

A new species of nightjar (*Caprimulgus*) from Timor and Wetar, Lesser Sunda Islands, Wallacea

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The nightjars of the *Caprimulgus macrurus* complex are distributed from Pakistan to Australia and comprise six morphologically similar but vocally distinct species. Fieldwork on Timor and Wetar, Lesser Sunda Islands, has resulted in the discovery of a seventh species in the complex, which we describe as a new species. This species has previously been confused with *Caprimulgus macrurus*, *Caprimulgus celebensis* and *Caprimulgus manillensis* but it differs from these and all other species in the complex by at least 13 vocal characters. Discriminant function analysis correctly classified all recordings in the complex to species. *Caprimulgus ritae* is known from five adult museum specimens, which are the smallest in the complex and which differ from other species in the complex in several morphological characters. A molecular phylogenetic analysis indicated that *C. ritae* is sister to *C. meesi* from Flores and Sumba, and that these species together are sister to *C. macrurus*. *C. ritae* is a tropical forest specialist occurring from sea level to at least 1500 m (probably mostly below 1000 m). Lowland and montane forests on Timor are threatened. Wetar is one of the least developed islands in Indonesia, and retains >95% natural vegetation, dominated by *Eucalyptus* woodlands, with tropical forests in river gorges and slopes in upland areas. Pressure for development is accelerating throughout the range of *C. ritae*, and a detailed assessment of its conservation status is urgently needed.

Keywords: acoustics, Caprimulgidae, cryptic species, morphology, taxonomy, Wallacea.

The Wallacean region has long been a source of insights in biogeography and evolutionary biology (Wallace 1869, Jönsson *et al.* 2016, Moyle *et al.* 2016). Despite its prominence in the evolutionary literature, the region remains relatively poorly known and avian species diversity is almost certainly underappreciated (Irestedt *et al.* 2013). This is underscored by the continued discovery of new species, which in the past three decades

included two rails (Lambert 1998a, 1998b), five owls (Lambert & Rasmussen 1998, Rasmussen 1999, Indrawan & Somadikarta 2004, Jönsson *et al.* 2013, Sangster *et al.* 2013), a nightjar (Sangster & Rozendaal 2004) and 11 passerines (Indrawan *et al.* 2008, Harris *et al.* 2014, Prawiradilaga *et al.* 2017, Ng *et al.* 2018, Irham *et al.* 2020, 2023, Rheindt *et al.* 2020). It is not surprising that most of these species have either a cryptic lifestyle or inhabit remote areas, which makes them difficult to study in the field.

Nightjars are among the most difficult bird species to study due to their unobtrusive and nocturnal behaviour and cryptic plumage. In recent

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years, vocalizations have been used to clarify species limits, which has resulted in the recognition of several additional species (Mees 1985, Hardy & Straneck 1989, Rozendaal 1990, Sangster & Rozendaal 2004). Previous studies of species limits in the Large-tailed Nightjar *Caprimulgus macrurus* complex revealed the existence of six species, of which each is diagnosable by up to eight acoustic differences (Sangster & Rozendaal 2004). Differences in song among species with allopatric breeding ranges are as large as those of the single pair of sympatric species in this complex (Jerdon's Nightjar *Caprimulgus atripennis*, *C. macrurus*; Fig. 1). Furthermore, allopatric species that have been subjected to playback tests discriminate between songs of their own species and those of other species (Sangster & Rozendaal 2004).

Due to the small number of museum specimens and a lack of sound recordings, assessments of the

taxonomic status of the 'Large-tailed Nightjars' on Timor and Wetar, Lesser Sunda Islands, have been problematic (Mayr 1944, Mees 1977, Sangster & Rozendaal 2004). Museum specimens are limited to three specimens from Wetar (two in the American Museum of Natural History, New York (AMNH) and one in the Naturalis Biodiversity Centre (NBC), Leiden, the Netherlands) and a newly collected specimen from Timor-Leste in the NBC. Due to their small size, these specimens have puzzled previous authors, who have assigned these specimens to either: Philippine Nightjar *Caprimulgus manillensis*, Sulawesi Nightjar *Caprimulgus celebensis* or *C. macrurus* (Finsch 1901, Hartert 1904, 1906, Mees 1977, and specimen label data). Recent fieldwork on Timor and Wetar by Ben F. King (B.F.K.) and Colin R. Trainor (C.R.T.) suggests that the territorial songs of the 'Large-tailed Nightjars' on these islands are distinct

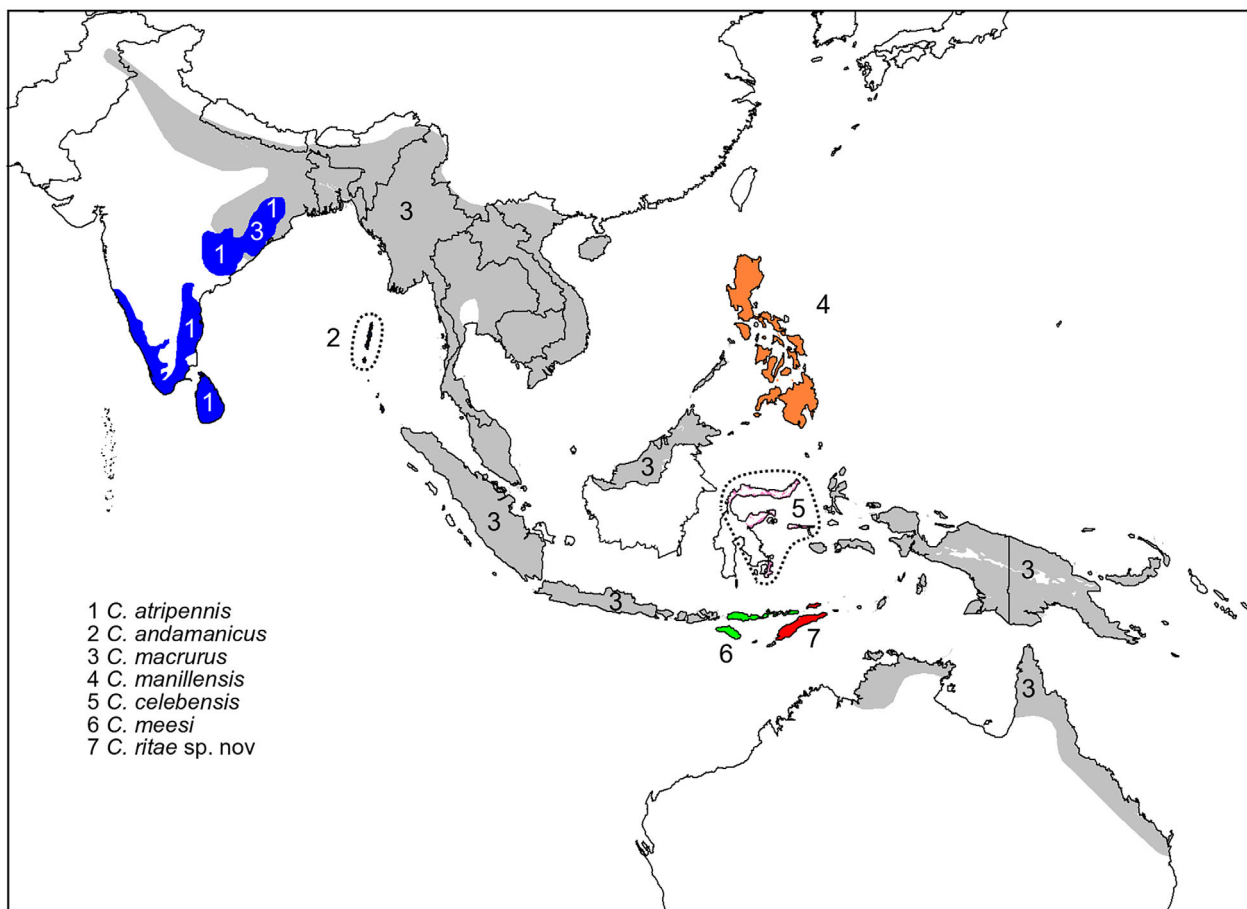


Figure 1. Map showing range of the *Caprimulgus macrurus* complex. Species limits are based on Sangster and Rozendaal (2004) and the present study.

from those of all other members of this complex. Here we analyse sound recordings, museum specimens and DNA sequences, and confirm the distinctiveness of these nightjars, which constitute a previously overlooked species in the *C. macrurus* complex.

METHODS

Molecular phylogenetics

We used tissue samples (toe-pads) of one 'Large-tailed Nightjar' from Timor, one from Wetar, one Mees's Nightjar *Caprimulgus meesi* (the holotype), one *C. atripennis* and 29 *C. macrurus* from South-East Asia, Indonesia, Papua New Guinea and Australia. Sequences from two additional *C. macrurus* individuals were obtained from GenBank. All samples are from vouchered museum specimens. Collection localities, dates of collection and museum voucher numbers are listed in Table S1.

Genomic DNA was extracted using the Qiagen DNeasy Tissue Kit (Qiagen, Valencia, CA, USA) following the manufacturer's protocol. Three modifications were made: the lysis procedure was extended to 15–20 h, the amount of proteinase K was increased to 35 μ L and 35 μ L of 1 M dithiothreitol solution was added to the initial lysis step to facilitate the breakdown of tissue.

Mitochondrial DNA sequences were used to assess the status and phylogenetic position of the nightjars on Timor and Wetar. We used the cytochrome *b* (*cyt b*) gene for polymerase chain reaction (PCR) amplification because this marker has been used successfully in a previous study to resolve phylogenetic relationships in nightjars (Han *et al.* 2010).

Because nearly all samples in our study are from old museum specimens, DNA is fragmented. Therefore, PCR amplification was performed in six partially overlapping fragments of 192–229 bp each. Primer sequences were newly designed (Table S2) using sequences obtained from fresh tissue samples. PCR products were Sanger sequenced in both directions using Big Dye 3.1 chemistry and run on an ABI 3100 capillary sequencer (Applied Biosystems, Foster City, CA, USA). Sequence fragments were aligned and edited using LASERGENE EDITSEQ (DNA Star, Madison, WI, USA).

To complement our dataset, we added GenBank sequences of Jungle Nightjar *Caprimulgus*

indicus (GU586640), *C. manillensis* (FJ588443), Chuck-will's-widow *Antrostomus carolinensis* (FJ588442), Nacunda Nighthawk *Chordeiles nacunda* (GU586685), Great Eared Nightjar *Lyncornis macrotis* (FJ588447), Collared Nightjar *Gactornis enarratus* (GU586637) and Spotted Nightjar *Eurostopodus argus* (GU586667) (Braun & Huddleston 2009, Han *et al.* 2010). The latter three sequences served as outgroup taxa for phylogenetic analyses.

Consensus sequences were aligned with ClustalW implemented in MEGA7 (Kumar *et al.* 2016). We used Bayesian inference and maximum likelihood (ML) to estimate phylogenetic relationships. Bayesian analysis was run in MrBayes 3.2.2 (Ronquist *et al.* 2012) as implemented on the CIPRES Science Gateway (Miller *et al.* 2010). The best substitution model was determined with MEGA7 using the Akaike information criterion. Accordingly, we ran analyses using the GTR + G + I model of nucleotide substitution. Analyses were partitioned by codon. Two runs with four metropolis coupled Monte Carlo Markov Chains were made for 2 million generations sampling every 1000 trees and discarding the first 25% (500 trees) as burn-in. The results were compared between runs to ensure that the chains had reached convergence (Nylander *et al.* 2008). We also checked that the potential scale reduction factor approached 1.0 for all parameters and that the average standard deviation of split frequencies converged towards zero. To validate the phylogeny obtained from MrBayes we calculated an ML tree with RAxML v7.7.1 (Stamatakis *et al.* 2008). We applied the GTR + G + I model, partitioned the dataset by codon and calculated support from 1000 bootstrap pseudoreplicates. Genetic divergence was measured as uncorrected parsimony values in MEGA7 excluding nucleotide positions with missing data to ensure a strictly comparable dataset (Fregin *et al.* 2012).

We applied four methods to verify the authenticity of newly generated DNA sequences: (1) inspection of electropherograms; (2) comparison of overlapping sequence fragments; (3) verification that stop codons or frameshift mutations were not present; and (4) assessment of the distribution of nucleotide substitutions among the three codons (Sangster *et al.* 2016). In addition, for the sequences of the holotype of *C. meesi* and those of the nightjars on Timor and Wetar, we assessed the phylogenetic position of the six fragments

separately in an ML analysis to verify that all fragments were derived from the same locus.

