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Functions and mechanisms of intra-group communication and song coordination during territorial defense in a group breeding bird species, the Yellow-breasted Barbet (*Trachyphonus margaritatus*)

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Funkcje i mechanizmy wewnątrzgrupowej komunikacji i koordynacji śpiewu podczas obrony terytorialnej u kolektywnie rozmnażającego się gatunku ptaka, wąsala perełkowanego (*Trachyphonus margaritatus*)

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A group of Yellow-breasted barbet singing in chorus

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Summaries

1. English summary

Introduction

Animals communicate to share information about their environment, physiological condition and their intention toward an audience, which allow both the emitter and the receivers to interact (Bradbury and Verhencamp, 2011). Communication often occurs in a social environment where multiple senders and multiples receivers share a common signaling space and thus form a communication network (Templeton and Carlson, 2019). One type of intended communication network is the emission of collaborative signals where multiple individuals signal altogether to send one cohesive signal to an audience (Templeton and Carlson, 2019). Such collective signal is often used by group-living species during between group-interactions.

One form of complex collective signal is the emission of vocal duet and chorus songs in birds. An acoustic duet defines the non-random combination of vocalisations emitted by two individuals, usually a mated pair, for the purpose of delivering a coordinated vocal performance (Farabaugh, 1982; Hall, 2009). In birds, acoustic duets have multiple functions depending on the context and the species, and one of the main functions is the joint territory defense (Hall, 2004). When more than two individuals join the group display, they perform a chorus which has similar functions. Chorus songs are usually performed by cooperative-group breeding bird species (Baker, 2004; Radford, 2003). Achieving such coordinated collective signal could be difficult and requires good communication between participants to reunite and agree to initiate such group vocal display. Yet few studies have investigated the use of intra-group communication in the context of coordinated group vocal displays.

The group-living African barbet species (*Lybiidae*) are a good model species to study the role of intra-group communication in the context of group collaborative signalling. Several species are cooperative breeding birds that perform duets and choruses (Soma and Brumm, 2020). Our knowledge regarding their within-group social interactions is limited but it seems that group vocal displays are led by the dominant breeding pair. Moreover, most species perform a pre-duet greeting ceremony in the beginning of a duet and chorus (Short and Horne, 1983). My main hypothesis is that the pre-duet greeting ceremonies could be used as a specific intra-group signal to initiate group

cooperative vocal displays that allow participants to start singing at the same time and deliver a coordinated collective signal.

Aims and hypotheses

The general aim of the thesis was to investigate the role of intra-group communication to initiate a group vocal display (duet or chorus) in a non-oscine group breeding bird species, as well as identify any pattern of song coordination that could differ from the "syllable-by-syllable" adjustments. This research project was motivated by the fact non-oscine duetting and chorusing bird species have generally received less attention than duetting songbirds. Moreover, performing coordinated group displays is a challenging task to achieve when several participants are involved. I chose to study the vocal and social behaviour of the Yellow-breasted barbet (*Trachyphonus margaritatus*), a group-breeding African barbet species that perform duet and chorus songs.

Aim n°1: In birds, an increase in social complexity via cooperative breeding is concomitant with an increase in vocal complexity, especially the number of distinct vocalisations used for within group communication (Leighton, 2017). It is thus important to identify the different vocalisation types of the Yellow-breasted barbet used during its daily vocal activity, especially those used for intra-group communication and their potential functions. This would allow us to better understand the vocal and social behaviour of the species and provide more details about the role of intra-group communication in the context of collective signalling.

Aim n°2: Investigate the usage of the greeting ceremony in the context of a group vocal display. ***Hypothesis 1***: The *chewp* notes are a specific signal used by the Yellow-breasted barbet during vocal duet and chorus introduction. The *chewp* notes should be directly followed by a duet or chorus song. If these vocalisations have a function in group singing initiation, I will not observe a duet or a chorus starting without such signal. ***Hypothesis 2***: The introductory sequence could act as a recruitment signal used by the initiator to attract other group members and trigger them to sing. If this is true, I expect that the initiator systematically gives an introductory sequence to induce a group vocal display, while the followers could answer simply by starting their song without an introductory sequence. Followers should immediately react to the signal and join the initiator. Alternatively, if both the initiator and the followers behave the same way during a duet

and chorus initiation, the introductory sequence could be a greeting ceremony in the sense of an intra-group social behaviour used as mutual agreement to sing in a group or to reinforce bonds.

Aim n°3: Investigate the context of collective vocal displays. ***Hypothesis* 3:** Since barbets are territorial birds, the primary function of group vocal displays might be joint territory defense. I thus expect that birds will react to playbacks that simulate a territorial intrusion by singing actively in duet or chorus. Moreover, I should observe that the group vocal displays are mostly emitted in the context of between-group interactions.

Aim n°*4:** Analyze the mechanisms of song coordination when the birds are duetting. The barbet species are considered to sing with a poor degree of song coordination when duetting (Payne and Skinner, 1970). However, several aspects of their vocal behaviour suggest that song coordination matters. First, duetting and chorusing barbet species rarely sing solo songs, they initiate their communal displays with greeting ceremony and start and stop singing altogether. Thus, a bird might exhibit some sort of mutual attention on its partner's song and could adjust its own vocal performance. ***Hypothesis 4: Barbets sing their phrase of syllables as a fixed action pattern, following a common cue (the pre-duet greeting ceremony) that initiates singing in both individuals. Once they start singing, each duetter sings with its internal-rhythmic pattern which is not influenced by its partner rhythm of calling. If it is true, both individuals should differ in their rhythm of calling and the timing changes made by one bird do not affect the timing of its partner. ***Hypothesis 5***: Alternatively, a barbet which is actively singing in duet might alter its rhythm of calling when it perceives a change in the timing of its partner' song. Instead of phrase-by-phrase timing adjustments, the bird could perceive the general acceleration or slowdown in the rhythm of calling of its partner and try to imitate such changes.

Methods

We conducted the research project in the Republic of Djibouti in the Horn of Africa, within the protected areas of Djalélo (11°21'16" N, 42°47'54" E) and Assamo (11°1'22." N, 42°52'53" E). We organized four fieldwork sessions between 2019 and 2023 to collect behavioural data related to the social and vocal behaviour of the Yellow-breasted barbet. We caught several groups of birds which received a colour rings combination. A first round of playback experiments was performed in the morning from 6:15 to 11:00 (average sunrise 6:20) during February and March 2019-2020 to investigate the way a group of birds introduce vocal duet and chorus songs. We recorded the

behavioural response of birds with a shotgun microphone connected to a Canon camera. The videos collected were analysed with BORIS (Behavioral Observation Research Interactive Software), to extract data regarding the visual displays. The acoustic features of the introductory vocal sequence (greeting ceremony) were analyzed using R software with the *Seewave* R package. We used autonomous recording units (SongMeter Micros from Wildlife Acoustics) to conduct a passive acoustic monitoring (PAM) from January to March 2022, to record the daily vocal activity of 11 groups of barbets near-by their roosting sites. We manually selected the different vocalisations using RavenPro software. In 2023, we recorded the vocal behaviour from 6 to 9 in the morning with PAM and conducted playback experiments to simulate the intrusion of an unknown pair that could compete for the roosting cavities site ownership during the nesting period. Each of the 10 groups were tested twice, one time with a short duration duet playback and a second time with a long duration duet playback to test whether long duration duet is perceived more threatening. To investigate whether duet and chorus songs were mainly used for between group-interactions and compare the duration of the displays, we classified the selected group vocal displays recorded under five distinct contexts: *Unanswered Spontaneous Display; Answered Spontaneous Display*; *Between Group Interaction*; *Playback Reaction* and *Playback Reaction - Between-Group Interaction*. Finally, we analyzed the temporal coordination of duetting songs to investigate whether birds are capable of rhythmic adjustment to match the rhythm of singing of their partner. All acoustic and statistical analyses were performed in R software. The methods of recording, sounds extraction, acoustic analysis and the statistical analysis are fully detailed in the corresponding chapters.

Results

Chapter 1*: The communal cavity roosting behaviour and the vocal activity of a group living bird species.* We found that the Yellow-breasted barbet is a group breeding species that use cavities both as roosting and nesting sites. All group members slept within the same cavity. The catching sessions conducted between 2019 and 2022 revealed that some individuals occupied the same cavities site for two consecutive years, even more. This confirms the year-round territorial behaviour of the species. The PAM allowed us to identify four distinct call types (cohesion calls, alarm calls, soft calls and *whoo* calls) used for intra-group communication. Cohesion calls and the group vocal displays were the most common vocalisations recorded. Moreover, we found that the

group vocal displays were often preceded by the emission of cohesion calls which suggest that cohesion calls could serve to localize and attract group members in the vicinity to perform a collective action and play an important role in the group cohesiveness.

Chapter 2*: The use of a multimodal intra-group signal to initiate a cooperative group vocal display.* Once the birds emitted cohesion calls to gather, they initiated the group vocal displays with an introductory vocal sequence which consists of a series of *chewp* notes emitted by one or several individuals. We found two variations of such vocalisations: the *high chewp* and the *low chewp*. The leading individual who initiated a duet or chorus emitted a higher number of *high chewp* notes than the followers who joined the display of the leader. We also found that the leading individual sometimes combined the emission of *chewp* notes with a specific tail posture. The combination of acoustic and visual signal constitutes a multimodal signal that is displayed to initiate duet and chorus songs.

Chapter 3*: Contexts of singing and the mechanisms of song coordination in a group living bird species that performs collective vocal displays*. We investigated the context in which collective vocal displays were given in 11 groups of barbets during the nesting period. To do so, we recorded their vocal activity close to the nesting cavity in the morning and in the afternoon. We found that the birds performed duets and choruses mainly in the morning. We also found that most of the collective vocal displays given by a focal group were emitted in the context of a between-group vocal interaction and all the 10 groups tested with playback stimulations reacted which suggested a function in joint territorial defense. Finally, we explored in more detail the degree to which a bird alters its rhythm of calling according to the vocal production of its partner by analyzing the temporal features of each duetters in 39 duet songs from 9 distinct pairs. We found that duetters sang with a rather similar rhythm even though each individual tends to follow its own internal-rhythmic pattern of singing. Finally, we did not find clear evidence of interactive timing adjustments in a way that the duetters could accelerate or slow down their rhythm of singing according to their partner's rhythmic variations. The birds simply reacted when the partner started and stopped singing.

Conclusion

The work carried out during my PhD study allowed to highlight the role of intra-group communication in a group living bird species that perform collective and coordinated vocal

displays, in the context of group territorial defense. The results presented in the thesis show that: (1) long and close-range vocalisations are used for intra-group communication; (2) the pre-duet greeting ceremony serves as a specific intra-group signal to initiate collective vocal displays; (3) the pre-duet greeting ceremony is initiated by a leading individual that combines specific vocalisations with a tail display to broadcast a multimodal signal; (4) the collective vocal displays are mainly used during between-group interactions which suggest a functions in territorial defense; (5) in the species of study, the birds start and stop singing at the same time, without fine temporal coordination. Overall, I hope that my work will stimulate further research on other group living bird species to investigate how do they mediate their intra-group relationships and coordinate their collective actions.

2. Streszczenie po polsku

Wstęp

Zwierzęta komunikują się by dzielić się informacją o środowisku, stanie fizjologicznym i intencjach wobec odbiorców, co pozwala zarówno nadawcom jak i odbiorcom na interakcję (Bradbury and Verhencamp, 2011). Komunikacja często odbywa się w środowisku społecznym gdzie wielu nadawców i wielu odbiorców równocześnie dzieli wspólną przestrzeń sygnalizacyjną, tworzą w ten sposób sieć komunikacyjną (Templeton and Carlson, 2019). Jednym z rodzajów intencyjnej sieci komunikacyjnej jest wydawanie wspólnych sygnałów, gdzie wiele osobników równocześnie sygnalizuje razem w celu wysłania jednego, spójnego komunikatu do odbiorców (Templeton and Carlson, 2019). Takie kolektywne sygnały są często używane przez gatunki żyjące w grupach podczas interakcji między różnymi grupami.

Jedną z form złożonych sygnałów kolektywnych są duety wokalne i chóry śpiewu u ptaków. Duet akustyczny definiuje się jako nieprzypadkową kombinację wokalizacji wydawanych przez dwa osobniki, zazwyczaj ze skojarzonej pary, w celu zaprezentowania skoordynowanego popisu wokalnego (Farabaugh, 1982; Hall, 2009). Duety u ptaków mają wiele funkcji, zależnie od kontekstu i gatunku, a jedną z głównych funkcji jest wspólna obrona terytorium (Hall, 2004). Kiedy więcej niż dwa osobniki łączą się we wspólnym popisie wokalnym, nazywamy to chórem a jego funkcje są zwykle podobne do duetu. Chóry są wykonywane zazwyczaj przez te gatunki ptaków, które w sposób kolektywny (grupowy) przystępują do rozrodu (Baker, 2004; Radford, 2003). Wytworzenie takiego skoordynowanego sygnału kolektywnego może być trudne i wymaga dobrego skomunikowania uczestników produkujących sygnały, aby rozpoczynać i kończyć sygnalizowanie w odpowiednim czasie. Jednak niewiele badań, jak do tej pory, podejmowało tematykę komunikacji wewnątrzgrupowej w kontekście skoordynowanych pokazów wokalnych.

Żyjące w grupach afrykańskie gatunki wąsali (*Lybiidae*) są dobrym modelem do badania znaczenia komunikacji wewnątrzgrupowej w kontekście sygnalizowania współpracy. Wśród nich mamy kolektywnie gnieżdżące się ptaki, które wykonują duety i chóry (Soma and Brumm, 2020). Nasza wiedza na temat wewnątrzgrupowych interakcji socjalnych jest ograniczona, ale wydaje się, że grupowe pokazy wokalne są prowadzone (przewodzone) przez dominującą parę lęgową. Co więcej, większość gatunków wykonuje ceremonię powitania przed duetem lub chóru (Short and Horne, 1983). Moja główna hipoteza zakłada, że takie przed-duetowe powitanie może być

używane jako specyficzny wewnątrzgrupowy sygnał, inicjujący kooperatywny sygnał wokalny, który pozwala uczestnikom rozpocząć śpiewanie w tym samym czasie, dzięki czemu produkowany jest wspólny i skoordynowany sygnał.

Cele i hipotezy

Zasadniczym celem rozprawy było zbadanie znaczenia komunikacji wewnątrzgrupowej w inicjowaniu grupowego pokazu wokalnego (duetu i chóru) u ptaków nie-wróblowych, a także zidentyfikowanie jakichkolwiek wzorców koordynacji śpiewu, które różnią się od wzorca dopasowywania „sylaba-po-sylabie". Motywacją do podjęcia się tego projektu był fakt, że ptakom duetującym i śpiewającym w chórach spoza *Oscines* (ptaków śpiewających), poświęcano dotąd niewiele uwagi. Ponadto, wykonywanie skoordynowanych pokazów jest zadaniem tym bardziej wymagającym im więcej jest jego uczestników. Dlatego zdecydowałem się wybrać do badań brodala perełkowanego (*Trachyphonus margaritatus*), którego socjalne i wokalne zachowania obejmują zarówno duety jak i chóry.

Cel nr 1: U ptaków wzrost złożoności społecznej grup w efekcie kooperatywnego rozrodu przebiegał wraz ze wzrostem komplikacji komunikacji wokalnej, a zwłaszcza ze wzrostem liczby różnych typów sygnałów używanych do komunikacji wewnątrz grupy (Leighton, 2017). Dlatego ważne jest, aby zidentyfikować różne typy wokalizacji brodali perełkowanych używane podczas ich codziennej aktywności, a szczególnie to jakie i dlaczego są używane do komunikacji wewnątrz grupy. Pozwoliłoby to lepiej zrozumieć zachowania wokalne i społeczne tego gatunku oraz dostarczyłoby więcej szczegółowych informacji na temat roli komunikacji wewnątrzgrupowej w kontekście zbiorowej sygnalizacji.

Cel nr 2: Zbadanie znaczenia ceremonii powitania w kontekście grupowego pokazu wokalnego. ***Hipoteza 1***: Dźwięki *chewp* są specyficznym sygnałem używanym przez brodale perełkowane w trakcie wstępu do duetów i chórów. Jeśli te dźwięki mają funkcję inicjalizacji duetów i chórów, to bezpośrednio po ich wydawaniu, ptaki powinny rozpoczynać duety lub chóry. Jednocześnie, nie powinno obserwować się zarówno duetów jak i chórów, które produkowane byłyby bez wcześniejszego zainicjowania przez dźwięki *chewp*. ***Hipoteza 2***: Sekwencja inicjalizująca duet czy chór, może działać jako sygnał przyciągający innych członków grupy po

to, aby ich zachęcić do wspólnego śpiewu. Jeśli tak rzeczywiście jest to oczekiwałem, że osobnik inicjujący pokaz systematycznie produkuje sygnał inicjujący, podczas gdy osobniki podążające za nim, mogą już same śpiewać bez wprowadzającej sekwencji dźwięków. Powinny po prostu natychmiastowo odpowiadać inicjatorowi i dołączać do niego w śpiewie. Alternatywnie, jeśli zarówno inicjator jak i jego naśladowcy zachowują się w ten sam sposób podczas inicjacji duetu i chóru, sekwencja wprowadzająca może być ceremonią powitania w sensie wewnątrzgrupowego zachowania społecznego wykorzystywania jako wzajemna zgoda na śpiewanie w grupie lub wzmacniania więzi społecznych.

Cel nr 3: Zbadanie kontekstu pojawiania się kolektywnych pokazów wokalnych. ***Hipoteza 3:*** Ponieważ wąsale są ptakami terytorialnymi, to podstawowa funkcja ich pokazów wokalnych może być związana ze wspólną obroną terytorium. Dlatego oczekiwałem, że ptaki będą odpowiadać na playback który symuluje wkroczenie w terytorium poprzez aktywne duetowanie lub śpiewanie w chórach. Co więcej, powinienem obserwować częstszą produkcję takich pokazów w kontekście interakcji między grupami.

Cel nr 4: Analiza mechanizmów koordynacji śpiewu podczas duetów u ptaków. Wąsale są uważane za ptaki, które charakteryzują się nikłym poziomem koordynacji śpiewu podczas duetów (Payne and Skinner, 1970). Jednak pewne aspekty ich wokalnych zachowań wskazują, że koordynacja ma znaczenie. Po pierwsze, śpiewające w duecie i chóralnie gatunki wąsali rzadko śpiewają solo. Zwykle inicjują swoje wspólne postępy wokalne ceremonią powitania i potem zaczynają bądź, po jakimś czasie, przestają śpiewać. W ten sposób ptaki mogą wykazywać pewnego rodzaju wzajemną uwagę na śpiew partnera i potencjalnie dostosować swoje własne wykonanie wokalne. ***Hipoteza 4***: Wąsale śpiewając swoją sekwencję sylab powielają stały wzorzec zachowania, podążając za wspólną wskazówką (ceremonia powitania przed duetem/chórem), która inicjuje śpiew obu (lub większej liczby) osobników. Po rozpoczęciu śpiewu każdy z duetujących osobników śpiewa wg swojego wewnętrznego wzorca rytmicznego, na który nie ma wpływu rytm nawoływanie partnera. ***Hipoteza 5***: Alternatywnie, wąsale perełkowane, aktywnie śpiewają w duecie w swoim wewnętrznym rytmie, który nie jest naruszany przez rytm partnera. A więc zamiast stosować dopasowywania sylaba-po-sylabie, ptak dostrzegałby ogólne zmiany w tempie, przyspieszanie czy spowolnianie rytmu swojego partnera i próbowałby imitować te zmiany.

Metody

Badania przeprowadziliśmy w Republice w Djibouti, zlokalizowanej w tzw. Rogu Afryki, na chronionych obszarach zwanych Djalélo (11°21'16" N, 42°47'54" E) oraz Assamo (11°1'22." N, 42°52'53" E). Prace terenowe prowadzone były podczas ekspedycji w latach 2019-2023, w trakcie których zbierano dane dotyczące zachowania i wokalizacji wąsali perełkowanych. Na obu obszarach badań odłowiono i zaobrączkowano ptaki kolorowymi obrączkami. Pierwsza tura eksperymentów z playbackiem została przeprowadzona między 6:15 a 11:00 (świty rozpoczynały się przeciętnie o 6:20) w lutym i marcu 2019-2020, w celu sprawdzenia w jak sposób ptaki rozpoczynają swoje duety i chóry. Odpowiedź behawioralna ptaków rejestrowana była z pomocą mikrofonu kierunkowego typu shotgun połączonego z kamerą Canon. Nagrane filmy wideo były analizowane z pomocą programu BORIS (Behavioral Observation Research Interactive Software), dzięki któremu wyekstrahowano dane dotyczące pokazów wizualnych obserwowanych ptaków. Parametry akustyczne sekwencji wokalnych (ceremonie powitania) były analizowane z użyciem pakietu *Seewave*, który działa w środowisku programu R. Automatyczne rekordery (SongMeter Micro, Wildlife Acoustics) były używane do przeprowadzenia pasywnego monitoringu od stycznia do marca 2022, w celu nagrania dziennej aktywności 11 grup wąsali w pobliżu ich miejsc noclegowych. Selekcja różnych typów wokalizacji była dokonywana poprzez wizualny przegląd spektogramów w programie *Raven Pro*. W 2023 roku nagrywaliśmy ptaki od 6 do 9 rano z pomocą Pasywnego Monitoringu Akustycznego (ang. skrót PAM) i przeprowadziliśmy eksperymenty symulujące wkroczenie obcej (nieznanej) pary ptaków, która potencjalnie mogłaby konkurować o miejsca noclegowe w norach aktualnych „właścicieli" w trakcie sezonu rozrodczego. Każda z 10 grup została przetestowana dwukrotnie, raz z duetem trwającym krócej a drugi raz z duetem długim, aby sprawdzić czy dłuższy czas trwania duetu odbierany jest jako większe zagrożenie. W celu sprawdzenia czy duety i chóry są używane głównie do interakcji międzygrupowych oraz porównania czasu trwania popisów, sklasyfikowaliśmy popisy wokalne ptaków do pięciu rożnych kategorii kontekstowych: Spontaniczny popis bez odpowiedzi; Spontaniczny popis z odpowiedzią; Interakcja między grupami; Odpowiedź na playback; oraz Odpowiedź na playback wraz z Interakcją między grupami. Na koniec przeanalizowaliśmy koordynację czasową śpiewu w duecie, aby stwierdzić, czy ptaki są zdolne do rytmicznego dostosowywania się do rytmu śpiewu partnera. Wszystkie analizy akustyczne i statystyczne zostały przeprowadzone w środowisku R. Metody

nagrywania, ekstrakcji dźwięków, analiz akustycznych i statystycznych zostały szczegółowo opisane w odpowiednich rozdziałach.

Wyniki

Rozdział 1*: Zachowania podczas nocowania wspólnie w norach oraz aktywność wokalna ptaków żyjących w grupach.* Stwierdziliśmy, że brodale perełkowane są kolektywnie rozmnażającym się gatunkiem, które używają nor zarówno do nocowania jak i do gnieżdżenia się. Wszyscy członkowie grupy śpią w tej samej norze. Sesje odłowów przeprowadzone w latach 2019-2022 wykazały, że niektóre osobniki zajmują te same nory przez dwa lata lub dłużej. Potwierdza to całoroczną terytorialność tego gatunku. PAM pozwolił na zidentyfikowanie czterech odmiennych typów głosów (głosy spajające grupę, głosy alarmowe, ciche głosy oraz głosy *whoo*). Głosy spajające oraz grupowe popisy wokalne były najczęściej rejestrowanymi wokalizacjami. Co więcej, stwierdziliśmy, że grupowe popisy wokalne były często poprzedzane wydawaniem głosów spajających, co wskazuje na to, że mogą one służyć jako pomoc do zlokalizowania i włączenia członków grupy znajdujących się w pobliżu do wspólnego działania, a więc odgrywają one istotną rolę dla utrzymywania spójności grupy.

