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Population estimates and trends of three Maui Island-endemic Hawaiian Honeycreepers

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ABSTRACT. Population monitoring is critical for informing the management and conservation of rare Hawaiian forest birds. In 2017, we used point-transect distance sampling methods to estimate population densities of birds on Haleakalā Volcano on east Maui island. We estimated the populations and ranges of three island-endemic Hawaiian honeycreepers, including the endangered ʻĀkohekohe (*Palmeria dolei*), the endangered Kiwikiu (Maui Parrotbill; *Pseudonestor xanthophrys*), and the Maui ʻAlauahio (*Paroreomyza montana newtoni*). We examined population trends back to 1980, and our 2017 density estimates were the lowest ever recorded for each species. Most concerning was the status of Kiwikiu, with a 71% decline in population since 2001 to a current population of 157 (95% CI 44–312) birds. The population of ʻĀkohekohe similarly decreased by 78% to a current population of 1768 (1193–2411) birds. For both species, population declines were due to declines in density and contraction of ranges from lower elevations. Both species are now restricted to ranges of less than 3000 ha. We surveyed ~ 91% of the range of Maui ʻAlauahio and estimated a population of 99,060 (88,502–106,954) birds, a 41% decrease since the highest estimate in 1992. Contraction of ranges to higher elevations is consistent with evidence that the impacts of avian malaria are being exacerbated by global warming trends. Our results indicate that the landscape control of either avian malaria transmission or its vector (*Culex* mosquitoes) will be a pre-requisite to preventing the extinction of endemic forest birds in Hawaii.

RESUMEN. **Estimaciones y tendencias poblacionales de tres especies endémicas de trepadores de miel hawaianos en la isla de Maui**

El monitoreo poblacional es fundamental para informar sobre la gestión y la conservación de aves forestales raras aves de Hawai. En 2017, utilizamos métodos de muestreo de distancia de transectos puntuales para estimar las densidades de población de aves en el volcán Haleakalā en la isla este de Maui. Estimamos las poblaciones y áreas de distribución de tres trepadores de miel hawaianos endémicos de la isla, incluido la especie en peligro de extinción ʻĀkohekohe (*Palmeria dolei*), la especie en peligro de extición Kiwikiu (Pico de loro de Maui; *Pseudonestor xanthophrys*) y el Alauahio de Maui (*Paroreomyza montana newtoni*). Examinamos las tendencias de la población desde 1980, y nuestras estimaciones de densidad de 2017 fueron las más bajas jamás registradas para cada especie. Lo más preocupante fue el estado de Kiwikiu, con una disminución del 71% en la población desde 2001 a una población actual de 157 (IC del 95%: 44–312) aves. La población de ʻĀkohekohe disminuyó de manera similar en un 78% a una población actual de 1768 (1193–2411) aves. Para ambas especies, la disminución de la población se debió a la disminución de la densidad y la contracción de los rangos de las elevaciones más bajas. Ambas especies están ahora restringidas a áreas de distribución de menos de 3000 ha. Muestreamos ~ 91% del rango del Alauahio Maui y estimamos una población de 99,060 (88,502-106,954) aves, una disminución del 41% desde la estimación más alta en 1992. La contracción de rangos hacia elevaciones más altas son consistentes con evidencia de que los impactos de la malaria aviar se ve agravada por las tendencias del calentamiento global. Nuestros resultados indican que el control del paisaje de la transmisión de la malaria aviar o de su vector (mosquitos *Culex*) será un prerrequisito para prevenir la extinción de l.

Key words: avian malaria, distance sampling, endangered species, Haleakalā, island-endemic species, population declines

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The avifauna of Hawai'i is characterized by a high level of endemism resulting from adaptive radiation (Fleischer et al. 1998, Pratt 2005, Lerner et al. 2011). Since human colonization of the Hawaiian Islands, the introduction of alien flora and fauna has caused the biota to become more continental in composition and ecology, almost invariably to the detriment of native species. The decline in populations of Hawaiian birds is often explained as the non-adaptive response of ecologically constrained or behaviorally naïve species to the arrival of new diseases, parasites, predators, and competitors (Atkinson 1977, Pratt 1994, van Riper and Scott 2001, Pratt and Jacobi 2009). Only 43 of 113 native forest bird species persist in the islands (Pyle and Pyle 2017), with 36 considered threatened or endangered and 11 not seen in the last 45 years (Banko and Banko 2009, Elphick et al. 2010).

