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STEVEN G. FANCY AND C. JOHN RALPH

'Apapane

Himatione sanguinea

The 'Apapane is the most abundant species of Hawaiian honeycreeper and is perhaps best known for its wide-ranging flights in search of localized blooms of ō'hi'a (*Metrosideros polymorpha*) flowers, its primary food source. 'Apapane are common in mesic and wet forests above 1,000 m elevation on the islands of Hawai'i, Maui, and Kaua'i; locally common at higher elevations on O'ahu; and rare or absent on Lāna'i and Moloka'i.

The 'Apapane and the 'I'iwi (*Vestiaria coccinea*) are the only two species of Hawaiian honeycreeper in which the same subspecies occurs on more than one island, although historically this is also true of the now very rare 'Ō'ū (*Psittirostra psittacea*). The highest densities of 'Apapane are found in forests dominated by 'ōhi'a and above the distribution of mosquitoes, which transmit avian malaria and avian pox to native birds. The widespread movements of the 'Apapane in response to the seasonal and patchy distribution of ' ōhi'a flowering have important implications for disease transmission, since the 'Apapane is a primary carrier of avian malaria and avian pox in Hawai'i.

The Birds of North America
Life Histories for the 21 st Century

The 'Apapane has an incredibly diverse array of songs and calls that vary between and even within islands. Their bright crimson plumage, black wings and tail, prominent white undertail-coverts and abdomen, and long, decurved bill are characteristic as they move quickly among ' ōhi'a flower clusters, probing for nectar and gleaning insects. 'Apapane

density may exceed 3,000 birds/km^2 at times of 'ōhi'a flowering, among the highest for a noncolonial species. Birds in breeding condition may be found in any month of the year, but peak breeding occurs February through June. Pairs remain together during the breeding season and defend a small area around the nest, but most 'Apapane

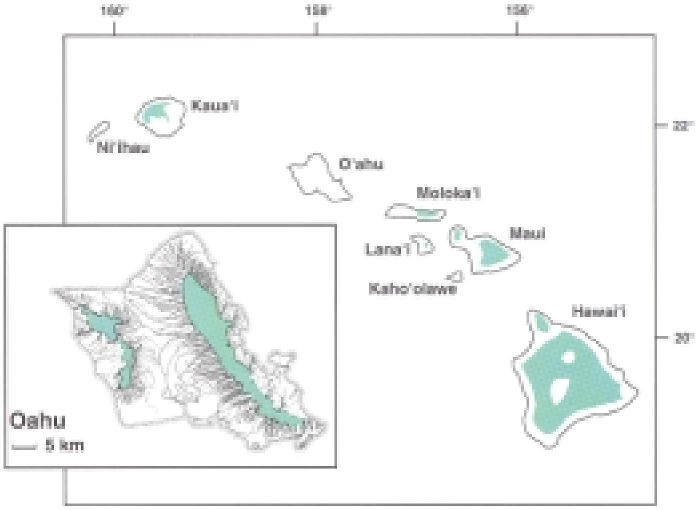

Figure 1.
Distribution of `Apapane.

Order PASSERIFORMES Family FRINGILLIDAE

disperse from breeding areas after nesting, and fidelity to local breeding areas seems low for most individuals.

Despite their seasonal high densities and widespread distribution in higher-elevation forests, no aspect of 'Apapane life history or biology has been well studied. Loss and modification of native forests for agriculture and development have greatly reduced the numbers and distribution of 'Apapane in the Hawaiian Islands, and introduced mammalian predators and avian diseases continue to limit populations of 'Apapane and other native Hawaiian birds.

The Laysan Honeycreeper *(Himatione sanguinea freethii),* a subspecies of 'Apapane from Laysan I. in the Northwestern Hawaiian Is., was first discovered in 1891 but became extinct in 1923 as a result of the almost complete destruction of the island's vegetation by introduced rabbits. This bird was described by Rothschild (1893-1900) as "by far the rarest of the Laysan Island birds, though I have observed a fair number, generally in pairs. They are very active in their movements, flitting about in the scrub. It feeds on very small insects as a rule, but I have also observed it sucking honey from the flowers."

DISTINGUISHING CHARACTERISTICS

Small (13 cm), sexually monochromatic songbird. Adults bright crimson with black wings and tail; long (15-17 mm), slightly decurved bluish black bill. Female distinguished from male only by measurements of birds in hand (Fancy et al.1993). Mean mass 16.0 g for males (*n* = 42), 14.4 g for females (*n* = 29; Baldwin 1953). Prominent white undertail-coverts and lower abdomen, and shorter, darker and less decurved bill distinguish it from the 'I'iwi which has longer, more decurved bill and vermilion abdomen and undertail-coverts. Juvenile has gray brown and buff body-feathers with white undertail-coverts. Juvenile secondaries and some greater-coverts with rufous or buff outer webs. Characteristic tail-up posture. Wings produce a distinctive whirring noise in flight.

Laysan subspecies (Fig. 2) had bright scarlet vermilion head, throat, breast, and upper abdomen, with faint tinge of golden orange; remainder of upperparts orange scarlet (Rothschild 1893-1900). Lower abdomen and underwing-coverts dull ashy brown, fading into brownish white on undertail-coverts. Laysan Honeycreeper distinguished from 'Apapane on main islands by shorter bill and scarlet vermilion (not blood red) coloration (Rothschild 1893-1900). Intense sunlight probably caused fading of plumage of Laysan form relative to nominate race (Olson and Ziegler 1995).

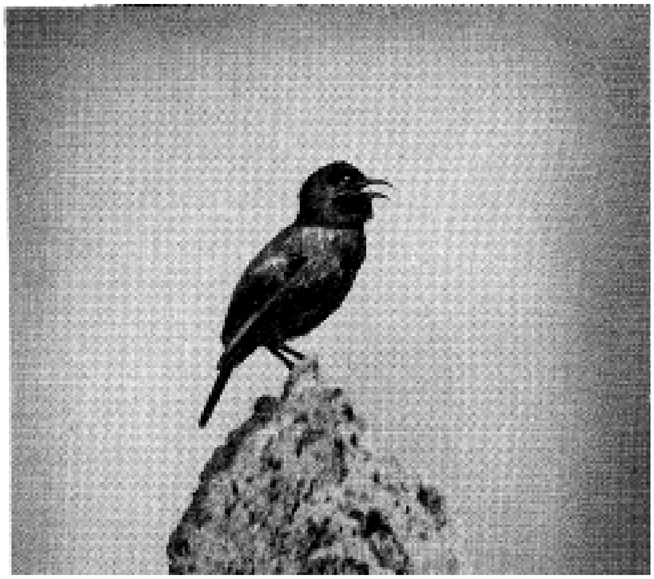

Figure 2. Laysan Honeycreeper. Photographed by Donald Dickey in 1923. Courtesy of the Denver Museum of Natural History/Photo Archives. All rights reserved.

