. This race is H. virens chloris.

At this point, a clear pattern of variation emerges. O'ahu and Hawai'i represent the variational extremes in every color character, with Maui-Moloka'i-Lana'i falling in between. A similar morphocline occurs in tail length. In all characters, these populations show broad overlap even when their means differ significantly. Such differences are characteristic of subspecies and all of these forms can be referred to Hemignathus virens, the Common 'Amakihi.

The Kaua'i population, stejnegeri, stands clearly apart from the others, and does not fit the morphocline of color variation exhibited by the races of Hemignathus virens. Kaua'i 'Amakihis resemble Maui birds in breast color and amount of yellow over the eye, but are like O'ahu birds in the extent of the black lores. In tail length, bill length, and bill depth stejnegeri is significantly different from all Common 'Amakihis. No overlap occurs in bill length, and in bill depth stejnegeri shows very narrow overlap with only one subspecies (H. v. wilsoni) of the Common 'Amakihi (Figure 16).

The great divergence of stejnegeri from other 'amakihis is attributable to its sympatry with the smaller Hemignathus parvus, with resulting character

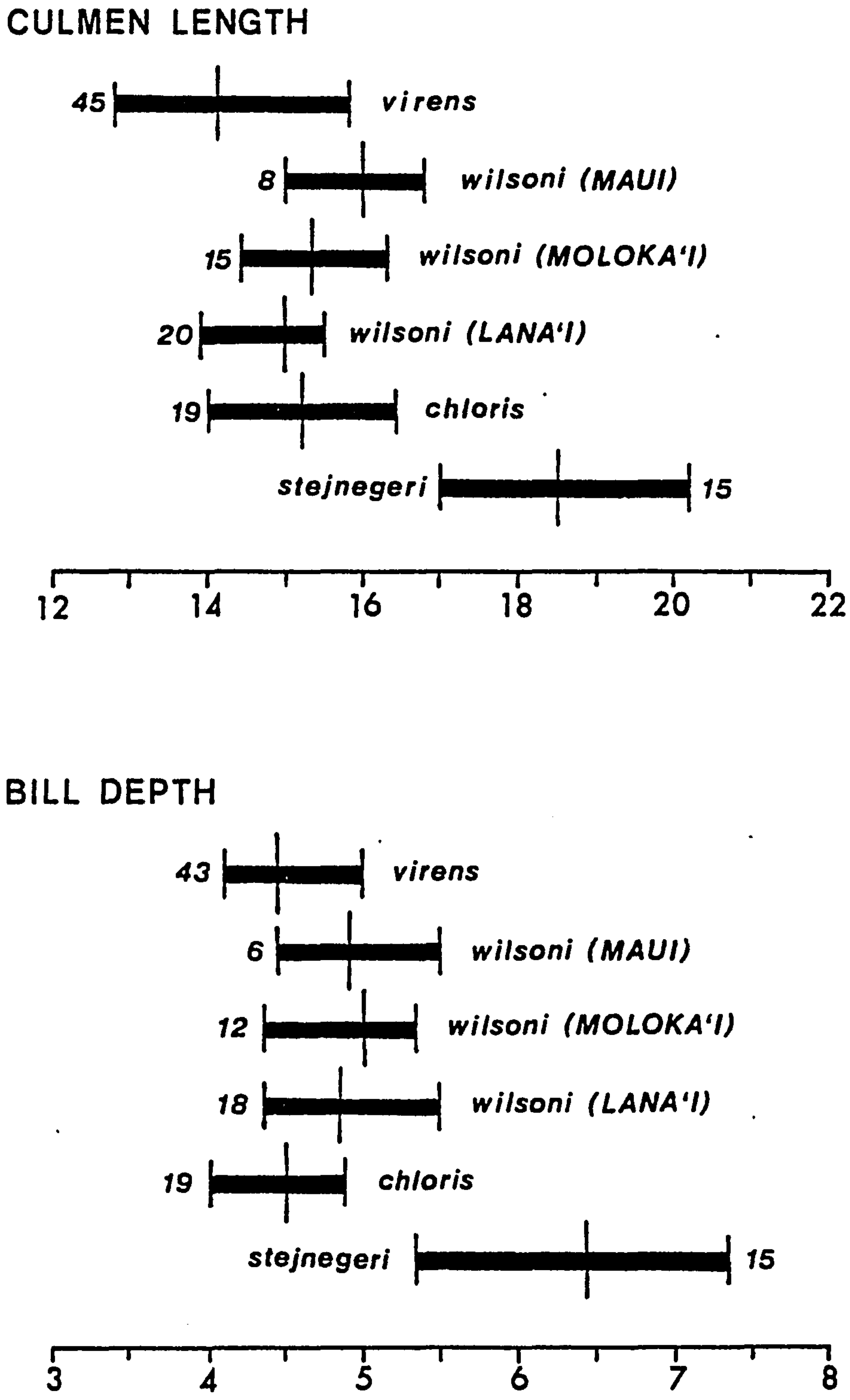

Figure 16. Measurements of bills of members of the Hemignathus [virens] superspecies. Means are indicated by long vertical lines, ranges by horizontal bars. Number of specimens examined given at ends of bars. All measurements in millimeters.

displacement (Bock 1970). Similar displacement can be seen on Hawai'i where H. sagittirostris occurred with H. virens, but there only the larger of the double-invasion species became drastically different from "typical" 'amakihis. The question that must be addressed, then, is whether stejnegeri has diverged far enough to be recognized as a species. Bock (1970) considered the point moot, but consideration of ecological and ethological factors can at least provide inferences that can be used in making the decision.

The feeding habits of stejnegeri are as different as its bill size. Not only do H. parvus and stejnegeri subdivide the usual 'amakihi niche, they broaden it considerably. The larger bird has become a bark foraging specialist, picking insects from crevices, prying with its bill, and hanging acrobatically to extract prey from the undersides of branches. In contrast, the 'Anianiau is mainly a foliage-gleaner. Both species take nectar. In general, the smaller bird more closely resembles H. virens in its movements. Certainly the possibility exists that stejnegeri could live in sympatry with H. virens.

The songs of the Kaua'i 'Amakihi (Fig. 11) differ noticeably from those of H. virens on Hawai'i and Maui (Fig. 9). The Kaua'i birds often utter a loud introductory note before the hemignathine trill, and also sing a descending trill (Fig. 11B) that may be an imitation of the song of Oreomystis bairdi (Fig. 18). To test whether these song differences might serve as isolating mechanisms, I conducted a series of playback experiments on Hawai'i and Kaua'i.

On Hawai'i the experiments occurred from 28 April to 4 May 1977. My procedure was to locate a Common 'Amakihi, preferably singing, and play a prepared tape of the Kaua'i bird's song. If the bird did not respond by vocal reply or approach, I then played a recording of a Maui 'amakihi. If still no response, I played the bird's own song or that of another Big Island individual. Many birds did not respond to any tape, but those that did showed a lack of recognition of the Kaua'i song. Only three individuals responded to that tape, and in no case did the birds utter a reply. However, 11 different birds responded by both approach and vocal reply to a Maui tape presented after the Kaua'i sequence, and in one experiment an individual that had ignored the Kaua'i tape responded to a Big Island song played inadvertently before the Maui tape.

On Kaua'i, however, the results were different. In experiments conducted on 27 and 28 January 1978 I found that Kaua'i 'Amakihis responded vigorously to playback of any 'amakihi song from any island. Perhaps noteworthy here is that the Kaua'i bird's vocal repertoire is considerably more varied than that of the Maui or Hawai'i 'amakihi. Thus stejnegeri may recognize the songs of Common 'Amakihis as being within its range of variation whereas the reverse is not true.

Other behavioral distinctions between H. virens and its Kaua'i relative include differences in territoriality. The Common 'Amakihi on Mauna Kea defends a large area that includes both the nest and major food sources (van Riper 1978), but the Kaua'i bird defends only the immediate vicinity of the nest (Eddinger 1970). Some variation is territoriality apparently can exist within a single population, however. Baldwin (1953) reported loosely held territories for 'amakihis in Hawai'i Volcanoes National Park on the Big Island.

The distinctive characters of the Kaua'i 'Amakihi seem sufficient to warrant classifying it as a separate species, *Hemignathus stejnegeri*. Nevertheless, the Kaua'i bird has only barely passed the species threshold. Incipient isolating mechanisms are present but not clearcut. Ecological and morphological differences are more striking, but the close relationship of *H. stejnegeri* and *H. virens* is obvious. These two forms are thus allospecies of the superspecies *Hemignathus* [*virens*].

The 'Akialoas

The subgenus *Hemignathus* includes birds with very long decurved bills, the mandibles being subequal in length. These birds are known collectively as 'akialoas. Forms have been described from Hawai'i (*obscurus*), Lana'i (*lanaiensis*), O'ahu (*ellisianus*), and Kaua'i (*procerus*). Originally considered separate species, all four forms were included in *H. obscurus* by Bryan and Greenway (1944). Amadon (1950: 169),however, stated that "*procerus* has such a strikingly larger bill that it is best treated as a species, forming with *obscurus* a superspecies." If Amadon's classification is correct, the 'akialoas exhibit a pattern of variation parallel to that of *Hemignathus* [*virens*].

Unfortunately, data on these birds are very limited. The O'ahu and Lana'i forms are known from only a few specimens. Amadon (1950) saw no examples of *ellisianus*, and only two immature specimens of *lanaiensis*. Good series of both *obscurus* and *procerus* exist, but the only sources of behavioral ecological information are accounts of early naturalists. The Hawai'i form is believed to be extinct, and the last published report of the Kaua'i bird was that by Huber (1966) of a sighting in 1964, although P. Bruner (pers. comm.) saw one individual in 1968 or 1969.

Perkins (1903: 422) stated that the various 'akialoas "differ but little in their habits from one another, centainly not more so than do the individuals of a single species." He also used a single description for vocalizations of both procerus and obscurus, with no indication that they differed in any noticeable way. Nevertheless, the bills of procerus and obscurus are highly divergent in both absolute and proportional size, and show no overlap. The question, then, is whether these measurements may simply represent the extremes of a morphocline. I believe the evidence indicates that they do.

Amadon (1950: 181) listed the mean culmen length of obscurus as 43.2mm, with a range of 41-47 mm. However, Wilson and Evans (1890-99) gave a measurement of 1.85 in (=47 mm), presumably an average. Amadon's (1950) data for 11 procerus males show a range of 65-72 mm, with a mean of 68.1, compared to 2.8 in (=71 mm) from Wilson and Evans (1890-99). The slightly larger measurements of Wilson and Evans probably indicate a difference in methods; Amadon measured from the anterior edge of the nostril, but earlier authors probably measured the culmen from its insertion into the feathers.

The first published measurements of lanaiensis were those of Rothschild (quoted by Wilson and Evans 1890-99), which indicate a culmen between 2.9 and 3.1 in (=74-79 mm), thus showing it, rather than procerus, to be the longest-billed form. Amadon's (1950) two immature specimens, however, have much shorter bills (both 53 mm).

Published data for bill length of ellisianus are difficult to interpret. Liechtenstein (quoted by Wilson and Evans 1890-99) gave a measurement of 1 3/4 in (=44.5 mm) for the bill, but this is surely an error. Such a measurement would give this form a bill as short as that of obscurus, and one proportionally the smallest of all among 'akialoas. In body length, ellisianus (7 in = 175 mm) is only slightly smaller than procerus (7.5 in = 191 mm) and considerably larger than obscurus (5.5 in = 140 mm) in measurements given by Wilson and Evans (1890-99). But these authors' figure, presumably done from a specimen, shows a bird with a bill proportionally longer than that of obscurus. In fact, the figure itself in a recent reprint of that work, although obviously reduced in size, has a bill measuring 39 mm.

The "strikingly larger bill" upon which Amadon (1950) based his recognition of procerus as a species is thus a spurious character. In the absence of any corroborating ethological or ecological differences, I see no basis for excluding procerus from the single 'Akialoa species Hemignathus obscurus.

The Nukupu'us

The subgenus Heterorhynchus comprises four forms of bark-picking curve-billed drepanidines in which the lower mandible is about half the length of the upper. All have been called nukupu'us, but the distinctive Big Island bird, whose lower mandible is straight rather than curved as in the Maui, O'ahu, and Kaua'i forms, is usually called the 'Akiapola'au. As with the 'Akialoa, the various island forms were considered four species by earlier writers. Bryan and Greenway (1944) considered them all conspecific, but Amadon (1950) separated the 'Akiapola'au from the typical Nukupu'u (Hemignathus lucidus) on the basis of its very different feeding apparatus. Amadon considered these two as comprising a superspecies, but I think their differences are great enough to cast doubt on the propriety of such classification.

These birds have not been previously grouped generically with the 'amakihis (subgenus Viridonia), but have usually been classed with the 'Akialoa (H. obscurus). Based on considerations of plumage color, feeding habits, and songs (see Section 5) I believe the 'Akialoa shares a more recent common ancestor with the 'amakihi group than with the nukupu'us. However, all three taxa are closely related and I consider them congeneric. This action has the unfortunate result of requiring a new specific epithet for the 'Akiapola'au. That species was originally named Heterorhynchus wilsoni (Rothschild, 1893 [November], The Avifauna of Laysan, pt. 2, p. 97). In April of that year, Rothschild (1893, Bull. Brit. Orn. Club, 1: 42) described the Maui 'amakihi as Himatione wilsoni. The latter name has priority in the genus Hemignathus, and is the name for the subspecies H. virens wilsoni found on Maui, Moloka'i, and Lana'i. I therefore propose that Rothschild's (1893) Heterorhynchus wilsoni (= Hemignathus wilsoni of Amadon 1950) be renamed

Hemignathus munroi nom. nov.

in honor of George C. Munro, Palmer's field assistant, author of Birds of Hawaii (Munro 1944 [1960]), and founder of the Hawaii Audubon Society.

The 'Ākepas

Each of the four largest Hawaiian Islands is inhabited by a small finch-like bird whose mandibles are slightly crossed at the tip. These birds comprise the genus Loxops. The forms inhabiting Hawai'i (coccineus), Maui (ochraceus), and O'ahu (rufus) are rather similar with red males and olive-green females, although the Maui males are apparently dimorphic with some adult males being a peculiar mustard yellow and others bright orange-red. Bryan and Greenway (1944) considered these forms to comprise a single species, the 'Ākepa, Loxops coccineus. The Kaua'i representative is somewhat larger and much less sexually dimorphic. Both males and females are green-backed yellow birds with black faces, but males are brighter. The Hawaiians used the name 'Ō'ū-holowai for the Kaua'i birds. The color difference between the two Loxops is so striking that Wilson (1889) placed the Kaua'i form in a separate genus, Chrysomitridops. However, the peculiar bill configuration clearly showed the relationship to Loxops and Chrysomitridops was soon synonymized with it (Henshaw 1902b; Perkins 1903). The 'Ō'ū-holowai, L. caeruleirostris, was considered conspecific with L. coccineus by Amadon (1950) who has been followed by all subsequent writers. The data presented below, however, indicate that L. caeruleirostris does indeed deserve species status.

Even a cursory examination of Loxops caeruleirostris and L. coccineus reveals that the bill of the former is larger. However, Amadon (1950) obscured the difference by measuring only the culmen length. My own measurements (Table 7), analyzed using Duncan's (1955) Multiple Range Test, show L. caeruleirostris to possess a significantly ($P < 0.05$) wider and deeper bill than L.

TABLE 7.
MEANS, RANGES, AND STANDARD DEVIATIONS (BRACKETS) FOR BILL MEASUREMENTS OF MALE *Loxops*

Taxon	n	Width	n	Culmen	n	Depth
caeruleirostris	23	5.3 [0.25] (4.8-5.8)	23	11.1 [0.37] (10.5-12.0)	24	5.4 [0.33] (4.4-6.0)
rufus	6	4.6 [0.19] (4.3-4.9)	6	10.0 [0.45] (9.6-10.8)	4	4.8 [0.26] (4.5-5.1)
ochraceus	12	4.9 [0.14] (4.7-5.2)	16	10.8 [0.67] (9.4-11.8)	11	5.0 [0.36] (4.4-4.5)
coccineus	41	4.9 [0.28] (4.5-5.8)	39	10.8 [ ] (9.9-11.6)	35	4.7 [0.28] (4.2-5.5)

coccineus, but with no significant difference in culmen length. Thus the bill of the Kaua'i bird is qualitatively different in shape. The other extreme is shown by *L. coccineus rufus*, with a significantly shorter and narrower bill than other 'Ākepas. These differences are probably all related to subtle ecological distinctions.

Both species of *Loxops* feed in the imbricated buds of *Metrosideros*. Richards and Bock (1973) describe possible ways in which the crossed bill is used in feeding. Both species also take nectar, but I have seen *L. caeruleirostris* feeding in flowers much more often than *L. coccineus*.

The two *Loxops* also differ vocally. Call notes (Fig. 14) as well as songs (Fig. 12) differ noticeably. The songs of *L. coccineus rufus* and *L. coccineus ochraceus* are unknown, but that of the nominate subspecies is a long, rather lackadaisical, loose trill. The song of the 'Ō'ū-holowai is also a trill, but is much more energetic than that of the 'Ākepa and has a ringing quality. Both songs vary considerably from one strophe to the next, unlike the stereotyped songs of *Hemignathus*. To test whether the two allopatric species could distinguish between their respective songs, I carried out a series of playback experiments similar to those described earlier for the 'amakihis, but the results were enigmatic. On Hawai'i during 1-5 May 1977 I found 'Ākepas to be generally unresponsive to playback of even their own songs. However, four individuals that had ignored the song of a Kaua'i bird gave vocal response (no approach) to a Hawai'i tape and four others responded to the latter tape by approach after showing no recognition of the Kaua'i tape. Two birds, however, did respond to the 'Ō'ū-holowai song, one by vocal reply, the other by approach. On Kaua'i during 27-30 January 1978 I again noted frustratingly low responsiveness to recorded songs. Two individuals, after ignoring the Hawai'i tape, responded vigorously to the Kaua'i one by approach and song. In one instance, I played the 'Ākepa tape close to a male 'Ō'ū-holowai that was calling and actively foraging. The bird did not alter its behavior in any noticeable way. After allowing about ten strophes of the Hawai'i song to play, I switched to the 'Ō'ū-holowai 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 strong response by any Kaua'i *Loxops* to the voice of the 'Ākepa. However, many of these experiments cannot be adequately evaluated because by the time I presented the 'Ō'ū-holowai song, the subject would often have wandered away. When Kaua'i songs were presented first, however, response was fairly consistent. Further experiments will be necessary before the significance of song in species recognition in *Loxops* can be adequately evaluated.

