Leiothrix lutea FRENCH: Léiothrix jaune

# Red-billed Leiothrix

nown in the cage bird trade as the Japanese Hill-Robin, Peking Robin, or Peking Nightingale, the Red-billed Leiothrix was first imported into the Hawaiian Islands in 1911 (Fisher and Baldwin 1947), with intentional releases to the wild occurring after 1918 (Caum 1933). A native of Southeast Asia, southern China, and the Himalayan regions of India, this species is a medium-sized, green and yellow babbler with a conspicuous red bill and strongly notched tail. The species is extremely active, but individuals are somewhat secretive and difficult to see as they flit around in the understory, often in small groups. The Red-billed Leiothrix is found in a wide variety of habitats in the Hawaiian Islands, including both native and exotic forests from sea level to near mountain summits exceeding 4,000 m elevation.

Leiothrix use a wide variety of native and introduced plants for foraging and nesting, and they feed on fruit and on invertebrates gleaned from foliage and dead wood. They forage and

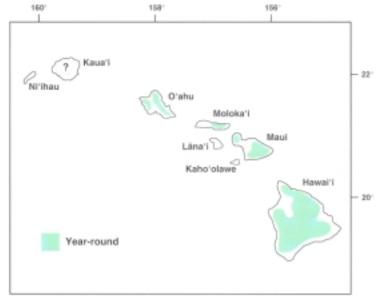


nest mostly among lower branches of dense vegetation, and rarely use canopy trees. The species is more gregarious and nomadic outside of the breeding season, when flocks of up to 100 birds have been observed. It sings most persistently during the breeding season, but also throughout the year, particularly when going to roost. Both sexes give a harsh, repetitive Chatter Call in response to human and other animal intruders.

# The Birds of North America

Life Histories for the 21st Century

Figure 1. Distribution of the Redbilled Leiothrix in the Hawaiian Islands. This species is also found in Asia.



Order PASSERIFORMES Family TIMALIIDAE

## 2 RED-BILLED LEFOTHRIX

Leiothrix populations have fluctuated widely on different islands. On O'ahu Island, this species was one of the most common birds seen on Christmas Bird Counts (CBCs) in the 1950s, but it declined dramatically in the 1960s. The O'ahu population persisted at barely detectable levels until the mid-1980s, but it has been increasing since then. In the 1940s, this may have been the most common bird species on Hawai'i Island, found from sea level in towns to the summits of Mauna Loa and Mauna Kea Volcanoes. Today, it is no longer common in many low-elevation sites and is rare in some districts of the island. The Red-billed Leiothrix was abundant on Kaua'i Island in the 1930s, persisting until the 1970s, but the breeding population may have disappeared since then (Male and Snetsinger in press). The cause or causes of these dramatic population fluctuations remain unknown.

## DISTINGUISHING CHARACTERISTICS

Small babbler with bright red bill. On adult, lores, crown, nape, and back are dull olive green, with bright yellow orange throat and yellow chin. Belly and undertail-coverts dull yellow. Ring around eye extending to bill is buffy to dull yellow. Primaries and secondaries black, with yellow orange edges on outer web; concealed portion of feathers olive brown. Basal section of secondaries yellow orange, forming small square patch on closed wing. Proximal third of all inner primaries bright orange to scarlet. Uppertail-coverts extend two-thirds the length of tail and terminate with thin white line. Tail deeply notched; rectrices curve outward at tip. Sexes similar, although females may be generally duller.

Juveniles have duller red and yellow wing-patches, yellow throat with rusty breast-band, and slaty gray upperparts. Cheeks and forehead slaty gray, with greenish wash; bill black, with varying amounts of red toward tip. Adultlike plumage apparently achieved by Prebasic I molt (age 3-4 mo). This distinctively plumaged species is unlikely to be confused with any others in Hawaiian Is.

#### DISTRIBUTION

## HAWAIIAN ARCHIPELAGO

Figure 1. From Scott et al. 1986, except where noted. Widespread on islands of Hawai'i, Maui, Moloka'i, and O'ahu in exotic and native forest with dense understory. Not present on Lana'i or Kaho'olawe Is. (M. Morin pers. comm.). No current information on Ni'ihau I., but not present in 1947 (Fisher 1951). More common above 1,000 m

elevation on Moloka'i, Maui, and Hawai'i Is., but present to near sea level in places with dense cover. Found on slopes of all mountains on Hawaii I., but less common in dry forests on Mauna Kea and in saddle between Mauna Kea and Mauna Loa. More common on East Maui than on West Maui and widespread throughout native and nonnative forest in Haleakalā National Park, valleys in Hana District, and most other areas on upper slopes of Haleakalā Volcano: present in low numbers in dry forest of Kaupō Gap (Conant and Stemmerman 1979). Common on Moloka'i I. above 1,000 m elevation throughout most valleys and gulches on eastern half of island. Previously found throughout upperelevation forest on Kaua'i I. and in northern coastal valleys, such as Kalalau Valley (Richardson and Bowles 1964), but may now be absent from this island (Male and Snetsinger in press). Nests found at maximum elevation of 1,860 m on Hawai'i I. and minimum elevation of 150 m on O'ahu and Moloka'i Is. (Fisher and Baldwin 1947).

Continues to occupy breeding range during nonbreeding season, but flocks are seen above 3,000 m elevation on Hawai'i and Maui Is. in Oct-Jan (Fisher and Baldwin 1947, Distasio 1997), suggesting wider postbreeding movements. Review of all issues of journal 'Elepaio indicated that between Oct and Jan from 1944 to 1954, flocks consistently moved into Honolulu suburb to visit fig trees (*Ficus* spp.; 'Elepaio 1944-1954).

