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ABSTRACT.　Mariana Swiftlets (*Aerodramus bartschi*) are federally listed as endangered, with populations currently limited to just three islands in the Mariana Islands plus an introduced population on the Hawaiian island of O'ahu. Before efforts are made to reintroduce Mariana Swiftlets to other islands in the Mariana archipelago, additional information is needed concerning their breeding biology. Therefore, our objective was to examine the reproductive biology of Mariana Swiftlets over five annual cycles on the Hawaiian island of O'ahu. This introduced population used a human-made tunnel for roosting and nesting, and was studied as a surrogate to negate interference with endangered populations in the Mariana Islands. Active nests ($N = 478$) were observed in every month of the year, with peak nesting activity between May and September. All clutches consisted of one egg. Mean duration of incubation and nestling periods were 23.9 d (range = 18–30 d, $N = 233$) and 55.0 d (range = 41–84 d, $N = 228$), respectively. Estimated nest success was 63%. Over half (52%) of nest failures were attributed to eggs found on the tunnel floor. Predation by rats (*Rattus* spp.) was also an important cause of nest failure and often resulted in the loss of most active nests. However, Mariana Swiftlets did re-nest after these predation events. Our results suggest that rat predation of both nests and adults may limit growth of the Mariana Swiftlet population on O'ahu, and could also affect the chances for successful establishment of relocated populations in the Mariana Islands. Another limiting factor on O'ahu is that only one nesting site is apparently available on the island. Current goals for downlisting Mariana Swiftlets from endangered to threatened include establishing populations on Guam, Rota, Aguiguan, and Saipan. To meet these goals, the population of Mariana Swiftlets on O'ahu can be important for testing reintroduction techniques, learning more about the natural history of these swiftlets, and providing individuals for reintroduction efforts in the Mariana Islands.

RESUMEN.　**Éxito reproductivo de *Aerodramus bartschi* en la isla de O'ahu en Hawaii**
Aerodramus bartschi está incluida en la lista federal de especies en peligro de extinción, con poblaciones actualmente limitadas a solo tres islas en las Islas Marianas más una población introducida en la isla hawaiana de O'ahu. Previo a esfuerzos para reintroducir *A. bartschi* en otras islas del archipiélago de las Marianas, se necesita información adicional sobre su biología reproductiva. Por lo tanto, nuestro objetivo fue examinar la biología reproductiva de *A. bartschi* durante cinco ciclos anuales en la isla hawaiana de O'ahu. Esta población introducida utilizó un túnel hecho por el hombre para posarse y anidar, y se estudió como un sustituto para negar la interferencia con poblaciones en peligro en las Islas Marianas. Se observaron nidos activos ($N = 478$) en todos los meses del año, con un pico de actividad de anidación entre mayo y septiembre. Todas las nidadas consistieron de un solo huevo. La duración promedio de los períodos de incubación y de polluelos fue de 23.9 días (rango = 18–30 días, $N = 233$) y 55.0 días (rango = 41–84 días, $N = 228$), respectivamente. El éxito estimado del nido fue del 63%. Las causas de más de la mitad (52%) de los nidos no exitosos fueron atribuidas a los huevos encontrados en el piso del túnel. La depredación por ratas (*Rattus* spp.), también fue una causa importante de mortalidad del nido y, a menudo, resultó en la pérdida de la mayoría de los nidos activos. Sin embargo, *A. bartschi* volvió a anidar después de estos eventos de depredación. Nuestros resultados sugieren que la depredación de ratas tanto de nidos como de adultos puede limitar el crecimiento de la población de *A. bartschi* en O'ahu, y también podría afectar las posibilidades de establecer con éxito poblaciones reubicadas en las Islas Marianas. Otro factor limitante en O'ahu es que solo un sitio de anidación está aparentemente disponible en la isla. Los objetivos actuales para bajar la categoría de *A. bartschi* de amenazada a en peligro, incluyen establecer poblaciones en Guam, Rota, Aguiguan y Saipan. Para alcanzar estos objetivos, la población de *A. bartschi* en O'ahu puede ser importante para probar técnicas de reintroducción, aprender más sobre la historia natural de estos vencejos y proporcionar los individuos para los esfuerzos de reintroducción en las Islas Marianas.

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The swiftlet genus *Aerodramus* consists of 28 species 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 (Gill and Donsker 2017). Known locally as "Yayaguak" (Guam) and "Chachaguak" (Commonwealth of the Northern Mariana Islands [CNMI]), Mariana Swiftlets (*Aerodramus bartschi*) were historically found on the Mariana Islands of Saipan, Tinian, Aguiguan, Rota, and Guam (Chantler and Driessens 2000). In the Marianas, the species is currently found only on Saipan, Aguiguan, and Guam (Cruz et al. 2008, Johnson 2015). In addition, an introduced population of Mariana Swiftlets has persisted on the Hawaiian island of O'ahu since 1962 (Wiles and Woodside 1999, Chantler and Driessens 2000, Johnson 2015).

