

## TERRITORIALITY, HABITAT USE AND ECOLOGICAL DISTINCTNESS OF AN ENDANGERED PACIFIC ISLAND REED-WARBLER

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**Abstract.**—Nightingale Reed-Warblers (*Acrocephalus luscini*a) were studied on Saipan, Mariana Islands from 1988 to 1991 to assess the territoriality, habitat use and morphology of this endangered, endemic, island species. Data were compared to those for closely related mainland forms to gain insights into differences evolved in an insular environment. Peak territorial activity was reached in January–February, the dry season. Males exhibited high site fidelity, but females had low mate fidelity between years. Birds inhabited mostly upland thicket-meadow vegetation, but they also used reed marshes, wetland thickets, and forest openings. Territory size in thicket-meadow complexes averaged  $9338 \pm 3433$  (SD) m<sup>2</sup>. Males were larger than females; mass, wing, tail, and tarsus length reliably distinguished sexes. Compared to the mainland *A. orientalis* and *A. arundinaceus*, *A. luscini*a had (1) polygyny largely or entirely absent, (2) much larger territories, (3) upland rather than marshes as the principal breeding habitat and (4) body size, particularly bill size, greatly increased. The shift to upland habitats may account for the difference in social behavior and territory size. Greater size is typical of island forms that may confront competitively impoverished or food-limited environments.

### TERRITORIALISMO, USO DE HABITAT Y SINGULARIDADES ECOLÓGICAS DEL AMENAZADO *ACROCEPHALUS LUSCINI*A

**Sinopsis.**—De 1988 a 1991 se estudió en Saipan (Islas Marianas) el territorialismo, uso de habitat y morfología del endémico y amenazado con desaparecer *Acrocephalus luscini*a. Se compararon los datos tomados con los de especies continentales similares, para hacer notar diferencias evolutivas que se dan en ambientes insulares. El pico de la conducta territorial se alcanzó en los meses de enero y febrero que corresponden a la temporada seca. Los machos exhibieron gran fidelidad a localidades, pero las hembras mostraron entre años poca fidelidad hacia sus parejas. Las aves habitan mayormente en matorrales de alturas, pero además utilizan anegados de junquillos y matorrales de pantanos y aperturas en bosques. El tamaño del territorio en complejo de matorrales promedió  $9338 \pm 3433$  (DE) m<sup>2</sup>. Los machos resultaron de mayor tamaño que las hembras; el peso, largo del ala, cola y tarso es confiable para distinguir entre los sexos. Comparado con *A. orientalis* y *A. arundinaceus*, *A. luscini*a tiene: (1) territorios de mayor tamaño, (2) áreas altas o montañas como habitat principal de anidamiento en vez de anegados costaneros, (3) tamaño, y (4) poliginia virtualmente o totalmente ausente. El cambio a habitats de alturas puede deberse a diferencia en la conducta social y tamaño del territorio. El mayor tamaño es típico de especies de islas que puedan confrontar empobrecimiento competitivo en ambientes limitados en alimentos.

Reed-warblers (Sylviinae: *Acrocephalus*) are widespread from Europe through Australasia, where many species inhabit marshes and are polygynous (review in Urano 1985). Members of the genus are strong island

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colonizers, presently represented in the tropical Pacific by as many as 10 species (Pratt et al. 1987). The relatively large, long-billed Nightingale Reed-Warbler (*A. luscinia*) of the Mariana Islands, Micronesia, is among the most distinctive of these. Baker (1951) believed it to be descended from the Eastern Great Reed-Warbler (*A. orientalis*), a species that has populations in the Bonin Islands, about 750 km N of the 812-km long Mariana chain (Baker 1951). These two species, along with the European–African *A. arundinaceus*, the Australasian *A. stentoreus* and all other Pacific island *Acrocephalus* form a superspecies that occurs over much of the Old World (Mayr et al. 1986).

Three subspecies of Nightingale Reed-Warbler are currently recognized (Mayr et al. 1986). *A. l. luscinia*, originally found on Guam, Saipan and Alamagan, has been extinct on Guam since the late 1960s (Engbring et al. 1986). *A. l. nijoi* of Aguijan, thought to be extinct, was rediscovered in May 1992, and *A. l. yamashinae* of Pagan became extinct ca. 1981 (Glass 1987). Steadman's (1989) findings of numerous, human-related prehistoric extinctions of Polynesian birds suggest that the species may have once inhabited additional islands as well.

