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Distribution and abundance of forest birds in low-altitude habitat on Hawai'i Island: evidence for range expansion of native species

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Summary

The Hawaiian honeycreepers are thought to be limited primarily to middle- and high-altitude wet forests due to anthropogenic factors at lower altitudes, especially introduced mosquito-transmitted avian malaria. However, recent research has demonstrated that at least one native species, the Hawai'i 'Amakihi (*Hemignathus virens virens*), is common in areas of active malaria transmission. We examined the current distribution and abundance of native and exotic forest birds within approximately 640 km² of low-altitude (0–326 m) habitat on south-eastern Hawai'i Island, using roadside variable circular plot (VCP) at 174 stations along eight survey transects. We also re-surveyed 90 stations near sea level that were last surveyed in 1994–1995. Overall, introduced species were more abundant than natives; 11 exotic species made up 87% of the total individuals detected. The most common exotic passerines were Japanese White-eye (*Zosterops japonicus*), House Finch (*Carpodacus mexicanus*) and Northern Cardinal (*Cardinalis cardinalis*). Two native species, Hawai'i 'Amakihi and 'Apapane (*Himatione sanguina*), comprised 13% of the bird community at low altitudes. Hawai'i 'Amakihi were the most common and widespread native species, being found at 47% of stations at a density of 4.98 birds/ha (95% CI 3.52–7.03). 'Amakihi were significantly associated with 'ohi'a (*Metrosideros polymorpha*)-dominated forest. 'Apapane were more locally distributed, being found at only 10% of stations. Re-surveys of 1994–1995 transects demonstrated a significant increase in 'Amakihi abundance over the past decade. This work demonstrates a widespread recovery of Hawai'i 'Amakihi at low altitude in southeastern Hawai'i. The changing composition of the forest bird community at low-altitudes in Hawai'i has important implications for the dynamics of avian malaria in low-altitude Hawai'i, and for conservation of Hawai'i's lowland forests.

Introduction

The Hawaiian honeycreepers (Fringillidae) are an endemic subfamily (Drepanidinae) of birds that originally comprised a minimum of 51 species, all descended from a single colonization event from North America approximately 4 million years ago (Tarr and Fleischer 1995, James 2004). These birds were once abundant in all forests throughout Hawai'i but have undergone large declines in species richness, distribution and abundance. Causes of these declines include habitat destruction (Cuddihy and Stone 1990), the introduction of predatory mammals (Tomich 1969, Atkinson 1977), exotic competitors (Mountainspring and Scott 1985) and introduced disease (Warner

1968, van Riper *et al.* 1986). Introduced avian malaria *(Plasmodium relictum*), which is transmitted primarily by introduced *Culex qinquefasciatus* mosquitoes, is currently thought to limit most honeycreeper populations to altitudes greater than approximately 900 m, where cooler temperatures begin to inhibit development of both mosquitoes and *Plasmodium* parasites (van Riper *et al.* 1986, LaPointe 2000). Honeycreepers have been found to be almost entirely absent from lower-altitude areas due to high mosquito densities, even in areas of otherwise suitable habitat (Scott *et al.* 1986, van Riper *et al.* 1986). As a result, low-altitude forests have generally been ignored in recent decades as suitable native bird habitat and little has been done to protect these areas from habitat destruction or to monitor the local avifauna. On the island of Hawai'i, the handful of surveys that were conducted in the late 1980s and 1990s found few honeycreepers at low altitudes (<400 m), and nearly none below 120 m (David 1995, Walker 1993, Reynolds *et al.* 2003).

Recently, however, breeding populations of Hawai'i 'Amakihi (*Hemignathus virens virens*), one of seven extant honeycreeper species on Hawai'i Island, have been documented at low altitude (<400 m) in the Puna District, often at greater densities than in high-altitude areas with comparable habitat (Woodworth *et al.* 2005). This small, 13–15 g non-migratory generalist has been shown to suffer high mortality rates from acute malaria infection (65%; Atkinson *et al.* 2000). However, nearly 90% of the birds sampled at low altitudes showed evidence of chronic malaria infections, evidence that they had contracted the disease and survived (Woodworth *et al.* 2005). The finding that Hawai'i 'Amakihi are persisting in low-altitude forests despite the high prevalence of avian malaria and evidence for local transmission, has raised the possibility that this species may be evolving resistance to avian malaria. However, the extent to which this recovery represents a localized versus a widespread phenomenon is unknown.

