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‘I‘iwi

Vestiaria coccinea

The 'I'iwi is one of the most spectacular of extant Hawaiian birds, with vermilion plumage, black wings and tail, and long, decurved bill. In pre-European Hawai'i, beautiful feather capes, sometimes containing hundreds of thousands of 'I'iwi feathers, were a symbol of power and prestige among native Hawaiians. The 'I'iwi is a bird of the Hawaiian forests. Its decurved bill seems well adapted to exploit nectar from the similarly shaped flowers of lobehoid plants (Campanulaceae). 'I'iwi and 'Apapane (*Himatione sanguinea*) are well known for their long flights over the forests in search of the flowers of the 'ōhi'a (*Metrosideros polymorpha*) tree, their primary food source. Probably as a consequence of their high flights, 'I'iwi, 'Apapane, and 'Ō'ū (*Psittirostra psittacea*) are the only 3 species of endemic Hawaiian honeycreepers in which the same subspecies occurs on more than one island. Contemporary inter-island movements have not been documented.

'I'iwi are common in mesic and wet forests above 1,500 m elevation on the islands of Hawai'i, Maui, and Kaua'i, but their populations consist of less than 50 birds on the lower-elevation islands of Oahu and Moloka'i, and they are now extinct on Lāna'i Island.

The Birds of North America

Life Histories for the 21 st Century

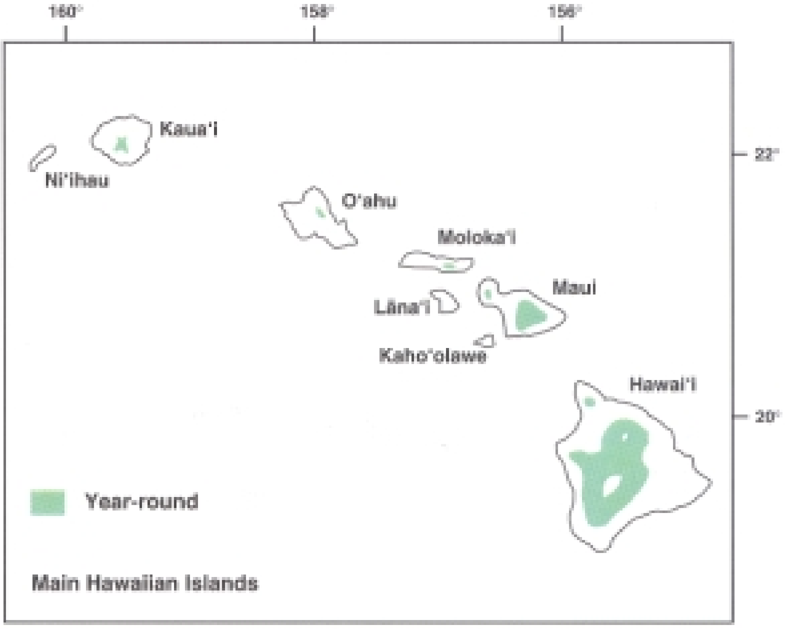

Figure 1.
Distribution of the 'I'iwi.

Order PASSERIFORMES Family FRINGILLIDAE

The species is highly susceptible to mortality from avian malaria, and viable populations persist only at higher elevations where disease-carrying mosquitoes are rare or absent. This species' range has contracted toward higher elevations during the past decade. One bite from a mosquito infected with *Plasmodium relictum* caused mortality in 90% of 10 juvenile 'I'iwi, and 100% of 10 other 'I'iwi bitten more than once died of malaria. One bird that survived malaria developed immunity and survived further challenges with multiple mosquito bites, but there is no evidence that 'I'iwi populations are developing disease resistance, as may be occurring with other Hawaiian species.

'I'iwi in breeding condition can be found in any month, but peak breeding occurs February to June, usually in association with the peak flowering of 'ōhi'a plants. 'I'iwi pairs remain together during the breeding season and defend a small area around their nest, but they usually disperse from breeding areas after breeding. Negative correlations in densities between 'I'iwi and the introduced Japanese White-eye (*Zosterops japonicus*) may result from interspecific competition for limited nectar resources.

Despite its seasonal high densities and widespread distribution in higher-elevation forests, no aspect of the 'I'iwi's life history or biology has been well studied. Short descriptive accounts with notes on 'I'iwi distribution in the late 1800s were written by Rothschild (1893-1900), Wilson and Evans (1890-1899), and Perkins (1903). Additional life history information based on collected birds was provided by Amadon (1950) and Baldwin (1953). Most information on breeding ecology comes from a single study of unbanded birds on Kaua'i Island by Eddinger (1970). Systematic surveys of forest birds on all the main Hawaiian islands in 1976-1982 (Scott et al. 1986) provided the most current data on population size and distribution within much of the 'I'iwi s range. Banding studies (Ralph and Fancy 1994, 1995, SGF) provide valuable information on timing of breeding and molting, local movements, site fidelity, and survival.

Habitat loss and modification because of development and agriculture, and introduction of disease vectors, avian diseases, mammalian predators, and alien plants all continue to threaten 'I'iwi populations, as well as those of other native Hawaiian birds.

DISTINGUISHING CHARACTERISTICS

Medium-sized: overall length 15 cm, mass 16-20 g; sexually monomorphic honeycreeper. Adult is brilliant vermilion; wings and tail black. Wings have contrasting white patch on inner secondaries. Long (25-28 mm), deeply decurved, peach- or salmon-colored bill. Yellow eye-ring visible at close range. Male larger than female in all measurements (see Table 1). Juveniles are dull yellow with black spots; bill dusky brown, becoming brighter with age. 'I'iwi wings produce distinctive whirring noise in flight.

'I'iwi similar to 'Apapane, but 'I'iwi lacks the white undertail-coverts and lower abdomen of 'Apapane. 'Apapane also has a shorter, less decurved, black bill, and has a deeper red color (crimson) than the 'I'iwi, which is slightly more orange (vermilion).

