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Taxonomic revision of the Savanna Nightjar (*Caprimulgus affinis*) complex based on vocalizations reveals three species

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Abstract

Background: The Savanna Nightjar (*Caprimulgus affinis*) is a widespread, polytypic species which was previously treated as two or three species. It is currently treated as a single species based on superficial similarity of their songs but no detailed comparisons of the songs in this complex have been made.

Methods: A total of 15 acoustic variables were measured for the songs of 86 individuals representing 8 of the 10 subspecies in the complex.

Results: Three major groups can be distinguished based on univariate and multivariate analyses: a northern group consisting of the subspecies *C. a. monticolus*, *C. a. amoyensis* and *C. a. stictomus*; a southern group consisting of *C. a. affinis*, *C. a. kasuidori*, *C. a. timorensis* and *C. a. propinquus*; and a third group in the Philippines consisting of *C. a. griseatus*.

Conclusions: It is here argued that these groups are best treated as species, and that Franklin's Nightjar (*C. monticolus*) and Kayumanggi Nightjar (*C. griseatus*) are reinstated as separate species.

Keywords: Caprimulgidae, Macrogeograpic variation, Taxonomy, Vocalizations

Background

Most species of nightjars and owls have a cryptic plumage which has long hampered taxonomic study of their species limits. During the last two decades, quantitative comparisons of songs have helped clarify species limits in several groups, including pygmy owls [*Glaucidium* [Howell and Robbins 1995; Gwee et al. 2019)], scops owls [*Otus* (Rasmussen et al. 2000; Sangster et al. 2013)], screech owls [*Megascops* (Krabbe 2017; Dantas et al. 2021)], hawk owls (*Ninox* [Rasmussen et al. 2012; Gwee et al. 2017]) and nightjars [*Caprimulgus* ([Sangster and Rozendaal 2004)]. Three aspects make songs in these groups useful for taxonomic purposes. First, in nearly all groups of non-passerines songs, including owls and nightjars, are not known to be learned (Kroodsma 2004). Variation is therefore likely inherited and may provide information about evolutionary relationships. Second, in some species of owls and nightjars songs are known to be involved in intra- and interspecific communication (reviewed by Sangster and Rozendaal 2004). This makes their songs a useful indicator of species limits (Marshall 1978). Third, songs in both groups are rather simple and stereotypical (Marshall 1978), which makes homology assessment easy. Vocalizations are therefore a useful avenue for clarifying and refining species limits in other species of nightbirds.

The Savanna Nightjar (*Caprimulgus affinis* Horsfield, 1821) is widely distributed in the Oriental region, ranging from northern Pakistan to Indonesia and Timor-Leste (Fig. 1). The song of the species is distinctive and can be described as a rasping "tschreep" note. Whereas