Haleakalā Volcano encompasses all of Haleakalā National Park (NP), several state-managed Forest Reserves (FR) and Natural Area Reserves (NAR), and private lands, most of which were included in the 2017 East Maui Island forest bird survey area (hereafter, East Maui). The area contains habitat for several honeycreepers, including three species endemic to East Maui: ʻĀkohekohe (*Palmeria dolei*), Kiwikiu (Maui Parrotbill; *Pseudonestor xanthophrys*), and Maui ʻAlauahio (*Paroreomyza montana newtoni*) (Scott et al. 1986). Disease, habitat conversion, and introduced plants and animals have had negative effects on populations of these birds. Species of honeycreepers that have fared better on East Maui include the Hawai'i ʻAmakihi (*Chlorodrepanis virens wilsoni*) and ʻApapane (*Himatione sanguinea*). These species have broad distributions across the main Hawaiian Islands (Gorresen et al. 2009) and have even demonstrated some localized resistance to avian malaria (Atkinson et al. 2000, Foster et al. 2007).

There have also been dynamic shifts in the avian community in Hawai'i as populations of native species decline and non-native species expand into new habitats. Over 170 species of birds have been introduced to the islands, and 54 have become naturalized (Foster 2009, Pyle and Pyle 2017). Species such as Japanese Bush-Warblers (*Horornis diphone*), Warbling White-eyes (*Zosterops japonicus*), and Red-billed Leiothrixes (*Leiothrix lutea*) have expanded their ranges into native forests on East Maui (Judge et al. 2013). Introduced ungulates and anthropogenic impacts have contributed to the conversion of more than 50% of lowland native forests to non-native habitat (Leopold and Hess 2017, Gon et al. 2018). Additionally, the encroachment of weedy shrubs into mesic- and wet-montane habitat threatens the unique ecological niches occupied by honeycreepers (Loope and Mueller-Dombois 1989, Pratt and Jacobi 2009). Control of invasive species has been the most challenging and critical management action for preserving habitat that supports honeycreepers (Loope and Medeiros 1995, USFWS 2006). This includes managing invasive predators such as cats (*Felis catus*), rats (*Rattus* sp.), and mongooses (*Herpestes javanicus*) as well as introduced disease spread by non-native mosquitoes. In some areas relatively free from disease-related impacts, habitat management (e.g., predator, ungulate, and weed control) has resulted in stable or increasing populations of native landbirds (Camp et al. 2010).

Methods for long-term forest bird population monitoring in Hawai'i were established by the Hawai'i Forest Bird Survey of 1976 to 1983 (HFBS; Scott et al. 1986) and were implemented on East Maui in 1980. Subsequently, HFBS transects have been surveyed using the same methods, and additional transects were added by private, state, and federal agency natural-resource managers. Recent surveys have been conducted by personnel from the Hawai'i State Division of Forestry and Wildlife (DOFAW), Maui Forest Bird Recovery Project (MFBRP), Haleakalā NP resource management, and the National Park Service (NPS) Pacific Island Inventory and Monitoring Network (PACN). In 2017, DOFAW, MFBRP, Haleakalā NP, and PACN collaboratively conducted surveys on almost all East Maui transects for the first time since 1980 to provide an updated status of native and non-native forest bird species for the entire region. Survey findings were reported in the NPS National Resource Report Series in Judge et al. (2019). Here we provide occurrence, density, and trend data from East Maui to examine the short- and long-term trajectories of populations of ʻĀkohekohe, Kiwikiu, and Maui ʻAlauahio from 1980 to 2017.

METHODS

The East Maui forest bird survey was conducted in a 146 km^2 inference area of

Haleakalā Volcano (3055 m asl). The area was divided into four regions, including Haleakalā NP, Windward, Leeward, and Kula (Fig. 1). The Haleakalā NP Region primarily includes the eastern portion of the Kīpahulu District. The northern Windward Region is contiguous with Haleakalā NP and includes areas managed by DOFAW and The Nature Conservancy (TNC). The Kula and Leeward Regions are disjunct units from the climatically wet Haleakalā NP and Windward regions, occurring on the drier southern and western slopes of Haleakalā Volcano.

Haleakalā National Park region. The Haleakalā NP region inference area included 29 km^2 of the upper portions of the Kīpahulu Valley Biological Reserve (Fig. 1). Bird monitoring stations range from 1500 to 2100 m in elevation. Habitat was dominated by a canopy of native ʻōhiʻa (*Metrosideros polymorpha*) and koa (*Acacia koa*) forest and predominantly native understory. Feral pigs (*Sus scrofa*) and goats (*Capra hircus*) occurred at low and mid-elevation areas where they negatively affect the native understory and spread seeds of invasive plants such as *Clidemia hirta*, *Psidium cattleainum*, and *Cyathea cooperi*. Typical northeast tradewinds pervade Kīpahulu Valley, and annual mean rainfall from weather stations in the area ranges from 5600 to 10,270 mm (Giambelluca et al. 2013).