With fewer than 6500 individuals remaining in the wild, Mariana Swiftlets are one of nine bird species federally listed as endangered in the Mariana Islands (U.S. Fish and Wildlife Service 2011). The swiftlets were listed as federally endangered throughout the Mariana archipelago in 1984 (U.S. Fish and Wildlife Service 1984) and as threatened/endangered by the CNMI government in 1991 (CNMI Public Law 2–51; Commonwealth Register Volume 13, Number 1). The U.S. Fish and Wildlife Service (USFWS) listed Mariana Swiftlets as endangered based on observed declines of swiftlet populations on Guam, Rota, and possibly Saipan (U.S. Fish and Wildlife Service 1991). Factors possibly contributing to these declines include (1) disturbance of caves by humans, (2) predation by brown treesnakes (*Boiga irregularis*), (3) pesticides, and (4) disease (U.S. Fish and Wildlife Service 1991).

Plans have been made to reintroduce Mariana Swiftlets to Rota and northern Guam from Saipan and southern Guam, respectively, provided supporting studies (e.g., life history assessment) are completed (Guam Division of Aquatic and Wildlife Resources 2006, Liske-Clark 2015). Reintroduction is considered possible because of the successful introduction of Mariana Swiftlets on O'ahu

in 1962 and 1965, when 175 and 210 Mariana Swiftlets, respectively, captured on Guam were released on O'ahu (Wiles and Woodside 1999). The introductions were for esthetic purposes and apparently to augment insect control (Woodside 1970). Fewer than 150 Mariana Swiftlets currently persist on O'ahu (Johnson 2015).

Studies of *Aerodramus* swiftlets have focused primarily on their breeding biology, behavioral ecology, population status, and diet (Medway 1962a,b, Tarburton 1986a,b, 1987, 1988, 1990, 2003, 2009a, Fullard et al. 1993, 2010, Nguyen Quang 1996). However, most of these studies were not conducted over full or multiple annual cycles. In addition, the few quantitative studies of Mariana Swiftlets have focused on their abundance and distribution, growth and development, and diet (Reichel et al. 2007, Cruz et al. 2008, Valdez et al. 2011). Thus, little is known about the full life cycle biology of this species. Therefore, our objective was to examine the reproductive biology of Mariana Swiftlets over five annual cycles. We studied the introduced population on O'ahu as a surrogate, thus avoiding any interference with indigenous populations in the Mariana Islands. When studying sensitive species, a surrogate population may provide an alternative for obtaining critical natural history and population biology information, ultimately assisting in recovery and conservation endeavors (Kesler and Haig 2007).

Rota, one of the proposed reintroduction locations for Mariana Swiftlets, is currently free of brown treesnakes, but introduced rats (*Rattus* spp.) and feral cats (*Felis catus*) are suspected or known predators of eggs, nestlings, and adults of endangered birds on the island (U.S. Fish and Wildlife Service 2007, Berry and Taisacan 2008, Zarones et al. 2015). Therefore, understanding the responses of swiftlets to potential predation by these invasive species is important when planning translocations. Consequently, we were interested in the effect that predators, such as rats, might have on Mariana Swiftlets on O'ahu, and hypothesized that rats in an enclosed tunnel could have significant effects on the reproductive output of the colony.

METHODS

O'ahu (21° 22'N, 157°55'W), the third largest Hawaiian island (1624 km^2), includes the Ko'olau and Wai'anae mountain ranges and a broad valley in between. Our study was conducted from January 2006 to January 2011 in and around a human-made tunnel that Mariana Swiftlets used for roosting and nesting on O'ahu. The tunnel was likely excavated prior to World War II as a possible water source for irrigation (Wiles and Woodside 1999) and is located near the base of a steep, seasonal waterfall in North Halawa Valley. The tunnel has one entrance (1.8 m high by 1.3 m wide) and is ~55 m long, averaging 1.7 ± 0.2 (SD) m high (range = 1.3–2.1 m, N = 12 measurements) and 1.3 ± 0.2 m wide (range = 0.9–1.6 m, N = 12 measurements). Tunnel width is relatively constant, but height steadily decreases after ~15 m. At an elevation of 424 m, the tunnel is located in the montane rain forest climatic vegetation zone (Mueller-Dombois and Fosberg 1998). The tunnel is wet throughout the year, with pools of water ~3–15 cm deep on the floor. Water constantly drips from the ceiling throughout the tunnel, but is more noticeable in the first 25 m, especially after heavy rains.

Nest monitoring. We monitored active nests every 8.4 ± 5.3 (SD) d (range = 1–41 d). With the exception of March 2007 and January and February 2008, our average nest visitation schedule was every 4.0 ± 2.9 d (range = 1–14 d) in 2006, 11.1 ± 8.6 d (range = 5–41 d) in 2007, 7.2 ± 1.8 d (range = 3–14 d) in 2008, 8.6 ± 5.7 d (range = 1–37 d) in 2009, 7.3 ± 2.1 d (range = 1–17 d) in 2010, and 29 d (only one check) in January 2011. Active nests were defined as those with either one egg or one nestling. A nest site was characterized by the presence of a nest or nest material on the tunnel wall.

