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SAIPAN REED WARBLER (*Acrocephalus hiwae*)

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INTRODUCTION

Reed warblers (Sylviinae: *Acrocephalus*) are strong island colonizers, presently represented in the tropical Pacific by perhaps 20 species. The Saipan Reed Warbler (*A. hiwae*) of the Mariana Islands, or Ga' ga' karisu in the Chamorro language, is among the largest and longest-billed of these. DNA evidence indicates that it is descended from an ancestral member of a superspecies including the Oriental Reed Warbler (*A. orientalis*). All Mariana Island reed warblers were once thought to comprise a single species, but DNA evidence also indicates that individual island populations are derived from several independent colonizations. Birds from the islands of Saipan and Alamagan are presently thought to represent a separate species from Nightingale Reed Warbler (*Acrocephalus luscinius*), Aguiguan Reed Warbler (*Acrocephalus nijoi*), and Pagan Reed Warbler (*Acrocephalus yamashinae*).

With its loud voice, large body size, monogamous mating system, defense of all-purpose territories and choice of earlier successional upland habitats, the Saipan Reed Warbler appears to be ecologically convergent with many members of the mockingbird family (Mimidae) and unlike the typically polygamous, smaller reed warbler species that are associated with marshes. On Saipan, reed warbler habitats are largely composed of such alien plant species as *Pennisetum purpureum* grass and *Leucaena leucocephala* shrubs, although the species is also found at mature forest edge, secondary forest and in marsh edge shrubbery, again like many mimids.

The Saipan Reed Warbler is considered endangered due to its low total population of ca. 3,687 pairs. Its numbers on Saipan and Alamagan are possibly declining and it appears to be extinct on Aguiguan. Habitat destruction through urbanization and the potential for introduction of the brown tree snake (*Boiga irregularis*) are principal threats faced by the species.

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IDENTIFICATION

Field identification

A loudly vocal species that often sings from exposed perches, the sexually monomorphic Saipan Reed Warbler is distinguished by its long bill, warm buffy plumage and large size compared with other island passerines. Its short, rounded wings and long tail are typical of birds that have evolved to maneuver in denser environments (Fig. 1).

Similar species

This is the only *Acrocephalus* species within its present range. No other species within this range can be confused with it. The extinct Guam species, believed to be derived from a separate colonization event (Cibos et al. 2011), was found to be indistinguishable in appearance from Saipan birds (Baker 1951). The presumed extinct Aguiguan species was described as shorter-billed, less rusty above and with darker flanks and belly than the Saipan population (Yamashina 1940). The presumed extinct Pagan species, also thought to be from a separate colonization event (Cibos et al. 2011), was described as having a shorter, more curved bill and being dark olive brown above, with breast, sides and flanks dusty grayish brown (Takatsukasa and Yamashina 1931) and being much smaller than other Marianas reed warblers (Saitoh et al. 2012). The Caroline Reed Warbler (*A. syrinx*) resembles the Saipan Reed Warbler but is smaller, with a much shorter, straighter bill, with the head and neck more reddish-brown, with back, rump, wing and tail edged with cinnamon and with flight feathers faintly tipped with white (Baker 1951).

PLUMAGES, MOLTS AND STRUCTURE

Plumages

The Saipan Reed Warbler has 10 primaries (numbered distally, from innermost p1 to outermost p10 and with the p10 reduced in length), 9 secondaries (numbered proximally from outermost s1 to innermost s9 and including 3 tertials, s7–s9 in passerines), and 12 rectrices (numbered distally, from innermost r1 to outermost r6 on each side of the tail). There is no geographic variation in appearance; the following is based primarily on plumage descriptions of Baker (1951) and Pratt et al. (1987), Mosher and Fancy (2002, Bairlein (2006), Kennerley and Pearson (2010), and examination of birds in the hand by RJC, along with examination of Macaulay Library Images; see Pyle et al. (2008), Radley et al. (2011) and Craig (2021a) for information on ageing and sexing this species. See Molts for molt and plumage terminology. Appearance of sexes is similar in all plumages; definitive-like plumage is assumed at the Formative

Plumage. Seasonal variation in plumages (e.g., fresh vs. worn) based on timing molts primarily in March–June and October–December following bi-annual breeding cycles (see Breeding: Phenology and Molts), but molting may also occur throughout the year.

Natal Down. Undescribed in the Saipan Reed Warbler. Mosher and Fancy (2002) indicate that this species may lack natal down.

Juvenile (first basic) plumage. Similar to later plumages, as in other *Acrocephalus* warblers (cf. Shirihai and Svensson 2018, Svensson 2023), but head plain, lacking a pale supercilium and dark lores; upperpart feathers finely fringed buff; breast, belly, vent, thighs, and undertail coverts washed or tinged more with pale yellow; flanks brownish yellow to buff (Mosher and Fancy 2002). As in the great majority of passerines, juvenile primaries and rectrices are thinner and more tapered or pointed at the tips than basic feathers and juvenile body feathers are likely weaker and more filamentous (barb density sparser) than in later plumages, especially the undertail coverts. In addition, iris and other bare-part colors of juveniles show average differences (see Bare Parts).

Formative and Definitive Basic Plumages. Following the complete Preformative Molt, Formative and Definitive Basic Plumages are indistinguishable. Plumage is warmer brown above and yellower below when fresh (e.g., ML83187271), becoming and faded brown and whiter below when worn (e.g., ML248130421). Upperparts medium-pale brown, the crown slightly darker and the nape, mantle, and rump warmer brown when fresh. Sides of head including supercilium creamy white or with slight yellowish tinge, with dusky lores and short eyeline behind eye, and darker brown auricular patch. Upperwing coverts, remiges, uppertail coverts and rectrices slightly darker or grayer brown than upperparts but with narrow fringing to the outer feather webs of same color as upperparts. Underparts cream when fresh, wearing to whitish or white, the flanks slightly darker buff or tawny and the undertail coverts pale buff or tinged yellowish. Underwing coverts grayish; axillars white tinged pinkish.

Definitive Basic Plumage is separated from Juvenile Plumage by having less yellowish tinge to the underparts; feathers less filamentous; outer primaries and rectrices broad, more truncate (less pointed), and relatively fresh compared with retained juvenile feathers. Breeding adults are more worn than juveniles within the same breeding season. See also Bare Parts.

