

Collapsing avian community on a Hawaiian island

Eben H. Paxton,^{1*} Richard J. Camp,² P. Marcos Gorresen,² Lisa H. Crampton,^{3,4} David L. Leonard Jr.,^{5†} Eric A. VanderWerf⁶

2016 © The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. Distributed under a Creative Commons Attribution NonCommercial License 4.0 (CC BY-NC).
10.1126/sciadv.1600029

The viability of many species has been jeopardized by numerous negative factors over the centuries, but climate change is predicted to accelerate and increase the pressure of many of these threats, leading to extinctions. The Hawaiian honeycreepers, famous for their spectacular adaptive radiation, are predicted to experience negative responses to climate change, given their susceptibility to introduced disease, the strong linkage of disease distribution to climatic conditions, and their current distribution. We document the rapid collapse of the native avifauna on the island of Kaua'i that corresponds to changes in climate and disease prevalence. Although multiple factors may be pressuring the community, we suggest that a tipping point has been crossed in which temperatures in forest habitats at high elevations have reached a threshold that facilitates the development of avian malaria and its vector throughout these species' ranges. Continued incursion of invasive weeds and non-native avian competitors may be facilitated by climate change and could also contribute to declines. If current rates of decline continue, we predict multiple extinctions in the coming decades. Kaua'i represents an early warning for the forest bird communities on the Maui and Hawai'i islands, as well as other species around the world that are trapped within a climatic space that is rapidly disappearing.

INTRODUCTION

Many Hawaiian forest birds were distributed from sea level to the upper-most alpine forests and shrublands before the arrival of humans and the non-native species they introduced. However, declining populations were evident as early as the late 1800s (1), and today, most of Hawai'i's forest birds are largely restricted to high-elevation forests because of the loss of low-elevation habitat, the invasion of non-native species into low- and mid-elevation habitats, and the distribution of introduced diseases (2, 3). In particular, non-native avian malaria (*Plasmodium relictum*) and avian poxvirus (*Poxvirus aviium*) have greatly influenced the distribution of native Hawaiian birds (3–5), restricting most species to high-elevation areas where avian malaria and its mosquito vector (*Culex quinquefasciatus*) are seasonally present or completely absent due to cool temperatures. Sporogonic development of avian malarial parasites and larval development of their mosquito vectors are increasingly slow below temperatures of 17°C and are largely inhibited at elevations where mean annual temperatures are below 15°C (corresponding to approximately 1500 m), making those high-elevation areas largely free of active disease transmission in Hawai'i (6). Of the main Hawaiian islands, only the Hawai'i and Maui islands have substantial intact forest above 1500-m elevations, and these forests still support diverse native avian communities (2). On Kaua'i, forest habitats occur at elevations from ~500 m to nearly the summit of the island (1500 m), elevations that should support the development of mosquitoes and disease throughout much of the year; however, Kaua'i forests have historically been ~3°C cooler than comparable elevations on other islands (6), which may have allowed the persistence of a diverse native avifauna at 1000 to 1500 m.

Given the strong relationship between elevation, temperature, and the distribution of disease, researchers have predicted negative consequences

of warming global temperatures to Hawaiian forest birds, specifically noting that these effects would first be seen on Kaua'i (7). The Hawaiian archipelago is already experiencing a warming trend (8), especially at higher elevations, which were historically disease-free (9). A recent study of avian malaria prevalence in upper-elevation forests on the Alaka'i Plateau of Kaua'i documented a sharp increase in disease prevalence over a 15-year period, with surveys in 2007–2013 indicating a more than doubling of disease prevalence from the 1994–1997 levels (10). Prevalence of malarial infections was highest in the lower elevations of the plateau and decreased upslope. Surveys for mosquitoes in 2011 found larval mosquitoes in multiple drainages, whereas extensive surveys in the 1990s found virtually none (10). Changes in disease and vector prevalence corresponded to shifting climatic conditions (>1°C increase in temperature on the plateau and reduced stream scouring, resulting from longer dry periods) (10), suggesting a climate-based mechanism for the increasing prevalence of disease on the plateau. Future projections of climate-based habitat suggest that nearly all of the current climatic space of native forest birds on Kaua'i will be lost by 2100 (11).

We present evidence of an ongoing collapse of the native Kaua'i avifauna. Although the scenario of a rapid increase in the distribution of disease driven by climate change is a prime suspect for the precipitous declines, other factors, such as the continued incursion of non-native plants and animals, are likely contributing factors. We hypothesize that each threat will produce a different pattern of response in the bird community, and examination of these patterns can provide insight into the drivers of the declines.

RESULTS

We used long-term survey data that cover much of Kaua'i's native forest birds' current range to understand how the abundance and distribution of avifauna on Kaua'i have changed over the last several decades. We found that six of seven native species are rapidly declining in abundance across their range (Table 1 and Fig. 1), based

¹U.S. Geological Survey Pacific Island Ecosystems Research Center, Hawai'i Volcanoes National Park, HI 96718, USA. ²Hawai'i Cooperative Studies Unit, University of Hawai'i, Hilo, HI 96720, USA. ³Hawai'i Division of Forestry and Wildlife, Hanapepe, HI 96716, USA. ⁴Pacific Cooperative Studies Unit, University of Hawai'i, Honolulu, HI 96822, USA. ⁵Hawai'i Division of Forestry and Wildlife, Honolulu, HI 96813, USA. ⁶Pacific Rim Conservation, Honolulu, HI 96839, USA.

*Corresponding author. Email: epaxton@usgs.gov

†Present address: U.S. Fish and Wildlife Service, Portland, OR 97232, USA.

