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Improved status of the conservation reliant Oahu Elepaio through effective management and natural adaptation

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Abstract

The Oahu Elepaio (*Chasiempis ibidis*) is an endangered forest bird endemic to the Hawaiian island of Oahu. The two most serious threats to the Oahu Elepaio are nest predation by nonnative black rats (*Rattus rattus*) and avian pox (*Avipoxvirus* spp.), a disease carried by nonnative mosquitoes. The Oahu Elepaio is conservation reliant because its continued existence depends on rat control. We used 27 years of data from 1995 to 2021 on pox prevalence, nest success, and fecundity with versus without rat control to reexamine the severity of these threats. Prevalence of avian pox declined over time. From 1995 to 2004, pox prevalence averaged 21% ± 4% per year and was positively related to annual rainfall. From 2005 to 2021, pox prevalence was only 2% ± 0.1% and despite several wet years there was no relationship with rainfall. The Oahu Elepaio appears to have evolved resistance to the pox variant currently in Hawaii. Elepaio nest success was higher with rat control (58% ± 1%) than without rat control (42% ± 6%). Nest success did not differ significantly between native tree species (52% ± 6%) and nonnative tree species (58% ± 6%) or between fruiting tree species (58% ± 1%) and nonfruiting species (61% ± 6%). Elepaio annual fecundity was higher with rat control (0.78 ± 0.02) than without rat control (0.48 ± 0.04) and varied among sites and years. The two primary threats to the species have been ameliorated through a combination of effective management and natural adaptation. The species' status should continue to improve if management is maintained, and someday, if patterns of natural adaptation continue, it could break free from conservation reliance.

KEYWORDS
avian pox, conservation reliant, Hawaiian birds, invasive predators, nest success, Oahu Elepaio

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1 | INTRODUCTION

Identifying the threats responsible for causing a species to decline is essential for implementing effective conservation actions (Moore et al., 2021). However, some threats can be difficult to manage or even impossible to eliminate on a permanent basis (Baxter et al., 2008; Doherty et al., 2016; McCallum, 2012), and species facing such threats have been called "conservation reliant" because their continued existence is reliant on management in perpetuity (Reed et al., 2012; Scott et al., 2010). Conservation reliance is especially common on islands because island environments are particularly vulnerable to invasion and island species that evolved in isolation often lack natural defenses to novel threats and may have reduced evolutionary capacity (Salo et al., 2007; Sih et al., 2010; VanderWerf, 2012).

Few species listed under the U.S. Endangered Species Act have been delisted because of effective management and consequent recovery, and many are likely to remain listed indefinitely and thus can be considered conservation reliant (Doremus & Pagel, 2001; Taylor et al., 2005). In this study, we describe how management of an invasive predator was used to indirectly facilitate natural adaptation to an invasive pathogen that was difficult to manage, and how this may provide a rare example in which an endangered island bird species eventually could break free from conservation reliance.

The Oahu Elepaio (*Chasiempis ibidis*), a territorial, non-migratory monarch flycatcher (Monarchidae) endemic to the Hawaiian island of Oahu (VanderWerf, 2020), has declined severely in the last few decades and occupies less than 4% of its presumed prehistoric range and only 25% of the range occupied in 1975 (VanderWerf et al., 2013). In 2011, the total population was estimated to be 1261 birds (95% CI = 1181–1343) and the fragmented range was estimated to be 5187 ha (Figure 1; VanderWerf et al., 2013). The Oahu Elepaio was listed as endangered under the U.S. Endangered Species Act in 2000 (USFWS, 2000, 2006).

The two most serious threats to the Oahu Elepaio are nest predation by nonnative black rats (*Rattus rattus*) and avian pox, a disease caused by a virus (*Avipoxvirus* spp.) that is carried by nonnative mosquitoes (hereafter "pox"; USFWS, 2006; VanderWerf et al., 2006; VanderWerf, 2009). VanderWerf and Smith (2002) showed that rat control is an effective tool for managing nest predation, resulting in higher nest success (61% vs. 33%), higher annual fecundity (0.71 ± 0.05 SE vs. 0.33 ± 0.07 SE fledglings per pair), and higher survival of nesting females. Following initial success of rat control, this management tool has been implemented in several areas by multiple agencies and has become the cornerstone of the conservation strategy for the species (VanderWerf, 2009; VanderWerf et al., 2011).