Molts

Molt and plumage terminology follows Humphrey and Parkes (Humphrey and Parkes 1959) as modified by Howell et al. (Howell et al. 2003). Under this

nomenclature, terminology is based on evolution of molts along ancestral lineages of birds from ecdysis (molts) of reptiles (cf. Pyle et al. 2024), rather than on molts relative to breeding season, location, or time of the year, the latter generally referred to as “life-cycle” molt terminology (Jenni and Winkler 2020). Saipan Reed Warblers appear to undergo a Complex Basic Strategy (cf. Howell et al. 2003, Howell 2010b), including complete prebasic and preformative molts but no prealternate molts (Pyle et al. 2008, Radley et al. 2011). As with most passerines, primaries are replaced distally (p1 to p10), secondaries are replaced proximally from s1 and proximally and distally from the central or innermost tertial (s8 or s9), s5 the last to be replaced, and rectrices are generally replaced distally (r1 to r6) on each side of the tail, though variation in sequence of rectrix molt may occur (Pyle et al. 2008, Radley et al. 2011).

Of 33 Saipan Reed Warbler individuals banded during the dry season (January–March), five displayed remains of feather sheaths in January, thereby indicating that they had just completed preformative or prebasic molt of flight feathers. Of preserved specimens examined for molt (Pyle et al. 2008), two from 1 February and one from 26 June were finishing molt, with p10 in pin and molt among the secondaries; and one from 9 July was worn and just beginning molt. The two 1 February specimens were labeled “immature” and “adult,” suggesting that they were finishing the Preformative and Definitive Prebasic Molts, respectively. A bird trapped on 1 July appeared to be a juvenile just commencing preformative body molt, and a 9 July bird appeared to have juvenile flight feathers and so may have been commencing preformative molt as well (Pyle et al. 2008, Radley et al. 2011). A single banded wet season (July–September) bird displayed no evidence of molt (Craig 2021), and three other adults collected 8 February–2 June and two captured 1–2 May were not in molt and appeared relatively fresh; one collected 26 June was not in molt and was worn.

During 1997–1998, observations made on banded and previously banded Saipan Reed Warblers indicated that flight feather molt was observed in both sexes in March–June and October–December, although not all captured individuals during these periods were undergoing molt. Body-feather molt was observed in all months except January and July, with peaks occurring in April and December (Mosher 2006). These observations potentially indicate a bimodal molting season corresponding to a bimodal breeding season, but how this varies among individual birds and differs between first-cycle and older birds requires further study. There is as yet no evidence for protracted, suspended, or arrested molts (Pyle et al. 2008, Radley et al. 2011) as can occur (in some cases suspended for breeding) in other tropical Pacific passerines (Pyle et al. 2016).

Bare parts

The following is based on descriptions in the literature (Mosher and Fancy 2002, Bairlein 2006, Pyle et al. 2008, Kennerley and Pearson 2010), examination of birds in hand by RJC, and examination of Macaulay Library Images.

Bill and Gape. The bill is proportionally very long among *Acrocephalus* warblers. Juveniles are notable for having a bill length that is less than half of the adult’s, slowly growing to the length of adults in the first year (Craig 2021).

In adults, the upper mandible is dark brown to blackish with a pink cutting edge and the mandible is similarly pink. The gape and mouth lining in adults is bright yellow, a color that stands out and may be part of sexual selection among singing birds. In nestlings, bill color is similar except the base is fleshy pink and the cutting edges of both mandibles are broadly yellow; three rectal bristles are present on each side of the mouth above the gape flanges; the palate is reddish pink, and the tongue is yellow with two oblong brown spots just below the tongue spurs. The egg tooth is still present 2–3 days prior to fledging (Mosher and Fancy 2002).

Iris. At all ages the iris is brown with that of adults averaging warmer or slightly redder brown than in juveniles (Pyle et al. 2008).

Tarsi and Toes. The adult has blackish to grayish-blue legs and feet with strong, well-developed black claws; nestlings have grayer legs and yellowish foot pads (Mosher and Fancy 2002).

Measurements

Because the Saipan Reed Warbler is highly territorial (Craig 1992) and pairs could be called to mist nets with song playback, all individuals banded even when not in breeding condition could be sexed. Based on measurements of these banded birds, male mass = 35.7 ± 2.0 g (32.1–40.0 g), $n = 22$, wing chord = 86.9 ± 1.7 mm (83.4–90.8 mm), $n = 23$, tail length = 82.1 ± 2.6 mm (75.9–88.0 mm), $n = 23$, bill length from proximal nares = 23.1 ± 1.0 mm (20.9–24.6 mm), $n = 23$, tarsus length = 34.0 ± 2.1 mm (28.6–37.2 mm), $n = 23$; female mass = 31.8 ± 2.8 g (27.0–38.5 g), $n = 10$, wing chord = 81.6 ± 2.1 mm (78.1–85.1 mm), $n = 11$, tail length = 78.3 ± 3.2 mm (74.0–83.0 mm), $n = 11$, bill length 23.1 ± 1.8 mm (21.5–28.0 mm), $n = 11$, tarsus length 32.8 ± 1.4 mm (29.1–33.9 mm), $n = 11$ (Craig 2021a).

The species is strongly sexually dimorphic, and discriminant function analysis demonstrated that means for sexes differed significantly, with 94.1% of cross-validated grouped cases correctly classified. Based on tests of equality of group means, only wing chord contributed substantially to the function. From the 95% confidence interval, birds with wing length > 82.9 mm were males and ≤ 82.9 mm were females (Craig 2021a). Additional measurements in mm

made on specimens are: male exposed culmen = 28–33, $n = 5$, bill depth at distal end of nares = 4.8–6.0, $n = 5$ female exposed culmen = 28–34, $n = 3$; bill depth = 4.5–4.8, $n = 3$ (Pyle et al. 2008). At ca. 14 ± 2 days of age, nestling mass was 28.4 ± 2.7 g, wing chord was 50.3 ± 4.9 mm, exposed culmen was 17.7 ± 1.7 mm, culmen was 10.4 ± 0.9 mm and tail length was 13.3 ± 4.0 mm (Mosher and Fancy 2002).

