Nest-site selection and breeding biology of the locally endangered Micronesian Starling (Aplonis opaca) informs its recovery on Guam

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ABSTRACT. Micronesian Starlings (Aplonis opaca) are one of two native forest bird species that have survived on the island of Guam despite predation by invasive brown tree snakes (Boiga irregularis). We report the first detailed account of the starling’s breeding biology to help understand how this species has persisted and guide management to conserve and expand the population. Our surveys indicated that although starlings continued to forage in nearby forest, nesting occurred almost exclusively in developed habitat on Andersen Air Force Base. We located 36 active nest sites in a variety of natural and artificial structures, many of which were likely difficult or impossible for snakes to access. We report reproductive data from those nest sites and also predator-resistant nestboxes (n = 48 pairs using 58 boxes) installed in our study area. Typical of tropical species, the average clutch was small (2.19 ± 0.55 [SD] over 431 nesting attempts), but pairs nested repeatedly throughout the year. Pairs showed high site fidelity, and nestboxes (n = 70) installed at least 34 m from forest edge were readily colonized with 77% occupied by the end of our study. Protected nestboxes in urbanized areas along with snake suppression may be useful strategies for expanding the population of Micronesian Starlings and consequently restoring seed dispersal in nearby forest on Guam.

La sélection des sites de nidification et la biologie de reproduction du Stourne de Micronésie (Aplonis opaca), espèce en voie de disparition localement, permettent d’envisager son rétablissement sur Guam

RÉSUMÉ. Les Stournes de Micronésie (Aplonis opaca) sont l'une des deux espèces d'oiseaux forestiers indigènes qui ont survécu sur l'île de Guam, malgré la prédation qu'ils subissent par les serpents bruns arboricoles envahissants (Boiga irregularis). Nous présentons le premier compte-rendu détaillé de la biologie de reproduction du stourne, visant à comprendre comment cette espèce a subsisté et à guider la gestion pour conserver et étendre sa population. Nos relevés ont montré que, bien que les stournes continuent de s'abriter dans les forêts avoisinantes, leur nidification a lieu presque exclusivement dans les milieux aménagés de l’Andersen Air Force Base. Nous avons localisé 36 sites de nidification actifs dans un large variety de structures naturelles et artificielles, nombre de ces sites étaient probablement difficiles ou impossibles d'accès par les serpents. Nous rapportons les paramètres de reproduction à ces sites de nidification ainsi qu'à des nichoirs à l'épreuve des prédateurs (n = 48 couples utilisant 58 nichoirs) installées dans notre aire d'étude. Typique des espèces tropicales, la taille moyenne de la ponte était petite (2,19 ± 0,55 [écart-type] sur 431 essais de nidification), mais les couples ont niché à plusieurs reprises tout au long de l'année. Les couples ont montré une grande fidélité à leur site, et les nichoirs (n = 70) installés à au moins 34 m de la lisière forestière ont été colonisés, avec 77 % d'occupation à la fin de notre étude. La protection des nichoirs dans les zones urbanisées et l'élimination des serpents peuvent être des stratégies utiles pour permettre une expansion de la population de Stournes de Micronésie et, par conséquent, restaurer la dispersion des graines dans les forêts avoisinantes sur Guam.

Key Words: Boiga irregularis; brown tree snake; conservation; Mariana Islands; nestbox; nesting; reproduction; Såli; Sturnidae

INTRODUCTION

The Micronesian Starling (Såli, Aplonis opaca) is a medium-sized (~80–85 g) passerine bird in the family Sturnidae that is distributed throughout much of Micronesia, with the subspecies A. o. guami occurring on the islands of Guam, Rota, Tinian, and Saipan in the Mariana archipelago (Baker 1951). Reproductive data are missing or sparse on most of the 25 extant and extinct species in the genus (Appendix I, Table A1.1), which mainly occur on islands in Indonesia and Oceania. Despite Micronesian Starlings being common in the region, remarkably little is known about the breeding biology and natural history of this cavity nester. Jenkins’ (1983) monograph on the avifauna of Guam provides the most detailed account for Guam, but like most other published literature (but see Brandt 1962 for A. opaca anga in Chuuk), descriptions are anecdotal or based on small samples for clutch size (n = 4 nests), nesting period (n = 2 nests), etc. Data on incubation period, reproductive phenology, nest construction, and nest site placement in urban areas are lacking.

Guam’s avifauna suffered precipitous declines following the introduction of the invasive brown tree snake (Boiga irregularis) around WWII (Savidge 1987). Although most resident bird species were extirpated (reviewed in Wiles et al. 2003),
Micronesian Starlings were one of two native forest species that persisted, albeit at greatly reduced abundance and range. The majority of Guam’s starling population is restricted to urbanized areas of Andersen Air Force Base (AAFB; Wiles et al. 1995, Pollock et al. 2021). Micronesian Starlings consume a variety of native fruits (Jenkins 1983, Pollock et al. 2020) and are a good candidate for maintaining and restoring seed dispersal on Guam (Rehm et al. 2018, 2019, Thierry and Rogers 2020, Kastner et al. 2021). Information on the breeding biology of Micronesian Starlings can potentially shed light on how this species has persisted and will be important for conserving and expanding the remaining population.

