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Species delimitation within the *Glaucidium brodiei* owlet complex using bioacoustic tools

Chyi Yin Gwee[1], James A. Eaton[2], Elize Y. X. Ng[1] and Frank E. Rheindt[1*]

Abstract

Background: The taxonomy of the Collared Owlet (*Glaucidium brodiei*) species complex is confused owing to great individual variation in plumage colouration seemingly unrelated to their distribution. Although generally recognised as a single species, vocal differences among the subspecies have been noted by field recordists. However, there is no study assessing the vocal differences among these four subspecies.

Methods: We obtained 76 sound recordings of the *G. brodiei* species complex comprising all four subspecies. We conducted bioacoustic examinations using principal component analysis and the Isler criterion to quantitatively test species boundaries within the *G. brodiei* complex. In addition, we compared plumage colouration among 13 specimens of the *G. brodiei* complex deposited at the Natural History Museum at Tring, UK and the Lee Kong Chian Natural History Museum, Singapore to ascertain the presence of plumage differences across taxa.

Results: We found the Bornean and Sumatran populations vocally similar to each other, but distinctly different from the mainland and Taiwan populations. The vocal pattern seems to corroborate plumage distinctions in the colouration of neck collars: the Bornean and Sumatran taxa share a white neck collar, whereas the continental and Taiwan taxa share a rufous neck collar.

Conclusions: We propose the taxonomic elevation of the Sumatran and Bornean populations to species level as Sunda Owlet *G. sylvaticum*, with one subspecies on Sumatra (*G. s. sylvaticum*) and Borneo (*G. s. borneense*) each. Our study corroborates the importance of bioacoustics in ascertaining species boundaries in non-passerines, and emphasises the significance of incorporating multiple species delimitation approaches when making taxonomic decisions.

Keywords: Borneo, Owl, Sumatra, Taxonomy, Vocalisation

Background

The genus *Glaucidium* consists mainly of small owl species, which are also known as owlets or pygmy owls. Owing to inter-specific plumage similarities, the taxonomy of this genus is confused, with a variation of 26 to 35 species recognised across different taxonomic treatments. Presently, approximately six species of *Glaucidium* owlets are recognised across Asia (Ritschard and Schweizer 2007; Dickinson and Remsen 2013; del Hoyo and Collar 2014). Among these, the taxonomic status of the Collared Owlet (*G. brodiei*) species complex is one of the most debatable among the Old World *Glaucidium*