Vocalizations

Twenty-three recordings of nightjars on Timor and Wetar were obtained by B.F.K. and C.R.T. One further recording from Timor-Leste by Frank Lambert was obtained from the AVOCET database (<http://avocet.zoology.msu.edu/>), and one from Wetar by Mike Nelson was obtained from the Xeno-Canto database (<https://www.xeno-canto.org/>). These recordings were compared with a set of 154 recordings of all species and subspecies in the *C. macrurus* complex (*sensu* Sangster & Rozendaal 2004). A list of recordings employed for all taxa with localities and recordists are provided in Table S3. All our recordings have been submitted to the Macaulay Library (Cornell University) or the British Library Sound Archive (London); accession numbers are provided in Table S3.

To enable a comparison with previous results, the methods of Sangster and Rozendaal (2004) were applied. Nineteen characters of the territorial songs were measured (Fig. S1): (1) number of notes in a song; (2) number of peaks in a song; (3) total song duration (measured from start of first element to end of last element); (4) maximum frequency of first peak; (5) minimum frequency of first low; (6) maximum frequency of second peak; (7) minimum frequency of second low; (8) maximum frequency of penultimate peak; (9) maximum frequency of last peak; (10) maximum frequency, which is the highest frequency present; (11) minimum frequency, which is the lowest frequency present; (12) frequency drop of first downward element; (13) frequency drop between penultimate peak and last peak, the 'drop' can be a positive or a negative value, in the latter case the last peak has a higher frequency than the penultimate peak; (14) peak frequency, which is the frequency with the highest amplitude; (15) peak frequency time, which is the point in time (measured from start of song) with the highest amplitude; (16) structure of first element, calculated by dividing the frequency range of the first element by the frequency range of the second element, rounded to the nearest 0.05; (17) song pace, which is the number of peaks divided by total song duration; (18) bout pace, which is the number of songs divided by the duration of the bout – if a sound file contains several cuts, the longest

uninterrupted bout was selected; and (19) frequency range. For each recording, up to five songs were measured. Means of these songs were computed and used as sample points from which ranges, means and standard deviations were computed.

Morphology

To identify morphological differences between the Timor and Wetar population and other taxa, 153 specimens of 11 species and subspecies in the complex were examined (Table S4). Specimens in juvenile or downy plumage or with damaged, extensively worn or moulting wing and tail feathers were excluded. Museum specimens are housed in the NBC, Leiden (formerly Rijksmuseum voor Natuurlijke Historie; RMNH), the AMNH, New York and the Swedish Museum of Natural History, Stockholm.

Whenever possible, we recorded the following information from each specimen: bill length (from gape, from anterior point of nostril), wing length (chord of flattened wing from bend of wing to tip of longest primary), emarginations of P9 and P8 (distance from tip of feather), wing formula, difference in length ('shortfall') between the longest primary and each of P1–P10, tail length (longest rectrix measured from point of insertion of central rectrices to tip of longest rectrix) and length of white terminal patch on R4 and R5 (measured along shaft on both inner and outer webs). Plumage colours were compared with published colour standards (Ridgway 1912, Smithe 1975).

Statistical analyses

Canonical discriminant function analysis (DFA) was applied to the acoustic and morphometric variables of individuals to test whether the individuals could be correctly assigned to species. DFA generates a set of criteria to assign individuals to groups that are defined before the analysis. Before DFA, a tolerance test was conducted to assess the independence of each variable. Variables that failed the tolerance test, i.e. that were an almost linear combination of other variables, were excluded from the analyses. Two DFAs were performed: (1) a 'descriptive' DFA, in which the observations used to develop the criteria were then subjected to these criteria; and (2) a 'predictive' DFA, which used a jackknife procedure to obtain a more

accurate test of the predictive performance of the DFA. In the jackknife procedure, the DFA was recalculated using the combination of variables of the initial DFA with one individual removed from the dataset. The criteria were then used to classify the removed individual. This process was repeated for all individuals of the dataset.

For univariate statistics of vocal differences, we used the non-parametric Mann–Whitney U test because all significant comparisons failed the Kolmogorov–Smirnov test, or Levene’s test of homogeneity of variance, or both. Holm’s sequential Bonferroni test (Holm 1979) was used to correct significance due to multiple tests being performed.

The effect size, expressed as Cohen’s d , was calculated to show the strength of the acoustic differences between taxa. For interpretation of effect size data, we used the classification of Cohen (1988), which was expanded by Sawilowsky (2009). We regard an effect size of $d \geq 0.01$ as ‘very small’, $d \geq 0.2$ as ‘small’, $d \geq 0.5$ as ‘medium’, $d \geq 0.8$ as ‘large’, $d \geq 1.25$ as ‘very large’ and $d \geq 2.0$ as ‘huge’.

SPSS version 27.0 (IBM, Armonk, NY, USA) was used to calculate all descriptive statistics, except Cohen’s d , and perform DFA, Mann–Whitney U test, Kolmogorov–Smirnov test and Levene’s test of homogeneity of variance. Cohen’s d was calculated in Microsoft Excel.

RESULTS

Molecular phylogenetics

We obtained 578–1055 bp of cyt b sequences of the samples from Timor and Wetar, *C. macrurus*, *C. meesi* and *C. atripennis*. Phylogenetic analyses based on ML and Bayesian interference produced almost identical phylogenies, which were generally well supported by both methods (Fig. 2). The samples from Timor and Wetar clustered together with strong support (99% bootstrap, 1.0 posterior probability (PP) and were sister to the holotype of *C. meesi*, again with strong support (99% bootstrap, 1.0 PP). All other samples of *C. macrurus* formed a monophyletic group (99% bootstrap, 1.0 PP), which was sister to the Timor/Wetar/*C. meesi* clade with moderate support (91% bootstrap).

Caprimulgus macrurus showed strong phylogeographical structure and consisted of three well-supported clades (PP 0.98–1.0), of which two

are found exclusively west of Wallace’s Line, whereas most members of the third clade are found east of Wallace’s Line. One clade corresponded to *C. m. macrurus* (Java, Bali, Salayer). Another clade corresponded to *C. m. bimaculatus* (mainland South-East Asia, Sumatra) and a third clade corresponded to *C. m. schlegelii* (Wallacea, New Guinea, northern Australia) but also included single representatives from Kalimantan (*C. m. salvadorii*) and *C. m. macrurus* (Java).

Mean sequence divergence (uncorrected p -distance) between the samples from Timor/Wetar and *C. meesi* was 2.9%. Sequences from the nightjars on Timor/Wetar differed from *C. macrurus* by 5.8%, whereas the holotype of *C. meesi* differed from *C. macrurus* by 5.2%. In contrast, mean intraspecific divergence of *C. macrurus* was 0.7%.

The authenticity of our sequences of *C. macrurus*, *C. meesi* and the population on Timor and Wetar is supported by multiple lines of evidence: chromatograms exhibited no double peaks; overlapping sequence fragments were identical; the alignment showed no stop codons, insertions or deletions; and the majority (86/112; 76.8%) of the nucleotide substitutions relative to two previously published sequences of *C. macrurus* based on fresh material (GU586643, GU586644) were found at the third codon position, and the fewest (8/112; 7.1%) were found at the second codon position. In ML analyses of the sequences of individuals sampled from Timor and Wetar, all fragments analysed separately were more closely related to *C. meesi* than to any other taxon (data not shown).

Discriminant function analyses of vocalizations

The songs of 150 individuals were included in a DFA using the seven species in the *C. macrurus* complex as group categories. All characters passed the tolerance test, except for maximum frequency ($n = 10$), frequency drop between penultimate and last peak ($n = 13$) and frequency range ($n = 19$), which were excluded from the test. The descriptive DFA was highly significant (Wilks’ $\lambda < 0.001$; Chi-square₉₆ = 2287.2; $P < 0.001$). The variables most important in the discrimination were: (1) number of notes, (2) number of peaks, (12) frequency drop of the first element and (16) structure of the first element. The descriptive DFA

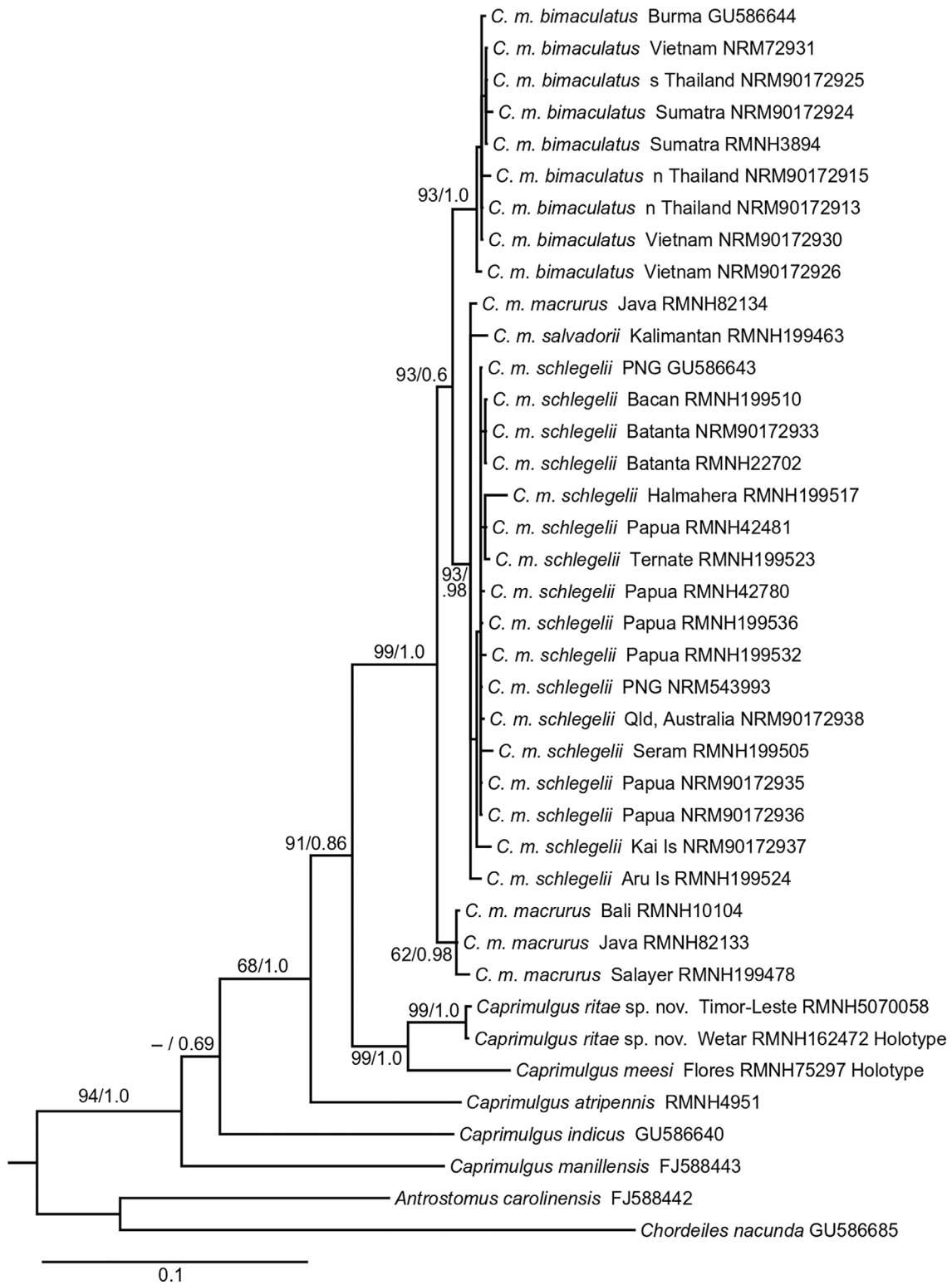


Figure 2. Bayesian phylogeny of nightjars. Numbers indicate bootstrap support from maximum likelihood analysis and posterior probabilities from Bayesian inference. Three outgroups are not shown.

led to a 100% correct classification of the individuals into the seven groups, whereas the predictive (jackknife) DFA classified 99.3% of the recordings correctly. The first of the six discriminant functions (DF1) accounted for 65.7% of the variation, and the second (DF2) and third (DF3) accounted for 18.3% and 10.4% of the variation, respectively (Fig. 3a).

