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ORIGINAL ARTICLE

On the natural history of duetting in White-browed Coucals: sex- and body-size-dependent differences in a collective vocal display

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Abstract Avian duets have long fascinated biologists, but much remains unknown about what information may be contained in these collective displays and how duet structures vary between taxa. In this study, we describe the structure and performance rules of duets in White-browed Coucals *Centropus superciliosus*, a tropical non-parasitic Cuckoo. We recorded vocal behaviours of 11 focal pairs and measured temporal, frequency, and amplitude characteristics of their duets. Molecular sexing and radio telemetry revealed that duets were initiated by both sexes, but the majority of them were led by the male. Moreover, we found that duet contributions were sex specific with females producing lower-pitched songs than males, reflecting the general size dimorphism in this species. Finally, we also found that song peak frequencies varied with body size within each sex, suggesting that songs used in duets may act as index signals of body size. We speculate that sexual selection has driven White-browed Coucals to sing as low as possible, a notion that is further supported by our observation of special singing postures that may help in lowering song pitch even further.

Keywords Acoustic communication · Bird song · Collective signalling · Cuculiformes · Duet · *Centropus superciliosus*

Zusammenfassung

Zur Naturgeschichte des Duettgesangs bei Weißbrauenkuckucken: geschlechts- und größenabhängige Unterschiede eines kollektiven akustischen Signals

Duettierende Vögel faszinieren Biologen seit langem, aber welche Informationen in ihren kollektiven Signalen kodiert sind und wie sich Duettstrukturen zwischen verschiedenen Taxa unterscheiden, ist nach wie vor meist unbekannt. In dieser Studie beschreiben wir die Struktur und die Performanzregeln des Duettgesangs von Weißbrauenkuckucken (*Centropus superciliosus*), die zur Gruppe der nistenden, tropischen Spornkuckucke gehören. Wir zeichneten die Lautäußerungen von elf Fokuspaaren auf und untersuchten die zeitlichen, spektralen und Amplitudencharakteristika der Duette. Beide Geschlechter initiierten Duette, die Mehrzahl wurde jedoch vom Männchen angeführt und durch das Einstimmen des Weibchens zum Duett. Die einzelnen Abschnitte des Duetts waren geschlechtsspezifisch: Die Weibchen produzierten dabei Gesänge mit tieferer Frequenz, den typischen Geschlechtsdimorphismus in der Körpergröße dieser Art widerspiegelnd. Auch innerhalb der Geschlechter variierten die Spitzenfrequenzen der Gesänge mit der Tarsuslänge, ein Hinweis darauf, dass Duettgesänge als Anzeiger der Körpergröße dienen können. Vermutlich führte sexuelle Selektion dazu, dass

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Weißbrauenkuckucke so tief wie möglich singen. Diese Auffassung wird auch dadurch gestützt, dass die Vögel während des Singens eine besondere Körperhaltung einnahmen, die einer Absenkung der Stimme förderlich ist.

Introduction

In most bird species, individuals communicate singly, broadcasting their songs or calls to others. But some species also produce duets, in which members of a pair coordinate their vocalizations to produce a combined signal pattern of overlapping or alternating notes—a striking behaviour that has been intriguing biologists for nearly a century (e.g. Huxley 1919; Moreau 1941; Robinson 1949; Dilger 1953). Following Thorpe's (1961, 1963; Thorpe and North 1965; Thorpe 1972) pioneering work on duetting songbirds in East Africa, two particularly fruitful lines of research emerged in the 1970s and 1980s. Wickler and his colleagues combined field observations and work on captive birds, mainly Boubous (*Laniarius* spp.) and other East African songbirds, to address questions of the structure, ontogeny, and function of duetting (e.g. von Helversen and Wickler 1971; Wickler 1972; Seibt and Wickler 1977; Wickler and Seibt 1980; Wickler and Sonnenschein 1989). In an influential paper, Wickler (1980) suggested that duetting may signal commitment between partners. Such commitment would be related to the amount of investment required to achieve song coordination: if attaining a high degree of coordination between partners takes time, then desertion will be costly because it requires investing again with a new partner. The other line of research was conducted by Todt and co-workers, who studied duet organization of several species (Todt 1970; Todt and Fiebelkorn 1980) and carried out a series of field and lab experiments on White-browed Robin-chats (*Cossypha heuglini*) investigating both proximate and ultimate aspects of duetting (Todt 1975; Todt et al. 1981; Hultsch 1983; Hultsch and Todt 1984). One noteworthy discovery was that the pair bond in Robin-chats was maintained even when their duetting had been disrupted, indicating that duetting was not essential for pair bonding, although it was for breeding (Todt and Hultsch 1982).