On Saipan, Nightingale Reed-Warblers are presently widespread, with populations estimated at 4867 in 1982 (Engbring et al. 1986). To provide basic data for future conservation and management of this largely unknown, endangered species, I document the social behavior, habitat use and morphology of the Saipan population. I also compare my data with those for related mainland forms to gain insights into differences evolved in an insular environment.

#### STUDY AREAS AND METHODS

I studied Nightingale Reed-Warblers on Saipan in 1988 and 1989 during January–February, dry season months that correspond to the time of peak singing and presumably peak breeding (Glass 1987). Additional observations were made from November 1990 to September 1991. I observed birds throughout the island (Fig. 1) but primarily in the Marpi region.

Detailed investigations of habitat use and territoriality were conducted on about 26 ha in the flat lowlands (about 10–40 m elevation) below the cliffs in the Marpi region and on the plateau (about 130–200 m elevation) near the top of these cliffs. These flat areas are vegetated by tangantangan (*Leucaena leucocephala*) thickets and elephant grass (*Pennisetum purpureum*) meadows (Fig. 2). The introduced tangantangan, aerially seeded after World War II to prevent erosion, often occupies land formerly cultivated for sugarcane (Fosberg 1960).

I studied territoriality by mist-netting birds in ATX (36 mm mesh) 12-m nets and color banding them. Birds were attracted to nets by playing tape recorded conspecific songs. Once banded, I confirmed the identity of territory holders visually with binoculars, and recorded their movements on field maps. Territory boundaries were determined with a variant of the minimum polygon method (Hill and Lein 1989) in which a curved

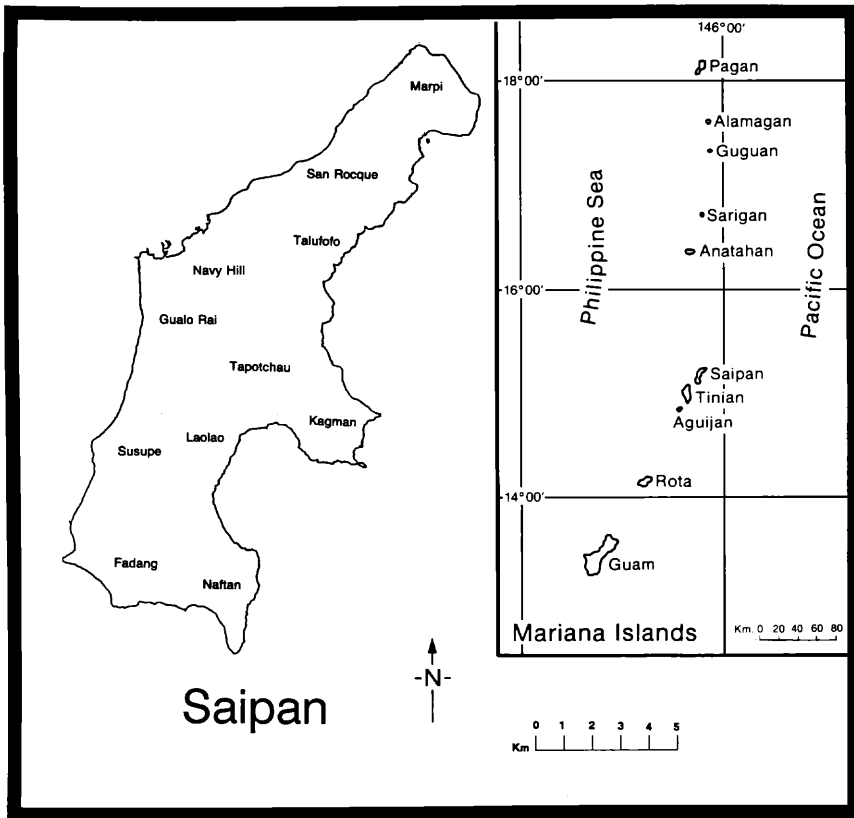


FIGURE 1. Principal study sites on Saipan, and the geographic relationship of Saipan to the neighboring Mariana Islands, Micronesia. Adapted in part from Jenkins (1983).

perimeter was fitted around outermost perches used by singing or intraspecifically aggressive males undisturbed by playback of taped calls.