DISTRIBUTION

HAWAIIAN ARCHIPELAGO

Figure 1. Breeds in native mesic and wet forests above about 1,250 m elevation on islands of Hawai'i, Maui, and Kaua'i. Occurs at greatly reduced densities below 1,000 m elevation, except in relatively dry areas of Kona, Hawai'i I., where moderate densities have been found as low as 300 m (Scott et al. 1986). Transient individuals occasionally reported near sea level on Hawai'i I. (SGF). On O'ahu, known to occur in only 3 isolated populations in Wai anae and Ko'olau Ranges, where numerous surveys in 1994-1996 found only 8 birds (VanderWerf and Rohrer 1996, E. VanderWerf pers. comm.). Also sighted on Moloka'i in 1995, the first confirmed sighting there in 7 yr (M. Reynolds pers. comm.). Extinct on Lānai by 1929 (Munro 1944). 'I'iwi reported by F. Sinclair on treeless Ni'ihau in late 1800s after they were "driven by gales from the adjacent island of Kaua'i separated by a channel 18 miles in width" (Wilson and Evans 1890-1899:13).

Seems to move more widely following breeding. Especially on Hawai'i I., many juveniles and adults found in high-elevation dry forests Jul-Nov, during flowering of mamane (*Sophora chrysophylla*).

HISTORICAL CHANGES

Formerly one of the most common forest birds in Hawaiian Islands, found on all forested islands to sea level (Wilson and Evans 1890-1899, Perkins 1903), but now restricted to higher elevations (Scott et al. 1986). In 1838, J. Townsend (in Perkins 1903) found 'I'iwi more abundant on O'ahu than on Kaua'i, but by 1905 W. Bryan (1905: 237) reported that 'I'iwi were "by far the rarest of the five species of mountain birds yet to be found on O'ahu." In 1970s, still found in small numbers in Poamoho, Kaukonahua, Kīpapa, Hālawa, and 'Aiea areas of Ko'olau Range (Shallenberger 1977), whereas in

1996 only a few individuals could be found there (VanderWerf and Rohrer 1996). Common on Moloka'i in late 1800s (Munro 1944), but now close to extinction on that island. Fairly common in Hawai'i Volcanoes National Park, Hawai'i I. in 1940s, but now rare or absent throughout much of the park (Baldwin 1953, Conant 1975, Scott et al. 1986). All low-elevation populations on Hawaii and Maui may be sustained primarily by recruitment from higher elevations (Scott et al. 1986).

Clearing of forests for food crops, grazing, and development, particularly below 1,250 m (Scott et al. 1986, Jacobi 1990), has greatly reduced 'I'iwi distribution. Estimated habitat loss since before human contact ranged from 52% on Hawai'i I. to 85% on O'ahu (Mountainspring 1986). Avian malaria and avian pox, transmitted by introduced mosquitoes and presumably brought in with introduced cage birds (see Demography and populations: disease and parasites, below), have had devastating effects on distribution and numbers of 'I'iwi and other native birds (Warner 1968, van Riper et al. 1986, Atkinson et al. 1995).

FOSSIL HISTORY

Known from fossils of unknown age at Barbers Point, O'ahu I. (Olson and James 1982a), and from similar collections on Maui and Hawai'i Is. (James and Olson 1991).

SYSTEMATICS

Described as *Certhia coccinea* by Forster (1780) from specimens collected by Barthold Lohmann, who had sailed with Cook's last expedition (Rothschild 1893-190). The name *Vestiaria coccinea,* established by Reichenbach (cited in Rothschild 1893-1900), has endured.

GEOGRAPHIC VARIATION

One form was found on all 6 largest Hawaiian Is. Lack of interisland variation may be result of recent range expansion, possibly in response to ecological changes (Pratt 1979, Tarr and Fleischer 1995). Interisland movements undocumented, but may play a role, since species is quite volant.

RELATED SPECIES

Most closely related to Crested Honeycreeper or 'Ākohekohe (*Palmeria dolei*) and 'Apapane, on basis of restriction fragment analyses of mitochondria) DNA (Tarr and Fleischer 1995). DNA and morphological evidence suggest that Hawaiian honeycreepers are most closely related to cardueline finches of North America (Raikow 1977, Sibley and Ahlquist 1982, Tarr and Fleischer 1995).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

A strong flier noted for relatively high, long flights to locate nectar sources, but these intra-island movements are not true migration, since the birds do not make regular movements to and from breeding and wintering areas. Well known for seasonal movements in response to patchy availability of 'ōhi'a and māmane flowering (Perkins 1903, Baldwin 1953, MacMillen and Carpenter 1980, Ralph and Fancy 1995). Some individuals relocated throughout year near breeding territory (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 are correlated with local 'ōhi'a availability (Ralph and Fancy 1995). 'I'iwi and 'Apapane are common in high-elevation mamane forests on Mauna Kea Volcano, Hawai'i I., during peak mamane bloom in Sep-Nov. Most birds seem to return down-slope 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 forests dominated by 'ōhi'a and koa (see Fig. 2; Scott et al. 1986). Range restricted mostly to elevations >1,250 m because of loss and destruction of forests and presence of cold-intolerant *Culex* mosquitoes that transmit avian diseases at lower elevations (Warner 1968, Scott et al. 1986, van Riper et al. 1986, Atkinson et al.1995). Windward slopes of Hawai'i, Maui, Moloka'i, O'ahu, and Kaua'i Is. receive 700-1,000 mm rainfall annually (Scott et al. 1986). Best habitat contains varying amounts of kolea (*Myrsine lessertiana*), naio (*Myoporum sandwicense*), and tree ferns (*Cibotium* spp.) in understory. Māmane is dominant in higher-

Figure 2. Typical breeding habitat of the `I`iwi-a wet forest site at Hakalau Forest National Wildlife Refuge on Hawai'i I. dominated by `ōhi'a and koa with an understory of ground ferns, `ōlapa (*Cheirodendron trigynum*), and `ōhelo. Photo by the authors.

elevation, dry forests used for foraging, but where breeding is uncommon.

