Vol. 53: 139–149, 2024
https://doi.org/10.3354/esr01296

ENDANGERED SPECIES RESEARCH
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Published February 15

Videographic monitoring at caves to estimate population size of the endangered yǻyaguak (Mariana swiftlet) on Guam

P. Marcos Gorresen[1,*], Paul Cryan[2], Megan Parker[3], Frank Alig[3], Melia Nafus[4], Eben H. Paxton[4]

[1]Hawai'i Cooperative Studies Unit, University of Hawai'i at Hilo, Hawai'i National Park, HI 96718, USA
[2]US Geological Survey, Fort Collins Science Center, Fort Collins, CO 80526, USA
[3]US Navy, NAVFAC Systems Command Marianas (NAVFACMAR), Guam 96915, USA
[4]US Geological Survey, Pacific Island Ecosystems Research Center, Hawai'i National Park, HI 96718, USA

ABSTRACT: The yǻyaguak (Mariana swiftlet; *Aerodramus bartschi*) is an endangered cave-nesting species historically found on Guam and the southern Mariana Islands, Micronesia. The population on Guam has been severely affected by the introduction of the brown treesnake *Boiga irregularis*. Population status assessments have, however, been challenging due to the limitations of traditional counting methods, which rely on visual observations at cave entrances and are prone to inaccuracies. To improve count accuracy, we estimated yǻyaguak population size and relative nesting activity using thermal and near-infrared videography. The population on Guam was surveyed at the island's 3 known occupied caves (Mahlac, Maemong, and Fachi) between 2019 and 2023. Mahlac Cave harbored the largest colony, which ranged from 506 to 665 birds; Maemong Cave held 144 to 196 birds; and Fachi Cave, which is sometimes flooded, had 28 (in 2019) and 35 birds (in 2023). Our estimates indicate a slight decline in the yǻyaguak population over the study period. This study demonstrates the potential of thermal and near-infrared videography for improved monitoring of yǻyaguak colonies and nesting activity, which will contribute to our understanding of population dynamics and the effectiveness of management strategies such as brown treesnake control.

KEY WORDS: Swiftlet colony · Autonomous camera systems · Apodidae · Micronesia

1. INTRODUCTION

The endangered yǻyaguak (Mariana swiftlet *Aerodramus bartschi* Mearns, 1909) is one of the last native bird species persisting in the wild on Guam (in Chamorro, Guåhan), with a distribution now restricted to southern Guam. Historically, yǻyaguak occurred on other southern Mariana Islands (Tinian and Rota; Steadman 1999), but today exists only on 3 islands: Guam, Aguiguan, and Saipan (Chantler et al. 2020). Yǻyaguak were once abundant on Guam (Jenkins 1983), but following the introduction of the brown treesnake *Boiga irregularis* in the 1940s, the population sharply declined, and the cave-dwelling species was largely extirpated from most of Guam by the late 1960s to early 1970s (Jenkins 1983, Savidge 1987, Rodda et al. 1992, Wiles et al. 2003). Additional threats including pesticides, cave disturbance, and disease may also have contributed to declines and extirpation from much of its native range (USFWS 1991).

The yǻyaguak population on Guam is currently known to inhabit 3 caves — Mahlac, Maemong, and Fachi — located less than 1 km from each other in the Talofofo watershed and within the administrative boundary of Naval Base Guam. Yǻyaguak were first found to occupy Mahlac Cave in the 1970s (USFWS

*Corresponding author: mgorresen@usgs.gov

Publisher: Inter-Research · www.int-res.com

1991), and the cave has consistently supported the largest known colony (Wiles & Aguon 1999, Brindock 2012a). A colony inhabited Maemong Cave (formerly called Firebreak 3 Cave) until at least 1965 (from which about 400 birds were captured for translocation to Oʻahu, Hawaii; Wiles & Woodside 1999). However, the cave was abandoned by 1981 and remained so until 1999, when 2–3 birds began roosting and nesting there again (Wiles & Aguon 1999). Numbers grew to 20–30 birds by 2004 (Brindock 2012a). A small colony of yå̄yaguak has been present in Fachi Cave since it was discovered in 1990 (Beck & Wiles 1990). From the mid-1980s to the mid-2000s, surveys of these 3 colonies indicated a population numbering only in the hundreds, followed by an increase that peaked at 1549 individuals in 2016 (Johnson et al. 2018). However, there is uncertainty about the actual population size, especially after 2005 when abundance became substantially larger (described below). Despite over 10 yr of snake control around these colonies (Sugihara et al. 2015), brown treesnakes continue to affect breeding and roosting swiftlets (Brindock 2012b, Klug et al. 2021), and the direct effects of snake control on swiftlet population size are poorly understood.

The standard method for estimating yå̄yaguak colony size in Guam and the southern Marianas is for observers to count birds in flight at cave entrances as they return to roost in the evening (e.g. Brindock 2010, Liske-Clark et al. 2018). This method of conducting arrival surveys of birds entering and exiting the caves has been used for more than 30 yr and provides an index of relative population size (Brindock 2010, Johnson et al. 2018). Since the mid-1980s, up to 12 evening cave entrance surveys per year have been conducted at the 3 caves on Guam. Observers arrive 60 min prior to sunset, conduct an in-cave count of birds and nests, then position themselves at cave entrances and count arriving and exiting birds until they are unable to detect birds due to low light or complete darkness. Arrival surveys of birds cannot account for 2 sources of uncertainty (Brindock 2010): (1) the extent to which swiftlets may repeatedly enter and exit caves and be double-counted; and (2) how many birds remain in the cave during a survey to roost (i.e. perched at or near nests) or attend nests (although counters generally survey the roosting/nesting area before conducting entrance counts to tally birds remaining in the cave). Additional uncertainty arises from the difficulty of counting in low-light conditions while birds rapidly fly in and out of a cave, often in groups, as well as regularly circling within the visual sample area. A yå̄yaguak colony can also be readily disturbed, and numerous birds might fly from the cave at once, thereby adding to the difficulty of visually tracking individuals. Surveyors that enter the cave for a count of birds and nests before the cave entrance count may risk additional disturbance to the colony. Because conditions and observers change over time, the reliability and replicability of population estimates across counts is difficult to assess.