In the wake of these early studies, a considerable body of literature on the structure and function of bird duets has accumulated (Hall 2009). To date, more than 400 species have been found to duet (Hall 2009), and since the majority of them breed in the tropics, it has often been suggested that tropical natural histories may be linked to the evolution of avian duetting (reviewed by Slater and Mann 2004; Hall 2009). However, two recent comparative studies challenge this view: Odom et al. (2015) suggest that the ecology and life history features that were thought to favour the evolution of duetting are rather associated with female song, and Logue and Hall (2014) argue that the evolution of duetting is primarily related to the absence of migration.

Avian duets are a particular example of collective signalling, in which the combination of the single contributions produced by different individuals forms a new entity, which then may act as a signal itself (Brumm and Slater 2007). Duetting in birds is characterized by the specific phrases that the two partners contribute and the temporal patterning between the individual song components (Todt and Naguib 2000). It is these meta-parameters that determine the collective signal parameters and establish the particular style of a duet (Brumm and Slater 2007). Duet styles vary considerably between species, ranging from rather loose temporal associations such as in Stripe-headed Sparrows (*Aimophila ruficauda*), in which the female and male simply overlap their parts with no further coordination (Illes and Yunes-Jimenez 2009), to cases of a stimulus response type, where the phrase of one partner is answered by the phrase of the other [e.g. in the Whipbird *Psophodes olivaceus* (Rogers 2005)], to rapid antiphonal cycles where female and male fit their song elements precisely in the brief pauses between the elements of their partner [e.g. in the Happy Wren, *Pheugopedius felix* (Templeton et al. 2013)]. In White-browed Sparrow Weavers (*Plocepasser mahali*), antiphonal phrases even alternate with unison phrases within a given duet, both coordinated with a high degree of temporal precision (Voigt et al. 2006). This astounding variety of duet styles (and the presence of duetting in a species in the first place) can be explained, at least in part, by evolutionary history. The strongest evidence for this notion comes from a comprehensive comparative study on singing modes in Neotropical Wrens (Mann et al. 2009). Combining molecular and bioacoustic methods, Mann et al. (2009) found that singing modes and duet styles map onto phylogeny in this group of songbirds. In other words, ancestry is a strong predictor of duet structure (Mann et al. 2009).

Similar to the variation in duet form, species also differ in the function of their collective vocal displays (Langmore 1998; Hall 2004). Although the significance of avian duetting is still debated, joint territory defence is considered one of the primary functions in many species (Todt and Naguib 2000; Hall 2009; Tobias et al. 2016). Other supported hypotheses for the function of duetting include mate guarding (Rogers et al. 2006; Seddon and Tobias 2006), recognition and contact between partners (Logue 2007; Mennill and Vehrencamp 2008), ensuring reproductive synchrony (Todt and Hultsch 1982; Hall 2006), and pair commitment (Wickler 1980; Templeton et al. 2012).

Taken together, this confusing variety in the current evidence suggests that duetting may serve more than one function within a species and different functions between them.

Previous duet studies have focused mainly on passeriform birds (Hall 2009; Logue and Hall 2014. But see Seddon 2002 and Wright and Dahlin 2007 for notable exceptions). Here we investigate duetting in a cuculiform bird, the White-browed Coucal (*Centropus superciliosus*). This species is a nesting Old World Cuckoo, occurring in sub-Saharan Africa (Fry et al. 1988). The breeding system and life history of White-browed Coucals have only recently been studied (Goymann et al. 2015, 2016). They are year-round resident birds that live in socially monogamous pairs, and both partners contribute to parental care. Thorpe observed that White-browed Coucals duet (Thorpe 1972) but he did not provide any further information on their song. The only published study that we are aware of on duet structure in a cuculiform bird is the one by Maurer et al. (2008) on Pheasant Coucals (*Centropus phasianius*). Maurer et al. (2008) found that duet phrases were sex specific, with females producing lower-pitched phrases than males. In Pheasant Coucals, as in most Coucals, females are larger than males, thus the difference in vocal frequency likely reflects the general size dimorphism of the sexes (Maurer et al. 2008). A similar connection between body size and song frequency was also found within female Black Coucals, *Centropus grilli* (Geberzahn et al. 2009; 2010), a non-duetting migratory Coucal species.