Common birds in same forest habitat include 'Apapane and introduced Japanese White-eye on all islands; Hawai'i 'Amakihi (*Hemignathus virens*),'Elepaio (*Chasiempis sandwichensis*), 'Ōma'o (*Myadestes* obscurus), and introduced Red-billed Leiothrix (*Leiothrix lutea*) on Hawai'i; Hawai'i 'Amakihi, Maui Creeper or 'Alauahio (*Paroreomyza montana*), and Red-billed Leiothrix on Maui; and Kaua'i 'Amakihi (*Hemignathus kauaiensis*), Kaua'i Creeper or 'Akikiki *(Oreomystis bairdi*), and 'Anianiau (*Hemignathus parvus*) on Kaua'i (Scott et al. 1986). See also Breeding: nest site, below.

FOOD HABITS

FEEDING

Main foods taken. Nectarivorous; also feeds on foliage insects and spiders (Perkins 1903, Amadon 1950, Conant 1981, Carothers 1986a, 1986b, Ralph and Fancy 1995). 'Ōhi'a, koa, naio, māmane, kōlea, 'dkala (*Rubus hawaiensis*), alani (*Melicope* sp.), kanawao (*Broussaisia arguta*), koki'o ke'oke'o (*Hibiscus arnottianus*), and native lobelioids used for foraging on nectar and insects. Banana poka (*Passiflora mollissima*) nectar is a major food source in some areas. The introduced banana poka forms tree-strangling curtains of vines that extend to canopy, and its presence has greatly increased density of 'I'iwi in parts of the Hakalau Forest National Wildlife Refuge on Hawai'i I. (SGF). Introduced tree alfalfa (*Cytisus palmensis*) on Maui I. used by large numbers of 'I'iwi when in bloom (Waring et al. 1993).

Now feeds primarily on open, nontubular corolla flowers of 'ōhi'a, but early accounts often asserted an apparent coevolution between the 'I'iwi's bill and the long, decurved corollas of Hawaiian lobelioids (Campanulaceae; reviewed by Smith et al. 1995). Reduction in bill size of 0.5 mm during past 86-100 yr may have resulted from dietary shift to 'ōhi'a because of declines and extinctions of lobelioids (Smith et al. 1995, Freed et al. 1996; but see Winker 1996).

Microhabitat for foraging. Forages mostly in mid- and upper strata of forest canopy, never on ground. Rarely seen foraging on larger trunks and branches. Frequently visits flowers of 'ākala and other plants in forest understory when in bloom. Observed <1 m from ground when robbing nectar from *Stenogyne* corollas (Engilis 1990).

Food capture and consumption. Active feeder, stopping at each flower for only a few seconds. Regularly obtains nectar by piercing or tearing holes in tubular corollas at their base, particularly with banana poka, koki'o ke'oke'o, *Stenogyne,* and *Clermontia* flowers (Engilis 1990). Approximately half of foraging time is spent on flowers of 'ōhi'a and other species (CJR). Feeding habits similar to those of 'Apapane, but longer bill enables 'I'iwi to obtain nectar from greater variety of flowers. Pollination by Hawaiian honeycreepers, particularly 'I'iwi and 'Apapane, is essential for high levels of seed set and outbreeding in 'ōhi'a (Carpenter 1976). Has tubular tongue with brushy tip, as do other drepanidines (Amadon 1950).

Often defends territory in flowering 'ōhi'a tree, and spends most time in trees that have greater numbers of flowers (Pimm and Pimm 1982). Single adult or mated pair, sometimes with offspring, often forage in same tree together (Carothers 1986a). Individuals not territorial at low or high flower abundances, but are territorial at intermediate flower abundances (Carpenter and MacMillen 1976a). Despite longer bill, 'I'iwi is more efficient than Maui Creeper or Hawai'i 'Amakihi at foraging on 'ōhelo (*Vaccinium reticulatum;* Carothers 1982).

When feeding on lobelioid flowers, perches on flower-bearing twig, just below flower pedicel, then quickly swings into upside-down position and simultaneously twists body so that head is under open corolla, with bill pointing upward (Spieth 1966). After probing into corolla for a few seconds, bird flies to another flower. May feed on dozens of flowers within a few minutes.

Forages throughout day, apparently making foraging flights away from areas where resident, even during breeding season (Ralph and Fancy 1995). Foraging flights most common during first and last 2 h of day. Most (94% of 791) 'I'iwi observed flying alone, but groups of 1-7 recorded (Ralph and Fancy 1995). One or more 'I'iwi sometimes fly with group of 'Apapane between feeding and roosting areas.

DIET

Primarily nectarivorous; nectar of 'ōhi'a and māmane make up major portion of diet (CJR). Time spent foraging on 'ōhi'a for nectar and insects was 80-90% at 3 sites (CJR). Frequency of occurrence of invertebrates in 32 'I'iwi stomachs: butterflies and moths (Lepidoptera), 100% of stomachs; hoppers (Homoptera), 73%; lacewings (Neuroptera), 60%; psocids (Psocoptera), 43%; bees, wasps, and ants (Hymenoptera), 33%; flies (Diptera), 30%; bugs (Hemiptera), 30%; spiders (Araneida), 30%; beetles (Coleoptera), 27%; and thrips (Thysanoptera), 7% (Baldwin 1953). Perkins (1903) noted fondness for looper caterpillars, which were fed to young.

FOOD SELECTION AND STORAGE

No information.

NUTRITION AND ENERGETICS

Specific requirements not known. Easily maintained in captivity on diet of artificial nectar, protein supplements, and fruit (Atkinson et al. 1995).

METABOLISM AND TEMPERATURE REGULATION

Standard metabolic rate of *7* 'I'iwi within thermal neutrality averaged 3.71 ml/g/h ± 1.39 (MacMillen 1981). Below thermal neutrality, oxygen consump tion had the following relationship with ambient temperature (T_a): $cm^3\ O_2 = 7.08 - 0.14T_a$. Territorial behavior during nonbreeding season increased energy costs by 17% over nonterritorial individuals (Carpenter and MacMillen 1976b).

