AN ABSTRACT OF THE THESIS OF

Nathan Christopher Johnson for the degree of Master of Science in Wildlife Science presented on June 18, 2015.

Title: Population Ecology of the Mariana Swiftlet (Aerodramus bartschi) on O‘ahu, Hawaiian Islands

Abstract approved: ______________________________________________________

Susan M. Haig

The Mariana Swiftlet (Aerodramus bartschi) (Aves: Apodidae) is endemic to the Mariana Islands, where it currently occurs on Saipan, Aguiguan, and Guam. An introduced population of Mariana Swiftlets is also present on O‘ahu in the Hawaiian Islands.

Sparing interference with the endangered population in the Marianas, the introduced, surrogate population on O‘ahu was studied in and around a human-made tunnel used for roosting and nesting from July to September 2005, and December 2005 to January 2011.

In order to implement effective conservation efforts, it is critical to understand species life history activities throughout multiple phases of the annual cycle. Information on Mariana Swiftlet life history is scarce. Therefore, this study was initiated to obtain critical data to provide the U.S. Fish and Wildlife Service, Commonwealth of the Northern Mariana Islands Division of Fish and Wildlife, and Guam Division of Aquatic and Wildlife Resources with the relevant information for addressing recovery criteria, as well as designing and implementing the proposed reintroductions of swiftlets from Saipan and southern Guam to their former ranges of Rota and northern Guam, respectively.
Mariana Swiftlets are open-air foragers that may be susceptible to the impacts of wind turbines if wind energy facilities become widespread in the Mariana Islands. Implementing effective survey methods is critical to determine a reliable baseline of Mariana Swiftlet population size, particularly if wind turbines are situated or proposed to be placed in the feeding ranges of these insectivores. I summarized the current and historic distribution and abundance, as well as described the survey methods used to evaluate the status of the Mariana Swiftlet. Using existing literature, correspondence from relevant biologists, and population surveys on O‘ahu, the present range-wide population of Mariana Swiftlets is estimated to be 6,532 individuals occurring in 17 caves on Saipan, Aguiguan, and Guam; and 142 individuals occupying one tunnel on O‘ahu. Based on a literature review, I confirmed that swiftlets have been extirpated from Rota and Tinian, and have declined on Aguiguan supporting their listing as an endangered species. Swiftlets have remained relatively stable on Guam and Saipan in recent years. An assessment of survey methods used for Mariana Swiftlets suggests changes are needed to more accurately reflect their distribution and abundance.

The behavioral ecology and reproductive biology of the Mariana Swiftlet on O‘ahu were examined at multiple temporal scales over five annual cycles. Tunnel emergence and arrival surveys indicated that peak entering and exiting activity occurred during crepuscular hours. Overnight surveys documented entering and exiting swiftlets at all hours of the night, with the latest arrival at 0402 hours. Active nests were observed in every month of the year. Peak nesting activity occurred between about May and September, and decreased from October to April. A clutch of one white egg ($n = 478$) was laid in a nest that was secured to a ledge or tunnel wall with copious amounts of
mucus-like salivary cement. Mean incubation and nestling periods were 23.91 ± 3.30 days (range = 18–30, n = 233) and 55.04 ± 6.61 days (range = 41–84, n = 228), respectively. Estimated nest success was 63%. Eggs found in the water or mud, or on the tunnel floor accounted for 52% of nest failures. Rat depredation was an important cause of nest failure and often resulted in simultaneous loss of most nests. Mariana Swiftlets completely recycled breeding activities following rat depredation events. The daily survival rate of nests was influenced by a quadratic effect of nest age and year. Having a surrogate population on O‘ahu to learn more about natural history, test reintroduction techniques, and provide individuals for population enhancement in the Marianas is an important advantage for Mariana Swiftlet conservation efforts.
POPULATION ECOLOGY OF THE MARIANA SWIFTLET
(AERODRAMUS BARTSCHI) ON O‘AHU, HAWAIIAN ISLANDS

by
Nathan Christopher Johnson

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APPROVED:

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Major Professor, representing Wildlife Science

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Head of the Department of Fisheries and Wildlife

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Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Nathan Christopher Johnson, Author
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This work was conducted in the laboratory of Dr. Susan Haig, who provided financial support, original thought, assistance with study design, aid in manuscript organization and development, field equipment, and office space throughout the project. Stephen Mosher contributed to the research presented in chapters two and three by collecting field data, and manuscript organization and development. Jeff Hollenbeck contributed to the research presented in chapter three by providing statistical and modeling guidance.
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Dedicated to the memory of my loving mother,

Pamela J. Johnson

1948–2009
POPULATION ECOLOGY OF THE MARIANA SWIFTLET 
(AERODRAMUS BARTSCHI) ON O‘AHU, HAWAIIAN ISLANDS

1. INTRODUCTION

1.1. INTRODUCTION

Oceanic islands represent valuable biological resources including unique ecosystems and high levels of endemism. However, insular flora and fauna are dangerously vulnerable to habitat change, human activities, species introductions, and extinction (Steadman and Martin 2003). Even though less than 20% of the world’s bird species are present on islands, more than 90% of bird extinctions in the past 400 years have been restricted to insular regions (Johnson and Stattersfield 1990). With islands in the Pacific Ocean experiencing over half of all avian insular extinctions (Johnson and Stattersfield 1990), island species are becoming extinct 12 times faster than continental species (Halliday 1978). In Oceania, 25,000 islands distributed across 13,000 km of the Pacific Ocean, 121 resident bird species are known to be extinct; the estimated range is thought to be 659–1,794 (Steadman 2006).

Of the 1,373 bird species categorized as Critically Endangered, Endangered, or Vulnerable by the International Union for Conservation of Nature, 25% occur on islands in the Pacific (i.e., Oceania, New Zealand, Papua New Guinea, and Hawai‘i) (International Union for Conservation of Nature 2014). The Hawaiian Islands alone comprise 35% of all U.S. listed threatened or endangered bird species (U.S. Fish and Wildlife Service 2015). In the Mariana Islands, nine bird species are included on federal
or local threatened or endangered lists (2 Northern Mariana Islands Administrative Code § 85–30.1–101, U.S. Fish and Wildlife Service 2011). On the Mariana island of Guam, 12–13 resident breeding bird species are extinct or extirpated (Wiles et al. 2003, Rodda and Savidge 2007), and the remaining are threatened with extirpation in the near future.

Translocation is one tool by which the preservation of threatened or endangered species is possible. Translocation is the capture and transfer of free-ranging animals from one part of their historic geographic range to another and can augment the local population or recolonize formerly occupied habitat (Kleiman 1989). Translocations have and remain a mainstay in many conservation-based programs. However, success of these programs has often been quite limited, frequently owing to poor planning efforts (Templeton 1996). Intended goals of translocations usually include strengthening genetic and demographic heterogeneity of small populations, creating satellite populations to decrease the threat of species loss attributable to catastrophes, reestablishing a former range, or accelerating species recovery (Griffith et al. 1989). The eventual measure of success for a translocation is establishment of a self-sustaining wild population (Scott and Carpenter 1987).

Translocation of threatened or endangered birds is possible as long as numerous challenging requirements are met (Fyfe 1978). Two important prerequisites are to thoroughly investigate the species to be translocated and carefully examine the target location. Komdeur (1994) stresses this point and utilized information about diet and habitat requirements of the Seychelles Warbler (*Acrocephalus sechellensis*) on Cousin Island (Seychelles Islands) and potential translocation sites on Cousine and Aride Islands before attempting translocation efforts. Fancy et al. (2001) considered many previously-
studied aspects of the ecology of the ‘Oma’o (*Myadestes obscurus*) before implementing a translocation on the island of Hawai‘i.

Understanding how and when a species is engaged in specific life history activities during multiple phases of the annual cycle and over their lifetime is crucial in order to carry out effective conservation efforts, particularly when reintroductions are being planned (Sillett and Holmes 2002, Webster et al. 2002). However, studies of the life history of a species throughout the annual cycle are uncommon because of limited personnel, time, and funding.

I had the unique opportunity to investigate aspects of behavioral ecology and reproductive biology of the endangered Mariana Swiftlet (*Aerodramus bartschi*) at multiple temporal scales over five annual cycles. In this case, I studied a surrogate population on O‘ahu, Hawaiian Islands; thus avoiding any interference with the indigenous population in the Mariana Islands, where there are plans to reintroduce Mariana Swiftlets to portions of their former range. Having a surrogate population on O‘ahu to learn more about natural history, test reintroduction techniques, and provide individuals for population enhancement in the Mariana Islands is an important advantage for Mariana Swiftlet conservation efforts.

### 1.2. BACKGROUND

The Mariana Swiftlet is historically known from the islands of Saipan, Tinian, Aguiguan, Rota, and Guam in the Mariana archipelago (Figure 1.1; Chantler and Driessens 2000). Currently, the species only occurs on Saipan, Aguiguan, and Guam (Cruz et al. 2008), although an introduced population persists on O‘ahu in the Hawaiian Islands (Wiles and
Woodside 1999, Chantler and Driessens 2000, this study). Mariana Swiftlets occupy natural and human-made caves throughout the year, and have the unique ability to echolocate, which allows them to penetrate, orientate, and navigate within darker regions of caves where roosting and nesting occurs (Pratt et al. 1987, U.S. Fish and Wildlife Service 1991, this study).

In 1981, the Guam population of the Mariana Swiftlet was locally protected by the Endangered Species Act of Guam (Guam Public Law 15–36, U.S. Fish and Wildlife Service 1991). The Mariana Swiftlet was listed as a federally endangered species throughout the Mariana archipelago in 1984 (U.S. Fish and Wildlife Service 1984) and listed as threatened/endangered by the U.S. Commonwealth of the Northern Mariana Islands (CNMI) government in 1991 (CNMI Public Law 2–51; Commonwealth Register Volume 13, Number 1; the CNMI law did not differentiate between threatened and endangered categories and are thus jointly classified). The U.S. Fish and Wildlife Service (USFWS) listed the Mariana Swiftlet as endangered based on observed declines of swiftlet populations on Guam, Rota, and potentially Saipan (U.S. Fish and Wildlife Service 1991). Despite no direct evidence of causal factors of population decline, the USFWS outlined hypothetical limiting factors possibly responsible for the decline in Mariana Swiftlets. These limiting factors included 1) disturbance of caves, 2) predation by Brown Treesnakes (*Boiga irregularis*), 3) pesticides, and 4) disease (U.S. Fish and Wildlife Service 1991).

Mariana Swiftlets were introduced to O‘ahu for aesthetic purposes and apparently to augment insect control (Woodside 1970). In 1962, approximately 175 swiftlets were captured from Guam and released in Niu Valley, O‘ahu; an additional 210 swiftlets were
captured on Guam and released at Waimea Valley, O‘ahu in 1965 (Wiles and Woodside 1999). In an effort not to disturb swiftlets in the Mariana Islands, fieldwork for this study focused on the introduced population of Mariana Swiftlets on O‘ahu and was concentrated in and around a human-made tunnel that swiftlets use for roosting and nesting in North Halawa Valley (Figure 1.2).

Information on Mariana Swiftlet life history is scarce. Therefore, this study was initiated to obtain critical behavioral ecology and reproductive biology data to provide the USFWS, CNMI Division of Fish and Wildlife, and Guam Division of Aquatic and Wildlife Resources with the relevant information for addressing recovery criteria, as well as designing and implementing the proposed reintroductions of swiftlets from Saipan and southern Guam to their former ranges of Rota and northern Guam, respectively (Berger et al. 2005, Guam Division of Aquatic and Wildlife Resources 2006, U.S. Fish and Wildlife Service 2009, 2010).

1.3. TAXONOMY

The Mariana Swiftlet belongs to the Order Apodiformes, Family Apodidae, Subfamily Apodinae, and Tribe Collocaliini (Chantler 1999). The nomenclature of the Mariana Swiftlet has been unstable and diverse since the late 19th century. English and Latin names of this swiftlet have included Collocalia fuciphaga (Oustalet 1895, Hartert 1898, Seale 1901); C. fuciphaga tachyptera (Oberholser 1912); Guam Island Swiftlet, C. bartschi (Mearns 1909); Guam Swiftlet, C. bartschi (American Ornithologists’ Union 1995, Chantler and Driessens 2000, Stattersfield and Capper 2000); Guam Swiftlet, C. vanikorensis bartschi (Sibley and Monroe 1990); C. inexpectata (Kobayashi 1970);
Edible Nest Swiftlet, *C. inexpectata bartschi* (Mayr 1945, Stott 1947, Baker 1951); Vanikoro Swiftlet, *A. vanikorensis* (Engbring et al. 1986); Island (Gray) Swiftlet, *A. vanikorensis* (Pratt et al. 1987); Gray Swiftlet, *A. vanikorensis bartschi* (Jenkins 1983); Vanikoro Swiftlet, *A. vanikorensis bartschi* (U.S. Fish and Wildlife Service 1991); and Guam Swiftlet, *A. bartschi* (Chantler 1999). In 2002, the American Ornithologists’ Union published an official English name change from Guam Swiftlet to Mariana Swiftlet (*A. bartschi*), which more accurately describes the distribution of the swiftlet (Banks et al. 2002). The International Ornithologists’ Union also recognizes this species as the Mariana Swiftlet, *A. bartschi* (Gill and Donsker 2015).

Ancestors of the Mariana Swiftlet evolved in the Malayan region and ostensibly colonized the Mariana Islands by way of the Philippines and Palau (Figure 1.1; Baker 1951). *A. bartschi* is one of 28 species, including 57 subspecies of *Aerodramus* swiftlets widely-distributed throughout the Indo-Pacific region from the Seychelles Islands, Reunion Island, Mauritius, India, and Sri Lanka; throughout Southeast Asia and Queensland, Australia; to islands in Melanesia, Micronesia, and Polynesia; reaching as far east as the Marquesas archipelago (Gill and Donsker 2015). Phylogenetic studies have placed the Mariana Swiftlet as a sister species of the Atiu Swiftlet (*A. sawtelli*) in the Cook Islands, over 6,900 km from the Mariana Islands (Lee et al. 1996, Thomassen et al. 2005, Rheindt et al. 2014).

**1.4. IDENTIFICATION**

The Mariana Swiftlet is mostly sooty-black and has slender wings (Figure 1.3). Wings comprised of 10 primary feathers each. Sooty-black upperparts sometimes with an
iridescent green tinge. Underparts are grayish-brown. Rump is slightly pale. The throat is silver-gray. Head is sooty-black. Minimal white coloration at the base of the lores. Iris is dark hazel to brown. Pupil is black. Eyelids are black. Tarsus is naked. Feet are dusky. Bill and claws are metallic gray. Upper mandible slightly curved and longer than the lower. The claws of the four toes are rather long and sharp. The hallux is relatively flexible. Abdomen is dull gray. The tail is slightly forked and consists of 10 feathers. The plumage of the sexes is similar (Seale 1901, Baker 1951, Berger 1981, Jenkins 1983, Pratt et al. 1987, U.S. Fish and Wildlife Service 1991, Chantler 1999, Drahos 2006, this study). Table 1.1 depicts morphometric measurements taken from Mariana Swiftlets captured at the North Halawa Valley tunnel on O‘ahu in 2005 and 2006, during this study.

1.5. OBJECTIVES

The primary objective of this study was to describe and quantify aspects of Mariana Swiftlet behavioral ecology and reproductive biology throughout the annual cycle. Chapter two is an overview of the distribution and status of the Mariana Swiftlet, with an assessment of survey methods for cave-nesting swiftlets. Chapter three summarizes temporal patterns of Mariana Swiftlet reproductive success throughout the annual cycle. Chapter four contains thesis conclusions.
1.6. LITERATURE CITED


Guam Division of Aquatic and Wildlife Resources. 2006. Guam comprehensive wildlife conservation strategy. Division of Aquatic and Wildlife Resources, Department of Agriculture, Mangilao, Guam.


Figure 1.1. Map of the Mariana Islands including the U.S. Commonwealth of the Northern Mariana Islands and the U.S. Territory of Guam. Mariana Swiftlets currently breed on Saipan, Aguiguan, and Guam. Formerly, they bred on Rota and occurred on Tinian.
Figure 1.2. Entrance to the Mariana Swiftlet roosting/nesting tunnel in North Halawa Valley, O'ahu, Hawaiian Islands. Photograph by NCJ.
Figure 1.3. Mariana Swiftlets inside the North Halawa Valley tunnel, O‘ahu, Hawaiian Islands, May 2006. Photographs by NCJ.
Table 1.1. Morphometric measurements of Mariana Swiftlets captured at the North Halawa Valley tunnel, O’ahu, Hawaiian Islands, 2005–2006.

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<th>Mean</th>
<th>SD</th>
<th>Range</th>
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<td>Body length (mm)</td>
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<td>4.29</td>
<td>80.00–99.50</td>
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2. DISTRIBUTION AND STATUS OF THE MARIANA SWIFTLET
(AERODRAMUS BARTSCHI): AN ASSESSMENT OF SURVEY METHODS
FOR CAVE-NESTING SWIFTLETS

2.1. ABSTRACT

Mariana Swiftlets (Aerodramus bartschi) are open-air foragers that may be susceptible to
the impacts of wind turbines if wind energy facilities become widespread in the Mariana
Islands. Implementing effective survey methods is critical to determine a reliable
baseline of Mariana Swiftlet population size, particularly if wind turbines are situated or
proposed to be placed in the feeding ranges of these insectivores. We describe the
distribution, abundance, and survey methods used to evaluate the status of the endangered
Mariana Swiftlet, a little-known echolocating cave swiftlet that presently inhabits three of
five formerly occupied islands in the Mariana archipelago. An additional population was
introduced and continues to survive on the island of O‘ahu, Hawaiian Islands. Using
existing literature, correspondence from relevant biologists, and population surveys on
O‘ahu, we estimate the present range-wide population of Mariana Swiftlets to be 6,532
individuals occurring in 17 caves on Saipan, Aguiguan, and Guam; and 142 individuals
occupying one tunnel on O‘ahu. Based on a literature review, we confirmed that swiftlets
have been extirpated from Rota and Tinian, and have declined on Aguiguan supporting
their listing as an endangered species. Swiftlets have remained relatively stable on Guam
and Saipan in recent years. An assessment of survey methods used for Mariana Swiftlets
suggests changes are needed to more accurately reflect their distribution and abundance.
2.2. INTRODUCTION

Wind energy has quickly emerged as a cost-saving alternative to oil and gas production, and wind turbines are being erected and employed worldwide. However, negative impacts to birds and insectivorous bats from turbines are continuing issues (Everaert and Stienen 2007, Kunz et al. 2007, Rydell et al. 2010a, Amorim et al. 2012, U.S. Fish and Wildlife Service 2012, Arnett et al. 2013). It has been estimated that in the United States, between 100,000 and 440,000 birds are killed by wind turbines each year (Subramanian 2012, Loss et al. 2013, Erickson et al. 2014). Between 2000 and 2011, approximately 650,000 and 1,300,000 bats were estimated to have been killed at wind facilities in the United States and Canada (Arnett and Baerwald 2013). In 2012, more than 600,000 bats may have died from interactions with wind turbines in the contiguous United States (Hayes 2013).