Although the data are limited, the two *Loxops* appear to differ also in nesting behavior. Several nests of the Kaua'i bird were built in the crowns of 'ōhi'a trees (Eddinger 1972a) but the only known nest of the Hawai'i form was found near the ground in a tree cavity (Sincock and Scott, in press). In view of this apparent difference, as well as the obvious morphological and vocal divergence, I feel justified in classifying the two *Loxops* as allospecies of the superspecies *Loxops* [*coccineus*].

The Koa Finches

Considerable taxonomic controversy has surrounded the genus *Rhodacanthis* since its discovery by Henry Palmer in 1891 (Munro 1944). When Rothschild (1893-1900) examined the specimens, he described two species: *R. palmeri*, a larger orange-headed form, and *R. flaviceps*, smaller and with a yellow head. The description of *R. flaviceps* was based on two males and six females. These specimens were, according to Munro (1944), obtained in the same locality, on the same days, and from the same koa trees as the larger specimens. The smaller finch was never again found, but *R. palmeri* was collected subsequently by Perkins (1903). He was skeptical of the validity of the smaller species, and Munro (1944), who participated in the collection of the type series, was particularly so. Bryan and Greenway (1944) listed *flaviceps* with a question mark, and expressed concern that the problem of its validity could never be solved since all *Rhodacanthis* were by then extinct. Amadon (1950) re-examined the specimens and considered the existence of two males in the group as removing "whatever doubt may still have existed as regards the specific validity of *flaviceps*."

I have also examined these specimens and I cannot share Amadon's confidence in the existence of two species. Several male specimens of *palmeri* are virtually identical to the type of *flaviceps* in color, but are marked "juv." or "imm." How these age determinations were made is not known, but certainly head color cannot be considered a diagnostic character for separating *flaviceps* from *palmeri*. Females of the two forms are indistinguishable in color.

Measurements likewise provide little support for the recognition of two species of *Rhodacanthis*. Four different measurements of the specimens in the Bishop Museum and the American Museum of Natural History are presented in Figure 17. The only clear dichotomy occurs in the length of the tail, a factor that is strongly affected by feather wear. Noteworthy, therefore, is that two of the female *flaviceps* and the single male (the type) are in a state of extreme wear, whereas four of the five female specimens and all but four of the males of *palmeri* are in fresh plumage. I believe feather wear can easily account for the shorter wing and tail measurements of *flaviceps*.

The two measurements of the bill show overlap between the two forms. An important observation is that the smallest-billed specimens of *palmeri* are immatures, perhaps indicating that the bill increases in size as the birds mature. Thus "*flaviceps*" may be merely the smallest and most heavily worn first-year individuals of *Rhodacanthis palmeri*. Of course, this hypothesis can be tested only if a remnant population of Koa Finches is found, an unlikely possibility. Recent searches in their former range have failed to rediscover the species (J. M. Scott, pers. comm.). However, the preponderance of evidence indicates that the specific validity of *R. flaviceps* is doubtful.

The Leeward Island Finches

My research included no first-hand observation of these birds in the field, and the following review is based mostly on the literature. The finches of Laysan (*Telespyza cantans*) and Nihoa (*T. ultima*) had been considered conspecific by all recent authors, but Banks and Laybourne (1977) believe, in my opinion correctly, that the two should be classed as separate species.

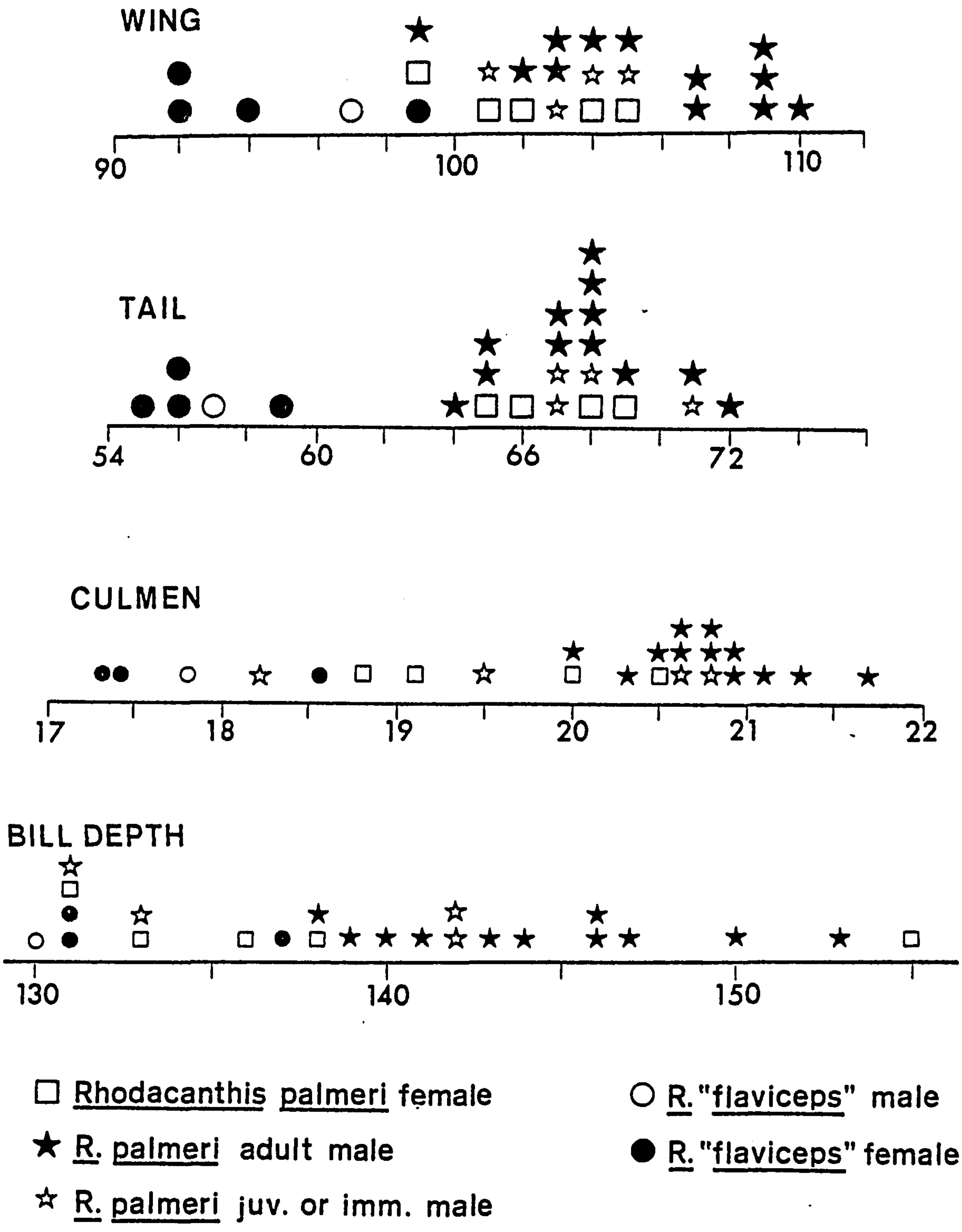

Figure 17. Measurements of Koa Finches, genus Rhodacanthis. Each symbol represents one specimen. All measurements in millimeters.

These authors found that T. cantans requires three years to attain its adult plumage whereas T. ultima does so in two. Also, the Laysan Finch has a single prebasic annual molt whereas the Nihoa bird has two molts (prebasic and a partial prealternate). Differences in size and color between the two finches are striking, T. cantans being a much larger bird (Banks and Laybourne 1977). Laysan Finch males are yellower than male Nihoa Finches, and the latter is blue-gray on the back whereas the former is brownish gray. The most obvious color differences, however, occur among females. Female Nihoa Finches are heavily streaked above and below with dark brown, but the streaks are much less prominent in Laysan females.

Some differences have also been reported in breeding biology. The Laysan Finch nests, with rare exceptions (Bailey 1956), at the bases of grass tussocks (Ely and Clapp 1973) but the Nihoa Finch nests in rock cavities (Richardson 1954; Clapp et al. 1977).

Vocalizations of the Leeward Island finches have not been adequately studied. I have listened to tape recordings of both species made by R. Coleman (USFWS) during the summer of 1978, and can report that the calls and songs, though similar, have noticeable differences. Evaluation of these distinctions must await additional data.

I believe these numerous biological differences between the two forms indicate a high degree of genetic divergence. I see nothing to be gained by considering these birds conspecific, and I believe to do so would obscure important distinctions.

SECTION 7.

SYSTEMATICS OF THE HAWAIIAN "CREEPERS"

Each of the six main Hawaiian Islands originally possessed an endemic, small, straight-billed, simple-tongued, insectivorous bird. These birds varied widely in plumage color, and their varying Hawaiian names reflect the distinctions. Several of the forms are now beyond the possibility of field study since the Lana'i population is extinct (Hirai 1978) and the Moloka'i (Scott et al. 1977) and O'ahu (Shallenberger and Pratt 1978) forms are nearly so. Although the Hawai'i form is endangered (USFWS 1975), it still occurs in sufficient numbers to provide meaningful data (Pratt et al. 1977) as do the healthier populations on Kaua'i and Maui. The relationships of these forms among themselves and within the Hawaiian honeycreeper complex provide one of the most difficult and intriguing systematic problems in the archipelago. In order to be as taxonomically noncommittal as possible, I shall initially discuss these forms using only their trivial scientific names as follows: bairdi (Kaua'i), maculata (O'ahu), flammea (Moloka'i), montana (Lana'i), newtoni (Maui), and mana (Hawai'i). The English name "creeper" was first asssociated with this complex when Henshaw (1902b) referred to mana as the Olive Green Creeper. Munro (1944) extended the use of the term to the other forms as well.

At first, the creepers were allocated among several genera (Wilson and Evans 1890-99; Rothschild 1893-1900) but soon a consensus developed that these birds were all closely related (Henshaw 1902b; Perkins 1903). These early authors considered all the forms different species in the genus *Oreomyza*. Perkins (1903) recognized two subgenera, *Oreomyza* and *Paroreomyza*, and when the former name was found to have been preoccupied, the latter became that of the genus, despite Stejneger's (1903) emendation of his earlier name to *Oreomystis*. The type of *Oreomystis* (=*Oreomyza* Stejneger 1887) was *bairdi* but that of *Paroreomyza* was *maculata*.

Perkins' (1903) subgenera were not recognized by subsequent authors, but Bryan and Greenway (1944) divided the genus into only two species along the same lines: *P*. *bairdi* (including *mana*) and *P*. *maculata* (including *flammea*, *montana*, and *newtoni*). Amadon (1950) considered all the creepers conspecific and made *Paroreomyza* a subgenus of *Loxops*. He considered this taxonomy more "convenient" (*ibid*.: 166) than the alternative of recognizing five species (*newtoni* and *montana* being conspecific by "almost any standard"). No author since Amadon has challenged the validity of "the Creeper" as a single species. However, Raikow (1977b) questioned the inclusion of the species in *Loxops* on the basis of differences in the limb musculature, and once again raised *Paroreomyza* to generic level. In Section 5 I outlined a new classification for the creepers that recognizes five species arranged in two genera. Although these genera correspond to the subgenera of Perkins (1903) and the two species of Bryan and Greenway (1944), I do not believe the two groups are, in fact, closely related.

My field studies of Hawaiian creepers have concerned only the forms of Kaua'i, Maui, and Hawai'i. From my earliest acquaintance with these birds I realized that those of Maui (newtoni) stood clearly apart from the other two. That realization was based initially only on an overall impression. The specific morphological and behavioral characters that contribute to the Maui creeper's distinctive "gestalt" all seem rather subtle individually, but taken together they give the bird a strikingly different image from that of mana and bairdi. That this divergence has not been emphasized by earlier authors is largely attributable to their lack of experience with the birds in life. But Perkins (1903), with his extensive field experience in the islands, recognized the dichotomy, and Henshaw (1902b: 49) remarked about the "marked difference in habits between species so closely allied" when discussing mana and newtoni.

Character Analysis

Perkins (1903) defined his subgenera on the basis of two characters, degree of development of the nasal setae and presence of sexual plumage dimorphism in adults. Amadon (1950) considered these characters to be of only subspecific nature, but did not consider any other characters that might have lent weight to Perkins' subdivisions. Of course, Perkins had behavioral and ecological observations to confirm his classification and simply used two obvious morphological ones to define the taxa. If these differences represented random variation among an array of subspecies, as Amadon claims, then other variation should occur as a mosaic of patterns among the geographical forms.

However, as I will demonstrate, every character that varies among the creepers does so along the same lines, with *mana* and *bairdi* standing in contrast to the other four forms.

Morphology

The shape of a bird's bill contributes to its characteristic "facial expression." However, subtle differences in shape may escape detection in the usual type of morphometric study, and such has been the case with the creepers. The different "look" of *newtoni* as compared to *mana* and *bairdi* is apparent both in the field and, to a lesser extent, in study skins. Its somewhat wood warbler-like look is shared by specimens of *montana*, *flammea*, and *maculata* and these four can be called the "*newtoni* group." The bills of the two groups are qualitatively different in shape, but bill measurements (Tables 8 and 9) do not reveal the difference. The Kaua'i and Hawai'i birds have slightly down-curved bills, whereas those of the *newtoni* group are essentially straight, even though the culmen is arched. The most important difference is in the profile of the gonys which in the *newtoni* group is straight or convex, *never concave*. In *bairdi* and *mana* the gonys is always at least slightly concave. Bills of Hawaiian creepers are illustrated in Figure 18. Richards and Bock (1973) described the bills of these birds in precisely opposite terms, considering the bill of *mana* to be straight and those of *newtoni* and *flammea* to be decurved. The difference may simply be semantic, but their description of *flammea* as having "the most decurved bill, one that is almost as curved as that of [*Hemignathus*] *virens* but stouter" (Richards and Bock

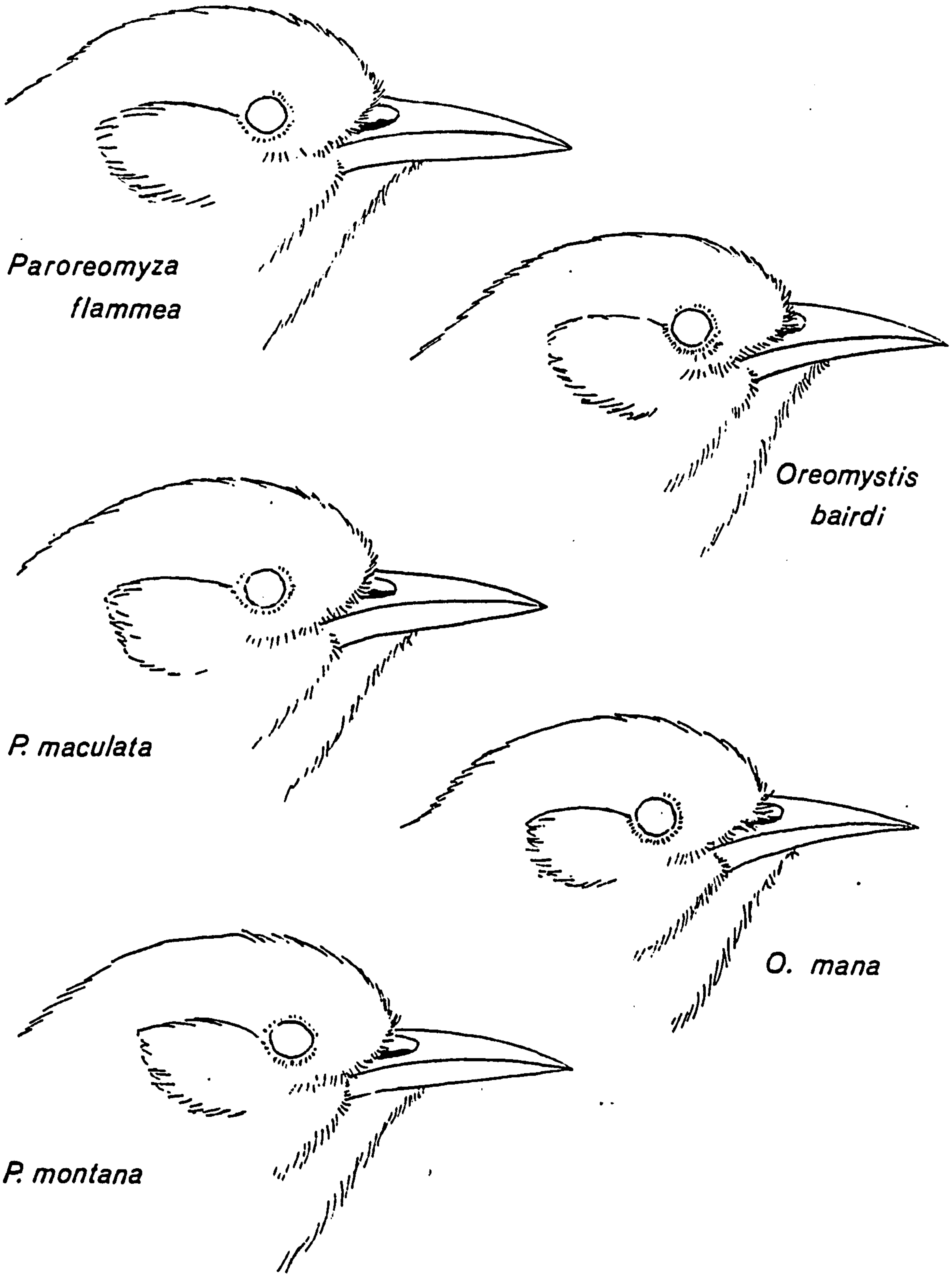

Figure 18: Heads of five species of Hawaiian "creepers."

