Factors Affecting Breeding Success of White Terns (*Gygis alba*; Aves: Laridae) in Urban Environments of Honolulu, Hawai'i[1]

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Abstract: The White Tern (*Gygis alba*) is a common seabird that nests on islands in tropical and subtropical oceans. In the southeastern Hawaiian Islands, White Terns breed only in urban and suburban areas of Honolulu. The Honolulu population has grown from a single pair in 1961 to 2,300 birds in 2016. We measured breeding success of White Terns in Honolulu and examined aspects of their breeding biology and the environment that may affect breeding. We documented 3,855 breeding events in Honolulu from 2016 to 2019. Breeding success was 68.3% and varied less than 3% among years. Breeding occurred in all months, with lowest activity in the summer and a peak in the winter and spring, but the pattern varied among years. White Terns bred in 64 tree species. Breeding success varied among tree species and was related to characteristics of the trees and their attractiveness to non-native predators. The height of breeding events was 9.26 ± 0.05 m and success was related to height, with higher success in events 5–10 m above ground. The diameter of branches on which breeding occurred was 10.2 ± 0.1 cm and success was related to branch diameter, with lower success on branches >20 cm. The high breeding success of White Terns in Honolulu is related to: the small size and isolation of the O'ahu population, which may result in reduced intra-specific competition for food; protection from predators provided by the urban environment; and trimming of trees by arborists, which unintentionally improves the value of trees as breeding sites for terns.

Keywords: White Tern, breeding success, urban environment, Honolulu, seabirds, urban forestry

The White Tern (*Gygis alba*) is a common seabird that nests on many islands in the tropical and subtropical Pacific, Atlantic, and Indian Oceans (Niethammer and Patrick 1998). It was formerly known as the Fairy Tern and is sometimes still referred to by that name (Pratt 2020). White Terns are common in the remote northwestern Hawaiian Islands, but in the larger southeastern Hawaiian Islands they are found only on O'ahu, where they were first found breeding in 1961 (Ord 1961, Niethammer and Patrick 1998, VanderWerf 2003). The White Tern population on O'ahu has increased rapidly since then, with the population estimated to be 50–100 pairs in the mid-1980s, 700 birds in 2002, and 2,300 birds in 2016 (Harrison 1990, VanderWerf 2003, VanderWerf and Downs 2018). The White Tern was designated the official bird of the City and County of Honolulu in 2007 (Morgan 2007).

White Terns are adaptable and breed in a variety of environments, including low-lying atolls with few trees, high rocky islands where they nest on sheer cliffs, such as the Hawaiian Island of Nihoa, and dense rainforest, such as

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Pacific Science (2022), vol. 76, no. 1:33–41
doi:10.2984/76.1.3

in Palau (VanderWerf 2007). On O'ahu, White Terns breed only in urban and suburban areas in the city of Honolulu, not in adjacent undeveloped land or other parts of the island (VanderWerf and Downs 2018). The first detailed information about the O'ahu population was provided by Miles (1985, 1986), who studied the breeding biology of White Terns near Kapiolani Park in the mid-1980s. Thorough surveys of the distribution and abundance of White Terns in Honolulu were conducted by VanderWerf (2003) and VanderWerf and Downs (2018). White Terns have persisted on islands where non-native predators are abundant and most other seabirds have been extirpated. Examination of their breeding biology in different environments will contribute to a better understanding of their ecology, conservation, and aspects of their life history that allow them to be so adaptable. In this study, our goals were to: (1) measure breeding success of White Terns in Honolulu; and (2) examine aspects of their breeding biology and the environment that may affect breeding success.

METHODS

White Terns do not build a nest, instead they lay their single egg directly on a branch, the ground, or other substrate (Niethammer and Patrick 1998). On O'ahu and most other islands, White Terns breed almost exclusively in trees (Carlile and Priddel 2015, VanderWerf and Downs 2018), but on some islands they nest on cliff ledges and man-made structures (Rauzon and Kenyon 1984, Niethammer and Patrick 1998). White Terns may make multiple breeding attempts per year and may raise as many as three chicks in a 12-month period (Miles 1985, VanderWerf 2003). This high fecundity is unusual among seabirds and presumably has contributed to their rapid population growth on O'ahu (VanderWerf and Downs 2018). Potential threats to White Terns on O'ahu include predation by non-native animals including feral cats (*Felis cattus*), black or ship rats (*Rattus rattus*), and Barn Owls (*Tyto alba*), cutting of trees in which they breed, disturbance from other human activities, and storms with strong wind and heavy rain that can damage trees or cause eggs and chicks to fall to the ground.

