



RESEARCH ARTICLE

# Increased nesting success of Hawaii Elepaio in response to the removal of invasive black rats

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## ABSTRACT

In Hawaii and other oceanic islands with few native land mammals, black rats (*Rattus rattus*) are among the most damaging invasive vertebrate species to native forest bird populations and habitats, due to their arboreal behavior and generalist foraging habits and habitat use. We evaluated the nesting response of Hawaii Elepaio (*Chasiempis sandwichensis*; Monarchidae), a generalist insectivore, to the removal of black rats using rodenticide in a before-after-control-impact study in high- and low-elevation mesic montane habitat recovering from long-term damage from introduced ungulates and weeds. We monitored nesting success and rat abundance during 2015–2016 before applying rodenticide bait in 2017 to remove rats from two 700 × 700 m treatment plots that were paired with 2 nontreatment plots of the same size. Rat abundance was reduced by 90% during treatment, with combined variables treatment and elevation best explaining the change using GLM methods and AIC model selection. The daily survival rate (DSR) of nests ( $n = 191$ ) was greater on treated plots after rodenticide application (mean  $\pm$  SE =  $0.980 \pm 0.004$  treatment;  $0.964 \pm 0.004$  nontreatment), modeled nest success increased from 29% to 50%, and apparent nest success (number of successful nests per total nests) increased from 37% to 52%. The most informative model for predicting DSR included the effect of treatment. Predation by rats was documented at 3 of 16 nests using video surveillance, and we observed additional evidence of rat predation during in-person nest monitoring. Rats targeted adults on the nest and sometimes removed intact eggs, leaving little trace of their activity. Our results demonstrate that reducing rat predation can immediately improve the nesting success of even a common bird species in habitat with a long history of forest restoration. Sustained predator control may be critical to accelerating the recovery of native forest bird communities.

**Keywords:** BACI, *Chasiempis sandwichensis*, Hawaii, invasive rat, nest success, predator control

## Aumento del éxito de nidificación de *Chasiempis sandwichensis* en respuesta a la eliminación de ratas negras invasoras

## RESUMEN

En Hawái y otras islas oceánicas con pocos mamíferos terrestres nativos, las ratas negras (*Rattus rattus*) están entre las especies de vertebrados invasores más dañinas para los hábitats y las poblaciones de aves de bosques nativos, debido a su comportamiento arborícola y sus hábitos generalistas de forrajeo y uso de hábitat. Evaluamos la respuesta de nidificación de *Chasiempis sandwichensis* (Monarchidae), un insectívoro generalista, a la eliminación de ratas negras usando veneno para ratas en un estudio de impacto antes-después-control en un meso-hábitat montano de alta y baja elevación recuperándose de un disturbio de largo plazo producido por ungulados y hierbas introducidas. Monitoreamos el éxito de nidificación y la abundancia de ratas durante 2015–2016 antes de aplicar el cebo venenoso en 2017 para eliminar las ratas de dos parcelas de tratamiento de 700 m × 700 m pareadas con dos parcelas sin tratamiento del mismo tamaño. La abundancia de ratas fue reducida en un 90% durante el tratamiento. La combinación de variables de tratamiento y elevación explicaron mejor el cambio usando métodos de modelos lineales generalizados (GLM) y la selección del modelo según el criterio de información de Akaike (AIC). La tasa de supervivencia diaria (TSD) de los nidos ( $n = 191$ ) fue mayor en las parcelas tratadas luego de la aplicación del veneno (media  $\pm$  EE =  $0.980 \pm 0.004$  tratamiento;  $0.964 \pm 0.004$  sin tratamiento), el éxito de nidificación modelado aumentó desde 29% hasta 50% y el éxito de nidificación aparente (número de nido exitosos del total) aumentó desde 37% hasta 52%. El modelo más informativo para predecir la TSD incluyó el efecto del tratamiento. La depredación por ratas fue documentada en 3 de los 16 nidos usando monitoreo por video, y observamos evidencia adicional de depredación por ratas durante el monitoreo en persona de los nidos. Las ratas atacaron adultos en los nidos y a veces removieron huevos intactos, dejando poca evidencia de su actividad. Nuestros resultados demuestran que la reducción de la depredación por ratas puede mejorar inmediatamente el éxito de nidificación de incluso una especie de ave común en un hábitat con una larga historia de restauración del bosque. El control sostenido de los depredadores puede ser fundamental para acelerar la recuperación de las comunidades de aves de los bosques nativos.

*Palabras clave:* *Chasiempis sandwichensis*, control de depredadores, éxito de nidificación, Hawái, impacto antes-después-control, rata invasora

## INTRODUCTION

In Hawaiian and other oceanic islands with few native land mammals, black rats (*Rattus rattus*) are generally considered the most damaging invasive vertebrate species to native forest bird populations and ecosystems due to their arboreal behavior and generalist foraging habits and habitat use (Atkinson 1977, Towns et al. 2006, Lindsey et al. 2009, Shiels and Pitt 2014, Shiels et al. 2014). Primarily rats, but also domestic cats (*Felis catus*) and other predators, account for about 16% of Hawaiian forest passerine nest failures overall (Woodworth and Pratt 2009), based on studies conducted mostly in wet montane forests dominated by the widespread native tree 'ōhi'a (*Metrosideros polymorpha*; Myrtaceae), or less often in forests co-dominated by 'ōhi'a and another widespread native tree, koa (*Acacia koa*; Fabaceae). At the community level, predation was observed or assumed to have caused the failure of 16% of 137 nests of 10 native and alien bird species in wet montane 'ōhi'a–koa forest at Hakalau Forest National Wildlife Refuge (Cummins et al. 2014). At the species or population levels, however, studies have often reported relatively low or inconclusive levels of nest predation, due partly to the research focus on rare or declining species, which typically yield few nests for observation, and because nests are often located in the canopies of tall trees, making them difficult to observe. Furthermore, assessing the response of birds to predator removal requires costly installation and operation of trap or rodenticide networks as well as having to split nest monitoring efforts between treatment and nontreatment areas or periods (Nelson et al. 2002, Malcolm et al. 2008, VanderWerf et al. 2011). Nevertheless, modeling suggests that even a 20% reduction in nest depredation can appreciably increase population growth rates for some Hawaiian species (Kilpatrick 2006), making predator control a potentially important if challenging method for protecting bird populations (Paxton et al. 2018).

