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PRODUCTIVITY OF FOREST BIRDS AT HAKALAU FOREST NWR

GEORGE C. CUMMINS[1], STEVE J. KENDALL[2], AND EBEN H. PAXTON[1]

[1] U.S. Geological Survey Pacific Island Ecosystems Research Center, P.O. Box 44, Hawai`i National Park, HI 96718
[2] U.S. Fish and Wildlife Service, Hakalau Forest National Wildlife Refuge,
60 Nowelo St, Suite 100, Hilo, HI 96720

Hawai`i Cooperative Studies Unit
University of Hawai`i at Hilo

200 W. Kawili St.

Hilo, HI 96720

(808) 933-0706

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ABSTRACT

Hawai'i has some of the most endangered avian species in the world, which face numerous threats from habitat loss, disease, climate change, and introduced species. This report details the results of a two-year productivity study of all forest bird species at Hakalau National Wildlife Refuge, Hawai'i Island. We found and monitored nests from seven native species and three common non-native species of forest birds at three sites across the refuge. In addition to gathering important baseline information on productivity of forest birds, we examined differences in productivity between years, sites, and as a function of nest height. The weather differed greatly between the two years, with much more rain occurring in 2014. The daily survival rate (DSR) of nests was found to have an inverse relationship with the amount of rainfall, and accordingly was much lower in 2014 compared to 2013. Nest success was lower at a regenerating forest site compared with mature rainforest, indicating negative environmental factors affecting nest success may be exacerbated in reforested areas which have lower canopies. Nest success was also impacted by nest height, with a positive relationship in the drier 2013, and a negative relationship in 2014 for the canopy nesting honeycreepers. The large difference in weather and DSR between years illustrates the need for long term demographic studies that can capture the vital rates of this community of birds.

INTRODUCTION

Native Hawaiian forest birds have experienced one of the highest rates of extinction in the world (Pratt 2009) because of habitat loss and the introduction of alien plants, animals, and diseases. Invasive species and landscape modification for agriculture, ranching, urban areas, and housing have largely removed most low elevation native forest bird habitats, leaving remaining intact lowland forests scattered and fragmented. Introduced diseases, specifically avian malaria and avian pox, along with an introduced mosquito (Southern House Mosquito, *Culex quinquefasciatus*) that efficiently transmits these diseases (LaPointe *et al*. 2009), have largely displaced native birds from remaining low and mid-elevation forests where rampant disease transmission occurs throughout the year (Warner 1968, van Riper *et al*. 1986, Atkinson & LaPointe 2009). These factors have interacted so that the highest diversity and densities of forest birds occurs in native forest above 1,500 m asl (Scott *et al*. 1986).

Hakalau Forest National Wildlife Refuge (Hakalau) was created in 1985 to protect endangered forest birds and their rainforest habitat. Hakalau supports a high diversity of native plants, invertebrates, and birds, including three endangered forest bird species ('akepa [*Loxops coccineus*], 'akiapola'au [*Hemignathus munroi*], and Hawai'i creeper [*Oreomystis mana*]), and a fourth species under consideration for listing, the 'i'iwi (*Vestiaria coccinea*). The refuge is one of the few places in the state where native forest bird populations are stable or increasing (Camp *et al*. 2010), but there are a number of continuing threats to habitats within the refuge, such as feral ungulate damage and incursion of weeds, and threats from climate change that could put new pressures on the refuge's forest bird populations. Management of forest birds requires information on threats, and how their populations respond to these threats. Long-term surveys are conducted in many locations across the islands, but they can only tell us about past and current population sizes, not what may be driving trends.

Refuge managers require information on the factors influencing the status of birds to develop effective management actions required to meet their mission. Detailed studies of population demography (survival, productivity, movement) are necessary in addition to population surveys to clearly assess population trends, response to management actions, and inform future decisions. Currently, efforts are being made to incorporate demographic information directly into the decision making process in multiple ways. These include determining management actions to respond to the impacts of climate change (Paxton *et al*. 2011) and development of Hakalau specific demographic models to evaluate potential threats and the effectiveness of management actions.

In 2012, three long-term banding sites were established at Hakalau to create a cohort of banded birds that could be tracked over time. A total of 2,173 birds have been banded over three years in this area since the project started. The three banding sites are at different elevations and in different habitats, ranging from mature closed-canopy forest to young reforested pastures, which will allow for comparison of demographic rates as a function of elevation and habitat. In 2013, a nesting study was added to evaluate productivity of forest birds.

We report the results of the first two years of this study (2013–2014) to quantify nest productivity of seven species of native forest birds and the three most common non-native forest bird species. The productivity sites were linked to ongoing demographic (banding) sites, which will allow us to relate productivity and survival to other variables driving population dynamics at Hakalau.

METHODS

Study Area
Located on the windward slope of Mauna Kea Volcano on Hawaiʻi Island, the 32,733 acre Hakalau Refuge contains some of the best and largest areas of remaining native rain forest in the state. The refuge also contains a large elevation gradient (793–2,000 m) and rainfall (254–635 cm) gradient, with lower slopes receiving the most rain. At the time of Hakalau's establishment, the refuge encompassed approximately 1,620 ha of once-forested pasture on these lands. In 1989, refuge staff began restoring the pasture area and open forest adjacent to pasture land to return it to mature forest habitat. After fencing and removing feral ungulates from the upper portions of the refuge, the restoration efforts expanded to include control of exotic plants and planting of native trees and shrubs, mostly koa (*Acacia koa*), ʻōhiʻa (*Metrosideros polymorpha*) and understory plants, but also several endangered plant species in the former pasture areas.

Nest searching and monitoring (along with banding and re-sighting) was centered around three sites within Hakalau: Pedro (PEDR; elevation 1,524 m), Koa Reforestation (KOAR; elevation 1,585 m), and Pua ʻĀkala (PUAK; elevation 1,890 m; Figure 1). The Pedro and Pua ʻĀkala sites are both mature ʻōhiʻa-koa forests with areas of dense, native understory as well as open areas of non-native grass. The Koa site is an even-aged, reforested koa stand (~ 16 years old) with little understory except non-native grasses and recently out-planted native shrubs.