## **OUTSIDE THE AMERICAS**

Native to China, including provinces of Hubei, Sichuan, Jiangxi, Zhejiang, Fujian, Guangdong, and Yunnan (Caldwell and Caldwell 1931); Myanmar, n. Vietnam, west to Himalayas of India, Bhutan, and Nepal in forests with understory (Etchecopar and Hue 1983). Introduced population established on Kyushu, Japan, where it is increasing (Hitoshi 1994). Also released in Australia, Tahiti, France, Colombia, and England (where nesting has occurred), but no populations yet established there (Long 1981).

## HISTORICAL CHANGES

Kaua'i 1. First deliberate release to the wild in Hawaiian Is. was on Kaua'i in 1918, with later introductions in 1920s-1930s to other islands (Caum 1933); some populations may have become established earlier from escaped cage birds (Fisher and Baldwin 1947). First mention of an established population was that "the species occurs in rather large flocks on Kaua'i" (Caum 1933: 39), but large numbers were never reported again. Richardson and Bowles (1964) found 9 birds in Jun 1960 at edge of Alaka'i Swamp and reported other sightings from Kalalau Valley. Sincock et al. (1984) surveyed forests between 1969 and 1973 and estimated that there were approximately 2.400 ± 2.200 SD Red-

billed Leiothrix on Kaua'i I., but they based this estimate on only a few sightings. Systematic surveys conducted in early 1980s failed to find any leiothrix (Scott et al. 1986), and none were detected during several forest bird surveys during 1990s (T. D. Male and T. J. Snetsinger unpubl.). Seen on a CBC in 1974, but none seen on counts since 1984, although 2 sightings by birders in 1982 and 1988; breeding population may be extinct or close to extinction on Kaua'i I. (Male and Snetsinger in press).

Oah'u 1. Uncommon in 1940s (Anonymous 1942), but CBC data indicated that its population increased dramatically in 1950s and it became one of the most abundant species. Review of issues of journal 'Elepaio indicated that it was common on edges of Honolulu suburbs and sighted during almost every bird hike undertaken by members of Hawaii Audubon Society from 1944-1955. Numbers declined drastically during 1960s to almost undetectable levels; persisted in extremely low numbers until mid-1980s (Williams 1987, Ralph 1990). Leiothrix populations have increased since that time, and are now commonly seen on CBCs and bird hikes (E. Vanderwerf pers. comm., TDM). This pattern is typical of rapid expansion and decline seen in some introduced species (Williams 1987).

Hawaii 1. Less than 20 yr after release, leiothrix were possibly the most common birds on Hawai'i L; found at sea level in valleys on Hāmākua coast and within city limits of Hilo (Amadon 1945). Found below 1,000 m elevation during surveys in 19401949 and 1962 in Hawai'i National Park (Conant 1975); surveys during 1972-1975, however, found none below 1,220 m (Conant 1975,1980, Banko and Banko 1980). At present (1997), species again occurs below 1,200 m in same area and has been reported again on CBCs, but no further reports of species at sea level or in Hilo City.

Maui 1. Numbers have increased since 1977 in Kula District on northwest slope of Haleakalā as introduced black wattle (Acacia mearnsii) forests have matured (C. B. Kepler in Scott et al. 1986).

FOSSIL HISTORY No information.

## **SYSTEMATICS**

## GEOGRAPHIC VARIATION

Brought to Hawaiian Is. from Shanghai and Hong Kong in China, from Kobe and Kokohama in Japan, and from San Francisco, CA (Fisher and Baldwin 1947). Fisher and Baldwin (1947:46) state that "H. G. Deignan, of the United States National Museum, has graciously examined 15 of our specimens from the Hawaiian Islands and has identified them as *Leiothrix lutea lutea*." However.

Ali and Ripley (1972) mention that L.1. calipyga was introduced to Hawaiian Is. without giving details of which specimens they examined. Range of L. 1. lutea is closest to all the Asian ports from which leiothrix were shipped (Fisher and Baldwin 1947), and specimens in Bishop Museum, Honolulu, lack black in center of outer primary webs (TDM), making *lutea* the more likely subspecies. Numerous subspecies may have been brought in at time of introduction. Within Hawaiian Is., there is no evidence that populations on different islands show any geographic variation in plumage (TDM). It is unknown whether there is any genetic differenttiation among islands. In native range, "cline of increasing color saturation runs from west to east" (Vaurie 1959: 440).

## **SUBSPECIES**

At least 4 subspecies in Asia (Vaurie 1959, Cheng 1987), possibly as many as 7 (Deignan 1964). Fifteen individuals from Hawaiian Is. were identified as nominate subspecies (Fisher and Baldwin 1947). *L. I. lutea* has brightest colors, no black on outer primary webs, and less yellow on belly (Vaurie 1959); found across w., central, and s. China from s. Sichuan east through Hunan, and Guangdong, China, to north of Gulf of Tonkin (Caldwell and Caldwell 1931). Deignan (1964) and Cheng (1987) maintain that *L. I. kwangtungensis*, of se. Yunnan, Tonkin, and Guangdong, China, is distinct from *lutea*.

L. 1. kumaiensis is found in Indian Himalayas between e. Punjab and nw. Uttar Pradesh, and in w. Nepal; dull crown, red edge of primaries reduced, and light overall color (Vaurie 1959). L. 1. calipyga, brighter in crown, with red-edged inner primaries, and darker overall than kumaiensis, is found from w. Nepal east and south to Bhutan, n. Bangladesh, Assam (in India), Myanmar, and Yunnan (in China). L. 1. yunnanensis, of n. Myanmar and n. Yunnan, China, is sometimes split off as darker subspecies with contrasting golden crown (Vaurie 1959, Deignan 1964). Neither Vaurie (1959) nor Cheng (1987) recognizes it as a distinct subspecies.