Reliable methods for accurate, verifiable, and repeatable counts of populations are necessary to monitor and assess the benefits of conservation actions (Dell et al. 2014). Despite the considerable challenges in censusing yå̄yaguak, methods to assess the efficacy of snake control techniques are needed to help guide management efforts and assess swiftlet population recovery or persistence. The use of thermal and near-infrared (NIR) videography in low-light or completely dark settings holds the greatest promise for producing accurate counts of swiftlets at roost and nest locations within caves (Brindock 2010, Johnson et al. 2018). Importantly, photo documentation can be reviewed post-count to assess accuracy, and computer vision algorithms can be developed to efficiently process imagery for rapid count estimation. This allows for high confidence and replicability across counts and minimizes human disturbance during counts. We describe the results of a study to derive colony-specific population estimates from thermal and NIR video monitoring over multiple years as part of a larger research program to understand yå̄yaguak population dynamics, population response to snake control, and factors affecting cave occupancy.

2. MATERIALS AND METHODS

2.1. Study site and surveys

Mahlac, Maemong, and Fachi Caves occur in the upper Talofofo watershed, within a region of low hills vegetated with limestone forest (Morton & Wiles 2002). The region receives an average of approximately 260 cm of rainfall per year (Lander & Guard 2003), broadly divided into a wet (July to December) and dry season. The caves are solution cavities in a limestone substrate, with interior volumes large enough to have low-light portions where swiftlets roost and nest. Mahlac Cave has 2 large entrances, and Maemong and Fachi Caves each have a small second entrance in addition to the main entrance. The entrances at Fachi Cave are partly inundated during periods of high rainfall (Morton & Amidon 1996).

We surveyed Mahlac and Maemong Caves during 24–29 April 2019, 12–17 November 2019, 22–29 March 2022, 13–18 November 2022, and 5–19 April 2023. The surveys occurred at the beginning of both the peak-breeding and non-peak-breeding seasons (the former delineated as the onset of the egg laying period, extending from about the middle of the dry season in April to the middle of the wet season in September; Reichel et al. 2007). Cameras were deployed both at cave entrances and within caves to image birds, nests, and roost areas. The interior of Fachi Cave was only video sampled in April 2019 and April 2023, as the cave was inundated during the other periods due to high rainfall.

2.2. Sampling equipment

For all surveys, we used thermal network video surveillance cameras (Q1922-E and Q1942-E; Axis Communications) that have a 640 × 480 pixel image sensor sensitive to the 'far' spectrum of infrared light (approximately 9000–14 000 nm) and require no illumination. These weatherproof thermal cameras record digital video to memory cards (with up to 256 GB capacity) at 30 frames per second and can be fitted with lenses of different focal lengths, including 10 and 19 mm (to provide a relatively large field-of-view) and 35 or 70 mm (to provide a smaller, but higher-magnification field-of-view). Depending on compression settings, camera recordings yielded between 4 and 14 h of video per GB. Thermal cameras were each powered with four 12 V, 7 amp hour (Ah) lithium–iron–phosphate ($LiFePO_4$) batteries (Dakota Lithium), connected in parallel to provide up to about 70 h of continuous recording. Batteries were set within a waterproof case (Pelican Vault V250 Ammo Case) with the camera mounted on a ball-head attached to the top of the case. Two thermal cameras were required to acquire full coverage of the colony at Mahlac Cave, whereas one camera sufficed for the Maemong and Fachi colonies.

The November 2022 and April 2023 surveys included the use of NIR network video surveillance cameras (Q1798-E; Axis Communications) equipped with a CMOS (complementary metal oxide semiconductor) sensor composed of 2592 × 1944 pixels, a built-in NIR illuminator (peak wavelength of 850 nm), and a 12–48 mm varifocal lens. Recordings at 30 frames per second were made to 256 GB memory cards, which yielded about 1 h of video per GB. The NIR cameras were each powered by two 12 V, 54 Ah lithium–iron–phosphate batteries (Dakota Lithium), connected in series to provide about 48 h of continuous recording and were set without a case below a tripod supporting the camera. A single NIR camera at each of Mahlac and Maemong Caves provided full coverage of the roost/nest areas.

