

# Evidence of change in a low-elevation forest bird community of Hawai'i since 1979

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## Summary

We evaluated the abundance and distribution of low-elevation forest birds on windward Hawai'i Island during August 1993–February 1994, and present evidence of changes in the species composition of the forest bird community since 1979. Endemic Hawaiian birds occurred in native-dominated forests as low as 120 m elevation. Non-native species were detected at all survey locations. We observed non-native Saffron Finch *Sicalis flaveola*, previously unrecorded in Puna. Variable circular plot surveys of Kahauale'a Natural Area Reserve indicated the disappearance of two native species ('Iwi *Vestiaria coccinea* and 'O'u *Psittitostira psittacea*), and two non-native additions (Red-billed Leiothrix *Leiothrix lutea* and Kalij Pheasant *Lophura leucomelana*) to the study area since the Hawai'i Forest Bird Survey conducted in 1979. We present evidence that native 'Elepaio *Chasiempis sandwichensis* has experienced a decrease in population density and an elevational range contraction since 1979. Surveys indicate Puna's forest bird community has had increasing aliens and declining native species since 1979. The persistence of some native bird species within the range of avian disease vectors such as *Culex quinquefasciatus* in forests below 1,000 m elevation presents an important enigma that requires additional study.

## Introduction

Hawai'i's endemic forest birds were historically found at all elevations on each island (Perkins 1903). Approximately 10% of the native passerine species known historically occur at elevations below 1,000 m (Scott *et al.* 1986). In the Hawaiian Islands, declining native bird species typically disappear from the lower elevation of their range and become restricted to higher elevations as their range contracts (Banko 1980–1984, Scott *et al.* 1986, van Riper *et al.* 1986). Today, the occurrence of native passerines at elevations below 500 m in Hawai'i is atypical.

A combination of limiting factors has caused low-elevation forest bird declines. Extirpation and extinction have been caused by low-elevation habitat loss and fragmentation (Kirsch 1982, Olson and James 1982, Jacobi and Scott 1985), depredation by introduced mammals (Atkinson 1977, Banko *et al.* 1999, Hodges and Nagata 2001) and introduced avian diseases (Warner 1968, Ralph and van Riper 1985, van Riper *et al.* 1986, Atkinson *et al.* 1995). Other less studied threats include habitat degradation (Mountainspring *et al.* 1990), competition from introduced birds (Mountainspring and Scott 1985) and impacts of introduced arthropods (Perkins 1903, Banko and Banko 1976). It appears that decline and extinction is due to "ecosystem collapse", where synergistic impacts limit native species,