Possible effects of wind turbines on birds include collision, displacement due to disturbance, barrier effects (birds alter their local flight paths or migration flyways), and habitat loss (Drewitt and Langston 2006, Everaert and Stienen 2007). While all these effects are concerning, collision results in direct mortality. Mortality associated with collision into wind turbines has been documented in numerous avian species groups (e.g., eagles, hawks, owls, gulls, ducks, terns, swallows; Everaert and Stienen 2007, Smallwood and Thelander 2007). Collision with wind turbines also impacts insectivorous bats, which are killed primarily by the moving rotor blades while feeding on migratory, high-altitude insects that congregate at turbine towers (Horn et al. 2008, Rydell et al. 2010a, 2010b). Baerwald et al. (2008) postulates that bat fatalities may also be due to barotrauma, resulting from changes in air pressure close to rotor blades.
Bat fatalities associated with wind turbines are known to include open-air foraging species (Rydell et al. 2010a). Mariana Swiftlets (*Aerodramus bartschi*) are open-air foragers and foraging behavior includes quick turning motions, almost stopping in mid-air, constant banking left and right, rapid fluttering, and occasionally circling upwards from a lower to higher altitude (NCJ, pers. obs.). Mariana Swiftlets forage solitarily or in flocks as low as 0.5 m and at least 50 m above a wide variety of vegetation and terrain, favoring ridge crests, open grassy areas, and riparian and ravine forests (Jenkins 1983, U.S. Fish and Wildlife Service 1991, Morton and Amidon 1996; NCJ, pers. obs.). Mariana Swiftlets presumably feed on a suite of insects belonging to several taxonomic orders (e.g., Hymenoptera, Coleoptera, Diptera, Homoptera, Hemiptera, Isoptera; Kershner et al. 2007, Valdez et al. 2011). Open-air foraging on an assortment of insects at variable heights above a diversity of habitats renders the Mariana Swiftlet susceptible to the impacts of wind turbines.

While similar in many ways to insectivorous bats, swiftlets have not been a common species of concern in discussions related to potential negative effects of wind turbine design and placement (two known examples: Sinclair Knight Merz 2005, Department of Energy 2013). Thus, accurately determining the distribution and abundance of aerial-foraging birds and bats throughout the annual cycle is essential, particularly if wind turbines are situated or proposed to be placed in the feeding ranges of these insectivores. An important issue related to determining these parameters is the lack of attention directed at developing appropriate survey methodologies for aerial-foraging birds and bats. With wind turbines planned or already constructed in the Mariana Islands (Brown 2011, Department of Energy 2013, REVE 2013) and reintroductions proposed...
for the endangered Mariana Swiftlet (Berger et al. 2005, Guam Division of Aquatic and Wildlife Resources 2006, U.S. Fish and Wildlife Service 2009, 2010), there is no better time to evaluate their status and the means by which it is ascertained, particularly in view of impending wind energy development.

Compilations of distribution, historical sightings, and population status information are important to science and essential for conservation efforts, particularly as species become extirpated from parts of their range for unknown reasons. However, surveys of volant species occupying caves (i.e., swiftlets and bats) can be challenging and unreliable (Sabol and Hudson 1995, Sankaran 2001, Frank et al. 2003, Kunz 2003, Betke et al. 2008, Ammerman et al. 2009, Hristov et al. 2010, Brindock 2013). Issues of detectability, disturbance, observer bias, impracticality, and determining the best time of day and phase of the annual cycle to survey, can confound ascertaining reliable population estimates within and among caves. Therefore, in this paper, we examine these issues by assessing applicable survey methods with respect to the Mariana Swiftlet.

The Mariana Swiftlet is a small (10 cm, 6–8 g), mostly sooty-black slender-winged bird (Figure 2.1) historically found on the Mariana Islands of Saipan, Tinian, Aguiguan, Rota, and Guam (Figure 2.2; Chantler and Driessens 2000). Presently, the species is found only on Saipan, Aguiguan, and Guam (Cruz et al. 2008; NCJ, pers. obs.), although an introduced population persists on O‘ahu in the Hawaiian Islands (Wiles and Woodside 1999, Chantler and Driessens 2000, this study). In 1981, the Guam population of the Mariana Swiftlet was locally protected by the Endangered Species Act of Guam (Guam Public Law 15–36, U.S. Fish and Wildlife Service 1991). The Mariana Swiftlet was listed as a federally endangered species throughout the Mariana archipelago in 1984.
(U.S. Fish and Wildlife Service 1984) and listed as threatened/endangered by the U.S. Commonwealth of the Northern Mariana Islands (CNMI) government in 1991 (CNMI Public Law 2–51; Commonwealth Register Volume 13, Number 1; the CNMI law did not differentiate between threatened and endangered categories and are thus jointly classified).

Introductions of Mariana Swiftlets to O‘ahu were made for aesthetic purposes and apparently to augment insect control (Woodside 1970). Approximately 175 swiftlets were captured from Guam and released in Niu Valley, O‘ahu on 22 May 1962 (Wiles and Woodside 1999). An additional 210 swiftlets were captured on Guam and released at Waimea Valley, O‘ahu on 29 January 1965 (Wiles and Woodside 1999). These two translocations were sponsored by the State of Hawai‘i and the Hui Manu Society, a local group devoted to the establishment of exotic bird species in the Hawaiian Islands (Woodside 1970, Wiles and Woodside 1999). The Mariana Swiftlet is considered established in Hawai‘i (American Ornithologists’ Union 1995).

Mariana Swiftlets are non-migratory and occupy natural and human-made caves throughout the year (Pratt et al. 1987, U.S. Fish and Wildlife Service 1991, this study). They have the unique ability to echolocate, which allows them to penetrate, orientate, and navigate within darker regions of caves where roosting and nesting occurs (U.S. Fish and Wildlife Service 1991). Mariana Swiftlets lay a single white egg in a saliva-structured nest composed of vegetative material and placed on a cave wall or ceiling (Jenkins 1983, Morton and Amidon 1996, Reichel et al. 2007; Johnson et al., In review).
2.3. Chapter Objectives

The objectives of this chapter were to 1) summarize the current and historic distribution and abundance of the Mariana Swiftlet to determine whether any changes have occurred, and 2) assess survey methods currently used or recently tested for cave-nesting swiftlets, in order to obtain accurate population estimates of the Mariana Swiftlet.

2.4. Methods

2.4.1. Literature Review

To obtain former and current distribution and abundance of the Mariana Swiftlet, and information about survey methods used for cave-nesting swiftlets, we reviewed available published and unpublished literature related to the Mariana Swiftlet and closely related *Aerodramus* species, as well as solicited comments from relevant biologists.

2.4.2. Study Area

The Mariana Islands are comprised of the CNMI (14 islands) and the U.S. Territory of Guam (Figure 2.2). These 15 islands stretch about 800 km between 13° 14’ N, 144° 45’ E and 20° 3’ N, 144° 54’ E, and constitute a total land area of 1,018 km². The islands are located approximately equidistant between Japan and New Guinea, and nearly 2,400 km east of the Philippines in the western Pacific Ocean. The Mariana Islands are the northern most islands in a region of the Pacific commonly referred to as Micronesia.

The climate of the Mariana Islands is tropical marine with distinct dry (December–June) and wet seasons (July–November) (Young 1989). Temperatures show
moderately little seasonal variation, with monthly averages between 24° and 27° C and extremes of 18° and 35° C (Mueller-Dombois and Fosberg 1998). Relative humidity is high with an annual mean of 82% recorded on Saipan (Falanruw et al. 1989). Average annual rainfall is about 200–250 cm (Engbring et al. 1986, Mueller-Dombois and Fosberg 1998), of which, 56–75% falls during the wet season (Bowers 1950, Stone 1970, Jenkins 1983, Engbring and Ramsey 1984, Young 1989). Located in the primary storm track of the western Pacific, typhoons routinely impact the islands between July and December; however, they have been recorded during every month of the year (Butler 1988, Young 1989).

Saipan (15° 12′ N, 145° 45′ E) is the second largest island in the Mariana archipelago and located in the southern, more volcanically stable region of the island chain. The island is 120 km² in size, 22 km long, and 3-10 km wide (Engbring et al. 1986). The highest point is Mt. Takpochao (474 m). Saipan is the most densely populated island in the Commonwealth and the center of the CNMI government.

Aguiguan (14° 51′ N, 145° 34′ E) is a small island located 30 km southwest of Saipan. It measures 7 km² in size, 5 km long, and 1.5 km wide (Engbring et al. 1986). It is comprised of several well-defined limestone plateaus or shelves; the uppermost plateau reaches approximately 150 m in elevation. The highest point on Aguiguan is 163 m.

Guam (13° 30′ N, 145° E) is the largest and southernmost island in the Mariana archipelago. The island is 49 km long and 7–15 km wide, and has an area of 550 km² (Engbring and Ramsey 1984). The northern half of Guam is a limestone plateau, while the southern half is more mountainous and volcanic in origin. Mount Lamlam (406 m) is the island’s highest point.
The Hawaiian Islands are the most isolated islands in the world, located 3,765 km from North America, the closest continental land mass. O‘ahu (21° 22′ N, 157° 55′ W) is the third largest Hawaiian Island and is comprised of the Ko‘olau and Wai‘anae mountain ranges and a broad valley in between. The island is 1,624 km² in size, 71 km long, and 48 km wide. O‘ahu is the most populated of the Hawaiian Islands and the seat of the state government.

In an effort not to disturb swiftlets in the Mariana Islands, we studied the introduced population of Mariana Swiftlets on O‘ahu. Fieldwork was concentrated in and around a human-made tunnel that Mariana Swiftlets use for roosting and nesting (Figures 2.3 and 2.4). The tunnel was likely excavated prior to World War II as a possible irrigation water source (Wiles and Woodside 1999). It is located near the base of a steep, seasonal waterfall in North Halawa Valley, 17 km and 32 km from the original Mariana Swiftlet release sites at Niu Valley and Waimea Valley, respectively (Figure 2.5; Wiles and Woodside 1999). The tunnel is a single-entrance (1.80 m high by 1.30 m wide) straight passage, which measures approximately 55 m long, averaging $1.67 \pm 0.20$ (SD) m high (range = 1.25–2.10, $n = 12$ measurements) and $1.25 \pm 0.19$ (SD) m wide (range = 0.91–1.58, $n = 12$ measurements). Tunnel width is relatively constant throughout, however height steadily decreases after about 15 m. The tunnel entrance faces northwest at 312° and travels southeast at 132°. Elevation is 424 m, placing the tunnel within the montane rain forest climatic vegetation zone (Mueller-Dombois and Fosberg 1998). The tunnel is wet throughout the year, with pools of water approximately 3–15 cm deep present on the floor. Standing water and mud are present throughout the tunnel; however it becomes progressively muddier towards the rear of the tunnel. Water
constantly drips from the ceiling throughout the tunnel, but is more noticeable within the first 25 m, especially following heavy rains.

**2.4.3. Data Collection**

Fieldwork was conducted on O‘ahu from July to September 2005, and December 2005 to January 2011. Multiple attempts were made to locate suitable or active roosting/nesting tunnels or caves following a review of swiftlet sightings (Bishop Museum Sightings Database), potential tunnel/cave habitats on O‘ahu, as well as results from requests for sightings from local birders. Local biologists and pig hunters assisted in these efforts, which were mostly concentrated in Halawa and Moanalua Valleys.

We conducted evening arrival surveys from inside the roosting/nesting tunnel in North Halawa Valley during 2005, 2006, 2009, and 2010. In 2005, we surveyed from the same dimly lit location in the tunnel as described in Wiles and Woodside (1999). In 2006, 2009, and 2010, we conducted surveys from a darker location against an indentation on the right side, 18 m into the tunnel. We used LOMO PVS-7 Recon II second generation night vision goggles or a Bushnell Night Vision 1x20 Tactical Monocular to detect and count swiftlets entering and exiting the tunnel. We are confident that most, if not all, entering and exiting swiftlets were counted during each survey. We determined beginning and ending survey times using prior experience conducting evening arrival surveys on Saipan, Aguiguan, and Guam. We included night vision technology in our surveys to determine its efficacy in small, single entrance caves/tunnels.

We derived population estimates by subtracting the number of exiting swiftlets
from the number of entering swiftlets, and adding any volant swiftlets that were present inside and outside the tunnel before and after the survey, respectively. We assessed the number of volant swiftlets present inside and outside the tunnel prior to and following the survey, respectively, and active nests (nests with one egg or one nestling) inside the tunnel before the survey, using night vision goggles or a monocular, a headlamp with a red filter, or a Sony Handycam DCR-HC21 camcorder (with NightShot Plus Infrared System). A Sony Infrared Light HVL-IRM was attached to the camcorder to extend the range of the NightShot Plus Infrared System. Because the tunnel was a straight and narrow passage with low clearance, nest detectability was high; thus, we are confident that all active nests were found.

We carried out rat trapping inside and outside the North Halawa Valley tunnel between March 2006 and January 2011. Using five types of snap trap (Ka Mate, Tomcat, Trapper T-Rex, Victor with metal tab, and Victor with plastic tab), 43 traps were distributed inside \((n = 5)\) and outside \((n = 38)\) the tunnel. Traps were baited with peanut butter, macadamia nuts, scented wax (peanut butter, coconut, grape), or sponges with essential oils (passion fruit, coconut), and situated on the tunnel floor and tree branches or the ground outside the tunnel. To avoid attracting rats near roosting and nesting swiftlets, two traps that were furthest inside the tunnel were not baited; these traps were positioned so that any approaching rat would be captured. We logged 252 visits, during which traps were checked and reset/rebaited, if necessary.

2.5. RESULTS
2.5.1. Assessment of Survey Methods

2.5.1.1. Evening arrival surveys

Evening arrival surveys are the primary method currently used to assess Mariana Swiftlet population size on Saipan, Aguiguan, and Guam (Cruz et al. 2008, Brindock 2013, Radley 2013). Observers in the Mariana Islands are typically situated just outside the cave entrance(s) during the survey and detection of swiftlets is visual (e.g., without night vision technology). Thus, issues related to observer bias may be confounding swiftlet population estimates at the largest known colony in Mahlac Cave on Guam (Brindock 2010, 2013), and other colonies in the Mariana Islands. For example, frequent and large (>100) “dumps” (swiftlets exiting the cave simultaneously during a survey) may cause inaccurate estimates (Brindock 2010). Counting numerous entering and exiting swiftlets at the end of a survey in low light and as birds arrive for nocturnal roosting may also result in count errors (Brindock 2010; NCJ, pers. obs.).

Evening arrival surveys (sometimes referred to as movement counts) have also been used to assess Aerodramus swiftlet population size in the Cook Islands (Atiu Swiftlets [A. sawtelli]; Fullard et al. 2010), Queensland, Australia (Australian Swiftlets [A. terraereginae]; Tarburton and Tarburton 2013), and Malaysia (Edible-nest Swiftlets [A. fuciphagus] and Black-nest Swiftlets [A. maximus]; Medway 1962, Leh and Kheng 2001). Nguyen Quang et al. (2002:236–237) state that:

movement counts include both breeders and non-breeders, and are highly variable due to bias associated with multiple observers and cave entrances, difficulty counting birds late in the evening or early in the morning (i.e., low light and high activity), double counts, different counting techniques, etc.
Nguyen Quang et al. (2002:237) mention that “they (movement counts) are extremely
difficult to use for assessing the actual size of populations,” presumably for the reasons
stated above.

2.5.1.2. Nest counts

The nest count method has been used to estimate the population size of the Edible-nest
Swiftlet in the Andaman and Nicobar Islands (Sankaran 2001, Manchi and Sankaran
2014), the Australian Swiftlet in Queensland (Tarburton and Tarburton 2013), and the
White-rumped Swiftlet (A. spodiopygius) in Fiji (Tarburton 1987). Counts typically
consist of an observer tallying the total number of active nests present inside the cave
(Tarburton 1987, Sankaran 2001, Tarburton and Tarburton 2013, Manchi and Sankaran
2014). An assumption is made that a specific ratio of birds is associated with one nest:
Edible-nest Swiftlet (two birds; Sankaran 2001, Manchi and Sankaran 2014), Australian
Swiftlet (two birds; Tarburton and Tarburton 2013), and White-rumped Swiftlet (three
birds; Tarburton 1987). Nest counts are probably not a reliable stand-alone indicator of
population size as observers need to consider the number of birds not associated with
active nests; these may include non-breeding individuals (e.g., recently fledged birds) or
breeding individuals that have yet to commence breeding activities.

2.5.1.3. Direct counts

Tarburton (1987) used direct counts to estimate population size of the White-rumped
Swiftlet in Fiji. Counts were made of roosting swiftlets late at night (Tarburton 1987).
Direct counts are only possible with small populations in small caves (Tarburton 1987),
presumably because with a small population, the observer would spend less time inside the cave and risk disturbance to the colony. This method assumes that all swiftlets that nest and roost inside a certain cave return to it each night and presence of the observer does not cause birds to fly out of the cave (Tarburton 1987).

2.5.2. Formerly Inhabited Islands

2.5.2.1. Rota

Rota has an extensive cave system comprising 120 known caves (Keel 2005) and Mariana Swiftlets may have been numerous at some point. There is evidence (old nests, nest stains, and nestling remains) that swiftlets nested in at least six caves on Rota: Coconut Crab, Payapai, Taiapu, Takta, Telang, and Tonga (Pratt 1984, Reichel and Glass 1988, Rice 1993, Kershner et al. 2007; J. Reichel, field notes). Bones discovered during excavations in As Matmos Cliffside and Payapai Caves in 1990 and 1994 also suggest possible former occupation by Mariana Swiftlets (Steadman 1992, 1999).

Swiftlets were observed on Rota as early as 1888 (Oustalet 1895). Large groups of swiftlets were observed in 1945 (Baker 1951). In July 1976, swiftlets were recorded in “fair numbers” on Rota (Pratt et al. 1979), with seven birds detected in three regions on the island: near Songsong Village \( (n = 3) \), near the Japanese cannon on the southwest coast \( (n = 2) \), and on the upper plateau of the Sabana region \( (n = 2) \) (Engbring et al. 1986). These are the last recorded swiftlet sightings on the island.

Multiple visits, surveys, and communications with reliable Rota residents between August 1977 and December 2012 have not resulted in subsequent observations of
swiftlets on the island (Ralph and Sakai 1979, Jenkins and Aguon 1981, Engbring et al. 1986, U.S. Fish and Wildlife Service 1991, Amar et al. 2008, National Audubon Society 2015); thus we affirm the Mariana Swiftlet is extirpated from Rota (Pratt et al. 1987, Reichel and Glass 1991, Stinson 1994). The reason(s) for the Mariana Swiftlet’s disappearance from Rota are unknown. However, heavy applications of pesticides, predominantly organochlorines, are suspected by reducing the prey base and/or causing physiological effects on the birds (Morton and Amidon 1996).