Rozdział 2*: Wykorzystanie multimodalnego sygnału wewnątrzgrupowego do inicjowania kolektywnego wokalnego popisu grupowego.* Kiedy ptaki wydadzą głosy spójajace, to następnie inicjują grupowy popis wokalny z wokalną sekwencją wstępną, składającą się z serii głosów *chewp*, które wydawane są przez jednego lub kilka osobników. Stwierdziliśmy występowanie dwóch rodzajów takich wokalizacji: *high chewp* oraz *low chewp*. Osobnik prowadzący, który inicjuje duet lub chór wydaje większą liczbę głosów *high chewp* niż osobniki, które wokalnie za nim podążały włączając się w popis wokalny lidera. Odkryliśmy również, że osobnik prowadzący czasami łączył emisję głosów *chewp* ze specyficzną pozycją ogona. Takie połączenie sygnału akustycznego i wizualnego tworzy nowy sygnał multimodalny, służący do inicjowania duetów i chórów.

Rozdział 3*: Okoliczności śpiewu oraz mechanizmy koordynacji śpiewu u żyjącego grupowo gatunku wytwarzającego kolektywne popisy wokalne.* Zbadaliśmy kontekst (okoliczności) w jakich pojawiały się kolektywne popisu wokalne w 11 grupach brodali perełkowanych. Aby to zbadać nagrywaliśmy aktywność wokalną ptaków w pobliżu nor rano oraz popołudniu.

Stwierdziliśmy, że ptaki produkowały duety i chóry głównie rano. Stwierdziliśmy również, że większość kolektywnych popisów wokalnych grupy była produkowana w kontekście interakcji międzygrupowych. Wszystkie 10 grup ptaków przetestowanych eksperymentalnie z użyciem playbacku jednoznacznie nań odpowiadały wskazując na funkcję śpiewu we wspólnej obrony terytorialnej. Wreszcie, zbadaliśmy bardziej szczegółowo stopień, w jakim ptak zmienia swój rytm wokalizacji w zależności od głosów wydawanych przez partnera. Przeanalizowaliśmy parametry czasowe każdego z osobników tworzących 39 duetów w wykonaniu 9 różnych par. Stwierdziliśmy, że duetujące osobniki śpiewają z dość podobnym rytmem, pomimo że każdy z ptaków ma tendencję do podążania za swoim własnym, wewnętrznym rytmem śpiewu. Wreszcie, nie udało nam się znaleźć wyraźnego dowodu na interaktywne dopasowywanie czasu produkcji głosów osobników duetujących, a więc takie gdzie partnerzy podążają za przyspieszającym czy spowalniającym rytmem śpiewu partnera. Wydaje się, że ptaki jedynie odpowiadają na rozpoczęcie i zakończenie śpiewu partnera.

Wnioski

Badania przeprowadzone w trakcie przygotowywania doktoratu pozwoliły na podkreślenie znaczenia komunikacji wewnątrzgrupowej u żyjącego grupowo gatunku ptaka, który wydaje kolektywne i skoordynowane pokazy wokalne, w kontekście grupowej obrony terytorium. Wyniki zaprezentowane w rozprawie wskazuję, że (1) wokalizacje o długim i krótkim zasięgu używane są do komunikacji wewnątrz grupy; (2) wykonywana przed właściwym duetem ceremonia powitania służy jako specyficzny, wewnątrzgrupowy sygnał inicjujący właściwy kolektywny popis wokalny; (3) ceremonia powitania przed właściwym popisem grupowym jest wydawana przez lidera, który łączy produkcję wokalizacji z pokazem specyficznej pozycji ogona, tworząc sygnał multimodalny; (4) kolektywne popisy wokalne są używane głównie podczas interakcji między grupami co wskazuje na ich znaczenie w grupowej obronie terytoriów; (5) osobniki badanego gatunku rozpoczynają i kończą śpiew w tym samym czasie, bez stosowania precyzyjnej koordynacji czasowej synchronizującej pokaz. Podsumowując, mam nadzieję, że moja praca pobudzi do dalszych badan nad gatunkami ptaków żyjącymi w grupach, aby zbadać charakterystykę wewnątrzgrupowych relacji oraz sposoby koordynacji wspólnych działań.

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List of original publications

My doctoral dissertation consists of four publications listed below:

Mahamoud-Issa, M., Sikora, B., Rusiecki, S., Łosak, K., Osiejuk, T.S. *in press*. The communal roosting behaviour and nesting of a group living bird species, the Yellow-breasted Barbet *Trachyphonus margaritatus* in Djibouti. *Scopus: Journal of East African Ornithology*.

Mahamoud-Issa, M., Sikora, B., Łosak, K., Osiejuk, T.S. 2023. The vocal repertoire and the daily calling activity of the Yellow-breasted Barbet (*Trachyphonus margaritatus*). *Journal of Ornithology* https://doi.org/10.1007/s10336-023-02112-5 (IF: 1.816)

Mahamoud-Issa, M., Sikora, B., Rusiecki, S., Osiejuk, T.S. 2023. The Yellow-breasted Barbet (*Trachyphonus margaritatus*) introduces vocal duets and choruses with a specific multimodal signal, during territorial advertisement. *Journal of Ornithology* 164: 183–192. https://link.springer.com/article/10.1007/s10336-022-02016-w (IF: 1.816)

Mahamoud-Issa, M., Osiejuk, T.S. *in prep*. Contexts of singing and the mechanisms of song coordination in a group living bird species that performs collective vocal displays.

Some of the data collected during this PhD work were used in the publication:

Sikora, B., **Mahamoud-Issa, M**., Unsoeld, M., Hromada, M., Skoracki, M. 2023. Species Composition of Parasitic Mites of the Subfamily Picobiinae (Acariformes: Syringophilidae) Associated with African Barbets (Piciformes: Lybiidae). Animals. 13: 2007. https://doi.org/10.3390/ani13122007 (IF: 3.2)

General Introduction

1. Introduction to Animal communication

1.1 Principles of animal communication

Animals communicate to share information about their environment, physiological condition, and their intention toward an audience, which allows both the sender of the information and the receiver(s) to interact and get some benefits (Bradbury and Verhencamp, 2011). As example, the scent marks led by felids in their environment serve as territorial boundaries that inform about the territory ownership and thus, help to avoid unnecessary physical conflicts between individuals, as well as finding a potential mate (Allen *et al*., 2016), the alarm calls given by birds and mammals can be monitored by several animal species to detect a potential threat (Magrath et al., 2020), and the colourful feathers and extravagant dances of males in the birds-of-paradise species serve during the courtship display to attract females (Ligon *et al*., 2018). In all these examples, the act of communication consists of transmitting information through a signal which can be defined as stimuli that affect the receiver by changing its behaviour and even its physiological condition **(**Bradbury and Verhencamp, 2011**, Figure 1**). Unlike cues that are by-products of animal behaviour generated unintentionally or any assessable properties of living organisms and environmental features that can be monitored by the sense organs of an animal, signals are stimuli selected for the purpose of transmitting intentional information and generating interaction between the sender and the receiver (Bradbury and Verhencamp, 2011; Smith *et al*., 2003). These stimuli can be acoustic, visual, olfactory, or physical contact. Indeed, animals often combine different modalities to transmit a multimodal signal (Higham and Hebets, 2013).

1.2 Communication Network, intra-group communication and collective signalling

Communication often occurs in a social environment where multiple senders and multiple receivers share a common signalling space and thus form a communication network (Templeton and Carlson, 2019). In this network, an individual could emit a broadcast signal to a large audience. As an example, the song of males in songbird species corresponds to a broadcast signal intended to attract females and compete with other males in the vicinity (Catchpole and Slater, 2008). On the other hand, an individual could emit a directed signal toward a specific receiver or small group of receivers for close-range interactions (Templeton and Carlson, 2019). In group-living species,

the intra-group communication is essential for individuals to regulate their within-group social interactions and affiliation such as assessing the dominance hierarchy (Tibbetts *et al*., 2022), reducing intra-group aggression (Weir *et al*., 2021), performing collective actions such as group hunting (Bailey *et al*., 2013), or to maintain group cohesiveness (Demartsev *et al*., 2023). In some cases, intra-group communication could serve to initiate and generate collaborative signals, when multiple individuals signal together to send one cohesive meta-signal to an audience (Templeton and Carlson, 2019).

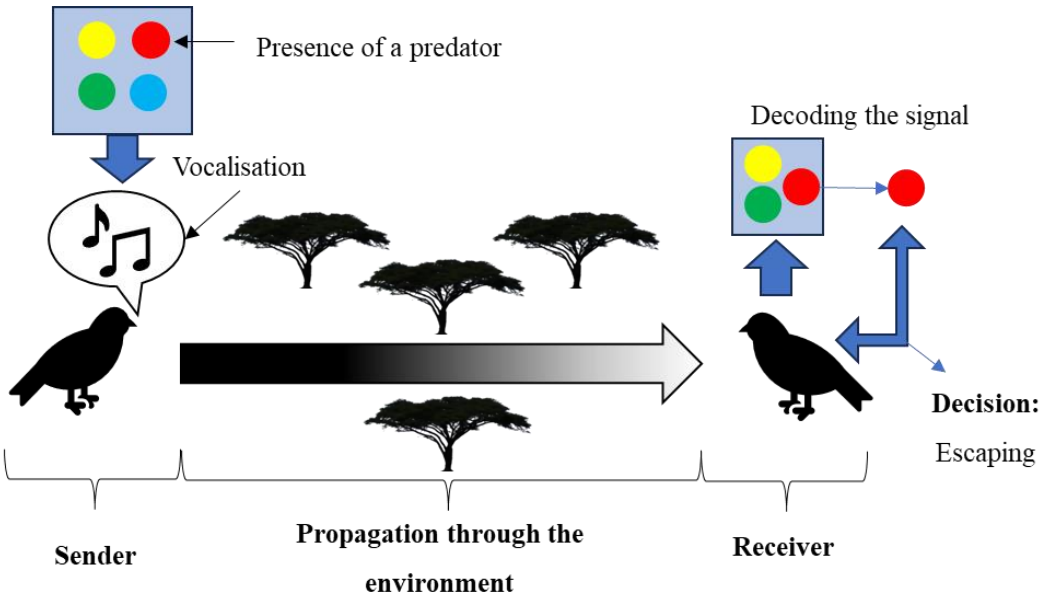

Figure 1: The process of acoustic communication (Shannon et Weaver, 1949; Bradbury and Verhencamp, 2011). The sender emits an acoustic signal trough which is encoded some information (colour circles). In this example, the yellow circle is the information about the species of the emitter, the green circle is its sex, the blue circle its individual identity and the red circle the information about the presence of a predator detected by the emitter. The acoustic signal propagates through the environment and some information might be lost due to the signal deterioration during the propagation. Then the receiver decodes the relevant information and could decide whether to react or not.

Group signalling performed by multiple individuals vocalising simultaneously occurs in many vertebrate and invertebrate species and constitutes a duet or a chorus display. The chorus of anurans and bush-crickets consists of males gathered in one place who vocalize together to attract females (Greenfield, 1994; Wells and Schwartz, 2006). In this context, the chorus is an acoustic competition between males for reproduction. On the other hand, collaborative signalling is one type of group signalling in which participants actively cooperate to achieve a common goal, and it mostly occurs in social mammals and birds. The duetting and chorusing bird species have probably

the most diverse and elaborate forms of collaborative vocal displays, which are described as duet or chorus songs when more than two individuals are displaying together.

2. Duetting and chorusing behaviour in birds

2.1 Classify the vocal production of birds

A vocalisation is the sound produced by an individual using its vocal apparatus. It can consist of a single sound unit named a syllable. The structure of a syllable can be simple with only one note/element or be more complex with several notes. A note is defined as a single line on a spectrogram. A complex vocalisation can be constituted of distinct sections or phrases which consist in the repetition of one syllable or the specific combination of several distinct syllables that is a motif (Catchpole and Slater, 2008) . It is common to classify avian vocal production into two broad categories: call and song. The song is generally a loud, long, and complex vocalisation made of different syllables and motifs which has as its main function to attract mates, compete with same-sex individuals during the breeding season, and in the case of territorial species, advertise about territory ownership (Lovette and Cornell University, 2016). Songs are typically emitted from an exposed perch, or in some species like the Short-clawed lark (*Certhilauda chuana*), songs are part of an aerial display during the breeding season (Engelbrecht and Grosel, 2022). Calls are usually simpler and shorter than the song and often consist of the emission of a single syllable or the repetition in rapid succession of the same syllable. Many birds produce non-vocal sounds as well, such as the drumming of the woodpeckers (Miles *et al*., 2018) or the wings sound produced during the courtship display of the male Club-winged manakin (*Machaeropterus deliciosus*, Bostwick and Prum, 2005).The measurements of the acoustics features, and the graphical representation of the different sounds allow to build of the acoustic repertoire of a species, which is a classification of the different sounds identified for a species. A catalogue of vocal production is useful to explore many aspects of animal behaviour, especially the functions of the different vocalisations.

2.2 Definition of the duetting behaviour

Over the years of studying the duetting behaviour in birds, the definition of such joint display has evolved. Avian duets consist of two birds that coordinate their songs with a certain degree of temporal precision to deliver a joint acoustic display (Farabaugh, 1982). Michelle Hall completed this definition with some precisions: the overlapping bouts of vocalisations are given

by paired individuals, usually a paired male and female, and there is a low coefficient of variation of the intervals between their vocal elements (Hall, 2004). It is a pair-level interaction with a vocalisation initiated by one individual that is answered by the second individual, which can lead to a series of alternating or overlapping answers from both duetters (Hall, 2009; Logue and Krupp, 2016). Few studies that investigated the mechanisms of song coordination in duetting songbirds revealed that the partners interactively adjust the timing of their vocalisations by listening to their own vocal production (autogenous feedback) and the vocal production of their partner (heterogenous feedback) and combine non-randomly different note types (Coleman *et al*., 2022; Hoffmann *et al*., 2019). The duet code defines the set of answering rules followed by birds when singing in duet (Logue and Krupp, 2016). Being able to choose the note type as well as adapt the timing of answering requires a fast auditory reaction time (Thorpe, 1963). Overall, an acoustic duet defines the non-random combination of vocalisations emitted by two individuals for the purpose of delivering a coordinated vocal performance (**Figure 2**). The local interaction between the paired birds generates a new collective signal directed both to the duetter and to a large audience (Brumm and Slater, 2007).

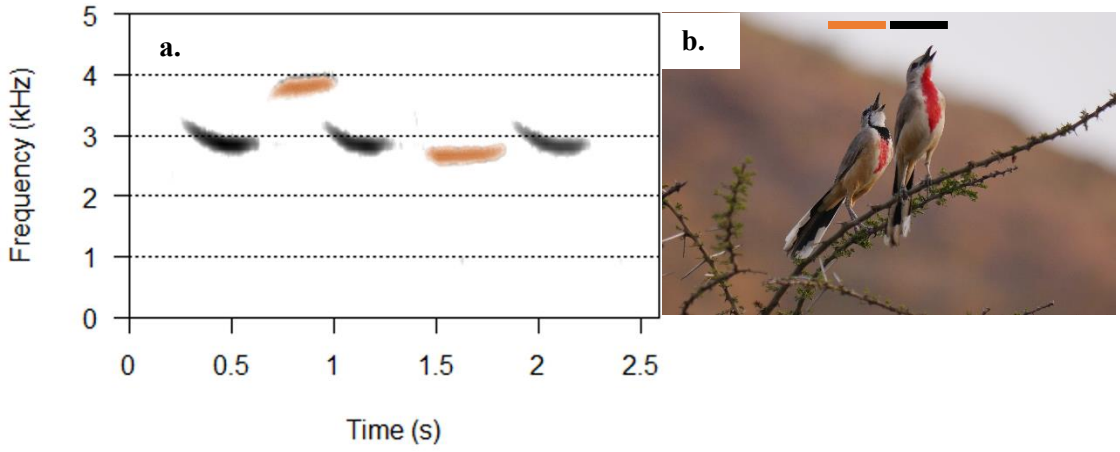

Figure 2a: Spectrogram of a duet song of a pair of Rosy-patched Bush-shrike (*Rodophoneus cruentus*). When duetting, the paired male (black notes) and female (orange notes) alternate non-randomly their syllables. **b**: Picture of the duetting pair (male is highlighted with the black stripe and female the orange stripe).

2.3 Sex roles and functions of duets

Several hypotheses have been formulated regarding the functions of duetting behaviour in birds (Dahlin and Benedict, 2014; Hall, 2004), as well as the different playback experiments that could be conducted to test them (Douglas and Mennill, 2010). Although in a few species, such as the Long-tailed manakin (*Chiroxiphia linearis*), the duet performance is a multimodal and collective courtship display performed by two males to attract a female (Lukianchuk and Doucet, 2014; Trainer *et al*., 2002), it is much common that duetting behaviour is performed by a paired male and female. Hence, vocal duets might be a form of intra-pair vocal communication that serves multiple purposes. In zebra finches (*Taeniopygia guttata)*, vocal duets and other forms of intra-pair interactive communication occur at the nest and could help mate recognition, reinforce pair bonds as well as help to coordinate other collaborative actions such as the time spent in incubating the eggs between partner and the exchange information during the nest reliefs (Boucaud *et al*., 2017, 2016; Elie *et al*., 2010). Another intra-pair function of vocal duets is to maintain contact between mates, especially in habitat where distant visibility is low. In the Rufous-and-white wren (*Thryothorus rufalbus*), the average distance between duetters was about 19.2 m which is relatively important for such tiny birds. Moreover, when duetting, the mates approached each other, which supports the acoustic-contact hypothesis function (Mennill and Vehrencamp, 2008). The wrens also emitted duets when close to one another near-by their nest, as well as at the edge of their territory, especially during between-pair interactions, which suggest a role in territory defense. The paired male and female of Purple-crowned fairy-wrens (*Malurus coronatus*) strongly reacted to playback stimulation, by approaching the loudspeaker and increased their within-pair cohesion by spending more time close to one-another and emitting numerous coordinated duet songs (Hall and Peters, 2008). Similar sex role convergence during territory defense is observed in many other duetting birds, such as the Ovenbird (*Seiurus aurocapilla*, Diniz *et al*., 2020). The join-territory defense seems to be one of the main functions of avian acoustic duets (Dahlin and Benedict, 2014).

Even though both the male and the female react to simulated intrusion during playback experiments; the function of solos and duets might be different at the individual-level and partners might not respond in a same way to same-sex solo songs as the opposite-sex solo song and duet. The reaction toward same-sex solo song could be as strong as the reaction toward a duet song or even higher, which suggest either sex-specific territorial defense or a form of mate guarding when

one individual increases its duet rate against same-sex solo song (van den Heuvel *et al*., 2014). Similarly, matching the song of a potential rival could mean an increase of aggressivity (Wheeldon et *al.*, 2021). The female Eastern whipbird (*Psophodes olivaceus*) matched her solo song type during same-sex song duets but when duetting with her mate, the female matched the song type of her mate, while the male preferentially matched the song type of the simulated male competitor. Therefore, the authors suggested that duet song in this species could be the result of sexual conflict where the female matches her mate 'song to signal to same-sex rivals their bond status and thus, it could be a form of mate guarding (Rogers et al., 2006). On the other hand, Levin suggested that the female song in the Bay wren (*Cantorchilus nigricapillus*) is primarily used in territory defense and the male song for mate guarding because it was usually the male that joined the female solo song to create a duet (Levin, 1996). To summarize, vocal duets are multifunctional depending on the species and the context of emission. It might signal the mated status or breeding activity, defend a territory, and reinforce pair bonds as well as intra-pair cooperation (Hall, 2009).

2.4 Occurrence of the duetting and chorusing behaviour in birds

Duetting behaviour has been reported in over 360 bird species (Dahlin and Benedict, 2014). These species mostly occur in tropical regions, and it was thought that environmental factors and lifestyle in the tropics might explain such occurrences (Farabaugh, 1982; Thorpe, 1972). In temperate regions, mostly the males sing to defend a territory and attract females during the short breeding season in spring and summer (Catchpole and Slater, 2008). The environmental conditions in the tropics such as temperature, daylength and food availability could be less variable over time which allows a longer breeding season or several short breeding opportunities during the year and, thus, promote a year-round territoriality. This might favour pair stability and enhance cooperation between mates that lead to sex role convergence and the emergence of duetting behaviour (Slater and Mann, 2004). However, a study done on 372 songbird species found a significant negative evolutionary relationship between migration and duetting (Logue and Hall, 2014). The authors concluded that duetting evolved in association with migration and not tropical breeding, and the perceived association between tropical breeding and duetting may be a by-product of the migration–duetting relationship. In the North American passerines, the duetting bird species are more frequently associated with long-term monogamy and year-round territoriality compared to none-duetting species (Benedict, 2008). Thus, a sedentary lifestyle, year-round territoriality and

monogamy could promote the development and maintenance of vocal duets in both temperate regions and in the tropics. The potential link between female song and duetting behaviour was also addressed in a study on the New World blackbirds. The phylogenetic analysis showed that the loss of female song was correlated with the loss of similar life-history traits: monogamy, territoriality, and non-migratory behaviour (Odom *et al*., 2015; Price, 2009). It also revealed that duets evolved in lineages where female song was common and likely ancestral, indicating that female song and duet behaviour are not evolutionarily independent in this clade (Odom *et al*., 2015). The authors suggested that "the apparent association between duets and these natural history traits may be a consequence of duetting behaviour evolving in species with female song, which is strongly associated with these traits, rather than these traits themselves driving the evolution of duets." Although the female song is an ancestral trait in most of the songbird species (Odom *et al*., 2014), it cannot constitute solely a general prerequisite to the evolution toward duetting as in many suboscines and non-passerine birds, females use other types of vocalisations to duet (Odom and Mennill, 2010; Seddon and Tobias, 2006).

3. The African Barbets (Lybiidae), a good model to study the role of the intra-group communication in the context of a duet and chorus displays

3.1 Vocal behaviour of the group-breeding African barbets species

Among the diversity of non-oscine duetting and chorusing bird species, the African barbets are well known to perform loud and conspicuous collective vocal displays (Hall, 2009; Soma and Brumm, 2020). The term "Barbet" refers to bird species that belong to the Piciformes order which includes seven families: Lybiidae (African Barbets); Megalaimidae (Asian Barbets); Capitonidae (New World Barbets); Semnornithidae (Toucan-Barbets); Ramphastidae (Toucans); Indicatoridae (Honeyguides); and Picidae (Woodpeckers). The Lybiidae family (African barbets) consists of 41 species from seven genera that inhabit sub-Saharan regions of Africa (Winkler *et al*., 2020). Most of the species from the *Trachyphonus* and *Lybius* genera are group-breeding bird species that perform vocal duets and chorus displays (Short and Horne, 1983; Soma and Brumm, 2020). Indeed, the group-breeding lifestyle might have facilitated the emergence of duetting and chorusing behaviour in barbet species, which could serve for multiple purposes such as pair bond maintenance, dominance against subordinates and territory defense (Soma and Brumm, 2020). Apart from the duet and chorus displays, barbets are known to perform "greeting ceremonies"

which is a form of intra-group communication. This behaviour has been documented in detail in the Black-collared barbet (*Lybius trochatus*). The authors said that "duetting and greeting ceremonies are major features of the social behaviour" of the species (Short and Horne, 1982). They described it as complex visual, and acoustics displays performed by group-members when gathering. When a greeting ceremony initiated the emission of duets or choruses, they called it "pre-duet". Pre-duet greeting ceremonies have been reported in at least eight species of African barbets, all of which are chorusing group-breeding species (Short and Horne, 1983). Such usage of greeting ceremonies to initiate a group vocal display suggests that intra-group communication is essential for group members who cooperate to perform a collective group vocal display. However, there is still a lack of knowledge regarding the usage of such pre-duet vocalisations and whether it could constitute a specific signal to initiate collective vocal displays or not.

Duetting and chorusing barbet species rarely sing solo, once a territory is established by a pair, birds usually sing in duet or chorus (Short and Horne, 1983). Such prevalence of duets and choruses displays instead of solo songs suggest that cooperation and song coordination is essential to achieve collective actions such as defending a territory or maintaining pair bond and group cohesion. Curiously, most of these barbet species perform poorly coordinated duets and choruses during which each participant sings following its own internal rhythmic pattern that seems independent from its partner's song, even though some degree of mutual attention and temporal adjustment was not excluded (Payne and Skinner, 1970). For example, when a pair of Green barbet (*Stactolaema olivacea*) is duetting, a certain degree of tempo shifting is observed as if the birds tend to match their rhythm of singing (Short and Horne, 1980). The song rhythmicity matching in barbets still needs investigation. Therefore, the chorusing African barbets are a good model to study the role of intra-group communication in the context of the emission of duets and choruses as well as the mutual attention and song coordination of duetters when they sing actively.

