Systematic notes on Asian birds. 41. Territorial songs and species-level taxonomy of nightjars of the *Caprimulgus macrurus* complex, with the description of a new species

G. Sangster & F.G. Rozendaal

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George Sangster, Stevenshof 17, 2312 GM Leiden, The Netherlands. (e-mail: g.sangster@planet.nl).
Frank G. Rozendaal, Akker 113, 3732 XC De Bilt, The Netherlands. (e-mail: kupau@worldonline.nl).

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The Large-tailed Nightjar *Caprimulgus macrurus* Horsfield, 1821, complex, as currently recognized, comprises 12 taxa which are grouped into four species based on their territorial songs. However, species limits are based on very small samples of a limited number of taxa in the complex. To further document species limits in the complex, we analysed 109 sound recordings representing all recognized taxa. Principal components analysis suggests the existence of six vocally distinct groups within the complex. Discriminant function analysis assigned 98-100% of individuals correctly to their group. Each of these groups differs diagnosably from all other groups by up to eight vocal characters, and each group is recognizable by ear. We propose to treat these six groups as species based on multiple differences in territorial songs, the lack of intermediate vocal types, the concordance of the geographic distribution of vocal types and morphology-based taxonomic boundaries and the sympatry of two groups in northeastern peninsular India without signs of intergradation. Three groups correspond to the currently recognized species *C. atripennis* Jerdon, 1845, *C. celebensis* Ogilvie-Grant, 1894, and *C. manillensis* Walden, 1875. '*C. macrurus*' comprises three vocally distinct species: (*i*) *C. macrurus* (s.s.), with a territorial song that is remarkably constant throughout its extensive range, (*ii*) *C. andamanicus* Hume, 1873, a population endemic to the Andaman Islands, and (*iii*) a previously unrecognized species from the east Indonesian islands of Flores and Sumba, which we describe in this paper. Known specimens of this new species were previously assigned to *C. macrurus schlegelii* A.B. Meyer, 1874, but the species differs from all other taxa in the complex by its vocalizations. Preliminary playback experiments support the recognition of these populations as a species. Finally, our acoustic data corroborate the allocation of the taxon *aequabilis* Ripley, 1945 to *C. atripennis*, of *jungei* Neumann, 1939 to *C. celebensis*, and of *johnsoni* Deignan, 1955 and *salvadorii* Sharpe, 1875 to *C. macrurus*.

Introduction

Nightjars are widely distributed in temperate, subtropical and tropical zones. They are difficult to study due to their cryptic plumage and nocturnal lifestyle and as a consequence, many species are poorly known. This is illustrated by recent taxonomic revisions within the family (Mees, 1985; Hardy & Straneck, 1989; Robbins & Parker, 1997; Garrido & Reynard, 1998) and by the continued discovery of new species taxa (Louette, 1990; Lencioni-Neto, 1994; Safford et al. 1995). Until the late 1970s, taxonomic studies of nightjars were based mainly on museum specimens although Davis (1962) proposed that vocalizations might prove useful in delimiting taxonomic relationships in nightjars. However, it was not until the influential study by Marshall (1978) that the importance of vocalizations for species-level taxonomy in owls and other nightbirds became fully accepted.

Crepuscular and nocturnal owls and nightjars are believed to rely more upon acoustic than visual communication signals (Oba 1996; Holyoak 2001). Detailed studies have demonstrated that vocalizations of nightjars and owls play an important role in intra- and interspecific communication (Mengel & Jenkinson, 1971; Cramp, 1985; Klatt & Ritchison, 1993; Oba, 1996; Cink, 2002). In these groups, there is at least one prominent vocalization which characterizes each species and may be comparable in complexity, manner of delivery and function to the songs of passerines (e.g. Oba, 1996; Holyoak, 2001). In contrast, plumage patterns and colouration in owls and nightjars seem more adapted for camouflage than for communication (Fry, 1988; Holyoak, 2001). Morphological characters are therefore considered to be less important for interspecific recognition than vocalizations (König, 2000). Marshall (1978) suggested that patterns of morphological variation may have obscured species limits and he proposed that vocalizations should be considered as a more reliable indicator of species limits. He showed that owls have distinct territorial songs and proposed to recognize vocally distinct populations as species, irrespective of the degree of morphological differentiation. Diagnostic differences in territorial vocalizations have been interpreted as evidence for reproductive isolation and, hence, as evidence for specific status under the Biological Species Concept (König, 1998, 2000). This is supported by the sympatric occurrence in southern India of two closely related, but morphologically poorly differentiated nightjars with distinct territorial vocalizations (Mees, 1985; Ripley & Beehler, 1987). Molecular analyses of some groups of New and Old World owls have demonstrated that closely related populations which are vocally distinct also differ in mitochondrial DNA sequences (Heidrich et al. 1995, 1996; König et al. 1996; Wink & Heidrich, 1999, 2000), which supports the view that each vocally distinct population may have an unique evolutionary history. The use of vocalizations in the taxonomy of owls and nightjars is now broadly accepted, and vocal characters have been used in various groups, including the nightjar genus *Caprimulgus* (Fry, 1988; Hardy & Straneck, 1989; Cleere, 1995; Robbins & Parker, 1997; Garrido & Reynard, 1998). In this study, we use patterns of variation in territorial songs to assess species limits in the Large-tailed Nightjar *C. macrurus* Horsfield, 1821 complex.

The *C. macrurus* complex is distributed from Pakistan to eastern Australia (fig. 1). In the past, taxonomic studies of the complex (e.g. Oberholser, 1915; Rothschild & Hartert, 1918) were primarily concerned with the delimitation of subspecies taxa and up to 30 populations have been formally named (Peters, 1940; Koeltz, 1954; Greenway, 1978). Many subspecies were synonymized by Mees (1977), who recognized one species with 11 subspecies. His taxonomy was primarily based on examination of museum specimens and has been widely accepted. Marshall (1978), who had recordings of three vocal types at his disposal (*aequabilis* Ripley, 1945 from Sri Lanka, *bimaculatus* Peale, 1848 from Thailand, and *manillensis* Walden, 1875 from Luzon, Philippines), felt unable to present a taxonomic revision without recordings from intervening areas, playback experiments and specimens. Based on Marshall´s (1978) recordings, Davis (1979) proposed to treat *C. atripennis* Jerdon, 1845 and *C. manillensis* as full species. Mees (1985) independently recognized *C. atripennis* and *C. manillensis* as full species based on his study of vocalizations, plumage patterns and the pattern and colouration

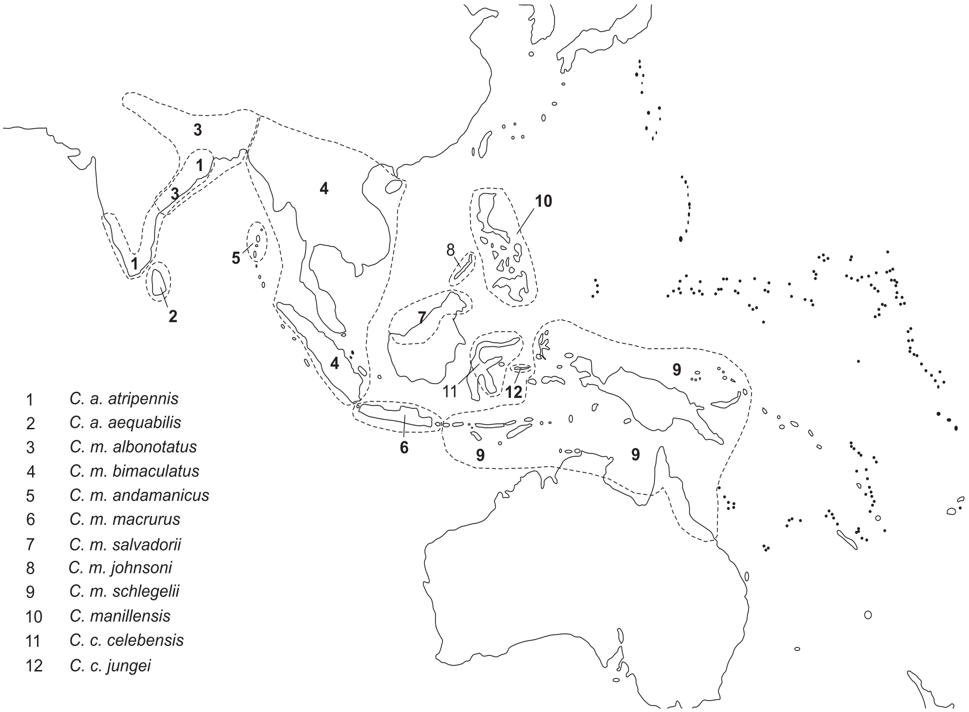


Figure 1. Map showing range of previously recognized taxa included in the *Caprimulgus macrurus* complex. Taxonomy follows Cleere (1998)

of egg shells, and sympatry of *C. atripennis* and *C. macrurus* in northeastern peninsular India. Ripley & Beehler (1987) provided additional evidence of sympatry of *C. atripennis* and *C. macrurus* and argued that the Sri Lankan form *C. atripennis aequabilis* was incorrectly included as a synonym of *C. atripennis* by Mees (1977). Rozendaal (1990) recognized a fourth species taxon, *C. celebensis* Ogilvie-Grant, 1894, for the Sulawesi population based on differences in vocalizations.

The arrangement of the *C. macrurus* complex into four species is now broadly accepted (e.g. Inskipp et al., 1996; Sibley, 1996; King, 1997; Cleere, 1998; Cleere, 1999; Holyoak, 2001; Dickinson, 2003). However, species limits in the *C. macrurus* complex are still incompletely known. Current species limits are primarily based on a small number of recordings of seven of the twelve recognized taxa in the complex (Davis, 1979; Mees, 1985; Rozendaal, 1990). Several taxa have not yet been analysed with the aid of sonagrams and may have been incorrectly grouped with other taxa. Therefore, both the validity of currently accepted species limits and the possible existence of additional vocally distinct populations need to be investigated. Here we analyse geographical variation in territorial songs and address the following questions: (1) Do the four vocal types described by Mees (1985) and Rozendaal (1990) hold up in an analysis of a larger sample and a broader selection of taxa? (2) Are there additional vocal types? (3) Are vocal types geographically restricted? (4) Should vocal types be treated as species?

Our study was prompted by F.G.R.'s observation during a field trip in 1989 that the population of '*C. macrurus*' on Flores sounded very different to birds from elsewhere within its large range. The distinct vocalizations of the birds on Flores have also been noted by others (D. Holmes in Coates & Bishop, 1997, K.D. Bishop in Verhoeye & Holmes, 1998) but the function of the vocalization has remained unclear. A monographic publication listed the vocalization as a variant of the grunting call (Holyoak, 2001). Additional recordings and fieldwork by G.S. on Lombok, Flores and Sumba in 2003 showed that vocalizations of the Sumba population are similar to the Flores population and provided additional information about the context and meaning of the vocalization.

Methods

Recordings and digital processing

To analyse vocalizations we assembled recordings of each of the recognized taxa in the complex (Cleere, 1998). Locations and recordists for all the recordings examined are listed in Appendix 1. To augment the sample size, we included recordings published by Marshall (1978), White (1984), Griffin & Swaby (1984), Swaby & Griffin (1984), Buckingham & Jackson (1991), Connop (1993), Smith (1993, 1995), Ranft & Cleere (1998), Breil & Roché (2000), Scharringa (2001), Warakagoda (2001), Jännes (2002), Stewart (2002) and van Gessel (2002).

Analog recordings were downloaded onto a computer using a Sound Blaster Audigy 2 sound card and transformed into wave files using the computer software CoolEdit 2000 (Johnston, 2000). Digital audio recordings were transformed into wave files using Cdex (Faber, 2001). All files were stored on hard disc as mono wave files at 44.1 kHz with 16 bit precision.

Vocalizations

We used recordings of the 'territorial song' (Holyoak, 2001) to delimit vocal types, because in nightbirds this vocalization is most likely to carry information concerning the bird´s identity (Oba, 1996), to function as sexual and territorial advertisement and may serve to attract and maintain contact with mates (Higgins 1999). This vocalization has also been described as a 'call' (Higgins, 1999; Kennedy et al. 2000), 'song' (Davis, 1978; Marshall, 1978; Cleere, 1998; Cleere, 1999) or 'territorial call' (Buckingham & Jackson, 1991). In the *Caprimulgus macrurus* complex, the territorial song is a commonly heard vocalization. Songs can be heard throughout the year but vocal activity may vary seasonally, geographically and according to moon phase. Variation in vocal activity may be related to the timing of breeding activity and population density (Mees, 1977; Higgins, 1999). Singing is most obvious during courtship and early breeding (Higgins, 1999). Songs are most often given at dusk and dawn (MacKinnon & Phillipps, 1993; Higgins, 1999; pers. obs.) but may continue through the night to dawn and the first half hour of daylight (Higgins, 1999; pers. obs.). Territorial songs are given by males (Robson, 2000) but it has been reported that they may also be given by females (Schodde & Mason, 1980). Singing takes place mostly from perches (Mees, 1977; Cleere, 1998, 1999; Holyoak, 2001) but occasionally in pursuit-flights during apparent courtship (Higgins, 1999).

An 'element' was defined as a part of a note. A 'note' was defined as an unbroken trace on a spectrogram (Isler et al. 1998). A 'song' was defined as the smallest stereotypic repetition of similar note sequences. A 'bout' was defined as a cluster of songs, separated from other clusters by a pause.

Measurements of vocal characters

We produced sonagrams of all recordings using CoolEdit 2000. Spectrograms used in illustrations were made with Syrinx (Burt, 2001). All measurements were made using CoolEdit 2000. Duration of elements, notes and songs were measured in seconds, expressed to the nearest thousandth. Frequency was determined using the option 'frequency analysis', which yields the frequency of the loudest sound at a given time. All frequencies were determined at an FFT size of 1024. Characters were defined on the basis of sonagrams and oscillograms. The following measurements were recorded: (1) number of notes in a song; (2) number of peaks in a song; (3) total song length (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 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 length; (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. The absolute amplitude was not used as a variable because of variation in recording distance and orientation towards the microphone. In order to give equal weight to individuals, means of five songs were computed for each recording. These means were used as sample points from which ranges, means and standard deviations were computed.

Statistical analysis

We initially treated each individual as an operational taxonomic unit (OTU). We have followed this analytical approach because it does not involve establishing groups *a priori* in a subjective manner and thus avoids the possibility of lumping vocally divergent populations in a single taxon based on previous taxonomies.

We used principal components analyses (PCA) to explore the data set and to generate hypotheses of diagnosable groups. PCA reduces multiple variables to a limited number of uncorrelated variables. We used ANOVA and Tukey's post-hoc comparisons to test whether the groups defined by PCA differed from each other.

We applied canonical discriminant function analysis (DFA) to the acoustic variables of individuals to test whether the individuals could be correctly assigned to the groups defined by PCA. DFA generates a set of criteria to assign individuals to groups that are defined prior to the analysis. Prior to DFA analysis, a tolerance test was conducted to assess the independence of each variable. Variables that fail the tolerance test, i.e. which are an almost linear combination of other variables, were excluded from the analyses. Two DFAs were performed: (*i*) a 'descriptive' DFA, in which the observations used to develop the criteria are then subjected to these criteria; (*ii*) a 'predictive' DFA, which uses a jackknife procedure to obtain a more accurate test of the predictive performance of the DFA. In the jackknife procedure, the DFA is recalculated using the combination of variables of the initial DFA with one individual removed from the data set. The criteria are then used to classify the removed individual. This process was repeated for all individuals of the data set.

We subsequently tested the diagnosability of these groups using the criteria developed by Isler et al. (1998). Characters which vary continuously were considered to differ diagnosably if two criteria are met. First, ranges of measurements should not overlap. Second, means (x) and standard deviations (SD) of the population with the smaller set of measurements (*a*) and the population with the larger set of measurements (*b*) should meet the following requirement:

$$x_a + t_a\,SD_a \leq x_b - t_b\,SD_b \qquad (1)$$

where t_i is the t-score at the 97.5 percentile of the t distribution for $n - 1$ degrees of freedom.

SPSS version 10.1 (SPSS, 2000) was used to calculate all descriptive statistics and perform analyses of variance (ANOVA), principal components analyses (PCA), and discriminant function analyses (DFA).

Playback experiments

Populations on Lombok, Flores and Sumba were subjected to playback experiments to assess whether individuals could discriminate between songs from local birds and those of *C. macrurus* (see below). We tested the null hypothesis that the populations do not differ in response to recordings from Flores or Sumba and elsewhere. For each trial, we used two recordings, one from the vocal type from Flores and Sumba and one from *C. macrurus*. For each trial, we used different recordings from these two groups (Kroodsma, 1989; design C). As representatives of the former type, we used recordings from Flores (n = 2) and Sumba (n = 1); as representatives of the latter, we used one recording each from Nepal, Bangladesh (*C. m. albonotatus* Tickell, 1833), Thailand, Singapore (*C. m. bimaculatus*) and Palawan (*C. m. johnsoni* Deignan, 1955) and two recordings from Papua New Guinea and Australia (*C. m. schlegelii* A.B. Meyer, 1874). Recordings are of similar quality, which was judged both visually on sonagrams and by ear. Amplitude of sound files was normalized to the same level and noise from insects was filtered out.

Songs were played from a portable Compact Disc player with separate loudspeakers. Songs were always played close to a known individual and inside a territory if boundaries were known. Trials were performed during dusk or dawn. For each trial, we played 1 minute of the heterospecific song, followed by a pause of 30 seconds to assess response, and 1 minute of conspecific song. Individuals were subjected to one trial only.

Morphology

To identify morphological differences between the Flores and Sumba population and other taxa, we examined 86 adult-plumaged specimens of nine taxa in the complex (Appendix 2). 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 National Museum of Natural History/Naturalis, Leiden (formerly Rijksmuseum voor Natuurlijke Historie; RMNH) and the American Museum of Natural History, New York (AMNH).