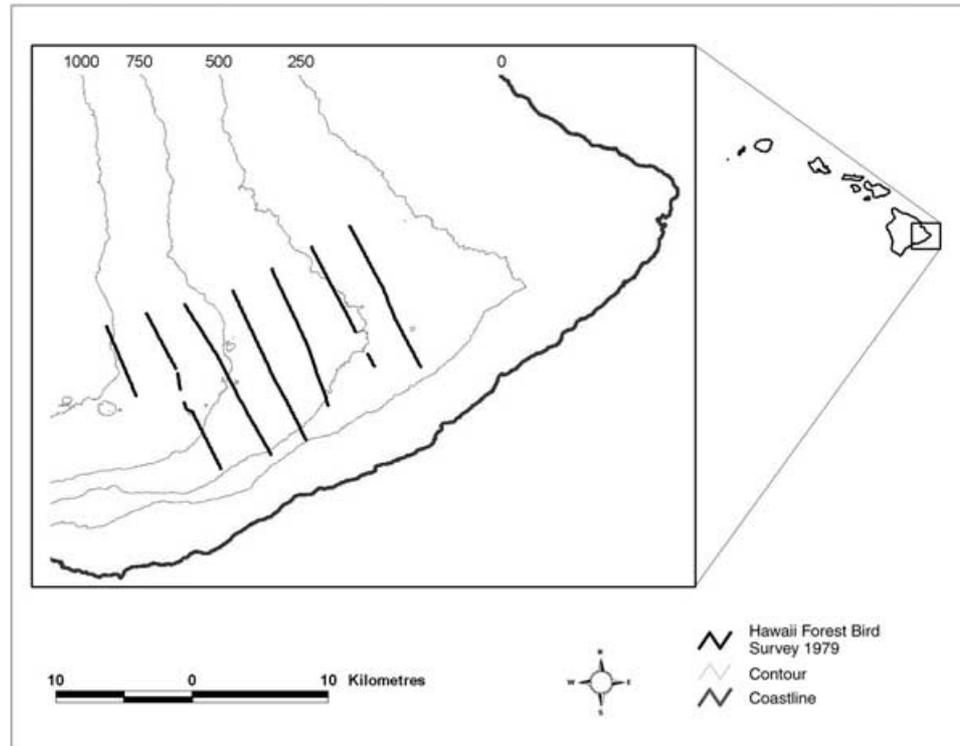


Figure 1. Map of the Hawaiian Islands and the low-elevation study site in the District of Puna, Hawai'i with a locator map showing the Hawaii Forest Bird Survey transects of 1979.

because no single factor is responsible for the loss of Hawaiian endemics. However, since the late 1800s and 1920s, avian pox *Avipox* sp. and malaria *Plasmodium relictum* respectively, have become important sources of mortality for native passerines in low- and mid-elevation forests (van Riper *et al.* 1986, Atkinson *et al.* 1995). Low- and mid-elevation forests, especially those degraded by feral pigs *Sus scrofa*, can harbour high densities of introduced mosquitoes, which serve as vectors for these diseases (LaPointe 2000).

We report on the status of bird species in the Puna District (hereafter Puna) between 0 and 1,000 m elevation, during an intensive, short-term study on Hawai'i Island in 1993–1994. Our objectives were to (1) determine relative abundance, distribution and species composition of the bird community in Puna, and (2) evaluate changes in the low-elevation bird community within the Kahauale'a Natural Area Reserve (NAR) since the last comprehensive survey of the area in 1979 during the island-wide Hawaiian Forest Bird Surveys (HFBS; Scott *et al.* 1986; Figure 1).

## Methods

### Study area

We surveyed forest birds on windward Hawai'i Island, in lower Puna (19°23' N 155°05' W) during August 1993–February 1994 (Figure 2). Vegetation character-