3.2 The Yellow-breasted barbet as a subject of study

I decided to focus my behavioural research on intra-group vocal communication and song coordination in the Yellow-breasted barbet (*Trachyphonus margaritatus*, Rüppell *et al*., 1826). It is a non-migratory bird, considered as a group-breeding species, usually found in pairs or small social groups that defend a territory year-round and emit loud vocal duets and choruses. Sexes are visually distinguishable; the male has a black patch on its throat that is lacking on the female

(Redman et al., 2016, **Figure 3**). The vocal repertoire and social behaviour of the Yellow-breasted barbet is poorly known. The song is described as the repetition of the same motif "tew-choo-to" by both sexes during a duet or a chorus, similar to the duetting song of the Red-and-yellow barbet (*Trachyphonus erythrocephalus*, Short and Horne, 2020a). Both the male and the female sing this song type together in duets and choruses. The species is also known to emit pre-duet greeting ceremonies described as *chewp* notes as well as some rattling alarm calls (Short and Horne, 2020b).

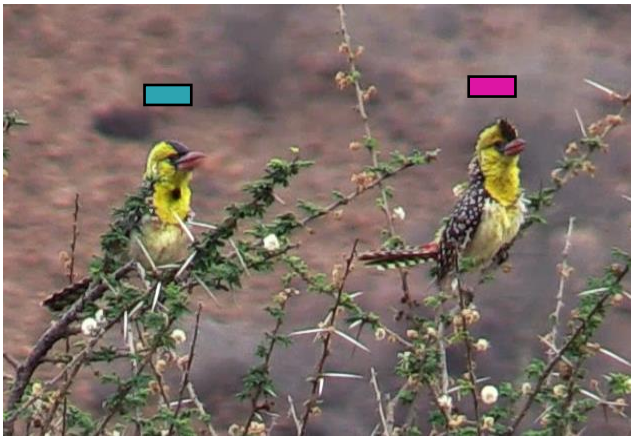

Figure 3: Picture of a duetting pair of Yellow-breasted barbet singing. The male has a black patch on its throat which is absent in on the female.

The very first aim of my research project was to collect behavioural data regarding the social behaviour of this group-living bird species, especially the group structure, its vocal repertoire as well as the daily vocal activity near the roosting cavities using passive acoustic monitoring (see **Chapter 1**). This data provided a better understanding of the vocal behaviour of the species. The second aim was to investigate the usage of greeting ceremonies in the context of a group vocal display (a duet or chorus song). My hypotheses were that *chewp* notes could be a specific intra-group signal used by the Yellow-breasted barbet to initiate vocal duet and chorus songs and that it could act as a recruitment signal used by the initiator to attract other group members and trigger them to sing. I conducted playback experiments to simulate an intrusion and elicit a vocal response from the tested groups and recorded the behavioural response of the birds with a video camera. Then, I analyzed the acoustic and visual features of the pre-duet greeting ceremony and its usage in the context of territorial defense (see **Chapter 2**). Finally, I investigated the context of singing and the mechanisms of song coordination in the Yellow-breasted barbet. I conducted passive acoustic monitoring to record the vocal activity of several groups close to their roosting cavity during the nesting period. I classified the collective vocal displays recorded into

different contexts of singing. I expected that if duet and chorus songs serve mainly for territorial ownership advertisement, most of the collective displays recorded should occur during between-group interactions. I also measured the song coordination in duets. My main hypothesis was that despite a poor degree of song coordination, duetters might try to match their rhythm of singing to deliver a synchronized collaborative acoustic signal (see **Chapter 3**).

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Chapter 1: The communal cavity roosting behaviour and the vocal activity of a group living bird species

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Mathieu Mahamoud-Issa, Bożena Sikora, Katarzyna Łosak, Tomasz S. Osiejuk (**2023**) The vocal repertoire and the daily vocal activity of the Yellow-breasted Barbet (*Trachyphonus margaritatus*). *Journal of Ornithology*. **Status: Published** Link: https://link.springer.com/article/10.1007/s10336-023-02112-5

Mathieu Mahamoud-Issa, Bożena Sikora, Katarzyna Łosak, Stanisław Rusieck, Tomasz S. Osiejuk (***in press***) The communal roosting behaviour and nesting of a group living bird species, the Yellow-breasted barbet (*Trachyphonus margaritatus somalicus*) in Djibouti. *Scopus: Journal of East African Ornithology*. **Status: Submitted and revised**

Abstract

The Yellow-breasted Barbet (*Trachyphonus margaritatus*) is a group living and chorusing bird species. Most of its vocal repertoire, breeding ecology and roosting behaviour are unknown or poorly described. In this study, we collected information about the usage of the roosting cavities during and outside the nesting period, for several group of barbets in Djibouti. We found that the group size ranged from a single pair to more than ten individuals per group. Each group occupied a specific roosting site where several cavities were dug. The group members slept together within one cavity, and the roosting site did not change over the years of the monitoring. During the nesting period, the group members slept with the eggs and chicks within a single cavity that served both as roosting and nesting cavity. We observed that other bird species used the barbet's cavities which suggests that inter-specific competition might occur with other cavity nester species. We recorded the daily calling activity of barbets at 11 roosting cavities sites to access the vocal repertoire and measured the acoustic features of four distinct vocalisations we could identify. These vocalisations were used for intra-group communication and were not part of the duet and chorus songs. We

found that bird's peak of calling activity was early in the morning and at the end of the day. The cohesion calls and group vocal displays were the most common vocalisations. Moreover, cohesion calls were often used before the start of a group vocal displays which suggest a function in the intra-group cohesiveness and recruitment.

Introduction

The vocal behaviour of duetting and chorusing bird species has been subject of growing interest over the last decades (Dahlin and Benedict, 2014; Hall, 2009). The studies have focused on understanding the functions of duet and chorus displays (Baker, 2004; Mennill and Vehrencamp, 2008), as well as the way that birds learn to coordinate their song with a partner (Rivera-Cáceres *et al*., 2018; Rivera-Cáceres and Templeton, 2019) and the mechanisms of song coordination (Hoffmann *et al*., 2019; Ręk and Magrath, 2020). But most of the work has been done on oscine duetting bird species and non-oscine species have received less attention. Moreover, the research tends to focus mainly on the conspicuous duetting and chorusing performance, with sometimes little information about the other vocalisations that birds might produce in their daily life.

In the case of group living species that perform coordinated choruses, assessing the functional vocal repertoire would provide a better understanding of the social structure and the inter-intra-group interactions (Hale, 2006; Radford, 2004). Leighton found that an increase in social complexity via cooperative breeding is concomitant with an increase in vocal complexity in birds (Leighton, 2017). He referred to the vocal complexity as the "functional repertoire size" (Bradbury and Verhencamp, 2011). In other words, the number of vocalisations given within specific contexts. The expansion of the vocal repertoire was significant for the vocalisations assigned to intra-group communication: contact calls and alarm calls. Since coordinated group vocal displays evolved in association with group breeding in African barbets species (Soma and Brumm, 2020), assessing the functional vocal repertoire will provide a better understanding of the social interactions and the role of the group members. This could help to understand the functions of the coordinated group vocal displays and the role of intra-group communication when a group of barbets is performing such collective signal.

The social behaviour of some of these barbet species has been described (Short and Horne, 1982, 1980), but for most of them, there is still a lack of knowledge regarding many aspects of the

social behaviour and the group breeding strategies. African barbets are cavity nesters, in which the breeding male and female (and sometimes helpers in group breeding species) incubate and feed the young (Short and Horne, 2001; Winkler *et al*., 2020). They are territorial birds that defend their roosting cavities against conspecific intrusion (Short and Horne, 2001). As an example, pairs of Crested barbets (*Trachyphonus vaillantii*) maintained a territory with several trees containing holes for roosting and nesting. Playback stimulation revealed that even though one hole was used as nesting site, the birds produced territorial displays in front of each hole owned (Ward, 1986). In the Black-collared barbet *(Lybius torquatus*), a group of birds defended a single territory year-round, and all group members slept into a single roosting cavity outside the breeding season, but the group split into subgroups that occupied different nesting cavities within the same territory during the breeding season (Grimes, 1976). In the Red-and-yellow barbet (*Trachyphonus erythrocephalus*), the group nests and roosts together or the helpers could roost in other holes nearby (Short and Horne, 2001).

Interspecific competition could occur between African barbet species as well as with other species to occupy cavities. It was observed that the Lesser Honeyguide (*Indicator minor*) responded to vocalisations of the Black-collared barbet (Ward, 1986), playback of duets of the Black-billed barbet (*Lybius guifsobalito*) might elicit a vocal response from the Spotted-flanked Barbet (*Tricholaema lachrymosa*,Short and Horne, 1983), and the Green barbet (*Stactolaema olivacea*) might react aggressively to calls of other sympatric barbet species such as the White-eared barbet (*Stactolaema leucotis*, Dowsett-Lemaire and Dowsett, 1987). In 2018, we witnessed a pair of White-eared barbet actively defending their cavity against a crested barbet in a tree in South Africa (Mahamoud-Issa pers.obs).

The aim of this study was to collect more information about the group size and the social behaviour of the Yellow-breasted barbet (*Trachyphonus margaritatus*), especially the collective usage of roosting cavities and the functional vocal repertoire of the species. We conducted four distinct field work session between 2019 and 2023 to investigate the communal roosting behaviour of the species, focusing on three questions: 1- Do the birds from the same group sleep communally within a single cavity or do they split into several ones at the same roosting site during and outside the nesting season? 2- Do the birds remain at the same site over the years? 3- Does any inter-specific competition with other bird species occur for cavity ownership? We also conducted regular

pictures of the eggs and chicks to estimate the duration of the nesting period. In 2022, we monitored the acoustic communication close-by the roosting cavities and analyzed the acoustic features of different long and short-range vocalisations emitted by birds. We discuss the context of the emission and potential functions of the different vocalisations and provide details about the calling activity per hour during the day, around the barbet's roosting cavities.

Methods

Sites of study and monitoring of birds at their roosting site

We conducted our study in the Republic of Djibouti, where the subspecies *T. m. somalicus* (von Zedlitz, 1910) is a common bird that inhabits thornbush and acacia savannah. The species is observable from coastal regions (sea level) up to the Day Forest in Goda Mountains (1,750 m altitude.). We conducted four distinct field work sessions between 2019 and 2023, in two areas: Djalélo: 11°21'16" N, 42°47'54" E and Assamo: 11°1'22." N, 42°52'53" E (**Figure 1a**, **Supplementary materials 1**). These field work sessions occurred during the fresh season from January to March. We selected these two areas because the size of the population was suitable for our study and the presence of a touristic camp that we used as basecamp during the fieldwork sessions. In these regions, the Yellow-breasted barbet is usually found along the dry watercourses. A territory owned by a group of barbets, encompasses a roosting cavities site dug along a sandy riverbank or found in rocky cliffs, where birds spend each night (**Supplementary materials 2**). Our work consisted first of localizing roosting cavities, accompanied with direct observation of birds in the surroundings. Once potential roosting sites were localized, we visited each site at the end of the day, observing with binoculars the birds gathering around their cavities from 17:30 until they entered the cavities at dusk. During this observation time, we documented the behaviour of the birds such as the time of arrival at the cavity site, when they entered, and any relevant interactions between group members. Since several cavities could be dug at the same site (**Figure 1b**), we carefully annotated which specific cavity the birds entered. In 2020, 2022 and 2023, we used an endoscope (wireless Depstech, model: WF010) to observe inside the cavities to document the shape of the entrance corridor and the aspect of the chamber (we wanted to estimate how large it was and determine if the birds put any materials within, such as small branches) and to check the presence of brood.

Catching session

We then placed a mist net in front of a roost cavity early in the morning before 6:00. When barbets woke and flew from the cavity at dawn, they were caught in the mist net. Once caught, we weighed each bird, determined the sex, and deployed colour rings. For each group, we deployed one colour to the group and one colour unique to the individual (**Figure 1c**). We took GPS coordinates (Garmin 64) of each cavities site and assigned a unique name for each group of barbets according to the site they were caught (**Figure 2a-b**). We caught birds in both areas from 01 February to 14 March 2019 and from 30 January to 04 March 2020. Another catching session occurred in Djalélo from 20 January to 09 March 2022.We caught birds in both areas from 01 February to 14 March 2019 and from 30 January to 04 March 2020. Another catching session occurred in Djalélo from 20 January to 09 March 2022.

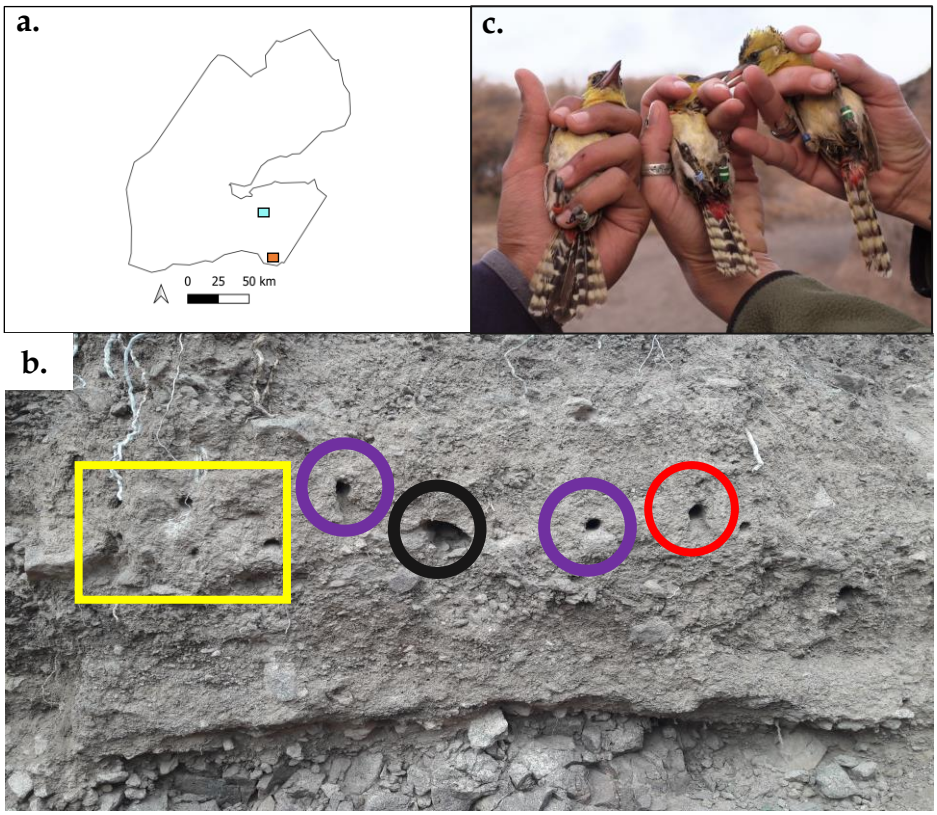

Figure 4a: The map of Djibouti, the blue square is the localization of Djalélo area (11°21'16" N, 42°47'54" E), and the brown square is Assamo area (11°1'22" N, 42°52'53" E); **b**: A site with one actively used cavity (red circle), two not used cavities (purple circles), one old and destroyed cavity (black circle) and several digging trials (yellow rectangle) at site DS03 in 2022; **c**: A picture of three birds caught together in 2022 at site DS05.

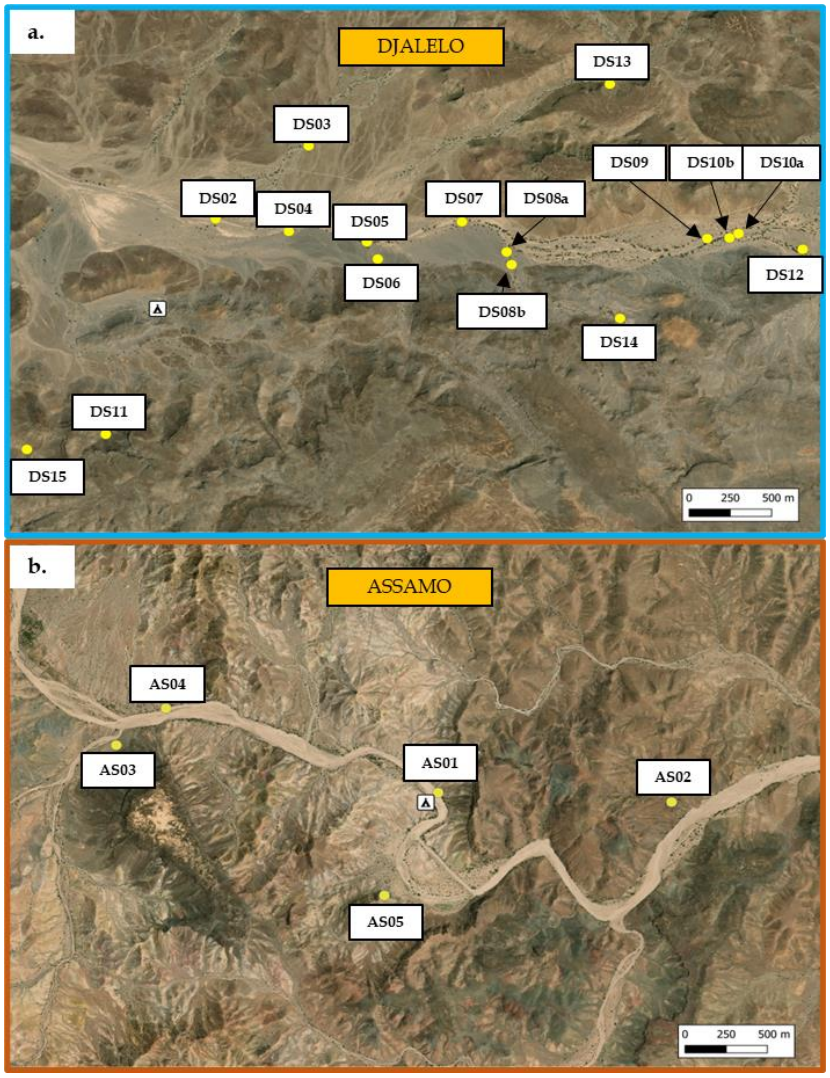

Figure 5 a-b: Satellite map of Djalélo area (11°21'16" N, 42°47'54" E) and Assamo area (11°1' 22" N, 42°52'53" E) with the GPS points of each roosting site monitored during the field study (21 sites in total).

Monitoring of the nesting activity

In March 2023, we monitored the nesting activity of 12 groups in Djalélo without catching the birds. During this period, we regularly visited each active site to make pictures and videos of the eggs and chicks with the endoscope. To calculate the duration of the incubation and the number of eggs laid, we visited each day the cavity where birds started to lay eggs. We recorded the begging calls of the hatchlings and the nestlings using a Sennheiser MKE600 connected to a H4n Zoom recorder (audio files: 44.1 kHz, 16 bits). The adult's vocalisations at the cavity entrance were recorded at the site DS14 with a SongMeter Micro deployed 50 cm from the hole (16 bits, sampling rate: 24,000 Hz, gain: + 18 dB, daily recording periods: from 06:00 to 9:00 and from 16:00 to

19:00, 13 recorded days). At the end of the day, we observed with binoculars whether the adult birds entered the nesting cavity or another cavity close-by to sleep.

Passive acoustic monitoring and acoustic analysis

We conducted passive acoustic monitoring (PAM) to record the daily vocal activity of 11 well-identified groups of barbets around their cavities site, from January to March 2022, in Djalélo. We put one SongMeter Micro from Wildlife Acoustics within each territory, near the cavities site (Supplementary Materials 3), to record birds for several days from 5:30 to 19:30 (16 bits, sampling rate: 24000 Hz, gain: +18dB, internal clock set using the same smartphone device Samsung galaxy A6 2016, mean sunrise 06:27, mean sunset 18:15).

Each recording was filtered with a bandpass filter above 800 Hz to 7000 and resampled to 22050 Hz. We used acoustic and behavioural data gathered in January - February 2019 and 2020 to identify the different vocalisation types. A same experienced person manually selected each vocalisations in our recordings from the PAM in 2022, using RavenPro software (version 1.6). The acoustic analyses were conducted under R software using the Seewave R package (wl=512, overlap=90%). We measured 19 temporal and frequency parameters of four different vocalisation types. We extracted the duration (ms), the mean, max and min of the fundamental and the first harmonic, the peak frequency, the difference between maximum and minimum values of the fundamental frequency, the fundamental frequency value at the start and end, the first and third quartiles (Q25, Q75) and inter-quartile (IQR) of each vocalisation (Hz). The average slope of the fundamental frequency is the intercept value based on a linear model to build using the frequency values from the beginning to the end of each note (dfreq function). To determine the time (ms) and frequency (Hz) of the main stationary point of modulated vocalisations, we tracked the fundamental frequency and used it to build a polynomial model that fits the dominant frequency modulation and calculated the first derivative. We also calculated the average number of vocalisations per sequence when birds emitted a series of the same vocalisation type and the time intervals between calls (s).

Statistical analysis

We assessed the daily vocal activity using the mean percentage of emission of alarm calls series (N=107), cohesion calls series (N=1116) and group vocal displays (a duet or chorus, N=375) emitted per day (N days = 82 10.9 ± 1.74, min = 2, max = 19) and recorded site (11 sites). To

identify the hours with the highest calling activity, we fitted an independent generalized mixed model (GLMMs, glmmTMB R package) with a negative binomial distribution for the cohesion calls and group vocal displays. We counted the number of vocalisations detected per hour and per day for each site as the response variable and the recording hour as a predictor (12 levels). The sites (11 levels) and recording day (27 levels) were used as random effects to control the inter-sites and days variation. We removed the potential double counting of acoustic events recorded simultaneously by two recording devices, by inspecting the recordings manually each time the delay of two acoustic events between recorders was shorter than 30 seconds. Finally, we selected 138 duets and choruses emitted close to our SongMeters during the hours with a significant peak of vocal activity and calculated the conditional probability that cohesion calls could be emitted within two minutes before a group vocal display. All statistical analyses were performed in R 4.2.0. The level of significance was $\alpha < 0.05$, and the results are expressed as the mean ± SEM.

Results

Site selection and communal roosting behaviour

We caught 139 birds from 21 cavity sites (**Figure 2**) comprising 37 individuals in 2019, 46 individuals in 2020 (12 individuals were recaptured from the previous year) and 56 individuals in 2022 (four individuals were recaptured from previous years). This resulted in 123 distinct birds with 16 recaptured. Some individuals escaped during the catching session which explains that the total number of individuals found during the study (Table 1) is superior to the total caught.

The total mean number of individuals per group was 4.53 ± 0.39 (N Sites = 21). The mean number of birds per group each year was 3.45 ± 0.45 in 2019 (N Sites = 11), 5.9 ± 0.9 in 2020 (N Sites = 10) and 4.38 ± 0.53 in 2022 (N Sites = 13). The maximum number of birds found in a single cavity was 11 adult birds in 2020 at site DS07 (**Table 1**). Of the 16 recaptured individuals, 14 were using the same roosting sites where we found them the previous season. We found that one female from the pair AS04 in 2019 joined the group AS01 in 2020 (distance between sites: 1745 m) and another female from DS05 in 2020 was in DS07 in 2022 (distance between sites: 593 m). All the four individuals from group DS07 of 2019 were still present in 2020 plus six new individuals, probably their offspring. One female caught at site DS06 in 2019 was caught again in 2020 and 2022 at the same roosting site. This data revealed that some individuals could occupy the same territory for more than four years and that recruitment of neighbours between seasons

occurred. However, most of the birds captured during one season had disappeared from the area the next field season and only 16 were recaptured.