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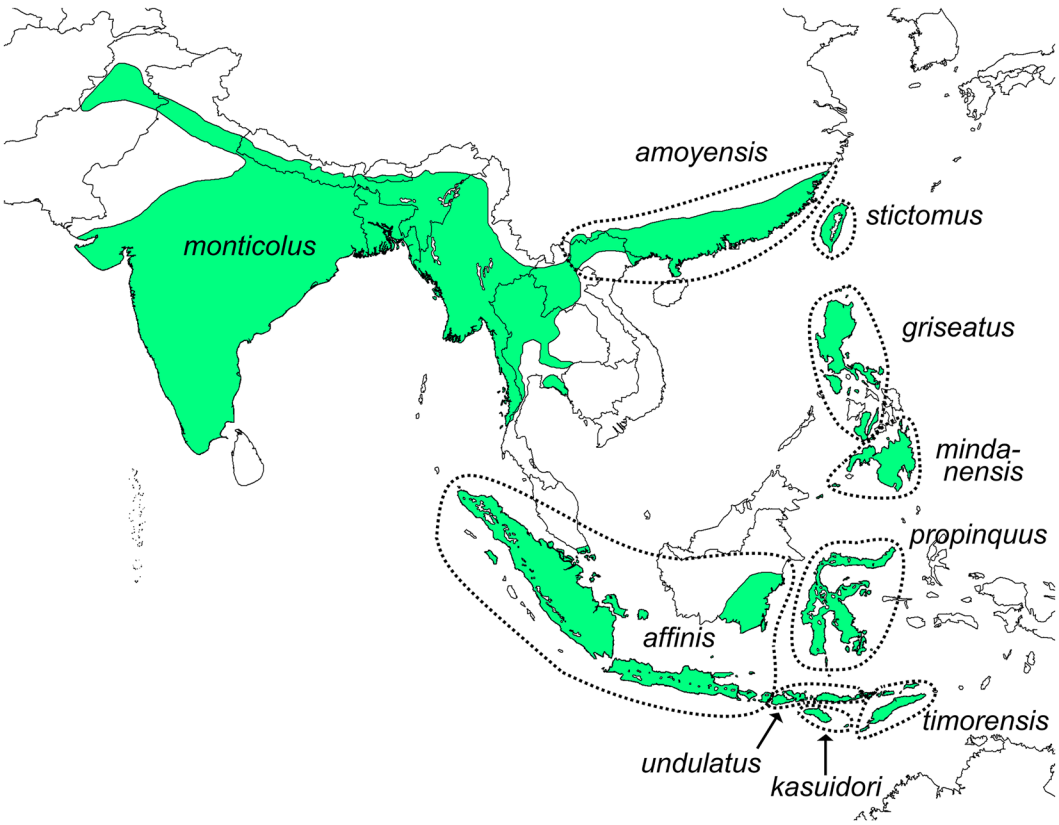

Fig. 1 Range map of *Caprimulgus affinis* (based on BirdLife International and Handbook of the Birds of the World 2017), indicating subspecies limits (sensu Cleere 1998). The taxa *undulatus* Mayr, 1944 and *kasuidori* Mayr, 1944 were included in *C. a. affinis* by Mees (2006) and Dickinson and Remsen (2013)

geographic variation in the vocalizations of Large-tailed Nightjar (*C. macrurus* Horsfield, 1821) has long been known (Marshall 1978) and has been used to delimit species (Mees 1985; Rozendaal 1990; Sangster and Rozendaal 2004), no such knowledge exists for *C. affinis*.

In the early twentieth century, taxonomic authorities recognized *C. monticolus* Franklin, 1831 and *C. affinis* as separate specis, the former occurring on mainland Asia and the latter in southern Peninsular Malaysia, Singapore and Indonesia east to Timor-Leste (Sharpe 1901; Peters 1940). Sharpe (1901) also recognized *C. griseatus* as a species. While discussing a letter from Erwin Stresemann on the birds of Yunnan, China, Rothschild (1927) noted that he disagreed with Stresemann that *C. monticolus* and *C. affinis* were conspecific. Mayr (1944) noted that the plumage of the Philippine taxon *C. a. griseatus* Walden, 1875 was intermediate between that of *C. monticolus* and *C. affinis* and regarded them as a single species. Sibley and Monroe (1990) ackowledged the occasional treatment of *C. monticolus* and *C. affinis* as species but noted that their calls are identical. These three opinions have formed the basis for recognizing a single species, a treatment which is now universally adopted in field guides (King et al. 1975; Robson 2000; Rasmussen and Anderton 2005; Allen 2020; Eaton et al. 2021), handbooks (Cleere 1998; Holyoak 2001) and taxonomic lists (Wolters 1976; Inskipp et al. 1996; Clements 2007; Dickinson and Remsen 2013; del Hoyo and Collar 2014; Gill et al. 2020). The only exception were Howard and Moore (1991), who presumably followed Peters (1940) in treating *C. monticolus* as a distinct species.

In this study, we revisit species limits in *C. affinis* using bioacoustic data on eight of the ten subspecies recognized by Cleere (1998) and Holyoak (2001).

