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MARIANA CROW (*Corvus kubaryi*)

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INTRODUCTION

The Mariana Crow (*Corvus kubaryi*), or Aga in the Chamorro language, is endemic to the Mariana Islands of the western tropical Pacific, where it is historically known from the islands of Guam and neighboring Rota. The native population on Guam was driven to extinction by 2003 due to predation by the brown tree snake (*Boiga irregularis*). Into the 1990s, it remained widespread on Rota, although since that time population surveys have documented a substantial decline. Phenomena driving the decline include a reduction of first year survival of young, which appears to be related to predation by feral cats and disease. Habitat degradation also has been suggested to be a contributing factor. Preferred habitat has been described historically as being mature native forest, although more recent study has demonstrated that the species appears to be more of an ecological generalist than typically assumed. Birds have been found to use low forest strand, mixed native-alien second growth forest, alien thickets and even savanna habitats in addition to mature native forest. Due to its endangered status, a captive breeding program has been established for it and primarily in recent years its biology has been studied intensively.

The species is relatively small and black, although it displays areas of green and blue-black iridescence. It is rather vocal, particularly during wet season courtship activity. In addition to studies into its population status and trends, investigations have been conducted into its spatial ecology, vocal behavior, foraging ecology, population dynamics, juvenile dispersal and nest site selection.

IDENTIFICATION

Field Identification

This comparatively large passerine is, however, small for a crow. It is primarily black except for areas of iridescent greenish-black gloss on its head and bluish-black gloss on the back, wings and tail (Baker 1951). It is also identifiable by its typical and commonly given crow-like vocalizations.

Similar Species

The only other all black bird species within the Mariana Crow's limited range is the introduced Black Drongo (*Dicrurus macrocercus*), which is far smaller and more delicately built.

PLUMAGES, MOLTS AND STRUCTURE

Plumages

The adult has a slight greenish-black gloss on its head. The back, wings and tail have a bluish-black gloss and the underparts are dull with a greenish-black

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gloss. The bases of the feathers are light grayish or more nearly white on the neck, which produces a ragged appearance. The nasal bristles are short but extend over the nostrils and base of the culmen (Baker 1951).

Juvenile (first basic) plumage. Juvenile feathers have less gloss and their wings and tail are browner than those of adults (Baker 1951, Jenkins 1983). Moreover, they have a brown gloss in the tail (MAC Working Group 2014).

Molts

From December to February, birds were observed to be in fresh plumage, but those shot in late March or later were faded and rough (Hartert 1898). Molting on Guam was thought to occur in May–September. Most birds collected in this period were in the process of molt. Skins obtained on Rota in late October also exhibited signs of molt. However, specimens taken in December–February were in fresh or slightly worn plumage. The species appears shabby when in molt, because the grayish and whitish basal parts of feathers are exposed (Baker 1951). The short gray feather bases are visible around the body and neck region and grow lighter toward the head (MAC Working Group 2014). Aside from these observations, the molt cycle is unstudied.

Bare Parts

Bill. The bill is black (Hartert 1898, Baker 1951).

Iris. The iris is variously described as dark brown (Baker 1951), van dyke brown (Hartert 1898) or dark hazel (Seale 1901).

Tarsi and toes. The tarsi and feet are black (Hartert 1898, Baker 1951).

Measurements

Linear measurements. The earliest reported measurements, although the details of measurement procedure and sample size are lacking, are apparently all from Guam: male culmen = 53–57 mm, wing = 230–245 mm, tail = 160–170 mm, tarsus = 50 mm; female culmen = 48–52 mm, wing = 220–230 mm, tail = 160 mm, tarsus = 50 mm. A dwarf Guam specimen of unknown sex was measured as culmen = 47 mm, wing = 212 mm, tail = 146 mm. Total length was 38–41 cm (Hartert 1898). Guam birds also were described as having total length = 380 mm, wing spread = 660 mm, wing = 241 mm, tail = 155 mm, tarsus = 51 mm, culmen = 46 mm, mid-toe and claw = 51 mm (Seale 1901). Means and ranges for specimens from Guam are males (*n* = 9): flattened wing = 236 (229−244 mm), tail = 165 (158−170 mm), exposed culmen = 55 (51−57 mm), tarsus = 51 (49−52 mm); females (*n* = 19): flattened wing = 227 (222−241 mm), tail = 151 (143−166 mm), exposed culmen = 50 (47−54 mm), tarsus = 50 (46−54 mm). Specimens of males from Rota measured (*n* = 3) flattened wing = 235 (233−236 mm), tail = 167 (166−169 mm), exposed culmen = 54 (53−56 mm), tarsus = 50 (49−51 mm) (Baker 1951).

Mass. Means and ranges of masses for Guam males (*n* = 5) = 256 (231−270 g) and for females (*n* = 11) = 242 (205−260 g). Mass of a Rota male = 256 and for a female = 260 g (Baker 1951).

SYSTEMATICS

Systematics History

The Guam population was first described as *Corvus solitarius* (Lutke 1836). It was then assigned to species *kubaryi* (Reichenow 1885), although the type locality was incorrectly reported as Palau (Hartert 1898). The Marianas population also was assigned to *Corone phillipina* and the incorrectly designated, non-existent Palau population was assigned to *Corone kubaryi* (Wiglesworth 1891). All later authors concurred with the species' placement into *Corvus* (e.g., Hartert 1898, Seale 1901, Baker 1951).

Geographic Variation

The Mariana Crow is monotypic, with both Guam and Rota populations showing low genetic variation. The populations are genetically distinct from one another, which suggests that little gene flow occurred between them (Cortes-Rodriguez et al. 2019). Rota birds initially appeared to show less genetic diversity than those on Guam, indicating that Rota was colonized from Guam (Tarr and Fleisher 1999). However, a more recent analysis indicates that the reverse is true, although this may reflect the recent genetic bottleneck that the Guam population experienced due to predation by the brown tree snake. Alternatively, it may reflect the small sample size from Guam compared with that from Rota (Cortes-Rodriguez et al. 2019). No differences in color or structure could be found between specimens obtained on Guam and Rota (Baker 1951).

Related Species

The monotypic Mariana Crow has been described as a modified species isolated on Guam and Rota for a long time. It was thought that the population was a relict of one once more widely distributed. Characters that showed distinctness from possible ancestral species included small size, slender bill and dull coloration. The species was initially thought to be derived from the *C. enca* group: *C. e. pusillus* of the Philippines or *C. e. celebensis* of the Celebes area. Small size, the shape of the culmen, the lack of pointed feathers on the breast and the presence of white on basal parts of feathers of the nape are char-

FIG. 1. A captive Mariana Crow from the now extinct Guam population.

acters that *C. kubaryi* has in common with *C. enca* (Baker 1951). However, more recent DNA evidence indicates that its closest relative is the Large-billed (formerly Jungle) Crow (*C. macrorhynchos*) of Asia, which is likely the ancestral species from which it is derived. These two species show a relationship with the House Crow (*C. splendens*) of south Asia. The *C. enca* group is instead rather distantly related to the Mariana Crow (Jonsson et al. 2012).

Fossil History

No prehistoric bones of *Corvus* have been found on Tinian, Aguiguan or Rota (Steadman 1999), which suggests that colonization of Rota may have been comparatively recent.

DISTRIBUTION

The Mariana Crow is known historically from Guam and Rota (Baker 1951). An unconfirmed and perhaps incorrect report exists for Aguiguan (Engbring et al. 1986). Still, long distance colonizations of birds to islands are well-documented (Thornton 1996), and in the Mariana Islands the Mariana Fruit Dove has recently colonized Sarigan on its own 100 km from the nearest population on Saipan (Radley 2012).

Historical Changes to the Distribution

It is extinct on Guam, with native birds reported gone by 2003 (MAC Working Group 2014).

