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Species-distinctiveness in the vocal behaviour of six sympatric bulbuls (genus *Pycnonotus*) in South-East Asia

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Abstract. Bulbuls (Passeriformes : Pycnonotidae) are a biodiverse group of birds that produce a variety of vocalisations, yet the vocal behaviour of most bulbuls has not been formally described or the subject of bioacoustical study. We present the first detailed descriptions of the song and singing behaviours of six species of bulbul in the genus *Pycnonotus*, based on recordings of birds in mixed-species flocks in the tropical forests of northern Thailand. All six species are frugivores that often forage together in the same fruiting tree. We compared nine fine structural features of the songs of these species to understand the vocal behaviour of each and the potential importance of vocalisations in species recognition in these mixed-species flocks. Our analyses reveal substantial differences in the structure of songs as well as marked differences in singing behaviour between species. Discriminant function analysis readily distinguishes the songs of the six species based on structural differences. Discriminant function analysis of species with the most similar plumage features (as assessed by human observers) readily distinguishes between phenotypically similar pairs of congeners. Our results provide evidence that vocalisations may be important in species recognition and as species-isolating mechanisms between closely related and sympatric *Pycnonotus* bulbuls. The species-typical features described here may be helpful to biologists and conservationists, particularly as several species of bulbul are of conservation concern.

Additional keywords: bird song, mixed-species flocks, Pycnonotidae, species recognition.

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Introduction

Bird song is important in territorial defence and mate-attraction and, consequently, it is important in speciation as a pre-mating isolation mechanism (Grant and Grant 1996; Slabbekoorn and Smith 2002; Catchpole and Slater 2008). Differences in vocalisations can serve to distinguish between different individuals (e.g. Brooks and Falls 1975), different populations (e.g. Koetz *et al*. 2007; Petrusková *et al*. 2010) or different species (e.g. Kirschel *et al*. 2009; Tobias and Seddon 2009). These differences arise from many factors, for example, vocal differentiation can result from acoustical adaptations to different habitats (Slabbekoorn and Peet 2003; Wood and Yezerinac 2006), differences in morphology (Podos 2001) or through spontaneous changes during the process of learning or cultural drift (Grant and Grant 1996).

Distinctive features of song enable birds to recognise each other as the same species and to make appropriate decisions about mates and territorial defence (Slabbekoorn and Smith 2002; Grether *et al*. 2009). Several previous studies suggest that assortative mating based on song can help to maintain population boundaries and lead to further speciation by preventing interspecific hybridisation (Patten *et al*. 2004; Ruegg *et al*. 2006). Song may be influenced by interspecific competition between different species, particularly for species that live in sympatry and share the same habitat. Sympatric species may show acoustical convergence for some signals, and divergence in other signals (e.g. Tobias and Seddon 2009). As a pre-mating isolation mechanism, species-specific song should reinforce recognition between closely related species or, at a minimum, differentiate between similar species to limit hybridisation, otherwise confusion in communication would reduce the fitness of both sender and receiver (Price 1998; Beckers and ten Cate 2001; Slabbekoorn and Smith 2002; Kirschel *et al*. 2009).

The *Pycnonotus* bulbuls (Aves : Pycnonotidae) are a diverse group of small passerines comprising 45 species, many of which live in sympatry and share common food resources (Fishpool and Tobias 2005; Woxvold *et al*. 2009). They are Asiatic birds, and they are understood to be distinct from their African counterparts based on molecular research (Moyle and Mark 2006; Pasquet *et al*. 2006). They are widely distributed throughout Asia, especially in the tropical forests of South and South-East Asia where vegetation diversity is very high (Fishpool and Tobias 2005). They are non-migratory, arboreal frugivores and live in various habitats, including scrub forest, bamboo forest, deciduous forest, broadleaf evergreen forest and coniferous forest. Bulbuls are a dominant frugivore in South-East Asia, foraging mainly on plant foods (leaves, ripe or unripe fruit and nectar; Corlett 1998; Kitamura *et al*. 2002; Wydhayagarn *et al*. 2009) and, very rarely, animal foods (insects and small lizards; Bhatt and Kumar 2001). They play an important role as seed dispersers in both mature and secondary forest (Corlett 1998; Kitamura *et al*. 2002; Wydhayagarn *et al*. 2009). Bulbuls often assemble in mixed-species flocks and feed together on highly productive fruit plants, especially when fruits are abundant (Sanitjan and Chen 2009; Wydhayagarn *et al*. 2009; Sreekar *et al*. 2010). During the non-breeding season, groups may contain as few as 10 or as many as several hundred individuals. Birds occur in smaller flocks or pairs during the breeding season.

Pycnonotus includes many highly vocal species. They are capable of producing a broad variety of sounds (Fishpool and Tobias 2005), although most of their sounds have only been described anecdotally, without any quantitative bioacoustical detail. Many birds in the genus produce complex vocalisations that are aesthetically appealing to humans. Consequently, many species have become popular cage-birds. For example, the wild population of Straw-headed Bulbuls (*P. zeylanicus*), which may have the most melodious song of the genus, is in extreme decline and may soon be extirpated from Thailand owing to the combination of trapping for the cage-bird trade and loss of habitat (Fishpool and Tobias 2005). Similarly, Red-whiskered Bulbuls (*P. jocosus*) are prized as cage-birds and are used in song competitions (Anderson 2005). Although escaped or released cage-birds have formed stable populations in other parts of the world (e.g. Carleton and Owre 1975, Amiot *et al*. 2007), they have become an increasingly threatened species in parts of their native range in Thailand.