Diseases carried by nonnative mosquitoes, primarily avian malaria (*Plasmodium relictum*) and avian pox, have been the most serious threat to endemic Hawaiian forest birds and continue to cause extinctions (Atkinson & LaPointe, 2009; Paxton et al., 2016; van Riper et al., 2002). The three elepaio species are less affected by mosquito–borne diseases than most Hawaiian forest birds, but pox is still a threat. Oahu Elepaio with pox lesions had 4%–10% lower annual survival than elepaio with no pox symptoms (VanderWerf, 2009). Pox prevalence in the Oahu Elepaio has been variable but high in some years, with up to 47% of birds captured exhibiting active lesions. VanderWerf et al. (2006) found that pox prevalence was higher in years with higher rainfall, which presumably created more breeding habitat for mosquitoes. Climate change is expected to allow altitudinal range expansion of mosquitoes in Hawaii, which would increase the severity of this threat for other Hawaiian forest birds (Atkinson & LaPointe, 2009; Benning et al., 2002; Garamszegi, 2011; Paxton et al., 2016, Fortini et al., 2017), but not for the Oahu Elepaio because the island has no mountains high enough to provide refuge from the cold-intolerant mosquitoes that carry the pathogens, and mosquitoes are already present throughout their range (VanderWerf et al., 2006).

The three elepaio species are adaptable in many ways, which likely has allowed them to persist while many other endemic Hawaiian forest birds have become extinct. Elepaio are flexible in foraging behavior and diet (VanderWerf, 1993, 1994, 2020) and readily forage and nest in a variety of tree species and forest types, including forest dominated by nonnative plants (VanderWerf, 2004; VanderWerf, 2020; VanderWerf & Young, 2016). VanderWerf (2012) showed that the Oahu Elepaio has evolved to nest higher off the ground in response to nest predation by rats. The Oahu Elepaio breeding season is flexible and has shifted in response to changing seasonal rainfall patterns and associated resource availability (VanderWerf et al., 2021). In addition, the Oahu Elepaio is the only Hawaiian bird that has been observed anting, a behavior that is thought to inhibit parasites or pathogens (VanderWerf, 2005, 2020). All the plant and animal species it has been observed to use for anting were introduced to Hawaii recently by humans, providing another, unusual demonstration of the capacity for learning and adaptation in this species.

There is an interface between management and evolution that offers opportunities to facilitate adaptations that increase resiliency to threats (Luo et al., 2011; Valenzuela-Sánchez et al., 2021). For example, VanderWerf and Smith (2002) advocated the use of rat control to accelerate evolution of disease resistance in the Oahu Elepaio. In this scenario, reducing predation through rat control would increase survival and reproduction

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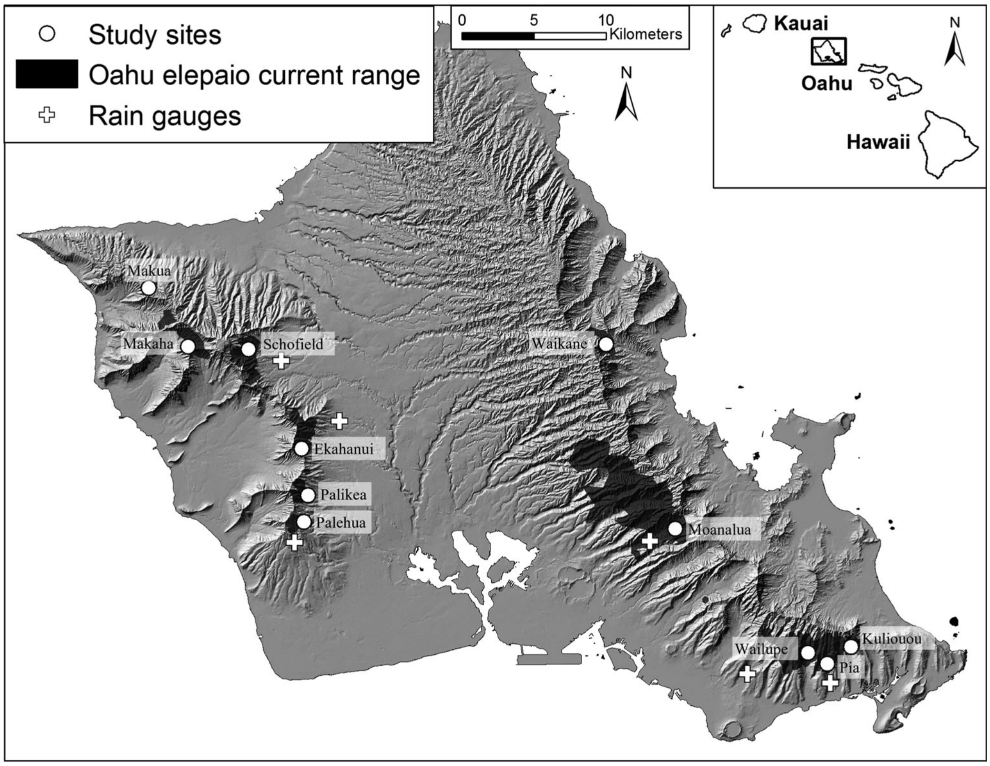

