

STATUS AND MONITORING METHODS OF A RED-TAILED TROPICBIRD COLONY ON O‘AHU, HAWAI‘I

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ABSTRACT

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The Red-tailed Tropicbird *Phaethon rubricauda* is a widespread seabird that nests in the tropical Pacific and Indian oceans. Most the global population nests in the predator-free Northwestern Hawaiian Islands. In the southeastern Hawaiian Islands, non-native predators restrict the species to nesting on coastal cliffs and small islets. I monitored 734 Red-tailed Tropicbird nests near Hālonā Point on O‘ahu during 2005–2020, controlled non-native predators to protect nests (beginning in 2006), and developed tools to facilitate monitoring of the species in other areas. The colony increased in size in response to predator control, from 18 eggs laid in 2006 to 94 eggs in 2020; this represented an overall growth rate of 520% and an annual growth rate of 11%. Egg laying (one egg per nest) peaked in March, hatching peaked in April, and fledging peaked in July. The mean incubation period was 44.3 days ($n = 504$ eggs) and the mean nestling period was 82.4 days ($n = 394$ chicks); together, this gives a mean breeding cycle length of 126.7 days. The apparent nest success rate was 0.631 ± 0.018 and the daily nest survival rate was 0.9962 ± 0.0002 , which resulted in a mean estimated nest success rate of 0.619. The number of adult tropicbirds flying over the colony was related to the number of active nests and varied monthly. I developed three correction factors to estimate the total number of nests in a colony, using the number of nests found during a single visit in any month. These results demonstrate that seabirds can thrive on islands inhabited by people, if predators are managed.

Key words: Hawai‘i, monitoring, predator control, Red-tailed Tropicbird, seabirds

INTRODUCTION

The Red-tailed Tropicbird *Phaethon rubricauda* is a widespread seabird that nests primarily in tropical areas of the Pacific and Indian oceans (Schreiber & Schreiber 1993, USFWS 2005). The species is common throughout the Northwestern Hawaiian Islands, but they have a much more restricted distribution on the larger southeastern Hawaiian Islands, which are inhabited by people and introduced predators (USFWS 2005, Pyle & Pyle 2017). In the southeastern Hawaiian Islands, these mammalian predators have limited tropicbirds and most other seabirds to nesting on steep cliffs and offshore islets (Harrison 1990, USFWS 2005, VanderWerf 2012).

There are many challenges to monitoring tropical seabirds and to measuring the effects of management actions (VanderWerf & Young 2018). For the Red-tailed Tropicbird, the primary challenges to monitoring are: 1) the inaccessibility of nests located on rocky cliffs or in dense vegetation, 2) the protracted nesting season, and 3) distinguishing between active and prospective nest sites. Including prospective nests in nest counts can result in inflated measures of breeding population size. However, Red-tailed Tropicbirds have an aerial courtship display in which two to several birds fly in a vertical circular pattern while giving loud calls (Schreiber & Schreiber 1993). These displays may offer a means of finding nesting colonies and of estimating both colony size and nesting phenology.

The status of a Red-tailed Tropicbird breeding colony on the Ka Iwi coast of southeastern O‘ahu and the effect of predator control on this colony was reported previously (VanderWerf & Young 2014). Since

predator control or exclusion can result in significant population increases among seabirds, monitoring effectiveness is important for refining management methods (VanderWerf *et al.* 2014, Spatz *et al.* 2017, Raine *et al.* 2020). The purposes of this paper are to: 1) update the status of the Red-tailed Tropicbird colony on O‘ahu, 2) report performance and improvements in predator control methods used to protect tropicbirds, and 3) describe new monitoring methods developed to facilitate the monitoring of this species in other locations or circumstances where they are more difficult to monitor.

STUDY AREA AND METHODS

I monitored a Red-tailed Tropicbird nesting colony located on the southeastern coast of O‘ahu, USA, between Lāna‘i Lookout and Hālonā Point over the 16-year period from 2005 to 2020 (Fig. 1). The frequency of nest checks varied among and within years, averaging 28.5 per year (range = 21–36 checks per year, $n = 427$ visits); the average duration between visits was 8.8 days (range = 6.7–10.7 days, $n = 15$ years). In 2005, I made fewer visits and thus determined only the number of eggs laid and number of chicks fledged. During each visit, I searched the colony area and noted where tropicbirds appeared to be sitting on nests, and I recorded the contents of each nest. Special effort was made to look under overhanging rocks, in small caves, and in other sheltered locations attractive to tropicbirds. I painted a small number on a rock next to each nest to allow identification. Most locations were used for nesting during multiple years. If an adult was present in a location not detected previously, I gently shifted the adult to see whether it was sitting on an egg or small chick, unless doing so might result in injury to the adult or damage to the egg. This never