owlets, with a discrepancy in treatments ranging from one (Dickinson and Remsen 2013; del Hoyo and Collar 2014; Gill and Donsker 2017; Clements et al. 2018) to two (Eaton et al. 2016) and possibly three species (Ritschard and Schweizer 2007). The species complex occurs in mostly montane and submontane forest (*G. b. brodiei* also occurs down to lowlands), and is widespread, with the taxon *brodiei* occurring from Afghanistan through the Himalayas to Central China and Southeast Asia, *sylvaticum* from Sumatra, *borneense* from Borneo and *pardalotum* from Taiwan Island (Fig. 1). Two other races, *tubiger* and *garoense* usually synonymised under the nominate subspecies, although *borneense* and *sylvaticum* have also been synonymised by König and Weick (2008).
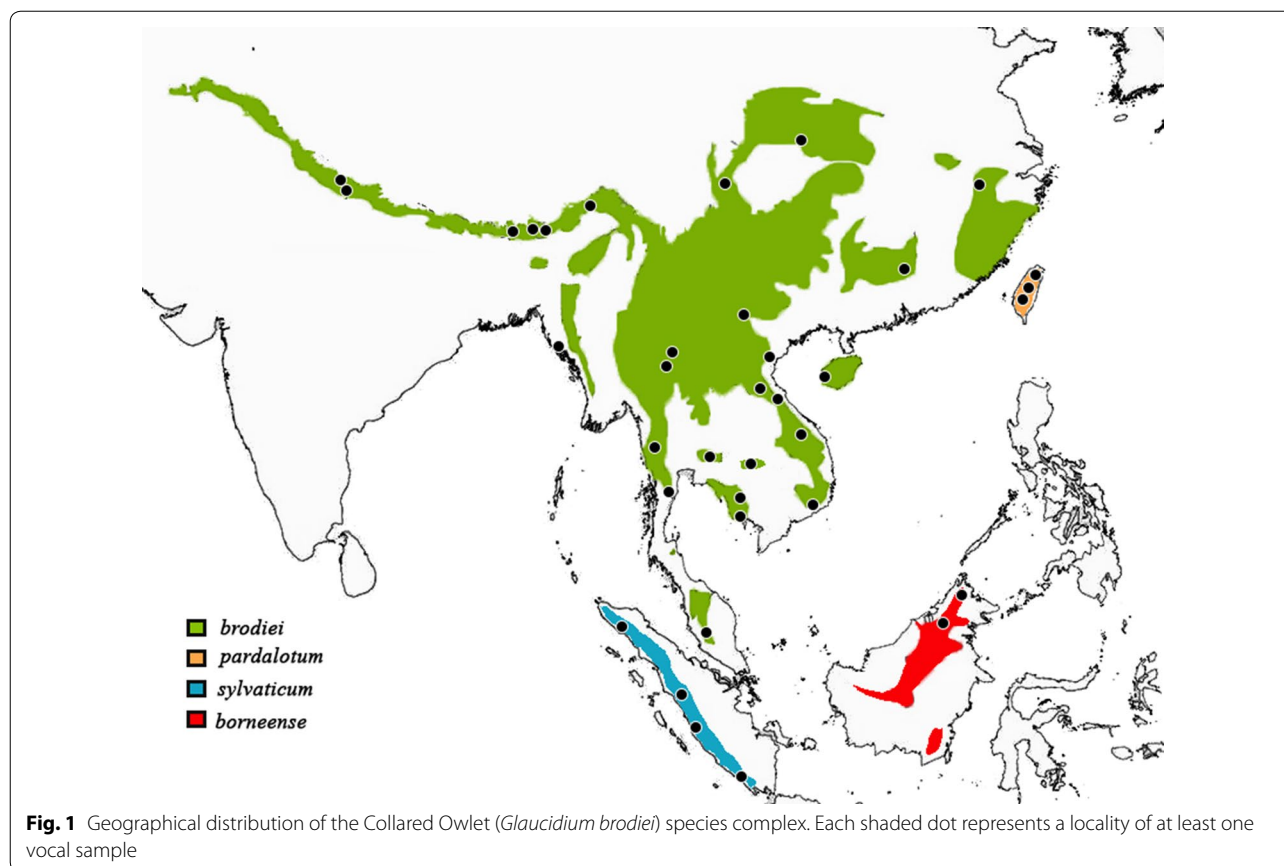
Discrepancies in the taxonomy of the *G. brodiei* species complex can be largely attributed to the variation of

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Fig. 1 Geographical distribution of the Collared Owlet (*Glaucidium brodiei*) species complex. Each shaded dot represents a locality of at least one vocal sample

plumage colours observed across individuals unrelated to their distribution (König and Weick 2008). Although these owlets were traditionally thought to exhibit true colour polymorphism (with grey and rufous morphs recognised), a study by Lin et al. (2014) suggests that this intra-specific variation in plumage colours may be age-dependent. At any rate, plumage comparison may be an unreliable species delineation tool for this group of owls and other species delimitation methods such as bioacoustics and genetics should be employed to accurately determine species boundaries within the *G. brodiei* complex. Furthermore, several studies have shown the pitfalls of relying solely on morphology in owl taxonomy, and the importance of bioacoustics in species delimitation of owls is well documented (König 1994; King 2002; Gwee et al. 2017).

Although regarded as a single species, vocal differences within the *G. brodiei* species complex have been noted by field observers. For example, Eaton et al. (2016) split the Sumatran and Bornean populations as a separate species from other members of the *G. brodiei* species complex based on notably different vocalisations, though quantitative analysis was unavailable. The pattern of species distribution proposed by Eaton et al. (2016) is

quite unusual as both islands have been repeatedly connected to the geographically intervening Malay Peninsula throughout the Pleistocene, suggesting the incidence of a leapfrog pattern (Remsen 1984) in which the terminal taxa *sylvaticum* and *borneense* are divided from peninsular *brodiei*. In the present study, we investigated potential species boundaries among each member of the *G. brodiei* species complex using bioacoustics as well as plumage comparison of museum specimens. These character suites allowed us to examine species delimitation in the complex in the absence of modern DNA material for the insular populations.