We searched for Micronesian Starling nests on AAFB (Fig. 1) to understand nest site selection by this remnant population. If nest sites are not limiting, we predicted pairs would select locations safe from predators, e.g., higher above the ground, larger diameter poles that are more difficult for snakes to climb (Savidge et al. 2021), and sites with nearby trees for perching but at a sufficient distance to prevent snake access. We used data on nest sites to inform the design and deployment of custom-made nestboxes installed in the urbanized areas of AAFB on large, smooth utility poles and electrical metallic tubing (EMT) protected by a predator baffle (Appendix 2, Fig. A2.1). We investigated factors affecting nestbox occupancy to determine if nestboxes could help expand the population. Specifically, we predicted urban starlings might avoid nesting close to forest if they perceive increased predation risk from brown tree snakes. Alternatively, Micronesian Starlings forage regularly in adjacent forest, and locations closer to forest may be more profitable if proximity to food resources is beneficial. Using data from both non-nestbox locations, i.e., natural and artificial cavities, and predator-resistant nestboxes, we provide the first complete account of the breeding biology of *A. opaca* on Guam.
METHODS

Study area
Guam (13.4° N, 144.7° E), the largest island in the Mariana Islands, is located in the western Pacific Ocean. It has a tropical climate with a dry (Dec–Jun) and wet season (Jul–Nov). We studied Micronesian Starlings from 2015 to 2018 on AAFB, an 8100-ha military installation in northern Guam (Fig. 1). Our main study area included urban housing, commercial and administrative areas, a golf course, secondary forest north and northwest of housing, and secondary and primary limestone forest along the eastern boundary of the installation (Fig. 1). Control methods for brown tree snakes in our study area include a combination of traps with live mouse bait, bait tubes with dead mice containing the toxin acetaminophen, and spotlight searches near the flight line and along the installation security fencing adjacent to housing (Vice 2011).

Nest surveys and nest site characterization
Initial observations in 2015 indicated birds were breeding in the urban area south of the flight line on AAFB (Fig. 1). Thus, we subdivided this area into 30 search areas, which also included patches of second-growth forest. From March through October 2015, we searched for nests on 41 occasions for a total of 117 hours. Additionally, authors TFS and JAS spent 68 hours in surrounding forest during 2017 (Apr, May, Jul, Aug, Nov) and 2018 (Jun, Jul, Nov), surveying for indications of nesting (Fig. 1). We identified potential starling nests using a combination of vocalizations, parental behavior, and presence of nesting material associated with cavities in natural and artificial structures. Potential nesting sites were inspected to confirm presence of nests and/or nest contents (eggs or nestlings). We used an iPhone mounted on an extendable pole and linked through a wireless base station or via Bluetooth to a second iPhone used for viewing and shutter control. We recorded the following characteristics of nests: substrate, entrance height, utility pole or tree diameter at breast height, and distance to the nearest tree as well as forest.

Nestbox occupancy
Nestboxes were constructed of cedar or PVC with sloped PVC roofs (inside floor dimensions: 184 x 146 mm; 70-mm entrance hole 136 mm above the floor); no differences were found in adoption of or nest survival in nestboxes made of the two materials (JAS and TFS, unpublished data). Nestboxes were installed on utility poles and on EMT with 91 cm long x 20–31 cm wide predator guards in the urban area of AAFB (Fig. 1; Appendix 2, Fig. A2.1). Most utility poles were round, smooth, concrete poles 36 cm in diameter, but 15 nestboxes were on utility poles of other materials and/or diameters. Numbers of nestboxes available for nesting during 2016–2018 ranged from 33 to 71, with a total of 78 boxes installed in different locations over the course of our study. Nestboxes ranged 11–212 m apart. To investigate nest spacing, we measured distance between an active nestbox and its nearest neighbor and if that box was being used by another pair.

We were interested in how quickly nestboxes were adopted after deployment and how distance from forest influenced starling use. Forty-six nestboxes were initially installed between 2 March and 22 April 2016 on utility poles > 30 m from forest edge. Given these were the first to be occupied, we assessed if their distance from forest edge influenced days until clutch initiation. We also compared days after nestbox deployment until clutch initiation in nestboxes > 30 m from forest edge and boxes within 15 m of forest edge. Last, we deployed five pairs of nestboxes between 16 December 2016 and 1 January 2017 to evaluate if placement on EMT versus utility poles affected selection. Each pair included a nestbox on EMT and a nearby (11–35 m) utility pole at similar distances (42–148 m) from forest edge.

Clutch initiation was estimated using known egg laying dates or backdating from hatch and fledging dates. Because nestboxes were deployed on different dates and for variable lengths of time, we evaluated data within the first 225 days of deployment, the minimum shared duration, for each nestbox.

