



Evolution of Nesting Height in an Endangered Hawaiian Forest Bird in Response to a Non-Native Predator

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Abstract: *The majority of bird extinctions since 1800 have occurred on islands, and non-native predators have been the greatest threat to the persistence of island birds. Island endemic species often lack life-history traits and behaviors that reduce the probability of predation and they can become evolutionarily trapped if they are unable to adapt, but few studies have examined the ability of island species to respond to novel predators. The greatest threat to the persistence of the Oahu Elepaio (*Chasiempis ibidis*), an endangered Hawaiian forest bird, is nest predation by non-native black rats (*Rattus rattus*). I examined whether Oahu Elepaio nest placement has changed at the individual and population levels in response to rat predation by measuring nest height and determining whether each nest produced offspring from 1996 to 2011. Average height of Oahu Elepaio nests increased 50% over this 16-year period, from 7.9 m (SE 1.7) to 12.0 m (SE 1.1). There was no net change in height of sequential nests made by individual birds, which means individual elepaios have not learned to place nests higher. Nests ≤ 3 m off the ground produced offspring less often, and the proportion of such nests declined over time, which suggests that nest-building behavior has evolved through natural selection by predation. Nest success increased over time, which may increase the probability of long-term persistence of the species. Rat control may facilitate the evolution of nesting height by slowing the rate of population decline and providing time for this adaptive response to spread through the population.*

Keywords: *Chasiempis ibidis*, Hawaii, island species, non-native predators, novel threats, Oahu Elepaio

Evolución de la Altura de Anidación en una Especie de Ave de Bosque Hawaiano en Peligro como Respuesta a un Depredador No Nativo

Resumen: *La mayoría de las extinciones de aves desde 1800 han ocurrido en islas, y los depredadores no nativos han sido la mayor amenaza para la persistencia de aves insulares. Las especies insulares endémicas a menudo carecen de atributos de historia natural y conductuales que reducen la probabilidad de depredación y pueden entramparse evolutivamente si no tienen la capacidad de adaptarse, pero pocos estudios han examinado la habilidad de especies insulares para responder a depredadores nuevos. La depredación por ratas no nativas (*Rattus rattus*) es la mayor amenaza para la persistencia del Elapaio de Oahu (*Chasiempis ibidis*), una especie de ave de bosque en peligro. Examiné si la ubicación de nidos de *C. ibidis* ha cambiado a nivel individual y de población en respuesta a la depredación de ratas midiendo la altura de los nidos y determinando si cada nido produjo crías entre 1996 y 2011. La altura promedio de nidos incrementó 50% en este período de 16 años, de 7.9 m (ES 1.7) a 12.0 m (ES 1.1). No hubo cambio neto en la altura de nidos secuenciales construidos por aves individuales, lo que significa que elepaio individuales no han aprendido a colocar sus nidos más arriba. Los nidos ≤ 3 m sobre el suelo produjeron menos crías, y la proporción de tales nidos declinó en el tiempo, lo que sugiere que el comportamiento de construcción de nidos ha evolucionado*

mediante selección natural por depredación. Los nidos exitosos incrementaron en el tiempo, lo que puede incrementar la probabilidad de persistencia de la especie a largo plazo. El control de ratas puede facilitar la evolución de la altura de anidación al disminuir la tasa de declinación poblacional y proporcionar tiempo para que esta respuesta adaptativa se disperse en la población.

Palabras Clave: Amenazas nuevas, *Chasiempis ibidis*, depredadores no nativos, Elepaio de Oahu, especies insulares, Hawái

Introduction

The majority of bird extinctions since 1800 have occurred on islands, and the most common cause of extinction has been the introduction of non-native predators, especially mammals (Blackburn et al. 2004; Trevino et al. 2007; Jones et al. 2008), sometimes in concert with habitat loss and modification (Owens & Bennett 2000). Many island species evolved in the absence of predators and do not possess the antipredator behaviors and life-history traits of continental species (Salo et al. 2007; Lima 2009; Sih et al. 2010). Island species are also particularly susceptible to introduced pathogens because they may lack a coevolved immunological response (Atkinson et al. 1995; Wikelski et al. 2004; Matson 2006). Because island species often fail to adapt to non-native predators and pathogens they are sometimes considered ecologically or evolutionarily trapped and may have relatively high probability of extinction (Schlaepfer et al. 2002). Rapid behavioral responses by native species to novel threats posed by non-native species are being described with increasing frequency (Griffin 2004; Schlaepfer et al. 2005; Strauss et al. 2006), but few of these examples involve island species (Woodworth et al. 2005; Foster et al. 2007; Massaro et al. 2009). Such responses provide opportunities to incorporate adaptive behavioral or evolutionary responses into conservation strategies for threatened taxa (Ashley et al. 2003; Stockwell et al. 2003; Kinnison et al. 2007).