A second DFA included Andaman Nightjar *Caprimulgus andamanicus*, *C. macrurus*, *C. atripennis* and the population on Timor and Wetar. All characters passed the tolerance test, except: (1) number of notes, (10) maximum frequency, (13) frequency drop between penultimate and last peak, and (19) frequency range, which were excluded from the test. The descriptive DFA was highly significant (Wilks' $\lambda < 0.001$; $\chi_{45} = 919.1$; $P < 0.001$). The variables most important in the discrimination were: (3) total song duration, (7) minimum frequency of the second low, (11) minimum frequency and (17) song pace. Both the descriptive DFA and the predictive (jackknife) DFA led to a 100% correct classification of the individuals into the four groups. The first three discriminant functions (DF1, DF2, DF3) accounted for 68.4%, 25.7% and 5.9% of the variation, respectively (Fig. 3b).

Univariate analyses of vocalizations

Territorial song characteristics of all taxa of the *C. macrurus* complex are given in Table 1 and statistical comparisons are given in Table 2. After Holm's sequential Bonferroni test, comparison of the 19 acoustic variables revealed 78 significant

differences between pairs of the Timor and Wetar vocal type and the six other groups (Table 2), representing 68% of 114 comparisons. The recordings from Timor and Wetar differed significantly from all other species by 8–17 acoustic variables (Table 2). Vocal differences were characterized by large effect sizes. In a total of 77 comparisons (68%) between pairs of the Timor and Wetar vocal type and the six other groups, the effect size was either 'very large' or 'huge' (Table 2).

Description of the Timor and Wetar song type

The territorial song of the nightjars on Timor and Wetar consisted of a single note with three (occasionally four) peaks (Fig. 4). As in other vocal types (Sangster & Rozendaal 2004), the first peak reached the highest frequency but in contrast to other song types, except that of *C. andamanicus*, the second and third peaks had a lower frequency than the preceding peak, and the second low was lower than the first one. The first low was at c.800 Hz, resulting in a much greater frequency drop of the first downward element than in *C. andamanicus* (Fig. 3, Table 1). Perhaps because of this, songs of the nightjars on Timor and Wetar sound lower pitched than those of *C. andamanicus*, and the difference is clear to the human ear. Songs are shorter than those of all other species, and total song duration is only 0.064–0.077 s. Vocalizations are often given in bouts of 5–16 rapidly repeated songs, followed by a pause of 1.0–2.5 s. We have not encountered this song pattern in any of the other species. A bout of five songs can be rendered as *choh-choh-choh-choh-choh*. The songs of this type sound less deep than those of *C. macrurus* and lack the deep *chonk* tone of that species. This song type is only known from Timor and Wetar; no other song types were recorded from these islands.

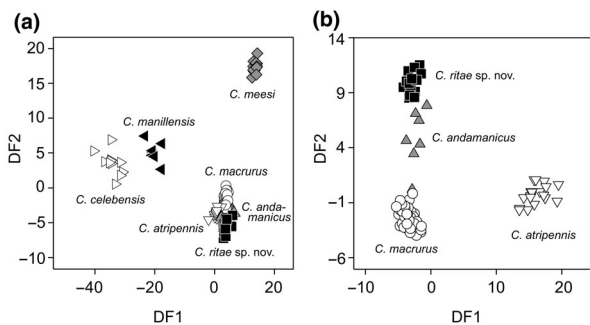


Figure 3. Discriminant function analysis scatterplots of acoustic variables measured for territorial songs of species of the *Caprimulgus macrurus* complex. (a) Seven species ($n = 150$); (b) four species ($n = 116$).

Morphometrics

Morphometric data on the specimens from Timor and Wetar, *C. andamanicus* and the four Indonesian subspecies of *C. macrurus* are given in Table 3 (males) and Table 4 (females). The small sample size of the specimens from Timor and Wetar (three males and two females) precluded meaningful tests of diagnosability. However, in both sexes, emargination of P9, wing length and tail length of

Table 1. Descriptive statistics of 19 acoustic variables measured for territorial songs of the *Caprimulgus macrurus* complex. Data presented are mean (standard deviation; sample size) and minimum and maximum values.

Variable	<i>C. ritae</i> sp. nov.	<i>C. andamanicus</i>	<i>C. macrurus</i>	<i>C. meesi</i>
1	1.0 (0.0; 16) 1.0–1.0	1.0 (0.0; 7) 1.0–1.0	1.00 (0.00; 76) 1.00–1.00	1.0 (0.0; 15) 1.0–1.0
2	3.1 (0.3; 16) 3.0–4.0	4.5 (0.5; 7) 4.0–5.0	4.01 (0.11; 80) 4.00–5.00	6.0 (0.0; 17) 6.0–6.0
3	0.071 (0.004; 16) 0.064–0.077	0.099 (0.012; 7) 0.083–0.122	0.147 (0.019; 80) 0.119–0.195	0.156 (0.013; 17) 0.131–0.172
4	1749.5 (103.4; 18) 1579.4–2008.0	1587.9 (77.3; 7) 1486.0–1669.0	1690.6 (114.0; 82) 1469.2–2123.6	2524.8 (147.0; 17) 2311.0–2813.2
5	776.8 (53.8; 16) 719.0–927.0	1011.2 (132.9; 7) 818.0–1170.6	658.9 (68.0; 80) 533.2–861.0	655.0 (140.3; 14) 380.0–861.0
6	973.5 (102.3; 18) 809.4–1226.0	1259.9 (46.9; 7) 1223.0–1347.0	913.9 (79.8; 81) 769.0–1134.4	1061.2 (147.6; 17) 849.6–1330.0
7	654.8 (62.9; 16) 521.0–794.8	702.8 (71.7; 7) 611.5–833.4	619.6 (85.4; 75) 431.0–797.6	681.7 (139.8; 14) 446.0–900.5
8	948.8 (134.0; 16) 735.4–1226.0	999.2 (49.3; 7) 966.0–1104.0	933.5 (84.0; 82) 749.4–1156.0	1000.9 (74.1; 15) 880.0–1141.0
9	752.3 (55.8; 16) 661.4–846.8	920.8 (33.9; 7) 860.0–966.0	934.4 (86.3; 81) 762.0–1126.8	881.1 (68.6; 15) 777.0–995.4
10	1749.5 (103.4; 18) 1579.4–2008.0	1587.9 (77.3; 7) 1486.0–1669.0	1690.6 (114.0; 82) 1469.2–2123.6	2524.8 (147.0; 17) 2311.0–2813.2
11	654.0 (58.5; 16) 521.0–752.6	702.8 (71.7; 7) 611.5–833.4	611.5 (82.2; 75) 431.0–797.6	637.3 (132.3; 14) 380.0–861.0
12	1059.1 (274.6; 18) 795.6–1758.0	576.7 (201.7; 7) 345.0–851.0	1031.2 (116.3; 80) 778.8–1352.0	1874.4 (228.0; 14) 1451.5–2198.0
13	196.5 (84.8; 16) 66.0–379.2	78.3 (46.6; 7) 45.2–173.0	1.5 (44.9; 81) –93.8–233.0	120.8 (69.4; 15) 6.0–290.0
14	1583.2 (251.2; 16) 805.6–1889.4	1397.4 (87.9; 7) 1265.0–1495.5	1502.9 (181.2; 82) 902.3–1811.2	2093.8 (195.5; 17) 1752.0–2466.6
15	0.007 (0.003; 16) 0.003–0.017	0.007 (0.003; 7) 0.004–0.011	0.011 (0.006; 82) 0.003–0.039	0.048 (0.015; 17) 0.015–0.066
16	0.06 (0.05; 19) 0.00–0.10	0.11 (0.02; 7) 0.10–0.15	0.17 (0.06; 82) 0.10–0.30	0.98 (0.03; 18) 0.90–1.00
17	43.818 (3.679; 16) 40.135–52.102	45.147 (3.509; 7) 40.984–49.024	27.653 (3.346; 80) 21.982–33.681	38.657 (3.369; 17) 34.935–45.802
18	3.409 (0.708; 25) 1.570–4.140	1.554 (0.727; 7) 0.922–3.095	1.347 (0.394; 81) 0.529–2.390	0.772 (0.423; 17) 0.148–1.572
19	1094.7 (123.4; 16) 955.4–1487.0	885.1 (139.2; 7) 670.8–1049.5	1082.8 (147.0; 75) 785.2–1380.6	1892.0 (214.9; 14) 1590.0–2248.0

Variable	<i>C. atripennis</i>	<i>C. celebensis</i>	<i>C. manillensis</i>
1	1.0 (0.0; 18) 1.0–1.0	7.8 (0.9; 14) 7.0–9.8	5.00 (0.37; 11) 4.20–5.83
2	4.0 (0.3; 19) 3.0–5.0	0.324 (0.026; 19) 0.270–0.397	5.28 (0.74; 11) 4.20–7.00
3	1330.9 (69.7; 19) 1179.4–1478.8	601.5 (41.9; 19) 550.0–700.2	0.387 (0.033; 11) 0.356–0.449
4	601.5 (41.9; 19) 550.0–700.2	1178.9 (60.3; 19) 1061.6–1292.2	1456.2 (89.8; 12) 1325.6–1682.6
5	1178.9 (60.3; 19) 1061.6–1292.2	568.6 (41.1; 19) 500.0–641.8	648.6 (51.5; 12) 535.5–727.4
6	568.6 (41.1; 19) 500.0–641.8	1125.1 (79.2; 19) 945.0–1224.8	1344.2 (271.2; 12) 754.0–1689.0
7	1125.1 (79.2; 19) 945.0–1224.8	903.1 (94.1; 19) 742.8–1127.8	689.3 (52.3; 12) 619.2–792.0
8	903.1 (94.1; 19) 742.8–1127.8	1330.9 (69.7; 19) 1179.4–1478.8	1012.8 (83.6; 10) 858.6–1165.4
9	1330.9 (69.7; 19) 1179.4–1478.8	566.1 (38.7; 19) 500.0–641.6	954.4 (95.2; 10) 834.4–1130.4
10	566.1 (38.7; 19) 500.0–641.6	734.5 (67.3; 19) 617.4–857.0	1465.4 (85.9; 12) 1359.0–1689.0
11	734.5 (67.3; 19) 617.4–857.0	221.7 (79.9; 19) 74.5–360.8	652.8 (34.2; 11) 609.4–712.4
12	221.7 (79.9; 19) 74.5–360.8	1291.0 (70.4; 19) 1139.2–1423.8	809.7 (101.1; 12) 718.4–1073.2
13	1291.0 (70.4; 19) 1139.2–1423.8	0.033 (0.009; 19) 0.015–0.045	58.3 (41.4; 10) –5.8–118.0
14	0.033 (0.009; 19) 0.015–0.045	0.26 (0.03; 19) 0.25–0.35	1367.2 (100.1; 12) 1123.4–1491.2
15	0.26 (0.03; 19) 0.25–0.35	12.341 (0.652; 19) 11.090–13.468	0.113 (0.092; 12) 0.002–0.270
16	12.341 (0.652; 19) 11.090–13.468	0.326 (0.071; 19) 0.187–0.435	0.44 (0.08; 13) 0.25–0.50
17	0.326 (0.071; 19) 0.187–0.435	762.2 (70.2; 19) 638.4–867.0	13.605 (0.983; 11) 11.429–15.590
18	762.2 (70.2; 19) 638.4–867.0		0.706 (0.306; 13) 0.320–1.418
19			821.8 (101.6; 11) 739.0–1079.6

Table 2. Summary of differences in vocalizations of nightjars in the *Caprimulgus macrurus* complex. Values are significance levels from Mann–Whitney *U* test, Cohen's *d*, and interpretation of effect size following Cohen (1988) and Sawilowsky (2009). *P* values marked with an asterisk remained significant after Holm's sequential Bonferroni test (Holm 1979).