Whenever possible, we recorded the following information from each specimen: bill length (from gape, exposed culmen, from anterior point of nostril), wing length (chord of flattened wing from bend of wing to longest primary), emarginations of P9 and P8 (distance from tip of feather), wing formula, shortfall of P1-P10 to tip of longest primary, 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 outher webs). We examined mensural characters with dial calipers (measured to the nearest 0.5 mm). Plumage colours of specimens were compared to published colour standards (Ridgway, 1912; Smithe, 1975).

Taxonomic rationale

We regard a 'species taxon' as a part of a population lineage. This concept of species is known as the General Lineage Concept of species (de Queiroz, 1999) or the Evolutionary Species Concept (Mayden, 1997). Although, in principle, many different criteria can be used to delimit species taxa (de Queiroz, 1999), we follow Marshall (1978) in treating as species only those taxa that have demonstrably diagnosable territorial vocalizations. This approach is consistent with current taxonomic practise in Caprimulgiformes and Strigiformes (Howell & Robbins, 1995; Robbins & Parker, 1997; Garrido & Reynard, 1998; König et al., 1999; König, 2000) and agrees with the Phylogenetic Species Concept (Cracraft, 1989) because species taxa are based on diagnosable character state differences. The differences in territorial vocalizations probably form the basis for reproductive isolation in nightbirds (König, 1998, 2000). Therefore, the units defined by this approach would also satisfy the criteria for species delimitation of the Biological Species Concept.

Throughout this paper we use the designation '*Caprimulgus macrurus* complex' for the group of species under consideration. Designation of this group as a superspecies (Sibley & Monroe, 1990; Cleere, 1998; Holyoak, 2001) is not appropriate (sensu Haffer, 1986; Amadon & Short, 1992) given the overlap of breeding ranges of *C. atripennis* and *C. macrurus* in northeastern peninsular India.

Results

Principal components analysis

The songs of 92 individuals representing all taxa were used in the PCA. The results of the PCA on the 18 measurements are summarized in table 1. Five components with eigenvalues >1 were extracted from the data set. The first principal component (PC1) accounted for 35.2% of the variance. PC2, PC3, PC4 and PC5 accounted for an additional 19.6, 15.0, 11.8 and 5.7% of the variance. PC1 was represented by most of the maximum frequency and duration measurements; PC2 was determined mostly by the structure of the first element, PC3 mostly by the minimum frequency measurements, PC4 and PC5 mostly by the frequency measurements of the last two peaks.

Plotting individuals of the 18 taxa on PC1 versus PC2 (fig. 2a) revealed six distinct clusters. Four groups are well-separated from all other groups, these correspond to *C. celebensis*, *C. m. andamanicus* Hume, 1873, the remaining six subspecies of *C. macrurus* and the population of Flores and Sumba. The groups corresponding to *C. atripennis* and *C. manillensis* did not overlap but are close to each other. A plot of PC1 versus PC3 (fig. 2b) revealed the same groups but *C. manillensis* and *C. atripennis* overlapped. Both plots clearly separated the population of Flores and Sumba from all other individuals, including *C. m. schlegelii* to which it is currently assigned (Mees, 1977). The plots also indicated a separate position of *C. m. andamanicus* from the other subspecies of *C. macrurus*.

Table 1. Factor loadings of the 18 acoustic variables on the five principal components. Numbers in boldface are variables that contributed >70% to individual components. Eigenvalues and percentage of variance explained by the respective components are given at the bottom of the table.

Acoustic variable	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
Number of notes	**-0.722**	0.418	0.049	-0.447	0.219
Number of peaks	-0.469	0.645	-0.130	-0.490	0.013
Total song length	**-0.833**	0.333	-0.070	-0.284	0.071
Maximum frequency of first peak	**0.850**	0.405	-0.270	-0.005	0.057
Minimum frequency of first low	0.347	0.184	**0.722**	-0.122	-0.343
Maximum frequency of second peak	-0.522	0.569	0.370	0.275	0.058
Minimum frequency of second low	0.366	0.540	0.651	-0.182	-0.057
Maximum frequency of penultimate peak	-0.075	0.204	0.265	**0.894**	0.090
Maximum frequency of last peak	0.389	-0.143	0.473	0.380	0.610
Maximum frequency	**0.835**	0.414	-0.270	0.001	0.082
Minimum frequency	0.378	0.430	**0.736**	-0.155	-0.096
Frequency drop of first downward element	**0.736**	0.344	-0.523	0.038	0.177
Frequency drop of penultimate and last peak	-0.438	0.356	-0.157	0.608	-0.482
Peak frequency	**0.752**	0.375	-0.321	0.059	-0.087
Peak frequency time	-0.369	0.535	0.100	0.100	0.351
Structure of first element	0.261	**0.841**	-0.302	0.062	0.021
Song pace	**0.906**	0.006	0.158	-0.179	-0.174
Bout pace	0.578	-0.470	0.285	-0.310	0.151
Eigenvalue	6.341	3.534	2.696	2.129	1.024
% variance explained	35.2	19.6	15.0	11.8	5.7

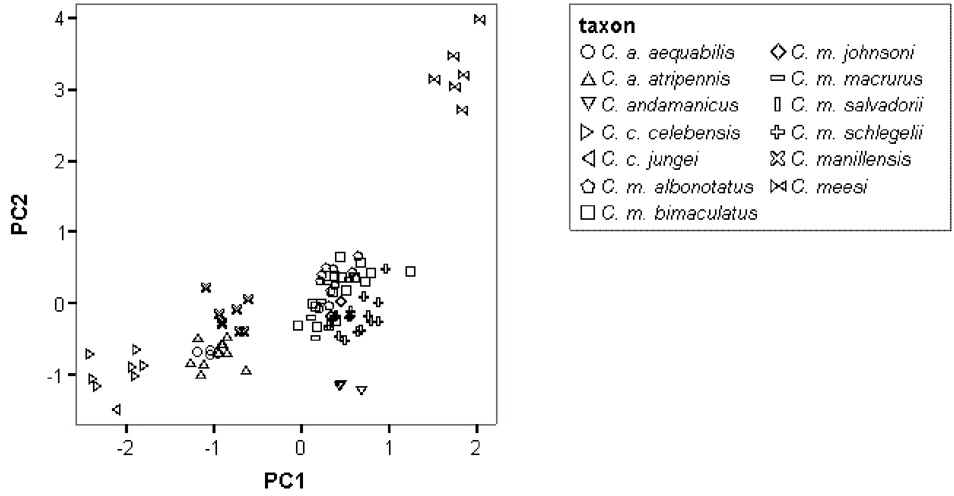


Figure 2a. Eigenvectors of the first and second principal components of 18 acoustic variables measured for territorial songs of the *Caprimulgus macrurus* complex.

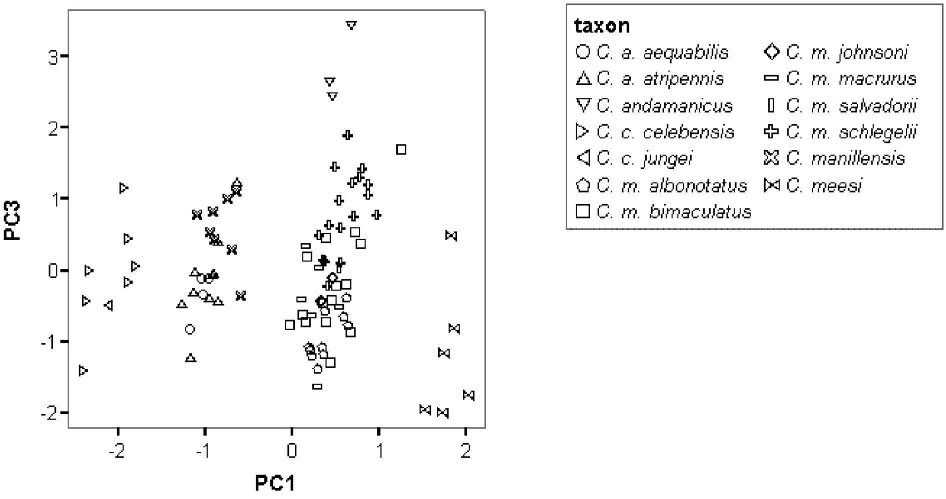


Figure 2b. Eigenvectors of the first and third principal components of 18 acoustic variables measured for territorial songs of the *Caprimulgus macrurus* complex.

Based on the plots, we recognize six potentially diagnosable groups, corresponding to *C. atripennis, C. manillensis, C. celebensis*, *C. m. andamanicus*, the remaining subspecies of *C. macrurus* and the populations of Flores and Sumba. We used one-way ANOVA to test whether the six groups identified by PCA differed in any of the five principal components. The groups differed for all five principal components ($P<0.001$). Each of the six groups differed from all other groups by at least two principal components (Tukey's post-hoc comparisons). All differences remained significant after Bonferoni correction.

Discriminant function analysis

The songs of 92 individuals representing all taxa were used in the DFA. All characters passed the tolerance test, except frequency drop of the first downward element which was excluded from the test. The descriptive DFA was highly significant (Wilks' ?<0.001; ?$^{2}_{85}$=1247.199; P<0.001). The variables most important in the discrimination were: number of notes, number of peaks, maximum frequency of penultimate peak, maximum frequency of last peak, maximum frequency, minimum frequency and structure of first element (table 2).

Table 2. Standardized canonical discrimination function coefficients examining trends in variance of 18 acoustic variables measured for territorial songs of the *Caprimulgus macrurus* complex. Numbers in boldface are variables that contributed >70% to individual roots. Eigenvalues and percentage of variance accounted for by each root are given at the bottom of the table.

Acoustic variable	**DF1**	**DF2**	**DF3**	**DF4**	**DF5**
Number of notes	**1.370**	0.329	0.656	-0.352	-0.459
Number of peaks	**-0.708**	0.122	**-0.716**	**0.726**	0.636
Total song length	-0.007	-0.303	0.137	0.267	**0.705**
Maximum frequency of first peak	-0.503	0.627	**0.803**	-0.678	0.419
Minimum frequency of first low	0.064	-0.053	0.515	1.119	**-0.852**
Maximum frequency of second peak	-0.002	-0.108	-0.483	0.196	-0.061
Minimum frequency of second low	-0.579	0.263	**1.209**	0.513	0.223
Maximum frequency of penultimate peak	-0.167	**-1.371**	**-3.482**	0.340	**-2.511**
Maximum frequency of last peak	0.355	**1.320**	**3.205**	-0.359	**2.758**
Maximum frequency	0.224	-0.186	-0.217	0.224	-0.034
Minimum frequency	**0.816**	0.000	**-1.725**	**-1.325**	0.416
Frequency drop of first downward element	excluded	excluded	excluded	excluded	excluded
Frequency drop of penultimate and last peak	0.230	0.536	**1.397**	-0.008	**1.259**
Peak frequency	-0.199	0.157	0.066	-0.005	0.038
Peak frequency time	0.001	0.086	-0.003	0.011	0.081
Structure of first element	-0.032	**0.828**	-0.412	-0.070	-0.325
Song pace	-0.476	0.108	**0.745**	0.330	-0.009
Bout pace	-0.217	-0.056	0.396	-0.205	-0.058
Eigenvalue	151.062	40.657	24.290	6.626	4.325
% variance explained	66.6	17.9	10.7	2.9	1.9

The initial DFA led to a 100% correct classification of the individuals into the groups defined by PCA. The first of the five discriminant functions (DF1) accounted for 66.6% of the variation, and the second (DF2) and third (DF3) accounted for 17.9% and 10.7% of the variation (table 2). The jackknife procedure also provided an extremely high degree of predictive discrimination, with 90 of 92 (97.8%) individuals being correctly assigned to their group defined by PCA. One *C. macrurus* was classified to *C. atripennis*, and one *C. atripennis* was classified to *C. macrurus*. In the original and jackknife analyses, the recordings from Java (*C. m. macrurus*), Borneo (*C. m. salvadorii* Sharpe, 1875), Palawan (*C. m. johnsoni*) and Lombok (previously separated as *C. m. oberholseri* Rothschild & Hartert, 1918) were assigned to *C. macrurus*. The single recording from the Sula Islands (*C. c. jungei* Neumann, 1939) was assigned to *C.*

celebensis. None of the recordings from Flores and Sumba was assigned to *C. macrurus*. Similarly, none of the three recordings from the Andaman Islands (*C. m. andamanicus*) was assigned to *C. macrurus*.

Univariate analyses

Territorial song characteristics of all taxa of the *Caprimulgus macrurus* complex are given in table 3. A total of 109 recordings was used to test the diagnosability of the six groups that were identified by PCA. Comparison of the 18 acoustic variables revealed 70 diagnosable differences between pairs of the six groups (table 4), representing 26% of 270 comparisons. In our data set, *C. macrurus* differs diagnosably from the other groups by 3-5 variables, *C. celebensis* by 2-8 variables, *C. atripennis* by 1-8 variables and *C. manillensis* by 1-8 variables. The population of Flores and Sumba differs diagnosably from *C. macrurus*, with which it is currently included, by 5 variables and differs from the other four groups by 7-8 variables. *C. m. andamanicus*, which also is included in *C. macrurus* by current taxonomies, differs from that species by 3 variables and from the other four groups in the complex by 4-7 variables. The pair with the least number of diagnosable differences was *C. atripennis* - *C. manillensis*; in our data set of acoustic characters, this pair is diagnosable only by the number of notes. The variables that resulted in the most diagnosable differences between taxon pairs were total song length (11 pairs), song pace (10 pairs), number of notes (8 pairs) and frequency drop of first downward element (8 pairs).

Three groups refer to polytypic species (*C. atripennis*, *C. celebensis* and *C. macrurus*). Comparisons of the 18 acoustic variables among the subspecies within these three groups did not yield any diagnosable differences between pairs of subspecies. Two subspecies (*C. c. jungei* and *C. m. salvadorii*) have a sample size of 1, making statistical analysis impossible. However, in most comparisons, measurements of these taxa fell either within the range of measurements of the other taxon, or below the 97.5% percentile of the t distribution of the other taxon, or both.

Description and taxonomic distribution of territorial song types

Sonagrams of the territorial songs of all taxa of the *Caprimulgus macrurus* complex are given in fig. 3. All territorial song types are robust-sounding pure tones and songs have almost no energy in their overtones. The fundamental frequency therefore is the only visible part in the spectrogram. All song types begin with an element that (slightly) rises in pitch, followed by a pronounced downward element and a repetitive series of elements at a lower frequency. In four song types, the elements form a single note; in two types the elements form separate notes. In almost all recordings, most of the energy is concentrated in the first downward element. All song types are clearly distinct to the human ear.

SONG TYPE 1.— Type 1 songs consist of a single note, a tremolo mostly consisting of four peaks (fig. 3a-c) although we have examined one recording each of songs with three and five peaks (fig. 3d). The first peak reaches a lower frequency than *C. macrurus* (table 3) although, due to variation in both species, the difference is not diagnosable (table 4). In

Table 3. Descriptive statistics of 18 acoustic variables measured for territorial songs of the *Caprimulgus macrurus* complex.