To locate nests and determine nest status, we surveyed the tunnel walls, ceiling, and chambers using second generation night vision goggles (LOMO PVS-7 Recon II; LOMO America, Inc., Northbrook, IL), a headlamp with a red filter, or a camcorder (Sony Handycam DCR-HC21 with Night-Shot Plus Infrared System; Sony Corp., Tokyo, Japan). 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 and unused, (4) building – nest materials being added to the nest site, (5) fledged – nestling was assumed to have successfully fledged if it was no longer in the nest and not observed dead on the tunnel floor, and (6) failed.

Nest sites were identified by placing ~2.54-cm^2 uniquely numbered reflective tape tags on the tunnel wall. Because the tunnel was straight and narrow with low clearance, we are confident that all active nests were found. We assumed that one pair of swiftlets was associated with each active nest site during each nesting attempt.

Reproductive success. 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. Because female Mariana Swiftlets only lay one egg, apparent nest success is equal to the proportion of successful nests. Transition dates (i.e., egg laying, hatching, fledging, and failure) were either directly observed or estimated by back-dating from known events during the nesting period, assuming an incubation period of 24 d and a nestling period of 55 d (79-d total nesting period; Johnson 2015). When no other data were available, we assumed that any change in status (i.e., egg laying, hatching, fledging, or failure) transpired halfway between nest-monitoring visits (Mayfield 1975). The durations of the incubation period, nestling period, nesting period, time to re-lay after young fledged, time to re-lay after a nest with an egg failed, and time to re-lay after a nest with a nestling failed were calculated using the estimated laying, hatching, fledging, and failure dates, and only when nest-monitoring visits occurred at one to 10-d intervals.

Rat trapping. Three species of rats occur on O'ahu, including black rats (*Rattus rattus*), Norway rats (*Rattus norvegicus*), and Polynesian rats (*Rattus exulans*) (VanderWerf 2009). We carried out rat trapping inside and outside the North Halawa Valley tunnel from March 2006 to January 2011. However, rat traps were not checked or rebaited in March 2007 and January and February 2008.

Using five types of snap traps (Ka Mate Medium Trap; Ka Mate Traps Ltd, Nelson,

Table 1. Candidate models describing daily nest survival (DNS) of Mariana Swiftlets in the North Halawa Valley tunnel, O'ahu, Hawaiian Islands, 2006–2010.

Model	K	Description
int	1	DNS constant
int + precip	2	DNS varies with daily precipitation
int + height	2	DNS varies with nest height
int + dist	2	DNS varies with tunnel depth
int + annrats	2	DNS varies with annual rat trapping
int + meantrap	2	DNS varies with rat trapping effort
int + sdate	2	DNS varies with Julian date (linear)
int + nage	2	DNS varies with nest age (linear)
int + dist + height	3	DNS varies with tunnel depth and nest height
int + dist + meantrap	3	DNS varies with tunnel depth and rat trapping effort
int + sdate + sdate²	3	DNS varies with Julian date (quadratic)
int + nage + nage²	3	DNS varies with nest age (quadratic)
int + year	6	DNS varies with year
int + year + precip	7	DNS varies with year and daily precipitation
int + year + sdate	7	DNS varies with year and Julian date (linear)
int + year + nage	7	DNS varies with year and nest age (linear)
int + year + nage + nage²	8	DNS varies with year and nest age (quadratic)

New Zealand; Tomcat Wooden Rat Trap; Scotts Company, Marysville, OH; Trapper T-Rex Rat Trap; Bell Laboratories, Madison, WI; Victor Metal Pedal Rat Trap and Victor Easy Set Rat Trap; Woodstream Corp., Lititz, PA), 43 traps were placed inside ($N = 5$) and outside ($N = 38$) the tunnel. Traps outside the tunnel were placed within 30 m ($N = 28$), 31–60 m ($N = 7$), and 61–70 m ($N = 3$) of the entrance. Traps were baited with peanut butter, macadamia nuts, scented wax (peanut butter, coconut, or grape), or sponges with essential oils (passion fruit or coconut) and placed on the tunnel floor, or secured to horizontal tree trunks/branches or on 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, but were positioned so that any approaching rat would encounter the traps. We logged 252 trap-check visits during which traps were checked for captures and reset/rebaited if necessary.