FIGURE 1 Range of the Oahu Elepaio as of 2011, with study site locations and rain gauges used in this study

of disease-resistant individuals, which would have disproportionately higher population growth, thereby increasing the frequency of genes responsible for disease resistance in subsequent generations. Kilpatrick (2006) expanded on this idea and quantitatively demonstrated the potential increase in population growth rates that might result from this approach in various species of Hawaiian forest birds.

VanderWerf (2009) speculated that the Oahu Elepaio suffers from higher rates of nest predation than the Kauai Elepaio (*C. sclateri*) and the Hawaii Elepaio (*C. sandwichensis*) because the forests where most remaining Oahu Elepaio occur are dominated by nonnative, fruit- or nut-bearing trees that that are attractive to rats. Determining whether nest success differs between native versus nonnative and fruiting versus nonfruiting tree species would be valuable. Variation in nest predation in forests with different species composition or structure could offer another opportunity to facilitate adaptation in the breeding biology of the Oahu Elepaio and perhaps other bird species.

The purpose of this paper is to provide an update on the conservation status of the Oahu Elepaio, focusing on the severity of the two primary threats to the species, nest predation by nonnative rats and avian pox. New tools for controlling rats have become available since this issue was last investigated (VanderWerf et al., 2011), and we expected that improved management may have resulted in increased elepaio reproduction. The potential to manage the threat from pox indirectly through rat control had been shown theoretically (Kilpatrick, 2006), but empirical data on pox prevalence had not been examined since 2004 (VanderWerf et al., 2006). We addressed these issues using a long-term data set spanning 27 years from 1995 to 2021.

2 | METHODS

2.1 | Study species

The Oahu Elepaio is nonmigratory and sedentary, and pairs defend all-purpose territories 1–2 ha in size (VanderWerf, 2020). They are insectivorous and eat insects, spiders, and other arthropods that they catch from many different substrates in a variety of forest types (VanderWerf, 1994, 2018). Both sexes build the nest, incubate the eggs, and feed the nestlings. Only the female incubates and broods at night, leading to higher predation on females by nocturnal rats and a skewed sex ratio in some areas (VanderWerf, 2009; VanderWerf et al., 2013). The clutch size is usually two eggs, occasionally one or three. Double-brooding is uncommon and occurs more often in years with higher rainfall (VanderWerf et al., 2019). Fledglings are fed by their parents for 4–6 weeks and are easy to locate by their persistent begging calls (VanderWerf, 2020).

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2.2 | Study sites

We studied elepaio in 11 sites that encompassed all large remaining subpopulations of the species (Figure 1). Six sites were located in the Waianae Mountains of western Oahu (Ekahanui, Makaha, Makua, Palehua, Palikea, and Schofield Barracks) and five sites were located in the Koolau Mountains of eastern Oahu (Kuliouou, Moanalua, Pia, Waikane, and Wailupe). Prevailing winds from the northeast cause generally higher rainfall in the Koolau Mountains and a rain shadow in the Waianae Mountains, with Moanalua and Waikane being the wettest study sites and Makaha and Makua being the driest. Forest in all sites was dominated by nonnative plants, but several sites (Ekahanui, Makaha, Makua, Palikea, and Schofield Barracks) also supported substantial amounts of native vegetation.

