The taxonomic position and breeding range of Golden Nightjar Caprimulgus eximius (Aves: Caprimulgidae)

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The taxonomic position and breeding range of Golden Nightjar *Caprimulgus eximius* (Aves: Caprimulgidae)

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Abstract

Golden Nightjar *Caprimulgus eximius* is an apparently sedentary sub-Saharan species with a breeding range extending from Senegal and Mauritania to Sudan. Although genetic studies of nightjars and related Caprimulgiformes have been published previously, none has included Golden Nightjar. In this study, mitochondrial and nuclear DNA of a Golden Nightjar found dead in Western Sahara in April 2016 was sequenced and compared to other species in the genus *Caprimulgus*. It was concluded with strong support that Golden Nightjar is closely related to Egyptian Nightjar *C. aegyptius*. It is hypothesised that Golden and Egyptian Nightjars may have arisen by splitting of a single ancestral species into migratory and sedentary populations.

Keywords: Golden Nightjar; Egyptian Nightjar *Caprimulgus*; *eximius*; *aegyptius*; systematics; molecular phylogeny; molecular sexing; Western Sahara; Nubian Nightjar; *nubicus*.

The avian Order Caprimulgiformes comprises oilbirds (family Steatornithidae), owlet-nightjars (Aegothelidae), frogmouths (Podargidae), potoos (Podargidae) and, most important in terms of species number, the Caprimulgidae, including nightjars and New World nighthawks (del Hoyo et al., 1999). Caprimulgid nightjars and nighthawks inhabit temperate and tropical zones worldwide. They share substantially nocturnal and crepuscular aerial feeding strategies with cryptic plumage that acts as camouflage at daytime roost sites. Such highly adaptive and constrained morphologies and plumage patterns have the potential to frustrate systematic and phylogeographic studies. Phylogenetic studies of Caprimulgiformes based on DNA sequence data have been published and compared to phylogenies based on morphological data (Barrowclough et al. 2006; Braun and Huddleston 2009; Dumbarcher et al. 2003; Larsen et al. 2007; Han et al. 2010; Mariaux and Braun 1996; Mayr 2010). They showed among other things that the genus *Caprimulgus* s.l. was polyphyletic and that traditional classifications based on morphological criteria may not accurately reconstruct patterns of evolution for these birds. Correct taxonomic arrangement of individual nightjar and nighthawk species requires molecular data. Current taxonomy (Dickinson and Remsen 2014) reflects the recent molecular data but many Caprimulgiform species have not yet been sequenced.

Omitted from previous studies was the Golden Nightjar *Caprimulgus eximius* Temminck 1826 of Subsaharan Africa. This attractive species has been poorly studied until recently (Jackson 2011), with few photographs and sound recordings (Cleere 1995; Jackson 2003). Because of its large range, it is not considered to be threatened (Birdlife International, 2016). Its striking yellow-orange plumage with black and white bars on most upperpart feathers is not approached by any other nightjar species, though the general paleness and subtlety of plumage is reminiscent of other some other desert and semi-desert species such as Egyptian Nightjar *C. aegyptius* and Sykes's Nightjar *C. mahrattensis*. Vaurie (1960), in his description of Vaurie's Nightjar *C. centralasicus*, noted the atypical speckled plumage and very long upper tail coverts of Golden Nightjar but placed it tentatively between Egyptian Nightjar and a group consisting of Jungle Nightjar *C. indicus*, European Nightjar *C. europaeus* and Red-necked Nightjar *C. ruficollis* (Vaurie 1960). The taxonomic affinities of Golden Nightjar therefore remain uncertain. Two subspecies are commonly recognised: nominate *C. e. eximius* of SW and Central Sudan, and *C. e. simplicior*, breeding from Central Chad to Senegal and Mauritania (Dickinson and Remsen 2014), and likely also to breed in Western Sahara (described below). The species appears to be sedentary, possibly with dispersive post-breeding movements (del Hoyo et al. 1999).

On 20 April 2016 a Golden Nightjar was found dead as roadkill by Jurrien van Deijk, Ruben Vermeer, Daan Drukker and Jacob Lotz in the Oued Jenaa in Oued Ad-Deheb province of Western

Sahara at coordinates 22.678119 N, 14.492028 E (see http://tinyurl.com/hlynyhr). Images of the specimen are presented in Figure 1. Plumage characteristics identify it as probably female (Fry et al. 1988; del Hoyo et al. 1999). The off-white tip of the outer tail feather was 19-20 mm which is normal for females (15-25 mm) and is not shown in males (30-40 mm). Wing length of 178 mm and tail length of 114 mm fell in the overlap zone for both sexes. The bird had a large brood patch, suggesting active breeding. Up to 4 singing males had been found in this area during the month (MahgrebOrnitho 2016), implying that Golden Nightjar breeds in this region.