Methods

Vocal sampling and measurements

We collected a total of 76 sound recordings of the *G. brodiei* species complex from the online sound library xeno-canto (https://www.xeno-canto.org) and from our personal collection (see Additional file 1: Table S1). In order to avoid duplicate recordings of the same individual, only one out of all the samples recorded by the same person at the same site and time was used for the study. Each sound recording was measured using the default settings on Raven Pro 1.5 (Bioacoustics Research

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Program, Cornell Laboratory of Ornithology, Ithaca, NY, USA). We measured a total of 8 vocal parameters: (1) number of elements per motif, (2) duration of a motif, (3) lowest frequency in a motif, (4) highest frequency in a motif, (5) bandwidth (= highest minus lowest frequency), (6) duration of first break within a motif, (7) duration of second break within a motif, and (8) duration of breaks between motifs. A motif is defined as a complete song that a bird usually repeats several times, while an element is defined as an individual note in the song.

Vocal analyses

Rstudio version 1.1.453 (https://www.rstudio.com) and R version 3.5.0 (R Core Team 2018) were used to conduct principal component analysis (PCA) on the vocal dataset to distinguish clinal bioacoustic variation from discrete variation. Pairwise comparison of each vocal parameter between two taxa were done using the criterion outlined by Isler et al. (1998), henceforth referred to as the Isler criterion. The Isler criterion is based on two conditions: (1) there must be no overlap between the ranges of measurements between the two taxa being compared, and (2) the means ($\overline{x}$) and standard deviations (SD) of the taxon (*t*) with the smaller set of measurements (a) and the taxon with the larger set of measurements (b) have to meet the following requirement: $\overline{x}_a + t_a SD_a \leq \overline{x}_b - t_b SD_b$, where t_i refers to the one-tailed *t*-score at the 97.5th percentile of the *t* distribution for $n-1$ degrees of freedom. Although Isler et al. (1998) first applied this method for the species delimitation of suboscine antbirds, this criterion has also been employed across non-oscines such as pigeons (Rheindt et al. 2011; Ng et al. 2016; Ng and Rheindt,

2016), nightjars (Sangster and Rozendaal 2004), owls (Gwee et al. 2017), as well as oscines (Cros and Rheindt 2017; Prawiradilaga et al. 2017; Gwee et al. 2019).

Plumage and biometric comparisons

A total of 13 adult specimens, including five mainland *brodiei*, six Bornean *borneense*, one Sumatran *sylvaticum* and one Taiwan *pardalotum*, were inspected at the Natural History Museum at Tring, UK (NHM Tring) and the Lee Kong Chian Natural History Museum, Singapore (LKCNHM). Photographic evidence of each specimen was taken and relevant plumage traits, such as the colouration of underparts, upperparts and neck collar, were visually assessed across specimens. Additionally, wing and tail measurements of the six specimens from the LKCNHM were obtained by C.Y. Gwee. Given the small sample size, biometric analysis was restricted to a mere comparison of ranges, with no significance testing.

Results

Spectrograms of song examples from across the *G. brodiei* species complex reflect the stark vocal differences between populations from Borneo and Sumatra versus populations from mainland Asia and Taiwan (Fig. 2). The vocalisation of Bornean and Sumatran populations comprises seven notes per motif, in contrast to the four notes per motif vocalisation of mainland and Taiwan populations (Fig. 2).

