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DEMOGRAPHY OF AN INTRODUCED RED-BILLED LEIOTHRIX POPULATION IN HAWAII[1]

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Abstract. Relative abundance, timing of breeding and molting, annual survival, and philopatry of an introduced population of Red-billed Leiothrix (*Leiothrix lutea*) were studied at four sites on the island of Hawaii. Numbers of leiothrix on our study areas showed a regular cyclical pattern, with highest numbers during the breeding season. Peak breeding occurred May–August, followed by peak molting of flight and body feathers in August–October. Flocking behavior increased post-breeding, and many leiothrix left the study areas during the fall and winter months. Populations on two intensive study areas were stable, with high annual survival ($x \pm SE = 0.581 \pm 0.115$ for hatching-year birds and 0.786 ± 0.047 for adults). Leiothrix seem to be relatively unaffected by avian diseases that have decimated some Hawaiian bird populations, and yet reasons for their large historical population fluctuations remain unexplained.

Key words: alien species, avian disease, demography, Hawaii, Leiothrix lutea, *Red-billed Leiothrix.*

INTRODUCTION

More species of passerine birds have been intentionally introduced to the Hawaiian Islands than to any other place on earth (Pratt 1994). It is sometimes assumed that these alien species compete with Hawaii's native birds (Mountainspring and Scott 1985, Scott et al. 1986), and yet little is known about the population ecology and life history of introduced passerines in Hawaii, or how they differ from their source population. One species that was successfully introduced to native forests on several islands in Hawaii is the Red-billed Leiothrix (*Leiothrix lutea*), a small babbler (family Muscicapidae) native to southern China, Southeast Asia, and the Himalayan region of India (Howard and Moore 1984). Known in the cagebird trade as the Peking Nightingale, Pekin Robin, or Japanese Hill Robin, it was recently added to Appendix II of CITES (Convention for International Trade in Endangered Species) because of habitat destruction in its native range and high levels of trade for the cagebird market.

In the Hawaiian Islands, deliberate attempts to establish leiothrix in the wild began in 1918 on Kauai, and in 1928 on the other main islands (Caum 1933). Breeding populations of leiothrix now occur in a wide variety of habitats in the islands, including both native and exotic forests from sea level to treeline, although populations on different islands have apparently fluctuated widely for unknown reasons (Scott et al. 1986, Williams 1987, Ralph 1990). Leiothrix are currently found on the islands of Oahu, Molokai, Maui, and Hawaii, but they are now rare or possibly extinct on Kauai (Scott et al. 1986, Male and Snetsinger, in press).

Fisher and Baldwin (1947) thought that the major characteristic of leiothrix habitat was a dense cover of vegetation near the ground. Leiothrix occur in the undergrowth of both native and non-native forests where they feed on a variety of fleshy fruits and on invertebrates gleaned from foliage and wood. Fisher and Baldwin (1947) reported that fruit comprised 40–60% of their diet and invertebrates the re-

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mainder, and Ralph and Noon (1986) found that leiothrix spent about 38% of their time foraging on a wide variety of fruits.

In this paper we present information on the population ecology of an introduced Red-billed Leiothrix population that was collected during a larger study of the demography and foraging ecology of Hawaiian forest birds.

METHODS

We studied Red-billed Leiothrix between November 1976 and January 1982 at four study sites on the island of Hawaii: Keauhou Ranch (19°31'N, 155°20'W; 1,740 m elevation), Kilauea Forest (19°31'N, 155°19'W; 1,630 m), Hamakua (19°47'N, 155°20'W; 1,770 m), and Kau Forest (19°13'N, 155°33'W; 1,750 m). Vegetation of the study areas was described by Mueller-Dombois et al. (1981) and Ralph and Fancy (1994a). All four sites were in mesic native forests with ohia (*Metrosideros polymorpha*) as the dominant or codominant canopy species, but sites differed in the abundance of other plant species and level of disturbance to the understory (see Ralph and Fancy 1994b).

Bird abundance was estimated using the variable circular-plot method (Reynolds et al. 1980) with 8-min counts, as described by Ralph and Fancy (1994b). The effective area surveyed around each counting station was determined by the program DISTANCE (Buckland et al. 1993, Laake et al. 1994) after pooling leiothrix detection distances for all surveys and adjusting for differences among observers (Fancy 1997). An effective detection area of 0.73 ha (radius = 48.1 m, CV = 3.0%) was calculated from 4,842 detection distances. Density at each station was calculated by dividing the number of leiothrix detected at each station by the effective area surveyed, and monthly density at each site was calculated as the mean of station densities. We used analysis-of-variance and Tukey's Studentized range test to compare densities among sites during May–August in 1979-1980 when all sites were surveyed. The May-August time period was selected to allow comparisons with density estimates obtained at several other study areas on the island of Hawaii in 1976–1979 (Scott et al. 1986).