2.5.2.2. Tinian

There are no records of Mariana Swiftlets breeding on Tinian (Reichel and Glass 1988) despite the presence of at least 88 caves on the island (Stafford 2003). However, swiftlet bones were discovered during excavations at one cave and a rockshelter on Tinian in 1994 (Steadman 1999). Swiftlet observations on Tinian have been sporadic and are suspected to be birds temporarily visiting, most likely from Saipan (5 km away) or Aguiguan (9 km away) (U.S. Fish and Wildlife Service 1991). Marshall (1949) observed a flock of swiftlets at the Marpo Valley region in mid-October 1945; by 20 October, he observed just four swiftlets, and between 22 October and mid-November, swiftlets were not detected on the island. In June 1945, Gleize (1945) noted a dozen or more swiftlets on Tinian, and Downs (1946) recorded two distant observations suspected to be the swiftlet sometime between May and October 1945. Pratt et al. (1979) saw Mariana Swiftlets in “fair numbers” during a June 1976 trip to Tinian.

Unfortunately, subsequent surveys and trips to the island between January 1979 and January 2015 failed to find any Mariana Swiftlets (Jenkins and Aguon 1981,
Engbring et al. 1986, Cruz et al. 2000b, Camp et al. 2012, National Audubon Society 2015); thus we confirm the Mariana Swiftlet is extirpated from Tinian (Reichel and Glass 1991). Additionally, a survey of 88 caves during 2002–2003 (Stafford 2003) provided no evidence of swiftlet use in any of the caves inventoried (K. W. Stafford, pers. comm.), although it is unclear what proportion of these caves might be suitable for swiftlet roosting and nesting activities.

2.5.3. Currently Inhabited Islands

Evening arrival surveys conducted on Saipan in 2013, Aguiguan in 2002, and Guam in 2015 suggest 6,532 Mariana Swiftlets reside in eight colonies on Saipan \( (n = 4,674) \), six colonies on Aguiguan \( (n = 267) \), and three colonies on Guam \( (n = 1,591) \) (Table 2.1; Esselstyn et al. 2003; K. M. Brindock, pers. comm.; P. M. Radley, pers. comm.). One additional colony exists on Saipan; however, the number of swiftlets within is unknown due to restricted access to the cave. Additional colonies are suspected to exist on all three islands, but we are unaware of any that have been confirmed. Evening arrival surveys completed on O‘ahu in 2010 indicate 142 volant Mariana Swiftlets reside in the North Halawa Valley tunnel.

2.5.3.1. Saipan

Saipan currently has the largest population of Mariana Swiftlets, representing 72% of the Mariana Islands population. However, population estimates have fluctuated since World War II. From December 1944 to December 1945, Marshall (1949) described swiftlets on Saipan as “abundant.” Between December 1945 and January 1946, Stott (1947) reported
swiftlets in “fair-sized concentrations” near cliffs throughout the island. During May–June 1976 and July 1978, Pratt et al. (1979) found swiftlets to be more “common” in the interior valleys. Ralph and Sakai (1979) encountered just 10 swiftlets during 7.3 census hours and 7.7 traversed km on the island in August–September 1977. A January 1979 roadside survey suggested low densities of swiftlets (0.21/km) on Saipan and the species was recommended for federal endangered status throughout its range (Jenkins and Aguon 1981). In May 1982, using the variable circular-plot (VCP) method (Reynolds et al. 1980), Engbring et al. (1986) estimated the Mariana Swiftlet population on Saipan to be 9,120 (84/km²) individuals.

Evening arrival surveys at the same five known active caves during 1983–1985 and 1986 resulted in population estimates of 3,160 and 2,155 swiftlets, respectively (U.S. Fish and Wildlife Service 1991). It is unknown whether the caves surveyed in the 1980s represented all known active caves. For a more detailed description of Saipan’s swiftlet population between 1985 and 1998, refer to Cruz et al. (2008). The sum of the annual mean of evening arrival surveys conducted at 10 caves each April and October between 1999 and 2005 was 3,730 swiftlets, with the maximum, 5,383 individuals recorded in 2005 (Cruz et al. 2008).

Saipan’s swiftlet population was assessed by evening arrival surveys in April 2009 and resulted in 6,111 birds at 10 caves (Radley 2009). The mean totals of evening arrival surveys conducted at eight caves in October 2009 and April 2010, and nine caves in October 2010 and April 2011 were 8,787 and 6,160 swiftlets, respectively (Radley 2010, 2011). The mean total of evening arrival surveys conducted at six caves in October 2012 and eight caves in April 2013 was 4,891 swiftlets (Radley 2013). A total of 4,674
swiftlets was counted during evening arrival surveys at eight caves in November 2013 (P. R. Radley, pers. comm.). There are currently nine known active swiftlet caves on Saipan; however due to chronic short-staffing, data collection discrepancies, and restricted access, only usable data are reported for surveys occurring between October 2009 and November 2013 (Radley 2010, 2011, 2012, 2013; P. R. Radley, pers. comm.). No swiftlet surveys were conducted on Saipan in April 2014, October 2014, or April 2015 (P. R. Radley, pers. comm.; T. P. Willsey, pers. comm.). Saipan contains at least 33 known caves (Wexel 2006), some of which might be suitable for Mariana Swiftlets. Unfortunately, Saipan caves are not as well inventoried as the caves on Tinian, Aguiguan, Rota, and Guam, because of challenging private land access, as well as the island’s complex geology and precipitous terrain (Jenson et al. 2006); hence, there are likely other undocumented caves on Saipan.

2.5.3.2. Aguiguan
The swiftlet population on Aguiguan appears to have declined since June 1982 when Engbring et al. (1986) approximated 1,022 (265/km²) birds using the VCP method. Surveys by CNMI Division of Fish and Wildlife (DFW) biologists in January 1985 estimated 970 swiftlets after censusing the five known roosting/nesting caves (Reichel and Glass 1988). Reichel and Glass (1988) counted 426 birds at three active caves in February 1987, and in 1988, a total of 381 swiftlets were tallied at four caves (Cruz et al. 2008). It is uncertain whether the caves surveyed in 1987 and 1988 represented all known active caves. Based on evening arrival surveys and daytime visits at the eight
known active caves in March and May–June 1995, 400–475 swiftlets were estimated on the island (G. J. Wiles, unpubl. data).

In 1995, 86 caves were inventoried on Aguiguan (Wiles and Worthington 2002). In addition to the eight caves occupied by swiftlets in 1995, eight more caves were described as potentially suitable for swiftlets (Wiles and Worthington 2002). A few eggshell fragments were detected at a ninth cave in 2003, but no birds were present during evening arrival surveys that year or in 1995 (G. J. Wiles, pers. comm.). Evening arrival surveys conducted by the CNMI DFW in April 2000 at the same five caves censused in 1985 totaled 408 swiftlets (Cruz et al. 2000a). These were the only known active caves on the island in 2000. In May 2002, 267 swiftlets were counted at the only six known active caves on Aguiguan (Esselstyn et al. 2003).

2.5.3.3. Guam

Mariana Swiftlets were frequently observed throughout Guam prior to World War II (Seale 1901, Bryan 1936) and considered “abundant” from December 1944 to December 1945 (Marshall 1949). Baker (1947) recorded the swiftlet as the third most common species during 125 counts along 3,154 km of roadway between 22 May and 5 October 1945. In October 1945, a group of about 50 swiftlets was observed at the base of Mt. Tenjo in southern Guam, and swiftlets were “common” at Ritidian Point in the north in November 1945 (Stophelet 1946). In April 1960, 10 swiftlets were observed in the Tarague Beach region in northern Guam (King 1962), and in July 1965, Tubb (1966) noted swiftlets as “common” at the northern end of Guam, with a colony of several hundred birds at Amantes Point. In April–May 1970, swiftlets were not seen during three
days of avian observations (Kobayashi 1970). Swiftlets were also not detected on the island during field trips in June 1976, August–September 1977, and June–July 1978 (Pratt et al. 1979, Ralph and Sakai 1979).

The largest group of swiftlets Jenkins (1983) observed during two years of fieldwork was 17 individuals in June 1978. He stated that the swiftlet was one of the rarest and most critically endangered of Guam’s native birds. Engbring and Ramsey (1984) recorded only one group of 18 swiftlets using the VCP method during an island-wide forest bird survey in June 1981, and thought that there were ≤100 swiftlets on Guam.

Evening arrival surveys at active caves on Guam presented a different scenario. In 1997, five evening arrival surveys in February, April, and August at Mahlac Cave, tallied 352 ± 36 (SD) swiftlets (range = 315–411; Wiles and Aguon 1997). Surveys at Mahlac Cave in January and March 1998 resulted in 430 and 396 swiftlets, respectively (Wiles and Aguon 1998). In January 1999, biologists counted 538 and 427–527 swiftlets during two surveys at Mahlac Cave (Wiles and Aguon 1999). Between January 2004 and January 2008, the mean population estimate at Mahlac Cave was 729 ± 124 (SD) swiftlets (range = 532–948, n = 12 surveys; A. P. Brooke, pers. comm.). Surveys at Mahlac Cave between November 2010 and April 2015 yielded a mean population estimate of 1,132 ± 156 (SD) swiftlets (range = 887–1,418, n = 17 surveys), with 1,243 individuals counted in March 2015 (Naval Facilities Engineering Command Marianas 2011, Brindock 2012, 2013; K. M. Brindock, pers. comm.).

Between November 2004 and December 2006, the mean population estimate combining the Mahlac Cave colony with the two smaller colonies in Maemong and Fachi
Caves was 822 ± 136 (SD) swiftlets (range = 611–976, \( n = 18 \) surveys; A. P. Brooke, pers. comm.). In 2008, nearly 1,000 swiftlets were estimated to inhabit all three caves (Grimm 2008). Evening arrival surveys of all three colonies between November 2010 and April 2015 resulted in a mean population estimate of 1,368 ± 238 (SD) swiftlets (range = 1,073–1,915, \( n = 48 \) surveys), with 1,591 individuals counted in March–April 2015 (Naval Facilities Engineering Command Marianas 2011, Brindock 2012, 2013; K. M. Brindock, pers. comm.). Mahlac, Maemong, and Fachi Caves, all in southern Guam, are presently the only known active swiftlet colonies on the island. With 192 known caves on Guam (Jenson et al. 2006), other colonies are suspected to exist; however, none have been confirmed.

2.5.3.4. O‘ahu

Despite thorough searches, focusing on Halawa and Moanalua Valleys, the only promising site was a single-entrance human-made tunnel located approximately 700 m northwest of the active roosting/nesting tunnel in North Halawa Valley. This straight tunnel was situated near the base of a steep waterfall and was about 25 m long. The entrance was 1.15 m high by 1.71 m wide. Measurements (height x width) taken inside the tunnel at 10 m, 20 m, and 24 m were: 1.51 m x 1.40 m, 1.70 m x 1.40 m, and 1.00 m x 1.15 m, respectively. The tunnel was similar to the active swiftlet roosting/nesting tunnel in terms of high humidity, muddy floor, and sections of dry wall. However, it was prone to major flooding events because it was positioned lower than the streambed outside; thus likely not suitable for swiftlets. High water and debris marks were visible on the walls at 0.80–1.10 m above the floor, and a substantial amount of woody debris.
was present in the rear. There was no evidence of swiftlet guano nor nests; although guano and nests could have been washed away. No additional active or suitable roosting/nesting tunnels or caves were discovered on O‘ahu during this study; however, we do not discount the possibility of other active or suitable roosting/nesting tunnels or caves existing on O‘ahu.

Population estimates of Mariana Swiftlets inside the North Halawa Valley tunnel were determined via 13 evening arrival surveys conducted in August–September 2005 ($n = 3$), March–July 2006 ($n = 8$), December 2009 ($n = 1$), and June 2010 ($n = 1$) beginning at a mean of 1642 hours (range = 1530–1740) Hawai‘i–Aleutian Standard Time and ending at a mean of 2007 hours (range = 1930–2045) (Table 2.2).

Mariana Swiftlets on O‘ahu appeared to breed throughout the annual cycle (Table 2.2). Estimated numbers of swiftlets exhibited substantial variation over an annual cycle. A low estimate on 17 March 2006 may be attributed to a suspected rat ($Rattus$ spp.) depredation event. Eighteen swiftlet feather piles, including three skulls and a carcass, were discovered 19–55 m into the tunnel on 6 March 2006. This depredation event occurred after the previous tunnel visit on 28 February 2006, when no active nests were recorded. Chewed common guava ($Psidium guajava$) exocarps and rat scat near and in the feather piles lead us to believe that rats were the suspected predators. Also found in the piles were aluminum bands belonging to two swiftlets banded as adults and two swiftlets banded as nestlings in August and September 2005.

Rats were also suspected predators when seven adult swiftlets were found dead 41–53 m into the tunnel on 28 January 2007. Five sets of wings, one feather pile, and the fresh remains of a swiftlet in a nest were distributed on and above the tunnel floor. Four
aluminum bands belonging to adult swiftlets were found. This depredation event occurred sometime after the previous tunnel visit on 29 December 2006, when no active nests were noted. Additional suspected rat depredation events occurred on 19, 20, and 27 September 2009, when at least 10 adult swiftlets were found dead and 17 nests failed (14 at the nestling stage and three at the egg stage) 33–54 m into the tunnel. During these depredation events, nine nests were knocked off the tunnel wall and two nestlings were displaced. While birds came back and resumed breeding, the resulting population declined considerably following these depredation events.

Increased population estimates in December 2009 and June 2010 (Table 2.2) may be the result of rat trapping efforts inside and outside the North Halawa Valley tunnel. Between March 2006 and January 2011, 406 rats were captured in snap traps inside (18) and outside (388) the North Halawa Valley tunnel (this study). The June 2010 count of 142 individuals represents 2% of the entire Mariana Swiftlet population, thus emphasizing the importance of the O‘ahu population.

2.6. DISCUSSION

Our results substantiate that the Mariana Swiftlet is extirpated from Rota and Tinian. Species-wide population estimates are relatively low (i.e., less than 7,000 birds, inclusive of O‘ahu). The Saipan population has declined since 1982, however it is presently the largest in the Mariana Islands. The Aguiguan population has also declined since 1982, yet has remained relatively stable from 1987 to 2000, with a slight decrease in 2002. The Guam population has remained relatively stable in recent years, and the O‘ahu population has increased since 1997. Our compilation of population and distribution information
provides a comprehensive perspective on potential populations that can contribute to conservation efforts, as well as those needing immediate intervention. Conversely, results must be considered with respect to the survey methods used.

2.6.1. Mariana Swiftlet Survey Methodology

Pacific island swiftlets have rarely been the focus of island-wide avian surveys, and approaches used in broader efforts do not adequately detect them. Thus, an assessment of survey methods provides perspective on the past and guidance for the future. Overall, a true population estimate for Mariana Swiftlets and other cave-nesting swiftlets (e.g., Edible-nest Swiftlet, White-rumped Swiftlet, Black-nest Swiftlet, Australian Swiftlet, Uniform Swiftlet [A. vanikorensis], Island Swiftlet [A. inquietus], Palau Swiftlet [A. pelewensis]) must include a survey of all active caves. This assumes that all active caves are known, which is often not the case. Observers need to report: number of caves surveyed, occupied, and known per island/location.

The VCP method (also known as point-transect surveys) is widely used for surveying avian populations in the Pacific (CNMI, Guam, Republic of Palau, Federated States of Micronesia, American Samoa, and Hawaiian Islands; Engbring and Ramsey 1984, 1989, Engbring et al. 1986, 1990, Scott et al. 1986, Engbring 1992, Amar et al. 2008, Camp et al. 2009, 2012, Amidon et al. 2014). However, because of the rapid aerial-foraging behavior exhibited by the Mariana Swiftlet, this is not an appropriate method for surveying this bird (U.S. Fish and Wildlife Service 1991, Camp et al. 2009); thus, population densities are overestimated, as is typically observed in highly mobile species (Scott and Ramsey 1981).
Using night vision goggles or a monocular to detect and count the number of entering and exiting swiftlets proved to be effective, if not a necessity, on O’ahu. Swiftlets were easily observed and differentiated during evening arrival surveys. This was also the case during field testing of night vision equipment at all three active swiftlet caves on Guam in 2011 (Sabol et al. 2011).

Thermal infrared imaging is popular for its use in censusing evening emergences of Brazilian Free-tailed Bats (*Tadarida brasiliensis*) from caves in Texas and New Mexico, and Mexican Long-nosed Bats (*Leptonycteris nivalis*) from caves in Texas, and has proven to be more accurate than preceding bat census efforts (Frank et al. 2003, Betke et al. 2008, Ammerman et al. 2009, Hristov et al. 2010). For example, 54 million Brazilian Free-tailed Bats were estimated among six colonies in Texas and New Mexico based on human visual observations in 1957; Betke et al. (2008) estimated four million bats in the same six colonies during a census between 2000 and 2006 using thermal infrared imaging. In an attempt to apply this technology to Mariana Swiftlets on Guam, the Navy tested thermal infrared imaging as a potential alternative to estimate population size (Sabol et al. 2011). However, due to comparable temperatures between swiftlets and warm cave walls, this method was ineffective because thermal contrast was low between the birds and their background (Sabol et al. 2011). In addition, due to the swiftlet’s rapid flight speed, images of flying swiftlets depicted an extended streak instead of a swiftlet-sized object (Sabol et al. 2011).

An alternative survey technique that has shown some promise with Mariana Swiftlets on Guam is near-infrared imaging (Brindock 2013). Near-infrared imaging has been successful in counting roosting swiftlets inside Maemong and Fachi Caves.
(Brindock 2013), but is questionable inside Mahlac Cave due to large, dense clusters of roosting birds (K. M. Brindock, pers. comm.). Comparing results from near-infrared imaging and evening arrival surveys without night vision technology at Maemong Cave revealed that evening arrival survey estimates were 38–45% greater than the actual number of swiftlets at the cave (Brindock 2013).

A survey method that should be considered for Mariana Swiftlets is terrestrial Light Detection and Ranging (LIDAR) laser scanning technology. Using scanning stations throughout the cave, an automatic detection algorithm that measures the intensity of the returning laser accurately calculated the number of roosting *Hipposideros* bats inside Gua Kelawar Cave in Malaysia (Azmy et al. 2013). This technology was also used to successfully differentiate Black-nest Swiftlet nests from roosting *Rhinolophus* bats inside Simud Hitam (the “Black Cave”) in Malaysia (McFarlane et al. 2015).