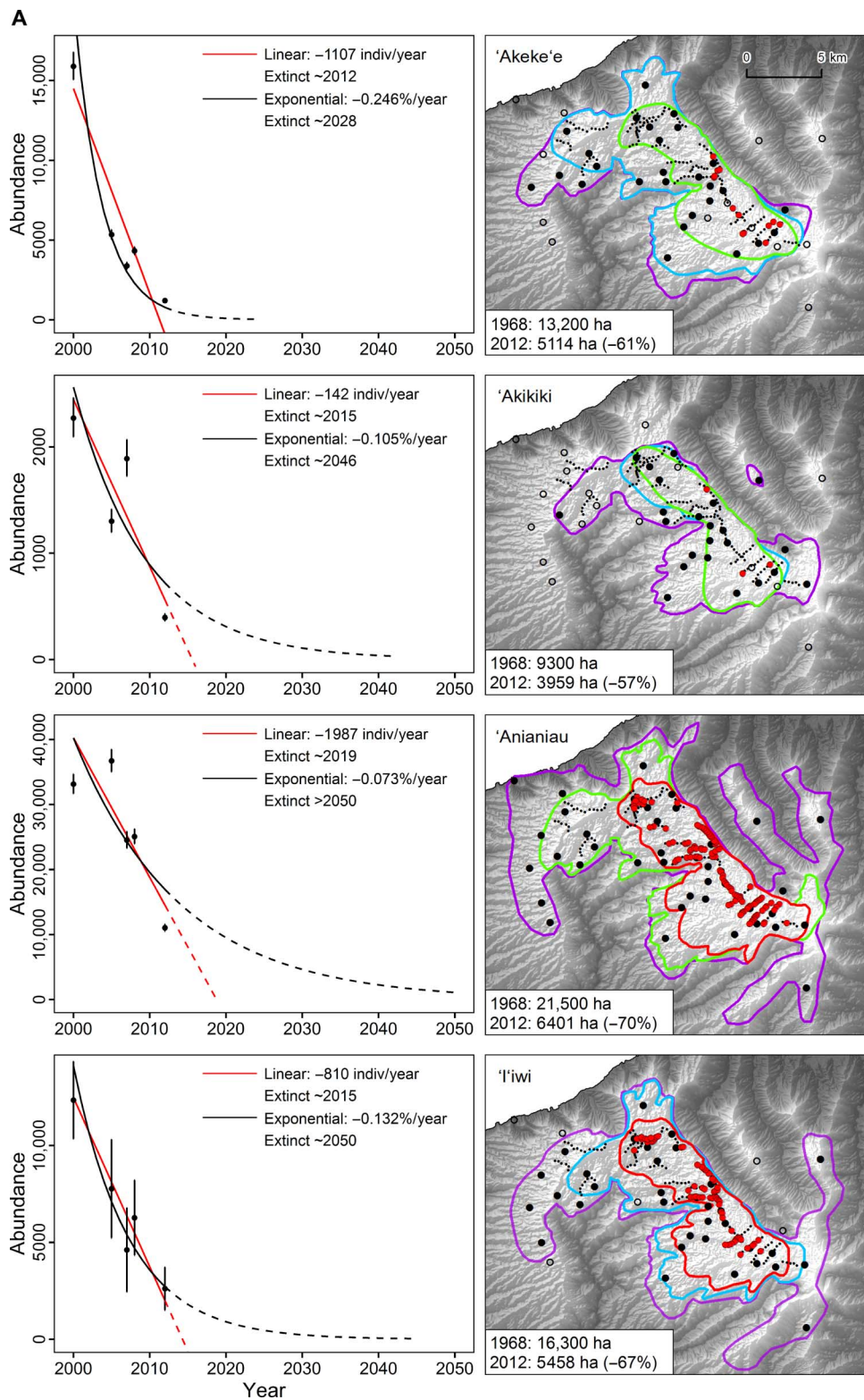
Table 1. Estimates of 2012 population density and abundance and trend for seven native species of forest birds and the five most common non-native species on Kaua'i. Trends (the average change in density over a 25-year period) are presented for both the interior (core area of most species' range, 1981–2012 and 2000–2012) and exterior areas of the Alaka'i Plateau (2000–2012). Trends were not calculated for species with few or no detections for one or more survey periods in a given area. Species abundances marked by an asterisk denote species that occur outside the survey area (<900 m), and abundance estimates do not include estimates from the unsurveyed area.

| Species | 2012 density (birds/ha) | | 2012 abundance | | Trend (25 years) | | |
|-----------------------|-------------------------|---------------|----------------|------------------|----------------------|----------------------|----------------------|
| | Mean | 95% CI | Mean | 95% CI | Interior (1981–2012) | Interior (2000–2012) | Exterior (2000–2012) |
| Native | | | | | | | |
| 'Akeke'e | 0.212 | (0.201–0.223) | 945 | (460–1,547) | –48% | –98% | — |
| 'Akikiki | 0.088 | (0.082–0.096) | 468 | (231–916) | –71% | –7% | — |
| 'Anianiau | 1.657 | (1.584–1.733) | 10,787 | (8,396–13,434) | –17% | –57% | –91% |
| 'I'iwi | 0.477 | (0.328–0.645) | 2,603 | (1,789–3,520) | –63% | –86% | –97% |
| 'Apapane | 8.489 | (8.313–8.670) | 98,506* | (62,863–117,435) | –27% | –67% | –89% |
| Kaua'i 'amakihi | 0.611 | (0.581–0.642) | 6,519* | (4,844–8,495) | –16% | –91% | –98% |
| Kaua'i 'Elepaio | 7.141 | (6.716–7.592) | 82,437* | (60,973–107,155) | 41% | 88% | –64% |
| Non-native | | | | | | | |
| Hwamei | 0.452 | (0.407–0.501) | 8,043* | (5,715–10,920) | 46% | –13% | 55% |
| Japanese bush-warbler | 0.177 | (0.163–0.192) | 5,682* | (3,987–8,011) | 311% | 13% | 508% |
| Japanese white-eye | 5.863 | (5.719–6.011) | 106,327* | (92,400–121,671) | –27% | –60% | –83% |
| Northern cardinal | 0.218 | (0.181–0.262) | 6,485* | (3,550–11,456) | –66% | — | –63% |
| White-rumped shama | 0.264 | (0.243–0.286) | 9,060* | (6,422–12,272) | — | — | 273% |