Nest monitoring
All nest sites were checked 1–2 times per week for signs of nesting and number of eggs recorded when an active nest was found. We usually removed old nesting material after 1–2 nesting cycles. Eleven nesting attempts in nestboxes found during nest building were checked daily to determine laying patterns, incubation and nesting periods. Because we did not know exactly when Micronesian Starlings start incubation, we defined the laying period as the day the first egg was found (if none were seen the day before) until the day before the last egg was laid, incubation as the period between laying of the last egg to the date of the last hatching, and the nesting period as the day nestlings hatched until they fledged (e.g., Nice 1937, Skutch 1945). Following Cornell Lab of Ornithology’s Nest Watch protocol (https://nestwatch.org/wp-content/uploads/2020/01/NestWatch_manual_20191106.pdf), we report ages associated with naked nestlings that were fully unfeathered, partially feathered young with feather sheaths emerging, and feathered young having feathers beginning to unfurl. Regular visits to nests allowed us to assess nesting development and behavior of nesting pairs. Six breeding females from separate pairs were banded, five of which were radio-tagged, as part of our other research, allowing us to confirm renesting intervals for these individuals. For assessing nest fidelity in non-banded birds, we considered behavioral characteristics (e.g., levels of aggression and aggressive behaviors employed, repeated perch locations), and typical renesting intervals observed in the banded birds.

RESULTS

Nest surveys and nest site characterization
Confirmed nests were confined to the urban and housing areas of AAFB. We never found a nest in forest fragments within the developed part of AAFB or in surrounding limestone forest. Within the nesting range on AAFB, we located 36 active nest sites and 26 other sites with indications of starling nesting activity and/or nesting material but that were inactive or inaccessible. Twenty-one of the latter locations were in coconut palms (Cocos nucifera), whose dense crowns made confirming nest presence difficult.

Active nests were found in cavities in a wide variety of substrates, including metal typhoon shutters, concrete streetlamp poles, coconut palm snags, and live coconut palms (Table 1; Appendix 2, Fig. A2.2). Thirteen nests located in coconut snags and metal and concrete utility poles were accessed by birds from the top of
Table 1. Substrates and characteristics of Micronesian Starling (*Aplonis opaca*) nests, including number of active nests (n), mean entrance height, mean substrate diameter at breast height (DBH), and mean distance to the nearest tree and forest edge. n/a = not applicable. Blanks indicate data not available.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>n</th>
<th>Mean entrance height (m) ±SD</th>
<th>Mean substrate DBH (cm) ±SD</th>
<th>Mean distance of nearest tree (m) ±SD</th>
<th>Mean distance to forest (m) ±SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Typhoon shutters†</td>
<td>10</td>
<td>2.3 (±0.2)</td>
<td>n/a</td>
<td>6.8 (±2.9)</td>
<td>428.1 (±190.4)</td>
</tr>
<tr>
<td>Concrete pole top</td>
<td>9</td>
<td>8.7 (±0.3) (n=7)</td>
<td>37.8 (±2.4) (n=8)</td>
<td>16.5 (±9.6)</td>
<td>323.0 (±135.4)</td>
</tr>
<tr>
<td>Concrete pole side</td>
<td>4</td>
<td>5.6 (±0.1)</td>
<td>32.0 (±0.0)</td>
<td>10.5 (±5.2)</td>
<td>912.3 (±211.1)</td>
</tr>
<tr>
<td>Cocos snag top</td>
<td>2</td>
<td>9.0</td>
<td>25.0 (±1.4)</td>
<td>17.3 (±17.3)</td>
<td>330.0 (±414.4)</td>
</tr>
<tr>
<td>Metal pole top</td>
<td>2</td>
<td>8.4 (±1.2)</td>
<td>19.0 (±1.4)</td>
<td>7.7 (±4.7)</td>
<td>420.5 (±283.5)</td>
</tr>
<tr>
<td>Live Cocos crowns</td>
<td>3</td>
<td>6.3 (±0.4) (n=2)</td>
<td>27.0 (±2.8) (n=2)</td>
<td>4.2 (±2.3)</td>
<td>557.8 (±132.8)</td>
</tr>
<tr>
<td>Jet exhaust hole</td>
<td>1</td>
<td>2.7</td>
<td>n/a</td>
<td>34.5</td>
<td>523.0</td>
</tr>
<tr>
<td>Roof gable</td>
<td>1</td>
<td>4.7</td>
<td>n/a</td>
<td>6.5</td>
<td>834.0</td>
</tr>
<tr>
<td>Cherry picker truck</td>
<td>1</td>
<td></td>
<td>n/a</td>
<td>71.7</td>
<td>546.0</td>
</tr>
<tr>
<td>Dead Cocos trunk cavity</td>
<td>1</td>
<td></td>
<td>8.0</td>
<td>296.0</td>
<td></td>
</tr>
<tr>
<td>Building exhaust fan</td>
<td>1</td>
<td></td>
<td>n/a</td>
<td>13.5</td>
<td>508.3</td>
</tr>
<tr>
<td>Building junction box</td>
<td>1</td>
<td></td>
<td>n/a</td>
<td>46.0</td>
<td>583.3</td>
</tr>
</tbody>
</table>

† Shown in Appendix 2, Fig. A2.2 (picture 8).

the snag or pole. Nest heights ranged from 2.0 to 9.2 m above ground level (Table 1). Round structures used (e.g., utility poles or palms) averaged 31.8 cm ± 6.9 (SD) in diameter at breast height (range = 18.0–41.0 cm). The nearest tree to a nest ranged from 1.7 to 71.7 m. Average distance from nests to forest was 480.6 m but varied greatly (SD = 247.1; range = 37–1196 m).