TABLE 8.
MEASUREMENTS OF MALE HAWAIIAN "CREEPERS" WITH MEAN, STANDARD DEVIATION (BRACKETS), AND RANGE (PARENTHESES)

Population	n	Wing Chord	n	Tail Length	n	Bill Width	n	Culmen	n	Bill Depth
bairdi	15	52.6 [2.61] (49 - 59)	15	39.3 [2.19] (35 - 44)	15	4.92 [0.21] (4.6 - 5.4)	15	13.0 [0.66] (12.2-14.6)	14	5.28 [0.24] (4.9 - 5.7)
maculata	20	53.1 [1.74] (50 - 56)	22	46.0 [2.65] (40 - 51)	20	5.01 [0.35] (4.3 - 5.5)	21	13.8 [0.50] (12.7-14.6)	20	4.56 [0.26] (4.2 - 5.0)
flammea	28	50.2 [1.72] (47 - 54)	25	51.7 [2.26] (47 - 56)	26	5.23 [0.26] (4.8 - 6.0)	27	14.3 [0.68] (13.1-15.5)	24	4.49 [0.31] (3.9 - 5.0)
newtoni	20	49.9 [1.86] (47 - 54)	19	45.4 [1.46] (42 - 48)	20	4.67 [0.29] (4.2 - 5.3)	21	12.2 [0.54] (11.2-13.2)	19	4.06 [0.25] (3.7 - 4.6)
montana	14	46.4 [1.31] (43 - 48)	14	47.2 [0.97] (45 - 49)	14	4.41 [0.17] (4.1 - 4.7)	15	12.7 [0.60] (11.4-13.7)	14	4.00 [0.24] (3.6 - 4.6)
mana	42	51.9 [1.68] (48 - 55)	45	40.8 [2.17] (37 - 47)	47	4.57 [0.20] (4.1 - 5.0)	48	12.6 [0.64] (11.1-14.1)	39	4.86 [0.33] (4.1 - 5.5)

TABLE 9.
MEASUREMENTS OF FEMALE HAWAIIAN "CREEPERS" WITH MEAN, STANDARD DEVIATION (BRACKETS), AND RANGE (PARENTHESES)

Population	n	Wing Chord	n	Tail Length	n	Bill Width	n	Culmen	n	Bill Depth
bairdi	11	52.0 [1.61] (49 - 54)	11	38.8 [1.94] (36 - 42)	11	5.05 [0.22] (4.8 - 5.5)	9	12.5 [0.37] (12.2-13.0)	10	5.02 [0.27] (4.6 - 5.5)
maculata	12	49.7 [1.92] (47 - 54)	21	42.2 [2.16] (38 - 46)	21	4.71 [0.22] (4.2 - 5.0)	21	12.5 [0.54] (11.6-13.7)	20	4.40 [0.37] (3.8 - 5.2)
flammea	15	48.0 [1.73] (45 - 51)	15	47.9 [2.50] (44 - 52)	11	4.90 [0.29] (4.5 - 5.4)	14	12.5 [0.80] (11.0-14.1)	10	4.26 [0.25] (3.8 - 4.6)
newtoni	6	48.7 [1.21] (47 - 50)	6	45.3 [2.07] (42 - 48)	6	4.63 [0.43] (4.2 - 5.2)	6	11.5 [0.56] (10.8-12.3)	6	3.82 [0.09] (3.7 - 4.0)
montana	4	46.3 [1.50] (44 - 47)	3	47.7 [2.08] (46 - 50)	3	4.26 [0.15] (4.1 - 4.4)	3	11.6 [0.05] (11.5-11.6)	3	3.93 [0.05] (3.9 - 4.0)
mana	21	50.2 [1.54] (48 - 53)	23	40.3 [2.00] (37 - 45)	21	4.53 [0.23] (4.0 - 5.2)	22	12.2 [0.54] (11.2-13.1)	18	4.69 [0.23] (4.4 - 5.1)

1973) must be challenged. Not only is the description incorrect, but their illustration (ibid.: 139) is either inaccurately drawn or based on an aberrant specimen. In my examination of skins of 43 adults of flammea, I found none with the proximal two-thirds of the gonys concave as shown in that drawing. Such differences in bill morphology are not trivial and can produce very different forces when the bill is used in feeding (Bock 1966) as has been shown by Bowman (1961) for the Galapagos finches. The differences are reflected in the feeding behavior of the Hawaiian creepers (see beyond).

Both mana and bairdi have the nasal setae "well developed, so as to be able to shield the whole length of the nasal openings" (Perkins 1903: 397) but those of the newtoni group are "entirely absent, or at least very short and little developed" (ibid.) Nasal operculae are fully developed in the latter group but less so in the former (Richards and Bock 1973; pers. obs.). These differences are probably also related to different feeding modes.

The feeding apparatus of two creepers, mana and newtoni, were included in Richards and Bock's (1973) detailed study of what they considered to be representative members of a single genus. The creepers were compared with Hemignathus virens, Loxops coccineus, and to a lesser extent with H. sagittirostris. Despite these authors' contention that mana and newtoni "are far more similar to one another than are any of the other species" (ibid.: 117) included in their study, their data belie such a generalization and appear to support the taxonomic separation of the two creepers studied. In two tables the authors compare the creepers with the 'amakihi and the 'akepa on the basis of 40 cranial characters. The tables reveal 15 instances in which mana agrees with *H. virens* in a character, 15 *newtoni*-*H. virens* agreements, 19 between *mana* and *L. coccineus*, and six between *newtoni* and *L. coccineus*. But the two creepers were alike in only six characters, and in three of these they shared the character with one of the other two species! In another table, Richards and Bock (1973) rank the various jaw muscles in order of size among the four taxa. In only five cases do the muscles of *mana* and *newtoni* hold adjacent ranks, while in 12 cases they are separated by one or two numbers.

The tongues of *mana* and *newtoni* are entirely different from those of *Hemignathus* and *Loxops* (Richards and Bock 1973) and indeed from all other drepanidine genera. Both are narrow, nontubular, and bifid at the tip, with small laciniae along the lateral margins of the distal half. Some differences between them are apparent from Richards and Bock's (1973) figures, however. The lateral laciniae of *newtoni* are very delicate as compared to those of *mana*, the latter resembling more closely the illustrated laciniae of *L. coccineus*, *H. virens*, and *H. sagittirostris*. A more striking difference can be seen at the proximal end of the corneous tongue. In *mana* it is obliquely truncate, but in *newtoni* it is deeply cleft. The tongue of *bairdi*, as illustrated by Gadow (1899) resembles that of *mana* in this respect. Since the proximally truncate tongue may be a uniquely derived character in the Drepanidinae (see Section 5), its presence in one creeper type but not the other argues for separation of the two at least at the generic level.

The post-cranial anatomy of the creepers has not been adequately studied. Raikow (1976; 1977a, b) dissected only *bairdi* and apparently assumed that the other "subspecies" would resemble it. That he did not also examine a member of the *newtoni* group is unfortunate. Raikow found that *bairdi* retains the plantaris muscle of the hind limb, a muscle lost in *Hemignathus virens*, and on that basis separated the creepers from the 'amakihis generically.

Body proportions also reflect the usual pattern of variation among the creepers. The wing/tail ratios of *flammea*, *newtoni*, and *montana* are near unity, but those of *bairdi* (1.33) and *mana* (1.25) reveal them to be relatively short-tailed birds. The distinction is not clear-cut, however, since *maculata* (1.15 male, 1.18 female) is intermediate in this respect.

Coloration and Plumages

Plumage variation among the creepers is striking. Only *newtoni* and *montana* exhibit the degree of similarity usually found among subspecies. In those two, adult males are bright yellow below and on the forehead with the dorsum olive green (*montana* being slightly yellower than *newtoni*). The pattern of coloration is similar in *flammea* but throughout the plumage yellow is replaced by brilliant flame red. Adult males of *maculata* are greener than those of *newtoni*, with white belly and undertail coverts, and a dark line from the bill through the eye. Green also predominates in the plumage of *mana* , but it is of a much grayer, less yellow tint than that of the *newtoni* group. Both *mana* and *maculata* are similar enough to certain plumages of *Hemignathus virens* on their respective islands to have caused considerable difficulty for field observers (Shallenberger and Pratt 1977; Scott et al. 1979). Dullest of the creepers is *bairdi*, drab greenish gray above and grayish white below.

Adult females of *bairdi* and *mana* are identical to the males in color, but the members of the *newtoni* group are more or less sexually dichromic. In *montana* and *newtoni* females are simply less bright than the males. In *flammea*, females are reddish brown above and buffy white below often with a trace of bright orange in the throat. Females of *maculata* are like the males in pattern but with the yellow of the plumage replaced by white, and with two prominent white wing-bars. Pale wing-bars are also found in all immature *maculata*, and are present in many immature specimens of *flammea*, *newtoni*, and *montana*. Immatures of *bairdi* and *mana* never have wing-bars, but differ from adults in the amount of white about the eyes.

Soft part colors vary along similar lines. The bills of *bairdi* and *mana* differ in color, but both are pale throughout except for a trace of dusky pigment along the culmen. In the *newtoni* group, the pattern is for the upper mandible to be dark and the lower one pale, but the contrast is not sharp. Thus both coloration and sequence of plumage pattern support the division of the creepers into *mana*/*bairdi* and *newtoni* groups.

Foraging Behavior

All Hawaiian creepers are primarily insectivorous, but *newtoni* and *montana* also take nectar (Perkins 1903). I have observed *bairdi* visiting flowers of *Metrosideros* on two occasions, and *mana* feeding once in *Myoporum* blossoms, but such behavior is very exceptional. The latter two birds appear to fill a nuthatchlike niche, feeding by creeping slowly over trunks and branches of trees. The favored foraging position of *bairdi* is among interior branches between 5 and 10 cm in diameter, but it also feeds clinging to the bark of large trunks. The Kaua'i bird rarely even perches among small branches. On Hawai'i, mana also is a true creeper, but prefers slightly smaller diameter branches than does bairdi and feeds and perches more often in thin outer branches. In their movements, bairdi and mana are very similar. Both frequently hold the body parallel to the branch on which they are foraging. Both crouch low on their legs, seldom perching upright with the tarsi visible. On large trunks and branches they may move with the head downward or upward but do not brace with the tail. Thus they forage in a manner intermediate between that of a nuthatch (Sitta) and a Black-and-white Warbler (Mniotilta varia).

In contrast to this type of creeping behavior is the foraging of newtoni. This bird also gleans much of its food from trunks and branches of trees, but in a manner rather different from that of mana and bairdi. A much more active, sprightly bird, newtoni virtually never clings close to the bark of a tree but rather sits upright, usually with tarsi clearly exposed. I have never observed any behavior of newtoni that could be described as nuthatch-like, but some of its movements are reminiscent of those of Mniotilta. I emphasize these points because considerable confusion has resulted from imprecise use of the term "creeping" in reference to these birds. For example, Henshaw (1902b), after describing the creeping behavior of mana, stated that newtoni is "noticeable for the same habit..." but then went on to discuss the "marked difference in habits" between them. Richards (in Richards and Bock 1973: 22) in reporting two days of observations of the Maui bird described its feeding "along the small branches...and among the twigs and leaves" and further discussed their foraging with "heads constantly moving, the bills being probed under lichens and among the leaves." While stating that "the creeping ability of this race seems as good as that of the Hawaii Creeper," his descriptions all involved feeding methods other than true creeping as described above. My observations have revealed that the most frequent foraging site of newtoni is among leaves rather than along large branches. In such situations, it gleans its prey in the manner of a Dendroica wood-warbler. Only about 20% of my observations involved birds foraging in any manner that could be called creeping in the broadest sense. Flycatching is rare among Drepanidinae, but newtoni at least occasionally takes flying insects by short sallying flights. Such behavior is inconceivable for mana or bairdi, which also rarely forage among leaves and almost always exhibit nuthatchlike creeping. This difference in foraging behavior may explain the differing wing/tail ratios mentioned earlier.

Early accounts reveal that montana (Perkins 1903) and flammea (Bryan 1908) were very similar to newtoni in foraging behavior. Although maculata is poorly known, its intermediate wing/tail ratio may indicate a foraging strategy that involves more creeping than that of the other members of the newtoni group. In three recent sightings of maculata, only one bird was seen to creep (Shallenberger, pers. comm.).

Vocalizations and Displays

One of the most noticeable behavioral traits of newtoni is a constantly uttered, loud chick call note. This note is one of the characteristic environmental sounds of the Maui forest and is apparently imitated by at least two other bark-foraging species, *Pseudonestor* and *Melamprosops*. Perhaps the note plays a role in the formation of mixed-species flocks, but this matter requires further study. Similar call notes have been described for *montana* (Perkins 1903), *flammea* (Bryan 1908), and *maculata* (Maile Stemmermann, pers. comm.). The call notes of *bairdi* and *mana* are, as Perkins (1903: 414) stated, "more or less different." In each case the typical call is a quiet, upwardly inflected *sweet* but each bird also has a louder version of the same call. Small parties of Hawai'i Creepers also utter a distinctive fast *whit-whit-whi-whi-whit*, etc. These calls may be those of young birds still following their parents. Figure 19 illustrates these calls.

The songs of the two creeper groups provide one of the clearest contrasts between them. That this difference has not been noted previously can be attributed to the birds' peculiar reticence with respect to song. Perkins (1903), who was a keen observer of vocalizations, claimed to have heard only the songs of *newtoni* and *montana* despite having seen "hundreds of the Oahuan bird and thousands of all the others." I suspect that he actually did hear the songs of *mana* and *bairdi*, but confused them with those of the 'amakihis *Hemignathus virens* and *H. stejnegeri*. To date no ornithologist has heard, let alone recorded, the songs of *maculata* or *flammea*, but I have obtained extensive recordings of those of *mana* and *newtoni*, as well as a single song strophe of *bairdi*. Perkins (1903) considered the song of the now-extinct *montana* identical to that of *newtoni*.

Both *mana* and *bairdi* sing a short trill, not greatly different from the songs of the various species of *Hemignathus* or *Loxops*. Elsewhere, (Scott et al. 1979) I have discussed the vocalizations of mana in some detail as they compare to these other songs. I have not found mana to be so sparing of its song as the other creepers, and have, in fact, never observed it for any length of time without hearing the song. Such has not been the case with bairdi. When finally I did successfully record this song, it was uttered but once. This fact may be partly explained by my discovery that the Kaua'i 'Amakihi sometimes sings an essentially identical, but somewhat louder trill. Thus I may have heard other bairdi songs, but failed to identify them correctly. For sonagrams of creeper and 'amakihi songs see Figures 9, 11, and 19.

In both bairdi and mana, the song is given from a perch. In the case of bairdi, the single recorded song was uttered by a bird foraging near the base of the trunk of a large koa tree. The Hawai'i Creeper often perches upright at right angles to a limb to sing, but may also do so from a creeping position.

The song as well as the attendant behavior of newtoni do not even remotely resemble that of mana and bairdi, except that singing is infrequent. On two visits in July and August to the native forests on the northeast slope of Haleakalā, I saw many Maui creepers but heard none sing. I finally obtained a fairly extensive series of recordings in April 1977 at Polipoli Springs. The songs of newtoni are varied, and in overall quality and pattern are unlike any other drepanidine songs I have heard. Henshaw (1902b), who heard only one song from newtoni, described it as "an ecstatic warbling song... quite unlike the voice of any other Hawaiian bird..." In my own experience, the voice of newtoni most closely resembles the lively songs of such wood-warblers as Dendroica pensylvanica and Wilsonia citrina. The most often heard variant is a monotonously repeated but lively whurdy-wheesy-whurdy-check..., the last syllable being identical to the call note. This song is apparently used in territory establishment. During aggressive encounters, the birds utter a more varied song that eventually grades into a loud version of the more stereotyped advertising song given by the victor. At other times, a bird may rise into the air singing an especially elaborate and vigorous version of this song, and then flutter back to a perch. I strongly suspect that these flight songs are part of a courtship display. The more complex songs of newtoni are often remarkably similar to the warbling song of the introduced House Finch Carpodacus mexicanus, but I cannot say whether true vocal mimicry is involved. A sonagram of the territorial song is given in Figure 19.