Nest survival analysis. We modeled daily nest survival following methods described in Rotella et al. (2004). We ranked 17 a priori candidate models (Table 1) using model selection and small-sample corrected AIC (AICc) comprised of nest age (linear and quadratic) and year. Nest age was the number of days since the first egg was laid and year

was the annual breeding season. In addition to nest age and season day (ordinal day), candidate models also incorporated nest site distance into tunnel, nest site height above tunnel floor, daily precipitation, mean number of active rat traps/night per year, and the cumulative total number of rats captured/ year. A successful nest was defined as one that fledged a nestling. An unsuccessful nest was one that had an egg, but failed to fledge a nestling. We considered candidate models with the lowest AICc or those within two ΔAICc units of the top-ranked model as those that best explained daily nest survival (Burnham and Anderson 2002). Prior to model ranking, we used a likelihood ratio test to assess goodness-of-fit of the global, or most parameterized, model. In addition to model ranking, we calculated apparent nest success (nest success = survival from laying to fledging) from the intercept-only model to facilitate comparison with published nest success values (i.e., Mayfield estimates). These estimates were derived for each year as the daily nest survival probability to the 79th power. We used the delta method to calculate standard errors for estimated model parameters (Powell 2007) and adjusted P values associated for multiple comparisons as appropriate (Benjamini and Hochberg 1995). We used R statistical software ver. 2.11.1 (R Development
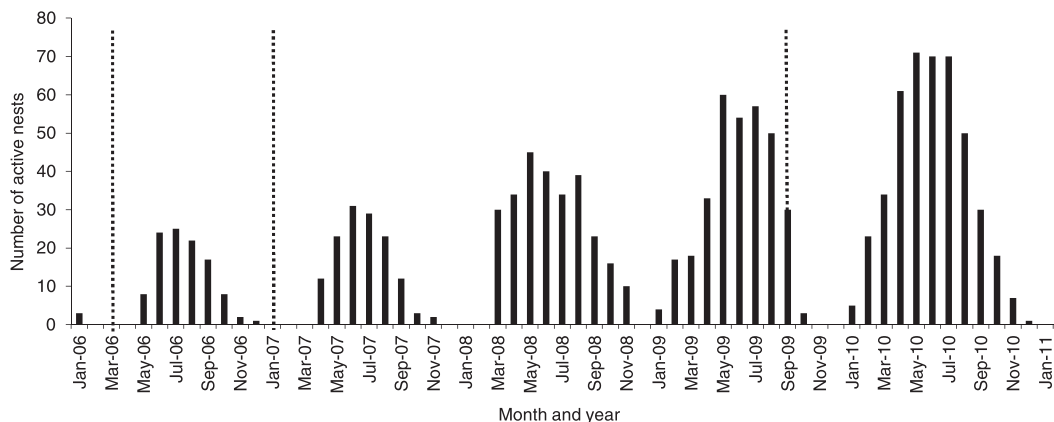
Fig. 1. Active Mariana Swiftlet nests observed per month in the North Halawa Valley tunnel, O'ahu, Hawaiian Islands, January 2006–January 2011. An active nest was a nest with one egg or one nestling. An active nest can occupy more than 1 mo. Nests were not monitored in March 2007 and January and February 2008. Rat predation events are indicated by dotted lines.

Core Team 2005), and values are presented as means ± 1 SD.

RESULTS

Annual cycle. Mariana Swiftlets on O'ahu exhibited a cyclical breeding pattern that extended across every month of the year (Fig. 1). Peak breeding activity was observed in July 2006, June 2007, and May 2008–2010. Predation by rats may have delayed the beginning of the 2006 breeding season (Fig. 1). Eighteen piles of swiftlet feathers were discovered in the tunnel on 6 March 2006. Chewed common guava (*Psidium guajava*) exocarps and rat scat near and in the feather piles confirmed that rats were the predators. The first active nest following rat predation was found on 4 May 2006.

Rat predation also likely delayed the onset of the 2007 breeding season (Fig. 1), with seven adult swiftlets found dead in the tunnel on 28 January 2007. Nests were not monitored in March 2007, but, based on back-dating from the first nestling of the year and using the average incubation period (24 d), the 2007 breeding season likely began in late March.

Nests were not monitored in January and February 2008, but back-dating from the first fledgling of the year and using the duration of the average nesting period (79 d), the 2008 breeding season likely began in mid-February. Rat predation in September 2009

essentially ended that breeding season (Fig. 1), with at least 10 adult swiftlets found dead and 17 nests failing (14 at the nestling stage and three at the egg stage). In addition, nine nests were found on the tunnel floor, and two nestlings were displaced and found roosting on the tunnel wall. In 2010, active swiftlet nests were recorded in every month, with a high of 71 in May (Fig. 1). Active nests per month and year markedly increased from 2006 to 2010 (Fig. 1).

Rat trapping. Overall, 18 rats were captured in snap traps inside the tunnel and 388 outside the tunnel. Of these, 89 were black rats and one was a Polynesian rat; the rest could not be identified to species due to the condition of partial remains left by scavengers.