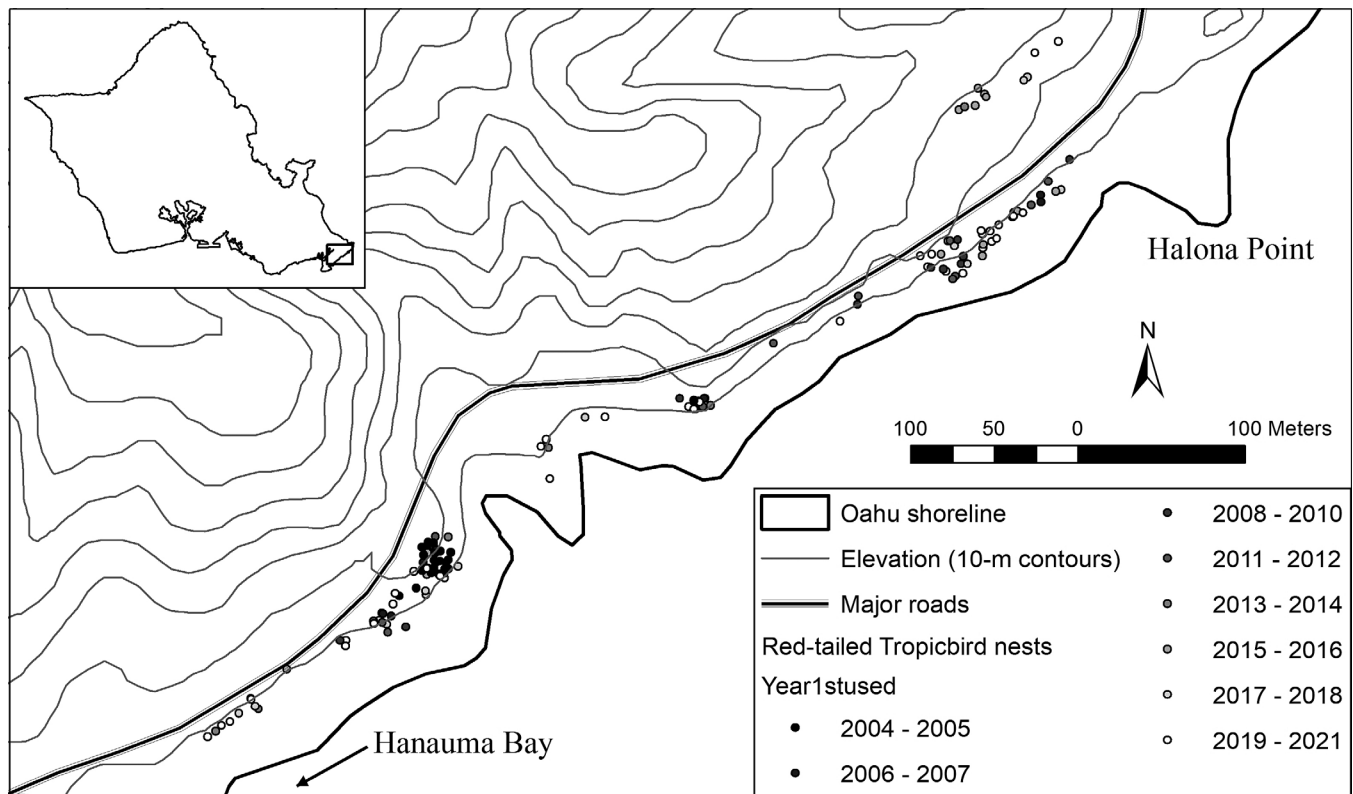


Fig. 1. Map of the study area at Hālonā Point, O'ahu. Points marking Red-tailed Tropicbird *Phaethon rubricauda* nests are shaded to indicate the year in which they were first used.

resulted in the adult leaving an active nest or ultimately abandoning the nest. The presence of recently hatched chicks was often evident from the eggshell or membrane next to the adult and was sufficient to assess nest status. If a nest failed, any evidence that might indicate the cause of failure was noted, such as the condition of the egg or chick, footprints, or other signs of predators. Beginning in 2011, I recorded the maximum number of tropicbirds flying over the colony at any one time, but only on visits between 11h00 and 15h00, when tropicbirds are most active (Felis *et al.* 2020; pers. obs.). This included birds engaged in courtship displays and others just flying.