Another behavioral feature that distinguishes newtoni from bairdi and mana is a propensity for mobbing predators. Perkins (in Wilson and Evans 1890-99) described seeing "twenty or thirty" Maui creepers gathered about a perched Short-eared Owl but keeping a "respectful distance" while uttering their loud call notes. In the rainforests of East Maui I once observed a group of these birds mobbing a feral cat. Perhaps as many as a dozen birds followed the cat as it crept slowly through the underbrush. Their loud calls created a very noticeable commotion. Maui creepers probably also perceive human intruders as predators. The birds are extremely curious and will approach an observer closely. Bryan (1908) described similar behavior in flammea, but I have seen no evidence of a mobbing instinct in mana or bairdi, or for that matter in any other drepanidine. Perkins (in Wilson and Evans 1890-99) thought this behavior in newtoni might result from greater predation

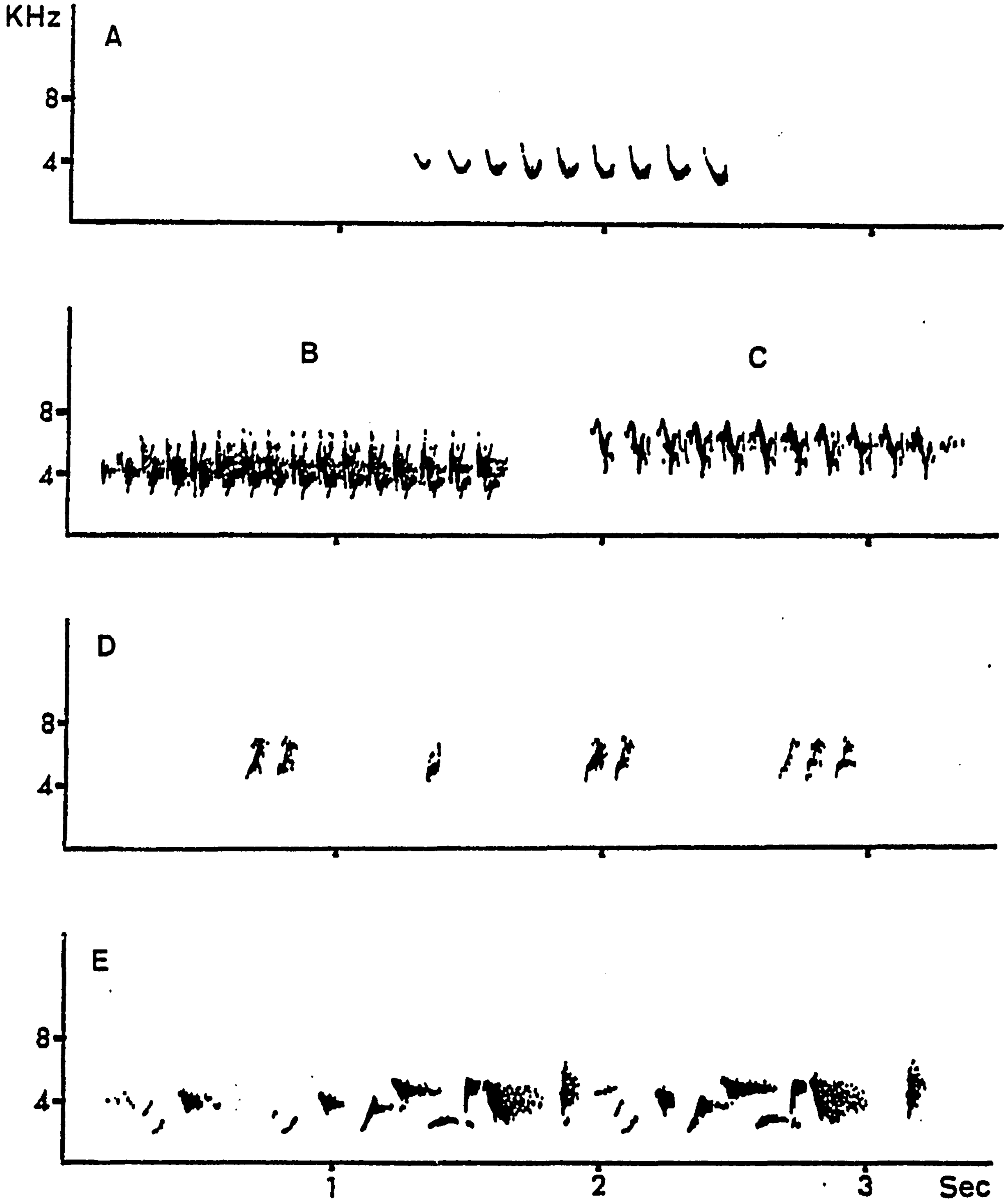

Figure 19. Vocalizations of Hawaiian "creepers." A) song of Oreomystis bairdi at Koke'e, Kaua'i, 14 May 1976; B) song of O. mana at 1800 m on northwest slope of Hualālai, Hawai'i, 3 May 1977; C) O. mana song at Keauhou Ranch, Hawai'i, 1 May 1977; D) Flock calls of O. mana, same data as B; E) segment of long song sequence of Paroreomyza montana, Polipoli Springs, Maui, 27 April 1977.

on this form than on other drepanidines by the native owl. He attributed this possibility to the fact that the Maui creeper lacks the characteristic scent of the subfamily. I doubt that the owl preys differentially on native birds in this manner, but the lack of drepanidine odor in the Maui bird is very interesting. Specimens of bairdi I collected in 1975 do possess the musty scent.

Taxonomy

I believe the current classification of the Hawaiian Creeper as a single species is erroneous. That such divergent forms as newtoni and bairdi could mate and produce viable offspring is inconceivable. Not only do they have obvious potential ethological isolating mechanisms, but they are ecologically so different that the survival of intermediate offspring, should such be produced, is highly unlikely. Even within the two groups of creepers, differences are great enough to justify recognition of most forms as full species.

Bock (1970) considered the difference in bill length between flammea and newtoni sufficient for the two to potentially coexist on a single island, and I believe the striking color differences between them provide an important potential isolating mechanism. Amadon (1950) de-emphasized the importance of this color difference because such shifts are "accomplished readily." Birds depend heavily on visual cues for species recognition, however, and thus that a visually very different phenotype may have been produced by a relatively minor genetic shift is irrelevant. On the other hand, newtoni and montana are almost surely conspecific. They differ only subtly in color, their songs and displays appear to be identical, and they are alike ecologically. Measurements

(Tables 8 and 9) of culmen length and bill depth reveal no statistically significant ($P > 0.05$) differences between *newtoni* and *montana*, but *flammea* differs significantly from both.

These three forms present an intriguing zoogeographical question. Maui, Moloka'i, and Lana'i were joined as a single island--I shall call it Maui Nui ("Greater Maui")--as recently as the last glaciation. Rising sea levels may have separated them as recently as 10,000 years ago (Terborgh 1975). As each island separated from the larger mass, first Moloka'i then Lana'i, it would undergo faunal readjustments as a result of reduced island size (Hamilton and Armstrong 1965; MacArthur and Wilson 1967; Lack 1969b, 1976), and some species, not necessarily the same in each case, would be eliminated. Thus we can reconstruct to some extent the avifauna of Maui Nui by combining the species lists for the three smaller islands. But should *flammea* and *montana* be listed as two species or one? Ten thousand years seems too short a time for potential species-level differences such as those that exist here to have evolved, particularly in the absence of closely related competitors. I believe this circumstantial evidence indicates that *flammea* and *montana* may well have been sympatric on Maui Nui, with only one of the pair managing to survive on the modern fragments of that island. Character displacement that could have occurred during this period of sympatry would help to explain why these two forms represent the extremes of bill measurements in the *newtoni* group. The O'ahu bird, which probably has never been sympatric with a congener, is intermediate in bill length. Plumage differences and a different wing/tail ratio indicate that *maculata* is best treated as a third species in this complex. The possibility that two of these three forms may have been sympatric precludes considering them as components of a superspecies.

Although *bairdi* and *mana* are clearly related, I believe they, too, are best classified as different species. Each has adapted to a different species milieu and fills a somewhat different feeding niche. Furthermore their plumage and vocal differences could well serve as isolating mechanisms.

A phylogenetically more important question than that of species limits is whether all the creepers should be considered congeneric. I believe the evidence indicates that the two groups are not closely related and that any similarities are due to convergence. The genus *Oreomystis* with species *O. mana* and *O. bairdi* can be seen as a slightly aberrant offshoot of the main line of drepanidine evolution. It possesses both the peculiar odor of the subfamily and the characteristic proximally truncate tongue. The songs are like those of the Hemignathini. The nontubular tongue of *Oreomystis* may well be secondarily derived, or possibly this genus branched from the hemignathine-drepanidine line before the tubular type evolved. The relict distribution of the species makes the latter possibility more likely.

The other three creeper species are peculiar among the Drepanidinae in almost every respect. They lack both the musty odor and the truncate base of the tongue. Their vocalizations are unique in the subfamily, as are such behavior patterns as predator mobbing. These facts suggest that, if these birds are drepanidines at all, they diverged very early from the ancestral stock, perhaps even before the ancestor of most modern thin-billed genera diverged from the finches. Ongoing biochemical studies (C. J. Ralph, pers. comm.) may shed further light on the relationships of this enigmatic genus. Because of their many wood-warbler-like attributes, the possibility that these birds actually belong to the Parulidae should be explored. For the present, *Paroreomyza* must be considered *incertae sedis*. The three species are *P. maculata*, *P. flammea*, and *P. montana* with subspecies *P. m. montana* and *P. m. newtoni*.

To avoid confusion, I believe that the name "creeper" should now be restricted to the genus *Oreomystis*. The Hawaiian names, with appropriate island modifiers, may be used as English vernaculars in the genus *Paroreomyza*. I have used these names in the Systematic List (Section 2).

SECTION 8.

PHYLOGENY AND SPECIATION OF HAWAIIAN THRUSHES

The Hawaiian thrushes have traditionally been placed in an endemic genus Phaeornis. Six forms have been described: obscura (Gmelin) 1789 of Hawai'i; lanaiensis Wilson 1891 of Lana'i; rutha Bryan 1908 of Moloka'i; oahensis Wilson and Evans 1899 of O'ahu; myadestina Stejneger 1887 and palmeri Rothschild 1893 both of Kaua'i. All were originally described as separate species. Although never seen by ornithologists, a thrush probably also existed on Maui (see Section 11). The O'ahu form became extinct shortly after its discovery and no skins of it exist, the name having been based upon written descriptions only (Wilson and Evans 1890-93). Thus its classification is purely conjectural. The two sympatric Kaua'i forms are obviously different species. The larger of the two, myadestina, has been regarded in all recent works as conspecific with the other allopatric forms, so that the genus has been considered to comprise only two species. Native Hawaiians gave different names to some of these forms: 'Ōma'o on Hawai'i; Oloma'o on Moloka'i and Lana'i; and Kāma'o on Kaua'i. The small Kaua'i thrush was called Puaiohi. As I will show, these aboriginal "taxonomists" probably understood these birds better than has been supposed. Since the nomenclature of Hawaiian thrushes is at issue in this discussion, I shall make frequent use of these taxonomically noncommittal native names.

The striking similarity of the Hawaiian thrushes to the American solitaires of the genus Myadestes was noted first by Stejneger (1887) in his description of Phaeornis myadestina. Later, Stejneger (1889) analyzed the relationships of Phaeornis and Myadestes in more detail. In comparing P. myadestina with M. townsendi, he stated that "were it not for the different proportions of wing, tail, and legs, the two birds could hardly be separated generically" (Stejneger 1889: 383). Other authors (Amadon 1942; Ripley 1952; Ames 1975) supported a close relationship of Phaeornis and Myadestes, but Bryan (1940) inexplicably associated Phaeornis with several Old World genera far removed from the American solitaires. Ripley (1962) later changed his opinion after hearing and seeing Phaeornis in the field. He thought that vocal behavior of the Hawaiian birds showed a close relationship with the Neotropical nightingale-thrushes of the genus Catharus. That, in Peters' Checklist of the Birds of the World (Ripley 1964), such limited and subjective evidence should have outweighed the overwhelming morphological evidence given by Stejneger (1889) is incredible and accentuates the need for a re-examination of the whole question of generic limits in the solitaire-Hawaiian thrush complex.

The Solitaires

The genus Myadestes (excluding Phaeornis) comprises seven or nine species depending on whether certain allopatric forms are considered full species. All except Townsend's Solitaire (M. townsendi) are sedentary tropical birds. The genus occurs from central Alaska south through Mexico, Central America, and the West Indies into South America. Solitaires are usually considered to be aberrant thrushes, although Sibley's (1973) study of egg white proteins and Ames' (1975) work on the morphology of the syrinx suggested that the relationships of *Myadestes* might lie outside the Turdinae. More recently, Sibley and Ahlquist (in press) have presented evidence from DNA hybridization experiments that contradicts the earlier protein data. The relationships of the solitaires as a group are outside the scope of this study, but perhaps an analysis of phylogeny within the group will be helpful in investigations of those relationships.

Are the Hawaiian thrushes solitaires? The following comparisons may answer that question.

Coloration

The most striking similarities between *Phaeornis* and *Myadestes* are in plumage coloration. Solitaires as adults are clad in somber tones of gray and brown, the brown tones usually confined to the upper surface. A few species possess eye rings and some have dark malar streaks. All but one species I have examined have the outer rectrices tipped with white. In some the white extends up the outer webs of the outer rectrices giving the folded tail a white border, while in others the outer webs are paler than the inner, but not white. The primaries are marked by a pale band at their base, and the outer webs form a pale rectangular patch on the folded wing. Only the West Indian *M. genibarbis* exhibits any striking patterns or color contrasts.

Immatures of all Myadestes are darker than adults. They are heavily spotted above and below but not in the usual manner of thrushes. For example, the feathers of the breast are pale in the center and have a dark border, producing a scalloped, rather than truly spotted breast. Feathers of the dorsum are brown or gray basally with a darker border and a subterminal buffy spot. The various species differ subtly in coloration, but show only very slight modification of the pattern described.

The above descriptions could be quoted almost verbatim for the Hawaiian thrushes, except that the various forms differ among themselves less than do the solitaires. All are olive brown above and gray below. All have more or less white tips and pale outer webs to the outer rectrices. All possess the characteristic solitaire wing-patch. The Puaiohi has both a narrow white eye ring and a trace of a dark malar line. Immatures are dark brown and scalloped in precisely the same peculiar manner as young solitaires. If the Hawaiian thrushes are placed in Myadestes, their somewhat duller and less contrasting plumage can be seen as illustrating trends noted elsewhere (Grant 1965b) in island representatives of mainland genera.

Thrushes of the genus Catharus are also generally dull plumaged, but often possess brightly colored "soft parts." The North American members of the genus, as well as some tropical species, are spotted below as adults. Plumages of immatures are not so distinctive as are those of young solitaires and Hawaiian thrushes. To this writer, no species of Catharus looks very much like a Hawaiian thrush.

External Morphology

Bill.--Solitaires stand clearly apart from typical thrushes in the shape of the bill, which is short and broad and resembles the bills of certain silky flycatchers (Sibley 1973). This design is apparently an adaptation for flycatching as well as frugivory. Bills of Hawaiian thrushes are more variable inter se than are those of solitaires. The extremes are represented by the two sympatric species on Kaua'i. The larger Kāma'o exhibits a bill that is, as Stejneger (1889) states "identical, though somewhat stouter and stronger" than bills of Myadestes. The Moloka'i, Lana'i, and Hawai'i birds have somewhat longer and narrower bills, and that of the Puaiohi approaches the more typical turdine configuration. The divergence of the two Kaua'i forms may have resulted from competition (Amadon 1947; Ripley 1962; but see Grant 1972). Selection has probably favored a more generalized bill structure on islands where only one thrush occurs. Even the insular solitaires M. elisabeth and M. genibarbis are sympatric with more typical thrushes. In fact, if Kaua'i had not been blessed with a double colonization of thrushes, we might expect all Phaeornis to have evolved away from a specialized ancestral bill type. Grant (1965a) has cited several examples of such broadening of feeding niche accompanied by changes in bill shape among birds of the Tres Marias Islands off Mexico. Figure 20 illustrates bills of selected solitaires and Hawaiian thrushes.

The divergence from continental Myadestes in bill shape exhibited by some Hawaiian thrushes in no way argues against considering the two groups congeneric. The greatest divergence from a myadestine ancestor, as shown

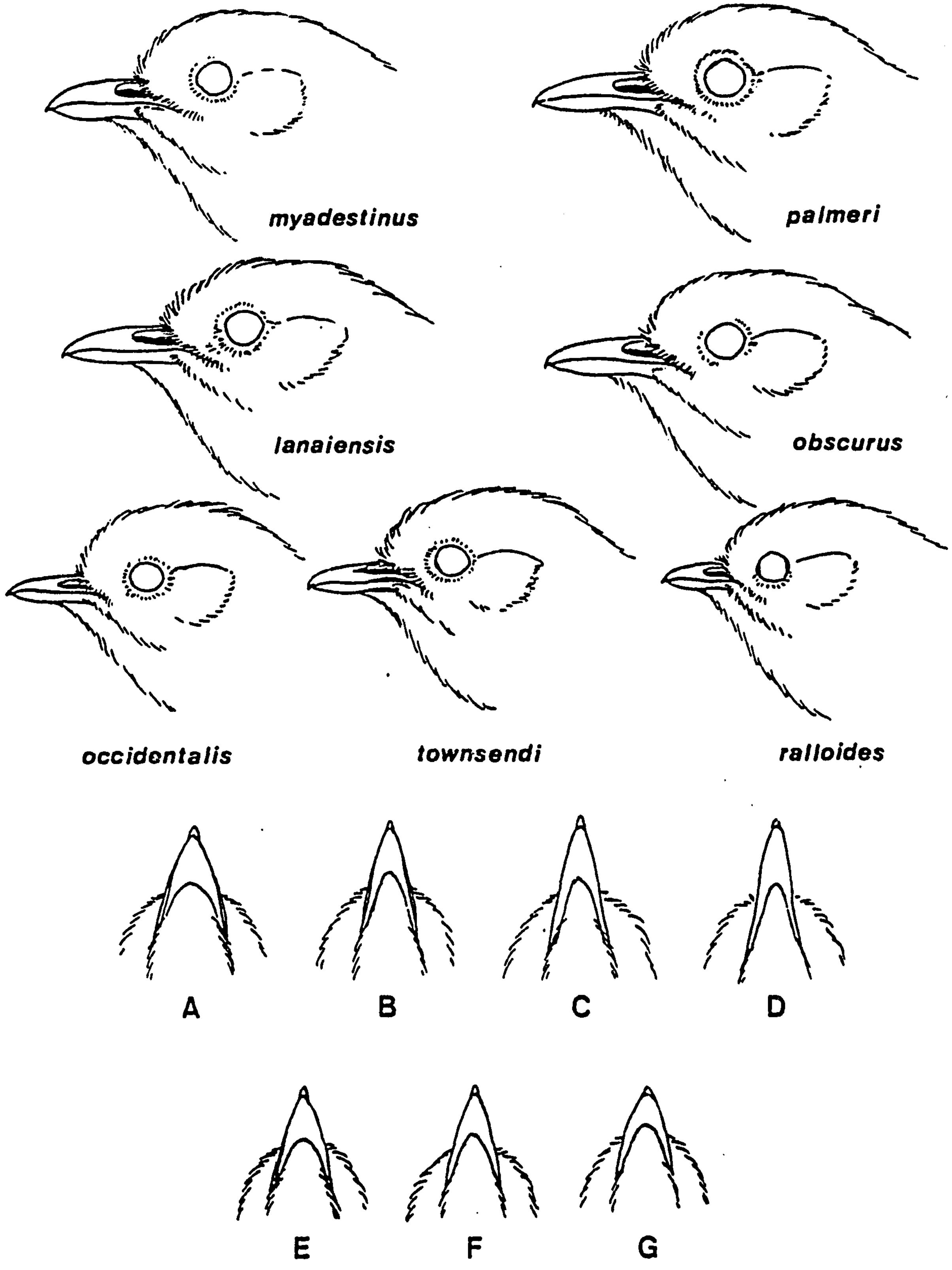

Figure 20. Bills of representative solitaires and Hawaiian thrushes, genus *Myadestes*. Ventral views as follows: A) *myadestinus* B) *obscurus* C) *lanaiensis* D) *palmeri* E) *occidentalis* F) *townsendi* G) *ralloides*. All natural size.

by the Puaiohi, is a reflection of the usual pattern of evolution on small islands where two congeners occur together (Grant 1968; Carlquist 1974). The generally larger bills of Phaeornis as compared to Myadestes parallel similar divergence in insular representatives of mainland genera elsewhere (Amadon 1953; Rand and Rabor 1960; Grant 1965a, 1968). Furthermore, the greater divergence inter se of Phaeornis is predictable from the findings of Schoener (1965). In fact, generic separation of Phaeornis and Myadestes obscures an important heuristic example of evolutionary trends in bill size and shape on islands.