DRINKING, PELLET-CASTING, AND DEFECATION

Most moisture obtained from nectar, but has been observed taking water from leaf surfaces and flowers.

SOUNDS

VOCALIZATIONS

Development. No information.

Vocal array. See Figure 3. From Eddinger 1970, except where noted. Most calls loud and squeaky, described as *eek* or *coo-eek*. One call is clear, distinct whistle; also used as alarm call. Another call is described as *ta-weet, ta-weet, ta-wee-ah* with flutelike clearness (Wilson and Evans 1890-1899). Often mimics other bird calls. Vocalization by female when soliciting food closely resembles begging calls of fledglings.

Song discordant, like "rusty hinge": *ii*-wi or *ee-vee,* rising in inflection. Both sexes sing throughout year. Sometimes sings in flight, but does not have special flight song.

Phenology. Sings throughout year, but is more persistent in Oct-Dec at beginning of breeding season (Ralph and Fancy 1994).

Daily pattern. Singing begins at dawn chorus and is most persistent during early morning and late afternoon; stops at sunset but while there is still some light (Eddinger 1970).

Places of vocalizing. From Eddinger 1970. Male sings from selected perches, usually live or dead 'ōhi'a branches. Sometimes sings in flight, but does not have specific flight song. Female does not call from nest.

Social context and presumed functions. Unstudied, but vocal and wing-whirring sounds (see Nonvocal sounds, below) appear to function agonistically in defending resources and reproductively in mating. Male uses call note, *eek* or *coo-eek,* to call female off nest for feeding (Eddinger 1970). "Distinct whistle" described by Perkins (1903) is used as alarm call (Eddinger 1970).

NONVOCALSOUNDS

While in flight truncate primaries produce whirring sound audible for 50-100 m (Amadon 1950).

BEHAVIOR

LOCOMOTION

Mobile and agile. Flight follows typical undulating finch pattern: a few rapid wing-beats upward, followed by brief descent on closed wings. Rarely seen on ground.

SELF-MAINTENANCE

From Eddinger 1970. Scratches head indirectly, bringing foot forward and upward over wing. Observed to perch in 'ōhi'a trees and sunbathe. Never observed bathing in pools, but typically

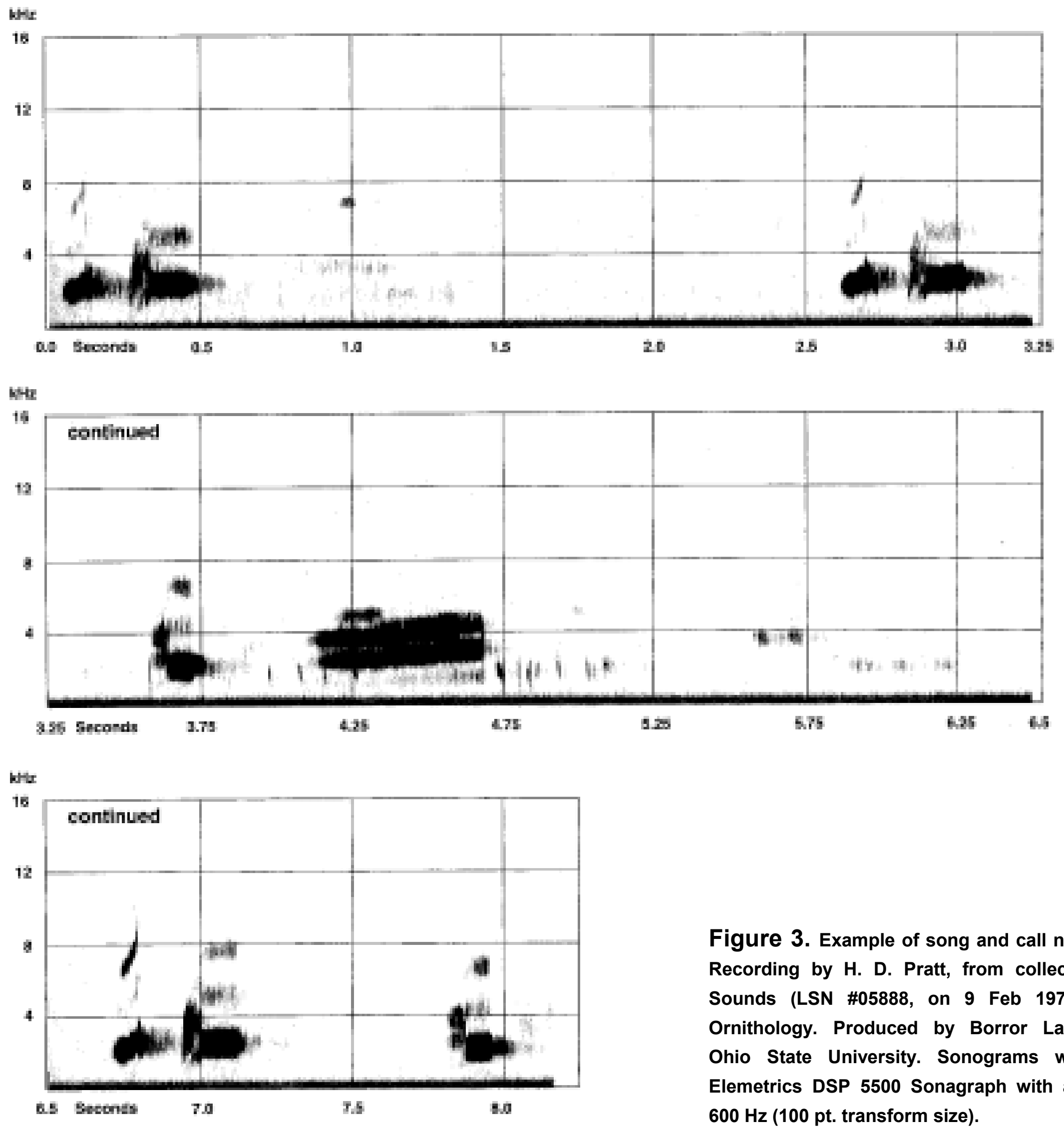

Figure 3. **Example of song and call notes of `I'iwi from Hawai'i I. Recording by H. D. Pratt, from collection of Library of Natural Sounds (LSN #05888, on 9 Feb 1978), Cornell Laboratory of Ornithology. Produced by Borror Laboratory of Bioacoustics, Ohio State University. Sonograms were prepared on a Kay Elemetrics DSP 5500 Sonagraph with an effective band width of 600 Hz (100 pt. transform size).**

bathes while perched during rain, or by flying into wet vegetation.