Until alternative methods are developed, refined, and fully operational for consistent use across all caves, we recommend evening arrival surveys with the use of night vision technology to facilitate detection and counting of entering and exiting swiftlets at active caves in the Mariana Islands. Incorporating night vision technology into evening arrival surveys on Saipan, Aguiguan, and Guam should improve population estimates. Similar to our surveys on O‘ahu, we suggest observers be situated at a position(s) inside the cave that will not disturb or impact swiftlet behavior, and provide an unimpeded view of the cave entrance(s). As on O‘ahu, we recommend assessing the total number of volant swiftlets and active nests inside the cave prior to the start of the evening arrival survey. This may be completed with night vision goggles or a monocular, a headlamp with a red filter, or a camcorder with a long-range infrared light. In any case,
the resulting number of volant swiftlets tallied inside the cave prior to and outside the
cave following the survey should be added to the net number of entering birds counted.
Finally, count results may vary based on the stage of the annual cycle and the time at
which the survey was conducted (as shown in Table 2.2). For example, obtaining
accurate population estimates becomes more challenging as daylight subsides and the
number of birds entering and exiting caves increases. Consequently, surveys must be
performed during similar months and time periods across years to obtain equivalent
results.

Estimating the number of breeding pairs also warrants a cautionary note. One
cannot assume that all volant individuals counted (e.g., during evening arrival surveys)
represents the number of nesting adults present in the colony. We know from nest and
adult surveys on O‘ahu that there may be many more birds counted than are associated
with active nests (Table 2.2). Birds not associated with active nests may be breeding
individuals that have yet to initiate breeding activities or non-breeding individuals (e.g.,
recently fledged birds). Therefore, simply dividing the total number of swiftlets counted
by two is not an accurate representation of the number of nesting pairs present in the
cave. A better approach is to carry out evening arrival surveys along with a count of
active nests. The resulting censuses produce a ratio of volant individuals to nesting
adults. This index of nesting and non-nesting birds provides insight into the natural
history of the Mariana Swiftlet (e.g., age at first breeding, operational sex ratios, annual
phenology, etc.) and is an indicator of the effective size/status of the population ($N_e/N$).
In small populations, such as with the Mariana Swiftlet, decreased ratios of $N_e/N$ can be
indicative of decreasing population viability as demonstrated by the Allee effect (Courchamp et al. 1999).

2.6.2. Population Estimates and Status Assessments

Population estimates for each island occupied by Mariana Swiftlets will be more accurate and reliable when additional caves are explored for nesting colonies and abundance estimates are calculated using consistent methods, preferably evening arrival surveys using night vision technology (until alternative methods are developed, refined, and fully operational) and active nest counts.

2.6.2.1. Saipan

The Mariana Swiftlet population on Saipan may have declined between the 1982 VCP surveys and evening arrival surveys conducted throughout the 1980s, 1990s, 2000s, and 2010s. However, we now know the VCP method overestimates swiftlet numbers (9,120 [84/km²] individuals estimated using the VCP method in 1982; 4,674 individuals counted at eight caves using evening arrival surveys in 2013), hence this decrease is questionable. Perhaps more reliable is the increase in known swiftlets in the late 1990s and 2000s from the 1980s evening arrival surveys, possibly due to discovery of five additional active caves (Cruz et al. 2008). Saipan presently contains the largest population of Mariana Swiftlets making it a potentially valuable source for reintroduction efforts. Although not representative of Saipan’s swiftlet abundance due to restricted access at one active cave, the November 2013 population estimate of 4,674 individuals at eight known active caves is the most current available.
2.6.2.2. Aguiguan

Similar to survey issues on Saipan, the status of Mariana Swiftlets on Aguiguan should not be evaluated based on comparisons of results from VCP estimates and evening arrival surveys. Thus, evening arrival surveys suggest their population remained relatively stable between 1987 and 2000, with a slight decrease in 2002. The most recent population estimate is 267 swiftlets at six known active caves in May 2002. Surveys are needed on Aguiguan to ascertain the island’s current swiftlet population size.

2.6.2.3. Guam

Observer bias is clearly an issue affecting accurate swiftlet population estimates on Guam, as the comparison between evening arrival surveys and near-infrared imaging at Maemong Cave indicated. Field testing of alternative swiftlet survey methods on Guam is to be commended; this can only be a step in the right direction to effectively determine accurate swiftlet estimates on that island, as well as Saipan and Aguiguan. Based on evening arrival surveys, the Mariana Swiftlet population on Guam appears to have remained relatively stable in recent years. The March–April 2015 population estimate of 1,591 swiftlets at three known active caves, including 1,243 birds in Mahlac Cave, is the most current available.

2.6.2.4. Oʻahu

Swiftlets on Oʻahu may be limited to the single colony in North Halawa Valley. There are presently no other known roosting/nesting tunnels or caves, and practically all swiftlet sightings since 1969 have been within approximately 5 km of the roosting/nesting tunnel,
suggesting that suitable roosting/nesting tunnels or caves may be a limiting factor preventing the Mariana Swiftlet population from expanding on O‘ahu (Wiles and Woodside 1999, this study). We documented potential evidence of this or tunnel fidelity during our study. One adult or sub-adult swiftlet that was banded in August 2005 was recaptured at the tunnel 334 days later. Also, the band of a nestling that was ringed inside the tunnel in August 2005 was found 193 days post-fledging in a feather pile following the 2006 suspected rat depredation event.

Our June 2010 population estimate of 142 swiftlets is the most current available and is substantially higher than the 21 November 1997 estimate of 66 birds (Wiles and Woodside 1999). In 1997, the survey ended at 1830 hours, and no swiftlets exited the tunnel throughout the entire census (Wiles and Woodside 1999). In 2010, the survey extended until 2020 hours, resulting in an additional 97 entering and 32 exiting sorties after 1830 hours. Longer daylight hours (sunset = 1914 hours) and 38 nests containing one nestling each, probably resulted in increased foraging activity after 1830 hours in 2010. There were only three nests containing one nestling each during the 1997 survey (Wiles and Woodside 1999), thus the shorter daylight hours (sunset = 1749 hours) and only three nestlings to feed may explain the absence of exiting forays. Additionally, in the 2010 survey, the 83 nestlings that successfully fledged during the remainder of the year had not yet done so. While in 1997, young of the year were probably counted as adults during the census (Wiles and Woodside 1999). Assuming no mortality, if we add the remaining young of the year \((n = 83)\) to the 142 individuals counted in June, the population potentially reached 225 by the end of 2010.

It is important to recognize the various stages of activity throughout the annual
cycle as it relates to survey results for the North Halawa Valley tunnel swiftlet colony (Table 2.2). On 11 June 2010, 76% of the colony was composed of nesting individuals (Table 2.2). In contrast, even at peak breeding, and during and prior to fledging activities on 13 August 2005 and 29 July 2006, respectively, nearly half of the colony was comprised of non-nesting individuals (Table 2.2). It is unclear how many non-breeding adults and sub-adults were present. The age at which a Mariana Swiftlet first enters the breeding cohort is unknown, although a study in Vietnam found that a large proportion of young Edible-nest Swiftlets bred at one year of age (Nguyen Quang et al. 2002).

The February–March 2006, December 2006–January 2007, and September 2009 rat depredation events likely caused some disruption to the colony on O‘ahu, although the swiftlets did not abandon the tunnel altogether. For example, during one subsequent evening arrival survey on 17 March 2006, 53 entering birds and 52 exiting birds were tallied from 1645 to 2015 hours; and during an overnight survey on 17–18 March 2006, 16 swiftlets entered and exited the tunnel from 2103 to 0459 hours. Tarburton (1987) mentioned that some White-rumped Swiftlets in Fiji remain away from their respective caves, perhaps roosting in the coil of a young banana leaf (according to Fijians). Thus, we cannot rule out the possibility of alternative roosting places by Mariana Swiftlets, especially following a disturbance to the colony. This possibility may rationalize discrepancies between the number of volant individuals counted during surveys (e.g., Table 2.2) (Tarburton 1987).

Rats may be a significant limiting factor thwarting Mariana Swiftlet population growth on O‘ahu. On O‘ahu, Black Rats (*Rattus rattus*) have been confirmed as primary nest predators of the endangered ‘Elepaio (*Chasiempis sandwichensis*) (VanderWerf

In Vietnam, Rice Rats (*R. tanezumi*) often enter caves and kill adult and nestling Edible-nest Swiftlets; from 1991 to 1997, an estimated 4,000 swiftlets were killed by rats in the Khanh Hoa region, including two caves that lost their entire swiftlet populations (Nguyen Quang and Voisin 2001, Nguyen Quang et al. 2002). Rats are also known predators of White-rumped Swiftlet adults and nestlings in Samoa and Australian Swiftlet nestlings in Queensland (Tarburton 1988, Tarburton 2009a, 2009b).

Implementing effective survey methods is critical to determine a reliable baseline of Mariana Swiftlet population size and for efficient conservation and management, particularly if wind turbines are situated or proposed to be placed in the feeding ranges of these insectivores. With reliable population estimates, managers will be able to accurately determine the context and impact of any wind-turbine-related fatalities to the overall population size, be able to mitigate where appropriate, and ultimately be able to determine whether any mitigation measures to reduce fatalities are working. In addition, accurate Mariana Swiftlet population estimates will assist the U.S. Fish and Wildlife Service in assessing whether the necessary minimum subpopulations for downlisting are established, facilitating progress toward recovery (U.S. Fish and Wildlife Service 1991).

In conclusion, this paper provides a summary of current and historic Mariana Swiftlet population and distribution information that will assist Mariana Islands natural resource managers with continued conservation efforts for Mariana Swiftlets, including proposed reintroductions from Saipan and southern Guam to their former ranges of Rota and northern Guam, respectively (Berger et al. 2005, Guam Division of Aquatic and Wildlife Resources 2006, U.S. Fish and Wildlife Service 2009, 2010). This paper also
provided perspectives on survey methods that can be used for the Mariana Swiftlet, as well as other cave-nesting swiftlets. Until alternative methods are developed, refined, and fully operational, we suggest the most accurate means of assessing the swiftlet population in the Mariana Islands will be via evening arrival surveys using night vision technology and active nest counts. Incorporating night vision technology into evening arrival surveys on Saipan, Aguiguan, and Guam should improve population estimates. Furthermore, given the endangered status of the Mariana Swiftlet in the Mariana Islands, the O‘ahu population of swiftlets is of significant conservation importance and may be a useful population to test reintroduction techniques, learn more about Mariana Swiftlet natural history, and provide individuals for population enhancement in the Mariana Islands.

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Government.
2.8. Literature Cited


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Figure 2.1. Mariana Swiftlet inside the North Halawa Valley tunnel, O’ahu, Hawaiian Islands May 2006. Photograph by NCJ.
Figure 2.2. Map of the Mariana Islands including the U.S. Commonwealth of the Northern Mariana Islands and the U.S. Territory of Guam. Mariana Swiftlets currently breed on Saipan, Aguiguan, and Guam. Formerly, they bred on Rota and occurred on Tinian.
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Figure 2.4. Interior of the Mariana Swiftlet roosting/nesting tunnel in North Halawa Valley, O‘ahu, Hawaiian Islands. Photograph by NCJ.
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Table 2.1. Current population estimates of Mariana Swiftlets on Saipan, Aguiguan, and Guam, Mariana Islands, and O‘ahu, Hawaiian Islands.

<table>
<thead>
<tr>
<th>Island</th>
<th>Population estimate</th>
<th>Number of known active caves/tunnels</th>
<th>Survey month and year</th>
<th>Survey type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Saipan</td>
<td>4,674&lt;sup&gt;a&lt;/sup&gt;</td>
<td>8&lt;sup&gt;c&lt;/sup&gt;</td>
<td>November 2013</td>
<td>Evening arrival</td>
</tr>
<tr>
<td>Aguiguan</td>
<td>267&lt;sup&gt;b&lt;/sup&gt;</td>
<td>6</td>
<td>May 2002</td>
<td>Evening arrival</td>
</tr>
<tr>
<td>Guam</td>
<td>1,591&lt;sup&gt;c&lt;/sup&gt;</td>
<td>3</td>
<td>March–April 2015</td>
<td>Evening arrival</td>
</tr>
<tr>
<td>O‘ahu</td>
<td>142&lt;sup&gt;d&lt;/sup&gt;</td>
<td>1</td>
<td>June 2010</td>
<td>Evening arrival</td>
</tr>
</tbody>
</table>

<sup>a</sup> P. M. Radley, pers. comm.
<sup>b</sup> Esselstyn et al. 2003.
<sup>c</sup> K. M. Brindock, pers. comm.
<sup>d</sup> This study.
<sup>e</sup> One additional active cave is present on Saipan; however, the number of swiftlets within is unknown due to restricted access.
Table 2.2. Mariana Swiftlet population estimates at the North Halawa Valley tunnel, O‘ahu, Hawaiian Islands, August–September 2005, March–July 2006, December 2009, and June 2010. Volant individuals were counted during evening arrival surveys. Nesting adults were calculated by doubling the number of active nests (i.e., two adults per nest). Active nest = nest with one egg or one nestling.

<table>
<thead>
<tr>
<th>Survey date</th>
<th>Volant individuals counted</th>
<th>Active nests</th>
<th>Nesting adults: other volant individuals</th>
<th>Phase of annual cycle</th>
</tr>
</thead>
<tbody>
<tr>
<td>13 August 2005</td>
<td>115</td>
<td>28</td>
<td>56:59</td>
<td>Active nests and young fledgingª</td>
</tr>
<tr>
<td>26 August 2005</td>
<td>131</td>
<td>24</td>
<td>48:83</td>
<td>Active nests, young fledgingª, and nest construction</td>
</tr>
<tr>
<td>9 September 2005</td>
<td>109</td>
<td>21</td>
<td>42:67</td>
<td>Active nests, young fledgingª, and nest construction</td>
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<tr>
<td>17 March 2006</td>
<td>2</td>
<td>0</td>
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<td>Following suspected rat depredation event</td>
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<tr>
<td>17 April 2006</td>
<td>62</td>
<td>0</td>
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<td>Nest construction</td>
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<td>1 May 2006</td>
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<td>15 May 2006</td>
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<td>5</td>
<td>10:70</td>
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</tr>
<tr>
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<tr>
<td>11 June 2010</td>
<td>142</td>
<td>54</td>
<td>108:34</td>
<td>Active nests and nest construction</td>
</tr>
</tbody>
</table>

ª Fledging refers to volant young leaving the nest site; these young are included in the number of other volant individuals counted.
3. TEMPORAL PATTERNS OF MARIANA SWIFTLET (*AERODRAMUS BARTSCHI*) REPRODUCTIVE SUCCESS THROUGHOUT THE ANNUAL CYCLE

3.1. ABSTRACT

In order to implement effective conservation efforts, it is critical to understand species life history activities throughout multiple phases of the annual cycle. Information on Mariana Swiftlet (*Aerodramus bartschi*) life history is scarce. Therefore, this study examined the behavioral ecology and reproductive biology of the Mariana Swiftlet at multiple temporal scales over five annual cycles on the island of O‘ahu in the Hawaiian Islands. This introduced population used a human-made tunnel for roosting and nesting, and was studied as a surrogate to spare the endangered population in the Mariana Islands from interference. Tunnel emergence and arrival surveys indicated that peak entering and exiting activity occurred during crepuscular hours. Overnight surveys documented entering and exiting swiftlets at all hours of the night, with the latest arrival at 0402 hours. Active nests were observed in every month of the year. Peak nesting activity occurred between about May and September, and decreased from October to April. A clutch of one white egg \(n = 478\) was laid in a nest that was secured to a ledge or tunnel wall with copious amounts of mucus-like salivary cement. Mean incubation and nestling periods were \(23.91 \pm 3.30\) days (range = 18–30, \(n = 233\)) and \(55.04 \pm 6.61\) days (range = 41–84, \(n = 228\)), respectively. Estimated nest success was 63%. Eggs found in the water or mud, or on the tunnel floor accounted for 52% of nest failures. Rat depredation was an important cause of nest failure and often resulted in simultaneous loss of most nests. Mariana Swiftlets completely recycled breeding activities following rat depredation.
events. The daily survival rate of nests was influenced by a quadratic effect of nest age and year. Results of this five-year study on a surrogate population provides important life history information for upcoming plans for swiftlet population enhancement in the Mariana Islands.
3.2. INTRODUCTION

Understanding how and when a species is engaged in specific life history activities during multiple phases of the annual cycle and over their lifetime is crucial in order to carry out effective conservation efforts, particularly when reintroductions are being planned (Sillett and Holmes 2002, Webster et al. 2002). Yet, studies of species life histories throughout the annual cycle are uncommon because of limited personnel, time, and funding. Perhaps not surprisingly, the best examples come from highly controversial, well-funded, non-migratory, endangered birds such as the Northern Spotted Owl (*Strix occidentalis caurina*; Forsman et al. 2011), Red-cockaded Woodpecker (*Picoides borealis*; Ziegler and Walters 2014), and California Condor (*Gymnogyps californianus*; Rivers et al. 2014). While seemingly simpler to study as they do not move as much, non-migrants still undergo seasonal changes and cross-seasonal interactions that are just as important to understand as with migratory species (Myers 1981, Haig et al. 2015). Even so, these species are fragile, hence the ability to examine a surrogate population prior to direct management provides an extra layer of safety in bringing the species back from the brink of extinction (see Toone and Wallace 1994, White et al. 2005).

In this paper, we report on aspects of the behavioral ecology and reproductive biology of the little-known, non-migratory, endangered Mariana Swiftlet (*Aerodramus bartschi*) at multiple temporal scales over five annual cycles. In this case, we had the opportunity to study a surrogate population in Hawai‘i, thus avoiding any interference with the indigenous population in the Mariana Islands.

*Aerodramus* swiftlets comprise 28 species, including 57 subspecies, and are
widely-distributed throughout the Indo-Pacific region from the Seychelles Islands, Reunion Island, Mauritius, India, and Sri Lanka; throughout Southeast Asia and Queensland, Australia; to islands in Melanesia, Micronesia, and Polynesia; reaching as far east as the Marquesas archipelago (Gill and Donsker 2015). Studies of *Aerodramus* swiftlets have primarily focused on breeding biology, behavioral ecology, population status, and diet (e.g., Medway 1962a, 1962b, Tarburton 1986a, 1986b, 1987, 1988, 1990, Fullard et al. 1993, Nguyen Quang 1996, Tarburton 2003, 2009a, Fullard et al. 2010). However, most of these investigations did not occur continuously over multiple annual cycles.

This paper is among few that have examined full life cycle biology of an *Aerodramus* swiftlet and will provide Mariana Islands natural resource managers with information necessary to assist with designing and implementing future reintroductions of Mariana Swiftlets, including the proposed movements of birds from Saipan and southern Guam to their former ranges of Rota and northern Guam, respectively.