The Hawaiian Islands are one of the most isolated groups of islands, and they exemplify the vulnerability of species evolved in isolation and the potentially catastrophic environmental consequences of non-native species. Hawaii has only one species of native terrestrial mammal, the insectivorous Hawaiian hoary bat (*Lasiurus cinereus semotus*), but many non-native predators have been introduced to the islands by humans. Polynesians colonized the Hawaiian Islands about 800 years ago (Rieth et al. 2011) and brought with them predators including the Pacific rat (*Rattus exulans*), domestic dog (*Canis familiaris*), and domestic pig (*Sus scrofa*) (Kirch 1982; Burney et al. 2001). The arrival of Europeans starting in 1778 increased the number of introductions of non-native predators, including the black or ship rat (*R. rattus*), Norway rat (*R. norvegicus*), domestic cat (*Felis silvestris*), small Indian mongoose (*Herpestes auropunctatus*), and European wild boar. These non-native predators and pathogens carried by non-native

mosquitoes have caused or contributed to the extinction of 74 of the 109 known endemic Hawaiian bird species and continue to threaten the remaining 35 species (Scott et al. 2001).

The Oahu Elepaio (*Chasiempis ibidis*) is an endangered, nonmigratory monarch flycatcher (Monarchidae) endemic to the Hawaiian island of Oahu (VanderWerf 1998; VanderWerf 2007). The primary threats to the persistence of the Oahu Elepaio are nest predation by black rats and mosquito-borne diseases, particularly avian poxvirus (*Poxvirus avium*) (USFWS 2006; VanderWerf et al. 2006; VanderWerf 2009). Feral cats, mongooses, and Pacific rats may prey on very low nests and recent fledglings, but are less serious threats because they do not climb as well as black rats (VanderWerf 2009). Rat control causes significant increases in elepaio nest success (i.e., number of chicks fledged), fecundity, and most importantly survival of nesting females (VanderWerf & Smith 2002; VanderWerf 2009). Rat control has been implemented in several areas on Oahu and has become the cornerstone of the conservation strategy for this species (U.S. Fish and Wildlife Service 2006). The decline of several Oahu Elepaio populations has been reversed by rat control, but not all rat-control programs have been effective, and only a fraction of some elepaio populations have been managed with this technique (VanderWerf 2009; VanderWerf et al. 2011b). In addition to the direct benefit of reducing nest predation, rat control may also provide an indirect means of accelerating the evolution of resistance to introduced pathogens in Hawaiian forest birds (VanderWerf & Smith 2002; Kilpatrick 2006).

Methods

Study Area

Wailupe, Pia, and Kuliouou Valleys are in the southern Koolau Mountains on the island of Oahu, Hawaii. These valleys support part of the largest remaining population of Oahu Elepaios which has been the subject of long-term ecological studies and the target of intensive conservation efforts (VanderWerf 2001; VanderWerf & Smith 2002; VanderWerf 2009). Vegetation in this area consists of mesic forest dominated by non-native plants, particularly strawberry guava (*Psidium cattleianum*), mango (*Mangifera indica*), kukui (*Aleurites moluccana*), and

Christmasberry (*Schinus terebinthifolius*). Elepaio are adaptable and can forage and nest in these non-native plants, although the rate of nest predation by non-native black rats is high (VanderWerf 2009). I collected baseline data on Oahu Elepaio demography at each of the 3 sites for 1–2 years, after which I began rat control. I reduced rat abundance by >90% each year at each site, but could not eradicate them completely because immigration from surrounding areas was continual (VanderWerf 2009). Thus, there was some predation, despite my control efforts.