Variable	<i>C. ritae</i> sp. nov. – <i>C. andamanicus</i>	<i>C. ritae</i> sp. nov. – <i>C. macrurus</i>	<i>C. ritae</i> sp. nov. – <i>C. meesi</i>	<i>C. ritae</i> sp. nov. – <i>C. atripennis</i>	<i>C. ritae</i> sp. nov. – <i>C. manillensis</i>	<i>C. ritae</i> sp. nov. – <i>C. celebensis</i>
1	n.s. 0.00	n.s. 0.00	n.s. 0.00	n.s. 0.00	<i>P</i> < 0.001* 18.01 (huge)	<i>P</i> < 0.001* 11.89 (huge)
2	PP < 0.001* 3.50 (huge)	PP < 0.001* 5.26 (huge)	PP < 0.001* 12.48 (huge)	<i>P</i> < 0.001* 2.67 (huge)	<i>P</i> < 0.001* 4.15 (huge)	<i>P</i> < 0.001* 7.56 (huge)
3	<i>P</i> < 0.001* 3.96 (huge)	<i>P</i> < 0.001* 4.47 (huge)	<i>P</i> < 0.001* 9.09 (huge)	<i>P</i> < 0.001* 13.36 (huge)	<i>P</i> < 0.001* 15.45 (huge)	<i>P</i> < 0.001* 7.78 (huge)
4	<i>P</i> < 0.001* 1.73 (very large)	<i>P</i> < 0.05 0.53 (medium)	<i>P</i> < 0.001* 6.31 (huge)	<i>P</i> < 0.001* 4.91 (huge)	<i>P</i> < 0.001* 3.09 (huge)	<i>P</i> < 0.001* 5.15 (huge)
5	<i>P</i> < 0.001* 2.91 (huge)	<i>P</i> < 0.001* 1.81 (very large)	<i>P</i> < 0.005 1.22 (large)	<i>P</i> < 0.001* 3.79 (huge)	<i>P</i> < 0.001* 2.52 (huge)	<i>P</i> < 0.001* 1.89 (very large)
6	<i>P</i> < 0.001* 3.28 (huge)	<i>P</i> < 0.05 0.71 (medium)	n.s. 0.72 (medium)	<i>P</i> < 0.001* 2.53 (huge)	<i>P</i> < 0.001* 2.04 (huge)	<i>P</i> < 0.001* 2.68 (huge)
7	n.s. 0.77 (medium)	n.s. 0.43 (small)	n.s. 0.26 (small)	<i>P</i> < 0.001* 1.70 (very large)	n.s. 0.61 (medium)	n.s. 0.13 (very small)
8	n.s. 0.45 (small)	n.s. 0.16 (very small)	n.s. 0.49 (small)	<i>P</i> < 0.001* 1.69 (very large)	n.s. 0.57 (medium)	n.s. 0.36 (small)
9	<i>P</i> < 0.001* 3.49 (huge)	<i>P</i> < 0.001* 2.24 (huge)	<i>P</i> < 0.001* 2.14 (huge)	<i>P</i> < 0.001* 1.97 (very large)	<i>P</i> < 0.001* 2.88 (huge)	<i>P</i> < 0.005 1.47 (very large)
10	<i>P</i> < 0.001* 1.73 (very large)	<i>P</i> < 0.05 0.53 (medium)	<i>P</i> < 0.001* 6.31 (huge)	<i>P</i> < 0.001* 4.91 (huge)	<i>P</i> < 0.001* 3.04 (huge)	<i>P</i> < 0.001* 5.05 (huge)
11	n.s. 0.82 (large)	<i>P</i> < 0.05 0.55 (medium)	n.s. 0.17 (very small)	<i>P</i> < 0.001* 1.86 (very large)	n.s. 0.02 (very small)	n.s. 0.82 (large)
12	<i>P</i> < 0.001* 1.95 (very large)	n.s. 0.18 (very small)	<i>P</i> < 0.001* 3.30 (huge)	<i>P</i> < 0.001* 1.69 (very large)	<i>P</i> < 0.001* 1.16 (large)	<i>P</i> < 0.001* 2.21 (huge)
13	<i>P</i> < 0.001* 1.63 (very large)	<i>P</i> < 0.001* 3.70 (huge)	<i>P</i> < 0.05 1.01 (large)	n.s. 0.32 (small)	<i>P</i> < 0.001* 2.01 (huge)	<i>P</i> < 0.001* 2.02 (huge)
14	<i>P</i> < 0.005 0.89 (large)	<i>P</i> < 0.05 0.42 (small)	<i>P</i> < 0.001* 2.35 (huge)	<i>P</i> < 0.001* 1.70 (very large)	<i>P</i> < 0.001* 1.11 (large)	<i>P</i> < 0.001* 2.24 (huge)
15	n.s. 0.09 (very small)	<i>P</i> < 0.005 0.77 (medium)	<i>P</i> < 0.001* 3.70 (huge)	<i>P</i> < 0.001* 3.83 (huge)	<i>P</i> < 0.001* 1.84 (very large)	<i>P</i> < 0.001* 1.12 (large)
16	<i>P</i> < 0.05 1.23 (large)	<i>P</i> < 0.001* 2.17 (huge)	<i>P</i> < 0.001* 22.10 (huge)	<i>P</i> < 0.001* 5.29 (huge)	<i>P</i> < 0.001* 6.49 (huge)	<i>P</i> < 0.001* 2.95 (huge)
17	n.s. 0.38 (small)	<i>P</i> < 0.001* 4.80 (huge)	<i>P</i> < 0.001* 1.51 (very large)	<i>P</i> < 0.001* 12.83 (huge)	<i>P</i> < 0.001* 10.77 (huge)	<i>P</i> < 0.001* 13.28 (huge)
18	<i>P</i> < 0.001* 2.69 (huge)	<i>P</i> < 0.001* 4.29 (huge)	<i>P</i> < 0.001* 4.43 (huge)	<i>P</i> < 0.001* 5.87 (huge)	<i>P</i> < 0.001* 4.51 (huge)	<i>P</i> < 0.001* 5.51 (huge)
19	<i>P</i> < 0.005 1.71 (very large)	n.s. 0.08 (very small)	<i>P</i> < 0.001* 4.80 (huge)	<i>P</i> < 0.001* 3.49 (huge)	<i>P</i> < 0.001* 2.46 (huge)	<i>P</i> < 0.001* 4.09 (huge)

the specimens from Timor and Wetar were shorter than those of *C. macrurus* and fell outside the range of variation of the latter.

Separate DFAs were performed for males and females. To maximize the number of specimens of *C. meesi*, *C. andamanicus*, and the Timor and Wetar population, we excluded characters with missing data. This resulted in the exclusion of five characters in both the male and the female datasets. In the DFA of males, shortfalls of P10, P6

and P1, bill from gape, and bill from nostril were excluded. In the DFA of females, shortfalls of P10, P9, P8 and P1, and bill to gape were excluded.

The DFA of male specimens was based on three specimens from Timor and Wetar, three specimens of *C. andamanicus*, two specimens of *C. meesi* and 44 specimens of the four Indonesian subspecies of *C. macrurus* (*C. schlegelii*, *C. macrurus*, *C. salvadorii*, *C. bimaculatus*). The descriptive DFA was highly significant (Wilks' $\lambda = 0.121$; $\chi_{45} = 87.6$;

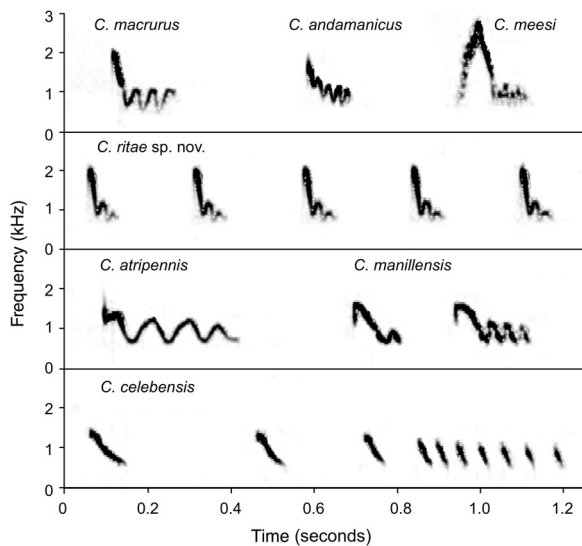


Figure 4. Sonograms of the territorial songs of the seven species of the *Caprimulgus macrurus* complex. A bout of five songs is depicted for *Caprimulgus ritae* sp. nov., whereas only a single song is depicted for each of the other species.

$P < 0.001$). The variables most important in the discrimination were: emargination of P9, shortfall of P4, wing length (flattened chord), tail length and length of the white terminal patch on the outer web of R4. The descriptive DFA led to a 98.1% correct classification of the individuals into the four groups, whereas the predictive (jackknife) DFA classified 82.7% of the specimens correctly. The first of the three discriminant functions (DF1) accounted for 67.1% of the variation, and the second (DF2) and third (DF3) accounted for 28.8% and 4.1% of the variation, respectively (Fig. 5).

The DFA of female specimens was based on two specimens from Wetar, one specimen of *C. andamanicus*, and 17 specimens of three Indonesian subspecies of *C. macrurus* (*C. schlegelii*, *C. macrurus*, *C. bimaculatus*). The descriptive DFA was significant (Wilks' $\lambda = 0.009$; $\chi_{30} = 46.9$; $P < 0.05$). The variables most important in the discrimination were: shortfalls of P3, P5 and P6, and the length of the white terminal patch on the outer web of R4 and R5. The descriptive DFA led to a 100% correct classification of the individuals into the seven groups, whereas the predictive (jackknife) DFA classified 65% of the specimens correctly. The first of the two discriminant functions (DF1) accounted for 78.1% of the variation, and the second (DF2) accounted for 21.9% of the variation (Fig. 5).

In both sexes, plots of DF1 against DF2 placed the specimens from Timor and Wetar outside the range of *C. macrurus* and *C. andamanicus* (Fig. 5). In addition, in males, the plot also separated the specimens from Timor and Wetar from those of *C. meesi* (no female specimens of *C. meesi* are known to exist).

Evidence for a single taxon on Timor and Wetar

A bird observed at Assalaino, Timor-Leste, on 24 September 2013, which was heard and which produced the vocalizations typical of the Timor and Wetar population was collected immediately afterwards (RMNH.5070058). Subsequent comparisons showed that its morphology and *cyt b* sequence were nearly identical to those of a specimen of the Wetar population. In addition, a bird that was sound recorded on Wetar on 13 October 2014 (XC204788 and XC204789) was photographed (Fig. 6) and showed two diagnostic characters of this species (coarsely barred lateral crown feathers and chestnut brown ear-coverts) providing further evidence that the vocally distinct nightjars on this island are the same as the specimens in AMNH and RMNH.

DISCUSSION

The results of this study show that the nightjars on Timor and Wetar are distinct from all other species in the complex, including *C. macrurus* with which they have been confused, and *C. meesi*, which is their closest relative, in mitochondrial DNA, territorial songs and morphometrics.

As in most other species in the complex, the Timor and Wetar vocal type is geographically restricted and not found in other parts of the range of the *C. macrurus* complex. In the *C. macrurus* complex, populations with distinctive vocalizations are concordant with traditionally defined taxonomic groups based on morphological differences (e.g. Mees 1977, Cleere 1998, Sangster & Rozendaal 2004). Lack of intergradation of vocal types in the sympatric *C. aripennis* and *C. macrurus* and discrimination between conspecific and heterospecific songs in playback tests of *C. macrurus* and *C. meesi* suggest that there are strong reproductive barriers among nightjars with different vocal types (Sangster & Rozendaal 2004). We conclude that the 'Large-tailed Nightjars' on Timor and Wetar

Table 3. Measurements of morphological variables for male *Caprimulgus ritae* sp. nov., *Caprimulgus meesi*, *Caprimulgus andamanicus* and Indonesian subspecies of *Caprimulgus macrurus*. Data presented are mean (standard deviation; sample size) and minimum and maximum values. *Caprimulgus meesi* and *C. macrurus* data from Sangster and Rozendaal (2004).