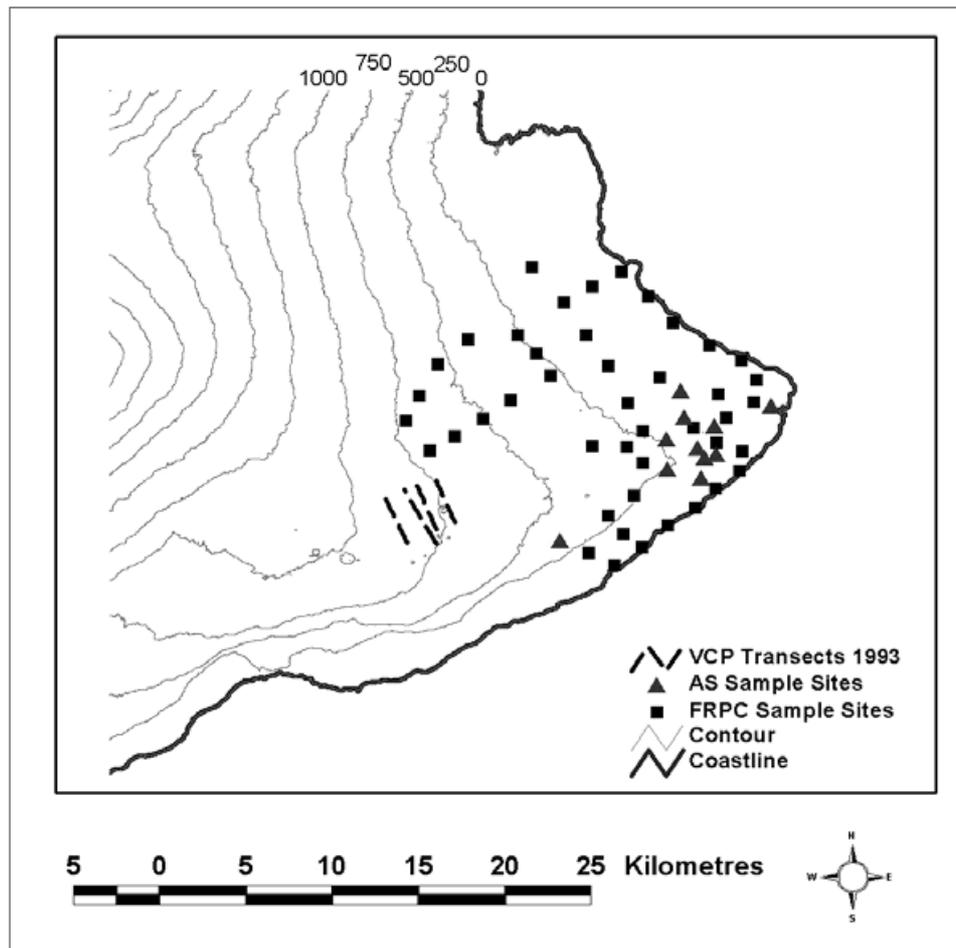


Figure 2. The 1993 sampling sites of bird surveys conducted August 1993–February 1994 in the district of Puna, Hawaii'i. VCP, variable circular plot; AS, area search; FRPC, fixed radius point count.

istics of the area ranged from wet to mesic native 'ohi'a *Metrosideros polymorpha* and tree fern *Cibotium* spp. forest with uluhe *Dicranopteris linearis* native fern or native shrub understorey, to fragmented transition forest with mixed native and introduced vegetation, and forests dominated by non-native vegetation.

#### *Bird surveys*

Variable circular plot (VCP) counts were conducted in December 1993 on four transects at 117 stations in the continuous forest of Kahauale'a NAR (19°22'14" N 155°05'18" W) following methods described by Scott *et al.* (1986) (Figure 2). Trained observers were dropped by helicopter in the roadless area of Kilauea Volcano's East Rift Zone to establish transects and conduct surveys. Transects were placed approximately 3 km apart, and stations were located every 150 m. Observers recorded the distance to each individual bird detected during eight-

minute count periods. Additional variables recorded were observer, time, location, cloud cover, wind, rain and vegetation structure. VCP counts were conducted during the first four hours after sunrise. Sampling was conducted when weather conditions did not interfere with bird detections (wind < 20 kph and during rainless or light rain periods). VCP surveys in May–June 1979 and December 1993 were conducted within the attenuated, low-elevation breeding season for many Hawaiian forest birds (Dr Pat Hart pers. comm.).

Changes in land ownership, land accessibility, and habitat loss from recent lava flows on Kilauea Volcano's East Rift, made resampling all 1979 HFBS Puna transects using VCP methods impossible (Figure 1). Therefore, we used additional survey techniques to sample extensively throughout the study area. These included area searches (AS), fixed radius point-counts (FRPC), and VCP methods. We conducted 20-minute AS at 11 sites accessible only by foot, but where transect sampling was not feasible (Ralph *et al.* 1993) (Figure 2). We conducted FRPC surveys at 44 stations for eight-minute sampling periods along secondary roads every 3.2 km and in highly fragmented habitats at 0.8 km intervals (Figure 2). All point-count surveys were censused between 07h00 and 11h00 by trained observers using 8×40 binoculars. Data collection was similar to methods described by Bystrak (1981) and Petit *et al.* (1995). Data recorded for AS and FRPC included: survey start and end time, elevation, location, vegetation association, wind scale, rain indices, species, number of birds, distance from observer to bird within or beyond 30 m radius and detection type for each bird. We pooled data from all survey methods to obtain species lists and distribution information. We determined detection rates (number of individuals per sample hour) for each species using AS and FRPC (55 points).

#### *Data analyses*

We analysed 117 stations from four transects (1993 data) and 117 stations on three transects HFBS (1979 data) within the Kahauale'a NAR. Data were analysed using the programs DISTANCE and VCPDATA (Fancy 1997, Scott *et al.* 1986, Thomas *et al.* 1998). We calculated the relative abundance for each species (birds/station, percentage of stations occupied, and birds/hour) and estimated densities (birds/km<sup>2</sup>) for species with adequate sample sizes. Densities were calculated by dividing the number of birds detected per station by the effective area surveyed per species. The variation in effective area surveyed was determined using bootstrapping methods described by Fancy (1997) and Thomas *et al.* (1998). The relative abundance and mean density estimates of four species were compared for 1979 and 1993 surveys using Mann–Whitney–Wilcoxon statistical tests. Statistical significance was determined at  $P \leq 0.05$ .