SYSTEMATICS

Systematics history

Conopoderas lusciniia hiwae Yamashina, 1942, Bulletin of the Biogeographical Society of Japan 12:81.—Saipan. The holotype, an adult female collected on 23 February 1931 by Orii Hyōjirō (1883–1970), is held at the Yamashina Institute for Ornithology, Abiko (YIO-00138).

Based on Baker's (1951) review, the first Marianas reed warblers were described from Guam. These were initially designated as *Thryothorus luscinius* (Quoy and Gaimard 1830), and next as *Sylvia syrinx* (Kittlitz 1836; *syrinx* now considered a separate species, the Caroline Reed Warbler; Cibois et al. 2011a), *Tatare luscinius* (Bonaparte 1850), *Hybristes [lusciniia]* (Reichenbach 1850), *Tatare lusciniia* (Gray 1859), *Tatares luscinius* (Giebel 1877), *Tatare mariannae* (Sharpe 1883) and *Conopoderas lusciniia* (Mathews 1930). Saipan and Alamagan birds were first considered subspecifically distinct as *C. lusciniia hiwae* (Yamashina 1942, Ornithological Society of Japan 1942), with Guam birds listed as *C. lusciniia lusciniia* (Ornithological Society of Japan 1942). Reed warblers from Pagan were considered subspecifically distinct as *C. lusciniia yamashinae* (Takatsukasa 1931) and those from Aguiguan were similarly considered distinct as *C. lusciniia nijoi* (Yamashina 1940), which arrangement was maintained by Watson et al. (Watson et al. 1986) and Kennerley and Pearson (Kennerley and Pearson 2010). Birds from Guam, Saipan, Aguiguan and Alamagan were later assigned to a single subspecies but in the genus *Acrocephalus*: *A. lusciniia lusciniia* (Mayr 1945). In addition, the virtually unknown, long extinct Mangareva Reed Warbler (*A. astrolabii*) was once considered conspecific with these populations until it was demonstrated to be distinct (Cibois et al. 2011b).

The Guam population was first assigned to *Acrocephalus* (*A. orientalis*) by Pelzeln (1865), and then considered *A. mariannae* (Tristram 1883), a name no longer in use for any *Acrocephalus*, and *A. lusciniia* (Hartert 1898). Based on recent DNA work, the Guam, Pagan and Saipan populations appear to be derived from distinctly separate colonizations and, thus, appear to represent separate species (Cibois et al. 2011a). Examination of DNA evidence from Al-

amagan and Aguiguan suggests that Saipan and Alamagan populations belong to the same species, *A. hiwae*, whereas Aguiguan individuals may constitute a separate species, *A. nijoi* (Saitoh et al. 2012).

Despite the DNA findings, the Aguiguan distinction is based on a single specimen and substantial variation in characters has been noted among Saipan individuals (Saitoh et al. 2012). Moreover, the distance between the Saipan and Alamagan populations is 254 km, whereas Saipan and Aguiguan are separated by only 30 km. Tinian, lying between these islands, also once had a reed warbler population (Steadman 1999). Considering the strong colonization capabilities of reed warblers (Cibois et al. 2011a) and that the appearance, behavior and habitat choice of Saipan and Aguiguan birds was observed to be indistinguishable (Craig and Chandran 1993), these two populations appear unlikely to be specifically distinct. Morphological analyses of three other Aguiguan passerine species showed that all had statistical differences with the same species on Saipan (Craig et al. 1993). Differences that arise through phenomena such as founder effect and genetic drift do not necessarily qualify as specific-level distinctions. Aguiguan birds have been distinguished morphologically based primarily on their ca. 3 mm shorter bill compared with Saipan birds (Baker 1951). However, these measures are based on five specimens all presumed to be adults. Particularly age is related to bill length in reed warblers (Craig 2021a).

Related species

With the exception of the Guam population, all Pacific *Acrocephalus* appear to be derived from a common ancestor. Guam birds appear to have colonized much earlier than on other Mariana islands. In total, the Marianas appear to have been independently colonized at least three times—on Guam (*A. luscinius*), Pagan (*A. yamashinae*) and Saipan (*A. hiwae*). A possible fourth colonization occurred on Aguiguan (*A. nijoi*). These colonizations thus gave rise to three and possibly four distinct species (Cibois et al. 2011, Saitoh et al. 2012).

Nomenclature

The common name Nightingale Reed Warbler has been recommended for the Saipan, Alamagan (Saitoh et al. 2012) and, likely, the now presumed extinct (Marshall et al. 2021) Aguiguan population—a viewpoint concurred with here. The extinct Guam and Pagan populations are better candidates for island-specific names.

Fossil history

Excavations on Tinian, Aguiguan and Rota yielded bones of *Acrocephalus*, tentatively identified



FIG. 1. The Saipan Reed Warbler is a large, long-billed passerine.

as *A. luscinius*, only on Tinian (Steadman et al. 1999).

DISTRIBUTION

The species is presently known from Saipan and Alamagan. Prehistorically, an *Acrocephalus* also occurred on Tinian (Steadman 1999), 5 km from Saipan, which was likely the same species. Agui-guan, 9 km from Tinian, also had a population that is now presumably extinct, and this was also likely the same species.

HABITAT

On Saipan, an early report of habitat use described the Saipan Reed Warbler as having a large, dense population in the marshes surrounding Lake Susupe, where birds occupied dense vegetation but avoided bulrushes growing in the water. Other habitats occupied included tall grass in moist gullies at island center mountains, in dense, low forest on the rocky edge of Laolao Bay, at the edge of woodland and in vegetation along a stream flowing through a wooded canyon. It was the only Saipan bird not found uniformly throughout a given kind of environment (Marshall 1949), a phenomenon also noted in 1988–1993 (RJC unpublished data).

More recent island-wide surveys revealed that the species occupied earlier successional habitats such as thicket-meadow mosaics, forest edge and forest openings as well as reed marshes, although it was not found in beach strand or native *Miscanthus floridulus* savanna (Craig 1996). Densities computed from point transect surveys in 1982, 1997 and 2007 were significantly greater in suitable habitats (secondary forest, introduced *Leucaena* thickets, open habitats) than in less suitable habitats (residential areas, golf courses, native forest) (Camp et al. 2009). Nests have been located in upland *Leucaena* thickets (84), a native mangrove (*Bruguiera gymnorhiza*) swamp (15) and a native reed (*Phragmites karka*) marsh (1) (Mosher and Fancy 2002). These observations support the contention that reed warblers on Saipan are primarily associated with uplands (Craig 1992), unlike the extinct Guam and Pagan populations, which were reported primarily although not exclusively from marshes (Seale 1901, Baker 1951, Reichel et al. 1992).