Reproductive success. We monitored 478 active Mariana Swiftlet nests with known outcomes during our study (Table 2), with the number of nests and their reproductive output gradually increasing throughout the study period (Table 2). Of 84 active nest sites, young fledged from 73 between January 2006 and January 2011. Of the 478 eggs laid during our study, 350 hatched and 300 young fledged. Annual apparent hatching success remained relatively stable throughout our study, with the highest recorded in 2006 and 2010 (Table 2). Annual apparent fledging and nest success were lowest in 2006 and 2009 and highest in 2007 and 2010 (Table 2). Causes of nest failure included

Table 2. Reproductive productivity and apparent reproductive success of Mariana Swiftlets in the North Halawa Valley tunnel, O'ahu, Hawaiian Islands, 2006–2010 (Proportions ± SE).

	2006	2007	2008	2009	2010	2006–2010
Eggs laid	38	51	105	129	155	478
Eggs hatched	29 (0.76 ± 0.07)	37 (0.73 ± 0.06)	76 (0.72 ± 0.04)	91 (0.71 ± 0.04)	117 (0.76 ± 0.04)	350 (0.73 ± 0.02)
Nestlings fledged	19 (0.66 ± 0.09)	34 (0.92 ± 0.05)	66 (0.87 ± 0.04)	72 (0.79 ± 0.04)	109 (0.93 ± 0.02)	300 (0.86 ± 0.02)
Apparent nest success[a]	0.50 ± 0.08	0.67 ± 0.07	0.63 ± 0.05	0.56 ± 0.04	0.70 ± 0.04	0.63 ± 0.02
Active nest sites[b]	23	25	39	57	67	84
Active nest sites that fledged young	17	23	32	48	61	73

[a]Apparent nest success = proportion of eggs that resulted in a fledged nestling.
[b]Active nest site = nest site with an egg or nestling.

eggs on tunnel floor (52%, $N = 92$), missing eggs or nestlings (13%, $N = 24$), nestlings on tunnel floor (13%, $N = 23$), rat predation (10%, $N = 17$), nests on tunnel floor (4%, $N = 8$), human (4%, $N = 7$; egg broken or damaged while taking measurements), nestling dead (2%, $N = 4$), and infertile eggs (2%, $N = 3$).

Nest survival. Of 478 nests monitored, 50 had insufficient data for nest survival analyses, resulting in 428 (35 [2006], 45 [2007], 98 [2008], 107 [2009], 143 [2010]) nests available for nest survival analyses. Goodness-of-fit of the global model was adequate ($\chi^2 = 54.7$, $P < 0.001$) to proceed with model selection. Our top model suggested daily nest survival varied as a quadratic function of nest age (Table 3, Fig. 2). The second-ranked model suggested that year was also an important predictor ($\Delta AIC_c = 1.79$), but this variable was not significant (Table 4). Overall, we found a *U*-shaped relationship between daily nest survival rate and nest age, with the daily nest survival rate decreasing during the incubation period, and increasing during the nestling to fledging period (Fig. 2). Daily nest survival varied among years, with the lowest survival rates in 2006 and highest in 2010. Models that received little support ($\Delta AICc \geq 12.30$; Table 3) included those that held the daily nest survival rate constant, or included only linear effects of nest age (with and without year), year alone, nest site distance into the tunnel, nest site height above the tunnel floor, daily precipitation, temporal variation within seasons (season-day; linear and quadratic), mean number of active and baited rat traps/night annually, and cumulative total number of rats captured.

To facilitate comparison with other studies, we present results of the constant survival (i.e., intercept-only) model (i.e., analogous to apparent nest success) for each year. Overall estimated nest success for the period from 2006 to 2010 was 63% ($N = 428$ nests). Yearly estimated nest success was 56% (95% CI = 41–68%) in 2006, 65% (95% CI = 50–80%) in 2007, 69% (95% CI = 52–73%) in 2008, 55% (95% CI = 44–63%) in 2009, and 71% (95% CI = 63–78%) in 2010. We found no significant differences in these Mayfield-analogue estimates of daily nest survival among years, although the difference between the 2009 and 2010

Table 3. Model selection results for 17 candidate models explaining daily nest survival of Mariana Swiftlets in the North Halawa Valley tunnel, O'ahu, Hawaiian Islands, 2006–2010.

Model[a]	K	AIC_c	ΔAIC_c	AIC_c weight
int + nage + nage²	3	1697.95	0.00	0.707
int + year + nage + nage²	8	1699.74	1.79	0.290
int + nage	2	1710.25	12.30	0.002
int + year + nage	7	1710.41	12.46	0.001
int + meantrap	2	1739.44	41.49	0.000
int + year + precip	7	1739.82	41.87	0.000
int + year + sdate	7	1739.83	41.88	0.000
int + sdate	2	1739.90	41.95	0.000
int + precip	2	1740.23	42.27	0.000
int + dist + meantrap	3	1740.76	42.81	0.000
int + year	6	1741.18	43.23	0.000
int + annrats	2	1741.70	43.75	0.000
int	1	1742.44	44.49	0.000
int + dist	2	1743.95	46.00	0.000
int + height	2	1744.43	46.48	0.000
int + sdate + sdate²	3	1745.23	47.28	0.000
int + dist + height	3	1745.94	47.99	0.000

[a]*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.

daily nest survival rates approached significance (adjusted *P* value = 0.07). Apparent nest success (simply the number of fledged nests/the number of active nests found) 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). Estimated and apparent nest success values were similar among years.