Nest Finding and Monitoring
The field studies were conducted February 27th to May 6th, 2013, and February 11th to June 6th, 2014. Typically each of the three sites were visited daily, although weather and logistics

prevented visits on several occasions in both years. Nests of all species present were searched for and monitored over the course of the season. Nests were found for the following ten species: 'akepa, Hawai'i 'amakihi (*Hemignathus virens*), 'apapane (*Himatione sanguinea*),
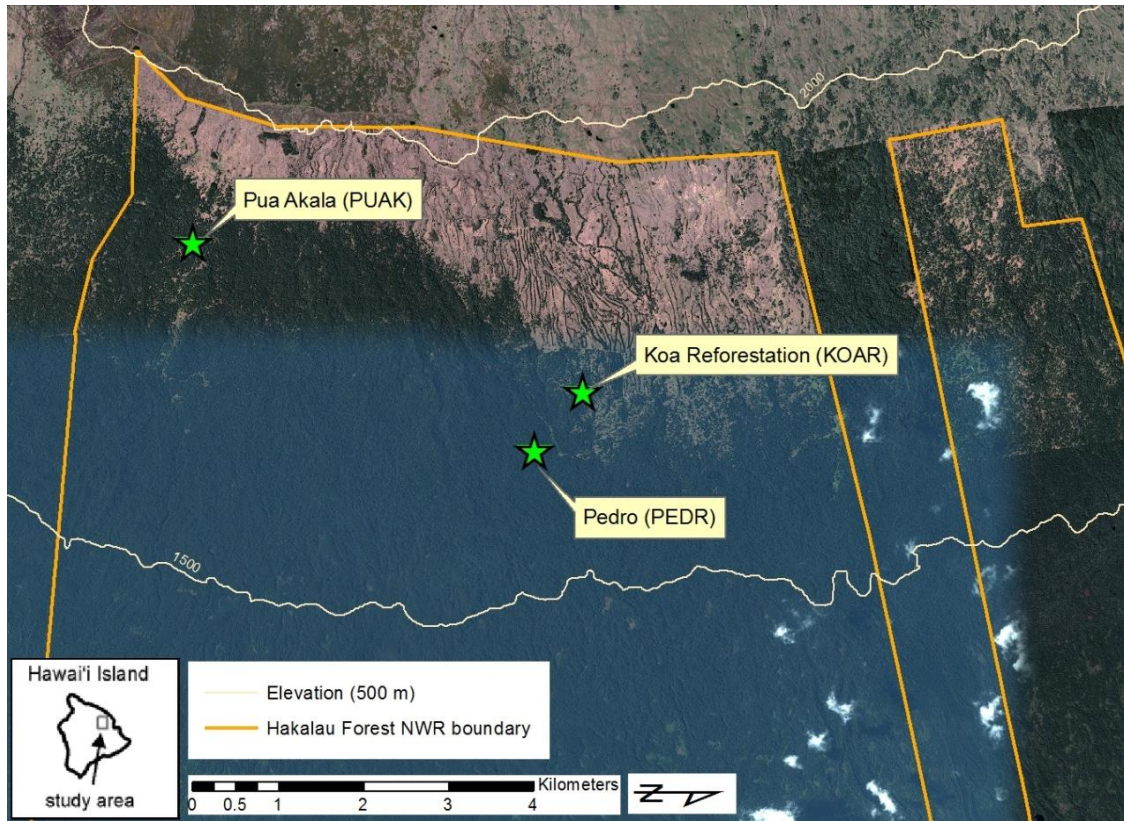
Figure 1. Location of the three forest bird productivity study sites within Hakalau Forest National Wildlife Refuge, Hawaii Island (outlined in orange).

Hawai'i creeper, Hawai'i 'elepaio (*Chasiempis sandwichensis*), 'i'iwi, 'ōma'o (*Myadestes obscurus*), Japanese white-eye (*Zosterops japonicus*), red-billed leiothrix (*Leiothrix lutea*), and northern cardinal (*Cardinalis cardinalis*). We did not locate any nests of the 'akiapola'au, one of the rare and endangered bird species also found in Hakalau. All species were being color-banded at these sites during the same period, and nest finding efforts were focused around capture locations (mist net lanes) to maximize the likelihood of finding nests with individually-marked adults. Nests were found most often using behavioral cues, but also by opportunistic searching in appropriate habitats.

Nests were monitored every two days until a transition date was determined (e.g. birds transitioned from nest building to incubating). Dates for the next transitions were then predicted, and the nest was visited every 3–4 days until nearing the next transition. Nests that were about to fledge were visited every day until they did so. Nest monitoring consisted of

watching a nest for up to 30 minutes with a spotting scope and using the birds' behaviors to determine the nest's stage. In 2013, some nests were low enough (<10 m) and in open enough vegetation that a mirror on an extendable fiberglass pole could be used to check nest contents (Figure 2). In 2014, we switched to wireless cameras (MBP26 Digital Wireless Video Baby Monitor, Motorola Mobility LLC, Chicago, IL) attached to the top of telescoping aluminum poles. A handheld video screen was used on the ground to see the contents of the nest in real time (Figure 2).

Figure 2. Checking contents of Hawai'i forest bird nests. We used a combination of wireless peeper video systems to check nests, such as an 'ōma'o nest (left), and a mirror mounted on an extendable pole, with the contents of a Hawai'i creeper nest showing nestlings (right).

A nest was not considered active until egg laying was confirmed, either by visually checking nest contents or observing (from afar) incubation behavior of attending adults. Once a nest was determined to be active, we used the following categories to classify eventual outcome of the specific nesting attempt:

1) **Successful** — Determined by seeing fledglings in the same tree as the nest on the fledge day, banded adults feeding fledglings after fledge day (Figure 3), or empty nests on fledge day that had healthy and active nestlings the day before

2) **Predated** — Determined either by witnessing a predation event, or assumed based on damage to the nest typical of a predator and/or the sudden disappearance of all nestlings/eggs prior to fledge age

3) **Abandoned** — Designated when nestlings or eggs are left unattended and nestlings are subsequently found dead in the nest, eggs went unhatched and there was no sign of adults for at least three nest checks prior to the full incubation period, or nest

became disheveled/dismantled while eggs are present, and no adult is seen at the nest for three nest checks

4) **Failed to Hatch** — Designated when a nest is incubated by parents beyond the normal incubation period, the eggs remained in the nest but never hatched, and the nest was eventually abandoned

5) **Storm/material Failure** — Designated when a nest is found blown out of a tree or destroyed by wind; or the nest structure is found otherwise broken, without predation of eggs or nestlings (e.g. the side of a cup droops and spills eggs on the ground, uneaten)

6) **Failure for Unknown Reasons** — Designated when a nest was determined to be no longer active prior to fledging, but for unknown reasons

7) **Unknown Fate** — Designated when a nest was not followed to completion, usually because the field season ended

In addition, we used the following two codes to designate nesting attempts that did not involve finding an active nest:

8) **Building Abandonment** — Designated when a nest was found in the building stage, but eggs were never laid

9) **Fledgling Found** — Noted when a banded adult was seen feeding a fledgling, but the physical nest was never found.

Fate numbers 7–9 are not included in known fate nest analysis. Nests were considered successful if meeting category 1 criteria, or failed if being categorized as 2–6.

Figure 3. ʻIʻiwi fledgling at Hakalau Forest National Wildlife Refuge. The visual sighting of fledglings is important evidence of successful fledgling.

Habitat and Weather Data
In 2014 the following data were taken for every active nest that was at least built to 50% completion: GPS location, nest and nest tree height, and nest tree species. Nest and tree height were measured using the sine method with a clinometer and laser rangefinder or a Nikon Forestry Pro (a device combining rangefinder and clinometer; Nikon Corporation, Tokyo, Japan).