In this study, we investigate the acoustical features of the songs of six sympatric species of *Pycnonotus* bulbul. We provide a detailed bioacoustical analysis of the song of all six species, and evaluate whether these species are distinguishable on the basis of song, particularly between pairs of species with similar plumage characters. These species provide an interesting system for evaluating acoustical divergence because they overlap in range and often associate in mixed-species flocks, but there have not been detailed acoustical descriptions or empirical comparisons of their vocalisations. All six species that we have studied are closely related, based on molecular data (Moyle and Mark 2006; Pasquet *et al*. 2006), and field observations confirm that all six species produce songs while defending resources from both conspecifics and other animals at flowering and fruiting trees. Based on the expectation that songs convey species-specific information, we predicted that song differentiation would occur between sympatric species, and that the most closely related species – where hybridisation should be most likely to occur – would be distinguished by the greatest differences in song structure. We also predicted that vocal distinctiveness would be greatest between species that are most often encountered together in mixed species flocks.

Materials and methods

Study site

Recordings were collected at two study sites in northern Thailand in the Chiang Dao Wildlife Sanctuary near the Chiang Dao Wildlife Research Station (19°21′N, 98°55′E) and on the campus of Chiang Mai University (18°48′N, 98°57′E). The altitude of these sites ranges from 300 to 700 m above sea level. The typical vegetation at Chiang Dao Wildlife Research Station is bamboo-deciduous, hardwood seasonal forest, and has many woody vines and abundant seedlings and saplings, as well as several species of bamboo (Ngoenjun and Sitasuwan 2009). The Chiang Mai University campus is an urban area where the typical vegetation is hardwood bamboo forest and deciduous, seasonal hardwood forest (Vaidhayakarn and Maxwell 2010). We collected sound recordings throughout an area of ~4 by 4 km at both sites.

Study species

We studied six sympatric tropical bulbuls, all in the genus *Pycnonotus*: Black-headed Bulbul (*P. atriceps*), Black-crested Bulbul (*P. flaviventris*), Streak-eared Bulbul (*P. blanfordi*), Stripe-throated Bulbul (*P. finlaysoni*), Red-whiskered Bulbul (*P. jocosus*) and Sooty-headed Bulbul (*P. aurigaster*). All six species occur in sympatry in seasonal tropical forest habitats at lower elevations in northern Thailand (Lekagul and Round 1991; Robson 2000). In the non-breeding season these birds usually forage in the same general area, and all six species are sometimes found in the same flowering or fruiting tree (S. Kamtaeja, unpubl. data). During the breeding season, birds spend most of their time close to their mate, and this is the only time of year when birds can be found outside of mixed foraging flocks. Previous studies indicate that bulbuls have small home-ranges associated with the fruiting trees (Fukui 1995; Sankamethawee *et al*. 2010).

Molecular data indicate these species are genetically related (Moyle and Mark 2006; Pasquet *et al*. 2006) and they share many similarities in behaviour, foraging techniques and diet (S. Kamtaeja, unpubl. data). These species are easily distinguished by plumage, as described in Lekagul and Round (1991), Robson (2000), and Fishpool and Tobias (2005). The six species can be separated into three morphological forms (see Figs 1, 2 for artist's depictions): (1) the 'yellow bulbuls' have bright yellow body parts and glossy black heads, and include Black-headed and Black-crested Bulbuls; (2) the 'plain bulbuls' are brownish-grey over the whole body and less elaborately ornamented than the other two groups, and include Streak-eared and Stripe-throated Bulbuls; and (3) the 'brown bulbuls' have a predominantly dull-brown body and a black head, and include Red-whiskered and Sooty-headed Bulbuls. We selected these six species for paired comparisons because, as well as their similar behaviour and diet (S. Kamtaeja, unpubl. data, as above), they form three pairs of visually similar species, at least from a human perspective.

Some ideas tested in this study rest on the assumption that all six species of bulbul interact with each other in sympatry. Our field observations confirm that this is the case. When collecting field recordings, we routinely encountered foraging groups comprising different combinations of the six species, confirming that they co-occur in mixed flocks. Our field observations suggest there is some partial segregation by micro-habitat: Black-headed and Black-crested Bulbuls were regularly found together in mature forests where the vegetation is dense and of multiple storeys; Streak-eared and Stripe-throated Bulbuls were often found together in the thicker understorey of deciduous forest