In order to determine the taxonomic affinity of Golden Nightjar, feather samples from the Oued Jenaa specimen were used to isolate genomic DNA, using the DNA Micro Kit (QIAGEN, UK) according to the manufacturer's instructions with addition of 0.01 M dithiothreitol to the digestion mix and elution in 80 µl of QIAGEN buffer AE. PCR fragments encompassing the entire coding region of the genes encoding cytochrome b (cytb) and cytochrome c oxidase subunit 1 (COI) were amplified from samples using primers L14993, H16065, BirdF1 and BirdR2, and conditions described in Helbig et al. (1995) and Hebert et al. (2004). Each 50 µl PCR reaction contained 28.5 µl of ddH_2O, 5 µl of 10x Optibuffer, 1 µl of 50 mM $MgCl_2$ solution, 3 µl of dNTPs (2 mM each), 5 µl of forward and reverse primers (10 mM each), 2 units (0.5 µl) of BIO-X-ACT Short thermostable DNA Polymerase (Bioline, UK) and 2 µl of template DNA. Fragment of the nuclear v-myc myelocytomatosis viral oncogene-like protein (MYC) gene were amplified using the MYC-F-01/MYC-R-04 and MYC-F-02/MYC-R-06 primers (Harshman et al. 2003) as above with 35 cycles at annealing temperature 55°C and 30 s extension. PCR products were separated by electrophoresis on a 1.5% agarose gel. The DNA from each gel fragment was then isolated using the QIAquick Gel Extraction Kit (Qiagen, UK) according to the manufacturer's protocols. Gel-extracted PCR products were sequenced by the Source BioScience (Cambridge) DNA sequencing service.

1008 bp of cytb, 695 bp of COI, and 545 bp of MYC were successfully sequenced from the Golden Nightjar. Open reading frames were consistent with these genes being functional, not pseudogenes, with no indels compared to database sequences. Sequences were deposited in the European Nucleotide Archive with Accession numbers: LT671509 (cytb), LT671510 (COI), LT671511 (MYC). BLAST searches performed at http://blast.ncbi.nlm.nih.gov/Blast.cgi confirmed that for all three genes, the most similar deposited sequences were of Egyptian Nightjar, from which there was 3.78% uncorrected divergence at the *cytb* locus. The 545 bp of MYC was 100% identical to the MYC sequence from Egyptian Nightjar (Accession number GU586565) and 2-4 bp different (>99% similarity) to multiple other nightjar sequences.

Molecular analysis of phylogeny was performed, comparing Golden Nightjar with representatives of the major clades of nightjars described by Han et al. (2000). Deposited gene sequences were downloaded from GenBank from all previously sequenced species (see Table 1). Sequences were aligned and appropriate models of evolution were selected using MEGA 7.0. Bayesian analysis was performed using the program BEASTv1.8.3 (Drummond *et al*., 2012) available from (http://beast.bio.ed.ac.uk). MCMC chains were run for 10,000,000 generations with trees sampled every 1000 generations using the lognormal uncorrelated relaxed clock model. All remaining parameters, such as the base frequencies, gamma shape parameter, and root height of the tree, were default. The phylogenetic tree estimate was carried out in TreeAnnotator v1.8.3 using the maximum tree clade credibility target tree and median node height. The resulting inferred phylogeny tree is presented as Figure 2. It confirmed with extremely high statistical support that Golden Nightjar falls within the 'Old World' (true) *Caprimulgus* clade (Han et al., 2000) and yields a sister relationship between Egyptian and Golden Nightjars.

Bayesian and Maximum Likelihood analysis based on 771 bp of cytb using the same sequences but also including a 771 bp fragment obtained from a juvenile Nubian Nightjar *C. nubicus* sampled by YP at Ne'ot Hakikar, Israel (30.930712 N 35.390312 E), on 21 June 2006 also resolved the sister relationship of Egyptian and Golden Nightjars and placed the Nubian Nightjar in a poorly resolved polytomy of the *C. eximius/aegyptius* clade, *C. affinis*, and the *C. nigriscapularis/pectoralis/policephalus* clade (Supplementary Figure S1). Further work will be needed to determine its taxonomic affinity of Nubian Nightjar, but it is clear that it is not a sister species to Golden or Egyptian Nightjars.