In 2019, we observed one individual being prevented from entering a roosting hole at site DS11. While the two females and one male were already inside the cavity at dusk, another male tried to enter several times but was systematically pushed out by the other male. He ended up sleeping alone in another hole at the same site. A similar situation occurred at site AS01 in 2020. During the catching session, we found that the whole group was sleeping within a specific hole, but a lone female slept in another cavity close-by. Regarding the potential competition for cavity usage with other bird species, on the 12 March 2023 we found a nest of Eurasian hoopoe (*Upupa epops*) within a cavity previously occupied by a group of barbets at DS06 in 2022. We sometimes observed a lone Blackstart (*Oenanthe melanura*) using unoccupied barbet's cavity to sleep during the night. The Blackstart did not enter inside the hole but stands at the entrance. When barbets saw a Blackstart at a cavity entrance, they chased it away.

The vocal repertoire and daily calling activity

Using our data collected with PAM in 2022, we could identify four different call types emitted by the Yellow-breasted barbet (**Figure 3**, **Table 2**). We observed a peak of group vocal displays between 6:00 to 8:00 and a peak of cohesion calls between 7:00 to 8:00. Alarm calls were given mainly between 6:00 to 7:00 but several small peaks occurred during the day (**Figure 4**). Our negative binomial GLMMs revealed that birds were significantly more active around their cavities in the morning between 6:00 to 9:00 and late in the afternoon (**Supplementary materials 4-5**). We found that the probability of a group vocal display to be preceded by the emission of cohesion calls was 44.9% while the probability of cohesion calls to be followed by a group vocal display was only 12,2% (N = 138 group vocal displays, 62 were preceded by cohesion calls and 505 cohesion calls series detected).

Nesting activity

Finally, in March 2023, we monitored the behaviour of 12 pairs/groups in Djalélo during the nesting period and all of them had a brood (**Figure 5 a-d**). One group had fledgling already on the 17/03/2023 while the groups DS02 and DS10 started to lay eggs. This suggests a breeding and nesting season from February to April 2023. Another brood with at least four chicks within a cavity was found on the 03 November 2022. We found that the Yellow-breasted barbet lays up to 8 eggs

in a single cavity, one egg per day. Although we were unable to document the exact incubation duration, we were able to identify that the incubation is > two weeks. At DS10 we found a single pair with five eggs. We determined that three weeks is necessary between hatchlings and fledglings, and about six weeks from laying eggs to fledglings (**Supplementary materials 6**). The maximum number of birds that occupied a cavity in 2023 was 13 individuals: seven fledglings and six adults that slept at site DS07. All adult birds of a group continued to sleep within the same cavity with eggs or chicks. Nestlings used rattling calls to beg for food from within the cavity (**Figure 5e**). Rattling calls were also emitted by adult birds from within the cavity during the incubation period and possibly the nest reliefs. When feeding young, adult birds emitted *whoo* calls (**Figure 6**). We often observed several adult birds of the same group queuing in front of their nesting cavity to feed the young one after another.

Table 1: Number of individuals per group for each year of monitoring. The number in parenthesis indicates the number of birds already caught from the previous field season (ex: AS01 in 2020 consists of eight individuals, two of them had rings from 2019). NA values indicate that no catching session was conducted.

Site_ID	2019	2020	2022
AS01	6	8 (2)	NA
AS02	3	9 (2)	NA
AS03	2	NA	NA
AS04	2	2	NA
AS05	2	2 (1)	NA
DS02	NA	NA	3
DS03	NA	NA	2
DS04	3	6 (1)	6
DS05	NA	6	6
DS06	6	5 (1)	6 (2)
DS07	4	11 (4)	7 (2)
DS08a	2	NA	NA
DS08b	NA	5 (1)	3
DS09	NA	NA	2
DS10a	4	NA	NA
DS10b	NA	NA	5
DS11	4	NA	2
DS12	NA	NA	5
DS13	NA	NA	3
DS14	NA	NA	7
DS15	NA	5	NA

Table 2: Acoustic features of four distinct call types: the cohesion calls (N=265), soft calls (N=93), alarm calls (N=78) and *whoo* calls (N=26). 19 acoustic parameters were measured (mean ± SEM).

Call type	Duration (ms)	Mean fundamental frequency (Hz)	Max fundamental frequency (Hz)	Min fundamental frequency (Hz)	Difference between Max and Min fundamental frequency (Hz)	Mean frequency 1st harmonic (Hz)	Max frequency 1st harmonic (Hz)	Min frequency 1st harmonic (Hz)	Start fundamental frequency (Hz)
Cohesion call	75.6 ± 0.8	1834 ± 11	2200 ± 13	1513 ± 15	687 ± 16	__	__	__	2190 ± 14
Soft call	58.8 ± 1.0	1445 ± 30	1590 ± 33	1255 ± 32	335 ± 27	__	__	__	1469 ± 36
Alarm call	47.3 ± 0.8	2203 ± 21	2308 ± 22	1948 ± 31	359 ±29	4443 ± 47	4713 ± 59	3962 ± 68	2223 ± 41
***Whoo* call**	62.8 ± 2.2	989 ± 25	1045 ± 29	868 ± 32	232 ± 54	1954 ± 27	2090 ± 54	1859 ± 22	2001 ± 54
End fundamental frequency (Hz)	**Peak frequency (Hz)**	**Slope (intercept)**	**Time stationary point (ms)**	**Frequency stationary point (Hz)**	**Q25 (Hz)**	**Q75 (Hz)**	**IQR (Hz)**	**Number of calls per series**	**Inter-call intervals within call series (s)**
1595 ± 17	1988 ± 20	-7.9 ± 0.2	__	__	1810 ± 10	2485 ± 28	675 ± 26	7.13 ± 0.85	1.00 ± 0.04
1377 ± 30	1465 ± 33	-2.4 ± 0.5	__	__	1602 ± 24	2189 ± 25	587 ± 26	__	__
1992 ± 33	3941 ± 16	-5.0 ± 0.5	18.1 ± 1.2	2299 ± 21	2571 ± 68	4326 ± 32	1754 ± 58	14.4 ± 3.09	0.11 ± 0.01
1919 ± 31	1800 ± 69	-0.8 ± 0.4	49.0 ± 6.1	1030 ± 27	1355.4 ± 57	2051 ± 42	696 ± 72	2.79 ± 0.29	0.27 ± 0.01

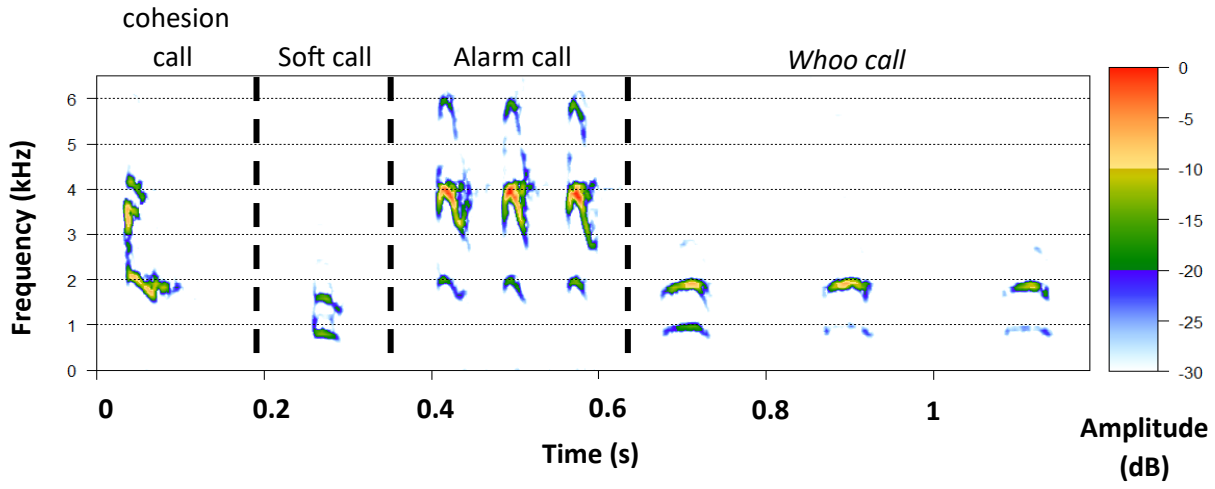

Figure 3: Spectrogram of four different call types identified. From left to right: cohesion call, soft call, alarm call and whoo call (wl=512, ovlp=90, f=44100).

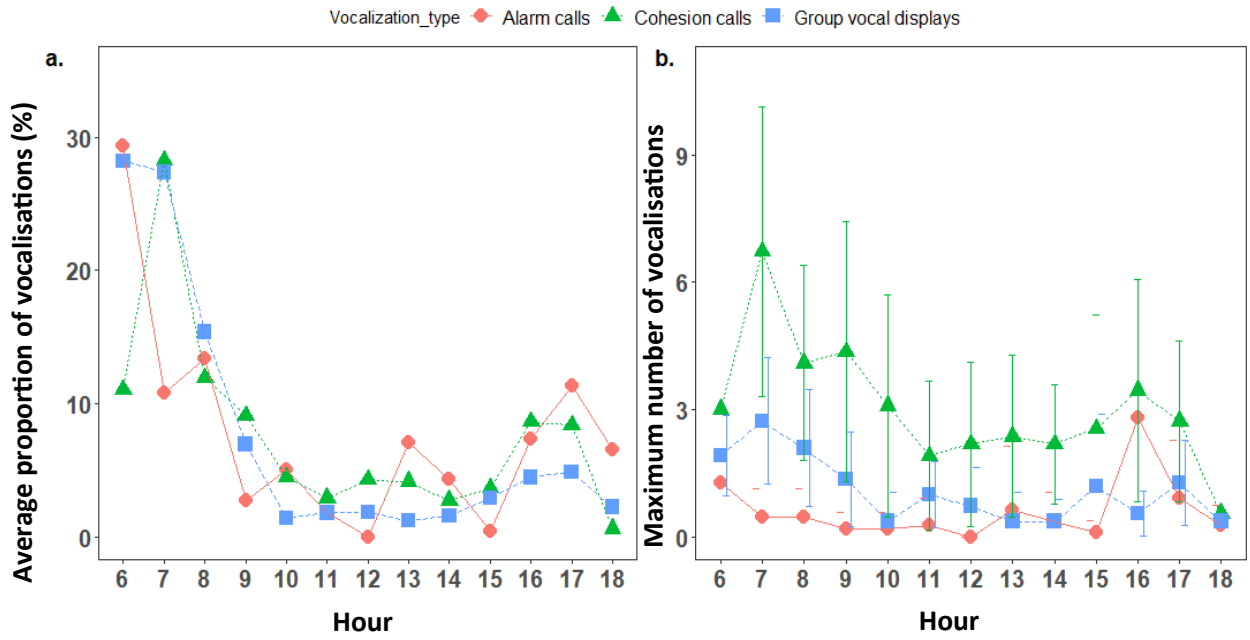

Figure 4: Daily vocal activity of the Yellow-breasted Barbet per hour. One point represents a full hour (x=6 is the time between 6:00 to 7:00). **a**: Each point is the average proportion of vocalisations per site (11 sites) and days (10.9 ± 1.74 days). **b**: The maximum number of vocalisations recorded per site for each hour of the day when the birds were vocally active. The blue squares represent the group vocal displays (duet or chorus), green triangles the cohesion calls series and the red diamonds the alarm calls series.

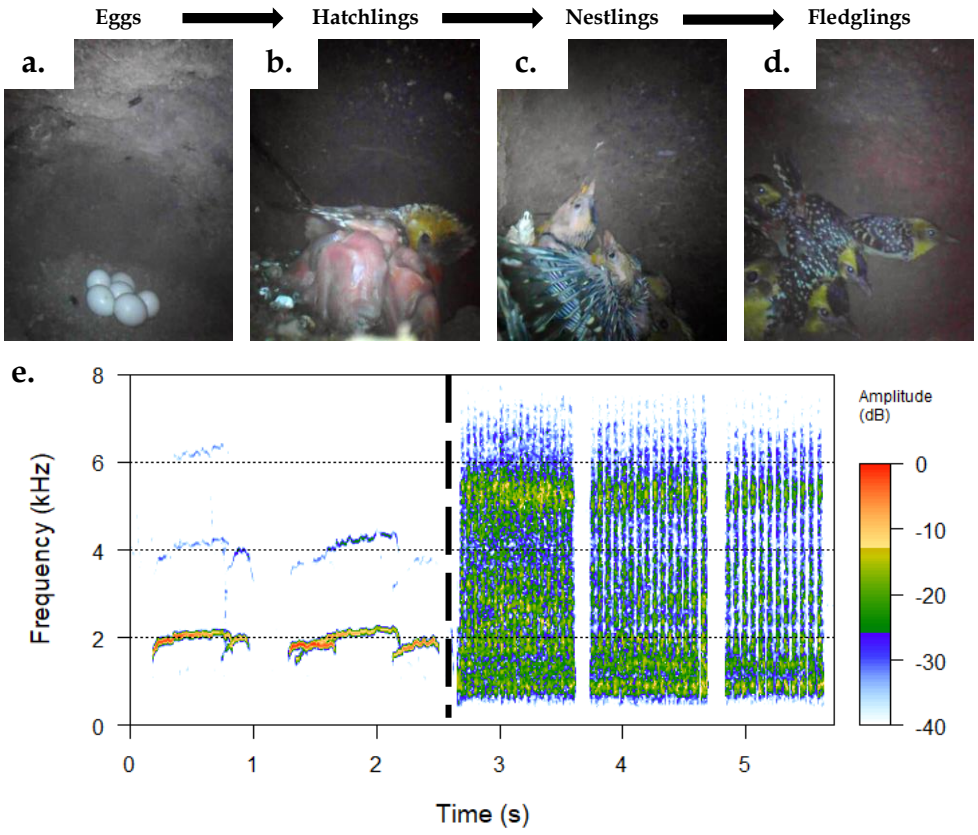

Figure 5a: Six eggs at site DS02, laid one per day. **b**: Hatchlings at site DS08a with an adult present within the cavity. **c**: 10-day old nestlings at site DS06. **d**: Fledglings about three weeks old at site DS07. **e**: Spectrogram of the begging calls of Yellow-breasted barbet chicks soon after they hatched (left) and few days later (right).

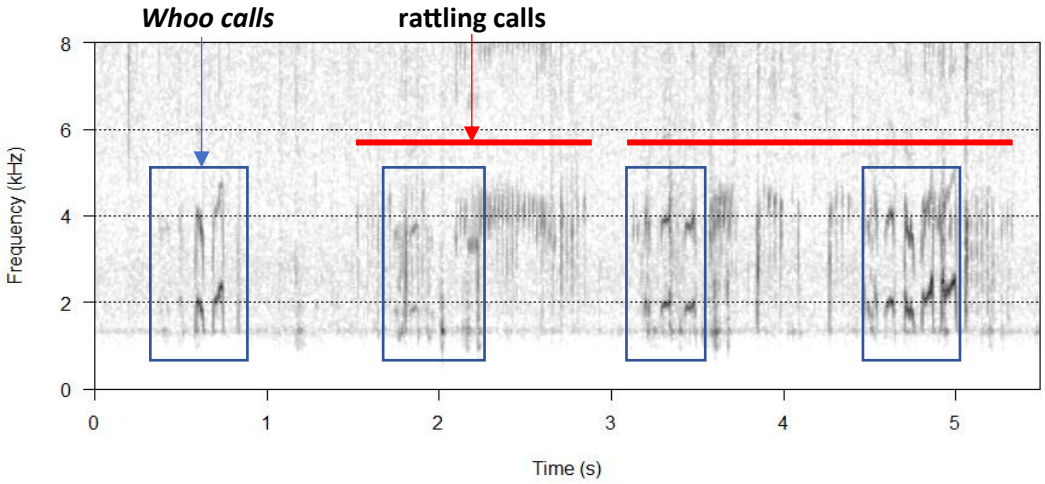

Figure 6: Vocal communication at the cavity. An adult Yellow-breasted barbet visiting the cavity emitted whoo calls (blue rectangles) at the cavity entrance, and a second bird replied with rattling calls from within the cavity (red lines), possibly an adult bird incubating

Discussion

Communal roosting

In this study, we found that the Yellow-breasted barbet live in pairs or small groups that communally roost within a single cavity, most of the time dug into steep sandy-river bank. Even though it was common to find several cavities at one site, the birds entered a specific cavity to spend the night. The usage of natural cracks and holes within rocky cliffs seems to be more common in the mountainous regions (pers. obs). The number of sites and their location did not change over the years of monitoring, suggesting there is a limited number of suitable sites to dig cavities in the studied areas. Hence, habitat saturation due to the limited number of suitable sites to dig cavities might be one of the factors that favour the retention of offspring within their family group. Since we often found one or several individuals that occupied the same site during at least two consecutive years, we suggest that once a pair has established a territory, the birds will occupy and defend their cavities site year-round. The offspring of the breeding pair could delay their dispersal to help their parents raise the next brood within the year. Eventually, one offspring might inherit the site (Downing *et al*., 2018; Kingma, 2017). Alternatively, the retention of offspring and the recruitment of newcomers could help the breeding pair to better defend its territory and resources ("group augmentation hypothesis", Kingma, 2017). Most of the birds caught in one year were not found in the area the next year. At some point, some individuals should be forced to leave their group due to the absence of breeding opportunity and the lack of space within the cavity. They might disperse over a long distance to find a new suitable site. Thus, the group formation might be driven by ecological constraints (a limited amount of suitable roosting and nesting sites) or the harsh life conditions in which alloparental care toward kin-relatives is favoured (Wild and Korb, 2017).

Nesting behaviour

In Djibouti, the period of the breeding season was not clear for the species. We found that a first breeding season occurred in September – November 2022. Then, a second breeding season from February to March 2023. These two seasons matched with the change between hot and fresh seasons, usually accompanied by rainfall. The timing of breeding of the Yellow-breasted barbets could be influenced by the temperatures and the amount of rainfall (Mares *et al*., 2017).

It was reported that the Yellow-breasted barbets lay 3 – 6 eggs with possibly two broods per year (Short and Horne, 2020a). We found two consecutive broods within a six-month period, but according to the number of eggs and chicks found in different cavities, the species can lay up to 8 eggs (one per day). According to our regular pictures of several nestlings at different stages, we suggested about three weeks for nestling period and an incubation time superior to two weeks. The suggested duration of nesting in a closely related species, the Red-and-yellow barbet is 23 - 24 days and a breeding season of 46 days with at least four broods (de Bont, 2009). In the Crested barbet, the incubation period lasts 13-17 days (Short and Horne, 2020b). A nesting season for a pair/group of Yellow-breasted barbets could last six weeks including incubation time until fledgling, the number of days could be variable according to the number of eggs laid. Once the young left the cavity, they stayed with the group and went back to the roosting cavity at night.

The group of Yellow-breasted barbets did not separate nesting and roosting cavity, all adults slept with the eggs, then with the chicks. At DS05, we observed that the hatchlings were placed in the center of the cavity while the four adults formed a circle around them. Communal roosting is advantageous for thermoregulation and saving energy (Paquet *et al*., 2016). However, it might also facilitate the spread of parasites such as mites (Sikora *et al*., 2023). Thus, we could expect that big groups provide better thermoregulation for chicks than single pairs, which might increase their survival or accelerate their growth. On the other hand, living in a group could increase the chance of parasite infestation of the brood. The regular communal sand baths we witnessed at the end of the day, before the birds entered their cavity could prevent, or at least limit the spread of parasites within the roosting cavity. Adults that roosted with nestlings were observed in other group breeding barbet species (Grimes, 1976; Short and Horne, 2001).

The vocal repertoire and the daily calling activity

In this study, we provided more details regarding the acoustic features of different vocalisations emitted by the Yellow-breasted barbet throughout the day. Birds left their roosting cavity between 5:50 to 6:20 in January – March. It coincided with a peak of emission of alarm calls. Similarly, the amount of alarm calls increased at the end of the day, when birds re-turned to their cavity. Birds are more vulnerable to a predator when entering or leaving their cavity which increases their vigilance. The regular small peaks of alarm calls emitted between 8:00 to 17:00 could coincide with the foraging periods or the time when birds came to monitor their roosting

cavities. We observed barbets emitting alarm calls during catching events, between-group interactions, against a Barbary falcon (*Falco peregrinus pelegrinoides*) and a Common kestrel (*Falco tinnunculus*), and when a pack of baboons or local shepherds were passing close by a barbet's roosting cavity.

From 6:00 to 8:00 the birds emitted a lot of cohesion calls. We found that cohesion calls are often used even before the start of a group vocal display, probably to recruit group members in the vicinity. When one bird emitted such cohesion calls, other birds in the vicinity replied with cohesion calls as well or just approached the emitter. The amount of cohesion calls also increased at the end of the day simply because birds gathered at their roosting site and often reunited to participate in a communal sand bath before entering their cavity (**Supplementary materials 7**). The cohesion calls seem to serve in intra-group communication to maintain group cohesiveness during joined actions such as foraging, taking a communal sand bath or heading back to the roosting cavity at dusk. Acoustic identity encoded in cohesion calls could allow other group members to recognize the different birds vocalising in their surroundings and decide whether to join or not.

Soft calls and *whoo* calls were the most difficult vocalisations to listen to in the field because of their low amplitude nature, not heard above a few meters from the emitter. Birds emitted soft calls when they were close to each other. We observed one male using such calls just after leaving its cavity. He stayed on a branch in front of the entrance while the two females were still inside the cavity. These calls were commonly used by adults when a threat was perceived close-by their cavity. Soft calls could serve during close-range interactions between group members. It could help to maintain contact. Few *whoo* calls were recorded during the PAM in 2022, usually emitted after the end of a group vocal display. However, we found that this vocalisation type was commonly used during the nesting season in 2023 when feeding the young. The adult birds emitted *whoo* calls close-by entrance and within the cavity. A similar behaviour was documented in the Green barbet who vocalises around and from within its cavity, especially during a nest relief (Short and Horne, 1980). Thus, we suggest that *whoo* calls serve primarily to attract young for feeding and between adult during nest relief. It might also have a function in affiliative behaviour within the group. For example, using such calls after a group vocal display could reduce the stress of the individuals and reinforce intra-group bond after a between-group conflict (Radford, 2008).

Possible competition with other species for cavity ownership

In Djibouti, we did not observe any competition between the Yellow-breasted barbet and the Black-throated barbet (*Tricholaema melanocephala*) which uses cavity dug in tree trunk and was present in the areas of study. It was mentioned that the Black-throated barbet sometimes reacted to duet playback of the Red-and-yellow barbet which sounds very similar to the Yellow-breasted barbet (Short and Horne, 1983). We found a nest of Eurasian hoopoe within a former barbet's cavity few meters far from the current nesting cavity of barbets. The Yellow-breasted barbet might also compete for cavities holding with the White-throated bee-eater (*Merops albicollis*) who migrates to Djibouti to breed in summer. It would be interesting to investigate the inter-specific competition between the Yellow-breasted barbet and the Red-and-yellow barbet where the two species ranges overlap in Somalia and Ethiopia. The Red-and-yellow barbet selects the same type of sites to dig roosting and nesting cavities (de Bont, 2009; Short and Horne, 2020b) and both barbet species are known to occasionally dig holes in human made structure (Yellow-breasted barbet in a mud wall: Fry *et al*. 1988, Red-and-yellow barbet in concrete wall: de Bont 2009). We wonder whether it could react to the vocalizations of other hole nesters species which might compete for cavity ownership.

Conclusion

A year-round monitoring study would be useful to determine the total number of broods per year in Djibouti, as well as the exact group breeding strategy. First, regular catching and re-catching sessions of several groups before, during and after each breeding season, with genetic analysis should be conducted. This will help to determine which birds in a group are breeders and non-breeders and whether non-breeders are delayed offspring or recruited newcomers. In a second time, the role of each group member during the nesting period needs to be clarified. We suggested using Passive Integrated Transponders (PIT tags) system accompanied with visual observations at the nesting cavity entrance to document the helping effort of each bird during the incubation period and when feeding the young. Finally, the deployment of colour rings and GPS trackers could help to determine when and where most of the birds leave their group and disperse. The study also showed that different call types are used for long- and short-range intra-group communication. Among these different vocalisations, the cohesion calls seem to be used as recruitment signals before the start of a duet or chorus. How birds initiate a coordinated group vocal display is investigated in the next chapter.