We surveyed for White Terns throughout Honolulu from 2016 to 2019 and collected the following information about White Tern breeding events: status when found (egg or chick), tree species, height off the ground (measured with a laser range finder or estimated if there was not a clear view), and branch diameter (estimated to the nearest inch, later converted to metric units). For breeding events found after the chick had hatched, we used the appearance of the chick to estimate its age and the approximate egg-laying date, based on an incubation period of 35 days (Niethammer and Patrick 1998, VanderWerf 2003). Each breeding site was categorized into one of six types based on its physical characteristics: branch, fork, branch junction, closed loop, crotch, or cup. A branch was simply a horizontal branch. A fork was where a branch split and both forks supported the egg. A branch junction was like a fork but with a perpendicular split, only one of which supported the egg. A closed loop consisted of two or more twigs or small branches that encircled the egg. A crotch was a vertical fork in a trunk or branch. A cup occurred where a branch was cut or had broken off, causing the tree to form a cup-shaped scar. We visited most breeding sites at approximately monthly intervals, but the frequency varied and in some cases was not sufficient to determine the outcome. For more information about survey methods, see VanderWerf and Downs (2018).

We defined breeding success as the proportion of breeding events that resulted in a fledged chick, excluding events in which the outcome was unknown. We tested whether breeding success varied among tree species with a chi-squared analysis. All tree species with sample sizes < 20 were lumped into "other." We tested whether success varied among breeding site types with a chi-squared analysis.

To examine the relationship between breeding success and height off the ground, we compared the height of failed versus successful events using a two-sample *t*-test, and we tested whether success differed among the following height categories using a chi-squared test: <5 m, 5–10 m, 10–15 m, and >15 m. To examine the relationship between breeding success and branch size, we compared branch diameter of failed versus successful events using a two-sample *t*-test, and we tested whether success differed among the following branch diameter categories using a chi-squared test: 2.5 or 5.0 cm (1 or 2 inches), 7.5 or 10.0 cm (3 or 4 inches), 12.5 or 15 cm (5 or 6 inches), 17.5 or 20 cm (7 or 8 inches), and >20 cm (>8 inches).

RESULTS

We documented a total of 3,855 White Tern breeding events in Honolulu from 2016 to 2019, of which 1,063 failed, 2,295 were successful, and 497 had an unknown outcome. Overall breeding success was thus 68.3%, not counting nests of unknown outcome. Breeding success did not differ among years and was very similar in all four years of the study (chi-squared = 2.49, df = 3, $P = .48$; 69.6% in 2016, 68.4% in 2017, 69.7% in 2018, and 66.7% in 2019), so data from all years were combined in other analyses.

Breeding occurred in all months and phenology was roughly similar in all four years but with some variation (Figure 1). The period of lowest breeding activity occurred in the summer months each year, with the fewest eggs laid in June in 2016 and in August in 2017–2019. A peak in breeding activity occurred in the winter months, but the pattern and timing varied among years. In 2017 and 2019 there was a distinct peak from January to March. In 2016 and 2018 the peak was less distinct and egg laying occurred over a longer period from October or November to April or May.

White Terns bred in 64 tree species, and breeding success varied among tree species (Table 1; chi-squared = 82.5, df = 22, $P < .001$). Success was similar in the four most frequently used tree species (monkeypod, kukui,