AGONISTIC BEHAVIOR

Immatures are subordinate to adults; intraspecific aggression usually results in mutually exclusive territories (Carothers 1986a). Modifies agonistic behaviors depending on density of canopy foliage (Carothers 1986b). Tolerates other species within nesting territory, but chases other 'I'iwi away. Female assists with territory defense only when intruder is close to nest (Eddinger 1970).

SPACING

Both sexes defend small territory around nest during breeding season, size of which depends on available singing perches nearby; territory size of 1 pair was 948 m^2 (Eddinger 1970). Individual trees with many flowers are often defended against conspecifics and other nectarivorous species (Pimm and Pimm 1982, Carothers 1986a).

SEXUAL BEHAVIOR

Mating system and sex ratio. Apparently monogamous within breeding season (CJR). On basis of body measurements (Fancy et al.1993), male-biased adult sex ratio is 1.44:1 (n = 264) at Hakalau Forest National Wildlife Refuge (SGF). Amadon (1950) reported male: female ratio of 2.3:1 for juvenile and adult museum skins, perhaps because males are more active and vocal and are collected more often. Adult sex ratio was 1.4:1 for 39 'I'iwi collected by Baldwin (1952).

Pair bond. From Eddinger 1970. Sexual chasing common before initiation of nest construction; most evident in Mar and Apr. Courtship-feeding, most often initiated by male, is important in maintaining pair bond. Female solicits feeding by depressing and quivering her wings, as do fledglings. Vocalization by soliciting female closely resembles food calls of begging fledglings. Before copulation, female crouches and flutters her wings on tree branch. Courtship display described by Berger (1972: 186): "A singing male, while perched near the top of a dead 'ōhi'a tree, slowly swayed first to one side and then the other. The bird then flew to a live 'ōhi'a nearby and continued to sing and flutter his wings as he hopped from branch to branch. A second bird flew into the tree and chased the male for several seconds, after which the male flew to another dead 'ōhi'a tree, singing in flight."

Extra-pair copulations. Not recorded.

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Found in pairs in breeding areas; males engage in aggressive interactions. Observed foraging in flocks of 2-9 'I'iwi and with other species, particularly after breeding season (Ralph and Fancy 1995, P. Hart pers. comm.).

Nonpredatory interspecific interactions. Behaviorally dominant over 'Apapane and Hawai'i 'Amakihi, but subordinate to Crested Honeycreeper (Pimm and Pimm 1982, Carothers 1986a). Intolerant of other 'I'iwi, but tolerates other species unless they approach 'I'iwi nest or a tree with many flowers (Eddinger 1970). May forage in flocks with 'Apapane and other species. Negative correlations in densities between 'I'iwi and introduced Japanese White-eyes may result from interspecific competition for limited nectar resources (Mountainspring and Scott 1985). See Agonistic behavior, above.

PREDATION

Predation on eggs and chicks by introduced mammals, particularly black rat (*Rattus rattus*) and feral cat (*Felis catus;* Atkinson 1977, Ralph and van Riper 1985, Snetsinger et al.1994). 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). The introduced Polynesian rat (*Rattus exulans*), Norway rat (*Rattus norwegicus*), mongoose (*Herpestes auropunctatus*), and Barn Owl (*Tyto alba*) may also take *'I'iwi.*

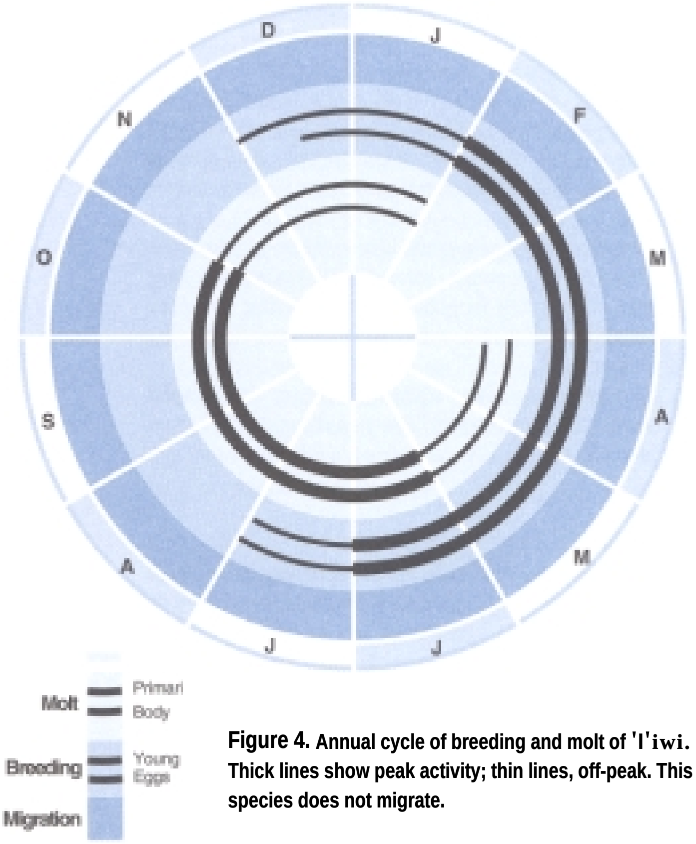

Figure 4. Annual cycle of breeding and molt of 'I'iwi. Thick lines show peak activity; thin lines, off-peak. This species does not migrate.