HABITAT

On Guam, the Mariana Crow was described as inhabiting forest (Lutke 1836, Engbring and Ramsey 1984), jungle (Seale 1901) or deep forest (Marshall 1949). Stophlet (1946) described it as being observed more frequently in forest than in open country. It also was described as confined to forested areas and coconut plantations on Guam and to avoid human habitation (Baker 1951). Later, it was described as being found in about equal numbers in mature forests, second growth and mixed woodlands on the northwesternmost portion of the island. It appeared to prefer native forest to agricultural areas. The species also frequented coastal strand, where it often perched or foraged in coconut palms. Staff notes from the early 1960s indicated that it once was common in ravine and coastal forests as well as the riparian habitats of southern Guam. Perhaps the only habitat in which it was not reported historically was savanna (Jenkins 1983). Crow sightings were found to decline with increasing proximity to roads and aircraft runways (National Research Council 1997).

On Rota, the Mariana Crow was described as occurring in all woodland habitats, including mature forest, second growth, mixed woodland and coastal strand (Engbring et al. 1986), although this description appeared to be derived from Jenkins' (1983) observations from Guam. When it was more common, birds were found to use not only mature forest but also stunted strand forest and to use both native and introduced trees. Plant species used for such

FIG. 2. Prime Mariana Crow habitat consisting of mature native limestone forest growing along the slopes of the Sabana plateau.

behaviors as vocalizing, playing, resting, and feeding young included for Guam: *Pandanus* sp., *Leucaena leucocephala, Cocos nucifera* and Rota: *Cocos nucifera, Scaevola taccada, Casuarina equisetifolia, Hernandia nymphaefolia, Maytenus thompsonii, Elaeocarpus sphaericus, Artocarpus mariannensis, Pandanus sp., Ficus prolixa, Tournefortia argentea, Neisosperma oppositifolia, Mangifera indica* (Tomback 1986).

Recent estimates indicate that 67.2% of Rota remains forested, with 78.7% of this being native forest. Habitat cover has not appreciably altered since 1976 (Donnegan et al. 2011). In level areas planted to sugarcane (*Saccharum officinarum*) prior to World War II, second growth comprised of mixed introduced and native trees constitutes 13.0% of forest cover, with many natives aggressive competitors with alien species. Areas of planted crop-producing trees like coconuts (*Cocos nucifera*), termed agroforest, account for 5.8% of forest area, and 1.8% is low coastal strand forest that occurs principally along the north-central coast. The remaining 32.8% of Rota includes 6.6% residential/commercial landscapes, 1.7% cropland, particularly on the Sabana, and 22.8% open ranch land with scattered individual trees and tree copses best termed savanna, although small amounts of native swordgrass (*Miscanthus floridulus*) savanna also exist on exposed volcanic soils (Craig 2023).

Of 156 nest sites found on Rota in 1996–1999, 39% were in mature forest, 42% were in secondary limestone forest and 19% were in coastal forest. The nests themselves were placed in interior forest, with an average distance from forest edge being 62 m. Although 18% of the forested area of Rota consists of *Leucaena leucocephala* or other introduced trees, no nests were in anything other than native trees (Morton et al. 1999). In 1992–1994, 90% of perching observations (n = 115) were in native trees, primarily in mid- to low heights of the canopy. Almost 61% of banded, pre-dispersal juvenile resightings (n = 398) were associated with young limestone forest. In contrast, only 49% of study blocks were categorized as young limestone forest, suggesting that juveniles showed a small preference for young forest (MAC Working Group 2014). In a 1992–1994 examination of 11 Rota nests, all were in native limestone forest (Lusk and Taisacan 1996). Similarly, more recent study has demonstrated that in the present small Rota population, nests are typically placed in mature native forest. Breeding pair densities averaged 1/22 ha of predominantly native forest on six 50 –130 ha study areas. Pair densities were 1/37 ha in a fragmented forest patch and 1/12 ha along the coastal terrace above Puntan Saguagahga (Ha et al. 2011). However, Faegre (2017) found no prey or vegetation factors that were predictive of either core use areas near nests or outer areas of home ranges.

Based on 63 measures of habitat occupancy by individuals on Rota during the wet season and an additional 45 measures made during the dry season in 1992–1993, forest was by far the principal habitat type occupied during both seasons, with savanna present less than half as often as forest, although individual birds occurred in solely savanna habitat. Wet season savanna occupancy showed a small increase and forest occupancy a showed similar small decrease compared with the dry season. Other habitat types were used in only nominal amounts during both seasons, although birds occupied areas that included beaches, cropland and a variety of forest types: coastal strand forest, low thicket-like forests, agroforest and mixed native/introduced forest. Habitat occupancy measures showed that forest use was greater than and savanna use less than its availability along transects, particularly during the dry season, although neither season yielded results significantly different from availability (Craig 2023).

MOVEMENTS AND MIGRATION

Movements

The Mariana Crow has not been recorded to make inter-island movements, although at some point in the past birds moved between Guam and Rota.

Dispersal and Site Fidelity

In a study of the Mariana Crow's spatial ecology, fledgling mobility was low during the first 31 days post-fledging. The effects of age (fledgling or sub-adult) and time (months post-fledging or post-dispersal) on mobility were often driven entirely by this period. However, home range size increased over time for both fledglings and sub-adults, with sub-adults on average using more than twice the area as fledglings. Sub-adults also tended to make longer daily movements than fledglings. Monthly home range areas did not increase over time but the average overlap between consecutive months in individuals' home range area was only 63%, suggesting that large shifts in space use occurred each month (Faegre et al. 2018). In a documented dispersal between the north and south ends of Rota, a female moved 12,687 m, whereas all other recorded dispersals were less than 5,000 m (Cortes-Rodriguez et al. 2019).

DIET AND FORAGING

Feeding

Microhabitat for foraging. Foraging has been described as taking place on the ground beneath the dense woodland canopy where birds were secretive and noiseless (Marshall 1949). On Guam, birds were recorded feeding from and perching in dense foliage (Baker 1951). Birds also were described as rustling noisily throughout the base of the leaf structure of *Pandanus.* The species often fed on the ground under thick forest canopy or scrub growth, where it rustled vigorously through leaf litter searching for insects, but it was not usually seen on the ground in open areas or along roadways (Jenkins 1983). It has been observed foraging in the canopy, subcanopy, understory, in forest undergrowth and on the ground (Engbring et al. 1986, Tomback 1986). On Rota, it was observed to search the leaves of *Cocos nucifera*, *Ficus prolixa* and the bark of *Scaevola taccada*, presumably to look for insects or lizards. On one occasion, a bird pulled vigorously at the dead leaves of a *Pandanus* (Tomback 1986). Rota crows were found to forage at an average of 4.9 m above the ground, which was significantly lower than the average canopy height of 7.5 m (USFWS 2005).

Foraging substrates used were 1) dead wood: rotten wood, either fallen or in a snag or live tree that is excavated by tearing and/or pecking to search for animal prey, 2) bark: dead or live bark that is peeled or flaked from trees in order to eat the live bark to find hidden prey, 3) foliage/branches: food items are gleaned directly from branches/twigs or foliage of any plant except *Pandanus*, 4) rolled leaves: dead or live, rolled or crumpled leaves that can be on a tree or on the ground that are searched for concealed prey, 5) ground debris: leaves, twigs, chunks of rotten wood or crevices between rocks or roots that are searched for food items, 6) *Pandanus* sp.: live or dead *Pandanus* leaves or debris accumulated in their crowns that are searched for food items (Faegre et al. 2019).

Food capture and consumption. On Guam, the Mariana Crow displayed complex foraging behavior. It selected a leaf and held it with the feet while tearing off and eating small chunks with the bill. Often, a bird delivered woodpecker-like blows to the branches, apparently to loosen chunks of edible size. Blows were delivered 4–5 at a time, and the series was repeated 3–4 times. The bird balanced with its feet and pulled back its head and upper body to deliver blows with the beak. This technique was observed to be used by one bird that was attempting to break through the outer layer of a newly emerging *Cocos nucifera* frond, which it pecked at persistently for ca. 40 minutes (Jenkins 1983).

An extensive learning period appears necessary for the development of foraging techniques by young. Fledglings on Guam closely followed parents. At times, juveniles mimicked the foraging patterns of the adults. Adults collected food items, which they fed one at a time to their young, but they did not regurgitate from the crop for young (Jenkins 1983).