I mapped seven 1988 territories on 1:2000 base maps made from 1:10,000 color aerial photographs using a Bausch and Lomb Zoom-transfer scope. Precise map scale was determined from taped measurements made in the field between distinct landmarks. Field data were transferred to these base maps, and territory area was measured with a compensating polar planimeter.

Data on habitat structure from these same seven territories were obtained by dividing them into eight "blocks" of approximately equal size and placing a 30-m transect in each block (stratified random sample). On each transect, habitat type (elephant grass meadow, tangantangan thicket, intergradation between these two types) and plant species composition were recorded at 1-m intervals (240 total sample points/territory). At 3-m intervals (80 points/territory) I recorded vegetation height in the following classes: <2, >2-3, >3-6 and >6 m.



FIGURE 2. Nightingale Reed-Warbler habitat at Marpi, Saipan, showing elephant grass meadows (foreground), tangantangan thickets (midground), and the Marpi cliffs vegetated by native forest.

To assess the morphology of this population, I made the following measurements on mist-netted individuals: mass, wing chord, tail length, tarsus length, and bill length (from the distal end of the nostrils). Breeding male Nightingale Reed-Warblers were distinguished by their cloacal protuberances, whereas breeding females were sexed by their brood patches. After color banding, sexes were verified by observing pairs on their territories. For comparison, I also made morphological measurements on museum skins of summering *A. orientalis* from China.

#### RESULTS

*Social behavior and territoriality.*—Male Nightingale Reed-Warblers defended territories by singing, and used either exposed treetops, interior thickets or elephant grass stems as song perches. Males responded vigorously to playback of tape recorded songs, and could be induced to leave their territories in pursuit of taped songs. I never observed females to sing, but they usually accompanied their mates during aggressive encounters, such as during response to playback. On no occasion did I observe any male on the 50 territories studied over three peak breeding seasons (28 individual males) to associate with more than one female.

Of 11 males banded in 1988, 9 (82%) were present on the same territory in 1989. One moved to a new territory 1900 m from its original one, and one disappeared. Hence, all males but one banded in 1988 (91%) were relocated. In 1991, I located 9 of 16 (56%) males banded by 1989. Taking

into account the missed January–February 1990 season, average annual male turnover for 3 yr was 18%. This turnover was not necessarily the same as male mortality, because males might have left the study area. Six of the 9 banded males present in 1991 were on the territory in which I originally banded them. One moved after at least 2 yr at one territory, and two moved to new territories after 1989.

Of eight females banded in 1988, three (38%) 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.

In January–February 1988 the study area contained 14 territories, whereas in January–February 1989 there were 19 territories, a 36% increase. Territorial activity changed seasonally, such that in November–December 1990 I could locate only 13 territories, but by January–February 1991 the number increased to 17. In May 1991, all 17 territories were still active. By July, however, only 15 territories were active, and in September I found only 14 territories, indicating that breeding activity was subsiding. Two territories active in 1989 but vacant in 1990–1991 were on land that had been partly cleared for grazing following 1989.

*Habitats.*—Most birds I found on Saipan inhabited areas with a mosaic of tangantangan and elephant grass. Birds also inhabited native reed (*Phragmites karka*) marshes near San Rocque, Gualo Rai and Lake Susupe. Contrary to Marshall's (1949) and H. D. Pratt's (pers. comm.) 1976 findings, however, the species was not abundant in the Susupe marshes, and birds located were mostly around the marsh edges. One reed-warbler singing near the shore of Lake Susupe seemed principally associated with a native pogo (*Hibiscus tiliaceus*) thicket bordering a band of bulrushes (*Scirpus littoralis*) edging the lake. Birds did not inhabit the grassy upper slopes of Mt. Tapotchau (elev. 465 m). They were first encountered at 400 m inhabiting native forest edge adjacent to a vegetable farm, and at 350 m in a protected valley vegetated by elephant grass, tangantangan thickets and *Pandanus* clumps. At Gualo Rai, I found reed-warblers in a vine-covered valley with bamboo (*Bambusa vulgaris*) and open woods of predominantly native tree species. At Talufofo, I found birds singing from open woods of bamboo, pogo, tangantangan, sosuge (*Acacia confusa*), elephant grass patches and vines. Elsewhere on the island, including at Navy Hill, Naftan Peninsula, Kagman Peninsula and Fadang, tangantangan and elephant grass were the principal vegetation in reed-warbler habitat. I found no territorial reed-warblers in interior native forest anywhere on the island, although on two occasions I found individuals foraging in relatively scrubby interior forest. In 1976, H. D. Pratt (pers. comm.) found several birds in native forest on the east coast of Marpi.