Acknowledgements

The study on *Trachyphonus margaritatus somalicus* was conducted with an official agreement of the Decan Wildlife Association (https://www.decandjibouti.org/) which is responsible for the management of the protected areas of Assamo and Djalélo in Djibouti where the study took place. We thank the Decan Wildlife association for the logistical support in the field, and Nathalie and Moustapha Mahamoud-Issa for their help with the transport of materials and other supplies during the fieldwork sessions. We thank Joshua De Freitas for his record of young barbets in November 2022. Funding: This study was supported by the Polish National Science Centre (Narodowe Centrum Nauki) under the grant no UMO-2017/27/N/NZ8/01554.

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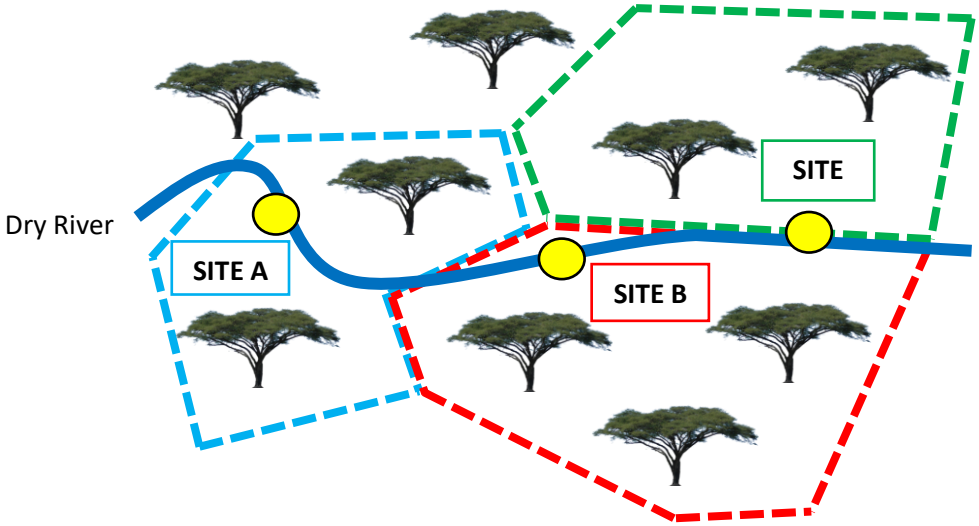
Supplementary materials

Supplementary materials 1: Pictures of the landscape of Djalélo (above) and Assamo (below)

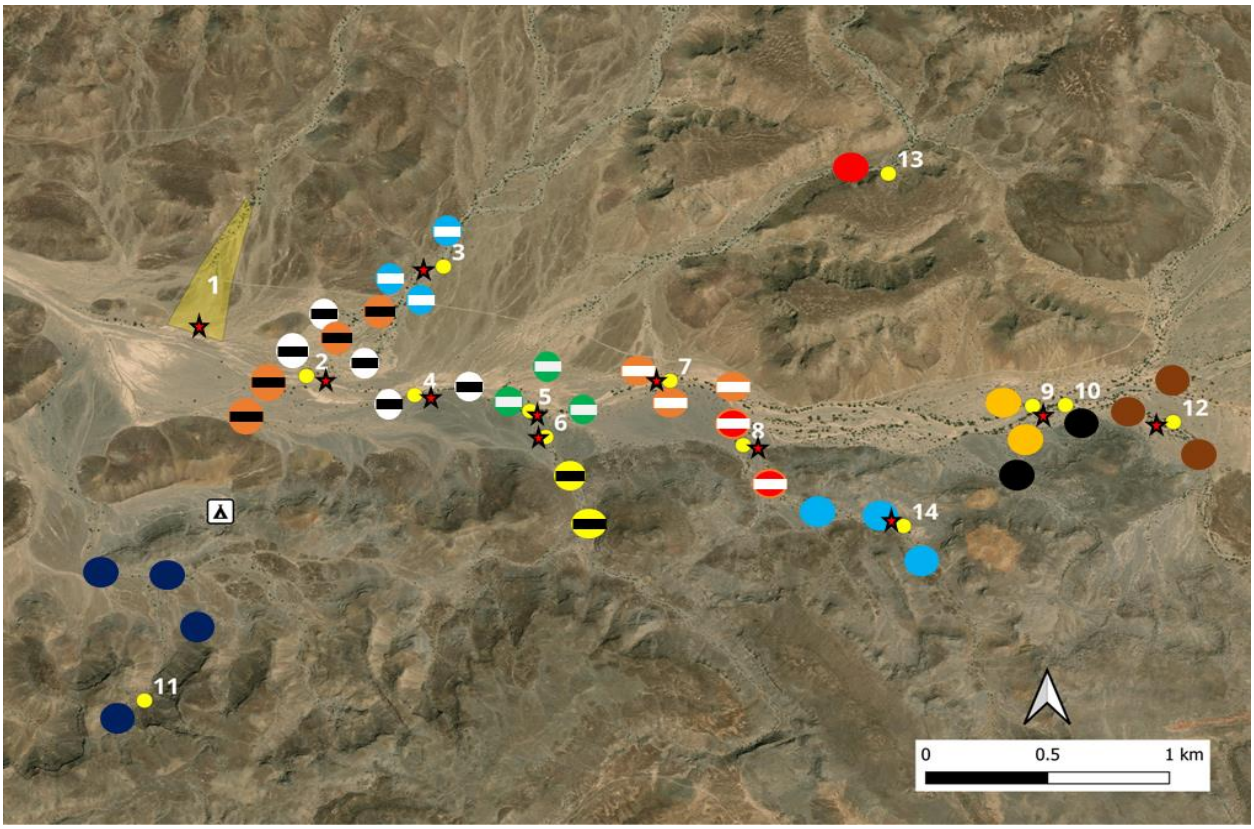
a.

b.



c.

Supplementary materials 2a: Views of the dry river along which several groups of Yellow-breasted barbet live. **b**: Schematic territorial organization of three groups of birds. Each yellow circle represents the specific site where the birds dig their cavities. **c**: Picture of a group of barbets taken within their roosting cavity early in the morning, with the endoscope Depstech.



SMM recorders

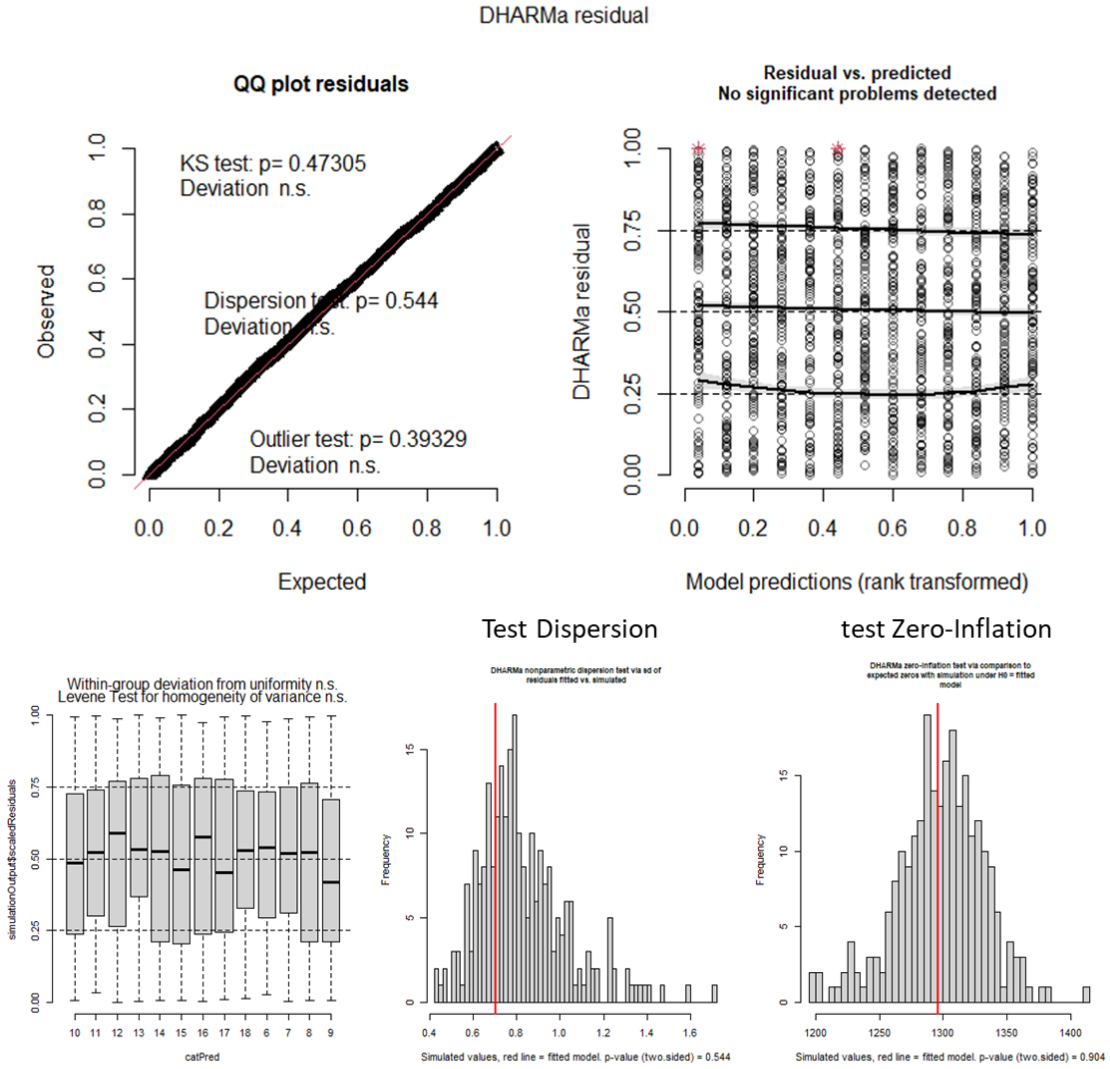
Group 02: 3 birds
Group 03: 2 birds
Group 04: 6 birds
Group 05: 6 birds
Group 06: 6 birds
Group 07: 7 birds
Group 08: 3 birds
Group 09: 2 birds
Group 10: 2 birds
Group 11: 2 birds
Group 12: 5 birds
Group 13: 3 birds
Group 14: 7 birds

Supplementary materials 3: Map of the Djalélo valley. The sites (small yellow dots) represent the cavities from which each group was caught. The red/black stars the SMM recorders that we put close by the cavities. The coloured dots represent the localization from where ringed birds were observed during the day. For the group 01 (1 on the map) we were not able to catch them even after three trials, although we identified their territory and a site with cavities where we put a SMM. In the current study, we did not include group 11 and 13.

Supplementary materials 4: Results of the Negative Binomial model for the Group vocal displays.

The negative binomial model: **modelnb**

glmmTMB(calling ~ Hour + (1 | Site) + (1 | Day_rec),family=nbinom1(link = "log"), data=data_DG)



The zero-inflated with negative binomial model: **modelinflnb**

glmmTMB(calling ~ Hour + (1 | Site) + (1 | Day_rec), ziformula = ~1, family=nbinom1(link = "log"), data=data_DG)

	dAICc	df
modelnb	0	16
modelinflnb	2	17

The negative binomial model: **modelnb**

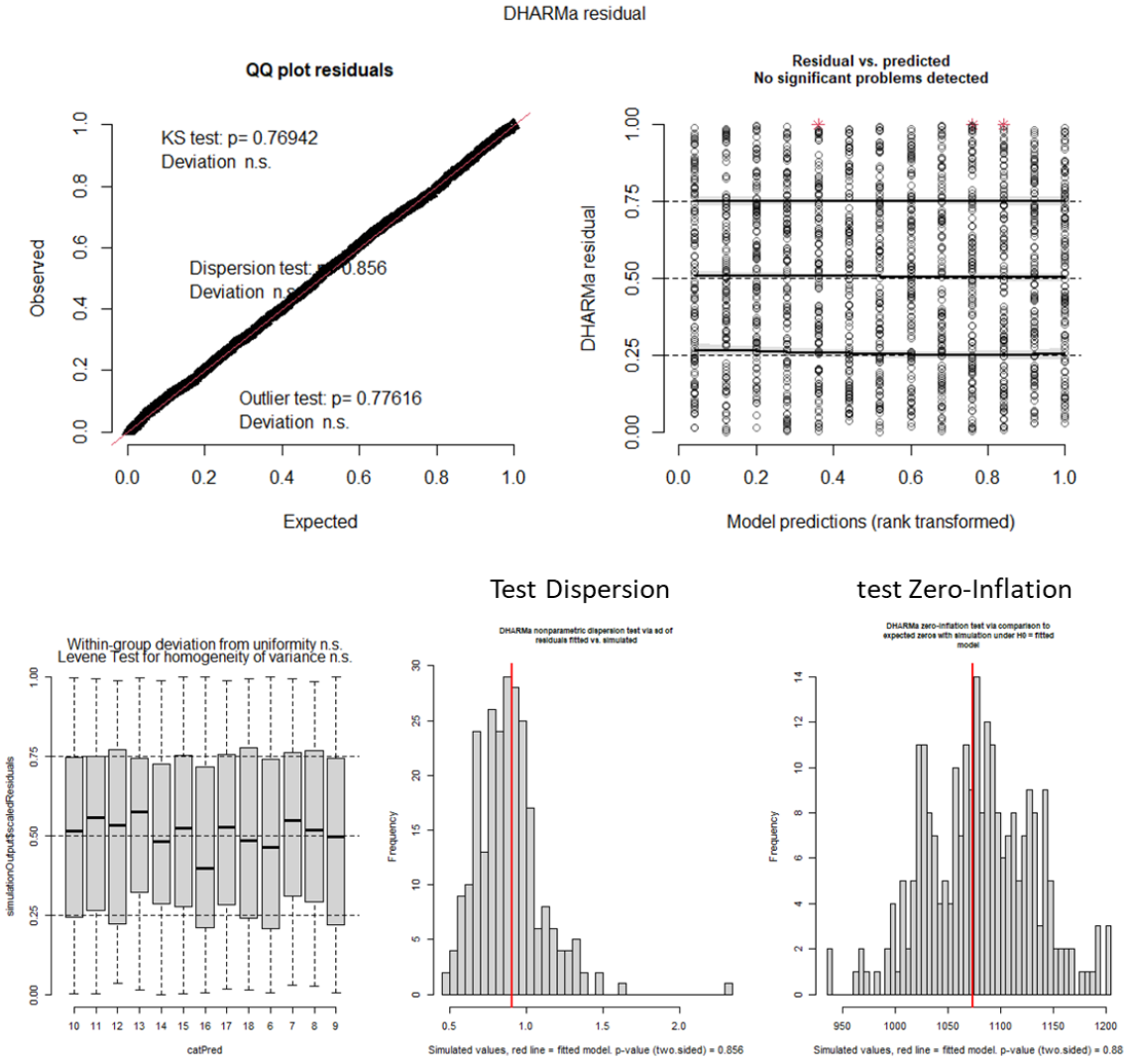
glmmTMB(calling ~ Hour + (1 | Site) + (1 | Day_rec),family=nbinom1(link = "log"), data=data_DG)

```
     AIC      BIC   logLik deviance df.resid
  1592.0   1677.6   -780.0   1560.0     1544

Random effects:

Conditional model:
 Groups  Name        Variance Std.Dev.
 Site    (Intercept) 0.1591   0.3989
 Day_rec (Intercept) 0.1324   0.3639
Number of obs: 1560, groups:  Site, 11; Day_rec, 27

Dispersion parameter for nbinom1 family (): 0.294

Conditional model:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -2.9481     0.4345  -6.785 1.16e-11 ***
Hour11        0.7470     0.4975   1.501  0.13323
Hour12        0.5107     0.5224   0.978  0.32832
Hour13       -0.6987     0.7066  -0.989  0.32275
Hour14       -0.4270     0.6451  -0.662  0.50803
Hour15        0.6100     0.5131   1.189  0.23453
Hour16        0.7516     0.4931   1.524  0.12743
Hour17        1.3108     0.4623   2.835  0.00458 **
Hour18       -0.1807     0.6047  -0.299  0.76502
Hour6         2.4758     0.4254   5.820 5.87e-09 ***
Hour7         2.7044     0.4222   6.406 1.49e-10 ***
Hour8         2.2171     0.4312   5.142 2.72e-07 ***
Hour9         1.1581     0.4726   2.450  0.01427 *
```

Supplementary materials 5: Results of the Negative Binomial model for the Cohesion calls.

The zero-inflated with negative binomial model: **modelinflnb**

glmmTMB(calling ~ Hour + (1 | Site) + (1 | Day_rec), ziformula = ~1, family=nbinom1(link = "log"), data=data_CC)

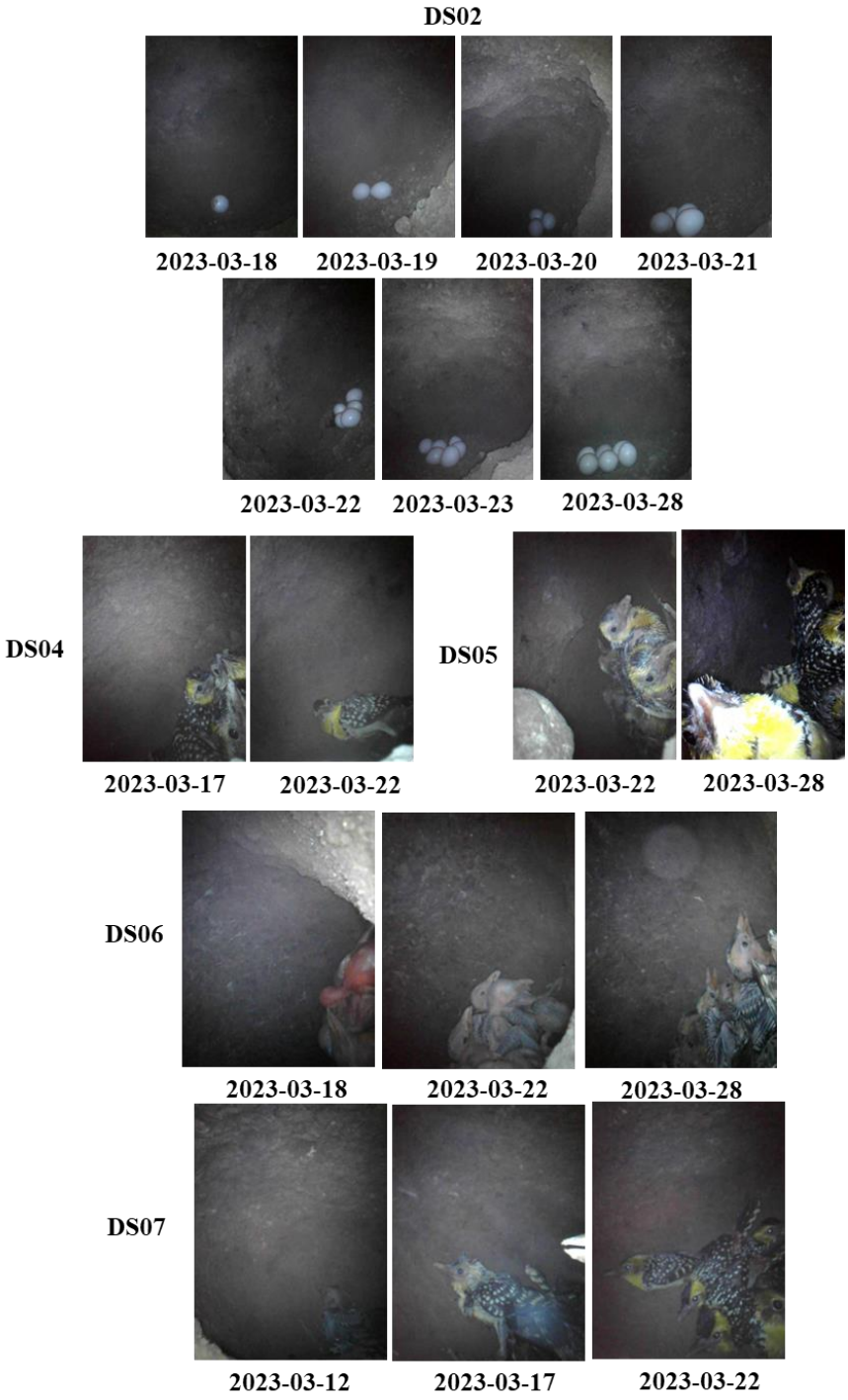


	dAICc	df
modelinflnb	0.0	17
modelnb	2.1	16

The zero-inflated with negative binomial model: **modelinflnb**

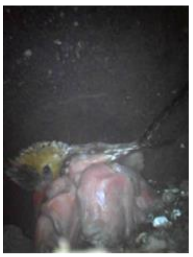
glmmTMB(calling ~ Hour + (1 | Site) + (1 | Day_rec), ziformula = ~1, family=nbinom1(link = "log"), data=data_CC)

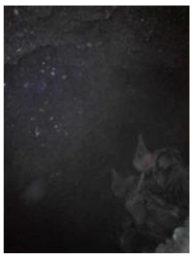
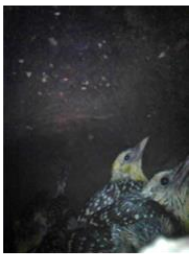
```
     AIC      BIC   logLik deviance df.resid
  3198.4   3289.3  -1582.2   3164.4     1543

Random effects:

Conditional model:
 Groups  Name        Variance Std.Dev.
 Site    (Intercept) 0.1390   0.3729
 Day_rec (Intercept) 0.1789   0.4229
Number of obs: 1560, groups:  Site, 11; Day_rec, 27

Dispersion parameter for nbinom1 family (): 1.18

Conditional model:
            Estimate Std. Error z value Pr(>|z|)
(Intercept) -0.63790    0.23114  -2.760 0.005783 **
Hour11      -0.35792    0.25834  -1.385 0.165917
Hour12      -0.08463    0.24355  -0.347 0.728222
Hour13      -0.38456    0.26161  -1.470 0.141572
Hour14      -0.56576    0.27643  -2.047 0.040693 *
Hour15      -0.30800    0.25529  -1.206 0.227641
Hour16       0.24197    0.22913   1.056 0.290947
Hour17       0.22969    0.22530   1.019 0.307970
Hour18      -1.68656    0.39265  -4.295 1.74e-05 ***
Hour6        0.50252    0.21614   2.325 0.020072 *
Hour7        1.32730    0.19400   6.842 7.83e-12 ***
Hour8        0.76828    0.20533   3.742 0.000183 ***
Hour9        0.36800    0.22600   1.628 0.103457
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Zero-inflation model:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -2.1116     0.5811  -3.634 0.000279 ***
---
```



Supplementary materials 6: Regular pictures of the brood at different sites. The date is displayed below each picture. The name of the site above each series of pictures.

DS08



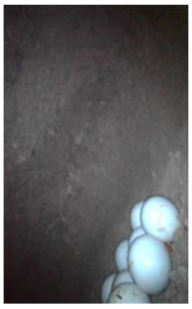
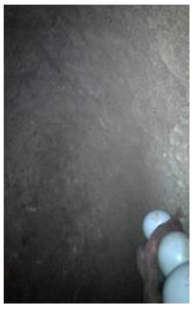



2023-03-12 **2023-03-18** **2023-03-21** **2023-03-28**

DS12


2023-03-12 **2023-03-18**

DS14


2023-03-18 **2023-03-21** **2023-03-23** **2023-03-30**

Supplementary materials 7: A group of barbets gathering and entering their cavity at dusk (pictures taken in 14/02/2020 in Site 07; Djalélo Valley in Djibouti). A video of the fieldwork is available here: https://www.youtube.com/watch?v=CQL4AZ7ltjY&ab_channel=M.Keisse

Chapter 2: The use of a multimodal intra-group signal to initiate a cooperative group vocal display

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Mathieu Mahamoud-Issa, Bożena Sikora, Stanisław Rusiecki, Tomasz S. Osiejuk (2023) The Yellow-breasted Barbet (*Trachyphonus margaritatus*) introduces vocal duets and choruses with a specific multimodal signal, during territorial advertisement. *Journal of Ornithology* 164, 183-192. **Status: Published**.