	<i>C. ritae</i> sp. nov.	<i>C. meesi</i>	<i>C. andamanicus</i>	<i>C. m. schlegelii</i>	<i>C. m. macrurus</i>	<i>C. m. salvadorii</i>	<i>C. m. bimaculatus</i>
P9 emargination from tip	64.7 (1.2; 3) 64–66	69.5 (6.4; 2) 65–74	75.0 (0.0; 3) 75–75	72.9 (2.3; 22) 69–77	77.0 (2.9; 20) 68–80	72.5 (2.5; 4) 70–76	77.8 (2.6; 5) 75–80
P8 emargination from tip	60.3 (1.2; 3) 59–61	65.0 (4.2; 2) 62–68	67.7 (2.1; 3) 66–70	67.0 (2.5; 22) 63–73	71.7 (2.7; 21) 65–74	68.3 (4.3; 4) 65–74	72.8 (4.7; 5) 67–79
Wing formulae	8 = 9 > 10 > 7 (n = 1)	8 = 9 > 10 > 7 (n = 1)	8 > 9 > 7 > 10 (n = 1)	8 > 9 > 7 > 10 (n = 19)	8 > 9 > 7 > 10 (n = 11)	8 > 9 > 7 > 10 (n = 2)	8 > 9 > 7 > 10 (n = 4)
	8 > 9 > 10 > 7 (n = 2)	8 > 9 > 10 > 7 (n = 1)		8 > 9 > 10 > 7 (n = 2)	8 > 9 > 7 > 10 (n = 2)	8 > 9 > 7 = 10 (n = 1)	8 > 9 > 7 = 10 (n = 1)
				8 > 9 > 7 = 10 (n = 1)	8 = 9 > 7 > 10 (n = 1)	8 > 9 > 10 > 7 (n = 1)	
				9 > 8 > 10 > 7 (n = 1)	8 = 9 > 7 = 10 (n = 1)		
					9 > 8 > 10 > 7 (n = 2)		
					9 > 8 > 7 > 10 (n = 1)		
Shortfall P10	11.0 (1.0; 3) 10–12	9.0 (0.0; 2) 9–9	15.0 (0.0; 2) 15–15	14.0 (5.4; 21) 8–35	12.9 (2.1; 19) 8–15	12.5 (0.6; 4) 12–13	14.4 (2.6; 5) 11–18
Shortfall P9	0.7 (0.6; 3) 0–1	0.5 (0.7; 2) 0–1	1.8 (1.3; 3) 0.5–3	1.6 (0.8; 21) 0–3	1.0 (0.9; 20) 0–3	2.0 (0.8; 4) 1–3	1.6 (0.9; 5) 1–3
Shortfall P8	0.0 (0.0; 3) 0–0	0.0 (0.0; 2) 0–0	0.0 (0.0; 3) 0–0	0.0 (0.2; 21) 0–1	0.2 (0.5; 21) 0–2	0 (0; 4) 0–0	0 (0; 5) 0–0
Shortfall P7	13.0 (2.6; 3) 11–16	11.5 (2.1; 2) 10–13	12.7 (2.1; 3) 11–15	10.0 (1.7; 22) 6–12	10.3 (1.7; 20) 7–14	11.8 (1.3; 4) 10–13	11.2 (1.8; 5) 9–13
Shortfall P6	39.8 (2.8; 3) 38–43	39.0 (4.2; 2) 36–42	41.5 (3.5; 2) 39–44	38.4 (2.0; 21) 34–42	39.3 (2.8; 21) 33–43	39.7 (4.0; 3) 35–42	40.7 (2.1; 3) 39–43
Shortfall P5	53.5 (2.2; 3) 52–56	53.5 (4.9; 2) 50–57	56.7 (3.1; 3) 54–60	52.9 (2.6; 21) 51–60	56.5 (2.4; 20) 49–59	56.8 (4.0; 4) 51–60	59.2 (2.9; 5) 55–63
Shortfall P4	61.2 (1.8; 3) 59.5–63	62.5 (4.9; 2) 59–66	67.0 (4.6; 3) 62–71	65.7 (4.0; 21) 60–77	67.0 (3.1; 21) 59–70	65.0 (2.9; 4) 61–68	70.6 (4.2; 5) 64–75
Shortfall P3	66.5 (2.8; 3) 63.5–69	67.5 (4.9; 2) 64–71	74.3 (4.7; 3) 69–78	72.9 (4.5; 21) 65–85	74.0 (3.0; 21) 67–76	72.8 (3.0; 4) 69–76	78.6 (4.8; 5) 71–84
Shortfall P2	72.3 (2.3; 3) 71–75	72.0 (4.2; 2) 69–75	80.7 (4.2; 3) 76–84	78.9 (3.7; 18) 72–84	81.1 (3.3; 21) 72–83	80.0 (2.2; 4) 78–83	84.8 (4.8; 5) 77–90
Shortfall P1	78.3 (2.1; 3) 76–80	80 (–; 1)	85.0 (3.6; 3) 81–88	84.3 (4.0; 17) 77–90	86.0 (3.3; 20) 77–88	85.0 (0.8; 4) 84–86	89.2 (6.1; 5) 79–95
Wing	162.3 (1.2; 3) 161–163	171.8 (8.8; 2) 165.5–178	183.3 (3.1; 3) 180–186	183.6 (5.2; 23) 171–194	189.2 (4.1; 22) 174–189	184.0 (2.4; 4) 182–187	193.8 (7.6; 5) 185–202
Tail	119.3 (1.5; 3) 118–121	129.5 (4.9; 2) 126–133	123.8 (1.3; 4) 122–125	135.4 (4.1; 25) 129–144	142.2 (5.9; 22) 128–146	136.0 (4.5; 4) 130–141	144.3 (8.3; 7) 134–160
Bill length (from gape)	30.0 (1.0; 3) 29–31	20.5 (0.7; 2) 20–21	32.0 (1.0; 3) 31–33	28.1 (3.8; 20) 22–33	29.0 (2.5; 20) 24–32	27.5 (2.5; 4) 25–31	30.1 (3.1; 7) 26–35
Bill length (from nostril)	6.7 (0.6; 3) 6–7	8.0 (0.0; 2) 8–8	6.7 (0.5; 3) 6–7	7.6 (0.9; 22) 6–9	7.6 (0.6; 24) 6–9	7.4 (0.5; 4) 7–8	7.0 (0.6; 7) 6–8
R5 white patch on outer web	32.0 (1.0; 3) 31–33	39.5 (3.5; 2) 37–42	31.0 (2.2; 4) 28–33	43.5 (6.1; 24) 34–55	41.8 (3.6; 22) 35–52	42.8 (3.2; 4) 40–46	42.8 (4.9; 6) 38–52

(continued)

Table 3. (continued)

	<i>C. ritae</i> sp. nov.	<i>C. meesi</i>	<i>C. andamanicus</i>	<i>C. m. schlegelii</i>	<i>C. m. macrurus</i>	<i>C. m. salvadorii</i>	<i>C. m. bimaculatus</i>
R5 white patch on inner web	38.0 (3.0; 3) 35–41	43.0 (0.0; 2) 43–43	35.0 (1.4; 4) 33–36	46.8 (5.1; 24) 38–55	45.0 (4.2; 22) 34–55	43.0 (2.2; 4) 40–45	45.2 (7.9; 6) 30–53
R4 white patch on outer web	33.0 (2.6; 3) 31–36	38.5 (2.1; 2) 37–40	32.0 (0.8; 4) 31–33	43.3 (6.1; 24) 31–54	41.9 (3.3; 21) 35–49	41.0 (2.2; 4) 38–43	42.8 (2.8; 6) 40–48
R4 white patch on inner web	35.7 (2.1; 3) 34–38	40.0 (0.0; 2) 40–40	33.5 (1.0; 4) 33–35	45.1 (6.5; 24) 31–54	42.7 (4.4; 21) 31–54	43.0 (2.4; 4) 41–46	43.7 (1.9; 6) 42–47

represent a diagnosably distinct and potentially reproductively isolated lineage that merits treatment as a species (de Queiroz 1999).

Caprimulgus ritae sp. nov.

Timor Nightjar

Cabak Timor

Zoobank

Publication: urn:lsid:zoobank.org:pub:ECAC43C0-E5BD-4928-B74B-D5BAEEC2CA2B.

Nomenclatural act: urn:lsid:zoobank.org:act:2D84AD2B-4D90-4B85-8D0C-0DDB3D19FB14.

Holotype

RMNH.AVES.162472. Collected by C. Schädler on Wetar, Indonesia, on 7 March 1898. Label data: “female” (Cab.), C. Schädler (No. 212). Previously identified as *C. macrurus celebensis* (label), *C. manillensis* (Finsch 1901; label) and *C. macrurus schlegelii* (Mees 1977).

Paratypes

AMNH 632998 male, Wetar (south coast), Indonesia, 13 October 1902. Collected by Heinrich Kühn. Field number 5777. Label data: Iris dark reddish brown; feet pale brown; bill black, brownish below.

AMNH 632999 female, Wetar (south Coast), Indonesia, 18 October 1902. Collected by Heinrich Kühn. Field number 5847. Label data: iris dark brown; feet dull brown red; bill black. This specimen and AMNH 632998 have previously been identified as *C. manillensis celebensis* (specimen labels), *C. manillensis* (Hartert 1904), *C. macrurus celebensis* (Hartert 1906) and *C. macrurus schlegelii* (Mees 1977).

RMNH 5070058, male, Assalaino, Bauro village, Lautem District, Timor-Leste, 24 September 2013. Collected by Colin R. Trainor.

On geographical grounds, a specimen of an immature bird, AMNH 345569 collected by Georg Stein at Tjamplong [Camplong], West Timor, Indonesia, on 12 January 1932 is probably this species but definitive identification should await verification by DNA analysis. Hence, we do not recognize this specimen as part of the type series. The specimen has been identified as a juvenile female (Mayr 1944), but we regard it as an

Table 4. Measurements of morphological variables for female *Caprimulgus ritaë* sp. nov., *Caprimulgus andamanicus* and Indonesian subspecies of *Caprimulgus macrurus*. Data presented are mean (standard deviation; sample size) and minimum and maximum values.

	<i>C. ritaë</i> sp. nov.	<i>C. andamanicus</i> (n = 1)	<i>C. m. schlegelii</i>	<i>C. m. macrurus</i>	<i>C. m. salvadorii</i> (n = 1)	<i>C. m. bimaculatus</i>
P9 emargination from tip	65.0 (1.4; 2) 64–66	72	73.2 (3.3; 13) 67–79	72.0 (3.3; 8) 68–76	77	76.0 (0.0; 2) 76–76
P8 emargination from tip	59.5 (0.7; 2) 59–60	67	66.8 (5.4; 13) 52–74	66.4 (1.8; 8) 64–70	70	68.5 (2.1; 2) 67–70
Wing formulae	9 > 8 > 10 > 7 (n = 1)	9 > 8 > 10 > 7	8 > 9 > 7 > 10 (n = 10) 8 = 9 > 7 > 10 (n = 1)	8 > 9 > 7 > 10 (n = 5) 8 = 9 > 7 > 10 (n = 1) 9 > 8 > 7 > 10 (n = 1)	8 > 9 > 7 > 10	8 > 9 > 7 > 10 (n = 2) 9 > 8 > 10 > 7 (n = 1)
Shortfall P10	11 (-; 1)	13	15.2 (2.1; 11) 10–18	13.5 (2.6; 8) 8–16	13	16.0 (4.2; 2) 13–19
Shortfall P9	0 (-; 1)	0	2.4 (1.3; 1) 0–5	1.9 (1.5; 7) 0–4	3	2.0 (1.4; 2) 1–3
Shortfall P8	0.5 (0.7; 2) 0–1	2	0.0 (0.0; 1) 0–0	0.1 (0.4; 8) 0–1	0	0.0 (0.0; 2) 0–0
Shortfall P7	14.0 (1.4; 2) 13–15	14	10.1 (1.6; 12) 8–12	10.8 (1.4; 8) 9–12	11	12.5 (2.1; 2) 11–14
Shortfall P6	39.0 (0.0; 2) 39–39	38	34.9 (1.2; 11) 33–37	36.4 (3.2; 8) 29–40	39	41.0 (5.7; 2) 37–45
Shortfall P5	53.5 (0.7; 2) 53–54	52	51.7 (1.9; 12) 49–55	52.7 (0.8; 6) 52–54	52	57.0 (4.2; 2) 54–60
Shortfall P4	59.5 (2.1; 2) 58–61	61	61.6 (2.4; 12) 58–65	61.9 (1.2; 7) 60–64	64	66.5 (3.5; 2) 64–69
Shortfall P3	66.5 (2.1; 2) 65–68	69	68.4 (2.5; 11) 64–72	68.6 (1.9; 7) 66–72	72	75.5 (3.5; 2) 73–78
Shortfall P2	73.5 (0.7; 2) 73–74	76	74.5 (2.8; 12) 70–80	73.6 (2.6; 7) 69–78	-	83.5 (0.7; 2) 83–84
Shortfall P1	79 (-; 1)	78	79.2 (2.7; 12) 76–83	77.7 (3.4; 6) 72–82	78	86.5 (0.7; 2) 86–87
Wing	162.0 (5.7; 2) 158–166	178	178.5 (4.7; 13) 170–186	180.1 (6.6; 8) 169–191	190	181.0 (12.3; 3) 167–190
Tail	120.0 (4.2; 2) 117–123	121	140.3 (5.4; 13) 133–148	139.1 (5.0; 8) 132–146	149	139.0 (4.4; 3) 134–142
Bill length (from gape)	29 (-; 1)	32	30.6 (3.6; 12) 23–35	30.6 (2.6; 8) 26–35	33	32.3 (2.1; 3) 30–34
Bill length (from nostril)	7.0 (1.4; 2) 6–8	7	7.8 (0.9; 13) 6–9	7.3 (1.0; 8) 6–9	7	7.0 (0.0; 3) 7–7
R5 white patch on outer web	20.5 (0.7; 2) 20–21	12	24.8 (5.7; 13) 11–35	23.6 (6.2; 8) 17–38	22	17.0 (6.1; 3) 10–21
R5 white patch on inner web	22.5 (2.1; 2) 21–24	13	27.6 (5.5; 13) 19–36	25.0 (7.9; 8) 17–43	24	17.7 (6.1; 3) 11–23
R4 white patch on outer web	13.0 (0.0; 2) 13–13	12	24.4 (6.6; 11) 12–32	20.0 (9.6; 8) 9–41	24	11.3 (5.8; 3) 8–18
R4 white patch on inner web	14.0 (4.2; 2) 11–17	13	22.3 (8.2; 11) 7–35	19.8 (9.3; 8) 9–39	17	11.7 (4.7; 3) 8–17

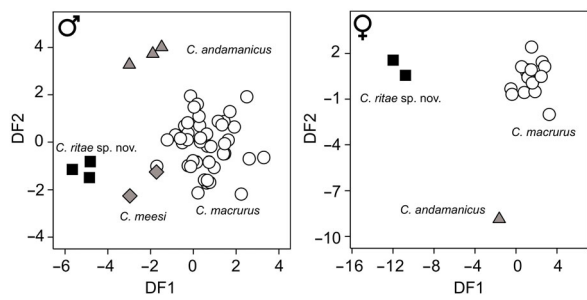


Figure 5. Discriminant function analysis scatterplot of morphometric variables measured for *Caprimulgus ritae* sp. nov., *Caprimulgus andamanicus*, *Caprimulgus meesi* and the four Indonesian subspecies of *Caprimulgus macrurus* (*C. m. schlegelii*, *C. m. macrurus*, *C. m. salvadorii*, *C. m. bimaculatus*), males left ($n = 52$) and females right ($n = 20$).