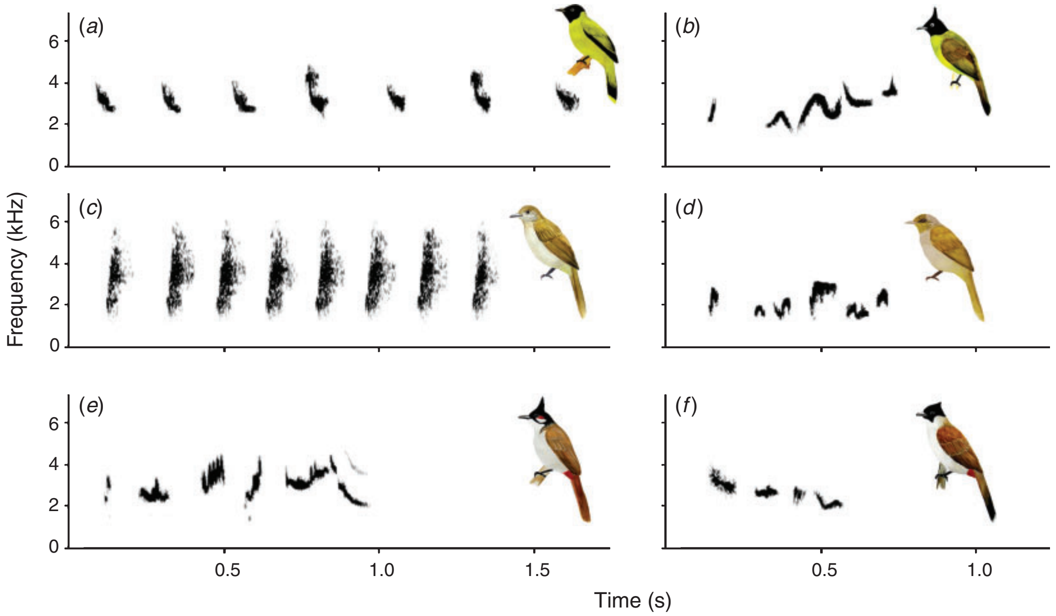

Fig. 1. Sound spectrograms (time *v*. frequency) showing the typical song recorded from each of six species of *Pycnonotus* bulbul in northern Thailand: (*a*) Black-headed Bulbul; (*b*) Black-crested Bulbul; (*c*) Streak-eared Bulbul; (*d*) Stripe-throated Bulbul; (*e*) Red-whiskered Bulbul and (*f*) Sooty-headed Bulbul.

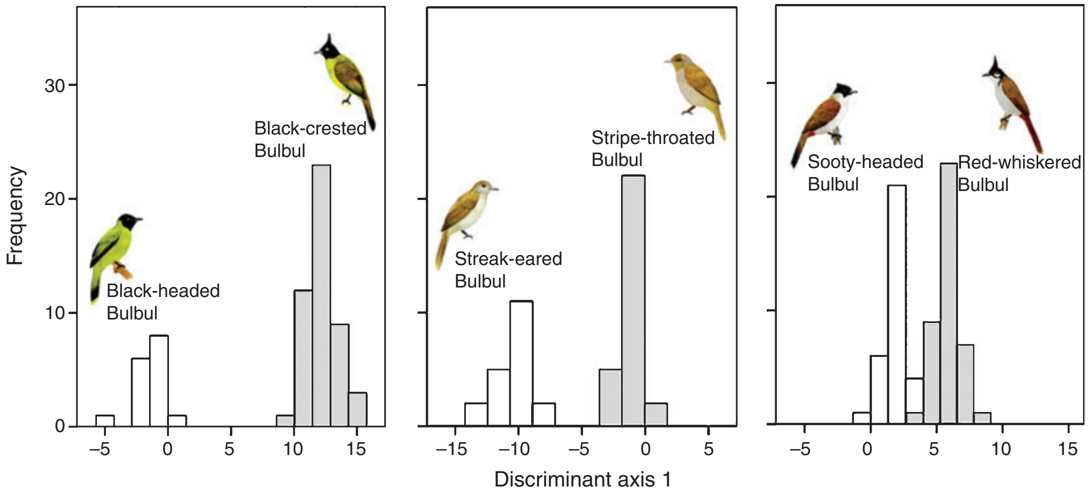

Fig. 2. Histograms showing the discriminant scores for pairwise comparisons of *Pycnonotus* bulbuls that share similar plumage and bare part features, based on three separate discriminant analyses of nine structural features of songs.

and secondary forest close to urban areas; and although Stripe-throated Bulbuls were not found in urban areas, Red-whiskered and Sooty-headed Bulbuls were often found together in urban areas with occasional occurrences in mature forest habitat.

Recordings of songs

We defined the 'songs' of each species as a repeated series of stereotyped elements, produced by one bird, often while singing from a post at the top of a tree or shrub. Songs were separated from other songs by a silent interval of >0.5 s. Within songs, we defined an 'element' as a continuous trace on a sound spectrogram (Thompson *et al*. 1994; Riebel and Slater 2003; Cardoso and Price 2010). Songs were the most conspicuous vocal signal in all six *Pycnonotus* species. For all six species, songs were common during the breeding period, and were less common, but still heard, outside the breeding period. This seasonal pattern is consistent with what is known of two other related species that have been studied previously (Red-vented Bulbul (*P. cafer*), Kumar 2004; Bare-faced Bulbul (*P. hualon*), Woxvold *et al*. 2009) and what is generally the pattern for many tropical birds (Stutchbury and

Morton 2001). We could not determine the sex of the recorded birds in this study because all six species are sexually monomorphic. Although size dimorphism might be used to distinguish male and female Red-whiskered Bulbuls in the hand (females are slightly smaller; Amiot *et al*. 2007), differentiating between subtle size differences is difficult in the field.