I controlled several species of non-native predators near the colony beginning in 2006 by using several methods: rat snap traps, automated rodent traps, live traps, kill traps, and rodenticide bait stations (Table 1). The targeted predator species were small Indian mongooses *Herpestes auro-punctatus*, feral cats *Felis catus*, rats *Rattus* spp., and house mice *Mus musculus*. Mongooses and feral cats were the predators that posed the greatest threat, but rats can kill eggs and small chicks, and both rats and mice can consume bait intended for other species, reducing trapping efficiency. All predator control was done using humane methods and, in the case of rodenticide, in compliance with the product label and State of Hawai'i regulations. The rodenticide bait contained 0.005% diphacinone, in the form of either Eaton's bait blocks® (J.T. Eaton Inc.; Twinsburg, Ohio, USA) or Ramik mini-bars® (HACCO Inc.; Randolph, Wisconsin, USA). Bait was placed in tamper-resistant plastic bait stations to shield it from rain and reduce the risk of poisoning to non-target species. The rat snap traps were the Victor professional model. The kill traps were DOC200 and

DOC250 spring traps made by the New Zealand Department of Conservation (DOC). The live traps were Tomahawk single-door traps of an appropriate size for cats. The automated rodent traps were pneumatic traps (A24 model) manufactured by Goodnature. A tally was kept of the number and species of predators caught with each method, allowing calculation of removal rate. I did not calculate captures per trap day, because the frequency of checks was relatively low and the bait was usually completely removed between checks, so the trap was unlikely to have been effective for the entire time between checks.

Nesting success of Red-tailed Tropicbirds was calculated using two methods: apparent nest success and daily nest survival rate. Apparent nest success was defined as the proportion of nests from which a chick fledged (Jehle *et al.* 2004). Similarly, apparent hatching success was the proportion of eggs that hatched, and apparent fledging success was the proportion of chicks that fledged. A chick was considered to have fledged if it was gone after a duration consistent with fledging (67–123 days; Schreiber & Schreiber 1993) and there was no evidence that it had died or been killed, e.g., feathers, body parts, or signs of a predator in or near the nest.

Measures of apparent nest success are useful for comparison with other studies, but they are often biased and usually overestimate true nest success because nests that fail are less likely to be found (Mayfield 1961, Jehle *et al.* 2004, Jones & Geupel 2007). I therefore also calculated the "Mayfield" daily nest survival rate using the number of mortalities and the number of exposure days. I assumed that any change in nest status (laying, hatching,

TABLE 1
Performance of different methods used to remove non-native predators around
a Red-tailed Tropicbird *Phaethon rubricauda* colony near Hālonā Point, O'ahu, 2006–2020

| Method | Years used | # traps | Target species ^a | Total # captures | Captures/check |
|-----------------------------|--------------------|---------|-----------------------------|------------------|----------------|
| Bait stations | 2008–2013 | 3–4 | Rats | unknown | unknown |
| Rat snap traps | 2010–2020 | 4–5 | Rats | 55 | 0.065 |
| | | | House mouse | 28 | 0.033 |
| | | | Mongoose | 1 | 0.001 |
| | | | Unknown | 73 | 0.086 |
| Automated rodent traps | 2013–2020 | 3–5 | Unknown (rats) | 703 | 1.151 |
| DOC ^b kill traps | 2010–2020 | 3–5 | Mongoose | 205 | 0.250 |
| | | | Rats | 23 | 0.028 |
| | | | Feral cat | 2 | 0.002 |
| | | | Unknown | 8 | 0.009 |
| Live traps | 2006–2010, 2020 | 2–5 | Mongoose | 6 | 0.130 |
| | | | Rats | 2 | 0.043 |
| | | | Feral cat | 2 | 0.043 |

^a Target species are listed in descending capture rate by method. The primary intended target is shown in bold type.

^b Department of Conservation (New Zealand)

fledging, failure) occurred mid-way between visits, as follows (from Johnson 1979):

$$dsr = 1 - \left(\frac{d}{exposure} \right)$$

where *dsr* is the daily (nest) survival rate, *d* is the number of deaths (i.e., nest failures), and *exposure* is the number of nest-days (i.e., the number of nests multiplied by the number of days exposed). Variance (*var*) was calculated as follows (also from Johnson 1979):

$$var(dsr) = (exposure - d) \times \frac{d}{exposure^3}$$

I then calculated the probability (*S*) that a nest would survive for the entire length of the nesting cycle (*t*, in days) and produce a fledged chick, using the formula:

$$S = (dsr)^t$$

Because there can be considerable variation in the length of the nesting cycle, I used its mean length in this population (126.7 days; see Results).