2.3 | Pox prevalence

We mist-netted and banded elepaio year-round from 1995 to 2021 and inspected them for visible signs of pox. As described by VanderWerf et al. (2006), we categorized each elepaio as being healthy or having active pox or inactive (healed) pox. We regarded elepaio with soft swellings, warty growths, open sores, or crusty scabs on the toes, feet, legs, bill, or face as having active pox, and those with missing or deformed toes, feet, or bill as having inactive or healed pox (Figure S1). We regarded elepaio with no visible symptoms as healthy. We categorized elepaio with healed pox separately because the deformities persist for the remainder of the bird's life and can obfuscate temporal patterns of pox prevalence. We did not confirm the pox diagnosis with histopathology or genetic testing because collecting a tissue sample by biopsy from such a small bird could have exacerbated the lesions and we did not want to risk increasing mortality in this endangered species (VanderWerf et al., 2006). No other pathogen known to occur in Hawaii causes cutaneous lesions like those observed in elepaio. Presence of the distinctive cutaneous lesions is a common method of identifying birds infected with pox and has been used in many previous studies (e.g., Atkinson et al., 2005; McNew et al., 2021; Parker et al., 2011; van Riper et al., 2002; Zylberberg et al., 2012).

We calculated annual pox prevalence as the number of individuals with active pox divided by the total number of birds captured each year. We examined active pox prevalence over time using multiple linear regression, with pox prevalence as the dependent variable and year and annual rainfall as continuous predictors. We calculated a single measure of annual rainfall by averaging rainfall from six National Weather Service gauges (Figure 1; Moanalua, Niu Valley, Palolo Fire Station, Kunia Substation, Schofield Barracks, and Palehua) that were closest to the study sites. We examined the relationship between pox prevalence during two time periods, 1995–2004, which was analyzed previously by VanderWerf et al. (2006), and 2005–2021, which has not been analyzed previously.

2.4 | Rat control

Rats were first controlled to protect Oahu Elepaio in the southeastern Koolau Mountains using an experimental approach in which rats were not controlled for 1 or 2 years, then rat control was implemented to allow measurement of the effects of rat control (VanderWerf & Smith, 2002). After initial demonstration of the efficacy of rat control, efforts have focused on protecting as many elepaio breeding pairs as possible in core populations across the island. Methods of rat control have changed and improved over time. From 1996 to 2012, the primary methods of rat removal were snap traps and poison bait containing 0.005% diphacinone in the form of either Eaton's bait blocks (J.T. Eaton Inc., Twinsburg, Ohio) or Ramik mini-bars (HACCO Inc., Randolph, Wisconsin). Bait was placed in tamper-resistant plastic bait stations to shield it from rain and reduce the risk of poisoning to nontarget species. Use of poison bait was discontinued in 2013 following a change in the product labels. Use of more efficient, automated, pneumatic rat traps made by the Goodnature company began in 2012. At first the Goodnature traps were deployed only in each elepaio territory, but at some sites managed by the Army Natural Resources Program (ANRP; Ekahanui, Palehua, Palikea) they were deployed in large grids of up to 300 traps. Finally, aerial broadcast of the rodenticide Diphacinone-50 was conducted at Schofield Barracks by the ANRP in November–December of 2017 and 2020. For more details on rat control methods, see VanderWerf and Smith (2002), VanderWerf (2009), and VanderWerf et al. (2011).

2.5 | Elepaio nest success and fecundity

We monitored Oahu Elepaio reproduction from 1995 to 2021 by visiting each territory at 1–2-week intervals to search for and monitor nests and document the presence of fledglings. For each nest we recorded the tree species and categorized the outcome as successful, failed, abandoned, or unknown. We counted nests as successful if they fledged at least one chick and we calculated nest success as the successful proportion of nests, not

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including abandoned nests or those of unknown outcome. We considered nests to have been abandoned if construction was not completed or if no eggs or incubation behavior were observed. It is possible that some nests counted as abandoned were depredated before incubation was observed, but there is no way to know this, and we have made this same assumption since the beginning of the study, so any bias has been consistent. For more details on Oahu Elepaio monitoring methods see VanderWerf and Smith (2002), VanderWerf (2009), and VanderWerf et al. (2011).

We investigated annual variation in nest success using mixed model logistic regression, with nest success (yes or no) as the response variable, and rat control (yes or no), year, site, and whether the nest tree was native (yes or no) and fruit-bearing (yes or no) as factors. We examined variation in elepaio fecundity using a General Linear Mixed Model, with number of fledglings per pair as the dependent variable, rodent control (yes or no), site, and year as factors. Although fecundity data ranged from zero to four and had a low mean value, McDonald and White (2010) demonstrated that regular regression based on a normal distribution performed better than Poisson or multinomial regression and was the best analytical method for fecundity data like these. We also examined temporal patterns of fecundity using regression of average annual fecundity as the response variable and year as the predictor, with separate regressions with and without rat control because of differences in the years for which data were available. We did not include fecundity data from Makaha or Waikane because it was already determined that rat control was less effective at those sites and management was discontinued in 2009 (VanderWerf et al., 2011). For analyses involving site, we lumped sites with small samples sizes that were geographically close (Pia and Kuliouou, and Palehua and Palikea) and we excluded data from two sites where very few nests were found (Makua and Waikane, three nests each). All analyses were done using Minitab 17 (2010).