At Marpi, where I gathered data on the structure of habitats chosen by Nightingale Reed-Warblers, I found that habitat choice was variable,

TABLE 1. Percent vegetation cover in the territories of seven Nightingale Reed-Warblers.

	Habitat		Plant species				
	Meadow	Thicket	Mixed	Elephant grass	Tangan-tangan	Vines	Other
Mean	26.3	50.1	23.7	49.9	70.8	9.0	15.7
SD	13.7	20.0	9.3	20.0	13.7	8.0	13.1

with neither elephant grass meadows nor tangantangan thickets consistently predominating in territories. Thickets averaged highest in coverage, however (Table 1). Aside from tangantangan and elephant grass, no plants other than vines had appreciable cover in reed-warbler territories. The predominant vegetation height in territories was >3–6 m, although variation among territories was again great (Table 2). In tangantangan the predominant height was >3–6 m, whereas in elephant grass it was <2 m.

Size of the seven territories mapped in 1988 averaged  $9338 \pm 3433$  (SD) m<sup>2</sup>. Regression of territory size with principal habitat parameters showed little relationship between area and cover by elephant grass meadow ( $r^2 = 0.02$ ,  $P > 0.5$ ) or tangantangan thicket ( $r^2 = 0.14$ ,  $P > 0.5$ ). In 1989, five of these territories appeared unaltered. Parts of the other two territories were usurped by adjacent territorial birds. One had a slight boundary change in 1989, but the other had substantially altered boundaries. As I spent less time determining territory boundaries after 1988, I was uncertain whether the males present in these two territories, the same ones that were present in 1988, compensated for their loss of some territory by expanding their territory elsewhere. Both of these males used the same preferred song perches as in 1988, however.

*Morphology.*—Male Nightingale Reed-Warblers were significantly larger than females in mass (equal variance model  $t = 4.1$ , 26 df,  $P < 0.001$ ), wing length ( $t = 7.7$ , 27 df,  $P < 0.0001$ ), tail length ( $t = 5.0$ , 27 df,  $P < 0.0001$ ) and tarsus length ( $t = 4.5$ , 27 df,  $P < 0.0001$ ), but did not significantly differ from females in bill length ( $t = 1.2$ , 27 df,  $P > 0.25$ ). For the 95% confidence interval, mass, and wing, tail and tarsus length had non-overlapping ranges, and were therefore useful in sexing

TABLE 2. Percent cover of vegetation heights (m) in the territories of seven Nightingale Reed-Warblers. Coverage for plant species was computed as observations/height category divided by total sampling stations (80).

	Plant species									
	Elephant grass		Tangantangan				Overall			
	<2	>2–3	<2	>2–3	>3–6	>6	<2	>2–3	>3–6	>6
Mean	33.6	15.0	11.1	19.6	41.3	3.2	26.1	29.6	41.3	2.9
SD	15.0	11.8	7.7	6.3	13.5	2.0	9.5	11.3	12.5	1.7

TABLE 3. Morphology of Nightingale Reed-Warblers.

	Mass (g)	Wing chord (mm)	Tail length (mm)	Tarsus length (mm)	Bill length (mm)
Male					
Mean	35.9	87	83	34.8	23.0
SD	1.9	2	2	1.0	1.0
CV	5.4	1.9	2.6	2.8	4.4
95% CI	0.9	0.8	1.0	0.5	0.5
<i>n</i>	19	19	19	19	19
Female					
Mean	32.0	82	78	33.2	22.6
SD	3.1	2	3	0.7	0.9
CV	9.8	2.7	3.8	2.0	3.9
95% CI	2.4	1.6	2.1	0.5	0.6
<i>n</i>	9	10	10	10	10

nonbreeding individuals (Table 3). Hence, birds with a mass >35.0 g, wing length >86.4 mm, tail length >81.5 mm or tarsus length >34.3 mm were males, and birds with a mass <34.4 g, wing length <83.2 mm, tail length <79.8 mm or tarsus length <33.7 mm were females.