As a first step in the study of the duetting behaviour of White-browed Coucals, we investigated the meta-structure of the collective signal and also the information content of each partner's duet component. In particular, we shall describe the structure and performance of White-browed Coucal duets and explore whether their vocal displays may be used as an index signal of body size.

Methods

General

Between 29 February and 13 March 2016 we studied the vocal behaviours of 12 pairs of White-browed Coucals in a grassland and savannah habitat located in the Usangu wetlands in southwestern Tanzania (8°40′S 34°03′E). For detailed information on the study population and the study area see Goymann et al. (2015). One or both members of each pair were colour banded and equipped with a Holohil BD-2 radio transmitter. The radio transmitter allowed us not only to find the birds in their dense habitat of acacia thickets but also enabled us to establish which sex produced which vocalization in cases when birds were out of sight.

Song recordings

We observed focal pairs between 0700 and 1900 hours and noted spontaneous duets from five of them. Thirty spontaneous duets from four pairs (average 7.5 duets per pair, range 2–12) were recorded with a Sennheiser ME 66 directional microphone (with a MZW 66 Pro windshield) connected to a Marantz PMD 660 solid state recorder (44.1-kHz sample rate, 16-bit resolution). In addition, we used duet playbacks to elicit duetting in ten pairs (including two from which we had recorded spontaneous duets). Two pairs did not duet in response to the duet playback. One of them could be triggered to duet with a male solo playback, but from the other pair we could only record male solo songs and so this pair was removed from the analysis. The source songs for the playbacks were recorded with the equipment described above from the same population but focal pairs were not exposed to their own songs or those of their neighbours because some duetting species can distinguish between duets of neighbours and those of strangers, responding less to the duets of familiar pairs (Wiley and Wiley 1977; Hall 2000; Grafe and Bitz 2004). We used three different duet sequences from three different pairs, each sequence consisting of three consecutive duets. Playbacks were broadcast from a Foxpro Scorpion remote-controlled playback device that we placed at a distance of about 20–50 m from the focal pair. Playbacks were conducted between 0730 and 0950 hours.

For one male that could be observed particularly well during the recordings, we measured the amplitude of 17 duet songs. The bird was recorded on 2 different days from a distance of 17.0 and 17.5 m, respectively, while he was perched in a bush at the height of the microphone with no obstacles between the bird and the microphone. Recordings were made from the front or the side of the bird. To be able to measure sound pressure level (SPL) values, the recording was calibrated with a reference tone that was recorded in an anechoic room with the same equipment and the same setting as the Coucal songs. While recording the calibration tone its amplitude was measured at the position of the microphone with a SPL meter (Casella CEL-242), and this value was then used to calibrate the analysis software. The song amplitude measurement was done according to standard procedures (Brumm 2004). Briefly, we measured the root mean square amplitude of the loudest song element (usually the second element), subtracted the background noise amplitude from it by logarithmic computation, and then calculated the song amplitude value for a standard distance of 1 m. For details of the procedures and calculations see Brumm and Zollinger (2011). All decibel values reported in this study refer to 20 μPa.

Body measurements

Coucals were caught with mist nets, measured and ringed with numbered aluminium rings and coloured plastic rings for individual identification. In addition, birds were equipped with a Holohil BD-2 radio-transmitter (<2 g; Holohil Systems, Carp, ON). Amongst other measures we took measurements of body mass (to the nearest gram), wing and tail length (to the nearest millimetre), and the length of the right tarsus (to the nearest 0.1 mm) following the methods detailed in Eck et al. (2011). For further details regarding capture, measurements, and tagging see Goymann et al. (2015).

A small blood sample was taken and stored in Queen's lysis buffer for DNA analysis (Seutin et al. 1991). All individuals were genetically sexed by polymerase chain reaction with the P2/P8 primer pair (Griffiths et al. 1988, for details see Muck et al. 2009).