The length of the nesting season for the whole colony was determined to be the number of days between the date the first egg was laid and the date the last chick fledged. Colony growth rate over the study period (2005–2020) was the number of eggs in 2020 divided by the number of eggs in 2005, taken to the 16th root. The relationship between colony size and the length of the breeding season was assessed with regression, using the number of eggs laid as the predictor variable and the season length (in days) as the response variable. I examined the relationship between the number of active nests and the number of adults flying over the colony using a general linear model, with the number of nests as the predictor and

the number of flying adults as the response, with month as a random factor to account for seasonal variation.

Causes of failure were assessed using the expected hatching and fledging dates, the condition of the egg or chick, and other evidence in the nest. Causes were then assigned to one of the following categories: abandoned (parents stopped incubating before the expected hatching date); egg breakage (egg cracked or broken in nest and no signs of predation); egg roll-out (egg found below nest, nests usually on sloping or uneven ground); failed to hatch (unhatched egg incubated beyond anticipated hatching date); exposure (small chick dead in nest with no sign of predation); starvation (chick found dead, appearing emaciated, with no signs of parents being predated); competition (broken egg in nest following an altercation with another tropicbird); disease (dead chick found in nest with signs of avian pox virus *Poxvirus avium*); human disturbance (broken egg or dead chick in nest with signs of humans in or near nest); predation (egg or chick missing or dead and evidence of a predator in the nest, such as footprints, droppings, chew marks on eggs, body dismembered or chewed open, or clumps of feathers); entanglement (chick or adult found dead and tangled in vegetation); and unknown (egg or chick missing and no evidence for other causes). Some failures that were categorized as unknown were probably the result of predation, but evidence was lacking.

RESULTS

I found and monitored a total of 734 Red-tailed Tropicbird nests between Lāna'i Lookout and Hālonā Point, O'ahu, during 2005 to 2020. The colony increased in size over time, from 18 eggs laid in 2005 to 94 eggs in 2020, and from 7 chicks fledged in 2005 to 59 chicks fledged in 2020 (Fig. 2). The average annual growth rate was 11% and the overall increase was 520%. The colony also expanded spatially, first along the cliffs to the east and west, then north onto the slopes of Koko Crater (Fig. 1).

In all years combined, the mean apparent hatching rate was 0.792 ± 0.015 ($n = 734$ eggs), the mean apparent fledging rate was 0.797 ± 0.017 ($n = 581$ chicks hatched), and the mean apparent nest success rate was 0.631 ± 0.018 ($n = 734$ nests). The apparent nest success rate varied among years, ranging from 0.400 ± 0.100 to 0.770 ± 0.049 ($n = 15$ years). The mean incubation period was 44.3 days ($n = 504$ eggs) and the mean nesting period was 82.4 days ($n = 394$ chicks), resulting in a mean breeding cycle length of 126.7 days.

The Mayfield daily nest survival rate in all years combined was 0.996 ± 0.0002 , ranging from 0.993 ± 0.002 to 0.998 ± 0.005 ($n = 15$ years). The mean daily nest survival rate resulted in a mean estimated nest success rate of 0.619. The Mayfield nest success rate thus was 0.012 lower overall than the apparent nest success rate, and the difference ranged from -0.018 to 0.076 among years. The apparent nest success rate was higher than the Mayfield estimate in 4 of 15 years.

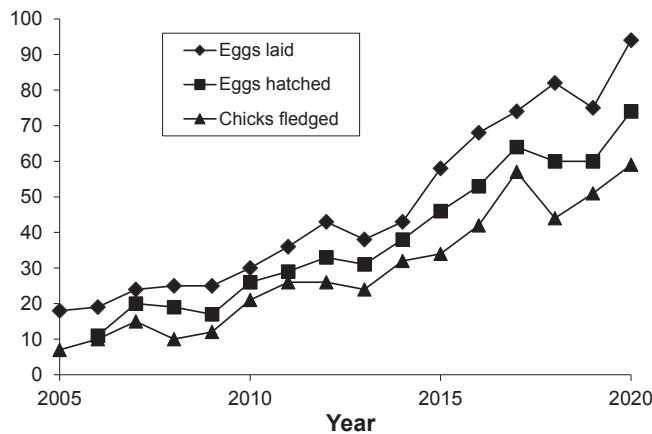


Fig. 2. Number of Red-tailed Tropicbird *Phaethon rubricauda* eggs laid, eggs hatched, and chicks fledged at Hālonā Point, O‘ahu, 2005–2020.