Diet. The Mariana Crow is omnivorous. On Guam, birds were described as pulling up corn seedlings and eating the eggs and nestlings of other birds (Seale 1901). Stomachs of five specimens contained grasshoppers and other insects, lizards, buds, flowers and other vegetable matter (Marshall 1949). The stomachs of four birds collected in the early 1960s contained mole crickets (*Gryllotalpa africana*) praying mantids (Orthoptera), earwigs (Dermaptera) and hermit crabs (*Coenobita* sp.). Birds also have been observed to feed on large caterpillars (Lepidoptera). On one occasion, a caterpillar was observed to be fed to a fledgling (Jenkins 1983). Observations from Guam and Rota indicated that skinks, geckos, immature rats and bird eggs are eaten. Moreover, the species has been observed foraging on the foliage, fruit, seeds, and buds of at least 26 different tree species (MAC Working Group 2014).

Plant material eaten by Guam birds primarily consisted of fruits, but also included seeds, flowers, buds, foliage and bark. The fruits of *Ficus* sp. were preferred, as were the fruits and flowers of *Hibiscus tiliaceus*, the large fruits of *Neisosperma oppositifolia* and the small umbelliferous fruits of *Premna obtusifolia*. Foliage also was consumed, with preference being shown for dead and dying (brown) leaves of *Neisosperma, Pandanus* and *Hibiscus*. The species was one of the few native birds that fed on the abundant *Pandanus*. In addition to eating its fruits and dead leaves, birds searched through leaves, presumably for insects. They also tore off and ate small chunks of wood and, more frequently, bark from broken branches. Plant food included: *Aglaia mariannensis*: bark; *Cestrum diurnam*: fruit, *Cocos nucifera*: leaves, flowers; *Ficus* sp.: fruit, *Hibiscus tiliaceus*: leaves, fruit, bark; *Momordica charantia*: seeds; *Neisosperma oppositifolia*: leaves; *Ochrosia* sp.: leaves, bark; *Pandanus* sp.: leaves, bark; *Premna obtusifolia*: fruits (Jenkins 1983). On Rota, the Mariana Crow was observed foraging on the fruit of *Artocarpus mariannensis* (Tomback 1986).

During 2010–2013 Rota observations of 36 Mariana Crows, principal food items taken included 21.6% termites, ants and insect larvae and eggs, 30.7% other adult insects, 4.0% wasp nests, 18.9% lizards, 7.6% crabs, 13.7% fruits, seeds and other plant material, 3.4% bird nestlings, eggs and miscellaneous items. Cumulatively, 14% were plant-based, 56% were insects or their larvae and eggs and 30% were non-insect animal prey. Most foraging occurred above ground, although ca 26% of fledgling foraging and ca. 42% adult foraging occurred on the ground. Two food categories, fruits/seeds/plants and ants/termites/larvae, which were procured and processed with simple behaviors, were taken more frequently by fledglings. Crabs, which were processed using complex behaviors, were captured more frequently by adults. Adults acquired more food items from the ground than did fledglings and sub-adults—a result driven by adults' high level of crab predation. Foraging behavior did not differ between wet and dry seasons, which indicated that the species maintained a similar diet year-round. Age-related differences in foraging behavior were prominent, which might drive differences in age-dependent survivorship. Complex trophic interactions between non-native snails and *Coenobita* hermit crabs may have modified crow foraging behavior, increasing the vulnerability of crows to feral cat predation. (Faegre et al. 2019).

SOUNDS AND VOCAL BEHAVIORS

Development

Juvenile crows on Guam were described as making immature squawks and begging food from adults (Jenkins 1983). The vocalizations of juveniles also have been described as being similar to those of adults: 1) locational calls (n = 3) were somewhat shorter in duration than those of adults but given in similar contexts; 2) monolog (n = 3), consisting of series of squalling, whining calls of varying inflection, given by a juvenile alone in the understory or with other crows perched nearby; 3) hunger calls (n = 3), consisting of a series of insistent *aaa* sounds with a rising inflection, often accompanied by wing flutters. The calls increased in intensity until the young bird was fed by a nearby adult. While gulping food, juveniles also made gurgling sounds and as juveniles swallowed food they emitted a choking, yelping sound (Tomback 1986).

Vocal array

Song. Calls described as a monolog, which include a variety of quiet or excited guttural and squalling sounds given for several minutes by members of a pair at the nest appear to be the song of the species. The song described by Brown (1985) for the American Crow (*Corvus brachyrhynchos*) seems homologous in sound structure and context to the monolog in the Mariana Crow (Tomback 1986).

Calls. An early description of calls by Guam birds described them as *Qu a a Qu a a* (Seale 1901). The call was later described as a high-pitched *caw*, given in a series of 2–3 notes. The call sounded more like the scream of a parrot than of a crow (Stophlet 1946). The *caw* also was reported to have conversational variations (Marshall 1949). Birds made harsh squawks higher-pitched and more nasal than the calls of the American Crow, with the loudest squawks given as birds hopped and made short flights through the forest, or when greeting one another when returning from short flights. The loud squawk also was given by birds in flight, when it likely served as a flocking call. A softer, squeakier call was uttered when groups of birds foraged on or near the ground (Jenkins 1983). The call carries great distances, especially on a calm, quiet day when a bird is flying high above the forest (Engbring and Ramsey 1984). Engbring et al. (1986) described presumably Rota birds as being fairly vocal when in groups flying above the forest canopy but less vocal when foraging in forest. Pratt et al. (1987) described vocalizations as a loud *kraa-ah* and quiet conversational notes.

In a more focused study (Tomback 1986), the vocalizations of adults on Guam and Rota were found to be of four general types: 1) locational calls (n = 8), consisting of high-pitched *caws* or *hi* sounds given 1–3 times in succession. Locational calls were probably used to maintain contact among individuals of a pair, family group or flock. Accompanying behaviors included perching, foraging, flying through or above the forest; 2) squally locational calls (n = 6), consisting of nasal *caws* with an *aaa* sound used by a nesting pair; 3) monolog, which included a variety of quiet or excited guttural and squalling sounds given for several minutes by members of a pair at a nest. These calls may serve some courtship or pair-bond function; 4) alarm calls, consisting of series of sharp, rapid *caws*. This vocalization was made by two crows perched in a *Casuarina* tree when they were startled by the sudden appearance of several people. Sonagraphic patterns are similar to those of *C. brachyrhynchos* but have higher frequencies. Squalling, persistent food-begging calls by juveniles were common throughout the coastal strand on Rota and were occasionally heard on Guam.

In 2017–2018 on Rota, six call types were identified using acoustic analysis of recorded vocalizations: 1) raspy, high to lower intensity aggression/alarm calls, of which there were three subtypes and which were the most common call type; 2) rising and abruptly falling slightly raspy calls of unknown function; 3) rising and abruptly falling clear calls of unknown function; 4) rising and slowly falling clear contact calls, which were the second most common call type; 5) whining, quieter contact calls; 6) quiet, grunting calls for intimate chatter. Call rate was highest in morning and declined throughout the day. Calls significantly differed among individuals, they were similar within mated pairs, they differed between males and females, with females vocalizing at higher frequencies than males, and they showed small but significant differences among genetic subgroups. Four call types were produced by nestlings.

Begging calls were produced as early as the first day after hatching, followed by chirps starting on the second day and gobbles by the end of the first week. Contact calls appeared to derive from begging calls (Stafford 2022).

Geographic variation. No geographic variation in vocalizations has been described.

BEHAVIOR

Locomotion

Birds on Guam were reported to hop (Jenkins 1983).

Self-Maintenance

Preening, head-scratching, stretching, sunbathing, bathing, anting, etc. Birds on Guam frequently allopreened, particularly mated adults, but an adult also preened a fledgling. When allopreening, birds perched next to each other and alternately allopreened, primarily on the back of the head and neck. They appeared to be plucking ectoparasites rather than solely preening feathers (Jenkins 1983). During one observation on Rota, a juvenile simultaneously preened and scratched its neck by lifting a leg over the wing (Tomback 1986).

Agonistic Behavior

Territories were described as being aggressively defended from July through January, although established pairs occupied these areas throughout the year (Wiles 1998, MAC Working Group 2014). Birds also were described as being territorial throughout year, with each pair defending 12–37 ha of forest (Zarones et al. 2014), although birds did not defend territories during non-nesting periods. The average distance to the nearest neighboring nest area was 687 m ± 427 m SD (Faegre et al. 2018).