2.3. Estimating population size

Video recordings were obtained over multiple days, from which a single 24 h period (starting at least 6 h from camera setup to avoid disturbance effects) was used to characterize diurnal and nocturnal bird counts and identify active nests. Video recordings were reviewed using free open-source video processing software (VirtualDub version 1.10.4). For the November 2022 and April 2023 surveys, bird counts were made directly from high-resolution NIR imagery. When high-resolution imagery (thermal or NIR) only covered a portion of the roost area (i.e. for surveys at Mahlac Cave before November 2022), counts were accomplished from nighttime recordings by first tallying birds settled at the nest or roost (inclusive of individuals roosting off-nest) for a focal area with a high density of nests (Fig. 1). Next, the bird tally was associated with a count of distinct thermal 'hot spots', indicative of a bird or a cluster of birds within the same extent in lower-resolution imagery, to produce a 'bird-to-spot' ratio (range: 1.7–1.8). The point locations of all thermal hot spots were then mapped and tallied from lower resolution imagery of the entire colony. Finally, the bird-to-spot ratio was applied to the tally for the entire field of view to extrapolate colony size. Bird counts were derived from recordings made between 20:00 and 05:00 h, when all birds were settled at the roost and within-cave flight activity was at its lowest. We evaluated the accuracy of the extrapolation method by producing counts both directly from high-resolution NIR imagery and independently by applying the 'bird-to-spot' ratio to a corresponding low-resolution thermal image and found that it underestimated counts by 3–5%. The trend in bird counts was assessed for the Mahlac and Maemong colonies with a generalized linear model using a Poisson distribution, and an ordinal interval for surveys over the 2019–2023 study period.

2.4. Tallying active nests

The identification and count of active nests at each yåyaguak colony was obtained either indirectly by an assessment of the duration of adult attendance at a

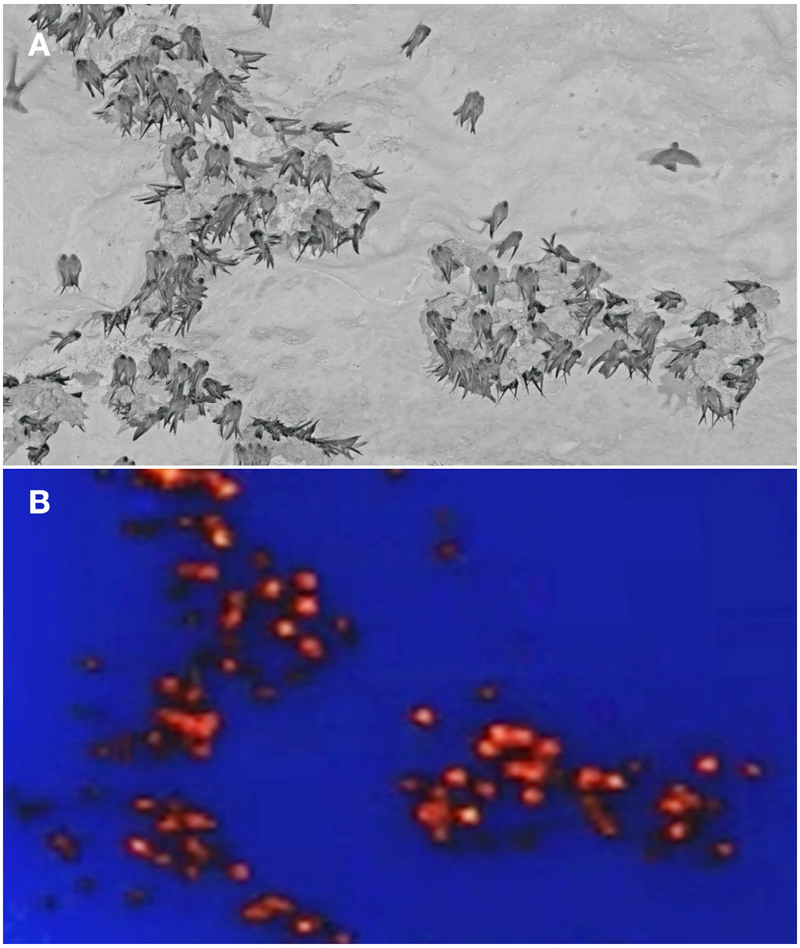

Fig. 1. Example of colony size estimation produced by (A) tallying individual birds from higher-resolution video associated with (B) 'hot spots' in lower-resolution thermal imagery of the same area (both images were recorded at Mahlac Cave at 22:00 h on 15 November 2022). A 'bird-to-spot' ratio was subsequently applied to a tally of spots in the remainder of the low-resolution field-of-view to extrapolate total colony size

nest or directly by observation of a nestling or inference of nestling occupancy. Diurnal patterns of egg incubation and parental attendance are not well known for yǻyaguak, but Tarburton (1986, p. 219) reported that incubation by white-rumped swiftlets (*Collocalia* [*Aerodramus*] *spodiopygius assimilis*) 'was shared by both parents and that they changed duties at about 24 h intervals'. Assuming that this also applies to yǻyaguak, consistent nest attendance at the incubation stage is likely a reliable indicator of active nesting. However, once a chick is hatched, identifying active nests based on attendance in the morning hours may underestimate counts if both adults are out foraging. Morton & Amidon (2008) found that the presence of adults at a nest decreased from 2 birds prior to emergence at sunrise to an average of one adult by about 08:00 h, and to 0.5 adult by 12:00 h (indicating either one or no bird at that time and that on-nest sitting by yǻyaguak may not occur continuously during daytime). Morton & Amidon (2008) also noted that adults (n = 5 pairs) returned to the nests to feed nestlings (i.e. 1–4 times per day, averaging 1.8 times during diurnal hours).

During night roosting, adult yǻyaguak not directly on the nest were usually perched at the side of nests, and sometimes clusters of multiple birds (likely composed in part of non-breeding 'floaters') obscured the view of the nest (see lower panel of Fig. 1). Therefore, to identify active nests, we examined imagery after the initial emergence of birds (beginning about 45 min before sunrise to 5 or 6 h after sunrise), when most volant birds were foraging outside the cave (Fig. 2). To identify a nest as 'active', we applied criteria based either on the consistent presence of an adult at a nest for a minimum of 3 h, or when an adult was not consistently present, the occurrence of a nestling as inferred by a sustained thermal glow evident in thermal imagery or direct observation from the high-resolution near-infrared recordings (Fig. 3).