PCA across eight vocal traits confirmed that Bornean *borneense* and Sumatran *sylvaticum* populations together form a cluster distinct from continental *brodiei* and Taiwan *pardalotum* populations (Fig. 3). This
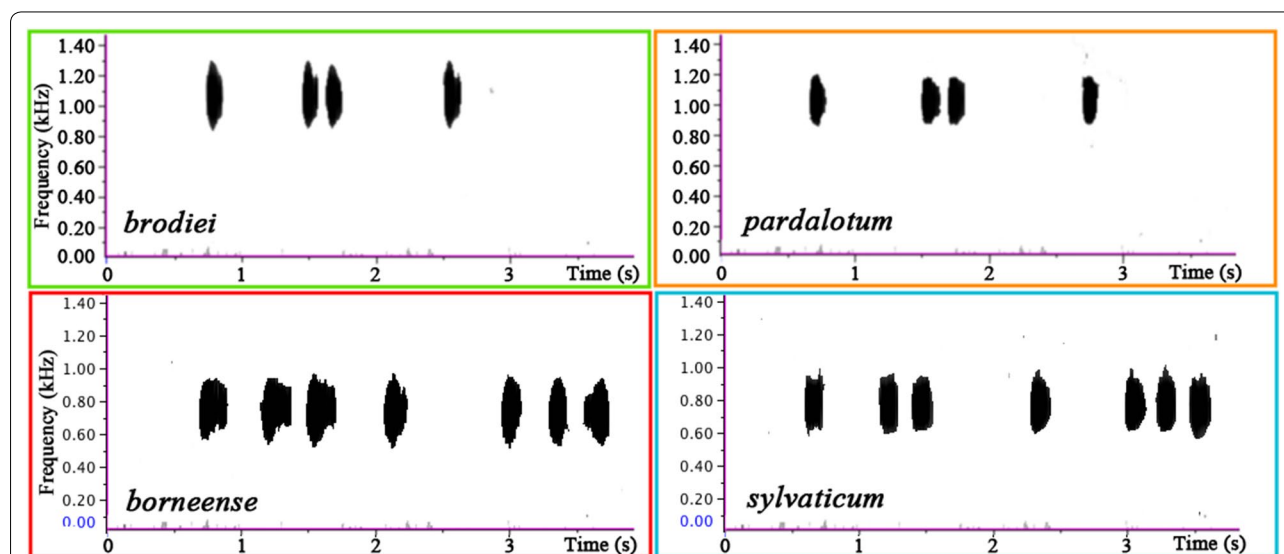
Fig. 2 Spectrograms of the vocalisation of each member of the *Glaucidium brodiei* species complex

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division was further corroborated by the Isler criterion results which showed at least two diagnosable vocal parameters between the Sundaic insular cluster and the other two taxa (Tables 1, 2). On the other hand, Bornean and Sumatran populations were vocally indistinguishable from each other (Fig. 3, Tables 1, 2). The mainland Asian and Taiwan populations were vocally indistinguishable, with large spatial overlap on PCA and an absence of any vocal parameter passing the
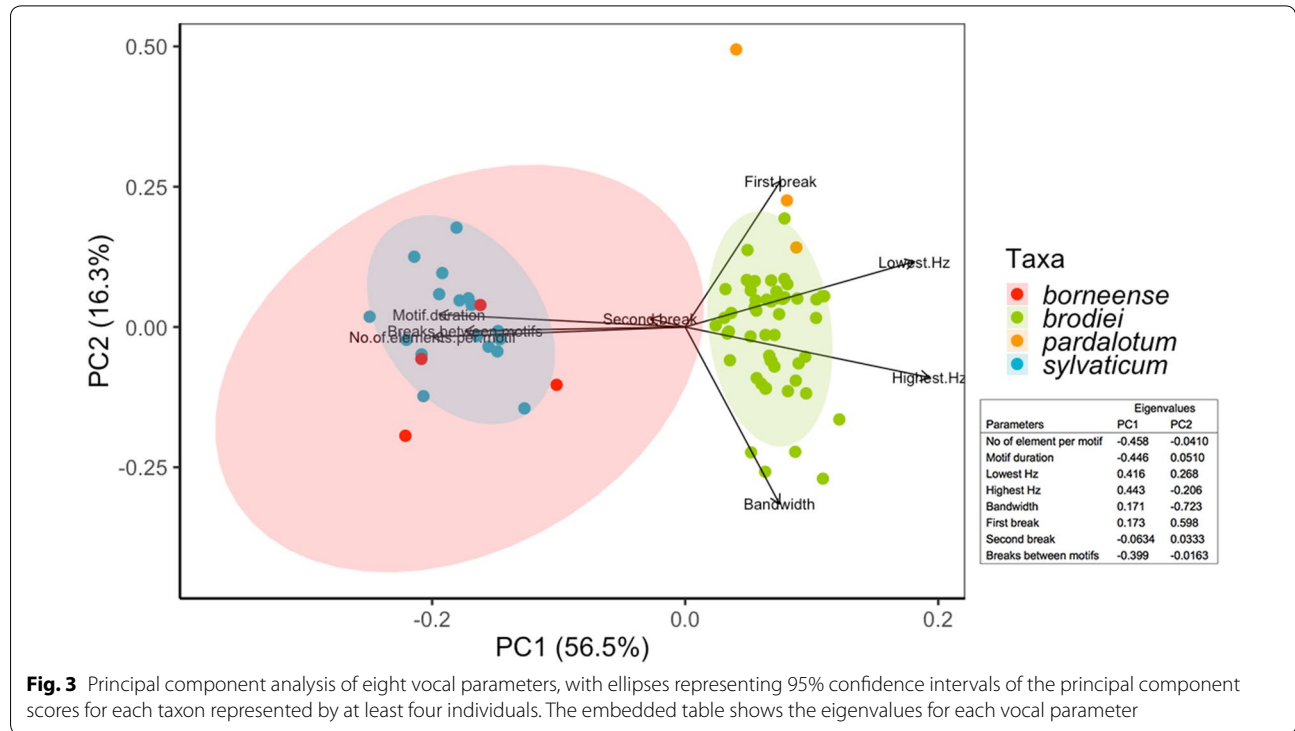
Fig. 3 Principal component analysis of eight vocal parameters, with ellipses representing 95% confidence intervals of the principal component scores for each taxon represented by at least four individuals. The embedded table shows the eigenvalues for each vocal parameter