Studies of endangered Hawaiian honeycreepers (Fringillidae; tribe Drepanidini) and other endemic species frequently report relatively low levels of nest predation by rats in wet montane 'ōhi'a forests, despite indications that predation could be limiting at least some populations (Simon et al. 2001, Becker et al. 2010, Hammond et al. 2015). Comparative studies of reproductive success at sites with and without rat removal have indicated only nominal increases in nesting success in wet montane 'ōhi'a forest (Mounce et al. 2013) and putatively higher ratios of young:adult birds in wet-mesic montane 'ōhi'a–koa forest (Lindsey et al. 2009).

In contrast, strong direct evidence that rat predation of eggs, nestlings, and incubating females reduces nesting success was found in studies of 2 endangered forest birds, the Puaiohi (*Myadestes palmeri*; Turdidae), which occurs in wet-mesic montane 'ōhi'a forest, and the Oahu Elepaio (or O'ahu 'Elepaio in Hawaiian) (*Chasiempis ibidis*; Monarchidae), which occurs in lowland mesic forest dominated by a variety of invasive trees that produce fruit attractive to rats (VanderWerf and Smith 2002, Snetsinger et al. 2005; VanderWerf 2009, 2018; VanderWerf et al. 2011). For species in which only the female incubates at night, nest predation by rats (and cats) may result in the loss of incubating females and lower female survival rates (Donald 2007), as has been reported for Hawaii Elepaio (or Hawai'i 'Elepaio in Hawaiian) (*Chasiempis sandwichensis*) in mesic montane forest dominated by koa and small native shrubs and trees (Sarr et al. 1998). Lower female survival rates have been attributed to nest predation by rats for a number of Hawaiian species (VanderWerf 2008, 2009; Vetter et al. 2012, Mounce et al. 2014, VanderWerf et al. 2014).

Artificial nest studies have corroborated rates of natural nest depredation reported in Hawaii and demonstrate that rats are the dominant nest predator in a variety of habitats (Amarasekare 1993, VanderWerf 2001, Sparklin et al. 2010). Nevertheless, the effects of predator control on artificial nest survival rates have varied considerably, possibly due to variation in rat abundance. For the Oahu Elepaio, survival of both artificial and natural nests increased dramatically following reduction of abundant rats (VanderWerf 2001), but not in wet montane 'ōhi'a forest where rat abundance was relatively low (Sparklin et al. 2010). Artificial nest studies have also shown that fruit availability can contribute to higher rates of nest depredation by rats (Amarasekare 1993, VanderWerf 2001, Sparklin et al. 2010).

In summary, Hawaiian forest bird nesting studies have indicated that rats are an important cause of nest failure for at least the Oahu Elepaio in lowland mesic forests dominated by invasive fruit-bearing tree species and for the Puaiohi in wet montane 'ōhi'a forests. The importance of nest predation by rats in other habitats is less definitive, and is sometimes combined with effects of cats (e.g., Sarr et al. 1998). The goal of our study was to broaden the scope of investigation of rat impacts to include mesic montane forests that were not dominated by 'ōhi'a or alien fruit trees and where changes in nest success in response to rat removal have not been evaluated. These habitats are important to native bird, arthropod, and plant communities and offer “the best opportunities” for meaningful landscape habitat

restoration in Hawaii (Price et al. 2009:402), becoming especially valuable as invasive species and climate change increase pressure on native species at lower elevations and wetter habitats (Fortini et al. 2015).

Reducing rat populations to low-impact levels in large tracts of native forest is one of the most challenging priorities in island conservation (Townes et al. 2006). In Hawaii, rat abundance has been reduced to <10% in relatively small (<120 ha) but biologically significant forest tracts using rodenticides (Spurr et al. 2013) or a combination of rodenticide and trapping (Nelson et al. 2002, Malcolm et al. 2008, VanderWerf et al. 2011). We used rodenticide to remove black rats in 2 mesic montane forest tracts (49 ha each) to evaluate changes in the nesting success of the Hawaii Elepaio in a before-after-control-impact (BACI) study. The widespread and locally abundant Hawaii Elepaio (Figure 1) is a habitat and feeding generalist (VanderWerf 1994, Banko et al. 2015) that maintains population viability even in moderately disturbed habitats and where rats are not controlled (VanderWerf 2004, 2008, 2018), making it a useful model for bird communities in mesic montane habitats. They also were abundant in our study area, their territories and nests were relatively easy to locate, and the local population was already known to be vulnerable to predators (Sarr et al. 1998).



**FIGURE 1.** Hawaii Elepaio (*Chasiempis sandwichensis*) at their nest, 4 m high in a mānele (*Sapindus saponaria*) sapling. The nestlings (deep in the nest) will be fed by the female (right), who has received from the male (left) a geometrid moth (*Scotorythra* sp.), a group of historical importance to Hawaiian forest bird nestlings (Banko and Banko 2009). Hawaii Elepaio nests are typically flecked with lichen and wrapped in spiderwebs, but this nest was unusually exposed because it was built before leaf-out on the mānele, the lone deciduous species in the forest canopy. The nest was woven into thin branches, which may have reduced its vulnerability to feral cats but not necessarily to rats. One nestling fledged from the nest.