Methods

Recordings were obtained from the Xeno-Canto (http://www.xeno-canto.org/) and AVoCet (http://avocet.zoology.msu.edu/) databases, and the bird sound collections of the Florida Museum of Natural History (https://www.floridamuseum.ufl.edu/bird-sounds/) and the British Library Sound Archive (http://cadensa.bl.uk/). The data set was supplemented by published recordings (Marshall 1978; Ranft and Cleere 1998; Jännes 2002; Supari 2003;

Scharringa 2005; Chappuis et al. 2009) and our own recordings, which we submitted to the Macaulay Library (https://www.macaulaylibrary.org/). In total, songs of 86 individuals of 8 of the 10 subspecies of *C. affinis* (sensu Cleere 1998; Holyoak 2001) were available for analysis: *C. a. monticolus* (34 individuals), *C. a. amoyensis* (2), *C. a. stictomus* (11), *C. a. affinis* (21), *C. a. kasuidori* (1), *C. a. timorensis* (5), *C. a. propinquus* (1) and *C. a. griseatus* (11). A list of recordings with localities and recordists is provided in Additional file 1: Table S1.

A total of 15 variables was defined on the basis of sonagrams (Fig. 2). The following measurements were recorded: (1) F1, frequency at the start of the song; (2) F2, frequency at the first low; (3) F3, frequency at the second peak; (4) F4, frequency at the second low; (5) F5, frequency at the third peak; (6) F6, maximum frequency, which is the highest frequency present; (7) F7, minimum frequency, which is the lowest frequency present; (8) DF1, the frequency drop between the second peak and the second low; (9) DF2, the frequency drop between the second and third peaks; (10) DF3, frequency range, which is the difference between the maximum and minimum frequency; (11) DT1, total song duration; (12) DT2, the duration of the first downward element at the point where the song begins to increase in frequency; (13) DT3, the interval between the second peak and the end of the song; (14) DT4, the interval between the second and third peaks; and (15) DT5, the interval between the first and second peaks. The first ten of these (F1 to DF3) are frequency-related variables, whereas the last five (DT1-DF5) are time-related variables.

Principal Component Analysis (PCA) was used to reduce the 15 acoustic variables to a limited number of uncorrelated variables. ANOVA was used to test whether the groups defined by PCA differed from each other.

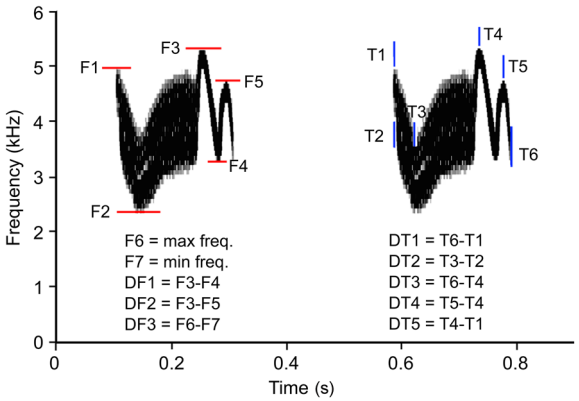

Fig. 2 Measurement of song variables. The left sonagram shows the frequency parameters and the right sonagram shows the time parameters

Canonical Discriminant Function Analysis (DFA) was applied 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 failed 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.

The effect size, expressed as Cohen's *d*, was calculated to show the strength of the acoustic differences between taxa. For interpretation of effect size data, we used the classification of Cohen (1988), which was updated and expanded by Sawilowsky (2009). Thus, we regard an effect size of $d \geq 0.1$ as "very small", $d \geq 0.2$ as "small", $d \geq 0.5$ as "medium", $d \geq 0.8$ as "large", $d \geq 1.2$ as "very large" and $d \geq 2.0$ as "huge".

SPSS version 27.0 (IBM Corp 2020) was used to calculate all descriptive statistics and perform analyses of variance (ANOVA), Mann-Whitney U-tests, Principal Components Analyses, and Discriminant Function Analyses.

Results

Principal component analysis

The songs of 86 individuals were used in the PCA. The results of the PCA on the 15 measurements are summarized in Table 1. Four components with eigenvalues > 1 were extracted from the data set. The first principal component (PC1) accounted for 46.0% of the variance. PC2, PC3 and PC4 accounted for an additional 24.0, 12.0, and 9.1% of the variance, respectively. PC1 was represented by most frequency variables, especially F3 and F6, and DF1. PC2 was determined mostly by F2 and F3, and PC3 mostly by DT1 and DT5.