DISTRIBUTION

HAWAIIAN ARCHIPELAGO

Breeding range. Figure 1. Native mesic and wet forests above about 1,250 m elevation on islands of Hawai'i, Maui, O'ahu, and Kaua'i. In Ko'olau Range on O'ahu, locally common from about 300-400 m elevation to summit at 946 m (E. VanderWerf pers. comm.). Generally less common and found only above 600 m in Wai'anae Range on Oahu (E. VanderWerf and J. Rohrer pers. comm.). Rare or absent on Moloka'i and Lanai Is. (Scott et al. 1986, U.S. Geological Survey Biological Resources Division unpubl. data).

Extinct Laysan Honeycreeper known only from Laysan I. in the Northwestern Hawaiian Is. No other records of 'Apapane on other islands.

Winter range. Same as breeding range, although found more often at elevations below 1,250 m in nonbreeding season. Many juveniles and adults found in high-elevation dry mamane *(Sophora chrysophylla)* forests on Hawaii in late summer and fall during mamane flowering. Small numbers may occur at low elevations on O'ahu in introduced vegetation, such as at Lyon Arboretum at 125 m.

HISTORICAL CHANGES

Nominate race formerly found on all forested islands in Hawaiian Archipelago to sea level (Wilson and Evans 1890-1899, Perkins 1903, Scott et al. 1986), but now restricted to higher elevations. Clearing of forests for grazing, food crops, and development, particularly below 1,250 m (Scott et al. 1986, Jacobi 1990), has greatly reduced the distribution of 'Apapane. Less than 40% of Hawai'i now covered by native-dominated vegetation, and only 10% of native forest remains below 600 m (Scott et al. 1986, Jacobi 1990). Estimated habitat loss since before human contact was 42% (Mountainspring 1986). Perkins (1903) found 'Apapane in the "scanty forest immediately behind the city of Honolulu," and Seale (1900) reported them in 'ōhi'a forest at 330 m on O'ahu. Found "in fair numbers" during 1935-1937 surveys on Hawai'i, Maui, O'ahu, and Kaua'i, but only 1 'Apapane found on Moloka'i (Munro 1960). Avian malaria and avian pox, transmitted by introduced mosquitoes and presumably brought to Hawai'i with introduced cage birds, have had devastating effects on distribution and numbers of 'Apapane (Warner 1968, van Riper et al. 1986, Atkinson et al. 1995).

Laysan Honeycreeper formerly found only on Laysan I. Rabbits, introduced by 1903 to provide food for guano miners, caused the almost total destruction of vegetation on Laysan that resulted in the extinction of 3 of the 5 endemic land birds (Ely and Clapp 1973). The last 3 known Laysan Honeycreeper individuals died in 1923 as a result of lack of cover during a storm (Olson 1996).

FOSSIL HISTORY

Known from deposits of unknown age at Barber's Point, O'ahu (Olson and James 1982a) and from collections on Maui and Hawai'i Is. (James and Olson 1991).

SYSTEMATICS

Described as *Certhia sanguinea* by Gmelin (1788). The name *Himatione sanguinea* established by Cabanis in 1851 (Museum Heineanum, Vol. 1, p. 99) has endured. Laysan Honeycreeper described as *H. fraithii* by Rothschild (1892), who named it after Captain Freeth, governor of Laysan I. Rothschild later corrected the spelling to *freethii* and later classified as a subspecies under *sanguinea* by Amadon (1950).

GEOGRAPHIC VARIATION

The nominate race is found on all of the main Hawaiian islands and has undergone little geographic differentiation. No documentation of current interisland movements.

SUBSPECIES; RELATED SPECIES

Two subspecies recognized: *H. s. sanguinea* on main Hawaiian islands, and *H. s. freethii* on Laysan I. The extinct Laysan subspecies differed in plumage characters and had a shorter, stouter bill than that of the nominate race (Schauinsland 1899, Fisher 1906, Berger 1981). Cranial osteology suggests that Laysan Honeycreeper is a distinct and possibly more primitive form that perhaps should be recognized as a full species (Olson and James 1982a, Olson and Ziegler 1995).

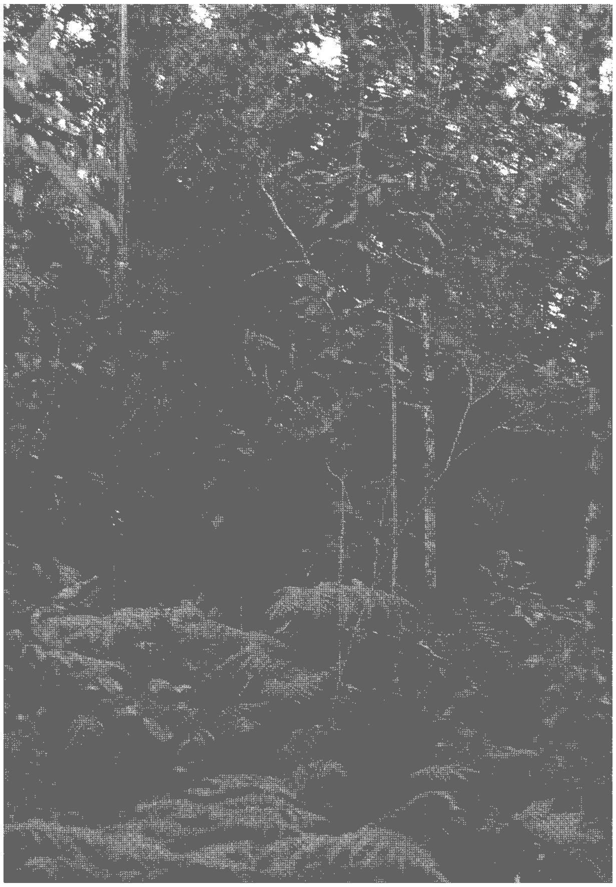

Figure 3. Typical breeding habitat of `Apapane-a wet forest at Hakalau Forest National Wildlife Refuge on Hawai'i I. dominated by `ōhi'a and koa with an understory of ground ferns, 'ōlapa, and pūkiawe (*Styphelia tameiameiae*). Photo by SGF.

Most closely related to Crested Honeycreeper (*Palmeria dolei*) on Maui and then to 'I'iwi (Tarr and Fleischer 1995). DNA and morphological evidence indicate that Hawaiian honeycreepers shared a more recent common ancestor with cardueline finches of North America than with any other group studied (Raikow 1977, Sibley and Ahlquist 1982).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Reported as making "regular migrations when the flowering season demands" within an island (Perkins 1903:407), but these local movements are not true migration. Well known for seasonal movements in response to 'ōhi'a availability (Perkins 1903, Baldwin 1953, MacMillen and Carpenter 1980, Ralph and Fancy 1995). Species reported to be resident by most studies (Perkins 1903, Baldwin 1953, van Riper et al. 1986, Ralph and Fancy 1995).

TIMING AND ROUTES OF MIGRATION

Population shifts within an island are more pronounced during Jun-Aug, presumably because of postbreeding dispersal and patchy 'ōhi'a flowering. Highest numbers of evening foraging flights recorded in Jul and Aug (MacMillen and Carpenter 1980). Foraging flights correlated with local 'ōhi'a availability (Ralph and Fancy 1995). 'Apapane common in high-elevation māmane forests on Mauna Kea Volcano, Hawai'i I., during peak māmane bloom in Sep-Nov. Most birds return downslope to 'ōhi'a and koa *(Acacia koa)* forests to roost.