Body proportions.--Stejneger (1889) could cite only the differing proportions of wing, tail, and legs in the two groups as a basis for generic diagnosis of Phaeornis and Myadestes. His analysis, based on M. townsendi, M. occidentalis (=obscurus), M. ralloides, and P. myadestina showed, however, that some solitaires differed less from Phaeornis in these respects than from other Myadestes. Using specimens from the American Museum of Natural History, Bernice P. Bishop Museum, and Louisiana State University Museum of Zoology, I calculated the wing/tail ratios for all available species in this complex. Figure 21 shows that the greater ratios of the Hawaiian birds can be seen as simply the extension of a morphocline. No gap exists between Myadestes and Phaeornis greater than that between species of Myadestes, but between species of Phaeornis, noticeable gaps occur. Some authors (e. g. Mayr and Vaurie 1948; Amadon 1953) suggest that island birds have longer wings (and presumably greater wing/tail ratios) than their mainland relatives, but more recent studies have failed to demonstrate any such trend (Grant 1965a,

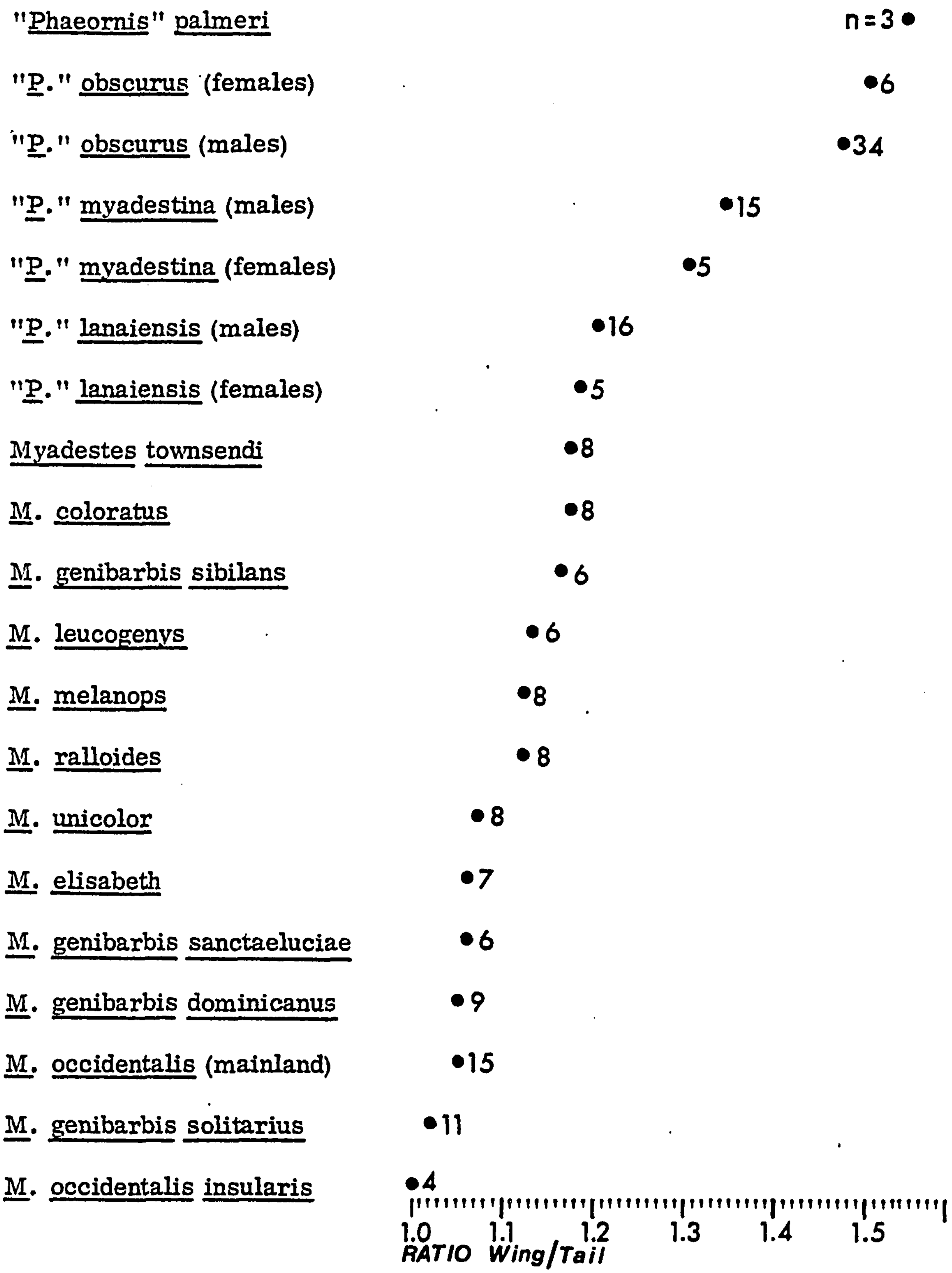

Figure 21: Ratios of wing to tail in the genus Myadestes.

1968).

Ridgway (1907) used the greater tarsus length of Phaeornis as a key character to separate that genus from Myadestes. But the longer tarsus of Phaeornis is shown by Stejneger's (1889) data to represent the extension of another morphocline. A tendency toward greater tarsus length in island birds has been demonstrated by Grant (1965a, 1966).

Internal Anatomy

Internal anatomical features of solitaires and Hawaiian thrushes have received relatively little attention. Gadow (1899) discussed the anatomy of the 'Ōma'o and concluded that if the bird was a thrush, it was a highly aberrant one. Unfortunately, he made no comparisons with Myadestes. Lucas (1894) compared skulls of the 'Ōma'o and the solitaire M. genibarbis, and his manner of discussion indicates that he considered the two genera closely related. Indeed, he usually referred to them collectively in pointing out those features that indicated a turdine relationship, peculiarities notwithstanding. In several skull features, Phaeornis is more thrush-like than Myadestes. In the configuration of the manubrium and the lack of a metapterygoid (see figures in Lucas 1894), Phaeornis and Myadestes resemble each other and stand apart from other thrushes.

Ames' (1975) study of syringeal morphology revealed another anatomical feature in which Phaeornis and Myadestes together differ from typical thrushes. While the syrinx of P. obscura resembles that of the solitaires in "overall proportions," the Hawaiian thrush has diverged somewhat further from the specialized turdine syrinx than has Myadestes. This pattern of variation supports the derivation of Hawaiian thrushes and American solitaires from a common ancestor.

Vocalizations

The songs of solitaires rank among the most aesthetically pleasing avian vocalizations and have been the subject of many eloquent descriptions (e. g. Sutton 1951; Skutch 1967; Lack 1976). In general, these songs are long and complex, comprising flutelike notes, trills, and some harsh sounds. Most have an ethereal cascading quality. Song reaches its highest musical development in M. unicolor, but that of M. occidentalis (=obscurus) is perhaps more complex (pers. obs.). Recorded examples of solitaire songs are presented by Davis (1958), Peterson (1962), and Gunn and Gulledge (1977).

Although not equalling the much-praised solitaires in this respect, Hawaiian thrushes have been considered by most writers to be the islands' most skilled songsters. The songs differ considerably from island to island (Munro 1944). The song of the Hawai'i representative is rather unthrushlike and jerky but "pleasing and, at times, sweet" (Henshaw 1902b: 29). On Moloka'i, the song is described as "irregular...somewhat jerky, though always melodious..." (Bryan 1908: 174), but the Lana'i bird was "no singer at all" (Munro 1944: 74). The song of the larger Kaua'i species is entirely different from that of the 'Ōma'o on Hawai'i, and has been described as resembling "that of an English thrush, but...less powerful" (Palmer in Rothschild 1893-1900) and composed "of flute-like double notes" (Richardson and Bowles 1964) or "mellow liquid phrases much like those of the Wood Thrush or Hermit Thrush" (Gauthey et al. 1968). That of the smaller Puaiohi, as might be expected, is very distinctive. Perkins (1903: 378) described it as "a simple trill with much resemblance to that of the...nukupuu [Hemignathus lucidus]." I have listened to a tape recording of this song made in 1968 (Gauthey et al. 1968) and while I concur in its general resemblance to that of H. munroi (Figure 13), whose song is said to be identical to that of the Nukupu'u by Perkins (1903), I would not call either song a trill. The Puaiohi's song is wheezy and high pitched, rather resembling the squeaking of a metal wheel in need of lubrication. Also present on the 1968 tape is an unidentified song fo clear flutelike notes. This song is distinct from any known Kaua'i bird song, and may be a second type of vocalization of the Puaiohi. Sonagrams of the songs of the 'Ōma'o, Kāma'o, and Puaiohi are presented in Figure 22. Unfortunately, the Oloma'o is now on the verge of extinction (Scott et al. 1977) and no recordings of its song exist.

Ripley (1962) considered the songs of Phaeornis so different from those of Myadestes as to warrant wide separation of the two genera in systematic lists (Ripley 1964). He likened the Hawaiian thrush songs instead to those of nightingale-thrushes (Catharus). Although he does not say so, his observations must surely have involved only the 'Ōma'o, since all the other Hawaiian thrushes were quite rare by the 1950s (Munro 1944). I believe Ripley (1962) was misled by taxonomies (Bryan and Greenway 1944; Amadon 1947) that had not taken into account interisland differences in vocalizations and considered the 'Ōma'o and Kāma'o conspecific. The Hawai'i bird's song is the least solitaire-like of any Hawaiian thrush's song. Even so, I cannot agree with Ripley's comparison of that song to those of nightingale-thrushes, recorded examples of which are given by Davis (1958) for C. aurantiirostris and by

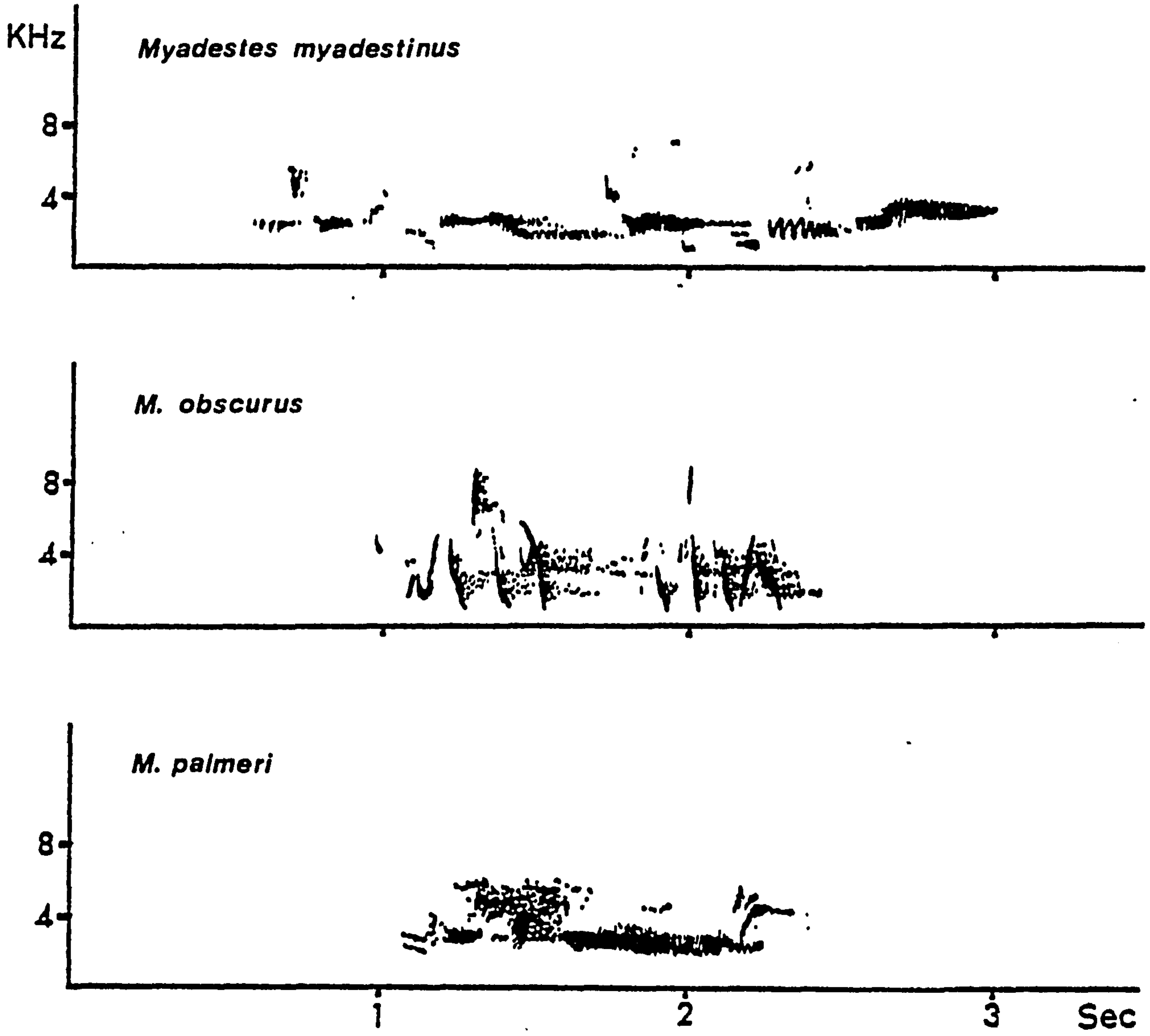

Figure 22: Songs of three species of Hawaiian thrushes.

Gunn and Gulledge (1977) for *C. dryas*. In my opinion, the songs of Hawaiian thrushes, particularly that of the Kāma'o, are very similar to those of solitaires. The larger Kaua'i thrush's song is most like that of *M. townsendi* in pattern (Peterson 1962), but often has the same ethereal quality heard in the song of *M. unicolor* (Davis 1958). The song of the 'Ōma'o is not so myadestine, but it resembles even less the songs of *C. aurantiirostris* and *C. dryas*. Certain elements in the songs of *M. unicolor* and *M. occidentalis* (=*obscurus*) rather closely resemble the jerky, liquid notes of the 'Ōma'o. Even the squeaky song of the Puaiohi resembles a short segment of the elaborate song of *M. occidentalis*. A further difficulty with Ripley's (1962) comparison is that the songs of several nightingale-thrushes are said to resemble those of solitaires (Slud 1964; Ridgely 1976). Hawaiian thrushes, like solitaires (Bent 1949; Skutch 1967), choose perches high in the forest canopy for singing. In contrast, tropical members of the genus *Catharus* sing on or near the ground (Skutch 1960; Wallace 1965).

Flight songs are unusual in the Turdinae (Skutch 1960), but virtually all writers have mentioned that Hawaiian thrushes sometimes sing on the wing. I have noted this behavior in both the Kāma'o and the 'Ōma'o. In both cases, the birds often end a bout of singing in the treetops with an upward flight, a brief period of "skylarking," and a sudden dive into the forest. Similar behavior has been noted in the Puaiohi (Perkins 1903). *Myadestes townsendi* (Bent 1949; Bailey and Niedrach 1965) and *M. occidentalis* (Gunn and Gulledge 1977) have a virtually identical song flight. In the genus *Catharus*, the migratory *C. minimus* exhibits somewhat similar behavior (Bent 1949), but I can find no report of song flights among the tropical nightingale-thrushes.

Ecology

Hawaiian thrushes, American solitaires, and nightingale-thrushes are solitary, highly sedentary birds (Skutch 1960, 1967; Slud 1964; Bond 1974; Edwards 1972; Ridgely 1976; De Schauensee and Phelps 1978). According to Bryan (1908: 173):

> the Olomao is by nature a shy, timid bird, and for that reason, instead of exposing itself in the open it prefers to proceed from place to place by short low flights, usually through the shade of the forest. Again, a flock of Olomao... has never been seen.

Similar behavior is characteristic of the 'Ōma'o, Kāma'o, and Puaiohi. Myadestes genibarbis exhibits seasonal altitudinal movements (Cruz 1976; Lack 1976) but M. townsendi is the only long-distance migrant in the genus (Bent 1949). The nightingale-thrushes are highly sedentary (Skutch 1960) but several North American Catharus are migratory (Bent 1949; Dilger 1956). The 'Ōma'o at least occasionally wanders in response to locally abundant food supplies (Perkins 1903).