For the smaller number of species for which both sequences (cytb and COI) were available, a comparable Bayesian tree was produced using a 1703 bp concatemer of cytb and COI. The tree is presented as Supplementary Figure S2 and is congruent with Figure 2 in placing Egyptian and Golden Nightjars together with very high statistical support.

Genetic sexing of the Golden Nightjar was performed by PCR using primer sets P2/P8 (Griffiths et al., 1998) and 2550F/2718R (Fridolfsson and Ellegren, 1999). Both P2/P8 and 2550F/2718R PCRs span introns of the sex-linked CHD1 gene, normally producing bands of different sizes from the Z and W chromosomes, such that males should yield one PCR band and females two. The P2/P8 PCR on Golden Nightjar yielded a single band of approximately 360 bp and the independent 2550F/2718R PCR yielded a single band of approximately 440 bp (Figure 3). At face value these data would suggest the bird was male. However the P2/P8 PCR is noninformative for

many species of non-passerines because the Z and W chromosome bands are often of too similar size to resolve on agarose gels (Griffiths et al. 1998 and pers. obs.). Whereas the 2550F/2718R PCR usually produces well separated bands from non-passerines of 650-750 bp from the Z chromosome and 440-480 bp from the W chromosome, in many species female samples only yield the shorter W chromosome product (Fridolfsson and Ellegren, 1999). In the case of the Golden Nightjar, the single band at ~440 bp is more consistent with a W chromosome product, hence we conclude that the bird is most probably genetically female, consistent with the plumage characteristics. However it remains possible that the morphological and plumage criteria are unreliable for determining sex. It is usually accepted that male nightjars do not develop a brood patch, but Camacho et al. (2014) found brood patches in breeding Red-necked Nightjars of both sexes, and it remains to be seen whether this might occur in other *Caprimulgus*. Biometric criteria for sexing Golden Nightjars used here were based on only 5 male and 5 female individuals (Fry et al. 1988) and secondary sexual features such as the size and number of the white patches in the rectrices and remiges are known to be extremely variable and may be subject to age-related and geographic variation (Forero et al., 1995; Forero and Tella 1997). In the case of Golden Nightjar, more samples of known sex are required to delimit the sexual, geographic and age-related variability of this species and to correlate with the results of molecular work.

Sequence data are not yet available for a further 18 of the 36 species currently included in *Caprimulgus* by Dickinson and Remsen (2013), eight of which have a substantially or completely African distribution. The semi-desert and scrubland-breeding Nubian Nightjar of northeast Africa and the Middle East shares generally pale plumage coloration and striking primary pattern of Golden Nightjar but our preliminary data analysis shows they are not sister species. Of the unsampled African species, (Freckled Nightjar *C. tristigma*, Slender-tailed Nightjar *C. clarus*, Prigogine's Nightjar *C. prigoginei*, Star-spotted Nightjar *C. stellatus*, Swamp Nightjar *C. natalensis*, Red-necked Nightjar *C. ruficollis*, Donaldson-Smith's Nightjar *C. donaldsoni* and the poorly known Nechisar Nightjar *C. solala*) none is intuitively more likely to be closely related to Golden Nightjar. The Star-spotted Nightjar is a semi-desert species with some plumage similarity to Golden Nightjar but is considered to possible form a superspecies with Plain Nightjar *C. inornatus* (del Hoyo et al. 1999). Further taxon sampling will be required to fully resolve sister relationships and patterns of evolution of species in this genus.

The phylogenetic trees in this study are broadly congruent with those produced previously in that all major strongly supported nodes in Han et al. (2000) are recapitulated, suggesting that the

strongly supported node linking Egyptian and Golden Nightjars (Figure 2) is robust. This study also provides further evidence of a breeding range extension of Golden Nightjar to include Western Sahara. The main breeding range of Golden Nightjar, from Senegal to the Sudan, closely matches the wintering range of Egyptian Nightjar (del Hoyo et al. 1999). If the two are indeed sister species then it is possible to speculate that their ancestral single species inhabited the desert and semi-desert zone of Africa and split into sedentary and migratory populations, that subsequently speciated. The relatively plain primary pattern Egyptian Nightjar contrasts strongly with the striking black and white patches of Golden Nightjar and may have evolved coincident with speciation, forming a pre-mating interspecific signal that acted as an accelerator for reproductive isolation.