MIGRATORY BEHAVIOR

No information.

CONTROL AND PHYSIOLOGY

No information.

HABITAT

Breeds and winters primarily in mesic and wet native forests dominated by 'ōhi'a (Fig. 3; Scott et al. 1986). Range limited mostly to elevations above 1,250 m because of disease-carrying mosquitoes that are restricted to lower elevations because of cold intolerance (van Riper et al. 1986, Atkinson et al. 1995). Windward slopes of Hawai'i, Maui, Moloka'i, O'ahu, and Kaua'i receive 700-1,000 mm rainfall annually (Scott et al. 1986). Koa also dominant in best habitat, with varying amounts of kōlea *(Myrsine lessertiana*), naio *(Myoporum sandwicense),* and tree ferns *(Cibotium* spp.) in forest canopy. Mamane dominant in higher-elevation, dry forests used for foraging but where breeding is uncommon.

Common birds in same forest habitat include 'I'iwi,'Amakihi (*Hemignathus* spp.), and introduced Japanese White-eye (*Zosterops japonicus*) on all islands; 'Elepaio (*Chasiempis sandwichensis*), 'Oma'o (*Myadestes obscurus*), and introduced Red-billed Leiothrix (*Leiothrix lutea*) on Hawai'i; Maui Creeper, or'Alauahio (*Paroreomyza montana*), and Red-billed Leiothrix on Maui; and Kaua'i Creeper, or 'Akikiki (*Oreomystis bairdi*), and 'Anianiau (*Hemignathus parvus)* on Kaua'i (Scott et al.1986).

FOOD HABITS

FEEDING

Main foods taken. Nectar; also foliage insects and spiders (Perkins 1903, Conant 1981, Carothers 1986a, 1986b; Ralph and Fancy 1995). Koa, naio, mamane, kolea, alani (*Melicope* sp.), kanawao (*Broussaisia arguta*), koki'o ke'oke'o (*Hibiscus arnottianus*), and 'ōlapa (*Cheirodendron trigynum*) also used for foraging on nectar and insects. Reported feeding on flowers of coconut palms (Cocos *nuci fera*) along seacoast in late 1700s (Perkins 1903). On Maui, feeds on nectar of introduced tree alfalfa (*Cytisus proliferus*) when in bloom (Waring et al. 1993). Takes nectar from introduced umbrella tree (*Schefflera actinophylla*) on O'ahu (E. VanderWerf and J. Rohrer pers. comm.).

Laysan Honeycreeper fed regularly on nectar from *Capparis sandwicheana,* but changed to *Portulaca* and *Sesuvium* when rabbits caused extinction of *Capparis* (Ely and Clapp 1973). Observed visiting flowers of *Tribulus* and *1pomoea* (Munro 1960). Also fed on caterpillars and moths (Fisher 1903).

Microhabitat for foraging. Forages mostly in mid- and upper strata of forest canopy, never on the ground, except for Laysan Honeycreeper which foraged on the ground. Most often seen feeding conspicuously on outer flower clusters of 'ōhi'a trees. Gleans small twigs and both upper and lower surfaces of leaves, mostly in outer crowns of trees. Foraging on larger branches and trunks rarely observed.

Food capture and consumption. Active feeder, stopping at each flower for only a few seconds. Usually inserts bill into flower for <1 s while perching; often probes neighboring flower or 2 before shifting sites (Waring et al.1993). At 4 wet-forest sites on Hawaii I., 61.6% of foraging motions were classified as flower probes, remainder as gleaning, pecking, and other probing motions (*n* = 3,883; CJR). Spent >90% of foraging time on 'ōhi'a at 1 study site, and >80% on 'ōhi'a at 2 other sites (CJR). Forages throughout day; makes foraging flights away from areas where resident, even during breeding season (Ralph and Fancy 1995). Foraging on introduced tree alfalfa inflorescences greatest at dawn and decreases throughout day, whereas foraging on 'ōhi'a increases throughout day (Waring et al. 1993). Increased foraging on 'ōhi'a nectar throughout day corresponds to nectar flow (Carpenter 1976, Waring et al. 1993).

Foraging flights most common during first and last 2 h of day (Ralph and Fancy 1995). Generally forages alone, but may form loose foraging flocks, sometimes containing several other species, during postbreeding season and at other times of year. Flock size ranges from 1 to 38, but 85% of flocks consist of 1 or 2 'Apapane (Ralph and Fancy 1995). Flocking by 'Apapane may thwart dominance behavior at flowering trees by 'I'iwi and Crested Honeycreepers (Carothers 1986a,1986b).

Pollination of 'ōhi'a by native birds, particularly 'Apapane, is essential for high levels of fruit set and outbreeding (Carpenter 1976). Robs nectar from

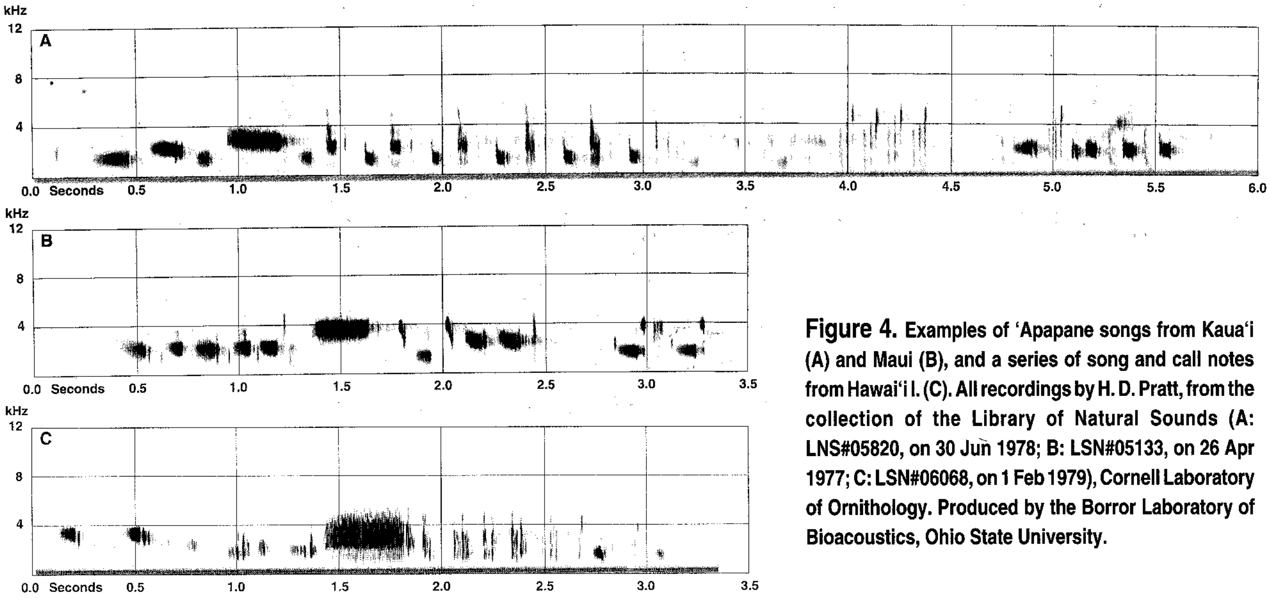

Figure 4. Examples of ‘Apapane songs from Kaua‘i (A) and Maui (B), and a series of song and call notes from Hawai‘i I. (C). All recordings by H. D. Pratt, from the collection of the Library of Natural Sounds (A: LNS#05820, on 30 Jun 1978; B: LSN#05133, on 26 Apr 1977; C: LSN#06068, on 1 Feb 1979), Cornell Laboratory of Ornithology. Produced by the Borror Laboratory of Bioacoustics, Ohio State University.

long, tubular flowers such as those of koki'o ke'oke'o (VanderWerf. and Rohrer 1996). Like other drepanidines, has tubular tongue with brushy tip (Amadon 1950).