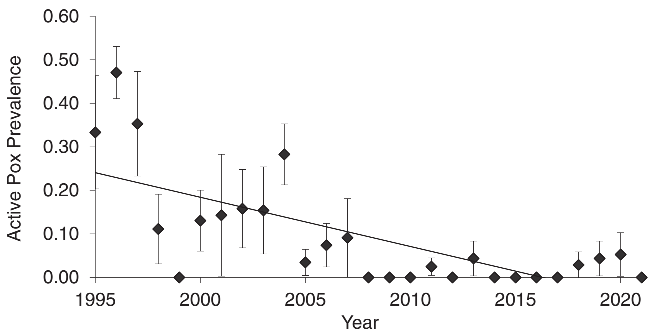

FIGURE 2 Proportion (SE) of Oahu Elepaio with active avian pox lesions from 1995 to 2021, with least squares regression line

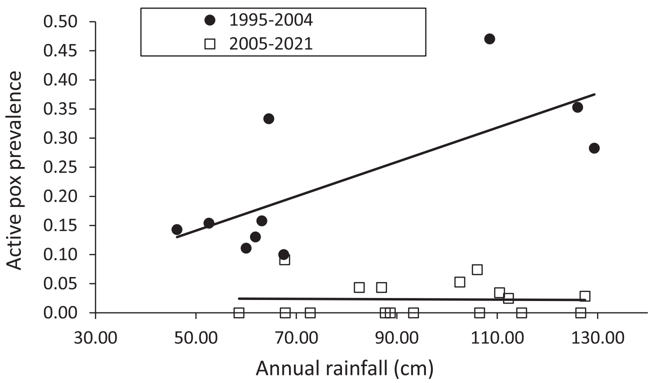

FIGURE 3 Relationship between active avian pox prevalence in Oahu Elepaio and annual rainfall in two time periods. There was a strong relationship until 2004 but since 2005 there has been no relationship

3 | RESULTS

3.1 | Pox prevalence

We mist-netted and banded 677 Oahu Elepaio from 1995 to 2021 (25 ± 3 SE birds per year), including initial captures and recaptures, of which 77 had active pox, 62 had inactive or healed pox, and 538 had no pox symptoms. Active pox prevalence was related to both year and annual rainfall ($F_{2,24} = 18.34$, $p < 0.001$, $R^2 = 60.5\%$), and declined from a peak of 0.47 in 1996 to zero in several recent years (Figure 2). From 1995 to 2004, pox prevalence averaged 21% ± 4%, as reported previously by VanderWerf et al. (2006). In contrast, from 2005 to 2021, pox prevalence averaged only 2% ± 0.1%. From 1995 to 2004 there was a positive relationship between pox prevalence and annual rainfall ($R^2 = 45.4\%$, slope $= 0.008$, $F_{1,8} = 6.64$, $p = 0.03$), but in 2005–2021 there was no relationship between rainfall and pox (Figure 3; $R^2 = 0.1\%$, slope $= -0.00009$, $F_{1,15} = 0.01$, $p = 0.92$).

3.2 | Elepaio nest success and fecundity

We found 1701 elepaio nests, of which 721 were successful, 540 failed, 287 were abandoned, and 153 had an unknown outcome. Nest success was higher with rat control (58% ± 1%) than without rat control (42% ± 6%; $F_{1,1212} = 3.28$, $p = 0.02$) and did not differ among study sites (range 52%–66%; $F_{10,1212} = 1.16$, $p = 0.31$) or years ($F_{25,1212} = 1.34$, $p = 0.12$). Elepaio nested in 35 different tree species, of which 10 were native and 25 were nonnative (Table S1). Nest success did not differ significantly between native tree species (52% ± 6%) and nonnative

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TABLE 1 Oahu Elepaio fecundity and SE with and without rat control at each study site

	With rat control		No rat control	
Site	**Fecundity**	**# pair-years**	**Fecundity**	**# pair-years**
Ekahanui	0.76 ± 0.03	469	0.50 ± 0.10	26
Moanalua	0.67 ± 0.04	228	0.51 ± 0.10	35
Palehua+Palikea	0.78 ± 0.06	174	0.33 ± 0.21	6
Pia + Kuliouou	0.67 ± 0.07	95	0.29 ± 0.08	34
Schofield Barracks	0.91 ± 0.05	296	0.57 ± 0.08	76
Wailupe	0.79 ± 0.04	411	0.41 ± 0.11	22
All sites combined	0.78 ± 0.02	1673	0.48 ± 0.04	199