In 1988–1991 studies on territorial pairs of reed warblers, birds principally inhabited areas with a mosaic of introduced *Leucaena* and *Pennisetum* (Fig. 3). Birds also inhabited native reed (*Phragmites karka*) marshes near San Roque, Gualo Rai and Lake Susupe. Contrary to Marshall's (1949) and H.D. Pratt's (pers. comm.) 1976 findings, the species



FIG. 2. This food-begging juvenile has a distinctly shorter bill than the adult.

was not abundant in the Susupe marshes, and birds located were mostly around the marsh edges (Fig. 4). One reed warbler singing near the shore of Lake Susupe was principally associated with a native *Hibiscus tiliaceus* thicket bordering a band of *Scirpus littoralis* edging the lake. Birds did not inhabit the grassy upper slopes of Mt. Tapotchau (elevation = 465 m) but were first encountered at 400 m in native forest edge adjacent to a vegetable farm and at 350 m in a protected valley of *Pennisetum* meadows, *Leucaena* thickets and *Pandanus* clumps. At Gualo Rai, they occurred in a vine-covered valley (Fig. 5) with introduced bamboo (*Bambusa vulgaris*) and open woods of predominantly native tree species, including *Barringtonia asiatica* and *Hibiscus tiliaceus*. At Talufofo, birds were singing from open woods of bamboo, *Hibiscus*, *Leucaena*, *Acacia confusa*, *Pennisetum* grass patches and vines. Elsewhere on the island, including at Navy Hill, Naftan Peninsula, Kagman Peninsula and Fadang, *Leucaena* and *Pennisetum* were the principal vegetation in reed warbler habitat. No territorial birds were present in interior native forest anywhere on the island, although on three occasions individuals were present foraging in relatively scrubby interior forest (Craig 1992, 1996, RJC unpublished data). In 1976, H.D. Pratt (pers. comm.) found several individuals in native forest on the east coast of Marpi. These observations suggest

that habitat structure rather than species composition is the principal factor determining species occupancy.

At Marpi, where data on the structure of habitats occupied by Saipan Reed Warblers were gathered, habitat choice was variable, with neither *Pennisetum* meadows nor *Leucaena* thickets consistently predominating in territories. Thickets averaged highest in cover, however. Aside from *Leucaena* and *Pennisetum*, no plants other than vines had appreciable cover in territories. The predominant vegetation height in territories was >3–6 m, although variation among territories was great. In *Leucaena*, the predominant height was >3–6 m, whereas in *Pennisetum* it was <2 m (Craig 1992)..

In examining the placement of 100 nests on Saipan, no reed warblers were found nesting in native limestone forest even when territories included limestone forest fragments or were adjacent to limestone forest. Moreover, birds that inhabited *Phragmites* marshes were not found to nest outside of the marsh in the wooded area surrounding the wetland (Mosher and Fancy 2002).

Many *Acrocephalus* are principally breeders of marshes, and marsh passerines are believed to develop polygyny because habitat is limited and territories differ strongly in quality. This situation may not hold in the upland habitats used on Saipan. Territories were 10 times larger than territories of some marsh-



FIG. 3. *Leucaena-Pennesetum* thickets at Marpi, Saipan where field studies on territoriality took place.

nesting *Acrocephalus*. Larger birds typically have larger territories than smaller birds, but the difference in territory size seemed disproportionately great, and is likely related to the habitat shift to uplands. Marshes are frequently highly productive, and in such productive habitats smaller territories are sufficient to provide adequate food (Craig 1992).

On Aguiguan, reed warblers were reported to be restricted to native forest, although observers appeared to have difficulty distinguishing the songs of reed warblers from those of other native passerines (Glass 1987, Reichel et al. 1992). Some observers have misidentified songs of Golden White-eyes (*Cleptornis marchei*) as those of reed warblers (Marshall et al. 2021). In 1992, two singing male reed warblers were directly observed to inhabit formerly disturbed areas vegetated by groves of *Casuarina equisetifolia* trees and 5 ha of 1–2 m tall *Lantana camara* thickets. Such habitats closely resembled those occupied on Saipan (Craig and Chandran 1993, RJC personal observation). In 1993, a male was found singing in native forest immediately adjacent to a 1–2 m tall *Lantana* thicket. A 1995 sighting was also of a male seen over several days singing in a similar forest edge area surrounded by open areas of *Lantana* and other introduced plants (USFWS 1998).

On Alamagan, birds were reported from partially open overstory and brushy understory in 1988. They also were seen in dense native swordgrass but within about 50 m of a wooded ecotone (Reichel et al. 1992). During 2008–2010 surveys, the greatest densities encountered were in secondary forest, with lower densities present in native and coconut (*Cocos nucifera*) forest. Feral ungulates on the island

browse woody vegetation and suppress forest regeneration, which is particularly severe at lower elevations where understory loss, open areas and forest fragmentation occur (Marshall et al. 2021).

MOVEMENTS AND MIGRATION

Reed warblers have proven to be strong island colonizers, having dispersed across the tropical Pacific through Micronesia, Melanesia and Polynesia, with the Saipan Reed Warbler dispersing in the past between Saipan and an island over 250 km away. The species also may have once occurred on islands between these two, making the dispersal distance less. However, paleontological evidence for this is lacking, although such evidence does exist for nearby Tinian. Although no conclusive evidence exists for movement of birds between islands, individuals found on Aguiguan in 1992 were suggested to have originated from Saipan, given their behavioral and habitat choice similarity to those on Saipan (Craig and Chandran 1993). The possibility that such a colonization event occurred appears plausible, as reed warblers did not use a stepping stone strategy in their colonization of the Pacific (Cibos et al. 2011). In a similar manner, the Marianas Fruit Dove (*Ptilinopus roseicapilla*) has recently colonized Sarigan, likely from Saipan, bypassing the intervening island of Anatahan in the process (de Cruz 2008).