Acknowledgements

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Table 1

Species	Cytb	COI
Caprimulgus eximius	LT671509	LT671510
Systellura longirostris	JQ988761	JN801536
Antrostomus vociferus	HQ696494	AY666512
Systellura longirostris	JQ988765	
Caprimulgus climacurus	GU586687	
Antrostomus saturatus	GU586657	
Antrostomus salvini	GU586656	
Antrostomus rufus	GU586655	JQ174302
Caprimulgus rufigena	GU586654	
Caprimulgus poliocephalus	GU586651	
Caprimulgus pectoralis	GU586650	
Caprimulgus nigriscapularis	GU586647	
Caprimulgus madagascariensis	GU586646	
Caprimulgus macrurus	GU586644	
Caprimulgus manillensis	GU586642	
Caprimulgus indicus	GU586640	
Caprimulgus fossii	GU586639	
Caprimulgus europaeus	GU586638	GU571785
Caprimulgus batesi	GU586636	
Caprimulgus affinis	GU586632	
Caprimulgus aegyptius	GU586631	JF498758
Antrostomus vociferus	GU586635	
Setopagis whitelyi	GU586659	JQ174303
Antrostomus ridgwayi	GU586653	
Setopagis parvula	GU586649	JQ174299
Hydropsalis maculicaudus	GU586645	JQ174294
Gactornis enarratus	GU586637	
Nyctidromus anthonyi	GU586633	
Caprimulgus carolinensis	FJ588442	JQ174284
Nyctipolus nigrescens	FJ588446	JQ174298
Hydropsalis cayennensis	FJ588444	JQ174285
Nyctibius grandis	GU586676	JQ175587

Accession numbers of DNA sequences used in this study.

Figure Legends

Figure 1. Female Golden Nightjar. A. Female Golden Nightjar, Aousserd Road, Western Sahara, 19 April 2016. **B**. Dry scrub habitat where Golden Nightjars were observed. **C.** The female Golden Nightjar *Caprimulgus eximius* sampled in this study, Oued Jenaa, Oued Ad-Deheb province of Western Sahara, 20 April 2016. **D**. Vascularised brood patch indicating local breeding.

Figure 2. Bayesian phylogeny of nightjars (beast analysis) based on cyt*b* (1008 bp) to identify the systematic position of Golden Nightjar. The tree was rooted with Great Potoo *Nyctibius grandis* as an outgroup. Support from posterior probabilities is indicated at nodes. See Table 1 for full scientific names and accession numbers.

Figure 3. Genetic sexing of Golden Nightjar. Lane 1: P2/P8 PCR. Lane 2: 2550F/2718R PCR. Lane 3: 100 bp ladder. Arrow: 500 bp.