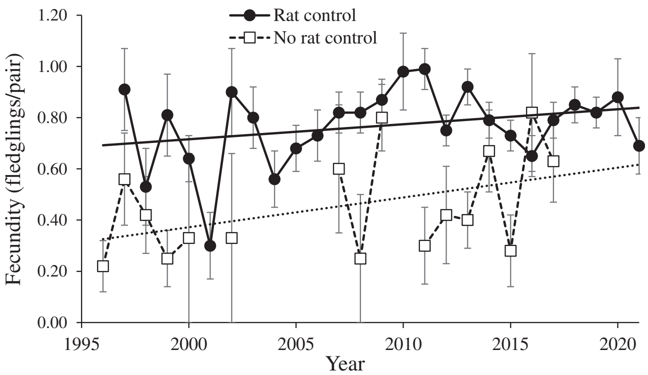

FIGURE 4 Fecundity (SE) of Oahu Elepaio over time with and without rat control, with least squares regression lines

tree species (58% ± 6%; $F_{1,1212}$ = 1.73, p = 0.19) or between fruiting (57% ± 1%) and nonfruiting species (62% ± 6%; $F_{1,1212}$ = 0.54, p = 0.46). Nest success was similar in the three tree species used most often (strawberry guava [*Psidium cattleianum*], 60%; kukui [*Aleurites moluccana*], 64%; and mango [*Mangifera indica*], 62%), which together accounted for 72% of all nests (Table S1).

Annual fecundity of elepaio pairs was higher with rat control (0.78 ± 0.02) than without rat control (0.48 ± 0.04; Table 1; $F_{1,1840}$ = 22.99, $p < 0.001$) and varied among sites ($F_{5,1840}$ = 3.26, p = 0.006) and years ($F_{25,1840}$ = 2.44, $p < 0.001$). Average annual fecundity showed some indication of increasing over time (Figure 4), with a stronger relationship ($F_{1,14}$ = 3.21, p = 0.09) and more rapid increase (coefficient = 0.012 per year) without rat control than with rat control ($F_{1,23}$ = 1.98, p = 0.17, coefficient = 0.006 per year).

4 | DISCUSSION

The conservation status of the Oahu Elepaio has improved because of effective management and natural adaptation. Effects of the two primary threats to the species, nest predation by nonnative rats and avian pox, have been ameliorated compared to several decades ago. Nest predation has been managed with rat control in many areas (VanderWerf, 2009; VanderWerf et al., 2011; VanderWerf & Smith, 2002), and evolution to nest higher off the ground also likely played a role in increased fecundity (VanderWerf, 2012). Elepaio appear to have evolved resistance to avian pox through natural selection, perhaps facilitated to some degree by rat control.

4.1 | Avian pox resistance

VanderWerf et al. (2006) found that pox was common in the Oahu Elepaio from 1995 to 2004 and that pox prevalence was higher during wet years. This pattern has changed; since 2005, pox prevalence has been lower and has not been related to rainfall. There have been several very wet years since 2005 (VanderWerf et al., 2021), and pox was common in other bird species on Oahu during that time (Krend, 2011; VanderWerf et al., 2019; VanderWerf & Young, 2016), yet pox prevalence in elepaio remained low. The most likely explanation for this change is that individuals that were most susceptible to pox died, and the remaining population has greater resistance overall. The role that rat control played in accelerating evolution of pox resistance, as advocated by VanderWerf and Smith (2002) and Kilpatrick (2006), is unknown, but nevertheless, the goal of disease resistance has been achieved. Similar resistance, to avian malaria, has been demonstrated in the Hawaii Amakihi (Foster et al., 2007; Atkinson et al., 2013) and the Oahu Amakihi (Krend, 2011). Garcia-Erill et al. (2022) found that resistance to novel diseases was one of the most potent drivers of evolution in warthogs (*Phacochoerus* spp.).