A second native species of interest is the 'Apapane (*Himatione sanguinea*). The 'Apapane, a 14–16 g nectivorous, non-territorial honeycreeper, also suffers mortality rates of approximately 65% to acute malaria infection (Yorinks and Atkinson 2000). Because recovered individuals carry chronic infections and are infective to mosquitoes for at least several years, 'Apapane are the primary reservoir of avian malaria in mid-altitude forests (Atkinson *et al.* 2000). In contrast to the sedentary and territorial lifestyle of 'Amakihi, 'Apapane only defend their nest-site while breeding, and move across the altitudinal gradient in the non-breeding season in response to availability of nectar resources (Ralph and Fancy 1995), inviting questions about their role in the transmission of disease across the landscape (van Riper *et al.* 1986, LaPointe 2000).

Exotic species are important players in the bird community as well. The extent to which lowland resources are available to native birds is dependent on the degree of competition they experience from exotic birds. Furthermore, because most exotic species are generally less susceptible to avian malaria than their native counterparts, their presence may decrease disease transmission in the community. In support of this idea, van Riper *et al.* (1986) studied a lowland avifauna dominated by exotic species and found little or no disease despite high numbers of mosquitoes.

Our study updates the status of a rapidly changing avifauna on Hawai'i Island. We document the present distribution and abundance of native and introduced forest birds in low-altitude habitats (<400 m) of Puna District, Hawai'i Island, providing a baseline from which to monitor future changes. We also compare the present abundance of Hawai'i 'Amakihi in coastal (<50 m) Puna District with its abundance in the

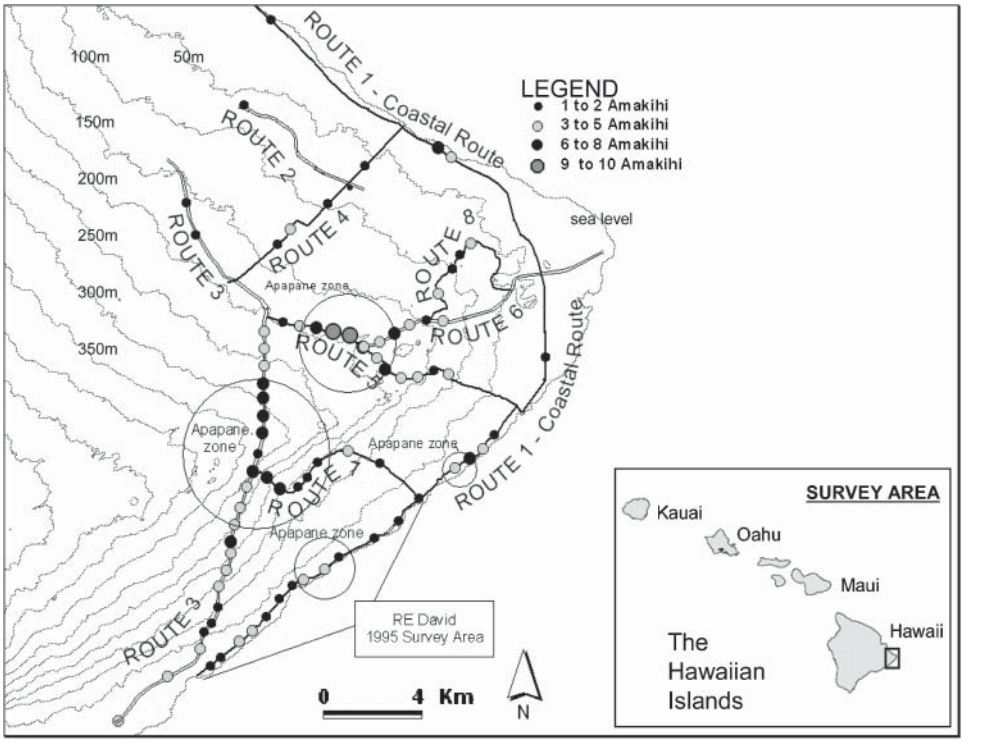

Figure 1. Map of the Hawaiian Islands with the study area indicated (Lower Puna District, Hawai'i Island). VCP survey transects (Routes), count numbers of 'Amakihi, areas of 'Apapane detection ('Apapane zones') and 50 m altitude contours are shown.

mid-1990s to document expansion of this species over the past decade. Finally, we examine the potential mechanisms of this expansion and discuss its implications with regard to the conservation of Hawaiian avifauna.

Methods

Survey area

Our survey area encompassed approximately 640 km^2 of low-altitude habitat on the east slope of Kilauea Volcano, lower Puna District on Hawai'i Island (Figure 1), and included some of largest areas of intact native lowland rainforest remaining in the State of Hawai'i. A variety of vegetation types were represented within the study area, including native 'ohi'a (*Metrosideros polymorpha*)-dominated forests, mixed native/exotic zones and exotic dominated forest. Some fragmented forest surrounded by urbanized areas, agricultural lands and bare lava flows were also present along our transects.