The proportion of non-nesting individuals in a colony was calculated as the difference between the total colony count and twice the associated active nest count (i.e. assuming one breeding pair per nest). To assess the nesting effort at a colony among surveys, we compared the proportion of active nests counted in the non-peak-breeding season relative to the peak-breeding season within the same calendar year. Finally, distinct nest clusters were tallied to provide a baseline for future monitoring and to determine whether parts of the colony may be undergoing nest gain or loss (e.g. attributable to snake control or, conversely, snake predation). Nest counts in April 2019 and April 2023 for Mahlac Cave relative to their general location and potential vulnerability to snake predation were compared with a Fisher's exact test. All statistical analyses were completed in R version 4.2.1 (R Core Team 2023), and statistical significance was assessed using a criterion of 0.05.

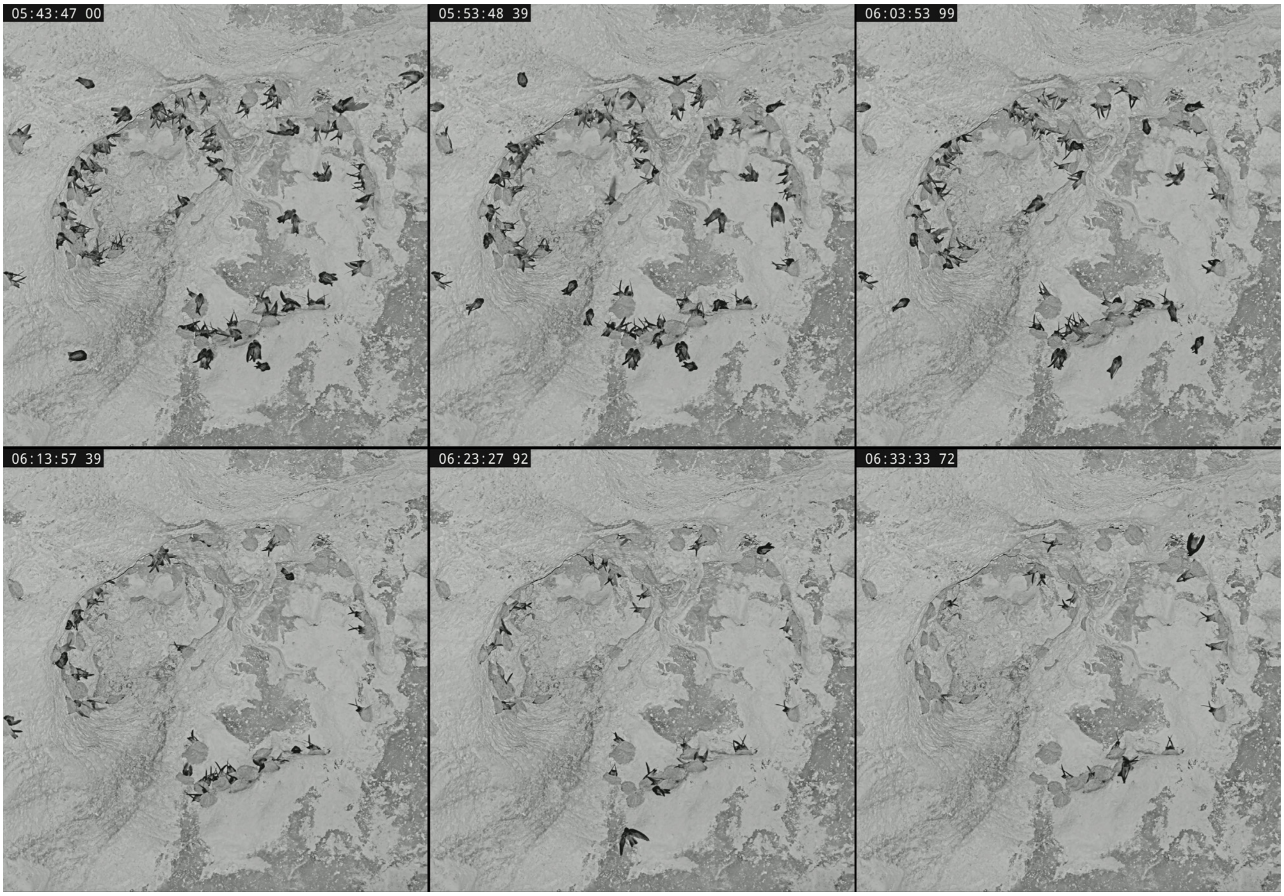

Fig. 2. Example of roost departure timing relative to sunrise (shown here for an image series recorded at 10 min intervals from 05:43 to 06:33 h at Maemong Cave on 16 November 2022, with sunrise at 06:20 h at this date and location). Yǻyaguak exit the roost up to 45 min before sunrise, with the majority leaving the cave about 15 min before sunrise