Weather data for 2013 and 2014 was downloaded from a remote weather station (RAWS station run by USFWS, elevation 1,950 m) near the refuge administration site at Hakalau (daily max/average wind speed, min/average air temperature, and total precipitation). This station is about 360 m higher than the lowest site (Pedro), but is within 5 km of all sites. However, because it is higher in elevation and weather varies dramatically with relatively small changes in elevation (e.g., less precipitation at higher elevations), the study sites may have received more precipitation than recorded by the weather station.

Data Analysis

Apparent Nest Success
Apparent nest success was calculated as the number of successful nests divided by the total number of nests with known outcomes. Apparent nest success was calculated separately by species for each site and year. The mean number of fledglings for each species was calculated by averaging the number of chicks that were fledged from all successful nests of that species. The number of fledglings for a given nest is the number of chicks seen on the days prior to fledge, when nestlings were easiest to count (being larger and having their heads sticking above the cup of the nest). This is a minimum estimate, but nestlings the day or two prior to fledging should be fully visible to nest observers. If numbers vary in successive counts, then the chronologically-last number was used.

Daily Survival Rate
We calculated a Daily Survival Rate (DSR) for every species in which at least six active, known fate nests (2013 and 2014 combined) had been monitored ('apapane, Hawai'i 'amakihi, Hawai'i 'elepaio, Hawai'i creeper, i'iwi, Japanese white-eye, and red-billed leiothrix). A DSR provides an estimate of the average survival rate, per day, of nests categorized by species, site, and other factors that may influence nesting success (Dinsmore *et al*. 2002). We used Program MARK (version 7.2) to estimate DSR, considering the covariates year (2013, 2014), site (Pua ʻĀkala, Pedro, and Koa Reforestation), and nest height (m). We ran a set of models separately for each species, and used AICc model selection criteria to choose among the models (various combinations of the three covariates). We did not consider any models with interactions among covariates given the small sample sizes. Nest success was calculated by exponentiation of the DSR for the average nesting attempt length (in days, as discerned using the BNA accounts for each species). In the case of the nest height covariate, the B-value coefficient is reported instead of the calculated DSR. This value gives an indication of the relationship between the variable involved and the survival rate; in this case negative values indicate an inverse relationship where nest survival rates decrease with increasing height.

Nest Height
Nest heights for each species across both seasons were averaged and reported with 95% confidence intervals and range (calculated using Excel). This analysis included both known and unknown fate nests. The beta-value (B-value) derived from Program MARK and associated odds ratios for known fate nests were also reported for all species for which it could be calculated. To assess an interaction between year and nest height, we evaluated the two most common

honeycreepers, ʻiʻiwi and ʻapapane, in Program MARK. ʻAmakihi were excluded due to 100% nest success in 2013. The B-value for each species by year was found by splitting nests from each year into two groups within MARK for analysis, and comparing the results.

Weather
The daily weather data was compared to a daily DSR failure rate for all species combined both graphically and using a linear regression. Species were combined to derive a community-level assessment of weather effects, as single species DSR data are too sparse for this analysis. Maximum precipitation for a given date was calculated as the maximum rainfall occurring on that day or the preceding day, allowing for some lag effects of weather on DSR to be captured. The all-species DSR was converted into a percentage of nests failed by taking 1 minus the average of 3 consecutive days of DSR centered on the day of interest (i.e., a 3 day moving window average). The average precipitation over 3 days, minimum and average temperature, and wind speed were also compared with the daily DSR failure rate.

RESULTS

Nest Summary
A total of 340 nests were found over the two field seasons. Of those, 290 were active nests (2013 n = 86; 2014 n = 204) and the fate was known for 233 of those (2013 n = 50; 2014 n = 183). In another 12 cases; nest numbers were assigned to color-banded adults seen with recent fledglings on site, although no nest had been found (fate code number 9). Across both years 38 nests were found abandoned prior to incubation (2013 n = 8; 2014 n = 30). The four most common species found were Hawaiʻi ʻamakihi (2013 n = 17; 2014 n = 45), ʻapapane (2013 n = 17; 2014 n = 35), ʻiʻiwi (2013 n = 21; 2014 n = 31), and Japanese white-eye (2013 n = 7; 2014 n = 47). The increased number of nests found in 2014 was due to a longer field season and a larger field crew, but the relative number of nests found in each stage was very similar between the two field seasons. For example, 61% (n = 59) of nests in 2013 were found during incubation, compared to 59% (n = 141) in 2014. In 2013, 13% (n = 12) and 20% (n = 19) of nests were found during incubation and nestling stages, respectively, which was similar to 2014 rates of 19% (n = 46) and 15% (n = 37), respectively. The most nests were found at the Pua ʻĀkala site (2013 n = 37; 2014 n = 92), followed by Pedro (2013 n = 34; 2014 n = 72) and Koa Reforestation (2013 n = 27; 2014 n = 78).

For species with at least five known fate nests, apparent nest success across all sites ranged from 100% for ʻamakihi in 2013 to only 17% for Hawaiʻi ʻelepaio and Japanese white-eye in 2014. Overall, nest success was much higher in 2013, with only Hawaiʻi ʻelepaio increasing in success in 2014, although only one Hawaiʻi ʻelepaio nest was found in 2013 (Table 1). Although nest success varied considerably, differences between site or year and the number of fledglings produced did not vary as much, although all species except Hawaiʻi creeper averaged more fledglings per successful nest in 2014 (Table 1). Two species are not shown in Table 1 because very few nests were found, and even fewer had known fates. These species are northern cardinal (2013 n = 0; 2014 n = 4) and ʻōmaʻo (2013 n = 2; 2014 n = 3), are listed with the total number of nests found. Although all three sites had relatively high and equal apparent nest success in 2013 (Pua ʻĀkala = 0.75; Koa = 0.75; Pedro = 0.72), the Koa site had even lower success than the other two sites in 2014 (Pua ʻĀkala = 0.37; Koa = 0.21; Pedro = 0.38). Overall success between sites was higher at Pedro (0.48) and Pua ʻĀkala (0.45) than Koa (0.30).

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Table 1. Apparent nest success (% succ) for all known-fate nests and mean number of fledglings per successful nest (mean FL) by species, site, and year.