on standardized 25-year trends of the core range (interior, 1981–2012) and peripheral range (exterior, 2000–2012). The exception is the Kaua'i 'elepaio (*Chasiempis sclateri*), which had mixed trends, decreasing by 64% in the periphery of its range (exterior area) but increasing by 88% in the core region of its range (interior area). In contrast, the remaining six native species (all Hawaiian honeycreepers) showed declines in both the periphery and core regions of their ranges by an average of –94 and –68%, respectively (Table 1 and Fig. 1). Moreover, declines in the core region appear to be accelerating, as evident from the 1.4 to 5.7 times greater declines in recent years (2000–2012) compared to the longer time period (1981–2012) (Table 1). The two endangered species, 'akikiki (*Oreomystis bairdi*) and 'akeke'e (*Loxops caeruleirostris*), have declined precipitously, with the 2012 population sizes estimated to be only 468 [95% confidence interval (CI), 231 to 916] and 945 (95% CI, 460 to 1547) individuals, respectively. Unlike in previous surveys (2000, 2005, 2007, and 2008), neither species was detected by our systematic surveys in the periphery of their ranges in 2012, although incidental sightings indicate continued but limited occurrence. Although less severe, long-term negative trends in 'i'iwi (*Drepanis coccinea*) and 'anianiau (*Hemignathus parvus*) have resulted in 2012 population size estimates of 2603 (95% CI, 1789 to 3520) and 10,787 (95% CI, 8396 to 13,434) individuals, respectively. Likewise, 'apapane (*Himatione sanguinea*) and Kaua'i 'amakihi (*Chlorodrepanis stejnegeri*) have also experienced severe declines but began from large, robust populations at the beginning of the survey period. The eighth native forest bird, the endangered puaiohi (*Myadestes*

palmeri), is a secretive thrush living in narrow river gorges, which were poorly sampled by the forest bird surveys; therefore, the surveys are unreliable measures of abundance and population trends for this species.

All of Kaua'i's native forest birds (including 'elepaio) have experienced sizeable range contractions over the last four decades (starting with presence-absence surveys from 1968), with reduction in range size varying from between 57 and 70% for the most range-restricted species to between 27 and 66% for the species with broader ranges. Four species ('akikiki, 'akeke'e, 'anianiau, and 'i'iwi) have experienced even more rapid range contractions since 2000 and are now limited to a small, remote area of the Alaka'i Plateau, with ranges encompassing only 40 to 64 km² of forest habitat. For the more common species, the contractions have been most severe in the periphery of their range, but density is rapidly decreasing in their core range as well. In contrast to native species, non-native forest birds demonstrated mixed abundance trends (Table 1), with the hwamei (*Garrulax canorus*), Japanese bush-warbler (*Cettia diphone*), and white-rumped shama (*Copsychus malabaricus*) increasing and the Japanese white-eye (*Zosterops japonicus*) and northern cardinal (*Cardinalis cardinalis*) declining. Similarly, patterns of occurrence by elevation were mixed for the non-native species, with some species showing no change in distribution, whereas the distribution of other species contracted. The hwamei and Japanese white-eye occurred throughout the elevation range surveyed (that is, from 1011 to 1455 m) and showed no changes in distribution over the 2000–2012 period.