The development of pox resistance shown in this study may represent the latest of several repeated adaptations to variants of avian pox since the virus became established in Hawaii in the late 1800s (Atkinson & LaPointe, 2009; van Riper et al., 2002). Pox has been reported in at least 374 bird species in 23 orders and there

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are 13 recognized variants of avian pox virus that are defined primarily by their association with particular host taxa (Atkinson & LaPointe, 2009; Williams et al., 2021), at least two of which are known in Hawaii and are most similar to fowl pox and canary pox (Atkinson et al., 2012). Atkinson et al. (2012) demonstrated that these variants differ in virulence in some Hawaiian bird species and that individuals that had recovered from one variant were not immune to the other variant. It is possible that different pox variants have arrived in Hawaii at various times, causing waves of population decline and sometimes extinctions in Hawaiian birds, and repeated selection for resistance to each variant. Waves of extinction occurred in Hawaiian birds in the late 1800s and early 1900s, shortly after pox is suspected to have arrived in Hawaii (Atkinson & LaPointe, 2009), and again in the 1960s and 1970s (Scott et al., 1986; Banko & Banko, 2009), perhaps associated with a newly arrived pox variant. VanderWerf (2001) documented the demographic effects of an epizootic of pox in the Hawaii Elepaio (*C. sandwichensis*) at Hakalau Forest National Wildlife Refuge in the early 1990s, from which the population recovered in several years. Another variant of avian pox virus could arrive in Hawaii at any time and could have renewed effects on the Oahu Elepaio and other native bird species. This risk makes the recent increase and expansion of the Oahu Elepaio population even more important, so if another pox variant does arrive there will be a robust population that can adapt again. Biosecurity measures to prevent the introduction of alien birds, mosquitoes, and pathogens must be maintained and strengthened (Kilpatrick et al., 2004).

Several other endemic Hawaiian bird species are in imminent danger of extinction, primarily because of increases in mosquito–borne diseases (Paxton et al., 2016), and pox also is an increasing threat to endemic birds in the Galápagos Islands (McNew et al., 2021; Williams et al., 2021). Evolution of pox resistance in the Oahu Elepaio required at least several decades, perhaps longer; similar evolution could occur in other species, and management of other threats, such as predation, parasitism, and habitat degradation, could help to minimize population declines so there is time for adaptation to occur before the species become extinct.

4.2 | Elepaio fecundity and rat control

Results of this study demonstrate that rat control remains an effective method of increasing reproduction of the Oahu Elepaio and justify the continued use of this management technique (VanderWerf, 2009; VanderWerf et al., 2011). In addition to the increase in elepaio fecundity caused by rat control, there was some evidence that fecundity increased over time, and there probably were several causes for this. First, improvements in rat control methods, particularly trap grids and aerial broadcast, allowed treatment of larger areas and resulted in less edge effect and immigration. Second, the decline in pox prevalence presumably resulted in fewer debilitated individuals that were unable to reproduce. Elepaio infected with pox often cannot attract a mate or are abandoned by their mate, and thus their lack of reproduction is not accounted for in per-pair fecundity measures. Third, evolution of increasing nest height resulted in less nest predation (VanderWerf, 2012), and this presumably was more important in areas where rats were not controlled, accounting for the faster increase in fecundity in areas without rat control (Figure 4).

Rat control was effective at all sites examined in this study, but there was variation in elepaio fecundity among sites and in the response by elepaio to rat control. Some of the variation among sites may be related to the methods of rodent control used, particularly at sites managed by the ANRP, where control methods have progressed to large grids consisting of hundreds of traps and aerial broadcast of rodenticide in 2017 and 2020. Elepaio fecundity was highest at Schofield Barracks, and that is the only site where aerial broadcast of rodenticide has been used. It is also possible there is variation in rat abundance among the study sites and in the efficacy of rat control methods caused by differences in terrain, forest structure, food availability, and other factors. It would be valuable to examine efficacy of different rat control methods in more detail to ascertain whether trapping grids and aerial broadcast are indeed more effective at reducing rat abundance and enhancing elepaio reproduction. Fecundity, and not nest success, should be used as the primary measure of efficacy because nest success is more affected by stochastic weather events among years and fecundity is a measure of reproduction throughout the year. Fecundity of Oahu Elepaio was lowest at Moanalua and rodent control had the least effect on elepaio at that site (Table 1). Moanalua is the wettest of the study sites and more often experienced weather conditions with heavy rain and strong winds that can cause elepaio nests to fail, and there was no large trapping grid.

Apart from rat control, much of the annual variation in elepaio fecundity among years is related to variation in rainfall, with elepaio producing more offspring in wet years because of higher food availability (VanderWerf et al., 2021), and this variation in fecundity has implications for the efficacy of rat control. In dry years, such as 1998 and 2001, fecundity of elepaio was low even with rat control, and the effect of rat control was lower than in

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other years, perhaps because rat abundance was lower in such years.