BREEDING

PHENOLOGY

Figure 4. Pair bonds form by mid-Feb on Kaua'i I. for some 'I'iwi; most have selected mates by mid-Mar (Eddinger 1970). Breeding season is probably earlier on Hawai'i I., beginning Oct-Nov, with peak breeding Feb-Jun (Baldwin 1953, Ralph and Fancy 1994). Breeding coincides with seasonal availability of 'ōhi'a nectar (Ralph and Fancy 1994). Enlargement of testes begins in Oct in older males (Baldwin 1953). Males in breeding condition can be found all year, and females with brood patches are found Dec-Jul. Nest construction requires 4-6 d;1-5 d between nest completion and laying of first egg (Eddinger 1970). Earliest eggs found on Kaua'i I. on 27 Feb; 1 clutch found in Feb, 8 in Mar, 5 in Apr, none in May or Jun (Eddinger 1970). Fledging dates reported in Hawai'i National Park from 3 Feb to late Jul (Baldwin 1953).

NEST SITE

From Eddinger 1970 (Kaua'i I.). Nest is usually a statant cup in terminal branches of 'ōhi'a tree. Places nest in terminal crown (*n* = 14), in cluster of branches growing upward from a horizontal limb (*n* = 6), or in cluster of branches along main vertical trunk (n = 2). Nest height averaged 7.2 m (range 4.3-9.8, n = 17).

NEST

From Eddinger 1970.

Construction process. Both parents build nest, but female does most of construction. Construction requires 4-6 d.

Structure and composition matter. Nests built largely of 'ōhi'a twigs, mixed with mosses, a few lichens, and bark fragments. Nest-lining consists primarily of lichens, with fibers from shredded leaves or bark.

Dimensions. Mean dimensions (cm): outside diameter 9.5, nest depth 7.44, cup diameter 5.4, cup depth 3.5 (n = 7).

EGGS

Shape. Ovate to short ovate.

Size. Mean length 20.7 mm (range 20.0-21.7), width 15.5 mm (range 15.0-15.8, n = 10; Eddinger 1970).

Mass. No information.

Color. Whitish background with irregularly shaped, dark chocolate brown markings (speckles, small spots, sometimes blotches). Markings concentrated at large end of egg. Amount and pattern of markings highly variable (Eddinger 1970).

Surface texture. No information.

Eggshell thickness. No information.

Clutch size. Typically 2 (range 1-3; Eddinger 1970). See also Demography and populations: measures of breeding activity, below.

Egg-laying. One egg laid each day, usually in early morning before 08:00. First egg laid 1-5 d after nest completion (Eddinger 1970).

INCUBATION

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

Incubation period. 14 days for each of 7 nests (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 46.6% on day 1, 81.1% on day 6, and 82.8% on day 12. Male feeds female away from nest after giving single loud call note.

Hardiness of eggs against temperature stress; effect of egg neglect. No information.

HATCHING

Eggs hatch most frequently in morning (n =14), complete clutch hatching before noon (Eddinger 1970).

YOUNG BIRDS

Condition at hatching. From Eddinger 1970 (Kaua'i I.). Altricial. Hatchlings weigh mean of 2.0 g (n = 3). Chicks have bright orange pink skin with tinge of yellow. Down is dirty white (80%) or dark gray (20%) mixed in feather tracts on top of head, above each eye, on middle of back, on each wing, and on thigh. Eyes closed.

Growth and development. From Eddinger 1970. Eyes open 5 d after hatching. Bill slightly decurved by day 6, then flesh pink with tinge of gray. Cream yellow feathers begin to unsheathe along sides of chest on day 9, and by day 11 green feathers on back begin to unsheathe. Wing-feathers completely unsheathed by day 15. After 12-14 d, young will jump out of nest if disturbed. Wing-feathers fully unsheathed by day 15.

PARENTAL CARE

Brooding. Female broods young closely during first few days as male continues to feed her away from nest. Female broods at night and during periods of heavy rain (Eddinger 1970).

Feeding. Both parents feed nestlings, but 71% of feedings are by female (n = 9 h of observation; Eddinger 1970). No quantitative data on nestling diet, but caterpillars may be important component (Perkins 1903, Eddinger 1970). Female and nestlings solicit feeding by depressing and fluttering their wings. During 9 h of observation at 1 nest, male fed female 12 times. Each time, male gave a single, loud call note, and female left nest, flew to male, crouched, fluttered her wings, and was fed (Eddinger 1970, Berger 1981).

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 21-22 d (n = 6; Eddinger 1970). Young able to fly well from tree to tree when they leave nest.

IMMATURE STAGE

Period of parental dependency <4 mo, on basis of proportion of observations of young with at least 1 parent (CJR). Juvenile follows parent during foraging and calls incessantly while crouching and fluttering wings (SGF).

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. Breeds during first year of life and annually thereafter (CJR).

Clutch. On Kaua'i I.,1-3 eggs (mean 2.0, *n* =14; Eddinger 1970).

Annual and lifetime reproductive success. From Eddinger 1970 (Kaua'i I.). Hatching success (% eggs laid that hatched): 83.3% (*n* = 30 eggs). Fledging success (% eggs laid that produced young that left nest): 53.3% (*n* = 22 nests). Nestling survival 64.0%.

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

LIFE SPAN AND SURVIVORSHIP

Annual survival based on 1,238 recaptures of 335 banded individuals and Jolly-Seber models: 55% ± 12 SE for adults and 9% ± 5 for juveniles (includes permanent emigration), the lowest of any Hawaiian honeycreeper (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 0.22, and low resighting probabilities can lead to imprecise estimates of survival (Pollock et al. 1990). Longevity in wild unknown.

DISEASE AND BODY PARASITES

Diseases. Highly susceptible to mortality from avian pox (*Avipoxvirus* spp.) and avian malaria (*Plasmodium relictum*), transmitted by mosquitoes that have had devastating effects on numbers and distribution of Hawaiian birds (Warner 1968, van Riper et al. 1986, Atkinson et al. 1995). Highest numbers of 'I'iwi with malaria found during late summer and fall, when birds move to lower-elevation forests where nectar is most available (van Riper et al.1986). Nine of 10 'I'iwi challenged with a single bite from a mosquito infected with *Plasmodium* died within 37 d (Atkinson et al. 1995). The single survivor apparently developed immunity to malaria and survived challenges with multiple mosquito bites. All of 10 'I'iwi challenged with multiple infective bites died from malaria.