Parental care. From 2006 to 2010, the mean duration of the incubation period for Mariana Swiftlets on O'ahu was 23.9 ± 3.3 d (range = 18–30 d, *N* = 233) and the mean duration of the nestling period was 55.0 ± 6.6 d (range = 41–84 d, *N* = 228), resulting in a mean nesting period of 79.5 ± 6.8 d (range = 63–113 d, *N* = 182). The mean time for females to lay another egg was 10.5 ± 6.6 d (range = 0–33 d, *N* = 129) after young fledged, 14.5 ± 7.5 d (range = 0–41 d, *N* = 69) after a nest with an egg failed, and 17.9 ± 11.9 d (range = 11–64 d, *N* = 18) after a nest with a nestling failed.

The average number of clutches attempted at each active nest site per year was 1.7 in 2006

(range = 1–3, *N* = 38), 2.0 in 2007 (range = 1–3, *N* = 51), 2.7 in 2008 (range = 1–5, *N* = 105), 2.3 in 2009 (range = 1–6, *N* = 129), and 2.3 in 2010 (range = 1–6, *N* = 155). As many as 17 clutches were laid at a single nest site during our study. The maximum number of young fledged at a nest site was two in 2006 and 2007, and three in 2008, 2009, and 2010.

DISCUSSION

Annual cycle. We recorded active nests in every month of the year, with peak nesting activity between May and September; swiftlets on Saipan exhibited a similar cycle (Rice 1993). Active Mariana Swiftlet nests have also been recorded in every month of the year on Guam, with peak nesting activity between about February and October (Wiles and Aguon 1997, 1998, 1999, Dicke et al. 2000).

Reproductive success. Estimated nest success (63%) and apparent nest success (64%) in our study were among the highest recorded for *Aerodramus* swiftlets known to lay one egg. Only Black-nest Swiftlets (*Aerodramus maximus*) in Vietnam (73%, *N* = 60
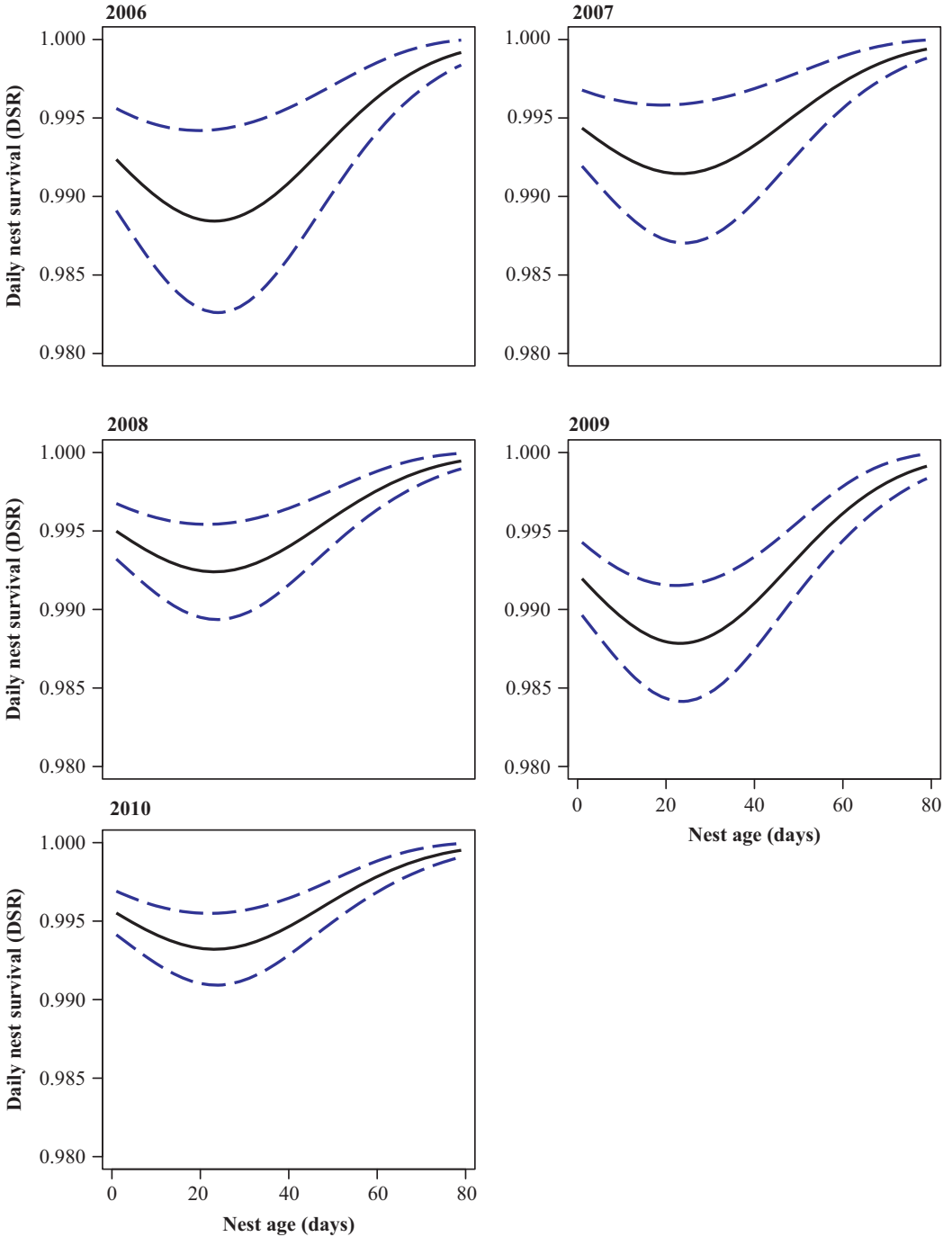
Fig. 2. Estimated daily nest survival (± 95% CI) of Mariana Swiftlets (North Halawa Valley tunnel, O'ahu, Hawaiian Islands, 2006–2010) from the top-ranked model that included nest age and year covariates. Daily nest survival varied as a quadratic function of nest age and by year. For reference, the mean duration of incubation, nestling, and nesting periods was 24, 55, and 79 d, respectively. Lowest nest survival probability is roughly coincident with hatching and highest probability near fledging.