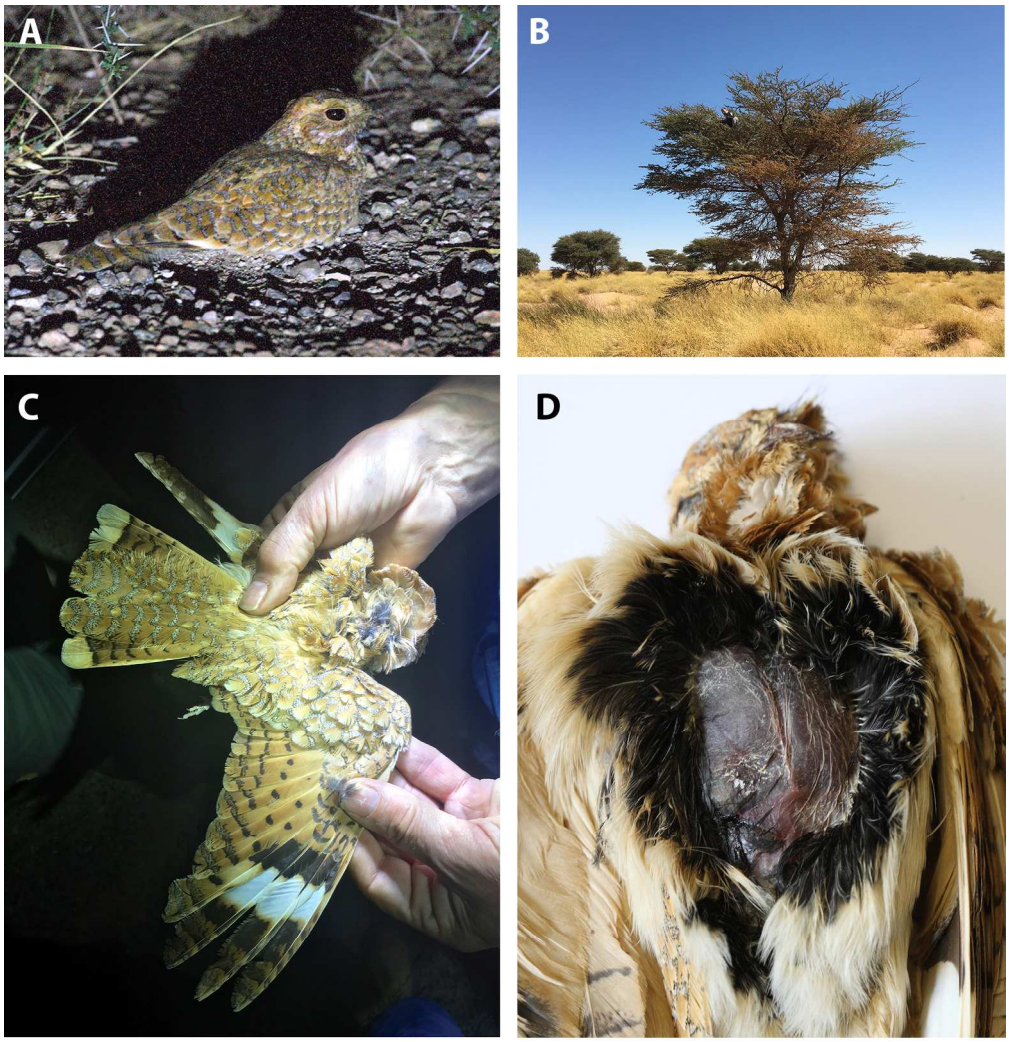

Figure 1. Female Golden Nightjar. A. Female Golden Nightjar, Aousserd Road, Western Sahara, 19 April 2016. B. Dry scrub habitat where Golden Nightjars were observed. C. The female Golden Nightjar Caprimulgus eximius sampled in this study, Oued Jenaa, Oued Ad-Deheb province of Western Sahara, 20 April 2016. D. Vascularised brood patch indicating local breeding.

171x177mm (300 x 300 DPI)