Bird surveys

We established eight survey transects with a total of 174 survey stations placed at 700 m intervals along primary and secondary roads, ranging in altitude from sea level

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Table 1. Attributes of each VCP survey transect showing the number of stations surveyed, altitudinal range, length of transect, and the percentage of stations with 'ohi'a making up over 25% of vegetation type within 100 m of the count station.

	Transect no.							
	1	2	3	4	5	6	7	8
No. of stations	57	9	36	15	17	16	13	11
Altitudinal range (m)	0–34	76–85	15–326	32–189	24–204	20–195	12–308	49–125
Transect length (km)	41.8	6.5	26.1	9.9	11.8	10.9	8.6	7.9
% stations with >25% 'ohi'a	45.6	100	77.8	100	76.5	56.3	38.5	45.5

to 326 m (Figure 1, Table 1). We conducted variable circular plot (VCP) counts (Reynolds *et al.* 1980) once at each station between 9 February and 11 June 2003. Counts were performed between 05:30 and 11:30 hours by five trained observers using 10 × 42 binoculars during favourable conditions (light or no rain and wind <25 kph). Observers recorded all birds seen or heard during 8 minute counts, and recorded the distance to each individual bird. Distance estimates among observers were pre-calibrated under field conditions using a Bushnell Yardage Pro 500 laser rangefinder. For most stations (158 of 174), we recorded the proportion of 'ohi'a forest (less than or greater than 25%) within a 100 m radius of the station (Table 1). Additional variables recorded at each station included time, wind, rain and percentage cloud cover.

Re-sampling count stations of prior studies

We conducted surveys of two transects in coastal Puna District (<50 m altitude) that were originally sampled in the mid-1990s. In January and February 1994, Reynolds *et al.* (2003) surveyed 11 stations spaced 3.2 km apart along a 35 km stretch of coastal road, encompassed by our transect 1 using 8 minute, 30 m fixed radius and unlimited radius point counts. We re-surveyed these stations in February 2004 using VCP methodology as described above (which can be converted for comparison with 30 m fixed radius and unlimited radius point counts). In April and July 1995, David (1995) and Cooper and David (1995) surveyed 79 count stations spaced 150 m apart along an 11.5 km subset of the Reynolds transect using VCP methods (Figure 1). We re-surveyed these 79 stations in April 2004 using VCP methodology. We performed these additional counts at the original sample locations during the same time of year to reduce spatial and temporal inconsistencies that would weaken direct comparisons between counts.

Data analyses

We present two measures of relative abundance for most species: mean birds per station (BPS) and its standard deviation; and frequency (the proportion of stations at which the species was detected). For Hawai'i 'Amakihi, we also present estimates of density (birds/ha). We used the program Distance 4.1 (Thomas *et al.* 2003) to produce 'Amakihi density estimates for (a) the entire survey area for 2003, (b) coastal Puna District <50 m altitude, as measured by the 57 stations on transect 1 in 2003 (the

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'Coastal Route') and (c) the 11.5 km southern section of the Coastal Route, comprising the 79 stations originally surveyed by David (1995). The effective detection radius (EDR), which may be defined as the distance at which the number of birds detected beyond the point equals the number missed within the point, was used to determine the effective area surveyed for each transect. Densities were then calculated as the number of birds detected per station divided by the effective area surveyed, and variance was estimated using bootstrapping methods (Buckland *et al.* 2001).

Model selection for effective detection radius (EDR) for calculating density was restricted *a priori* to half normal, hazard rate and uniform functions with up to two adjustment terms. These models have generally been shown to best approximate the curve that is generated by plotting the probability of detection as a function of distance from the station. Detection histograms, Akaike's Information Criterion (AIC) values and associated statistics were compared with truncated and untruncated data to select 'best fit' models (Buckland *et al.* 2001). We explored the need to adjust our models by analysing environmental variables (wind, rain and cloud cover) as covariates using the 'Multiple Covariate Distance Sampling Module' of Distance 4.1, but in no case did the inclusion of these variables improve the fit of the model.

Results

Overall, we detected 3,164 individuals of 15 species throughout the study area. Three year-round endemic resident birds species, Hawai'i 'Amakihi, 'Apapane and I'o (Hawaiian Hawk, *Buteo solitarius*), and one seasonal resident species, Pacific Golden Plover (*Pluvialis fulva*), were detected, along with 11 non-native species (Table 2).