Laysan Honeycreeper fed on nectar and insects (Fisher 1903), and was observed walking around on ground within patches of a prostrate succulent *Portulaca* (Fisher 1906). Observed walking on rocks and ground picking up small flies (Olson 1996:132). Captured moths and held them with 1 foot while removing wings and eating only the soft parts (Ely and Clapp 1973).

DIET

Primarily nectarivorous; nectar of 'ōhi'a and māmane constitute major portion of diet. Frequency of occurrence of invertebrates in 63 'Apapane stomachs: butterflies and moths (Lepidoptera) 87%, hoppers (Homoptera) 75%, lacewings (Neuroptera, mostly larvae) 60%, spiders (Arachnida) 43%, bees, wasps, and ants (Hymenoptera) 43%, bark lice (Psocoptera) 41%, flies (Diptera) 21%, beetles (Coleoptera 17%), thrips (Thysanoptera)14%, true bugs (Hemiptera) 10%, and mites (Acarina) 3% (Baldwin 1953).

Frequency of occurrence in 195 fecal samples collected throughout year: adult psyllids (Psyllidae) 40%, psyllid eggs 20%, spiders 20%, Lepidoptera larvae (18%), Lepidoptera adults (18%), common bark lice (Psocoptera: Psocidae) 18%, leafhopper (Homoptera: Cicadellidae) adults (12%), and Hymenoptera (10%; CJR).

FOOD SELECTION AND STORAGE

No information.

NUTRITION AND ENERGETICS

Specific requirements not known. Easily maintained in captivity on diet of artificial nectar with protein supplement.

METABOLISM AND TEMPERATURE REGULATION

Basal metabolic rate of 8 'Apapane fasted for 6-12 h was 27.5 kJ/d, 18% higher than that predicted for a 14.5-g passerine (Weathers et al. 1983). Metabolic rate of 7 'Apapane fasted 24 h was 21.5 kJ/d (MacMillen 1981).

DRINKING, PELLET-CASTING, AND DEFECATION

Obtains most moisture from nectar, but has been observed taking water from leaf surfaces.

SOUNDS

VOCALIZATIONS

Development. No information.

Vocal array. Described, and supported with sonographs, by Ward (1964). Incredibly varied calls and songs, including squeaks, whistles, rasping notes, clicking sounds, and melodic trills. Variations found in different locations (Fig. 4), even within the same island. Both sexes sing at all times of year. One song described as "a rolling call, followed by 3 whistles, 5 chucks, a drawn-out note, and a faint squawk at the end" (Ward 1964). Common call described as a "feeble though clear *tweet* twice repeated" (Wilson and Evans 1890-1899). Contact calls (Fig. 4C) are frequent in small, fast-moving foraging flocks during nonbreeding season and in nesting pairs. Calls often while flying, but rarely sings during flight.

Song of Laysan Honeycreeper described as low, sweet, and consisting of several notes (H. Palmer in Rothschild 1893-1900).

Phenology. Sings throughout year, but more persistently during breeding season (Ralph and Fancy 1994). Singing rate highest in Feb at beginning of breeding, and lowest in Jul-Oct when 'ōhi'a flowering is more patchy and 'Apapane are more mobile (Ralph and Fancy 1994). Singing begins with dawn chorus and is most persistent during early morning and late afternoon (Eddinger 1970). Less singing during hotter part of day. Henshaw (1902:56) reported singing "at all seasons of the year and at all times of the day."

Laysan Honeycreeper silent except during breeding season, Dec-mid-Jun (Rothschild 1893-1900).

Places of vocalizing. Often sings from perch at 10- to 30-s intervals (Ward 1964). Sometimes gives flight song while flying straight or while circling nest tree. Sometimes flies upward from a perch, sings in hesitating flight, and then flies downward to a perch, giving call notes on its way (Berger 1981).

Social context and presumed functions of vocalizations. Unstudied, but both vocal and wing-whirring sounds appear to function agonistically in defending of resources and reproductively in mating.

NONVOCAL SOUNDS

Whirring sound during flight produced apparently by obliquely truncate primaries (Amadon 1950).

BEHAVIOR

LOCOMOTION

Mobile and agile. Flight follows typical undulating finch pattern: a few rapid wing-beats upward are followed by brief descent on closed wings. Rarely seen on ground except for Laysan Honeycreeper. Laysan Honeycreeper "weak, low flier" (Munro 1960).

SELF-MAINTENANCE

Scratches head by bringing foot forward and up over wing (Eddinger 1970). Occasionally seen sunbathing in 'ōhi'a trees: "The bird ruffs out its feathers, opens the bill, spreads the tail feathers, points the head and open bill upward, and eyes being open, stretches one wing and then the other" (Eddinger 1970). Bathes while perched on branch while it is raining, or by flying into wet vegetation (Eddinger 1970). Not observed bathing in water pools.

AGONISTIC BEHAVIOR

Aggressive toward other 'Apapane during breeding season (Eddinger 1970, Carothers 1986a, 1986b). During nonbreeding season, usually travel together in small flocks with no noticeable aggression. Behaviorally subordinate to other nectarivorous bird species. Forced to spend majority of time on relatively poor patches of resources because of aggressive behavior by ‘I’iwi and Crested Honeycreeper (Pimm and Pimm 1982, Carothers 1986a,1986b).

SPACING

Both sexes defend small territory around nest during breeding season by singing; defense may also include chases and use of claws (Eddinger 1970). Males show increased animosity toward other 'Apapane during nesting, but groups of up to 6 'Apapane, including nesting pair, observed in tree with active nest (Baldwin 1953:343).

SEXUAL BEHAVIOR

Mating system and sex ratio. Monogamous. Male-biased adult sex ratio of 1.7:1 at Keauhou Ranch (n = 504; CJR) and 1.5:1 at Hakalau Forest National Wildlife Refuge (*n* =182; SGF), on basis of discriminant analyses of body measurements. Sex ratio 1.3:1 for 119 'Apapane collected by Baldwin (1953). Adult sex ratio of museum collections of Laysan Honeycreeper is 1.7:1 (Ely and Clapp 1973).

Pair bond. Pairs usually form Jan-Mar; during pair formation males sing and sometimes show aggression toward other males (Eddinger 1970). Sexual chasing common before initiation of nest construction (Eddinger 1970). Before copulation, female crouches on tree branch and flutters wings. Both birds then usually fly off without post-copulation display, and male sings. Female solicits feeding by depressing and fluttering her wings, as do fledglings. Courtship-feeding observed before and throughout nest construction, but highest rate during incubation (Eddinger 1970). Pairs remain together during breeding season, but no information on reuniting of pairs between seasons.