Table 1 Mean and standard deviation of each vocal parameter across individual taxa

Taxon	a	b	c	d	e	f	g	h
sylvaticum	7.00 ± 0.00	3.05 ± 0.117	618 ± 39.6	959 ± 48.1	342 ± 60.1	0.382 ± 0.0481	0.115 ± 0.0158	17.8 ± 11.8
borneense	7.00 ± 0.00	2.83 ± 0.0771	614 ± 26.2	988 ± 76.8	374 ± 61.8	0.326 ± 0.0802	0.149 ± 0.0432	17.8 ± 13.8
brodiei	3.98 ± 0.139	1.41 ± 0.180	806 ± 53.0	1210 ± 56.7	400 ± 63.9	0.415 ± 0.0553	0.0953 ± 0.143	0.901 ± 0.223
pardalotum	4.00 ± 0.00	1.89 ± 0.00416	879 ± 42.3	1170 ± 97.6	290 ± 140	0.601 ± 0.0185	0.102 ± 0.0259	1.95 ± 0.116

The following parameters were assessed: (a) number of elements per motif, (b) duration of a motif, (c) lowest frequency, (d) highest frequency, (e) bandwidth, (f) first break length within a motif, (g) second break length within a motif, and (h) break length between motifs

**Table 2 List of vocal parameters identified as Isler diagnosable (denoted by 'X')**

	a	b	c	d	e	f	g	h
sylvaticum vs *borneense*								
sylvaticum vs *brodiei*	X	X		X				
sylvaticum vs *pardalotum*	X	X				X		
borneense vs *brodiei*	X	X	X					
borneense vs *pardalotum*	X	X						
brodiei vs *pardalotum*								

The following parameters were assessed: (a) number of elements per motif, (b) duration of a motif, (c) lowest frequency, (d) highest frequency, (e) bandwidth, (f) first break length within a motif, (g) second break length within a motif, and (h) break length between motifs

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threshold of diagnosability under the Isler criterions (Fig. 3, Table 2).

Plumage inspection of the 13 specimens from the NHM Tring and the LKCNHM revealed continental *brodiei* and

Fig. 4 **a** Upperparts and **b** underparts of *pardalotum* (1907.12.12.115), *brodiei* (86.2.1.683) and *borneense* (93.6.21.1) specimens, respectively, from the Natural History Museum at Tring, UK. **c** Upperparts of specimens from the Lee Kong Chian Natural History Museum, Singapore. First four specimens from left are *brodiei* (ZRC3.8606, ZRC3.8607, ZRC3.8610, ZRC3.8612), second from right is *sylvaticum* (ZRC3.8604) and rightmost is *borneense* (ZRC3.8603). All specimens show mainland *brodiei* has a rufous neck collar in contrast to the white neck collar in Sumatran *sylvaticum* and Bornean *borneense*