Two native birds species, Hawai'i 'Amakihi and 'Apapane, together made up approximately 13% of all detections, but their abundance varied widely throughout the study area. Three transects (numbers 3, 5 and 7) in the lower half of the study area each had bird communities comprised of about 20% native birds. In contrast, transects 2, 4, and 8, all of which were concentrated in the northern part of the study area, had extremely low percentages of native birds (<5% each; Figures 1 and 2, Table 2).

Hawai'i 'Amakihi were distributed throughout the entire survey area. 'Amakihi were detected at 47% (81 of 174) of all stations, making up nearly 10% (289 of 3,164 individuals) of all birds recorded. An average of 1.66 ± 2.4 'Amakihi were detected at each station. Overall 'Amakihi density within the survey area was 4.98 birds/ha (95% CI 3.52–7.03; half normal model, no expansion; truncation = 43.1 m; EDR = 30.39 m; %CV = 3.75). 'Amakihi were more regularly distributed in the southern half of the study area than in the northern half (Figure 1), and their greatest abundance was found along transect 5 at approximately 200 m altitude. Along the lowest-altitude transect (transect 1), which averages under 20 m in altitude, 'Amakihi were detected at over 33% of all stations (20 of 57) and averaged 0.93 ± 1.7 birds per station. 'Amakihi density along transect 1 was estimated at 2.5 birds/ha (95% CI 1.5–4.3; hazard rate model, no expansion; truncation = 42.5 m; EDR = 32.07; %CV = 7.63). Throughout the study area, 'Amakihi were associated with 'ohi'a-dominated forests ('Amakihi were detected at 58 of 85 stations with >25% 'ohi'a coverage vs 20 of 79 stations with <25% 'ohi'a coverage; $\chi^2 = 30.24$, d.f. = 1, $P < 0.001$).

'Apapane were patchily distributed in the study area, localized to four sections along three transects ('Apapane Zones' on Figure 1). They comprised less than 1%

Table 2. Mean number of birds per station (BPS) and frequency of bird detections during VCP counts of eight transects in south-eastern Hawai'i Island, February–June 2003.

	Transect no.																	
	1		2		3		4		5		6		7		8		All transects	
Species	BPS	Frequency	BPS	Frequency	BPS	Frequency	BPS	Frequency	BPS	Frequency	BPS	Frequency	BPS	Frequency	BPS	Frequency	BPS	Frequency
'Apapane*	0.11 ± 0.6	0.04	0.00 ± 0.0	0.00	0.31 ± 0.7	0.22	0.00 ± 0.0	0.00	0.47 ± 0.9	0.29	0.06 ± 0.3	0.06	0.08 ± 0.3	0.08	0.00 ± 0.0	0.00	0.16 ± 0.6	0.10
Hawai'i ' Amakihi*	0.93 ± 1.7	0.35	0.22 ± 0.4	0.22	2.83 ± 2.7	0.67	0.47 ± 0.9	0.27	3.53 ± 3.2	0.71	1.38 ± 2.1	0.38	2.62 ± 2.9	0.69	0.82 ± 1.3	0.36	1.66 ± 2.4	0.47
House Finch	3.14 ± 2.1	0.95	2.33 ± 1.4	0.89	1.44 ± 2.4	0.44	1.27 ± 1.9	0.33	2.88 ± 2.5	0.88	6.00 ± 2.9	1.00	4.08 ± 1.8	1.00	6.91 ± 3.0	1.00	3.13 ± 2.8	0.79
House Sparrow	0.00 ± 0.0	0.00	0.00 ± 0.0	0.00	0.14 ± 0.8	0.03	0.67 ± 1.5	0.20	0.06 ± 0.2	0.06	0.00 ± 0.0	0.00	0.00 ± 0.0	0.00	0.00 ± 0.0	0.00	0.09 ± 0.6	0.03
Japanese White-eye	3.49 ± 1.9	0.91	3.67 ± 1.0	1.00	7.19 ± 3.6	0.92	7.27 ± 3.1	1.00	9.47 ± 3.5	1.00	6.88 ± 3.4	1.00	4.54 ± 1.1	1.00	10.00 ± 3.9	1.00	5.98 ± 3.6	0.95
Melodious Laughing-thrush	0.07 ± 0.2	0.07	0.33 ± 0.5	0.33	0.47 ± 0.8	0.33	0.47 ± 0.5	0.47	0.88 ± 0.9	0.59	0.63 ± 0.5	0.63	0.31 ± 0.5	0.31	0.91 ± 0.7	0.73	0.40 ± 0.6	0.33
Common Myna	0.46 ± 0.8	0.28	0.33 ± 0.7	0.22	1.47 ± 1.8	0.53	3.40 ± 3.1	0.80	2.29 ± 2.0	0.76	2.44 ± 1.8	0.75	1.15 ± 1.6	0.46	3.27 ± 2.2	0.91	1.51 ± 2.0	0.52
Northern Cardinal	1.54 ± 1.1	0.77	2.22 ± 1.3	0.89	2.97 ± 1.7	0.94	2.67 ± 1.1	1.00	3.59 ± 1.7	1.00	2.56 ± 1.6	0.88	3.38 ± 1.6	1.00	4.36 ± 1.4	1.00	2.58 ± 1.6	0.90
Nutmeg Manikin	0.18 ± 0.6	0.07	0.22 ± 0.7	0.11	0.92 ± 4.2	0.14	0.00 ± 0.0	0.00	0.88 ± 1.2	0.41	0.50 ± 0.8	0.31	0.54 ± 1.3	0.15	0.55 ± 0.9	0.36	0.47 ± 2.1	0.16
Spotted Dove	0.39 ± 0.6	0.30	0.78 ± 1.1	0.44	1.36 ± 2.1	0.44	0.73 ± 1.0	0.47	1.00 ± 0.9	0.71	1.63 ± 1.2	0.81	1.31 ± 1.2	0.69	3.09 ± 1.7	0.91	1.05 ± 1.4	0.51
Zebra Dove	0.60 ± 0.9	0.35	1.67 ± 1.7	0.67	1.11 ± 1.4	0.58	2.27 ± 1.8	0.80	0.65 ± 1.1	0.41	1.94 ± 1.4	0.75	1.23 ± 1.4	0.62	3.00 ± 1.8	0.91	1.23 ± 1.5	0.55