Song analyses

All sound analyses were done with the software Avisoft SASLab Pro (version 5.2.08; Avisoft, Berlin). We measured temporal song features with automatic threshold detection in waveforms and peak frequencies in power spectra (Zollinger et al. 2012). The temporal resolution of the measurements was 11.6 ms, and for the frequency measures it was 3.9 Hz. Prior to the measurements the recordings were filtered to remove background noise outside the frequency band of White-browed Coucal songs (finite impulse response band pass, cut-off frequencies 0.2 and 0.7 kHz, Hamming window, 1024 tabs). We defined a song as separated temporally from all other songs by more than 1 s, which means that two (or more) phrases of a pair were considered as a duet when they were spaced apart by less than 1 s (Mennill and Vehrencamp 2005). Likewise, a song phrase by one of the two partners was considered as a solo song when it was spaced apart by more than 1 s from a solo of the other partner or a duet of the pair. Following standard birdsong terminology, a 'song element' is defined as the smallest building block of song organisation, visible as a continuous line on a spectrogram (Catchpole and Slater 2008). Thus, several elements form a phrase, a single phrase from one of the two members of a pair may be a solo song, and two or more phrases from both partners may form a duet song. Duty cycles for both members of a duetting pair were calculated as the ratio between the time spent vocalizing and the total duration of the duet.

Statistical analyses

Statistical analyses were performed with R version 3.3.1 (R Development Core Team, Vienna) and a Bayesian statistical approach using the R package Bayesian First Aid following the procedures described by Kruschke (2013). In contrast to a frequentist statistical approach Bayesian statistics allows the estimation of the likelihood of a true difference between groups. Specifically, we investigated the likelihood of differences between the song characteristics of male and female duetting partners by comparing the posterior means and their respective 95% credible intervals (typically reported in brackets). Further, we tested whether the size of a bird (using tarsus length as a proxy) predicts the peak frequency of the lowest element of a duet phrase using a Bayesian correlation test. For all tests we used uninformative priors.

Results

During both solo and duet singing, female and male White-browed Coucals adopted a striking posture leaning forward and stretching their necks (often parallel to the ground) with their head pointing downwards, beak closed and their throats heavily inflated (Fig. 1). Spontaneous duets were observed during nest building or when pairs re-nested after nest failure, but not during incubation or after young had hatched. The amplitude of male duet song phrases ranged between 83 and 88 dB SPL at 1-m distance (median 85 dB SPL).

On average, we recorded 9.8 duets per pair (range 2–15; $n = 10$ pairs). In most cases (66%), the two members of a pair formed a duet by combining the same vocalization types that they also used as solo songs (Fig. 2a). In the remaining instances, one of the partners (mostly the female) sang an undulating song (Fig. 2b), a song variant that was only observed in duetting.

The majority of all duets had the form A–B (22%) or A–B–A (73%), with A being the contribution of one partner and B being that of the other. Other observed duet types were A–B–A–A (4%) and A–B–A–B (1%). The temporal associations between successive duet contributions were rather flexible; they either alternated with inter-song intervals ranging from 12 to 981 ms or they overlapped by 22 to 2268 ms (Fig. 3). This pattern was mainly due to the variable phrase latencies within pairs, as most of them sang both alternating and overlapping duet phrases, whereas only one pair only alternated and one only overlapped.

Fig. 1 *Right panel* male White-browed Coucal singing a solo song, showing the typical singing posture with outstretched neck and inflated throat. *Left panel* pair of duetting White-browed Coucals. The first picture (*top*) shows the partners immediately before duetting. In the second frame, the male (*right*) starts to sing; in the third frame, the female (*left*) joins in, thus initiating a duet. The last frame shows the male finishing the duetting sequence. In this case both partners were close together while duetting, but usually the two members of a pair were spaced between 3 and 40 m apart when performing their collective song. (Photographs W. Goymann)

Moreover, the average variance in phrase latencies within pairs was bigger than the variance of the average latencies between them (SD within pairs, 626 ms; SD between pairs, 355 ms), which is further evidence for a rather loose temporal association of duet phrases within pairs.

Undulating songs were considerably longer than descending ones and the following duet contribution by the partner could be completely overlapped by them (Fig. 2d). Although mostly females sung undulating songs, the sexes did not differ considerably in the degree of song overlap/alternation (0.03% likelihood of a difference).