TABLE 1

White Tern Breeding Success by Tree Species in Honolulu from 2016 to 2019

Common Name	Scientific Name	Total No. Breeding Events	No. Failed Breeding Events	No. Successful Breeding Events	No. Unknown Outcome Breeding Events	Breeding Success (%)
Monkeypod	*Samanea saman*	855	214	523	118	71.0
Kukui	*Aleurites moluccana*	684	174	436	74	71.5
Shower	*Cassia* spp.	580	163	350	67	68.2
Mahogany	*Swietenia mahagoni*	324	102	191	31	65.2
Indian banyan	*Ficus benghalensis*	285	99	151	35	60.4
Chinese banyan	*Ficus microcarpa*	200	33	136	31	80.5
Umbrella	*Schefflera actinophylla*	92	28	57	7	67.1
Tamarind	*Tamarindus indica*	60	29	25	6	46.3
Yokewood	*Catalpa longissima*	59	28	23	8	45.1
Narra	*Pterocarpus indicus*	50	11	29	10	72.5
Gold tree	*Tabebuia donnell-smithii*	43	10	29	4	74.4
Moreton Bay fig	*Ficus macrophylla*	40	17	11	12	39.3
Royal poinciana	*Delonix regia*	36	10	22	4	68.8
False olive	*Elaeodendron orientale*	33	7	19	7	73.1
Kiawe	*Prosopis pallida*	32	8	21	3	72.4
Yellow poinciana	*Peltophorum pterocarpum*	31	6	22	3	78.6
Autograph tree	*Clusia rosea*	28	5	19	4	79.2
Bischofia	*Bischofia javanica*	27	9	16	2	64.0
Mango	*Mangifera indica*	27	3	19	5	86.4
Tropical almond	*Terminalia catalpa*	26	1	19	6	95.0
Hala	*Pandanus tectorius*	24	12	10	2	45.5
Other		283	82	151	50	64.8
Total		3589	1063	2299	497	68.4

"Other" included all species in which there were <20 breeding events ($n = 42$ species).

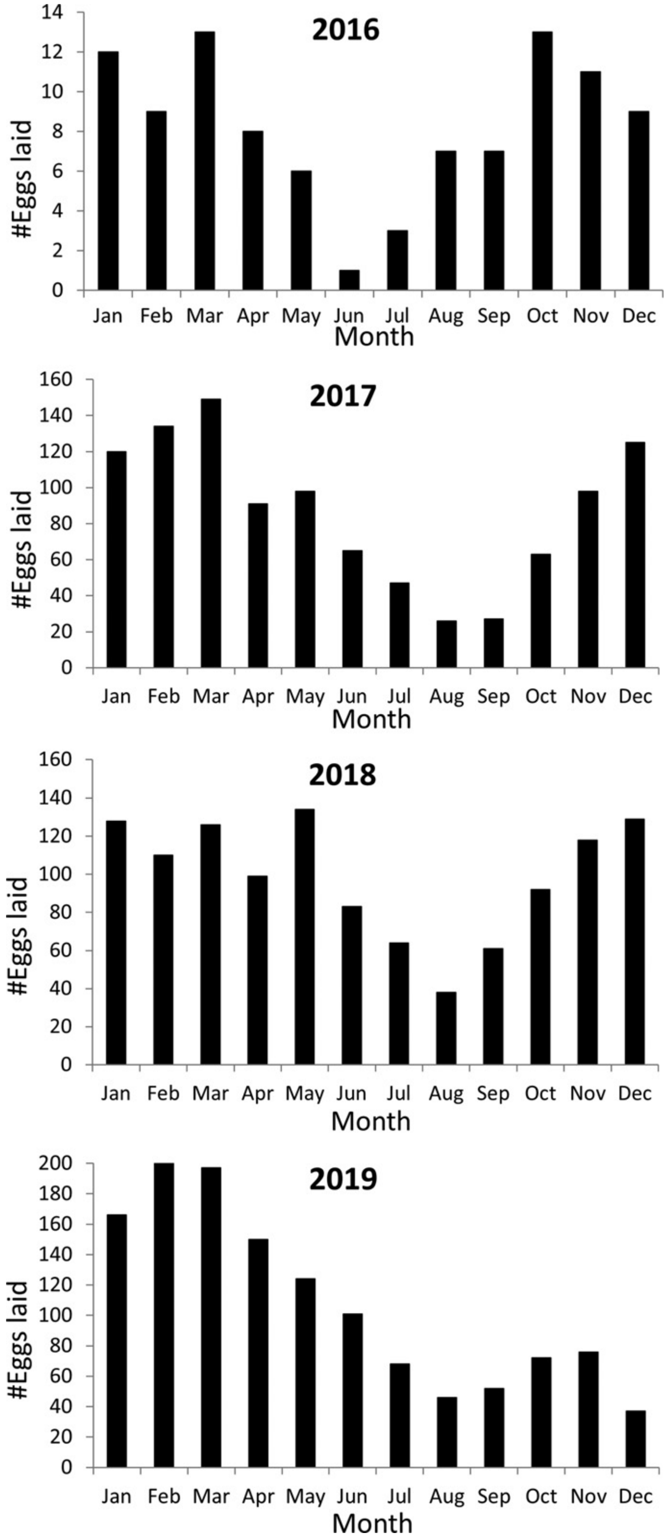

FIGURE 1. Breeding phenology of White Terns in Honolulu, Hawai'i from 2016 to 2019. Note the different axis units in 2016, when survey effort was lower.