The apparent low annual survival compared to other Hawaiian honeycreepers may be directly related to avian disease (Ralph and Fancy 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). Pox is transmitted directly by contact or mechanically by vectors, including mosquitoes (Cavill 1982).

Body parasites. Known parasites for 'I'iwi include the protozoan *Plasmodium relictum,* the nematode *Viquiera hawaiensis,* the cestode *Anonchotaenia brasilense,* 4 genera of mites (Acariformes; Goff 1980), lice, hippoboscid flies (Perkins 1893), and the bacteria *Staphylococcus epidermis* and *Citrobacter fruendii* (van Riper and van Riper 1985). Voge and Davis (1953) found numerous cestodes (*Anonchotaenia* spp.) in 1 'I'iwi specimen collected in Kau, Hawai'i I.

CAUSES OF MORTALITY

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

RANGE

Initial dispersal from natal site. No information.

Fidelity to breeding site and winter home range. Some birds are resident throughout year, but individuals make long foraging flights, and population shifts have been observed in response to nectar availability (Ralph and Fancy 1995). Fidelity to local breeding area is low for most individuals: 82% of 891 banded 'I'iwi were never captured or sighted again at 2 study areas (Ralph and Fancy 1995). Individuals may change breeding sites between years to take advantage of differences in nectar availability. All 'I'iwi remaining on study sites for >4 yr were adult males.

POPULATION STATUS

Density. Most abundant in mesic to wet forests at higher elevations. Densities highly correlated with 'ōhi'a flowering, with mean monthly densities on Hawai'i I. as follows: 371 individuals/km^2 ± 37 SE at Keauhou Ranch, 225 ± 33 at Kīlauea Forest, 586 ± 140 at Ka'ū Forest, and 680 ± 289 at Hāmākua (Ralph and Fancy 1995). Densities may exceed 2,000 individuals/km^2 in nectar-rich areas (Scott et al. 1986, Ralph and Fancy 1995). Densities on Maui I. generally lower than in similar vegetation types on Hawai'i I. (Scott et al.1986). Estimated at 318 individuals/km^2 ± 135 in 1988 in Hanawī Natural Area Reserve on Maui I. (Engilis 1990).

Numbers. Of total population in 1976-1981, 93.3% (340,000 ± 12,000; 95% confidence interval [CI]) found on Hawai'i I.; Scott et al.1986); 88% of these in Hāmākua. East Maui had 19,000 individuals ± 2,000 (95% CI), with a localized, relict population on West Maui of 180 ± 150. Relict populations on Moloka'i in Kamakou Preserve and Oloku'i Plateau numbered 80 ± 65 in 1979. Population estimate for Alaka'i Swamp on Kaua'i in 1981 was 5,400 ± 500. Only 8 'I'iwi found during repeated surveys on O'ahu in 1994-1996; total population probably <50 (VanderWerf and Rohrer 1986, E. VanderWerf pers. comm.).

Trends. Difficult to determine because of highly variable seasonal densities in each area, but seems to be declining except at higher elevations. In Alaka'i Wilderness Area on Kaua'i I., mean number of individuals/8-min count decreased from 1.22 in 1981 to 1.06 in 1989, and percentage of stations where 'I'iwi were present declined from 96 to 77% (T. Pratt unpubl. data). On Moloka'i, 12 'I'iwi recorded during 120 counts in 1979-1980, but only 2 detected during 148 counts in 1988 (Scott et al. 1986, T. Pratt unpubl. data).

POPULATION REGULATION

Habitat loss, avian disease, and introduction of alien species have had the greatest impacts on 'I'iwi populations. Forests have been cleared for agriculture, cattle-ranching, and development. Patchy distribution of 'I'iwi on Maui I. may have been related to pig damage of understory (Engilis 1990). Avian diseases, which resulted from 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 'I'iwi populations (C. Atkinson unpubl. data).

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Shooting and trapping. Feather cloaks and helmets, some containing more than half a million feathers of 'I'iwi, 'Ö'ö (*Moho nobilis*), and other birds, were symbols of prestige and power in pre-European Hawai'i (Brigham 1899, Kaeppler 1970). Cook (1784) reported that large numbers of 'I'iwi were offered for sale in bundles of 20 or more on Kaua'i. Birds caught for feathers were often killed and eaten. In the case of 'Ö'ö, the tens of thousands of birds captured for featherwork probably led to population declines, but it is considered unlikely that feather-collecting by early Hawaiians caused any bird extinctions (Rose et al. 1993).

Degradation of habitat. Loss and modification of habitat by humans and introduction of alien species to Hawai'i have greatly reduced numbers and distribution of 'I'iwi and other endemic birds. Polynesians colonized Hawaiian Is. around 400 A.D. and radically changed ecosystems by burning vast areas of forest for agriculture and introducing nonnative plants and animals (Kirch 1982, Olson and James 1982b). The great majority of Hawaiian bird species went extinct before European contact (Olson and James 1982b), and 27% of endemic Hawaiian birds have gone extinct since 1778 because of human activities (Smith and Fancy 1997).

MANAGEMENT

Primary conservation strategy for endemic Hawaiian forest birds is protection and restoration of native forests above 1,500 m elevation, where malaria-carrying 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 control 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*) has converted vegetation in some areas to open mire, and seriously degraded many mesic and wet forests in Hawaiian Is. Mammalian predators such as rats have been controlled in only a few localized areas. Control of alien vegetation has had only limited success, but prompt action has probably prevented establishment and spread of several species that could have devastating effects on Hawaiian forests.

APPEARANCE

MOLTS AND PLUMAGES

Hatchlings. From Eddinger 1970. Mixed dirty white (80%) and gray (20%) down. Dark gray down most plentiful on top of head and over each eye.