Mist nets were operated on 16-ha grids at the Keauhou Ranch (n = 62,006 net hr, November 1976 to January 1982) and Kilauea Forest (n = 16,958 net hr, April 1978 to November 1979) sites as described by Ralph and Fancy (1994a, 1995). Captured birds were banded with numbered U.S. Fish and Wildlife Service aluminum bands and a unique combination of plastic colored bands. We aged birds by skull ossification or plumage characteristics, and determined their molt status as described in Ralph and Fancy 1994a, 1994b, 1994c. We were unable to sex birds in the field because there are no differences in plumage between sexes, and both sexes are known to incubate in captivity (Gibson 1978) so that the presence of a brood patch is not a reliable characteristic.

At least monthly, observers walked throughout Keauhou Ranch and Kilauea Forest sites and recorded activities of at least 35 leiothrix, as well as the locations of color-banded birds (Ralph and Fancy 1994b). Activity observations were used to calculate seasonal patterns in vocalizations, as well as pairing and flocking behavior (Ralph and Fancy 1994a). Resightings of color-banded birds were used in conjunction with data from net captures to calculate survival rate using Jolly-Seber models (Pollock et al. 1990). The complement of survival probability that we report here includes both mortality and permanent emigration. We selected a 4-month sampling period each year from May through August based upon goodness-of-fit tests from preliminary runs. Birds captured or resighted during the 8-month period of September through April were coded as resightings for calculating survival probabilities (Pollock et al. 1990). Estimates of population size and recruitment from the program JOLLYAGE were based only on leiothrix captured in mist nets.

Unless otherwise stated, values presented are means ± SE.

RESULTS

SEASONAL VARIATION IN POPULATIONS

Density of Red-billed Leiothrix, and the percent of stations where at least one leiothrix was detected, followed a cyclical pattern with highest values usually occurring during the May–August breeding season each year (Fig. 1). The highest density (birds ha^{-1}) during the May–August time period was at Keauhou Ranch (7.17 ± 0.82), which was greater than densities at Kilauea Forest (4.15 ± 0.45), Hamakua (0.56 ± 0.27), and Kau Forest (0.14 ± 0.14) (Tukey's test, df = 24, all $P < 0.05$).

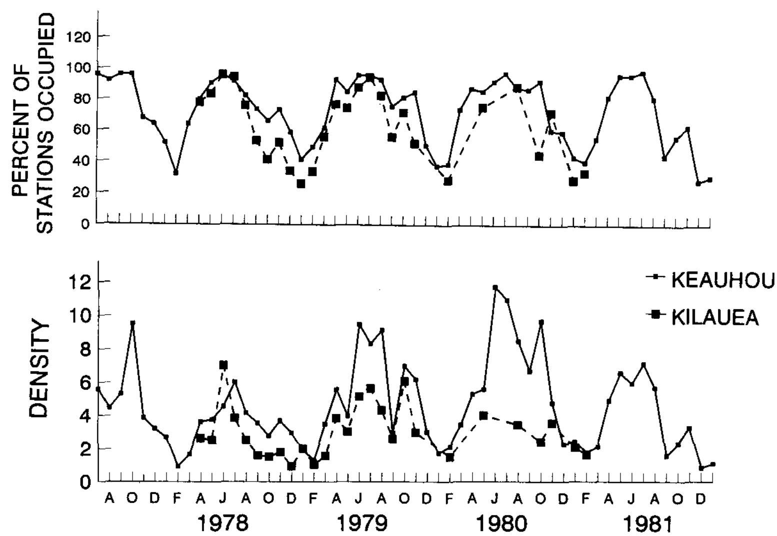

FIGURE 1. Mean density (birds ha^{-1}) of Red-billed Leiothrix during monthly counts at Keauhou Ranch and Kilauea Forest, Hawaii, and percent of stations where at least one leiothrix was detected, 1977–1982.

SURVIVAL PROBABILITY

Survival probabilities at Keauhou Ranch were calculated from 2,719 captures and resightings of 227 adult and 111 hatching-year leiothrix. Mean survival probability of hatching-year birds (0.581 ± 0.115) was lower ($\chi^2_5 = 12.2$, $P = 0.03$) than that for adult leiothrix (0.786 ± 0.047). The probability of resighting an individual during the May–August sampling interval if the bird was alive and on the study area was 0.18 ± 0.03.

Mean population size at Keauhou Ranch based upon mark/recapture data was 219 birds. The home ranges of some birds captured on the study area probably overlapped the study area boundaries, so the area to which this population estimate applies is unknown. The mean number of leiothrix recruited into the population each year, as calculated by JOLLYAGE, was 56 birds, or 25.6% of the mean population size. This value includes immigration as well as births.