Eighty-three percent of the duets were led by males, i.e. duets were mainly established by the female who turned a male solo into a duet. With a likelihood of 99.9%, males contributed more songs to the collective signal than their female partners (Table 1), mainly because males were more likely to lead duets of the A–B–A type.

The 95% credible intervals of the phrase duration of males and females overlapped and there was only a 25% likelihood that females sang longer phrases than males (Table 1). Likewise, the number of song elements per

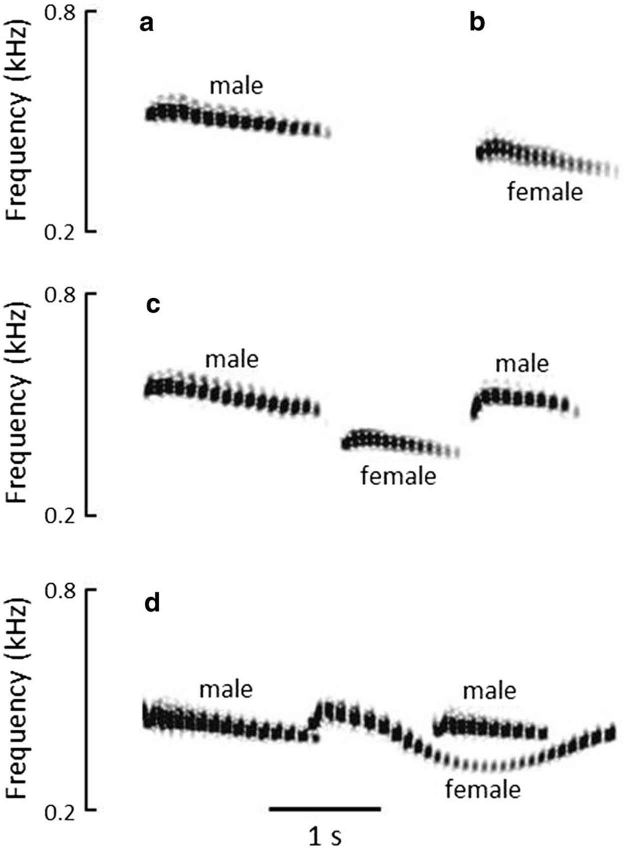

Fig. 2 Examples of White-browed Coucal songs. **a**, **b** Solo songs of each member of a selected pair and **c** a duet of the A–B–A type by the same individuals. **d** Duets could contain a more complex song phrase than the descending songs shown above. This complex phrase rose in frequency again after the typical fall of element pitches [similar to the 'scale' call of Pheasant Coucals (Maurer et al. 2008)]. This undulating song variant was mostly observed in females and it only occurred during duetting. (Spectrogram settings: FFT size 1024, frame size 100%, window Flat Top, temporal overlap 98%.) For the sound recordings see the Electronic supplementary material

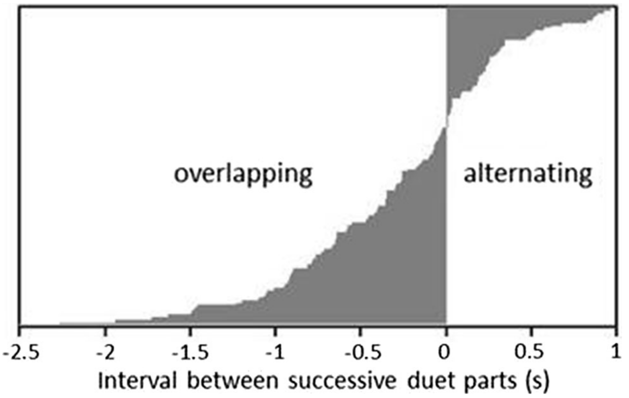

Fig. 3 Latencies between duet contributions. *Negative values* indicate that the successive phrase overlapped the preceding one and *positive values* indicate that the duet phrases were alternating ($n = 132$ successive duet phrases from ten pairs)

Table 1 Characteristics of White-browed Coucal duets. Posterior means (95% credible intervals), $n = 10$ pairs