Character	*C. (m.) andamanicus*	*C. atripennis* (all subspecies)	*C. celebensis* (all subspecies)	*C. macrurus* (all subspecies, except *C. m. andamanicus*)	*C. manillensis*	*C. meesi* (Flores and Sumba)
1	1.0 (0; 3) 1.0-1.0	1.0 (0.0; 14) 1.0-1.0	8.0 (1.0; 10) 7.0-9.8	1.0 (0.0; 54) 1.0-1.0	5.0 (0.4; 10) 4.2-5.8	1.0 (0; 7) 1.0-1.0
2	4.4 (0.5; 3) 4.0-5.0	4.0 (0.4; 15) 3.0-5.0	8.0 (1.0; 10) 7.0-9.8	4.0 (0.1; 58) 4.0-5.0	5.3 (0.8; 10) 4.2-7.0	6.0 (0; 9) 6.0-6.0
3	0.099 (0.005; 3) 0.093-0.102	0.326 (0.028; 15) 0.270-0.397	0.968 (0.200; 10) 0.816-1.375	0.149 (0.018; 58) 0.119-0.194	0.388 (0.035; 10) 0.356-0.449	0.149 (0.017; 9) 0.113-0.172
4	1509.2 (26.1; 3) 1486.0-1537.4	1321.0 (63.1; 15) 1179.4-1418.0	1238.7 (104.2; 10) 1044.8-1375.8	1680.7 (116.2; 60) 1469.2-2123.6	1435.6 (57.3; 11) 1325.6-1522.5	2509.4 (167.2; 10) 2330.0-2813.2
5	1138.1 (46.8; 3) 1084.4-1170.6	597.7 (41.2; 15) 551.8-700.2	642.2 (86.9; 9) 507.8-779.4	656.3 (64.0; 58) 533.2-813.0	652.2 (52.4; 11) 535.5-727.4	705.4 (45.8; 7) 656.0-790.0
6	1228.3 (5.9; 3) 1124.0-1235.0	1172.5 (58.6; 15) 1061.6-1262.8	1228.4 (106.8; 10) 1029.8-1390.6	904.5 (71.3; 59) 769.0-1114.0	1312.8 (260.6; 11) 754.0-1515.3	1045.5 (170.1; 10) 849.6-1330.0
7	750.5 (78.5; 3) 677.4-833.4	565.7 (42.4; 15) 500.0-641.8	629.6 (71.7; 9) 542.0-748.5	619.7 (85.6; 53) 466.4-797.6	679.9 (43.1; 11) 619.2-750.3	750.4 (68.3; 7) 666.0-855.6
8	980.1 (9.1; 3) 971.0-989.2	1118.4 (85.1; 15) 945.0-1222.4	897.9 (64.4; 9) 782.2-975.2	923.8 (77.8; 60) 749.4-1127.8	995.8 (68.0; 9) 858.6-1105.0	995.7 (55.9; 8) 939.4-1079.0
9	927.9 (18.1; 3) 907.4-941.6	898.0 (100.8; 15) 742.8-1127.8	823.9 (61.5; 9) 708.8-897.6	930.1 (78.8; 59) 784.4-1115.6	934.9 (76.8; 9) 834.4-1088.0	890.1 (74.2; 8) 813.6-995.4
10	1509.2 (26.1; 3) 1486.0-1537.4	1321.0 (63.1; 15) 1179.4-1418.0	1244.2 (103.5; 10) 1045.0-1391.2	1680.7 (116.2; 60) 1469.2-2123.6	1445.0 (51.6; 11) 1359.0-1522.5	2509.4 (167.2; 10) 2330.0-2813.2
11	750.5 (78.5; 3) 677.4-833.4	564.0 (38.1; 15) 500.0-641.6	589 (59.1; 8) 506.0-699.0	611.2 (81.4; 53) 466.4-797.6	657.1 (32.7; 10) 615.0-712.4	698.1 (46.8; 7) 650.0-790.0
12	371.1 (28.5; 3) 345.0-401.6	722.1 (59.0; 15) 617.4-815.2	589.3 (106.4; 9) 464.8-748.8	1023.5 (117.5; 58) 778.8-1352.0	785.7 (60.6; 11) 718.4-907.5	1806.4 (152.8; 7) 1615.6-2088.4
13	52.1 (10.0; 3) 45.2-63.6	216.9 (91.0; 15) 29.8-360.8	72.8 (27.5; 9) 32.4-112.5	-3.1 (33.4; 59) -91.4-80.6	60.9 (43.0; 9) -5.8-118.0	107.5 (30.3; 8) 58.8-161.0
14	1446.7 (50.0; 3) 1391.0-1487.8	1279.5 (69.5; 15) 1139.2-1371.2	1121.1 (113.3; 10) 913.6-1268.2	1490.0 (164.1; 60) 1073.2-1787.8	1355.9 (96.6; 11) 1123.4-1487.2	2136.2 (166.5; 10) 1947.2-2466.6
15	0.006 (0.001; 3) 0.004-0.007	0.038 (0.020; 15) 0.015-0.105	0.065 (0.081; 10) 0.006-0.206	0.011 (0.004; 60) 0.004-0.024	0.121 (0.092; 11) 0.002-0.270	0.050 (0.015; 10) 0.015-0.066
16	0.12 (0.03; 3) 0.10-0.15	0.26 (0.03; 15) 0.25-0.35	0.24 (0.08; 10) 0.10-0.35	0.19 (0.05; 60) 0.10-0.30	0.45 (0.09; 11) 0.25-0.50	0.98 (0.03; 10) 0.90-1.00
17	44.462 (3.895; 3) 41.484-48.870	12.469 (0.882; 15) 11.090-14.698	8.420 (1.014; 10) 5.980-9.511	27.340 (3.107; 58) 21.982-33.681	13.628 (1.033; 10) 11.429-15.590	39.721 (2.969; 9) 34.935-44.229
18	1.319 (0.325; 3) 1.069-1.686	0.295 (0.070; 15) 0.187-0.435	0.347 (0.068; 10) 0.227-0.420	1.295 (0.389; 59) 0.529-2.390	0.777 (0.311; 10) 0.396-1.418	0.600 (0.237; 9) 0.148-1.003

Character	*C. a. aequabilis*	*C. a. atripennis*	*C. c. celebensis*	*C. c. jungei*	*C. m. albonotatus*
1	1.0 (0; 4) 1.0-1.0	1.0 (0; 10) 1.0-1.0	8.0 (1.0; 9) 7.0-9.8	7.4	1.0 (0; 12) 1.0-1.0
2	4.0 (0; 4) 4-4	4.0 (0.4; 11) 3.0-5.0	8.0 (1.0; 9) 7.0-9.8	7.4	4.0 (0; 12) 4.0-4.0
3	0.321 (0.006; 4) 0.314-0.327	0.328 (0.033; 11) 0.270-0.397	0.983 (0.206; 9) 0.816-1.375	0.832	0.162 (0.013; 12) 0.132-0.181
4	1310.7 (16.3; 4) 1287.6-1325.6	1324.8 (73.8; 11) 1179.4-1418.0	1260.2 (83.6; 9) 1083.6-1375.8	1044.8	1713.5 (71.9; 13) 1606.8-1820.8
5	583.6 (19.1; 4) 560.8-607.4	602.8 (46.5; 11) 551.8-700.2	650.0 (89.5; 8) 507.8-779.4	580.0	616.2 (37.7; 13) 558.6-677.6
6	1176.2 (46.2; 4) 1151.8-1245.4	1171.1 (64.5; 11) 1061.6-1262.8	1250.4 (85.8; 9) 1097.0-1390.6	1029.8	870.7 (49.0; 13) 798.2-950.8
7	553.5 (38.3; 4) 508.4-600.4	570.1 (44.7; 11) 500.0-641.8	637.0 (72.9; 8) 542.0-748.5	570.0	551.1 (65.6; 11) 466.4-652.0
8	1144.6 (61.6; 4) 1054.2-1189.0	1108.8 (92.9; 11) 945.0-1222.4	912.4 (50.9; 8) 814.2-975.2	782.2	883.2 (74.7; 13) 751.0-995.0
9	869.9 (103.5; 4) 742.8-959.6	908.2 (102.9; 11) 748.6-1127.8	833.2 (58.6; 8) 708.8-897.6	749.8	891.3 (63.8; 12) 784.4-993.8

Table 3. Continued.

10	1310.7 (16.3; 4) 1287.6-1325.6	1324.8 (73.8; 11) 1179.4-1418.0	1266.4 (80.9; 9) 1107.0-1391.2	1045.0	1713.5 (71.9; 13) 1606.8-1820.8
11	552.9 (37.8; 4) 508.4-599.2	568.0 (39.1; 11) 500.0-641.6	591.7 (63.3; 7) 506.0-699.0	570.0	541.2 (53.2; 11) 466.4-622.6
12	727.4 (13.4; 4) 709.2-741.0	720.2 (69.4; 11) 617.4-815.2	604.9 (102.2; 8) 481.0-748.8	464.8	1097.1 (75.8; 13) 992.0-1234.2
13	274.8 (73.7; 4) 209.6-360.8	195.9 (90.3; 11) 29.8-324.8	77.8 (24.5; 8) 38.6-112.5	32.4	4.7 (21.2; 12) -31.8-34.2
14	1298.5 (14.0; 4) 1282.6-1316.2	1272.5 (80.6; 11) 1139.2-1371.2	1131.2 (115.4; 9) 913.6-1268.2	1030.4	1561.0 (138.2; 13) 1321.0-1786.8
15	0.026 (0.003; 4) 0.025-0.031	0.042 (0.023; 11) 0.015-0.105	0.072 (0.083; 9) 0.014-0.206	0.006	0.009 (0.003; 13) 0.004-0.013
16	0.25 (0; 4) 0.25-0.25	0.26 (0.03; 11) 0.25-0.35	0.25 (0.07; 9) 0.10-0.35	0.15	0.22 (0.06; 13) 0.10-0.30
17	12.479 (0.222; 4) 12.241-12.733	12.466 (1.037; 11) 11.090-14.698	8.366 (1.060; 9) 5.980-9.511	8.909	24.854 (2.189; 12) 22.068-30.344
18	0.302 (0.060; 4) 0.302-0.435	0.266 (0.062; 11) 0.187-0.383	0.339 (0.067; 9) 0.227-0.411	0.420	1.253 (0.431; 13) 0.630-2.222

Character	*C. m. bimaculatus*	*C. m. salvadorii*	*C. m. johnsoni*	*C. m. macrurus*	*C. m. schlegelii*
1	1.0 (0; 16) 1.0-1.0	1.0	1.0 (0; 2) 1.0-1.0	1.0 (0; 6) 1.0-1.0	1.0 (0; 17) 1.0-1.0
2	4.1 (0.2; 20) 4.0-5.0	4.0	4.0 (0; 2) 4.0-4.0	4.0 (0; 6) 4.0-4.0	4.0 (0; 17) 4.0-4.0
3	0.160 (0.015; 20) 0.133-0.194	0.119	0.129 (0.011; 2) 0.121-0.137	0.141 (0.007; 6) 0.128-0.150	0.134 (0.009; 17) 0.123-0.150
4	1744.2 (132.5; 20) 1569.8-2123.6	1562.4	1579.6 (96.7; 2) 1511.2-1648.0	1580.7 (105.2; 6) 1469.2-1753.0	1637.6 (81.6; 18) 1491.4-1807.4
5	657.6 (62.9; 18) 575.6-788.2	666.4	599.3 (1.0; 2) 598.6-600.0	603.0 (60.7; 6) 533.2-671.0	707.6 (47.9; 18) 613.0-813.0
6	916.9 (91.3; 20) 771.6-1114.0	801.8	833.3 (59.3; 2) 791.4-875.2	886.4 (66.4; 6) 769.0-967.2	936.7 (38.4; 17) 859.2-1001.4
7	600.7 (77.2; 15) 473.8-778.2	612.0	569.1 (17.1; 2) 557.0-581.2	580.4 (61.8; 6) 517.6-687.8	696.6 (58.0; 18) 579.4-797.6
8	934.0 (89.8; 20) 820.5-1127.8	819.4	942.4 (93.1; 2) 876.6-1008.2	892.9 (74.7; 6) 749.4-969.6	955.8 (49.0; 18) 855.6-1039.6
9	916.3 (94.8; 20) 790.2-1115.6	910.8	966.3 (66.3; 2) 919.4-1013.2	918.2 (72.0; 6) 800.0-1000.2	972.3 (57.6; 18) 857.6-1100.2
10	1744.2 (132.5; 20) 1569.8-2123.6	1562.4	1579.6 (96.7; 2) 1511.2-1648.0	1580.7 (105.2; 6) 1469.2-1753.0	1637.6 (81.6; 18) 1491.4-1807.4
11	591.7 (72.8; 15) 473.8-763.8	612.0	582.4 (17.3; 2) 570.2-594.6	567.0 (43.5; 6) 517.6-637.6	688.1 (55.6; 18) 579.4-797.6
12	1091.0 (103.6; 18) 955.2-1352.0	896.0	980.3 (95.7; 2) 912.6-1048.0	977.6 (116.9; 6) 862.8-1095.6	930.0 (82.1; 18) 778.8-1086.8
13	17.5 (27.3; 20) -30.8-80.6	-91.4	-23.9 (26.7; 2) -42.8- -5.0	-25.4 (38.2; 6) -80.4-29.4	-16.7 (28.2; 18) -68.4-34.3
14	1485.5 (203.8; 20) 1073.2-1742.4	1400.6	1425.3 (112.4; 2) 1345.8-1504.8	1462.3 (129.7; 6) 1313.0-1625.8	1465.0 (148.7; 18) 1166.2-1787.8
15	0.013 (0.005; 20) 0.006-0.024	0.011	0.010 (0.008; 2) 0.005-0.015	0.12 (0.004; 6) 0.005-0.017	0.011 (0.004; 18) 0.006-0.017
16	0.17 (0.05; 20) 0.10-0.25	0.25	0.20 (0.07; 2) 0.15-0.25	0.19 (0.05; 6) 0.15-0.25	0.19 (0.05; 18) 0.10-0.25
17	25.483 (2.019; 20) 21.982-30.083	33.681	31.149 (2.634; 2) 29.286-33.012	28.487 (1.546; 6) 26.671-31.317	30.054 (1.867; 17) 26.612-32.541
18	1.213 (0.396; 19) 0.558-1.981	1.462	1.398 (0.412; 2) 1.107-1.690	1.153 (0.211; 6) 0.888-1.378	1.439 (0.395; 18) 0.529-2.390

Table 4. Summary of diagnostic vocal characters of nightjars in the *Caprimulgus macrurus* complex.

	Characters																		
PCA-defined groups	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Total
C. meesi / C. macrurus		X		X						X		X				X			5
C. meesi / C. atripennis		X	X	X						X		X		X		X	X		8
C. meesi / C. manillensis	X		X	X						X		X		X		X	X		8
C. meesi / C. celebensis	X		X	X						X		X		X		X	X		8
C. meesi / C. andamanicus				X	X					X		X		X	X	X			7
C. macrurus / C. atripennis			X														X	X	3
C. macrurus / C. manillensis	X		X														X		3
C. macrurus / C. celebensis	X	X	X														X	X	5
C. macrurus / C. andamanicus					X	X						X							3
C. atripennis / C. manillensis	X																		1
C. atripennis / C. celebensis	X	X	X																3
C. atripennis / C. andamanicus			X		X							X					X		4
C. manillensis / C. celebensis			X														X		2
C. manillensis / C. andamanicus	X		X		X							X				X	X		6
C. celebensis / C. andamanicus	X		X		X												X		4
Total diagnosable	8	4	11	5	5	1	0	0	0	5	0	8	0	4	1	6	10	2	70

1 = number of notes; 2 = number of peaks; 3 = total song length; 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; 11 = minimum frequency; 12 = frequency drop of first downward element; 13 = frequency drop of penultimate and last peak; 14 = peak frequency; 15 = peak frequency time; 16 = structure of first element; 17 = song pace; 18 = bout pace.

recordings with songs of 4-5 peaks the last peak has a lower frequency than the previous peak. Songs are clearly longer than those of *C. m. andamanicus*, *C. macrurus*, and the Flores and Sumba population, but much shorter than those of *C. celebensis*. Songs are given in long bouts of evenly-spaced songs which are repeated every 2-3.5 s. This is the only song type with a tremolo clearly audible to the human ear. A single song with four peaks can be rendered as *toowowowo*. This song type is known from *C. a. atripennis* and *C. a. aequabilis* only; no other song types were recorded from these subspecies.

SONG TYPE 2.— This song type consists of two parts, separated by an interval of 0.10-0.15 s (fig. 3e-f). The first part consists of a single note which on average rises to c. 1436 Hz (table 3) and then descends rapidly. In two of 11 recordings, there is a second peak at much lower frequency (754-843 Hz). The second part consists of 3-5 notes, the first of which on average rises to c. 1427 Hz, followed by notes with peaks of lower amplitude (834-1105 Hz). Songs are given at variable rate and can be rendered as *took toorrrr* or *chook choorrr*. This song type is only known from *C. manillensis*; no other song types were recorded from this subspecies.

SONG TYPE 3.— Song type 3 consists of a rapid accelerating series of 7-10 notes (fig. 3g-i), lasting c. 0.8-1.4 s. This song type has the longest duration of all taxa in the complex. The first notes are of higher frequency and amplitude than the last notes which trail off. The first notes rise slightly and then descend rapidly; the last notes

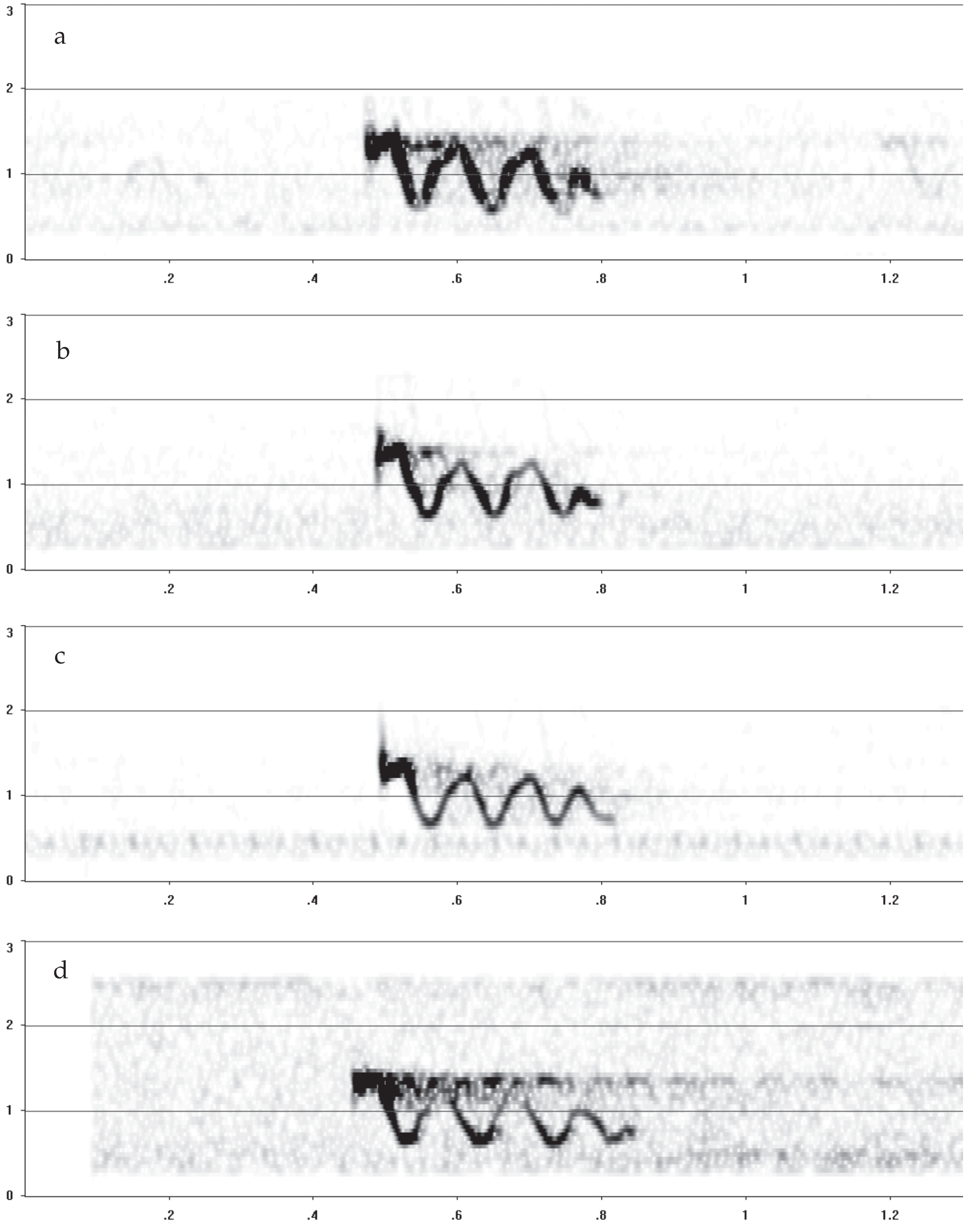


Figure 3a-d. Sonagrams of territorial songs of *Caprimulgus atripennis*. From top to bottom: (a) *C. a. aequabilis*, Lahogala, Sri Lanka, January 1982, R.K. Templeton; (b) *C. a. aequabilis*, Yala N.P., Sri Lanka, January 1995, S. Smith; (c) *C. a. atripennis*, Mudumalai N.P., Tamil Nadu, India, February 2002, H. Jännes; (d) *C. a. atripennis*, Chandaka-Dampara Wildl. Res., Orissa, India, February 2002, P. Singh. X-axis in seconds, Y-axis in kHz.