Windward region. The Windward region inference area covered 67 km^2 jointly managed by TNC and DOFAW. The region includes TNC's Waikamoi Preserve, Hanawī NAR, Koʻolau FR, Makawao FR, and Hāna FR (Fig. 1). Transects range from 600 to 2300 m elevation. The habitat varied from wet ʻōhiʻa-dominated forests in the eastern portion to transitional wet-mesic forests with

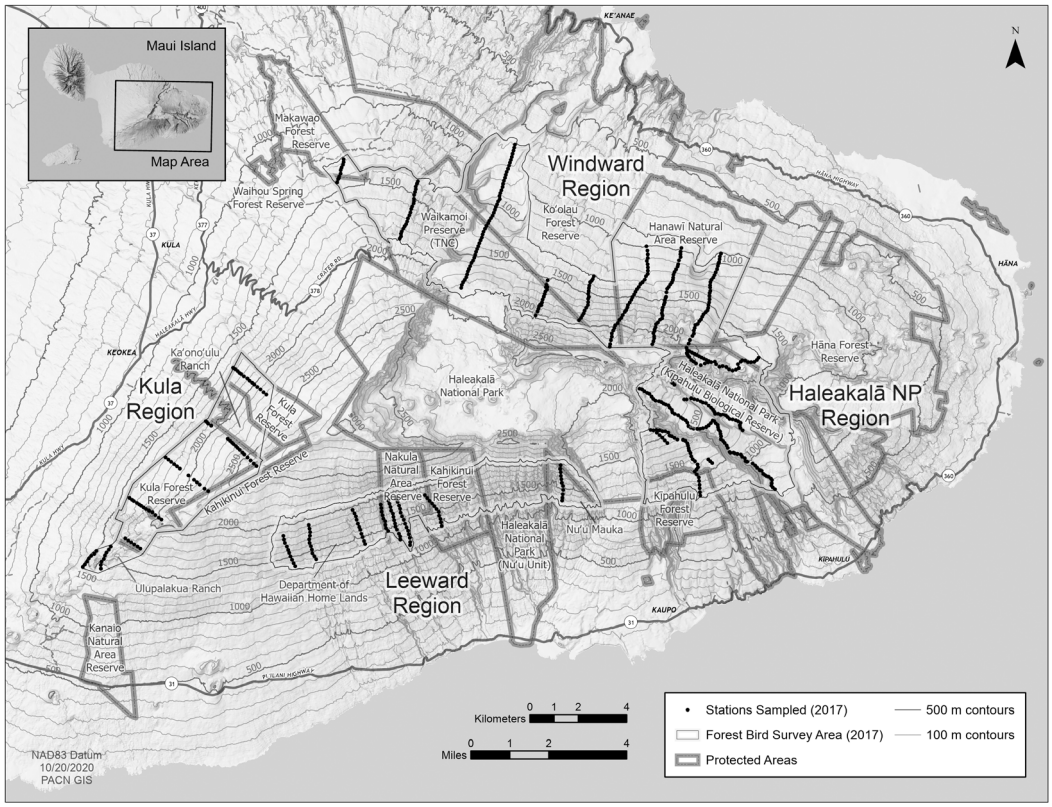


Fig. 1. The 2017 East Maui forest bird survey area. The area was divided into four regions: Windward, Haleakalā National Park, Leeward, and Kula. These regions include lands managed by the State of Hawaiʻi, National Park Service, The Nature Conservancy, and private landowners. [Colour figure can be viewed at wileyonlinelibrary.com]

a mixed koa and ʻōhiʻa canopy along the western edge. Mean annual rainfall in the area ranged from 6600 to 10,270 mm (Giambelluca et al. 2013).

Leeward region. The Leeward region encompassed 26 km^2 on the south-facing slope of Haleakalā (Fig. 1). DOFAW manages Nakula NAR and Kahikinui FR in the central portion of the region. The Haleakalā NP Nuʻu Unit is located east of Kahikinui FR. The state of Hawaiʻi Department of Hawaiian Home Lands (DHHL) manages the western portion of the region and the privately owned Nuʻu Mauka Ranch manages the land on the eastern end (Fig. 1). Forest quality in this region generally declines from west to east. In DHHL and Nakula NAR, there are large intact patches of koa and ʻōhiʻa woodland and savanna in the west, whereas only scattered ʻōhiʻa and severely eroded, non-native grass-covered slopes remain in the east. Thus, most of the remaining habitat for forest birds is in the western portion of the Leeward region. Transects ranged from 1100 to 2000 m elevation and the region experiences dry conditions, with a mean annual rainfall ranging from 720 to 1000 mm (Giambelluca et al. 2013).