3. RESULTS

3.1. Population size

Cave-specific estimates of colony size for 2019, 2022, and 2023 demonstrated that Mahlac Cave harbored about 77% of the known yǻyaguak population on Guam, and an equivalent proportion (79%) of active nests (Table 1). The estimated colony size for Mahlac Cave over the 3 years ranged from 506 to 665 across all surveys and averaged 577 birds (standard deviation [SD] = 66; coefficient of variation [CV] = 11%) during the peak-breeding season. The Maemong Cave population estimate ranged from 144 to 196 across all surveys, with a mean of 157 birds (SD = 13; CV = 8%) during the peak-breeding season. Due to the difficulty of accessing the flooded cave interior, the colony in Fachi Cave was only sampled twice, both in the dry season during April 2019 (28 birds) and April 2023 (35 birds). However, videographic monitoring of bird entry and exit at the east entrance of Fachi Cave confirmed yǻyaguak use of the cave during all survey periods. Count estimates for Mahlac and Maemong colonies declined on average about 1% per consecutive survey over the 2019–2023 study period (Mahlac: β_{count} = −0.018, standard error [SE] = 0.006, p = 0.001, exp(−0.018) = 0.982, 95% confidence interval [CI] = 0.975–0.993; Maemong: β_{count} = −0.020, SE = 0.011, p = 0.057, exp(−0.020) = 0.980, 95% CI = 0.960–1.001). Counts at Fachi Cave from April 2019 to April 2023 increased by 7 birds (25%), a magnitude amplified by its small population size. Post-peak-breeding season counts for the Mahlac and Maemong colonies demonstrated a combined gain of 69 birds (8%) in 2019 and 67 birds (9%) in 2022 relative to the peak-breeding season of the same year.

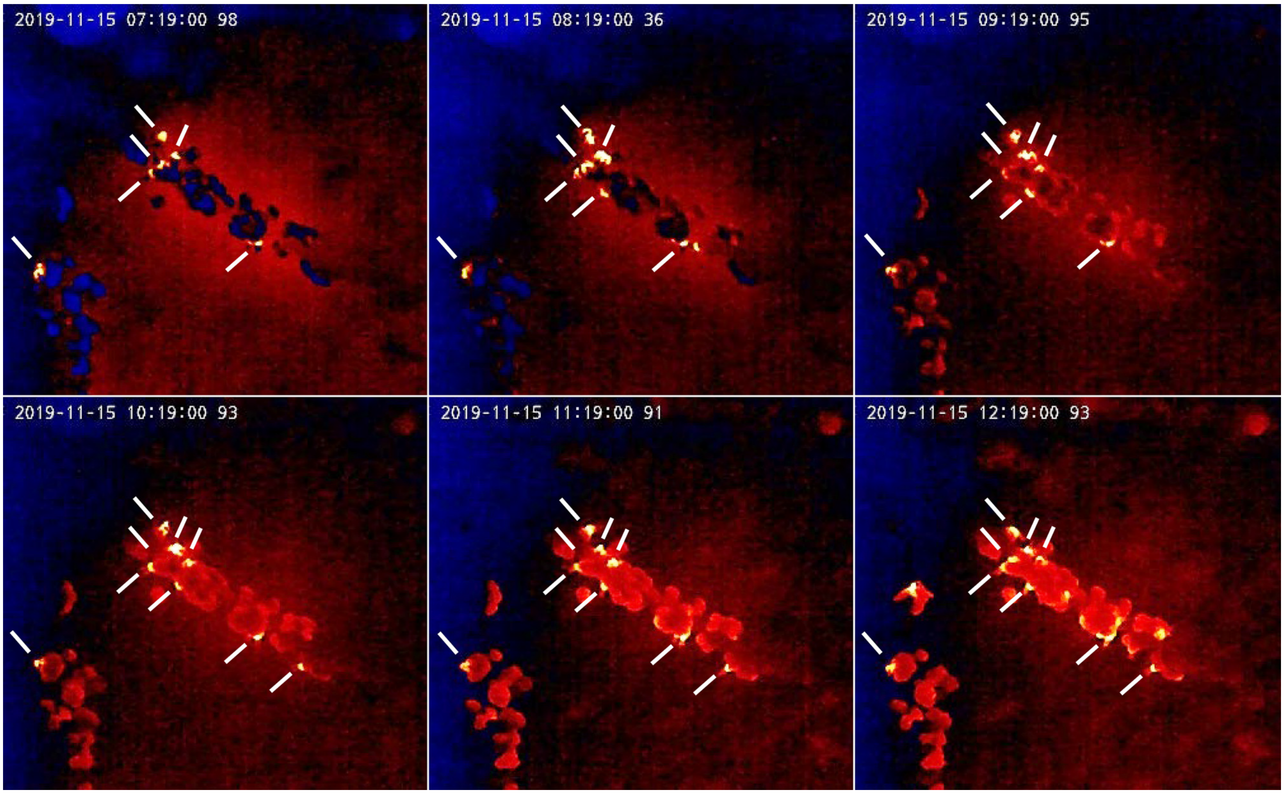

Fig. 3. Example of active nest identification from thermal imagery based on consistent occupancy for at least a 3 h period between 06:00 and 13:00 h (shown here for an image series recorded at 1 h intervals from 07:19 to 12:19 h at Mahlac Cave on 15 November 2019). Active nests are indicated with a line; unmarked points of thermal 'glow' show nests not consistently attended by an adult or with a nestling

3.2. Active nest counts

The number of active nests over the 3 years averaged 248 nests (SD = 18; CV = 7%) at Mahlac Cave and 63 nests (SD = 5; CV = 8%) at Maemong Cave during the peak-breeding season, and 31 nests (SD = 18; CV = 58%) and 6 nests (SD = 0; CV = 0%) during the non-peak-breeding season, respectively (Table 1). On average, 83% of adults (range: 73–90%) appeared to be actively nesting at these 2 colonies during the peak-breeding season, whereas a smaller proportion of birds were observed nesting at Fachi Cave (60%) during the peak-breeding season. As expected, the proportion of non-nesting individuals increased during the non-peak-breeding season, averaging 93% for the Maemong and 91% for Mahlac colonies.