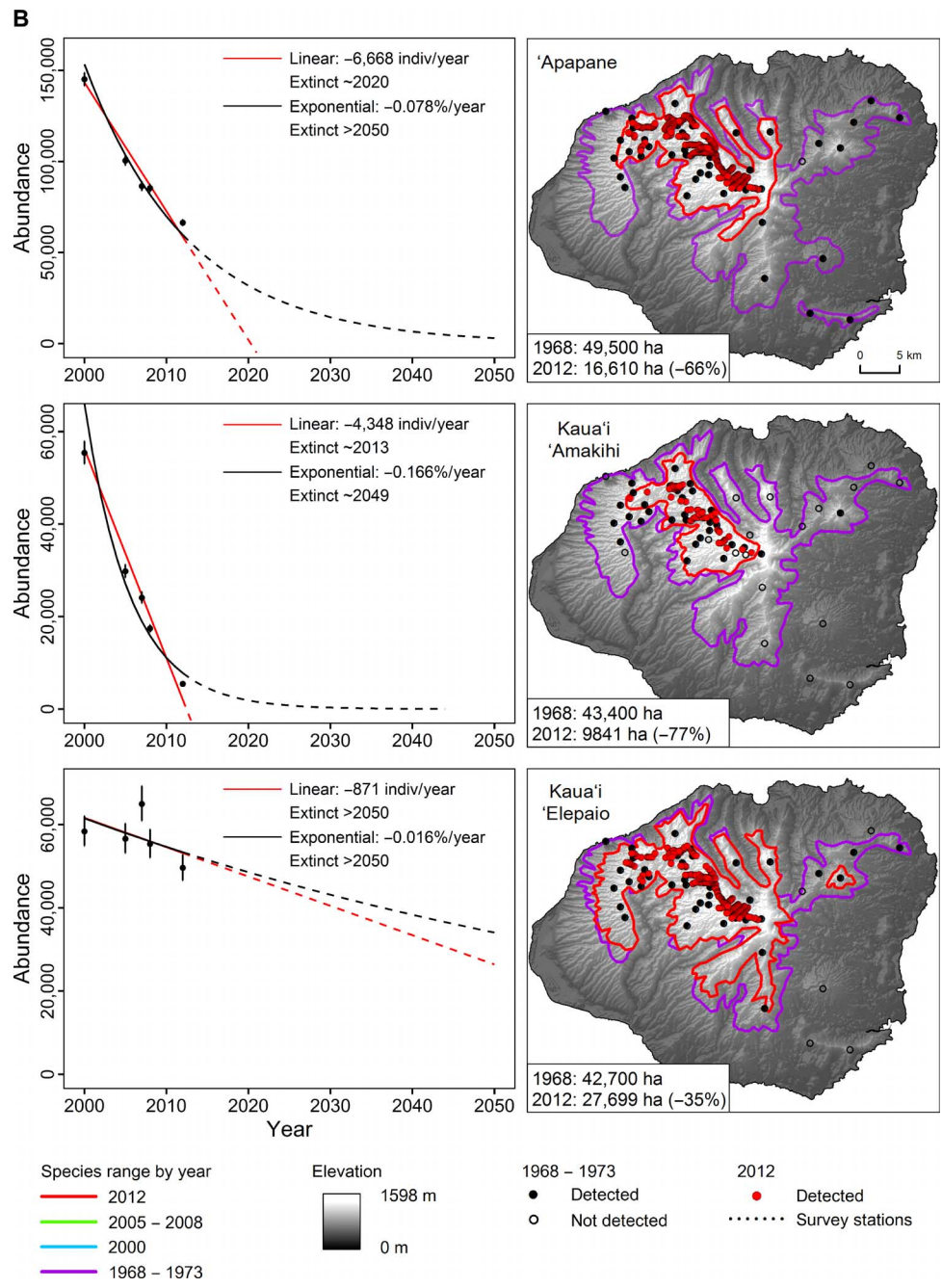


Fig. 1. Population estimates and distributions for native Kaua'i forest birds. Population estimates (left panels) are from surveys conducted in 2000, 2005, 2007, 2008, and 2012 across both the interior and exterior portions of the Alaka'i Plateau (with error bars representing the 95% CI of each estimate). Linear and exponential population change models fitted to the 2000–2012 data are projected from 2013 to 2050 or estimated year of extinction (when abundance is less than 30 individuals, which is a quasi-extinction level). The projections are just one possible outcome of many, assuming that the rate of change is accurate and does not change over the coming decades. Areas of distributional range (right panels) from 1968 through 2012 were determined from presence or absence at count stations and extrapolated across similar elevations and habitats. For 'apapane, Kaua'i 'amakihi, and Kaua'i 'elepaio, estimated distributions from 2000 to 2012 were very similar, and only the 2012 range is shown.

If native species linearly decline at a rate similar to or greater than that of the past decade, then multiple extinctions are likely in the next decade (Fig. 1). Alternatively, if populations decline in a negative logistic fashion (proportional to population size), then we would expect a somewhat longer persistence by an increasingly smaller number of individuals (Fig. 1). Although a proportional, density-dependent response is more typical in declining species (12), disease mortality may be density-independent (that is, linear trend); many species of birds can act as reservoirs for disease and keep prevalence high, even if a given species is diminishing in density (10).

DISCUSSION

We hypothesize that the observed patterns of decline will differ depending on which potential drivers have the strongest effect on the declines. Likely drivers of declines include increased distribution and prevalence of disease, decreased habitat quality from the continued incursion of invasive weeds, competition from non-native forest birds, ongoing threats from predators (for example, rats), and continued habitat changes from hurricane damage in the 1980s and 1990s (13). Whereas the forest on the Alaka'i Plateau of Kaua'i has historically been dominated by native plants and animals (14), non-native species have been invading from the surrounding areas, into the core forest. If non-native plants are sufficiently degrading habitat quality to drive the observed declines, then we would expect moderate to no declines in the interior wherein non-native plant species are still rare or are being actively controlled. Non-native birds are increasing in abundance even in the core range of native birds, but non-native bird densities are still fairly low in the core areas. If habitat degradation or competition with non-native species were contributing to declines of native birds, it is unlikely that the pattern of decline would be similar for all native birds, given the differences in feeding guilds and habitat requirements of the native species. Nonetheless, the spread of non-native birds is likely facilitated by environmental and habitat changes that already negatively affect native birds, and the increase in non-native species is likely contributing to population stress. Rats can be important nest predators of Hawaiian forest birds, but studies on the Alaka'i Plateau do not indicate high levels of impact (15, 16). Additionally, two hurricanes in the 1970s and 1980s resulted in extensive damage of the forest across the Alaka'i Plateau (14); however, habitat damage should affect native species differently, and it is not apparent why there would be an accelerated response from bird species some 20+ years later.

Although multiple factors likely contribute to negative population dynamics, the pattern of rapid population contraction to the highest elevations, with declines in abundance observed even within the species' core range, is consistent with a scenario of disease invading from the lower elevations and recently spreading across the plateau to encompass the entire range of all species. Disease would affect most native species similarly, given their general susceptibility to introduced avian malaria (3, 5), and all of Kaua'i's honeycreepers are rapidly declining. One exception, the 'elepaio, comes from a lineage that colonized the Hawaiian Islands more recently than did the Hawaiian honeycreepers (17), and all three 'elepaio species have demonstrated greater tolerance to introduced diseases than have most of the Hawaiian honeycreepers (18). Likewise, the puaiohi, a thrush, may be more tolerant of avian malaria (19), and although population trends are uncertain, there is no evidence of rapid declines based on the monitoring of several breeding populations for

this species (20). The wide overlap of foraging and habitat needs of the native and non-native species and the low susceptibility of non-native species to introduced disease (5) further point to disease as being the likely causal factor for the strong and accelerating declines in native species, which are not evident in non-native species. Thus, the sudden and rapid declines in all malaria-susceptible native bird species, which are not as severe in species that are more tolerant, are consistent with sudden changes in disease prevalence. However, even 'elepaio are declining across their outer range, suggesting that multiple factors are affecting these native bird populations.