TABLE 2

White Tern Breeding Success by Breeding Site Type (See Text for Type Descriptions)

Site Type	No. Failed	No. Successful	% Success	% of Events
Branch	302	612	67.0	27.7
Branch junction	36	89	71.2	3.6
Closed loop	74	146	66.4	6.6
Crotch	18	41	69.5	1.8
Cup	431	951	68.8	40.4
Fork	202	460	68.5	19.9

shower, and mahogany, see Table 1 for scientific names of tree species), which together accounted for 63% of all breeding events. Success was higher than expected in Chinese banyan, mango, and tropical almond, and lower than expected in Indian banyan, Moreton Bay fig, yokewood, tamarind, and hala (Table 1). Breeding success did not differ among the six site types (chi-squared = 2.26, df = 5, $P = .81$; Table 2).

The mean height of all breeding events was 9.26 ± 0.05 m ($n = 3{,}843$), and success was related to height. The height of failed breeding events (9.35 ± 0.1 m, $n = 1{,}061$) was marginally higher than that of successful events (9.14 ± 0.06 m, $n = 2{,}288$; $t = 1.72$, df = 1387, $P = .08$). Breeding success was higher in events 5–10 m above the ground than in higher and lower height categories (Table 3; chi-squared = 25.7, df = 3, $P < .001$).

The mean diameter of branches on which breeding events occurred was 10.2 ± 0.1 cm ($n = 2{,}501$), and breeding success was related

TABLE 3

White Tern Breeding Success by Height Off the Ground

Height Category (m)	No. Failed	No. Successful	% Success
<5	62	98	61.3
5–10	595	1384	69.9
10–15	302	469	60.8
>15	95	156	62.2
Total	1054	2107	66.7

Success was higher in events 5–10 m above the ground.

TABLE 4

White Tern Breeding Success by Branch Size

Diameter Category in cm (in)	No. Failed	No. Successful	% Success
2.5 or 5.0 (1 or 2)	258	563	68.6
7.5 or 10.0 (3 or 4)	448	1064	70.4
12.5 or 15.0 (5 or 6)	196	397	66.9
17.5 or 20.0 (7 or 8)	72	163	69.4
>20 (>8)	89	103	53.6
Total	1063	2290	68.3

Success was lower only in the largest size category.

to branch diameter. The diameter of branches in failed events (10.7 ± 0.2 cm, $n = 743$) was larger than that in successful events (10.0 ± 0.1 cm, $n = 1{,}403$; $t = 2.52$, df = 1337, $P = .01$). Breeding success was similar among most diameter categories, but success was lower on branches >20 cm (8 inches) in diameter (Table 4; chi-squared = 22.69, df = 4, $P < .001$).

DISCUSSION

Breeding success of White Terns in urban and suburban areas of Honolulu was remarkably high (68.3%), especially considering the many sources of anthropogenic disturbance and presence of non-native predators including feral cats, mongooses, and rats. All previous measurements of breeding success in the Oʻahu White Tern population have been similarly high and are the highest known in the species (76%, Miles 1985; 74%, VanderWerf 2003; 57%, VanderWerf and Downs 2018). On Tern Island, Hawaiʻi, where there are no introduced predators, breeding success was 30% (Niethammer and Patrick 1998). On Ascension Island in the Indian Ocean, breeding success was 29% (Dorward 1963). On Lord Howe Island, where White Terns also nest in urban and suburban areas, breeding success was just 17% because of predation by native and non-native birds (Carlile and Priddel 2015). The high rate of breeding success undoubtedly has contributed to the rapid growth of the Honolulu population (VanderWerf and Downs 2018).