Kula region. The Kula region encompassed 24 km^2 on the east- and northeast-facing slopes of Haleakalā. Most of the region is managed by DOFAW, which includes the Kula FR and a portion of Kahikinui FR. Privately owned Kaʻonoʻulu and Ulupalakua ranches own smaller areas in the region (Fig. 1). The region is dominated by non-native tree species (conifers, eucalyptus, and *Acacia* spp.), with a mix of native tree and shrub species. Upper-elevation areas are dominated by native shrubland. Transects ranged from 1700 to 2700 m in elevation. Mean annual rainfall ranges from 800 to 920 mm (Giambelluca et al. 2013).

Distance sampling. Surveys were conducted from 13 March to 28 June 2017. We surveyed for birds at 570 stations along 32 transects in the four regions (Fig. 1). Transects were 350 to 3500 m apart and ranged from eight to 72 stations long. Stations were ~ 150 m apart and surveyed using point-transect distance sampling methods lasting 8 min. Surveys began soon after dawn and concluded by 11:00 in Haleakalā NP and by 12:00 in the Leeward, Kula, and Windward regions. We recorded species, horizontal distance in meters from observers to each bird detected, and detection type (seen, heard, or both). Weather conditions were also recorded at each station. Point-transect distance sampling methods allow for estimating detection probabilities by modeling a species-specific detection function to estimate absolute abundance using design-based methods (Buckland et al. 2001). Distance sampling analysis accounts for individuals that go undetected and produces unbiased absolute abundance. Robust estimates are reliant upon the critical assumptions that all birds are detected with certainty at the station center point, birds are detected before any movement, and distances are measured without error. Details of Hawaiian forest bird sampling can be found in Camp et al. (2011). Data are available from the U.S. National Park Service (https://irma.nps.gov/DataStore/Reference/Profile/2279288).

Range delineation. We used transect locations, contour intervals, vegetation, and the current and historical distribution of landbird species to determine the inference area for abundance estimates. Methods for defining study area boundaries and inference of broadly occurring species are described in detail by Judge et al. (2019). We used survey records, banding records, and spot-mapping studies conducted from 2006 to 2017 to determine the upper- and lower-elevation extents occupied by each species. Using only records obtained since 2006 ensured that inference areas reflected the current range of each species. The lower edge of each range followed the lowest contour interval where each species was observed in each geographic region and thus varied among regions. Transitions between contour intervals were spanned using straight lines, management boundaries, or other physical features (e.g., fence lines). The upper edge for the range of each species was created using contour intervals, habitat layers, or management boundaries.

The ranges of ʻĀkohekohe and Kiwikiu were smaller than the overall survey inference so we were able to provide global population estimates for those species. ʻĀkohekohe and Kiwikiu occur in habitat dominated by native forests in Haleakalā NP and the Windward Regions. We used habitat layers for native forest, excluding all other habitats (i.e., native

shrubland and bare rock) to create the upper edge of their ranges (Jacobi 1989). Camp et al. (2009) defined ranges using the same methods, but compiled a history of detections from surveys conducted from 1980 through 2001. Scott et al. (1986) determined the ranges of ʻĀkohekohe and Kiwikiu to be 5800 ha and 5000 ha, respectively. Using more recent survey records, Camp et al. (2009) revised the ʻĀkohekohe range to 5990 ha and the Kiwikiu range to 5063 ha. We calculated the percent change in species ranges between the previous (1980–2001) and current (2006–2017) estimates.

Maui ʻAlauahio occupy native shrubland, some non-native forests, and native-dominated habitat in the Haleakalā NP, Windward, and Kula Regions. For this species, we primarily used contour intervals as the upper edge of the inference area. This generally followed the same upper edge as the overall inference area. Based on habitat characteristics and incidental observations, we determined that portions of their range extended outside the overall 2017 inference area so we provide an inference area for frequently surveyed areas and an updated range for the species by including incidental observations and habitat descriptions. Based on surveys conducted in 1980, Scott et al. (1986) estimated the range for the species to be 13,500 ha. Using more recent data, Camp et al. (2009) reported a range contraction to 9800 ha, a 27% decrease.