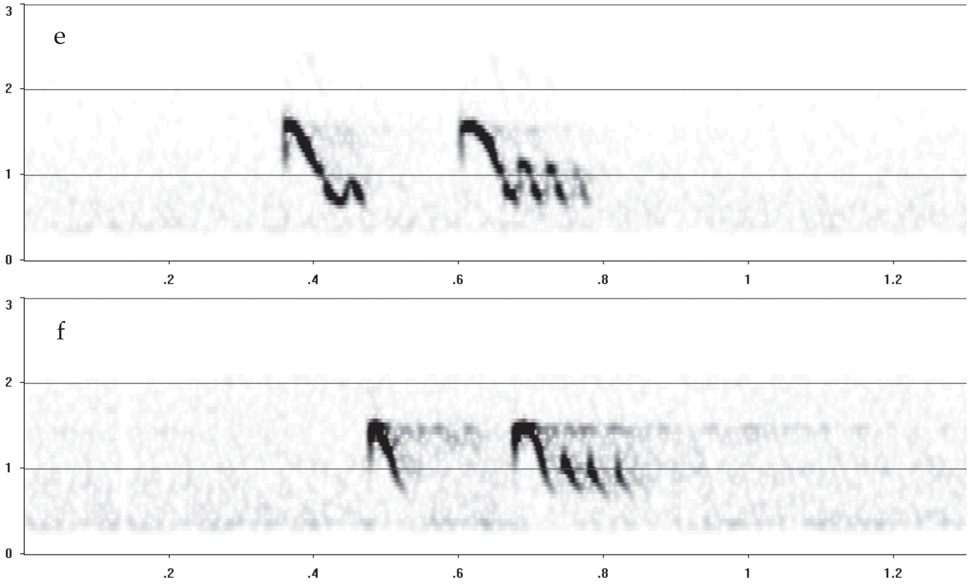


Figure 3e-f. Sonagrams of territorial songs of *Caprimulgus manillensis*. From top to bottom: (e) Mt Katanglad, Mindanao, Philippines, March 1990, A. Greensmith; (f) Mt Katanglad, Mindanao, Philippines, May 1995, N. Gardner.

only consist of a downward element. The song lacks any indication of a tremolo. An eight-note song can be rendered as *chuck chuck chuck chuck-chuck-tr-rr-r*. This song type is known from *C. c. celebensis* and *C. c. jungei* only; no other song types were recorded from these subspecies.

SONG TYPE 4.— Songs of this type consist of a single note (fig. 3j-p). The note is a tremolo of four peaks (one recording from Thailand shows five peaks). The song starts at a relatively high frequency, rises slightly, then descends rapidly, followed by three peaks. These peaks are of similar frequency, although some individual variation occurs; in some recordings, the last peak is of higher frequency than the previous peak, in other recordings it is of lower frequency. Songs are often given in long monotonous bouts at variable rate but songs are sometimes uttered in series of only two or three songs. This song type has a deep resonating quality and can be recognized from long distances. A series of three songs can be rendered as a deep *chong-chong-chong*. This song type is known from *C. m. albonotatus, C. m. bimaculatus, C. m. macrurus, C. m. johnsoni, C. m. salvadorii* and *C. m. schlegelii*; no other song types are known for these subspecies.

SONG TYPE 5.— Songs of this type are a single note, a tremolo consisting of four to five peaks (fig. 3q-r). As in other types, the first peak reaches the highest frequency, but in contrast to other song types, each of the following peaks has a lower frequency than the preceding peak, and each of the lower parts of the tremolo is lower than the

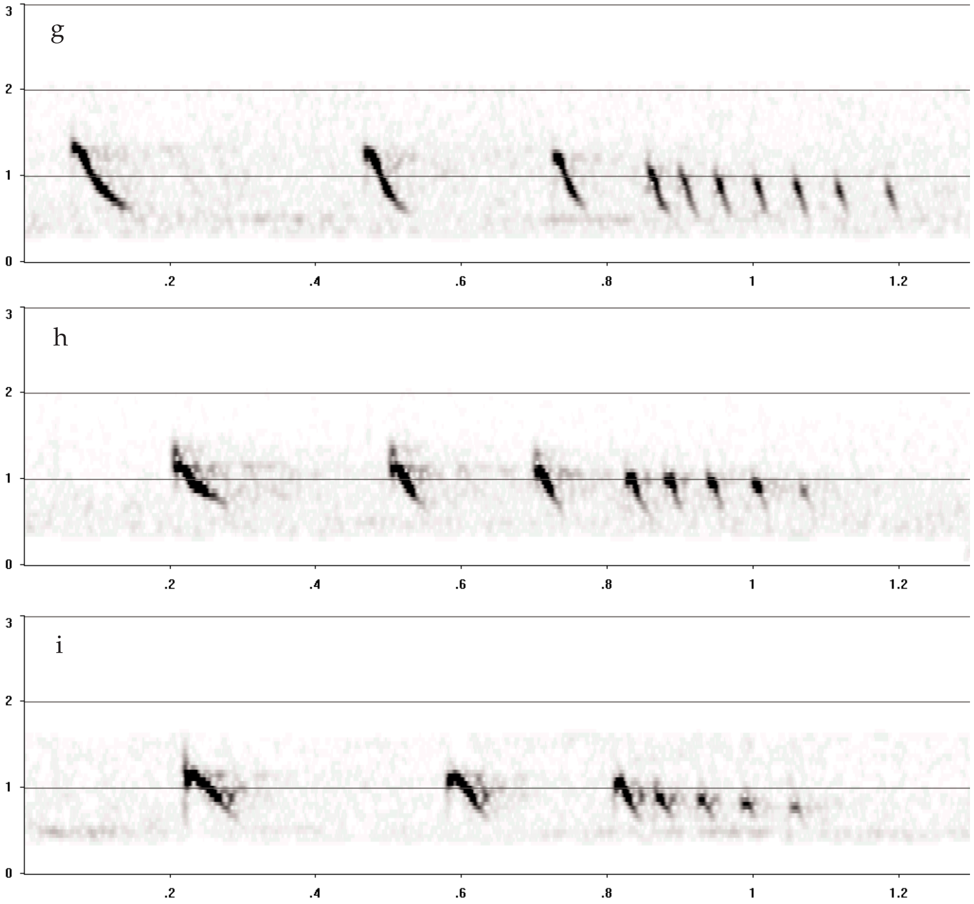
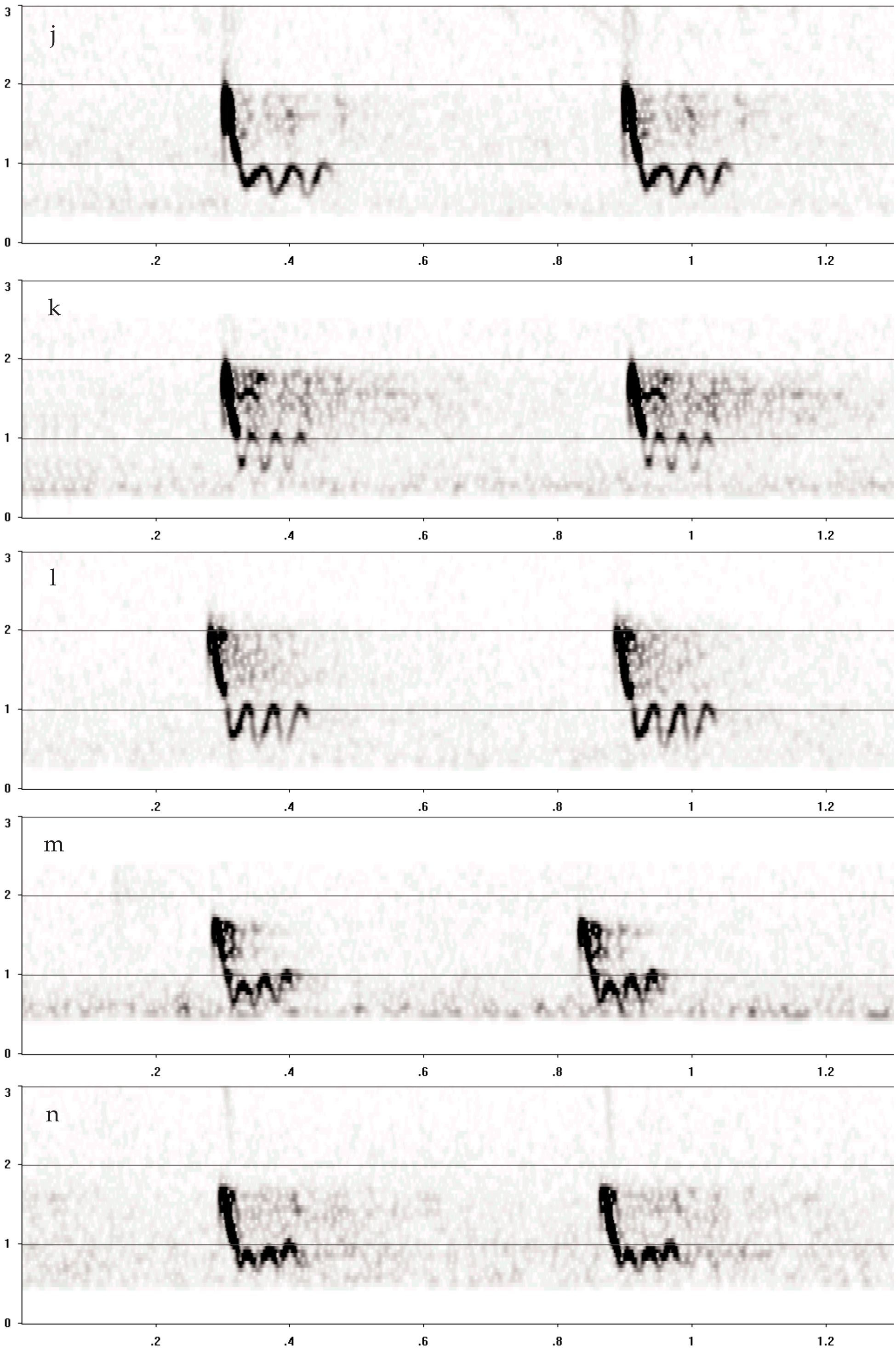


Figure 3g-i. Sonagrams of territorial songs of *Caprimulgus celebensis*. From top to bottom: (g) *C. c. celebensis*, Morowali Res., Sulawesi, Indonesia, c. 1980, D. Watling; (h) *C. c. celebensis*, Tangkoko Batuangus N.P., Sulawesi, Indonesia, November 1998, R. Drijvers; (i) *C. c. jungei*, Mangole Isl., Sula Is, Indonesia, December 1988, D. Yong.

preceding one. The frequency of the first low is higher than in all other taxa and as a consequence, the frequency drop of the first downward element is smaller than in all other taxa, except *C. celebensis*. Songs are shorter than in all other song types, and total song length is almost always <0.1 s. Songs are often given in bouts of four to seven rapidly repeated songs, followed by a pause of 2.5-4 s. We have not encountered this song pattern in any of the recordings of other song types. A bout of five songs can be rendered as *tow-tow-tow-tow-tow* or *chow-chow-chow-chow-chow*. The songs of this type sound less deep than those of the other subspecies of *C. macrurus* and lack the deep *chonk* tone of that species. This song type is only known from *C. m. andamanicus*; no other song types were recorded from this subspecies.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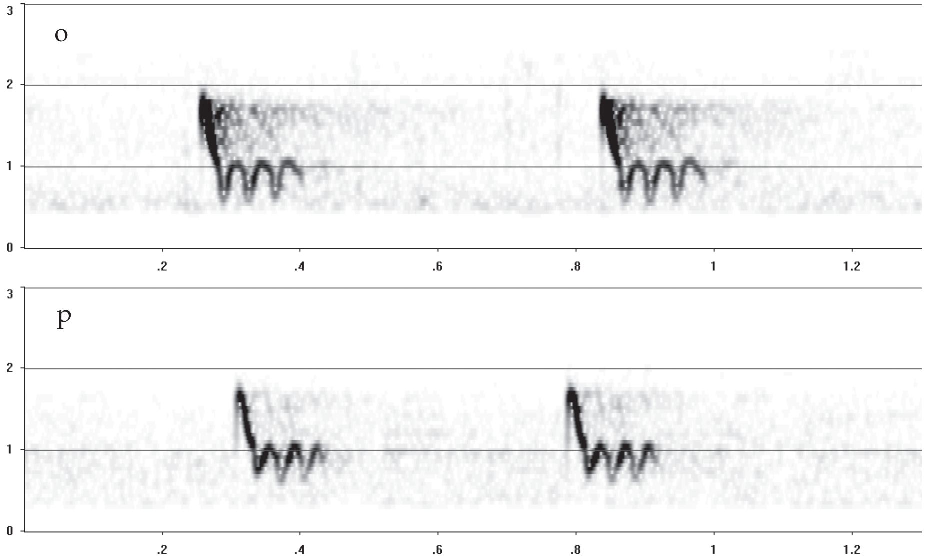

Figure 3j-p. Sonagrams of territorial songs of *Caprimulgus macrurus*. From top to bottom: (j) *C. m. albonotatus*, Corbett N.P., Uttaranchal, India, March 1997, P. Holt; (k) *C. m. albonotatus*, Bhitarkanika, Orissa, India, February 2002, P. Singh; (l) *C. m. bimaculatus*, Ban Bang Tiao, Khao Nor Chuchi, Krabi Prov., Thailand, April 1987, F.G. Rozendaal; (m) *C. m. johnsoni*, Puerto Princesa, Palawan, September 1978, R.S. Kennedy; (n) *C. m. salvadorii*, Pulau Tiga, Sabah, Malaysia, April 1995, A. Greensmith; (o) *C. m. macrurus*, Carita, Java, Indonesia, July 1989, A.B. van den Berg; (p) *C. m. schlegelii*, Gunung Rinjani N.P., Lombok, Indonesia, September 2003, G. Sangster.

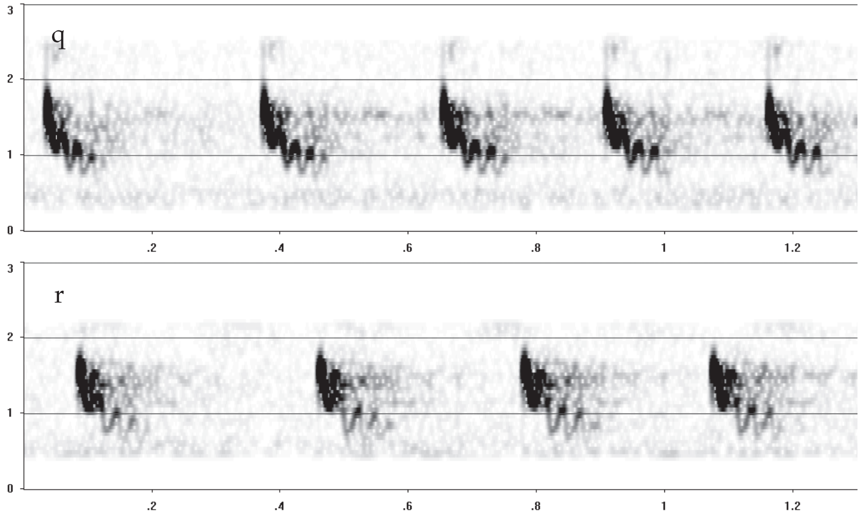

Figure 3q-r. Sonagrams of territorial songs of *Caprimulgus andamanicus*. From top to bottom: (q) Hut Bay, Little Andaman Isl., Andaman Is, April 2002, P. Singh; (r) Bakultala, Middle Andaman Isl., Andaman Is, April 2001, P. Singh.