Model selection for effective detection radius (EDR) was restricted a priori to half normal, hazard-rate and uniform functions with expansions series of two orders. Observations were adjusted to standard survey conditions by analysing independent variables, factor, continuous or continuous categorical, as covariates (Fancy 1997). Observer (factor) was the only variable with significant effects on detection distances collected during the 1979 survey. Observer, time of detection (continuous), cloud cover (continuous), rain and wind (continuous categorical) were treated as covariates potentially influencing the EDR of species detected in

1993. Adjustments for observers were made for all species, except 'Elepaio, while adjustments for time of detection were made for 'Oma'o, and cloud cover, wind and time of detection for 'Apapane. Detection histograms and associated statistics for each species were compared with untruncated data, 10% truncation, and  $g'(x) = 0.10$  truncation to select "best-fit" models (Buckland *et al.* 1993, Thomas *et al.* 1998) (see Appendix).

## Results

Pooling the results of all sampling methods, we detected 25 bird species in the Puna District during August 1993–February 1994 (Table 1). Seven of these were endemic to the Hawaiian Islands. Two of these were recorded incidentally: Hawaiian Noddy *Anous minutus melanogenys* and 'A'o or Newell's Shearwater *Puffinus auricularis newelli*. Three seasonal migrants and 15 non-native species were also observed.

The most common species during AS and FRPC was Japanese White-eye *Zosterops japonicus*, with a detection rate of 28.6 birds/hour. House Finch *Carpodacus mexicanus* followed closely with 25.2 birds/hour. Other common species (> 6 bird/hour) included the introduced Nutmeg Mannikin *Lonchura punctulata* (16.3 birds/hour), Northern Cardinal *Cardinalis cardinalis* (14.5), Common Myna *Acridotheres tristis* (13.9) and Spotted Dove *Streptopelia chinensis* (6.3), and the native Hawai'i 'Amakihi *Hemignathus virens virens* (8.9 birds/hour) and 'Apapane *Himatione sanguinea* (7.8 birds/hour).

Hawai'i 'Amakihi and 'Apapane were detected at several survey locations at 120 m elevation. The lowest elevation detection of 'Oma'o *Myadestes obscurus* was a single individual at about 470 m. We detected 'Elepaio *Chasiempis sandwichensis* within the Kahauale'a NAR at and above 700 m. Notable records of alien species included Saffron Finch *Sicalis flaveola* at 800 m, Kalij Pheasant *Lophura leucomelana* between 150 and 1,000 m, and unknown parrots at 240 m. Records of migrant species included Wandering Tattler *Heteroscelus incanus* at sea level, Pacific Golden Plover *Pluvialis fulva* throughout Puna from 0 to 1,000 m, and a possible but unconfirmed Green-winged Teal *Anas carolinensis* at 50 m.

We detected 10 species in the Kahauale'a NAR in 1993 (Table 2), of which 'Apapane (526 counted) and Japanese White-eye (357 counted) were the most abundant. 'Apapane, 'Elepaio, 'Oma'o, Japanese White-eye, Hwamei *Garrulax canorus* and Northern Cardinal were also recorded here in 1979. The 'Io or Hawaiian Hawk *Buteo solitarius*, Red-Billed Leiothrix *Leiothrix lutea*, Kalij Pheasant, and Spotted Dove were recorded during 1993 in Kahauale'a NAR, but were located elsewhere in Puna during the 1979 surveys (Scott *et al.* 1986). 'O'u *Psittitostira psittacea* and 'Yiwi *Vestiaria coccinea*, both rare during the 1979 counts, were absent in 1993. Hawai'i 'Amakihi and House Finch were not detected in the Kahauale'a NAR during our 1993 VCP survey, although they occurred commonly in other areas of Puna (Table 1).

For each species, we compared VCP count results from the 1979 survey with those of the 1993 survey (117 stations in both years; Table 2). Four species common during both the 1979 and 1993 VCP counts had sample sizes large enough for density comparisons: 'Apapane, Japanese White-eye, 'Oma'o and 'Elepaio (see Appendix and Figure 3). 'Apapane was the most abundant species

Table 1. Bird species detected during Puna surveys: August 1993–February 1994 between 0 and 1,000 m.