TABLE 2

Causes of nest failure in a Red-tailed Tropicbird *Phaethon rubricauda* colony near Hālonā Point, O‘ahu, 2006–2020

| Cause of failure | # | % |
|-------------------|------------|--------------|
| Unknown | 61 | 23.2 |
| Predation | 57 | 21.7 |
| Exposure | 45 | 17.1 |
| Failed to hatch | 33 | 12.5 |
| Egg breakage | 26 | 9.9 |
| Starvation | 19 | 7.2 |
| Abandonment | 11 | 4.2 |
| Competition | 4 | 1.5 |
| Egg roll-out | 3 | 1.1 |
| Disease | 2 | 0.8 |
| Human disturbance | 1 | 0.4 |
| Entanglement | 1 | 0.4 |
| Total | 263 | 100.0 |

The most common cause of nest failure was predation, accounting for 21.7% of failures (Table 2). The second most common cause of failure was exposure, in which a small chick was found dead in the nest with no sign of injuries. Failing to hatch also was common, accounting for 12.5% of failures; some parents continued to incubate eggs for up to 121 days. One large chick was found entangled and dead in the thorny branches of a kiawe *Prosopis pallida* tree in 2010. One chick was found crushed into the soil, with human footprints next to it. Four eggs were cracked or broken during fights for nest sites, with three of the four instances occurring during interactions between a Red-tailed and a Red-billed tropicbird *P. aethereus*. Three eggs were found below nests on sloping or uneven ground but were not damaged, apparently having rolled from the nest.

The length of the breeding season became longer as the colony grew ($F_{1,12} = 17.66$, $P < 0.001$, $R^2 = 57.6\%$; Fig. 3). Active nests were present in all months except December, with peaks in egg laying, chick hatching, and chick fledging occurring in March, April, and July, respectively (Fig. 4). The proportion of nests active in each month ranged 3% to 70%, peaking in May (Fig. 5). I developed a correction factor to estimate the total number of nests in a colony based on the number of nests found during a single visit in any month (Table 3).

The number of adult tropicbirds flying over the colony was related to the number of active nests ($F_{58,252} = 1.87$, $P = 0.001$) and to

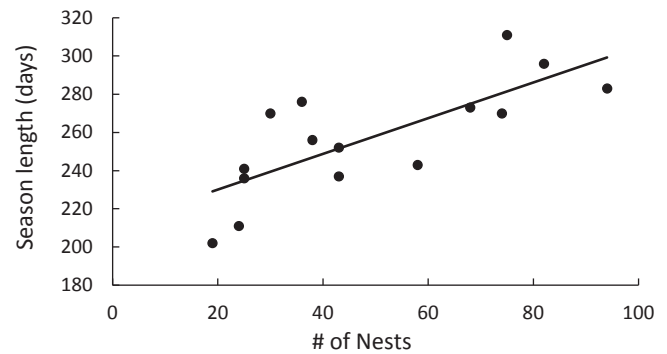


Fig. 3. Length of the breeding season in a Red-tailed Tropicbird *Phaethon rubricauda* colony at Hālonā Point, O‘ahu, in relation to colony size. The colony grew from 19 to 94 nests between 2006 and 2020.

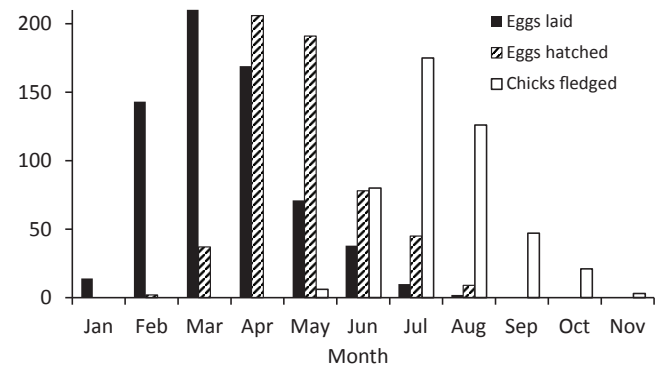


Fig. 4. Seasonality of egg laying, hatching, and fledging in Red-tailed Tropicbirds *Phaethon rubricauda* at Hālonā Point, O‘ahu, 2006–2020.

month ($F_{9,252} = 2.99, P = 0.002$; Fig. 6). I developed a correction factor to estimate the number of active nests present based on the number of flying adults on any given day, varying by month (Table 3). Most adults sitting on the ground were on an active nest, and only a few sat on prospective nests that had no egg or chick. Another correction factor was developed to estimate the number of active nests based on the total number of adults observed on the ground, also varying by month (Table 3).