#### DISCUSSION

Like most territorial passerines (Morse 1980), Nightingale Reed-Warbler males defended territories against conspecifics with song and by pursuit of intruders. High site fidelity by males and low mate fidelity by females are also typical of passerines (e.g., Nolan 1978), although male fidelity, and perhaps survivorship, appeared higher (82%) in this sedentary species than in Nolan's (1978) migratory population of Prairie Warblers (*Dendroica discolor*) (65%). Low female mate fidelity may be particularly favored in this small island population if genetic reassortment leads to higher average offspring survivorship.

Unlike *A. orientalis*, in which 17–43% of males are polygynous (Urano 1985), and *A. arundinaceus*, in which 12% are polygynous (Dyrce 1977), *A. luscinia* appeared entirely monogamous. *A. orientalis* (Saitou 1976) and *A. arundinaceus* (Dyrce 1977) are principally breeders of reed marshes, and marsh passerines are believed to develop polygyny because habitat is limited and territories differ strongly in quality. Females maximize their reproductive output by mating polygynously with a male on a superior territory (Verner and Willson 1966). This situation may not hold in the upland habitats used by *A. luscinia* on Saipan, hence, polygyny does not appear to be favored in this population.

Also unlike the marsh nesting *A. orientalis* and *A. arundinaceus*, *A. luscinia* on Saipan has a wide range of breeding habitats (the historically rare Guam [Jenkins 1983] and Pagan [Glass 1987] populations might have been restricted to wetlands, although H. D. Pratt [pers. comm.] suspects this perception to be artifactual). The elephant grass-tangan-

tangan mosaics now most frequently used by *A. luscini*a are, however, comprised of introduced species (More and McMakin 1979). The range of habitats I observed birds use, from reed marshes to forest openings, suggests that *A. luscini*a initially expanded its habitat use from reed marshes to adjacent *Hibiscus* thickets and structurally similar disturbed sites, such as typhoon-created forest openings of meadow and thicket vegetation. Moreover, reed-warblers may have used native tangantangan (*Leucaena insularum*) that now grows mixed with *L. leucocephala* along the coast.

Territories of *A. luscini*a were 10 times larger than territories of *A. orientalis*, which Saitou (1976), using methods similar to mine, found to have reed marsh territories averaging 830 m<sup>2</sup> at the peak breeding season. Larger birds typically have larger territories than smaller birds (Schoener 1968), but the difference in territory size of *A. orientalis* compared to the 50% larger (by mass) *A. luscini*a (Nisbet and Medway 1972) seems disproportionately great, and is likely due to the habitat shift to uplands by *A. luscini*a. Marshes are frequently highly productive, and in such productive habitats smaller territories are sufficient to provide adequate food (Orians 1971).

The population increase in Nightingale Reed-Warblers after 1988 may have been a result of population recovery from the effects of a 1987 supertyphoon, whose >300 km/h winds destroyed much of the island's thicket habitats (P. Glass, pers. comm.). In contrast, the loss of two territories after 1989 appeared due to agricultural activity.

Compared to mainland members of the *A. arundinaceus* complex, such as *A. orientalis*, *A. luscini*a is a large, very long-billed species. Mean male *A. orientalis* fall mass is 24.1 g (Nisbet and Medway 1972), whereas male bill length measured on museum specimens is 12.8 ± 0.7 mm (*n* = 8). Both these differences are observed frequently among island populations when compared to mainland relatives (Blondel 1985). Larger bill size is related to a greater range of food size selection (Hespenheide 1973), a potential advantage in a competitively impoverished or food limited island. Indeed, unlike its mainland relatives, which are insectivorous, the Nightingale Reed-Warbler has extended its prey selection to include insects of at least 3 cm in length (pers. obs.) and lizards (Marshall 1949).

The Nightingale Reed-Warbler on Saipan is, therefore, a sedentary, sexually size dimorphic species of thicket-meadow complexes. Unlike close mainland relatives, it is largely or entirely monogamous, it defends comparatively large territories principally in uplands rather than in marshes, and it is larger and longer billed.

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