Plotting individuals on PC1 versus PC2 revealed three distinct clusters, corresponding to songs from the *affinis*-group (subspecies *C. a. affinis*, *C. a. kasuidori*, *C. a. timorensis* and *C. a. propinquus*), the *monticolus*-group (subspecies *C. a. monticolus*, *C. a. amoyensis* and *C. a. stictomus*) and the *griseatus*-group (subspecies *C.*

Table.1 Factor loadings of 15 acoustic variables on the 4 principal components in the *Caprimulgus affinis* complex. Eigenvalues and percentage of variance explained by the respective components are given at the bottom of the table

Variable	PC1	PC2	PC3	PC4
F1	0.788	0.341	0.110	−0.261
F2	0.129	0.905	−0.239	0.202
F3	0.940	0.194	0.212	0.156
F4	0.080	0.595	0.582	−0.440
F5	0.693	0.467	0.384	−0.315
F6	0.941	0.194	0.217	0.146
F7	0.129	0.905	−0.239	0.202
DF1	0.910	−0.084	−0.060	0.365
DF2	0.826	−0.097	−0.001	0.491
DF3	0.847	−0.338	0.352	0.025
DT1	−0.636	−0.046	0.621	0.417
DT2	0.634	−0.321	−0.325	0.224
DT3	−0.660	0.566	0.190	0.349
DT4	−0.688	0.554	0.159	0.333
DT5	−0.230	−0.578	0.641	0.227
Eigenvalue	6.906	3.599	1.795	1.372
Variance explained	46.0%	24.0%	12.0%	9.1%
F (ANOVA)	8606	6604	15.0	15.1
Significance (ANOVA)	$P<0.001$	$P<0.001$	$P<0.001$	$P<0.001$
Degrees of freedom (ANOVA)	85	85	85	85

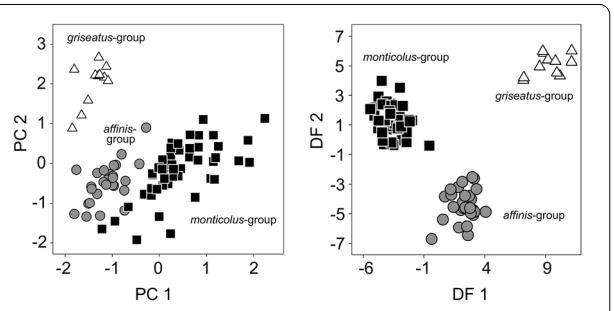

Fig. 3 PCA (left) and DFA (right) scatterplots of acoustic variables measured for songs of the *Caprimulgus affinis* complex ($n=86$)

a. griseatus) (Fig. 3). One-way ANOVA showed that the three groups identified by PCA differed in all four principal components (Table 1).

Discriminant function analysis

The songs of the three groups identified by PCA were used in the DFA. Most variables passed the tolerance test, except F7, DF1, DF2, DF3 and DT5 which were excluded from the test. The descriptive DFA was highly significant (Wilks' lambda = 0.004; Chi Square$_{20}$ = 435.6; $P<0.001$). The variables most important in the discrimination were F2, F3, F4, F6 and DT4 (Table 2). The initial DFA led to a 100% correct classification of the individuals into the three groups. The jackknife procedure also provided a high degree of predictive discrimination, with 85 of 86 (98.8%) individuals being correctly assigned to their group defined by PCA.