Figure 6. Male *Caprimulgus ritae*, Wetar, 13 October 2014 (James Eaton). This bird was sound recorded (XC204788 and XC204789).

immature male (see below). Field number 3896. Label data (translated from German): iris blackish; feet grey; bill dark grey-black.

Diagnosis: DNA

Compared with a *cyt b* sequence of the holotype of *C. meesi*, *C. ritae* shows unique nucleotides at 52 positions (see Appendix S1 for character states). Compared with 31 *cyt b* sequences of *C. macrurus*, *C. ritae* shows unique nucleotides at 46 positions (see Appendix S1 for character states).

Diagnosis: Vocalizations

Caprimulgus ritae differs diagnosably from *C. meesi* by its smaller number of peaks, shorter total song

duration, lower maximum frequency of first peak, lower maximum frequency, smaller frequency range of the first element and smaller frequency range.

Caprimulgus ritae differs diagnosably from *C. macrurus* by its shorter total song duration (c.50% of song duration of *C. macrurus*) and its much greater song pace. The territorial song of *C. ritae* also differs from that of *C. macrurus* by its less deep sound caused by the shorter tremolo consisting of only two closely spaced peaks (Fig. 4). Furthermore, the pitch of the tremolo in *C. ritae* is falling, rather than level as in *C. macrurus*.

Caprimulgus ritae differs diagnosably from *C. andamanicus* by its shorter total song duration and lower maximum frequency of the last peak.

Caprimulgus ritae differs diagnosably from *C. atripennis* by its much shorter total song duration, higher maximum frequency of first peak, higher minimum frequency of the first low, higher maximum frequency, the small frequency range of the first element, faster song pace, faster bout pace and greater frequency range.

Caprimulgus ritae differs diagnosably from *C. celebensis* and *C. manillensis* by its single note song, smaller number of peaks, much shorter total song duration, and much faster song pace and bout pace. It further differs from *C. celebensis* in higher maximum frequency of the first peak, higher maximum frequency, greater frequency drop of the first downward element and greater frequency range, and from *C. manillensis* by a difference in the structure of the first element.

The only other nightjar known from Timor and Wetar is *C. affinis* (Cleere 1998 and B.F.K., G.S. and C.R.T pers. obs.). Compared with *C. ritae*, songs of *C. affinis* have a very different structure (reflected by a rising broad-band element in sonagrams), a much longer duration (c.0.240 s), and a much higher minimum (c.2000 Hz) and maximum frequency (c.5000 Hz). To the human ear, songs of *C. affinis* are high-pitched and have a rasping quality that is lacking in all members of the *C. macrurus* complex, including *C. ritae*.

Diagnosis: Morphology

Male *C. ritae* differs from male *C. meesi* by: (1) ear-coverts darker chestnut; (2) uppertail-coverts with dark diamond-shaped spots in centre (in *C. meesi*, dark shaft, streaks only); (3) belly rusty buff with narrow blackish bars (buffy white with

broader blackish bars on *C. meesi*); (4) dark banding on undertail-coverts more regular; (5) smaller white patches on R4 and R5 (Table 3); (6) lesser upperwing-coverts with cinnamon fringe (cinnamon buff apical spot in *C. meesi*); (7) tail darker and more coarsely marked with black, with more distinct barring. (There are no known female specimens of *C. meesi*, thus precluding comparisons of females of the two species.)

Caprimulgus ritae differs from *C. macrurus* by a combination of: (1) smaller size; (2) coarsely marked lateral crown feathers (finely marked in most *C. macrurus*, although *C. m. schlegelii* from the Kei Islands and Waigeo also have coarsely marked feathers); (3) lack of buff to rufous collar (present in *C. macrurus*); (4) darker, chestnut brown to dark rusty brown ear-coverts (rufous in most *C. macrurus*, although some have dark rusty brown ear-coverts). Male *C. ritae* further differs from male *C. macrurus* by (5) upper throat and sides of throat darker, due to narrower and darker irregular rusty buff tips on black feathers.

Both sexes of *C. ritae* differ from *C. andamanicus* by: (1) smaller size; (2) lack of rusty tinge on hindneck or upper back (rusty tinge present in male *C. andamanicus*); (3) darker, chestnut brown ear-coverts (in *C. andamanicus* paler rusty brown).

Male *C. ritae* further differs from male *C. andamanicus* by: (4) darker tail (in male *C. andamanicus* black areas of tail are smaller and pale area paler, more rusty grey); (5) tail darker than uppertail-coverts (in male *C. andamanicus* tail is concolorous with uppertail-coverts); (6) darker upper throat and sides of throat due to narrower rusty buff feather tips; (7) smaller, less conspicuous rufous notches on basal part of outer vane of underside of R5; (8) tip of outer vane of R5 white with irregular blackish edging (in *C. andamanicus* edging on white tip of outer vane of R5 rusty buff with blackish mottling).

Female *C. ritae* further differs from female *C. andamanicus* by: (4) larger and whiter patch on tips of R4 and R5 (in female *C. andamanicus* pale patches on tips of R4 and R5 are smaller and rusty buff); (5) larger pale rufous patch in outer primaries, which is visible in field (small patch on outer primaries of female *C. andamanicus* is probably not visible in field).

Male *C. ritae* differs from male *C. atripennis* by: (1) smaller size; (2) darker and greyer overall plumage; (3) crown greyer and much more coarsely vermiculated, with broader black crown

stripe; (4) lack of strong rusty tinge on hindneck and upper back; (5) scapulars and tertials darker and more coarsely vermiculated, contrasting less with Sepia markings on scapulars; (6) tail darker than uppertail-coverts; (7) smaller white patch at tip of tail (R4 and R5); (8) smaller white patches on primaries; (9) darker, chestnut brown to dark rusty brown ear-coverts; (10) darker, rusty brown upper throat and sides of throat; (11) darker, greyer, more coarsely vermiculated breast.

Female *C. ritae* differs from female *C. atripennis* in the same characters as male, except character (6). Female *C. ritae* further differs from female *C. atripennis* in having smaller, darker rusty buff patches on outer primaries (larger and paler in *C. atripennis*), and white patches on R4 and R5 (in *C. atripennis* pale tips of R4 and R5 tinged rusty buff, especially on outer vane).

Male *C. ritae* differs from male *C. manillensis* by: (1) tail darker than uppertail-coverts (in male *C. manillensis* tail is concolorous with uppertail-coverts); (2) larger white patch on outer vane of R5; (3) outer edge of basal part of outer vane on R5 has tiny rufous notches (narrow rusty buff bands in *C. manillensis*); (4) upper throat and sides of throat darker (narrower pale tips to feathers); (5) smaller white patches in outer primaries; (6) tertials and inner vane of scapulars somewhat darker and more coarsely vermiculated, contrasting less with upperparts.

Female *C. ritae* differs from female *C. manillensis* in the same characters as male, except character (1). Female *C. ritae* further differs from female *C. manillensis* in smaller white patch on R4, and rusty buff patches on outer primaries smaller and darker.

Caprimulgus ritae differs from the sympatric *C. affinis* primarily by its longer tail, darker and less grey plumage, and white on the outer tail feathers restricted to the tips (in *C. affinis*, R5 mostly white in male, no white in tail of female).

Description of the holotype

Head

Chin and throat feathers barred Sepia (219, cf. Smithe 1975; no equivalent colour in Ridgway 1912) and Orange-Cinnamon* (* = Ridgway 1912). Lower throat with pure white patch in centre. Central feathers on lower throat white, broadly tipped Sepia (219) and with Cinnamon Buff* subterminal band. White throat patch

demarcated by a narrow band of Clove Brown* and Sepia*, with two to four small Cinnamon Buff* subterminal spots. Feathers of forehead, crown and nape with brownish-white (Light Drab*) ground colour (without cold aspect of the holotype of *C. meesi*). Central feathers on forehead, crown and nape with dagger-shaped Sepia (219) median crown stripe and coarse Sepia (219) spots. Lateral feathers of forehead, crown and nape with narrow Sepia (219) stripe along shaft. Vermiculations on crown coarser than in most *C. macrurus schlegelii* but less so than in the holotype of *C. meesi*. Lower nape feathers with Sepia (219) centre and two or three Cinnamon Buff* lateral bars. Supercilium narrow, tinged Orange-Cinnamon*. Rictal bristles with greyish base, Cinnamon Buff* and brownish centre and broad black tips. Loes and ear-coverts mottled Sepia (219) and Cinnamon Buff*. Rictal bristles well developed; nine on each side.

Upperparts

Back, rump and uppertail-coverts with greyish-white (Drab*) ground colour, and with fine, sharply demarcated Sepia (219) vermiculations. Overall aspect of upperparts less brown than in *C. macrurus schlegelii* but without cold aspect of the holotype of *C. meesi* due to slight brownish tinge on some feathers. Feathers on upper back with diamond-shaped Sepia (219) centres. Uppertail-coverts with four to five Sepia (219) diamond-shaped spots in centre. Anterior upper scapulars Sepia (219) with broad Cinnamon Buff* fringe on outer webs. Some feathers with small Cinnamon Buff* apical spot on both inner and outer webs. Anterior lower scapulars with narrow Cinnamon Buff* fringe on outer webs, vermiculated Sepia (219). Outer webs of anterior lower scapulars with a large, round to oval, subterminal Sepia spot, and Cinnamon Buff*, Sepia (219) and Drab Gray* bars. Inner webs of anterior lower scapulars marbled Drab Gray* and Sepia (219). Posterior upper and lower scapulars marbled Drab Gray* and Sepia (219) and with Sepia (219) line along shaft and large Sepia (219) spots.

Underparts

Upper breast feathers with Light Drab* to Drab* ground colour, large Sepia (219) patches on feather centres and diffuse Sepia (219) vermiculations. Upper breast much darker than *C. macrurus schlegelii* and *C. meesi*. Feathers of lower breast,

belly and flanks Light Drab* with broad Pinkish Buff* to Cinnamon Buff* terminal fringe and fine Clove Brown* bars. Undertail-coverts broadly barred Pinkish Buff* and Clove Brown*, with banding more regular than in *C. meesi* (holotype) and Clove Brown* bands much wider than in *C. macrurus schlegelii*.