Table 4. Estimated model coefficients for top-ranked models describing daily nest survival of Mariana Swiftlets in the North Halawa Valley tunnel, O'ahu, Hawaiian Islands, 2006–2010.

Model	Coef	Estimate	SE	95LCI	95UCI
Nest age (quadratic)	int	5.145	0.274	4.597	5.693
	nage	−0.038	0.018	−0.074	−0.003
	nage^2	0.0008[a]	0.0002	0.0004	0.0013
Year + Nest age (quadratic)	2006	4.904	0.217	4.469	5.338
	2007	5.209	0.218	4.773	5.646
	2008	5.328	0.181	4.966	5.690
	2009	4.853	0.150	4.553	5.154
	2010	5.441	0.160	5.122	5.761
	nage	−0.039	0.008	−0.055	−0.024
	nage^2	0.0008[a]	0.0002	0.0005	0.0012

[a] ± 95% CI, shown to four decimal places (logit scale) for clarity.

nests) (Lee and Kang 1994) and White-rumped Swiftlets (*Aerodramus spodiopygius*) in Samoa (72%, $N = 18$ nests) (Tarburton 2009a) had higher nest success (albeit smaller sample sizes) than Mariana Swiftlets in our study. Mountain Swiftlets (*Aerodramus hirundinaceus*) in New Guinea had 61% nest success ($N = 56$ nests) (Tarburton 2003). Our 2010 nest success was among the highest known for a swiftlet species and may have been greatest because of the highest mean number of active and baited rat traps/night ($N = 33.7$) and greatest number of rats captured ($N = 114$) that year. The ability of female Mariana Swiftlets to re-nest following successful and unsuccessful nesting attempts, in conjunction with a year-round nesting season, provide multiple opportunities to augment nest success throughout the year.

Apparent nest success estimates are considered reasonably accurate if the assumption of high nest detectability ($\geq 75\%$) is met (Johnson and Shafer 1990). In the North Halawa Valley tunnel, we are confident that all active and inactive Mariana Swiftlet nests were found so detectability was 100%. Consequently, measures of Mariana Swiftlet (and possibly other cave-nesting swiftlets) apparent nest success may be treated as accurate approximations of true nest success.

Daily nest survival. Our results suggest that nest age was the best predictor of daily nest survival. However, daily nest survival declined during incubation to a minimum around the day of hatching, followed by increasing daily survival until fledging (Fig. 2). During our study, 70% of all nest failures occurred during the egg stage/incubation period, yet there was 86% apparent fledging success. Similarly high fledging success was documented for White-rumped Swiftlets in Samoa (Tarburton 2009a).

Following rat predation in 2006, 2007, and 2009, swiftlets in our study did not abandon the tunnel. However, population expansion on O'ahu may not be possible because swiftlets are apparently limited to the single colony in North Halawa Valley. There are no other known roosting/nesting tunnels or caves, and almost all swiftlet sightings since 1969 have been within 5 km of the roosting/nesting tunnel (Wiles and Woodside 1999, Bishop Museum Sightings Database). Thus, a lack of suitable roosting/nesting tunnels or caves may limit the Mariana Swiftlet population on O'ahu (Wiles and Woodside 1999, Johnson 2015).