Table.2 Standardized canonical discriminant function coefficients examining trends in variance of ten acoustic variables measured for songs of three groups of *Caprimulgus affinis*

Variable[a]	DF1	DF2
F1	0.109	0.079
F2	0.150	1.428
F3	2.608	1.556
F4	1.025	−1.148
F5	−0.412	−0.711
F6	−3.294	−0.561
DT1	0.109	−0.275
DT2	−0.441	0.389
DT3	0.093	0.195
DT4	0.930	0.120
Eigenvalue	20.270	11.082
Variance explained	64.7%	35.3%

Eigenvalues and percentage of variance accounted for by DF1 and DF2 are given at the bottom of the table

[a] Variables F7, DF1, DF2, DF3 and DT5 were excluded because these failed the tolerance test

Univariate analysis

Song characteristics of the three groups identified by PCA are given in Table 3 and illustrated in Fig. 4. All 15 variables differed significantly in comparisons of the *monticolus*-group with the *affinis*-group, and some of these also showed non-overlapping ranges (DF1 and DF2 in *monticolus*-group vs. *affinis*-group. Similarly, 14 variables differed significantly in comparisons of the *monticolus*-group with the *griseatus*-group, and 4 (DF1, DF3, DT3 and DT4) showed no overlap. Comparisons of the *affinis*-group with the *griseatus*-group revealed seven significant differences and five variables that showed no overlap between the 2 groups (F2, F7, DF3, DT3 and DT4).

The effect size of the differences between the three groups is given in Table 3. The three groups showed multiple "very large" (Cohen's $d>1.2$) or "huge" (Cohen's $d>2.0$) differences in both frequency-related and time-related variables (Table 3).

The differences between the three groups are visible on sonagrams (Fig. 4). The songs of the *griseatus*-group differ most prominently from the *monticolus*- and *affinis*-groups by their lack of a raspy quality (shown on

Table.3 Descriptive statistics of 15 variables measured for songs of 3 species in the *Caprimulgus affinis* complex (mean ± SD, range)