Variance of BPS is presented as standard deviation from the mean. Four other species ('Io (Hawaiian Hawk)*, Pacific Golden Plover*, Ring-necked Pheasant and Yellow-billed Cardinal) were detected during the surveys in numbers ≤3 individuals per species, and are not included in this table.
*Native species.

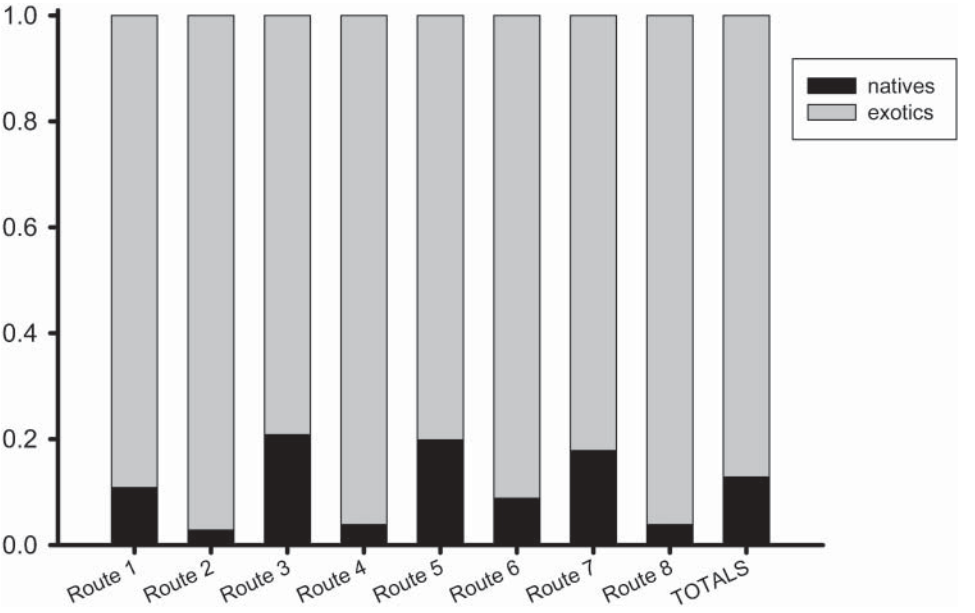

Figure 2. Percentage of native ('Amakihi and 'Apapane) and exotic detections by VCP survey transect (Route).

of detections (Table 2). On average, 0.16 ± 0.6 birds per station were detected, and 'Apapane were present at just under 10% (17 of 174) of all stations surveyed. 'Apapane were most widely distributed along transect 3 at an altitude of approximately 300 m. Two other natives, the 'Io (Hawaiian Hawk) and Pacific Golden Plover, were only incidentally recorded during the surveys (<3 each).