With less than 7,000 individuals remaining in the wild, the Mariana Swiftlet is one of nine bird species listed as federally endangered in the Mariana Islands (U.S. Fish and Wildlife Service 2011). In 1981, the Guam population of the Mariana Swiftlet was locally protected by the Endangered Species Act of Guam (Guam Public Law 15–36, U.S. Fish and Wildlife Service 1991). The Mariana Swiftlet was listed as a federally endangered species throughout the Mariana archipelago in 1984 (U.S. Fish and Wildlife Service 1984) and listed as threatened/endangered by the U.S. Commonwealth of the Northern Mariana Islands (CNMI) government in 1991 (CNMI Public Law 2–51; Commonwealth Register Volume 13, Number 1; the CNMI law did not differentiate
between threatened and endangered categories and are thus jointly classified). Known locally as “Yayaguak” (Guam) and “Chachaguak” (CNMI), the Mariana Swiftlet is a small (10 cm, 6–8 g), mostly sooty-black slender-winged bird historically found on the Mariana Islands of Saipan, Tinian, Aguiguan, Rota, and Guam (Chantler and Driessens 2000). Presently, the species is found only on Saipan, Aguiguan, and Guam (Cruz et al. 2008; NCJ, pers. obs.), although an introduced population persists on O‘ahu in the Hawaiian Islands (Wiles and Woodside 1999, Chantler and Driessens 2000, this study).

Mariana Swiftlets occupy natural and human-made caves throughout the year (Pratt et al. 1987, U.S. Fish and Wildlife Service 1991, this study). They have the unique ability to echolocate, which allows them to penetrate, orientate, and navigate within darker regions of caves where roosting and nesting occurs (U.S. Fish and Wildlife Service 1991). Mariana Swiftlets lay a single white egg in a saliva-structured nest composed of vegetative material and placed on a cave wall or ceiling (Jenkins 1983, Morton and Amidon 1996, Reichel et al. 2007, this study).

Currently, there are plans to reintroduce Mariana Swiftlets to Rota and northern Guam (Berger et al. 2005, Guam Division of Aquatic and Wildlife Resources 2006, U.S. Fish and Wildlife Service 2009, 2010) provided appropriate groundwork, including understanding the species life history, is completed. Assisted movements of Mariana Swiftlets have proven successful in the past. In May 1962 and January 1965, respectively, 175 and 210 individuals were captured from Guam and released approximately 6,000 km away on O‘ahu (Wiles and Woodside 1999). They have survived to this day although, presently less than 150 birds persist on O‘ahu (Johnson et al., In review). While Rota is currently free of Brown Treesnakes (Boiga irregularis),
introduced rats (*Rattus* spp.) and feral cats (*Felis catus*) are or suspected to be a source of mortality for avian eggs, nestlings, and adults on the island (U.S. Fish and Wildlife Service 2007, Berry and Taisacan 2008, Zarones et al. 2015). Thus, swiftlet response to depredation is an important aspect to understand when planning the reintroduction. Therefore, we were interested in the effect predators such as rats might have on Mariana Swiftlets on O‘ahu, and predicted that one to a very few rats in an enclosed tunnel could have a significant effect on the reproductive output of the entire colony.

The paucity of research on Mariana Islands avifauna poses difficulties when planning important conservation efforts such as reintroductions. The ecology and behavior of most indigenous birds in the Mariana Islands are scantily documented and most of the avifauna has typically received only qualitative attention (e.g., Marshall 1949, Baker 1951, Pratt et al. 1979, Engbring and Pratt 1985, Pratt et al. 1987, Stinson 1995). Jenkins (1983) summarized natural history facets of Guam’s birds, of which most are now extinct or extirpated (Savidge 1987, Wiles et al. 2003, Rodda and Savidge 2007). Results of island-wide avian population surveys on Guam, Rota, Aguiguan, Tinian, and Saipan were described by Engbring and Ramsey (1984), Engbring et al. (1986), Amar et al. (2008), Camp et al. (2009, 2012), and Amidon et al. (2014).

marchei; Craig 1990, Stinson and Stinson 1994), Mariana Common Moorhen (Gallinula chloropus guami; Takano and Haig 2004a, 2004b), Guam Rail (Gallirallus owstoni; Jenkins 1979, Haig et al. 1990, Haig et al. 1994, Haig and Ballou 1995), and Guam Micronesian Kingfisher (Todiramphus cinnamominus cinnamominus; Marshall 1989, Haig and Ballou 1995, Haig et al. 1995). Unfortunately, the Mariana Swiftlet has not received this type of attention until recently (Reichel et al. 2007, Cruz et al. 2008, Valdez et al. 2011, this study).

When faced with a sensitive species, studying surrogate populations is one alternative for obtaining critical natural history and population biology information, ultimately assisting in recovery and conservation endeavors (Kesler and Haig 2007). Taking a comparative approach similar to that of the Guam Micronesian Kingfisher (Kesler and Haig 2007), we determined that a safer method to investigate the Mariana Swiftlet was to study the introduced population on O‘ahu.

3.3. **Chapter Objectives**

The objectives of this chapter were to 1) describe and quantify aspects of Mariana Swiftlet behavioral ecology and reproductive biology over the three temporal scales (daily cycle, annual cycle, five-year period) the population was studied on O‘ahu, 2) determine the most significant factors affecting the survival of Mariana Swiftlet nests on O‘ahu, and 3) ascertain whether rats had an effect on the annual reproductive success of Mariana Swiftlets on O‘ahu.
3.4. METHODS

3.4.1. Study Area

The Hawaiian Islands are the most isolated islands in the world, located 3,765 km from North America, the closest continental land mass. O‘ahu (21° 22’ N, 157° 55’ W) is the third largest Hawaiian Island and is comprised of the Ko‘olau and Wai‘anae mountain ranges and a broad valley in between. The island is 1,624 km² in size, 71 km long, and 48 km wide. O‘ahu is the most populated of the Hawaiian Islands and the seat of the state government.

Fieldwork was concentrated in and around a human-made tunnel that Mariana Swiftlets use for roosting and nesting on O‘ahu. The tunnel was likely excavated prior to World War II as a possible irrigation water source (Wiles and Woodside 1999). It is located near the base of a steep, seasonal waterfall in North Halawa Valley, 17 km and 32 km from the original Mariana Swiftlet release sites at Niu Valley and Waimea Valley, respectively (Wiles and Woodside 1999). The tunnel is a single-entrance (1.80 m high by 1.30 m wide) straight passage, which measures approximately 55 m long, averaging 1.67 ± 0.20 (SD) m high (range = 1.25–2.10, n = 12 measurements) and 1.25 ± 0.19 (SD) m wide (range = 0.91–1.58, n = 12 measurements). Tunnel width is relatively constant throughout, however height steadily decreases after about 15 m. The tunnel entrance faces northwest at 312° and travels southeast at 132°. Elevation is 424 m, placing the tunnel within the montane rain forest climatic vegetation zone (Mueller-Dombois and Fosberg 1998). The tunnel is wet throughout the year, with pools of water approximately 3–15 cm deep present on the floor. Standing water and mud are present throughout the
tunnel; however it becomes progressively muddier towards the rear. Water constantly drips from the ceiling throughout the tunnel, but is more noticeable within the first 25 m, especially following heavy rains.

3.4.2. Data Collection

Fieldwork was conducted from July to September 2005, and December 2005 to January 2011. Two individuals carried out all fieldwork during this study (NCJ and SMM).

3.4.2.1. Activity surveys

Three types of Mariana Swiftlet surveys were carried out in 2005, 2006, 2008, 2009, and 2010 inside the North Halawa Valley tunnel: evening arrival, morning emergence, and overnight. Evening arrival surveys were performed to estimate population size and describe activity patterns, whereas morning emergence and overnight surveys were a record of activity patterns. See Johnson et al. (In review) for population estimates resulting from the evening arrival surveys. This paper discusses activity patterns recorded during all three survey types.

In 2005, we surveyed from the same dimly lit location in the tunnel as described in Wiles and Woodside (1999). In 2006, 2008, 2009, and 2010, we conducted surveys from a darker location against an indentation on the right side, 18 m into the tunnel. We used LOMO PVS-7 Recon II second generation night vision goggles or a Bushnell Night Vision 1x20 Tactical Monocular to detect and count swiftlets entering and exiting the tunnel. Because swiftlets are easily observed and differentiated with night vision devices (Johnson et al., In review), we are confident that most, if not all, entering and exiting
swiftlets were counted during each survey. We determined beginning and ending evening arrival and morning emergence survey times using prior experience conducting swiftlet surveys on Saipan, Aguiguan, and Guam.

3.4.2.2. Nest monitoring

We monitored the status of active Mariana Swiftlet nests inside the North Halawa Valley tunnel from January 2006 to January 2011. The only months in which monitoring did not occur were March 2007, and January and February 2008. An active nest was defined as containing one egg or one nestling. A nest site was characterized by the presence of a nest or nest material on the tunnel wall; consequently, an active nest site was one that produced at least one egg. Nest sites were identified by placing 2.54 cm$^2$ uniquely numbered reflective tape tags on the tunnel wall 1.27–10.16 cm from each nest. Because the tunnel was a straight and narrow passage with low clearance, nest detectability was high; thus, we are confident that all active and inactive nests were found. We assumed that one pair of swiftlets was associated with an active nest site during each breeding season.

To verify nest status, we examined the tunnel walls, ceiling, and chambers using night vision goggles, a headlamp with a red filter, or a Sony Handycam DCR-HC21 camcorder (with NightShot Plus Infrared System). A Sony Infrared Light HVL-IRM was attached to the camcorder to extend the range of the NightShot Plus Infrared System. Nest status categories included 1) egg – one egg in the nest; 2) nestling – one nestling in the nest; 3) empty – nest empty; 4) building – nest materials added to the nest site; 5) fledged – nestling was assumed to have successfully fledged from the nest if it was no
longer in the nest and not observed dead in the water or mud, or on the tunnel floor; and
6) failed (see below).

We assigned nest failures to one of eight categories based on the following
evidence: 1) egg in water or mud – egg in the water or mud, or on the tunnel floor; 2) 
nestling in water or mud – nestling in the water or mud, or on the tunnel floor; 3) nest fell
off wall – nest containing an egg or nestling fell off the tunnel wall; 4) human – egg
broken or damaged in the hand while taking measurements; 5) depredation – remains of
an egg or nestling with evidence of depredation, such as feather piles, body parts, or a
carcass; 6) missing – egg or nestling missing from the nest, and not located in the water
or mud, or on the tunnel floor; 7) nestling dead in or on nest – nestling dead inside or
hanging on the outside of the nest; and 8) egg infertile – egg in the bottom of the nest
with a new egg laid on top of it, or egg manually removed from the nest because in the
nest >40 days or shell flaking off membrane.

We calculated apparent hatching success as the proportion of eggs laid that
hatched, apparent fledging success as the proportion of hatched nestlings that fledged,
and apparent nest success as the proportion of eggs that resulted in a fledged nestling.
Since Mariana Swiftlets are known to lay one egg, apparent nest success is equal to the
proportion of successful nests. Transition dates (i.e., egg laying, hatching, fledging,
failure, building) were either directly observed; or estimated by back dating from known
events during the nesting period, assuming an incubation period of 24 days and nestling
period of 55 days. When no other data were available, we assumed that any change in
status (i.e., egg laying, hatching, fledging, failure, building) transpired halfway between
nest monitoring visits (Mayfield 1975). Incubation period, nestling period, nesting
period, time to re-lay after a fledged nest, time to re-lay after a failed nest with egg, time to re-lay after a failed nest with nestling, and nest construction period were calculated using the estimated laying, hatching, fledging, failure, and building dates, and only for instances when nest monitoring visits occurred at 1–10 day intervals.

3.4.2.3. Nest and nest site measurements

Nests known to be active were measured when unattended by adults, or soon after fledging or failure with Fowler electronic or SPI dial calipers, and a plastic ruler (cup depth). Nest measurements included outer length (outer portion of the nest perpendicular to the tunnel wall), outer width (outer portion of the nest parallel to the tunnel wall), cup length (inner portion of the nest perpendicular to the tunnel wall), cup width (inner portion of the nest parallel to the tunnel wall), cup depth (center of the cup), external height (height of the front rim), and front rim thickness. Internal nest volume was also calculated for individual nests and was the product of cup length x cup width x cup depth, providing an average internal volume index for all nests (Tarburton 1990, 2009a).

Measurements were taken with a tape measure at active nest sites, and included height above the tunnel floor and distance into the tunnel. Also recorded was the distance from each active nest site to the nearest active nest site on the same tunnel wall. Additionally, we documented the placement location of each active nest site inside the tunnel (e.g., right wall, left wall).

3.4.2.4. Egg measurements

Eggs were measured when first observed or soon thereafter, and when unattended by
adults. Length and breadth (maximum diameter) measurements were taken with Fowler electronic or SPI dial calipers. Egg volumes (Volume = 0.51 x Length x Breadth²; Hoyt 1979) and egg shape indices (Breadth/Length x 100; Romanoff and Romanoff 1949) were calculated for individual eggs.

3.4.2.5. Rat trapping

We carried out rat trapping inside and outside the North Halawa Valley tunnel between March 2006 and January 2011. Using five types of snap trap (Ka Mate, Tomcat, Trapper T-Rex, Victor with metal tab, and Victor with plastic tab), 43 traps were distributed inside (n = 5) and outside (n = 38) the tunnel. Traps were baited with peanut butter, macadamia nuts, scented wax (peanut butter, coconut, grape), or sponges with essential oils (passion fruit, coconut), and situated on the tunnel floor and tree branches or the ground outside the tunnel. To avoid attracting rats near roosting and nesting swiftlets, two traps that were furthest inside the tunnel were not baited; these traps were positioned so that any approaching rat would be captured. We logged 252 visits, during which traps were checked and reset/rebaited, if necessary.

3.4.2.6. Nest survival analysis

We calculated daily nest survival rates using Program R, following methods described in Rotella et al. (2004). We included nest age (linear and quadratic effects; number of days since the first egg was laid), year (breeding season), nest site distance into the tunnel, nest site height above the tunnel floor, daily precipitation, temporal variation within seasons (linear and quadratic effects), mean number of active and baited rat traps/night annually,
and cumulative total number of rats captured annually as independent predictor variables of daily survival rates of Mariana Swiftlet nests. Likelihood functions in Program R were used to fit our a priori candidate models. We used second order AICc to assess candidate models and selected models with the lowest AICc or those within two $\Delta$AICc units, which suggests substantial evidence for the model (Burnham and Anderson 2002). The delta method was used to calculate variance for model parameter estimates (Powell 2007). We used the likelihood ratio test as a goodness-of-fit test to determine whether the global or most parameterized model was adequate (i.e., fit the data). The Benjamini and Hochberg method (Benjamini and Hochberg 1995) was used to correct for multiple comparisons of the daily nest survival rates between all years; adjusted $P$-values < 0.05 were considered significant.

We used a two-sample $t$-test to test for differences in nest and egg measurements between successful and unsuccessful nests. We were interested in whether nest and egg size were important to the success of a nest. $T$-tests were two-tailed, and the level at which we accepted significance was $P < 0.05$. A successful nest was defined as a nest that fledged a nestling. An unsuccessful nest was one that had an egg, but failed to fledge a nestling. Unless otherwise noted, results are presented as mean ± SD.

3.5. RESULTS

3.5.1. Nests and Eggs
3.5.1.1. Nest structure and composition

Mariana Swiftlet nests on O‘ahu were circular cups composed entirely of plant materials (Table 3.1 and Figure 3.1). Approximately 80% of two nests examined were composed of two liverwort species, *Herbertus gracilis* and *H. helleri*. *Bazzania trilobata*, also a liverwort, was the third most abundant material in the two nests and was the primary material in another. Overall, the three intact nests were composed of four species of liverworts (*B. trilobata, H. gracilis, H. helleri, Plagiochila deflexa*), one liverwort identified to genus (*Metgeria*), three identified moss species (*Acroporium fuscoflavum, Aerobryopsis wallichii, Macromitrium piliferum*), at least one unidentified moss species, and one species of fern (*Adenophorus pinnatifidus*).

3.5.1.2. Nest placement

Mariana Swiftlet nests were secured to ledges or the tunnel walls with copious amounts of mucus-like salivary cement (Figure 3.1). Nests on the tunnel walls exhibited the bracket and cup construction that is characteristic of swiftlets (Medway 1966). At the onset of a new nest attempt, fresh materials were either added to the cup, rim, and base of an existing nest (Figure 3.1), or an entirely new nest was constructed. Twelve nests observed throughout the entire construction cycle, commencing with salivary cement on the tunnel wall and concluding with an egg in the cup took an average of $33.83 \pm 15.47$ days (range = 6.00–55.00) to complete.

Of the 133 nest sites we documented inside the North Halawa Valley tunnel, 84 were active throughout the period of study. Inactive nest sites ranged from one piece of material adhered to a ledge or the tunnel wall with salivary cement, to an intact nest that
was never active. All 84 active nest sites were located in complete darkness of the tunnel. Mean distance into the tunnel for the 84 active nest sites was 47.65 ± 5.63 m (range = 32.58–54.51). Approximately 82% \((n = 69)\) of the active nest sites were situated between 45.01 and 54.51 m into the tunnel, and 18% \((n = 15)\) were located between 32.58 and 45.00 m into the tunnel. Of the 84 active nest sites, 50% \((n = 42)\) were located on the right wall of the tunnel, 44% \((n = 37)\) were on the left wall, 4% \((n = 3)\) were on the rear wall, 1% \((n = 1)\) were placed on a ledge in a small chamber on the right side ceiling, and 1% \((n = 1)\) were situated on a ledge in a small chamber on the left center ceiling. Mean height above the tunnel floor for the 84 active nest sites was 1.17 ± 0.25 m (range = 0.57–1.73). Active nest sites on the right, left, and rear walls of the tunnel averaged 0.51 ± 0.97 m (range = 0–5.20, \(n = 42\); 0.58 ± 1.16 m (range = 0–6.53, \(n = 37\); and 0.17 ± 0.02 m (range = 0.15–0.18, \(n = 3\)) from the nearest active nest site, respectively.

There were no differences in nest measurements between successful and unsuccessful nests: outer length (two-sample t-test: \(t_{59} = -0.94, P = 0.35\)); outer width (two-sample t-test: \(t_{59} = 0.06, P = 0.95\)); external height (two-sample t-test: \(t_{60} = -0.72, P = 0.48\)); front rim thickness (two-sample t-test: \(t_{22} = -0.39, P = 0.70\)); cup length (two-sample t-test: \(t_{43} = -0.98, P = 0.34\)); cup width (two-sample t-test: \(t_{43} = -1.03, P = 0.31\)); and cup depth (two-sample t-test: \(t_{43} = 1.44, P = 0.16\)).

3.5.1.3. Eggs

The clutch of the Mariana Swiftlet on O‘ahu consisted of one egg \((n = 478)\) and is presumed to be attended by both adults. Eggs were elliptical in shape, nonglossy, smooth
in texture, and white in color (Figure 3.1). No markings were observed on any of the 452 eggs examined. Egg dimensions, volume, and shape index are presented in Table 3.2.