Variable	*C. monticolus* (*n* = 47)	*C. affinis* (*n* = 28)	*C. griseatus* (*n* = 11)	*C. monticolus* vs. *C. affinis* Significance Cohen's *d* (interpretation)	*C. monticolus* vs. *C. griseatus* Significance Cohen's *d* (interpretation)	*C. affinis* vs. *C. griseatus* Significance Cohen's *d* (interpretation)
F1	5139 ± 394 (4033–6262)	4726 ± 205 (4366–5161)	4780 ± 281 (4115–5074)	$P < 0.001$[b] 1.25 ("very large")[d]	$P < 0.005$[b] 0.97 ("large")[c]	n.s.[b] 0.25 ("small")[c]
F2	2242 ± 206 (1712–2720)	1856 ± 195 (1435–2332)	2948 ± 150 (2663–3156)	$P < 0.001$[b] 1.94 ("very large")[c, d]	$P < 0.001$[b] 3.64 ("huge")[d]	$P < 0.001$[b] 6.10 ("huge")[d]
F3	5773 ± 627 (4514–7399)	4879 ± 269 (4366–5587)	5034 ± 249 (4503–5264)	$P < 0.001$[b] 1.73 ("very large")[c, d]	$P < 0.001$[b] 1.30 ("very large")[c, d]	n.s.[b] 0.60 ("medium")[c]
F4	3428 ± 303 (2859–4088)	3634 ± 273 (3256–4403)	3685 ± 246 (3243–4091)	$P < 0.005$[a] 0.71 ("medium")[c]	$P < 0.001$[b] 0.89 ("large")[c]	n.s.[a] 0.20 ("small")[c]
F5	4931 ± 416 (4079–5799)	4723 ± 235 (4376–5374)	4746 ± 287 (4143–5082)	$P < 0.001$[b] 0.59 ("medium")[c]	n.s.[b] 0.47 ("small")[c]	n.s.[b] 0.10 ('very small')[c]
F6	5777 ± 630 (4514–7399)	4895 ± 253 (4505–5587)	5034 ± 249 (4503–5264)	$P < 0.001$[b] 1.71 ("very large")[c, d]	$P < 0.001$[b] 1.30 ("very large")[c, d]	n.s.[b] 0.57 ("medium")[c]
F7	2242 ± 206 (1712–2720)	1856 ± 195 (1435–2332)	2948 ± 150 (2663–3156)	$P < 0.001$[a] 1.94 ("very large")[c, d]	$P < 0.001$[b] 3.64 ("huge")[d]	$P < 0.001$[b] 6.10 ("huge")[d]
DF1	2345 ± 463 (1618–3486)	1246 ± 187 (647–1563)	1349 ± 184 (1035–1617)	$P < 0.001$[b] 2.90 ("huge")[d]	$P < 0.001$[b] 2.37 ("huge")[d]	n.s.[b] 0.57 ("medium")[c]
DF2	842 ± 389 (407–1914)	156 ± 109 (-175–324)	288 ± 83 (182–420)	$P < 0.001$[b] 2.20 ("huge")[d]	$P < 0.001$[b] 1.59 ("very large")[c, d]	$P < 0.001$[b] 1.32 ("very large")[c, d]
DF3	3535 ± 587 (2543–4956)	3039 ± 237 (2608–3496)	2087 ± 204 (1710–2338)	$P < 0.001$[b] 1.03 ("large")[c]	$P < 0.001$[b] 2.73 ("huge")[d]	$P < 0.001$[b] 4.28 ("huge")[d]
DT1	0.194 ± 0.020 (0.154–0.245)	0.226 ± 0.017 (0.197–0.276)	0.230 ± 0.017 (0.200–0.257)	$P < 0.001$[b] 1.75 ("very large")[c, d]	$P < 0.001$[b] 1.92 ("very large")[c, d]	n.s.[a] 0.23 ("small")[c]
DT2	0.023 ± 0.004 (0.015–0.035)	0.014 ± 0.002 (0.010–0.018)	0.012 ± 0.003 (0.006–0.017)	$P < 0.001$[a] 2.58 ("huge")[d]	$P < 0.001$[b] 2.69 ("huge")[d]	n.s.[b] 0.59 ("medium")[c]
DT3	0.050 ± 0.006 (0.035–0.066)	0.065 ± 0.007 (0.048–0.073)	0.098 ± 0.008 (0.080–0.106)	$P < 0.001$[a] 2.33 ("huge")[d]	$P < 0.001$[b] 7.34 ("huge")[d]	$P < 0.001$[b] 4.82 ("huge")[d]
DT4	0.042 ± 0.005 (0.031–0.059)	0.056 ± 0.006 (0.044–0.064)	0.087 ± 0.006 (0.075–0.097)	$P < 0.001$[b] 2.91 ("huge")[d]	$P < 0.001$[b] 9.13 ("huge")[d]	$P < 0.001$[b] 5.38 ("huge")[d]
DT5	0.144 ± 0.016 (0.119–0.184)	0.162 ± 0.017 (0.134–0.209)	0.132 ± 0.015 (0.117–0.155)	$P < 0.001$[a] 1.07 ("large")[c]	$P < 0.05$[b] 0.79 ("medium")[c]	$P < 0.001$[b] 1.90 ("very large")[c, d]

The right three columns present significance levels of ANOVA or Mann-Whitney *U*-tests, the effect size (expressed as Cohen's *d*) and the interpretation of effect size by Cohen (1988) and Sawilowsky (2009)

[a] ANOVA

[b] MW*U*-test

[c] sensu Cohen (1988)

[d] sensu Sawilowsky (2009)

sonagrams as a narrow line in the first upward-inflected element). The differences between the *monticolus*- and *affinis*-groups are reflected by (i) the broader basis (i.e. longer duration) of the first downward element of the songs of the *monticolus*-group than in those of the *affinis*-group, and in the much larger frequency drops between (ii) F3 and F4 and (iii) F3 and F5 in the *monticolus*-group.

Discussion

The results of this study show that the northern subspecies *C. a. monticolus*, *C. a. amoyensis* and C. a. *stictomus*, the southern subspecies *C. a. affinis*, *C. a. kasuidori*, *C. a. timorensis* and *C. a. propinquus* and the Philippine subspecies *C. a. griseatus* represent separate groups in Principal Component Analysis of variation in vocalizations, and that individuals can be classified correctly at high proportions in Discriminant Function Analysis. The three groups show significant differences in the three principal components and in all univariate variables and there are "very large" to "huge" differences in effect size between the three groups in both frequency-related and time-related variables.