Radio-tracked birds demonstrated that pairs had overlapping home ranges with neighbors even though they aggressively defended territories against conspecifics. Within the home range, core areas were present where birds concentrated their activi-



FIG. 4. *Phragmites* marsh habitat at Susupe, Saipan.

ties. Home range size was 4.35 ± 2.85 ha ($n = 26$) and core area size was 0.85 ± 0.52 ha ($n = 26$). Home ranges in mangrove swamps averaged largest, whereas those in *Phragmites* marshes averaged smallest (Mosher 2006), which provides some evidence that marsh environments were superior breeding habitats.

Dispersal and site fidelity

During a 1988–1991 study of territoriality at Marpi, Saipan, 9 of 11 males banded in 1988 were present on the same territory in 1989. One moved to a new territory 1900 m from its original one and one was not relocated. In 1991, 9 of 16 males banded by 1989 were relocated, making average annual male turnover 18%. Of eight females banded in 1988, three were relocated in 1989 and two of these were mated to the same male on the same territory. The third female, the mate of the only male to disappear, remained on its 1988 territory with a new mate. Of 10 females seen well during 1990–1991, one was banded in 1988 and one was banded in 1989, both on territories other than those they initially occupied (Craig 1992).

DIET AND FORAGING

The foraging ecology of the Saipan Reed Warbler is largely unstudied. Stomach contents from four Guam birds contained adult and larval insects (Seale 1901). The species also has been reported to prey from the ground upon lizards, snails, spiders and large insects. The stomach contents of collected specimens included a coccinelid beetle, Hemiptera

and Orthoptera (Marshall 1949). Because it generally occupies dense vegetation, observing foraging is difficult. Of seven observations made on foraging, birds ate insects (3), gleaned invertebrates from leaves (3) and probed a dead stub (1) (Craig 1996). The species' large bill size is associated with the ability to eat a greater range of prey sizes, including insects to at least 3 cm (Craig 1992). Nestlings have been fed small caterpillars, large spiders, beetles, millipedes, grasshoppers, skinks, geckos, ants, moths and praying mantids (USFWS 1998, Mosher 2006). A food-begging juvenile was fed a large winged insect (Engbring et al. 1986).

SOUNDS AND VOCAL BEHAVIORS

Males have been reported to sing loudly in a dawn chorus but to sing less during the day (Marshall 1949). However, more recent quantitative observations indicate that male song frequency averages a slow but variable increase from morning to evening. Moreover, individual males may not sing throughout the day, which may be related to breeding status (E. Roark unpublished data). One male can elicit singing by adjacent territorial males and adjacent males engage in song duels. Singing also can occur during moonlit nights and birds often raise their crest feathers during song. Song perches are high exposed treetops, dead snags, interior thickets or *Pennisetum* grass stems, sometimes nearly at the ground, with songs most typically given from 2–3 m in height. Males also have been observed to sing during flight. Midday singing can be from the concealment of reeds when birds inhabit marshes (Marshall 1949, RJC personal observation).



FIG. 5. Vine covered valley habitat at Gualo Rai, Saipan with native and introduced tree species.

Birds from Guam were described as having a rising and falling liquid, sweet song (Seale 1901). In contrast, the song of Saipan birds is variable but often begins with 2–3 spaced, raspy notes, has a several note whistle in the middle and ends with 1–3 higher pitched whistles. The whole sequence may last 4–5 sec. The species also gives an extended jumble of raspy, whistled notes, often with series of the same note repeated, and this may continue for minutes. The call note is a harsh, raspy *chut* or, alternatively, a low, raspy *kwa*. Both members of a pair have been observed to make soft, sputtering, chattering or twittering calls during their interactions (RJC unpublished data). Females have not been observed to sing, although a mist-netted female made a *kreee* call upon release and females also utter raspy *tschoww* notes and make peeping, whining calls. A fledgling was observed to make thin *wheep* begging calls (RJC unpublished data).

Songs are reminiscent of those given by various members of the family Mimidae, although they also share striking similarities in cadence to the North American Orchard Oriole (*Icterus spurius*). All such species are associated with edge/successional environments, which suggests that this type of vocal repertoire is effective in typically dense habitats (RJC personal observation). There are no reported non-vocal sounds.

BEHAVIOR

During 1988–1991, male Saipan Reed Warblers were observed to distinguish territorial boundaries with song. Males defended territories against conspecifics with song and by pursuit of intruders. Song

duels between neighboring territorial males were frequent. Males responded vigorously to playback of tape-recorded songs and could be induced to leave their territories in pursuit of recorded songs. Females usually accompanied their mates during aggressive encounters. However, birds mist-netted using playback became net shy after an initial capture (Craig 1992, RJC personal observation). The movements of individual reed warblers have been observed to be highly variable, with some females travelling >800 m away from their territory and returning hours later. Some birds occasionally left territories to forage (USFWS 1998).

Over three peak breeding seasons, no male on the 50 territories studied associated with more than one female, unlike mainland *Acrocephalus* that are often polygynous. An aggressive, singing banded male observed with a perched fledgling stayed within 10 m of it. When bill-wiping, the species did so slowly compared with shorter-billed species, wiping the entire length of the bill. During rain, birds repeatedly shake the rain from themselves. In the only interspecific interaction noted, three Micronesian Starlings (*Aplonis opaca*) supplanted a male reed warbler from a perch (Craig 1992, RJC unpublished data). During times when temperatures were >32.5°C, birds would gape to assist with regulation of body temperature (Mosher 2006).

BREEDING

Phenology

In January–February 1988, the study area contained 14 territories, whereas in January–February

1989 there were 19 territories. Territorial activity changed seasonally, such that in November–December 1990 only 13 territories were present, but by January–February 1991 the number increased to 17. In May 1991, all 17 territories were still active. However, by July only 15 territories were active, and in September only 14 territories were present. Two territories active in 1989 but vacant in 1990–1991 were on land that had been partly cleared for grazing following 1989 (Craig 1992).

In a 1997–1998 study on Saipan, 51 of 100 reed warbler nests located were active. Two nesting peaks occurred: January–March (dry season) and July–September (wet season). Active nests were located in all months but November–December (Mosher and Fancy 2002).