Song trait	Male part	Female part	Mean difference	Likelihood (%)
Number of phrases per duet song	1.7 (1.4–2.0)[a]	1.1 (1.0–1.2)[a]	0.61 (0.27−0.93)[a]	99.9[a]
Phrase duration (s)	2.1 (1.5–2.8)	2.4 (1.9–2.9)	−0.27 (−1.20 to 0.61)	25.0
Number of elements per phrase	15 (12–19)	18 (15–23)	−2.8 (−11.0 to 5.0)	22.2
Duty cycle	0.61 (0.54–0.68)	0.53 (0.47–0.60)	0.075 (−0.02 to 0.16)	94.8
Peak frequency highest element (Hz)	496 (476–514)[a]	437 (409–467)[a]	56 (22–90)[a]	99.7[a]
Peak frequency lowest element (Hz)	424 (409–439)[a]	341 (325–358)[a]	84 (65–102)[a]	99.9[a]
Mean peak frequency (Hz)	458 (442–473)[a]	377 (362–393)[a]	85 (65–102)[a]	99.9[a]

Likelihood Probability that the mean difference between males and females is larger than zero

[a] Mean differences (effect sizes) with 95% credible intervals that did not include 0

phrase did not differ considerably between the sexes (Table 1; 22.2% likelihood of a difference).

In contrast, we found a marked difference between the sexes in the spectral characteristics of their duet phrases: with a likelihood of 99.7–99.9%, females had lower voices than males (Table 1). Moreover, also within each sex, song pitch was related to body size (Fig. 4). Larger females produced lower elements in their duet phrases than smaller ones [Bayes correlation coefficient, −0.74 (−0.99 to −0.13), $n = 7$ birds with a likelihood of 97.1% that the correlation was negative; Fig. 4a]. A similar pattern was also found in male birds, but with a lower confidence in the likelihood that the true relationship is negative [Bayes correlation coefficient, −0.49 (−0.91 to 0.13); $n = 9$ birds, likelihood of a negative correlation = 91.7%; Fig. 4b].

Discussion

We found sex-specific duetting songs in White-browed Coucals and also discovered that duetting strategies differed between the sexes, as males were more vocal than females, while females were responsible for most duets. In most duetting bird species, the female initiates duetting by responding to the male and turning his solo song into a duet (Hall 2009). White-browed Coucals were no exception to this, with 83% of all the duets led by the male. The observed pairs sang duets with a rather loose temporal association, in which the partners alternated or partly overlapped their songs to varying degrees.

Our analyses of song frequencies revealed that females had lower voices than males, which was evident in the peak frequencies of the highest and lowest note of the duet phrases, as well as the mean peak frequency. This difference in song pitch reflects the general size dimorphism between the sexes in White-browed Coucals. Females in this species are on average 13% larger than males (Goymann et al. 2015), and bigger birds, with bigger syrinxes and vocal tracts, can often produce deeper sounds (Wallschläger 1980; Ryan and Brenowitz 1985). The same pattern of females producing lower-pitched duet phrases than males has also been described for Pheasant Coucals (Maurer et al. 2008). In a similar vein, female ‘Thryothorus’ Wrens are usually smaller than males and they have higher duet songs (Mann et al. 2009). Most interestingly, we did not only find a divergence of song frequencies between the sexes, but also a correlation between body size and song pitch within sexes, with bigger individuals producing lower pitched song elements (but the strength of this correlation was much higher in females than in males). Thus, Coucals could potentially recognize not only males and females by their voices, but they might also assess the size of an individual, at least for females, by the pitches of the lowest song elements. Such a role of low-frequency notes as an index signal of body size has also been suggested for female Black Coucals (Geberzahn et al. 2010).

It is not only interesting that the song frequencies varied with body size, but also that they were generally unusually low in pitch. We measured a mean lowest peak frequency in male and female White-browed Coucals of 381 Hz. This value is low compared to the vocalizations of other cuculiform species of similar size, e.g. male Eurasian Cuckoos (*Cuculus canorus*) are similar in size to male White-browed Coucals, but the lower end of male White-browed Coucal songs is more than 120 Hz lower on average than the lower note of the famous[1] Cuckoo interval (mean 548 Hz, $n = 12$ Eurasian Cuckoo males; Brumm, unpublished data), which, in musical terms, is a difference of slightly more than four semitones. This low voice is most likely achieved by anatomical adaptations of the syrinx and the vocal tract, as well as behavioural modulations. In White-browed Coucals the parts responsible for sound production are located far down in the two bronchi, whereas in Eurasian Cuckoos (and songbirds) they are located more cranially at the bifurcation of the two bronchi

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[1] August Heinrich Hoffmann von Fallersleben (ca. 1827): “Kuckuck, Kuckuck ruft’s aus dem Wald.”