Perch pounding and foraging are two behaviors that may appear similar but which have different functions. Foraging can involve using the bill to chip away bark from a branch to collect food. Perch pounding involves pounding on a solid section of the branch, which acts as a warning to an intruder in a nesting territory (Mariana Crow Recovery Project 2025).

Social and Interspecific Behavior

On Guam, an early report said that the Mariana Crow could be approached and observed (Seale 1901). Guam birds were seen as singles or in small flocks, often along roadways. They were often noisy when flying in flocks or pairs, but when observed in the jungle they were generally quiet when feeding and perching in dense foliage (Baker 1951). In the 1970s, Guam birds were instead described as being unusually wary and more often heard than seen (Pratt et al. 1979). However, during these same years, others still considered the species to be one of the least wary of forest birds. It would perch and vocalize within 2–3 m from an observer (Jenkins 1983).

The Mariana Crow is typically found in families containing a monogamous pair and 1–3 young (MAC Working Group 2014). On Guam, it indeed occurred in family groups of 2–5, with single birds seen only infrequently. The largest group observed was 14, with the next largest being 11 (Jenkins 1983). Flock size counts from 32 crow sightings had a range of 1–6. Mean flock sizes on Guam and Rota were 2.2 and 2.7, respectively, although these measures did not differ significantly. On Rota, family groups were initially thought to occupy a defined home range, with one group found in the same 2 km stretch of coastal strand for three consecutive mornings (Tomback 1986).

Home range size on Rota was first estimated to be 64 ha (Morton et al. 1999). Home ranges among adjacent family groups was found to overlap by 42.0 ± 19.5% (*n* = 18) and, using the local convex hull method, averaged 52.7 ± 23.4 ha SD (*n* = 17) for fledglings, 83.2 ± 72.0 ha SD (*n* = 7) for sub-adults of known age and 274.6 ± 249.5 ha SD (*n* = 3) for sub-adults of unknown age, with daily movement distances increasing with age. Cumulative home range measures increased with time although measurements from 30-day intervals did not show an increase. Sub-adults ranged more widely than family groups. During active nesting, the species had high nest area fidelity. The average location of nest attempts was 100 m ± 112 m SD) from that of the previous season's nest attempts (Faegre et al. 2018).

Sightings of large groups of birds have been reported for both Rota and Guam. Counts of at least 66 and 25 birds were made at a roost on Guam over a two-week period in 1984. The causes of the flocking were uncertain, but were perhaps related to encounters with the introduced, predatory brown tree snake. Such groups typically appeared in late summer, prior to territory establishment for breeding. Temporary aggregations of 5-15 were common on Rota in the 1980s but large aggregations were not observed on Rota during the late 1990s, with observations of larger groups attributable to brief mixing of family groups. Notable exceptions included observations of 16 in June 1989, nine in September 1997 and seven in February 1998. Generally, however, sub-adults appeared to avoid social congregation, particularly after 2007, when the population dropped below 200 individuals (Faegre et al. 2018).

Sightings of crows in flight were common on both Guam and Rota. The wings appeared comparatively short and broad, with such architecture typically permitting greater maneuverability in forests. Occasionally, the flight pattern was like that of a woodpecker. For fast flying, flapping was of the pumping type typical of crows. Birds commonly flew above the forest canopy on Guam and Rota (Tomback 1986). On Rota, birds were observed to fly above the canopy for up to 250 m (R. Craig pers. obs.).

Nonpredatory interspecific interactions. Interspecific interactions with other forest birds were frequent on Guam. Birds were observed pursuing Mariana Fruit Doves, but Micronesian Starlings, kingfishers and introduced Black Drongos harassed crows (Baker 1951, Jenkins 1983). Similarly, on Rota Micronesian Starlings and Black Drongos frequently chased crows (USFWS 2005, R. Craig pers. obs.).

Predation

Kinds of predators. The introduced brown tree snake on Guam (Savidge 1987) and such introduced species such as cats (*Felis catus*), rats (*Rattus* spp.), Black Drongos and monitor lizards (*Varanus indicus*) have been listed as Mariana Crow predators (Zarones et al. 2014, Faegre 2017).

BREEDING

Phenology

The Mariana Crow appears to breeds year-round (Engbring et al. 1986, Morton et al. 1999), with peak breeding described variously: concentrated in the winter and spring (Baker 1951) curtailed May–July (Marshall 1949, Engbring et al. 1986), primarily October–March (Lusk and Taisacan 1996), August–December (National Research Council 1997), August –February (Morton et al. 1999) and August–April (Zarones et al. 2014). Presumably on Guam in spring 1945, a nest was observed on March 8. Specimens collected May–September were not in breeding condition, although an adult was observed feeding a young bird on May 8 (Baker 1951). Guam observers also noted fledglings with adults in May, June, September and October, and found a recently fledged juvenile in September. An adult with enlarged testes was collected in September, an active nest was found in November and adults have been observed carrying nesting material in November and December (Jenkins 1983).

In 1996–1999, nest initiation on Rota was observed as early as July 31 and fledging were seen as late as May 22. June was the only month that active nests were not found. Peak nesting timing appeared to vary depending on typhoon activity during the previous breeding season (Morton et al. 1999). Breeding activity in the remnant crow population (including translocated individuals from Rota) on Guam in 1998–2007 was truncated, apparently due to nest predation, poor physiological vigor of the adults and egg nonviability. During these years, nesting was recorded only in October–mid-April (MAC Working Group 2014).

As with most crows, the Mariana Crow commonly builds and abandons multiple nest platforms before constructing a full nest, which can be constructed in as little as a week. New nests are constructed by a pair throughout a season after nest failure. Renesting five times within a season is not uncommon, and 7–10 successive nests have been documented. Prolific renesting is likely an adaptation to the species' variable environment in which typhoons can destroy nests (National Research Council 1997). Birds reinitiate the nest cycle within two weeks after abandoning an empty nest and within four weeks after losing a clutch or brood (MAC Working Group 2014).

Nest

Nest site. On Guam, an early description of nest sites was of two nests found in introduced *Pithecellobium dulce* and *Psidium guajava* trees, 1–2 m from the ground (Hartert 1898), respectively, although nests were generally placed high in trees (Marshall 1949, Jenkins 1983). A nest also was reported high in a native *Ficus* tree (Baker 1951). Observers similarly recorded nests in *Ficus* trees at >13 m (Jenkins 1983). On Rota, a July 1980 pair was found constructing a nest in coastal strand vegetation. The nest site was at the junction between two large branches 8 m up in a large *Hernandia nymphaeifolia*, which bore abundant fruit. Located near a dirt road parallel to the strand, the nest tree was 20 m from the beach (Tomback 1986). Nesting by one pair on Rota was 100 m from two houses and nesting by a second pair was 150 m from a building. The mean distance of nests to nearest roads was,however, 290 m ± 38 SE (*n* = 75). High quality forest habitat appears to permit close proximity to human habitation, albeit at lower densities than in extensive forest (USFWS 2005).

Rota crow nests were recorded in 20 native tree species. Of 161 nest trees, 63% were of four species: *Neisosperma oppositifolia*, *Eugenia reinwardtiana*, *Intsia bijuga* and *Premna obtusifolia.* These trees were usually about the height of the forest canopy although sometimes shorter (Morton *et al.* 1999). Nest location and type of trees selected for nesting differed between Guam and Rota, with birds on Rota typically building nests toward the inner part of the tree canopy. In contrast, birds on Guam usually built nests in the outer portions of the tree canopy and choose a small number of mainly emergent native tree species. Individual nest trees averaged 16.9 cm dbh and 8.7 m high. Canopy cover at nest sites averaged 93% and was never <79% (MAC Working Group 2014). On Rota, the harassment of crows by Black Drongos may encourage birds to choose nest sites in dense foliage. Mobbing may be less frequent in dense limestone forests, especially near cliff lines, and more frequent in secondary vegetation, pastures and open areas (USFWS 2005).