SPECIES		Pua 'Ākala n	% succ	mean FL	SE	Koa Reforestation n	% succ	mean FL	SE	Pedro n	% succ	mean FL	SE	Total n	% succ	mean FL	SE
AKEP	2013	2	0.50	1.00	0.00	0	--	--	--	0	--	--	--	2	0.50	1.00	0
	2014	2	0.00	--	--	0	--	--	--	1	1.00	2.00	0.00	3	0.33	2.00	0
	TOTAL	**4**	**0.25**	**1.00**	**0.00**	**0**	**--**	**--**	**--**	**1**	**1.00**	**2.00**	**0.00**	**5**	**0.40**	**1.50**	**0.5**
APAP	2013	3	1.00	2.00	0.58	1	1.00	2.00	0.00	5	0.80	2.50	0.29	9	0.89	2.25	0.25
	2014	10	0.40	2.50	0.29	5	0.20	3.00	0.00	17	0.35	2.20	0.37	32	0.34	2.40	0.22
	TOTAL	**13**	**0.54**	**2.29**	**0.29**	**6**	**0.33**	**2.50**	**0.50**	**22**	**0.45**	**2.33**	**0.24**	**41**	**0.46**	**2.33**	**0.16**
HAAM	2013	5	1.00	2.40	0.24	4	1.00	2.50	0.29	3	1.00	2.00	0.00	12	1.00	2.33	0.14
	2014	19	0.47	2.44	0.18	16	0.19	2.33	0.33	7	0.43	2.67	0.33	42	0.36	2.47	0.13
	TOTAL	**24**	**0.58**	**2.43**	**0.14**	**20**	**0.35**	**2.43**	**0.20**	**10**	**0.60**	**2.33**	**0.21**	**54**	**0.50**	**2.41**	**0.10**
HAEL	2013	0	--	--	--	1	0.00	--	--	0	--	--	--	1	0.00	--	--
	2014	2	0.00	--	--	4	0.25	2.00	0.00	0	--	--	--	6	0.17	2.00	0.00
	TOTAL	**2**	**0.00**	**--**	**--**	**5**	**0.20**	**2.00**	**0.00**	**0**	**--**	**--**	**--**	**7**	**0.14**	**2.00**	**0.00**
HCRE	2013	1	1.00	2.00	0.00	2	0.50	2.00	0.00	0	--	--	--	3	0.67	2.00	0.00
	2014	7	0.29	1.50	0.50	3	0.00	--	--	1	1.00	1.00	0.00	11	0.27	1.33	0.33
	TOTAL	**8**	**0.38**	**1.67**	**0.33**	**5**	**0.20**	**2.00**	**0.00**	**1**	**1.00**	**1.00**	**0.00**	**14**	**0.36**	**1.60**	**0.24**
IIWI	2013	7	0.71	1.60	0.24	2	0.50	2.00	0.00	8	0.63	1.80	0.20	17	0.65	1.73	0.14
	2014	19	0.53	1.78	0.15	0	--	--	--	9	0.56	2.00	0.32	28	0.54	1.86	0.14
	TOTAL	**26**	**0.58**	**1.71**	**0.13**	**2**	**0.50**	**2.00**	**0.00**	**17**	**0.59**	**1.90**	**0.18**	**45**	**0.58**	**1.80**	**0.10**
JAWE	2013	0	--	--	--	2	1.00	1.00	0.00	0	--	--	--	2	1.00	1.00	0.00
	2014	9	0.00	--	--	31	0.26	2.25	0.16	6	0.00	--	--	46	0.17	2.25	0.16
	TOTAL	**9**	**0.00**	**--**	**--**	**33**	**0.30**	**2.11**	**0.20**	**6**	**0.00**	**--**	**--**	**48**	**0.21**	**2.11**	**0.20**
RBLE	2013	1	0.00	--	--	0	--	--	--	2	0.50	1.00	0.00	3	0.33	1.00	0
	2014	6	0.33	2.50	0.50	1	0.00	--	--	4	0.25	3.00	0.00	11	0.27	2.67	0.33
	TOTAL	**7**	**0.29**	**2.50**	**0.50**	**1**	**0.00**	**--**	**--**	**6**	**0.33**	**2.00**	**1.00**	**14**	**0.29**	**2.25**	**0.48**

AKEP = 'akepa, APAP = 'apapane, HAAM = Hawai'i 'amakihi, HAEL = Hawai'i 'elepaio, HCRE = Hawai'i creeper, IIWI = 'i'iwi, JAWE = Japanese white-eye, RBLE = red-billed leiothrix

Most nests failed for unknown reasons (62%). These uncertainties were largely due to our inability to see inside many nests. However, abandonment contributed to 13% of all failed nests, while predation was the assumed cause of failure in 16% of nests (Table 2). The causes of abandonment and the main predators are unknown, although we did have one observation of an ʻio predating an ʻapapane nest. The only two species with more than two nests thought to be predated are the low nesting Japanese white-eye and red-billed leiothrix, which might indicate a ground-based predator (e.g., rats). The koa forest site also had higher recorded depredation events than the other two sites. While the Koa site did have proportionally more failures than other sites, we also have higher certainty in outcome because more nests could be reached with peeper cameras than other sites. In 2013, we could only determine the cause of failure of four nests due to much higher nest success and fewer total nests [two depredated red-billed leiothrix nests (Pedro and Pua ʻĀkala sites), one depredated Hawaiʻi creeper nest (Koa site), and one ʻelepaio with a clutch that failed to hatch (Koa site)].

Table 2. Nest failure causes for both years combined, with percentages of total failures. For each site and species, number predated, abandoned, failed to hatch, destroyed by storm or material failure, and failed for unknown reasons are listed (see Methods section for detailed explanations of each category).

Site/Species	Predated		Abandoned		Failed to Hatch		Storm/Material Failure		Unknown Reason		Total
	n	%	n	%	n	%	n	%	n	%	
KOAR	12	0.23	9	0.17	5	0.10	3	0.06	23	0.44	**52**
PEDR	4	0.12	1	0.03	0	0.00	0	0.00	28	0.85	**33**
PUAK	6	0.12	8	0.15	2	0.04	2	0.04	34	0.65	**52**
	22	**0.16**	**18**	**0.13**	**7**	**0.05**	**5**	**0.04**	**85**	**0.62**	**137**
AKEP	0	0.00	1	0.33	0	0.00	0	0.00	2	0.67	**3**
APAP	2	0.09	0	0.00	0	0.00	1	0.05	19	0.86	**22**
HAAM	1	0.04	3	0.11	1	0.04	1	0.04	21	0.78	**27**
HAEL	1	0.17	0	0.00	4	0.67	0	0.00	1	0.17	**6**
HCRE	2	0.22	3	0.33	0	0.00	1	0.11	3	0.33	**9**
IIWI	0	0.00	0	0.00	0	0.00	0	0.00	19	1.00	**19**
JAWE	10	0.26	9	0.24	1	0.03	1	0.03	17	0.45	**38**
NOCA	1	0.50	0	0.00	0	0.00	0	0.00	1	0.50	**2**
OMAO	0	0.00	1	1.00	0	0.00	0	0.00	0	0.00	**1**
RBLE	5	0.50	1	0.10	1	0.10	1	0.10	2	0.20	**10**