Extra-pair copulations. Not recorded.

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Occur as pairs in breeding areas, and neighboring males interact aggressively. Forms loose-knit flocks of 2-38 individuals during foraging flights. Immatures are subordinate to adults (Carothers 1986a).

Nonpredatory interspecific interactions. Forced to spend time on relatively poor patches of resources because of the behaviorally dominant 'I'iwi and Crested Honeycreeper (Pimm and Pimm 1982; Carothers 1986a, 1986b). On Maui in 1980s'Apapane counteracted to dominance by 'I'iwi and Crested Honeycreeper by foraging in flocks: this behavior reduced chase frequencies, increased 'Apapane foraging time, and let 'Apapane forage in trees from which they were otherwise excluded (Carothers 1986a). Often observed in mixed-species foraging flocks with 'Akepa (*Loxops coccineus*), 'Akeke'e (*Loxops caeruleirostris*), Hawai'i Creeper (*Oreomystis* mana),'Amakihi,and other native birds during nonbreeding season. Little evidence of competition with nonnative birds as found for 'I'iwi (Mountainspring and Scott 1985).

PREDATION

Kinds of predators. Suspected predation on eggs and chicks by introduced mammals, particularly black rat (*Rattus rattus*) and feral cat (*Felis catus*; Atkinson 1977). Density of rats in 1 study area on Hawai'i estimated at 60 rats/ha, the highest reported for a forest habitat (SGF). Hawaiian Hawk (*Buteo solitarius*) and Pueo, or Short-eared Owl (*Asio flammeus sandwichensis*), are also known predators on adults or chicks of Hawaiian honeycreepers (Snetsinger et al. 1994). Introduced Polynesian rat (*Rattus exulans*), Norway rat (*Rattus norvegicus*), mongoose (*Herpestes auropunctatus*), and Barn Owl (*Tyto alba*) may also take some 'Apapane.

Response to predators. Predator-mobbing and alarm-calling not documented.

BREEDING

PHENOLOGY

Figure 5. Breeding activity begins Oct-Nov; peak breeding Feb-Jun (Ralph and Fancy 1994). Males in breeding condition all year, and females with brood patches found Dec-Jul. Breeding coincides with seasonal availability of 'ōhi'a nectar.

Nest-building. Nest construction requires 5-8 d; 1-6 d between nest completion and laying of first egg (Eddinger 1970).

First/only brood per season. Fledging dates in Hawai'i National Park from 3 Feb to early Aug (Baldwin 1953).

NEST SITE

Uses wider variety of nest sites than most other bird species in Hawai'i. Nest is usually a cup on a high terminal branch of 'ōhi'a, but nests have also been found in tree cavities and lava tubes (van Riper 1973, Sakai 1983), and on upper branches of koa, ilex (*Ilexanomala*) and *Cibotium* tree ferns (Sakai 1983).

Laysan Honeycreeper nested mainly in center of high grass bunches, but sometimes in very thick ***Chenopodium sandwichensis shrubs*** (Schauinsland 1899).

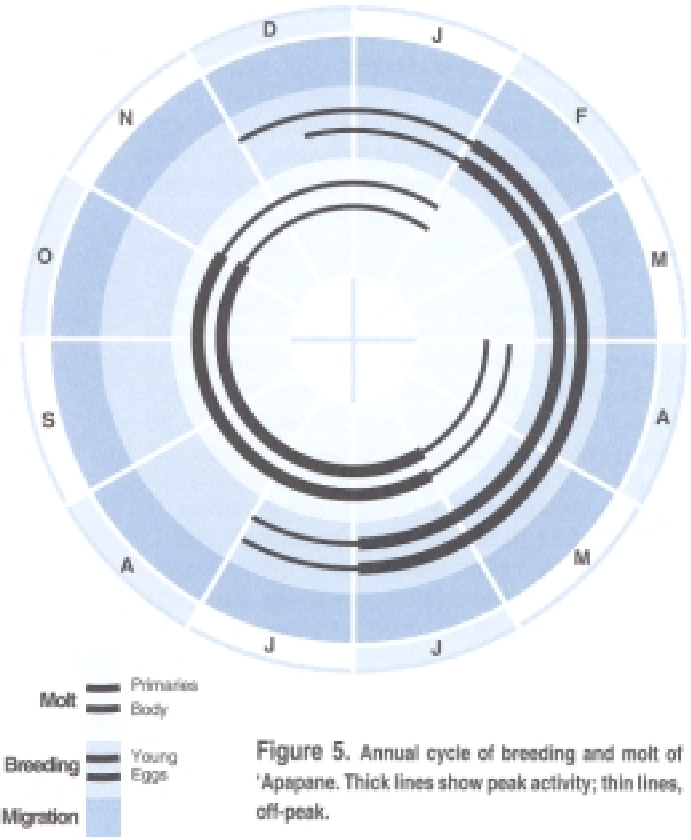

Figure 5. Annual cycle of breeding and molt of 'Apapane. Thick lines show peak activity; thin lines, off-peak.

Sixty-eight nests constructed between and woven around small vertical branches 30-61 cm below terminal cluster of leaves in 'ōhi'a trees; average nest height 8.4 m ($n = 38$ nests; Eddinger 1970). Usually nests in trees without flowers, presumably to make nest defense easier. Both parents defend small territory around nest from other 'Apapane.

NEST

Construction process. Both parents build nest; construction takes 5-8 d. Often dismantle deserted nests of other 'Apapane or other species (Eddinger 1970, Sakai 1983). One nest in a lava tube was superimposed on 3 nests from previous seasons (van Riper 1973).

Structure and composition matter. Body of nest composed mostly of mosses, with a few 'ōhi'a twigs and leaves, a few lichens, bark fragments, roots, and small rhizomes woven among nest materials (Eddinger 1970, Sakai 1983). Nest cups lined with shredded grass or sedge fibers.

Laysan Honeycreeper nest consisted predominantly of fine rootlets, with a few interwoven grass blades, firmly fitted together but not deep (Schauinsland 1899). One nest contained down from a young albatross (*Diomedea* spp; Fisher 1903).

Dimensions. Mean nest dimensions (cm) for 6 nests: outside diameter 9.5, nest depth 10.2, cup diameter 5.1, cup depth 3.8 (Eddinger 1970).

EGGS

Shape. Ovate to short ovate.

Size. Mean length 24.1 mm (range 22.6-25.8); mean width 18.4 mm (range 17.9-19.1, *n* = 16; Eddinger 1970). Lengths of 3 Laysan Honeycreeper eggs were 19.75, 20.5, and 20.5 mm, widths 14.0, 14.5, and 14.5 mm, respectively (Schauinsland 1899). Fisher (1903) reported typical Laysan Honeycreeper egg measurements of 18 x 13.75 mm.

Color. Whitish background with irregularly shaped markings that vary from tan to reddish brown to dark chocolate. Markings concentrated at large end of egg.

Surface texture. No information.