We recorded birds while they fed together on fruiting plants, often in large mixed-species flocks, between 0600 and 1800 hours during all months of the year, between January 2008 and April 2010. We visited both study sites on at least 2 days every month. Birds were recorded with digital recorders (Marantz PMD661, D&M Professional, Kanagawa, Japan, and EDIROL R-09, Roland, Swansea, UK), using the built-in microphone of each unit (frequency responses of 20–24 000 Hz and 20–22 000 Hz respectively). Files were recorded as 16-bit WAV files at a sampling frequency of 44.1 kHz. All birds were recorded from as close as possible, with distances between the recorder and the bird ranging from 10 to 15 m.

To record as many individuals as possible, we travelled around these sites recording birds opportunistically. Recordings were made continuously from the time we first encountered a singing bird or a flock of birds, until birds stopped singing or moved to a different location. When recording birds in mixed flocks, we recorded one or two individuals of each species, for as many species present as possible, distinguishing between individuals on the basis of their position in the vegetation. Based on their position, we ensured that each recording represented a different individual, and we rejected recordings if it was not clear whether they came from unique individuals. We then moved 300–500 m to a new recording location. In this study, of unbanded birds, we considered a separation distance of 300–500 m to be adequate for sampling different groups of bulbuls, based on previous studies that report the home-range diameters of congeneric bulbuls as 200–300 m (e.g. 225 m in Olive-winged Bulbul (*P. plumosus*), 300 m in Cream-vented Bulbul (*P. simplex*), Peh and Ong 2002), and also for another bulbul genus (311 m in Puff-throated Bulbul (*Alophoixus pallidus*), Sankamethawee *et al*. 2010).

All six species are abundant at our study sites, with hundreds of birds of each species at both. We made the assumption that the birds recorded at each location in each month were an independent sample and that each recording location (300–500 m apart) contained unique individuals of each species. In each month, we recorded from different localities inside the 4 × 4-km study sites, avoiding repeated recordings from the same species at the same location. In a few cases where we recorded multiple birds from similar locations (<500 m apart), we calculated an average value for that species at that location.

Owing to a current lack of research on these species, it is unclear what times of the year correspond to mixed-species flocking behaviour or territorial behaviour in the six species we studied. A recent study of Puff-throated Bulbuls showed that birds live in pairs or social groups of 2–7 individuals and defend territories year-round; the average size of groups during the breeding season was 3.2 birds, increasing to 4.1 birds during the non-breeding season (Sankamethawee *et al*. 2010). In the *Pycnonotus* bulbuls we studied, we found that birds were often found in pairs during what we assumed was the breeding season (based on six nests we found for four of the species we studied), and in groups of up to >100 birds per flock in non-breeding season. We found roosting sites of birds with 100–200 birds per group. Given the extremely different group sizes between the breeding and non-breeding season, we conclude that birds do not defend territories year-round.

All recordings were visualised using Syrinx-PC sound analysis software (J. Burt, Seattle, WA). We generated sound spectrograms of all field recordings and used the time and frequency cursors to select and annotate sounds of interest. We estimated the signal-to-noise ratio of each recording by assigning it a value between 1 and 3 (1, low quality signal containing high level of background noise that impaired parameter measurement; 2, signal of moderate quality with some background noise but sufficient signal strength for structural analysis; 3, good quality recording with little background noise). The songs chosen for fine structural analysis were of rating 2 or 3.

We analysed song structure using SASLab Pro (*v*. 4.40; Avisoft Bioacoustics, Berlin). For each song we generated a spectrogram (512 points, 87.5% overlap, FlatTop window, time resolution 2.9 ms, frequency resolution 22 Hz). We measured nine fine structural features: (1) song duration, the length of entire song (s); (2) maximum frequency of the entire song (Hz); (3) minimum frequency of the entire song (Hz); (4) duration of elements, expressed as an average for all elements per song (s); (5) maximum frequency of each element, as an average of all elements per song (Hz); (6) minimum frequency of each element, as an average of all elements per song (Hz); (7) duration of the longest element (s); (8) average interelement interval (s); and (9) the number of types of element within a song; elements of a song were considered to be different types when they had a different shape, duration or frequency range. Illustrations of four of these fine structural features are summarised in Fig. 3. All measurements were made using the automatic parameter measurements feature of SASLab Pro to minimise the influence of human subjectivity (hold time: 20 ms; amplitude relative to maximum: –20 dB). Measured song elements were checked by eye using the red cursors in SASLab Pro to ensure accurate measurements of the target signal; in rare cases that background noise at different frequencies appeared to influence the automated parameter measurements, we used the eraser tool in SASLab Pro

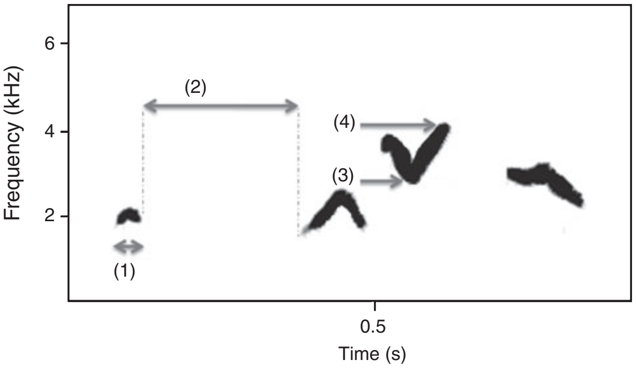

Fig. 3. Sound spectrogram (time *v*. frequency) of the song of a Black-crested Bulbul demonstrating four of the acoustical features that we measured from sympatric species of *Pycnonotus* bulbuls: (1) duration of element; (2) interelement interval; (3) minimum frequency and (4) maximum frequency. All measurements were collected using the automatic parameter measurements feature of SASLab Pro (Avisoft Bioacoustics).