Data Collection

As part of a long-term demographic research project (VanderWerf & Smith 2002; VanderWerf 2009), I monitored 293 Oahu Elepaio nests from 1996 to 2011 and recorded information about each nest, including nest height and nest-tree height each year. I either estimated the height of each nest and tree relative to the height of a human observer or I measured these heights with a clinometer and tape measure. To determine the amount of error associated with estimating nest heights, in 2009 and 2010 I estimated nest height and then measured it with a clinometer and tape measure. There was no difference between estimated (11.7 m [SE 0.9]) and measured (11.3 m [SE 0.9]) heights, and estimated values were not consistently higher or lower than measured values ($T = 0.38$, $df = 54$, $p = 0.70$). Elepaios nested in a variety of tree species, but the most commonly used species were strawberry guava ($n = 88$), mango ($n = 73$), kukui ($n = 69$), and Christmasberry ($n = 32$). The remaining 31 nests were in 9 different tree species.

Analyses

I calculated the average height of all nests and all nest trees each year. I calculated the proportional height of each nest by dividing the nest height by the height of the tree in which it was built. I calculated the proportion of nests that were successful (i.e., fledged at least one chick), not including nests that were abandoned before eggs were laid. I examined temporal patterns in nest height, nest-tree height, proportional nest height, and nest success with linear regressions in which the average value of each variable was the response variable and year was the predictor. I used analysis of covariance, with year as the common predictor, to test whether the rates of change in nest height and nest-tree height were similar.

To determine whether elepaio may have learned to adjust nest height from previous nesting attempts, I examined the sequence of nest heights of individual birds that were uniquely color banded. I assigned numbers to nests of each bird in the order they were built in the same year and in successive years. The most nests built by an individual bird in 1 year was 4, and the longest time span over which an individual bird built nests was 10 years.

I then conducted a linear regression of nest height on nest sequence of each bird and used a t test to determine whether the average slope of the individual regressions was different from zero. Both sexes of elepaio participate in nest construction, but females may play a larger role in selection of nest sites (VanderWerf 1998). During the day the male and female take turns sitting on the nest, but females are more likely to be preyed on at the nest because they alone incubate and brood at night, when rats are most active (VanderWerf 2009). Females therefore may be more likely than males to change the height at which they build nests, but I had a larger sample and generally longer histories for males, so I conducted separate analyses for males and females.

To examine whether lower nests were more likely to fail, I constructed histograms of the height of failed and successful nests, I calculated the success rate of nests grouped into 3-m height increments, and I performed a chi-square test of the number of successful and failed nests higher or lower than 3 m. I examined whether the proportion of low nests changed over time with linear regressions of the proportion of nests ≤ 3 m high and of nests ≤ 6 m high.

Results

Nest height varied from 2.0 to 24.0 m. The height of Oahu Elepaio nests increased about 50% over 16 years, from an average of 7.9 m (SE 1.7) in 1996 to 12.0 m (SE 1.1) in 2009 (Fig. 1) ($F_{1,14} = 25.20$, $R^2 = 0.64$, $p < 0.001$). The height of trees in which elepaio nested also increased over the same period (Fig. 1) ($F_{1,13} = 22.43$, $R^2 = 0.63$, $p < 0.001$). The rates of increase in nest height (0.2 m per year) and nest tree height (0.3 m per year) were

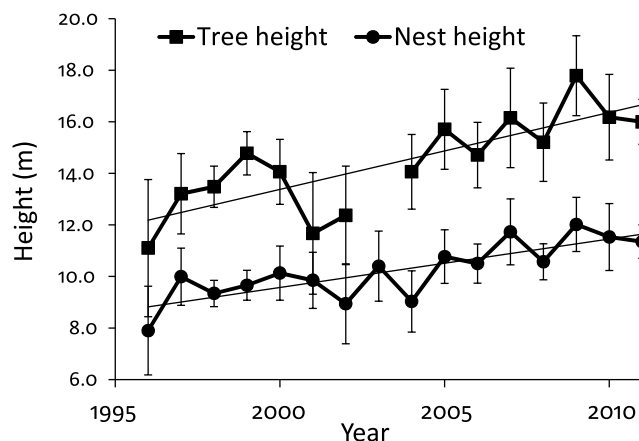


Figure 1. Average height (SE) of Oahu Elepaio nests and trees used for nesting from 1996 to 2011 in the southern Koolau Mountains (Oahu, Hawaii) (lines, best-fit least-squares regression).