During 2006–2010, the mean incubation period was 23.91 ± 3.30 days (range = 18–30, \( n = 233 \)) and the mean nestling period was 55.04 ± 6.61 days (range = 41–84, \( n = 228 \)), resulting in a mean nesting period of 79.47 ± 6.76 days (range = 63–113, \( n = 182 \)). Incubation period, nestling period, and nesting period are depicted by individual year in Figure 3.2.

During 2006–2010, mean time to re-lay after a fledged nest was 10.53 ± 6.56 days (range = 0–33, \( n = 129 \)); mean time to re-lay after a failed nest with egg was 14.48 ± 7.54 days (range = 0–41, \( n = 69 \)); and mean time to re-lay after a failed nest with nestling was 17.89 ± 11.89 days (range = 11–64, \( n = 18 \)) (Figure 3.3).

The average number of clutches attempted at each active nest site per year was 1.65 in 2006 (range = 1–3, \( n = 38 \)); 2.04 in 2007 (range = 1–3, \( n = 51 \)); 2.69 in 2008 (range = 1–5, \( n = 105 \)); 2.26 in 2009 (range = 1–6, \( n = 129 \)); and 2.31 in 2010 (range = 1–6, \( n = 155 \)). As many as 17 clutches were laid at a single nest site throughout the entire study. The maximum number of young fledged at a nest site in 2006 and 2007 was two; and three in 2008, 2009, and 2010.

There were significant differences in egg measurements between successful and unsuccessful nests: egg length (two-sample \( t \)-test: \( t_{418} = 3.66, P < 0.001 \)) and egg breadth (two-sample \( t \)-test: \( t_{418} = 2.61, P < 0.01 \)). Eggs resulting in a fledgling were on average 0.27 mm longer and 0.08 mm wider than those from unsuccessful nests.
3.5.2. Daily Cycle

Daily activity patterns were determined via 12 morning emergence surveys conducted in August–September 2005 \((n = 3)\), March–July 2006 \((n = 8)\), and October 2008 \((n = 1)\), beginning at a mean of 0504 hours \((\text{range} = 0500–0520)\) Hawai‘i–Aleutian Standard Time and ending at a mean of 0758 hours \((\text{range} = 0700–0919)\); and 13 evening arrival surveys carried out in August–September 2005 \((n = 3)\), March–July 2006 \((n = 8)\), December 2009 \((n = 1)\), and June 2010 \((n = 1)\), beginning at a mean of 1642 hours \((\text{range} = 1530–1740)\) and ending at a mean of 2007 hours \((\text{range} = 1930–2045)\).

Morning emergence surveys indicated that peak exiting activity occurred between 0600 hours and 0630 hours, with a mean of 28 swiftlets per survey recorded during this period (Figure 3.4). The earliest swiftlet to depart the tunnel during morning emergence surveys was at 0508 hours. During morning emergence surveys, entering swiftlets were tallied throughout all phases of the annual cycle (Table 3.3).

Evening arrival surveys showed that peak entering activity was between 1830 hours and 1900 hours, with a mean of 34 swiftlets per survey recorded during this period (Figure 3.4). The latest returning swiftlet during evening arrival surveys was at 2029 hours. During evening arrival surveys, exiting swiftlets were noted throughout all phases of the annual cycle (Table 3.4).

Eight overnight surveys were carried out in March–July 2006, beginning at a mean of 2115 hours \((\text{range} = 2050–2145)\) and ending at 0459 hours. Entering and exiting swiftlets were documented at all hours of the night and during all phases of the annual cycle (Table 3.5 and Figure 3.5). The latest individual returned to the tunnel at 0402 hours.
Additional opportunistic observations with the night vision goggles and camcorder with infrared capabilities revealed that adult Mariana Swiftlets inside the North Halawa Valley tunnel incubate eggs, as well as brood and feed nestlings during most diurnal hours. Incubating and brooding swiftlets were recorded between 1036 hours and 1812 hours, and 1329 hours and 1739 hours, respectively. Adult swiftlets were observed feeding a nestling between 1342 hours and 1658 hours \((n = 8 \text{ nests, } 16 \text{ observations})\).

### 3.5.3. Annual Cycle

From January 2006 to January 2011, Mariana Swiftlets on O‘ahu exhibited a cyclical breeding pattern that extended throughout the year (Figure 3.6). Peak breeding activities were observed in July (2006), June (2007), and May (2008–2010).

A suspected rat depredation event may have interrupted the beginning of the 2006 breeding season (Figure 3.6). Eighteen swiftlet feather piles, including three skulls and a carcass, were discovered 19–55 m into the tunnel on 6 March 2006. This depredation event occurred after the previous tunnel visit on 28 February 2006, when no active nests were recorded. Chewed common guava \((Psidium guajava)\) exocarps and rat scat near and in the feather piles lead us to believe that rats were the suspected predators. Also found in the piles were aluminum bands belonging to two swiftlets banded as adults and two swiftlets banded as nestlings in August and September 2005. The first active nest following the 2006 rat depredation event was observed on 4 May.

Another suspected rat depredation event likely delayed the onset of the 2007 breeding season (Figure 3.6). Seven adult swiftlets were found dead 41–53 m into the
tunnel on 28 January 2007. Five sets of wings, one feather pile, and the fresh remains of a swiftlet in a nest were distributed on and above the tunnel floor. Four aluminum bands belonging to adult swiftlets were found. This depredation event occurred sometime after the previous tunnel visit on 29 December 2006, when no active nests were noted. Nest monitoring did not occur in March 2007; however, back dating from the first nestling of the year and using the average incubation period (24 days), the 2007 breeding season began in approximately late March.

Nest monitoring was not conducted in January and February 2008; however, back dating from the first fledgling of the year and using the average nesting period (79 days), the 2008 breeding season began in approximately mid-February. Suspected rat depredation events in September 2009 essentially terminated that breeding season (Figure 3.6). These events occurred on 19, 20, and 27 September 2009, when at least 10 adult swiftlets were found dead and 17 nests failed (14 at the nestling stage and three at the egg stage) 33–54 m into the tunnel. During these depredation events, nine nests were knocked off the tunnel wall and two nestlings were displaced.

In 2010, active nests were recorded in every month, with a study-high of 71 observed in May (Figure 3.6). Active nests per month and year markedly increased from 2006 to 2010 (Figure 3.6), perhaps the result of rat trapping efforts inside and outside the North Halawa Valley tunnel. Between March 2006 and January 2011, 406 rats were captured in snap traps inside (18) and outside (388) the North Halawa Valley tunnel (this study).
3.5.4. Reproductive Success

The number of Mariana Swiftlets nesting inside the North Halawa Valley tunnel and their reproductive output gradually increased throughout the study period (Table 3.6 and Figure 3.7). Of the 84 active nest sites, 73 successfully fledged young between January 2006 and January 2011. Of the 478 eggs laid throughout the study period, 350 hatched young, and subsequently 300 successfully fledged.

Annual apparent hatching success remained relatively stable throughout the study period, with the highest recorded in 2006 and 2010 (Table 3.6 and Figure 3.8). Annual apparent fledging and apparent nest success were lowest in 2006 and 2009, and highest in 2007 and 2010.

The leading reasons for nest failure were egg in the water or mud, 52% (n = 92); missing egg or nestling, 13% (n = 24); nestling in the water or mud, 13% (n = 23); rat depredation, 10% (n = 17); and nest fell off the wall, 5% (n = 8) (Table 3.7).

We monitored 478 active Mariana Swiftlet nests with known outcomes during this study. Of this total, 50 had insufficient data for the nest survival analysis, resulting in a sample of 428 (35 [2006], 45 [2007], 98 [2008], 107 [2009], 143 [2010]) nests to estimate nest survival. We considered a total of 17 nest survival models in our analysis (Table 3.8). Our results suggest that the nest survival of Mariana Swiftlets was influenced by a quadratic effect of nest age and year (Table 3.8). The top model included a quadratic effect of nest age (Table 3.8). This model was 1.79 ΔAICc units better than the second-top model, which included year and a quadratic effect of nest age, and was ≥12.30 ΔAICc units better than all other models evaluated. Our top model indicated that the daily nest survival rate increased as a quadratic effect of nest age (β = 0.001 on a logit
scale, SE = 0.000, 95% CI was 0.000, 0.001), suggesting that nests were more likely to
survive at the beginning and end of the nesting period (Figure 3.9). In addition to a
quadratic effect of nest age, our second-top model suggested that year was also important
to the daily survival rate of swiftlet nests. For each year, there was a u-shaped
relationship between the daily nest survival rate and the age of the nest, with the daily
nest survival rate decreasing during the incubation period, and increasing during the
nestling period through fledging (Figure 3.9). Our data indicate that Mariana Swiftlet
nests were most vulnerable at the end of the incubation period each year (Figure 3.9).
The global model was found to be adequate and convincingly fit the data (goodness-of-fit
chi-square = 54.71, df = 2, $P < 0.001$).

Models that held the daily nest survival rate constant or included only linear
effects of nest age (with and without year), only year, nest site distance into the tunnel,
nest site height above the tunnel floor, daily precipitation, temporal variation within
seasons (linear and quadratic effects), mean number of active and baited rat traps/night
annually, and cumulative total number of rats captured received no support ($\Delta AIC_c \geq
12.30$; Table 3.8).

The daily survival rate of Mariana Swiftlet nests was lowest in 2006 ($\beta = 4.904$ on
a logit scale, SE = 0.217, 95% CI was 4.469, 5.338) and 2009 ($\beta = 4.853$ on a logit scale,
SE = 0.150, 95% CI was 4.553, 5.154), and highest in 2010 ($\beta = 5.441$ on a logit scale,
SE = 0.160, 95% CI was 5.122, 5.761) (Figure 3.10). There were no significant
differences in the daily nest survival rate between each of the years. Evidence of a
difference between the 2009 and 2010 daily nest survival rates was convincing, but
inconclusive (adjusted $P = 0.07$; Benjamini and Hochberg method). All other adjusted $P$-values were between 0.15 and 0.85.

The overall nest success rate (i.e., estimated nest success) for 2006–2010 was 63% for an average 79-day nesting period ($n = 428$ nests). Estimated nest success for each year was 56% (2006), 65% (2007), 69% (2008), 55% (2009), and 71% (2010). Apparent nest success for the same 428 nests included in the nest survival analysis was 49% (2006), 69% (2007), 65% (2008), 55% (2009), 71% (2010), and 64% (2006–2010).

### 3.6. DISCUSSION

Results from this study provide the first in-depth activity descriptions of the Mariana Swiftlet and evidence of the significance rat depredation can bring to an enclosed colony. Following birds throughout five annual cycles afforded insight into constant breeding activities and other important factors that would not have been predicted from shorter observation periods.

#### 3.6.1. Nests and Eggs

Mariana Swiftlet nest sizes on O‘ahu and the Marianas were similar. Average measurements for two nests on Guam (inner cup 47.5 mm in diameter, and outer cup dimensions 55 by 67.5 mm) were comparable to our O‘ahu nests (Drahos 1975). Nest height on Guam was rather variable with one at 51 mm and the other at 125 mm, while cup depth tapered from 0 mm at the cave wall to 10 mm at the front lip of the nest (Drahos 1975).

The variability in our external height measurements was likely an artifact of nest
materials being added to the rim at the onset of a new attempt. Our mean internal volume index resembled values recorded for the Australian Swiftlet (*A. terraereginae*) (25 cm³) and White-rumped Swiftlet (*A. spodiopygius*) in Samoa (23.2 cm³); nests of which are also known to contain one nestling (Tarburton 1988, 2009a).

Swiftlets inhabiting the Micronesian islands of Palau (Palau Swiftlet [*A. pelewensis*]), and Pohnpei and Kosrae (Island Swiftlet [*A. inquietus*]) build nests that also contain one nestling (Brandt 1966, Pratt and Etpison 2008). Our mean outer nest length was similar to the average of 11 Island Swiftlet nests on Kosrae (65 mm) (Brandt 1966). Nest cup dimensions of Palau Swiftlets (50 mm diameter), Island Swiftlets on Pohnpei (40 mm diameter, 10–15 mm depth), and Island Swiftlets on Kosrae (50 mm diameter, 12.5 mm depth, *n* = 11) (Brandt 1966) were within or slightly exceeded our ranges.

Mariana Swiftlet clutches on Saipan also contained a single white egg (*n* = 404) (Reichel et al. 2007). Our mean egg length, egg breadth, incubation period, and nestling period for 2006–2010 were within the ranges of those recorded on Saipan (mean egg length: 18.21 ± 0.55 mm [range = 17.0–19.7, *n* = 106]; mean egg breadth: 12.05 ± 0.40 mm [range = 10.3–13.0, *n* = 106]; mean incubation period: 22.95 days [range = 17–31, *n* = 22]; and mean nestling period: 47 days [range = 40–58, *n* = 28]) (Reichel et al. 2007).

Our egg measurements were comparable to the Island Swiftlet, which lays one egg on Pohnpei and Kosrae (Brandt 1966). On Pohnpei, mean egg length and breadth were 19.0 mm (range = 18.0–22.0, *n* = 17) and 12.9 mm (range = 11.0–13.5, *n* = 17), respectively; and on Kosrae, mean egg length and breadth were 19.1 mm (range = 18.0–20.0, *n* = 11) and 12.9 mm (range = 12.5–13.5, *n* = 11), respectively (Brandt 1966).

The mean incubation period of Mariana Swiftlets on O‘ahu was similar to other
*Aerodramus* swiftlets that lay one egg. Black-nest Swiftlets (*A. maximus*) in Sarawak, Singapore, and Vietnam incubated the egg for an average of 28 days (range = 21–39, $n = 19$), 25.5 ± 2.2 days ($n = 11$), and 29 days (range = 26–30, $n = 7$), respectively (Medway 1962a, Lee and Kang 1994, Nguyen Quang 1996). The Australian Swiftlet’s mean incubation period was 26.6 ± 0.23 (SE) days (range = 25–29, $n = 27$) (Tarburton 1988). Two single-egg clutches laid by the White-rumped Swiftlet in Samoa took 25 and 26 days (both ± 1 day) to hatch (Tarburton 2009a).

Our mean nestling period was comparable to other *Aerodramus* swiftlets that raise one chick. Mean age at fledging for Black-nest Swiftlets in Sarawak, Singapore, and Vietnam was 58.5 days (range = 41–77, $n = 10$), 45.9 ± 2.6 days ($n = 41$), and 53 days (range = 50–55), respectively (Medway 1962a, Lee and Kang 1994, Nguyen Quang 1996). During a normal wet season and a noticeably dry season, the Australian Swiftlet’s mean nestling periods were 46.1 ± 0.8 (SE) days ($n = 8$) and 51.0 ± 1.3 (SE) days ($n = 5$), respectively (Tarburton 1988). Two Mountain Swiftlet (*A. hirundinaceus*) nestlings in New Guinea were 67 and 74 days old upon fledging (Tarburton 2003). In Samoa, the mean age at fledging for White-rumped Swiftlets was 51.5 ± 4.8 days (range = 47–57, $n = 4$) (Tarburton 2009a).

Mariana Swiftlets on O‘ahu took less time to re-lay after fledging young than after the premature loss of an egg or nestling; swiftlets took longest to re-lay following the loss of a nestling. The average time for a Mariana Swiftlet on O‘ahu to re-lay after a fledged nest and a failed nest with an egg were similar to other *Aerodramus* swiftlets with a single-egg clutch. Australian Swiftlets re-laid a mean of 10.4 ± 0.4 (SE) days (range = 6–18 days, $n = 41$) after losing an egg (Tarburton 1988). Black-nest Swiftlets in Vietnam
re-laid about 3–7 days after a fledgling has left the nest (Nguyen Quang 1996). In Sarawak, Black-nest Swiftlets replaced 28% of lost clutches, 26% of lost broods, and 11% of fledglings (Medway 1962a). That Mariana Swiftlets re-lay an egg following a successful or unsuccessful nesting attempt suggests that adults remain attached to individual nest sites in the North Halawa Valley tunnel.

Eggs from successful nests were significantly longer and wider than those from unsuccessful nests. Since the length and breadth of bird eggs do not change during incubation (Hoyt 1979), reasons for this difference are unknown. Perhaps young, inexperienced birds, or females with a reduced nutritional condition, lay shorter and narrower eggs.

3.6.2. Daily Cycle
Our surveys showed that there are at least two primary pulses of Mariana Swiftlet activity during diurnal hours at the North Halawa Valley tunnel (Figure 3.4). These pulses are associated with 1) the emergence of volant individuals in the morning hours, presumably to forage on the wing all day if a non-breeder, and if a breeder, for feeding and food gathering forays if nestlings are present; and 2) the arrival of volant individuals in the evening hours, for nocturnal roosting inside the tunnel.

During morning emergence and evening arrival surveys, entering and exiting swiftlets, respectively, were tallied during all phases of the annual cycle; we do not discount that some of these sorties were associated with constructing nests and attending to eggs or nestlings (Tables 3.3 and 3.4). Swiftlets are known to only visit their roosting/nesting tunnels or caves during the daytime if they are breeding; otherwise, they
enter and exit during twilight (Tarburton 2003). Using a closed-circuit video system with infrared illuminators in the largest Mariana Swiftlet colony on Guam (Mahlac Cave) in 1996, observations of five pairs revealed that adults returned to their nests an average of 1.8 times/day to feed nestlings during diurnal hours (range = 1–4, SE = 0.14; Morton and Amidon 1996).

It is unknown what activities Mariana Swiftlets were engaged in outside the tunnel at night on O‘ahu. Foraging (for consumption and provisioning nestlings) and gathering nest materials for construction are possibilities (Table 3.5). Both entering and exiting swiftlets were recorded only on nights with a gibbous moon phase and when ≥82% of the visible disk was illuminated (U.S. Naval Observatory 2014). Since echolocation in Aerodramus swiftlets is believed to be strictly for navigation and not sensitive enough to detect insect prey (Medway 1959, 1962b, Fullard et al. 1993, Fullard et al. 2010), bright moonlight would have probably facilitated any foraging activities (Medway 1962b). Urban lighting appears to assist swiftlets with night foraging. Australian Swiftlets were observed feeding on insects near fluorescent lights about one hour following sunset (Tarburton 1987).

We cannot rule out that swiftlets returning to the North Halawa Valley tunnel after dark were younger individuals with underdeveloped echolocation abilities. Nevertheless, the observation of one Mariana Swiftlet returning to the tunnel on O‘ahu at 0402 hours is one of the latest arrival times recorded for a swiftlet. During that overnight survey, 82% of the moon’s visible disk was illuminated during a gibbous moon phase (U.S. Naval Observatory 2014). Medway (1962b) recorded Black-nest Swiftlets
returning to Niah Cave, Sarawak as late as 0400 hours. In Fiji, White-rumped Swiftlets returned to the roost as late as 2230 hours (Tarburton 1987).