## METHODS

### Experimental Design and Study Area

We assessed the response of Hawaii Elepaio to reduced predator abundance using a before-after-control-impact (BACI) study design to compare nest success and nest daily survival rates (DSR). We monitored rat and bird activity on 4 plots (2 pairs of matched treatment and nontreatment plots) before and after rodenticide application in mesic montane forest in Hawaii Volcanoes National Park (HAVO). Baseline (pretreatment) monitoring was conducted for 2 yr (2015–2016), and monitoring continued at all sites as we reduced rat numbers with rodenticide at the treatment plots from January through August 2017.

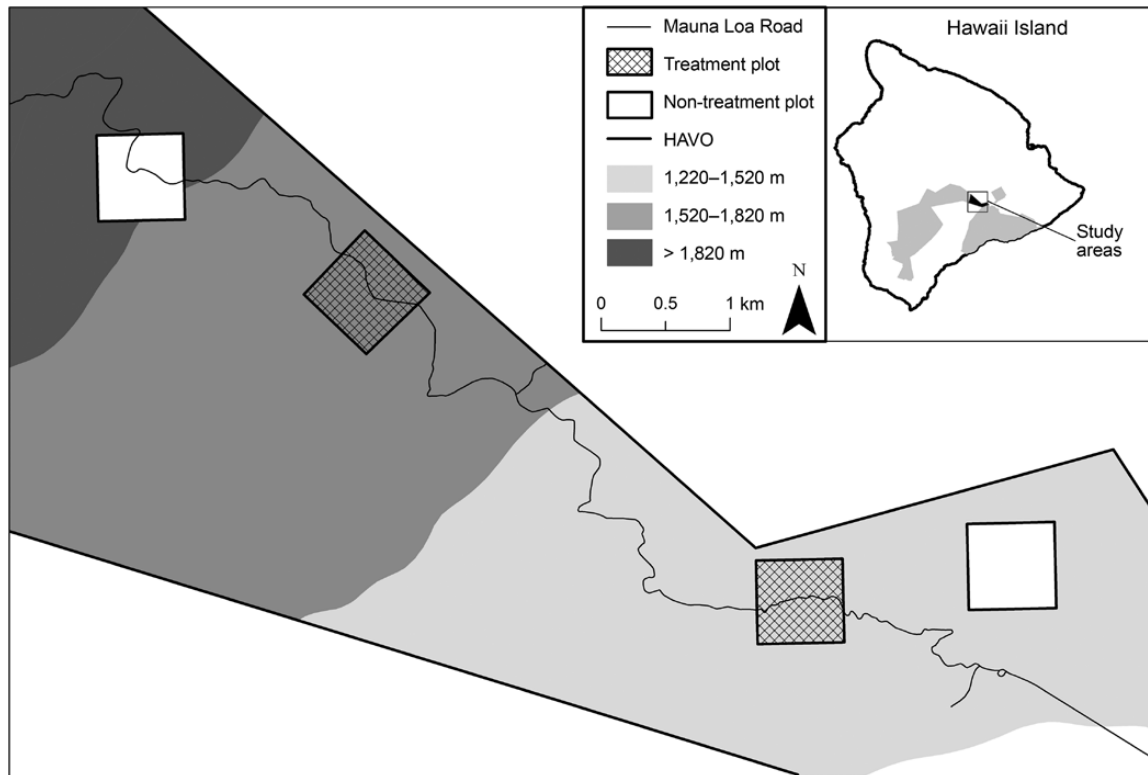
The 4 sites (Figure 2), each 700 × 700 m (49 ha), were located along or near the Mauna Loa Strip Road. One pair of sites was located at lower elevation (1,220–1,340 m a.s.l.; Kipuka Ki [KKI], Kipuka Puaulu [PUA]) and the other pair was located at higher elevation (1,700–1,830 m a.s.l.; Lower Ke‘āmoku [LKE], Upper Ke‘āmoku [UKE]). Rodenticide treatment was applied to KKI (nontreatment: PUA) and to LKE (nontreatment: UKE). Within each 700 × 700 m grid, stations were established at 50-m intervals along parallel transects. The UKE site overlapped the Hawaii Elepaio study site used by Sarr et al. (1998).

The region has been free of introduced ungulates for >25 yr (Tunison and Stone 1992, Katahira et al. 1993, National Park Service 2013), resulting in dynamic vegetation still recovering from long-term, severe browse damage. Habitats are also being restored by controlling weeds and planting rare species. Although our study sites shared common tree and shrub species, vegetation structure varied by elevation (Pratt et al. 2010). The 2 lower-elevation sites (KKI and PUA) were dominated by koa, ‘ōhi‘a, and mānele (*Sapindus saponaria*; Sapindaceae) in the canopy and by pāpala kēpau (*Pisonia brunoniana*; Nyctaginaceae), pilo (*Coprosma rhynchocarpa*; Rubiaceae), and native shrubs and ferns in the subcanopy (Belfield et al. 2011). Koa dominated the canopy at the 2 higher-elevation sites (LKE and UKE), and ‘a‘ali‘i (*Dodonaea viscosa*; Sapindaceae), māmane, and pūkiawe (*Leptecophylla tameiameia*; Ericaceae) dominated the subcanopy (Belfield and Pratt 2002).