The rapid decline in almost all native forest birds on Kaua'i is of great concern and indicates the imminent collapse of the native avian community. An earlier set of Kaua'i forest birds that have gone extinct [kama'o (*Myadestes myadestinus*), Kaua'i 'o'o (*Moho braccatus*), 'ou (*Psittirostra psittacea*), and Kaua'i 'akialoa (*Akialoa stejnegeri*)] were also last seen in the core high-elevation forests of the Alaka'i Plateau. Our findings differ from an earlier assessment of Kaua'i native birds species based on a subset of the same survey data from 1981 to 2000 (21), in which the authors were "cautiously optimistic," given that most species were stable with relatively large population sizes (>20,000). The 'akikiki and 'akeke'e were identified as having low but stable populations, although subsequent surveys (post-2000) suggested that they were declining, leading to their listing as endangered species in 2010. However, the relatively sudden change in abundance and distribution of most native bird species in Kaua'i post-2000, as was found in this study, suggests that a threshold has been crossed. The Alaka'i Plateau has been an anomaly, supporting a diverse avifauna at elevations that should have high disease prevalence. Therefore, only a small change in climatic conditions was likely necessary to tip this region into a new state with seasonal or year-round disease transmission throughout the plateau. We suggest that such habitats, which are close to climatic envelope boundaries for species and disease ranges, will be the most susceptible to threshold events such as this.

Multiple management responses to the crisis are possible, although their likelihood of success is unclear. The evolution of disease resistance is one of the great hopes for Hawaiian forest birds, and evidence of immunity to malaria has been shown in the Hawai'i 'amakihi (*Chlorodrepanis virens*) (22) and possibly the O'ahu 'amakihi (*C. flava*) (23). However, some species of Kaua'i forest birds have been experimentally shown to be highly susceptible to introduced disease (4), and the small remnant populations that exist today may not have sufficient genetic variability to develop immunity. Alternatively, control of mosquitoes could be used to reduce the distribution of vector-borne disease. Localized efforts to target mosquito larval habitat around core breeding areas may help to slow declines in bird populations, but these methods are labor-intensive, would have to be sustained indefinitely, and may not be a practical solution for controlling mosquitoes in many areas of the large and roadless Alaka'i Plateau. However, there is great potential in the development of genetically modified mosquitoes to provide large-scale vector control (24), and the use of these methods may be one of the most effective management actions for preserving Kaua'i forest birds. Rat control around active nests of the rarest species could increase productivity, thus slowing declines. Additionally, management actions to improve habitat, including fencing, feral ungulate control, and control of non-native plants, will help reduce habitat degradation. Intact forests are likely to be more resistant to mosquito invasion (by providing less larval habitat) and non-native bird incursion and may also support higher productivity and survival of birds, which can offset increased

incidence of malaria-related mortality, providing forest birds more time to evolve immunity (25). Beginning in 2015, there has been an ongoing effort to collect eggs from the wild to establish a captive population of 'akikiki and 'akeke'e to prevent imminent extinction. However, attention should also be focused on improving Kaua'i forest conditions to ensure habitat for future generations of Kaua'i forest birds. The implications of the loss of many of Kaua'i native birds go far beyond the birds themselves. The potential extinction of the 'akikiki and 'akeke'e, two insectivores, and the 'iwi, the dominant nectarivore, will likely continue to reduce the ecological integrity of the island's forest and result in continued degradation of ecosystem processes (26). Our findings clearly demonstrate the rapid effects that climate change can have on species with small geographic ranges and specific climatic constraints, and unless an effective conservation response can be developed, provide a glimpse of what the future holds for species on other Hawaiian islands and beyond.

MATERIALS AND METHODS

Study area

Bird surveys were conducted on the Alaka'i Plateau of Kaua'i, a highly eroded crater of an extinct volcano 5.1 million years old. The plateau gradually slopes downward from the eastern summits (1598 m) to the west, with bird survey locations occurring at elevations between 1011 and 1455 m. Prevailing northeasterly trade winds produce annual rainfall ranging from 11.5 m at the highest elevations in the east to 1.5 m in the southwest (27). The terrain is extremely rugged with deep canyons that eroded into the plateau on all sides, and even the relatively flat central plateau is etched with numerous streams and narrow ravines. Much of the area is covered in dense montane forest and shrubland, and bogs occupy some depressions. The dominant canopy tree is 'ohi'a (*Metrosideros polymorpha*), with koa (*Acacia koa*) co-dominant in drier areas in the west. The higher elevations contain some of the most intact native ecosystems left in Hawai'i, but invasive alien plants occur throughout the native forest and are dominant in some parts of the plateau, especially in lower elevation areas (28). All eight native forest bird species on Kaua'i are restricted to the Alaka'i Plateau. These include six Hawaiian honeycreeper (Drepanidinae) species ('akikiki, 'akeke'e, 'apapane, 'iwi, Kaua'i 'amakihī, and 'anianiau), a monarch flycatcher (Kaua'i 'elepaio), and a thrush (puaiohi). The 'akikiki, 'akeke'e, and puaiohi are endangered; however, the puaiohi, which occurs primarily in steep, narrow stream valleys where few survey stations are located, was not included in this analysis because standard forest bird survey is an unreliable sampling method for the species (20).