**Nestbox occupancy**

Forty-eight pairs of Micronesian Starlings nested in 58 of our 78 nestboxes on utility and EMT poles from 2016 to 2018 (Fig. 1), with 12 of these pairs nesting in more than one nestbox. Distances among nestboxes of actively nesting pairs of birds suggest a preferred spacing of at least 75 m; 11 of the 48 pairs nested in two nestboxes and a 12th pair in three, all of which were in close proximity to the original box (range: 11–75 m). In four additional cases, nearest nestboxes within 24–70 m of an active nestbox remained unoccupied. Twenty pairs of nearest neighboring nestboxes had different breeding pairs that overlapped in nesting attempts; 14 of these were ≥ 75 m apart while only six pairs were within 28–68 m of each other.

Pairs showed high nest fidelity based on five of the six radio-tagged and banded females we monitored over 5–12 months (range: 3–10 nesting attempts; \( \bar{x} \) renesting interval = 70 days ± 44.2 [SD], range: 25–226 days, n = 18 nesting intervals), and an unbanded juvenile/subadult that retained distinctive plumage during three nesting attempts over five months.

There was no relationship between days until nest initiation in the initial nestboxes installed on utility poles and distance to forest (\( R^2 = 0.01; n = 38; P = 0.511; \) Appendix 2, Fig. A2.3). Sixty-one percent of the 70 nestboxes 34–877 m from forest edge (i.e., interior nestboxes) were nested in within 225 days of box deployment (first nest initiated at 8 days, \( \bar{x} \) days until nest initiation = 78.9 ± 57.5 [SD]). Additional nests initiated between 259–653 days resulted in 77% occupancy (Fig. 2). Only one (12.5%) of the eight nestboxes (seven on EMT and one on a utility pole) within 15 m of forest edge (Fig. 1) was used within 225 days (first nest initiated at 223 days). Three other boxes on forest edge were nested in after 288, 346, and 407 days post deployment, resulting in 50% occupancy.

For the subset of five paired EMT and utility pole nestboxes, Micronesian Starlings nested in all five nestboxes on utility poles within the first 225 days following installation. Three of five nestboxes on the paired interior EMT poles were also used within this time period, in two cases, by a pair that had first nested in the nearby utility pole. In the third case, a different pair nested unsuccessfully in the paired EMT nestbox 35 m away. Nestboxes on utility poles were always selected before the paired box on EMT.

Fig. 2. Frequency histogram and cumulative frequency for time from nestbox deployment until nest initiation by Micronesian Starlings (*Aplonis opaca*) utilizing nestboxes (n = 70) on Andersen Air Force Base, Guam. Nestboxes were on utility and EMT poles > 30 m from forest edge. By the end of our study, 77% of the nestboxes were used. The first nest was initiated 8 days after nestbox deployment.
Nest construction and defense

Most nests consisted of an outer ring of green *Casuarina equisetifolia* branch tips (“needles”), an inner ring of strips of coconut leaflets, and a bottom carpet of whole or partial broadleafs (often *Ficus* sp. or *Calophyllum inophyllum*). Sometimes *Casuarina* needles and coconut leaves were interwoven or with other materials such as grass. Occasionally human-made material such as thread, wire or plastic wrappers was added. Nest thickness varied considerably. The broadleaf carpet was at times absent, and eggs laid directly on the coconut leaflets or even the bare cavity or nestbox floor. Non-nestbox nests were built to fit the cavity birds were using. In non-nestbox nests or when we did not remove the nesting material from nestboxes, starlings sometimes cleared out part of the old nesting material, or reused the same nesting material (particularly if the previous clutch was not successful). Often they built a new nest on top of the old one.

Duration of nest building varied, with some pairs completing nests in a few days and others continuing to add new material for several weeks and even after laying eggs. Occasionally, pairs added nesting material to cavities different from the one where they ultimately laid eggs.

Some breeding pairs displayed agonistic interactions (e.g., dive-bombing and fly-bys) toward other Micronesian Starlings, introduced Black Drongos (*Dicrurus macrocercus*) and Eurasian Tree Sparrows (*Passer montanus*), dogs, cats, and humans. However, starlings were not always aggressive toward conspecifics, and there were often 2 to > 15 Micronesian Starlings (sometimes but not always related, based on banded birds) of all age classes in trees near active boxes.

Egg traits, laying patterns, and clutch size

Eggs were white to pale greenish-blue with a variable extent of brownish-red spots distributed primarily on the larger end (Appendix 2, Fig. A2.4). Eggs (*n* = 8) measured with dial calipers averaged 27.85 mm ± 1.09 (SD) by 21.36 mm ± 0.81 (SD). Nests that were checked daily (*n* = 11) indicated eggs were laid on consecutive days. We documented 431 nesting attempts (non-nestbox and nestbox) in the egg laying or incubation stage with an average clutch size of 2.19 ± 0.55 (SD; 31 nesting attempts (non-nestbox and nestbox) in the egg laying or incubation stage with an average clutch size of 2.19 ± 0.55 (SD; 31 nesting attempts with 1 egg, 290 with 2 eggs, 109 with 3 eggs, and 1 with 4 eggs). Occasionally, unhatched eggs from the previous clutch remained in the nest while new eggs were laid, eventually being removed by the breeding pair.