During 2006–2020, a total of 1108 predators were trapped from the area around the tropicbird colony, including 4 feral cats, 212 mongooses, 80 rats, 28 mice, and 784 predators of unknown species (Table 1). Most of the unknown predators were removed with

automated rat traps and most probably were rodents. An additional unknown number of predators were removed with the poison bait stations during 2009–2013, but there is no way to know how many predators consumed the bait or how many died. For mongooses, the DOC kill traps were the best removal method and were twice as effective as live traps. For feral cats, live traps were more effective than the DOC kill traps, but the capture rate was low. The automated rodent traps were most effective for rodents, but most carcasses were scavenged quickly, and few could be identified. Mongoose carcasses were present under an automated rat trap on two occasions.

DISCUSSION

The Red-tailed Tropicbird colony on the Ka Iwi coast of southeastern O'ahu grew in response to predator control, reaching 94 nests in 2020. It is now the fourth largest colony of this species in the southeastern Hawaiian Islands, after Kilauea Point on Kaua'i (449 pairs), Lehua Islet (200 pairs), and Ka'ula Islet (119 pairs; Pyle & Pyle 2017, VanderWerf *et al.* 2007, Felis *et al.* 2020; see below). Most growth was likely the result of local recruitment, but some immigration was involved, indicated by the discovery of a breeding adult banded as a chick on Johnston Atoll, 1330 km away. Since Varela *et al.* (2021) found little genetic population structure of Red-tailed Tropicbirds within the entire Hawaiian archipelago, movement must exist among the Hawaiian colonies. Evidence exists of tropicbirds moving between islands 6000 km apart (Le Corre *et al.* 2003).

The apparent nest success rate (63%) was high compared to other colonies, despite a continuing low level of predation. On Lehua Islet, where the only land predators present were Pacific rats *R. exulans*, apparent nest success was 57%–58% and Mayfield nest success was 38%–47% (VanderWerf & Raine 2016). On Kure Atoll, where Pacific rats were also the only mammalian predator, apparent nest success was 17% and 38% in 1964 and 1965, and predation accounted for 54% and 65% of nest failures (Fleet *et al.* 1974). On Midway Atoll, apparent nest success was 38% and 41% in two years before rats were eradicated (Tyler 1991, as cited in Laniawe 2008) and 41% in the 11 years after rats were eradicated in 1997 (Laniawe 2008). At Kilauea Point, where feral cats and rats are present but their numbers are controlled, apparent nest success was a maximum

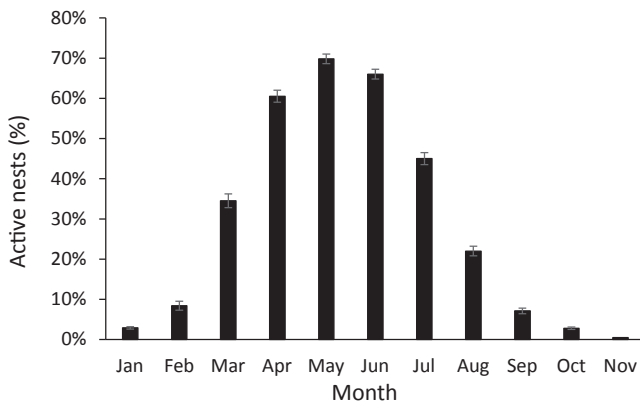


Fig. 5. Nesting phenology of Red-tailed Tropicbirds *Phaethon rubricauda* at Hālonā Point, O'ahu. Error bars show standard error.