Wing

Primaries dark brown (between Olive Brown* and Clove Brown*). Margin of outer web of outermost primary (P10) with narrow, irregularly shaped spots that are Cinnamon* proximally and Pinkish Buff* distally (at emargination); two diffuse Buffy Brown* spots near tip. P10 (right wing) with three or four small, irregularly shaped and poorly demarcated Pinkish Buff* spots on inner web, which do not extend to shaft. The most distal spot is largest. P10 on left wing not fully grown. P9 with four to five small Cinnamon* spots or bars on both inner and outer webs. Distal half of P9 with large Pinkish Buff* spots at emargination on both inner and outer webs. On both webs spot extends from fringe to shaft. P9 diameter of spot maximum 11 mm. P8–P1 Clove Brown* with irregularly shaped markings which are Cinnamon* proximally and Pinkish Buff* distally. Secondaries dark brown (between Olive Brown* and Clove Brown*). Secondaries with bands of small, irregular Cinnamon* markings on inner and outer webs. Tertiaries with Drab Gray* ground colour, Clove Brown* line along shaft and fine, poorly demarcated Clove Brown* vermiculations. Greater upperwing-coverts Clove Brown* along shaft; outer webs with large Cinnamon Buff* spot near tip and small Cinnamon Buff* proximally; inner webs vermiculated Drab Gray* and Clove Brown*. Median upperwing-coverts similar to greater upperwing-coverts, although some feathers with paler (Pinkish Buff* rather than Cinnamon Buff*) spot near tip on outer webs. Lesser upperwing-coverts Clove Brown* with Cinnamon* fringe and one or two Drab Gray* bands. Underwing-coverts Clove Brown* with broad and clear-cut Cinnamon Buff* to Cinnamon* barring.

Tail

Uppertail (R1–R3) brown (Drab*), with irregularly marked Clove Brown* bars which are broadest and most distinct near shaft but very diffuse near fringes, and with coarse Clove Brown* vermiculations. Ground colour of uppertail warmest

(between Pinkish Cinnamon* and Cinnamon*) near shaft. R4 and R5 Clove Brown* with c.11 narrow, irregularly shaped Pinkish Buff* bars; bars most distinct on outer web but more diffuse on inner web. R5 with pure white terminal patch on inner web, with diameter maximum 30 mm (21 mm along shaft). Outer web of R5 with pale terminal patch, mostly Olive Brown* merging into Pinkish Cinnamon*, with pure white only along shaft. R4 with pure white terminal patch on inner web, with diameter maximum 21 mm (13 mm along shaft). Outer web of R4 with pale terminal patch, mostly Pinkish Cinnamon* with Olive Brown* blotches.

Description of the paratypes

AMNH 632998, male, Wetar. Upper throat and sides of throat black with dark rusty buff feather tips. Band across lower throat white, the tips of the feathers mixed pale rufous and black. Crown and nape pale brownish grey, the feathers finely vermiculated whitish to buffy and dark grey to blackish, with a narrow black shaft streak, the black streaks very broad in the centre of the crown, covering most of the feather and forming a broad black band down the centre of the crown and nape. Loes and supercilium area vermiculated rusty brown and black. Cheeks and ear-coverts dark rusty brown. Sides of neck (behind ear-coverts) rufous, the feathers with irregular narrow black bars. Narrow white whisker stripe below gape. Upper back dark brownish grey, the feathers broadly and irregularly black in the centre, the paler edges finely vermiculated greyish buff and dark grey to black. Lower back and uppertail-coverts brownish grey, the feathers finely vermiculated pale buff to buffy grey and dark grey to blackish, with black shaft streaks, the bases of the uppertail-coverts with broad irregular blackish bars. Anterior scapulars black with broad rusty buff edge on outer web and narrow irregular rusty buff bars, passing to pale brownish grey posterior scapulars (finely vermiculated whitish buff to buff and dark grey) with irregular black centres. Breast pale brownish grey (as crown), the feathers finely vermiculated black and greyish buff, with black shaft streaks, a few of the feathers in the centre of the breast broadly tipped rusty buff. Belly rusty buff with irregular narrow blackish bars. Undertail-coverts mixed whitish buff and rusty buff, the longer coverts with narrow black bands. Primaries black with fine irregular rufous bars

(except distal half of P7–P9), the four outermost with a broad white patch (inner vane only on 10th primary). Secondaries blackish with fine irregular bars (rufous on outer vane, rusty buff on inner vane). Tertiaries pale brownish grey (finely vermiculated buff and blackish brown). The outer vane of greater upperwing-coverts black with a rufous spot, the inner vane brownish grey (vermiculated buff and blackish brown). Median upperwing-coverts black with broad buff to rusty buff tips. Lesser upperwing-coverts black with rufous fringe on tip. Underwing-coverts mottled pale rufous and black. Uppertail dark brownish grey with irregular blackish bars and mottling and tiny pale rusty notches on the edges, the outer two pairs (4 and 5) broadly tipped white with dusky edging on the outer vane. Undertail black (except for broad white tips to outer tail feathers) with tiny rusty notches on edges.

AMNH 632999, female, Wetar—Differs from male AMNH 632998 by: narrower black central crown stripe; slightly paler brownish grey tertiaries; somewhat paler rump and uppertail-coverts; paler tail (the black bars and mottling smaller in area); smaller white patches on tips of outer two pairs of tail feathers, the outer webs mostly dusky; broader, more conspicuous rufous bars on primaries and secondaries; the pale band on four outermost primaries smaller in area and rusty buff (rather than white); upper throat and sides of throat somewhat paler, the rusty buff feather tips broader; white whisker mark and lower throat as male; breast slightly paler and browner grey; undertail-coverts as male but lacking white.

RMNH 5070058, male, Timor-Leste—Differs from holotype in: vermiculations on sides of crown and nape coarser; Light Drab* with broad Cinnamon* terminal fringe and fine Clove Brown* bars; primaries dark brown with fine irregular rufous bars on outer webs (except distal half of P7–P9), the four outermost with a broad white patch (inner vane only on 10th primary); tertiaries paler and with coarser pattern; underwing-coverts Clove Brown* broad and clear cut Cinnamon* barring. R5 with pure white terminal patch on inner and outer webs, with maximum diameter 40 mm (35 mm along shaft) on inner web. Outer web of R5 with Olive Brown* smudge along lateral margin and at tip extending onto inner web. R4 with pure white terminal patch on both webs, with maximum diameter 35 mm (35 mm along shaft) but with Olive Brown* blotches at tip.

A further specimen (AMNH 345569), which we do not consider part of the type series, is an immature male from Timor. This specimen is classed as an immature based on somewhat disintegrated feathers on underparts. It is sexed as female on label, but it appears to be mis-sexed as it has white patches on primaries as adult male and larger white patches on outer tail feathers as adult male. The body plumage is more like that of the female. This specimen is like AMNH 632999 (female, Wetar), but has less black on central crown stripe; rufous bands in primaries and secondaries narrower; ear-coverts paler dull rusty brown; upper throat and sides of throat paler, the feathers rusty buff with narrow blackish markings; breast paler, many of the feathers with whitish tips; belly and undertail-coverts paler buff with somewhat narrower blackish bars.

Phylogenetic position and generic placement

Phylogenetic studies of relationships among nightjars and allies have shown that Caprimulgidae (*sensu* Sibley & Monroe 1990) consists of four major clades, of which only one is found in the Old World (Barrowclough *et al.* 2006, Han *et al.* 2010; see also Larsen *et al.* 2007). These studies also indicate that species formerly included in the genus *Caprimulgus* do not form a monophyletic group. A revision of the generic limits of nightjars retained *C. macrurus* and all other species in the Old World clade in the genus *Caprimulgus* (Han *et al.* 2010). Our phylogenetic analysis (Fig. 2) placed *C. ritae/C. meesi* firmly as the sister of *C. macrurus*, corroborating their placement in the genus *Caprimulgus*.

Etymology

The species is named after B.F.K.'s long-time friend, Rita Bobbin (née Alexander). The English name Timor Nightjar refers to the largest of the two islands where the species is known. This is also the name used for this species in a recent field guide (Eaton *et al.* 2016).

Distribution

Caprimulgus ritae is only known from Timor (both West Timor and Timor-Leste) and Wetar. In West Timor, there are six site records (Fig. 7). Four of

these sites are among the most frequently visited birding locations in West Timor: (1) Bipolo, Kupang district, heard/observed at 30 m altitude (Noske & Saleh 1997); (2) Camplong, Kupang, specimen collected, 12 January 1932 (Mayr 1944), also heard/observed at 230 m (Noske & Saleh 1997); (3) near Oel Nasi, South Central Timor, heard and observed at c.400–600 m, 15 September 2008 (B.F.K.), heard, 2 September 2009 and 8–10 September 2010 (C. Robson in litt.); (4) Fatumnasi (Gunung Mutis area), South Central Timor, heard at 1500 m, 2 October 1995 (highest known record, Verbelen 1996); (5) Besi Pae, South Central Timor, heard/observed at 290 m (Noske & Saleh 1997); (6) near Kapan, South Central Timor, heard, observed and/or sound recorded at 1055 m on 30 August 1987, 20 August 1989, 12 August 1991, 23 August 1993, 27 August 1995, 16 August 1997 and 8 September 2006 (B.F.K.); and heard at Oel Bubuk, near Kapan, 6 August 2008 (Hendriks 2008).

In Timor-Leste, the species is known from 17 sites (Fig. 7). Mauro (2003) found *C. ritae* at two of five (40%) sites sampled over a 12-day period in March 2003 on the south-central coast area of Timor-Leste (0–50 m): (1) Lake Modo Mahut, Manufahi district, 5 m; and (2) Welaluhu-Natarbora, Manufahi, 20 m. C.R.T. found *C. ritae* at 14 of 24 (58%) sites surveyed (20 in Lautem district). Each of these sites was surveyed over 1–20 nights at altitudes ranging from 0 to 1420 m (August 2002–April 2008) with nocturnal surveys along transects at most sites generally in the first 2 h after dusk (Trainor *et al.* 2008). The sites where *C. ritae* were found are: (3) Laleia, Manatuto, 55 m; (4) Daudere River, Lautem, 30 m; (5) Ili lapa, Lautem, 420 m; (6) Chin River, Lautem, 130 m; (7) Iramalaro Camp, Lautem, 425 m; (8) Nari, Lautem, 510 m; (9) Assalaino Camp, Lautem, 500 m; (10) Assalaino, Lautem, 500 m; (11) Loré, Lautem, 5 m; (12) Muapitine Ridge, Lautem, 470 m; (13) Malahara, 6 km south, Lautem, 60 m; (14) Com-Loikeri, Lautem, sea level; (15) Maca Beach, Lautem, 65 m; (16) Vero River, Lautem, 20 m. In addition, the species was sound recorded near Los Palos, Lautem, 400 m, on 12 May 2005 by Frank Lambert (<http://avocet.zoology.msu.edu/recordings/4162>).

The three specimens from Wetar lack precise locality data. The first modern records were obtained almost simultaneously by C.R.T. and B.F.K. in 2008, with further records in 2010.