Nest site

Site characteristics. Nests have been located in seven tree species. In uplands, 79 nests were in introduced *Leucaena leucocephala*, four were in native *Ochrosia mariannensis* and one was in an introduced *Pithecellobium dulce*. Of 15 nests found in mangrove swamps, six were in native *Casuarina equisetifolia*, four were in *Hibiscus tiliaceus*, three were in *Bruguiera gymnorhiza*, one was in *Thespesia populnea* and one was in *Pithecellobium dulce*. A nest found in *Phragmites* was attached to stems. Vegetative cover above, below and around nests varied among substrates (Mosher and Fancy 2002).

In *Leucaena* thickets, nests were attached to a main stem and several lateral branches, with at least one branch supporting from below. Some *Leucaena* nests were constructed on the top of typhoon-damaged trunks and supported by regrowth branchlets. Nests in *Ochrosia* were supported by the main trunk and by 3–5 branches that forked from the center of the tree. Four of six nests in *Casuarina* were attached to high, drooping branches that extended away from the main trunk. In one instance, a nest was at the terminal branch end of a *Bruguiera*. A reed marsh nest was supported by three vertical *Phragmites* stems and two leaning stems from below. Nests were attached using vines looped around or weaved through supports (Mosher and Fancy 2002).

A large, bulky May 1982 nest composed of grasses was 6 m up in the fork of a *Leucaena* (Engbring et al. 1986). A 1988 nest was 4 m up in a 4.6 m *Leucaena* at the edge of a 2–3 m high *Pennisetum* patch. Other similar *Leucaena* were present in the thicket, as were several *Morinda citrifolia*. A 1989 nest was 4.6 m up in a 5.2 m *Leucaena* (RJC unpublished data). Of 83 nest trees recorded in 1997–1998, nest height was 4.3 ± 1.3 m, tree height was 6.1 ± 3.4 m and diameter was 60.7 ± 59.7 mm. The number of support branches for 76 nest trees was 3.9 ± 1.2 . Diameter of support branches was 8.0 ± 4.6 mm ($n = 282$ supports). A nest found

in a reed marsh was 2.2 m high and 0.8 m below the tops of the reeds (Mosher and Fancy 2002).

In a 1997–1998 study on Saipan, birds had a principal nesting area within a territory where several unused nests from previous breeding could be present (Mosher and Fancy 2002).

Nest

Construction process. A female usually gathered nesting material and constructed the nest while the male sang from a nearby perch. On a few occasions, a male carried material to the nest (Mosher and Fancy 2002).

Structure and composition. Stems and tendrils of introduced *Momordica charantia* and *Passiflora foetida* vines were the primary components of the outer nest ($n = 73$). The cup lining of nests in *Leucaena* thickets was primarily *Leucaena* petioles, whereas nests in the mangrove swamp had a larger amount of *Casuarina* branchlets. A nest in *Phragmites* had an outer structure of dry vines, coarse reed blades, a spider web and a cup lined with *Phragmites* panicles. Nests were of two forms: tightly woven, compact nests, and larger, tightly woven nests with bulky outer material. Nests had open cups circular to ovoid in shape. In some nests, the inner rim had an overhanging lip (Mosher and Fancy 2002).

A 1988 nest supported from below by *Leucaena* branches had the upper portion composed of fine fibers, the lower portion composed of coarser materials and had strands of fibers hanging from the bottom of the nest. A 1989 nest was composed of fine material, bark shreds and *Leucaena* pods (RJC unpublished data).

Dimensions. The nest outer diameter was 10.6 ± 1.0 cm and height was 9.0 ± 2.0 cm ($n = 66$). Cup diameter was 6.5 ± 0.6 cm and cup depth was 4.5 ± 0.7 cm. Rim width at the lip was 2.0 ± 0.4 cm and rim width at base was 2.8 ± 0.6 cm. The *Phragmites* nest had an outer diameter of 11.7 cm, height of 9.8 cm, cup diameter of 5.7 cm, cup depth of 4.3 cm, rim width at lip of 2.5 cm and rim width at base of 3.2 cm (Mosher and Fancy 2002). 1988 and 1989 nests measured 15 x 15 cm (RJC unpublished data).

Maintenance and reuse of nests. Two nests were observed to be constructed directly on top of an old nest, although individual nests did not appear to be used more than once. On three occasions, nests in the beginning stages of construction were dismantled and reconstructed nearby (Mosher and Fancy 2002). In instances where a first nest failed, pairs were observed to re-nest (Mosher 2006).

Eggs

Eggs were sub-elliptical and varied from dull white to cream to ivory-buff. Eggs were spotted and blotched with irregularly shaped markings, commonly with a heavier zone of overlapping markings

around the broader end. Markings were gray, brown, black, or rust colored and ranged from pinpoints to 2.3 mm in diameter. The depth of markings was variable within the cuticle and the egg surface was smooth, nonglossy and with a slightly granular appearance. Egg length was 23 ± 1.2 mm and egg width was 16.9 ± 0.5 mm ($n = 50$). Mass was 3.1 ± 0.5 g ($n = 49$). Clutch size has been reported as 2.5 ± 0.7 ($n = 20$ nests) (Mosher and Fancy 2002) and 2.3 ± 0.6 ($n = 39$ nests) (Mosher 2006).

Incubation

Incubation lasted 16 ± 0.84 days ($n = 7$). Eggs were laid on consecutive days and incubation began with the first egg. Both sexes participated in incubation although the female spent the most time doing so (Mosher 2006).

Young birds

Nestlings hatched naked and had closed eyelids, dark gray to black skin and bright yellow gape flanges. Prior to fledging, nestlings were almost completely feathered except around the eyes, ears, chin and throat ($n = 43$). The mean number of tail feathers was 10.2 ± 0.8 ($n = 21$) (Mosher and Fancy 2002).

In 1997–1998, brood the nestling period lasted 16.7 ± 1.7 days ($n = 15$). Both sexes brooded and fed young, with nestlings fed 7.7 ± 2.0 times/hr ($n = 59$ hr). Adults either consumed or deposited fecal sacs away from the nest until nestlings could stand at the edge of the nest. Nestlings then dropped fecal sacs over the nest edge (Mosher 2006).