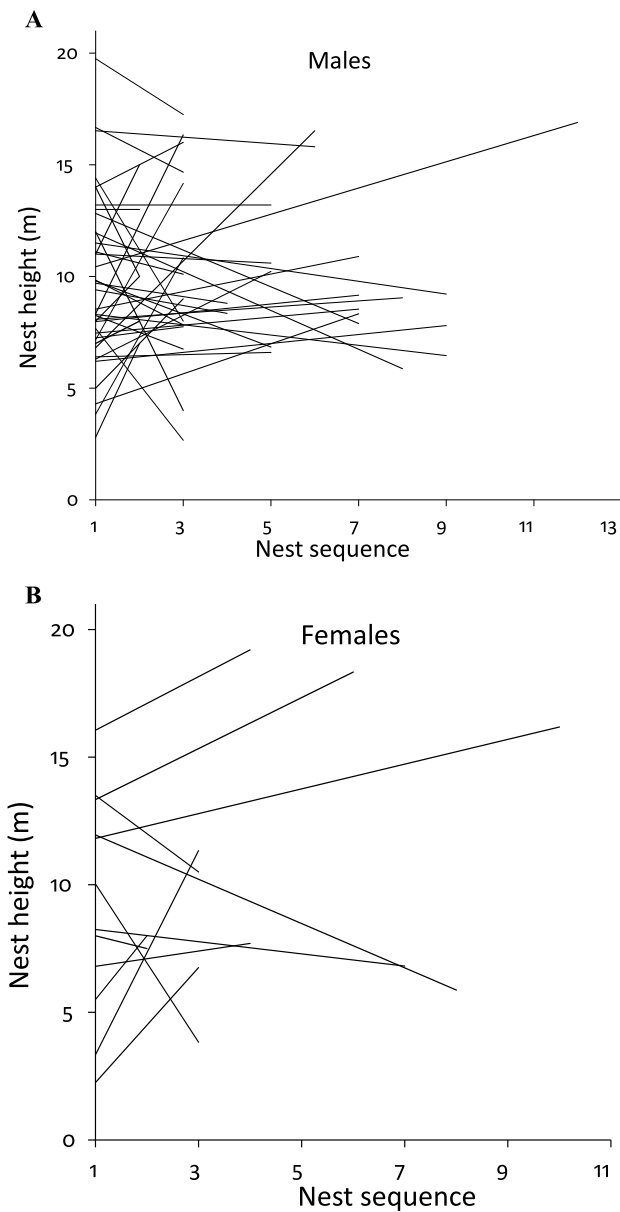


Figure 2. Least-squares regression lines of height of nests built in sequence by individual male and female Oahu Elepaios.

not significantly different ($F_{1,27} = 2.30, p = 0.14$), which resulted in a similar average proportional nest height over time (0.74 [SE 0.01], range 0.66–0.79, $F_{1,13} = 0.30, p = 0.59$). There was no significant difference in nest height or nest-tree height among the 3 study sites ($F_{1,287} = 1.05, p = 0.35, F_{1,276} = 2.41, p = 0.10$, respectively), so I pooled data from all 3 sites.

The height of nests made by individual birds varied considerably (Fig. 2). Moreover, there was no net change in height of sequential nests made by individual birds (Fig. 2) in either males ($T = 0.18, p = 0.86, n = 33$) or females ($T = 0.54, p = 0.60, n = 12$).

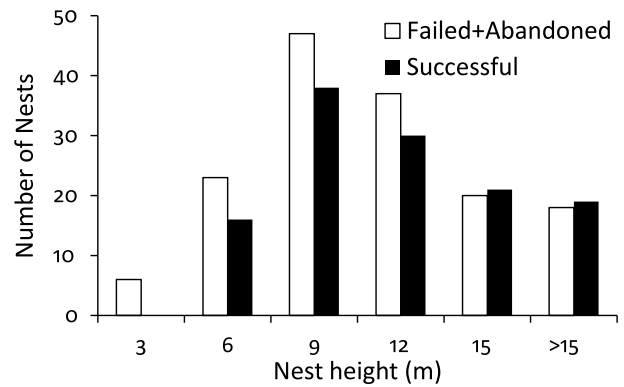


Figure 3. Number of Oahu Elepaio nests at different heights that failed or were abandoned and were successful from 1996 to 2011.