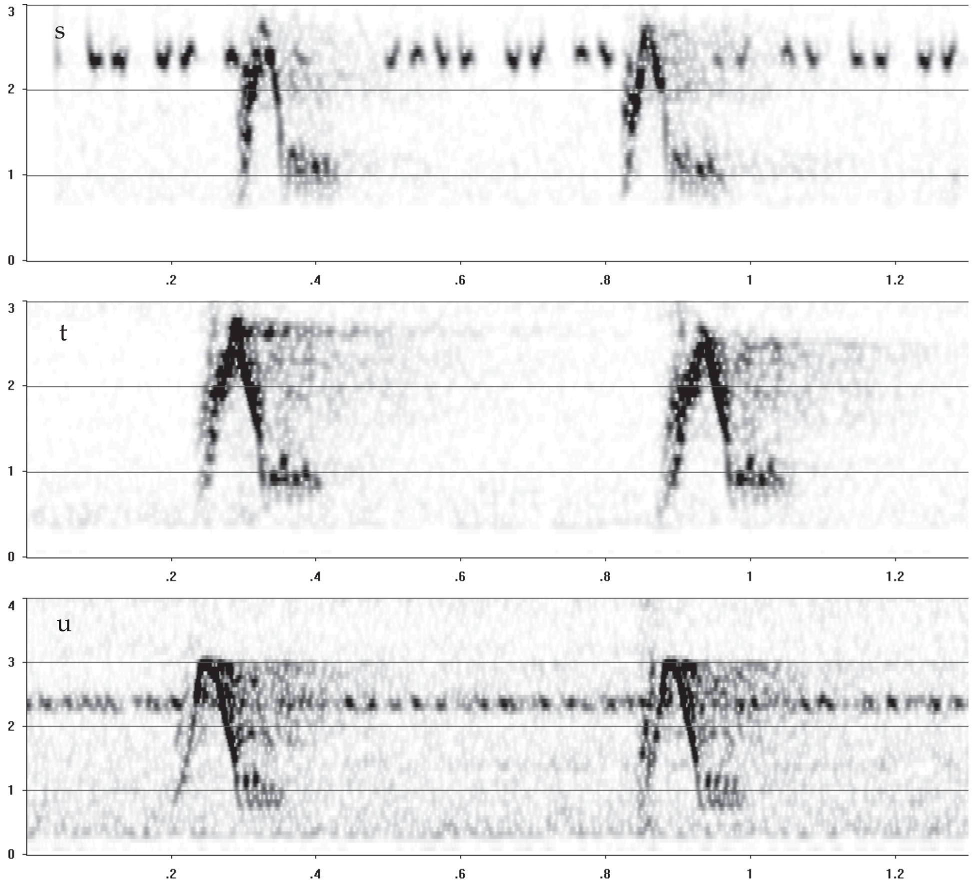

Figure 3s-u. Sonagrams of territorial songs of *Caprimulgus meesi*. From top to bottom: (s) Ili Wengot, Flores, Indonesia, September 1998, R. Drijvers; (t) Wolo Tado, near Riung, Flores, Indonesia, August 2003, G. Sangster; (u) Lewapaku, Sumba, Indonesia, August 2003, G. Sangster. The notes at c. 2.4 kHz in Figure 3s and 3u are insect sounds.

SONG TYPE 6.— Song type 6 consists of a single note with six peaks (fig. 3s-u). The song begins with a distinct rising element, which reaches a frequency of at least 2330 Hz at the first peak, the highest in the complex. The song then descends rapidly and is followed by a tremolo with five rapidly repeated peaks. The song has an explosive quality, reminiscent of the song of *C. affinis* Horsfield, 1821. The tremolo is not audible to the human ear but can be seen in sonagrams. Songs are often, but not always, given twice and are then followed by an interval of variable length before the next two songs are given. A pair of songs can be transcribed as a high-pitched *piok-piok* or *weelp-weelp*. The song lacks the deep tone of *C. macrurus*. In our experience, the song appears as loud as that of *C. macrurus* at short distances but, being more high-pitched, it propagates less well over longer distances. This song type is only known from Flores and Sumba; no other song types have been recorded on these islands.

Playback experiments

We performed nine trials involving two vocally distinct populations. Six trials were performed on the Flores and Sumba populations and three on the population of *C. macrurus* on Lombok. In both the Flores and Sumba populations and in *C. macrurus*, there was a clear difference in response towards playback of heterospecific and conspecific songs (table 5). In each trial, playback of heterospecific songs elicited no response but playback of conspecific songs brought an immediate response from all tested individuals.

Table 5. Response of nightjars from Flores, Sumba and Lombok to playback of hetero- and conspecific territorial songs.

Trial	**Playback**	**Response**
Caprimulgus meesi		
Lewapaku, Sumba, 19.viii.2003	*C. m. schlegelii*	No response
	C. meesi	Immediate response from one bird, which started singing for two minutes; then approached the speaker and flew around a few times at a height of c. 10 m.
Lewapaku, Sumba, 20.viii.2003	*C. m. schlegelii*	No response
	C. meesi	One bird responded immediately by flying directly towards the speaker after which it flew several times back and forth at a height of c. 7 m. After one minute a second bird joined in.
Wolo Tado, Flores, 25.viii.2003	*C. m. albonotatus*	No response
	C. meesi	One bird responded immediately by flying towards the speaker; it settled on a nearby branch where it started singing for c. 2 minutes.
Wolo Tado, Flores, 25.viii.2003	*C. m. schlegelii*	No response
	C. meesi	One bird responded instantaneously by singing but apparently did not approach the speaker.
Wolo Tado, Flores, 25.viii.2003	*C. m. johnsoni*	No response
	C. meesi	One bird responded immediately by singing, which continued for c. 8 minutes.
Labuhanbajo, Flores, 28.viii.2003	*C. m. bimaculatus*	No response
	C. meesi	One bird responded immediately by singing, but stopped when playback trial ended.
Caprimulgus macrurus schlegelii		
Sapit, Lombok, 4.ix.2003	*C. meesi*	No response
	C. m. bimaculatus	One bird responded immediately by singing but apparently did not approach the speaker.
Gng. Rinjani NP, Lombok, 4.ix.2003	*C. meesi*	No response
	C. m. albonotatus	Two birds responded within seconds. One bird started singing, the other, which was already singing when the trial started, flew towards the speaker, settled in a nearby tree and continued singing close to the speaker for c. 5 minutes, after which it flew to a different tree and continued singing.
Gng. Rinjani NP, Lombok, 5.ix.2003	*C. meesi*	No response
	C. m. schlegelii	One bird responded immediately by singing.

Discussion

Homology

The distinctive vocalizations of the Flores and Sumba populations have been regarded as a possible variant of the grunting call of *C. macrurus* (Holyoak, 2001), which implies that they are not homologous to the territorial song of *C. macrurus* and other taxa in the complex. Our data do not support this view and strongly indicate that the vocalizations of the Flores and Sumba populations that we used in this study are homologous to the territorial song of the other taxa in the complex.

First, the sonagraphic structure of the songs of the Flores and Sumba populations shows several similarities to those of the other taxa in the complex and differs from other call types, such as the grunting call. For instance, songs of all taxa, including the Flores and Sumba populations, consist of a relatively high-pitched element followed by a lower-pitched series of 2-9 waves or downward notes. Grunting calls are only known from *C. atripennis* (*C. a. atripennis*) and *C. macrurus* (*C. m. albonotatus, C. m. bimaculatus, C. m. macrurus, C. m. schlegelii*) but it seems likely that they are also given by other taxa in the complex. Grunting calls are very different from territorial songs. They are best described as a series of deep, low-pitched *wroww* calls at c. 500 Hz (*C. atripennis*, fig. 4a) or a series of fast-repeated, frog-like *wrrrog* or *grrrog* notes at c. 700-800 Hz (*C. macrurus*, fig. 4b). Second, the vocalizations of the Flores and Sumba populations are loud, repetitive, easily located and are given from prominent perches, characteristics which are a general feature of territorial songs in nightjars

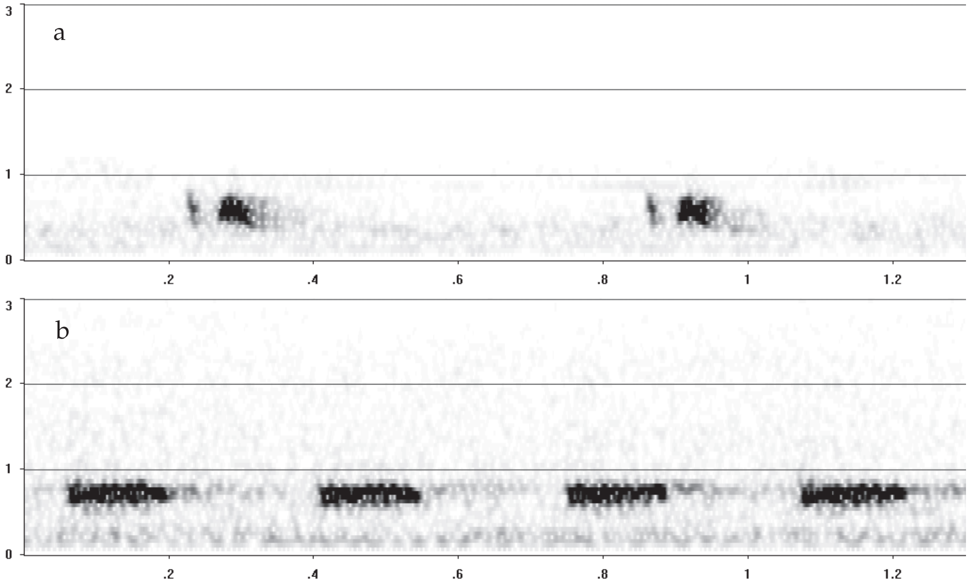

Figure 4a-b. Sonagrams of grunting calls. (a) *C. a. atripennis*, Goa, India, March 2002, H. Jännes; (b) *C. m. bimaculatus*, Kuala Lumpur, Malaysia, February 1970, R. Kersley.

(Holyoak, 2001). Finally, playback of conspecific songs elicits similar behavioural responses. The Flores and Sumba populations often strongly responded to playback of songs recorded on these islands by calling back and by flying towards the speaker and displaying above the speaker. These observations are similar to the responses that we observed in *C. macrurus* on Lombok (this study) and in Malaysia (G.S., unpubl. data), and of *C. celebensis* in Sulawesi (F.G.R., unpubl. data), to playback of conspecific songs. These observations strongly suggest that the vocalizations of the Flores and Sumba populations included in this study represent the territorial song.

Two other possible explanations for the distinct vocalizations of the Flores and Sumba populations are that they refer to individual variation or to seasonal variation within *C. macrurus*. Again, our data do not support these hypotheses. The vocal type of the Flores and Sumba populations has never been recorded outside Flores and Sumba and none of the other five vocal types have been recorded on Flores or Sumba. Our evidence indicates that these vocal types are geographically restricted and hence do not reflect individual variation. The recording dates of the Flores and Sumba populations and *C. macrurus* in Indonesia extensively overlap, which is inconsistent with the view that these vocalizations reflect seasonal variation within a single population. For instance, territorial songs of the Flores and Sumba populations are known from June to November (Schmutz, 1977; Verhoeye & Holmes, 1998; Appendix 1). This period overlaps extensively with those of *C. m. macrurus* (May to August) and *C. m. schlegelii* (January, March, July, September and November) in our data set. Moreover, we have recorded the Flores and Sumba vocalizations on Flores in the same week as *C. macrurus* on Lombok. We conclude that the recordings of the Flores and Sumba populations are of the territorial song and that this vocalization is homologous to the songs of the other taxa.

Taxonomy

Our data show that there are six discrete types of territorial songs in the *Caprimulgus macrurus* complex. Like other species of nightjars (e.g. Hardy et al., 1997; Ranft & Cleere, 1998), these vocal types are readily distinguishable by ear in the field. We propose to recognise all six vocally distinct populations in the complex as species taxa based on the following considerations.

Firstly, each group is diagnosable from all other groups, and most groups differ by multiple acoustic characters. No diagnosable differences exist within these groups, even in populations that are separated by thousands of kilometres (e.g. *C. m. albonotatus* in India vs. *C. m. schlegelii* in Australia). Secondly, our data set does not include any vocalizations intermediate between the vocal types defined in this study. Thirdly, vocal types are not randomly distributed but are geographically restricted. With the exception of the population on Flores and Sumba, which will be discussed below, the distribution of vocal types coincides with taxonomic boundaries based on morphology (Mees, 1977). There is no indication that individuals use more than one territorial song type, and we have never observed individuals switching between songs, neither in the field nor in tape recordings made by others. Fourthly, 13 of 15 combinations of species are diagnosable by three or more vocal characters, which equals the number of differences shown by *C. atripennis* and *C. macrurus*, two taxa that are reported to occur sympatrically in northeastern peninsular India (Mees, 1977, 1985; Ripley & Beehler, 1987) and for which species status is not in doubt. Our data set includes four recordings from the reported zone of overlap in northeastern peninsular India: three recordings of *C. a. atripennis* (two from Orissa, one from West Bengal; see also Gauntlett, 1995), and one *C. m. albonotatus* from Orissa. Measurements of these recordings are typical of *C. atripennis* and *C. macrurus*, respectively, and do not show any signs of intergradation. Finally, our approach to recognize populations of nightjars with diagnosable song types as species is consistent with current taxonomic practise in other nightbirds including owls (e.g. Howell & Robbins, 1995; König et al., 1999; Rasmussen et al., 2000) and nightjars (Hardy & Straneck, 1989; Robbins & Parker, 1997; Garrido & Reynard, 1998).

Three of the six species proposed here correspond to previously accepted species taxa. Our results confirm the diagnosability of *C. atripennis* (Song type 1), *C. manillensis* (Song type 2) and *C. celebensis* (Song type 3), and provide the first acoustic evidence in support of the inclusion of *C. a. aequabilis* in *C. atripennis*, the inclusion of *C. c. jungei* in *C. celebensis*, and the inclusion of *C. m. johnstoni* and *C. m. salvadorii* in *C. macrurus*.

A surprising result of our study was that '*C. macrurus*' (sensu Cleere, 1998; Holyoak, 2001) comprises three vocal types (Song types 4-6), which are supported by the PCA, DFA and univariate analyses in our study. Song type 4 is the well-known 'chopping' song described for *C. macrurus* in numerous field guides and handbooks. This type is given by *C. m. albonotatus, C. m. bimaculatus, C. m. macrurus, C. m. johnsoni, C. m. salvadorii* and *C. m. schlegelii*, which we include in the species *C. macrurus*.

Song type 5 refers to the population of the Andaman Islands, *C. m. andamanicus*. Based on its distinctive territorial song, we propose to treat it as a separate species (*C. andamanicus*). The name Andaman Nightjar is that previously used and is appropriate; this is also the name used in Rasmussen & Anderton (in press). The morphological and other characters of this species will be discussed elsewhere (N. Cleere, P.C. Rasmussen & P. Holt, in prep.).

Song type 6 is only known from Flores and Sumba. There are two known museum specimens from these islands, one each from Flores and Sumba. Mayr (1944), who examined the Sumba specimen, and Mees (1977), who examined both specimens, felt unable to determine the taxonomic identity of these specimens. The geographically closest named population is that of the island of Lombok, for which the name *C. m. oberholseri* has been proposed (Rothschild & Hartert, 1918). This subspecies has been synonymized with *C. m. schlegelii* based on a lack of distinct morphological characters (Mees, 1977). During field work on Lombok in September 2003, the territorial songs of this population could be instantly recognized as that of *C. macrurus* (i.e. Song type 4), and this designation is supported by sonagrams (fig. 3p) and by PCA, DFA and univariate analysis of these recordings. Thus, the populations on Flores and Sumba do not correspond to a previously named population but represent an undescribed taxon. We propose to name this taxon:

Caprimulgus meesi spec. nov.
Mees's Nightjar

Holotype.— RMNH 75297, adult male, 15.ix.1975, Nisar, Flores, 8°47'S, 119°58'E, 250 m, collected by Erwin Schmutz (Mees, 1977; Schmutz, 1977). Label data: "habitat:

shrub-land", "iris dark brown. In stomach: a conglomerate of tiny insects and an undamaged cricket". Schmutz (1977) further noted that the bird had very large gonads, that the eyelid was pale brown, that the gape was pink as in *C. affinis*, and that the undamaged cricket in the stomach was white and had very long antennae.

Paratype.— AMNH 346702, adult male, 9.vi.1932, Mao Marru, Sumba, 9°58′S, 120°28′E, collected by Georg Stein (Mayr, 1944). Label data: "Iris schwarzblau", "Schnabel und Füße schwarzbraun", "expedition G. Stein no. 4730", "Sumba, Mao Marroe, Ost-Sumba".

Diagnosis: vocalizations.— Territorial songs of *C. meesi* differ diagnosably from those of all other taxa in the complex in the following characters (table 3, 4): (1) maximum frequency of first peak; (2) maximum frequency; (3) frequency drop of first downward element; and (4) structure of the first element. Differs further from *C. andamanicus, C. atripennis, C. celebensis* and *C. manillensis* in (5) peak frequency; from *C. atripennis, C. celebensis* and *C. manillensis* in (6) total song length and (7) song pace; from *C. atripennis* and *C. macrurus* in (8) number of peaks; from *C. celebensis* and *C. manillensis* in (9) number of notes; and from *C. andamanicus* in (10) minimum frequency of the first low and (11) peak frequency time.

Territorial songs of *C. meesi* have been confused with those of *C. affinis* with which it occurs sympatrically and possibly even syntopically (see below). However, songs of *C. affinis* (fig. 5) differ from those of *C. meesi* in structure and duration (c. 0.240 s) and have a much higher minimum (c. 2000 Hz) and maximum frequency (c. 4800 Hz). Songs of *C. meesi* resemble those of *C. affinis* in having an explosive quality but songs of *C. affinis* are higher-pitched and have a rasping quality which is lacking in *C. meesi* and other nightjars of the *C. macrurus* complex. The rasping sound of *C. affinis* is reflected by a rising broad-band element in sonagrams (fig. 5).