Incubation and nesting periods

The average incubation period was 14.2 days ± 0.75 (SD; range = 13–16; *n* = 11 nests). Males and females took turns incubating during the day. However, based on data from five radio-tagged females, apparently only females incubated at night (HSP and JAS, unpublished data). The average nesting period was 25.1 days ± 1.15 (SD; range = 23.5–27.5; *n* = 8 nests). The naked young stage lasted roughly 9 days. Pin feathers in the alar, dorsal, and caudal tracts began emerging around 10 days (partially feathered stage), and flight feathers began unfurling around 16 days (fully feathered stage). Juvenile plumage was fully grown by 22 or 23 days (Appendix 2, Fig. A2.4).

Age at breeding and seasonality

Micronesian Starlings reached full adult plumage at approximately one year of age, but some individuals retained remnants of juvenile plumage up to 16 months (MK, personal observation). Nearly all birds in breeding pairs were in full adult plumage, implying they generally do not breed until at least one year of age. However, there were two instances of birds with juvenile plumage being part of a breeding pair. In the first case, the pair laid one egg that disappeared shortly afterwards. Although we do not know the exact age or sex of the bird in the second case, it retained some evidence of juvenile plumage for more than five months after the initial sighting. This pair nested 12 times over our study period, laying an average of 2.3 ± 0.49 (SD) eggs per clutch and having a 67% nest success rate.

Active nests occurred in every month of the year (Fig. 3). However, there was a period of higher breeding during March–September and less breeding from October–February. Except for March and April 2016 when the initial boxes were installed and November 2017, > 40% of nestboxes were occupied each month with a maximum of 90% occupied in June 2017.

![Fig. 3. Percent of nestboxes occupied by Micronesian Starlings (*Aplonis opaca*) out of nestboxes available each month on utility poles, Guam.](http://www.ace-eco.org/vol17/iss1/art18/)

DISCUSSION

Although historically considered common in Guam forests, Micronesian Starlings appear to have stopped nesting in these habitats sometime in the mid-1980s to early 1990s based on population surveys (Wiles et al. 1995, 2003). We did not find nests in forest adjacent to AAFB in our searches or other fieldwork regularly done in the area (e.g., radio-tracking, mist-netting), despite starlings foraging extensively in those forests during the day. Micronesian Starlings are conspicuous near their nests, emitting numerous vocalizations; it was easy to locate nests when attentive to their behaviors, and we feel confident nesting birds were not overlooked in the forested areas visited.

AAFB, and particularly its developed areas, has been an important stronghold for Micronesian Starlings. Summarizing the drastic avian decline due to brown tree snakes, Savidge (1987) stated starlings had been observed nesting on artificial structures
located on AAFB. Subsequently, Wiles et al. (1995) found starlings nesting in the developed part of AAFB and suggested the potential safety of this refuge from brown tree snake predation. Brown tree snakes occupy all habitats on Guam, including urbanized areas (Roddia and Savidge 2007, Siers et al. 2017), but may be present at reduced abundances relative to forest habitat. Additionally, brown tree snake control activities employed since 1993 on AAFB (Hall 1996) reduce snake encroachment into the urban area, and the numerous roads and maintained lawns presumably hinder brown tree snake movement (Siers et al. 2016). However, snakes are still present and known to consume fledglings at AAFB (Wagner et al. 2018, Pollock et al. 2019).

A less hospitable environment to brown tree snakes and access to foraging locations in nearby forest for Micronesian Starlings has undoubtedly contributed to starling persistence on AAFB. Additionally, starlings benefit from aspects of their breeding biology, such as their ability to utilize human-made structures. The Singing Starling (A. cantoroides) and Asian Glossy Starling (A. panayensis) are the only other members of Aplonis that have been reported using human-made structures (Finch 1986, Shieh et al. 2016; Appendix 1, Table A1.1). Unlike nests in forest habitat, many urban nesting locations are difficult or impossible for snakes to access. Most poles used for nesting on Guam were of a larger diameter, preventing lasso climbing by brown tree snakes (Savidge et al. 2021). Brown tree snakes can bridge horizontal gaps having 58% of their snout-vent length unsupported; thus, a large snake could cross a 1.5-m horizontal gap (Byrnes and Jayne 2012). None of the 36 non-nestbox locations had a tree within this distance.

Clutch sizes ranging from 1 to 3 eggs have been reported for Micronesian Starlings on various islands (e.g., Yamashina 1932, Brandt 1962, Pratt et al. 1980, Jenkins 1983). Although no sample size was provided, Seale (1901) found clutches of three to four eggs on Guam. Only one of our 431 nesting attempts had a clutch of four eggs; however, some pairs consistently had nonviable eggs, and clutches occasionally overlapped, leading to as many as five eggs being present in the nesting cavity at one time. The modal clutch size of two for Micronesian Starlings is more typical of tropical birds (Jetz et al. 2008) and within the range reported for other Aplonis species (Appendix 1, Table A1.1). Our work confirms that nesting occurs throughout the year in the Mariana Islands, as has been suggested by others (Marshall 1949, Craig 1996, Jenkins 1983). Year-long data for Aplonis species are rare, but it is likely that at least some other species nest continuously (Appendix 1, Table A1.1). Although Micronesian Starlings have a small clutch size, the year-long breeding season allows a continual influx of young into the population, which is undoubtedly partially responsible for their survival on Guam.