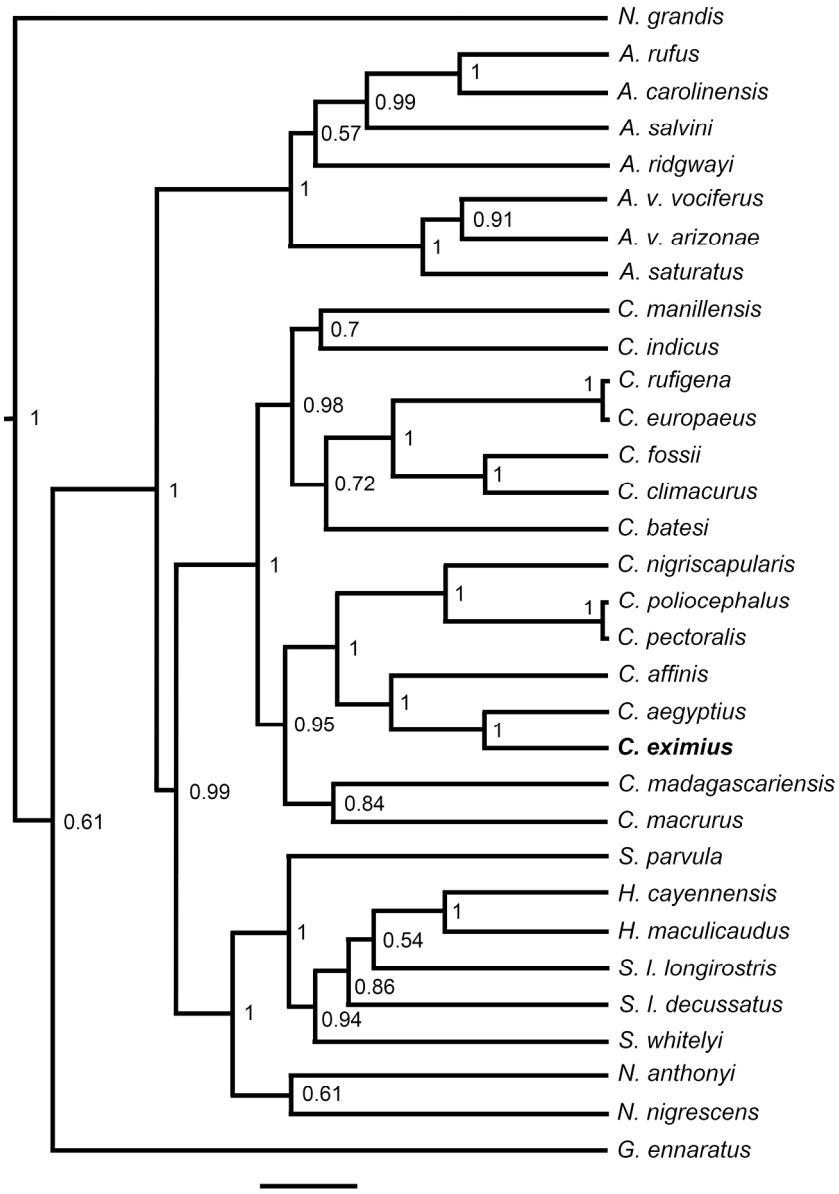

Figure 2. Bayesian phylogeny of nightjars (beast analysis) based on cytb (1008 bp) to identify the systematic position of Golden Nightjar. The tree was rooted with Great Potoo Nyctibius grandis as an outgroup. Support from posterior probabilities is indicated at nodes. See Table 1 for full scientific names and accession numbers.

200x281mm (300 x 300 DPI)

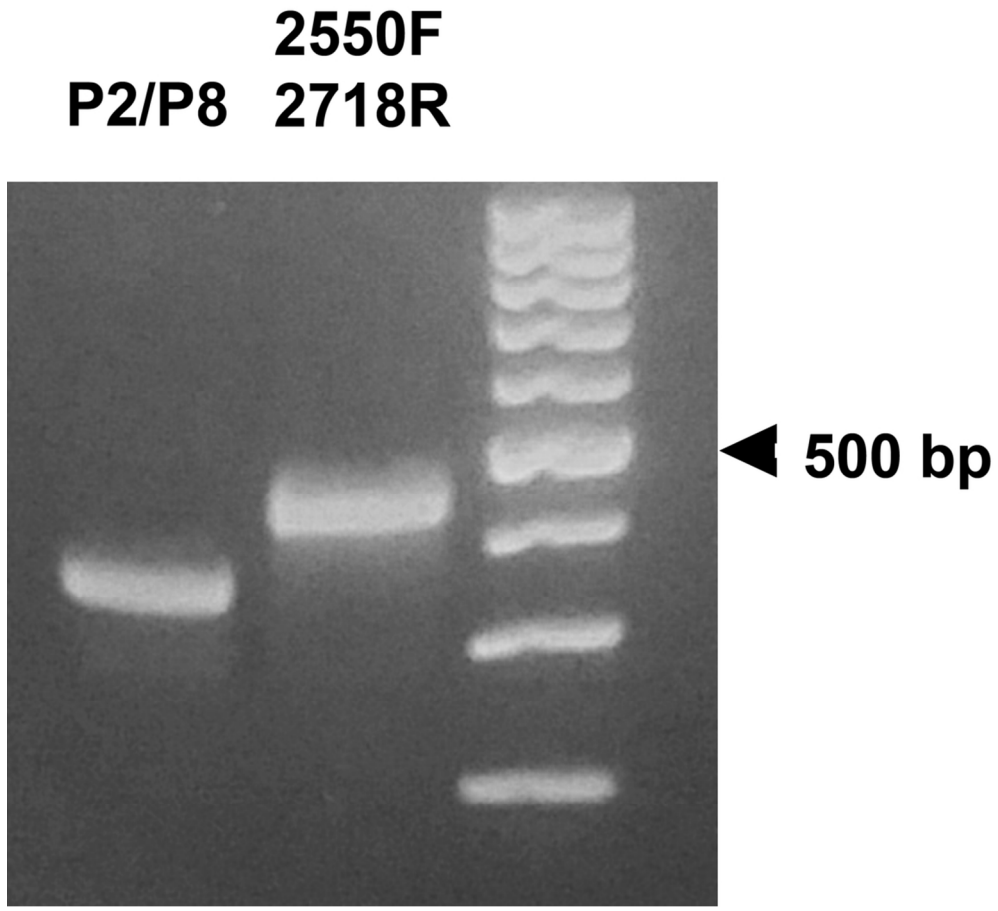

Figure 3. Genetic sexing of Golden Nightjar. Lane 1: P2/P8 PCR. Lane 2: 2550F/2718R PCR. Lane 3: 100 bp ladder. Arrow: 500 bp.