Breeding success of White Terns in Honolulu also was remarkably consistent among years, with less than 3% annual variation, especially given the extreme variation in ocean and climate conditions that occurred in the Pacific during the four years of this study. In 2016, the north Pacific was still under the influence of the "warm blob," a huge mass of unusually warm water that caused a large number of tropical storms and extreme rainfall events (Cavole et al. 2016, Brainard et al. 2018, Herring et al. 2018). In contrast, 2017–2019 were not typical El Niño years but still exhibited unusual variability. Evans et al. (2021) found that annual variation in climatic and oceanographic conditions during this time period affected the foraging distributions of many seabirds in the Pacific. Eizenberg et al. (2021) found that increased marine temperatures reduced breeding success of two Procellariform seabirds in Australia during this time period, but that one of the two species maintained consistent breeding success and phenology while another did not. Environmental variability likely caused annual variation in breeding phenology of White Terns, but it did not reduce their breeding success.

The high breeding success by White Terns in Honolulu probably is related to several factors. First, the relatively small size and isolation of the O'ahu population may result in reduced intraspecific competition for food. Food abundance near large seabird colonies can become locally depleted, causing lower breeding success and longer foraging ranges, which ultimately can limit the size of seabird colonies; this pattern is commonly referred to as Ashmole's halo (Ashmole 1963, Lewis et al. 2001, Gaston et al. 2007). The nearest White Tern colony to O'ahu is on Nihoa, 463 km away. White Terns return to land to feed their chick every day (Niethammer and Patrick 1998, VanderWerf and Downs personal obs.), and the distance from O'ahu to Nihoa is farther than the foraging range of White Terns during the breeding season, so there is no overlap in foraging range with terns from other colonies. Relatively high food availability also may account for the higher incidence of double and triple brooding and short fledging period in the O'ahu population (VanderWerf and Downs 2018). If intraspecific competition for food on O'ahu is low, breeding success would be expected to decline as the population increases in size (Lewis et al. 2001).

Second, although non-native predators are ubiquitous in urban Honolulu, the abundance of predators may be low compared to nearby agricultural and natural areas, and, paradoxically, aspects of the urban environment may help to protect terns. Many of the trees used by terns in Honolulu were located next to busy roads on which road-killed predators were common, and vehicle traffic may inhibit predators from reaching some trees. Rodents are controlled with rodenticide bait stations by commercial pest control companies in many areas of Honolulu to protect human health and property, and this may provide some benefit to terns too. In contrast, most natural areas on O'ahu receive little or no non-native predator control, with a few exceptions (VanderWerf 2009). Feeding of feral cats by the public remains a problem in some locations because it results in an increase in cat numbers and the fed cats still instinctively hunt.

Third, trimming of trees by arborists may help to increase tern breeding success, provided it is done carefully to avoid branches with eggs or chicks (Liu et al. 2019). Techniques used by arborists to protect human safety and property, maintain tree health, and create tree shapes that are aesthetically pleasing to people also may unintentionally improve the value of trees as breeding sites for terns. For example, removal of dead branches that could break and fall also removes dangerous breeding sites for terns. Low branches that are removed to prevent collisions with vehicles and damage to utility poles, lines, and other structures also would be most accessible to predators. Trimming of branch clutter results in more open tree crowns that provide easier access for terns and reduced interaction of branches within and among trees that could knock eggs or chicks from the tree.

Variation in breeding success among the different tree species used by White Terns in Honolulu appeared to be related to physical characteristics of the tree species and their attractiveness to non-native mammalian predators. One of the most common causes of breeding failure was eggs or chicks falling from the tree; we frequently found broken eggs and chicks on the ground, especially following storms with high winds. The tree species used most have physical characteristics that seem to make the egg and chick more secure. Kukui has an angular branching geometry with many sharp bends that create corners and nooks suitable for balancing an egg. Mahogany and monkeypod trees grow very large and have rough bark that may prevent eggs from rolling and be easier for a chick to grasp with its feet. Kukui and shower trees readily form circular, cup-shaped scars where branches were broken or trimmed, creating ideal nest cups for tern eggs. Hala, the only tree species native to Hawai'i in which we found terns breeding, had low breeding success, likely because its branches are round and smooth and were precarious for eggs and chicks.

Miles (1986) found that ironwood (*Casuarina equisetifolia*) was the most commonly used tree species in Kapiolani Park, but we found no breeding events in ironwood. The ironwood trees are still present and terns are still common in the area, but many of the trees are now used by large numbers of feral pigeons (*Columba livia*) and Rose-ringed Parakeets (*Psittacula krameri*). The pigeons produced large amounts of droppings that could have attracted rats, and the parakeets occasionally acted aggressively toward terns, and it is possible the terns have stopped using ironwood trees to avoid pigeons and parakeets. The tree used most often by White Terns on Lord Howe Island, Norfolk Island Pine (*Araucaria heterophylla*) is fairly common on O'ahu and is commonly planted as an ornamental, as is the closely related Cook Pine (*A. columnaris*), but neither species was used by terns in Honolulu.