### Rat Monitoring and Rodenticide Application

We periodically estimated rat activity with a live mark-recapture scheme on each of the 4 sites to evaluate variation in rat abundance and activity over time. Nested centrally within each 700 × 700 m site grid was a smaller 300 × 300 m grid where we deployed 49 wire cage traps (Haguruma, Osaka, Japan), spaced 50 m apart. To account for seasonal variation in rat activity, we sampled during 4 periods: Fall 2015, Spring 2016, Fall 2016, and Spring 2017. Each sampling period consisted of two 4-night trapping sessions spaced about 1 mo apart. However there were a





**FIGURE 2.** Location of study plots (each  $700 \times 700$  m) in the Mauna Loa Strip section of Hawaii Volcanoes National Park. Plots are paired according to elevation and treatment or nontreatment with rodenticide, from left to right: Upper Ke'āmoku (UKE; Nontreatment), Lower Ke'āmoku (LKE; Treatment), Kīpuka Kī (KKI; Treatment), Kīpuka Puāulu (PUA; Nontreatment).

few exceptions: in Fall 2015 the low-elevation plots were trapped for a third session to increase capture numbers and the high-elevation plots were trapped for 3 days instead of 4 in the second session, and in Fall 2016 KKI was trapped for an extra day to account for excessive trap interference by mongoose (*Herpestes javanicus* [sym. *H. auro-punctatus*]).

To pre-bait traps, we wired open the doors and sprinkled ~30 mL (~2 tablespoons) of fresh, shredded coconut inside traps and in front of trap doors (Sugihara 1997, Shiels 2010, Spurr et al. 2013). We pre-baited traps at least 3 days prior to each trapping session. We set traps by piercing a chunk (approximately  $2 \times 2$  cm) of fresh coconut onto the bait hook trigger mechanism. We then checked traps each day before 1000 hours, resetting traps and replenishing baits throughout the week.

Rats were marked by applying a uniquely numbered ear tag (National Band and Tag, Newport, Kentucky, USA) in each ear. Tag numbers were recorded for recaptured rats, and missing tags (as indicated by the presence of only 1 tagged ear or 2 torn ears with tags found in trap) were replaced as needed. All rats were released at their point of capture, and on the few occasions when house mice (*Mus musculus*) and mongoose were captured, the animals were released on site or were transferred to HAVO staff for disposal.

To reduce rat abundance on the 2 treatment sites, we distributed Ramik Mini Bars (HACCO, Randolph, Wisconsin, USA) containing 0.005% diphacinone in a compressed cereal grain bait in tamper-proof Protecta Bait Stations (Bell Laboratories, Madison, Wisconsin, USA) that were placed on the ground and spaced 50 m apart throughout each  $700 \times 700$  m grid (225 bait stations per plot), in accordance with federal and state regulations. We pre-baited the stations with fresh, shredded coconut for 1 week prior to initial deployment, which required 2 days (12 person-days). Each station was then continually supplied with 0.45 kg of fresh bait (16, 1-ounce Ramik mini bars) from January 20 through July 2017. Stations were initially checked twice per week to replace bait that was consumed or spoiled, although the interval was gradually increased to once per month as bait consumption slowed. We estimate that the rodenticide treatment was effective through August 2017, based on the low rate of bait consumption and deterioration during the summer months. To minimize consumption by nontarget species and to comply with pesticide label requirements, all bait blocks were secured on metal rods inside the station, which was then securely closed with a zip-tie. Dead rodents were recorded and collected when discovered within the treatment plots, and we were alert for dead or injured nontarget wildlife. Hawaiian

Hawks (*Buteo solitarius*) were monitored throughout the rodenticide treatment phase to assess potential risks of secondary poisoning from scavenging or predation upon dead or dying rodents, as required by US Fish and Wildlife Service.

### Elepaio Nest Monitoring

We searched for nests within each site during the breeding season from mid-February to mid-July in 2015, 2016, and 2017. Hawaii Elepaio build small, cup-shaped nests made of grasses, moss, dried leaves, and spiderwebs, often in the forks of branches near the canopy, and males and females contribute nearly equal effort in nest building, incubating, and feeding young (VanderWerf 2018). Nests were often found using behavioral cues, such as birds carrying nest material or food items, or replacing one another on the nest. In order to identify pairs and territories, throughout the study we individually marked mist-netted birds with unique colored and numbered bands. We monitored nests every 2–3 days, with no more than 5 days in between checks, and tried to visit nests daily when close to fledging. Nest monitoring continued from the point of discovery until chicks fledged or the nest failed. During each visit, observers watched nests from >3 m away using binoculars, and recorded behavior of the parents, nest contents when possible, and nest stage (build, incubation, nestling, or inactive). Observation time was kept as brief as possible and was limited to 30 min. In most cases the nests were too high or vegetation too dense for mirror poles; without other evidence, nests were considered to have failed if no activity was observed on at least 2 consecutive visits.

### Nest Cameras

We opportunistically monitored nests for evidence of predation with video cameras in all 3 breeding seasons and in 2–4 plots in any given season. Infrared security cameras (DWC-B5661TIR550, Digital Watchdog, Tampa, Florida, USA) were mounted on tripods and set up at least 5 m from nest trees to monitor nests continuously. The cameras were equipped with two 12 V batteries and a small digital video recorder (DVR-T8, Shenzhen Wantong Gongchuang Technology Development, Guangdong, China) with removable data card. Camera surveillance was limited to nests with an adequate line of sight to the nest, which typically included nests below 5 m. We were careful to not remove or displace the vegetation between the camera and the nest, and stored the batteries and DVR an additional 3–5 m behind the tripod to minimize attraction or disturbance to the nest.