Of 55 nest sites vs. 60 random sites examined on Rota in predominantly native limestone forest during 1997–1999, actual nest sites differed from random sites in having a higher percent of canopy cover and greater dbh of introduced *Carica papaya* and woody vines, as well as a higher stem count of native species associated with limestone forest. These findings resulted in correct classification of a potential site as nesting vs. random in 92% of cases. Nests averaged >300 m from buildings, whereas random sites were 226.7 (SE =71.6) m from buildings. Nests were a mean distance of 223.9 m from a road, whereas random plots were 133.5 m from roads on average. Nests in native forests were associated with higher reproductive success than nests in more disturbed areas. Tree species used for nesting included *Eugenia reinwardtiana, Neisosperma oppositifolia, Intsia bijuga* and *Guettarda speciosa* and were chosen significantly more often than 16 other species of nest trees. The mean height of nest trees was 7.8 m, their dbh was 0.17 m and their slope was 10.8°. Nests were high in the canopy (6.6 ± 0.3 m SE) but were placed, on average, 2 m below the crown (nest tree height = 8.7 ± 0.3 m SE). Successful nests were more likely on sites within the closed-canopy limestone forest with smaller *Ficus tinctoria*, greater stem densities of *Psychotria* spp, and larger *Ochrosia mariannensis, Polyscias grandifolia*, and *Pouteria obovata*. *Ficus tinctoria* is associated with the beach or back strand vegetation, and was associated with unsuccessful nests. Collectively, the presence of such native species describes forest composition and structure that is consistent with a maturing, undisturbed, native limestone forest. Damage to habitat from anthropogenic or natural causes may, therefore, contribute to limiting nesting success (Ha et al. 2011).

Structure and composition. An inactive nest found on Guam was crudely fashioned from large branches (Jenkins 1983). In a 1992–1994 examination of 11 Rota nests, including the detailed composition of two, a nest typically consisted of an outer platform of sticks and an intermediate and inner cup of vines, rootlets, and fibers, with 84.0% of materials the native vine, *Jasminum marianum*. Qualitative observations of other crow nests on Rota indicated that this vine is the preferred platform building material. It also was the most common material used in crow nests on Guam. Notably, one nest contained twigs that showed evidence of mechanical cutting and roots likely obtained from freshly worked earth, suggesting that birds occasionally used material from human-disturbed sites. Although a Guam nest was reported as being composed primarily of *Elaeocarpus joga* twigs, in this study the tree species was infrequent in nests. There was a mean of 200 (range = 130–270) twigs in two nests examined, with most 2.1–4.0 mm in diameter, similar to the 2–6 mm (Michael 1987) and 1–1.5 mm (Jenkins 1983) reported for Guam nests. Of twig lengths, 46.6% were 151–300 mm, similar to the 150–200 mm (Michael 1987) and 200–300 mm (Jenkins 1983) reported for Guam nests (Lusk and Taisacan 1996). Another Rota nest had 300–500 mm lengths, however (Tomback 1986). Nest construction, carried out by both parents, typically takes a week to complete and develops through three stages in which progressively smaller-diameter materials are used: platform, cup, and nest lining (Lusk and Taisacan 1996, MAC Working Group 2014).

Intermediate nest cups were composed of an interwoven mesh of small branches, rootlets, vines and *Cocos* fibers in the 1992–1994 study. *Jasminum* accounted for most material in two nests examined. Of measurable components, 84% were 0.0–2.0 mm diameter and 60% were the 101–200 mm length. *Ficus prolixa* rootlets and *Jasminum* vines averaged 31.6% of total cup mass, whereas *Cocos nucifera* fibers composed 4.5%. Inner cups were constructed of finely interwoven fibers, rootlets, and small vines. These materials were all <2 mm in diameter. *Cocos* fibers were 55.4% of the mean total mass of the inner cup and a mix of *Ficus* rootlets, *Jasminum* vines and unknown vines, branches and rootlets formed 44.6% of the mean total mass. There was no evidence of *Pandanus* or *Casuarina* presence. Components of two nests included *Jasminum marianum*, which comprised 84% of the platform and 97.3% of the intermediate cup; *Alyxia torresiana*, which comprised 3.1% of the platform and 0.5% of the intermediate cup; *Meiogyne mariannae,* which comprised 1.5% of the platform and 0.5% of the intermediate cup; *Psychotria mariana*, which comprised 1.9% of the platform; *Guettarda speciosa* , which comprised 0.8% of the platform; *Maytenus thompsonii*, which comprised 0.8% of the platform; *Ficus prolixa*, which comprised 0.2% of the platform and 0.9% of the intermediate cup (Lusk and Taisacan 1996). Nests on Guam, in contrast, were often lined with fine fibers from *Flagellaria* sp. (MAC Working Group 2014).

In a 1980 examination of nest construction by a pair of crows on Rota, an adult was observed to fly to the nest carrying a long strand of *Casuarina* foliage. Apparently, the same bird also flew into *Hernandia* foliage above the nest, picked up twigs and placed them into the nest. Only one crow appeared to engage in nest construction (Tomback 1986). However, on Guam observers found that two different adults carryied nesting material, indicating that both adults shared in nest construction (Jenkins 1983).

Dimensions. An inactive nest found on Guam had twigs 10–15 mm in diameter and 20–30 cm long, with twigs laid in a criss-cross manner (Jenkins 1983). In a 1980 nest on Rota, at an early stage the nest consisted of a skeletal platform and ring of twigs ca. 50 cm in diameter. In a 1992–1994 examination of Rota nests (n = 8), mean nest diameter was 37 .2 cm (SD = 8.6, range = 24.0–53.0 cm) and mean height was 15.4 ± 3.4 cm SD, range = 10.0–21.0 cm. Mean cup diameter was 13.3 ± 1.9 cm SD, range = 10.3–16.0 cm, and mean cup depth was 6.9 cm ± 2.1 cm SD, range = 4.5–9.5 cm. The platform mass of the two nests averaged 347.5 g, with the platform 284.1 g, intermediate cup 42.1 g, and inner cup 21.3 g. (Lusk and Taisacan 1996).

Eggs

The eggs were first described as glossless white and pale yellow if held against a light. Three eggs measured 31.5 x 23, 31.6 x 21.4 (almost fusiform) and 35 x 22 mm (Hartert 1898). Mean 1996–2009 clutch size was 2.57 ± 0.08 SD (n = 82) (Zarones et al. 2014). Large clutches (four eggs) have been observed on Rota but not on Guam. This occurred in 7 of 8 nests during the year following the 1997 Supertyphoon Paka. In 1998, one female even deposited a second four-egg clutch immediately after losing the first clutch of four eggs (Morton et al. 1999).

Incubation

A minimum of 65 days is necessary to build the nest, incubate the eggs, and rear the brood through fledging, with the incubation period being 21–23 days (Morton *et al.* 1999). Both parents generally participate in all aspects of breeding, although the female incubates and broods most of the time, whereas the male provisions the female and nestlings (National Research Council 1997, MAC Working Group 2014).

Young Birds

Clutch and brood sizes on Guam were unknown to Jenkins (1983), but on one occasion, he saw a pair with two fledglings and, on two occasions he saw a single adult with one fledgling. On Rota in 1996–1999, the nestling period was 36–39 days and an average of 1.2 fledglings were produced/nest for 33 successful nests (Morton et al. 1999). Number of nestlings and number of fledglings for nests monitored in 1996–2009 was 1.39 ± 0.05 SD (n = 106) and 1.25 ± 0.04 SD (n = 68), respectively (Zarones et al. 2014).

In 1980 on Rota, food-begging calls by juveniles were accompanied by wing flutters and bill gaping. Begging juveniles were fed intermittently by a parent. Between feedings or when parents did not respond, the juveniles often perched quietly or moved alone through dense *Scaevola* understory. While juveniles traveled through the understory, moving from perch to perch or searching the ground, they would encounter and manipulate a variety of objects, apparently not consuming them. They snipped or ripped leaves from trees, hammered on branches and played with seeds, snail shells, twigs, live leaves and dead leaves. One juvenile was observed shredding bark from a twig by sliding the twig between the mandibles. Another placed a seed in a cup-like hollow, where two large branches joined in a *Hernandia* tree, and removed and replaced the seed in the hollow at least twice. The juveniles were particularly tame and occasionally perched in the understory ca. 1 m from an observer. As in other corvid species, juveniles appeared to have a long period of dependency, as several observed at close range did not have rictal flanges (Tomback 1986).