Juvenal plumage. No information on Prejuvenal molt. Juvenal plumage characterized by black-tipped, green body-feathers that fade with age to pale yellowish (Fancy et al.1993). May have feathers with reddish blush on face or scapulars. Primaries, secondaries, and rectrices grayish black. Juvenal plumage lacks the white inner secondary characteristics of adults.

Basic I plumage. From Fancy et al. 1993. Most Juvenal body-feathers replaced during Prebasic I molt with brilliant scarlet or vermilion feathers. Breast- and belly-feathers are first to molt and are nearly entirely or entirely replaced. Head (particularly nape), back, and scapulars molt last and incompletely. Also retained are all primaries, secondaries 1-4 (sometimes 5 and 6), and all rectrices. Secondaries 6-9 (and sometimes others) are usually replaced near end of Prebasic I molt. New secondaries are larger and darker than ones

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

Age	Hatch-year	Second-year	Adults
Wing			
Male	75.3 ± 0.63 (15)	75.7 ± 0.71 (7)	80.9 ± 0.33 (33)
Female	70.7 ± 0.50 (14)	73.5 ± 1.50 (2)	76.0 ± 0.71 (14)
Tail			
Male	47.6 ± 0.80 (11)	48.0 ± 2.00 (2)	51.9 ± 0.38 (32)
Female	44.7 ± 0.84 (7)	46.5 ± 1.00 (2)	49.2 ± 0.54 (13)
Exposed culmen			
Male	25.0 ± 0.63 (12)	27.4 ± 0.27 (8)	27.5 ± 0.17 (32)
Female	24.3 ± 0.25 (14)	24.3 ± 1.10 (2)	25.2 ± 0.28 (14)
Culmen			
Male	20.0 ± 0.88 (8)	21.5 ± 0.79 (3)	22.4 ± 0.19 (31)
Female	20.0 ± 0.18 (7)	19.2 ± 0.55 (2)	20.4 ± 0.23 (14)
Tarsus			
Male	25.2 ± 0.47 (11)	24.7 ± 0.25 3)	25.8 ± 0.16 (33)
Female	23.6 ± 0.47 (7)	23.4 ± 0.55 (2)	23.9 ± 0.22 (11)
Mass			
Male			19.9 ± 0.38 (21)[1]
Female			16.7 ± 0.40 (12)[1]

[1] Source: Baldwin 1953.

replaced, extend beyond adjacent secondaries, and have darker, matte black color, contrasting with gray black Juvenal secondaries and primaries.

'I'iwi in Basic I plumage is predominately vermilion, with a few yellowish Juvenal feathers on head, back, and scapulars, and grayish black remiges and rectrices except for new inner secondaries, which are black.

Definitive Basic plumage. Definitive Prebasic molt complete. This single annual molt occurs primarily between Jun and Oct in adults (Baldwin 1953), following or partly overlapping breeding season (Fancy et al. 1993, Ralph and Fancy 1994). Primaries molt in sequence from Pl to P9. Secondary replacement sequence is S8, S9, S7, S1-S6. Secondaries 1-6 begin molting when primary molt is almost complete (Baldwin 1953, Fancy et al. 1993). Flight-feather molt usually completed by late Oct (Baldwin 1953).

From Rothschild 1893-1900 and Wilson and Evans 1890-1899. Plumage bright vermilion on upperparts and underparts; deepest on breast and abdomen; distinctly lighter on top of head and on throat (Rothschild 1893-1900). Wings and tail black. Primary-coverts black; smaller wing-coverts red. Innermost (S9) secondary white; next one blackish; outer web ashy gray or ashy brown. Wing-lining and edge of wing whitish, tinged with pinkish vermilion.

BARE PARTS

Bill and gape. Long, strongly decurved bill is peachor salmon-colored in adults (SGF).

In hatchlings, bill is short and straight, its color changing from lightbrown with rose-colored edges to yellow (immature) to salmon (subadult). Gape is rose pink, with tinge of orange in center of roof of mouth and bright yellow edge along margins of bill (Eddinger 1970).

Iris. Iris dark hazel.

Legs and feet. Legs salmon pink. Tarsi and toes brown, soles orange (Wilson and Evans 1890-1899, Rothschild 1893-1900).

Juvenile legs and feet yellow orange, with tinge of pink.

MEASUREMENTS

Male larger and heavier than female (Table 1). In linear measurements, male 5-10% larger than female; on average, male has 19% greater body mass. Adults sexed from measurements of exposed culmen and wing-chord (Fancy et al.1993). Hatch-year 'I'iwi with wing-chords ≥73 mm should be classified as males, and second-year 'I'iwi with exposed culmens ≥25.5 mm should be classified as males (Fancy et al. 1993).

PRIORITIES FOR FUTURE RESEARCH

The devastating effects of avian disease and negative effects of introduced predators, feral ungulates, and some alien plants on the distribution and numbers of native Hawaiian forest birds place a premium on research and management to control disease and alien species in Hawai'i. A top priority is to determine if certain individuals have a genetic or immunological basis for resistance to disease and whether those that survive malarial infections can pass antibodies to their offspring. The use of 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 'I'iwi in the 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 characterization. There is a need to study strain differences among islands and identify 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 development of techniques for controlling vector populations are needed. Control of feral pigs and other ungulates can reduce mosquito breeding sites, but studies to determine the effects of ungulate control on disease transmission are necessary. Simulation models to predict disease epizootics and effects of different control strategies should be developed.

Improved methods are needed to control rat and feral cat populations in native forests, with additional work on responses of bird populations to predator control. Supporting data for toxicant registration that leads to improved toxicants and dispersal methods are urgently needed in Hawai'i.

Relatively few data on the demography of the 'I'iwi 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 population decline. 'I'iwi are being used as surrogates in captive propagation programs focusing on recovery of critically endangered species. Information on the basic reproductive biology of 'I'iwi, specifically details on pair-bonding, nesting season, nest requirements, nest attendance, incubation, and dietary requirements at all life phases, is needed to increase the chances of a successful captive breeding program and to aid in conservation of the 'I'iwi and other species.

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