Taiwan *pardalotum* share a rufous neck collar, whereas Sumatran *sylvaticum* and Bornean *borneense* share a while neck collar (Fig. 4, Additional file 2: Fig. S1). Furthermore, biometric comparisons of specimens from the LKCNHM suggest *brodiei* has a slightly shorter wing (85 to 91 mm) than *sylvaticum* and *borneense*, though the latter two taxa were represented by only one specimen each (Table 3). On the other hand, the tail measurement of *brodiei* (44 to 57 mm) overlapped with that of *borneense* (52 mm). The tail length of the *sylvaticum* specimen was significantly shorter (29 mm), possibly due to tail moult. Given small sample sizes, no statistic comparison was attempted on the basis of our biometric measurements.
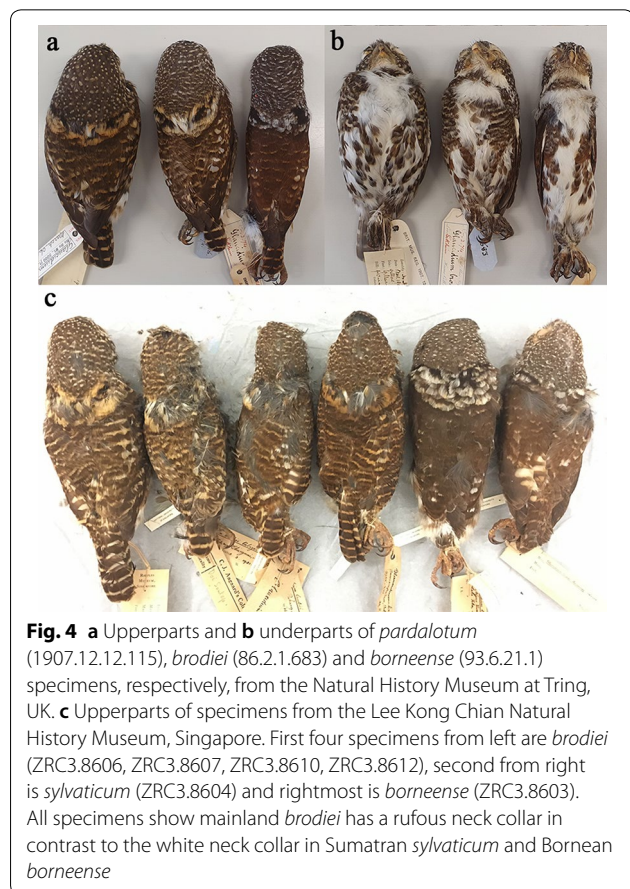
Discussion

Vocalisations and plumage agree on two species in the *G. brodiei* complex

The innate vocalisations of owls are an important taxonomic indicator of species limits as they are inherited and subject to strong pressure for mate selection in nocturnal birds (King 2002; Gwee et al. 2017). Our bioacoustic data reflected a stark contrast between the well-known homogenous four-note song separated only by short pauses from other motifs of the Collared Owlet throughout mainland Asia and the seven-note song widely separated from other motifs uttered by insular populations in Sundaland (Fig. 2). Similarly, plumage differences in these owlets, particularly the neck collar colouration, seem to mirror the vocal pattern (Fig. 4). Although Sharpe (1875) commented *sylvaticum* differs from *brodiei* by its "rufous brown back", we failed to observe this in specimen ZRC3.8604 (Fig. 4c). Given potential age-related plumage variation in *Glaucidium* owlets, we caution that such

Table 3 Specimen information and morphometric measurements, if any, of the *Glaucidium brodiei* complex collection from the Natural History Museum at Tring, UK and the Lee Kong Chian Natural History Museum, Singapore

Taxon	Voucher number	Sex	Locality	Wing measurement (mm)	Tail measurement (mm)
sylvaticum	ZRC3.8604	Female	Northeast Sumatra, Indonesia	105	29
borneense	ZRC3.8603	Male	Sarawak, Malaysia	107	52
borneense	1900.2.14.11	Male	Sarawak, Malaysia	–	–
borneense	95.11.15.57	Male	Sabah, Malaysia	–	–
borneense	98.11.24.62	Female	Sabah, Malaysia	–	–
borneense	93.6.22.3	Male	Sabah, Malaysia	–	–
borneense	93.6.21.1	Male	Sarawak, Malaysia	–	–
brodiei	ZRC3.8606	Female	Chiang Mai, Thailand	91	57
brodiei	ZRC3.8607	Male	Chiang Mai, Thailand	88	50
brodiei	ZRC3.8610	Male	Pahang, Malaysia	85	44
brodiei	ZRC3.8612	Female	Pahang, Malaysia	91	53
brodiei	86.2.1.683	Male	Sikkim, India	–	–
pardalotum	1907.12.12.115	Male	Mt Ho Ho, Taiwan, China	–	–

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plumage comparisons should be conservatively regarded (Ritschard and Schweizer 2007; Lin et al. 2014). Our biometric results seem to suggest *sylvaticum* and *borneense* have a greater wing length than *brodiei* regardless of their sex (Table 1). However, the measurements in Sharpe's (1875) record show the wing length of *sylvaticum* (3.8 in.) and *borneense* (3.65 in.) overlapped with the female *brodiei* (3.6 to 3.8 in.) which are greater than the male *brodiei* specimens (3.2 to 3.4 in.). Nevertheless, the distinct vocalisations and consistent neck collar colouration pattern of the Sunda Owlet support an elevation of *G. sylvaticum* to species status, with the junior Bornean taxon *G. s. borneense* to be reclassified as a subspecies of *G. sylvaticum* based on the Principle of Priority (ICZN 1999: Art. 23.1).