Our data suggests only females incubated at night, making them susceptible to nocturnal predation. We witnessed no nest defense when time-lapsed cameras being used for other research recorded snakes defeating baffles during the night and entering nestboxes on four EMT poles at the forest edge (JAS and TFS, unpublished data). However, even birds that have evolved with snakes and aggressively defend their nests against them during the day, often will not defend their nests against nocturnal snake predation (Carter et al. 2007, DeGregorio et al. 2015).

Micronesian Starlings readily used nestboxes on both EMT and utility poles. Extensive pruning of Cocos nucifera in parts of the Base near the time of our nestbox deployment, leading to the destruction of many nests (MK, personal observation), probably was responsible for rapid adoption (e.g., within eight days of deployment) of some nestboxes. Pairs appeared to have high nest fidelity, with virtually all pairs occupying the same nestbox or adjacent boxes throughout our study.

Nestboxes on most utility poles appear safe from predation (JAS and TFS, unpublished data). We recorded some predation events in nestboxes on EMT, but modifications to baffles are being investigated. An obvious benefit of EMT is that it allows expansion of nest sites into locations where utility poles are unavailable. In our small experiment where nestboxes were simultaneously provided on a utility pole and a nearby EMT pole, the former was always selected first. Noise or movement from baffles on EMT poles may be a slight deterrent to nestbox use on this substrate. Because there is little development along forest edge in our study area (and thus no artificial structures to nest in), we could not discern if the more interior locations of non-nestbox nests reflect edge avoidance. Nonetheless, our findings suggest birds avoided nesting in boxes within close proximity to forest (Fig. 1). Given high fledging mortality due to brown tree snakes (Pollock et al. 2019), placing nestboxes close to forest, even if protected, is not recommended. Lastly, our data suggest that nestboxes should be spaced approximately 75 m or more apart to maximize occupancy.

Until brown tree snakes can be heavily controlled in forest habitats, or for that matter in other urban locations, developed areas on AAFB will likely remain the stronghold for nesting Micronesian Starlings on Guam. The ability to protect nestboxes based on placement or with protective baffles and the rapid adoption we recorded, combined with high nest fidelity, suggest nestboxes could be used to augment the starling population in other urban areas on Guam, helping restore seed dispersal in adjacent forests. Given the devastation to coconut palms caused by the recently introduced rhinoceros beetle (Oryctes rhinoceros), nestboxes may become even more important for the maintenance and expansion of Micronesian Starling populations. However, snakes in other areas must be suppressed enough to allow the susceptible fledging stage to have reasonable survival. Despite consistent long-term control aimed at brown tree snake interdiction near key cargo areas and housing on AAFB, starling fledgling survival is one of the lowest rates recorded for passerine birds (Pollock et al. 2019). Small populations of starlings are found in urban locations outside of AAFB (Pollock et al. 2021), and while brown tree snake interdiction efforts were also started in 1993 in commercial port facilities and other military installations in central and south-central Guam (Hall 1996), no apparent sustainable starling populations have established outside of AAFB on Guam. Possible explanations include snake control has not suppressed snake numbers to the level at AAFB, safe nest sites and locations for fledglings are lacking, and/or Micronesian Starlings, that were locally extinct in these areas at the time control started, have not been able to recolonize in sufficient numbers to sustain a population. A small population of urban-nesting Micronesian Starlings was still present when interdiction began on AAFB (Wiles et al. 1995), and these served as the source for the present population. Thus, active
reintroduction of Micronesian Starlings to urban locations with nearby forest for foraging, combined with intensive snake suppression and possible use of well-placed protected nestboxes, may be necessary to allow their range expansion on Guam.

Responses to this article can be read online at:
https://www.ace-eco.org/issues/responses.php/2106

Acknowledgments:
This research was a result of funding provided by U.S. Navy, Joint Region Marianas, Guam to investigate Micronesian Starlings as a surrogate for guiding reintroduction efforts for the endangered Guam Micronesian Kingfisher (Todiramphus cinnamominus cinnamominus). We appreciate support from the following Naval Facilities Engineering Systems Command Marianas personnel: K. Brindock, A. Brooke, S. Garcia, M. Hall, J. Horeg, D. Lujan, M. Mazurek, S. Mosher, and J. Watkins, and R. Reed, U.S. Geological Survey (USGS). We thank the Guam USGS BTS team and CSU technicians that assisted in various aspects of the research. S. Siers initiated work on this project. All field work was conducted in accordance with Colorado State University IACUC Protocols.

LITERATURE CITED


**Appendix 1. Table A1.1.** Geographic distribution, general breeding biology, and conservation status of the 25 *Aplonis* species. Distribution and breeding data are largely taken from literature summaries by Craig and Feare (2020) and Feare and Craig (1999). Conservation status is from BirdLife International (2021). Additional sources used are listed. Much of the reproductive data are anecdotal or based on limited observations and sample sizes.