## RELATED SPECIES

Only 1 other species in genus: Silver-eared Mesia (*Leiothrix argentauris*), found in Indonesia, Thailand, n. Vietnam, Bangladesh, and s. China across to Himalaya Mtns. of sw. China (Cheng 1987). The 2 species are frequently found together where ranges overlap (Ali and Ripley 1972).

## **MIGRATION**

Nonmigratory in Hawaiian Is., but flocks seen at higher elevations during nonbreeding (Oct-Jan) season. In China, some altitudinal migration may

occur, with individuals found at elevations of 800-2,000 m in summer and 75-1,400 m in winter; may migrate between central provinces in summer and southern provinces in winter (Caldwell and Caldwell 1931).

## **HABITAT**

Found in native and exotic wet forests on all Hawaiian islands and in dry forests on Maui and Hawaii Is. Common in native forests with 'ōhi'a (Metrosideros polymorpha) or mixed 'ōhi'a and koa (Acacia koa) canopy, less common in mixed mamane (Sophora chrysophylla) and naio (Myoporum sandwicense) forest. Often found in areas with dense understory of nonnative plants such as Christmasberry (Schinus terebinthifolius) or hau (Hibiscus tiliaceus), and in dense stands of strawberry guava (Psidium cattleianum) and guava (Psidium guajava). Absent from introduced ironwood (Casuarina spp.) and eucalyptus (Eucalyptus spp.) forest with scant understory (Fisher and Baldwin 1947).

Most abundant in wet forests and woodlands above 1,000 m on Moloka'i, Maui, and Hawai'i Is. (Scott et al.1986). On O'ahu, found at all elevations in mountain valleys with dense vegetation and some flowing or standing water and not along exposed, windswept ridges (Fisher and Baldwin 1947). On Hawai'i I. and East Maui, most common in mesic 'ōhi'a-koa forest and wet 'ōhi'a forest (Scott et al. 1986). Presence of fruiting plants may partly influence population densities. In a partial regression analysis using habitat variables, abundance was positively related to elevation, tree biomass, and abundance of native and introduced shrubs, ground ferns, banana poka (Passiflora mollissima) vines, and 'olapa (Cheirodendron trigynum) fruit, and negatively related to presence of matted ferns in understory (Scott et al. 1986).

## FOOD HABITS

## **FEEDING**

*Main foods taken*. Generalist; adults consume approximately equal amounts of fruit and invertebrates (Fisher and Baldwin 1947) and use wide variety of foraging motions (Ralph and Noon 1988). No information on diet of wild nestlings, but in captivity, parents fed young nestlings live invertebrates exclusively, even though adults ate other items (Gibson 1978).

*Microhabitat for foraging*. Almost always forages in lower strata of vegetation, usually below 3 m, typically plucking fruit or gleaning and probing in foliage. Also gleans and probes twigs and dead wood; rarely seen on trunks. Will go to ground to

drink from pools or to investigate fallen branches. Spent >60% of time on small branches and twigs at 4 wet forest sites on Hawai'i I. (CJR).

Food capture and consumption. Forages low in trees, with numerous short flights and rapid hopping between branches within a tangle; moves quickly. Reported foraging activities on Hawai'i I. divided as follows: foliage-gleaning and -probing (45%), fruit-feeding (41%), bark-gleaning and -pecking (11%), fly-catching (2%), and flower-probing (1%; Ralph and Noon 1988).

#### DIET

Major food items. Adults consume fruits of native'ākala (Rubus hawaiiensis),'ōlapa, naio, 'ōhelo (Vaccinium reticulatum), and introduced strawberry (Fragaria vesca), thimbleberry (Rubus rosifolius), strawberry guava, and papaya (Carica papaya; Fisher and Baldwin 1947, Ralph and Noon 1988). Invertebrates found in 13 stomachs from birds collected in Hawai'i National Park included larval and adult butterflies and moths (Lepidoptera), bees and wasps (Hymenoptera), adult flies (Diptera), and snails (Gastropoda; Fisher and Baldwin 1947).

Quantitative analysis. Percent occurrence of food items in fecal samples from Hawai'i I. (n =187) were adult flies (25%), larval and adult butterflies and moths (22%), millipeds (Diplopoda;17%), 'ōlapa seeds (14%), bees and wasps (10%), spiders (Aracnida;10%), strawberry seeds (9%), and 'ohelo seeds (8%; CJR). Of over 350 observations of fruitfeeding on Hawai'i I.,'ākala (34%), naio (29%), and '61apa (26%) were primary fruiting species used (CJR).

FOOD SELECTION AND STORAGE No information.

NUTRITION AND ENERGETICS No information.

METABOLISM AND TEMPERATURE REGULATION No information.

DRINKING, PELLET-CASTING, AND DEFECATION Frequently seen drinking from pools of water on fallen leaves (Fisher and Baldwin 1947). Does not produce pellets. No information on defecation.