to remove the background noise to ensure that they did not interfere with the automated signal measurements. We inspected these nine variables for possible multicollinearity by examining variance inflation factors. Variance inflation factors that exceed 10 indicate strongly correlated variables (Chatterjee and Price 1977); our variance inflation factors were between 1.99 and 7.25.

Statistical analyses

To evaluate whether song structure could distinguish among the recorded species of *Pycnonotus* bulbuls, we conducted discriminant function analysis (DFA) with cross-validation. We used our recordings at each recording location (i.e. each flock) as the unit of replication. A total of 1149 songs was recorded: 93 of Black-headed Bulbuls, 318 of Black-crested Bulbuls, 85 of Streak-eared Bulbuls, 122 of Stripe-throated Bulbuls, 265 of Red-whiskered Bulbuls, and 266 of Sooty-headed Bulbuls. We calculated an average value for each recording location, resulting in a total of 186 average measurements: 16 Black-headed Bulbuls, 48 Black-crested Bulbuls, 20 Streak-eared Bulbuls, 29 Stripe-throated Bulbuls, 41 Red-whiskered Bulbuls, and 32 Sooty-headed Bulbuls. We constructed the DFA using a randomly selected subset of 80% of the data (minimum of 12 songs, maximum of 39 songs representing each species), and describe the three resulting canonical axes based on their correlation coefficients with the original nine variables in this subset of the data. We performed cross-validation to determine whether this analysis could predict the correct species based on fine structural features; we tested our ability to correctly identify species using the remaining 20% of the data. We report the accuracy of the discriminant function analyses as the percentage of songs assigned to the correct species for this 20% of songs. In addition to a DFA based on the songs of all six species, we ran three additional DFA on pairs of species with highly similar plumage. As with the six-species DFA, we constructed the DFA using a randomly selected 80% of the data, and cross-validated the analysis with the remaining 20% of the data.

All statistics were calculated using JMP 8 (SAS Inc., Cary, NC) or SPSS 16 (SPSS Inc., Chicago, IL).

Results

The structural and behavioural features of songs of the six species of *Pycnonotus* bulbuls from northern Thailand are presented in Table 1.

Descriptions of songs and vocal behaviour

Black-headed Bulbul

The songs of Black-headed Bulbuls consist of repeated down-slurred tonal elements (Fig. 1*a*). This species has the highest number of elements per song, but songs comprise only a single element type, with a narrow frequency bandwidth of ~2.3 kHz. This song of repeated notes is very distinctive compared with the songs other species of this group, and is the longest of the songs of the six species. This species was most often recorded singing in dense vegetation, such as within bamboo thickets and inside the middle storey of the forest.

Black-crested Bulbul

Black-crested Bulbuls have complex songs composed of frequency modulated tones (Fig. 1*b*). Their short songs contain various element types, which usually start at a low frequency, then increase to a high terminal frequency, with a frequency bandwidth of ~2.0 kHz. This species is among the most common birds in low-elevation forest habitats in Thailand, and was the most frequently encountered of the six species (28% of recorded songs). Birds were most often recorded singing from the topmost part of the canopy of the forest.

Streak-eared Bulbul

Streak-eared Bulbuls sing trilled songs, consisting of repeated notes with elements of short duration (<0.1 s; Fig. 1*c*). The repeated element is a harsh, rising note, with a frequency bandwidth of ~4.0 kHz. In contrast with other bulbuls, this shy and plain-coloured bulbul was often found in dense shrubby vegetation where it was difficult to observe, such as dense bamboo thickets, thicket habitat along the forest edge, and forest understorey.

Stripe-throated Bulbul

Stripe-throated Bulbuls sing a complex song composed of various frequency modulated elements (Fig. 1*d*). Among the six species, Stripe-throated Bulbuls show the highest element diversity per song. Their songs had the lowest frequency range, the lowest maximum frequency, and also the lowest minimum frequency, with an average frequency bandwidth of ~1.8 kHz. Morphologically, this plain-coloured bulbul is very similar to the Streak-eared Bulbul; in the absence of vocalisations, distinguish-

Table 1. Measurements of the fine structural features of the songs of six species of *Pycnonotus* bulbuls recorded in northern Thailand
Values are given as means ± s.e.