Daily Nest Survival Analysis

Our analysis of daily survival rate (DSR) indicated that year (presumably correlated with weather) was the strongest factor considered in terms of explaining variation in nest survival overall. Models with year-effect only were within two delta AIC values for all species except the Hawai'i creeper (Table 3). DSR decreased for every species in 2014 (except 'elpaio and red-billed leiothrix, which had only n = 1 and n = 3 in 2013, respectively) (Table 4). Differences between years were especially apparent for 'apapane and 'amakihi which decreased by 57% and 76% for a 33 day nesting period, respectively. Nest height appeared to be the second most important factor in explaining DSR, followed by site differences (Table 3). Site was important for some species, such as Hawai'i 'amakihi which showed markedly lower survival overall at the Koa site (30%) compared with 42% and 59% at the Pua 'Ākala and Pedro sites, respectively (Table 4). Nest height had a negative relationship with the four honeycreeper species (Table 4), suggesting decreasing nest survival with increasing nest height. Contrarily, the 'elepaio and the two non-native species had a positive relationship with nest height (Table 4). Null models, which have only the intercept (average values), also received model support, especially for the species with smaller sample sizes (with 'i'iwi a notable exception). This indicates that the factors considered have weak explanatory power for some species, or that nest survival is so variable that large sample sizes are needed to discern the effects from the measured factors.

Table 3. AICc model selection results of Daily Nest Survival modeling. Models selection was performed using all main-effect combinations of year, site, and nest height. The Year covariate represents 2013 and 2014, the Site covariate represents each site (Koa, Pedro, Pua 'Ākala), and the Nest height represents height measured in meters. A null model (intercept only) was included for each species. Only species with at least 6 known fate nests monitored are shown.

APAP

Model	AICc	Delta AICc	AICc weights	Model Likelihood	Num. Par	Deviance
Year	127.660	0.000	0.498	1.000	2	123.64
Nest height + year	129.221	1.562	0.228	0.458	3	123.18
Year + site	130.747	3.087	0.106	0.214	4	122.68
NULL	131.938	4.278	0.059	0.118	1	129.93
Nest height	132.259	4.600	0.050	0.100	2	128.24
Year + site + nest height	132.549	4.889	0.043	0.087	5	122.44
Site	135.685	8.026	0.009	0.018	3	129.64
Nest height + site	136.117	8.458	0.007	0.015	4	128.05

HAAM

Model	AICc	Delta AICc	AICc weights	Model Likelihood	Num. Par	Deviance
Nest height + year	180.238	0.000	0.621	1.000	2	176.22

Year	181.876	1.639	0.274	0.441	2	177.86
Year + site	184.668	4.430	0.068	0.109	4	176.62
Year + site+ nest height	185.865	5.627	0.037	0.060	5	175.80
NULL	203.782	23.545	0.000	0.000	1	201.78
Site	205.390	25.152	0.000	0.000	3	199.36
Nest height	205.736	25.499	0.000	0.000	2	201.72
Nest height + site	206.495	26.257	0.000	0.000	4	198.45

HAEL

NULL	35.194	0.000	0.375	1.000	1	33.16
Site	36.895	1.701	0.160	0.427	2	32.79
Year	37.185	1.991	0.138	0.370	2	33.08
Nest height	37.227	2.033	0.136	0.362	2	33.12
Year + site	38.759	3.566	0.063	0.168	3	32.54
Nest height + site	38.910	3.716	0.058	0.156	3	32.69
Nest height + year	39.288	4.094	0.048	0.129	3	33.07
Year + site+ nest height	40.889	5.695	0.022	0.058	4	32.53

HCRE

Site	59.738	0.000	0.267	1.000	2	55.69
NULL	60.447	0.710	0.188	0.701	1	58.43
Nest height + site	60.846	1.108	0.154	0.575	3	54.74
Year + site	60.919	1.181	0.148	0.554	3	54.82
Year	62.123	2.386	0.081	0.303	2	58.07
Nest height	62.471	2.734	0.068	0.255	2	58.42
Year + site+ nest height	62.644	2.907	0.063	0.234	4	54.47
Nest height + year	64.012	4.275	0.032	0.118	3	57.91

IIWI

Year	141.808	0.000	0.423	1.000	2	137.79
NULL	143.249	1.441	0.206	0.486	1	141.24
Nest height + year	143.782	1.975	0.157	0.373	3	137.75
Nest height	144.973	3.165	0.087	0.206	2	140.96
Year + site	145.739	3.932	0.059	0.140	4	137.68
Site	147.008	5.200	0.031	0.074	3	140.97
Year + site+ nest height	147.643	5.836	0.023	0.054	5	137.56
Nest height + site	148.608	6.800	0.014	0.033	4	140.55

JAWE

Nest height + year	214.793	0.000	0.460	1.000	2	210.77
Year	215.446	0.653	0.332	0.722	2	211.42
Year + site	218.404	3.611	0.076	0.164	4	210.33
NULL	219.328	4.535	0.048	0.104	1	217.32
Year + site+ nest height	220.083	5.291	0.033	0.071	5	209.97
Nest height	220.336	5.543	0.029	0.063	2	216.31
Site	221.496	6.703	0.016	0.035	3	215.45
Nest height + site	223.019	8.227	0.008	0.016	4	214.95

RBLE

Nest height	50.001	0.000	0.306	1.000	2	45.89
NULL	50.250	0.249	0.271	0.883	1	48.21
Year	51.590	1.589	0.138	0.452	2	47.48
Nest height + year	51.812	1.812	0.124	0.404	3	45.59
Nest height + site	53.105	3.105	0.065	0.212	4	44.72
Site	53.836	3.836	0.045	0.147	3	47.61
Year + site+ nest height	54.879	4.878	0.027	0.087	5	44.30
Year + site	55.094	5.093	0.024	0.078	4	46.71

Table 4. Daily Nest Survival (DSR) estimates for each factor by species. For a given level (as well as overall average), sample size, average DSR, standard error (SE), confidence interval, and average nest success are shown. Average nest success is calculated as the DSR raised to the average number of days a nest is active by species, with average being 33 days for APAP and HAAM; 34 days for HAEL; 35 days for HCRE; 36 days for IIWI; and 23 and 24 days for JAWE and RBLE, respectively. In the case of nest height, the B-value coefficient is reported, which represents the slope of the relationship between nest height and DSR, with negative values indicating decreasing DSR with increasing nest height. Only species with at least 6 known fate nests monitored are shown. Results not shown for a particular factor if sample size is less than 3.