98x91mm (300 x 300 DPI)

The taxonomic position and breeding range of Golden Nightjar *Caprimulgus eximius* (Aves: Caprimulgidae)

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SUPPLEMENTARY MATERIAL

Figure S1

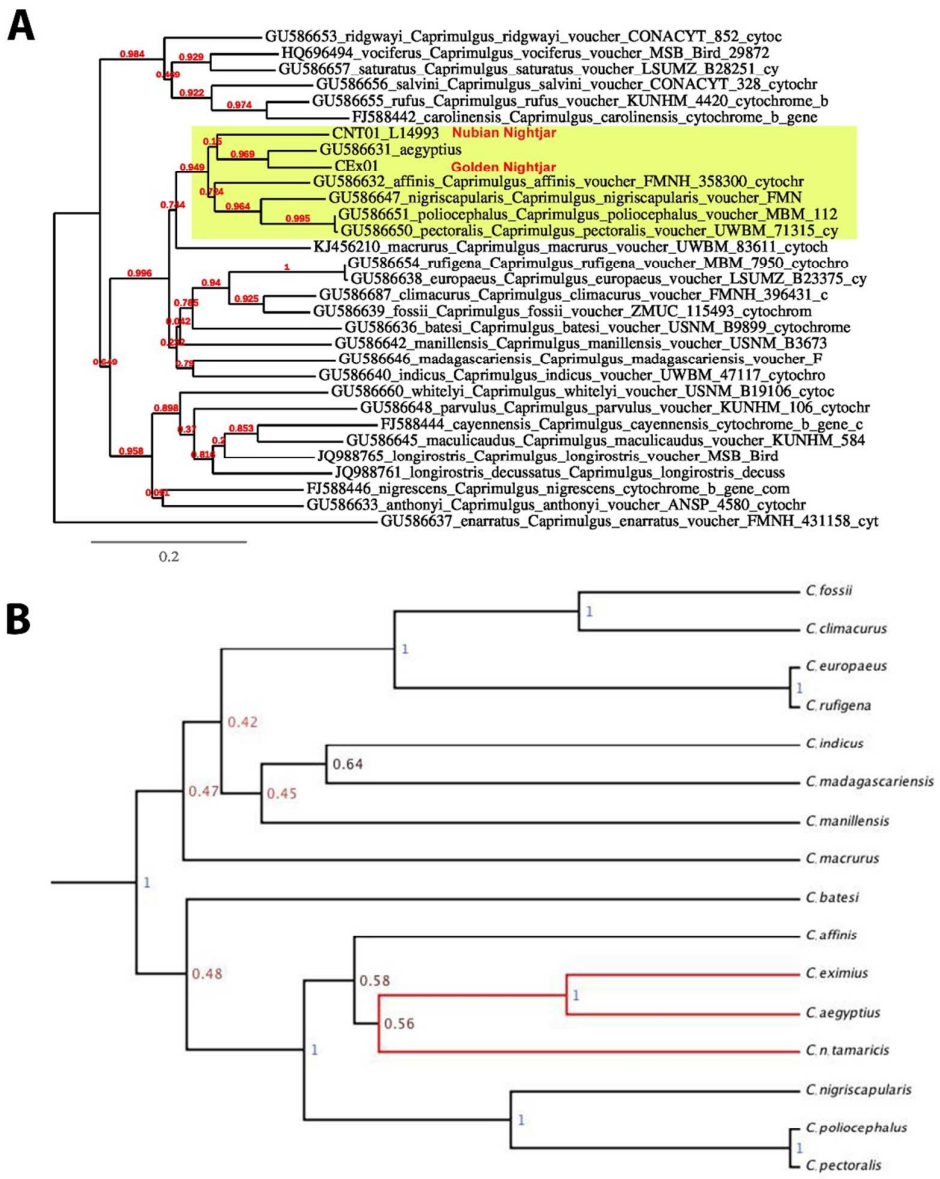

Figure Legend: A. Maximum likelihood tree based on 771 bp of cytb sequence to resolve position of Nubian Nightjar ('CNT01') relative to Golden Nightjar ('CEx01'). Alignments and phylogenetic reconstructions were performed with CLC Sequence Viewer (http://www.clcbio.com/products/clc-sequence-viewer/), PhyML (Dereeper et al., 2008) and TreeDyn (Chevenet et al., 2006) online using the South of France Bioinfomatics Platform (http://www.atgc-montpellier.fr/index.php?type=pg). **B.** Bayesian Inference tree using the same dataset with Golden, Egyptian and Nubian Nightjar *C. n. tamaricis* highlighted in red. See main text for details.