Diagnosis: morphology.— Exceedingly similar to, and not diagnosably different, from *C. macrurus schlegelii*. All morphological characters (plumage, measurements) of the two male specimens of *C. meesi* are within the range of variation of males of *C. macrurus*. Hence, *C. meesi* differs from other species taxa in the complex in the same way as reported for *C. macrurus* (Cleere, 1998; Holyoak, 2001). *C. meesi* differs from

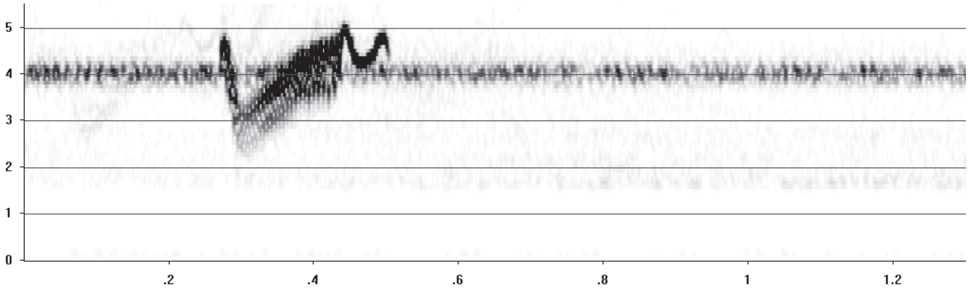

Figure 5. Sonagram of territorial song of *Caprimulgus affinis kasuidori* Hachisuka, 1932, Wanga, Sumba, Indonesia, August 2003, G. Sangster. The horizontal band at 4 kHz is formed by insect sounds.

sympatric *C. affinis* by its larger size, browner plumage, and the presence of large white spots on the outer tail feathers.

Phylogenetic position and generic placement.— We regard *C. meesi* as a member of the *C. macrurus* complex based on similarities in morphology and territorial songs. Morphological similarities include the conspicuous and contrasting pattern of the upperparts, and upper scapulars with solid, sharply defined black centres and a conspicuous, white or buff, immaculate border (Marshall, 1978). Vocalizations of the members of the complex share the same basic sonagraphic structure: a high-pitched element followed by a lower-pitched series of 2-9 waves or downward notes. Phylogenetic relationships among the six species in the complex are unknown.

In the absence of detailed cladistic study of relationships among Caprimulginae, monophyly of the genus *Caprimulgus* and hence inclusion of the *C. macrurus* complex in *Caprimulgus* remains poorly supported. Sibley & Ahlquist's (1990) DNA-DNA hybridization study suggests that the genus *Caprimulgus* is polyphyletic. Based on patterns of acoustic variation, Davis (1978, 1979) recognized several additional genera of nightjars for species that are traditionally included in *Caprimulgus*. He placed the *C. macrurus* complex in the genus *Rossornis* Mathews, 1918. Until a better supported hypothesis of relationships among Caprimulginae becomes available, we suggest that the *C. macrurus* complex is best kept in *Caprimulgus*.

Description of the holotype.— Head. Central chin and uppermost throat feathers absent. Lateral chin and throat feathers barred Sepia (119, cf Smithe, 1975; no equivalent colour in Ridgway, 1912) and Cinnamon Buff* (*= Ridgway, 1912), with terminal fringes closest in colouration to Orange-Cinnamon*. Lower throat with pure white patch in center. Central feathers on lower throat feathers white, broadly tipped Sepia (119) and with Cinnamon Buff* subterminal band. Subterminal band is broadest on central feathers. White throat patch demarcated by narrow band of Clove Brown* and Sepia* (NB cf Ridgway, 1912), with two small Cinnamon Buff* subterminal spots. Feathers of forehead, crown and nape with cold greyish-white (Drab Gray*) ground colour, without brownish or rufescent wash (as in most *schlegelii*) and fine, sharply demarcated blackish-brown (Sepia, 119) vermiculations. Vermiculations coarser than in most *schlegelii*. Feathers on center of forehead, crown and nape with broad blackish-brown (Sepia, 119) diamond or arrow-head in center extending towards tip, forming a coarsely blotched median crown-stripe. Nape as forehead and crown, without rufous hindneck collar (possibly due to wear). Some feathers with broad Pinkish Buff* to Cinnamon Buff* spots. Supercilium narrow, tinged rufous-buff (between Cinnamon Buff* and Orange-Cinnamon*. Rictal bristles with horn-coloured base, brown centre, and blackish tips. Lores mottled Sepia (119) and rufous-buff (between Cinnamon Buff* and Orange-Cinnamon*). Ear-coverts mottled Sepia (119) and Hazel*, paler, more Cinnamon Buff* on lower and posterior ear-coverts. Submoustachial stripe white, progressively more pale buff towards posterior. Rictal bristles well-developed; twelve on both sides. Upperparts. Mantle, back, rump, and uppertail coverts with cold greyish-white (Drab*) ground colour, without brownish or rufescent tinge, and with fine, sharply demarcated blackish-brown (Sepia, 119) vermiculations. Feathers on mantle with diamond-shaped Sepia (119) centres. Uppertail-coverts with Sepia (119) shaft-streak. Anterior upper and some lower scapulars Sepia (119) with broad Pinkish Buff* to Cinnamon Buff* fringe on outer webs, forming Pinkish Buff* line. Some feathers with small Pinkish Buff* apical spot on inner webs, and some small buff spots at base. Posterior upper and lower scapulars marbled cold greyish-white (Drab-Gray*) and Sepia (119). Line of Sepia (119) spots along shaft. Underparts. Upper breast with cold greyish-white ground colour, between Pale Drab-Gray* and Pale Smoke Gray*, finely mottled and vermiculated blackish-brown (Clove Brown*). Feathers of lower breast, belly, and flanks Drab-Gray* with broad Pinkish Buff* terminal fringe and fine blackish-brown (Clove Brown*) cross-bars and shaft streak. Undertail-coverts Pale Pinkish Buff* with coarse Clove Brown* banding and vermiculations. WING. Primaries Clove Brown*. P10-P7 outer vanes paler and closer to Sepia*. Margin of outer web of outer primary (P10) with narrow, irregularly shaped spots which are Cinnamon-Buff* distally and Cinnamon* proximally. P10 with large, round, white spot on inner web which does not extend to the shaft. P9 with white spots on both outer and inner webs, on outer web centered on emargination. Spot on inner web ellipsoid from shaft to feather edge. On both webs spot extends from fringe to shaft. P9, P8, P7 with irregularly shaped Cinnamon* markings. White spots on P8 and P7 form broad white band. Spot on inner web trapezoid and more diffuse, less sharply demarcated than on P9. P9 diameter of ellipse max. 18 mm. P8 extent of white measured along shaft, 12 mm. P7 extent of white measured along shaft, 14 mm. P7 with very indistinct, diffuse Drab-Gray* subapical markings. P6 with c. five Cinnamon* bands with irregular outline on outer web and indistinct, diffuse Drab Gray* subapical vermiculations. Diffuse dirty-white spot on inner vane. Extent of white measured along shaft, 6 mm. P5-P1 Clove Brown* with c. six bands of irregular Cinnamon* markings on outer and inner vane, distally more Pinkish Buff*. Secondaries Clove Brown*. Secondaries with bands of irregular Cinnamon* to Cinnamon-Buff* spots on outer and inner webs. Tertials are palest part of wing (and upperparts). Tertials cold greyish-white, Drab Gray*, coarsely marbled greyish brown (Clove Brown*), with Clove Brown* shaft streak. Greater upper-wingcoverts similar to median upper-wingcoverts but large Cinnamon-Buff* to Cinnamon* patch only on outer webs. Median upper-wingcoverts Clove Brown* marked with small Cinnamon-Buff* spots and large Cinnamon-Buff* to Cinnamon* patch on both inner and outer webs; patch on outer webs larger than on inner webs. Lesser upper-wingcoverts Clove Brown* with Cinnamon-Buff apical spot on outer webs. Outer webs with c. four narrow irregularly marked bands on outer web. Inner webs cold greyish-white, between Pale Drab-Gray* and Pale Smoke Gray*, finely mottled and vermiculated blackish-brown (Clove Brown*). Under-wingcoverts Clove Brown* coarsely barred Cinnamon*. TAIL. Tail brown (Drab*), with irregularly marked Clove Brown* bars, broadest along shaft, and coarse Clove Brown* vermiculations. R4 and R5 Clove Brown* with c. 11 narrow, irregularly shaped Pinkish Buff* to Cinnamon Buff* bars; bars most distinct on outer web but very diffuse on inner web. Bars are blotched Clove Brown*. R4 and R5 with large white terminal patch on both inner and outer webs (table 6).

Description of the paratype.— Differs from the holotype, to which it was directly compared, as follows: feathers of forehead, crown and nape with fine vermiculations as in most *C. m. schlegelii* and more diffuse, not as sharply demarcated as the holotype.

Nape with narrow rufous nuchal collar formed by Pinkish Buff* to Cinnamon Buff* spots on lowermost hindneck feathers. Ear-coverts virtually uniform rufous-buff, between Cinnamon Buff* and Cinnamon*. Mantle, back, rump, and uppertail coverts with slightly darker ground colour, Drab*, appearing slightly darker than head and nape; this effect is accentuated by the presence of a nuchal collar. Anterior upper and some central scapulars with broad Pinkish Buff* fringe on outer webs. Feathers of lower breast, belly, and flanks Drab-Gray* with broad Pale Pinkish Cinnamon* to Pale Pinkish Buff* terminal fringe and fine blackish-brown (Clove Brown*) cross-bars and shaft streak. Pale crossbars appearing paler than in holotype. Undertail-coverts with bands coarser than in holotype. Margin of outer webs of outer primary (P10) with less extensive and more diffuse spots than in holotype. P9 diameter of ellipse max. 14 mm. P8 extent of white measured along shaft, 7.5 mm. P7 extent of white measured along shaft, 11 mm. P7 without subapical markings. P6 with narrower and less distinct Cinnamon* band than in holotype, white spot in inner vane very indistinct. Secondaries with less extensive and more diffuse and paler (Cinnamon-Buff*) spots. Tertials more finely marbled than in holotype. Lesser upper-wingcoverts Clove Brown* with Cinnamon-Buff* apical spot on outer webs, slightly paler, more Pinkish-Buff* on inner webs. Very diffuse, narrow bands on outer webs. Inner webs cold greyish-white (Drab Gray*), marbled greyish brown (Clove Brown*).

Measurements.— Measurements of the holotype and paratype of *C. meesi*, and of male specimens of *C. macrurus* are presented in table 6. Tarsus length and bill width could not be reliably measured in the holotype and paratype of *C. meesi* without damaging the specimens; these characters are therefore not included.

Distribution.— *C. meesi* is only known from Flores and Sumba (fig. 6) where it has been recorded at elevations ranging from sea level to 265 m on Sumba (Coates & Bishop, 1997; pers. obs.) and to 800 m on Flores (Schmutz, 1977). On Flores, it is known from the following localities: (1) Labuhanbajo (8°33′S, 119°55′E; sound recording), (2) Paku (8°38′S, 119°57′E; field observation; Schmutz, 1977), (3) Nisar (8°47′S, 119°58′E; specimen; Schmutz, 1977), (4) Nunang (8°44′S, 120°00′E; field observation; Schmutz, 1977), (5) Gunung Pacandeki (Poco Ndeki), near Kisol (8°46′S, 120°41′E; sound recording), (6) Wolo Tado, near Riung (8°28′S, 121°02′E; sound recording), (7) Ili Wengot (8°29′S, 122°40′E; sound recording). On Sumba, *C. meesi* is known from: (1) Lewapaku (9°43′S, 119°55′E; sound recording) and (2) Mao Marru (9°58′S, 120°28′E; specimen; Mayr, 1944). Reports

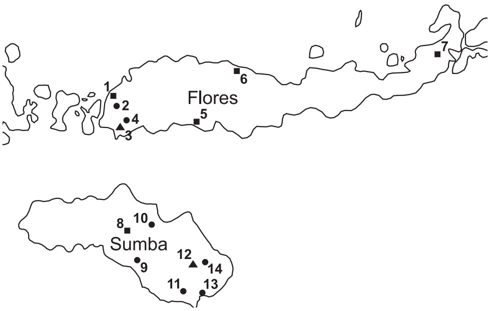

Figure 6. Map of Flores and Sumba showing localities where *Caprimulgus meesi* has been recorded. Symbols: ■ = sound recording, ▲ = specimen record, ● = sight or hearing record. Localities: (1) Labuhanbajo, (2) Paku, (3) Nisar, (4) Nunang, (5) Gunung Pacandeki, (6) Wolo Tado, (7) Ili Wengot, (8) Lewapaku, (9) Praingkareha, (10) 'km 14', (11) Tanjung Ngunju Protected Area, Pangaduharar, (12) Mao Marru, (13) Baing, (14) Luku Melolo.

Table 6. Measurements of morphological variables for *Caprimulgus meesi* and Indonesian subspecies of *C. macrurus*.

	C. meesi Holotype male	*C. meesi* Paratype male	*C. m. schlegelii* males	*C. m. macrurus* males	*C. m. salvadorii* *males*	*C. m. bimaculatus* males
P9 emargination from tip	74	65	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	68	62	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	P8 = P9 > P10 > P7	P8 > P9 > P10 > P7	P8 > P9 > P7 > P10 (n=19) P8 > P9 > P10 > P7 (n=2) P8 = P9 > P7 = P10 (n=1) P9 > P8 > P10 > P7 (n=1)	P8 > P9 > P7 > P10 (n=11) P8 > P9 > P7 > P10 (n=2) P8 > P9 > P7 = P10 (n=1) P8 > P9 > P7 = P10 (n=1) P9 > P8 > P10 > P7 (n=2) P9 > P8 > P7 > P10 (n=1)	P8 > P9 > P7 = P10 (n=2) P8 > P9 > P7 = P10 (n=1) P8 > P9 > P10 > P7 (n=1)	P8 > P9 > P7 > P10 (n=4) P8 = P9 > P7 > P10 (n=1)
shortfall P8	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 P9	0	1	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 P10	9	9	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 P7	13	10	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	42	36	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	57	50	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	66	59	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	71	64	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	75	69	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	80	-	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 (flattened chord)	178 (right), 175 (left)	165.5 (right), 165.5 (left)	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	133	126	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)	20	21	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 (exposed culmen)	14	11	11.3 (1.3; 23) 9-14	12.4 (1.1; 24) 10-14	12.8 (0.5; 4) 12-13	10.7 (1.0; 7) 10-12
Bill length (from anterior point of nostril)	8	8	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 length of white patch on outer web	42 (right)	37 (right)	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
R5 length of white patch on inner web	43 (right)	43 (right)	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 length of white patch on outer web	40 (right)	37 (right)	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 length of white patch on inner web	40 (right)	40 (right)	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

(sight or aural records) of '*Caprimulgus macrurus*' at the following sites probably also refer to *C. meesi*: (3) Praingkareha (10°03'S, 120°03'E; Jones et al., 1994), (4) 'km 14', 14 km west from Waingapu, along the Waingapu-Lewa road (9°43'S, 120°11'E; S. van Balen, in litt.), (5) Tanjung Ngunju Protected Area, Pangaduharar (10°13'S, 120°26'E; Jones et al., 1994, Jepson et al., 1996), (6) Baing (10°15'S, 120°34'E; Jones et al., 1994), (7) Luku Melolo (9°58'S, 120°36'E; Jones et al., 1994, Jepson et al., 1996). Based on the availability of suitable habitat, we suspect that *C. meesi* will be found at other sites on Flores and Sumba as well.

Ecology and life history.— *Caprimulgus meesi* occurs in open to dense scrubland with scattered small trees or at the edges of open forest. We never encountered *Caprimulgus meesi* inside dense forests or at the edges of dense forests. Verhoeye & Holmes (1998) characterized it as common along forest edge and in wooded cultivation. *C. meesi* occurs sympatrically with *C. affinis* on Flores (Schmutz, 1977; Verhoeye & Holmes, 1998) and Sumba (Mayr, 1944; Jepson et al., 1996; Linsley et al., 1998). It is possible that *C. meesi* occurs syntopically with *C. affinis* at some localities. Schmutz (1977) noted that on Flores, the former inhabits scrubland, the latter inhabits 'steppes' and that both species meet in savanna with scrub ('Gebüschsavanne'). At Lewapaku, Sumba, we once recorded *C. meesi* within 50 m from of a singing *C. affinis*, although these species were found in slightly different habitats, with *C. affinis* singing in flight over dry grassland and *C. meesi* singing from nearby small trees in the same dry grassland but closer to forest.

In June 1989 and August 2003, we recorded spontaneous singing only during dawn (5:15-5:35) and dusk (18:10-18:45). Playback of songs in known territories in August resulted in territorial behaviour (singing, approach towards speakers) only during dawn and dusk; no response to playback was observed in daylight in early morning or late afternoon, or in solid darkness before dawn or after dusk. Schmutz (1977) reported hearing territorial songs in western Flores in July between 18:10 and 18:30, in August at 20:45, in September between 18:10 and 18:30, and in November until 22:30; he did not hear songs in May 1972 at a locality where he heard songs in November 1971 and September 1972.

We observed *C. meesi* singing only from exposed perches at c. 5-10 m above the ground. One unseen bird probably sang from the ground. No singing was observed from birds in flight. Feeding occurs in flight and as sallies from exposed perches that were also used as song points. We did not record *C. meesi* during the day but Pilgrim et al. (2000) saw a number of birds roosting during the day on islands just offshore at Riung, Flores, and observed them flying over the sea and mudflats to the mainland at dusk.

Very little information is available about breeding. Available evidence suggests that territorial songs are given from June to November (Schmutz, 1977; Verhoeye & Holmes, 1998; Appendix 1). It is as yet unclear if *C. meesi* also sings during other times of the year. An egg collected on 11.x.1956 at Djinggor, Flores was originally identified as an egg of *C. affinis* by its collector J.A.J. Verheijen but was later referred to *C. macrurus* by Mees (1977) and is therefore most likely referable to *C. meesi*. In his discussion of the breeding seasons of birds on Flores, Verheijen (1964) reported that nests and eggs of *C. affinis* were found from August to November, with a peak in September and

October. It is likely that Verheijen´s data included the egg and perhaps other data on *C. meesi*. Schmutz (1977) suggested that the breeding period identified by Verheijen for *C. affinis* on Flores may also be valid for *C. macrurus* (= *C. meesi*).