The lack of evidence for vocal learning in most non-passerines, including nightjars, implies that vocal differences are innate and likely have a genetic basis. Thus, population-level differences in vocalizations may reflect

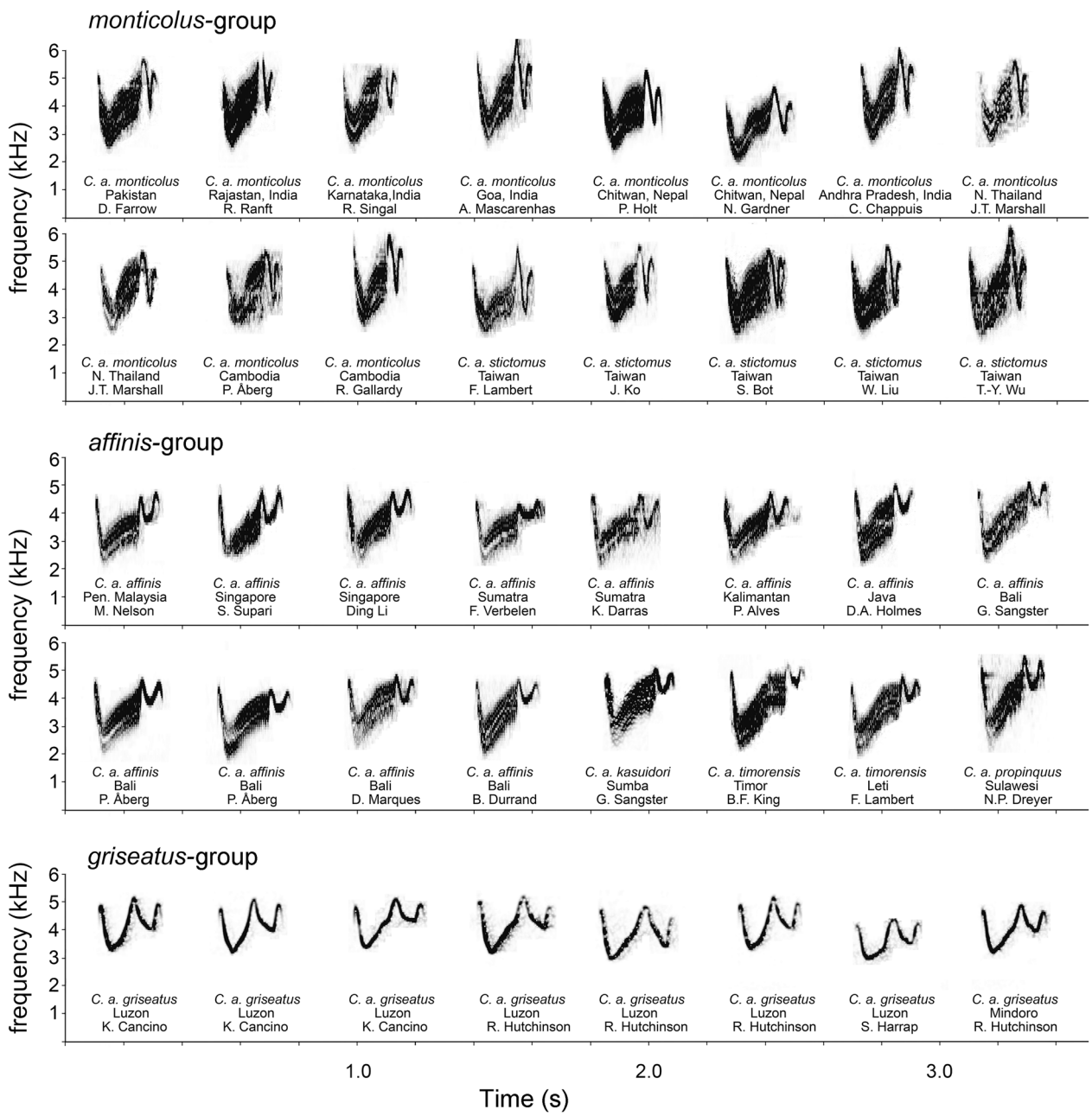

Fig. 4 Sonagrams of songs of the *monticolus*-group, *affinis*-group and *griseatus*-group illustrating the differences among the three groups