APAP

Factor	Level	n	DSR/B	SE	Average (Lower CI, Upper CI)	Nest Success	(Lower CI, Upper CI)
Average		38	0.966	0.007	(0.948, 0.978)	0.324	(0.175, 0.484)
Habitat	PUAK	12	0.972	0.013	(0.934, 0.988)	0.387	(0.104, 0.675)
	KOAR	5	0.969	0.018	(0.907, 0.990)	0.348	(0.040, 0.714)
	PEDR	21	0.963	0.011	(0.936, 0.979)	0.287	(0.112, 0.494)
Year	2013	9	0.994	0.006	(o.955, 0.999)	0.807	(0.222, 0.970)
	2014	29	0.957	0.010	(0.933, 0.972)	0.234	(0.103, 0.397)
Nest height (m)	m	38	-0.059	0.046	(-0.151, 0.032)		

HAAM

Factor	Level	n	DSR/B	SE	Average (Lower CI, Upper CI)	Nest Success	(Lower CI, Upper CI)
Average		54	0.973	0.005	(0.960, 0.981)	0.404	(0.267, 0.537)
Habitat	PUAK	24	0.974	0.008	(0.952, 0.986)	0.423	(0.202, 0.629)
	KOAR	20	0.964	0.010	(0.938, 0.978)	0.296	(0.123, 0.494)
	PEDR	10	0.984	0.008	(0.958, 0.993)	0.587	(0.243, 0.819)
Year	2013	12	1.000	0.000	(1, 1)	1.000	(1, 1)
	2014	42	0.958	0.008	(0.939, 0.971)	0.244	(0.128, 0.380)
Nest height (m)	m	54	-0.012	0.050	(-0.11, 0.086)		

HAEL

Average		6	0.964	0.016	(0.916, 0.984)	0.289	(0.051, 0.598)
Habitat	KOAR	4	0.970	0.017	(0.911, 0.990)	0.358	(0.043, 0.719)
Year	2014	5	0.966	0.017	(0.913, 0.987)	0.309	(0.045, 0.645)
Nest height (m)	m	6	0.029	0.145	(-0.25, 0.311)		

HCRE

Average		14	0.964	0.012	(0.932, 0.981)	0.280	(0.087, 0.517)
Habitat	PUAK	8	0.959	0.018	(0.904, 0.982)	0.228	(0.029, 0.542)
	KOAR	5	0.958	0.020	(0.894, 0.984)	0.226	(0.020, 0.575)
Year	2013	3	0.978	0.022	(0.861, 0.996)	0.463	(0.005, 0.898)
	2014	11	0.961	0.013	(0.924, 0.980)	0.250	(0.063, 0.501)
Nest height (m)	m	14	-0.012	0.120	(-0.24, 0.222)		

IIWI

Average		45	0.975	0.006	(0.961, 0.984)	0.403	(0.241, 0.560)
Habitat	PUAK	26	0.972	0.008	(0.950, 0.984)	0.364	(0.161, 0.571)
	PEDR	17	0.978	0.008	(0.954, 0.989)	0.447	(0.186, 0.682)
Year	2013	17	0.985	0.006	(0.967, 0.993)	0.580	(0.298, 0.783)
	2014	28	0.964	0.010	(0.939, 0.979)	0.269	(0.104, 0.467)
Nest height (m)	m	45	-0.041	0.077	(-0.19, 0.110)		

JAWE

Average		48	0.938	0.010	(0.915, 0.954)	0.227	(0.130, 0.340)
Habitat	PUAK	9	0.919	0.026	(0.850, 0.957)	0.142	(0.024, 0.365)
	KOAR	33	0.946	0.011	(0.920, 0.964)	0.282	(0.149, 0.431)
	PEDR	6	0.913	0.034	(0.818, 0.960)	0.122	(0.010, 0.393)

Year	2014	46	0.933	0.011	(0.908, 0.950)	0.201	(0.110, 0.312)
Nest height (m)	m	48	0.050	0.050	(-0.04, 0.148)		

RBLE

Average		13	0.927	0.023	(0.865, 0.961)	0.163	(0.031, 0.391)
Habitat	PUAK	6	0.933	0.032	(0.835, 0.974)	0.190	(0.013, 0.541)
	PEDR	6	0.930	0.034	(0.828, 0.973)	0.176	(0.010, 0.526)
Year	2013	3	0.869	0.087	(0.595, 0.967)	0.034	(4.016, 0.451)
	2014	10	0.935	0.024	(0.870, 0.968)	0.201	(0.035, 0.468)
Nest height (m)	m	13	0.448	0.334	(-0.20, 1.102)		

Nest Height

Species that typically nest lower (Japanese white-eye and red-billed leiothrix) had greater nest success with increasing nest height, while the opposite was true of species that typically nest higher (honeycreepers; Tables 3–5). We evaluated whether this relationship held true across both years, but could only do so for two species, 'i'iwi and 'apapane. The relationship between nest success and nest height was similar for the two species analyzed, with a positive relationship in 2013 (B-value coefficient = 0.0084 for 'i'iwi and 0.1328 for 'apapane), but a negative relationship in 2014 (B-value = -0.0536 for 'i'iwi and -0.0278 for 'apapane).

Table 5. Mean nest height by species, including unknown fate nests. Coefficient values (B-value) from Daily Nest Survival analysis of known fate nests only (only for those species with sufficient information; Table 3) is included with its associated odds ratio (the odds of nest success for each additional meter in height from ground level; values below 1.0 indicate decreasing odds with increasing height).