Both solitaires (Slud 1964; Skutch 1967; Edwards 1972; Bond 1974; Cruz 1976; Ridgely 1976; De Schauensee and Phelps 1978) and Hawaiian thrushes (Berger 1972b) are primarily inhabitants of dense montane forests. Myadestes ralloides (De Schauensee and Phelps 1978), M. occidentalis (Edwards 1972), and M. townsendi (Bent 1949) also occur in open scrubby vegetation at higher elevations. I have found 'Ōma'o commonly in scrubby 'ōhi'a-lehua trees growing on relatively recent lava flows in the Saddle area of the Big Island. Above tree line on Mauna Loa, an isolated population of the 'Ōma'o lives among low shrubs and uses rocks rather than trees as perches (Dunmire 1961), and thus closely parallels the adaptations exhibited by high-elevation populations of *M. townsendi* (Bent 1949). Although *Catharus minimus* occurs in arctic regions, it never truly forsakes trees (Bent 1949), and I know of no other reports of alpine adaptations in the genus.

The feeding habits of Hawaiian thrushes also parallel those of solitaires. The larger species are frugivorous but also take insects, and the Puaiohi is primarily insectivorous (Perkins 1903). Such mixed diet has been reported for *Myadestes melanops* (Skutch 1967), *M. genibarbis* (Cruz 1976), and *M. townsendi* (Bent 1949). The latter species varies its diet seasonally, taking more fruit on its wintering grounds and more insects when breeding (Salomonsen and Balda 1977). *Catharus* thrushes are primarily insectivorous (Bent 1949; Dilger 1956; Skutch 1960).

Not only are the diets of Hawaiian thrushes similar to those of solitaires, but the birds forage in similar ways. The flycatching propensities of both have been noted by several authors (Henshaw 1902b; Bent 1949; Cruz 1976), but such behavior is virtually unknown in the genus *Catharus* (Bent 1949; Dilger 1956; Skutch 1960; Slud 1964). *Myadestes melanops* feeds "in the manner of either a flitting, neck-stretching tanager or a hovering trogon" (Slud 1964) and similar behavior has been reported for *M. ralloides* (Wallace 1965). The characterization would be equally appropriate for the 'Ōma'o. Solitaires and Hawaiian thrushes forage primarily in the upper strata of the forest (Perkins

1903; Bent 1949; Wallace 1965; Cruz 1976; Salomonsen and Balda 1977; pers. obs.), whereas Catharus thrushes forage almost exclusively on or near the ground (Bent 1949; Dilger 1956; Skutch 1960; Slud 1964; Wallace 1965).

Nests and Eggs

The nesting of Myadestes townsendi is probably the best known of the genus. The nest is often built on or near the ground, the most frequently mentioned site being a nook in a steep bank with an overhanging shelter (Bent 1949). Similar nest sites have been reported for M. elisabeth and M. genibarbis (Bond 1974) in the West Indies, for M. melanops and M. occidentalis in Central America (Skutch 1967), and for M. ralloides in Colombia (Wallace 1965). Other low sites mentioned include a nook in the side of a leaning moss-covered tree (Skutch 1967) as well as a cavity in a stub or the heart of a tree-fern (Bond 1974). Myadestes genibarbis sometimes chooses higher nest sites such as a bromeliad 15 m from the ground or the fork of a tree at 4 m (Cruz 1976).

Bryan (1908) reported a possible Oloma'o nest in a fork about 9 m up in an 'ōhi'a tree, but the first confirmed nest of a Hawaiian thrush (the 'Ōma'o) was found by Berger (1969b) not surprisingly about 1.3 m above the ground against the trunk of a tree-fern. The details of the nest's construction (Berger 1969b) are similar to those of solitaire nests (Bent 1949; Skutch 1968; Cruz 1976), both of which are fairly large bulky structures. More recently, other 'Ōma'o nests have been found in nooks or cavities in trees (J. M. Scott, C. J. Ralph, pers. comms.). No Hawaiian thrush nest has yet been found on the ground, but the alpine population of the 'Ōma'o (Dunmire 1961) almost surely uses such sites. Tropical Catharus build small compact nests in low shrubbery (Skutch 1960; Wallace 1965).

The eggs of solitaires are white to pale blue, liberally spotted with reddish brown (Bent 1949; Reed 1965; Skutch 1967; Bond 1974), the spots often concentrated toward the larger end (Bent 1949). The eggs of M. townsendi are said to be "entirely different from the eggs of other North American thrushes..." (Bent 1949: 320). Thus the similarity of the eggs of the 'Ōma'o and Puaiohi as described by Berger (1972b) to those of solitaires may be noteworthy. However, Lack (1958) considered egg color a useless taxonomic tool among thrushes. The Puaiohi eggs described by Berger (1972b) were laid by a single captive female in the Honolulu Zoo. Perhaps coincidental, but remarkable nonetheless, is that two of the three eggs were laid after a male Myadestes unicolor was placed in the same aviary.

Probability of Myadestine Ancestry

That Phaeornis and Myadestes are closely related appears inescapable on morphological, behavioral, and ecological grounds. Certainly, little evidence exists to support Ripley's (1962, 1964) hypothesized Phaeornis-Catharus affinity. A further point that argues against such a relationship is that Catharus thrushes have not successfully colonized the West Indies, even though several members of the genus winter there (Bond 1974). But despite the fact that Myadestes is widespread in the Caribbean islands, this mostly sedentary tropical genus does not in general seem to be a likely colonizer of a remote archipelago such as Hawai'i. One species, M. townsendi, however, is exceptional in this regard. It is highly migratory in the northern part of its range, which extends north to east-central Alaska (Bent 1949). During migration, Townsend's Solitaires sometimes forsake their solitary habits and form aggregations of many individuals (Eent 1949; Phillips et al. 1964). Such an aggregation, trapped by some meteorological phenomenon, could be carried to Hawai'i as a propagule. The birds would find no competitors in their accustomed niche, and their habit of defending winter feeding territories (Salomonsen and Balda 1977) might enable them to better exploit the island resources and to have a better chance of successful breeding than a species that required a return migration sequence to trigger territorial behavior prior to nesting. Thus a proto-townsendi solitaire would be pre-adapted to survival in isolation on a remote archipelago.

These observations, as well as the close resemblance of the songs of Townsend's Solitaire and the Kāma'o, ecological similarities such as the alpine adaptations of the 'Ōma'o, and the almost identical wing/tail ratios (Fig. 21) of that solitaire and the Oloma'o, may indicate that the Hawaiian thrushes and M. townsendi share a recent common ancestor and may therefore be sister groups in a cladistic sense. If that is indeed the case, the two are more closely related to each other than either is to the other species of Myadestes, and the maintenance of a separate genus for the Hawaiian birds is logically untenable. Therefore I have included the Hawaiian thrushes in the genus Myadestes Swainson 1838 in the systematic list, and made Phaeornis Sclater 1859 a junior synonym. One unfortunate consequence of combining these two genera is that the long-established name of the Brown-backed Solitaire (M. obscurus Lafresnaye 1839) must yield to the priority of Myadestes (=Phaeornis) *obscurus* (Gmelin) 1788, the name of the 'Ōma'o. The name of the Brown-backed Solitaire will now become *Myadestes occidentalis* Stejneger 1882, and the former nominate subspecies *M. o. obscurus* (based on *Myadestes obscurus* Lafresnaye, 1839, Rev. Zool., 2, p. 98--Mexico; probably Veracruz) must be renamed. Since this subspecies is confined to the mountains of eastern Mexico, I propose that it be called

Myadestes occidentalis orientalis, nom. nov.

in the hope that the seemingly contradictory epithets will cause less confusion than other possible new names for the eastern subspecies.

Radiation of Hawaiian *Myadestes*

Amadon (1947) was the first to propose a phylogeny for the Hawaiian thrushes. He considered the allopatric larger forms (*obscurus*, *lanaiensis*, *rutha*, *oahensis*, and *myadestinus*) to be components of a single polytypic species with *palmeri* as a second species sympatric with *myadestinus* on Kaua'i. For such a classification to be logical, *Myadestes palmeri* must represent the older of the two species on Kaua'i, and Amadon (1947) states that to be the case. In bill shape, and consequently in diet, *M. palmeri* appears to be the most divergent member of the complex. An analysis of variance of four variables (culmen length, bill width, wing chord, and tail length) show that *M. palmeri* is significantly different ($P < 0.05$) in feather dimensions from other Hawaiian *Myadestes*, but closest to *obscurus*. In bill dimensions, *M. palmeri* reveals no significant differences in width from *obscurus* or in culmen length from *lanaiensis* and *rutha*. Since *lanaiensis* and *obscurus* are not statistically different in culmen length, little differentiation can be demonstrated for *palmeri* in these characters. Vocally, *palmeri* is distinctive, as are the other forms that have been studied (see below), and represents a step in the trend toward song simplification in insular *Myadestes* that reaches its culmination in the apparently songless *lanaiensis* on Lana'i.

The larger Kaua'i representative, *myadestinus*, is statistically distinctive in wing chord and bill width. It differs from *obscurus* and *palmeri* in tail length and bill length. By differing from all other forms in width of the bill but not in length, *myadestinus* exhibits a bill shape unique in the Hawaiian group, but one that closely resembles the bills of mainland *Myadestes*. The song of *myadestinus* is as distinctive as any, but is much closer than that of either *palmeri* or *obscurus* to songs of American congeners. Thus *palmeri* and *myadestinus* can be considered about equally distinctive among the Hawaiian thrushes. No reason exists for considering, a priori, either species to be the older colonizer of Kaua'i. However, the close resemblance of *myadestinus* to mainland relatives in a variety of particulars, and the great distinctiveness of *palmeri* when compared to the same forms argues that *myadestinus* is the older. Otherwise the ancestral Hawaiian *Myadestes* must have lost the continental bill shape and song type, only to regain them after a reinvasion of Kaua'i from another island, a much less parsimonious hypothesis.

Two other facts support the idea that *palmeri* is the latecomer on Kaua'i. First, the two forms on the island appear to be ecologically isolated through differences in food (Perkins 1903). The mostly frugivorous *myadestinus* resembles the thrushes of other islands in this respect, while the mostly insectivorous palmeri is distinctive. Grant (1968) has shown that divergence in feeding habits is the most likely accommodation that would allow coexistence of two congeners on a small island, and that the second colonizer is the one that must adopt a novel feeding niche unless its predecessor has already done so in allopatry. In the absence of congeneric or other competitors, such divergence in the first colonizer of Kaua'i seems unlikely. The second fact is that in double invasions, the second colonizer is at a decided disadvantage in competition with a well-established congener. Selection for divergence in the newcomer will be initially very strong, and the second congener may never become as widespread as the first since it must find a niche to which its predecessor is less well adapted (Grant 1968). On Kaua'i, palmeri has always been rare and restricted to a small area on the Alaka'i Plateau (Perkins 1903; Richardson and Bowles 1964) while myadestinus was historically the most common forest bird on the island (Munro 1944). Again, evolutionary parsimony requires that palmeri be the more recent of the two Kaua'i species.

If myadestinus is the older colonizer of Kaua'i, then a minimum of three thrush species must be present in the archipelago. In other words, the ancestor of palmeri must already have reached the species level relative to the ancestor of myadestinus or the second colonization would have been impossible (Mayr 1942).

To test the possibility that potential reproductive isolating mechanisms exist between allopatric Hawaiian Myadestes, I conducted a series of vocal playback experiments on the island of Hawai'i. On 28 and 29 April I visited Keauhou Ranch, which lies between Kilauea Forest Reserve and Hawaii

Volcanoes National Park. The area has a very high density of 'Ōma'o, and the birds were vigorously singing at the time of my investigations. I had prepared tapes of call notes and songs of the Kāma'o from recordings made by me and Robert J. Shallenberger in 1975 in the Alaka'i Swamp on Kaua'i, and also tapes of homologous vocalizations of the 'Ōma'o from Keauhou Ranch. Before I began experimenting with the Kaua'i vocalizations, I tested the responsiveness of singing thrushes to playback of the prepared 'Ōma'o tape.

The raspy call notes elicited no response whatever. Singing birds continued uninterrupted and birds giving the same call did not alter their behavior when the tape was played. A higher pitched call was likewise ignored. This latter result is surprising in light of Perkins' (1903) comment that 'Ōma'o can be attracted by imitation of that call. Response to the song was, however, immediate and obvious. First, the bird, singing vigorously, flew upward from its perch and then dived into the forest understory near the playback speaker. Then the bird approached the sound silently in a series of short flights as if attempting a surreptitious investigation. When only one or two meters from the speaker, the bird stared intently at the sound source, but did not appear agitated. In fact, the characteristic wing-shivering behavior noted by every writer on Hawaiian thrushes, ceased during the bird's approach to the recorded sound. The bird remained, seemingly oblivious to human presence, as long as the playback continued. When it ceased, the bird flew back into the forest canopy and resumed singing.

Having established that the birds were responsive to song playback, I began playing the Kāma'o tape first, followed by the 'Ōma'o recordings. Limitations of equipment prevented a simultaneous presentation, and thus these experiments were less "controlled" than those conducted by Lanyon (1967) in his study of species limits in West Indian Myiarchus flycatchers. However, since my results are unequivocal, I believe they are valid.

In the first experiment, I played the tape for an apparently territorial, vigorously singing 'Ōma'o. Neither the two different call notes, nor the complex Kāma'o song (Fig. 22) elicited any response, or even any indication that the bird heard the tape. The subject's vocalizations continued until the taped 'Ōma'o song began. The bird then ceased singing abruptly and flew directly to an open perch about four meters above the playback speaker. Its behavior closely matched that previously described. I conducted nine such playback experiments during the two-day period, involving nine different individuals. None of these birds responded in any way to recordings of the Kaua'i bird. Seven responded in the vigorous manner described to subsequent presentation of the 'Ōma'o song. Two others responded to neither tape, but one of these may have been distracted by the passage of a helicopter overhead during the 'Ōma'o portion of the tape.

Lanyon (1967) interpreted similar differential responses of flycatchers to taped vocalizations as indicating that two allopatric forms in question were not conspecific. Thrushes are noteworthy in possessing species that are similar in appearance but differentiated vocally and ecologically (Dilger 1956; Rowley and Orr 1964). Thus the interpretation of vocal differences among allopatric thrushes as potential isolating mechanisms is reasonable, and I consider the specific distinctness of three Hawaiian Myadestes (obscurus, palmeri, and myadestinus) to be well established.

But what of the other described forms? The status of the O'ahu bird cannot be determined at present. But that of the Lana'i and Moloka'i forms can at least be surmised. These two were considered to be a single taxon until Bryan (1908) described the Moloka'i population (rutha) as distinct. Having re-examined Bryan's (1908) type series and other more recent specimens in the Bishop Museum, I cannot appreciate the color differences he noted. Perhaps the apparent difference was an artifact of comparing a fresh series from Moloka'i with older Lana'i specimens. The previously mentioned analysis of variance revealed no statistically significant differences between rutha and lanaiensis in any of the four mensural parameters examined. Thus I can find no morphological justification for taxonomic seapration of the Lana'i and Moloka'i thrushes. However, Munro (1944) mentioned their vocal differences as supporting Bryans (1908) position. In the absence of morphological distinctions, I believe the best course is to synonymize rutha with lanaiensis. The two have been separated for a relatively short time, geologically speaking, since, as noted previously, Moloka'i, Lana'i, and Maui were united during the last glaciation. Probably a single thrush species inhabited "Maui Nui." Henshaw (1902b) and Perkins (1903) believed thrushes once occurred on Maui, though none was ever collected and zoogeographical evidence supports their belief (see Section 11). The vocal differences between birds on Moloka'i and Lana'i may be viewed as incipient subspeciation, but I do not believe that such minor differences should be recognized taxonomically unless they can be shown to represent potential isolating mechanisms. Since the Oloma'o is now extinct on Lana'i (Hirai 1978) and nearly so on Moloka'i (Scott et al. 1977), good comparative studies of their vocalizations are impossible.

Whether lanaiensis (including rutha) is potentially reproductively isolated from the three well-established species of Myadestes in Hawai'i is moot. However, using the reasoning recommended by Mayr (1969: 197) for such decisions, I believe the best course is to consider lanaiensis a species of equal rank with the others. Myadestes lanaiensis is morphologically as distinct as the other Hawaiian species. Furthermore, lumping it with any of the others would be purely arbitrary, since it is about equally distinct from the Kāma'o and the 'Ōma'o, and very different from the Puaiohi in mensural characters. The same can be said of coloration. The problem presented by oahensis is insurmountable at present, and I propose that it be listed in checklists, as I have done (Section 2), as a questionable species, Myadestes ?oahensis. Recently discovered fossil thrushes from O'ahu (Olson, pers. comm.) may help to solve the problem.

The Hawaiian Myadestes probably represent one superspecies and a single additional species, but the superspecies cannot be delimited. The allopatric species could be grouped with equal justification with either of the sympatric Kaua'i species. Therefore I recommend that the four (or five if oahensis is valid) Hawaiian Myadestes be simply considered a species group.

SECTION 9.

SYSTEMATICS OF HAWAIIAN HONEYEATERS, WARBLERS, AND CROWS

The remaining Hawaiian passerines present few systematic problems at the species level, but all are more or less enigmatic as to their provenance. Furthermore, they are difficult to study both because of extinctions and because of the inaccessibility of the surviving representatives. I have had little field experience with any of these birds, but I offer the following discussions to complete the survey of Hawaiian passerines.

The Honeyeaters

The family Meliphagidae is represented by two endemic genera. The large Chaetoptila is known historically from four specimens collected before 1859 on Hawai'i (Greenway 1967). Virtually nothing is known of its habits other than that it was a nectar-feeding woodland bird with a musical voice (Henshaw 1902b reporting the account of Peale). In plumage, the bird most closely resembles the Australian friar-birds (Philemon). Chaetoptila may once have occurred throughout the Hawaiian Islands. Dole (1879) reported it, without corroboration, from Moloka'i and fossil specimens have recently been found on O'ahu (Olson, pers. comm.).