DEMOGRAPHY AND POPULATIONS

Measures of breeding activity

In 1997–1998, brood sizes ranged from 1–3 and nestlings sometimes disappeared from nests after hatching. Of active nests studied, 44% successfully fledged nestlings ($n = 50$ nests). Of nest failures, 68% occurred during the egg stage and 32% occurred during the nestling stage. In 1997, there were 2.11 ± 0.78 fledged/nest ($n = 9$) and in 1998 there were 1.85 ± 0.55 fledged/nest ($n = 13$) (Mosher 2006).

Life span and survivorship

Daily survival was 0.95 ± 0.01 ($n = 40$ nests) during incubation and 0.98 ± 0.01 ($n = 32$ nests) during the nestling stage (Mosher 2006).

Causes of mortality

In 1997–1998, 75% of nest failures were due to predation, 7% were due to a super-typhoon, 3.5% were due to an unknown cause and 14.5% appeared to be the consequence of aggression with other avian

species, including the Golden White-eye (*Cleptornis marchei*) ($n = 28$ nests). Predators included rats (*Rattus* spp.) and feral cats (*Felis catus*). Possible predators were monitor lizards (*Varanus indicus*), green tree skinks (*Lampropeltis smaragdina*), Micronesian Starlings (*Aplonis opaca*) and Mariana Kingfishers (*Todiramphus albicilla*) (Mosher 2006).

Population spatial metrics

Of 11 males banded on Saipan in 1988, 82% were present on the same territory in 1989, one moved to a new territory and one disappeared. In 1991, 56% of males banded by 1989 were located and annual male turnover for three years was 18%. Six of the nine banded males present in 1991 were on the territory in which they were originally banded. One moved after at least two years at one territory and two moved to new territories after 1989. Of eight females banded in 1988, 38% were relocated in 1989, and two of these were mated to the same male on the same territory. The mate of the only male to disappear remained on its 1988 territory with a new mate. Of 10 females seen well during 1990–1991, one was banded in 1988 and one was banded in 1989, both on territories other than those they initially occupied. High site fidelity occurred in males and low mate fidelity occurred in females, although mate fidelity appeared higher in this sedentary species (Craig 1992) than in other migratory *Acrocephalus* species (Dyrce 1977, Urano 1985) that have been studied. Low female mate fidelity may be favored in this small island population if genetic reassortment yields higher average offspring survivorship (Craig 1992).

In January–February 1988, the study area contained 14 territories, whereas in January–February 1989 there were 19 territories. Territorial activity changed seasonally, such that in November–December 1990 only 13 territories were present but by January–February 1991 the number increased to 17. In May 1991, all 17 territories were still active. However, by July only 15 territories were active, and in September only 14 territories were present, indicating that breeding activity was subsiding (Craig 1992).

On Alamagan, surveys up a long, wooded gully yielded territories at 60–100 m intervals (Reichel et al. 1992).

Population status

On Saipan, populations appear to have been localized following World War II, likely a consequence of extensive agricultural use of land during the Japanese administration. Stott (1947) reported finding only a single pair. Five small populations and a dense population in the marshes surrounding Lake Susupe were reported by Marshall (1949). The Lake Susupe population was estimated at <300 in 1978

(Engbring et al. 1986). Later, Pratt et al. (1979) characterized the species as common, and Ralph and Sakai (1979) estimated a population density of 45 birds/km² based on their 7.3 hours of Emlen (1971) transect counts.

The first island-wide population survey was performed in May 1982 using the variable circular plot (VCP) technique (Buckland et al. 2001). Survey of 14 transects yielded an estimate of 46 birds/km² (better interpreted as males/km², as virtually all VCP detections are of singing males), with a total island population estimate of 4,867 males (Engbring et al. 1986). The same transects were resurveyed in 1997 and 2007 and data from these and the 1982 survey were analyzed with improved computational procedures that employed covariates and larger sample sizes. Population estimates were 57.7 ± 6.0 males/km² in 1982, 40.2 ± 4.5 males/km² in 1997 and 22.5 ± 2.8 males/km² in 2007, with a total 2007 population computed as $2,742 \pm 1,056$ males (Camp et al. 2009). The date of surveys for 1997 and 2007 were not reported, although based on analyses of population variance, little seasonal change occurred in reed warbler population estimates (Craig 1996, 2021b) even though breeding activity changed seasonally (Craig 1992, Mosher and Fancy 2002).

In an examination of habitat effects on 1982, 1997 and 2007 densities, suitable habitats (open, secondary and *Leucaena* thickets) were observed to have higher densities than less suitable habitat (golf course, limestone forest and residential). Moreover, densities declined in unsuitable habitats over time, with the most dramatic decline occurring in residential habitats. In 1982, 60 males/km² were present, whereas in 1997 13 males/km² were present and in 2007 0.05 males/km² were present. A decline was also observed in golf course habitats (Camp et al. 2009).

Additional surveys performed along six VCP transects in 1991–1993 yielded population densities for earlier successional habitats (e.g., *Leucana-Pennisetum* communities) of 52.5 ± 26.1 males/km². Individuals detected incidentally during native limestone forest surveys produced estimates of 11.6 ± 13.8 males/km² in the wet season and 13.2 ± 13.5 males/km² in the dry season, although birds encountered were almost all calling from outside of native forest. Annual wet/dry season comparisons of 1991, 1992 and 1993 surveys yielded limited differences among years and seasons (Craig 2021b).

Birds on Aguiguan were first reported in 1940 by a Japanese collector, and a 1954 visit to the island revealed the species to be rare (Reichel et al. 1992). Perhaps three individuals were found in 1982, with a total population estimate of 4–15 (Engbring et al. 1986). Surveys conducted in 1983–1985 yielded a maximum of six individuals. During eight visits in 1987–1990, no birds were found and the population was thought to have become extinct (Reichel et al. 1992). However, in 1992 two singing males were

located (Craig and Chandran 1993). In 1993, a male was found and in 1995 a male was again observed (USFWS 1998). No birds were detected during a 2008 survey of the island and this population is now thought to be extinct (Marshall et al. 2021).

Birds on Alamagan were first recorded in 1931 by a Japanese collector (Reichel et al. 1992). No other historical records for this island exist. Based on 1988 and 1990 surveys, the Alamagan population was estimated at 350 to 1,000 pairs (Reichel et al. 1992). In 1992, surveys at the north end of Alamagan estimated a population that approached or exceeded the 1992 estimate (USFWS 1998). A 2000 population survey yielded an estimate of 1,125 pairs and one from 2010 yielded an estimate of 946 pairs (Marshall et al. 2021).