3.6.3. Annual Cycle

Previous visits to the North Halawa Valley tunnel documented active Mariana Swiftlet nests in all months but February, May, September, and December (Wiles and Woodside 1999, Bishop Museum Sightings Database). Our study recorded active nests in every month of the year, with peak nesting activity occurring between about May and September, and decreasing from October to April (Figure 3.6); swiftlets on Saipan exhibited a similar cycle (Rice 1993). Active swiftlet nests have also been recorded in every month of the year on Guam (Wiles and Aguon 1997, 1998, 1999, Dicke et al. 2000). Peak nesting activity on O‘ahu may follow periods of high rainfall (Figure 3.11), which is presumably when insects are more readily available to support adults and nestlings during the nesting cycle.

3.6.4. Reproductive Success

For the 428 nests that were included in the nest survival analysis, it is not surprising that apparent nest success and estimated nest success for each year and all years were similar. Apparent nest success estimates are considered reasonably accurate if the assumption of high nest detectability (≥75%) is met (Johnson and Shafer 1990). Within the North Halawa Valley tunnel, we are confident that all active and inactive Mariana Swiftlet nests were found during our study; thus, detectability was 100%. If time and resources are
limited during future studies of the Mariana Swiftlet and other cave-nesting swiftlets, apparent nest success should be relatively accurate if nest detectability is high. Our study included one of the largest known sample sizes of active nests for a swiftlet species. Estimated nest success (63%) and apparent nest success (64%) for the 428 nests included in the nest survival analysis, as well as apparent nest success (63%) for all 478 nests rank among the highest recorded for *Aerodramus* swiftlets known to lay one egg. Only Black-nest Swiftlets in Vietnam (73%, *n* = 60 nests) (Lee and Kang 1994) and White-rumped Swiftlets in Samoa (72%, *n* = 18 nests) (Tarburton 2009a) had higher nest success than Mariana Swiftlets on O‘ahu. Mountain Swiftlets in New Guinea had 61% nest success (*n* = 56 nests) (Tarburton 2003). If we only include 2010, our nest success was nearly the highest known for a swiftlet species. Nest success may have been greatest in 2010 because of the highest mean number of active and baited rat traps/night (*n* = 33.7) and most number of rats captured (*n* = 114) that year. The Mariana Swiftlet’s capability to re-lay an egg following successful and unsuccessful nesting attempts, in conjunction with a year-round nesting season, may provide multiple opportunities to augment nest success throughout the year.

Model results suggest that factors related to a quadratic effect of nest age were most predictive of daily nest survival and it goes to reason that the older the nest, the greater chance it has for future success (Figure 3.9). The daily survival rate of Mariana Swiftlet nests on O‘ahu declined and was lowest during the incubation period each year (Figure 3.9). Of the 428 nests included in the nest survival analysis, 70% of all failures were during the egg stage/incubation period. Our data indicate that if a Mariana Swiftlet egg on O‘ahu successfully hatches, the probability of fledging increases. This is
supported by 86% apparent fledging success for all 478 nests throughout the five-year study (Table 3.6). Similarly high fledging success was documented in White-rumped Swiftlets in Samoa, with 86% and 87% recorded at two separate colonies (Tarburton 2009a).

Although models including the mean number of active and baited rat traps/night annually and cumulative total number of rats captured annually received no support, we feel that rats influenced Mariana Swiftlet colony success when the overall pattern of nesting and re-nesting are examined. Figure 3.6 shows the complete recycling of breeding in the colony following a rat depredation event (years 2006, 2007, 2009). When we examine our top models for factors related to nest failure, adding the factor year provides clarity to the results as year is directly related to the recycling of nests when a rat depredation event has occurred. We suspect that year was included in our second-top model because of a rat effect (i.e., year was a surrogate for rats). Rat trapping did not occur every day and the mean number of active and baited rat traps/night varied each year; thus, the number of rats captured was not representative of their abundance. If rat trapping efforts were carefully planned with an equal number of traps monitored every day, we believe the top models would have included rat traps and/or captured rats.

The 2006, 2007, and 2009 rat depredation events likely caused some disruption to the colony, but the swiftlets did not abandon the tunnel altogether. However, population expansion on O‘ahu may not be an option as swiftlets could be limited to the single colony in North Halawa Valley. There are presently no other known roosting/nesting tunnels or caves, and practically all swiftlet sightings since 1969 have been within approximately 5 km of the roosting/nesting tunnel, suggesting that suitable
roosting/nesting tunnels or caves may be a limiting factor preventing the Mariana Swiftlet population from expanding on O‘ahu (Wiles and Woodside 1999, Johnson et al., In review).

Without rat trapping, it is probable that reproductive activity and nest success would not have been as high during this study. Considering the 2006, 2007, and 2009 depredation events, rats may be a significant limiting factor precluding Mariana Swiftlet population growth on O‘ahu. However, their effect may be greater in adult survivorship than nest success. In Vietnam, Rice Rats (*Rattus tanezumi*) often enter caves and kill adult and nestling Edible-nest Swiftlets (*A. fuciphagus*); from 1991 to 1997, an estimated 4,000 swiftlets were killed by rats in the Khanh Hoa region, including two caves that lost their entire swiftlet populations (Nguyen Quang and Voisin 2001, Nguyen Quang et al. 2002). Rats are also known predators of White-rumped Swiftlet adults and nestlings in Samoa and Australian Swiftlet nestlings in Queensland (Tarburton 1988, Tarburton 2009a, 2009b).

3.6.4.1. Nest failures

Nestlings discovered in the water or mud in the North Halawa Valley tunnel were possibly the result of nestlings either 1) backing themselves over the front rim of the nest to defecate and losing grip of the nest, consequently falling into the water or mud, or onto the tunnel floor (see Medway 1962a, Lim and Cranbrook 2002); or 2) crawling from the nest and subsequently falling into the water or mud, or onto the tunnel floor. In any case, starvation or drowning was likely the outcome. Underfed swiftlet nestlings are known to become hypersensitive and restless, and eventually crawl out of the nest (Lim and
Cranbrook 2002). Falling out of the nest was a common cause of nestling mortality for the White-rumped Swiftlet in Fiji, Atiu Swiftlet (*A. sawtelli*) in the Cook Islands, and Australian Swiftlet (Tarburton 1986a, 1988, 1990). Nests probably fell from the tunnel wall when the wall became too wet and moisture saturated the nest material and salivary cement, weighting the nest down to the point where it lost its adhesive properties (see Medway 1962a, Lim and Cranbrook 2002). Rats were the only suspected predator that negatively affected active nests (in 2009). The seven human-caused failures were the result of broken or damaged eggs during measurements. Eggs and nestlings missing from the nest could have decomposed and sunk below the water’s surface and out of observation. We do not discount that depredation could have been the cause of the missing eggs and nestlings; however, unlike our observations following the suspected rat depredation events, there were no noticeable signs of a predator (e.g., footprints, scat, bones, feathers).

Eggs discovered in the water or mud, or on the North Halawa Valley tunnel floor may have been accidentally knocked out or deliberately kicked out of the nest by adults. Some form of disturbance may have resulted in eggs accidentally knocked out of the nest, especially if the egg was caught between the swiftlet’s feet (see Lim and Cranbrook 2002). While we do not dismiss that our presence may have caused some eggs to be accidentally knocked out of the nest, we are confident we were not the primary cause as we were particularly cautious entering and exiting the tunnel. In addition, many of the eggs found in the water or mud, or on the tunnel floor, had been there for some time (i.e., the egg was not knocked out upon our entry into the tunnel), suggesting some other form of disturbance. Dog tracks were commonly observed on the tunnel floor throughout the
study. Noise associated with a dog(s) entering and exiting the tunnel could disturb incubating swiftlets, ultimately resulting in eggs knocked out of the nest. Human tracks other than ours were also observed inside the tunnel. Without the cautious approach we took, these humans could have certainly caused swiftlets to accidentally knock out eggs. During overnight surveys, noises outside the tunnel (e.g., thunder, large rocks falling into the pool at the base of the waterfall) were audible inside the tunnel, but did not disrupt the swiftlets. Eggs could have also been accidentally knocked out of the nest when a changeover of incubation duties occurred or during disputes between birds at the nest (see Tarburton 1988).

Eggs are believed to be accidentally knocked out of the nest by Mariana Swiftlets in Mahlac Cave on Guam (Morton and Amidon 1996, Wiles and Aguon 1999). Wiles and Aguon (1999) thought some form of nighttime disturbance was the cause. Morton and Amidon (1996) postulated various reasons for eggs accidentally knocked out of the nest, including depredation or attempted nest depredation, explosions on the Navy’s nearby Ordnance Annex, research activity, antagonistic encounters among swiftlets, and aggressive exchanges between swiftlets and wasps (mud dauber wasps [Vespula sp.] are known to construct nests on swiftlet nests, weighting down the latter and causing it to fall to the cave floor).

Mariana Swiftlets on O‘ahu may have also deliberately kicked eggs out of the nest. If a nest became too saturated with moisture and indicated signs of falling from the tunnel wall, we cannot dismiss the potential for an aborted nesting attempt (i.e., an egg deliberately kicked out). On one occasion during this study, a nest containing an egg fell to the tunnel floor. It is unknown whether the egg was deliberately kicked out prior to the
nest falling. Morton and Amidon (1996) hypothesized that swiftlet eggs on Guam may be deliberately kicked out of the nest because of a deterioration in the female’s nutritional condition, possibly due to a decline in insect abundance. In Sarawak, eggs of the Black-nest Swiftlet, Mossy-nest Swiftlet (*A. salangana*), and Glossy Swiftlet (*Collocalia esculenta*) were believed to be deliberately kicked out after being in the nest substantially longer than the mean incubation period (Medway 1962a). Of the 92 eggs that were found in the water or mud, or on the tunnel floor on O‘ahu, ≥49 (≥53%) of these had surpassed the mean incubation period and thus may have been deliberately kicked out of the nest. It remains unclear whether eggs found in the water or mud, or on the tunnel floor were the result of infertility, a female’s reduced nutritional condition, changeover of incubation duties, disputes between birds at the nest, or some type of disturbance inside or outside the tunnel. Eggs accidentally knocked out or deliberately kicked out the nest may have been significant contributing factors to the lower daily nest survival rate observed during the incubation period each year on O‘ahu (Figure 3.9). Future studies that investigate reasons for eggs in the water or mud, or on the tunnel floor may lend insight into understanding this phenomenon better.

### 3.6.5. Conclusion

Understanding these facets of Mariana Swiftlet behavioral ecology and reproductive biology would not have been possible had we not studied the birds over the annual cycle and across five years. This longer view of Mariana Swiftlet biology further provides confidence in the annual repeatability of our results, which is not often attained in shorter studies.
During this study, we documented rats as a predator of Mariana Swiftlets on O‘ahu. It is important to recognize the relative influence that rats had on swiftlet colony success; however, their toll may be more in terms of adult survivorship. Our results point to the significance that even a few rats can bring to the decline of a swiftlet colony. Thus, the reintroduction program needs to address this factor in order to grow the populations in the Mariana Islands. Identifying the reasons for eggs in the water or mud, or on the tunnel floor will expand our knowledge of swiftlet reproductive biology and facilitate reintroduction efforts.

Current goals for downlisting the Mariana Swiftlet from endangered to threatened include establishing subpopulations of 2,000 birds on Guam; 2,000 birds on Rota; 1,000 birds on Aguiguan; and 2,000 birds on Saipan distributed among a minimum of five caves on each island except Rota (U.S. Fish and Wildlife Service 1991). Given these goals and the endangered status of the Mariana Swiftlet in the Mariana Islands, the O‘ahu population of swiftlets is of significant conservation importance and may be a useful population to test reintroduction techniques, learn more about Mariana Swiftlet natural history, and provide individuals for population enhancement in the Mariana Islands.

3.7. ACKNOWLEDGEMENTS

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and J. C. Hagar. We thank G. J. Wiles for insights on Mariana Swiftlets, E. A. VanderWerf for securing the necessary permits and field assistance on O‘ahu, and M. Waite for his detailed identification of Mariana Swiftlet nest materials. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.
3.8. Literature Cited


Guam Division of Aquatic and Wildlife Resources. 2006. Guam comprehensive wildlife conservation strategy. Division of Aquatic and Wildlife Resources, Department of Agriculture, Mangilao, Guam.


Figure 3.1. Mariana Swiftlet nest with egg inside the North Halawa Valley tunnel, O’ahu, Hawaiian Islands, June 2006. Photograph by NCJ.
Figure 3.2. Mean incubation, nestling, and nesting periods for Mariana Swiftlets in the North Halawa Valley tunnel, O‘ahu, Hawaiian Islands, by individual year, 2006–2010. Bars around the mean estimates represent the standard errors. Numbers above the standard error bars are sample sizes.
Figure 3.3. Mean time to re-lay after a fledged nest, failed nest with egg, and failed nest with nestling for Mariana Swiftlets in the North Halawa Valley tunnel, O‘ahu, Hawaiian Islands, combined years, 2006–2010. Bars around the mean estimates represent the standard errors. Numbers above the standard error bars are sample sizes.
Figure 3.4. Mean number of Mariana Swiftlets entering and exiting from the North Halawa Valley tunnel, O'ahu, Hawaiian Islands, during 12 morning emergence surveys in August–September 2005, March–July 2006, and October 2008; and 12 evening arrival surveys in August–September 2005, March–July 2006, and June 2010. During the October 2008 survey, individual times were not recorded for two entering swiftlets between 0554 hours and 0722 hours, and 13 exiting swiftlets between 0540 hours and 0722 hours; thus, these data are excluded from the figure. During a December 2009 evening arrival survey, individual times were not recorded for all entering and exiting swiftlets; thus, these data are excluded from the figure.
Figure 3.5. Number of Mariana Swiftlets entering and exiting from the North Halawa Valley tunnel, O'ahu, Hawaiian Islands, during eight overnight surveys, March–July 2006.
Figure 3.6. Number of active Mariana Swiftlet nests observed per month in the North Halawa Valley tunnel, O‘ahu, Hawaiian Islands, January 2006–January 2011. Active nest = nest with one egg or one nestling. An active nest can occupy more than one month. Nest monitoring was not completed in March 2007, and January and February 2008. Rat depredation events are demarcated with red dotted lines.
Figure 3.7. Mariana Swiftlet reproduction in the North Halawa Valley tunnel, O‘ahu, Hawaiian Islands, 2006–2010.
Figure 3.8. Apparent reproductive success for Mariana Swiftlets in the North Halawa Valley tunnel, O‘ahu, Hawaiian Islands, 2006–2010. 2006 (38 nests); 2007 (51 nests); 2008 (105 nests); 2009 (129 nests); 2010 (155 nests). Apparent hatching success = the proportion of eggs laid that hatched; apparent fledging success = the proportion of hatched nestlings that fledged; apparent nest success = the proportion of eggs that resulted in a fledged nestling.
Figure 3.9. Mariana Swiftlet daily nest survival rates in relation to a quadratic effect of nest age (number of days since the first egg was laid) in the North Halawa Valley tunnel, O'ahu, Hawaiian Islands, by individual year, 2006–2010. The mean incubation, nestling, and nesting periods are 24, 55, and 79 days, respectively. The dashed lines represent the 95% confidence limits.
Figure 3.10. Mariana Swiftlet daily nest survival rate (on a logit scale) in the North Halawa Valley tunnel, O‘ahu, Hawaiian Islands, by individual year, 2006–2010. Bars around the mean estimates represent the 95% confidence limits. DSR = daily survival rate.
Figure 3.11. Number of active Mariana Swiftlet nests observed per month in the North Halawa Valley tunnel and monthly rainfall, O‘ahu, Hawaiian Islands, January 2006–January 2011. Rainfall from the following gage on O‘ahu: USGS 212428157511201 771.11 North Halawa Valley at the Interstate H-3 Trans-Koolau Tunnel. Months and years with incomplete rainfall data include March (five days), May (16 days), and November (five days) 2006, and January 2007 (six days). Active nest = nest with one egg or one nestling. An active nest can occupy more than one month. Nest monitoring was not completed in March 2007, and January and February 2008.

<table>
<thead>
<tr>
<th></th>
<th>Mean</th>
<th>SD</th>
<th>Range</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Outer length (mm)</td>
<td>59.69</td>
<td>5.24</td>
<td>47.79–76.80</td>
<td>70</td>
</tr>
<tr>
<td>Outer width (mm)</td>
<td>64.40</td>
<td>4.64</td>
<td>53.83–76.25</td>
<td>70</td>
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<tr>
<td>External height (mm)</td>
<td>31.62</td>
<td>8.29</td>
<td>20.58–71.27</td>
<td>71</td>
</tr>
<tr>
<td>Front rim thickness (mm)</td>
<td>11.24</td>
<td>1.90</td>
<td>8.60–14.60</td>
<td>24</td>
</tr>
<tr>
<td>Cup length (mm)</td>
<td>40.38</td>
<td>4.32</td>
<td>31.64–49.00</td>
<td>45</td>
</tr>
<tr>
<td>Cup width (mm)</td>
<td>38.14</td>
<td>3.39</td>
<td>31.21–48.40</td>
<td>45</td>
</tr>
<tr>
<td>Cup depth (mm)</td>
<td>14.85</td>
<td>3.80</td>
<td>7.00–22.40</td>
<td>45</td>
</tr>
<tr>
<td>Internal volume index (cm³)</td>
<td>23.45</td>
<td>8.41</td>
<td>8.07–38.87</td>
<td>45</td>
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</table>
Table 3.2. Egg measurements for Mariana Swiftlets in the North Halawa Valley tunnel, O‘ahu, Hawaiian Islands, 2005–2010.

<table>
<thead>
<tr>
<th></th>
<th>Mean</th>
<th>SD</th>
<th>Range</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg length (mm)</td>
<td>18.67</td>
<td>0.72</td>
<td>16.30–20.50</td>
<td>452</td>
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<tr>
<td>Egg breadth (mm)</td>
<td>11.69</td>
<td>0.30</td>
<td>10.75–12.50</td>
<td>452</td>
</tr>
<tr>
<td>Egg volume (cm³)</td>
<td>1.30</td>
<td>0.09</td>
<td>1.00–1.56</td>
<td>452</td>
</tr>
<tr>
<td>Shape index (%)</td>
<td>62.67</td>
<td>2.44</td>
<td>55.72–71.30</td>
<td>452</td>
</tr>
</tbody>
</table>
Table 3.3. Number of Mariana Swiftlets entering and exiting from the North Halawa Valley tunnel, O’ahu, Hawaiian Islands, during 12 morning emergence surveys, August–September 2005, March–July 2006, and October 2008. Active nest = nest with one egg or one nestling.