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Common name</th>
<th>Geographic distribution</th>
<th>Breeding season</th>
<th>Nest substrate</th>
<th>Nest type</th>
<th>Colonial breeder (yes/no)</th>
<th>Clutch size</th>
<th>Incubation</th>
<th>Incubation / Nestling periods (X ±SD)</th>
<th>Comments including status</th>
<th>Additional Sources †</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. atrifusca</em></td>
<td>Samoan Starling</td>
<td>Samoan Islands</td>
<td>Mar-Nov; likely lower level of breeding year-round</td>
<td>tree, including coconut palm cavity</td>
<td>n</td>
<td>Island group endemic; least concern, common in range.</td>
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<td>Pyle et al. 2016; Tarburton 2018</td>
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<tr>
<td><em>A. brunneicapillus</em></td>
<td>White-eyed Starling</td>
<td>Bougainville; Choiseul, Rendova and Guadalcanal, Solomon Islands</td>
<td>Guadalcanal: Jul-Aug; Bougainville: Jan</td>
<td>among epiphytes, tree cavity</td>
<td>y</td>
<td>Island group endemic; vulnerable, range-restricted, patchily distributed.</td>
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<td>Marki et al. 2014; Woxvold and Novera 2021</td>
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<tr>
<td><em>A. cantoroides</em></td>
<td>Singing Starling</td>
<td>New Guinea and surrounding islands; Bismarck Archipelago; Solomon Islands; Arus</td>
<td>New Guinea: Sep-Feb; smaller islands: Mar, Jul, Aug</td>
<td>tree, including coconut palm; sometimes in cliffs, coral rock, buildings or other human-made structures</td>
<td>cavity</td>
<td>sometimes colonial 2-3</td>
<td></td>
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<td></td>
<td>Wide-ranging island species; common, expanding range into developed areas; one nest of 4 young found (Bradley and Wolff 1958).</td>
<td>Bradley and Wolff 1958; Filardi et al. 1999; Kratter et al. 2001; Ripley 1964; Sibley 1951; Smith 1947</td>
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<tr>
<td><em>A. cinerascens</em></td>
<td>Rarotonga Starling</td>
<td>Rarotonga, Cook Islands</td>
<td>Aug-Dec</td>
<td>tree</td>
<td>cavity</td>
<td>n</td>
<td>at least 2</td>
<td></td>
<td></td>
<td></td>
<td>Island endemic; vulnerable.</td>
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<tr>
<td><em>A. corvina</em></td>
<td>Kosrae Starling</td>
<td>Kosrae, Caroline Islands</td>
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<td></td>
<td></td>
<td>Island endemic; extinct; no breeding data.</td>
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<tr>
<td>Species</td>
<td>Common Name</td>
<td>Distribution</td>
<td>Breeding Season</td>
<td>Nest Type</td>
<td>Breeding Notes</td>
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<td><em>A. crassa</em></td>
<td>Tanimbar Starling</td>
<td>Tanimbar Island, Lesser Sundas</td>
<td>Aug-Nov</td>
<td>tree cavity</td>
<td>Island endemic; near threatened; breeding recorded with hetero-specifics (Mioduszewska et al. 2018); breeding poorly known.</td>
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<td><em>A. dichroa</em></td>
<td>Makira Starling</td>
<td>Makira Island, Solomon Islands</td>
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<td>tree dome; possibly in cavity</td>
<td>Island endemic; restricted range but common to locally common; breeding poorly known.</td>
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<tr>
<td><em>A. feadensis</em></td>
<td>Atoll Starling</td>
<td>Bismarck Archipelago; Solomon Islands; assorted small islands northeast of Papua New Guinea</td>
<td>Jun-Jul</td>
<td>tree, including coconut palm cavity</td>
<td>Island group endemic; near threatened; breeding data limited.</td>
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<tr>
<td><em>A. fusca</em></td>
<td>Norfolk Starling</td>
<td>Norfolk and Lord Howe Islands</td>
<td>Sep-Nov and Feb-Mar (A. f. fusca); Sep-Dec and May-Jun (A. f. hulliana)</td>
<td>tree or tree fern cavity</td>
<td>Island endemic; extinct; Hindwood (1949) reported clutch of 3-5 but no sample sizes.</td>
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<td><em>A. grandis</em></td>
<td>Brown-winged Starling</td>
<td>Bougainville; Solomon Islands</td>
<td>Bougainville: May-Sep; New Georgia: Nov; Kolombangara: Sep-Nov; extended season likely</td>
<td>dome; cavity</td>
<td>Island group endemic; least concern, common within range.</td>
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<td>Species</td>
<td>Common Name</td>
<td>Geographic Range</td>
<td>Nesting Habitat</td>
<td>clutch size</td>
<td>Notes</td>
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<tr>
<td>A. insularis</td>
<td>Rennell Starling</td>
<td>Rennell and Bellona Islands, Solomon Islands</td>
<td>tree, including coconut palm cavity</td>
<td>n 3</td>
<td>Island endemic; least concern, but status not well known; one clutch of 3 eggs recorded,</td>
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<td>published without associated date. Filardi et al. 1999</td>
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<tr>
<td>A. magna</td>
<td>Long-tailed Starling</td>
<td>Biak and Numfor Islands, Western New Guinea</td>
<td>tree</td>
<td></td>
<td>Island endemic; restricted distribution but reported abundant in range; breeding poorly</td>
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<tr>
<td>A. mavornata</td>
<td>Mysterious Starling</td>
<td>Mauke, Cook Islands</td>
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<td>Island endemic; extinct; no breeding data available.</td>
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<tr>
<td>A. metallica</td>
<td>Metallic Starling</td>
<td>New Guinea; Lesser Sundas; Moluccas; NE Australia; Bismarck Archipelago; Solomon</td>
<td>New Guinea: variable, year round;</td>
<td>y 1-4</td>
<td>Wide distribution, adaptable; possibly some cooperative breeding; highly colonial.</td>
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<td>Islands</td>
<td>NE Australia: Aug-Feb</td>
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<td>Ripley 1964; Smith 1947</td>
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<tr>
<td>A. minor</td>
<td>Short-tailed Starling</td>
<td>S Philippines (Mindanao); widely distributed throughout Indonesia</td>
<td>tree, including coconut palm cavity</td>
<td>sometimes</td>
<td>Wide-ranging island species and generally locally common; breeding seems concentrated Sep-</td>
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<td>colonial</td>
<td>Dec but may extend later. Linsley et al. 1998; Noske 2003; Trainor and Soares 2004</td>
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<tr>
<td>Species</td>
<td>Common Name</td>
<td>Distribution and Habitat</td>
<td>Breeding Information</td>
<td>Notes</td>
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<td>A. mysolensis</td>
<td>Moluccan Starling</td>
<td>Indonesia: Banggai and Sula Is, the Moluccas and Western New Guinea islands</td>
<td>Aug-Nov, tree cavity</td>
<td>Island group endemic; common and adaptable in most of range; breeding poorly known.</td>
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<tr>
<td>A. mystacea</td>
<td>Yellow-eyed Starling</td>
<td>New Guinea Island group endemic; near threatened; breeding poorly known.</td>
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<tr>
<td>A. opaca</td>
<td>Micronesian Starling</td>
<td>Caroline Islands; Mariana Islands; Palau</td>
<td>Guam: year-round; Yap and Pohnpei: Aug; Chuuk: Oct-Dec, tree, especially coconut palm; buildings and other human-made structures; nest boxes</td>
<td>Wide-ranging island species; least concern; common in much of range except Guam where exotic brown treesnakes have decimated population (Savidge 1987).</td>
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<tr>
<td>A. panayensis</td>
<td>Asian Glossy Starling</td>
<td>SE Asia (NE India, Myanmar, Thailand, Singapore, Peninsular Malaysia); Borneo; Philippines; Indonesia</td>
<td>India: Feb-Apr; Andamans/Nicobars: Apr; Myanmar: Mar-Jun; Peninsular Malaysia: Jan-Aug; Java/Bali: Jan-Jun; Borneo: Jun-Sep; Philippines: Feb-Jun, tree, including coconut palm; cliffs, banks; buildings and other human-made structures; nest boxes</td>
<td>Widespread and common in native range; introduced in parts of Malaysia and Taiwan (at least); highly adaptable; nests apparently year-round in native range; breeding in urban sites.</td>
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</table>