	Black-headed Bulbul (*n* = 16)	Black-crested Bulbul (*n* = 48)	Streak-eared Bulbul (*n* = 20)	Stripe-throated Bulbul (*n* = 29)	Red-whiskered Bulbul (*n* = 41)	Sooty-headed Bulbul (*n* = 32)
Song duration (s)	3.8 ± 1.2	0.7 ± 0.1	1.5 ± 0.6	0.7 ± 0.3	0.6 ± 0.1	0.4 ± 0.1
Maximum frequency of the song (kHz)	4.6 ± 0.2	3.7 ± 0.4	5.2 ± 0.6	3.0 ± 0.5	3.9 ± 0.4	3.5 ± 0.5
Minimum frequency of the song (kHz)	2.3 ± 0.2	1.7 ± 0.2	1.3 ± 0.3	1.2 ± 0.2	1.7 ± 0.2	1.9 ± 0.3
Average element duration (s)	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.1
Average maximum frequency of elements (kHz)	4.1 ± 0.2	3.1 ± 0.3	4.5 ± 0.5	2.6 ± 0.4	3.6 ± 0.4	3.1 ± 0.3
Average minimum frequency of elements (kHz)	2.6 ± 0.1	2.0 ± 0.2	1.7 ± 0.4	1.6 ± 0.3	2.0 ± 0.2	2.2 ± 0.2
Longest element (s)	0.1 ± 0.0	0.2 ± 0.1	0.0 ± 0.0	0.1 ± 0.0	0.2 ± 0.1	0.2 ± 0.1
Average interelement interval (s)	0.3 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.1 ± 0.0
Number of types of element	1.0 ± 0.0	3.6 ± 0.8	1.0 ± 0.0	3.9 ± 1.0	3.5 ± 0.9	2.5 ± 0.7

ing between these two species is difficult, particularly as both live in dense vegetation and are too difficult to observe.

Red-whiskered Bulbul

Red-whiskered Bulbuls sing a complex song of various frequency modulated element types (Fig. 1*e*). The song has a moderate frequency range, with an average frequency bandwidth of ~2.3 kHz. Birds typically sang from high, exposed perches, such as treetops, electric wires and rooftops, particularly in the early mornings. This species was often found in anthropogenically modified habitats, such as forest edges and parks, and near human habitation.

Sooty-headed Bulbul

The songs of Sooty-headed Bulbuls have a simple structure (Fig. 1*f*). Their songs are the shortest of the six described and contain the fewest elements. Their songs span a narrow frequency bandwidth of ~1.6 kHz, usually comprised of a series of elements that descend in pitch. We recorded birds of this species singing from treetops, and the birds were observed feeding in small groups of 5–10 individuals at all times of the year.

Multispecies comparison

Discriminant function analysis distinguished between the six species of *Pycnonotus* bulbuls based on the nine fine structural variables we measured (Wilks' lambda = 0.003, d.f. = 45, $P < 0.0001$; Fig. 4). Our analysis, with cross-validation, correctly predicted the species identity with an accuracy of 91.9% ($n = 37$ of the 186 average measurements used for cross-validation), which is significantly higher than the 16.7% level expected by chance (binomial test $P < 0.0001$). Discriminant function analysis generated three canonical axes that explained 93.3% of the total variance in structural characteristics of the songs of the six species (Table 2). The first canonical axis explained 65.6% of the variance, and showed a strong positive relationship with song duration, maximum frequency of the song, average maximum frequency of each element in the song, and strong negative relationship with the number of elements in the song; high values for this canonical axis indicate long songs with a high maximum frequency and few types of elements. The second canonical axis explained 14.0% of the variance, and showed a strong positive relationship with interelement interval; high values for this canonical axis indicate songs with elements separated by very small silent intervals. The third canonical axis explained 13.5% of the variance, and showed a strong positive relationship with minimum frequency of the entire song and average minimum frequency of each element in the song; high values for this canonical axis indicate songs with a high minimum frequency.

We performed three additional pairwise discriminant function analyses to evaluate whether song structure could differentiate between pairs of species with similar plumage characters (as assessed by human observers; see Figs 1, 2). We compared acoustical differences between pairs of species with the greatest plumage similarities, based on the assumption that similar plumage indicates closely related species with heightened chances of hybridisation. Our field data demonstrate that these pairs of visually similar species routinely encounter one another, based on the proportion of locations where the pairs of species were encountered: Black-headed Bulbuls (13 of 16 locations) *v.* Black-crested Bulbuls (13 of 48 recording locations included both species); Streak-eared Bulbuls (17/20 locations) *v.* Stripe-throated Bulbuls (17/29 recording locations included both species); and Red-whiskered Bulbuls (23/41 locations) *v.* Sooty-headed Bulbuls (23/32 recording locations included both species). On at least one occasion we detected all six species in the same foraging flock, and on multiple occasions we encountered flocks containing four or five of the species in different combinations.

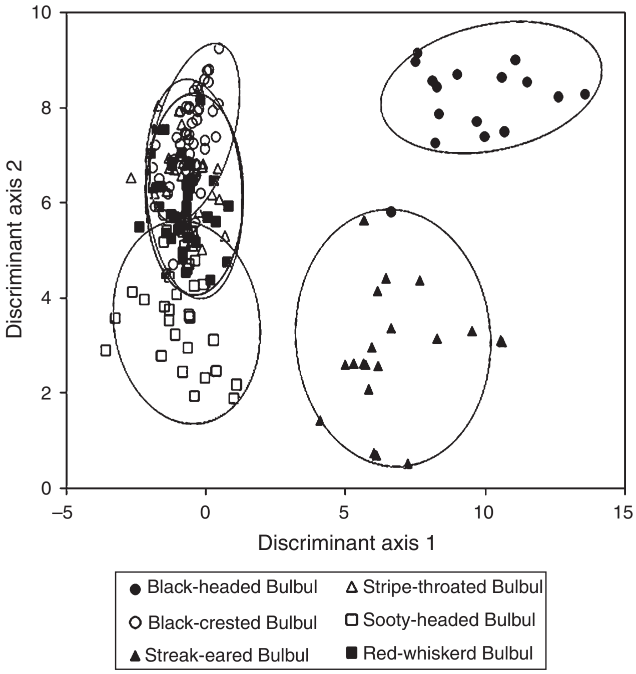

Fig. 4. Scatterplot of the first two canonical axes resulting from a discriminant analysis of nine structural features of the songs of six sympatric species of *Pycnonotus* bulbul recorded in northern Thailand. Ellipses represent 95% confidence spaces for each species.