### Data Analysis

We estimated rat abundance on each 300 × 300 m trapping grid as rats captured per 100 corrected trap-nights (CTN),

whereby sprung or compromised traps were counted as 0.5 trap night (Nelson and Clark 1973, Beauvais and Buskirk 1999). Compromised traps included those with recaptured rats, house mice, or mongooses, and those that were otherwise unavailable to a new rat for at least part of the night. We measured the relative abundance of rats by calculating the percentage of traps that caught rats at each of the 4 plots.

We compared measures of rat abundance and Hawaii Elepaio nesting success separately, using generalized linear models of biologically relevant variables, as well as likelihood-based information-theoretic methods (Burnham and Anderson 2002) to identify the variables with the greatest predictive abilities. Specifically, we built generalized linear mixed models using a binomial link function via the package lme4 (Bates et al. 2015) in R 3.4.0 (R Core Team 2017) to estimate the probability of catching a rat based on a set of predictor variables. We considered the effects of rat removal (treatment) and regional variation in climate and habitat types (elevation) to be the most biologically relevant predictor variables on the probability of catching a rat, but we included local variation in vegetation (plot) and temporal variation in trapping success (session) as potentially important random effects. We then used Akaike's information criterion corrected for small sample size ( $\Delta AIC_c$ ) via the R package AICcmodavg (Mazerolle 2017) to evaluate our best candidate models explaining variation in rat abundance.

To evaluate nest success we calculated DSR using the nest survival model in program Mark via the R package RMark (Laake 2013) following the methods described by Rotella et al. (2004). In a way similar to that used to evaluate rat abundance (above), we included treatment, elevation, and plot, as well as year and nest age (number of days since first egg was laid) as predictor variables on DSR of nests. In both scenarios, we ranked the models by differences in Akaike's information criterion corrected for small sample size ( $\Delta AIC_c$ ) and Akaike model weights ( $w_i$ ), where models with less than  $-2 \Delta AIC_c$  units were considered to have substantial empirical support to explain variation in the data set.

The nest survival model in program RMark requires information on the length of the breeding season, the age of the nest when found, the day of the breeding season the nest was found, the day the nest was last known to be active, the last day the nest was checked, and the fate of the nest. The length of the breeding season varied slightly from year to year and for our analysis was defined as beginning with the earliest date a nest was discovered, and ending with the latest date a nest was active through all 3 yr of monitoring. We were confident in determining nest age ( $\pm 2$  days) for the 129 nests that were discovered during the building phase, or when actual fledge dates were known.

When fledging was not observed directly, we inferred the duration of nest activity using the chronology of behavioral observations or appearance of nestlings to produce a reasonable estimate. The model does not require an exact failure date, and instead uses the interval between the last day a nest was known to be active and the first day it was found to be inactive to estimate the time of failure. We were not able to determine the exact cause of nest failure in most cases. In 9 cases where parents continued to incubate past full-term (18 days), the nest was considered to be unsuccessful and the failure to have taken place within the check interval surrounding the expected hatch day. In 8 cases, nests with intact eggs were abandoned around the expected hatch date and these nests were also considered to have failed after the last check when birds were seen incubating. Even though the nest could have been considered “active” because a rat could have scavenged the dead eggs after the end of the incubation period, the cause of nest failure had already occurred and could be related to a variety of unknown causes, including previous disturbance to the nesting pair by rats that may have disrupted or ended incubation.

We estimated overall nest survival in treatment and nontreatment sites by raising the DSR derived from the top-ranking model to the power of 34, the number of nesting days for elepaio (18-day incubation and 16-day nestling; VanderWerf 2018). We used the delta method (Powell 2007) to calculate variance and 95% confidence intervals for the cumulative survival probabilities.

## RESULTS

### Rat Distribution and Abundance

We captured 681 individual rats (1,236 captures) during 5,595 CTN during the study: 402 captures and 1,685 CTN in 2015, 661 captures and 2,553 CTN in 2016, and 173 captures and 1,357 CTN in 2017. Rats were distributed widely across the study sites during the 3 pretreatment sampling periods (2015–2016). Rats were caught in 78% of all traps on KKI and at least 95% of traps on each of the other 3 trapping grids (300 × 300 m; 49 cage traps each). Rats were consistently caught less often at KKI during the pretreatment period, which accounted for much of the variation in capture rates between sites (Table 1). Pretreatment capture rates were not consistently higher at any of the other

3 sites or during any particular trapping period. Capture rates varied by nearly 2-fold between trapping periods within sites and by nearly 3-fold between sites within trapping periods. During the treatment period (Spring 2017), rats were captured on 16 occasions at treatment sites and 156 occasions at nontreatment sites. Between the last pretreatment period (Fall 2016) and Spring 2017, capture rates declined by 77–90% at treatment sites but only by 1–19% at nontreatment sites (Table 1).

### Factors Affecting Rat Abundance

We modeled the influence of treatment (rodenticide), elevation, plot, and trapping session on rat abundance. The AIC<sub>c</sub> score of our best model (treatment) was within ~2 points of the 2 next-best models (treatment+elevation; treatment\*elevation; Table 2). Models without treatment were not supported. The odds ratio of the treatment effect was 0.092, indicating that rat abundance was reduced by over 90% in treatment plots.

### Elepaio Nest Survival and Success

We monitored 256 Hawaii Elepaio nests throughout the study, but only 191 were used for analysis because we could not determine the fate of 14 nests, 46 nests were abandoned during the building phase (cause unknown), and 5 were located off-plot. The most convincing models for predicting nest survival included the combined effect of nest age+treatment and the sole effect of treatment (Table 3 and Figure 3). The nest age model yielded a negative slope ( $\beta = -0.02$ , SE = 0.01), indicating that nests were more susceptible to failure with increased age. The treatment model yielded a positive coefficient ( $\beta = 0.61$ , SE = 0.24), signifying that survival improved when rats were removed. Cumulative nest survival was calculated from the treatment model for treatment and nontreatment areas. DSR was greater on treated plots after rodenticide application (mean  $\pm$  SE =  $0.980 \pm 0.004$  treatment;  $0.964 \pm 0.004$  nontreatment). Mean  $\pm$  SE (95% LCL, 95% UCL) nest survival was  $0.50 \pm 0.07$  (0.36, 0.65) in treatment plots (KKI and LKE in 2017) and  $0.29 \pm 0.04$  (0.22, 0.36) in nontreatment plots (all plots before 2017, PUA and UKE in 2017). Mean survival estimates were derived from the treatment model.