## **SOUNDS**

## **VOCALIZATIONS**

**Development**. No information.

**Vocal array**. During breeding season, captive males sing long, complex song (Fig. 2A), with wide array of syllables; 1 male used 99 qualitatively different syllables in series of these songs (Gerhard

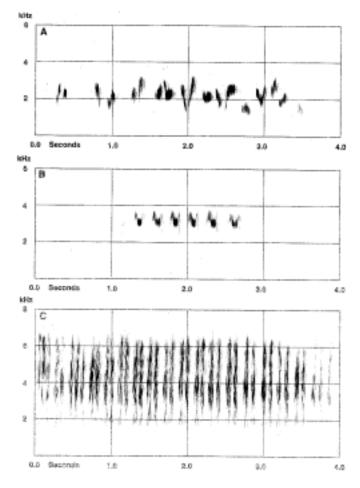


Figure 2. Songs and alarm call of male Red-billed Leiothrix. A. Complex song, sung during breeding season. B. Simple song, sung throughout year. C. Chatter Call (alarm call). A and B were recorded in upper Hana rain forest, Maui, HI, 11 Apr 1979; from the collection of Library of Natural Sounds [LNS], Laboratory of Ornithology, Cornell University, LNS no. 06074; C was recorded at Polipoli Springs, Maui, HI, 25 May 1977; LSN no. 05142. Prepared by staff of Borror Laboratory of Bioacoustics, Ohio State University, on a Kay Elemetrics DSP 5500 Sonagraph with an effective band width of 600 Hz (100 pt. transform size).

and Thielcke 1970). A second song (Fig. 2B) is heard year-round, is shorter, and has fixed sequence of syllables. A third song, quieter and less melodic than the others, is heard only when males are courting and following females (Gerhard and Thielcke 1970). Both sexes give harsh Chatter Call that is very repetitive and loud (Fig. 2C); directed at human intruders, at other bird species, and at other leiothrix near nest (Gerhard and Thielcke 1970). Usually when 1 adult begins giving Chatter Call, others appear from vegetation and begin returning the call (TDM). In captivity, both sexes often utter "a single quiet chirp" when foraging near other birds (Gibson 1978).

**Phenology**. Sings throughout year, but more frequently during breeding season (CJR). Songs most noticeable as birds go to roost, but may occur

throughout daylight hours. Calling frequency constant throughout year (CJR).

*Daily pattern*. No information.

**Places of vocalizing.** Usually sings and calls from within low bushes and shrubs.

Repetoire and delivery of songs. No information.

Social context and presumed functions. For captive birds, Contact Calls of males and females are sex-specific and distinct among individuals; the unique characteristics of individuals' Contact Calls last for many years and make it possible to identify individuals (Gerhard and Thielcke 1970). Female's Contact Call is "simple two syllable whistle repeated 3-5 times," while male's call sounds like its simple song, but is shorter (Gibson 1978: 6). Contact Call is most frequently heard while pairs or flocks are foraging in dense vegetation, which suggests that they use it to stay together (TDM).

NONVOCAL SOUNDS None reported.

## **BEHAVIOR**

#### LOCOMOTION

*Walking, hopping, climbing, etc.* Very active. Usually remains in dense understory vegetation, flitting from plant to plant with short flights and hops between branches (TDM).

**Flight.** Not studied. Seldom flies >15 m except in open habitats, where flights of >60 m have been observed (Fisher and Baldwin 1947).

## SELF-MAINTENANCE

Frequently observed bathing in shallow pools (Fisher and Baldwin 1947). Captive birds bathed daily (Gibson 1978). No other information.

## AGONISTIC BEHAVIOR

No information.

## **SPACING**

Home ranges of pairs in 1 study site overlapped extensively (CJR). Captive pairs behaved aggressively toward others that were put in same cage, suggesting some degree of spacing (Gibson 1978).

## SEXUAL BEHAVIOR

*Mating system and sex ratio*. Apparently monogamous (Gerhard and Thielcke 1970, Gibson 1978). Of 230 birds caught in mist-nets in 2 study areas on Hawaii L, sex ratio was female biased: 1:1.35 (CJR).

**Pair bond.** In captivity, pairs remain mated for life (Gerhard and Thielcke 1970, Gibson 1978).

Extra-pair copulations. No information.

## SOCIAL AND INTERSPECIFIC BEHAVIOR

**Degree of sociality.** Outside of breeding season, >50% of birds join flocks of 20-100 individuals (Fisher and Baldwin 1947). Flocks begin to break up at beginning of breeding season in Feb-Mar, although some birds remain in flocks throughout year (Fisher and Baldwin 1947).

*Play*. No information.

*Nonpredatory interspecific interactions.* On numerous occasions, 'Ōma'o (*Myadestes obscurus*) observed repeatedly chasing leiothrix out of fruiting 'ōlapa trees (E. Vanderwerf pers. comm.).

#### **PREDATION**

Kinds of predators. Red-billed Leiothrix remains found in Barn Owl (Tyto alba) pellet from Hakalau Forest National Wildlife Refuge, Hawai'i 1. (C. Mostello pers. comm), and in Barn Owl pellet and feral cat (Felis catus) scat collected on Mauna Kea, Hawai'i 1. (Snetsinger et al.1994). A Hawaiian Hawk, or'Io (Buteo solitarius), was observed feeding nestling leiothrix to its own young (P. Hart pers. comm.). Rats (Rattus spp.) known to take eggs (SGF).

*Manner of predation.* 'Io removed leiothrix nestlings from their nest (P. Hart pers. comm.). No other information.

**Response to predators.** When disturbed from nest, females flush silently; once near the ground, chatter loudly while fluttering wings and hopping away (CJR).

## **BREEDING**

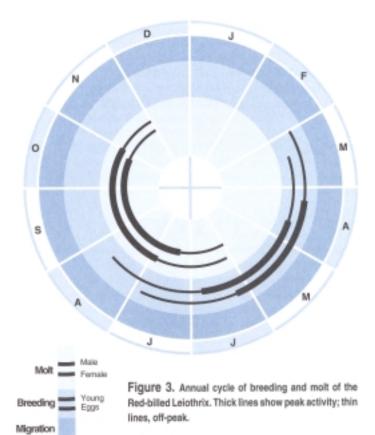
#### PHENOLOGY

Extended nesting season (Fig. 3). Breeding activity begins Mar-Apr; peak breeding Apr-Aug at 1 site on Hawai'i 1. (CJR).