More nests ≤ 3 m in height failed than expected by chance (Fig. 3) ($\chi^2 = 5.08, df = 1, p = 0.02$), and the proportions of nests ≤ 3 and ≤ 6 m high decreased over time (Fig. 4) ($F_{1,13} = 5.36, R^2 = 0.29, p = 0.03, F_{1,13} = 6.72, R^2 = 0.34, p = 0.02$, respectively), which indicates the change in nest height was caused by a decrease in the number of low nests. The success rate of nests increased as the height of nests increased, but this pattern was caused primarily by the low success of nests built at ≤ 3 m. The success rate of nests at ≤ 6 m but ≥ 3 m was only slightly lower than that of nests at >6 m. The nest success rate increased over time (Fig. 5) ($F_{1,13} = 12.80, R^2 = 0.50, p < 0.03$).

Discussion

In continental areas, birds often exhibit plasticity in behaviors and traits such as nest placement, microhabitat selection, clutch size, parental activity, and nestling

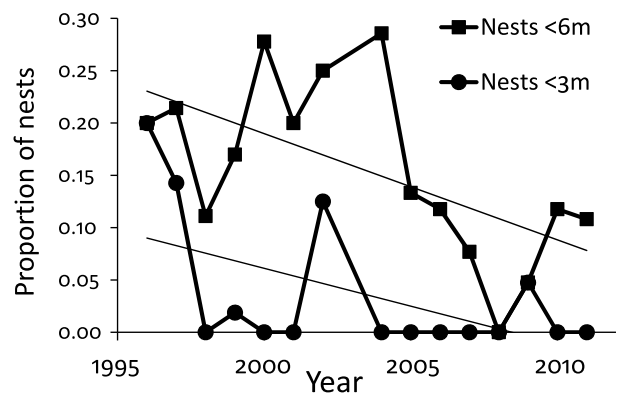


Figure 4. Proportion of Oahu Elepaio nests below 3 m and below 6 m over time (lines, best-fit least-squares regression).

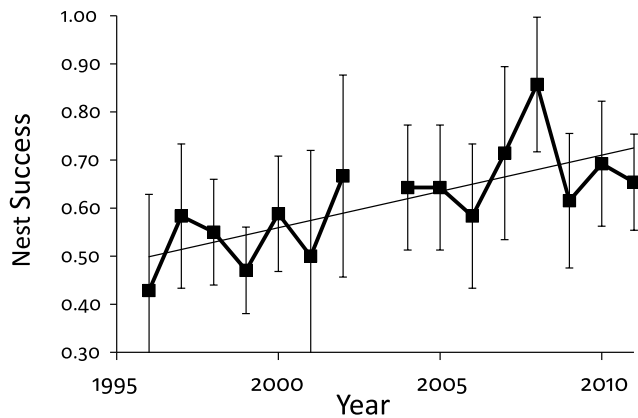


Figure 5. Mean (SE) nest success rate of Oahu Elepaio by year.

begging calls, in response to differences in predation risk (Martin 1995; Peluc et al. 2008; Lima 2009), but in island species such plasticity is rare. The increase in nest height of Oahu Elepaios is one of few documented examples of an island species responding adaptively to a threat from a non-native predator. Female New Zealand Bellbirds (*Anthornis melanura*) in areas where predation risk is relatively high spend longer periods on the nest during incubation and make fewer visits to provision nestlings than females in areas with lower probability of predation (Massaro et al. 2009). Both these behaviors reduce activity at the nest and make it less conspicuous to predators. Peluc et al. (2008) found that a population of Orange-crowned Warblers (*Vermivora celata*) on the Channel Islands of California (U.S.A.) vary the height at which they build nests on the basis of the presence of avian predators and that nest placement and parental activity can be altered experimentally by manipulating perceived predation risk.