TIMING OF BREEDING AND MOLTING

We captured leiothrix with active brood patches in every month (Fig. 2), but most breeding occurred during April–August. All birds with ≤ 10% ossification were captured during May–October (Fig. 2). Molting of flight feathers and body feathers occurred at the same time, with peak molting during August–October (Fig. 2). The rate of calling was fairly constant throughout the year (Fig. 2), but frequency of singing increased during March–May at the beginning of the breeding season.

Approximately one-third of leiothrix were observed paired with another adult bird during monthly observations throughout the year (Fig. 3). Occurrence of flocks (3 or more adult birds together), however, was highest during the nonbreeding season. The capture/resighting history of individual birds suggested that some individuals left the study area during the nonbreeding season.

DISCUSSION

We found large differences in abundance of Red-billed Leiothrix at our four study sites. The highest density occurred at Keauhou Ranch, which had a discontinuous forest because of grazing and logging, but had a variety of fruiting plants in the understory available throughout the year including naio (*Myoporum sandwicense*), akala (*Rubus hawaiiensis*), olapa (*Cheirodendron trigynum*), and ohelo (*Vaccinium reticulatum*). In contrast, density was 92% lower at the Hamakua site, which had a continuous canopy, but little ground cover or understory because of intensive grazing. The very low density at Kau Forest (0.14 birds ha^{-1}) is an enigma, because this site had a dense and diverse native understory with an abundance of the fruiting plants such as kolea (*Myrsine lessertiana*) and kawau

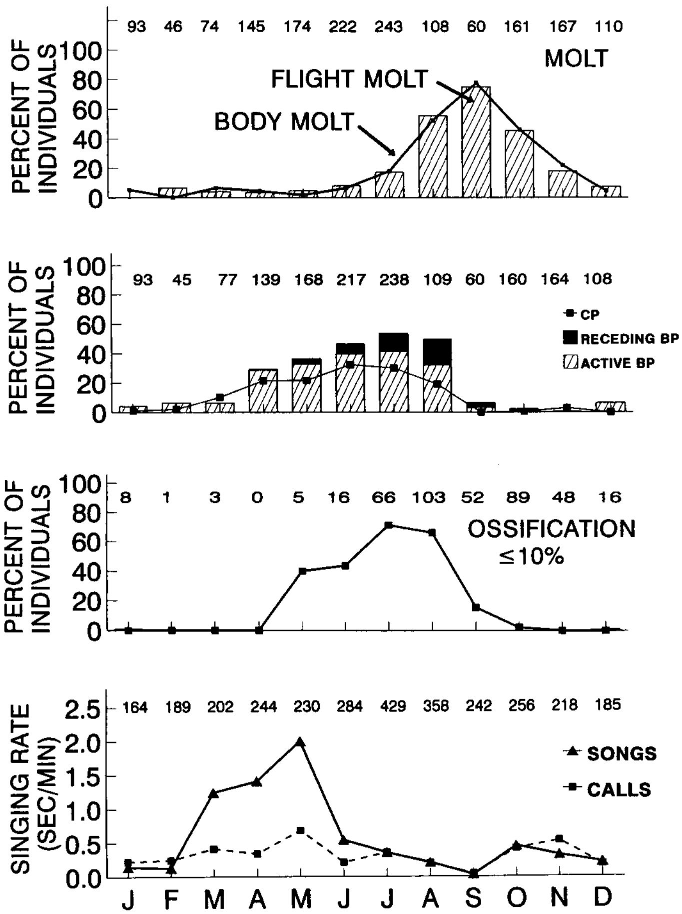

FIGURE 2. Timing of molting and breeding at Keauhou Ranch and Kilauea Forest, Hawaii. Percentage of birds with swollen cloacal protuberance (CP) or brood patch (BP) is shown, as is the proportion of birds with incomplete skull ossification that had ≤ 10% ossification. Sample sizes for each month are shown.

(*Ilex anomala*). Scott et al. (1986) also found relatively low density of leiothrix (< 0.5 birds ha^{-1}) throughout much of the Kau Forest, despite the closed canopy and relatively undisturbed understory throughout much of the forest. Ralph and Noon (1986) found positive correlations between leiothrix numbers at Keauhou Ranch and seasonal changes in abundance of olapa fruit and naio flowers.

Our density estimates from variable circular-plot counts are comparable to those found by Conant (1975) and Scott et al. (1986) for areas near our Keauhou Ranch and Kilauea Forest sites, despite differences in data analysis methods. At Kilauea Forest, Conant (1975) estimated a leiothrix density of 3.80 birds ha^{-1} during year-round surveys, compared to our mean density of 3.01 birds ha^{-1} for all months of the year. Conant (1975) estimated 3.28 leiothrix ha^{-1} for a transect near our Keauhou Ranch site, compared to our estimate of 4.6 birds ha^{-1} for all 55 surveys. Scott et al. (1986) found a patchy distribution of areas with high leiothrix abundance within each of their study areas, and they noted an association with understory fruit plants and average understory density.