**Pair formation.** At 2 Hawaii 1. sites, 33% of monthly observations of Red-billed Leiothrix were of pairs of birds; peak occurrence of pairs in Mar (CJR).

First/only brood per season. Figure 3. A completed clutch found on 3 Mar is the earliest recorded (Fisher and Baldwin 1947). Earliest hatching date recorded is 14 Mar (Fisher and Baldwin 1947). In Kohala Mtns., Hawai'i I., first nest was found in Apr; peak in May and Jun (van Riper 1982). In captivity, clutches laid in early Apr (Gibson 1978). In China, breeds Apr-Oct (Etchecopar and Hue 1983).

Second/later brood(s) per season. Latest nests with eggs found 23 Jul on Hawai'i 1. (Berger 1972). Latest active nest found with feathered young on 5 Aug on Maui I. (Berger 1977). No information on whether wild birds double-clutch or only lay replacement clutches. In captivity, up to 7 clutches laid /season (Apr-Aug) and a second brood fledged on 1 occasion (Gibson 1978).



NEST SITE

Selection process. No information.

*Microhabitat*. Only requirement may be dense vegetation around nest site (Fisher and Baldwin 1947).

Site characteristics. Builds pendulous nest in fork of low horizontal branches in dense native or nonnative vegetation (Fisher and Baldwin 1947). Nest height ranges from 0.5 to 3 m on O'ahu and from 1 to 7 m on Hawai'i 1. (Fisher and Baldwin 1947, CJR). Average nest height on Hawai'i I. 2.6 m ± 1.5 SD (n = 17; CJR). Nests found in 'ō1apa, 'ohe (Tetraplasandra sp.), of (Stachytarpheta dichotoma), 'a'ah'i (Dodonea viscosa), pūkiawe (Styphelia tameiameiae), mamane, hāpu'u Ti (Cibotium chamissoi), uluhe or staghorn fern (Dicranopteris linearis), palm foxtail (Setaria palmifolia), guava, hau, ti (Cordyline terminalis), and 'ohi a.

#### **NEST**

*Construction process.* In captivity, both male and female build (Gibson 1978). No other information on wild populations.

Structure and composition matter. Open, semipendant cup composed of leaves, dried grass, and occasionally animal hair (Fisher and Baldwin 1947). Cup usually lined with plant fiber, leaves (including koa phyllodes), and fine grass. Sheep wool found in 1 of 8 nests on Mauna Kea (van Riper 1977). **Dimensions.** Two nests measured by Fisher and Baldwin (1947) and 3 by CJR had the following mean measurements (in cm,  $\pm$  SE): largest outside diameter 10.7  $\pm$  0.44; largest inside diameter 6.28  $\pm$  0.24; smaller outside diameter 8.90  $\pm$ 0.10; smaller inside diameter 5.04  $\pm$  0.25; outside depth 8.14  $\pm$  0.44; inside depth 4.98  $\pm$  0.32.

*Microclimate*. No information.

Maintenance or reuse of nests, alternate nests. No information.

#### **EGGS**

Shape. No information.

*Size*. Mean length and breadth of 7 eggs from 2 clutches were 20.6 mm (range 20.0-21.3) and 15.9 mm (range 15.4-16.5), respectively (Fisher and Baldwin 1947).

*Mass*. Mean egg mass in one 3-egg clutch, which hatched 3 d later, was 2.6 g (range 2.4-3.0; Fisher and Baldwin 1947).

**Color.** Pale blue, with reddish spots at blunt end (Fisher and Baldwin 1947). For eggs from captive nests (n = 50), color ranged from greenish to bluish, with large reddish brown spots at blunt end (Gibson 1978).

Surface texture. No information.

Eggshell thickness. No information.

Clutch size. Typically 2-4 eggs in captivity (Gibson 1978). Mean clutch size from published data is 3.0 eggs (n = 5; Fisher and Baldwin 1947, Berger 1977). Mean 2.64 eggs (range 1-3) for 11 nests found in Kilauea Forest Reserve and Keauhou Ranch, Hawai'i I. (CJR).

*Egg-laying*. No information.

## **INCUBATION**

Onset of broodiness and incubation in relation to laying. In captivity, both sexes incubate after first egg laid; female incubates at night (Gibson 1978). Almost synchronous hatching of eggs suggests that incubation is not constant until clutch is close to completion (Fisher and Baldwin 1947, Gibson 1978).

**Incubation patches.** Females develop highly vascularized brood patch. On Hawai'i I. (CJR), >50% of females captured (n = 526) during AprAug had active brood patch; <1% of males (n = 338) had any trace of brood patch during same interval. Most brood patches disappear by Sep, when adults are molting (CJR).

*Incubation period*. Incubation in captivity lasts 11.5-12.5 d from date of laying; most eggs in a clutch hatch on same day (Gibson 1978). Three eggs in 1 nest all hatched within 1 h (Fisher and Baldwin 1947). No information on wild nests.

**Parental behavior**. In captivity, both members of pair incubate; female incubates at night. Incubation period usually 30-120 min (Gibson 1978).

Female incubates more frequently as eggs near hatching (Gibson 1978). No reports of male feeding female. No information on behavior during change of incubating parent.

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

## **HATCHING**

**Preliminary events and vocalizations.** No information

Shell-breaking and emergence. Egg is pipped near greatest diameter, and hatchling uses legs to kick its way free; 3 slightly pipped eggs each took <2 h and 35 min to hatch (Fisher and Baldwin 1947).