Better known are the 'ō'ōs (*Moho*), represented by species on Hawai'i (*M. nobilis*), Moloka'i and probably Maui (*M. bishopi*), O'ahu (*M. apicalis*), and Kaua'i (*M. braccatus*). Only the small 'Ō'ō'a'a of Kaua'i still survives, and it may soon follow its congeners into extinction. For comparisons of the four 'ō'ōs we must rely on Perkins (1903). The three larger species were somewhat similar morphologically, with long modified rectrices that were used in various displays. Both the Moloka'i and the Hawai'i 'Ō'ō had yellow axillary tufts that were displayed during aggressive encounters, although probably not in the manner shown in many illustrations (e. g. Rothschild 1893-1900; Wilson and Evans 1890-99). The yellow plumes are soft and lax in specimens I have examined, and according to Perkins (1903) were visible only when the bird raised its wings. The O'ahu 'Ō'ō lacked axillary plumes, but exhibited long yellow flank feathers. The vocalizations, at least of *M. nobilis* and *M. bishopi*, were rather similar (Perkins, *ibid.*). The three larger 'ō'ōs were alike enough to be considered allospecies in the superspecies *Moho* [*nobilis*].

I exclude *M. braccatus* from that complex in recognition of its many distinctive characters. It "differs considerably from its allies in its general appearance and structure, as well as in its habits and song"(Perkins 1903: 443). The most obvious anatomical difference is the lack of long, elaborate rectrices in the Kaua'i species. The short stiff tail is, according to Perkins (*ibid.*), used as an aid in climbing trees, but I noted no such behavior in my brief studies of the bird. The marked difference in elaboration of the tail probably indicates fundamental differences in displays, particularly since the 'Ō'ō'a'a also has no yellow plumes, the only yellow feathers being confined to the thighs. The song of *Moho braccatus* is elaborate, melodic, and flute-like. It resembles rather closely certain parts of the songs of the New Zealand Tui (*Prosthemadera novaeseelandiae*) and Bellbird (*Anthornis melanura*), and surprisingly is not very much like the songs of meliphagids occurring much closer to Hawai'i (e. g. *Foulehaio* and *Gymnomyza* of Fiji and Samoa). Possibly the Tui, the Bellbird, and the 'ō'ōs are all ancient relicts that have been replaced by more advanced meliphagids on the intervening islands.

The origins of the Hawaiian meliphagids cannot be clearly discerned without additional data. Indeed, no one can say whether these birds are the products of one or two colonizations. Perhaps the recently discovered fossils will provide the needed information.

The Millerbird

The Old World warbler *Acrocephalus familiaris* once occurred on both Laysan (*A. f. familiaris*) and Nihoa (*A. f. kingi*) but the nominate form is now extinct. This genus is widespread in the Old World, where the members are known as reed-warblers. Various species occur on some of the most remote islands of the Pacific, and in some cases are the only passerines present (e. g. *A. vaughani* on Pitcairn, *A. aequinoctialis* in the Line Islands). Many forms occur on low, dry islands similar ecologically to Laysan and Nihoa, but others occur on high, wet islands in Micronesia (Baker 1951) and southeastern Polynesia (Holyoak and Thibault 1977). Many Pacific island *Acrocephalus* are large, long-billed birds quite different in overall aspect from the diminutive species of Europe. Furthermore, many Pacific species have forsaken the reed-bed or marsh habitats typical of continental members of the genus. Some authors

(Thibault and Thibault 1973; duPont 1976) place the Pacific forms in the genus *Conopoderas*. However, Rothschild (1893-1900) considered the two genera inseparable. Certainly the Hawaiian species is a typical *Acrocephalus*, and all stages of morphological and ecological divergence from typical reed-warblers occur among Pacific island forms.

Whether all Pacific island *Acrocephalus* are related inter se or are the products of multiple invasions cannot be determined at present. Baker (1951) reviewed the history of the group and noted the likelihood that the continental *A. arundinaceus* was ancestral to it. That species occurs throughout the western Palearctic (including the Bonin Islands) and Oriental Realms, and extends eastward in the Australian Realm to the Solomons. Thus the Micronesian species *A. luscinia* and *A. syrinx* are completely surrounded by *A. arundinaceus*. However, a broad gap occurs in the distribution of *Acrocephalus* in the Pacific. The genus is absent from seemingly suitable islands in the Marshalls and Gilberts and central Polynesia (Baker 1951), yet is widespread in eastern Polynesia (duPont 1976). Thus the possibility clearly exists that the eastern Pacific species of the Northwest Hawaiian Islands, the Line Islands, and southeastern Polynesia may represent one or more separate invasions.

The larger Pacific *Acrocephalus* are noteworthy for their complex and varied vocalizations (Marshall 1949; pers. obs.). The Millerbird has a quiet, rather tinny song (Berger 1972b) that seems to me, based on recordings made by USFWS personnel in 1978, rather different although not unusual within the genus as a whole.

The Hawaiian Crow

The 'Alalā, or Hawaiian Crow (_Corvus tropicus_) has been found in historic times only in the Kona and Ka'ū Districts of the Big Island. The reasons for its confinement to this one area remain obscure, since crows were once widely distributed in the islands as evidenced by fossil remains (Olson, pers. comm.). _Corvus tropicus_ is a distinctive corvid, and its ancestry is not readily apparent. Bryan (1940) suggested a relationship to _C. macrorhynchus_ of South-east Asia, as well as to another insular species, _C. kubaryi_ of Guam and Rota. Baker (1951) argued, rightly in my opinion, against such a relationship. _Corvus kubaryi_ differs in both habits and voice from _C. tropicus_. The Mariana Crow is a rather secretive bird of semiopen forests. It forages frequently on the forest floor and in the underbrush, whereas the Hawaiian Crow is more of a canopy dweller. The voice of _C. kubaryi_ is a typically crowlike _caw_, whereas _C. tropicus_ has a varied repertoire of notes reminiscent of some calls of the Common Raven, _C. corax_, in addition to various crowlike notes. Some ornithologists working in Hawai'i (e. g. Winston and Paul Banko, pers. comm.) have suggested the adoption of the name "Hawaiian Raven" for this bird to recognize the possible relationship. However, since these birds are all congeneric and the terms "crow" and "raven" have no precise taxonomic meaning, I see no reason for coining a new English name for _Corvus tropicus_.

SECTION 10.

HAWAIIAN NONPASSERINES

The nonpasserine land and freshwater birds of the Hawaiian Archipelago present few systematic problems. As discussed in Section 2, most of them are conspecific or congeneric with forms found elsewhere. A few nevertheless deserve further comment with regard to their alpha taxonomy. Several species were originally described in endemic genera that were synonymized with widespread taxa when more information became available. Such is the case with the Nēnē, Branta sanvicensis, originally placed in the monotypic genus Nesochen. This genus was merged with Branta by Delacour and Mayr (1945). Also, I follow Olson (1973) in merging the two Hawaiian rail genera Porzanula and Pennula in Porzana. The following discussions deal only with species-level taxonomic problems.

The Hawaiian Stilt

Most 20th Century authors on Hawaiian birds list the Hawaiian stilt (knudseni) as a subspecies of Himantopus himantopus. Such a classification can only be correct if Old World and New World stilts are considered conspecific. North American ornithologists regard the form mexicanus as a distinct species (AOU Check-list Committee, 1957), however. The Hawaiian stilt differs from

H. mexicanus only in relatively minor plumage differences as compared to the striking color pattern differences shown by H. himantopus. Mayr and Short (1970) considered the Hawaiian form an allospecies of a worldwide stilt superspecies, mainly because of "insufficient knowledge," but admitted that some of the allospecies would "undoubtedly prove conspecific." I believe the plumage similarities are sufficient to warrant considering the Hawaiian stilt a subspecies, H. mexicanus knudseni, of the Black-necked Stilt of the New World.

The Hawaiian Coot

The Hawaiian Coot, originally considered an endemic species Fulica alai, has been classed in all recent works as a subspecies of the American Coot, F. americana. However, the relationship is not, in my opinion, obvious a priori. The various species of Fulica differ primarily in the size, color, and configuration of the bill and frontal shield, and in the distribution of white feathers in the generally dark gray plumage. The American Coot has a small maroon frontal shield, a pied bill, and white undertail coverts. The Old World F. atra lacks the white undertail, and has a much larger white frontal shield. The Caribbean Coot, F. caribaea, also has a large white shield. Mayr and Short (1970) consider F. atra, F. americana, F. caribaea, and the South American F. leucoptera to comprise a superspecies.

The Hawaiian form resembles the American Coot in plumage, but its frontal shield is much like those of F. atra or F. caribaea. The shield is large and bulbous, extending posteriorly to a point above and between the eyes, unlike the small knobby shield of F. americana. Most Hawaiian Coots have pure white shields and bills, but some are cream colored or yellow, and others (about 15 %, pers. obs.) have bright red shields and black-appearing spots near the tips of the mandibles. Unfortunately, the red-shielded variety is not represented in specimen collections. One specimen with a small, maroon frontal shield is in the collections of the Bishop Museum, but I believe this bird, taken on Hawai'i in the winter, is referable to F. americana. In the Andes of South America occurs another population of coots that is also dimorphic with respect to the color of the frontal shield (Gill 1964). Mayr and Short (1970) and Gill (ibid.) consider this population conspecific with F. americana, but de Schauensee (1966; 1970) disagrees. Obviously, considerably more data will be necessary before the systematics of coots can be adequately analyzed. At the present time, I see no reason for considering the Hawaiian form conspecific with F. americana. Zoogeographic considerations aside, the bird more closely resembles F. caribaea or the controversial Andean form F. "ardesiaca." However, F. alai is equally distinct from all allospecies of the F. [atra] superspecies and should therefore be given equivalent taxonomic rank until new data suggest otherwise.

In recent years, sightings of supposed American Coots have been made during the winter months in Hawai'i (Pratt 1978). Studies are needed to determine whether such birds may occasionally remain during the breeding season. Such observations might demonstrate whether differences in frontal shields actually function as species recognition factors in coots.

The Hawaiian Mallards

Two endemic ducks occur in the Hawaiian Islands, one on Laysan and the other on the main islands. Both are obviously related to the Common Mallard, *Anas platyrhynchos*. The Laysan form (*laysanensis*) is much smaller than continental mallards, and has undergone considerable adaptation in order to survive in the harsh environment of a coral island. The Koloa-maoli (usually simply called Koloa for short), of the main islands (form *wyvilliana*) is also smaller than continental birds but is much closer to them in habits and plumage than is *laysanensis*. The adult Koloa resembles the female Common Mallard, but is darker. Drakes sometimes show a trace of green about the head and a darker brown chest than hens. First-year males are more similar to drake Common Mallards than are the adults. These birds exhibit black around the base of the tail, pale lateral tail feathers, upturned central rectrices, and sometimes even a neck ring. Such bright plumage is lost the second year (Swedberg 1967). Waterfowl taxonomists have long considered these similarities to indicate that *wyvilliana* and *laysanensis* are conspecific with *A*. *platyrhynchos* (Delacour and Mayr 1945; Mayr and Short 1970), but most publications on Hawaiian birds have retained the species status of the two local forms (Berger 1972b; Shallenberger 1978).

Delacour and Mayr (1945) did not consider the possibility of isolating mechanisms between Hawaiian mallards and *A*. *platyrhynchos*, but simply stated that, on the basis of plumage similarities, all were conspecific. Such thinking has also been applied to other mallards such as *A*. *fulvigula* of southeastern North America, which Mayr and Short (1970) consider conspecific with the Common Mallard. These authors believe these forms to be allopatric, and thus no doubt feel justified in lumping them. However, such a belief ignores one very important aspect of mallard breeding biology. According to Schorger (in Palmer 1976), the breeding cycle of mallard-type ducks begins in the fall _on the wintering grounds_. Pair formation occurs throughout the winter and is virtually complete before the ducks return to their nesting grounds. Thus the phase of the cycle in which species recognition is most important usually occurs when Common Mallards may be in the company of other mallards.

Common Mallards, while not particularly numerous, winter in some numbers in the Hawaiian Islands every year. In addition, I have seen domestic mallards at Hanalei National Wildlife Refuge on Kaua'i and at Kawainui Marsh on O'ahu, both of which are important nesting grounds for the Koloa. Although biologists have frequently expressed concern that such populations might interbreed with the native ducks (Shallenberger 1978), no case of Common Mallard/Koloa hybridization has been documented. The Hawaiian Duck breeds throughout the year (Swedberg 1967), and thus has ample opportunity to form mixed pairs with migrant Common Mallards, which are forming pair-bonds while in the islands. But the local ducks and the migrants do not associate with each other. Swedberg (1967: 13) states: "Even in an area as small as Ahukini reservoir on Kauai (about ten acres) the Koloa tend to keep to one end, while the migrants keep to the other." Thus the two species form pair-bonds within sight of each other. Mayr (1969: 413) defines "sympatry" as "the existence of a population in breeding condition within the cruising range of individuals of another population." I interpret "breeding condition" to include the pair-formation phase of the breeding cycle, and thus consider that the Koloa, _Anas wyvilliana_, and the Common Mallard have met the test of sympatry without interbreeding and are therefore good species. They are components of the _Anas_ [platyrhynchos] superspecies as is the aberrant Anas laysanensis.

These observations may explain why the drake Koloa reverts to a somber brown plumage after the first year. Selection has probably favored divergence in plumage color to prevent mixed matings of Common Mallards and Koloa. Such divergence would be advantageous to both species by preventing wasteful expenditure of energy in the formation of pair-bonds that would be broken when the A. platyrhynchos member flew northward. Even if the pair-bonds were strong enough to hold a Common Mallard on its wintering grounds, the bird would be ill-adapted to nesting on mountain streams in the manner of most Koloa (Swedberg 1967). Similar mechanisms would undoubtedly prevent mixed pair formation on Laysan should migrant Common Mallards find their way there.

SECTION 11.

TAXON CYCLES AND ZOOGEOGRAPHY OF HAWAIIAN BIRDS

In earlier sections of this paper I have alluded to the existence of what has come to be known as the "taxon cycle." The idea that taxa exhibit life cycles roughly comparable to those of individuals has been widely discussed in the last quarter century. Brown (1957) provided the theoretical basis for modern studies of the phenomenon. Such a cycle begins with the expansion of a species over a broad geographic area. Then follows a period of taxonomic differentiation as populations adapt to local conditions. These differentiated populations may become isolated, speciate, and diverge further from the founder species. In time some of these derived species will die out leaving isolated relicts. These relicts may die out as well, ending the process, or one of them may be able to initiate a new cycle. Most data on the subject have come from studies of insular faunas (Wilson 1961; Greenslade 1968; Ricklefs and Cox 1972) because archipelagos provide natural controlled experiments. The term "taxon cycle" has been used in the island context only (Wilson 1961; Ricklefs 1970; Ricklefs and Cox 1972, 1978). Various authors have outlined the stages of such cycles in somewhat different ways (Wilson 1961; Dillon 1966; Greenslade 1968), the most recent, and I believe most successful attempt being that of Ricklefs and Cox (1972). These authors present an outline of the island taxon cycle in four stages. In Stage I, a species invades an archipelago and occurs undifferentiated on all the islands. Stage II is characterized by subspeciation among the islands and the loss of some island populations. In Stage III, the isolated populations become well-differentiated species with fragmented or disjunct distributions, and in Stage IV only highly derived single-island endemics remain. Ricklefs and Cox (1972) dealt with the West Indies, islands that are close to continental source areas for invading species, and whose fauna shows clear affinities to that of the continent. Most endemic taxa above the species level are relicts in late stages of the taxon cycle.

The assumption is made, based on numerous examples, that species invade an archipelago by systematic island-hopping, without leaving distributional gaps (Ricklefs and Cox, ibid.) Any species that shows gaps is interpreted as being in a later stage of the cycle. This assumption probably is not valid in every case, but the data seem to indicate that it is a good working hypothesis. Ricklefs and Cox (ibid.) showed that most documented invasions of the West Indies had occurred in the manner described. Also, the degree of taxonomic differentiation seems to be positively correlated with the degree of fragmentation of distribution.

In Hawai'i, distributional gaps have traditionally been unexplained or attributed simply to vagaries of interisland colonizations. However, the history of several exotic species introduced to the islands supports the "no gap" hypothesis. The Barred Dove (Geopelia striata) was introduced to O'ahu, Kaua'i, and Maui in the 1920s but now occurs on all islands (Berger 1972b, 1977). Schwartz and Schwartz (1949) found it abundant on Moloka'i in 1947. These same authors documented the dove's spread to the Big Island in 1937. The birds appeared first at the northwest end of the island, immediately opposite the source area on Maui. Since all of the Hawaiian Islands (even Kaua'i on a clear day) are visible from their nearest neighbors, this type of spread through the archipelago is what would be expected, rather than a haphazard appearance of birds on scattered islands. Therefore I believe the assumption that birds with fragmented distributions are in later stages of the taxon cycle is valid for Hawai'i. Thus, disjunct distributions such as that of Chasiempis sandwichensis (Table 1) can be explained in terms other than fortuitous colonizations (see below).

Likewise, the widespread, undifferentiated forms must be viewed as Stage I species. Since the time of Perkins (1903) the lack of subspeciation in Drepanis coccinea, Himatione sanguinea, and Psittirostra psittacea has been attributed to frequent interisland dispersal. I agree with Berger (1972b), however, that this idea has been overemphasized. No other evidence of frequent interisland movements exists. Furthermore, the occurrence of vocal dialects in Himatione sanguinea (Ward 1964) and Drepanis coccinea (pers. obs.) may indicate that these species are much too sedentary to provide the level of genetic interchange necessary to preclude subspeciation. Thus, as discussed in Section 5, I consider these three species to represent Stage I of the taxon cycle.