Eggshell thickness. No information.

Clutch size. Typically 3, range 1-4 (*n* = 38; Eddinger 1970). See also Demography and populations: measures of breeding activity, below. Clutch size of Laysan Honeycreeper reported as "four or five" (Bailey 1956: 122); several sets of 3 taken by early collectors (Ely and Clapp 1973).

Egg-laying. First egg laid 1-6 d after nest completion; 1 egg laid /d, usually in early morning, before 08:00 (Eddinger 1970).

INCUBATION

Onset of broodiness and incubation in relation to laying. Incubation begins with laying of last egg, by female exclusively (Eddinger 1970).

Incubation patch. Females with brood patches found Dec-Jul.

Incubation period. Mean 13 d (*n* = 8; Eddinger 1970).

Parental behavior. Male forages near nest and sings from perches nearby, but does not visit nest. Female does not sing or call from nest. Proportion of time that 1 female covered eggs was 57.8% on day 1, 70.0% on day 6, and 94.4% on day 12 (Kauai I.; Eddinger 1970). Male feeds female away from nest: Female leaves nest, flies to male's singing perch, and depresses and quivers her wings as a fledgling begging for food does (Eddinger 1970). Male either feeds female immediately or flies off to collect food from 'ōhi'a blossoms before returning to feed female.

HATCHING

Eggs hatch most frequently in morning; complete clutch hatches before noon (Eddinger 1970).

YOUNG BIRDS

Condition at hatching. Young altricial. Nestlings weigh 3.0 g at hatching. Chicks essentially naked, with small amount of gray down on head, back, and wings. Eyes closed at hatching. Inside of mouth is bright pink, rictal flanges cream-colored (Eddinger 1970).

Growth and development. Eyes open 4 d after hatching (Eddinger 1970). Feather tracts begin to appear on wings and back on day 6. Feathers begin to unsheath on day 8 and are unsheathed by day 14. Nestlings weigh 13-15 g on day 10. After 11 d of age, young will jump out of nest if disturbed.

PARENTAL CARE

Brooding. Female broods young closely during first few days after eggs hatch as male continues to feed her away from nest (Eddinger 1970). Female broods at night and during periods of heavy rain. Feeding rate decreases during heavy rains, since male does not increase frequency of feeding trips to compensate for female's reduced number of trips.

Feeding. Both parents feed nestlings. No data on nestling diet, but caterpillars are a large part of it (Eddinger 1970). Feeding rate 2.7 trips/h on day 1, 1.3 on day 7, and 2.3 on day 14 (*n* = 3 h/d observation time; Eddinger 1970). Female fed nestlings 73.7% of times (Eddinger 1970). Female and nestlings solicit feeding by depressing and fluttering their wings. Male feeds female most frequently during incubation, but also before and during nest construction (Eddinger 1970).

Nest sanitation. Both parents remove fecal sacs (Eddinger 1970).

Carrying of young. Not reported.

COOPERATIVE BREEDING

None reported.

BROOD PARASITISM

None reported.

FLEDGLING STAGE

Mean nestling period 16 d (range 15-17, *n* = 19; Eddinger 1970). Young can fly well from tree to tree when they leave nest. Fledglings present Feb-Jul (Baldwin 1953).

IMMATURE STAGE

Period of dependency <4 mo, on basis of proportion of observations with young and at least 1 parent (CJR). Proportion of immatures in population peaked in Jul on Hawai'i and Kaua'i Is. (CJR).

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding. First year of life (Baldwin 1953); annually thereafter.

Clutch. One to 4 eggs (mean 2.8, *n* = 38; Eddinger 1970).

Annual and lifetime reproductive success. Fledging success 70.2%, hatching success 79.8%, nestling survival 88.0% (*n* = 53 nests; Eddinger 1970).

Number of broods normally reared per season. One, but may renest if first nest unsuccessful.

LIFE SPAN AND SURVIVORSHIP

Annual survival based on 1,584 recaptures of 429 banded individuals and Jolly-Seber models was 0.72 ± 0.11 SE for adults and 0.13 ± 0.07 SE for juveniles (includes permanent emigration; Ralph and Fancy 1995). However, probability of resighting an individual in a given year if that individual was alive and in the study area was only 0.07, and low capture probabilities can lead to imprecise estimates of survival (Pollock et al. 1990). Longevity in wild unknown. In captivity, a 2+-yr-old 'Apapane captured on 7 Mar 1981 died on 10 Feb 1990 at the Honolulu Zoo; its life span was >-11 yr (P. Luscomb pers. comm.).

DISEASE AND BODY PARASITES

Diseases. Avian pox (*Avipoxvirus* spp.) and avian malaria (*Plasmodium relictum*) kill Hawaiian honeycreepers and devastate bird numbers and distributions (Warner 1968, van Riper et al. 1986). 'Apapane has highest prevalence of *Plasmodium* parasites of any native or alien bird species in Hawaiian Is. (van Riper et al. 1986, C. Atkinson unpubl. data). Parasitemia levels (parasites/ 10,000 red blood cells) in'Apapane also were significantly higher than in other island species (van Riper et al. 1986). Some 'Apapane now appear to breed in midelevation forests where high rates of malaria transmission have been demonstrated; thus these birds may be developing resistance (Atkinson et al. 1995).

Individuals with lesions characteristic of avian pox on their feet, legs, or face were more likely to have malaria than individuals without lesions (van Riper et al.1986). The primary disease vector, the mosquito *Culex quinquefasciatus,* may have expanded recently to higher elevations: *Culex* larvae have been found at 1,800 m elevation on Hawai'i I. (D. Lapointe pers. comm.), and incidence of poxlike lesions on birds captured at 1,600 m elevation increased from 0.9% of 1,361 'Apapane at Keauhou Ranch in 1976-1981 (Ralph and Fancy 1995) to 5.6% of 266 'Apapane at Hakalau Forest National Wildlife Refuge in 1994-1996 (SGF).

Body parasites. Known parasites of 'Apapane include the protozoa *Plasmodium relictum* and *Trichomonas gallinae,* nematodes *Procyrnea longialatus* and *Viquiera hawaiensis,* cestode *Anonchotaenia brasilense,* trematode *Urotocus rossittensis,* 6 genera of mites (Goff 1980), lice, and the bacteria *Klebsiella pneumoniae, Escherichia coli, Pseudomonas pseudoalcaligens,* and *Enterobacter cloacae* (van Riper and van Riper 1985). Voge and Davis (1953) found numerous cestodes (*Anonchotaenia* spp.) in 10 'Apapane specimens collected in 1948-1949 in Kau, Hawai'i I.

CAUSES OF MORTALITY

Little direct information. Avian malaria and avian pox, and predation by black rats and feral cats thought to be major factors. Nestlings may die from exposure during cold, rainy periods or be blown from nest during high winds.

RANGE

Initial dispersal from natal site. No information.

Fidelity to breeding site. Fidelity to localbreeding area low for most individuals: 78% of 1,361 'Apapane were never captured or seen again at 2 study areas on Hawai'i I. (Ralph and Fancy 1995). Only 3% of 236 hatch-year 'Apapane were recaptured or sighted in subsequent years at same site on Hawai'i I. (CJR).