The three most common exotic birds detected throughout the survey area were Japanese White-eyes (*Zosterops japonicus*; 32.8% of individuals counted), House Finches (*Carpodacus mexicanus*; 17.2%) and Northern Cardinals (*Cardinalis cardinalis*; 14.2%) (Table 2). Together these three species made up 64% of all detections and each was detected at >75% of stations. The remaining eight exotic species, in decreasing order of abundance, were Common Myna (*Acridotheres tristis*; 8.3%), Zebra Dove (*Geopelia striata*; 6.7%), Spotted Dove (*Streptopelia chinensis*; 5.8%), Nutmeg Mannikin (*Lonchura punctulata*; 2.5%), Melodious Laughing Thrush (*Garrulax canorus*; 2.2%), House Sparrow (*Passer domesticus*; <0.1%), Ring-necked Pheasant (*Phasianus colchicus*; <0.1%) and Yellow-billed Cardinal (*Paroaria capitata*; <0.1%).

Re-surveys of 1990s coastal transects

We detected 13 individual 'Amakihi at four of 11 stations originally surveyed by Reynolds in 1994 (36.4% of stations, 1.18 ± 1.9 BPS), whereas Reynolds *et al.* (2003) had found no 'Amakihi during their surveys (Fisher's exact test, $P = 0.09$). We detected a total of 62 'Amakihi at 33 of 79 stations (41.8%, 0.78 ± 1.09 BPS) originally surveyed by David (1995) and Cooper and David (1995), compared with zero 'Amakihi at the same 79 stations in April and July 1995 (David 1995, Cooper and

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David 1995). This represents a significant increase in 'Amakihi in this area over a 9 year period ($\chi^2 = 39.2$, d.f. = 1, $P < 0.0001$). Density of 'Amakihi along David's transect in 2004 was estimated at 0.81 birds/ha (95% CI 0.52–1.27; hazard rate model, no expansion; truncation = 45.0 m, EDR = 38.02; %CV = 8.08).

Discussion

Our data represent the highest densities of Hawai'i 'Amakihi and 'Apapane ever recorded for this altitudinal range, and suggest an expansion in distribution and abundance within a large area of Hawaiian lowlands that were previously thought uninhabitable due to habitat fragmentation, exotic predators and competitors, and especially avian disease. Over the past decade, Hawai'i 'Amakihi have become common at altitudes below 100 m where they were previously rare or absent. A renewed presence of native birds, especially 'Amakihi, in these areas suggests a low-altitude re-colonization by populations that were historically reduced or extirpated. This expansion appears to be driven by reproduction from lowland individuals, as there is no evidence for an increase in either middle- or high-altitude populations (USGS unpubl. data).

Birds have been known to naturally re-colonize areas originally made uninhabitable by major disturbance such as logging or fires (e.g. Dranzoa 1998). Re-colonizations have also been aided by human conservation efforts, either through remediation of habitat (Johns 1996, Findlay and Bourdages 2000), regulation and mitigation of processes that originally affected the population (Newton and Wylie 1992, Lensink 1997, Elliott and Harris 2001/2002) or direct re-introduction (Franklin and Steadman 1991, Clout and Craig 1995, Tarr and Fleischer 1999). There are few reports, however, of natural re-colonization events by species that were historically reduced or eliminated by disease from a habitat where they once were abundant. The New Zealand Bellbird (*Anthornis melanura*) represents one of few examples on record of an apparent re-colonization by a bird species after near extirpation by introduced disease (Steadman *et al.* 1990); however, this process occurred over 90 years ago and was not well documented. Hawai'i 'Amakihi re-colonization in the face of introduced disease as the likely primary limiting factor may be a unique event.

Although we most frequently detected Hawai'i 'Amakihi in areas dominated by native forest, they were regularly observed in exotic vegetation, on barren lava flows and in housing subdivisions. The O'ahu 'Amakihi (*Hemignathus flavus*), a close relative of the Hawai'i 'Amakihi, has also been reported foraging and nesting in exotic tree species and suburban areas below 100 m in altitude (VanderWerf 1997, Shehata *et al.* 2001, Lovich 2003). Plasticity in ecological requirements has apparently allowed 'Amakihi to persist under adverse conditions such as habitat fragmentation and destruction, extreme interspecific competition with exotic bird species, and growing human populations (Lindsey *et al.* 1998). The increase in 'Amakihi in our study area is notable because it has occurred during a period of rapid habitat degradation and human population growth.

Potential mechanisms by which 'Amakihi are expanding in our study area include the evolution of increased disease resistance in the host, evolution of decreased virulence in the malaria parasite, increased annual survival or productivity resulting from greater food availability, lower predator abundance, or other ecological factors at low altitudes (Woodworth *et al.* 2005). Understanding the processes that allow 'Amakihi

to persist and expand in low-altitude areas may be important to managing remaining populations of honeycreepers throughout the Hawaiian islands. If a low-altitude disease-resistant population of Hawai'i 'Amakihi is identified, individuals could be translocated to other lowland forests where native birds have been extirpated by disease. This would serve the additional purpose of enhancing the function of lowland native forests by restoring an important pollinator and arthropod predator.