Population estimates. Species-specific density estimates (birds/ha) were calculated for ʻĀkohekohe, Kiwikiu, and Maui ʻAlauahio. Species-specific detection probabilities were modeled, and densities were estimated using program DISTANCE, version 6.0, release 2 (Thomas et al. 2010). Because we had relatively few detections of ʻĀkohekohe and Kiwikiu, fewer than the recommended 100 survey-specific detections (Buckland et al. 2001), their detections were pooled with data from all previous surveys to model detectability (2172 and 261 additional detections, respectively). Pooling allowed us to fit detection functions to a larger number of detections than was possible for a single survey, and we used the global detection probability to estimate survey-specific densities using post-stratification procedures. This approach is useful for estimating densities of rare species where detections are sparse and are described by Buckland et al. (2001, 2015). Similarly, preliminary analysis of Maui ʻAlauahio data yielded unrealistic uncertainty (percent coefficient of variation > 80) so our 2017 data were pooled with data from all previous surveys (3559 additional detections). The candidate detection function models were limited to half normal and hazard rate detection functions with an expansion series of order two (Buckland et al. 2001). Following recommendations by Buckland et al. (2001), the half normal was paired with cosine and Hermite polynomial adjustments, and the hazard rate was paired with cosine and simple polynomial adjustments. Model precision was improved by incorporating sampling covariates in the multiple covariate distance sampling (MCDS) engine of DISTANCE (Thomas et al. 2010). Covariates included cloud cover, rain, wind and gust speed, observer, time of detection, and detection type. All covariates were treated as a factor, except time of detection was treated as a continuous covariate. Assessing time of detection as a continuous covariate helped us determine if detection rates varied during the morning. Detection type 4, a bird first detected aurally, but later confirmed visually, was pooled with both detection type 1 and 2, and fitted independently. Pooling of covariates was used to increase sample size and increase the likelihood of model convergence. Covariates for survey and year were also assessed for all three species because of pooling. Each detectability model in the candidate set was fit, and the model selected was that with the lowest 2nd-order Akaike's Information Criterion corrected for small sample sizes (AICc; Buckland et al. 2001, Burnham and Anderson 2002). Covariates were incorporated with the most parsimonious model to improve model precision, again choosing the model with the lowest AICc value. Due to concerns about small sample sizes, combinations of covariates were not considered. Data were truncated at a distance where the detection probability was ~ 10%. This procedure facilitates modeling by deleting outliers and reducing the number of parameters needed to modify the detection function. Species-specific densities, variances, and confidence intervals were derived by bootstrap methods in DISTANCE from 999 iterations (Thomas et al. 2010) from a global

detection function using post-stratification procedures stratifying by region and species range. Absolute abundance was calculated as mean density weighted by area.

Trend assessment. Changes in estimated densities between our 2017 survey and the most recent survey (2011 for Haleakalā NP or 2012 for the Windward Region) were compared using end-point *z*-tests by region. A standard two-sample *z*-test was modified to incorporate testing for differences within and outside an equivalence region (Camp et al. 2008). Equivalence tests allowed us to distinguish between cases where there was no trend versus an inability to statistically detect a trend (Dixon and Pechmann 2005, Camp et al. 2008). Equivalence bounds were set to identify a 25% change in the population over 25 years, or a −0.0119 and 0.0093 annual rate of change. Changes in population density, or trends, were defined as increasing, decreasing, negligible (i.e., stable population), or inconclusive. A biologically meaningful trend occurred when the difference in density estimates was greater than the equivalence region. A negligible trend occurred when the difference lay within the equivalence region. An inconclusive result occurred when densities were imprecise and precluded obtaining conclusive results (Dixon and Pechmann 2005).

We investigated long-term trends using linear regression models to evaluate overall changes in population densities. Preliminary analyses revealed that the trend assessment model could not accurately recover parameters (Appendix S1). We, therefore, compared difference in densities with end-point *z*-tests and used loess smoothers to illustrate the qualitative population patterns of the species-specific time series.

RESULTS

We detected 108 ʻĀkohekohe and only eight Kiwikiu (Table 1). All detections were above 1600 m elevation in wet-mesic and montane ʻōhiʻa-dominated rainforest in Haleakalā NP and on Windward transects in Hanawī NAR and TNC's Waikamoi Preserve (Figs. S1 and S2). There were few detections on Windward transects in eastern Waikamoi Preserve, Koʻolau FR, and Kīpahulu Valley, areas that included portions of the former and current estimated ranges of each species (Figs. S1 and S2). Neither species was detected in the Kula or Leeward regions. For ʻĀkohekohe, we estimated a density of 0.75 ± 0.13 birds/ha (SE) and an abundance of 1768 ± 315 (95% CI 1193–2411) individuals in their 2363 ha range. For Kiwikiu, we estimated a density of 0.05 ± 0.02 birds/ha (SE) and a total abundance of 157 ± 67 (95% CI 44–312) individuals in their 2992 ha range.

We had 454 detections of Maui ʻAlauahio (Table 1) that were broadly distributed in native and non-native forest at elevations ranging from 1200 to 2300 m in Haleakalā NP, Windward, and Kula regions, but no detections in the Leeward region (Fig. S3). Population density of Maui ʻAlauahio was 10.79 ± 1.04 birds/ha (SE) and we estimated an abundance of 99,060 ± 9510 (95% CI 88,502–106,954) individuals in the 9179 ha inference area. However, based on habitat characteristics and incidental detections, our abundance estimates did not include 1542 ha of their range (see below).