Home range. Some birds resident throughout year, but individuals make long foraging flights and the population shifts in response to nectar availability (Ralph and Fancy 1995).

POPULATION STATUS

Density. Densities >3,000 birds/km^2,among the highest for noncolonial species, found in 'ōhi'a-koa forests near Hawai'i National Park (Ralph and Fancy 1995). Densities highly correlated with 'ōhi'a flowering; mean monthly densities (birds/km^2± SE) at 4 forest sites: 1,563± 404, 1,368 ± 163, 1,274 ± 77, and 715 ± 210, respectively (Ralph and Fancy 1995). Densities in 'ōhi'a-koa forests usually higher than in forests with few '6hi'a (Scott et al. 1986).

Numbers. Of total population, 86% found on Hawai'i I.:1,080,000 ± 25,000 birds (95% confidence interval; Scott et al. 1986). Maui population estimated at 109,643, with 86% on Haleakala Volcano in e. Maui. Moloka'i population 38,643 ± 2,360; Kaua'i population 30,327 ± 716. 'Apapane is the only remaining honeycreeper on Lana'i; population there was 540 ± 213 birds in 1979 (Scott et al.1986).

The only population estimates for Laysan Honeycreeper were 300 in 1911, 1,000 in 1915, and 3 just before extinction in 1923 (Ely and Clapp 1973).

Trends. Difficult to determine because of highly variable seasonal densities in each area. Population estimates at 1 site were higher after 15 yr for surveys in Feb but lower for surveys in Jun (Ralph and Fancy 1995). No major changes in distribution since late 1970s.

POPULATION REGULATION

Habitat loss, avian disease, and introduction of alien species have had the greatest impacts on 'Apapane populations. Forests have been cleared for agriculture, cattle-ranching, and development. Avian diseases, which resulted from the introduction by humans of mosquitoes and cage birds to Hawai'i, effectively limit breeding populations to elevations above 1,500 m and cause seasonal die-offs and measurable fluctuations in 'Apapane populations (C. Atkinson unpubl. data).

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Shooting and trapping. Feather cloaks, some containing more than half a million feathers of 'Apapane and other birds, were a symbol of prestige and power in pre-European Hawai'i (Brigham 1899, Kaeppler 1970). 'Apapane feathers were not as desired as feathers of other species, and given the high population density of 'Apapane and their habits, it is unlikely that populations were affected by taking of feathers.

Degradation of habitat. Loss and modification of habitat by humans and the introduction of alien species to Hawai'i have greatly reduced numbers and distribution of 'Apapane and other endemic birds. The introduction of rabbits to Laysan I. as a food source for guano miners led to the extinction of the Laysan Honeycreeper in 1923 (Ely and Clapp 1973). Polynesians colonized Hawai'i around 400 A.D. and radically changed the ecosystem by burning vast areas of forest for agriculture and introducing nonnative plants and animals (Kirch 1982, Olson and James 1982b). Most Hawaiian bird species went extinct before European contact (Olson and James 1982b), and 27% of endemic Hawaiian birds have gone extinct since first western contact (in 1778) because of human activities (Smith and Fancy 1997).

MANAGEMENT

The primary conservation strategy for endemic Hawaiian forest birds is protection and restoration of native forests above 1,500 m elevation, where mosquitoes are less common. Refuges, parks, and reserves have been established by federal and state agencies and by private conservation organizations. Many conservation areas are fenced to exclude or control feral ungulates. Compaction of soils and felling and hollowing of tree ferns by feral pigs (*Sus scrofa*) create favored breeding sites for *Culex* mosquitoes (Atkinson et al. 1995), and feral pig management may help reduce avian disease transmission. Overbrowsing and girdling of young trees by feral goats (*Capra hircus*), feral cattle (*Bos taurus*), feral sheep (*Ovis aries*), mouflon (*Ovis musimon*), axis deer (*Axis axis*), and black-tailed deer (*Odocoileus hemionus*) have converted vegetation in some areas to open mire and seriously degraded many mesic and wet forests in Hawaiian Archipelago. Mammalian predators such as rats have been controlled in only a few localized areas. Control of alien vegetation has had only limited success for most species, but prompt action has probably prevented the establishment and spread of several species that could have devastating effects on Hawaiian forests.

APPEARANCE

MOLTS AND PLUMAGES

Hatchlings. Chicks mostly naked; small amount of gray down on head, back, and wings. (Eddinger 1970).

Juvenal plumage. Feather tracts appear on wings and back on day 6. Feathers begin to unsheath by day 8, and are unsheathed by day 14 (Eddinger 1970).

Juvenal plumage characterized by gray brown and buff body-feathers, and by secondaries and some greater-coverts with rufous or buff outer webs (Fancy et al. 1993). Pink or orange wash on auriculars, throat, or scapulars of some birds is distinct from crimson color of adults. Wing and tail black. Primaries edged narrowly with white on outer web; secondaries broadly edged with buffy brown (Rothschild 1893-1900). Wing-lining ashy. Underparts brownish buff, shading into whitish buff on abdomen.

Juvenal plumage of Laysan Honeycreeper described by Rothschild (1893-1900) as generally dull brown on upper surface and light ashy brown on underparts, many of the feathers margined with rich buffy brown. Head- and hindneck-feathers had blackish terminal and buffy subterminal spot, producing somewhat mottled appearance. Wings and tail dark brown; primaries narrowly and secondaries broadly margined with rich brownish buff. Chin and upper throat orange buff; lower abdomen and undertail-coverts white, tinged with buff.

Basic I plumage. Prebasic I molt partial. Molt occurs between Jul and Dec (Baldwin 1953). Birds captured in Sep were molting body and capital tracts and posterior portion of ventral and spinal tracts. S8-S9 may molt by Sep, but never primaries. Molt completed in most birds by Dec; sparse molt in parts of capital tract in a few birds (Baldwin 1953). During first Prebasic molt, 'Apapane attains crimsonbody plumage of adults, but retains juvenal primaries, all or some buff-edged secondaries (particularly S5 and S6), and, frequently, a few gray brown feathers on head. Head becomes almost blackish, intermixed with orange (Rothschild 1893-1900). Sexes similar.

Definitive Basic plumage. Definitive Prebasic molt complete. This single annual molt follows or partly overlaps breeding season (Fancy et al. 1993, Ralph and Fancy 1994). Molt occurs mostly Jun-Nov in adult birds (Baldwin 1953). Primaries replaced in order from P1 to P9, and secondaries replaced in the following order: S8, S9, S7, S1-S6. S5 and S6 molt at same time or slightly later than P9 (Baldwin 1953). Molt of flight-feathers usually completed by late Oct.

Adult male plumage described by Rothschild (1893-1900) as dark blood-red crimson, lighter and much brighter on head. Underparts deep crimson, shading into brownish white or white on lower abdomen and undertail-coverts. Thighs brownish black. Nine functional primaries (Berger 1982) are black, the longer ones narrowly, but distinctly edged on outer web with white or whitish. Nine secondaries, the innermost smallest and shortest, black broadly edged with crimson on outer web. Only 2 alular feathers. Inner webs of all remiges lined with pale ashy. Rectrices black. Underwing-coverts ashy. Distinct apteria were found between humeral tract and dorsal spinal tract of Nihoa Finch (*Telespyza ultima*) and Hawaii 'Amakihi (*Hemignathus virens*), but this space filled by regularly spaced feathers in 'Apapane, possibly as adaptation to colder and wetter conditions in its forest habitat (Berger 1982). Sexes similar.