3.3. Nest distribution

The locations of nests and roosts in each cave remained relatively unchanged during our study

Table 1. Yáyaguak colony size and active nest counts by survey and cave. On-nesting proportion is the percentage of individuals in the colony that were not associated with active nesting. The March and April surveys occurred at the beginning of the peak-breeding season (i.e. egg laying period from April to September) and the November surveys occurred during the non-peak-breeding season. (–) birds present, but frequent flooding at Fachi Cave prevented access and within-cave videographic monitoring during this survey period

Cave	Colony size (no. of birds)					Active nests (no. of nests)					Non-nesting proportion (%)				
	Apr '19	Nov '19	Mar '22	Nov '22	Apr '23	Apr '19	Nov '19	Mar '22	Nov '22	Apr '23	Apr '19	Nov '19	Mar '22	Nov '22	Apr '23
Mahlac	636	665	506	595	590	254	43	228	18	263	20	87	10	94	11
Maemong	156	196	170	148	144	68	6	62	6	58	13	94	27	92	19
Fachi	28	–	–	–	35	8	–	–	–	11	43	–	–	–	37
Total/Avg.	820	861	676	743	769	330	49	290	24	332	25	91	19	93	22

period, but there was evidence of changes in locations historically. The distribution of nests for the Mahlac colony encompassed approximately 10–15 groups, each composed of multiple closely packed nests, although a small proportion were attached singly to the cave wall and ceiling (Fig. 4). The Mahlac nests were limited to a ceiling area of approximately 6 × 6 m. There were large guano piles under an adjacent and currently unoccupied area closer to the northwest ('front') cave entrance that may previously have supported numerous nests for a long period of time. The nests at the lower left side of Fig. 4 were less than 2 m from a ledge near the cave floor, with other clusters situated relatively higher in the roost area. Several nest clusters in Mahlac Cave demonstrated relatively large gains and losses from 2019 to 2023, but those with large gains occurred near those with large losses (Fig. 4). A Fisher's exact test comparing nest counts in relation to their general location and potential vulnerability to brown treesnake predation (i.e. the 7 relatively compact clusters on the left and the more widely spaced clusters on the right in Fig. 4) demonstrated no significant difference between the 2 surveys ($p = 0.859$). Spatially distinct roost and nest areas were not observed at the colonies, and roosting birds were always located within about 1 m of nest locations.

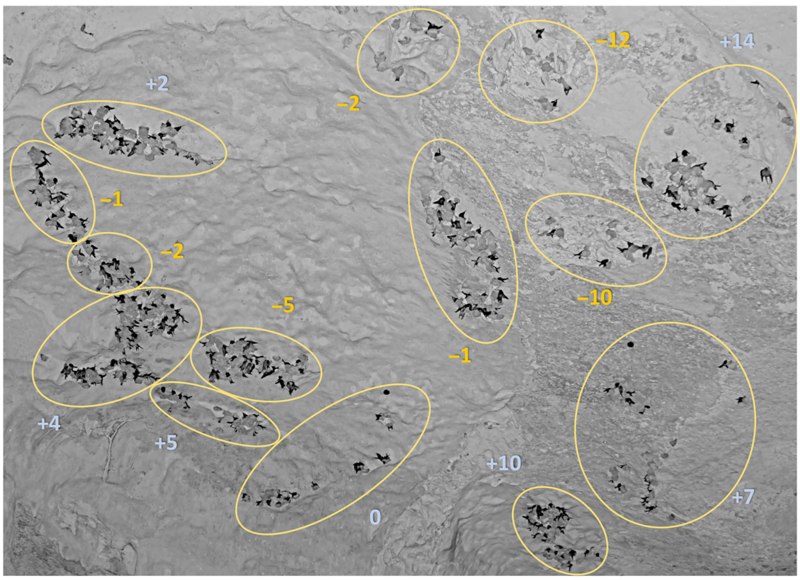

Fig. 4. Relative difference in active nest counts by cluster from surveys conducted at Mahlac Cave in April 2019 and April 2023 (shown here for an image recorded on 7 April 2023). Orange and light blue values indicate negative and positive differences in counts between periods. A Fisher's exact test compared nest counts between the 2 surveys in relation to their general location and potential vulnerability to brown treesnake predation (i.e. the 7 relatively compact clusters on the left and the more widely spaced clusters on the right)

The colony at Maemong Cave is presently restricted to a single 2 × 2 m area of cave ceiling, with nests concentrated in 2 adjacent dome-shaped cavities that are less densely clustered than at Mahlac Cave (Fig. 2). In Maemong Cave, we observed a secondary cluster of about a dozen nests approximately 10 m towards the west ('back') entrance and away from the active nest cluster; this secondary cluster of nests appeared to have been established and subsequently abandoned sometime between our surveys in 2019 and 2022.

4. DISCUSSION

Our videographic system allowed us to consistently measure colony sizes over multiple sampling periods, providing the first reliable and repeatable population estimates for yá̊yaguak on Guam. This work provides baseline information for long-term population monitoring, an important step in the conservation and management of this species. Accurate counts of populations are key for sound resource management (Dell et al. 2014). Thus, methods that reduce uncertainty will provide better tools for resource managers to assess the benefits of management actions or detect changes in yá̊yaguak numbers. The videographic system used in this study can be applied to monitoring other cave-dwelling swiftlet species.