Link: https://link.springer.com/article/10.1007/s10336-022-02016-w

Abstract

Cooperative behaviour is a prominent feature among many group-living species and continues to pose challenges to our understanding about the evolution of social relationships and task coordination between members of the same social group. Individuals who are willing to cooperate to achieve a joined action need to communicate their intentions and somehow make a common agreement. We investigated how a coordinated chorus song is initiated in a cooperative-breeding bird species, The Yellow-Breasted Barbet (*Trachyphonus margaritatus*). A chorus can be defined as an interactive vocal display involving several individuals who are synchronizing their behaviour to sing in a time coordinated manner. Synchronizing behaviour to sing in chorus might become quite challenging when several individuals are involved. Thus, group members could use a specific signal to induce such collective action. Yet, few studies have investigated the mechanisms of communal display initiation in chorusing bird species. We conducted playback experiments to induce and record territorial defensive reactions from birds with a video camera. We recorded 26 different groups from distinct wild populations in Djibouti which belonged to 17 sites. We found that barbets use a specific vocalization named chewp note to introduce their duet and chorus. Moreover, we found that the individual that initiates such communal displays may broadcast a multimodal signal by combining chewp note series with a typical body posture with

the tail raised and fanned. We suggest that the multimodal signal could serve to attract attention and elicit a response from other group members or could enhance the song coordination.

Introduction

Birds that perform coordinated vocal displays are known as duetting or chorusing bird species (Hall, 2004). A vocal duet occurs when two individuals combine their vocalizations non-randomly, usually for the purpose of delivering a conspicuous synchronized vocal performance (Thorpe, 1972; Farabaugh, 1982). It is usually broadcasted by a mated pair, in order to defend its territory, advertise the mated status and maintain pair bond (Grafe and Bitz, 2004; Logue and Gammon, 2004; Odom *et al*., 2017; Odom and Omland, 2017; Wheeldon *et al.*, 2021). It also occurs during the courtship display (Soma and Iwama, 2017) and it can be performed even by two or more males (Foster, 1981; Trainer *et al*., 2002). When birds perform such coordinated display, the interplay of single components produced by each individual form a new meta-signal also known as a collective signal (Brumm and Slater, 2007). Such collective signal has its own properties that are shaped at the individual level by the acoustic features of each bird, and the manner through which the partners combine their song (Logue and Krupp, 2016). Duets have many functions and could transmit different information depending on the context and the species (Dahlin and Benedict, 2014; Hall, 2004; Mennill and Vehrencamp, 2008). When more than two birds, usually from the same social group, join their song to broadcast a collective and cooperative vocal display, they perform a chorus. It has similar functions in territorial defense to duets (Baker, 2009, 2004; Radford, 2003; Seddon and Tobias, 2003; Wu, 2013).

There is a lack of knowledge regarding the coordination strategies used by chorusing bird species where all participants start singing at the same time. Such group coordinated display requires that individuals share information and agree to perform a collective action. In this context, a specific intra-group signal could be used by group members to synchronize their song. In several African barbet species (Piciformes, Lybiidae), specific vocalizations combined with visual displays precede vocal duets and choruses and may play such role. This was first described by Skead (Skead, 1950) in the Black-collared Barbet (*Lybius torquatus*). The author provided three significant points: the pre-duet calls sound different than the song; the bird who initiated the duet gave the pre-duet calls while its mate simply replied by starting its own song sequence (Payne and Skinner, 1970); finally, birds combined their calls with visual display. Later on, the presence of

pre-duet/chorus vocalizations combined with visual postures defined as “greeting ceremony” was reported in at least eight species of the African barbets (Short and Horne, 1983). The authors suggested that because these pre-duet notes are relatively soft compared to the loud duet/chorus song and can hardly be heard beyond 20-30 meters away from the birds, they might have a function in intra-group relationships and pair-bond maintenance. However, there is a lack of studies among the different barbet species that describe how birds use these vocalizations, making any assumptions regarding their exact functions difficult.

The aim of our study is to describe the use of the pre-duet and chorus vocalizations notes (described as "*chewp* note" by Short and Horne, 2001) to determine whether it might constitute a specific signal used by the Yellow-breasted Barbet (*Trachyphonus margaritatus somalicus*) to initiate a group vocal display. This barbet species is considered as a chorusing species that introduces its communal songs with greeting ceremonies, but the group vocal behaviour has not been studied yet. We used the term “introductory sequence” instead of “greeting ceremony” because we considered the former more neutral since the function of this behaviour remains unknown. We organized our investigations around two mains hypotheses:

Hypothesis 1: The *chewp* notes are a specific signal used by the Yellow-breasted barbet during vocal duets and choruses introduction. The *chewp* notes should be directly followed by a duet or chorus song. If these vocalizations have a function in group singing initiation, we will not observe a duet or a chorus starting without such signal.

Hypothesis 2: The introductory sequence could act as a recruitment signal used by the initiator to attract other group members and trigger them to sing. If this is true, we expect that the initiator systematically gives an introductory sequence to induce a group vocal display, while the followers could answer simply by starting their song without an introductory sequence. Followers should immediately react to the signal and join the initiator. Alternatively, if both the initiator and the followers behave the same way during a duet and chorus initiation, the introductory sequence could be a greeting ceremony in the sense of an intra-group social behaviour used as mutual agreement to sing in a group or to reinforce bonds.

To investigate these hypotheses, we used playback stimulations and we recorded with a video camera the duets and choruses of different groups of Yellow-breasted barbet in Djibouti. We analysed the vocal and visual components of their group displays.

Methods

Species and sites of study

The Yellow-breasted Barbet occurs in thorn-bush and acacias savannah, usually along dry watercourses in the semi-desert sub-Saharan regions. It is a non-migratory bird species that lives in pairs or small social groups which defend their territory throughout the year and is described as a group-breeding species (Soma and Brumm, 2020, personal field observations). We monitored and recorded two wild populations of the species in the Republic of Djibouti, during February – March 2019 and 2020 (Djalélo population: 11°21'16" N, 42°47'54" E; Assamo population: 11°1'22." N, 42°52'53" E). We put colour rings combination on each individual and saved GPS coordinates (Garmin 64) of each pair / group territory. In total, 72 individuals were ringed in 12 distinct sites (in total, we identified 18 sites in 2 years, **Supplementary materials 1, Supplementary materials 9**).

Playback experiments

We conducted playback experiments that simulated a territorial intrusion to induce a group defensive display. The aim was to attract birds close enough to allow us to film with a video camera their group display. The playbacks were performed in the morning from 6:15 to 11:00 (average sunrise 6:20) during February and March 2019-2020. In 2019, we used "Natural playback song" created with barbet songs previously recorded in 2016 in Djibouti (recorded either with or without playback of songs obtained from xeno-canto). We selected the best quality recorded songs, filtered (high pass filter 800 Hz), and normalized. In 2020, we had enough data and knowledge to create "Synthesized playback song" made with the Soundgen package under R software. Each playback consisted of 30 seconds of a solo, a duet, or a chorus song that included an introductory vocal sequence directly followed by the song sequence itself. Playbacks were broadcasted through a JBL CHARGE3 loudspeaker (power: 20 W, frequency response: 65 Hz-20 kHz, signal-to-noise ratio: >80 dB), just after we visually localized the tested group in their territory. The amplitude of the playback was adapted to the natural amplitude of barbet's song that we obtained using a sound meter (model: testo 816, automatic mode, range from 30 to 130 dBA, fast time weighting mode A). The behavioural response of birds was recorded with a shotgun microphone Sennheiser MKE600 connected to a Canon XF400 camera (audio: 44.1 kHz, 16 bits; video: 1080p, 30fps). We conducted 55 recording sessions in total (two field recordings done in 2016 were included in

our data due to their good quality and the similar way the playback sessions were done). We selected 49 of the best quality of the 55 recordings for the analysis. It corresponds to 26 groups of barbets recorded in 17 sites (one group in 2016, 12 groups in 2019 and 13 groups in 2020). The highest number of groups than sites is due to the fact that in many cases a group of birds caught in 2019 on a specific site was different from the group of birds caught in the same site in 2020 (**Supplementary materials 1, Supplementary materials 9**).

Data extraction

To describe the bird behaviour when replying to playback stimulations and investigate the possible existence of a multimodal signal, we created a list of behavioural variables inspired by what was observed in the closely related D'Arnaud's Barbet (*Trachyphonus darnaudii*) and the Black-collared Barbet (Short and Horne, 1982):

- Tail display: we considered that the tail is raised and fanned over the back when the tilt angle was greater than 45 degrees and it was not caused by the bird's balance adjustment while perching or moving.
- Song sequence: the individual song sequence during a duet or chorus.
- Introductory sequence: the *chewp* notes series emitted before the start of the song sequence.

The videos collected were analysed with BORIS (Behavioral Observation Research Interactive Software, Friard and Gamba, 2016) to extract data regarding the visual displays. We analysed the audio part of our recordings under PRATT software (version 6.1.15; method: Fourrier; window shape: Gaussian; time steps: 1000; frequency steps: 250), to precisely annotate the start and end of acoustic events of the individuals recorded. We then combined both the acoustic and visual data to construct the behavioural timeline (s). In each group display analysed, we divided the participants in two categories: The leader is the individual that gives the very first vocalisation either of the introductory sequence or the song sequence. The follower is the individual that replies to the leader's vocalisations.

Acoustic analysis of the chewp notes

We isolated 54 *chewp* notes from our recordings using Raven Lite 2 software, filtered with a high pass filter 800 Hz to reduce background noise, and resampled to 16000 Hz. The acoustic analyses were conducted under R software using the Seewave R package (wl=128, overlap=75%).

We extracted the mean, max and min of the fundamental and the first harmonic, the peak frequency, the first and third quartiles (Q25, Q75) and inter-quartile (IQR) of each chewp notes analysed. The average slope of the fundamental frequency was calculated using the frequency values at the beginning and the end of each note. To determine the time and frequency of the main stationary and inflexion points, we tracked the dominant frequency and used it to build a polynomial model that fits the dominant frequency modulation and calculated the first and second derivatives. The stationary and inflexion points gave us more details about the modulation pattern (increasing or decreasing frequency signal as well as the curvature of the signal).

Statistical analyses

We first classified by hand each of the 54 chewp notes into two categories based on their acoustic features: 33 *high chewp* notes (n = 11 individuals, 3 notes per individual) and 21 *low chewp* notes (n = 7 individuals, 3 notes per individual). Then, we conducted a Hierarchical Clustering on Principal Components (HCPC) using the package Factoextra in R, to determine if our two categories *high* and *low chewp* notes were meaningful. The first step was to perform a Principal Component Analysis (PCA) based on the acoustic measurements to reduce the dimensionality of the dataset (FactoMineR package in R, data scaled, three dimensions kept). We computed the results of the PCA to perform an HCPC based on the first two principal components (Factoextra package in R). We limited the hierarchical clustering to 2 clusters, focusing on the main distinction between *high* and *low chewp* notes, and to not continue the clustering based on other acoustic similarities or dissimilarities (ex: sex acoustic specificity, acoustic similarities between individuals).

We counted the number of duets and choruses that started with or without an introductory sequence. We then calculated the mean time delay of answering of the follower after the emission of the first leader's vocalization in each group. We compared the use of *chewp* notes between leader and follower individuals. First, we calculated the percentage of the introductory sequence that contained only *high chewp* notes, only *low chewp* notes, or both *chewp* note types using one group display per group recorded. Then, we performed a Mann-Whitney-Wilcoxon test (Wilcoxon Sum-Rank test, two-sided with continuity correction) to test whether leaders emit more introductory notes than followers do, we used the average values of leaders and followers per group to allow each group to contribute equally to the statistics. We also analysed in which manner

birds combine acoustic and visual components by determining when the visual display occurred during the full vocal sequence timeline (introductory vocal sequence + song sequence). Finally, using one recording per group, we counted the number of individuals that introduced their song only with the introductory vocal sequence: “acoustic only”; the individuals who used the visual display only: “visual display only”; those who displayed both the introductory vocal sequence and the visual tail posture: “multimodal display”; and the individuals that did not perform any visual display nor used pre-duet and chorus calls and just directly started their song: “no display”. We conducted a Pearson’s Chi-Squared Test for Homogeneity to know whether the two categories Leader and Follower differ in the way birds introduce their song and compared the Pearson’s residuals to determine on which categorical variables they differ the most with the R package corrplot. All statistical analyses were conducted with R software (version 4.0.3).

Results

Acoustic analysis of the chewp notes

The Yellow-breasted barbet initiates its song sequence with a serie of *chewp* notes which we defined as the introductory vocal sequence (**Figure 1a**, **Supplementary materials 3**). We divided these introductory notes into two categories according to their loudness and frequency shape: “*High chewp*” are short-medium range, high-pitched notes (mean fundamental frequency = 1931 Hz ± 47, mean 1st harmonic = 3804 Hz ± 89.6, the dominant frequency was on the fundamental or the 1st harmonic according to the individual, **Figure 1b-right**, **Table 1**); “*Low chewp*” are the softer version of the *high chewp*, meaning they are lower in intensity and frequency range (mean fundamental frequency = 1405 Hz ± 47, the 1st harmonic was too soft to get consistent measurements, **Figure 1b-left, Table 2**). We performed a PCA using 13 acoustic parameters of the 54 *chewp* notes. The cumulative variances of the two principal components explained 68% of the variances. The 1st PC accounts for 52% with the main contribution of frequency features (freq _stationary, mean_fundfreq, Q25, fund_min and fund_max). The 2nd PC explains 16% of the variance with mainly time related features (IQR, duration, Q75 and slope). For more details about eigen values and variables contribution, please refer to Supplementary Information S4. The HCPC assigned 20 *chewp* notes in cluster 1 and 34 *chewp* notes in cluster 2. We found that cluster 1 contained 20 *low chewp* notes, the cluster 2 contained all the 33 *high chewp* notes and one *low*

chewp note. Overall, HCPC correctly assigned high and *low chewp* notes in two distinct groups based on their acoustic features. Only one *low chewp* was misclassified.

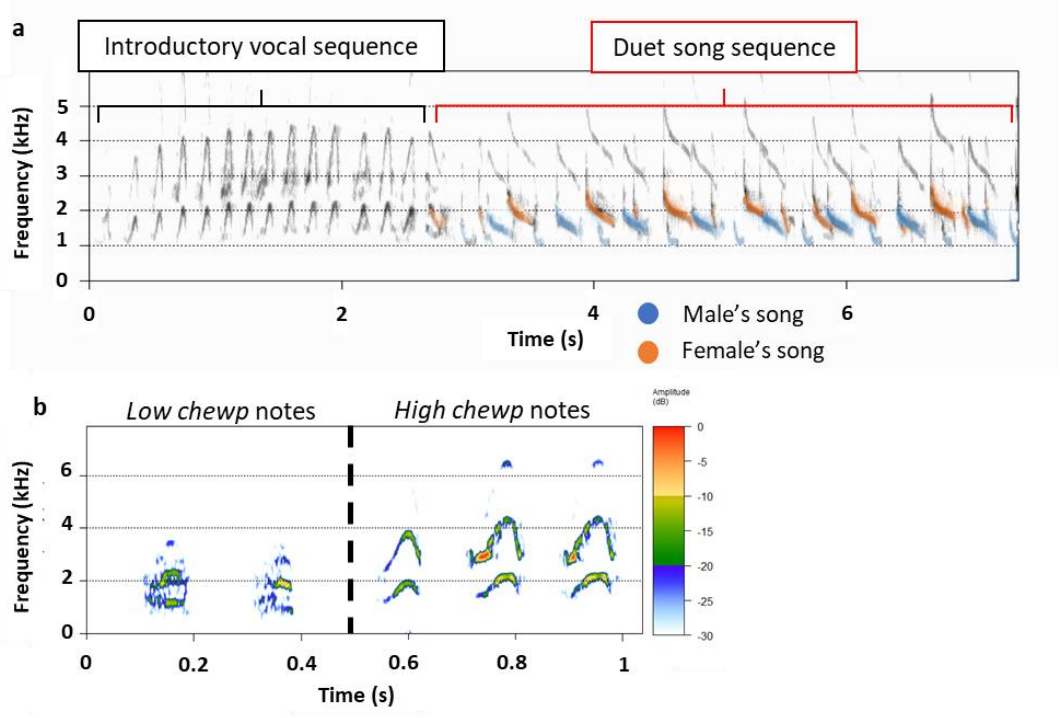

Figure 6a: Spectrogram of the beginning of a duet song with the introductory vocal sequence (black grey), given here by the female, consisting of a series of *chewp* notes. Then, the duet sequence with the song of each duetter colored (blue for the male and orange for the female). **b**: Spectrogram of the two types of *chewp* notes series: on the left the *low chewp* notes, on the right the *high chewp* notes.

Table 2: Mean ± SEM of 16 acoustics measurements conducted on 54 *chewp* notes (21 *low chewp* and 33 *high chewp* notes). All the measurements were conducted with the Seewave package in R package (wl=128, overlap=75%). Clusters 1 and 2 refer to the assignment of each note type into a group based on a Hierarchical Clustering on Principal Components (**Supplementary materials 4**). Acoustic measurements on the 1st harmonic are not reported for the *low chewp* notes due to weak accuracy of detection.

call type	cluster	duration (s)	mean fundamental frequency (Hz)	max fundamental frequency (Hz)	min fundamental frequency (Hz)	mean 1st harmonic frequency (Hz)	max 1st harmonic frequency (Hz)	min 1st harmonic frequency (Hz)
low *chewp*	1	0.083 ± 0.084	1405.26 ± 47.08	1750 ± 63.97	1107.14 ± 46.68	_	_	_
high *chewp*	2	0.055 ± 0.03	1931.74 ± 46.91	2200.76 ± 61.72	1530.30 ± 44.73	3804.12 ± 89.61	4333.33 ± 109.46	3068 ± 81.85
slope	peak frequency (Hz)	Q25 (Hz)	Q75 (Hz)	IQR (Hz)	stationary point time (sec)	stationary point frequency (Hz)	inflexion point time (sec)	inflexion point frequency (Hz)
0.07 ± 0.01	1910.71 ± 162.55	1720.23 ± 112.76	3261.90 ± 148.63	1541.66 ± 126.57	0.042 ± 0.004	1454.57 ± 86.86	0.000	0.000
0.018 ± 0.01	2878.78 ± 229.28	2348.48 ± 83.45	4136.36 ± 127.64	1787.88 ± 76.40	0.040 ± 0.003	4327.59 ± 111.97	0.019 ± 0.002	3606.49 ± 68.79

Acoustic structure of the duet and chorus introduction

All of the duets and choruses recorded started with an introductory vocal sequence from at least one individual. The mean reaction time of followers per group to reply to the leading individual was 2.88 ± 0.61 s (mean ± SEM, n = 19 groups). This reaction time concerns only the individuals that were present when the playback simulation started. We did not account for the individuals that joined the chorus with some delay due to the fact that they were far from the rest of the group at that moment. When looking at the first follower only, the mean reaction time per group was 1.73 ± 0.48 s (n = 19). Half of the introductory sequences of leaders were pure series of *high chewp* notes, and the second half were a combination of *high* and *low chewp* notes. Only 3.8% were pure series of *low chewp* notes (**Figure 2a** – LEADER, n = 26 leaders). Regarding followers, 53.1% of the introductory sequences contained a mix of *high* and *low chewp* notes, and 25.0% high chewp notes series only. However, 21.9% were composed of *low chewp* notes only (**Figure 2a** – FOLLOWER, n = 32 followers). We also found that leaders produced a significantly higher amount of *high chewp* notes than followers did per introductory sequence (W = 63.5, n = 22 groups for leader category, 25 groups for the follower category, $p < 0.001$, **Figure 2b**). However, we did not find any significant difference regarding the number of *low chewp* notes per introductory sequence emitted between leaders and followers (W = 182, n = 20 groups for leader category, 17 groups for the follower category, $p = 0.72$, **Figure 2c**). We controlled for the sex of individuals, and we found that there is no significant difference between males and females in the number of *chewp* notes emitted, regardless of whether they are leaders or followers. It suggests that the emission of *chewp* notes did not depend on the sex of the individual but rather its role as leader or follower during a group display initiation.

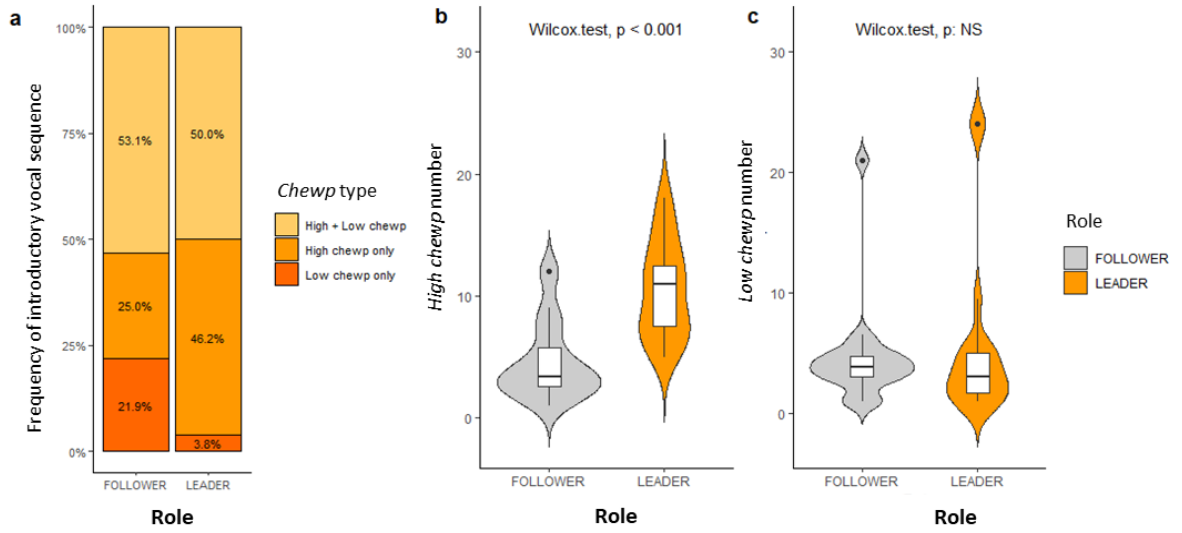

Figure 7a: Frequency of use of three types of introductory vocal sequence: with *high chewp* notes only, *low chewp* notes only and sequences with a combination of *high* and *low chewp* notes. Almost all the Leaders emitted *high chewp* notes, half of them used *high chewp* notes series only, while the other half used a mix of *high* and *low chewp* notes. Most of the followers also used *high chewp* notes only or combined with *low chewp* notes. However, around 22% of the sequences recorded contain only *low chewp* notes. **b-c**: Violin plots representing the number of *high* and *low chewp* notes per introductory sequence for both the leaders and followers. Leaders emitted significantly more *high chewp* notes to introduce their song than followers did (Mann-Whitney-Wilcoxon Test: W = 63.5, n = 22 groups for Leader category, 25 groups for the Follower category, $p < 0.001$). There was no difference in the number of *low chewp* notes emitted by leaders and followers (Mann-Whitney-Wilcoxon Test: W = 182, n = 20 groups for Leader category, 17 groups for the Follower category, $p = 0.72$). We also noticed that the number of *high chewp* notes emitted by followers did not differ from the number of *low chewp* notes emitted both by followers and leaders, while Leaders emitted a higher number of *high chewp* notes per sequence than *low chewp* notes.

Who is displaying? The use of a multimodal signal

We found that the visual tail posture occurred at the beginning of the vocal display (**Figure 3a**). The average duration of introductory vocal sequences was 4.24 ± 0.35 s (n = 16). All visual displays started during the *chewp* notes series with some delay (average delay = 2.06 ± 1.41 s) and ended for most of the individuals after the end of the introductory vocal sequence (n = 12/16: average delay after the end of the vocal introductory sequence: 3.43 ± 1.09 s). These results show that some birds combined the *chewp* notes with a tail visual display but without fine temporal coordination. Birds also erected their dark forehead crest, but we did not find it constituted a specific signal used during duet and chorus introduction and seemed to rely more on the general emotional state (excitation, stress, aggressivity) of the individual during the group vocal displays, as well as in other contexts. Finally, we found that leaders and followers did not introduce their

song the same way (χ^2 = 18.1, df = 2, n = 20 leaders, 35 followers, $p < 0.001$, **Figure 3b**). Though both leaders and followers mostly used purely acoustic displays, leaders performed multimodal displays as often, while some followers did not introduce their song with *chewp* notes nor tail display (Pearson's residuals, **Figure 3c**).