Figure S2

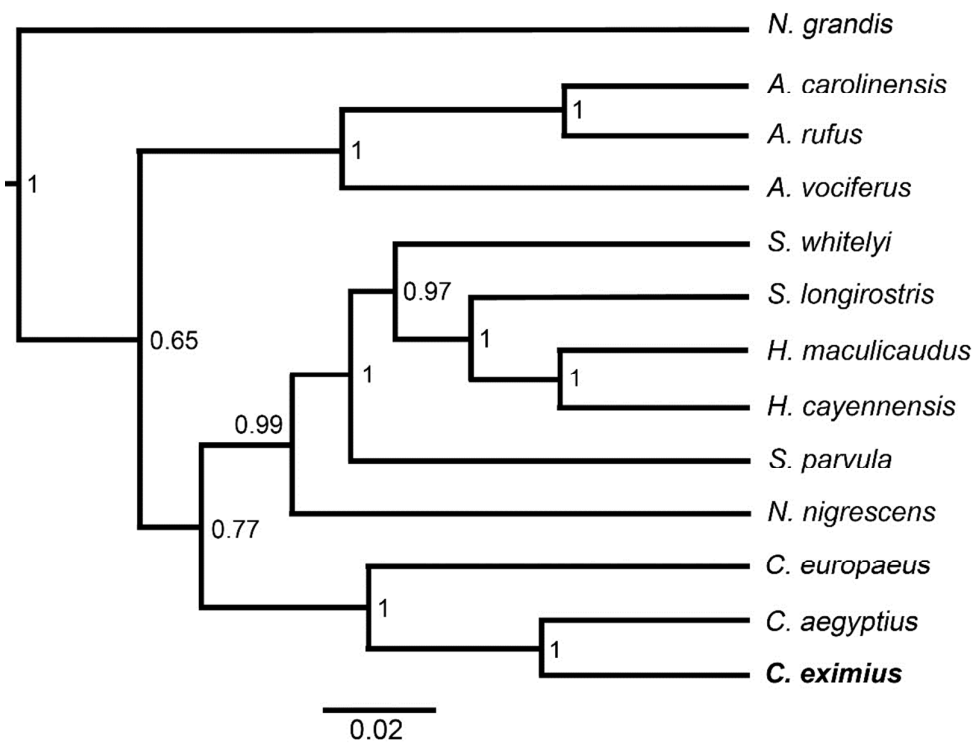

Figure Legend

Bayesian inference tree based on 1703 bp concatemer of cytb and COI for all relevant species for which both sequences were available. See main text for methodology.

Nubian Nightjar *Caprimulgus nubicus*

Partial cytb sequence will be completed and uploaded to GenBank as part of a future study of the systematics of this species.

TCTAGATCTGCCTAGCAACACAAATCCTAACCGGACTACTACTAGCTACACATTACACCGCAGACACAACCCTG
GCCTTCTCATCTGTTGCCCACACTTGCCGAAACGTACAATACGGCTGACTAATCCGTAATCTGCACGCAAATGG
AGCCTCACTCTTCTTCATTTGCATTTACCTCCACATTGGACGAGGCCTATACTACGGATCCTACCTCTACAAAGA
AACCTGAAACACAGGAGTAATCCTCTTACTCACCTTAATAGCAACAGCCTTCGTAGGCTACGTCCTACCATGAG
GACAAATATCATTCTGAGGGGCTACAGTCATCACCAACCTATTCTCAGCTATCCCATATATTGGCCAAACCCTT
GTAGAATGAGCATGAGGTGGATTTTCCGTAGACAACCCCACACTAACCCGATTTTTTGCCCTACACTTCCTCCT
TCCCTTTATAATTGCCGGCCTCACCCTAATCCACCTAACATTCCTCCATGAATCTGGCTCAAACAACCCCCTCGG
AATTGTATCAAACTGCGACAAAATTCCATTCCACCCCTATTTTTCCCTAAAAGACATCCTAGGCTTCGCACTAAT
ACTCACCCCATTAATAACACTCGCCATATTCGCCCCAAACCTGCTAGGGGACCCAGAAAACTTTACCCCAGCAA
ATCCCCTAGTCACACCCCCACATATCAAACCCGAGTGATACTTCCTATTTGCATACGCCATCTTACGCTCAATCC
CGAACAAACTAGGAGGTGTCCTAGCCC