The standard method of human observers counting yá̊yaguak returning to a cave before dusk can be inaccurate given the difficulty of visually tracking birds constantly entering and exiting as well as circling in the cave entrance (some of which go unobserved) in very low light conditions. In addition, the accuracy of counts varies by cave, colony size (larger colonies are typically harder to count), and skill level differences among observers (Johnson et al. 2018). The application of thermal and NIR video systems resolves many of the issues with past counting methods. These systems are not affected by low light conditions, are deployable for long periods under wider ranges of conditions, provide a relatively non-intrusive method of monitoring, and can produce quantitative measures that can be readily standardized and reanalyzed from archived recordings for long-term monitoring. A camera set-up was generally accomplished in less than 15 min and involved minor disturbance to birds, which appeared to settle within minutes of our exit from a cave. The videography system we deployed did not require technical proficiency in electrical wiring, was portable by backpack, and relatively low cost. The system cost primarily involved the commercially available camera and battery components.

Our analysis of roost-site imagery from 2019, 2022, and 2023 yielded total population estimates ranging from 676 to 861 yǻyaguak for the 3 caves on Guam. These counts were considerably lower than the most recent published estimate of 1549 birds in March 2016 (Johnson et al. 2018 citation of a pers. comm. with K. M. Brindock, Naval Facilities Engineering Command Marianas). We propose 2 hypotheses that potentially explain this near halving of the yǻyaguak population estimate. First, the population may have undergone a rapid decline. A population change from 1549 birds in 2016 to 820 in 2019 would represent a total decline of 47%, or a mean of 16% yr^{-1} during this 3 yr period. Second, some of the difference could be due to methodology; i.e. the difference between cave entrance and roosting area counts. For example, Brindock (2013) reported that comparisons of population estimates using 'near-infrared imaging equipment (goggles)' from within Maemong Cave to counts derived from evening arrival surveys outside the cave with unaided eyes revealed that the latter method generated estimates 38–45% greater than the estimated number of swiftlets inside the cave. Applying this percent difference to the 2016 population estimate yields values ranging from 852 (= 1549 − [0.45 × 1549]) to 960 (= 1549 − [0.38 × 1549]), which fall closer to our counts (e.g. 820 birds in April 2019). Currently, cave entrance counts are the standard method for estimating population size. However, if that approach overestimates population sizes, then adoption of different survey methods such as the approach we present here would provide more accurate and reliable estimates for current and future conservation planning and monitoring purposes.

Considerable intra- and inter-annual variation in yǻyaguak survey results has been documented at all 3 colonies on Guam (Brindock 2012a) and colonies on Saipan (Cruz et al. 2008). The variation may be from imperfect survey methods and the impacts of brown treesnake predation and control (Wiles et al. 2003), as well as natural biological variation. For example, the timing of surveys relative to the breeding season could be an important intra-annual source of variation, as young of the year will contribute more to post-breeding counts later in the year than counts conducted before the breeding season. Additionally, metapopulation exchange between colonies at the 3 caves and possibly with colonies at unknown caves could also account for some of the variability in consecutive yǻyaguak surveys on Guam. On Saipan, swiftlets have been documented switching nesting and roosting locales and can recolonize abandoned caves (e.g. recolonization of 2 caves on Saipan occurred within 12–18 mo of abandonment; Cruz et al. 2008). Additionally, the colony at Maemong Cave, known to have been occupied in the early 1960s (Wiles & Woodside 1999), was abandoned from at least 1981 to 1999, after which it was re-occupied by roosting and nesting swiftlets. With videographic systems such as we applied, all known colonies could be monitored simultaneously or in near-real time to account for any inter-cave movements. In addition, using radio telemetry technology to track yǻyaguak over space and time could provide important insights into how much movement among caves contributes to observed population and colony size dynamics.

Intra-annual variation in active nesting was evident in our surveys, which demonstrated higher counts in the peak-breeding season (March–April; mean = 317) than in the non-peak breeding season (November; mean = 37; Table 1). These results are in accord with Cruz et al. (2008, citing unpubl. data by C. Rice), who noted that nesting occurs year-round on Saipan (with peak activity between May and September). On O'ahu, Hawaii, the introduced population of yǻyaguak is also considered to breed year-round, although a distinct period with little to no nesting is evident for this population from November to January (Johnson et al. 2017). These results appear to differ somewhat from the pattern on Guam, which demonstrated a higher proportion of active nests during the non-peak breeding period (mean = 8%). In addition, a larger proportion of individuals are engaged in nesting on Guam during the peak breeding season (mean = 78%) compared to the O'ahu population, of which less than half the colony consisted of nesting individuals (Johnson et al. 2018).

Seasonal changes in prey availability are known to regulate the timing of breeding and reproductive success in swiftlets (e.g. Medway 1962, Tarburton 1993), which in turn may contribute to population size variability. Inter-annual differences in monthly rainfall on Guam can be pronounced (Gingerich 2003), which in turn may affect insect availability and influence the onset and cessation of breeding between years. Kershner et al. (2007) observed that swiftlet guano on Saipan revealed a more species-diverse diet during the wet season compared to the dry season (particularly for hymenopterans, which Valdez et al. 2011 determined to be the main prey consumed by yấyaguak during a 2 wk survey period at the onset of the rainy season on Aguiguan). Reichel et al. (2007, p. 690) speculated that 'heavy rains would depress aerial insect food resources and swiftlet foraging time' and curtail yấyaguak breeding during the height of the wet season. Tarburton et al. (2023) also noted the correspondence between a favorable rainfall regime and the ensuing supply of insects for swiftlet species in the Pacific. These reports indicate that the timing of breeding and resultant yấyaguak counts may be influenced by seasonal conditions, inclement weather, and available food resources.