The height of Oahu Elepaio nests increased by about 50% over the 16 years of my study, but information from early naturalists indicates nests were lower historically than when I began my research. Thus, nest height has been increasing for some time. Henshaw (1902) commented that the Oahu Elepaio was the only Hawaiian forest bird that habitually built nests low. He reported that nests usually were placed from 3 to 9 m high in small trees, and he found one nest on a fern within 0.6 m of the ground. MacCaughy (1919) also thought the Oahu Elepaio was the only Hawaiian forest bird that habitually built its nests low. He reported the average nest height was about 6 m and that the bird did not nest in the high tree tops. Perkins (1903) remarked that nest height varied from 2 to 12 m. Conant (1977) reported an average height of 7.6 m in 32 nests in Manoa Valley from 1966 to 1968.

I think it is unlikely that Oahu Elepaio nest heights will continue to increase substantially. It was primarily nests

≤ 3 m high, and to a lesser degree nests >3 and ≤ 6 m high, that were the most depredated, and by the end of my study few birds still built nests at ≤ 3 m. This pattern is consistent with the results of Shiels (2010), who found that the average height of above-ground activity by individual black rats on Oahu was 2.8 m (SE 0.5) and that average maximum height was 7.4 m (SE 0.9). Most Oahu Elepaios now build nests higher than 7.4 m and thus may be nesting sufficiently high to avoid predation, although rat behavior could change or differ among forest types. Elepaio could have nested higher in the trees they selected for nesting, but the proportional height of Oahu Elepaio nests in the present study (0.74 ± 0.01) did not vary over time and was similar to that in Hawaii Elepaio (*Chasiempis sandwichensis*) at Hakalau Forest National Wildlife Refuge (0.76 [SE 0.01]) (VanderWerf 2004), which indicates that elepaios nest in consistent locations in a tree and that the primary means by which elepaio nest height can increase is through selection of larger trees. Nest-site selection is evolutionarily conservative in some respects, and most open-cup nesting birds, such as the Oahu Elepaio, build nests on particular substrates at particular heights (Martin 1993; Hansell 2000; Lima 2009).

Training native species to recognize non-native predators has been suggested as a conservation strategy, but this technique may be more effective in species that have previous experience with similar predators (Griffin et al. 2000; Griffin 2004; Sih et al. 2010). Some prey species may retain antipredator behaviors, or at least the ability to relearn them, for some time (Blumstein & Daniel 2002; Berger 2007; Sih et al. 2010), but the elepaio lineage in the Hawaiian Islands has been isolated from mammalian predators for approximately 2.3 million years (VanderWerf et al. 2009). The mechanism for the increase in nest height of Oahu Elepaio was evolution, not learning, and elepaios do not appear to be able to learn about rats and other mammalian predators. Oahu Elepaios are thus naïve to mammalian predators, which suggests training them to recognize predators would not be successful (Caro 2005; Sih et al. 2010).

The increase in Oahu Elepaio nest height cannot be explained simply by tree growth. Individual trees in the study sites undoubtedly grew, but forests in the study sites are dynamic and contained abundant seedlings and saplings in the smaller size classes. There is no reason to suspect abundance of trees in different size classes has changed. Although tree growth was not responsible for the increase in height of Oahu Elepaio nests, forest succession may affect nest predation and thus play a role in regulating elepaio abundance. In areas where land-use practices have changed forest structure, and particularly increased tree height, Oahu Elepaio nest success can be expected to increase.

Predator control has been an important tool in preventing extinction of many species (Côté & Sutherland

1997; Butchart et al. 2006). Control efforts that result in complete eradication of predators without risk of recolonization, as is feasible on some remote islands, may be sufficient to ensure survival of the species for the foreseeable future. Long-term persistence is less certain in situations where predators cannot be eradicated and must be controlled indefinitely. In such cases, species persistence depends on continued financial and political support for predator control (Scott et al. 2010). However, predator control and other management actions that increase the probability of persistence of a threatened species may give the species time to evolve natural defenses. In the case of the Oahu Elepaio, nest predation by black rats is a strong selective force and has caused substantial and rapid declines in elepaio abundance (VanderWerf 2009; VanderWerf et al. 2001; VanderWerf et al. 2011a). Without rat control, loss of breeding females and consequent population declines may occur too rapidly for a response to evolve and could result in populations that are so small that they would have difficulty recovering. Rat control may help facilitate the evolution of nest-building behavior because it may allow sufficient time for the adaptive response to spread through the population, thereby enhancing the long-term persistence of the species and perhaps eventually obviating the need for rat control.

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