4.3 | Nest success and tree species

Contrary to our prediction, nest success did not differ between fruiting and nonfruiting tree species, but this comparison alone may not be sufficient to resolve the issue of whether fruit abundance influences nest predation. Most areas on Oahu where elepaio remain are dominated by nonnative, fruit-bearing trees, particularly strawberry guava, mango, kukui, and Christmasberry (*Schinus terebinthifolius*). In most areas, the few native trees are surrounded by nonnative fruit-bearing trees, and rats can easily travel from crown to crown through the forest canopy. Even if nonfruiting trees are less attractive to rats, such trees are not isolated and nests in them likely are subjected to similar predation pressure as nests in fruiting trees. It would be valuable to examine Oahu Elepaio nest success in an area dominated by nonfruiting native trees, if such a place still exists. Alternatively, measuring nest success in relation to broader scale habitat variables, such as canopy height, spacing between trees, understory density, and relative density of fruiting and nonfruiting trees in the neighborhood of elepaio nests, might reveal other important factors and more subtle variation in predation pressure. Elepaio have persisted in some areas of nonnative forest without any management, and the habitat in some of those areas has peculiar characteristics, such as an exceptionally tall canopy and a sparse understory, that could make it more difficult for rats to find elepaio nests.

There were some noteworthy patterns in nest success among individual tree species (Supplemental Table S1). The two most-commonly used native trees were papala kepau (*Pisonia umbellifera*; $n = 43$ nests) and ohia (*Metrosideros polymorpha*; $n = 13$ nests), but nest success was very different in these two species. Nest success was 100% in ohia, which has tiny wind-dispersed seeds that are not attractive to rats, and this dominant native canopy tree is the species used for nesting most often by the Hawaii Elepaio and Kauai Elepaio in many areas (VanderWerf, 2020; VanderWerf et al., 2006). Conversely, nest success was only 35% in papala kepau, which has large fruit clusters with very sticky sap that can cause entanglement and possibly mortality of elepaio (EAV personal observation), and which were used by the Hawaiian people to snare birds in the past. Among nonnative trees, nest success was low in Christmasberry (43%), a shorter, shrubby tree in which elepaio nests are usually lower off the ground and thus more accessible to rats and more subject to predation (VanderWerf, 2012). Nest success also was low, 35%, in mountain apple (*Syzygium malaccense*), which has large, soft fruits that are thought to be especially attractive to rats.

Apart from nest predation, the most common cause of nest failure was extreme weather events with heavy rain and strong wind, and the frequency of these storms varied among years (VanderWerf et al., 2021). Many pairs renested after failure and eventually fledged chicks, but nest success alone was not a good indicator of reproduction because of stochastic variation in storms.

5 | CONCLUSIONS

The population of the Oahu Elepaio is still relatively small and the range is still fragmented, but both of these parameters are improving. Ongoing surveys by P. Taylor have shown that elepaio numbers have increased in the Waianae Mountains by 240% compared to previous surveys of the same areas in 2006–2011 (VanderWerf et al., 2013) and that spatial gaps between some subpopulations have been filled, but surveys are not yet complete. Similar surveys are needed in the Koolau Mountains to provide updated information for the entire island.

The overall management strategy for the Oahu Elepaio has been effective, which was to control rats in the remaining core populations so they acted as sources of emigrants that supported surrounding sinks where nest predation caused local population decline (USFWS, 2006; VanderWerf & Smith, 2002). Rat control gave pox-resistant elepaio disproportionate ability to reproduce (Kilpatrick, 2006; VanderWerf & Smith, 2002) and protected low nests that otherwise would have been vulnerable, allowing some margin for error in nest site selection and more time for evolution of nest height to occur. Dispersal of young birds from managed areas not only supported the surrounding sinks demographically, but also may have spread the accelerated increase in genes for pox resistance, thereby transferring some of the management benefits to areas that were not managed. If the natural adaptations in pox resistance and nest height continue, rat control may become less important for ensuring survival of the species, and it is possible that someday the Oahu Elepaio could break free from conservation reliance (Reed et al., 2012; Scott et al., 2010). In Figure 4, both regression lines of fecundity over time are increasing, but they are converging and eventually may meet (or at least may overlap broadly in standard errors), which would indicate a release from conservation reliance. This is not likely to occur for several decades, and monitoring will be needed to determine whether that point is ever reached.

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