Conservation status.— Although only two museum specimens have been collected, *C. meesi* probably is not rare in suitable habitat. It has been characterized as ′common′ in western Flores, ′rare′ in central Flores, and ′never heard in the east′ (J. Verhoeye in Verhoeye & Holmes, 1998). D.A. Holmes (in Verhoeye & Holmes, 1998) recorded the species on Flores only near Labuhanbajo in the extreme west of the island. It is unclear whether this reflects the true status of the species in the different parts of the island or merely a greater bias of observers towards western Flores. It is common at Wolo Tado, in central Flores (Pilgrim et al., 2000; pers. obs.). A sound recording from Ili Wengot demonstrates that it also occurs in eastern Flores. We suspect that *C. meesi* is also widely distributed on Sumba, although only a few records are known. A factor that may contribute to the scarcity of records on both islands is that *C. meesi* is easily overlooked when silent (e.g. outside the breeding season) or if territorial songs are not known.

Near Labuhanbajo and in Wolo Tado, Flores, we recorded *C. meesi* along paths that were frequently used by motorized vehicles during the day and early evening. *C. meesi* may thus be tolerant to moderate levels of disturbance. On Sumba, *C. meesi* is known to occur in one protected area: Tanjung Ngunju Protected Area (Pangaduharar), and in an area for which formal protection is proposed: Luku Melolo (Praimbana Lakatang) Protected Area (Jepson et al., 1996). On Flores, it has been recorded in one protected area, Wolo Tado Nature Reserve, near Riung.

Etymology.— We name this new species after Gerlof F. Mees, curator of the bird department of the Rijksmuseum van Natuurlijke Historie (currently Nationaal Natuurhistorisch Museum) in Leiden, The Netherlands between 1963 and 1991 and mentor of F.G.R. It serves as a long overdue acknowledgement of his contributions to Asian and Pacific ornithology, comprising numerous meticulous systematic and faunistic studies, as exemplified by his monumental review of the Indo-Australian white-eyes (Zosteropidae; Mees, 1957, 1961, 1969); for further biographic details, see Voous (1995). As demonstrated in this paper, it was Gerlof Mees who has laid the foundations of our current understanding of the taxonomy of the *Caprimulgus macrurus* complex.

We propose ′Mees's Nightjar′ as the vernacular name of this new species. This name is appropriate considering the English names of other little-known Asian Caprimulgidae, which were named after authorities who also have left an indelible mark on Asian ornithology, notably Jerdon's Nightjar *C. atripennis*, Vaurie's Nightjar *C. centralasicus* Vaurie, 1960, Bonaparte's Nightjar *C. concretus* Bonaparte, 1850 and Salvadori's Nightjar *C. pulchellus* Salvadori, 1879 (e.g. Mearns & Mearns, 1998; Walters, 2003).

Vocal differentiation and species recognition

Although acoustic differences between the six species of the *Caprimulgus macrurus* complex are clearly audible to the human ear, the sonagraphic structure of each of the territorial songs of these species appears to represent a variation on a similar theme.

The most obvious differences between the species are differences in song duration. In our study, total song length differentiated most species in pairwise comparisons (table 4). Sonagraphically, the song of *C. atripennis* looks like a slower version of the song of *C. macrurus* and the song of *C. macrurus* in turn appears as a slower version of that of *C. andamanicus*. The song of *C. celebensis* may be characterized as an extendend and drawn out version of that of *C. manillensis*. In addition to temporal differences there are also interspecific differences in the number of repetitive elements or notes. Thus, after an initial high-pitched peak, most *C. atripennis* and *C. macrurus* have three similar elements, *C. andamanicus* has three or four, *C. meesi* has five, *C. manillensis* has 4-7 and *celebensis* has 7-10 notes. Some parts of the song show interspecific differences in frequency. For instance, compared to all other species, the first peak is very high-pitched in *C. meesi*, the first low is high-pitched in *C. andamanicus* and the last peak is distinctly lower than the second-last in most *C. atripennis*. Finally, the structure of the song shows interspecific differences in the first element (in *C. meesi* the first element covers a much larger frequency range than in all other species) and in the number of notes in the song (*C. manillensis* and *C. celebensis* have multiple notes, the other species have a song comprised of a single-note). Interspecific differences in the territorial songs of *C. macrurus* complex therefore are a combination of temporal differences, differences in the number of elements or notes, frequency differences and differences in structure. No other detailed quantitative studies have been published for other groups of closely-related nightjar species but similar patterns of differentiation appear to be present in *C. sericocaudatus* (Cassin, 1849), *C. badius* (Bangs & Peck, 1908) and *C. salvini* Hartert, 1892 (Hardy & Straneck, 1989), and *C. rufus* Boddaert, 1783 and *C. carolinensis* J.F. Gmelin, 1789 (Robbins & Parker, 1997).

Playback tests have been succesfully applied to study several aspects of nightjar ecology and behaviour. For instance, the method has been used to study factors contributing to species recognition (Abs, 1963), to determine the presence of species (e.g. Marion et al., 1981; Robbins et al., 1994), to assess population density (e.g. Kalcounis et al., 1992) and to study territoral behaviour (Jackson, 2002). To our knowledge, the present study represents the first application of playback methods in species-level taxonomy of nightjars. Due to its small sample size our playback study must be regarded as preliminary. The results nevertheless are promising because they indicate that *C. meesi* and *C. macrurus* can distinguish between territorial songs of their own species and those of another taxon. We therefore suggest that playback may prove useful as an additional source of information in nightjar taxonomy. The quantitative method used in our study in combination with playback studies may be helpful in resolving species limits in other difficult groups (e.g. *C. poliocephalus* Rüppell, 1840, *C. ruwenzorii* Ogilvie-Grant, 1908, *C. pectoralis* Cuvier, 1816 and *C. nigriscapularis* Reichenow, 1893; Fry, 1988; Dowsett & Dowsett-Lemaire, 1993; Cleere, 1995).

The *C. macrurus* complex in Nusa Tenggara

Mees (1977), in his analysis of subspecies limits in *C. macrurus*, merged all populations from Nusa Tenggara and the Moluccas east to New Britain and Queensland into the subspecies *C. m. schlegelii*. The identity of the populations in Nusa Tenggara remains problematic because very few (or no) samples are available from most islands, and because some of the specimens are not typical. Our study clearly shows that two vocally distinct species occur in Nusa Tenggara (*C. macrurus* on Lombok, *C. meesi* on Flores and Sumba). The identity of other populations in Nusa Tenggara remains uncertain. We tentatively include the populations on Sumbawa and Timor in *C. macrurus* because territorial songs have been positively identified as *C. macrurus* by reliable observers (R. Noske, in litt.; C. Trainor, in litt.). Museum specimens from Wetar are distinctive in being the smallest in the complex. Mees (1977) suggested that the two known specimens he examined in the RMNH and AMNH are juveniles or immatures. However, the single specimen that we examined (RMNH Cat. No. 1) does not show any indication of immaturity, and all primaries and rectrices appear to be fully grown. Therefore, in the absence of sound recordings or reliable field observations, we suggest that the identity of the Wetar population is best regarded as unresolved.

The recognition of the Flores and Sumba populations as a distinct species results in a break of the range of the subspecies *C. m. schlegelii* into two disjunct areas: *(i)* Lombok and Sumbawa, and (*ii*) the Moluccas and Timor east to New Britain and Queensland, Australia. This pattern may be due to recent immigration from one of these areas to the other. An implication of this distribution pattern is that the populations on Lombok and Sumbawa are more closely related to the geographically distant *C. m. schlegelii* than they are to the geographically close populations of Bali and Java. However, subspecies limits in *C. macrurus* may not be consistent with the evolutionary history of this species. Morphological differentiation between *C. m. schlegelii* and *C. m. macrurus* is not strong; *C. m. schlegelii* is slightly darker than *C. m. macrurus*, has less cinnamon in its plumage and more pronounced vermiculations on the head (Mees, 1977). Schodde & Mason (1980) even questioned the validity of *C. m. schlegelii* as a separate subspecies. It is therefore possible that the Lombok/Sumbawa populations are more closely related to those on Java and Bali than to *C. m. schlegelii* occurring in eastern Nusa Tenggara. A detailed molecular phylogeographic analysis may be able to resolve the evolutionary history of the *C. macrurus* complex in Nusa Tenggara. Previous phylogeographic studies have shown that the colonization history of island birds may be complex and inconsistent with subspecies limits (e.g. Klein & Brown, 1994; Seutin et al., 1994).

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References

Abs, M., 1963. Field tests on the essential components of the European Nightjar's song.— Proc. Int. Orn. Congr. 13: 202-205.

Amadon, D. & L.L. Short, 1992. Taxonomy of lower categories: suggested guidelines.— Bull. Brit. Orn. Cl. Cent. Suppl. 112A: 11-38.

Breil, F. & J.C. Roché, 2000. Oiseaux de l'Inde et du Népal. Compact Disc.— Le Verdier.

Buckingham, R. & L. Jackson, 1991. A field guide to Australian bird song 6. Audiocassette.— Nunawading, Australia.

Burt, J., 2001. Syrinx. Version 2.2b. Published on the internet <http://SyrinxPC.com>.

Cink, C.L., 2002. Whip-poor-will *Caprimulgus vociferus*.— In: A. Poole & F.B. Gill (eds). The birds of North America, no. 620: 1-20. Philadelphia & Washington D.C.

Cleere, N., 1995. The identification, taxonomy and distribution of the Mountain Nightjar *Caprimulgus poliocephalus* / Fiery-necked Nightjar *C. pectoralis* complex.— Bull. Afr. Bird Club 2: 86-97.

Cleere, N., 1999. Caprimulgidae (nightjars): 302-386.— In: J. del Hoyo, A. Elliot & J. Sargatal (eds). Handbook of the Birds of the World. Vol. 5. Barn-owls to hummingbirds. Barcelona.

Cleere, N., 1998. Nightjars, a guide to nightjars and related nightbirds: 1-317.— Robertsbridge.

Coates, B.J. & K.D. Bishop, 1997. A guide to the birds of Wallacea: 1-535.— Alderley.

Connop, S., 1993. Birdsongs of Nepal. Audiocassette.— Ithaca.

Cracraft, J., 1989. Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation.— In: D. Otte & J.A. Endler (eds). Speciation and its consequences: 28-59. Sunderland, Mass.

Cramp, S., (ed.) 1985. The birds of the Western Palearctic. Vol. 4: 1-960.— Oxford.

Davis, L.I., 1962. Acoustic evidence of relationship in *Caprimulgus*.— Texas J. Sci. 14: 72-106.

Davis, L.I., 1978. Acoustic evidence of relationship in Caprimulginae.— Pan. Am. Studies 1: 22-57.

Davis, L.I., 1979. Review of recent literature and tape discussions of nightjars.— Pan. Am. Studies 2: 20-35.

de Queiroz, K., 1999. The general lineage concept of species and the defining properties of the species category.— In: R.A. Wilson (ed). Species: new interdisciplinary essays: 49-89. Cambridge, Mass.

Dickinson, E.C. (ed.) 2003. The Howard & Moore complete checklist of the birds of the world. Third edition: 1-1039.— London.

Dowsett, R.J. & F. Dowsett-Lemaire, 1993. Comments on the taxonomy of some Afrotropical bird species.— Tauraco Res. Rep. 5: 323-389.

Faber, A.L., 2001. Cdex. Version 1.40. Published on the internet <http://www.cdex.n3.net>.

Fry, C.H., 1988. Skulls, songs and systematics of African nightjars.— Proc. Sixth Pan-African Orn. Congr.: 105-131.

Garrido, O.H. & G.B. Reynard, 1998. Is the Greater Antillean Nightjar *Caprimulgus cubanensis* (Aves: Caprimulgidae), a composite species?— Orn. Neotrop. 9: 1-12.

Gauntlett, F.M., 1995. What is the range of Jerdon's Nightjar?— Oriental Bird Cl. Bull. 22: 55.

Greenway, J.C., 1978. Type specimens of birds in the American Museum of Natural History. Part 2.— Bull. Am. Mus. Nat. Hist. 161: 1-306.

Griffin, A.C.M. & R.J. Swaby, 1984. Bird calls of North Queensland rainforests. Audiocassette.— Paluma.

Haffer, J., 1986. Superspecies and species limits in vertebrates.— Z. Zool. Syst. Evol. Forsch. 24: 169-190.

Hardy, J.W., G.B. Reynard & B.B. Coffey, 1997. Voices of New World nightjars & their allies. Revised edition. Audiocassette.— Gainesville, Florida.

Hardy, J.W. & R. Straneck, 1989. The Silky-tailed Nightjar and other Neotropical caprimulgids: unraveling some mysteries.— Condor 91: 193-197.

Heidrich, P., C. König & M. Wink, 1995. Molecular phylogeny of South American screech owls of the *Otus atricapillus* complex (Aves: Strigidae) inferred from nucleotide sequences of the mitochondrial cytochrome b gene.— Z. Naturforsch. [C] 50: 294-302.

Heidrich, P., C. König & M. Wink, 1996. Bioakustik, Taxonomie und molekulare Systematik amerikanischer Sperlingskäuze (Strigidae: *Glaucidium* spp.).— Stuttgarter Beitr. Naturk. Ser. A (Biol.) 534: 1-47.

Higgins, P.J., (ed.), 1999. Handbook of Australian, New Zealand & Antarctic birds. Vol. 4. Parrots to Dollarbird: 1-1248.— Melbourne.

Holyoak, D.T., 2001. Nightjars and their allies: the Caprimulgiformes: 1-773.— Oxford.

Howell, S.N.G. & M.B. Robbins, 1995. Species limits of the least pygmy-owl (*Glaucidium minutissimum*) complex.— Wilson Bull. 107: 7-25.

Inskipp, T., N. Lindsey & W. Duckworth, 1996. An annotated checklist of the birds of the Oriental region: 1-294.— Sandy.

Isler, M.L., P.R. Isler & B.M. Whitney, 1998. Use of vocalizations to establish species limits in antbirds (Passeriformes: Thamnophilidae).— Auk 115: 577-590.

Jackson, H.D., 2002. Comparison of vocal behaviour in two Afrotropical nightjars: a whistler and a churrer.— Ostrich 73: 173-174.

Jännes, H., 2002. Bird sounds of Goa & South India. Compact Disc.— Helsinki.

Jepson, P., S. Rais, A.B. Ora & W. Raharjaningtrah, 1996. Evaluation of a protected area network for the conservation of forest values on Sumba Island, East Nusa Tenggara. Laporan No. 5: 1-36.— Bogor.

Johnston, D., 2000. CoolEdit 2000. Version 1.1.— Phoenix.

Jones, M.J., D. Juhaeni, H. Banjaransari, L. Lace, M.D. Linsley & S.M. Marsden, 1994. The status, ecology and conservation of the forest birds and butterflies of Sumba, Indonesia. A report to the Indonesian Directorate General of Forest Protection and Nature Conservation (PHPA), the Indonesian Institute of Sciences (LIPI) and BirdLife International: 1-111.— Manchester.

Kalcounis, M.C., R.D. Csada & R.M. Brigham, 1992. The status and distribution of the Common Poorwill in the Cypress Hills, Saskatchewan.— Blue Jay 50: 38-44.

Kennedy, R.S., P.C. Gonzales, E.C. Dickinson, H.C. Miranda & T.H. Fisher, 2000. A guide to the birds of the Philippines: 1-369.— Oxford.

King, B.F., 1997. Checklist of the birds of Eurasia: 1-105.— Vista, U.S.A.

Klatt, P.H. & G. Ritchison, 1993. The duetting behavior of eastern screech owls.— Wilson Bull. 105: 483-489.

Klein, N.K. & W.M. Brown, 1994. Intraspecific molecular phylogeny in the Yellow Warbler (*Dendroica petechia*), and implications for avian biogeography in the West Indies.— Evolution 48: 1914-1932.

Koeltz, W.N., 1954. New birds from Iran, Afghanistan, and India.— Contr. Inst. Reg. Expl. 1: 1-32.

König, C., 1998. Lautäußerungen als interspezifische Differenzierungsmerkmale bei Eulen und ihren Bedeutung für die Taxonomie (Aves: Strigiformes).— Zool. Abhandl. Staatl. Mus. Tierk. Dresden 50 Suppl.: 51-62.

König, C., 2000. Owl vocalizations as interspecific differentiation patterns and their taxonomical value as ethological isolating mechanisms between various taxa: 781-794.— In: R.D. Chancellor & B.-U. Meyburg (eds). Raptors at risk. Berlin & Blaine.

König, C., P. Heidrich & M. Wink, 1996. Zur Taxonomie der Uhus (Strigidae: *Bubo* spp.) im südlichen Südamerika.— Stuttgarter Beitr. Naturk. Ser. A 540: 1-9.

König, C., F. Weick & J.-H. Becking, 1999. Owls: a guide to the owls of the world: 1-462.— Robertsbridge.

Kroodsma, D.E., 1989. Suggested experimental designs for song playbacks.— Anim. Behav. 37: 600-609.

Lencioni-Neto, F., 1994. Une nouvelle espèce de *Chordeiles* (Aves, Caprimulgidae) de Bahia (Brésil).— Alauda 52: 241-245.

Linsley, M.D., M.J. Jones & S.J. Marsden, 1998. A review of the Sumba avifauna.— Kukila 10: 60-90.

Louette, M., 1990. A new species of nightjar from Zaire.— Ibis 132: 349-353.

MacKinnon, J. & K. Phillipps, 1993. The birds of Borneo, Sumatra, Java, and Bali: 1-491.— Oxford.

Marion, W.R., T.E. O'Meara & D.S. Maehr, 1981. Use of playback recordings in sampling elusive or secretive birds.— Stud. Avian Biol. 6: 81-85.

Marshall, J.T., 1978. Systematics of smaller Asian night birds based on voice.— Orn. Monogr. 25: 1-58.