Common name	Scientific name	Status	Survey type <sup>a</sup> 1993–1994
'A'o (Newell's Shearwater)	<i>Puffinus newelli</i>	Native	Incidental detections
'Apapane	<i>Himatione sanguinea</i>	Native	AS, FRPC
Barn Owl	<i>Tyto alba</i>	Non-native	Incidental detections
Common Myna	<i>Acridotheres tristis</i>	Non-native	AS, FRPC
Hawai'i 'Amakihi	<i>Hemignathus virens virens</i>	Native	AS, FRPC, VCP
Domestic chicken	<i>Gallus domesticus</i>	Non-native	AS, FRPC
'Elepaio	<i>Chasiempis sandwichensis</i>	Native	VCP
Green Pheasant	<i>Phasianus colchicus</i>	Non-native	Incidental detections
Hawaiian Noddy	<i>Anous minutus melanogenys</i>	Native	Incidental detections
House Finch	<i>Carpodacus mexicanus</i>	Non-native	AS, FRPC
'Io (Hawaiian Hawk)	<i>Buteo solitarius</i>	Native	AS, FRPC, Incidental detections
Japanese White-eye	<i>Zosterops japonicus</i>	Non-native	AS, FRPC, VCP
Kalij Pheasant	<i>Lophura leucomelana</i>	Non-native	VCP, incidental detections
Pacific Golden Plover	<i>Pluvialis fulva</i>	Migrant	AS, FRPC, VCP
Hwamei	<i>Garrulax canorus</i>	Non-native	AS, FRPC, VCP
Northern Cardinal	<i>Cardinalis cardinalis</i>	Non-native	AS, FRPC, VCP
Nutmeg Manikin	<i>Lonchura punctulata</i>	Non-native	AS, FRPC
'Oma'o (Hawaiian Thrush)	<i>Myadestes obscurus</i>	Native	VCP, Incidental detections
Red-billed Leiothrix	<i>Leiothrix lutea</i>	Non-native	AS, FRPC, VCP
Saffron Finch	<i>Sicalis flaveola</i>	Non-native	Incidental detections
Spotted Dove	<i>Streptopelia chinensis</i>	Non-native	AS, FRPC, VCP
Teal sp.	<i>Anas sp.</i>	Migrant	Incidental detections
Wandering Tattler	<i>Heteroscelus incanus</i>	Migrant	Incidental detections
Parrot sp.	Family: <i>Psittacidae</i>	Non-native	AS, FRPC
Zebra Dove	<i>Geopelia striata</i>	Non-native	AS, FRPC, VCP

<sup>a</sup>Survey methods: AS, Area search; FRPC, Fixed radius point count; VCP, Variable circular plot.

in 1979 with 2,353 birds/km<sup>2</sup> (95% C.I. 2,070–2,658) compared with a lower density estimate of 605 birds/km<sup>2</sup> (95% C.I. 501–718) in 1993. The density of Japanese White-eye increased from 746 birds/km<sup>2</sup> (95% C.I. 656–842) in 1979 to 1,094 birds/km<sup>2</sup> (95% C.I. 980–1,217) in 1993. 'Elepaio density was 126 birds/km<sup>2</sup> (95% C.I. 98–156) in 1979 and 46 birds/km<sup>2</sup> (95% C.I. 24–71) in 1993. The 'Oma'o densities were 169 birds/km<sup>2</sup> (95% C.I. 147–193) and 128 birds/km<sup>2</sup> (95% C.I. 111–148) in 1979 and 1993, respectively.

We found significant differences between 1979 and 1993 relative abundance (birds/station) and densities (birds/km<sup>2</sup>) for the four species tested (Mann–Whitney–Wilcoxon Rank Sum adjusted for ties;  $\alpha = 0.05$ ,  $n = 117$  stations). Both relative abundance and densities per station were significantly less in 1993 than 1979 for the native 'Apapane (Birds/station  $W = 16,854$ ,  $P = 0.0001$ ; Tot. Density  $W = 19,303$ ,  $P = 0.0001$ ), 'Oma'o (Tot. Birds/station  $W = 16,568.5$ ,  $P = 0.001$ ; Tot. Density  $W = 15,160$ ,  $P = 0.0032$ ), and 'Elepaio (Tot. Birds/station  $W = 16,284$ ,  $P = 0.001$ ; Tot. Density  $W = 16,034$ ,  $P = 0.0001$ ). The Japanese White-eye population was significantly higher in 1993 than 1979, also based on total birds/station ( $W = 12,543$ ,  $P = 0.0084$ ) and density estimates ( $W = 11,271$ ,  $P = 0.0001$ ).