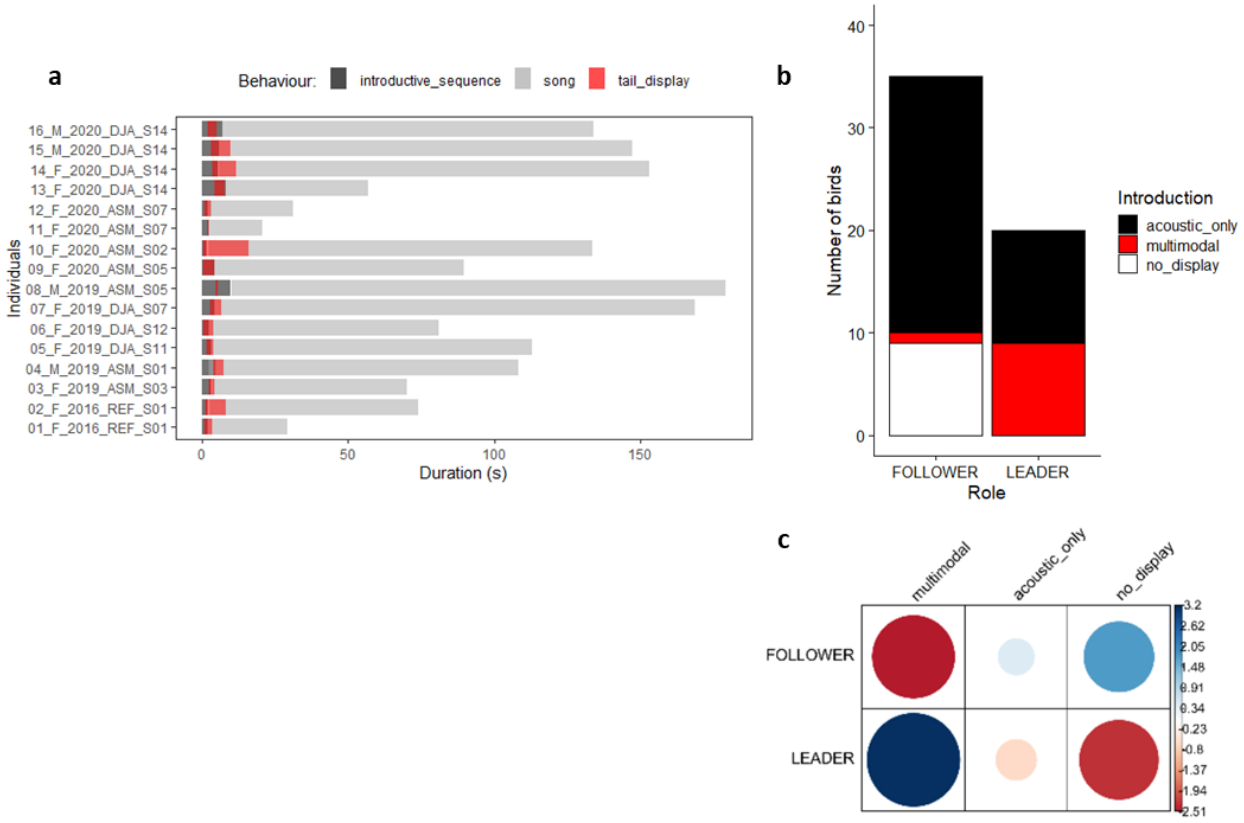

Figure 8a: Gantt chart of the 16 individuals that displayed a multimodal signal in barplots. The introductory vocal sequence in dark grey is followed by the song sequence in light grey. The visual tail display starts with the introductory vocal sequence and end during the beginning of the song sequence. **b**: Barplots comparing whether leaders and followers introduce or not their song with a specific display when duetting or chorusing. A chi-square test of homogeneity reveals a significant difference between the two categories (χ^2 = 18.1, df = 2, n = 20 leaders, 35 followers, $p < 0.001$). **c:** Pearson's residuals show which variables account the most for the difference between leaders and followers. Leaders are positively associated (blue) with multimodal display while followers are positively associated (red) with no display.

Discussion

In this study, we investigated how the Yellow-breasted Barbet starts a coordinated group vocal display. We found that barbets initiate their song with a specific vocalization named *chewp* notes. Acoustic measurements allowed us to identify two variations of such call type: the *high chewp*, which is louder with a "wave shape" frequency modulation, the dominant frequency can

be on the fundamental or the 1st harmonic; the *low chewp* is softer in intensity, lower in frequency range and more variable in terms of frequency modulation and duration. We also found that the initiator of a group vocal display used more *high chewp* than followers and sometimes combined *chewp* notes with a tail visual display to perform a multimodal display.

The pre-duet and chorus vocalizations were previously interpreted as a "greeting ceremony", which is according to its initial definition, a kind of ritualized social behaviour executed by two or more individuals that takes the form of a multimodal display involving specific calls and visual postures. Such display may or may not lead to a duet/chorus song (Short and Horne, 1982). The authors defined the term "greeting ceremony" based on what they observed in the Black-collared Barbet. They found that greeting ceremonies were more common than duets and identified three kinds of calls: grating, chatter, and "*tyaw*" calls. Moreover, they found that most greeting ceremonies that led directly to a duet sequence were shorter in duration and contained "*tyaw*" calls, while greeting ceremonies that did not introduce a duet song were longer in duration and ended with soft grating or chatter calls. According to this information, we suppose that greeting ceremonies might encompass two distinct social behaviours, one exclusively serves in "meeting" or "joining" events (which we consider as true greeting ceremony) while the second serves specifically in duet initiation. It is important to mention that David Ward admitted that it was difficult to perceive any differences between these calls though, because frequency and volume were quite variable. He then grouped all these vocalizations as grating calls (Ward, 1986).

In our study on the Yellow-breasted Barbet, we found that *chewp* notes are a specific vocalization used during a group vocal display initiation and we did not record these calls in any other contexts than duet and chorus displays. Moreover, we made few observations when the group members did not reply to the *chewp* notes of an individual. In this case, the bird that gave *chewp* notes did not start its song sequence or gave just a few syllables and quickly stopped. Another use of *chewp* notes that was not mentioned in the results due to the very few occasions we observed it, was during troop movements. When birds were actively singing, and one individual suddenly flew away to another tree location, the moving individual broke its song sequence with *chewp* notes while flying. The rest of the group immediately followed to continue their chorus on the other tree. However, if the group did not follow, the individual that moved remained silent after it had landed. Finally, in three instances the leading individual broke its song sequence with few *chewp* notes

during a chorus when one individual that was absent initially, joined with some delay the chorusing group. These additional observations combined with our main results led to two conclusions. First is that these *chewp* notes are used specifically in the context of duet and chorus displays. Second, that barbets use these vocalisations for intra-group interactions to induce an immediate behavioural response from the other group members. Similarly, in the Laughing Kookaburras (*Dacelo novaeguineae*), typical introductory syllables usually emitted by one individual appear to cause others in the group to join and sing in chorus (Baker, 2004). Introductory vocal elements are also mentioned in the song of the duetting White-eared Ground-sparrows (*Melozone leucotis*) and described as the first part of the song (Sandoval *et al*., 2016). In the White-browed Sparrow Weavers (*Plocepasser mahali*), a duet initiation consists of harsh notes emitted by both sexes, or one to three introductory syllables at the beginning of a duet (Voigt *et al*., 2006). The emission of introductory vocal elements to initiate a coordinated group display seems to be common in many duetting and chorusing bird species and therefore needs more attention and dedicated studies about their usage and possible functions.

We found that the leader and follower individuals did not behave in the same way when introducing their song. This result is consistent with the "leader-follower strategy", where the follower is the individual who adapts its behaviour according to the leading individual who promotes the activity (Fairhurst *et al*., 2014). A leader within a group is generally necessary to induce a joined action from other members (Wheatcroft and Price, 2018). For example, troop movements are usually initiated by one individual considered as a leader, who gives specific calls when flying to invite the rest of the group members to follow (Koykka and Wild, 2015; Radford, 2004). Synchronizing the behaviour to sing in a coordinated way can become quite challenging when several individuals are involved. Thus, the emission of *chewp* notes could serve as a recruitment signal that informs all the group members in the vicinity about the start of a communal vocal display and that they must join the leading individual. Since followers could also reply with *chewp* notes, and we did not find significant difference in the number of *low chewp* notes given by both leaders and followers, the introductory vocal sequence could serve as agreement between participants to act together. *Chewp* notes could also be used as a coordination signal that helps participants to coordinate their song sequences from the beginning. In the White-browed Sparrow, it was hypothesized that the song onset of the bird that joins the duet represents the common cue that defines the onset of vocal coordination in both birds (Hoffmann *et al*., 2019). Thus, the

introductory part of the duet in this species might not be used by duetters as a common cue to coordinate their song. In duetting Songbirds in general, partners coordinate their song by following a precise set of rules known as the duet code (Logue and Krupp, 2016), that needs to be learnt when they are young birds and even in adult stage (Rivera-Cáceres *et al*., 2018, 2016). However, many duetting, and chorusing bird species such as barbets are non-oscine-birds, and the strategies of song coordination for those species have been subject of less attention.

We found that the leading individual sometimes combined *chewp* notes with a specific visual display consisting of the tail raised and fanned. Visual display synchronized with the vocalizations is observed in several duetting barbet species e.g. *Lybius torquatus*, *Lybius vieilloti* and *Trachyphonus darnaudii* (Payne, 1971). The author suggested that those displays may be directed toward the mate. In the Black-collared Barbet, all birds engaged in duetting or chorusing behaviour may combine both acoustic and visual display. However, the most active bird considered as the leading individual during greeting ceremonies and duets was the bird with the cocking tail, and it was never reported that more than one bird in a group displayed in such way (Short and Horne, 1982). They thus concluded that such specific visual display might be associated with sex and/or dominance status. These observations are consistent with our findings in the Yellow-breasted Barbet. However, in our case, both the male and female could lead the duet and chorus and used the tail display. Performing a multimodal signal in the context of a group collective behaviour could increase the detection and/or the discrimination of the leading individual from the rest of the group, helping followers to focus their attention on the right individual. The visual component could serve as "amplifier" of the vocal component or "alerting signal" in order to decrease the receiver's reaction time to the *chewp* notes sequence (Hebets and Papaj, 2005). In the D'Arnaud's Barbet, one individual constantly performs oscillation movements with its tail raised when it is actively singing in a duet (Payne and Skinner, 1970; Wickler, 1973). This suggests that the tail display may play a role in the song coordination in this barbet species. Recent work on the Australian Magpie-larks (*Grallina cyanoleuca*) also revealed that mated pairs use wing movements as conductor baton to enhance their song coordination, resulting in a more threatening signal for neighbours (Ręk and Magrath, 2020). In our model species, however, the tail display was restricted to the song introduction.

Further investigations are needed to understand the role of *chewp* notes and the tail display in the Yellow-breasted Barbet and how such signal affects the group cohesion and song coordination. It would be interesting to investigate whether the *chewp* notes sequence could give some information regarding the threat perceived and the level of investment the participants must provide during the group vocal performance. The *chewp* notes features could transmit information related to the emitter identity, its sex and status in the group, as well as information on how intensively the participants must sing in terms of rhythm and song duration. Females often started the duets and choruses, but we did not find any difference in the number of *chewp* notes emitted between males and females whether they are leaders or followers. Moreover, we recorded one chorus where three males started together, joined later by a female of the group. These observations suggest that sex roles in communal display are similar, even though there is a sexual dimorphism with the presence or absence of the black patch on the throat, as well as with the pitch frequency of the song sequence which is higher for the female compared to the male (Short and Horne, 2001). In the D'Ardaud's Barbet, experimental removal of one duetter resulted in its replacement by another subordinate group member that sang the appropriate duet role, with male singing the duet part that was assigned to the female and vice versa (Short and Horne, 1983).

More data need to be collected on duetting and chorusing barbet species to conduct a comparative behavioural analysis in order to investigate the role of sex during group displays, as well as the different strategies of song coordination and mutual attention. This would certainly help to understand why and how certain species perform coordinated chorus displays while others do not.

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Association (https://www.decandjibouti.org/) which is responsible for the management of the protected areas of Assamo and Djalélo in Djibouti.

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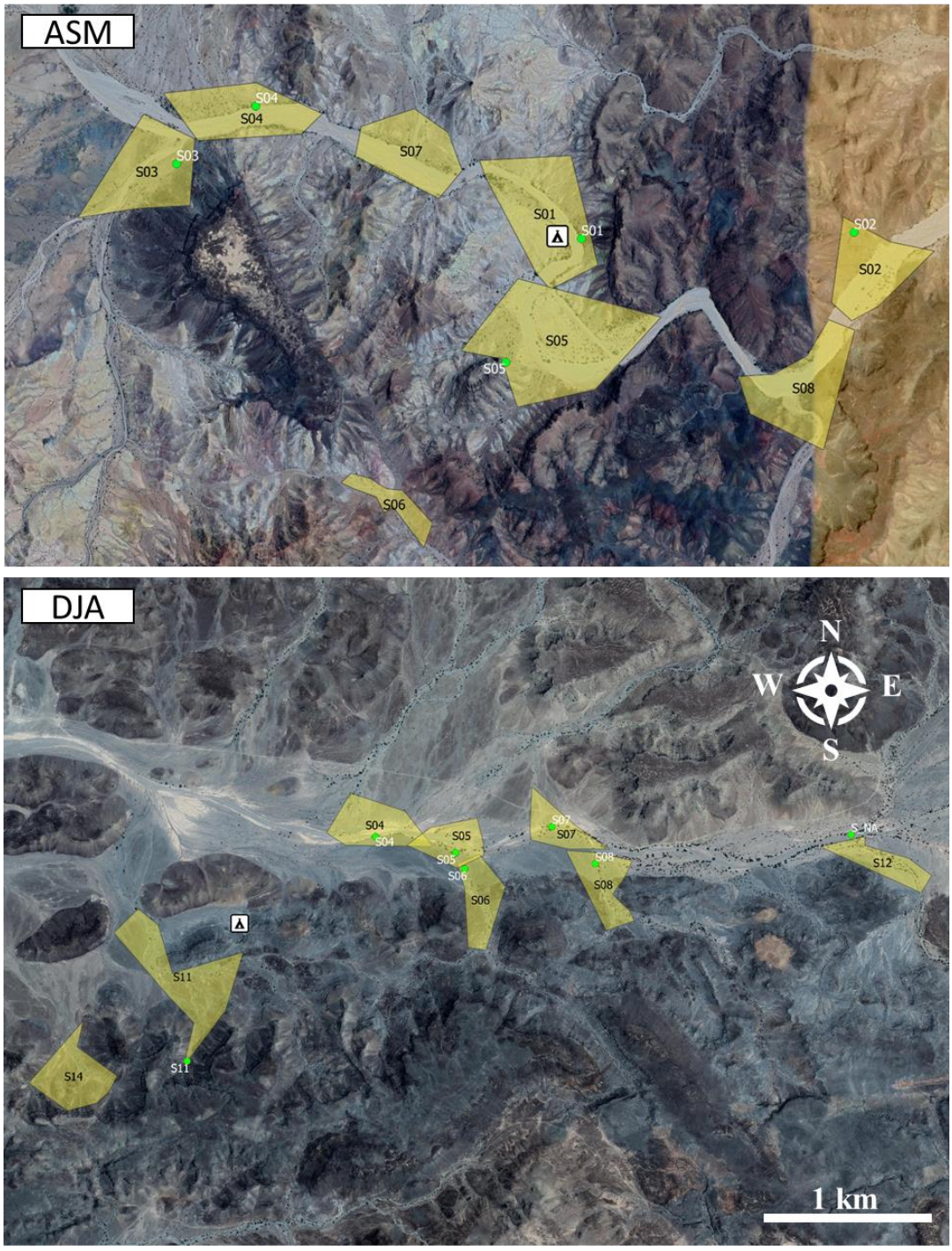
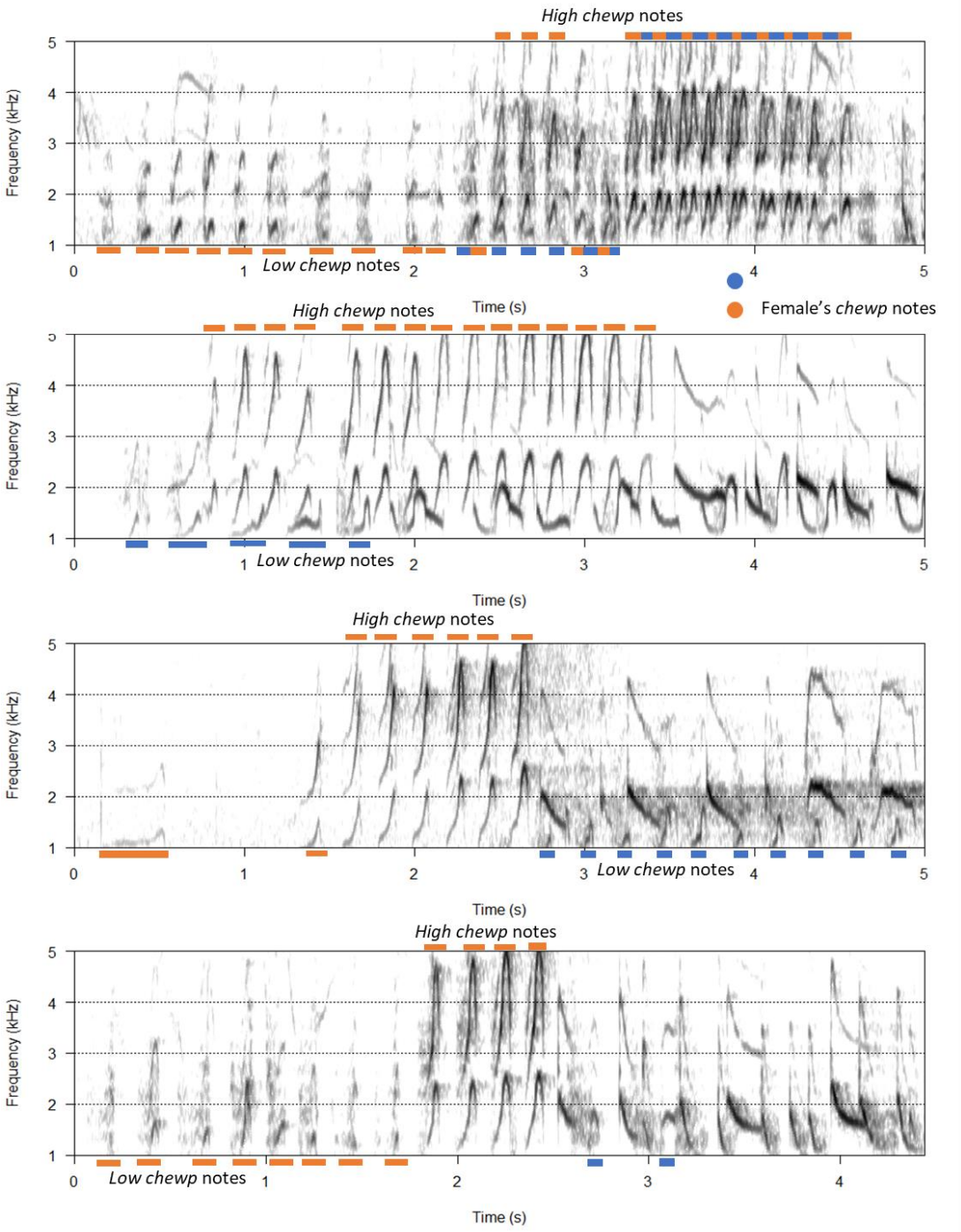
Supplementary materials



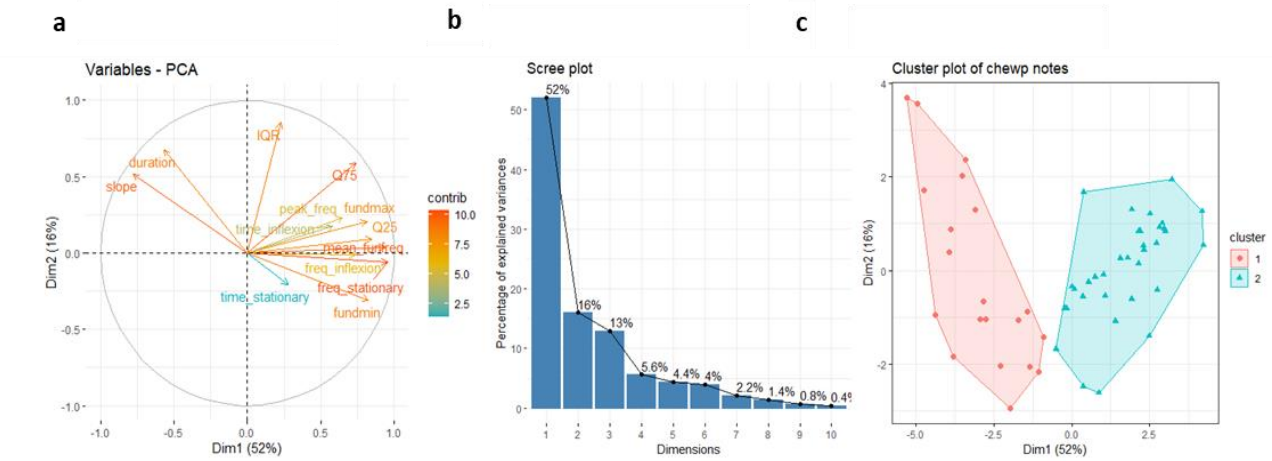
Supplementary materials 8: Localizations of all the sites (green dots) where we caught the different groups of barbets in Assamo (ASM) and Djalélo (DJA). The yellow areas are the territory of each group, at least the place we observed them regularly and recorded. For some groups (without green dots), we identified their territory but failed to find their cavity.

Area	Site	2016_group_recorded	2019_group_recorded	2020_group_recorded
ASM	S01		2019_ASM_S01	2020_ASM_S01
ASM	S02		2019_ASM_S02	2020_ASM_S02
ASM	S03		2019_ASM_S03	
ASM	S04		2019_ASM_S04	2020_ASM_S04
ASM	S05		2019_ASM_S05	2020_ASM_S05
ASM	S06			2020_ASM_S06
ASM	S07			2020_ASM_S07
ASM	S08		2019_ASM_S08	
DJA	S04		2019_DJA_S04	2020_DJA_S04
DJA	S05			2020_DJA_S05
DJA	S06		2019_DJA_S06	2020_DJA_S06
DJA	S07		2019_DJA_S07	2020_DJA_S07
DJA	S08		2019_DJA_S08	2020_DJA_S08
DJA	S11		2019_DJA_S11	
DJA	S12		2019_DJA_S12	
DJA	S14			2020_DJA_S14
DJA	S_NA			
REF	S01	2016_REF_S01		2020_REF_S01
total	**18**	**1**	**12**	**13**
			Total recorded groups	**26**

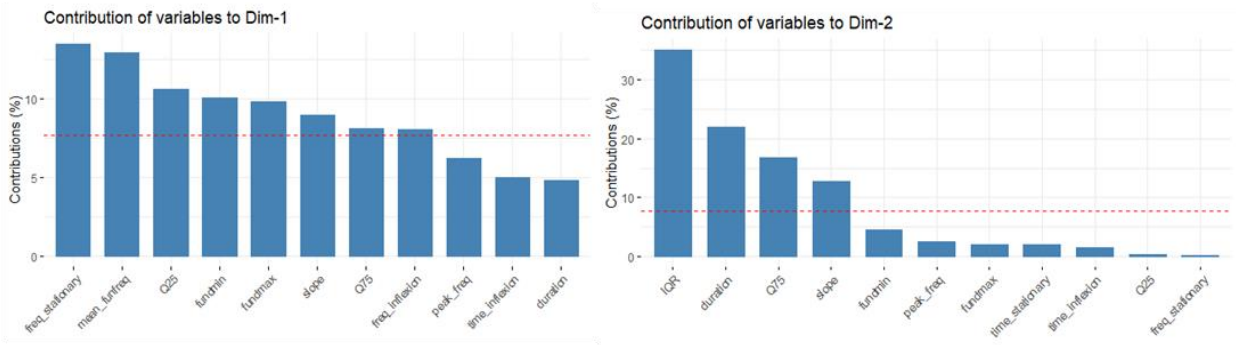
Supplementary materials 9: Groups recorded during the two fieldwork sessions. A site defines a cavity localization (see maps **Supplementary materials 1**). There are 17 sites in total for DJA (Djalélo) and ASM (Assamo) areas. REF is the wildlife shelter owned by DECAN association. A group of barbets have settled in this shelter attracted by the food and water availability; however, we did not find their cavity. One site in Djalélo area is named S_NA. In 2019 we caught a group of barbet at the site S_NA, but did not manage to record them. The next year this site was destroyed, and the barbet group left the area. At the end, we recorded groups from 17 sites**.**



Supplementary materials 10: Introductory sequence of four duetting pair with a combination of *high* and *low chewp* notes.