Bird sampling

Bird surveys were conducted in 1981, 1989, 1994, 2000, 2005, 2007, 2008, and 2012 using point-transect distance sampling methods (21, 29). Six transects, with count stations located at 150-m intervals, were established in 1981 across the southeastern Alaka'i (29), termed interior (fig. S1). In 2000, an additional 26 transects were established in the northern Alaka'i, southwestern Alaka'i, and western (Kōke'e) areas, termed exterior (fig. S1), to improve the spatial coverage of sampling across the forested portion of Kaua'i above 1000 m (21). The interior area has received eight surveys over 31 years (1981–2012; average span between surveys, 4.4 years), whereas the exterior area has been surveyed five times over 12 years (2000–2012; average span between surveys, 3.6 years). In general, the interior corresponds to

the core range of the native species, whereas the exterior represents the periphery of native species, although several species extend beyond the exterior into lower-elevation forest habitats, which are not surveyed (but where densities are believed to be quite low).

Coverage of transects varied somewhat among years (table S1), but densities were averaged across the set of surveyed transects for trends assessment. Several stations established in 2000 occur within the interior of the plateau (21) and were included in the survey results for this area. At each station, observers recorded the horizontal distance to each bird detected, the species, and detection type (heard, seen, or both) during an 8-min count. Cloud cover, rain, wind strength, gust strength, and time of day were also recorded at each station. Sampling started within 30 min of dawn and continued until 11:00 a.m., and ceased during adverse weather conditions.

Density, distribution, and population size

We used distance sampling methods to calculate species-specific density estimates, using the program DISTANCE (version 6.0, release 2) (30). We modeled detection functions and calculated detection probabilities for each species, then used the Akaike information criterion (AIC) to select the best model. Candidate models included the half-normal and hazard-rate detection functions with expansion series of order two. Data were right tail-truncated at a distance where the detection probability was <10%. Detection function precision was improved by incorporating the sampling covariates in the multiple covariate distance sampling engine of DISTANCE (30). Covariates included cloud cover, rain, wind strength, gust strength, observer, time of detection, and month and year of survey, and AIC was used to determine whether covariates improved model fit. Annual density estimates were calculated from the global detection function, poststratified by year. The 2.5th and 97.5th percentiles were used to estimate 95% CIs for the annual density estimates from bootstrap methods in DISTANCE with 999 iterations. All species included in this analysis had more than 300 detections pooled over the eight surveys.

To estimate the abundance of each species based on the most recent surveys (2012), we multiplied the estimated density by the size of the projected 2012 species range (table S2), although for Fig. 1, we estimated the abundance by multiplying the average density for the interior and the exterior by their respective areas (3097 and 5049 ha, respectively) (table S3). For species whose distributions were contained entirely within our study area ('akikiki, 'akeke'e, 'anianiau, and 'iwi), the estimates represent the global population or, in the case of 'iwi, the total island population. For the other native species (Kaua'i 'elepaio, Kaua'i 'amakihī, and 'apapane), distributions extend beyond the surveyed area; for these species, we extrapolated their range by projecting into adjacent areas with the same elevation and habitat classification as found in the study area, out to 900-m elevation and above [the lowest elevation interval (900 to 1100 m) surveyed in 2012]. The extent of the range below 900 m is believed to contain few native birds and contributes a negligible number of individuals for overall population estimates. Estimates of abundance for non-native species were also only estimated for areas above 900 m, but in most cases, these species occur widely at lower elevations, and the estimates presented here represent only a fraction of the total population size on Kaua'i.

Trend in density

Because two areas were surveyed over different time spans, we conducted separate analyses for the interior [long (1981–2012) and short

(2000–2012)] and the exterior (surveyed 2000–2012) (fig. S1 and table S4). We estimated trends in density within a Bayesian framework for each region. Following standard model diagnostic procedures, we fitted the density-per-station data with a traditional least-squares model, with the “lm” command and the “blinreg” function in R (R version 2.15.1; R Development Core Team, 2011) for sampling from the joint posterior distribution of slope and variance. Histograms of the simulated posterior draws of the regression coefficients slope and deviation variance were plotted and visually inspected to detect deviations from a normal distribution. Outliers were also identified using Bayesian residuals and were visually inspected. Temporal autocorrelation in annual abundance was assessed with the “acf” function, and AIC procedures were used to select the lag autocorrelation that removed serial correlation. For each analysis, there was no evidence that the model residuals differed from a normal distribution (no evidence of skewness or kurtosis), and although there were some outlier points, the outliers did not occur at either the first or last time points; therefore, the trends were conservative in that the variance was greater when outliers were included rather than excluded. Furthermore, there was no conclusive evidence that an autoregressive model was necessary to control for temporal correlation. Although the data did not substantially deviate from linear forms, we log-transformed the data to control error variance.

Log-linear regression was performed with WinBUGS (31) in the statistical program R. We computed the trend using the equation by Camp *et al.* (32), where α is the density at time t equals 0 (intercept), β is the rate of change (slope) with each unit increase in time t , and τ equals variance⁻¹ (precision). The parameters α and β were given vague normal priors (0, 0.000001), and τ was given a vague γ prior (0.01, 0.01). Year values were centered on a year corresponding to the midpoint of the time series. The model parameters were estimated from 100,000 iterations for each of three chains (that is, model runs) after discarding the first 50,000 iterations (a “burn-in” period). The three chains were pooled (150,000 total samples) to create a posterior distribution. The Gelman-Rubin convergence statistic (R hat) was inspected to ensure convergence. Convergence was problematic for species with zero or very low densities. For these species, we increased the number of iterations to 2,100,000 and sampled from every 10th iteration for inference with a burn-in of 50,000 iterations to yield a total of 150,000 samples. The “overRelax” argument was applied to generate multiple samples at each iteration to reduce within-chain correlation by selecting a value that was negatively correlated with the current value.

We used a log-linear regression model to calculate the distribution of the posterior probabilities (P) of trend parameters. The proportion of the posterior distribution that was within or outside threshold bounds was assessed, corresponding to a 25% change in the population over 25 years. We categorized the trends as increasing, decreasing, negligible (stable population), or inconclusive (trend uncertain). The evidence for a particular trend was based on how the distribution of posterior probabilities was apportioned by category, and was interpreted as very weak ($P < 0.5$), weak ($0.5 \leq P < 0.7$), strong ($0.7 \leq P < 0.9$), or very strong ($P \geq 0.9$) (table S4). An inconclusive result occurred when variance was high and the posterior distribution gave only very weak evidence across the increasing, decreasing, and negligible trend categories.