Parental Care

Observations at an active nest on Guam showed that a pair exchanged incubation duties and both adults accompanied a fledgling (Jenkins 1983). On

Rota, birds typically remained in family groups after +fledging until the following breeding season—a period averaging 241 days (median = 197 days, range = 99–537 days; *n* = 15 banded groups). Although the species typically produced 0–1 broods/year, one pair successfully raised two broods of single birds in one breeding season and another pair tended a single juvenile for 18 months. Over three years, four of 30 pairs were deemed nonbreeders during at least one year due to continued attendance of juveniles produced during the previous breeding season (Morton et al. 1999).

DEMOGRAPHY AND POPULATIONS

Causes of Mortality

Depredation. After its accidental introduction to Guam from the north Australia-New Guinea-Solomon Islands region, the brown tree snake progressively decimated the entire native avifauna of Guam (Savidge 1987). Introduced species such as cats (*Felis catus*), rats (*Rattus* spp.), Black Drongos and monitor lizards (*Varanus indicus*) have been suggested as additional factors influencing the population decline. The single chick that fledged in 1989 from a nest tree protected with a steel-wrap and tanglefoot barrier was killed soon after fledging by a monitor lizard. However, the brown tree snake is believed to be the overriding factor in the extirpation of the Mariana Crow from Guam. From necropsies of snakes in 1982–1986, a time when birds had virtually disappeared from Guam, the percent of birds and bird eggs in their diets was lower than in the 1970s. By releasing Coturnix Quails (*Coturnix japonica*), domestic chickens, Canaries (*Serinus canaria*), and wild-caught Bridled White-eyes (*Zosterops conspicillatus*) into the forest from Saipan, predation on eggs and young birds was determined to be high (National Research Council 1997). Phenomena driving the population decline on Rota include particularly a reduction of first year survival of young (Ha et al. 2010), which appears to be related primarily to predation by feral cats (Zarones et al. 2014, Faegre 2017). Evidence also suggests that human persecution may occur (Sussman et al. 2015). In a 2003-2004 study on the relationship between rat and crow abundance, breeding success was found to be significantly higher where rats were most abundant, suggesting that rats were unlikely to be a major driving force behind the decline in this species. The positive association between crow breeding success and rat abundance suggests these species may be responding to similar habitat needs or a shared predator (Amar and Esselstyn 2014).

Exposure. Major typhoons have struck Guam and Rota in recent years. The destruction of Mariana Crow nests and deaths of nestlings have been documented on both islands. Although native birds in the Mariana Islands have evolved with the periodic occurrence of major typhoons, their effects on small, remnant populations could be especially severe (National Research Council 1997). Indeed, 1982–2003 variable circular plot surveys on Rota and U.S. Fish and Wildlife Service roadside surveys showed that increasing typhoon severity was negatively related to the species' abundance (Ha et al. 2012).

Disease. A potential threat from West Nile virus exists, although to date this virus has not been detected in the Mariana Islands (USFWS 2007). Infectious disease monitoring and 1982–1984 Guam studies on potential exposure to environmental contaminants did not reveal evidence that population declines were caused by disease (Savidge 1987). On Rota, health examinations on captured Mariana Crows did not reveal the presence of pathogenic organisms or parasites (National Research Council 1997). However, the chigger, *Trombicula* sp., had previously been found on crows on Guam (Wharton 1946). Moreover, in the early 1960's Guam birds were found to be infested with *Menopon gallinae* and other unidentified lice (Jenkins 1983). The crow population decline on Rota has more recently been attributed in part to disease (Zarones et al. 2014, Faegre 2017). Ectoparasites also have been speculated to be related to population declines. Observations of juveniles suggest that they suffer from feather lice (unknown species), and observations of adults with missing feathers suggests feather mites damage (Amar et al. 2008).

Population Status

Numbers and trends. In a 1945 Mariana Crow count on Guam, individuals made up 2.4% of all birds counted and they were observed on 21.6% of 125 roadway counts. Birds were distributed through most parts of the island but were usually infrequent near populated areas. Field notes from the early 1960s indicated that the species was common in southern Guam but by the 1970s it was extirpated from that region. In the 1970s, its population was centered primarily on Andersen Air Force Base in northwest Guam. Birds were less common along the northeastern coastline and rare in the central portion of the northern plateau (Jenkins 1983). In a 1977 survey, 12 birds were counted on 8.45 km of transect surveys, yielding a density estimate of 0.418/ha and a population estimate of 4,694 based on the amount of forest present. From 1978 to 1981, Guam wildlife staff found that birds/count increased from 0.577 to 1.169. In 1981, a variable circular plot survey counted 180 birds and yielded a population estimate of 2,329 (Engbring and Ramsey 1984). A 1985 survey estimated >100 birds (USFWS 2005) and a 1990 repetition of the 1981 survey counted 107 birds. Estimates of numbers on Guam fell from ca. 100 in 1990–1991 to 18 territorial birds and a few nonterritorial birds by 1995–1996; observational evidence suggested a sex ratio skewed in favor of males. Only one of the pairs remaining in 1995–1996 produced eggs (National Research Council 1997). From 1997 to 2004, counts of Guam birds declined from 13 to 0, with the last recorded in 2003 (USFWS 2005).

No chicks were fledged from unprotected nests on Guam after 1987 and only six fledged from protected nests after 1989. Five chicks were fledged from nest trees protected with electric barriers in 1992–1994. Two additional chicks, collected from wild nests in 1995–1996, were successfully hatched and hand-raised in captivity (National Research Council 1997). Translocations from Rota to Guam began in 1997. In 1997–2003, 26 birds were released on Guam: two were captive-bred birds of Guam origin, six were of Rota origin from mainland zoos and 18 were translocated from Rota. As of 2005, 10 translocated birds from Rota remained (USFWS 2005) but it is now extirpated (BirdLife International 2018).

On Rota, early observers found the species to be fairly common (Baker 1951). Counts on Rota during 1979 showed, however, that it appeared to be uncommon despite the species' high visibility and loud vocalizations (Jenkins and Aguon 1981). By the 1980s, Jenkins (1983) believed that the Rota population had declined by perhaps 50%. In a 1977 survey, 12 birds were counted on 6.94 km of transect surveys, yielding a density estimate of 0.263/ha and a population estimate of 1,496 based on the amount of forest present. In April 1982, Engbring et al. (1986) used the variable circular plot (VCP) procedure at 254 stations to estimate 1,491 individuals (as revised by Camp et al. 2015). A 1988 informal estimate was 600–1000 (USFWS 2005). Other population estimates, standardized by Camp et al. (2015), include 891 (95% CI = 500−1935) from a Oct.−Nov. 1995 survey of 311 VCP stations (Fancy et al.1999) and a 1998 estimate of 407 (95% CI = 212−899) for VCP data (Camp et al. 2015). In contrast, Plentovich et al. (2005) counted 117 breeding pairs in 1998, whereas Zarones et al. (2014), based on counts of paired and unpaired birds, found 144 individuals in 2007−2008. Camp et al. (2015) also reported a 2003 VCP estimate of 244 (95% CI = 115−620) and a 2012 VCP estimate of 81 (95% CI = 30−202), with birds appearing at 4% of 666 station visits for this latter estimate. A 2010 estimate based on a population model was 164 (Ha et al. 2010). The most recent estimate is 178 for 2013-2014 (Kroner and Ha 2018). Hence, despite some variation in results among studies, populations appear to have declined steadily to the present, with data suggesting that the critical turning point was after 1995 (Craig 2023).

A series of wet/dry season population estimates made in 1992–1993 were consistently far lower than that of Engbring et al (1986). Two April surveys of 321 station visits yielded an average estimate of 496 crows. In contrast, an October 1992 estimate from 160 stations was 1058 (95% CI = 788−1421) (Craig 2023). However, Jenkins and Aguon (1981) found birds at 16% of 19 survey stations in April, whereas this study found them during 21.5% of 1048 station visits overall and 17% of 321 April visits. Moreover, 1988 roadside counts reported by Camp et al. (2015) had occurrences of 26.0% at 96 December stations and 20.8% at 90 August stations compared with 15.2% at 322 January stations and 27.5% at 160 July stations in this study. These observations provide evidence of count-to-count variation but also some evidence that Engbring et al. (1986) may have overestimated the population due to overcounting and that numbers may not have changed dramatically from 1982 to 1992−1993 (Craig 2023).