## Discussion

Our 1993–1994 survey detected 'Apapane and Hawai'i 'Amakihi to 120 m in elevation, and 'Oma'o at 470 m, representing some of the lowest elevational

Table 2. Relative abundances and median densities (birds/km<sup>2</sup>) of forest birds from 117 stations in the Kahauale'a Natural Area Reserve from variable circular plot surveys 1979 and 1993.

Species	1979 per station mean (SE)	1993 per station means (SE)	1979 median density	1993 median density	% Occurrence 1979	% Occurrence 1993	birds/hour 1979	birds/hour 1993
'Apapane	7.11 (0.34)	4.50 (0.28)	1941.2	345.9	99.1	94.9	54.6	33.7
'Oma'o	3.24 (0.14)	2.27 (0.13)	130.65	105.24	95.7	90.6	24.9	17.0
Japanese White-eye	2.56 (0.14)	3.05 (0.12)	689.0	936.9	94.9	100	19.8	22.9
'Elepaio	0.86 (0.10)	0.21 (0.05)	140.66	0	50.4	14.5	6.6	1.6
Hwamei	0.26 (0.06)	0.15 (0.04)	-	-	18.8	12.8	1.9	1.2
Northern Cardinal	0.24 (0.06)	0.03 (0.02)	-	-	17.9	3.4	1.9	0.3
I'iwi	0.05 (0.02)	0	-	-	4.3	0	0.38	0
Hawai'i 'Amakihi	0.02 (0.01)	0	-	-	1.7	0	0.12	0
Red-billed Leiothrix	0	0.04 (0.02)	-	-	0	4.3	0	0.3
'Io	0	0.02 (0.01)	-	-	0	1.7	0	0.1
Kaliij Pheasant	0	0.03 (0.2)	-	-	0	1.7	0	0.3
Spotted Dove	0	0.01 (0.01)	-	-	0	0.9	0	0.1
House Finch	0.01 (0.01)	0	-	-	1.7	0	0.06	0
'Ou	0.01 (0.01)	0	-	-	0.9	0	0.06	0