Use of different tree species also appeared to affect the risk of predation. All fig trees produce large quantities of fruit that could be attractive to black rats (*Rattus rattus*), which are good climbers and are known to prey on bird eggs and chicks (VanderWerf 2009), but breeding success of White Terns was lower in fig species with multiple trunks, large leaves, and large fruit (Indian banyan and Moreton Bay fig) than in species with smaller leaves and fruit (Chinese banyan). Indian banyans often grew in dense clusters composed of numerous trunks and complex interwoven crowns, resulting in an extensive canopy that likely supported a high density of rats. Some large clusters of Indian banyan trees were used as shelters by homeless people and had garbage and food waste under them, which often attracted feral pigeons and likely contributed to rat abundance. In contrast, Chinese banyan produces smaller fruit and usually grew as isolated trees rather than clumps, which may make it less attractive to rats. The high success in mango was surprising because that species produces large fruits that are attractive to rats, but some mango trees had rodenticide bait stations at their base and a metal band on the trunk to prevent rats from climbing to protect the fruit for human consumption. The low breeding success in tamarind was attributable to a high failure rate in a single large tree that had the second-most breeding events of any tree (40) in Honolulu, and where feral cats were fed by members of the public within a few meters of the tree. The causes of the high success in tropical almond and the low success in yokewood are unknown.

Other aspects of breeding site location that influenced breeding success also were related to predation risk and severe weather. Lower nests and larger branches were easier for predators to reach by climbing up from the ground, especially cats. Reduced success of breeding attempts higher in trees may have been related to greater exposure to winds and rain. We found the remains of several adult terns that appeared to have been depredated by Barn Owls (*Tyto alba*), which are not native to Hawai'i. Some of the depredated adults were found near nests and likely were the parents, which led to failure of the breeding attempt.

The lack of variation in success among the nest type categories was surprising; we had expected success to be higher in closed loops and cups because it seemed less likely that an egg could fall from those locations. However, we still believe cups are beneficial for White

Terns because they are uncommon yet were the most commonly used type site, accounting for 40% of all breeding events. Miles (1986) reported intense aggression over nest sites, and cups seemed to attract a lot of attention, suggesting that some breeding attempts may have failed because of intraspecific interference. Success in closed loops was the lowest in any type, indicating the security they appear to provide is an illusion. Loops sometimes were formed by twigs from different branches, allowing them to move independently in the wind, which could cause the loop to change in size or shape, possibly causing the egg or chick to fall through or be pushed out. On the other hand, it is possible that some loops may have been too secure and had such a tight fit that it prevented the parents from rolling the egg, which could impede development of the embryo. In a few cases, photographs of the spotting pattern visible on the underside of an egg in a loop was always the same, indicating it probably had not been rolled. Some eggs remained apparently wedged in the same position for weeks after they should have hatched.

The White Tern population on Oʻahu has thrived over the past 60 years, growing rapidly and exhibiting the highest breeding success rate known in the species. White Terns are not disturbed by the noise, lights, traffic, and other aspects of the urban environment in Honolulu. They are not seriously affected by non-native predators that have contributed to the extirpation of all other native seabirds and forest birds in urban Honolulu, and, paradoxically, may be protected to some degree from predation by the urban environment. White Terns still do not breed in most areas of Oʻahu, and their population can be expected to continue to grow and expand, perhaps until their numbers are limited by competition for food in the surrounding ocean.

ACKNOWLEDGMENTS

We thank the Hui Manu o Ku and many volunteers that helped to monitor tern breeding events, particularly Melody Bentz, Tiana Bolosan, Tersha Carpenter, Yvonne Chan, Catherine Fuller, Madison Kai, Satoko Lincoln, Jami Muranaka, Calvin Proctor, Antonio Querubin, Shalane Sambor, and Miriam Swann. We are grateful to Lake Gibby for helping to replace tern chicks rescued from the ground back in their tree using his climbing skills. Funding for surveys by EAV in 2016 was provided by the Hawaii Division of Forestry and Wildlife. The paper was improved by comments from David Duffy and two anonymous reviewers.

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