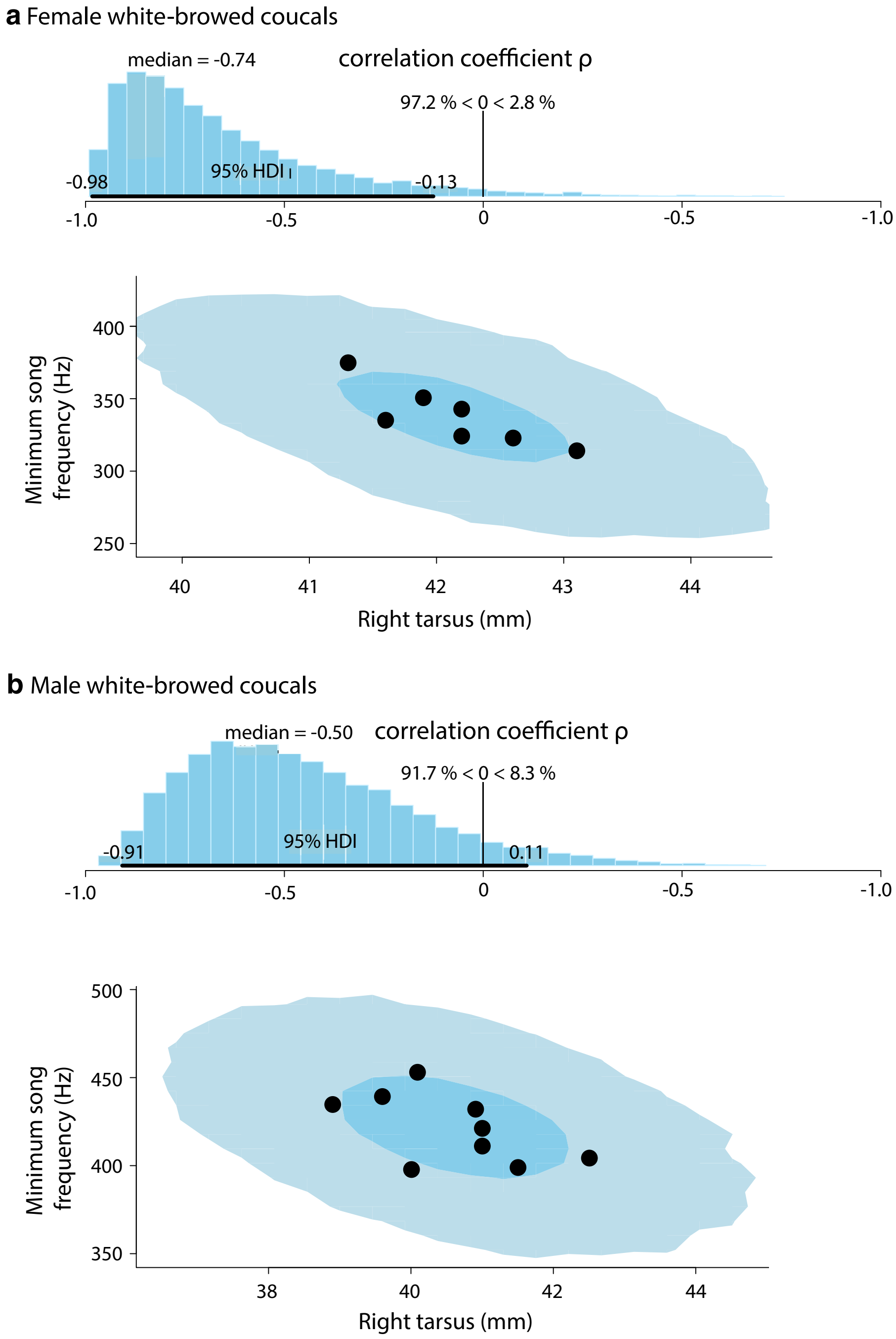

Fig. 4 Relationship between body size and minimum frequency of duet songs in **a** female and **b** male White-browed Coucals. The minimum song frequency is the peak frequency of the lowest song element of a duet phrase (averaged for each individual). *Upper panels* in **a** and **b** show the posterior distribution for the correlation (ρ) with a 95% highest density interval (*HDI*). *Lower panels* show the original data with superimposed posterior predictive distributions that we would expect new data points to have (the *darker* of the two ellipses shows the 50% and the *lighter* one the 95% highest density regions)

at the base of the trachea (Berger 1960). In terms of sound production, the bronchial syrinx of the White-browed Coucal means that the vocal tract is longer relative to body size than in a tracheobronchial syrinx and thus it may sustain lower pitched vocalizations.