|	n	Mean Height (m)	L 95% CI	H 95% CI	Min Height	Max Height	B-value	Odds Ratio
AKEP	12	11.94	9.21	14.66	3.2	18.2		
APAP	51	13.54	12.26	14.81	4.4	23.5	-0.059	0.942
HAAM	60	12.85	11.89	13.80	5	20	-0.012	0.988
HAEL	19	9.99	8.72	11.26	3.6	15.2	0.029	1.029
HCRE	15	9.38	7.87	10.90	4.4	12.8	-0.012	0.988
IIWI	52	12.85	11.90	13.79	4.8	21	-0.041	0.960
JAWE	54	7.11	6.23	7.99	1.5	14.2	0.050	1.051
NOCA	3	5.40	-0.13	10.93	3	7.4		
OMAO	4	5.20	1.41	8.99	2	7.6		
RBLE	18	2.69	1.82	3.56	0.5	6.8	0.448	1.566
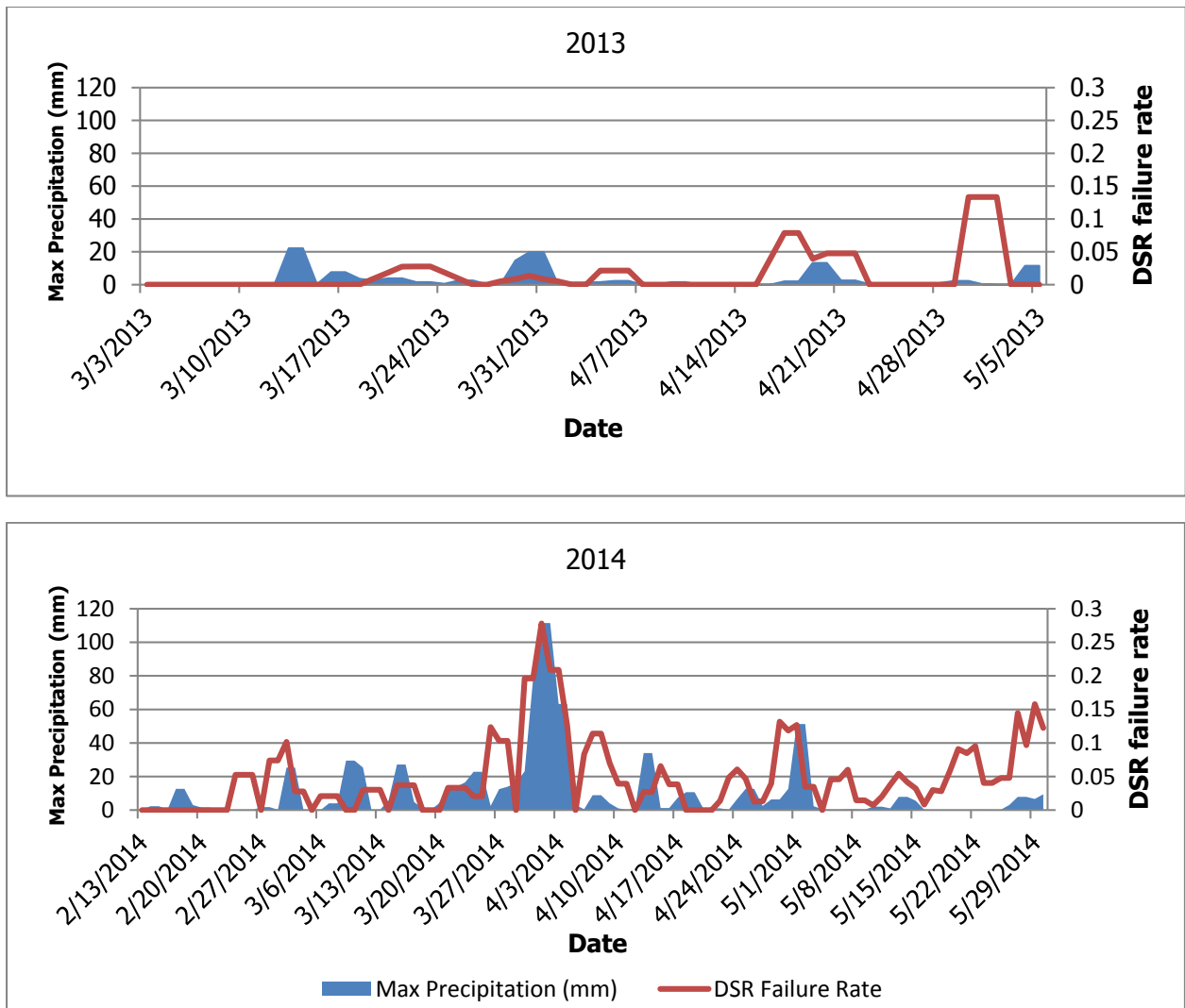
Figure 4. Relationship between precipitation (2-day maximum) and daily nest failure rate (1-Daily Survival Rate; 3-day average) for 2013 (top panel) and 2014 (bottom panel).
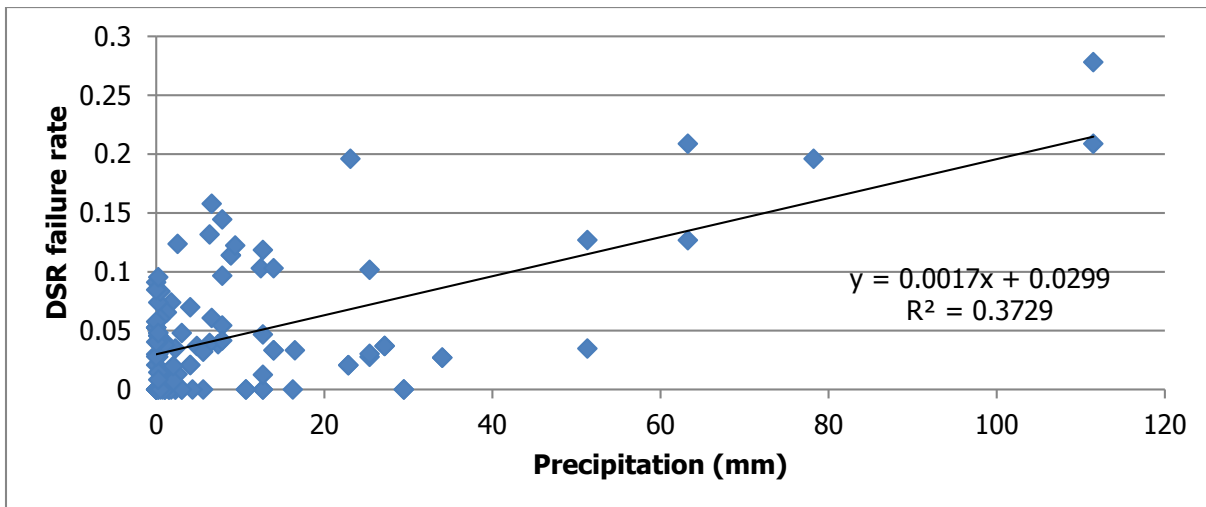
Figure 5. Statistically significant relationship ($R^2 = 0.37$, $P < 0.001$) between maximum precipitation (two-day moving maximum) and DSR failure rate (1-daily survival rate, 3-day moving average) for 2014. In 2013, there was only one storm with rainfall > 20 mm, and no statistical relationship between nest failure and rainfall.

DISCUSSION

Nest survival was dramatically different between the two years of this study and analysis of DSR showed Year as one of the strongest covariates. Almost all species showed a decrease in success in the second year, which was much wetter throughout the season. In both years, we found similar proportions of nests in each of the different nesting stages, so any differences in nest success should be due to reasons other than search effort. However, sample sizes were very different in the two years and more years are needed to understand year to year variation. Winter storms have been shown to have a large impact on productivity of 'i'iwi at Hakalau, potentially because of high precipitation amounts and cooler temperatures associated with these events (Kuntz 2008). Weather data collected during 2014 shows a correlation between higher rain events and lower DSR for all species combined. Along with several weather-damaged nests, there were almost as many abandoned nests as depredation events in 2014, and more abandonments than depredations in native species. Despite nest predation being identified as a key cause of nest failure and a strong driver of avian life histories (Conway and Martin 2000, Payevsky 2008, Woodworth and Pratt 2009), this study indicated that storm system effects on the breeding success of these species may play a larger role in the islands of Hawai'i than in other systems. Heavy rain may cause parents to choose between incubation/feeding young and maintaining their own health. Under especially heavy or long-lasting rain, it may be too difficult to shelter eggs/nestlings from water and cooler temperatures. 'Apapane and Hawai'i 'amakihi had relatively large sample sizes in both years and showed large decreases in success between the years (55% and 64% reductions, respectively). Interestingly, both of these species also showed lower success at the Koa site compared with the other two sites in 2014. The generalist, Hawai'i 'amakihi, live in a variety of habitats, and are early colonizers of koa reforested areas (Camp *et al*. 2010), yet our data suggest they have lower nesting success in reforested forests, at least during rainy years. During the drier 2013 however, there was no difference in success between the habitats. This difference may indicate that restoration forest is less protective in adverse weather conditions. The only species with

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ample sample size that showed more success at the Koa site was the Japanese white-eye, and even it had low success in 2014 (but zero success at the other sites).