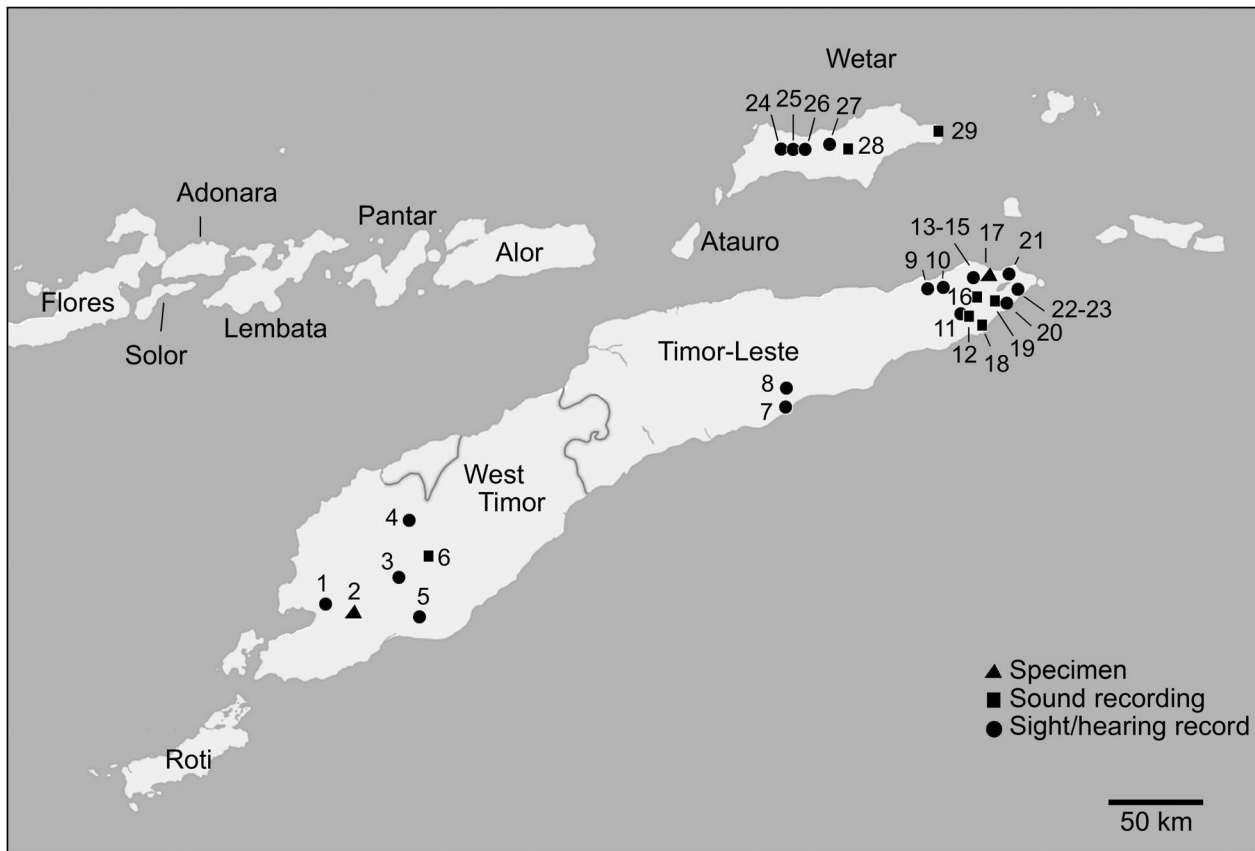


Figure 7. Map of eastern Lesser Sunda Islands showing localities where *Caprimulgus ritae* has been recorded. Localities: (1) Bipolo, (2) Camplong (immature bird tentatively assigned to this species), (3) Oel Nasi, (4) Fatumnasi, (5) Besi Pae, (6) Oel Bubuk/Kapan, (7) Lake Modo Mahut, (8) Welaluhu-Natarbora, (9) Laleia, (10) Daudere River, (11) Ili Iapa, (12) Chin River, (13) Iramalaro Camp, (14) Nari, (15) Assalaino Camp, (16) Los Palos, (17) Assalaino, (18) Loré, (19) Muapitine Ridge, (20) Malahara, 6 km south, (21) Com-Loikeri, (22) Maca Beach, (23) Vero River, (24) Naumatang Gorge (upper), (25) Naumatang Gorge (mid), (26) Naumatang Gorge (lower), (27) Ili Moso/Gunung Botak, (28) Lake Tihu, (29) Ilway. The three specimens from Wetar lack precise locality data and are not plotted on this map.

C.R.T. surveyed and camped at 10 forest sites over a total of 31 nights (or days) between 27 September and 3 November 2008, mainly in the north and northwest of the island at elevations of 0–930 m (Trainor *et al.* 2009a, 2009b; Fig. 7). Although few nocturnal surveys were carried out, C.R.T. camped in forest habitat at all sites. Nightjars were recorded at four sites: at three sites along Naumatang Gorge, and at Lake Tihu. *Caprimulgus ritae* was also heard at Ili Moso (Gunung Botak), south of the former Lerokis Gold Mine (north coast), on 4 October 2010 at 1000 m (C.R.T.). B.F.K. spent 6 days (28 September–3 October 2008) and five nights near the coastal village of Ilway, on the east coast of the island (Fig. 7). *Caprimulgus ritae* were heard, observed and sound

recorded c.2 km south of Ilway at c.80 m on 29–30 September 2008 and c.3 km southeast of Ilway at c.230 m on 2 October 2008. Search time was 2–4 h following sunset each evening and 1–3 h before sunrise on five mornings, using playback.

No nightjars of the *C. macrurus* complex have been reported from Lembata (Trainor 2003), Atauro (Trainor & Soares 2004) or Romang (off Wetar: Hartert 1904, C.R.T. pers. obs.) although efforts should be made to determine their presence on these islands.

Ecology and behaviour

Caprimulgus ritae is a forest specialist that has been recorded from a wide range of tropical forests

from tall evergreen to highly deciduous dry forest mostly in the lowlands below 1000 m, with one record from 1500 m. There are records from the edge of tropical dry forest–savanna interface, but lowland savannas are the typical habitat for *C. affinis*. At Gunung Mutis, West Timor and on Wetar, there are records from *Eucalyptus*–tropical forest edge/mosaics. Additional details about ecology and behaviour are included in Appendix S1.

Conservation status

Timor and Wetar and associated islands (Sawu, Roti and Semau) represent an Endemic Bird Area with at least 23 endemic species (Stattersfield *et al.* 1998). Most of these species, like *C. ritae*, are largely dependent on tropical forests, and their fate is tied to the sustainable use and conservation management of forest habitat. There is a particularly strong push for development throughout the entire range of *C. ritae*, which will continue to threaten forest resources. Recent analysis of forest cover trends on Timor Island from 1990 (33.5% forest cover) to 2020 (18% cover) showed a loss or conversion of forest to shrubland and savanna of ~5899 km² (Fu *et al.* 2022).

Associated with its low human population, Wetar (3600 km²) retains >95% natural vegetation cover, including extensive *Eucalyptus alba* and *Eucalyptus urophylla* woodlands on slopes and ridges, with tropical forests (ranging from evergreen montane and gallery forests to tropical dry) dominating in gorges and upland slopes (perhaps 30% of island cover). Deep gorges and exceptionally steep and dissected terrain are likely to protect extensive forest on Wetar for perpetuity, though accessible coastal forest will continue to be converted for agriculture including cashew and coconut plantations.

In 1982, a total of 18 sites were identified on Timor (nine in the west; eight in the east) and Wetar (one site) as key representative natural areas as part of the Indonesia-wide National Conservation Plan (FAO/UNDP 1982). Nine Important Bird Areas have been identified in West Timor, and 15 in Timor-Leste, based on the occurrence of threatened and restricted-range birds (Rombang *et al.* 2002, Trainor *et al.* 2007). In Timor-Leste, the Monte Paitchau–Iralalora area (c.250 km²) in Los Palos district was subsequently identified as one of the highest site priorities in the Indonesian Biodiversity Action Plan (BAPPENAS 1993). In August 2007, this site was established as

Timor-Leste's first protected area, Nino Konis Santana National Park, with a land component of 654 km². The park includes the most pristine tropical evergreen forest on Timor Island (Trainor *et al.* 2007) including eight of the 16 *C. ritae* sites. We estimate a substantial population of hundreds to thousands of individuals in this park. Recent surveys revealed that the FAO/UNDP proposed Gunung Arnau area in western Wetar retains exceptional natural values with pristine *Eucalyptus* woodlands and tropical forests supporting all the resident landbirds including a substantial population of *C. ritae* (Trainor *et al.* 2009b). In 2009, the biologically important Lake Tihu area was designated as a Nature Reserve (Cagar Alam) (C. Farmer pers. comm.).

Biogeography

Caprimulgus ritae is the fourth bird species known to be endemic to both Timor and Wetar. Other species are Timor Imperial Pigeon *Ducula cineracea*, Wetar Ground Dove *Pampusana gallicolumba hoedtii* and Iris Lorikeet *Saudareos iris* (Noske & Saleh 1997, Stattersfield *et al.* 1998, Trainor & Soares 2004). Six additional species on Timor and Wetar are otherwise found only on Atauro, Roti and/or Semau (Jonquil Parrot *Aprosmictus jonguillaceus*, Black Cuckoo Dove *Turacoena modesta*, Timor Blue Flycatcher *Cyornis hyacinthina*, Fawn-breasted Whistler *Pachycephala orpheus*, Plain Gerygone *Gerygone inornata* and Timor Oriole *Oriolus melanotis*). Hence, the distribution of *C. ritae* is mirrored by that of several other bird species. Wetar is closer to Timor (51 km) than to Alor (76 km), with the stepping-stone Atauro Island only 23 km off Timor and 21 km off Wetar. The lack of divergence between the *cyt b* sequences from Timor and Wetar suggests that colonization of Wetar from Timor, or vice versa, was probably very recent. Additional comments on biogeography are included in Appendix S1.

We thank our two field assistants during the Wetar expedition, Imanuddin and A. Firma, for their help and companionship. We also thank the many sound recordists who contributed their recordings (listed in Sangster & Rozendaal 2004 and Table S3) either directly to us or to the British Library Sound Archive, London, the Macaulay Library of Natural Sounds, Ithaca, NY, USA, and the Xeno-Canto (<http://www.xeno-canto.org/>) and AVOCET (<http://avocet.zoology.msu.edu/>) databases.

We continue to be indebted to the British Library Sound Archive and the Macaulay Library of Natural Sounds for providing sound recordings. We further thank Philippe Verbelen for sharing details of field observations on Alor, Craig Robson for providing details of his records of nightjars on Timor, James Eaton for letting us use his photograph of *C. ritae* and Marc Guyt for his help with the photograph. B.F.K. wishes to thank Raja Raja for much assistance with fieldwork. For access to museum specimens, we thank P. Kamminga, S. van der Mije, H. van Grouw, R. Dekker (NBC, Leiden (formerly Rijksmuseum voor Natuurlijke Historie, RMNH)), P. Sweet (AMNH, New York), G. Frisk and U. Johansson (NRM, Stockholm). M. Shanley (AMNH) photographed the three paratypes of *Caprimulgus ritae*. We are grateful to Frank Rheindt, Rauri Bowie and two anonymous referees for their helpful comments.

AUTHOR CONTRIBUTIONS

Ben F. King: Conceptualization; investigation; supervision; validation; writing – original draft; writing – review and editing. **George Sangster:** Conceptualization; data curation; formal analysis; investigation; methodology; project administration; writing – original draft. **Colin R. Trainor:** Conceptualization; funding acquisition; investigation; resources; validation; writing – review and editing. **Martin Irestedt:** Methodology; supervision; writing – review and editing. **Dewi M. Prawiradilaga:** Writing – review and editing. **Per G. P. Ericson:** Resources; supervision; writing – review and editing.

ETHICAL NOTE

For permission to collect a specimen on Timor-Leste we thank Manuel Mendes, and for help collecting the specimens in the field we thank Arceno Lopes, Pedro Pinto, Fernando Santana and Alcantra Xavier. For navigating the tangled bureaucratic process to gain an export permit we are indebted to Rick Jacobsen. Great assistance was provided by the staff of the Ministry of Agriculture and Fisheries, Timor-Leste, to secure permission to export the specimen; in particular we thank Estanislau da Silva, the late Sergio Pereira, Rui Daniel de Carvalho, Almeida Xavier, Adelino Rojario, Raimundo Mau and Manuel Mendes. The export permit number was 03/AD-DQA/IV/2015.

FUNDING

C.R.T.'s fieldwork on Wetar in 2008 was part of a State Ministry of Research and Technology

(RISTEK) and Indonesian Institute of Sciences (LIPI) supported project on behalf of Columbidae Conservation – a UK-based charity that works towards the conservation of pigeons and doves, and their habitat, with funding from Birdfair/RSPB Research Fund for Endangered Birds, Sophie Danforth Conservation Biology Fund and Oregon Zoo Foundation's Future for Wildlife Conservation Fund. C.R.T.'s fieldwork on Wetar in 2010 was supported by Chris Farmer and P.T. Batutua Tembaga Raya. C.R.T.'s fieldwork on Timor was supported by a Charles Darwin University scholarship, with additional funding from the Tropical Savannas Management Cooperative Research Centre, and Birdlife International-Asia Programme. G.S., M.I. and P.G.P.E. were supported by the Swedish Research Council (grant no. 2015-06455 to G.S., grant no. 621-2014-5113 to M.I. and grant no. 621-2013-561 to P.G.P.E.).

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

All new sequences are deposited at GenBank (Accession numbers ON109348–ON109380). All our recordings have been submitted to the Macaulay Library (Cornell University, Ithaca, NY, USA) or the British Library Sound Archive (London, UK). Unpublished sound recordings by others are available from the corresponding author.

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Received 24 July 2021;
Revision 3 November 2023;
revision accepted 31 May 2024.
Associate Editor: Yang Liu

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Measurement of vocal character states.

Table S1. Collection and locality data for newly generated sequences.

Table S2. Primers used for PCR amplification and sequencing.

Table S3. Recording localities and recordists.

Table S4. List of specimens examined.

Table S5. Standardized canonical discrimination function coefficients examining trends in variance of 16 acoustic variables measured for territorial songs of seven species in the *Caprimulgus macrurus* complex.

Table S6. Standardized canonical discrimination function coefficients examining trends in variance of 15 acoustic variables measured for territorial songs of *Caprimulgus ritae* sp. nov., *C. meesi*, *C. macrurus* and *C. andamanicus*.

Table S7. Standardized canonical discrimination function coefficients examining trends in variance of 15 morphometric variables measured for males.

Table S8. Standardized canonical discrimination function coefficients examining trends in variance of 15 morphometric variables measured for females.

Table S9. Raw morphometric data, males.

Table S10. Raw morphometric data, females.