The peculiar singing posture of White-browed Coucals with stretched out neck and inflated throat that we describe in this study probably plays a crucial role in further lowering the voice. The stretched neck likely elongates the vocal tract by increasing the length of the trachea, and the inflation of the throat may indicate an increase in the volume of the oropharyngeal-oesophageal cavity and/or the usage of inflatable vocal sacs potentially associated with it. All of these modifications may lower the peak frequency of the vocalization through changes in the resonance properties of the vocal tract (reviewed by Suthers and Zollinger 2008). The closed beak of White-browed Coucals during duetting allows for the inflation of the oesophagus (and/or associated vocal sacs) and means that the birds vocalize into the closed, inflated cavity with the sound radiating through the skin of the neck. Thereby, the inflation of the throat may act to boost radiation of the signal, amplifying the low sounds (Riede et al. 2016). Generally, the fundamental frequency of vocalizations in birds that vocalize with the mouth closed is lower than predicted from body size alone (Riede et al. 2016), and thus, the duetting posture of White-browed Coucals described in this study is most likely a mechanism to support the production and radiation of particularly low-frequency vocalizations.

Low-frequency vocalizations of birds are thought to be candidates of honest signals of body size (Ryan and Brenowitz 1985; Gil and Gahr 2002) because their production is constrained by difficulties with producing loud low-pitched sounds (reviewed by Zollinger and Brumm 2014). If White-browed Coucals advertise their body size to mating partners or to conspecific competitors, then sexual selection has most likely driven them to sing as low as possible. Such a scenario might be widespread within the genus *Centropus*, since many species of this taxon have particularly low-pitched songs and they also adopt the striking singing posture with stretched out necks, closed beaks and inflated throats, e.g. Coppery-tailed Coucals (*Centropus cupreicaudus*), Senegal Coucals (*Centropus senegalensis*), and Black Coucals (W. Goymann, unpublished observation), as well as Lesser Coucals (*Centropus bengalensis*) and Greater Coucals [*Centropus sinensis* (H. Brumm, unpublished observation)]. In their comprehensive review Riede et al. (2016) noted that, apart from a few exceptions, closed-mouth vocalizations are mainly used by advertising males. In duetting Coucal species, however, this vocalization mode appears to be used by both males and females.

Another potentially common feature of Coucal duets was also found in the amplitude pattern of White-browed Coucal songs; as in Pheasant Coucals (Maurer et al. 2008), the second element of White-browed Coucal song phrases was usually the loudest. Interestingly, the second note had also the highest pitch, which hints at a coupling between amplitude and pitch that has previously been described in songbirds (Dabelsteen 1984; Nelson 2000; Goller and Cooper 2008; Ritschard and Brumm 2011; Nemeth et al. 2013) and a Dove (Elemans et al. 2008). This comparative view suggests that, in the absence of any vocal adjustments to counter it, frequency-amplitude coupling is a general trait of bird vocalizations.

Although we do not have individual longitudinal data on how duetting activity varied with breeding stage in White-browed Coucals, our cross-sectional data are in line with previous studies that demonstrated a peak in duetting rates during nest building and when pairs re-nest after nest failure (Sonnenschein and Reyer 1983; Hall 2006; Topp and Mennill 2008). Increased duetting during this breeding stage may hint at a function in ensuring reproductive synchrony. In addition, our observation that duet playback triggered duetting in White-browed Coucals is consistent with a function in territorial defence and/or mate guarding. Probably, duetting serves more than one function within this species, as is the case in other birds, too (Langmore 1998; Hall 2004).

To conclude, this study has characterized the structure and performance rules of duet songs in White-browed Coucals; it has revealed sex-specific song characteristics as well as the potential of duet phrases to serve as an index signal of body size.

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