Rainy weather seems to affect all species, leading to dramatic differences in nest success during the same period of the breeding season. This kind of climatic effect can particularly impact species with small populations (such as many of the Hawaiian honeycreepers) because environmental stochasticity and catastrophes are associated with higher rates of extinction (Shaffer 1981). This effect is especially an issue on the Hawaiian Islands because habitat loss in low and high elevation areas and mosquito-borne disease has restricted native species to a relatively narrow band of high elevation forests, leaving no room for population expansion regardless of available habitat at lower elevations. This restricted distribution of native species at the highest elevations may make their reproductive efforts more vulnerable to storms that will be colder at higher elevations, when historically they occupied a much larger elevation range, including the warmer lower elevation habitats. However, these species are relatively long lived (Woodworth and Pratt 2009), and this may dampen environmental stochastic effects on productivity by allowing an individual more time to reproduce successfully (and indeed, these effects may have led to a low productivity life history strategy). The long breeding season in Hawaiʻi also helps boost productivity, and allows more chances for a successful season. Many hatch-year birds were observed and captured for the banding study throughout Hakalau at the beginning of the 2014 season, indicating a significant amount of successful breeding prior to the beginning of the nesting study. This suggests that while we documented very low success in the 'peak' period of the breeding season, many birds may have had successful seasons when considering the full breeding season.

Although weather seems to be the primary factor affecting nest success at Hakalau, other variables may also be important. Nest survival rates at the lower and higher elevation mature forest sites (Pedro and Pua ʻĀkala, respectively) were similar, but there were differences when comparing those two sites to the third site — the even-age, reforested koa stand. Both Pedro and Pua ʻĀkala have breeding populations of all species while the Koa site does not — ʻiʻiwi and ʻakepa have not been detected breeding there at all, and ʻōmaʻo and red-billed leiothrix nests were found in very limited numbers. During the drier 2013, there was no difference in ʻamakihi nest survival among the sites, while in the wetter 2014 season, success dropped off more at Koa than the other two sites. Also in 2014, Japanese white-eye showed higher success (albeit still very low) at the Koa site than the other sites (not enough Japanese white-eye nests with known fates were found at any site in 2013 to make statistical comparisons). This difference reflected in part the lack of successful Japanese white-eye nests found in the mature forest sites and a notably high level of nesting activity in the Koa site. Both species are foraging and nesting generalists, and in recent years have been able to expand populations into all types of habitat in Hawaiʻi. This study shows that although ʻamakihi utilize young (approximately 16–20 year old) reforested habitat, they may not be as productive there during years of poor weather. If regenerating forests provide less protection from large storms, this could reduce the quality of the habitat, something surveys alone would not detect. Japanese white-eyes, which nest in high numbers at the Koa site, did not have higher success there than ʻamakihi in 2014, but they were unsuccessful in all attempts in the mature forests. This suggests the white-eyes may be better adapted to young regenerating forests, although more years are needed to understand general patterns.

The results also show an interesting trend in nest height, potentially indicating opposite selective pressures acting to keep nest heights towards a middle range. Within species that

have higher nest placement, individuals had more success at lower nest heights in the wetter 2014 season, while the opposite was true in the drier 2013. Inclement weather may cause the highest nests to fail, as placement in the highest terminal branches may make them more vulnerable to wind buffeting, expose them more directly to rainfall, and may provide less microclimate buffering compared to lower canopy locations. These possible negative effects of high nest placement in stormy years may place an upper limit on ideal nest placement for these canopy-nesting species. However, nest success was also low at the other end of the height spectrum, with both red-billed leiothrix and Japanese white-eye (the lowest nesting species) gaining success as nest height increased. These two species also recorded the most depredation events. Predation from small mammals is probably greatest among the lowest nests, especially those placed in small trees and shrubs in the understory, which both species utilize. For the two species that we could evaluate differences between nest height and DSR in 2013 and 2014 ('i'iwi and 'apapane), there was evidence of a positive relationship in DSR and nest height in the non-stormy year (2013), and a negative relationship in the stormy year (2014). If the positive relationship in 2013 was driven by predation (e.g., rats), and the negative relationship in 2014 driven by weather, the pressures of constant predation and stochastic weather events may combine to balance selection within a species for nests not too high, and not too low.

This study has provided valuable information on the productivity of Hakalau's forest bird community, but it also shows how difficult it is to draw conclusions from just two years of data at three sites of different types. Attempting to estimate productivity for a whole community of birds requires several years of investigation, and ideally replicated sites, especially for species with few or difficult to locate nests. Additionally, interpreting the many factors involved in nest success, both at an individual and landscape level, is difficult when unpredictable variables such as weather can profoundly affect the system. Many questions are left to be investigated for tropical bird species in general, such as how climate and weather affect resource availability, nest predators activity levels and behavior, and the annual timing of breeding (Young 1994, Brawn *et al.* 2011). Combining a long term demographic data set with in depth studies targeting individual aspects of productivity can shed light on these issues. Parental nesting behaviors, responses to predators, and movement patterns in relation to breeding, food resources, and weather are some examples of such studies.

The productivity rates in this study compare favorably with those reported for some native Hawaiian species, but are different for others. 'I'iwi had much higher nest success in our study, even in 2014, with both apparent nest success (58%) and DSR (0.975) greater than the maximum reported in Woodworth and Pratt (2009; 53% and 0.973, respectively). In contrast, our overall estimates for 'apapane were lower than the minimum that they reported — 46% and 0.966 compared to 48.5% and 0.973, respectively. Other species such as Hawai'i 'amakihi were within the range of reported nest survival rates. The main causes of failure (predation and abandonment or starved chicks) are the same for our study as that reported in Woodworth and Pratt (2009). Our estimates for the number of chicks fledged per successful nest was within the range of those reported for 'apapane, Hawai'i creeper, and 'i'iwi. Other species did not have enough information, either in our data or in reported estimates, showing a need for further research into this vital demographic rate.

Given that surveys show population trend patterns alone, they cannot give managers all the information they need to protect these species and their habitats. Noting the large difference in nest survival and the very different conditions between the first two years of this demographic

study, it is highly desirable to continue monitoring of these populations for at least a further two years to enable more accurate predictions of productivity over time. Combined with concurrent parental behavior, survival, and landscape movement studies, the factors affecting nest success and overall productivity can be determined. Identifying these factors and their intensity is crucial for efficient management and the use of limited conservation funds. The results from this long-term study will not only apply to Hakalau, but to the whole state of Hawaiʻi, as these environments share many of the same unique features that also separate them from other ecological systems.

ACKNOWLEDGEMENTS

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