The distribution of nest clusters at a colony may shift over time. For example, we noted old guano piles over 5 m away from the area below the current colony at Mahlac Cave, indicating a long-term shift or contraction of the nest and roost area. These shifts may be due to population changes or result from predation. Predators may have large effects on shaping the distribution of nests within caves. For example, white-rumped swiftlets *Aerodramus spodiopygius* will clump when nesting on smooth overhanging rock surfaces that are presumably safer from predation, but in areas where they are more vulnerable to predation, they space nests farther apart to decrease detection by predators (Tarburton 2009). In general, nests of colonial birds located at the center of a roosting group are typically considered safer due to lower accessibility to approaching predators, increased time to respond to detected predators, and deterrence of predators compared to peripheral nests (Minias 2014). Klug et al. (2021) found brown treesnakes near the periphery of active yấyaguak nests, indicating that such nests may be vulnerable to predation by snakes. However, we found no evidence of a significant difference between 2019 and 2023 in the number of nests in the clusters closer to the ground and the more widely spaced clusters higher up the cave ceiling. Long-term photo documentation of the location and distribution of nests can help us to understand how dynamic nest distribution is over time.

Deploying videographic cameras for extended periods of time could provide important information on seasonal variation in nesting and roost activity as well as quantify the occurrence and activity of predators and pests. High-resolution NIR cameras can capture detail sufficient for imaging snakes and other animals that may pose a threat to roosting and nesting yấyaguak. Brown treesnakes have been observed high up on cave walls near nests (Klug et al. 2021). However, the impracticality of regular in-cave human observation makes it difficult to assess the frequency of predation events and to gather detailed information on where, how, and at what life-stage(s) snakes are depredating swiftlets. We have incidentally detected snakes near nests during roost-site monitoring, as well as occasionally observed rodents on cave floors. Rats, particularly the widespread black rat *Rattus rattus*, are notorious predators of island birds (Shiels et al. 2014) and a documented predator of Mariana swiftlets on Oʻahu (Johnson et al. 2017, 2018). However, these non-native predators may have little effect on the yấyaguak population as they may be unlikely to reach nests high on the walls or cave ceilings. Other known or potential threats include American cockroaches *Periplaneta americana* and mud dauber wasps (likely *Delta* or *Sceliphron* sp.), both of which can affect nest longevity and disturb nesting and roosting birds (Morton & Amidon 1996, Cruz et al. 2008). Morton & Amidon (1996) routinely observed both cockroaches and wasps in low-resolution NIR video of yấyaguak nests at Mahlac Cave in 1996. Our review of over 400 h of high-resolution NIR imagery obtained at Mahlac and Maemong Caves in November 2022 and April 2023 did not reveal any cockroach or wasp activity directly at swiftlet nests, although inactive dauber nests were prevalent in some roost areas and wasps were sometimes seen at cave entrances. We made incidental observations of geckos around yấyaguak nests in NIR recordings. This is noteworthy because brown treesnake control on Guam has been shown to increase the abundance of curious skink *Carlia ailanpalai* and geckos *Lepidodactylus lugubris* and *Hemidactylus frenatus* (Campbell et al. 2012), whose predatory activity in turn may contribute to reduced cockroach and wasp infestations within caves.

Dark-imaging videographic systems such as we used in our study, coupled with potential new ways of analyzing the resulting imagery data, have great potential to reveal important information about the ecology and conservation of swiftlets. Unlike standard methods of counting yấyaguak that involved human observers periodically visiting roost caves to census birds in various ways, autonomous camera systems could be adopted for near-continuous and more precise long-term monitoring. Additional benefits of video over human counting include reducing error estimates, characterizing the spatial distribution of counted birds over time, providing data-rich archival recordings for future reference and analysis, and decreasing the likelihood of disturbing the sensitive wildlife being monitored. Long-term sampling can document the incidence of bird depredation, colony size response to predator control, phenology of nesting during peak-breeding and non-peak-breeding periods, diurnal patterns of parental care and nest attendance, and changes in colony size as a function of reproductive effort. Our methods might also help estimate vital demographic metrics such as nest success and fledging rates. Furthermore, automated videographic monitoring at unoccupied caves can provide information on whether yǻyaguak explore and reoccupy historically used caves, which could help plans to encourage recolonization of previously inhabited sites. Dark-imaging camera systems show great potential for gaining valuable insights into the habits and wellbeing of cryptic wildlife populations, as exemplified by yǻyaguak colonies at caves on Guam, and can be an important tool for species conservation efforts.

Acknowledgements. Funding was provided by the US Navy, both through Joint Region Marianas and NAVFAC Marianas. We appreciate the access to the Naval Munitions Site provided by Naval Base Guam. We thank R. Camp, N. Johnson, G. Wiles, and an anonymous reviewer for comments that improved the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government. Supporting data are available at https://doi.org/10.5066/P90R04RD (Gorresen et al. 2023).

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Editorial responsibility: Brendan Godley,
University of Exeter, Cornwall Campus, UK
Reviewed by: N. Johnson, G. Wiles and 1 anonymous referee

Submitted: June 19, 2023
Accepted: November 16, 2023
Proofs received from author(s): January 29, 2024