TABLE 3
Correction factors for estimating the number of active Red-tailed Tropicbird *Phaethon rubricauda* nests at Hālonā Point, Oahu

| Month | Correction factor | | |
|-----------|----------------------------|--------------------------|--------------------------|
| | Flying adults ^a | False nests ^a | Seasonality ^b |
| January | 0.14 ± 0.03 | 0.30 ± 0.04 | 34.5 ± 3.57 |
| February | 1.29 ± 0.27 | 0.63 ± 0.08 | 11.9 ± 1.56 |
| March | 5.65 ± 1.06 | 0.92 ± 0.22 | 2.9 ± 0.14 |
| April | 7.79 ± 1.57 | 0.97 ± 0.19 | 1.7 ± 0.04 |
| May | 8.12 ± 1.38 | 0.98 ± 0.20 | 1.4 ± 0.02 |
| June | 6.10 ± 0.71 | 0.97 ± 0.19 | 1.5 ± 0.03 |
| July | 7.42 ± 1.57 | 0.97 ± 0.21 | 2.2 ± 0.07 |
| August | 2.92 ± 0.45 | 0.96 ± 0.22 | 4.5 ± 0.25 |
| September | 3.93 ± 0.88 | 1.00 ± 0.00 | 14.1 ± 1.39 |
| October | - | 1.00 ± 0.00 | 35.7 ± 3.83 |

^a The corrections for flying adults and false nests can be multiplied by the number of adults observed in the air or sitting on the ground to derive the number of active nests present at the time of observation.

^b The correction for seasonality can be multiplied by the number of nests observed on a single visit to derive the total number of nests throughout the year.

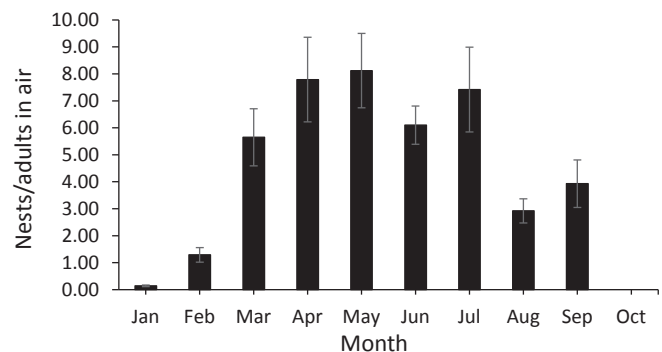


Fig. 6. Seasonal relationship between number of Red-tailed Tropicbird *Phaethon rubricauda* nests and number of adults flying over Hālonā Point colony, determined by counts during 11h00–15h00 each day. Error bars show standard error.

of 42% (Felis *et al.* 2020). On Johnston Atoll, where predators are absent, apparent nest success averaged 56% during 1967–1969 (Amerson & Shelton 1976) and 85% during 1982–1984 (Schreiber 1994). If predation at the O'ahu colony could be eliminated and the 57 nests that failed from predation had succeeded at the rate of other nests, the apparent nest success rate would be 68%.

Apparent nest success often is an overestimate of true nest success because nests that fail are present for less time and thus are less likely to be found, especially if visits are infrequent (Jehle *et al.* 2004, Jones & Geupel 2007). However, in this study apparent nest success was accurate, resulting in an average overestimate of just 1.2% compared to the Mayfield estimate. Apparent nest success was accurate in this case because: 1) most nest sites were used for several years and thus easy to find; 2) the colony was limited in spatial scope and few nests were missed; 3) visits were frequent (28.5 times per year) and most nests were found shortly after the egg was laid. The difference between the apparent and Mayfield nest success was larger (15%; 57%–58% vs. 38%–47% in two years, respectively) in a study of Red-tailed Tropicbirds on Lehua Islet (VanderWerf & Raine 2016) because only four visits per year were made and more nests were either missed or found later in the nesting cycle.

The nesting phenology of Red-tailed Tropicbirds varies considerably, even within the southeastern Hawaiian Islands. On Kure Atoll, the first eggs were laid in the first week of March in two years and the peak in laying was in April and May (Fleet 1972). At Kīlauea Point, the first egg was laid in early to mid-March in five of six years (Felis *et al.* 2020), six weeks later than on O'ahu. Tracking studies have shown that Red-tailed Tropicbirds breeding at Kīlauea Point and Lehua Islet foraged primarily north and west of the islands, while tropicbirds from O'ahu primarily foraged to the south (Adams *et al.* 2020, Townsend *et al.* unpubl. data.). This offers the possibility that differences in nesting phenology could be related to geographic variation in prey availability.