Table 2. Discriminant analysis of the songs of six species of *Pycnonotus* bulbuls produced three factors summarising nine fine structural features of songs, represented here as the correlation coefficients between the original data and the three factors

Variables with the strongest relationships (correlations > 0.60) are indicated in bold

Variable	Factor 1	Factor 2	Factor 3
Song duration	**0.92**	0.21	0.02
Maximum frequency of the entire song	**0.68**	–0.28	–0.19
Minimum frequency of the entire song	0.22	0.20	**0.85**
Element duration	–0.47	0.12	0.13
Maximum frequency of each element	**0.66**	–0.32	–0.10
Minimum frequency of each element	0.21	0.23	**0.70**
Duration of longest element	–0.44	0.06	0.27
Interelement interval	0.50	**0.61**	–0.23
Number of types of element within a song	**–0.71**	0.38	–0.30
Eigenvalue	12.06	2.56	2.47
Percentage of variance explained	65.87	13.99	13.46

In pairwise comparisons of species with very similar plumage and bare parts, we found substantial divergence in acoustical features of song (Fig. 2). In a comparison of Black-headed *v*. Black-crested Bulbuls (Wilks' lambda = 0.027, d.f. = 9, $P < 0.0001$), cross-validated DFA separated the species based on song measurements (100% correct assignment; $n = 13$ of the 64 average measurements used for cross-validation, significantly higher than the chance rate of 50%; binomial test $P < 0.0005$); the canonical axis showed a strong negative relationship with song length, maximum and minimum frequency, and a strong positive relationship with average length of element and length of the longest element. Similarly, in a comparison of Streak-eared *v*. Stripe-throated Bulbuls (Wilks' lambda = 0.052, d.f. = 9, $P < 0.0001$), cross-validated DFA separated the species based on song measurements (100% correct assignment; $n = 10$ of the 49 average measurements used for cross-validation, significantly higher than the chance rate of 50%; binomial test $P < 0.002$); the canonical axis showed a strong negative relationship with song length and maximum frequency measures, and a strong positive relationship with the length of the longest element and the total number of types of elements. Similarly, in a comparison of Red-whiskered *v*. Sooty-headed Bulbuls (Wilks' lambda = 0.20, d.f. = 9, $P < 0.0001$), cross-validated DFA separated the species based on song measurements (100% correct assignment; $n = 15$ of the 73 average measurements used for cross validation, significantly higher than the chance rate of 50%; binomial test $P < 0.0001$); the canonical axis showed a strong positive relationship with song length, interelement interval, and number of types of elements.

Discussion

Our bioacoustical analyses of the songs of six sympatric species of *Pycnonotus* bulbuls are the first quantitative description of the vocalisations of each species. Our multivariate analyses reveal that each species produces distinctive vocalisations that provide acoustical cues for species identity. These features may be the basis for species-recognition signals, which may be particularly important in the context of mixed-species flocks (Baker and Boylan 1999; Slabbekoorn and Smith 2002; Päckert *et al*. 2003; Cadena and Cuervo 2010). Although all six species sing songs in overlapping parts of the frequency spectrum (1.2–5.1 kHz), results of cross-validated discriminant analysis reveal significant acoustical differences for the six species of bulbul. Pairwise analyses are consistent with the idea that sympatric species with similar plumage features show pronounced acoustical differences.