Time to extinction

Using abundance estimates for native species from 2000 to 2012, we fit a linear and exponential growth model to the population numbers of each

species using the “nls” function in R (excluding the 2008 estimate for ‘akikiki because it was a clear outlier). The model estimated the initial population size and the rate of change, and these were used to project population change moving forward in time using a population-independent (linear) and population-dependent (exponential) rate of change. Time to extinction (extinction year) was determined for the year that the projected population becomes less than 30 individuals, which was chosen as a number that species are no longer likely to be viable in the wild. The projections are just one possible outcome of many, assuming that the rate of change is accurate and does not change over the coming decades.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/2/9/e1600029/DC1>

fig. S1. Spatial extent of interior and exterior survey areas used for the estimate of trends by region and period.

table S1. Survey date and numbers of transects and stations sampled for forest birds on Kauaʻi from eight point-transect surveys.

table S2. Density and population abundance estimates of Kauaʻi forest birds by elevation (900 to 1500 m) from the 2012 Kauaʻi surveys.

table S3. Density of Kauaʻi forest birds by study area (interior and exterior) for each survey period (1981–2012).

table S4. Trends in forest birds on Kauaʻi in the consistently sampled interior and exterior areas by survey period.

REFERENCES AND NOTES

1. G. C. Munro, *Birds of Hawaii* (Tongg Publishing Company, Honolulu, 1944).
2. T. K. Pratt, C. T. Atkinson, P. C. Banko, J. D. Jacobi, B. L. Woodworth, *Hawaiian Forest Birds: Their Biology and Conservation* (Yale Univ. Press, New Haven, 2009).
3. C. T. Atkinson, D. A. LaPointe, Introduced avian diseases, climate change, and the future of Hawaiian honeycreepers. *J. Avian Med. Surg.* **23**, 53–63 (2009).
4. R. E. Warner, The role of introduced diseases in the extinction of the endemic aawaiian avifauna. *Condor* **70**, 101–120 (1968).
5. C. van Riper III, S. G. van Riper, M. L. Goff, M. Laird, The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecol. Monogr.* **56**, 327–344 (1986).
6. D. A. LaPointe, M. L. Goff, C. T. Atkinson, Thermal constraints to the sporogonic development and altitudinal distribution of avian malaria *Plasmodium relictum* in Hawaiʻi. *J. Parasitol.* **96**, 318–324 (2010).
7. T. L. Benning, D. LaPointe, C. T. Atkinson, P. M. Vitousek, Interactions of climate change with biological invasions and land use in the Hawaiian Islands: Modeling the fate of endemic birds using a geographic information system. *Proc. Natl. Acad. Sci. U.S.A.* **99**, 14246–14249 (2002).
8. T. W. Giambelluca, H. F. Diaz, M. S. A. Luke, Secular temperature changes in Hawaiʻi. *Geophys. Res. Lett.* **35**, L12702 (2008).
9. H. F. Diaz, T. W. Giambelluca, J. K. Eischeid, Changes in the vertical profiles of mean temperature and humidity in the Hawaiian Islands. *Global Planet. Change* **77**, 21–25 (2011).
10. C. T. Atkinson, R. B. Utzurrum, D. A. Lapointe, R. J. Camp, L. H. Crampton, J. T. Foster, T. W. Giambelluca, Changing climate and the altitudinal range of avian malaria in the Hawaiian Islands—An ongoing conservation crisis on the island of Kauaʻi. *Glob. Chang. Biol.* **20**, 2426–2436 (2014).
11. L. B. Fortini, A. E. Vorsino, F. A. Amidon, E. H. Paxton, J. D. Jacobi, Large-scale range collapse of Hawaiian forest birds under climate change and the need 21st century conservation options. *PLOS One* **10**, e0140389 (2015).
12. M. D. Fonzo, B. Collen, G. M. Mace, A new method for identifying rapid decline dynamics in wild vertebrate populations. *Ecol. Evol.* **3**, 2378–2391 (2013).
13. W. E. Banko, P. C. Banko, Historic decline and extinction, in *Conservation Biology of Hawaiian Forest Birds: Implications for Island Avifauna*, T. K. Pratt, C. T. Atkinson, P. C. Banko, J. D. Jacobi, B. L. Woodworth, Eds. (Yale Univ. Press, New Haven, 2009), pp. 25–58.
14. S. Conant, H. D. Pratt, R. J. Shallenberger, Reflections on a 1975 expedition to the lost world of the Alakaʻi and other notes on the natural history, systematics, and conservation of Kauaʻi birds. *Wilson Bull.* **110**, 1–22 (1998).
15. R. L. Hammond, L. H. Crampton, J. T. Foster, Breeding biology of two endangered forest birds on the island of Kauai, Hawaii. *Condor* **117**, 31–40 (2015).
16. R. L. Hammond, L. H. Crampton, J. T. Foster, Nesting success of native and introduced forest birds on the island of Kauaʻi. *J. Avian Biol.* **47**, 252–262 (2016).