Unusual biogeographical divide

The Isthmus of Kra is a prominent biogeographical and avifaunal divide between northern Southeast Asian monsoon forests and equatorial Sundaic rainforests (Hughes et al. 2003). Numerous Oriental bird species pairs are characterised by a more monsoon-adapted northern and rainforest-adapted southern species that abut somewhere around this transition zone, including owl pairs such as Sunda Scops Owl (*Otus lempiji*) versus Collared Scops Owl (*O. lettia*), and Spot-bellied Eagle Owl (*Bubo nipalensis*) versus Barred Eagle Owl (*B. sumatranus*). However, in the case of the Collared Owlet complex, the Sundaic population from the Thai-Malay Peninsula is vocally and morphologically undifferentiated from the more northerly monsoon populations, generating an unusual division between continental (Peninsula Malaysia and other parts of mainland Asia) versus archipelagic populations (Sumatra and Borneo). Despite regular linkage through Quaternary land bridges via the geographically intervening Malay Peninsula (Bintanja et al. 2005), the islands of Sumatra and Borneo are known to share multiple montane and submontane species which are absent on the continental mainland. This pattern is observed in the Collared Owlet complex, as well as other avian species such as Rajah's Scops Owl (*Otus brookii*) and Black-capped White-eye (*Zosterops atricapilla*).

Differentiation of Taiwan population

While our bioacoustic data did not support distinct divergence between Taiwan *pardalotum* and continental *brodiei* (Tables 1, 2), we note that one of the three sound recordings of *pardalotum* was quite different from continental *brodiei* (Fig. 3). More samples are required to ascertain whether this vocal difference is clinal as Taiwan forms a continuous landmass with the mainland during the Pleistocene glaciation, or that sample was an anomalous recording. Although the *pardalotum* specimen

seems to have a darker brown upperpart than the *brodiei* specimens (Fig. 4), intra-specific plumage variation may be present (Ritschard and Schweizer 2007; Lin et al. 2014). Furthermore, Sharpe (1893) found the two taxa to be indistinguishable in plumage during specimen inspection. Therefore, we propose that Taiwan *pardalotum* be retained as a subspecies of *G. brodiei*.

Conclusions

Our study leads to a taxonomic division of an important and well-known Asian owl species complex into two resultant species on the basis of bioacoustic and morphological data. It is therefore one of numerous contributions that highlight the importance of bioacoustics as a tool for species delineation in Strigiformes, which are often challenging to identify by plumage due to age-related or ecomorphological variation (König and Weick 2008; Lin et al. 2014; Mikkola 2014; Sadanandan et al. 2015; Gwee et al. 2017). Modern genetic materials of owl species can be difficult to obtain due to their elusive behaviours and ancient genetic materials can be challenging to work with, thus bioacoustics serve as a reliable tool to scan for cryptic diversity in the absence of genetic data. Future studies can look into using molecular tools to investigate the level of genetic divergence within the *G. brodiei* species complex, as well as playback experiments to assess species recognition between the Sunda Owlet and Collared Owlet (Freeman and Montgomery 2017). In conclusion, we found vocal evidence further supported by plumage comparisons differentiating the insular Sumatran and Bornean taxa from the mainland and Taiwan taxa. We thereby propose the elevation of *G. sylvaticum* to species status under the common name Sunda Owlet.

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s40657-019-0175-4.

Additional file 1: Table S1. Information of all recordings used in the study and measurements of all vocal parameters.

Additional file 2: Fig. S1. Photos of all *borneense* specimens inspected at the Natural History Museum at Tring, UK.

Authors' contributions

CYG analysed the vocal data and was the main contributor in writing the manuscript. JAE acquired and measured the sound recordings. EYXN interpreted the results. FER designed the research. All authors read and approved the final manuscript.

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