Mayden, R.L., 1997. A hierarchy of species concepts: the denouement in the saga of the species problem.— In: M.F. Claridge, H.A. Dawah & M.R. Wilson (eds). Species, the units of biodiversity. Systematics Association Special Volume 54: 381-424. London.

Mayr, E., 1944. The birds of Timor and Sumba.— Bull. Am. Mus. Nat. Hist. 83: 123-194.

Mearns, B. & R. Mearns, 1998. The bird collectors: 1-472.— San Diego.

Mees, G.F., 1957. A systematic review of the Indo-Australian Zosteropidae (part I).— Zool. Verh. Leiden 35: 1-204.

Mees, G.F., 1961. A systematic review of the Indo-Australian Zosteropidae (part II).— Zool. Verh. Leiden 50: 1-168.

Mees, G.F., 1969. A systematic review of the Indo-Australian Zosteropidae (part III).— Zool. Verh. Leiden 102: 1-390.

Mees, G.F., 1977. Geographical variation of *Caprimulgus macrurus* Horsfield (Aves, Caprimulgidae).— Zool. Verh. Leiden 155: 1-47.

Mees, G.F., 1985. *Caprimulgus macrurus* Horsfield and related forms, a re-evaluation (Aves, Caprimulgidae).— Proc. K. Ned. Acad. Wetensch. (Biol. Med. Sci.) 88: 419-428.

Mengel, R.M. & M.A. Jenkinson, 1971. Vocalizations of the Chuck-will´s-widow and some related behavior.— Living Bird 10: 171-184.

Oba, T., 1996. Vocal repertoire of the Japanese Brown Hawk Owl *Ninox scutulata japonica* with notes on its natural history.— Nat. Hist. Res., Spec. Issue 2: 1-64.

Oberholser, H.C., 1915. A synopsis of the races of the Long-tailed Goatsucker, *Caprimulgus macrurus* Horsfield.— Proc. U.S. Natl. Mus 48: 587-599.

Peters, J.L., 1940. Check-list of birds of the world. IV: i-xii, 1-291.— Cambridge, Mass.

Pilgrim, J., J.D. Leadley & Saifuddin, 2000. Bird surveys and conservation status of four forests on Flores, Indonesia: 1-76.— Cambridge, U.K.

Ranft, R. & N. Cleere, 1998. A sound guide to nightjars and related nightbirds. Compact Disc.— London.

Rasmussen, P.C. & J.C. Anderton, in press. Birds of South Asia: the Ripley guide.— Barcelona.

Rasmussen, P.C., T.S. Schulenberg, F. Hawkins & R. Voninavoko, 2000. Geographic variation in the Malagasy Scops-Owl (*Otus rutilus* auct.): the existence of an unrecognised species on Madagascar and the taxonomy of other Indian Ocean taxa.— Bull. Br. Orn. Cl. 120: 75-102.

Ridgway, R., 1912. Color standards and color nomenclature: 1-43, plate I-LIII.— Washington D.C.

Ripley, S.D. & B.M. Beehler, 1987. New evidence for sympatry in the sibling species *Caprimulgus atripennis* Jerdon and *Caprimulgus macrurus* Horsfield.— Bull. Br. Orn. Cl. 107: 47-49.

Robbins, M.B. & T.A. Parker, 1997. Voice and taxonomy of *Caprimulgus* (*rufus*) *otiosus* (Caprimulgidae), with a reevaluation of *Caprimulgus rufus* subspecies.— Orn. Monogr. 48: 601-607.

Robbins, M.B., R.S. Ridgely & S.W. Cardiff, 1994. Voice, plumage and natural history of Anthony's Nightjar (*Caprimulgus anthonyi*).— Condor 96: 224-228.

Robson, C., 2000. A field guide to the birds of South-east Asia: 1-504.— London.

Rothschild, L. & E. Hartert, 1918. Further notes on the birds of Sudest Island, or Tagula, in the Louisiade Group.— Novit. Zool. 25: 313-326.

Rozendaal, F.G., 1990. Vocalizations and taxonomic status of *Caprimulgus celebensis*.— Dutch Birding 12: 79-81.

Safford, R.J., J.S. Ash, J.W. Duckworth, M.G. Telfer & C. Zewdie 1995. A new species of nightjar from Ethiopia.— Ibis 137: 301-307.

Scharringa, J., 2001. Birds of tropical Asia. Second edition. CD-ROM.— Westernieland, Netherlands.

Schmutz, E., 1977. Die Vögel der Manggarai (Flores): 1-95.— Ruteng.

Schodde, R. & I. Mason, 1980. Nocturnal birds of Australia: 1-136.— Melbourne.

Seutin, G., N.K. Klein, R.E. Ricklefs & E. Bermingham 1994. Historical biogeography of the Bananaquit (*Coereba flaveola*) in the Caribbean region: a mitochondrial DNA assessment.— Evolution 48: 1041-1061.

Sibley, C.G., 1996. Birds of the world. Version 2.0.— Cincinnati.

Sibley, C.G. & J.E. Ahlquist, 1990. Phylogeny and classification of Birds: i-xxiii, 1-976.— New Haven.

Sibley, C.G. & B.L. Monroe, 1990. Distribution and taxonomy of birds of the world: i-xxiv, 1-1111.— New Haven.

Smith, S., 1993. Bird recordings from the Moluccas. Audiocassette.— Swanage, U.K.

Smith, S., 1995. Bird recordings from Sri Lanka. Audiocassette.— Swanage, U.K.

Smithe, F.B., 1975. Naturalist's color guide.— New York.

SPSS Inc., 2000. SPSS for Windows. Version 10.1.— Chicago.

Stewart, D., 2002. Australian bird calls: tropical north east. Compact Disc.— Mullumbimby, NSW, Australia.

Swaby, R.J. & A.C.M. Griffin, 1984. Bird calls from the Iron Range Area, Cape York Peninsula. Audiocassette.— Nunawading, Australia.

Van Gessel, F., 2002. Australian bird call series 4. Nightbirds – owls, nightjars and frogmouths. Compact Disc.— Woy Woy, NSW, Australia.

Verheijen, J.A.J., 1964. Breeding season on the island of Flores, Indonesia.— Ardea 52: 194-201.

Verhoeye, J. & D.A. Holmes, 1998. The birds of the islands of Flores – A review.— Kukila 10: 3-59.

Voous, K.H., 1995. In de ban van vogels: 1-605.— Utrecht.

Warakagoda, D., 2001. The bird sounds of Sri Lanka, an identification guide. Part 1. non-passerines. Second edition. Audiocassette.— Nugegoda, Sri Lanka.

Walters, M., 2003. A concise history of ornithology: 1-255.— London.

White, T., 1984. A field guide to the bird songs of South-east Asia. Two audiocassettes.— London.

Wink, M. & P. Heidrich, 1999. Molecular evolution and systematics of the owls (Strigiformes): 39-57.— In: C. König, F. Weick & J.-H. Becking. Owls: a guide to the owls of the world. Robertsbridge.

Wink, M. & P. Heidrich, 2000. Molecular Systematics of Owls (Strigiformes) based on DNA-sequences of the mitochondrial cytochrome b gene: 819-828.— In: R.D. Chancellor & B.-U. Meyburg (eds). Raptors at risk. Berlin & Blaine.

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Appendix 1

Recording localities and recordists. Numbers following each name represent the number of recordings from the recordist at each site.

Caprimulgus affinis affinis (2 recordings).— INDONESIA: Muara Angke, Jakarta, Java (D. Holmes, 1); Kuta, Bali (G. Sangster, 1).

Caprimulgus affinis kasuidori (1 recording).— INDONESIA: Wanga, Sumba (G. Sangster, 1).

Caprimulgus affinis monticolus (5 recordings).— INDIA: Keoladeo Ghana N.P., Bharatpur, Rajastan (R. Ranft, 1). NEPAL: Royal Chitwan N.P. (N. Gardner, 2; P. Holt, 1); THAILAND: south-west of Chiang Mai, Chiang Mai Prov. (J.T. Marshall, 1).

Caprimulgus andamanicus (3 recordings).— INDIA: Middle Andaman Isl., Andaman Is (P. Singh, 1); Barathang Isl., Andaman Is (P. Singh, 1); Little Andaman Isl., Andaman Is (P. Singh, 1).

Caprimulgus atripennis aequabilis (4 recordings).— SRI LANKA: Lahogala (R.K. Templeton, 1; Wirawila (B. F. King, 1); Yala N.P. (S. Smith, 1); Udawalawe N.P. (D. Warakagoda, 1).

Caprimulgus atripennis atripennis (11 recordings).— INDIA: Baga Hills, Goa (H. Jännes, 1); Nagarhole N.P., Katarnaka (D. Farrow, 1); Thrissur, Kerala (P. Singh, 1); Mudumalai N.P., Tamil Nadu (H. Jännes, 1); Indira Ghandi Wildl. Res., Tamil Nadu (R. Drijvers, 1; D. Farrow, 1; P. Holt, 1; P. Singh, 1); Chandaka-Dampara Wildl. Res., Orissa (P. Singh, 2); Durgapur, West Bengal (M. Gauntlett, 1).

Caprimulgus celebensis celebensis (9 recordings).— INDONESIA: Tangkoko Batuangus N.P., Sulawesi (C. Carter, 1; R. Drijvers, 1; F.G. Rozendaal, 3); Manado, Sulawesi (D. Farrow, 1); Lore Lindu N.P., Sulawesi (P. Morris, 1); Morowali Res., Sulawesi (D. Watling, 1); east of Maligano, Buton (J.G. Corbett, 1).

Caprimulgus celebensis jungei (1 recording).— INDONESIA: Mangole Isl., Sula Is. (D. Yong, 1).

Caprimulgus macrurus albonotatus (13 recordings).— INDIA: Chandigarh, Haryana (P. Singh, 1); Corbett N.P., Kumaria, Uttaranchal (P. Holt, 2; J.C. Roché, 1); Bhitarkanika, Orissa (P. Singh, 1); Manas N.P., Assam (B. Bertram, 1); Kohora, Assam (B. & L. Coffey, 1); Kaziranga N.P., Assam (H. Jännes, 1). NEPAL: Royal Chitwan N.P. (S. Connop, 1; L. Macaulay, 1); Pokhara (B. & L. Coffey, 1). BHUTAN: Hatisar (B. Bertram, 1). BANGLADESH: West Bhanugach Res. (S.P. Gittins, 1).

Caprimulgus macrurus bimaculatus (20 recordings).— VIETNAM: Buon Luoi, Kon Ha Nung, Gia Lai Prov. (F.G. Rozendaal, 1); Nam (Bai) Cat Tien N.P., Dong Nai Prov. (A. Meijer, 1). THAILAND: Salween River, Kanchanaburi Prov. (J.T. Marshall, 1); Kaeng Krachan N.P., Phetchaburi Prov. (D. Farrow, 1); Khao Sam Roi Yot, Prachuap Khiri Khan Prov. (T. Luijendijk, 1); Ban Bang Tiao, Khao Nor Chuchi, Krabi Prov. (F.G. Rozendaal, 1). MALAYSIA: Taman Negara N.P., Pahang (R. Drijvers, 1); Kuala Selangor, Selangor (A.B. van den Berg, 2; G. Sangster, 1; J. Scharringa, 3); Kuala Lumpur (R. Kersley, 4); Kenang, Johor (T.C. White, 1). SINGAPORE (C. Hails, 1; P. Morris, 1).

Caprimulgus macrurus johnsoni (2 recordings).— PHILIPPINES: St. Pauls, Palawan (A. Greensmith, 1); Puerto Princesa, Palawan (R.S. Kennedy, 1).

Caprimulgus macrurus macrurus (6 recordings).— INDONESIA: Carita, Java (A.B. van den Berg, 3); Muara Angke, Jakarta, Java (D. Holmes, 1); Depok, Java (S. van Balen, 1); Alas Purwo, Java (S. van Balen, 1).

Caprimulgus macrurus salvadorii (1 recording).— MALAYSIA: Pulau Tiga, Sabah (A. Greensmith, 1).

Caprimulgus macrurus schlegelii (18 recordings).— INDONESIA: Gunung Rinjani N.P., Lombok (G. Sangster, 2); Kali Batu Putih, Halmahera (T. Luijendijk, 1; S. Smith, 1); Bataka, Halmahera (F.G. Rozendaal, 1). PAPUA NEW GUINEA: Mt Hagen (J.C. Roché, 1); River Fly (I. Redmond, 1). AUSTRALIA: Iron Range, Cape York, Queensland (S. Bennett, 1; R. Swaby/A. Griffin, 1); Rocky River, McIlwraith Range, Cape York, Queensland (D. Stewart, 1); Murray Falls N.P., Queensland (F. van Gessel, 1); Broadwater State Forest, near Ingham, Queensland (F. van Gessel, 3); Mt Spec, Paluma Range, Queensland (H. Pollock, 1; A. Griffin/R. Swaby, 1); Cape Hillsborough N.P., Queensland (F. van Gessel, 1); Cape Wilderness Lodge, Queensland (G. Beruldsen, 1).

Caprimulgus manillensis (11 recordings).— PHILIPPINES: Mt Arayat, Pampanga, Luzon (J.T. Marshall, 1); Talustuson, Biliran (R.S. Kennedy, 1); Raja Sikatuna N.P., Bohol (P. Morris, 1); Mt Katanglad, Mindanao (R. Drijvers, 1; D. Fisher, 1; N. Gardner, 3; A. Greensmith, 2; P. Morris, 1).

Caprimulgus meesi (10 recordings).— INDONESIA: Labuhanbajo, Flores (G. Sangster, 1); Gunung Pacandeki, near Kisol, Flores (C. Carter, 1; F.G. Rozendaal, 1); Wolo Tado, near Riung, Flores (J. Leadley, 1; G. Sangster, 3); Ili Wengot, Flores (R. Drijvers, 1); Lewapaku, Sumba (F. Verbelen, 1; G. Sangster, 1).

Appendix 2

List of specimens examined. Where relevant, new spelling of localities is given in square brackets.

Caprimulgus atripennis aequabilis (1 male).— SRI LANKA: Kalutara District (RMNH, 1 male).

Caprimulgus atripennis atripennis (1 male).— INDIA: Nagargale, Wynaad (RMNH, 1 male).

Caprimulgus macrurus albonotatus (1 male).— INDIA: Darjeeling (RMNH, 1 male).

Caprimulgus macrurus bimaculatus (7 males).— THAILAND: Salanga (RMNH, 1 male); MALAYSIA: Malakka (RMNH, 1 male); INDONESIA: 'Sumatra' (RMNH, 1 male); Medan, North Sumatra (RMNH, 2 males); Sungai Putih, Serdang, South Sumatra (RMNH, 2 males).

Caprimulgus macrurus macrurus (26 males).— INDONESIA: Goenoeng Koepak [Gunung Kupak], West Java (RMNH, 2 males); Bolang, West Java (RMNH, 2 males); Palabuhan [Pelabuan] District, West Java (RMNH, 1 male); Goenoeng Massigit [Gunung Masigit], West Java (RMNH, 4 males); Tjipetir [Cipetir], west of Soekaboemi [Sukabumi], West Java (RMNH, 1 male); Tjilangkat [Cilangkat], north of Buitenzorg [Bogor], West Java (RMNH, 1 male); Batavia [Jakarta], West Java (RMNH, 1 male); Pasir Kananga, Djampang [Jampang] Tengah, West Java (RMNH, 1 male); Gunung Pangerango [Pangrango], West Java (RMNH, 1 male); Kalidjati [Kalijati], West Java (RMNH, 1 male); Tjilandak [Cilandak], Tjiboengoer [Cibungur], West Java (RMNH, 1 male); Tjiodeng [Ciodeng], West Java (RMNH, 1 male); Bandjar [Banjar], Preanger, West Java (RMNH, 4 males); Cheribon [Cirebon], West Java (RMNH, 2 males); Gedangan, Semarang, Central Java (RMNH, 2 males); Koeta [Kuta], Bali (RMNH, 1 male).

Caprimulgus macrurus salvadorii (4 males).— MALAYSIA: Kuching, Sarawak (RMNH, 2 males); INDONESIA: Pontianak, West Kalimantan (RMNH, 2 males)

Caprimulgus macrurus schlegelii (25 males, 17 females).— INDONESIA: Salayar (RMNH, 1 male); Wetar (RMNH, 1 female); Buru (RMNH, 3 males, 3 females); Ambon (RMNH, 3 males); Seram (RMNH, 4 males); Obi Latoe [Obilatu] (RMNH, 1 female); Damar, off southern Halmahera (RMNH, 1 female); southern Halmahera (RMNH, 1 male, 1 female); Batjan [Bacan] (RMNH, 1 female); Ternate (RMNH, 4 males, 1 female); Misool (RMNH, 2 males, 2 females); Wammer, Aru Is (RMNH, 1 male); Wailibit, Batanda [Batanta] (RMNH, 1 male); Mansinam, Arfak, Irian Jaya (RMNH, 1 male); Kaukas, Onin Peninsula, Irian Jaya (RMNH, 1 male); Geitenkamp, Noord R. [Lorentz River], Irian Jaya (RMNH, 1 male, 1 female); Kloofbivak, Noord R. [Lorentz River], Irian Jaya (RMNH, 1 male); Alkmaar, Noord R. [Lorentz River], Irian Jaya (RMNH, 1 female); Ongari [near Kumbe River], Irian Jaya (RMNH, 1 female); Koerik [Kurik], Irian Jaya (RMNH, 3 females); Wanggo, Irian Jaya (RMNH, 1 male).

Caprimulgus manillensis (4 males).— PHILIPPINES: Bulacan, Luzon (RMNH, 1 male); Vijcaya, Luzon (RMNH, 1 male); Silliman Farm, Negros (RMNH, 1 male); Inalad, Siaton, Negros (RMNH, 1 male).

Caprimulgus meesi (2 males).— INDONESIA: Nisar, Flores (RMNH, 1 male); Mao Marru, Sumba (AMNH, 1 male).