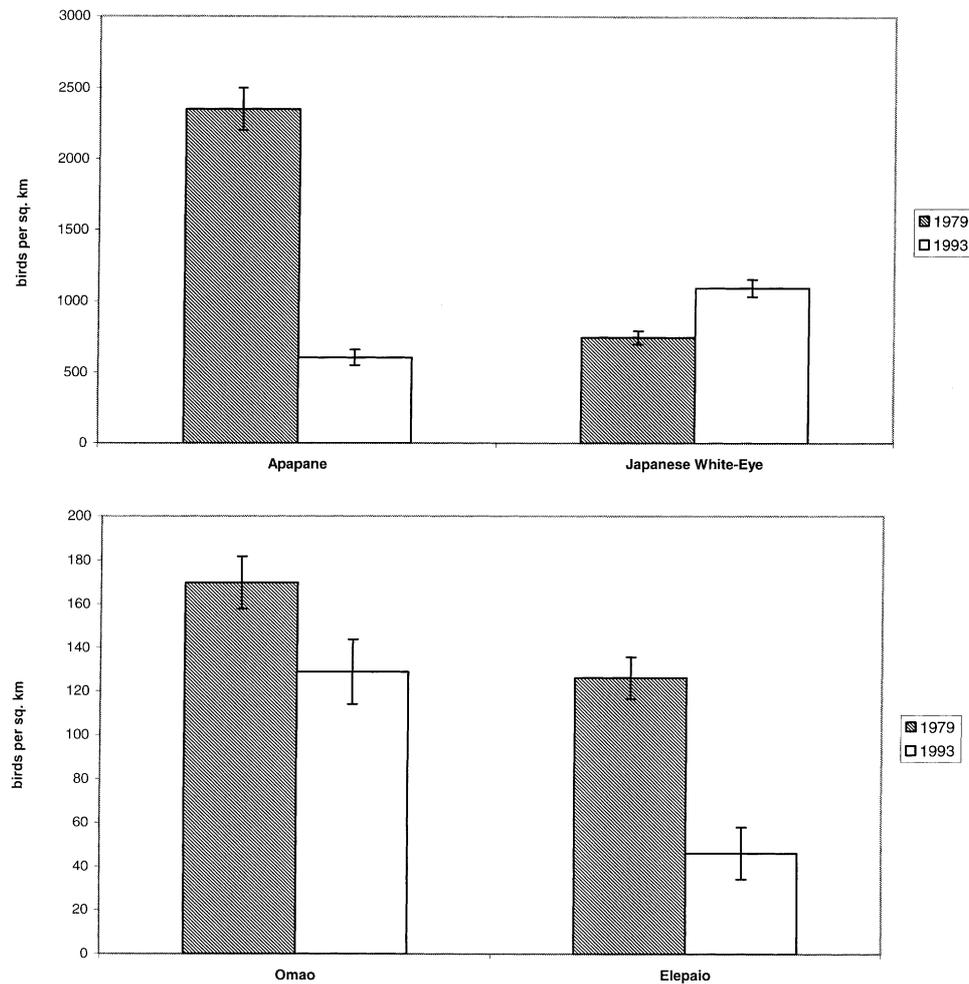


Figure 3. Variable circular plot estimates of forest bird densities (with SE) from Kahauale'a Natural Area Reserve 1979 and 1993. Population densities are significantly different between 1979 and 1993 ( $P < 0.01$ ).

records for these species on Hawai'i Island in recent years. The fragments of native-dominated ('ohi'a-uluhe) forest below 600 m in which these birds were found, remain scattered throughout lower Puna in pit craters, cinder cones, successional forests on lava flows and in forest reserves and parks. The HFBS recorded 'Apapane, Hawai'i 'Amakihi and 'Oma'o at the lowest elevations sampled in Puna (from 300 to 500 m). Field biologists with mist-netting sites in Puna have recently reported capturing Hawai'i 'Amakihi at 10 m elevation, Apapane at 120 m (Kelly Kozar, USGS, pers. comm.), and observing 'Elepaio at a forested cinder cone at approximately 330 m in 2001–2002 (Erik Tweed and Carlie Henneman, USGS, pers. comm.). 'Elepaio was not found below 700 m during our surveys, yet the species was recorded at high densities (range 5–100 birds/km<sup>2</sup>) to 300 m in Puna by the HFBS in 1979 (Scott *et al.* 1986). 'Elepaio was also

absent from all of our AS and FRPC sampling sites in Puna below 700 m (refer to Figures 1 and 2). Much of the habitat sampled in 1979 below 700 m has been lost to lava flows. Since 'Elepaio is territorial and sedentary year round (Vanderwerf 1998), our data provide evidence that 'Elepaio has experienced an elevational range contraction of approximately 400 m across most of this region since 1979.

In Kahauale'a NAR, the 'Elepaio's relative abundance and density were significantly less in 1993 than in 1979. Vanderwerf (1998) reported population declines in other areas of Hawai'i Island and O'ahu due to habitat degradation, habitat loss, predation and avian disease. 'Iwi and 'O'u were at low densities in 1979 (1–10 birds/km<sup>2</sup>; Scott *et al.* 1986), and are likely to have been extirpated from the reserve. 'Iwi was absent below 700 m in 1979, and recent surveys from Puna and elsewhere in windward Hawai'i, suggest its range has contracted, and that it is rare below 1,500 m (USGS-BRD unpubl. data). 'Iwi are highly susceptible to avian malaria which is prevalent at mid elevations (Atkinson *et al.* 1995). 'O'u was seen last in 1987 and is likely to be extinct, as intensive surveys for 'O'u in 1994–1996 did not confirm its existence on any of the Hawaiian Islands (Snetsinger *et al.* 1998, Reynolds and Snetsinger 2001).

Several new species of introduced birds have appeared since the 1979 forest bird surveys. Saffron Finch, Kalij Pheasant and an unidentified parrot Psittacidae were not recorded below 1,000 m in Puna during 1979 HFBS surveys. Red-Billed Leiothrix, introduced in 1918, has experienced large population fluctuations (Male *et al.* 1998) and has moved into Kahauale'a NAR since 1979.

Japanese White-eye, a seasonally territorial generalist, was first introduced to the island of Hawai'i in 1937 (van Riper 2000). It is found in all forested habitats of all of the main Hawaiian Islands, and is suspected of being a competitor with native forest birds (Mountainspring and Scott 1985, van Riper 2000). The density of Japanese White-eyes has increased in Kahauale'a NAR since the 1979 survey, and was the most common species detected during AS and FRPC surveys.