Previous observers have noted that few crows inhabited the high elevation Sabana plateau (Engbring et al. 1986, Camp et al. 2015) and indeed in the 1992−1993 study no birds were found on 48 visits to the eight transect points present at the summit of the Sabana, although detections of birds on the slopes leading to the Sabana were frequent. Similarly to Engbring et al. (1986), a transect east of Songsong Village, which is at the western end of Rota, had the least sightings of any transect, although a second transect just southeast of Songsong in the approximate location of Engbring et al.'s (1986) Songsong transect produced multiple observations to the edge of residential development (Craig 2023).

Comparison of wet and dry season population estimates during the 1992−1993 study provided strong evidence that the apparent size of the Mariana Crow population is influenced by the season of survey. Breeding appears frequent in at least portions of both the wet and dry season. However, population estimates were consistently highest in both wet season measures and particularly in October, which suggests that increased vocalization and, thus, detectability occurred during these times. This observation may be related to findings for several other Marianas bird species that showed evidence of molt in the late wet season and peak breeding in the dry season, which thereby segregates these energetically expensive activities (Craig 2021). A peak in wet season vocalization could indicate courtship or family group activity preceding dry season nesting when birds become more secretive (Craig 2023).

Population Regulation

On Guam, nest failures were attributed to premature abandonment (either as a result of predators or human-induced disturbance), interference by unmated males due to skewed sex ratios, Black Drongo mobbing and possibly senescence (i.e., poor physiological vigor and infertility). The installation of electric barriers on nest trees helped to decrease the loss of eggs to brown tree snakes, but these barriers did not result in greatly increased reproductive success. Apparent abandonment of nests occurred at 63% of 93 nests with known fates and was the dominant form of nest failure. Failure of eggs to hatch was the second greatest cause of nest failure. This occurred at 16% of the nests with known fate. Even protected nests that were not abandoned rarely produced young. Of 42 eggs that remained in the nest through incubation, 83% failed to hatch. Many eggs showed no development and appeared to be infertile, whereas others were intact or were cracked and contained dead embryos (nonviability can be caused by infertility, inbreeding depression, thin or cracked egg shells, poor parental nutrition, or inadequate incubation). Many of the crows on Guam may have been exhibiting reproductive senescence—a suggestion based on the premises that the population has been progressively declining for a number of years, that recruitment to the population has been extremely low, and that most of the birds in the population are reaching the end of their life span (National Research Council 1997).

In addition to low nesting success, productivity for the Guam population was low because many pairs did not lay eggs. Only 0.3–0.5% of pairs laid clutches in any year. Six young fledged in 1989–1996, all in nests that were protected by electric barriers. Even during four years when nearly every nest was protected with barriers, only four young were produced, and two of these were hatched and hand-raised in captivity in 1995–1996. In 1993–1994, 33% of 12 pairs lost one or more pair members, and in 1994–1995 22% of 9 pairs did so. Average annual survivorship for females was 71%. In the 1993–1994 breeding season, only 56% of 27 crows were accounted for two years later, yielding an annual survivorship for sexes combined of 75%. Most long-lived birds like crows have annual survivorship between 80–90% (National Research Council 1997).

On Rota, birds were assumed to enter the breeding cohort at 3.5 years, and the oldest known breeding bird was a 13-year-old male (MAC Working Group 2014). One Rota male was recorded to be 18.5 years old (Mariana Crow Recovery Project 2025). Although the species generally produces a single brood/year, nest failure and other factors can lead to multiple nest attempts. In 1993–1996, of 21 nests with known fates, there was a success rate of 48% and 10 nests fledged 14 young. Success rates for other species of corvids vary considerably (mean = 58 ± 19% for 15 species) (National Research Council 1997). In 1996–1999, 32 pairs on Rota constructed a mean of 2.2 nests a year (n = 78), nesting as many as seven times in one season. Not all nests resulted in egg laying, however. Over a 3-year period, of 148 nests with known fates, 18% were only partially constructed, 13% were abandoned after completion, 4% had inviable clutches, 28% were depredated, 16% were destroyed by typhoons and the remaining 22% fledging young (Morton et al. 1999). Nests that produced fledglings in 1996–2006 varied from 12%–50% and Mayfield estimates of nest success ranged from 13% to 41% (Ha et al. 2008). An overall estimate of nest success was 25·7% in 1996–2009 (n = 204). On average, 49% of pairs produced at least one fledgling per season and the mean number of fledglings/pair/year was 0.66 (Zarones et al. 2014). Population viability simulations found that for population growth to occur, annual adult survivorship needed to be >90% and fledgling survivorship needed to be >60%. Using 97 birds marked and resighted over the course of a 21-year period, Ha et al. (2010) showed there was a rapid decline in first-year (fledgling to one year old) survival from 0.7 to 0.4 between 1990 and 2010, representing a doubling in mortality, and a smaller reduction in adult survival from 0.86 to 0.82 over the same period.

CONSERVATION AND MANAGEMENT

Conservation Status

The Mariana Crow is listed as critically endangered on the IUCN Red List because of its small range and decline of the Rota population due to predation, disease and habitat loss. Moreover, the potential introduction of the brown tree snake to Rota could result in rapid elimination of the population (BirdLife International 2018). The first legal protection of the species occurred on Guam in 1981 with the passage of Guam Public Law 16-39. It was declared endangered by the Endangered Species Act of Guam in June 1981 and later was given endangered status on Guam and Rota under the U.S. Endangered Species Act in 1984. It is also listed as endangered by the Commonwealth of the Northern Mariana Islands (National Research Council 1997).

Effects of Human Activity

Habitat loss and degradation. The effects of World War II were considerably less on Rota than on Guam. More recent habitat changes on Rota are associated with economic and commercial development (Engbring et al. 1986). However, substantial tracts of native forest remain on Guam and forest is extensive on Rota. Moreover, some pairs of crows on Rota have continued to occupy territories despite modification of habitats within them (National Research Council 1997) and recent evidence, although indicating that mature forest is the principal habitat occupied, points toward the species being more of a habitat generalist that previously recognized (Craig 2023). Still, continued habitat modification and fragmentation are likely to have a negative impact on populations.

The Mariana Crow has traditionally been considered an agricultural pest. Moreover, Chamorro superstition held that illness would follow hearing a crow call. Although such cultural prejudices may have resulted in killing of crows in the past, there is no evidence that such killing was responsible for the crow's population decline on Guam. By the early

1980s, the population on Guam was restricted largely to military lands, where the hunting of native species is prohibited and tight security has minimized poaching. On Rota, however, some illegal killing may occur. In at least one instance, a nesting pair was killed on forest lands that were being cleared for commercial development. With increasing pressure for development on Rota and negative attitudes toward protection of endangered species, the species' endangered status may have contributed to illegal killing (National Research Council 1997).

From World War II until the early 1970s, pesticides such as DDT and malathion were used extensively on Guam for vector control and agricultural purposes. Malathion was applied by the military around beaches and buildings up to three times a week. Malathion also was aerially applied over approximately a third of the island in 1975 to prevent a potential outbreak of dengue fever. However, a 1981 survey of pesticides in guano, birds, and small mammals indicated that it was unlikely that pesticides were responsible for the decline of Guam's avifauna. On Rota, malathion was used to control insects in 1988 and 1989. Although there is no indication that crows on either island have been adversely affected by pesticides, no thorough studies have been conducted (National Research Council 1997, USFWS 2005).

Increases in the number of non-laying pairs and in the production of nonviable eggs in the Guam population might have been related to food resources, as the brown tree snake has greatly reduced the potential prey for crows. However, the species' omnivorous diet would have reduced the importance of such a reduction. One study showed that lizard populations densities and biomass were about 33% less with predation by snakes (National Research Council 1997). Moreover, logistic regression modeling of crow distribution on Andersen Air Force Base suggested that birds were more affected by visible human disturbance than by auditory human disturbance. Roads, runways and housing areas appeared more disturbing to aga populations than ambient noise from flyovers. (USFWS 2005).