We believe that variable circular-plot counts underestimate density because characteristics of leiothrix violate important assumptions of the method. One critical assumption of distance estimation is that birds do not react to the observer (Buckland et al. 1993, McCracken 1994), but leiothrix often remain hidden and silent in the understory while an observer is near, or they

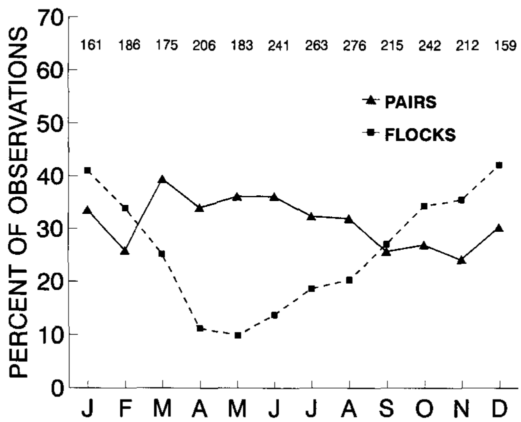

FIGURE 3. Percentage of observations that consisted of observations of two adult Red-billed Leiothrix (pairs) or three or more leiothrix together (flocks). Numbers at top of figure are sample sizes for each month.

make repeated scolding and alarm calls in the presence of an observer. These behaviors have opposite effects on the density estimate. Another important assumption is that observations are independent, but leiothrix frequently move in flocks or pairs and some individuals in the group may not be detected.

Ali and Ripley (1972) reported that in their native range Red-billed Leiothrix make minor seasonal movements. Seasonal movement patterns in Hawaii are not well understood, but flocks that form during the fall and winter months seem to disperse through many habitats, and leiothrix are at times recorded above 3,000 m (Montgomery and Howarth 1980, Distasio 1997). These observations suggest that seasonal differences in flocking behavior may be even greater outside of areas used for breeding. We captured fewer unbanded birds and recaptured or sighted fewer banded individuals outside the breeding season, suggesting that some birds leave the study area at this time, although it also is possible that birds were simply less vocal and less active during the winter months when few sightings and captures occurred. Seasonal abundance in the high-elevation mamane (*Sophora chrysophylla*) and naio woodlands on Mauna Kea volcano follow the same pattern that we found in lower-elevation forests (C. J. Ralph, unpubl. data; Biological Resources Division of U.S. Geological Survey [BRD], unpubl. data), and it is unclear where birds leaving our study areas spent the winter months if there was a distribution shift.

Estimates of annual survival for Red-billed Leiothrix were higher than those reported for most tropical and temperate forest birds (Karr et al. 1990), but are within the range reported for other passerines in Hawaii (Ralph and Fancy 1994c, 1995, Lepson and Freed 1995). Although survival and distribution of other species of forest birds in Hawaii have been greatly affected by avian malaria and avian pox (van Riper et al. 1986, Atkinson et al. 1995), there is no evidence that avian disease has affected leiothrix populations. Prevalence of avian malaria in leiothrix is extremely low, with only 3 of 42 birds captured at Waikamoi Preserve on Maui positive for malaria by serology tests, and none of 131 leiothrix captured near Kulani Prison on the island of Hawaii positive for malaria by blood smear and serology tests (C. Atkinson, unpubl. data). Most of the leiothrix population on Oahu occurs below 1,000 m elevation where mosquitos may be present year-round, suggesting that they are resistant to avian malaria. Incidence of avian pox in leiothrix also seems very low, with only 1 of 226 birds captured in mamane forest on Mauna Kea and 18 of 899 leiothrix captured at the Hakalau Forest National Wildlife Refuge having crusty lesions or missing toes characteristic of avian pox (BRD, unpubl. data).

The Red-billed Leiothrix has successfully colonized a variety of wet- and dry-forest types in Hawaii, and its omnivorous diet of fleshy fruits and invertebrates makes it a generalist among the relatively few remaining species of native passerines. Our findings indicate that its populations are stable, with relatively high recruitment and survival in our study areas. Leiothrix seem relatively tolerant of the avian diseases that have caused large population changes in other forest birds in Hawaii, and yet leiothrix populations have still undergone large fluctuations, to the point of possible extinction on Kauai (Male and Snetsinger, in press). An understanding of these fluctuations could provide great insight into the dynamics of island populations, and provide information that could assist in the conservation of Hawaii's native forest birds.

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