Parental assistance and disposal of eggshells. Hatchling breaks its way out of egg unassisted, but parents subsequently remove eggshells from nest area (Gibson 1978).

#### YOUNG BIRDS

Condition at hatching. From Fisher and Baldwin 1947. Naked, with eyes closed. Skin reddish apricot, with gray over feather follicles. Feet and bill apricot, except bill gray between nares and tip. Soon able to lift head to food-begging posture; three 1-d-old hatchlings weighed 3.0, 3.1, and 3.2 g.

Growth of body parts. From 1 nest with 3 nestlings (Fisher and Baldwin 1947): at day 7, sheathed outer primary was 15.5 mm long; at day 11, outer primary 33.5 mm long and two-thirds unsheathed, and central rectrices 3 mm long and one-third unsheathed; mean nestling mass was 3.1 g on day 1, 13.5 g on day 7, and 15.1 g on day 11. Eyes open after 5 d (Gibson 1978).

## PARENTAL CARE

**Brooding**. No information.

**Feeding.** In captivity, both parents fed young nestlings exclusively invertebrates, but switched to other food sources for older nestlings (Gibson 1978).

**Nest sanitation**. In captivity, parents "fastidious" about removing fecal sacs from nest, checking for them every time they return to nest (Gibson 1978).

Carrying of young. No information.

## **COOPERATIVE BREEDING**

No information.

## **BROOD PARASITISM**

No brood parasites in Hawaiian Is. Cuculus *canorus* parasitizes *L.1. calipyga* in native range (Ali and Ripley 1972).

## FLEDGLING STAGE

**Departure from nest.** Nestling period 10-12 d (Fisher and Baldwin 1947, Gibson 1978).

*Growth.* Wing- and tail-feathers still partly sheathed at fledging (Fisher and Baldwin 1947, Gibson 1978). No other information.

Association with parents or other young. No information.

Ability to get around, feed, and care for self. No information.

## IMMATURE STAGE

Young birds join flocks at unknown time after fledging (Fisher and Baldwin 1947).

## **DEMOGRAPHY AND POPULATIONS**

## MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. No information.

Clutch. See Breeding: eggs, above.

Annual and lifetime reproductive success. Following based on unpublished data collected on 12 nests found in 2 study sites on Hawai'i I. (CJR): 24 of 29 (82.6%) eggs hatched, and 44.6% fledged young. On basis of daily survival rates averaged through egg and nestling stages, 78.0% of nests fledged  $\geq 1$  young. No information on brood size at fledging or lifetime reproductive success.

*Number of broods normally reared per season.* In captivity, usually rear 1 brood, occasionally 2 (Gibson 1978). No information on wild populations.

Proportion of total females that rear at least one brood to nest-leaving or independence. No information.

## LIFE SPAN AND SURVIVORSHIP

From 1977 to 1979, annual survival based on Jolly-Seber models based on mist-net captures on 16-ha grid at Keauhou Ranch, Hawai'i L.,was  $0.786\pm0.047$  SE for 227 adults and  $0.581\pm0.115$  SE for 111 hatch-year birds (includes permanent emigration; SGF). In wild, some individual adult birds recaptured 4 yr after initial banding (CJR).

## DISEASE AND BODY PARASITES

**Diseases.** Low prevalence of avian malaria and avian pox. One of 11 blood smears collected from wild birds on Hawaii I. contained malarial parasites (*Plasmodium vaughani*; Fisher and Baldwin 1947). *P. relictum* also collected, and specimens identified as *P: vaughani* may have been *P. relictum* misidentified (van Riper and van Riper 1985). Malarial parasites were not found in 20 birds from Hawaii National Park (van Riper et al. 1986), 6 from Hakalau Forest National Wildlife Refuge, Hawai'i I. (Feldman et al. 1995),141 from Kulani Prison, Hawai'i I. (C. Atkinson unpubl. data). However, 3 of 42 individuals from Waikamoi Preserve, Maui I., tested positive (C. Atkinson unpubl. data). In challenge experiments, no

leiothrix contracted P. relictum (n = 5; van Riper et al. 1982). Yersina enterocolitica isolated from 1 captive individual (Hacking and Sileo 1974).

**Body parasites.** Two genera of mites (*Ornithocheyletia sp.* and *Ornithocheyla* sp.) collected from birds captured at Hawai'i National Park (Goff 1980); 2 others from unknown areas of Hawaiian Is. (*Ornithocheyletia leiothrix* and *Neocheyletiella media;* Goff 1983). One captive individual had heavy infestation of spinning mites (*N. media;* Kniest and Hoffman 1982); 2 of 3 captive birds had coccidian parasites (*Isospora leiothrixi;* McQuistion et al. 1996).

## CAUSES OF MORTALITY

Exposure. Numerous recoveries at high elevations (3,706-4,180 m) on Mauna Kea and Mauna Loa on Hawai'i I.; presumed to have died from exposure (Montgomery and Howarth 1980). Fisher and Baldwin (1947) state that flocks were frequently seen at elevations above tree line on these mountains and usually died from exposure.

**Predation.** See Behavior: predation, above. Predators destroyed 1 nest with nestlings out of 7 knownfate nests in study area on Hawai'i I. (CJR).

Competition with other species. Some dietary overlap with endemic 'Ōma'o on Hawaii I., but no significant negative correlations between abundance of these 2 species when habitat variables were considered (Mountainspring and Scott 1985). Ralph and Noon (1988) found significant positive correlation between leiothrix and 'Ōma'o numbers, after controlling for fruit and flower abundance but not other habitat variables. 'Ōma'o chase leiothrix from fruiting 'olapa trees (E. Vanderwerf pers. comm.).