The number of nests that failed due to rat predation may have been higher if the 2006 and 2007 rat predation events occurred when active nests were present. Without rat trapping, reproductive activity and nest success of Mariana Swiftlets in our study likely would have been lower. Our results suggest that rat predation may limit growth of the Mariana Swiftlet population on O'ahu. However, their effect may be even greater on adult survivorship than nest success, with 35 adults killed in our study. Similarly, in Vietnam, rice rats (*Rattus tanezumi*) often enter caves and kill adult and nestling Edible-nest Swiftlets (*Aerodramus fuciphagus*). From 1991 to 1997, an estimated 4000 swiftlets were killed by rice rats in the Khanh Hoa region, including two

caves where entire swiftlet populations were lost (Nguyen Quang and Voisin 2001, Nguyen Quang et al. 2002). Rats are also known predators of adult and nestling White-rumped Swiftlets in Samoa and nestling Australian Swiftlets (*Aerodramus terraereginae*) in Queensland (Tarburton 1988, 2009a,b).

Nest failures. Nestlings discovered on the tunnel floor in our study may have accidently fallen when they were either backing over the front rim of nests to defecate (Medway 1962a, Lim 2002) or attempting to move from nests to the wall. In any case, starvation or drowning were the likely outcomes. Underfed swiftlet nestlings are known to become hypersensitive and restless, and eventually crawl out of nests (Lim 2002). Falling from nests was also a cause of nestling mortality for White-rumped Swiftlets in Fiji, Atiu Swiftlets (*Aerodramus sawtelli*) in the Cook Islands, and Australian Swiftlets (Tarburton 1986a, 1988, 1990). In cases where nests fell to the tunnel floor, the wall likely became too wet and moisture saturated the nest material and salivary cement, weighing the nest down to the point where adhesive properties failed (Medway 1962a, Lim 2002).

Eggs found on the tunnel floor may have been either accidentally or deliberately ejected from nests by adults. Eggs could have accidentally fallen from nests when a changeover of incubation duties occurred or during disputes between birds at nests (Tarburton 1988). Factors that may have led to the accidental ejection of eggs from nests by adult Mariana Swiftlets in Mahlac Cave on Guam included predation or attempted predation, explosions at a nearby Navy Ordnance Annex, research activity, antagonistic encounters among swiftlets, and aggressive interactions between swiftlets and mud dauber wasps (*Vespula* sp.) that sometimes construct nests on swiftlet nests, weighing them down and causing them to fall (Morton and Amidon 1996).

Mariana Swiftlets on O'ahu may have deliberately ejected eggs from the nest, perhaps having the ability to detect inviable eggs. Of 92 eggs found on the tunnel floor in our study, ≥ 53% had surpassed the duration of the mean incubation period and may have been deliberately ejected from nests. Morton and Amidon (1996) hypothesized that swiftlet

eggs on Guam may be deliberately ejected from nests due to deterioration in the nutritional condition of adult females, possibly due to declines in insect abundance. In Sarawak, eggs of Black-nest Swiftlets, Mossy-nest Swiftlets (*Aerodramus salangana*), and Glossy Swiftlets (*Collocalia esculenta*) were believed to be deliberately ejected after being in nests substantially longer than the mean incubation period (Medway 1962a).

Parental care. The mean incubation period of Mariana Swiftlets on O'ahu was similar to that on Saipan (22.95 d, $N = 22$; Reichel et al. 2007) and to other *Aerodramus* swiftlets that lay one egg (Medway 1962a, Tarburton 1988, 2009a, Lee and Kang 1994, Nguyen Quang 1996). Our mean nestling period on O'ahu was also comparable to that of Mariana Swiftlets on Saipan (47 d, $N = 28$; Reichel et al. 2007) and to those of other *Aerodramus* swiftlets that raise one chick (Medway 1962a, Tarburton 1988, 2009a, Lee and Kang 1994, Nguyen Quang 1996).

Mariana Swiftlets on O'ahu took less time to re-lay after fledging young than after the loss of an egg or nestling; swiftlets took longest to re-lay following loss of a nestling. The average time for Mariana Swiftlets on O'ahu to re-lay after young fledged and nests with an egg failed were similar to that of other *Aerodramus* swiftlets with single-egg clutches (Medway 1962a, Tarburton 1988, Nguyen Quang 1996). Re-nesting by Mariana Swiftlets after successful and unsuccessful nesting attempts suggests that adults may remain attached to individual nest sites, and perhaps mates, in the North Halawa Valley tunnel.

Conservation implications. We found that rats preyed on Mariana Swiftlets on O'ahu and this suggests that rats could also affect the chances for successful establishment of relocated populations in the Mariana Islands. Additional study to determine how or why eggs are ejected from nests (accidentally or deliberately) would fill another gap in our knowledge of swiftlet reproductive biology and facilitate reintroduction efforts.

Current goals for downlisting Mariana Swiftlets from endangered to threatened include establishing populations of 2000 birds on Guam, 2000 birds on Rota, 1000 birds on Aguiguan, and 2000 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 Mariana Swiftlets in the Mariana Islands, the O'ahu population of swiftlets is of significant conservation importance and may be useful for testing reintroduction techniques, learning more about the natural history of Mariana Swiftlets, and providing individuals for population enhancement in the Mariana Islands.

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