CONSERVATION AND MANAGEMENT

Conservation status

Reed Warbler populations in the Mariana Islands, all originally considered to comprise a single species, were federally listed as endangered (USFWS 1970). The Saipan Reed Warbler is listed as critically endangered on the IUCN Red List (Birdlife International 2023). With 2010 populations of ca. 3,687 pairs (Camp et al. 2009, Marshall et al. 2021) distributed over at least two islands, of which only one is inhabited, and with populations appearing to be slowly declining, it has a recovery priority of 8 on a scale of 1–18. This indicates a moderate degree of threat and high potential for recovery (USFWS 1983, 1998).

Effects of human activity

Habitat loss and degradation. During the 1914–1944 Japanese administration, agricultural activity, particularly sugarcane (*Saccharum officinarum*) cultivation, is thought to have reduced available habitat and, therefore, populations of reed warblers on Aguiguan and Saipan. Agricultural activities also resulted in the cutting of reed beds and draining of some wetlands used by birds on Saipan. Since World War II, reversion of agricultural land to earlier successional habitats appears to have benefitted the population on Saipan. However, recent development for agriculture, homesteads and tourist-related facilities has again reduced available habitat, although even when the species was at its commonest the Saipan population did not appear to saturate available habitat. This indicates that additional factors are involved in population regulation (RJC personal observation). Populations also may be impacted from predation by introduced rat (*Rattus* spp.), monitor lizards (*Varanus indicus*) and feral cats (*Felis catus*), as all of these prey upon forest birds or nests. They may account for the reported high proportion of reed

warbler nest failures (Reichel et al. 1992, USFWS 1998, Camp 2009, Marshall et al. 2021).

Effects of invasive species. Whether a brown tree snake (*Boiga irregularis*) population has become established on Saipan is as yet unclear. In 1986, an unidentified snake was seen at the commercial port facility. In 1987, a brown tree snake was seen crawling out of a container at the port. In 1990, a dead brown tree snake was found inside a container arriving from Guam. In 1994, a live brown tree snake was captured at Saipan International Airport. There were two sightings in 1994, two more in 1995, in 1996 two were caught when they swam to the port shore from Guam cargo ships and in 1997 a female snake was captured at the Saipan International Airport. In all, 31 snake sightings have been reported on Saipan from 1986 to 1998 and sightings increased toward the end of that period, suggesting that an incipient population is present. If the brown tree snake becomes established on Saipan, it would likely decimate the reed warbler population much as it did on Guam (USFWS 1998, Rodda and Savidge 2007).

On Aguiguan, the historical presence of feral goats (*Capra hircus*) has degraded some types of understory vegetation used by reed warblers. Unlike on Saipan, the population remained low there during the post-war period, presumably because of goat activity (Engbring et al. 1986). In 1989, a goat removal program reduced the Aguiguan goat population such that in 1992 only three goats were detected during a week of wildlife surveys. By 1995, however, goat numbers had begun to rebound as hunting pressure was reduced (Craig and Chandran 1993, USFWS 1998).

On Alamagan, the species is common despite the presence of feral ungulates, perhaps because a human population present until 1990 controlled goats. The difference in populations between Alamagan and Aguiguan may be attributable to the denser understory on Alamagan (Reichel et al. 1992). Recent observations indicate that feral ungulates are damaging woody vegetation and this may result in future population reduction (Marshall et al. 2021).

Management

Wetlands, with which the species shows some association, are protected by Section 404 of the Clean Water Act. This act prohibits unpermitted alteration of wetlands. The U.S. Army Corps of Engineers must take into consideration the effects of a project on endangered species when issuing a permit for wetland alteration. Similarly, Presidential Executive Order 11990 directs federal agencies to protect wetlands, and the Emergency Wetland Resource Act assists in wetland acquisition for conservation. The welfare of reed warblers is also considered during the permitting phase of major land development projects. Provisions to protect habitat and to mitigate for loss of habitat are included in Commonwealth of the

Northern Marianas (CNMI) permits for such projects. In addition, a habitat conservation plan is being developed that includes establishment of an upland mitigation bank to maintain and enhance habitat for reed warblers and other native species (USFWS 1998).

Efforts in the CNMI directed at controlling the spread of brown tree snakes have included maintaining trap lines at ports, conducting night searches and investigating snake reports. A sniffer dog program is also used to check cargo at ports. Publicity campaigns are used to raise awareness among island residents, including port workers, about the dangers of brown tree snake introduction. On Guam, control work involves interception of snakes at ports and setting snake traps around the airport to help prevent export of snakes (USFWS 1998).

Recent stochastic population models that did not consider inbreeding still indicated that declines of Saipan Reed Warbler populations are expected. The inclusion of inbreeding into models increased the rate of population decline. Initial population size, carrying capacity and male survival had comparatively little influence on reed-warbler populations, whereas female and juvenile survival as well as fecundity more strongly influenced them (Fahtle-Lepczyk et al. 2018).

PRIORITIES FOR FUTURE RESEARCH

To date, no translocations of reed warblers to other islands have been attempted. The islands of Rota, Aguiguan, Tinian, Anatahan, Pagan and Agrihan have been proposed as potential sites for introduction of new populations or reestablishment of extinct populations. Of these islands, at least Tinian, Aguiguan and Pagan formerly supported populations and the species also may have once inhabited other islands in the chain (Craig 1992, USFWS 1998, Marshall et al. 2021).

In order for the species to be delisted from endangered or threatened status, U.S. Fish and Wildlife Service (USFWS) guidelines call for the Marianas population to be comprised of $\geq 4,000$ individuals on Saipan, 2,000 on Alamagan and 2,000 in ≥ 3 additional island populations. Rota, Aguiguan, Tinian, Anatahan, Pagan and Agrihan are target islands. These populations must be stable or increasing for ≥ 5 consecutive years. Once delisted, USFWS must monitor populations for a minimum of five years to ensure that protections provided by the Endangered Species Act are no longer required (USFWS 1998).

Based on population modeling, collecting updated survival data for all life stages, but particularly for females and juveniles is recommended. Given model predictions of the species' vulnerability to extinction, management actions that increase survival of juveniles and females are also recommended (Fahtle-Lepczyk et al. 2018).

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