We recognize several limitations in interpreting VCP comparisons between 1979 and 1993. First, both surveys constitute snapshots in time of populations that vary both temporally and spatially. The 1993 survey was conducted at a different time of year than that done in 1979, but both were conducted within the extended low-elevation breeding season for many species, December–June (USGS data). Therefore, we assumed that detection differences due to time of year were not significant. Density estimates are susceptible to inter-observer variability (Ralph and Scott 1981), but we calibrated all observers using the same techniques as Scott *et al.* (1986) and corrected for observers' differences within survey years to reduce the influence of this variability (Ralph and Scott 1981, Fancy 1997). Lastly, due to landscape and access changes since 1979, we were not able to duplicate all sample sites of the HFBS (Figure 1). Thus, we limited our statistical comparisons to the areas that could be re-sampled within the Kahauale'a NAR (Figure 2), and report only change in species composition from 1979 and 1993–1994 for the rest of the study area.

Despite these cautions, we believe the range contraction of endemic 'Elepaio, disappearance of 'Iwi and 'O'u, and additional populations of introduced species in Kahauale'a NAR, and other areas of Puna represent evidence of change

in the low-elevation forest bird communities. Statistically significant differences between 1979 and 1993 in populations of 'Oma'o and Japanese White-eye may also indicate biological significance. However, survey efforts nearly 15 years apart generate more hypotheses than conclusions. Long-term inventory and monitoring of low-elevation forests is needed to evaluate forest bird population trends.

Population decrease of 'Oma'o, a territorial and sedentary endemic solitaire, seems likely. In contrast, 'Apapane is primarily nectarivorous and known for wide-ranging movements in response to 'ohi'a blossom availability (Ralph and Fancy 1994), thus high variability in population density at a given locality is likely. With our survey, population declines of Apapane in the lower elevations of Puna may be confounded by their seasonal movements for nectar. Extensive surveys of bird communities and analyses of landscape factors influencing distribution and abundance are needed for evaluating species status.

Absence or reduced populations of native birds in Puna may be attributed to habitat fragmentation, degradation and loss and/or competition from introduced species. The entire study area is within the distribution of *Culex quinquefasciatus*, a vector of avian malaria and pox. However, it is unlikely the mosquito distribution and associated diseases directly explain all survey locations with and without native birds. Susceptibility to avian diseases varies widely between species (Atkinson *et al.* 1995). Currently we do not know whether native forest birds detected at the lowest elevations are residents with disease resistance (see Atkinson *et al.* 2001, Shehata *et al.* 2001), seasonal migrants from higher elevation (MacMillen and Carpenter 1980), or "doomed" sink populations from dispersal of higher elevations source populations.

We recommend protection of remaining native forest in low-elevations of Hawai'i where native birds persist. Ongoing research on the occurrence and resistance of avian malaria (USGS data), and the population dynamics of low-elevation forest birds may provide information on the evolution of avian disease resistance essential to the conservation of Hawaii's native forest birds.

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Appendix. Model parameters, effective detection radius (EDR), percentage of coefficient of variation (%CV), and population estimates in the Kahauale'a Natural Area Reserve from variable circular plot surveys 1979 and 1993.

Species	1979						1993					
	Model	Truncation	EDR	%CV	Mean density	SE <sup>a</sup>	Model	Truncation	EDR	%CV	Mean density	SE <sup>a</sup>
'Apapane	Half normal function, simple polynomial expansion, order 2.	$g'(x) = 67.3$ m	40.49	5.25	2352.6	149.5	Hazard-rate function, no expansion series.	$g'(x) = 74.8$ m	51.70	2.70	605.1	55.6
Japanese White-eye	Hazard-rate function, simple polynomial expansion, order 1.	10%	37.22	3.00	746.4	47.5	Hazard-rate function, no expansion series.	10%	31.93	2.31	1093.7	60.7
'Oma'o	Hazard-rate function, simple polynomial expansion, order 1.	$g'(x) = 97.3$ m	69.81	3.42	169.8	12.0	Half normal function, simple polynomial expansion, order 1	$g'(x) = 126.0$ m	89.25	4.83	129.0	9.5
'Elepaio	Half normal function, no expansion series.	10%	47.57	7.34	126.3	14.8	Uniform function, cosine expansion, order 1	$g'(x) = 63.6$ m	38.68	8.31	46.3	11.9

<sup>a</sup>Standard errors estimated with bootstrapping methods (Thomas *et al.* 1998).

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