On O'ahu I., Ralph (1990) found a significant negative correlation between abundance of leiothrix and that of another introduced bird, White-rumped Shama (Copsychus malabaricus), as detected during CBCs. However, no evidence of direct competitive interactions between the 2 (E. Vanderwerf pers. comm.). Leiothrix populations are again increasing on O'ahu I., with no apparent decline in Shama numbers (TDM).

## RANGE

Initial dispersal from natal site. Dead individuals found at summits of Mauna Kea and Mauna Loa, Hawai'i I. (Montgomery and Howarth 1980), were primarily young birds (TDM), suggesting some initial dispersal. At 2 sites on Hawai'i I., 62.8% of hatch-year individuals (n=43) that returned in subsequent years were female, suggesting greater philopatry in this sex (CJR). No other information.

Fidelity to breeding site and winter home range. Over 4 yr, average of 25.6% of 1 Hawai'i I. population composed of new recruits (CJR).

Dispersal from breeding site or colony. No information.

*Home range*. On basis of 3 yr of resighting/recapture data, minimum convex polygon size (mean  $\pm$  SE) was 3.07 ha  $\pm$ 0.32 for males and 2.68ha  $\pm$ 0.27 for females for 50 total individuals in a study site on Hawai'i 1. (CJR).

## POPULATION STATUS

**Densities.** Conant (1975) estimated densities of 23-380 birds/km2 along transects in Hawai'i National Park. Mean monthly densities from point count data (birds/km2  $\pm$  SE) at 3 forest sites on Hawai'i L: 152  $\pm$  14, 1.5  $\pm$  0.83, and 17  $\pm$  7.2, respectively (CJR). At a fourth site, point count data provided estimate of 240  $\pm$  19 birds/km², mark/recapture model estimated 1,370 birds/km², and monthly surveys of banded birds estimated 1,190 birds/km², suggesting that point counts underestimate both flocking leiothrix and leiothrix that avoid observers (CJR).

*Numbers.* From Scott et al. 1986, except where noted. Population estimated at  $98,000 \pm 4,000$  SD in  $3,539\text{-km}^2$  study area on Hawai'i I.,  $19,000 \pm 1,200$  in  $404 \text{ km}^2$  East Maui study area and  $800 \pm 200$  in  $44 \text{ km}^2$  on West Maui, Maui I., and  $1,800 \pm 200$  birds in  $131\text{-km}^2$  study area on Moloka'i I. None were found in  $125\text{-km}^2$  study area on Kaua'i I., but population of that island was estimated at  $2,367 \pm 2,200$  in 1970s (Sincock et al. 1984). No population estimates for O'ahu I.

Trends. See Distribution: historical changes, above.

## POPULATION REGULATION

Scott et al. (1986) suggested that higher temperatures at lower elevations may not be favorable for leiothrix, but there is no physiological data to support this hypothesis, and the species is once again common at lower, warmer elevations on O'ahu I.. May be limited by availability of naio fruit and water in mamane-naio forest on Mauna Kea, Hawai'i I. (Scott et al. 1986).

## CONSERVATION AND MANAGEMENT

## EFFECTS OF HUMAN ACTIVITY

Leiothrix are quicker than other introduced or native birds at recolonizing the regrowth that develops after land is cleared (Sakai 1988). They may feed on fleshy fruit of some introduced plants and spread seeds of these plants.

## **MANAGEMENT**

Leiothrix appear to have no adverse effect on populations of native Hawaiian birds directly, but they may be vectors for spread of introduced plants and reservoirs for avian disease (van Riper et al.1986). It is unlikely that any management action will be taken to directly enhance or reduce leiothrix numbers, but the species will probably benefit from the control of

feral pigs and ungulates, which tend to have adverse effect on fruiting plants in forest understories.

## **APPEARANCE**

## MOLTS AND PLUMAGES

Capitalized color names follow Smithe 1975-1981, and numbers in parentheses follow Munsell color notation.

Hatchlings. See Breeding: young birds, above.

Juvenal plumage. No information on Prejuvenal molt. Juveniles distinguished from adults by duller red and yellow wing-patches, yellow throat with rusty breast-band, and slaty gray upperparts. Cheeks and forehead slaty gray, with greenish wash. Gibson (1978) states that young birds molt into adult plumage at 3 mo of age. No information on whether this molt is partial or complete (TDM).

**Definitive Basic plumage.** Single annual (Definitive Prebasic) molt follows breeding season, with peak in Aug-Oct (CJR). No information on sequence of molt.

Crown Yellowish Olive-Green (8Y 4.5/6); lores, supraloral stripe, and eye-ring Cream (3.5Y 8.5/4). Ear-coverts, back, wing-coverts, rump, uppertailcoverts, and rectrices Blackish Neutral Gray (N2.5); rectrix-tips Jet Black (3.2PB 1.6/0.5). Longest tail-coverts have white tips. Tail is deeply notched, and ends of outer rectrices curve outward. Secondaries and primaries jet Black, with Orange Yellow (10 YR 8/14) edges on outer vanes of all primaries and Orange Yellow patch at base of exposed secondaries. Exposed basal portion of all inner primaries Flame Scarlet (10R 5/16) to Spectrum Orange (5YR 6.5/16). Chin Orange Yellow; throat Spectrum Yellow (6Y 8.5/12). Breast Straw Yellow (5Y 8/6), fading to Chamois (17Y 8/6) on lower belly, with Glaucous (6Y 6/1) flanks. Sexes similar, although males tend to be brighter than females.

## **BARE PARTS**

**Bill and gape.** Varies from Yellow Ocher (10YR 6.7/7.7) to Flame Scarlet, sometimes with jet Black at base. Bill of juveniles is mostly Jet Black.