17. E. A. VanderWerf, L. C. Young, N. W. Yeung, D. B. Carlton, Stepping stone speciation in Hawaii's flycatchers: Molecular divergence supports new island endemics within the elepaio. *Conserv. Genet.* **11**, 1283–1298 (2010).
18. E. A. Vanderwerf, M. D. Burt, J. L. Rohrer, S. M. Mosher, Distribution and prevalence of mosquito-borne diseases in O'ahu 'Elepaio. *Condor* **108**, 770–777 (2006).
19. E. A. VanderWerf, L. H. Crampton, J. S. Diegmann, C. T. Atkinson, D. L. Leonard, Survival estimates of wild and captive-bred released Puaiohi, an endangered Hawaiian thrush. *Condor* **116**, 609–618 (2014).
20. B. L. Woodworth, A. A. Lieberman, J. T. Nelson, J. S. Fretz, Puaiohi, in *Conservation Biology of Hawaiian Forest Birds: Implication for Island Avifauna*, T. K. Pratt, C. T. Atkinson, P. C. Banko, J. D. Jacobi, B. L. Woodworth, Eds. (Yale Univ. Press, London, 2009), pp. 499–512.
21. J. T. Foster, E. J. Tweed, R. J. Camp, B. L. Woodworth, C. D. Adler, T. Telfer, Long-term population changes of native and introduced birds in the Alaka'i Swamp, Kaua'i. *Conserv. Biol.* **18**, 716–725 (2004).
22. B. L. Woodworth, C. T. Atkinson, D. A. LaPointe, P. J. Hart, C. S. Spiegel, E. J. Tweed, C. Henneman, J. LeBrun, T. Denette, R. DeMots, K. L. Kozar, D. Triglia, D. Lease, A. Gregor, T. Smith, D. Duffy, Host population persistence in the face of introduced vector-borne diseases: Hawaii amakihi and avian malaria. *Proc. Natl. Acad. Sci. U.S.A.* **102**, 1531–1536 (2005).
23. K. L. Krend, *Avian Malaria on Oahu: Disease Ecology, Population Genetics, and the Evolution of Resistance in Oahu Amakihi*, dissertation, University of Hawaii, Manoa (2011).
24. L. Alphey, Genetic control of mosquitoes. *Annu. Rev. Entomol.* **59**, 205–224 (2014).
25. A. M. Kilpatrick, Facilitating the evolution of resistance to avian malaria in Hawaiian birds. *Biol. Conserv.* **128**, 475–485 (2006).
26. A. G. Boyer, W. Jetz, Extinctions and the loss of ecological function in island bird communities. *Glob. Ecol. Biogeogr.* **23**, 679–688 (2014).
27. T. W. Giambelluca, Q. Chen, A. G. Frazier, J. P. Price, Y.-L. Chen, P.-S. Chu, J. K. Eischeid, D. M. Delparte, Online Rainfall Atlas of Hawai'i. *Bull. Am. Meteorol. Soc.* **94**, 313–316 (2013).
28. L. A. H. Behnke, L. Pejchar, L. H. Crampton, Occupancy and habitat use of the endangered Akikiki and Akekee on Kauai Island, Hawaii. *Condor* **118**, 148–158 (2016).
29. J. M. Scott, S. Mountainspring, F. L. Ramsey, C. B. Kepler, Forest bird communities of the Hawaiian Islands: Their dynamics, ecology, and conservation. *Stud. Avian Biol.* **9**, 1–431 (1986).
30. L. Thomas, S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques, K. P. Burnham, Distance software: Design and analysis of distance sampling surveys for estimating population size. *J. Appl. Ecol.* **47**, 5–14 (2010).
31. D. J. Lunn, A. Thomas, N. Best, D. Spiegelhalter, WinBUGS—A Bayesian modelling framework: Concepts, structure, and extensibility. *Stat. Comput.* **10**, 325–337 (2000).
32. R. J. Camp, N. E. Seavy, P. M. Gorresen, M. H. Reynolds, A statistical test to show negligible trend: Comment. *Ecology* **89**, 1469–1472 (2008).

Acknowledgments: We thank the many people over the years who conducted bird surveys of Kaua'i forest birds in the very remote and rugged terrain of Kaua'i. C. Atkinson, K. Paxton, and S. Yelenik provided important comments on earlier drafts. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. **Funding:** Funding for the analysis was provided by the State of Hawai'i Department of Forest and Wildlife (agreement #13WSZB000-PA2983) and the U.S. Fish and Wildlife Service State Wildlife Grant Program (agreement #F13AF00964). **Author contributions:** R.J.C., P.M.G., L.H.C., D.L.L., and E.A.V. performed field surveys; E.H.P., R.J.C., and P.M.G. analyzed the data; E.H.P. wrote the paper; R.J.C., P.M.G., L.H.C., D.L.L., and E.A.V. read and commented on the manuscript. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Original bird survey data is available through the USGS ScienceBase Catalog (doi:10.5066/F7ZG6QC1) at the following URL: <https://www.sciencebase.gov/catalog/item/579bcc73e4b0589fa1c982e2>.

Submitted 8 January 2016

Accepted 7 August 2016

Published 7 September 2016

10.1126/sciadv.1600029

Citation: E. H. Paxton, R. J. Camp, P. M. Gorresen, L. H. Crampton, D. L. Leonard, E. A. VanderWerf, Collapsing avian community on a Hawaiian island. *Sci. Adv.* **2**, e1600029 (2016).

Collapsing avian community on a Hawaiian island

Eben H. Paxton, Richard J. Camp, P. Marcos Gorresen, Lisa H. Crampton, David L. Leonard, Jr. and Eric A. VanderWerf

Sci Adv 2 (9), e1600029.
DOI: 10.1126/sciadv.1600029

ARTICLE TOOLS

<http://advances.sciencemag.org/content/2/9/e1600029>

SUPPLEMENTARY MATERIALS

<http://advances.sciencemag.org/content/suppl/2016/09/06/2.9.e1600029.DC1>

REFERENCES

This article cites 27 articles, 2 of which you can access for free
<http://advances.sciencemag.org/content/2/9/e1600029#BIBL>

PERMISSIONS

<http://www.sciencemag.org/help/reprints-and-permissions>

Use of this article is subject to the [Terms of Service](#)