Male Laysan Honeycreeper described by Rothschild (1893-1900) as having bright scarlet vermilion feathers on head, throat, breast, upper abdomen, lower back, and uppertail-coverts, with faint tinge of golden orange that was more pronounced in freshly molted and living birds. Remainder of upperparts orange scarlet. Lower abdomen and underwing-coverts dull ashy brown, with brownish white undertail-coverts. Primaries narrowly edged with whitish on outer web, inner web becoming buff, and secondaries edged pale scarlet on outer web. Adult female similar to male, but red somewhat paler. Freshly molted individuals have deeper red and are not easily distinguished from 'Apapane on main islands, but red feathers apparently fade in direct sunlight on Laysan I. (Rothschild 1893-1900, Olson and Ziegler 1995).

BARE PARTS

Bill. The long (15-17 mm), slightly decurved bill is primarily bluish black, although basal portion of lower mandible maybe straw-colored (Berger 1981). Base of lower mandible orange in immatures.

Iris. Brown (Rothschild 1893-1900).

Legs and feet. Black; brownish in immatures (Rothschild 1893-1900).

MEASUREMENTS

Nominate race is of uniform size throughout its range (Amadon 1950). Males slightly larger and heavier than females (see Table 1).

MASS

No seasonal trend in body mass (CJR). Males are 11% heavier than females.

LINEAR

According to linear measurements, males are 4-9% larger than females. Adults can be sexed from measurements of exposed culmen and wing-chord (Fancy et al.1993). Laysan Honeycreeper had shorter bill and perhaps slightly shorter wing and longer tail (Amadon 1950).

PRIORITIES FOR FUTURE RESEARCH

The devastating effects of avian disease and negative effects of introduced predators, feral ungulates, and alien plants on the distribution and numbers of native Hawaiian forest birds place a premium on research on methods to control disease and alien species in Hawai'i. A top priority is to determine whether there is a genetic or immunological basis for resistance to disease by certain individuals, and whether individuals that survive malarial infections are able to pass antibodies to their offspring. The possibility of using disease-resistant individuals as founders for new populations as a means of "speeding up evolution" needs to be researched. Further research on the role of the 'Apapane in dispersal of disease parasites and viruses between low- and high-elevation forests is badly needed. The pathogenicity of avian pox needs to be determined, and its interaction with malarial infections needs to be characterized. There is also a need for studies of strain differences among islands and identification of vaccine candidates that can be used to immunize critically endangered species.

Research on the ecological requirements of *Culex* mosquitoes in mid- and high-elevation habitats and the development of techniques for controlling vector populations are needed. Control of feral pigs and other ungulates may reduce disease transmission, but field experiments to determine the effect of ungulate control on disease transmission are necessary. Mathematical models to predict disease epizootics and simulate effects of

Table 1. Linear measurements (mm) and mass (g) of 'Apapane. From Fancy et al. 1993, except as noted. Data shown as mean ± SE (*n*).

	Hatch-year	Second-year	Adults
Wing length			
Male	71.4 ± 0.49 (15)	74.4 ± 1.08 (5)	76.1 ± 0.51 (20
Female	67.9 ± 0.62 (22)	68.3 ± 0.53 (12)	70.6 ± 0.41 (23)
Tail length			
Male	45.8 ± 0.50 (14)	47.6 ± 1.60 (5)	51.2 ± 0.44 (19)
Female	44.2 ± 0.48 (18)	44.3 ± 0.62 (11)	47.0 ± 0.37 (18)
Exposed culmen length			
Male	15.8 ± 0.18 (15)	16.0 ± 0.22 (5)	16.6 ± 0.16 (21)
Female	15.8 ± 0.17 (22)	15.4 ± 0.18 (10)	15.8 ± 0.10 (21)
Culmen length			
Male	12.4 ± 0.16 (14)	12.6 ± 0.19 (5)	13.2 ± 0.13 (19)
Female	12.3 ± 0.10 (18)	12.4 ± 0.20 (9)	12.7 ± 0.11 (16)
Tarsus length			
Male	23.5 ± 0.22 (14)	23.7 ± 0.41 (5)	23.4 ± 0.16 (19)
Female	22.5 ± 0.01 (17)	22.9 ± 0.25 (10)	22.3 ± 0.15 (18)
Mass (g)			
Male[1]	15.4 ± 0.24 (7)	15.4 ± 0.56 (3)	14.7 ± 0.09
Male[2]			16.0 ± 0.20 (42)
Female[1]		13.7 ± 0.70 (4)	14.0 ± 0.13 (106)
Female[2]			14.4 ± 0.29 (29)

[1] CJR.

[2] Baldwin

different control strategies should be developed.

Improved methods are needed to control rat and feral cat populations in native forests, and additional field experiments should be conducted to determine the response of bird populations to predator control. Studies that provide supporting data for toxicant registration and lead to improved toxicants and dispersal methods are urgently needed in the Hawaiian Archipelago.

Few data on the demography of the 'Apapane and other native forest birds exist, and information on age structure, age-specific mortality, and age-specific reproductive rates is needed to understand and counteract the causes of population decline. 'Apapane are being used as surrogates in captive propagation programs focusing on recovery of critically endangered species. Information on the basic reproductive biology of the 'Apapane---specifically details on pair-bonding, nesting season, nest requirements, nest attendance, incubation, and dietary requirements at all life phases-is needed to increase chances of successful captive breeding programs and to aid in conservation of this and other species.

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ABOUT THE AUTHORS

Steven G. Fancy received his B.S. and M.S. degrees from Humboldt State University before migrating to Alaska, where he received a Ph.D. in wildlife biology from the University of Alaska, Fairbanks, for his work on the energy metabolism of barren-ground caribou. Since 1986 he has worked as a research biologist for the U.S. Department of the Interior, and is now based at the Pacific Island Ecosystems Research Center in Hawai'i. Recent research has focused on factors limiting populations of endangered forest birds in Hawai'i and Micronesia. Current address: USGS Biological Resources Division, P.O. Box 44, Hawai'i National Park, HI 96718. E-mail: Steve Fancy@usgs.gov.

C. John Ralph received his bachelors degree in wildlife from the University of California, Berkeley, his master's degree from San Jose State University, and his doctorate from Johns Hopkins University. Most of his early research was on bird migration and orientation. He was cofounder (with L. R. Mewaldt) of the Point Reyes Bird Observatory and served as its Director for a period. After teaching at Dickinson College in Pennsylvania, he moved to Hawai'i with the U.S. Forest Service's research branch, investigating forest birds. Since 1981 he has been involved with land bird and seabird research, primarily in the Pacific Northwest. Current address: U.S. Forest Service, Redwood Sciences Laboratory, 1700 Bayview Drive, Arcata, CA 95521. E-mail: cjr2@axe.humboldt.edu.

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