The correction factors developed will facilitate the monitoring of Red-tailed Tropicbirds in other areas that are more difficult to access or in situations where only one or a few visits can be made per year. For example, in a seabird survey of Ka'ula Islet conducted with ultra-high-resolution digital photographs taken from an aircraft during a single visit in March 2016, 16 sitting Red-tailed Tropicbirds were observed on the ground but no nest contents were ascertained (Normandeau Associates & APEM 2016). Using correction factors from the present study and values from February instead of March to account for difference in nesting phenology between these areas, $63\% \pm 8\%$ of those nests, or 10.0 ± 1.3 nests, probably were active (Table 1). Since the survey was conducted near the start of the nesting season, probably 11.90 ± 1.56 times as many nests were present throughout the year, resulting in a total estimate of 119.0 ± 15.6 nests on the island throughout the year. This estimate is comparable to that on Lehua Islet, which has similar topography, is 1.71 times larger (110 ha vs. 64 ha, or 1.1 km^2 vs. 0.64 km^2), and supports 200 breeding pairs (VanderWerf *et al.* 2007) or 1.68 times as many as estimated on Ka'ula. Similarly, Felis *et al.* (2020) surveyed Red-tailed Tropicbirds at Kīlauea Point on three visits from April to July 2019, and they found 387 active nests and 64 potential nests in which the contents could not be determined. Using the correction factor for false nests, $97\% \pm 19\%$ of the potential nests probably were active (62.1 ± 12.2 nests), resulting in a total estimate of 449.0 ± 12.2 active nests on the refuge.

There are several possible explanations for the increasing breeding season duration as the colony grew, the most likely of which is avoidance of intraspecific competition for food by pairs nesting at slightly different times of year (Ainley *et al.* 1995, Lewis *et al.* 2001). The pattern also could be an effect of statistical sample size; in a larger colony there is a higher chance that a pair will breed very early or very late in the season, resulting in a longer season overall. However, some pairs consistently nested early or late, indicating that the asynchrony was not random.

The prevalence of avian pox virus was low among Red-tailed Tropicbirds on O'ahu (2 of 394 chicks = 0.5%; 2 of 16 years = 12.5%), as it is in other seabirds elsewhere (VanderWerf & Young 2016). However, both chicks that showed signs of the pox died from severe infections that caused their bill to become so deformed that they probably could not eat. Both instances occurred during particularly rainy years, presumably because the abundance of mosquitoes (the primary vector) was higher than normal in the colony area, owing to more standing water where mosquitoes can breed. A single Red-tailed Tropicbird chick with pox was found on Lehua Islet, but the infection was not severe, and the chick survived to fledge (VanderWerf & Raine 2016). Locke *et al.* (1965) found pox on two adult and 19 juvenile Red-tailed Tropicbirds on Midway Atoll in September 1963, with four additional chicks with pox infections found dead. The prevalence of avian pox was found to be similar in White-tailed Tropicbirds *P. lepturus* in Bermuda by Wingate *et al.* (1980), who reported that 6 of 81 fledglings in 4 of 20 years had lesions suggestive of pox infection, with an overall infection rate of 0.3% in all nests.

Competition for nests sites accounted for a small number of failures (four), but three of them occurred following fights between a Red-tailed and a Red-billed tropicbird; it is possible that competition was involved in other failed nests as well (VanderWerf & Young 2007). Tropicbirds are known to engage in vigorous fights during competition for nesting sites (Schreiber & Schreiber 1993), and Diamond (1975) speculated that interference from White-tailed Tropicbirds may have been a cause of nest failure in Red-tailed Tropicbirds on Aldabra Atoll. The amount of competition in the O'ahu colony did not increase despite colony growth, and it is possible that spatial expansion of the colony resulted from new breeders attempting to avoid competition for nesting sites with established breeding pairs (Fig. 1).

The predator control was generally effective at keeping predator numbers low and protecting tropicbird nests, but there still was some predation. Most instances appeared to have been by mongooses, which are known to be a serious predator of many seabirds in Hawai'i (Hays & Conant 2007, VanderWerf *et al.* 2014). However, mongoose predation occurred on only eggs and chicks (not adults) in the present study. Predation on adults was rare and involved only feral cats, only a few of which were trapped. However, feral cats can cause a lot of damage in a short time, as occurred in 2020, when a single cat killed six adult tropicbirds in two weeks before it was removed. Raine *et al.* (2020) also found that only cats killed adult Hawaiian Petrels *Pterodroma sandwichensis*, and that rats preyed on eggs and chicks. The dry, rocky habitat around the O'ahu tropicbird colony is probably not that attractive to cats, but two areas where feral cats regularly are fed by members of the public are located at Hanauma Bay and Koko Head Regional Park, less than one kilometer from the nearest tropicbird nest. Thus, there is significant potential for cats

to reach this colony. Predator control will be required in perpetuity to allow this colony to continue thriving, but the required effort is low and easily manageable.

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