To facilitate comparisons with other studies, we calculated apparent nest success; 24 of 46 (52%) nests were successful when rodenticide was applied compared to

**TABLE 1.** Capture frequency of rats at paired treatment and nontreatment plots during 3 pretreatment sessions (2015–2016) and 1 treatment session (2017). Values shown are mean (SE) rats per 100 CTN (corrected trap-nights).

Plot	Elevation	Treatment	Fall 2015	Spring 2016	Fall 2016	Spring 2017
KKI	low	rodenticide	10.7 (3.0)	17.6 (1.1)	8.2 (2.3)	0.8 (0.8)
PUA	low	no rodenticide	17.7 (7.2)	29.6 (3.2)	19.3 (1.5)	19.6 (5.9)
LKE	high	rodenticide	26.3 (3.9)	27.1 (1.7)	14.4 (2.4)	3.3 (2.3)
UKE	high	no rodenticide	32.5 (2.3)	23.2 (4.4)	24.2 (0.4)	19.5 (0.1)

**TABLE 2.** Rat capture probability models, ranked by Akaike's Information Criterion ( $\Delta AIC_c$ ). Capture probabilities were estimated at paired treatment and nontreatment plots during 3 semiannual pretreatment sessions (2015–2016) and 1 treatment session (2017). The number of parameters ( $K$ ), maximized log likelihood ( $-2\ln L$ ), and cumulative weight ( $\Sigma w_i$ ) are also provided. Variables: TRT (application of rodenticide); ELV (elevation); PLT (random plot effect); and SES (random temporal effect).  $AIC_c$  value of top-ranked model = 801.70.

Model	$K$	$\Delta AIC_c$	$-2\ln L$	$w_i$	$\Sigma w_i$
TRT + ELV + (PLT) + (SES)	5	0.00	791.24	0.59	0.59
TRT + (PLT) + (SES)	4	2.12	795.52	0.21	0.80
TRT * ELV + (PLT) + (SES)	6	2.14	791.19	0.20	1.00
ELV + (PLT) + (SES)	4	103.79	907.45	0.00	1.00
(PLT) + (SES)	3	104.24	909.97	0.00	1.00
(PLT)	2	258.70	1062.96	0.00	1.00

**TABLE 3.** Daily nest survival rate models, ranked by Akaike's Information Criterion ( $\Delta AIC_c$ ). Daily nest survival ( $S$ ) was modeled at paired treatment and nontreatment plots during 3 semiannual pretreatment sessions (2015–2016) and 1 treatment session (2017). The number of parameters ( $K$ ), maximized log likelihood ( $-2\ln L$ ), and cumulative weight ( $\Sigma w_i$ ) are also provided. Variables as in Table 2, except with an effect of nest age (AGE), a random year effect (YR), and an intercept-only model (NULL).  $AIC_c$  value of top-ranked model = 748.34.

Model	$K$	$\Delta AIC_c$	$-2\log L$	$w_i$	$\Sigma w_i$
S(AGE + TRT)	3	0.00	742.33	0.52	0.52
S(TRT)	2	1.63	745.97	0.23	0.75
S(TRT + ELV)	3	2.71	745.04	0.13	0.88
S(AGE)	2	5.36	749.69	0.04	0.92
S(AGE + ELV)	3	6.17	748.49	0.02	0.94
S(NULL)	1	6.73	753.07	0.02	0.96
S(PLT)	4	7.11	747.44	0.01	0.97
S(ELV)	2	7.62	751.95	0.01	0.98
S(YR)	3	8.30	750.63	0.01	0.99
S(ELV + YR)	4	9.51	749.83	0.00	1.00

54 of 145 (37%) nests when rodenticide was not applied ( $\chi^2 = 3.22$ ,  $P = 0.07$ ).

### Evidence of Rat Predation

We considered the cause of nest failure to be rat predation at 46 (24%) of 191 nests, based on evidence from in-person nest checks and surveillance cameras. In-person evidence of predation included a hole in the side of the nest, feathers or eggshell fragments, disappearance of the clutch, or an abrupt renesting attempt following a short incubation period. Rats were the most abundant potential nest predators and were the likely predators when video and physical evidence were not available. We did not observe claw marks, fur, or other evidence of climbing or nest predation by feral cats or mongooses. Elepaio nests are deep and narrow, but we found no evidence of nest disturbance by Hawaiian Hawk or owls (Hawaiian Short-eared Owl [*Asio flammeus sandwichensis*] or Barn Owl [*Tyto alba*]). Nevertheless, these raptors may have contributed to nest failure by killing nesting adults.