Effects of invasive species. After its accidental introduction to Guam from the north Australia-New Guinea-Solomon Islands region, the brown tree snake progressively decimated the entire native avifauna of Guam (Savidge 1987). Introduced species such as cats (*Felis catus*), rats (*Rattus* spp.), Black Drongos, monitor lizards (*Varanus indicus*) have been suggested as additional agents of population decline (National Research Council 1997). The population decline on Rota indeed appears to be primarily related to predation by feral cats (Zarones et al. 2014, Faegre 2017).

The only introduced species on Guam and Rota that is a potential competitor with the Mariana Crow is the much smaller Black Drongo. Study on Guam suggested that drongos were not competing directly with native species because of differences in its habitat use and foraging techniques (Maben 1982). However, they have been seen harassing nesting crows. Nest placement by crows on Rota in the subcanopy whereas on Guam it was in the canopy. This difference has been hypothesized to be related to the greater density of drongos on Rota (Tomback 1986).

Management

Conservation areas. Critical habitat on Guam was not designated under the original federal listing but was proposed in June 1991. However, this proposal was withdrawn in 1994 after the establishment of the Guam National Wildlife Refuge. In 1993, the military and U.S. Fish and Wildlife Service entered into an agreement that created the Guam National Wildlife Refuge. The refuge consists of about 150 ha of newly protected areas and more than 9,000 ha of military lands at the northern end of Guam. These lands include the 281 ha Pati Point Natural Area, the Haputo Ecological Reserve and the Orote Peninsula Ecological Reserve. No Disturbance areas also have been established around Mount Almagosa and Mahlac Cave. In addition, the government of Guam manages 1,620 ha of forest. The Anao and Y-Pigua Conservation areas are located in the north and the Cotal and Bolanos Conservation areas are located in the south (National Research Council 1997, USFWS 2005).

On Rota, wildlife-conservation areas have been established, including the Sabana Conservation Area, Tapingot Conservation Area and Mariana Crow Conservation Area (USFWS 2005). The Marianas Crow Conservation Area was created by the Commonwealth of the Northern Mariana Islands (CNMI) Division of Fish and Wildlife to protect the area as a refuge for the Mariana Crow (CNMI Department of Lands and Natural Resources 2025).

Conservation measures and habitat management. Keeping brown tree snakes out of ships, planes, cargo, cargo facilities and trucks moving cargo is key to conservation efforts. Snake traps, barriers, snake detection dogs and toxicants have been employed for controlling snakes spread. Prey reduction also has been conducted in warehouses and at other key facilities. On Rota, an enclosure was built at the port to hold cargo from Guam overnight to allow detection and capture of any snakes present. In addition, the following have been proposed for Rota: 1) increase inspection of cargo departing from Guam to Rota, 2) expand the barrier in off-loading areas and 3) quarantine all high-risk cargo in the port barrier. Preventing the spread of snakes from Guam to other islands is viewed as more cost effective than attempting to control snakes once they reach other islands. As part of this effort, trapping was attempted in a 42-ha area on Andersen Air Force Base. The number of snakes captured declined rapidly, but snake capture continued, presumably because of immigration of snakes into the area (USFWS 2005).

On Guam, an electric and mechanical barrier was developed to exclude snakes and monitor lizards from Mariana Crow nest trees. Tree-barrier technology was developed in 1985 and by 1989 it was combined with trapping snakes around protected trees. In 1989, the first chick fledged from a protected nest. Improvements in tree-barrier technology led to the fledging of three chicks in 1991–1992. Females laid larger clutches (3 vs. 1–2 eggs) in nests in protected trees during the 1992–1993 breeding season, which provided evidence that eggs were being lost to snakes (National Research Council 1997, USFWS 2005).

Since 1993, member zoos of the American Zoo and Aquarium Association have participated in the Marianas Archipelago Rescue and Survey (MARS) program's efforts for captive-propagation. A captive population of Mariana Crows was founded with wild birds captured on Rota in 1993–1995. The first birds captured included seven in July 1993, one in July 1994 and two in January 1995 (National Research Council 1997). In addition, the Pacific Island Recovery Team of U.S. Fish and Wildlife Service was charged with developing a recovery plan, with a revised plan published in 2005 (USFWS 2005).

In 1993–1994, Guam researchers discovered that a high percentage of eggs were nonviable, so an aviculture intervention program was begun to study this, artificially incubate eggs and hand-rear chicks. Because crows readily renest, taking eggs encourages birds to produce more. One chick was successfully hatched in 1994–1995. In 1995–1996, a male and female were successfully reared from eggs (National Research Council 1997). In 1997, eight birds from zoo populations, with eight from Rota, were released on Guam. In 1997–1998, nine nests were located but three eggs collected proved nonviable. In 1998–1999, three pairs including two females of Rota origin produced no offspring. In 1999, two chicks were translocated from Rota but neither survived. In 2000–2001, 12 adult and juvenile birds were translocated from Rota and into 2004 10 had survived. One captive pair produced no surviving young in 1996 – 2001 (USFWS 2005).

On Rota in 2016, researchers began collecting eggs from nests to be reared in captivity as part of a program to keep birds until they passed the period of highest mortality before release into the wild. The first cohort of five captive birds was released in 2017. An additional 10 were released in 2018, 13 more were released in 2019, 13–14 were released in 2020, 11 were released in 2022 and 14 were released in 2023. A bird from the 2019 release cohort was found with a fledgling in 2022, making it the first hand-reared individual to reproduce successfully in the wild. All released birds were 11–18 months old, which is the age at which birds become independent from parents. Observers monitored the released birds and observed them as they learned to forage wild foods, avoid predators and socialize with wild birds. Researchers also worked with island residents to encourage maintenance of bird habitats, especially through a landowner incentive program. With these efforts, the population appears to have stabilized — albeit at a low number (Eckart 2018, Maurin 2021, Mariana Crow Recovery Project 2025).

As of 2005, there has been no large-scale control or removal of ungulates on Rota and Guam. Several attempts have been made to remove deer and feral pigs completely from a 24-ha limestone forest surrounded by a chainlink fence on Andersen Air Force Base on Guam, but these have been unsuccessful. In 1996, immunocontraception along with the capture, relocation and culling of water buffalos has reduced the population on the U.S. Navy Ordnance Annex by 60% (USFWS 2005). A cat control program commenced on Rota in 2012, targeting Mariana Crow breeding areas. Since the program commenced, survival rates of first-year birds have increased, as shown from radio-telemetry and mark-resight analysis (BirdLife International 2018, Faegre et al. 2019).

Habitat protection. Critical habitat was designated on Guam and Rota in 2004; 152 ha were designated on Guam and 2,552 ha were designated on Rota. Establishment of a Rota habitat conservation plan also began in 1994. The process was initiated during the planned development of agricultural homestead sites, which contained crow breeding and foraging habitat. Although the plan was not completed, a plan for the agricultural homestead sites was under development in 2005 (USFWS 2005).

PRIORITIES FOR FUTURE RESEARCH

1. A high priority is continued monitoring and implementation of interdiction efforts at ports to prevent the establishment of a brown tree snake population on Rota.
2. As the highest densities of the Mariana Crow are attained in mature native limestone forest, a second priority is the preservation of this habitat by setting it aside from any encroachment by agriculture, residential or commercial development. In addition, much of secondary forest that is presently dominated by alien species, particularly that adjacent to seed sources in native forest, has the potential to be revegetated by native forest species (Craig 1994). Native birds and Mariana fruit bats (*Pteropus mariannus*) are major dispersers of native seeds (Caves et al. 2013), so further research into facilitating conversion of alien forest into that dominated by native species is needed.
3. High feral cat densities on Rota are interfering with survivorship of Mariana Crows. Hence, ongoing efforts to control feral cats appear to be imperative for permitting successful natural reproduction. Present efforts directed at releasing

captive-reared birds onto Rota can help to sustain the population in the short term but it does not solve the underlying causes of population decline.

4. Develop translocation efforts to additional Mariana islands that do not have introduced predators. The Mariana Islands of Sarigan, Alamagan, Pagan, Agrihan and Asuncion, all have apparently suitable areas of forest habitat for translocation efforts.
5. Continue periodic population surveys to evaluate the status of the Rota population.

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