The expansion of Hawai'i 'Amakihi into low-altitude areas underscores the importance of fragmented and disturbed forest habitats in Hawai'i to the conservation of the native avifauna. Understanding population dynamics and factors influencing habitat selection within and among disturbed or fragmented habitats can be crucial when assessing potential conservation concerns of species living within those areas (MacNally and Horrocks 2002, Hames *et al.* 2001). Marginalized habitat of the past could become future refugia for species adapting to changing environments under large-scale and complex processes (e.g. taxon cycles; Ricklefs and Bermingham 2002) that are difficult to ascertain within short periods of study (Johns 1996, Schmiegelow and Moenkkoenen 2002). Furthermore, populations within these areas, which have uniquely adjusted to constraints imposed by the habitat, could one day become source populations, replacing individuals that have become imperiled in other areas of the species' range, resulting in secondary expansions (Channell and Lomolino 2000, Ricklefs and Bermingham 2002).

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References

Atkinson, C. T. (1977) A reassessment of factors, particularly *Rattus rattus*, that influenced the decline of endemic forest birds in the Hawaiian Islands. *Pacific Sci.* 31: 109–133.

Atkinson, C. T., Dusek, R. J., Woods, K. L. and Iko, W. M. (2000) Pathogenicity of avian malaria in experimentally infected Hawaii Amakihi. *J. Wildl. Dis.* 36: 197–204.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. and Thomas, L. (2001) *Introduction to distance sampling*. Oxford: Oxford University Press.

Channell, R. and Lomalino, M. V. (2000) Dynamic biogeography and conservation of endangered species. *Nature* 403: 84–86.

Cooper, A. B. and David, R. E. (1995) *Radar and visual surveys of seabirds in the HELCO SSPP Unit 71, Puna, Hawaii, during July 1995*. Technical report prepared for: R. M. Towill Corporation and Hawaii Electric Light Co.

Clout, M. N. and Craig, J. L. (1995) The conservation of critically endangered flightless birds in New Zealand. *Ibis* 137: S181–S191.

Cuddihy, L. W. and Stone, C. P. (1990) *Alteration of native Hawaiian vegetation: effects of humans, their activities and introductions*. Honolulu, HI: University of Hawaii Press.

David, R. E. (1995) *Faunal survey of Helco SSPP Unit 71 — Rauenhorst, Kehena-Keekee, Homestaed, Puna, Hawaii*. Technical report prepared for: R. M. Towill Corporation and Hawaii Electric Light Co.

Dranzoa, C. (1998) The avifauna 25 years after logging in Kibale National Park, Uganda. *Biodiv. Conserv*. 7: 777–797.

Elliott, J. E. and Harris, M. L. (2001/2002) An ecotoxicological assessment of chlorinated hydrocarbon effects on bald eagle (*Haliaeetus leucocephalus*) populations. *Rev. Toxicol*. 4: 1–60.

Findlay, S. C. and Bourdages, J. (2000) Response time of wetland biodiversity to road construction on adjacent lands. *Conserv. Biol*. 14: 86–94.

Franklin, J. and Steadman, D. W. (1991) The potential for conservation of Polynesian birds through habitat mapping and translocation. *Conserv. Biol*. 5: 506–521.

Hames, R. S., Rosenberg, K. V., Lowe, J. D. and Dhondt, A. A. (2001) Site reoccupation in fragmented landscapes: testing predictions of metapopulation theory. *J. Anim. Ecol*. 70: 182–190.

James, H. F. (2004) The osteology and phylogeny of the Hawaiian finch radiation (Fringillidae: Drepanidini), including extinct taxa. *Zool. J. Linn. Soc*. 141: 207–255.

Johns, A. G. (1996) Bird population persistence in Sabahan logging concessions. *Biol. Conserv*. 75: 3–10.

LaPointe, D. (2000) Avian malaria in Hawaii: the distribution, ecology, and vector potential of forest dwelling mosquitoes. PhD dissertation, University of Hawaii, Honolulu.

Lensink, R. (1997) Range expansion of raptors in Britain and the Netherlands since the 1960s: testing an individual-based diffusion model. *J. Anim. Ecol*. 66: 811–826.

Lindsey, G. D., VanderWerf, E. A., Baker, H. and Baker, P. E. (1998) Hawai'i 'Amakihi (*Hemignathus virens*), Kaua'i 'Amakihi (*Hemignathus kauaiensis*), O'ahu 'Amakihi (*Hemignathus chloris*) and Greater 'Amakihi (*Hemignathus sagittirostris*). In A. Poole and F. Gill, eds. *The Birds of North America*. Philadelphia, PA: The Birds of North America, Inc.