Breeding data in this manuscript; Savidge 1987; Mukhlisi et al. 2021; Shieh et al. 2016 (incubation and nestling periods).
<table>
<thead>
<tr>
<th>Species</th>
<th>Range</th>
<th>Habitat</th>
<th>Status</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. pelzelni</td>
<td>Pohnpei, Caroline Islands</td>
<td>Jul tree cavity</td>
<td>Island endemic; critically endangered and possibly extinct; female in breeding condition in Jul; breeding poorly known.</td>
<td></td>
</tr>
<tr>
<td>A. santovestris</td>
<td>Espiritu Santo Island, Vanuatu</td>
<td>tree cavity</td>
<td>Island endemic; endangered; breeding poorly known.</td>
<td></td>
</tr>
<tr>
<td>A. striata</td>
<td>New Caledonia, Loyalty Islands</td>
<td>Dec-Jan tree cavity</td>
<td>Island group endemic; common; breeding poorly known.</td>
<td></td>
</tr>
<tr>
<td>A. tabuensis</td>
<td>Vanuatu; Temotu Islands; Samoan Islands; Fiji and surrounding islands</td>
<td>Samoa: Jan-Oct; Tonga: Oct-Jan, May; Niue: Aug tree, including coconut palm cavity</td>
<td>Wide-ranging island species; common and adaptable in range; breeding records in Tarburton 2018 span Jan-Oct and Göth and Vogel 1999 suggest Oct-Jan, so perhaps year round.</td>
<td></td>
</tr>
<tr>
<td>A. ulietensis</td>
<td>Raiatea, Society Islands</td>
<td></td>
<td>Island endemic; extinct; no breeding data.</td>
<td></td>
</tr>
<tr>
<td>A. zelandica</td>
<td>Vanuatu; Nendo and Vanikoro in Santa Cruz Islands</td>
<td>tree cavity</td>
<td>Island group endemic; near threatened; uncommon to scarce; breeding poorly known.</td>
<td></td>
</tr>
</tbody>
</table>
Addional sources:

Figure A2.1. Micronesian Starling nestbox on a utility pole (left) and a nest being checked on an EMT pole (right). Insert shows a pair of starlings utilizing a nestbox.
Figure A2.3. Scatterplot of days until nest initiation in nestboxes on utility poles and distance to the forest edge. Data is from the first nestboxes installed in March and April 2016. No significant relation was found.
Figure A2.4. Eggs of Micronesian Starlings (A) and representative photos of nestling stages: (B) naked young (~1-9 days), (C) partially feathered (~10-15 days), and (C) fully feathered (~16 days to fledging).