In an oceanic archipelago as isolated as the Hawaiian Islands, immigration is virtually a negligible factor. More species enter the fauna by autochthonous speciation than by immigration. Thus, even though the nature of the taxon cycle in Hawai'i is not fundamentally different from those seen in other archipelagos, these cycles often represent a long succession of "recycling" of relict senile taxa. Such relicts, subjected to extreme selection, may evolve novel solutions to the problems of survival either by exploiting new niches, as when a new type of food plant colonizes the islands, or by becoming more efficient in old ones. When such adaptations are perfected, they can open the door to a rapid expansion on the part of the former relict, which spreads from its island of origin to occupy most or all of the archipelago. The remainder of the cycle is essentially the same in a remote oceanic archipelago as elsewhere. First, a period of "fine tuning" of adaptations on the respective islands leads to subspeciation. Further changes produce first a superspecies complex, then a species group too disparate to be so classed. Eventually divergence may be so great that the relationships of the descendant forms are no longer readily apparent, or perhaps only one single island endemic remains to represent a once thriving group of species. Usually, these specialized relicts are the ones that begin new cycles, although rarely one may begin with a new colonization from outside the archipelago.

The Hawaiian avifauna possesses taxa in all stages of the taxon cycle (Table 10). The three Stage I species clearly illustrate the point that new cycles can begin with relicts. Each belongs to a tribe whose members are highly divergent, with the "links" missing. In fact, the Drepanidini and

TABLE 10.

STAGE OF TAXON CYCLE OF LAND AND FRESHWATER BIRDS OF THE MAIN HAWAIIAN ISLANDS

STAGE I

- *Nycticorax nycticorax*
- *Anas wyvilliana*
- *Gallinula chloropus*
- *Fulica alai*
- *Himantopus mexicanus*
- *Asio flammeus*
- *Psittirostra psittacea*
- *Himatione sanguinea*
- *Drepanis coccinea*

STAGE II

- *Hemignathus obscurus*
- *Hemignathus* [*virens*]

STAGE III

- *Myadestes obscurus* species group
- *Chasiempis sandwichensis*
- *Moho* [*nobilis*]
- *Loxops* [*coccineus*]
- *Hemignathus lucidus*
- *Paroreomyza maculata* species group

STAGE IV

- *Branta sandwichensis*
- *Buteo solitarius*
- *Porzana sandwichensis*
- *Corvus tropicus*
- *Chaetoptila angustipluma*
- *Moho braccatus*
- *Rhodacanthis palmeri*
- *Loxioides bailleui*
- *Chloridops kona*
- *Pseudonestor xanthophrys*
- *Oreomystis bairdi*
- *Oreomystis mana*
- *Hemignathus munroi*
- *Hemignathus parvus*
- *Hemignathus sagittirostris*
- *Ciridops anna*
- *Drepanis pacifica*
- *Drepanis funerea*
- *Palmeria dolei*
- *Melamprosops phaeosoma*

Psittirostrini include only Stage I and Stage IV species.

Species in Stages II and III of the cycle include most members of the Hemignathini, as well as the endemic Meliphagidae, Monarchinae, Sylviinae, and Turdinae. The boundary between these two stages is, of course, arbitrary, since the taxon cycle is a dynamic process. Many species are progressing from Stage II to Stage III, without precisely corresponding to either. An example of such intermediacy is the genus Loxops, wherein the distribution pattern is that of a Stage II species, but one of the four isolates has already reached the species level of divergence. A clearcut Stage II species is Hemignathus obscurus, with subspecies on four islands and a few distributional gaps, and Stage III is illustrated by the Moho [nobilis] group, with geographically representative species on three islands. Moho braccatus has already reached Stage IV.

The most remarkable attribute of taxon cycles in Hawai'i is that the pattern of geographic differentiation and island extinctions is so similar among so many taxa. The most strongly differentiated forms of complexes in Stages II and III are usually found on Kaua'i. Such is the case with Loxops [coccineus], Hemignathus [virens], and Moho. This pattern is probably related to the relative isolation of Kaua'i in the archipelago. Less frequently, a strongly differentiated form occurs on Hawai'i, as in the subgenus Heterorhynchus. On the other hand, Kaua'i does not seem to function as a refugium for the bizarre relicts of Stage IV. Only Moho braccatus can be classed as a Stage IV species on that island, and it barely so. Virtually all Hawaiian species in Stage IV are found on either Hawai'i or the Maui Nui complex. The Big Island harbors seven such species (*Rhodacanthis* here considered monotypic), five of which comprise monotypic genera, while Maui Nui has four such species and three monotypic genera. Neither O'ahu nor Kaua'i harbors a monotypic genus. Perhaps such relicts survive only on larger, younger islands.

In Hawaiian taxon cycles, distributional gaps typically first appear on the smaller islands, as shown by the *Loxops* [*coccineus*] superspecies (Table 1). As the cycle proceeds, some populations may thrive while others decline. Sometimes the result is a single-island endemic such as *Ciridops anna*, now known as fossils from other islands (Olson, pers. comm.), but historically confined to the Big Island. The subgenus *Heterorhynchus* illustrates a case of differential success, with some declining members and one species poised for a new cycle. The three subspecies of *Hemignathus* (*Heterorhynchus*) *lucidus* exist at such a low population level that they can be considered extinction prone. These forms have always been considered rare (Perkins 1903) and the O'ahu form is now extinct. In contrast, the 'Akiapola'au, *Hemignathus* (*Heterorhynchus*) *munroi*, is a very successful species on the Big Island (or at least was until recent artificial ecological changes). Its bizarre "combination tool" bill has enabled it to exploit a new niche, one only partially and probably less well exploited by its sister species *Hemignathus lucidus*. Thus the 'Akiapola'au is just the sort of Stage IV species likely to be "recycled" by expanding its range to other islands. Other Stage IV species, such as *Pseudonestor xanthophrys*, may have become so specialized that such an expansion is no longer possible.

Taxon cycles in Hawai'i appear to be driven by "counteradaptation" similar to that seen in West Indian islands (Ricklefs and Cox 1972). In other words, taxa advance through the cycle because of readjustments of each island's fauna following the successful invasion of a new species. Invading species in the West Indies are usually ecological generalists. As such, they enjoy an initial competitive advantage over the more specialized older residents of the islands. However, the older fauna eventually "counteradapts" to the newcomer, forcing it into more specialized niches and thus through the taxon cycle (Ricklefs and Cox 1972). The phenomenon differs in Hawai'i only in that expanding, invading species rarely originate outside the archipelago, and in the fact that these species need not be ecological generalists. The spectacular adaptive radiation of the Drepanidinae has occurred precisely because of this absence of invading continental taxa.

Taxon Cycles Among Introduced Species

Do artificially introduced birds illustrate the same phenomena as the products of natural colonizations? This question has not heretofore been addressed, but no account of Hawaiian birds would be complete without at least a cursory look at the possibility inasmuch as these islands have proportionally more introduced bird species than anywhere else (Berger 1972b, 1977). Many of these exotics are inhabitants exclusively of man-altered habitats and thus are not good subjects for comparisons with birds in natural environments. A few species, however, have invaded the native forests of the islands and have apparently found "open niches." One such species, the Red-billed Leiothrix

(Leiothrix lutea), is perhaps the best studied exotic bird in Hawai'i.

Introduced to all islands except Lana'i early in this century, the leiothrix became numerous everywhere (Caum 1933; Fisher and Baldwin 1947). By 1960, however, it was rare on Kaua'i (Richardson and Bowles 1964), and is now virtually extinct there. I have not seen it on Kaua'i despite extensive field work throughout the island. This pattern was repeated on O'ahu. The leiothrix was still abundant there in 1960 (Richardson and Bowles 1964) but about 1968 a drastic decline began that is clearly documented by data from Honolulu Christmas Bird Counts (CBCs) of the period published annually in the journal 'Elepaio, as well as various field trip reports in the same publication. Shallenberger and Vaughn (1978) summarized recent published records on O'ahu, and found that only ten sightings of the leiothrix had been reported between 1971 and 1976. Shallenberger and Vaughn's (1978) thorough surveys of the Ko'olau Range turned up only 27 individuals. Thus the Red-billed Leiothrix is now only slightly more numerous on O'ahu than on Kaua'i. Furthermore, the bird is now relatively scarce on Moloka'i (Scott et al. 1977; pers. obs.). No evidence of such a decline on the other islands has been forthcoming, and I have found the leiothrix still common to abundant on Maui and Hawai'i.

Kaua'i may have been ecologically overfull following the wave of introductions of the 1930s (Caum 1933; Munro 1944). In the faunal readjustments that followed, the leiothrix proved less tenacious than other species. This result may be an example of what Ricklefs and Cox (1972) call "counteradaptation." O'ahu, larger than Kaua'i, can maintain more species, which could explain the longer tenure of the leiothrix there. But O'ahu has continued to receive input of exotic forest-dwelling species, which Kaua'i has not (Berger 1972b). Two such birds, Cettia diphone and Pycnonotus cafer, underwent spectacular increases in the 1950s and 1960s (see CBC and field trip reports in 'Elepaio). No evidence exists of direct competition between these two and the Red-billed Leiothrix, but none need be hypothesized. In order to accommodate these successful newcomers, a saturated O'ahu avifauna would have to undergo various shifts and readjustments, and as on Kaua'i, the leiothrix was among the species eliminated.

Similar patterns can be seen in some other foreign species that occur in native Hawaiian forests. The Varied Tit (Parus varius) was introduced to O'ahu and Kaua'i and became established for a time on both (Caum 1933; Munro 1944; Berger 1972b, 1977) but disappeared from the latter island before 1960 (Richardson and Bowles 1964) and from O'ahu more recently ('Elepaio CBC and field trip reports). The tit was probably eliminated by the same pressures that have reduced the leiothrix populations. In contrast, some exotic species have undergone spectacular Stage I expansions following their introduction. The Japanese White-eye (Zosterops japonicus) is now probably the most abundant bird in the islands and occurs in virtually every habitat (Berger 1972b, 1977). Introduced to O'ahu in 1931 (Caum 1933), the white-eye spread apparently unaided to the other islands and has even been taken on Johnston Atoll, 1328 km southwest of Honolulu (Amerson and Shelton 1976). Probably the white-eye will eventually feel the effects of counteradaptation as did the leiothrix.

These phenomena could be interpreted as illustrating taxon cycles on a much shorter time scale than occurs with natural colonizations. On O'ahu at least, true counteradaptation may have been replaced recently by the continued influx of new competitors. Thus the exotic birds in Hawai'i can be said to undergo artificial taxon cycles.

Distributional Anomalies

An understanding of the taxon cycle can help to explain some of the seemingly peculiar distributions of Hawaiian birds. One of the most intriguing questions in zoogeographic studies in these islands has been why the 'Elepaio (Chasiempis sandwichensis) is absent from Maui, Moloka'i, and Lana'i when it is so successful on the other three large islands. The answer, I believe, lies in the interactions of the 'Elepaio with the members of the genus Paroreomyza. Henshaw (1902b) considered the 'Elepaio and the Maui 'Alauahio (P. montana) so similar in habits that the latter could exclude the former from the island. I fully agree that the two species are very similar in their ecology. The 'Elepaio is more of a leaf-gleaner and bark-picker than most writers have indicated, and the 'alauahio is as much a flycatcher as is Chasiempis. However, members of these two genera coexist on O'ahu. Why, then, would Chasiempis be excluded from Maui, a somewhat larger island?

In Section 7 I discussed the possibility that Maui Nui, the large composite island of Moloka'i-Maui-Lana'i that existed during the last glaciation, may have had two sympatric species of Paroreomyza. If that indeed were the case, then a model can be suggested to account for the present absence of the 'Elepaio. I hypothesize that Maui Nui and O'ahu originally had one representative each of

Chasiempis and Paroreomyza. The latter may have been the older of the two taxa, or may have been evolving at a faster rate and thus have undergone speciation on the two islands. The O'ahu form then could have colonized Maui Nui, giving that island three species to subdivide a niche originally occupied by two. The 'Elepaio may have been the loser in the three-way competition. An important point to remember here is that Maui has two specialized endemics (Melamprosops and Pseudonestor) that may well have reduced the "ecological room" on that island allowing the ultimate survival of only one "flycatcher-warbler" on the island. These postulated events would be examples of the counteradaptation that forces species through the taxon cycle, and can explain why Chasiempis sandwichensis is in Stage III rather than Stage II of the cycle.

The 'Elepaio represents only one of several enigmatic gaps in the Maui avifauna. With the apparent absence of both an 'o'o (Moho) and a thrush (Myadestes), Maui presents an avifauna that is disharmonic even within the context of Hawai'i. If Melamprosops and Paroreomyza are drepanidine, then all Maui passerines are members of a single subfamily! This bizarre taxonomic situation is, I believe, an artifact.

Recent biogeographical theorists (e. g. Hamilton and Armstrong 1965; MacArthur and Wilson 1967; Lack 1969b, 1976) have demonstrated that a direct correlation exists between island size and species diversity, with larger islands having more species than smaller ones. In general, the Hawaiian Islands follow this model. Lana'i (363 sq km) has nine land and freshwater species, Moloka'i (676 sq km) has 15, Kaua'i (1432 sq km) 19, and Hawai'i (10,458 sq km) 30. However, Maui (1888 sq km) with 16 species and O'ahu

(1575 sq km) with 17 appear to be species-poor. Perhaps the historic avifaunas of these two islands are less well known than has been supposed.

Maui was sadly neglected by the few naturalists who worked in the Hawaiian Islands before Scott Wilson began his studies in 1887. A perusal of his history of ornithological exploration of the islands (Wilson and Evans 1890-99: vii-xix) reveals that he may have been the first serious collector to set foot on Maui. Noteworthy is the fact that both O'ahu and Hawai'i lost species of birds long before 1887. In the case of O'ahu, a thrush taken by Bloxam in 1824 was never again recorded, an 'ō'ō was last seen in 1837, and the Nukupu'u and 'Akialoa were either extinct or very rare by the time of Wilson's visit. O'ahu and Maui are similar in size and both have extensive lowland areas separating two mountain masses. Since Maui was the site of the original capital of the Kingdom of Hawai'i at Lahaina, one would expect that it, as has been documented for O'ahu (Greenway 1967), also suffered the early destruction of its lowland forests. That three of the early extinctions on O'ahu (*Moho apicalis*, *Myadestes* sp., and *Hemignathus obscurus*) represent species or genera missing from the known avifauna of Maui is probably not coincidental. Henshaw (1902b) saw, but did not collect, an 'ō'ō on Maui in 1901 which he suspected might be *Moho bishopi*. Also, Perkins (1903) presented rather convincing anecdotal evidence of the occurrence of a thrush on Maui before the time of intense scientific collecting. Perhaps the discovery of a new species on Maui in 1973 (Casey and Jacobi 1974) should not have been so surprising after all. That event is further evidence that the avifauna of Maui was incompletely surveyed by early naturalists.

O'ahu, despite its position as a commercial center, was also virtually ignored by naturalists of the late 19th and early 20th centuries. This neglect occurred undoubtedly because the island's avifauna was already so degraded by various human disturbances that it was much less interesting from an explorer's point of view than those of the less developed islands (Seale 1900).

That the same fate has now befallen the other islands is tragic, but should not discourage further studies. Much remains to be learned about almost every aspect of the biology of Hawaiian birds, and the loss of some species should only impress those of us who study them with the necessity of preserving what remains of this, the world's greatest natural laboratory of avian evolution.

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VITA

Harold Douglas Pratt, Jr. was born 23 July 1944 at Charlotte, Mecklenburg County, North Carolina. He attended elementary and secondary school there and was graduated from South Mecklenburg High School in 1962. He entered Davidson College, Davidson, North Carolina and received the degree of Bachelor of Science from that institution in 1966.

From 1966 to 1970, Pratt was employed as a teacher of biology in the high schools of Charlotte and Gastonia, North Carolina. He also served as a ranger-naturalist in the Great Smoky Mountains National Park during the summers of 1969 and 1970.

In 1970, he began graduate studies at Louisiana State University, where he received the Master of Science Degree in 1973. In addition to his purely academic activities, Pratt has pursued a career as a scientific illustrator and wildlife artist. His first major published illustrations appeared in the late George H. Lowery, Jr.'s *Mammals of Louisiana and its Adjacent Waters* (1974). His works have also appeared in Lowery's *Louisiana Birds* (1974), *Defenders* (1975), *National Wildlife* (1977), *The Wilson Bulletin* (1977), and *The Living Bird* (1977). In 1976, Pratt was commissioned by the State Foundation on Culture and the Arts (Hawaii) to paint a series of 10 portraits of endangered

Hawaiian forest birds. Others of Pratt's paintings are permanently displayed in the Hall of Hawaiian Natural History at the Bernice P. Bishop Museum in Honolulu. Currently Pratt is preparing the color plates for a field guide to the birds of the Pacific, under the auspices of the Hawaii Audubon Society.

In 1977, Pratt participated in an environmental survey of Hawaiian wetlands conducted by Ahuimanu Productions, Kailua, Hawaii under contract to the U. S. Army Corps of Engineers. Subsequently he has conducted environmental impact studies for airport developments in Palau and Yap in Micronesia, these latter two under contract to AECOS of Kaneohe, Hawaii and Parsons-Brinckerhoff, Inc., of Honolulu. Other incidental employment has included guiding nature tours in Hawaii (1976) and Micronesia (1978) for World Nature Tours, Inc., and in Hawaii for the University of Houston (1978, 1979) and the Oakland Museum (1979).

Pratt is a member of the American Ornithologists' Union, Wilson Ornithological Society, Cooper Ornithological Society, an elective member of the American Birding Association, and an Associate of the Laboratory of Ornithology, Cornell University. He is now a candidate for the degree of Doctor of Philosophy at the May, 1979 commencement of Louisiana State University.

EXAMINATION AND THESIS REPORT

Candidate: Harold Douglas Pratt, Jr.

Major Field: Zoology

Title of Thesis: A Systematic Analysis of the Endemic Avifauna of the Hawaiian Islands

Approved:

J M Fitzsimons
Major Professor and Chairman

James G. Traynham
Dean of the Graduate School

EXAMINING COMMITTEE:

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Date of Examination:

18 April 1979