Lovich, R. (2003) Habitat use by the 'Amakihi, *Hemignathus chloris* (*Aves: Drepanidinae*) in a suburban setting: possible evolutionary and conservation consequences. *'Elepaio* 63: 51–54.

MacNally, R. and Horrocks, G. (2002) Relative influences of patch, landscape and historical factors on birds in an Australian fragmented landscape. *J. Biogeogr*. 29: 395–410.

Mountainspring, S. and Scott, J. M. (1985) Interspecific competition among Hawaiian forest birds. *Ecol. Monogr*. 55: 219–239.

Newton, I. and Wyllie, I. (1992) Recovery of a sparrowhawk population in relation to declining pesticide contamination. *J. Appl. Ecol*. 29: 476–484.

Ralph, C. J. and Fancy, S. G. (1995) Demography and movements of Apapane and Iiwi in Hawaii. *Condor* 97: 729–742.

Reynolds, M. H., Camp, R. H., Nelson, B. M. B. and Jacobi, J. D. (2003) Evidence of change in a low-altitude forest bird community of Hawai'i since 1979. *Bird Conserv. Int*. 13: 179–187.

Reynolds, R. T., Scott, J. M. and Nussbaum, R. A. (1980) A variable circular-plot method for estimating bird numbers. *Condor* 82: 309–313.

Ricklefs, R. E. and Bermingham, E. (2002) The concept of the taxon cycle in Biogeography. *Global Ecol. Biogeogr*. 11: 353–361.

Schmiegelow, F. K. A. and Moenkkoenen, M. (2002) Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. *Ecol. Appl*. 12: 375–389.

Scott, J. M., Mountainspring, S., Ramsey, F. L. and Kepler, C. B. (1986) *Forest bird communities of the Hawaiian islands: their dynamics, ecology, and conservation*. Lawrence, KS: Allen Press and Cooper Ornithological Society (Studies in Avian Biology 6).

Shehata, C., Freed, L. and Cann, R. (2001) Changes in native and introduced bird populations on O'ahu: infectious diseases and species replacement. Pp. 264–273 in J. M. Scott, S. Conant and C. van Riper III, eds. *Evolution, ecology, conservation, and management of Hawaiian birds: a vanishing avifauna*. Lawrence, KS: Allen Press and Cooper Ornithological Society (Studies in Avian Biology 22).

Steadman, D. W., Greiner, E. C. and Wood, C. S. (1990) Absence of blood parasites in indigenous and introduced birds from the Cook Islands, South Pacific. *Conserv. Biol.* 4: 398–404.

Tarr, C. L. and Fleischer, R. C. (1995) Evolutionary relationships of the Hawaiian honeycreepers (Aves, Drepanidinae). Pp. 147–159 in W. L. Wagner and V. A. Funk, eds. *Hawaiian biogeography: evolution on a hotspot archipelago*. Washington, DC: Smithsonian Institution Press.

Tarr, C. L. and Fleischer, R. C. (1999) Population boundaries and genetic diversity in the endangered Mariana crow (*Corvus kubaryi*). *Mol. Ecol.* 8: 941–949.

Thomas, L., Laake, J. L., Strindberg, S., Marques, F. F. C., Buckland, S. T., Borchers, D. L., Anderson, D. R., Burnham, K. P., Hedley, S. L., Pollard, J. H. and Bishop, J. R. B. (2003) Distance 4.1, release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, U.K.

Tomich, P. Q. (1969) *Mammals in Hawaii*. Honolulu, HI: Bishop Museum Press.

VanderWerf, E.A. (1997) O'ahu 'Amakihi nest in Manoa Valley. *'Elepaio* 57: 125–126.

van Riper III C., van Riper, S. G., Goff, M. L. and Laird, M. (1986) The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecol. Monogr.* 56: 327–344.

Walker, R. L. (1993) *Kikala — Keokea wildlife survey*. Technical report prepared for the State of Hawaii.

Warner, R. E. (1968) The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *Condor* 70:101–120.

Woodworth, B. L., Atkinson, C. T., LaPointe, D. A., Hart, P. J., Spiegel, C. S., Tweed, E. J., Henneman, C., LeBrun, J. J., Denette, T., DeMots, R., Kozar, K. L., Triglia, D., Lease, D., Gregor, A., Smith, T. and Duffy, D. C. (2005) 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.

Yorinks, N. and Atkinson, C. T. (2000). Effects of malaria on activity budgets of experimentally infected juvenile apapane (Himatione sanguinea). *Auk* 117: 731–738.

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