Quantitative acoustical measurements of the voices of most tropical birds are lacking, in spite of the high biodiversity that characterises the tropics and the conservation pressures that imperil the future of many tropical ecosystems (Gaston 2000; Stutchbury and Morton 2001). Our study provides quantitative descriptions of the songs of six species of *Pycnonotus* bulbul (Table 1). Black-headed and Streak-eared Bulbuls both sing trilled songs composed of one type of element sung in repetition; the former sings narrow-bandwidth, downslurred elements at a slower pace, whereas the latter sings broad-bandwidth, upslurred elements at a faster pace. Consequently, the two species that sing trilled songs can be readily distinguished from each other based on these differences. These trilled songs match the published description of the trilled song of another congener, the Bare-faced Bulbul (songs consisting of 3–15 elements, frequency range of 2–5 kHz; Woxvold *et al*. 2009). In contrast to these trilled songs, the remaining four species that we studied produce songs composed of various frequency modulated tones. Red-whiskered Bulbuls have the most complex songs, with many elements featuring rapid frequency modulations. Their complex songs are one of the reasons that Red-whiskered Bulbuls are of conservation concern in Thailand; although this species has been introduced in many parts of the world, and is even a pest in some regions, they continue to face conservation pressure in their native range owing to the pet trade (Clergeau and Mandon-Dalger 2006), including trade for song competitions (Anderson 2005). Sooty-headed Bulbuls have the simplest songs of those described here, with few elements, which descend in pitch over the course of the song. The remaining two species can be distinguished on the basis of their frequency range (Stripe-throated Bulbuls have the lowest-pitched frequency-modulated songs in the group) and the organisation of elements (Black-crested Bulbul songs tend to rise in pitch much more noticeably than the other species). These four species are most similar to published descriptions of the songs of Red-vented Bulbul (songs of 2–6 elements, frequency range of 0.9–4.5 kHz; Kumar 2004) and the Common Bulbul (*P. barbatus*) (songs of 4–7 elements, frequency range of 1.2–3.5 kHz; Lloyd *et al*. 1999). Our acoustic descriptions can assist ornithologists, ecologists and conservation biologists in their future research endeavours. Based on these quantitative differences in the songs of the six species, sound recordings should provide a useful tool for monitoring bulbuls. Acoustic survey techniques may be particularly advantageous in dense habitats where visual monitoring is difficult, and where recordings may be collected unobtrusively at a distance from the animals (Waide and Naring 1988; Haselmayer and Quinn 2000; Grava *et al*. 2008).

Discriminant analysis of the nine fine structural features revealed significant vocal differences between the six species. The acoustical features that contributed most strongly to our discriminant analysis may be the features that are most important for interspecific recognition. Features that strongly influenced discrimination included frequency measurements (both maximum and minimum frequency), temporal measurements (particularly song duration and interelement interval), and compositional features (the number of types of element within a song). Acoustic distinctiveness is expected to increase when birds live in the same habitat (Kirschel *et al*. 2009; Seddon and Tobias 2010), and may be particularly important in the close associations of a mixed-species foraging flock. Song is an important feature as a heterospecific pre-mating isolation mechanism (Irwin *et al*. 2001; Balakrishnan and Sorenson 2006). We found that all six species of bulbul regularly occur together, creating a complex acoustical and social environment. Many prior studies have found acoustic, species-typical differences in closely related, allopatric congeners (e.g. Price and Lanyon 2002; Valderrama *et al*. 2007; Kirschel *et al*. 2009). Our results reveal pronounced acoustic differences in sympatric congeners that share the same habitat.

Results of our pairwise comparisons are consistent with the idea that song provides a mechanism for discriminating between species that are visually similar. It is well known that both visual and acoustic signals are important in avian matechoice (Bradbury and Vehrencamp 2011), and both types of signals are expected to be used in distinguishing territorial opponents and prospective mates. We subdivided our six study species into three pairs of visually similar bulbuls, based on similar patterns of plumage and bare parts (we assessed similarity through visual inspection; careful spectrophotometric comparisons is an important avenue for future research). Our first pairing included Black-headed and Black-crested Bulbuls, both of which have bright yellow body parts and glossy black heads (Fig. 1). These species were regularly found in the same areas of mature forests where vegetation is dense and comprised of multiple storeys. Discriminant analysis readily distinguished these two species on the basis of both length of elements and frequency measurements; Black-headed Bulbuls sing longer, trilled songs whereas Black-crested Bulbuls sing shorter songs made up of varied frequency modulated elements that rise in pitch. Our second pairing included Streak-eared and Stripe-throated Bulbuls, both of which have plain, brownish-grey plumage (Fig. 1). These two species co-occur, often in dense vegetation of deciduous forests, where their cryptic plumage makes them difficult to observe. Discriminant analysis readily distinguished these two species on the basis of both length of elements and frequency measurements; Streak-eared Bulbuls have longer, trilled songs whereas Stripe-throated Bulbuls have shorter, lower pitched songs made up of varied frequency modulated elements. Our third pairing included Red-whiskered and Sooty-headed Bulbuls, both of which share similar plumage patterns of black facial ornaments and bright-red undertail coverts (Fig. 1). These two species also co-occur, frequently singing from treetops in urban areas and secondary forests. Discriminant analysis showed less separation between this pair of species owing to their similarly complex, frequency modulated songs. Nevertheless, discriminant analysis significantly separated the two species, primarily on the basis of song length; Red-whiskered Bulbuls have longer songs with more elements uttered in rapid succession than Sooty-headed Bulbuls.

This multispecies comparison adds to our understanding of song differentiation between closely related birds. Many multispecies comparisons focus on species that are closely related but do not live in the same habitats (e.g. Martens *et al*. 2004; Valderrama *et al*. 2007; Uy *et al*. 2009; Petrusková *et al*. 2010; but see Tobias & Seddon 2009 for an interesting case where sympatric congeners have highly similar vocalisations). Our study focuses on acoustical comparisons of six sympatric bulbul species that routinely forage in mixed-species flocks, and draws attention to acoustic differences between animals that live in the same habitat. Our study provides the first detailed description of song of six frugivorous birds that are widespread in tropical Asia. Further comprehensive study on the sexual and breeding behaviour would help to clarify communication mechanisms influencing song divergence in this group. Playback studies are an important area for further study, as they would allow us to confirm that birds respond to the species-typical acoustic cues we have identified here, and which may provide insight into the function of these vocalisations.

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