We calculated a 61% contraction in the ʻĀkohekohe range compared to estimates reported by Camp et al. (2009) from surveys conducted from 1980 through 2001 (Table 2). The range of Kiwikiu contracted by an estimated 41% (Table 2). Range reductions for ʻĀkohekohe and Kiwikiu were due to a lack of detections at lower elevations in surveys conducted from 2006 through 2017. We estimated the species range of Maui ʻAlauahio to be 10,721 ha, representing a 9% increase from the 9800 ha range reported by Camp et al. (2009). The largest discrepancy between our range-size estimates and those of Camp et al. (2009) was our inclusion of additional areas in the Kula region and TNC's Waikamoi Preserve where the species is known to occur. We do not consider this a true increase in the species' range, but, rather, increased precision in certain portions of the Maui ʻAlauahio range based on additional information (Mounce et al. 2007).

We assessed short-term trends of ʻĀkohekohe, Kiwikiu, and Maui ʻAlauahio by comparing the 2017 densities to estimated densities based on range-wide surveys conducted in 2011 and 2012. Results were inconclusive for each species because of relatively small changes in densities and large

Table 1. Total detections and population density and abundance estimates of three Maui island-endemic Hawaiian honeycreepers. Birds per station was calculated as the number of detections divided by the 570 total stations surveyed in 2017.

Species	Total detections	Stations occupied	Birds per station	Birds/ha ± SE (95% CI)	Abundance (95% CI)
ʻĀkohekohe	108	35	0.12	0.75 ± 0.13 (0.50–1.02)	1768 ± 315 (1193–2411)
Kiwikiu	8	6	0.01	0.05 ± 0.02 (0.01–0.10)	157 ± 67 (44–312)
Maui ʻĀlauahio	454	175	0.66	10.79 ± 1.04 (9.64–11.65)	99,060 ± 9510 (88,502–106,954)

Table 2. Areas of current and previously reported ranges of three Maui island-endemic Hawaiian honeycreepers. Current ranges were determined from surveys and other observations conducted since 2006. Previous estimates for each species were reported by Camp et al. (2009) based on surveys conducted from 1980 through 2001.

Species	1980–2001 Range (ha)	2006–2017 Range (ha)	Percent change
ʻĀkohekohe	5990	2363	−61
Kiwikiu	5063	2992	−41
Maui ʻĀlauahio	9800	10,721	+9

uncertainties in the differences (all coefficient of variations > 0.75; Table 3). Long-term population trajectories of ʻĀkohekohe, Kiwikiu, and Maui ʻĀlauahio have fluctuated since 1980 (Fig. 2, Table S1). Throughout their ranges, densities appeared to increase in the 1990s and peak for ʻĀkohekohe and Kiwikiu in 2001 (Fig. 2, Table S1). Range-wide densities of ʻĀkohekohe subsequently decreased by 78% in both density and abundance to our 2017 estimates (Fig. 2, Table S1). Further, the lack of overlap in the 95% CI of density estimates of the most recent two surveys versus prior surveys also indicates that this species has experienced substantial declines in population over the last two decades (Fig. 2). Similarly, range-wide densities and abundance of Kiwikiu decreased 72% and 71%, respectively, since 2001 (Fig. 2, Table S1). The highest estimated density and abundance of Maui ʻĀlauahio were in 1992, with subsequent estimates declining by 41% in density and 48% in abundance to our 2017 estimates (Fig. 2, Table S1).

DISCUSSION

We observed simultaneous declines in the density and abundance of the three Maui island-endemic honeycreepers, with a more than 70% decline in abundance of ʻĀkohekohe and Kiwikiu since 2001 and a 48% decline in Maui ʻĀlauahio abundance since 1992. The abundance of Kiwikiu in 2017 was alarmingly low, with an estimated 44 to 312 individuals remaining in the wild. ʻĀkohekohe also warrants concern, with an estimated abundance of 1193 to 2411

Table 3. Short-term trends and differences in population densities of ʻĀkohekohe, Kiwikiu, and Maui ʻAlauahio between 2011/2012 and 2017. The null hypothesis that density has not changed over time was tested with a *z*-test. Equivalence tests were used to determine if the difference was within the threshold bounds (−0.0199, 0.0093) of a 25% change in density over 25 years. LCL and UCL = Lower and Upper 90% Confidence Limits, LEL and UEL = Lower and Upper Equivalence Levels (*t*-values), and LELp and UELp = Lower and Upper Equivalence Level *P* values. Trends were interpreted as increasing, decreasing, stable, or inconclusive.