<table>
<thead>
<tr>
<th>Survey date</th>
<th>Survey type</th>
<th>Number of entering swiftlets</th>
<th>Number of exiting swiftlets</th>
<th>Phase of annual cycle</th>
</tr>
</thead>
<tbody>
<tr>
<td>14 August 2005</td>
<td>Morning emergence</td>
<td>19</td>
<td>72</td>
<td>Active nests (14 eggs, 14 nestlings) and young fledgingª</td>
</tr>
<tr>
<td>28 August 2005</td>
<td>Morning emergence</td>
<td>18</td>
<td>114</td>
<td>Active nests (4 eggs, 16 nestlings), young fledgingª, and nest construction</td>
</tr>
<tr>
<td>11 September 2005</td>
<td>Morning emergence</td>
<td>22</td>
<td>109</td>
<td>Active nests (3 eggs, 16 nestlings), young fledgingª, and nest construction</td>
</tr>
<tr>
<td>18 March 2006</td>
<td>Morning emergence</td>
<td>15</td>
<td>14</td>
<td>No active nests</td>
</tr>
<tr>
<td>18 April 2006</td>
<td>Morning emergence</td>
<td>9</td>
<td>41</td>
<td>No active nests, nest construction</td>
</tr>
<tr>
<td>2 May 2006</td>
<td>Morning emergence</td>
<td>19</td>
<td>72</td>
<td>No active nests, nest construction</td>
</tr>
<tr>
<td>16 May 2006</td>
<td>Morning emergence</td>
<td>18</td>
<td>84</td>
<td>Active nests (5 eggs, 0 nestlings) and nest construction</td>
</tr>
<tr>
<td>8 June 2006</td>
<td>Morning emergence</td>
<td>12</td>
<td>69</td>
<td>Active nests (12 eggs, 2 nestlings) and nest construction</td>
</tr>
<tr>
<td>22 June 2006</td>
<td>Morning emergence</td>
<td>21</td>
<td>78</td>
<td>Active nests (15 eggs, 5 nestlings) and nest construction</td>
</tr>
<tr>
<td>6 July 2006</td>
<td>Morning emergence</td>
<td>31</td>
<td>90</td>
<td>Active nests (8 eggs, 12 nestlings) and nest construction</td>
</tr>
<tr>
<td>30 July 2006</td>
<td>Morning emergence</td>
<td>26</td>
<td>87</td>
<td>Active nests (5 eggs, 15 nestlings) and nest construction</td>
</tr>
<tr>
<td>12 October 2008</td>
<td>Morning emergence</td>
<td>8</td>
<td>116</td>
<td>Active nests (0 eggs, 15 nestlings), young fledgingª, and nest construction</td>
</tr>
</tbody>
</table>

ª Fledging refers to volant young leaving the nest site.
Table 3.4. Number of Mariana Swiftlets entering and exiting from the North Halawa Valley tunnel, O‘ahu, Hawaiian Islands, during 13 evening arrival surveys, August–September 2005, March–July 2006, December 2009, and June 2010. Active nest = nest with one egg or one nestling.

<table>
<thead>
<tr>
<th>Survey date</th>
<th>Survey type</th>
<th>Number of entering swiftlets</th>
<th>Number of exiting swiftlets</th>
<th>Phase of annual cycle</th>
</tr>
</thead>
<tbody>
<tr>
<td>13 August 2005</td>
<td>Evening arrival</td>
<td>123</td>
<td>24</td>
<td>Active nests (12 eggs, 16 nestlings) and young fledging&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>26 August 2005</td>
<td>Evening arrival</td>
<td>162</td>
<td>48</td>
<td>Active nests (7 eggs, 17 nestlings), young fledging&lt;sup&gt;a&lt;/sup&gt;, and nest construction</td>
</tr>
<tr>
<td>9 September 2005</td>
<td>Evening arrival</td>
<td>119</td>
<td>15</td>
<td>Active nests (3 eggs, 18 nestlings), young fledging&lt;sup&gt;a&lt;/sup&gt;, and nest construction</td>
</tr>
<tr>
<td>17 March 2006</td>
<td>Evening arrival</td>
<td>53</td>
<td>52</td>
<td>No active nests</td>
</tr>
<tr>
<td>17 April 2006</td>
<td>Evening arrival</td>
<td>99</td>
<td>40</td>
<td>No active nests, nest construction</td>
</tr>
<tr>
<td>1 May 2006</td>
<td>Evening arrival</td>
<td>67</td>
<td>8</td>
<td>No active nests, nest construction</td>
</tr>
<tr>
<td>15 May 2006</td>
<td>Evening arrival</td>
<td>85</td>
<td>8</td>
<td>Active nests (5 eggs, 0 nestlings) and nest construction</td>
</tr>
<tr>
<td>7 June 2006</td>
<td>Evening arrival</td>
<td>92</td>
<td>13</td>
<td>Active nests (10 eggs, 2 nestlings) and nest construction</td>
</tr>
<tr>
<td>21 June 2006</td>
<td>Evening arrival</td>
<td>117</td>
<td>48</td>
<td>Active nests (15 eggs, 5 nestlings) and nest construction</td>
</tr>
<tr>
<td>5 July 2006</td>
<td>Evening arrival</td>
<td>137</td>
<td>54</td>
<td>Active nests (9 eggs, 11 nestlings) and nest construction</td>
</tr>
<tr>
<td>29 July 2006</td>
<td>Evening arrival</td>
<td>148</td>
<td>63</td>
<td>Active nests (5 eggs, 15 nestlings) and nest construction</td>
</tr>
<tr>
<td>31 December 2009</td>
<td>Evening arrival</td>
<td>141</td>
<td>14</td>
<td>No active nests</td>
</tr>
<tr>
<td>11 June 2010</td>
<td>Evening arrival</td>
<td>181</td>
<td>41</td>
<td>Active nests (16 eggs, 38 nestlings) and nest construction</td>
</tr>
</tbody>
</table>

<sup>a</sup> Fledging refers to volant young leaving the nest site.
Table 3.5. Number of Mariana Swiftlets entering and exiting from the North Halawa Valley tunnel, O‘ahu, Hawaiian Islands, during eight overnight surveys, March–July 2006. Active nest = nest with one egg or one nestling.

<table>
<thead>
<tr>
<th>Survey date</th>
<th>Survey type</th>
<th>Number of entering swiftlets</th>
<th>Number of exiting swiftlets</th>
<th>Phase of annual cycle</th>
</tr>
</thead>
<tbody>
<tr>
<td>17–18 March 2006</td>
<td>Overnight</td>
<td>16</td>
<td>16</td>
<td>No active nests</td>
</tr>
<tr>
<td>17–18 April 2006</td>
<td>Overnight</td>
<td>27</td>
<td>40</td>
<td>Nest construction</td>
</tr>
<tr>
<td>1–2 May 2006</td>
<td>Overnight</td>
<td>7</td>
<td>0</td>
<td>Nest construction</td>
</tr>
<tr>
<td>15–16 May 2006</td>
<td>Overnight</td>
<td>4</td>
<td>5</td>
<td>Active nests (5 eggs, 0 nestlings) and nest construction</td>
</tr>
<tr>
<td>7–8 June 2006</td>
<td>Overnight</td>
<td>10</td>
<td>7</td>
<td>Active nests (10–12 eggs, 2 nestlings) and nest construction</td>
</tr>
<tr>
<td>21–22 June 2006</td>
<td>Overnight</td>
<td>1</td>
<td>0</td>
<td>Active nests (15 eggs, 5 nestlings) and nest construction</td>
</tr>
<tr>
<td>5–6 July 2006</td>
<td>Overnight</td>
<td>0</td>
<td>0</td>
<td>Active nests (8–9 eggs, 11–12 nestlings) and nest construction</td>
</tr>
<tr>
<td>29–30 July 2006</td>
<td>Overnight</td>
<td>0</td>
<td>0</td>
<td>Active nests (5 eggs, 15 nestlings) and nest construction</td>
</tr>
</tbody>
</table>
Table 3.6. Reproductive activity and apparent reproductive success for Mariana Swiftlets in the North Halawa Valley tunnel, O‘ahu, Hawaiian Islands, 2006–2010. (Proportions ± SE). Apparent nest success = proportion of eggs that resulted in a fledged nestling. Active nest site = nest site that produced at least one egg.

<table>
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<tr>
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<th></th>
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<tbody>
<tr>
<td><strong>Eggs laid</strong></td>
<td>38</td>
<td>51</td>
<td>105</td>
<td>129</td>
<td>155</td>
<td>478</td>
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<tr>
<td><strong>Eggs hatched</strong></td>
<td>29</td>
<td>37</td>
<td>76</td>
<td>91</td>
<td>117</td>
<td>350</td>
</tr>
<tr>
<td></td>
<td>(0.76 ± 0.07)</td>
<td>(0.73 ± 0.06)</td>
<td>(0.72 ± 0.04)</td>
<td>(0.71 ± 0.04)</td>
<td>(0.76 ± 0.04)</td>
<td>(0.73 ± 0.02)</td>
</tr>
<tr>
<td><strong>Nestlings fledged</strong></td>
<td>19</td>
<td>34</td>
<td>66</td>
<td>72</td>
<td>109</td>
<td>300</td>
</tr>
<tr>
<td></td>
<td>(0.66 ± 0.09)</td>
<td>(0.92 ± 0.05)</td>
<td>(0.87 ± 0.04)</td>
<td>(0.79 ± 0.04)</td>
<td>(0.93 ± 0.02)</td>
<td>(0.86 ± 0.02)</td>
</tr>
<tr>
<td><strong>Apparent nest success</strong></td>
<td>0.50 ± 0.08</td>
<td>0.67 ± 0.07</td>
<td>0.63 ± 0.05</td>
<td>0.56 ± 0.04</td>
<td>0.70 ± 0.04</td>
<td>0.63 ± 0.02</td>
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<tr>
<td><strong>Active nest sites</strong></td>
<td>23</td>
<td>25</td>
<td>39</td>
<td>57</td>
<td>67</td>
<td>84</td>
</tr>
<tr>
<td><strong>Active nest sites that fledged young</strong></td>
<td>17</td>
<td>23</td>
<td>32</td>
<td>48</td>
<td>61</td>
<td>73</td>
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<table>
<thead>
<tr>
<th>Failure Type</th>
<th>Number</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg in water or mud</td>
<td>92</td>
<td>52</td>
</tr>
<tr>
<td>Missing – egg</td>
<td>22</td>
<td>12</td>
</tr>
<tr>
<td>Missing – nestling</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Nestling in water or mud</td>
<td>23</td>
<td>13</td>
</tr>
<tr>
<td>Rat depredation – egg</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Rat depredation – nestling</td>
<td>14</td>
<td>8</td>
</tr>
<tr>
<td>Nest fell off wall – egg</td>
<td>1</td>
<td>&lt;1</td>
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<tr>
<td>Nest fell off wall – nestling</td>
<td>7</td>
<td>4</td>
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<tr>
<td>Human</td>
<td>7</td>
<td>4</td>
</tr>
<tr>
<td>Nestling dead in or on nest</td>
<td>4</td>
<td>2</td>
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<tr>
<td>Egg infertile</td>
<td>3</td>
<td>2</td>
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<tr>
<td><strong>Total</strong></td>
<td>178</td>
<td>100</td>
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Table 3.8. Summary of model selection results for the nest survival of Mariana Swiftlets in the North Halawa Valley tunnel, O‘ahu, Hawaiian Islands, 2006–2010. Daily survival rate maximum likelihood estimation using Program R, following methods described in Rotella et al. (2004). int = intercept; nage (linear effect of nest age) = number of days since the first egg was laid; nage2 (quadratic effect of nest age); year = breeding season; meantrap = mean number of active and baited rat traps/night annually; precip = daily precipitation; sdate (linear effect of season) = temporal variation within seasons; sdate2 (quadratic effect of season); dist = nest site distance into the tunnel; annrats = cumulative total number of rats captured annually; height = nest site height above the tunnel floor.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameters</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AICc weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>int+nage+nage2</td>
<td>3</td>
<td>1697.95</td>
<td>0.00</td>
<td>0.707</td>
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<tr>
<td>int+year+nage+nage2</td>
<td>8</td>
<td>1699.74</td>
<td>1.79</td>
<td>0.290</td>
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<td>int+nage</td>
<td>2</td>
<td>1710.25</td>
<td>12.30</td>
<td>0.002</td>
</tr>
<tr>
<td>int+year+nage</td>
<td>7</td>
<td>1710.41</td>
<td>12.46</td>
<td>0.001</td>
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<tr>
<td>int+meantrap</td>
<td>2</td>
<td>1739.44</td>
<td>41.49</td>
<td>0.000</td>
</tr>
<tr>
<td>int+year+precip</td>
<td>7</td>
<td>1739.82</td>
<td>41.87</td>
<td>0.000</td>
</tr>
<tr>
<td>int+year+sdate</td>
<td>7</td>
<td>1739.83</td>
<td>41.88</td>
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</tr>
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<td>int+sdate</td>
<td>2</td>
<td>1739.90</td>
<td>41.95</td>
<td>0.000</td>
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<tr>
<td>int+precip</td>
<td>2</td>
<td>1740.23</td>
<td>42.27</td>
<td>0.000</td>
</tr>
<tr>
<td>int+dist+meantrap</td>
<td>3</td>
<td>1740.76</td>
<td>42.81</td>
<td>0.000</td>
</tr>
<tr>
<td>int+year</td>
<td>6</td>
<td>1741.18</td>
<td>43.23</td>
<td>0.000</td>
</tr>
<tr>
<td>int+annrats</td>
<td>2</td>
<td>1741.70</td>
<td>43.75</td>
<td>0.000</td>
</tr>
<tr>
<td>int</td>
<td>1</td>
<td>1742.44</td>
<td>44.49</td>
<td>0.000</td>
</tr>
<tr>
<td>int+dist</td>
<td>2</td>
<td>1743.95</td>
<td>46.00</td>
<td>0.000</td>
</tr>
<tr>
<td>int+height</td>
<td>2</td>
<td>1744.43</td>
<td>46.48</td>
<td>0.000</td>
</tr>
</tbody>
</table>

-continued-
Table 3.8. Continued. Summary of model selection results for the nest survival of Mariana Swiftlets in the North Halawa Valley tunnel, O‘ahu, Hawaiian Islands, 2006–2010. Daily survival rate maximum likelihood estimation using Program R, following methods described in Rotella et al. (2004). \( int = \) intercept; \( nage \) (linear effect of nest age) = number of days since the first egg was laid; \( nage2 \) (quadratic effect of nest age); \( year \) = breeding season; \( meantrap \) = mean number of active and baited rat traps/night annually; \( precip \) = daily precipitation; \( sdate \) (linear effect of season) = temporal variation within seasons; \( sdate2 \) (quadratic effect of season); \( dist \) = nest site distance into the tunnel; \( annrats \) = cumulative total number of rats captured annually; \( height \) = nest site height above the tunnel floor.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameters</th>
<th>( AIC_c )</th>
<th>( \Delta AIC_c )</th>
<th>( AIC_c ) weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>( int+sdate+sdate2 )</td>
<td>3</td>
<td>1745.23</td>
<td>47.28</td>
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<td>( int+dist+height )</td>
<td>3</td>
<td>1745.94</td>
<td>47.99</td>
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4. CONCLUSIONS

This thesis investigates survey methods, behavioral ecology, and reproductive biology of the O‘ahu surrogate population of Mariana Swiftlets (*Aerodramus bartschi*) in an attempt to better understand the indigenous population in the Mariana Islands. I began with an evaluation of current and historic Mariana Swiftlet abundance and distribution. Using existing literature, correspondence from relevant biologists, and population surveys on O‘ahu, this study estimated the entire Mariana Swiftlet population to be currently comprised of 6,674 individuals occurring in eight caves on Saipan \( (n = 4,674) \), six caves on Aguiguan \( (n = 267) \), three caves on Guam \( (n = 1,591) \), and one tunnel on O‘ahu \( (n = 142) \) (Esselstyn et al. 2003; K. M. Brindock, pers. comm.; P. M. Radley, pers. comm.; this study). Population surveys on O‘ahu revealed that night vision technology was effective in detecting and counting the number of entering and exiting swiftlets. An assessment of survey methods used for Mariana Swiftlets suggests changes are needed to more accurately reflect their distribution and abundance. Until alternative methods are developed, refined, and fully operational, I suggest the most accurate means of assessing the swiftlet population in the Mariana Islands will be via evening arrival surveys using night vision technology and active nest counts. Incorporating night vision technology into evening arrival surveys on Saipan, Aguiguan, and Guam should improve population estimates.

In chapter three, I examined the behavioral ecology and reproductive biology of the Mariana Swiftlet on O‘ahu at multiple temporal scales over five annual cycles. I found that peak entering and exiting activity occurred during crepuscular hours during
tunnel emergence and arrival surveys. Overnight surveys documented entering and exiting swiftlets at all hours of the night. Nest monitoring revealed active nests in every month of the year, with peak nesting activity occurring between about May and September, and decreasing from October to April. Nesting biology of swiftlets on Oʻahu was similar to their Marianas counterparts, with a clutch of one egg, and mean incubation and nestling periods of $23.91 \pm 3.30$ days (range = 18–30) and $55.04 \pm 6.61$ days (range = 41–84), respectively. Nest survival modeling suggested that the daily survival rate of nests was influenced by a quadratic effect of nest age and year. I estimated nest success of swiftlets on Oʻahu to be 63%, ranking among the highest recorded for *Aerodramus* swiftlets known to lay one egg. Eggs found in the water or mud, or on the tunnel floor accounted for 52% of nest failures. Future studies that investigate and identify the reasons for this will expand our knowledge of swiftlet reproductive biology and facilitate reintroduction efforts. Rat depredation was considered an important cause of nest failure that often resulted in simultaneous loss of most nests. Mariana Swiftlets on Oʻahu completely recycled breeding activities following rat depredation events. It is important to recognize the relative influence that rats had on swiftlet colony success; however, their toll may be more in terms of adult survivorship. My results point to the significance that even a few rats can bring to the decline of a swiftlet colony. Thus, the reintroduction program needs to address this factor in order to grow the populations in the Mariana Islands. Results of this study illustrate the significant conservation importance of the Oʻahu surrogate population of swiftlets: they may be useful to test reintroduction techniques, learn more about Mariana Swiftlet natural history, and provide individuals for population enhancement in the Mariana Islands.
Collectively, results of this study should provide the U.S. Fish and Wildlife Service, Commonwealth of the Northern Mariana Islands Division of Fish and Wildlife, and Guam Division of Aquatic and Wildlife Resources with the relevant information for addressing recovery criteria, and continued conservation efforts for Mariana Swiftlets, including designing and implementing the proposed reintroductions of swiftlets from Saipan and southern Guam to their former ranges of Rota and northern Guam, respectively (Berger et al. 2005, Guam Division of Aquatic and Wildlife Resources 2006; U.S. Fish and Wildlife Service 2009, 2010).
4.1. Literature Cited


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