*Iris*. Brown.

Legs and feet. Greenish (Berger 1981).

## **MEASUREMENTS**

Males slightly larger and heavier than females (see Table 1).

## LINEAR

Table 1. Adult and hatch-year males significantly larger than respectively aged females in wing length (CJR) and adult males appear to have longer tail than adult females.

<b>Table 1.</b> Linear measurements (mm) and mass (g) of Red-billed Leiothrix. Data shown as mean $\pm$ SE (n).				
D:01 d	USGS/BRD¹	Freed <sup>2</sup>	Ralph <sup>3</sup>	Male <sup>4</sup>
Bill length Male Female Hatch-year	$11.66 \pm 0.09 (8)$ $11.85 \pm 0.14 (9)$ $11.19 \pm 0.65 (3)$	$12.90 \pm 0.14$ (18) $12.26 \pm 0.10$ (22) $11.48 \pm 0.31$ (5)		$12.10 \pm 0.25 (10)$ $11.98 \pm 0.28 (5)$ $11.25 \pm 0.47 (4)$
Wing length Male Female Hatch-year	$68.11 \pm 0.35 (8)$ $67.24 \pm 0.47 (9)$ $67.64 \pm 1.40 (3)$	$68.13 \pm 0.48 (20)$ $66.92 \pm 0.47 (38)$ $65.49 \pm 0.31 (5)$	$67.21 \pm 0.16 (158)$ $65.89 \pm 0.15 (222)$ $64.17 \pm 0.14 (323)$	$66.35 \pm 0.86$ (8) $66.40 \pm 0.37$ (5) $65.92 \pm 1.26$ (4)
Tail length Male Female Hatch-year	$56.39 \pm 0.30 (8)$ $55.11 \pm 0.47 (9)$ $54.86 \pm 1.43 (3)$	$56.38 \pm 0.99$ (4) $54.79 \pm 0.57$ (17) $54.40 \pm 0.48$ (19)		$55.54 \pm 0.37$ (9) $54.03 \pm 0.52$ (4) $54.03 \pm 0.54$ (4)
Tarsus length Male Female Hatch-year	$23.88 \pm 0.20 (8)$ $23.79 \pm 0.21 (9)$ $23.77 \pm 0.30 (3)$	$23.19 \pm 0.23$ (19) $23.41 \pm 0.17$ (38) $23.57 \pm 0.23$ (24)		$24.63\pm0.26$ (10) $23.84\pm0.33$ (5) $24.25\pm0.36$ (4)
Mass Male Female Hatch-year	$21.30 \pm 0.28$ (8) $21.21 \pm 0.24$ (9) $21.55 \pm 0.80$ (2)	$21.33 \pm 0.24$ (20) $21.54 \pm 0.26$ (40) $20.88 \pm 0.45$ (24)	$21.77 \pm 0.12 (150)$ $21.49 \pm 0.11 (216)$ $21.35 \pm 0.08 (315)$	

<sup>1</sup>From U.S. Geological Survey Biological Resources Division (USGS/BRD) for birds banded at Pu'u La'au, Hawai'i I.

## **MASS**

Table 1. Adult and hatch-year males are slightly more massive than respectively aged females (CJR).

## **OTHER**

Hematocrit levels (ratio of red blood cells to total blood cells after centrifugation) of males averaged 50.90 (n = 12); of females, 48.26 (n = 17; J. Rohrer unpubl. data).

Highest spectral sensitivity in UV (380 nm maxima); other peaks at 470 and 530 nm, and flattened peak between 590 and 650 nm; 5 times more sensitive to equal-quanta light at 380-nm peak than at 530-nm peak (Burkhardt and Maier 1989). Females spent more time near males behind UV-transmittent plexiglass than near males behind UV-blocking plexiglass, suggesting that ultraviolet wavelengths may be important for species recognition (Maier 1993).

## PRIORITIES FOR FUTURE RESEARCH

The Red-billed Leiothrix is poorly known in both its native and its introduced range, despite its abundance. Populations have increased and declined dramatically throughout the Hawaiian Islands during the past 80

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years. Although this pattern may be typical of the population cycles of many introduced species (Williams 1987), there is no information on the causes underlying the high variability in abundance of this species. For most native Hawaiian birds, avian disease is thought to be a major factor limiting bird populations and distribution. The Red-billed Leiothrix, however, seems to be resistant to avian malaria and pox, yet its populations have undergone major numerical and distributional changes. This species is an ideal candidate for future population studies because there are separate populations on each island that seem to vary independently of one another.

Leiothrix and the native *Myadestes* thrushes are potential competitors for fruits and insects, but little has been done to systematically document diet and resource use for these species in areas where they both occur. Leiothrix may also be dispersing seeds of native and exotic plants. It is important to know if their diet biases their dispersal toward weeds or if they provide an important service for native plants.

While there is clear evidence that leiothrix and other introduced species carry avian malaria (Fisher and Baldwin 1947, van Riper and van Riper 1985), we still need information as to whether disease is spread from exotic to native bird species. Research on the spread of disease is critical to managers charged with protecting remaining native birds on the Hawaiian Islands.

<sup>&</sup>lt;sup>2</sup>From Lyon Arboretum, O'ahu I., Hanawī, Maui I., and Hakalau National Wildlife Refuge, Hawai'i I.

<sup>&</sup>lt;sup>3</sup>From Keauhou Ranch and Kīlauea Forest on Hawai'i I.

<sup>&</sup>lt;sup>4</sup>From specimens in Bishop Museum, Honolulu, that were collected on Moloka'i, Maui, and Hawai'i Is.

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