evolutionary divergence. The multiple differences documented between the geographically separate *monticolus* and *affinis* groups likely means that these populations have been subjected to a long period of genetic isolation. Consequently, the three non-overlapping groups in the DFA plot are therefore best interpreted as evidence that the *monticolus*-group, the *affinis*-group and the *griseatus*-group represent separate evolutionary lineages, i.e. separate branches in the tree of life. According to the General Lineage Concept (de Queiroz 1999, 2007) such lineages are best considered as species: *C. monticolus*, *C. affinis* and *C. griseatus*. As English names we propose to reinstate the name Franklin's Nightjar for *C. monticolus* and to maintain Savanna Nightjar for *C. affinis*. For *C. griseatus* we suggest the name Kayumanggi Nightjar, in recognition of the Filipino name Kayumanggi for brownish-coloured, particularly with reference to tan coloured skin. The three species reinstate species last

recognized by Sharpe (1901) and reflect differences in size and plumage coloration. *C. monticolus* is larger and browner than *C. affinis* (Cleere 1998). Indeed, data in Cleere (1998) show no overlap in wing length between *C. monticolus* (males 181–208 mm; females 177–208 mm) and *C. affinis* (males 150–172 mm; females 152–170 mm). *C. griseatus* is greyer than *C. affinis* and the barring on its underparts is finer and extends lower on the belly (Cleere 1998; Holyoak 2001).

Unfortunately, no recordings were available of the Philippine taxon *C. a. mindanensis* Mearns, 1905. Thus, it is not clear if this taxon belongs to *C. griseatus* or to *C. affinis*, or perhaps represents another vocally distinct group. Pending further analysis, we suggest that *C. a. mindanensis* be treated as conspecific with *C. griseatus* on geographic grounds. We are not aware of any reliable recent records of *C. a. mindanensis*, and we hope our paper provides impetus to find and study this poorly known taxon.

Taxonomic study of the *C. affinis* complex, and that of other groups of nightjars, could further benefit from molecular phylogenetic and phylogeographic analyses. This could (i) corroborate and refine of species limits based on morphological or bioacoustic patterns, (ii) facilitate the discovery of additional lineages, and (iii) provide a historical perspective on the biogeography of the group. Conversely, modern morphological and bioacoustic studies of species limits may benefit phylogenetic and phylogeographic analyses by indicating which populations should be sampled and where additional cryptic species may be located.

Conclusions

In recent decades, avian species-level taxonomy shows two major trends: improved documentation of species taxa and a refinement of species limits. As a consequence, the scientific underpinnings of avian taxonomy continue to be improved and the number of taxonomically-recognized species increases steadily (Sangster and Luksenburg 2015; Sangster 2018). The increase of species is not a goal of taxonomy but results from the improved understanding of species limits due to new information on groups that often have long been neglected. This process is especially important in birds due to the large-scale lumping of species in the first half of the twentieth century without detailed study (reviewed by Haffer 1992; Sangster 2018). The Savanna Nightjar complex is an example of three valid species that have long been treated as a single species without a solid scientific basis. The results of this study thus underscore the importance of identifying and revisiting poorly-documented taxonomic changes.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40657-021-00288-z.

Additional file 1: Table S1. Recording localities, recordists and accession numbers/sources.

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Authors' contributions
GS conceived and designed the study, collated the data, performed analyses and wrote the manuscript. KMC and ROH contributed materials and improved the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials
All but one of the recordings used in this study are available from the Xeno-Canto (http://www.xeno-canto.org/), AVoCet (http://avocet.zoology.msu.edu/) databases, and the bird sound collections of the Florida Museum of Natural History (https://www.floridamuseum.ufl.edu/bird-sounds/), Macaulay Library (https://www.macaulaylibrary.org/) and British Library Sound Archive (http://cadensa.bl.uk/). One recording, by Ben F. King, will be archived at the Macaulay Library, Cornell University, NY, USA.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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