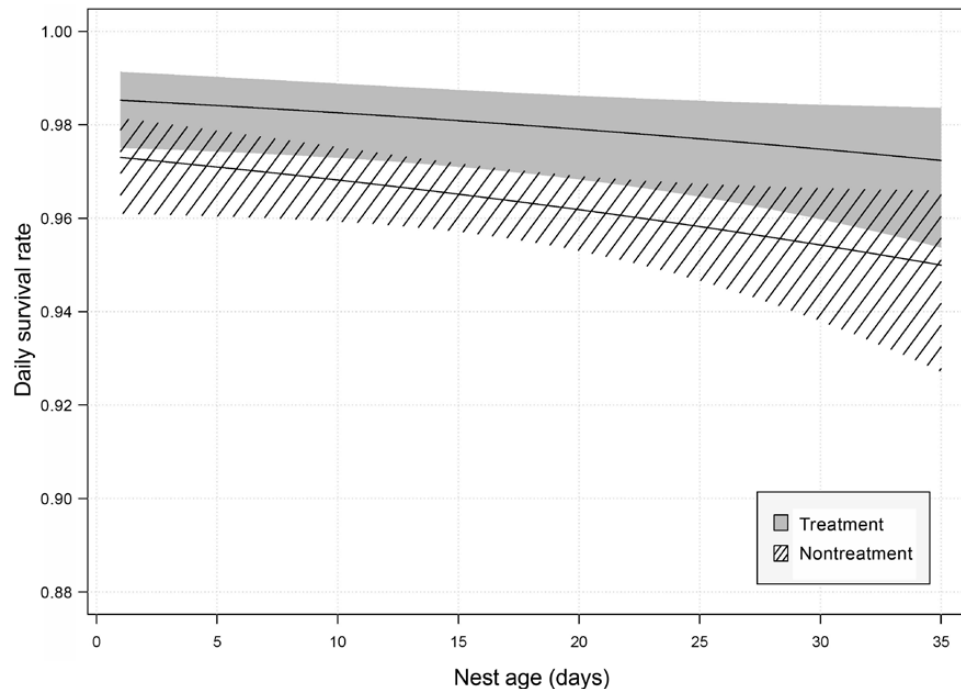
Of 21 nests monitored with video cameras, 12 fledged, 5 failed for unknown reasons, 3 had eggs depredated by black rats, and 1 failed to hatch any eggs despite attentive incubation. In one of the predation events, a rat lunged

unsuccessfully after the incubating female before returning moments later to consume eggs in the nest. This rat was recorded in the camera's field of view ( $\leq 0.5$  m from the nest) on 9 occasions over 4 nights. We assume that the same rat was recorded on each occasion based on the rat returning to the exact portion of a branch where it occasionally groomed itself and seemed unaware of or uninterested in the nest nearby. The video suggests that the rat was finally attracted to the nest when the incubating female shifted her position when the rat was nearby. The female returned to the nest about an hour after the rat had eaten the eggs, and the rat again attacked her unsuccessfully. In a different predation event, a female escaped seconds before a rat reached the nest. The rat removed an egg from the nest and returned on 2 different occasions to consume the remaining egg.

### DISCUSSION

Rats were abundant and widespread throughout our study, and predation rates of 14% (3 of 21 nests monitored by video camera) to  $\geq 24\%$  (46 of 191 nests monitored in-person) affected the nest DSR of Hawaii Elepaio, a relatively widespread, locally abundant species. Substantially reducing





**FIGURE 3.** Elepaio DSR as a function of nest age at rat removal treatment (KKI and LKE in 2017) and nontreatment plots (PUA and UAE 2015–2017; LKE and KKI 2015–2016). The shaded areas indicate 95% confidence intervals, and solid black lines depict slopes of the regressions.

rat abundance improved nesting success during a single season. Our results help fill a gap in our knowledge of rat impacts in mesic montane habitat, where high rates (52%) of nest predation have been reported but where cats have also been assumed to be important predators (Sarr et al. 1998). Although we cannot rule out cat predation in our study, we found no evidence of it. Furthermore, our large sample of nests allowed us to document the frequency of rat predation with a level of reliability that is difficult to achieve for species that are rare or otherwise difficult to study. Although several studies have produced compelling evidence of nest predation and the benefits of rat control, they have occurred in lowland habitats that are dominated by alien fruit-bearing tree species that are highly attractive to rats (VanderWerf and Smith 2002, VanderWerf 2009, VanderWerf et al. 2011) or in wet montane habitat dominated by ‘ohi‘a (Snetsinger et al. 2005), which does not produce fruit attractive to rats (Sparklin et al. 2010). The inferences drawn from most other studies have been somewhat equivocal about the value of rat control.

In our study, rodenticide application reduced rat abundance by more than 90% during 4 mo of treatment and monitoring (January–May) and likely afterward through mid-August, a month after our last bait treatment. VanderWerf (2009) found that about a 90% level of rat suppression resulted in increased nest success (from 33% to 62%), fecundity (from 0.33 to 0.69 fledglings per pair), and

female survival (from 0.55 to 0.82) of the closely related Oahu Elepaio. Although we did not evaluate changes in fecundity or female survival during the short period when rats were controlled, the increase in nest success (from 29% to 51%) was similar to VanderWerf’s results. A longer-term rat removal program, therefore, would also likely result in increased fecundity and female survival of the Hawaii Elepaio population in our mesic montane study area. Adaptive management trials could also reveal the conservation and practical benefits of varying levels of control frequency and intensity. For example, higher-intensity predator management resulted in greater increases in productivity and survival of Oahu Elepaio (VanderWerf et al. 2011). The potential value of predator management is also evident from the immediate response of Hawaii Elepaio to rat removal, even where forests have been recovering for decades through ungulate removal, weed suppression, and planting of native species (Belfield et al. 2011, Loh et al. 2014). Moreover, the effect of elevation contributed little to our model of nest DSR, suggesting that Hawaii Elepaio respond positively to rat removal where mosquito-borne avian malaria (*Plasmodium relictum*) transmission is sustained (Samuel et al. 2015).