Species	Difference	SE	LCL	UCL	*z*-test *P*	LEL	UEL	LELp	UELp	Result
ʻĀkohekohe	−0.19	0.20	−0.51	0.14	0.34	0.59	−1.24	0.72	0.11	Inconclusive
Kiwikiu	−0.04	0.03	−0.10	0.01	0.17	−0.82	−3.11	0.20	< 0.00	Inconclusive
Maui ʻAlauahio	0.32	1.50	−2.15	2.80	< 0.00	−0.26	0.18	0.40	0.57	Inconclusive

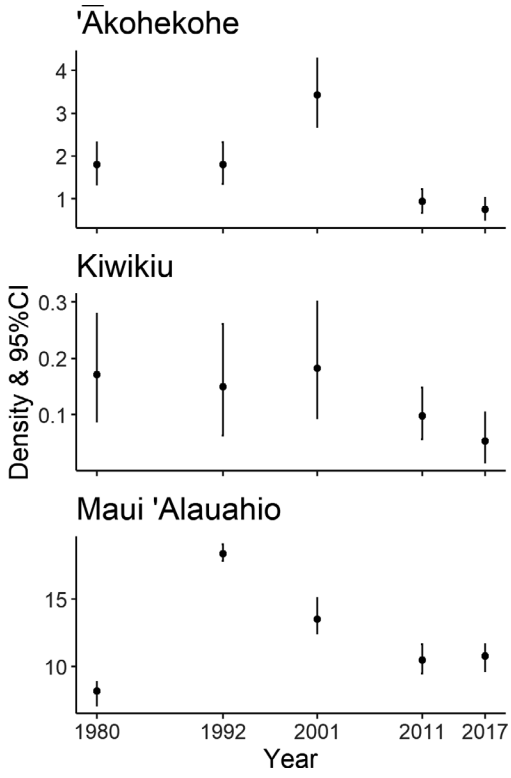


Fig. 2. Range-wide density estimates (birds/ha) for ʻĀkohekohe, Kiwikiu, and Maui ʻAlauahio since the first survey on East Maui in 1980. Error bars indicate 95% CI. Y-axis values vary between panels and survey years.

individuals. Declines in populations of Kiwikiu and ʻĀkohekohe have been exacerbated by upward range restrictions of more than 40% since 1980, evidenced by the lack of detections in the lower-elevation range of the study area just 15 to 20 years before 2017.

The abundance of Maui ʻAlauahio was higher than that of the other two Maui endemics, with an estimate between 88,502 and 106,954 individuals. Declines in density were more pronounced in Maui ʻAlauahio than range contraction because this generalist species still occurs in some drier leeward areas in mixed native and non-native habitat. Scott et al. (1986) reported dramatic differences in Maui ʻAlauahio densities above and below 1200 m elevation, whereas our results indicate that nearly the entire range of the species is above 1500 m elevation, suggesting greater declines in low-elevation areas. Declines in abundance of each species suggest that landscape-level dynamics are affecting native avian communities on East Maui.

Since 1980, most detections of ʻĀkohekohe and Kiwikiu have been above 1500 m elevation, where disease prevalence has traditionally thought to be reduced because avian malaria has a strict thermal threshold for reproduction (van Riper et al. 1986, Atkinson and LaPointe 2009, LaPointe et al. 2010, Atkinson et al. 2014). Consequently, native species of Hawaiian birds struggle to persist in a "climatic space" as higher mean global temperatures, declining precipitation, and changes in streamflow push both the disease and its vector, the southern house mosquito (*Culex quinquefasciatus*), higher into native forest (Atkinson et al. 2014). Climate-based models project a loss of > 75% of the current estimated range of ʻĀkohekohe and Kiwikiu by 2100 (Fortini et al. 2015). However, population trajectories suggest Kiwikiu is unlikely to persist beyond 25 years and

will likely become functionally extinct in as few as 10 years (Mounce et al. 2018). The species is dependent on high adult survivorship and limited by low fecundity so may have difficulty rebounding from the loss of breeding adults (Mounce et al. 2018). The scarcity and decline of Maui endemics bear similarities to the current catastrophic decline of honeycreeper populations elsewhere in Hawai'i. On Kaua'i Island, populations of four forest bird species have declined by ~ 90% (Paxton et al. 2016). The climatic space is even smaller there and multiple extinctions of native forest birds are predicted in the coming decades because of the increase in elevational range of avian malaria and its mosquito vector (Paxton et al. 2016).