The rapid response of Hawaii Elepaio to rat removal indicates that predator management could be a powerful tool for restoring the entire forest bird community (Kilpatrick 2006, U.S. Fish and Wildlife Service 2006, VanderWerf



2009). Hawaii Elepaio are representative of other forest bird species because they nest in a variety of widespread, abundant tree species and they build their nests throughout the forest canopy. Similar to most forest birds, Hawaii Elepaio tend to place their nests in the terminal branches and upper crowns of the larger available trees, which results in nest height increasing with canopy height (van Riper 1995, Sarr et al. 1998, VanderWerf 2018). VanderWerf (2012) determined that Oahu Elepaio nest height increased over a 16-yr period due to higher frequencies of predation by rats in the lower canopy, lending support to the idea that Hawaiian birds are adapting to invasive mammalian predators by nesting more frequently and successfully among the smaller branches high in the forest canopy rather than near the ground (Pratt 2009, Woodworth and Pratt 2009). In considering the impacts of black rat predation and other factors on island forest birds in the southeastern Pacific, Thibault et al. (2002) found no significant difference between nest heights of a locally abundant native species, the Tahiti Reed Warbler (*Acrocephalus caffer*), and 5 threatened monarch flycatchers (Monarchidae; *Pomarea* spp.), although the monarchs tended to nest in branches that were significantly more horizontal in orientation than the reed warbler, which also nested closer to the tops of trees. They also noted that monarchs nested at lower heights on islands without black rats or where they had only recently appeared, compared to Tahiti, where black rats had a relatively long history. We could not observe a change in nest height because we removed rats in only the last year of the study, but we would expect to find nests at lower heights with sustained predator control. Nevertheless, our estimate of predation at nests monitored in person ( $\geq 24\%$ ) was nominally higher than that for nests monitored with video cameras (14%), suggesting that in our study area nests located lower in the canopy (where video monitoring was possible) were not necessarily more vulnerable to rats.

Another factor that influences the location and success of nests in tree canopies is exposure to solar radiation, wind, and rain (Kern and van Riper 1984, Pratt 2005, Woodworth and Pratt 2009), but adverse weather was implicated in the loss of only 2 nests during our study. Nevertheless, if nest placement is affected by multiple factors that vary temporally or geographically in selection pressure, nest locations within the forest canopy may differ between and even within species (Woodworth and Pratt 2009). Cummins et al. (2014) found that mean nest height of 2 species varied annually, potentially in response to the strength of different selection pressures. In a relatively stormy season, DSR was higher for low-canopy nests compared to high-canopy nests, possibly due to increased exposure to storms at the outermost branches. During a more moderate season, DSR was higher for high-canopy nests, which may have been less vulnerable to mammalian predators.

DSR decreased with nest age in our study, which may be typical for altricial species where parental activity

increases as nestlings develop (Dinsmore et al. 2002, Weston et al. 2018). Rates of feeding are high for both sexes of Hawaii Elepaio, and although eggs are rarely left unattended, nestlings may be exposed more frequently to cool, damp conditions as well as predators when parents are away foraging (VanderWerf 2018). At night, broods (and brooding parents) may become increasingly restless and perhaps noisy as nestlings increase in size and activity, which may more readily draw the attention of nocturnal rats. Although Hawaii Elepaio maintain relatively clean nests (VanderWerf 2018), olfactory cues may nevertheless become stronger as the total surface area, respiration, and weight of the brood increases. The probability of nest detection by rats might also increase over time if they do not explore their entire territory each night and if territories do not extensively overlap (Shiels 2010). Additionally, video surveillance revealed that rats do not always depredate nests as soon as they come within close range, which would contribute to lower daily nest survival later in the nesting cycle.

Our video cameras revealed narrow escapes of adult birds from rat attacks at nests, and feathers found at failed nests suggest that rats sometimes catch nesting birds (also see Sarr et al. 1998), potentially with serious demographic consequences. Adult survival as well as nesting success of Oahu Elepaio improved when rat populations were reduced (VanderWerf 2009, VanderWerf et al. 2011), and we may find similar results for Hawaii Elepaio in future analyses.

Invasive predators, habitat degradation, diseases, and food web disruption have all contributed to the historical decline of Hawaiian forest birds (Banko and Banko 2009), and a multi-faceted approach is needed to recover the forest bird community (U.S. Fish and Wildlife Service 2006). To the extent that rats may suppress Hawaiian forest bird populations, modeling suggests that reducing predation rates and improving habitat conditions can facilitate the evolution of resistance to introduced avian malaria where transmission rates are moderate (Kilpatrick 2006). Hawaii Elepaio and other birds contract malaria in our lower-elevation study sites (Samuel et al. 2015), which suggests that sustained rat control could most benefit them. That even relatively common, widespread species, such as Hawaii Elepaio, can at least be partially constrained by rats and other predators has also been reported in New Zealand forests where disease has little impact and habitat quality is high (Elliott et al. 2010). Habitat improvements over the past 50 yr and relatively high reproductive output (Sarr et al. 1998) may partly account for the large and approximately stable population of Hawaii Elepaio in our study area. Populations have disappeared or are declining elsewhere on Hawaii Island (Gorresen et al. 2009, Judge et al. 2011), where habitats may be less favorable and rates of disease

transmission may be higher. A problem that complicates management strategies is that restoring habitats benefits rats (Shiels et al. 2017) as well as birds. Nevertheless, controlling predators and restoring habitats, in addition to reducing the frequency of disease transmission, are among the highest priorities in Hawaiian forest bird conservation (Kilpatrick 2006, U.S. Fish and Wildlife Service 2006, VanderWerf 2009, Paxton et al. 2018). At least where habitat conditions are improving, reducing rates of rat predation may be a critical next step toward reestablishing rare species and stabilizing or bolstering populations of even some relatively widespread species.

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