Populations on East Maui are declining faster than anticipated, given that avian malaria was first observed in lower-elevation habitats of Kiwikiu 10 to 15 years ago (Aruch et al. 2007, Atkinson and LaPointe 2009). Several factors could be interacting to obscure a clear relationship between the uppermost elevation ranges of malaria and differences among species, including (1) episodic transmission of malaria in mid- and high-elevation forests due to seasonal or annual temperature differences (Samuel et al. 2015), some of which may occur infrequently, but result in large population impacts, (2) microhabitat use and behavioral differences by birds in lower- or upper-elevation forests that limit or increase their exposure to malaria due to differences in microclimate, (3) seasonal or exploratory movements of adult birds and dispersal of juvenile birds that facilitate disease exposure in birds that spend most of their time in largely malaria-free habitat (Wang et al. 2020), or (4) other unknown species-specific differences in response to avian malaria. The sporadic nature of these factors, the logistical difficulty of working in the habitats of endemic birds on East Maui, and the virulence of avian malaria in Hawaiian birds suggest that determining the factor or factors responsible for the declining populations of each species could be challenging even with extensive research efforts.

Predation and habitat degradation could also be contributing to declines in native-bird populations on East Maui. Quantifying the extent or relative impacts of these factors is currently not possible. Native forest habitat has remained relatively intact in the current range of endemic species and effects of predation are unlikely to have been altered dramatically in the last 30 years because no new predators have been introduced to East Maui over the last 50+ years. This is not to suggest that addressing these two factors are not critical to bird conservation, but does imply that they are either not solely responsible for the observed declines or that disentangling the relative impacts of these factors, especially given the threat of malaria, will be difficult.

In an ecological context, little time remains to conserve Kiwikiu and ʻĀkohekohe populations. Managers face a myriad of choices on where to focus limited resources and would like a detailed understanding of the causes of declines before proceeding with time-intensive and costly management actions. However, for the above-stated reasons, research actions may not be sufficient. Paxton et al. (2018) suggested that future work take place in an adaptive context through the implementation of management actions. This would provide a greater understanding of how to implement the actions and the potential responses of birds; a lack of response to any management action would still provide important insights and further improve our knowledge of actions needed to save these species.

Landscape control of both avian malaria and predators may be the management actions most likely to benefit the native Hawaiian bird community in East Maui. Preventing habitat degradation is also critical, but habitat restoration efforts have been in place for decades and we assume they will continue. Ideally, landscape control of malaria and predation would occur simultaneously, but either alone would benefit a variety of native-bird species and help managers better understand and target the causes of declines. The most likely route to controlling malaria is by reducing or eliminating the only vector of this disease in Hawai'i, the invasive mosquito *Culex quinquefasciatus*. Pursuing this goal via *Wolbachia* cytoplasmic incompatibility may have the quickest regulatory pathway to deployment while other techniques are pursued (Liao et al. 2017). Predator control can be locally successful in Hawai'i (VanderWerf 2001, Banko et al. 2019), but landscape controls have rarely been implemented in native-bird habitats on the main Hawaiian Islands due to expense, logistical constraints, and concerns about public perceptions. The method most likely to achieve landscape control of rodents is

the repeated widespread aerial delivery of diphacinone throughout the ranges of endemic Maui species (Spurr et al. 2015). Landscape control of malaria and predation will be expensive and outcomes are uncertain, but a growing body of evidence suggests they are the only two actions with the potential to halt or reverse the long-term decline of communities of native Hawaiian birds (Paxton et al. 2018). Adding to the urgency of this situation is the finding that efforts to establish new populations or propagate Kiwikiu in captivity have had limited and inconsistent success (Mounce et al. 2018). Other investigators have concluded that now is the time to act, even with imperfect knowledge (Samuel et al. 2011, Fortini et al. 2015).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Fig. S1. Detections of 'Ākohekohe (*Palmeria dolei*) during distance sampling efforts on East Maui in 2017. The former range (1980–2001) is outlined in light green with striped hatching, the current range (2006–2017) is outlined in dark green with light green shading, and the entire 2017 survey area is outlined in yellow.

Fig. S2. Detections of Kiwikiu (Maui Parrotbill, *Pseudonestor xanthophrys*) during distance sampling efforts on East Maui in 2017. The former range (1980–2001) is outlined in light green with striped hatching, the current range (2006–2017) is outlined in dark green with light green shading, and the entire survey 2017 area is outlined in yellow.

Fig. S3. Detections of Maui 'Alauahio (*Paroreomyza montana newtoni*) during distance sampling efforts on East Maui in 2017. The former range (1980–2001) is outlined in light green with striped hatching, the current range (2006–2017) is outlined in dark green with light green shading, and the entire 2017 survey area is outlined in yellow.

Table S1. Range-wide population density and abundance estimates of 'Akohekohe (*Palmeria dolei*), Kiwikiu (Maui Parrotbill; *Pseudonestor xanthophrys*), and Maui 'Alauahio (*Paroreomyza montana newtoni*) on East Maui (1980–2017).

Appendix S1. Population trend assessment.