	Eigenvalues	Variance.percent	Cumulative.variance.percent
Dim.1	6.76	51.99	51.99
Dim.2	2.08	15.99	67.98
Dim.3	1.68	12.96	80.95



Supplementary materials 11: Results of the PCA conducted on 13 parameters (duration, minimum, maximum and mean of the fundamental frequency, Q25, Q75, IQR, peak frequency, frequency slope, time of stationary and inflexion point, frequency of stationary and inflexion point) from 54 *chewp* notes (33 *high chewp* from 11 individuals and 21 *low chewp* from 7 individuals). **a**: The circle shows the correlation and the level of contribution of each acoustic parameter on the first and second principal components. **b**: The first component explains 52% of the variance and the second component explains 16%. **c**: The two clusters obtained by HCPC using the first two principal components of the PCA. The cluster 1 contains the 20 *low chewp*, the cluster 2 contains all the 33 *high chewp* notes and one *low chewp*.

Chapter 3: Contexts of singing and the mechanisms of song coordination in a group living bird species that performs collective vocal displays

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Keywords: Lybiidae, Trachyhonus margaritatus, collective behaviour, duet, chorus

Abstract

Collective and collaborative signalling consists of multiple individuals that signal together to send one cohesive meta-signal to an audience. In birds, such collaborative signal takes the form of the acoustic duet and chorus displays. These coordinated group vocal displays serve multiple functions depending on the context and the species. Most of the investigations regarding the forms and functions as well as the mechanisms of vocal coordination have been investigated in songbirds, with little attention to non-oscine species. In this study, we investigated the contexts of collective signalling as well as the mechanisms of song coordination in a group living bird species, the Yellow-breasted barbet (*Trachyphonus margaritatus*). We recorded with passive acoustic monitoring the vocal activity of 11 groups of birds during the nesting period in March 2023. We found that duet and chorus displays performed near the nesting cavity occurred mainly during between-group interactions. Moreover, playback experiments with 10 groups showed that all the groups reacted to the playback. This suggests that group vocal displays serve in territorial defense. The analysis of the singing patterns when the birds were duetting revealed that males often sang faster than the females and we did not find any evidence of interactive rhythmic adjustments between the duetters. Each bird might sing following its own rhythm of singing.

Introduction

Definition of a collective signal and the duet and chorus song

Collective signaling, in which two or several individuals combine their vocalisations into duets or choruses, occurs in many social insects, anurans, mammals and birds (Pika *et al*., 2018). Among the variety of collective signals, avian acoustic duets are one of the most structurally complex and well-coordinated (Hall, 2009; Logue and Krupp, 2016). An acoustic duet defines the non-random combination of vocalisations emitted by two individuals to deliver a synchronized vocal performance (Farabaugh 1982). Synchronization often occurs in space, as duetters are seen close to each other when duetting, as well as in time because in many species, the timing between partner's vocalisation is short and regular (Hall, 2004). Such collective signal possesses two levels of organization: the individual level and the pair/group level (Logue and Krupp, 2016), and the interplay between the temporal and frequency features of each participant's contribution constitutes a new signal on itself (Brumm and Slater, 2007).

Contexts and functions of collective singing in group living bird species

Acoustic duets and choruses in group-living bird species are generally considered as collaborative signals (Templeton and Carlson, 2019) that serve multiple functions depending on the context of emission and the species (Dahlin and Benedict, 2014). The loud and conspicuous nature of such collective displays have been suggested to serve in between-pair and group interactions to collectively defend the territory (Baker, 2004; Dowling and Webster, 2013; Hall and Peters, 2008), discriminate neighboring groups (Radford, 2005) and assess the number of individuals within the chorusing group (Hale, 2006; Seddon and Tobias, 2003). On the other hand, in some species, duet and chorus songs serve primarily for intra-group interactions to maintain within-group cohesiveness and bonds, and rarely during between-group interactions (Savagian and Riehl, 2023). Such collective signals might also serve within the group to enforce dominance hierarchy (Radford, 2003) or advertise about the mated status of the dominant breeding pair (Voigt *et al*., 2006).

Is it important to be coordinated or not?

Most duetting songbird species perform highly coordinated collective vocal displays (Dahlin and Benedict, 2014). Such precise coordination could be costly to achieve for duetters and might reflect the pair quality and pair's bond stability (Brumm and Slater, 2007; Hall and Magrath,

2007; Logue *et al.*, 2008). Thus, it could be used as an honest signal to advertise the strength of the pair to defend their territory (Hall, 2009). For example in the Australian Magpie-larks (*Grallina cyanoleuca*) well-coordinated duets are perceived as a more threatening signal for neighbours (Ręk and Magrath, 2022, 2020).

How Does birds achieve song coordination

To maintain regular timing during a duet bout, each bird could fix its singing rhythm based on a common cue when initiating a duet. On the other hand, one or both duetters could adjust their timing intervals with a syllable-by-syllable adjustments mechanism. It requires a fast auditory-reaction time, which is the delay for a bird to listen and answer its partner vocalisation (Thorpe, 1963). In the Black-bellied wren (*Pheugopedius fasciatoventris*), the timing calculation of duetters song revealed that the male timing of vocal production was primarily influenced by the time of the beginning of the previous female phrase and secondarily influenced by the male's own internal tempo. The female was primarily influenced by the end of the previous male phrase and secondarily influenced by her own internal tempo (Logue *et al*., 2008). In this species, birds achieve good phrase coordination by minimizing overlaps and gaps between their phrases using syllable-by-syllable adjustments, based both on autogenous and heterogeneous sensory feedback. In other words, when duetting, a bird controls its own vocal production by listening to its own vocalisation (autogenous sensory feedback) as well as the vocalisations of its partner (heterogeneous sensory feedback). In the Plain wrens (*Cantorchilus modestus zeledoni*), the female uses heterogeneous sensory feedback by modifying her inter-phrase intervals based on the phrase type her mate sings. The male modifies his inter-phrase intervals based on both the phrase that he sang and the phrase the female chose to answer, which suggest that male uses both autogenous and heterogeneous feedbacks (Rivera-Cáceres, 2015). Similar inter-phrase intervals adjustments to achieve well-coordinated duets using both autogenous and heterogeneous feedback were described in the Plain-tailed wren (*Pheugopedius euophrys*, Fortune *et al*., 2011), the Happy wren (*Pheugopedius felix*, Templeton *et al*., 2013) and the White-browed sparrow-weaver (*Plocepasser mahali*, Hoffmann *et al*., 2019). Duetting birds of Large-footed finch (*Pezopetes capitalis*) adjust both their temporal and frequency coordination pattern (Trejos-Araya and Barrantes, 2018). Coordinated antiphonal duets where the male and female sing distinct phrase types have received most of the attention and songbirds seem to have become a good model species

to study the neurophysiological mechanisms for song coordination in duetting birds (Brenowitz, 2021; Coleman *et al*., 2022, 2021; Fortune *et al*., 2011; Hoffmann *et al*., 2019).

What about non-oscine duetting bird species

Although the emission of duet and chorus is observed both in passerines and non-passerines (Hall, 2009; Tobias *et al*., 2016), there is a real prevalence of such collective displays in some groups of non-passerines birds like the rail species (Goldberg *et al*., 2023) or the African barbets (Soma and Brumm, 2020). Yet, little information is known regarding the mechanisms of song coordination in these species. The degree of mutual attention, the ability of a bird to listen to its partner's song features and alter its own vocal production according to it, was poorly investigated.

The case of the African barbets

The African barbets family (*Lybiidae*) which contains several duetting and chorusing bird species (Hall, 2009; Short and Horne, 1983; Soma and Brumm, 2020) is a good example. Duetting barbets such as the Black-collared barbet (*Lybius torquatus*) and the Darnaud's barbet (*Trachyphonus darnaudii*) seem to perform duets with a good temporal coordination (Short and Horne, 1982; Wickler and Uhrig, 1969). However, the studies on the song rhythmicity and temporal patterns of duets in most duetting barbet species concluded that the rhythm of calling is different between the two duetters. The mechanisms of song coordination in these species involve individual rhythms of calling which are in large degree independent of the timing of the call of the partner (Payne, 1971; Payne and Skinner, 1970). The authors suggested other mechanisms than syllable-by-syllable response in which the temporal patterns of singing may involve an autochthonous behavioural rhythm with the possible influence of the partner's song. Yet, the degree to which a bird alters its rhythm of singing according to the vocal production of its partner was not investigated in detail. Even though both partners sing with different rhythms, one bird could accelerate or slow down its rhythm of singing if it perceives a change in the timing of its partner' song. It was observed once in the Green barbet (*Stactolaema olivacea*) that the faster-singing bird slows down its tempo as if to accommodate the slower tempo of its partner (Short and Horne, 1980). Such tempo shifting still requires investigations to understand better the mechanisms of song coordination in the duetting barbets.

In this study, we investigated the contexts in which different groups of Yellow-breasted barbet (*Trachyphonus margaritatus somalicus*) emitted vocal collective displays during the nesting

period in Djibouti, as well as the temporal pattern of singing in duets. We focused on several questions: Does the Yellow-breasted barbet perform group vocal displays mainly to defend its territory? Does the duration of a group vocal display depend on the context of singing? What are the temporal features of duet songs? Do duetters adapt their rhythm of singing according to their partners? We analyzed the rhythm of singing only in duet, because of the limited possibility to differentiate many individuals singing in chorus.

Our hypothesis is that collective vocal displays are used mainly during between-group interactions to defend the territory. In this case we expect that playback of duet songs as well as neighbour's songs would induce an immediate vocal reaction from the focal group. On the other hand, if the collective vocal displays are used primarily for intra-group interactions, duet and chorus songs emitted by distant neigbours should rarely trigger a vocal answer from the focal group, especially when the birds are close to their own nesting cavity.

Singing continuously could be demanding for birds, and thus long duration duet and chorus songs could show the stamina of the individuals and their capacity to fight during between-group conflicts (Radford and du Plessis, 2004). We expect that the birds sing longer vocal sequences during between-group interactions and after playback stimulation than in less threatening contexts. Moreover, we expect that chorus songs might be longer in duration than duet songs. When duetting, if one individual stops singing it stops the duet while in chorus, when at least two individuals sing continuously, the collective song might continue even if one individual in the group stops to sing.

When duetting, the barbets could sing their song sequence following a fixed action pattern. Once they start singing, each duetter sings with its internal-rhythmic pattern which is not influenced by its partner rhythm of calling. Both individuals should differ in their rhythm of singing and the timing changes made by one bird do not affect the timing of its partner. Alternatively, barbets could be capable of some adjustments in their rhythm of singing to match their partner's rhythm. In this case we should observe that the difference in the mean rhythm of singing between duetters is lower within duet than between duet songs. Moreover, barbets could be capable of interactive rhythmic adjustments. Instead of phrase-by-phrase timing adjustments, the bird could perceive the general acceleration or slowdown in the rhythm of calling of its partner and try to imitate such changes.

To test the hypotheses and answer the questions, we monitored the vocal activity of several groups of barbets close to their nesting cavities for a few days during the nesting period with autonomous recording units. We also conducted playback experiments to simulate an intrusion within the territory. We classified in which contexts the different groups of birds performed collective vocal displays close to their nesting cavity and analyzed the rhythmic coordination in duet songs.

Methods

Species of study

The Yellow-breasted barbet is a group-breeding bird species that lives in arid semi-desert, sub-Saharan regions of Africa, that perform loud acoustic duets and choruses (Short and Horne, 2020). The main functions of such group vocal displays might be to maintain family social bonds as well as territorial defense (Payne and Skinner, 1970; Short and Horne, 1983). Its song was described as the repetition of descending notes "*tew-choo-to*" with an introductory sequence of *chewp* notes (Short and Horne, 2020). The phrase *tew-choo-to* is repeated by both the male and female during the whole duet sequence as well as in chorus, with a slight difference in the pitch frequency between sex, somehow similar to the Red-and-Yellow barbet (*Trachyphonus erythrocephalus*, Short and Horne, 1983). We can distinguish two distinct parts within the phrase: the *twe* part and the *choo-to* part. The note *choo* is the highest pitched in frequency within the phrase. It is followed by one up to six descending *to* notes. All together they constitute the *choo-to* part of the phrase. The *twe* part is softer in amplitude and lower in frequency compared to the *choo-to*, and consists usually of one, up to three *twe* notes (**Figure 1**).

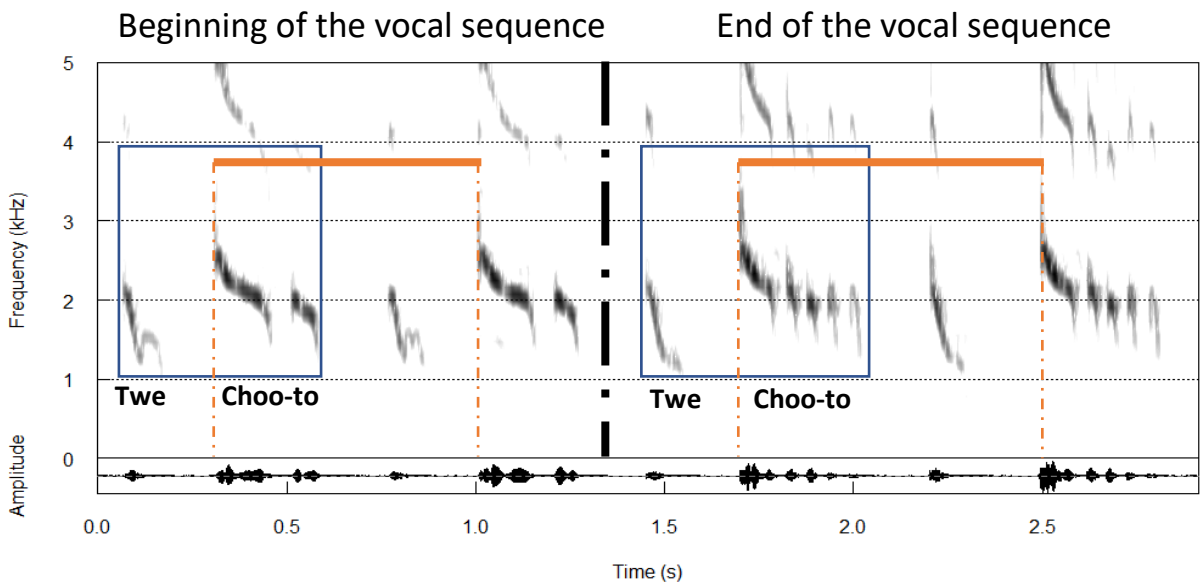

Figure 9: Spectrogram of the beginning and the end of a Yellow-breasted barbet's song sequence. The song of the species consists of a repetition of "*tew choo-to*" motif (blue square). The "*choo-to*" part evolves during the song sequence. In the beginning, the motif consists of one note "*choo*" accompanied with one "*to*". The number "*to*" notes will progressively increase up to 5-6 notes as the individual is singing will be added. To calculate the rhythm of singing, we measured the time interval between two successive "*choo*" notes.

Sites and methods of recordings

We studied 11 groups of Yellow-breasted barbet from the Djalélo valley in Djibouti (11°21'16" N, 42°47'54" E) during the nesting period in March 2023 (**Figure 2**). We deployed an array of autonomous recording units (ARUs) using Song Meters Micro (Wildlife Acoustics). We put one recording unit in the vicinity of each cavities site owned by a group of birds. African barbets are known to be territorial and aggressive toward conspecifics as well as other species which might compete for roosting and nesting cavities (see Chapter 1). Moreover, all the monitored groups were having nestlings, which might reinforce their aggression toward any intrusion. We recorded the vocal behaviour of birds (audio files: Mono, 16 bits, 22.5 kHz) from 6h to 9h in the morning, which corresponds to the peak of vocal activity near the cavities site in this species, as well as late in the afternoon from 16h to 19h. when birds gathered around the roosting site before going to sleep.

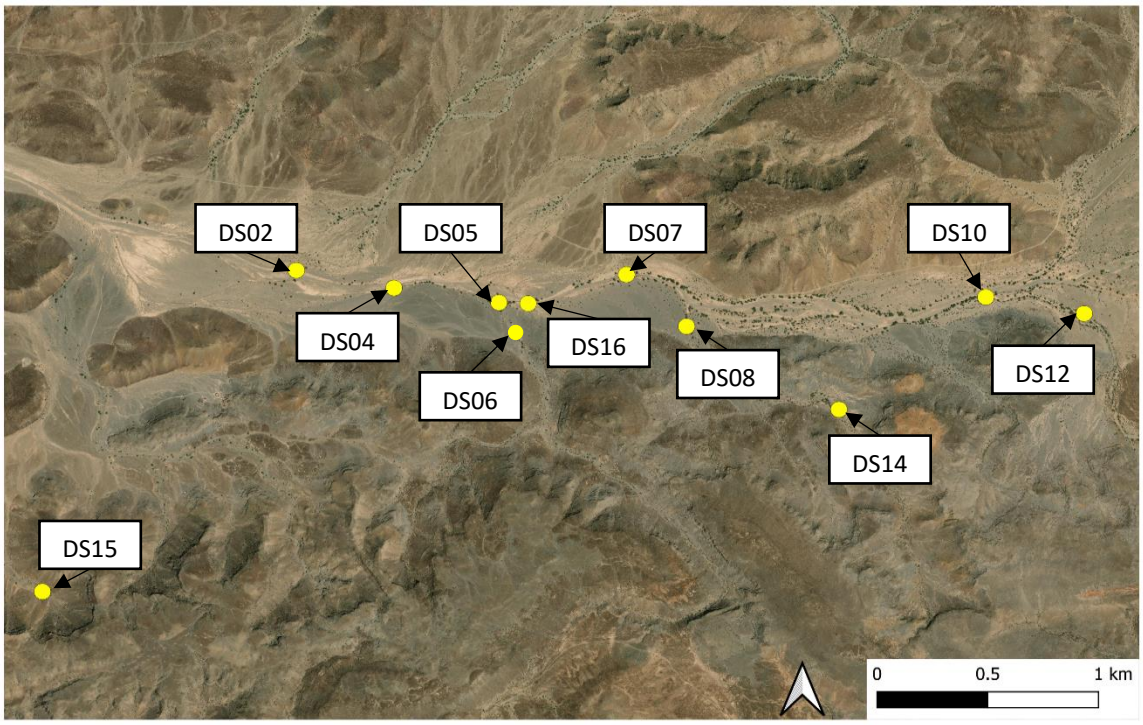

Figure 10: MAP of the Djalélo area (11°21'16" N, 42°47'54" E). The yellow dots represent the cavity site of a distinct group of birds. All the 11 groups were having eggs or nestlings during the study.

Playback experiments

Playback experiments were conducted in the morning when the autonomous ARUs were recording on 10 groups. All the playbacks consisted of a duet song broadcasted near-by a roosting cavity to simulate the intrusion of an unknown pair that could compete for the roosting cavities site ownership. We prepared two categories of playback stimulation based on the duration of the acoustic duet (sec). One category of playback consisted of about one minute of duet song (playback medium duet: PMD), while the second category consisted of about two minutes of duet song (playback long duet: PLD). Each of the 10 groups monitored received the two playback treatments (PMD and PLD), one playback treatment a day, with at least one day of no playback between the two treatments. Only the group DS15 received one treatment a day for two consecutive days due to the lack of time. The duets used as playbacks were recorded during a previous fieldwork session that occurred in February 2019 in another region in the South of the country (sampling rate 44.1 kHz, 16 bits, normalized -3 dB, high pass filter 800 Hz). The playback stimulations were broadcasted through a loudspeaker JBL CHARGE3 (power: 20 W, frequency response: 65 Hz–20 kHz, signal-to-noise ratio: > 80 dB) with the amplitude adapted to the song amplitude perceived

in the field for the species. We calculated the time delay of answer (sec) after the start of the playback as well as the duration (sec) of the vocal collective displays sung by the tested birds in response to the playbacks.

Sound selection and contexts of singing

A same experienced person visually scanned spectrograms the audio recordings (high-pass filter 800 Hz, normalized -3dB) and annotated all vocalisations assigned to the Yellow-breasted barbets and we selected the best quality duets and choruses (best signal-to-noise ratio) using RavenPro software 1.6.5. Such good quality recorded songs were obtained when the birds displayed very close to the autonomous recorders, and thus, close to their cavities site. It ensured that we recorded the targeted group and that we got a good quality signal for acoustic analysis. We classified the selected group vocal displays recorded under five distinct contexts: *Unanswered Spontaneous Display* (USD): a group of birds started a duet or chorus song without directly answering a neighbor group nor playback. Such group vocal displays did not get any immediate answer from a neighboring group within a delay inferior to 5 minutes; *Answered Spontaneous Display* (ASD): a group of birds spontaneously broadcasted a collective vocal display which was answered by neighbors; *Between-Group Interaction* (BGI): a group of birds answered the duet or chorus of a neighbouring group within a delay inferior to 5 minutes; *Playback Reaction* (PR): a group of birds reacted to a playback stimulation; *Playback Reaction - Between-Group Interaction* (RP-BGI): When a playback was broadcasted, the answer of the focal group was classified as RP. However, either the playback or the answer of the focal group could trigger a vocal reaction from other neighboring groups. In that case, the collective songs from neighbors were classified as a between-group interaction that was triggered by playback.

Temporal analysis

We calculated the delay of the answer to a playback stimulation. To investigate the mechanisms of song coordination, we analyzed the temporal features of the duets only, at the individual level. Selected duet songs were resampled to 16 kHz for a better temporal resolution. For each duetter, we measured the start and end of the *twe* part and *choo-to* part of each phrase (sec). We then calculated the inter-phrase interval (sec) using time delay between start between the beginning of two consecutive *choo* notes (**Figure 1**). Finally, we calculated the individual rhythm of singing by dividing the total number of *choo-to* by the duration of the whole song sequence

(from the first to the last note *choo*). These temporal features of the duetting barbets were measured under RavenPro software 1.6.5 (window: Hann, DFT size = 128 samples, sampling rate 16 kHz).

Statistical analysis

We compared the mean number of collective vocal displays emitted per group and per day in the morning and in the afternoon using a Wilcoxon signed rank test. We assessed the context in which collective vocal displays were emitted during the passive acoustic monitoring session by fitting generalized mixed models with negative binomial distribution. To build the model, we used the number of collective vocal displays (duet and chorus) as response variable, the context (BGI, USD and ASD) and the period of the day (Morning and Afternoon) as predictors. We also added the interaction between the period of the day and the context. The recorded site (level = 11 sites or group ID) as well as the day of recording (level = 13, mean number of recording days per site = 8.8 ± 0.8) were included as random effects. To test whether the types of playbacks used might impact the time delay of answer or the duration of the vocal answer we fitted generalized mixed models with gamma distribution. The type of playback (PMD and PLD) as well as the order of the playback session (1^{st} and 2^{nd}) were used as fixed factors, the day of the playback, the tested group (N=10) as well as the audio file used for the playback (account for the pseudo replication) were used as random factors. Finally, we fitted another generalized mixed model with gamma distribution with the collective vocal display's duration (s) as response variable and the contexts (BGI, USD, ASD, PR, PR-BGI) as well as the type of collective displays (duet or chorus) as predictors and the recorded sites as random factor.

To determine whether the male and female sang with their own rhythm of singing when duetting, we used a Wilcoxon (Mann-Whitney U) test using the difference in the mean of the *choo-to* intervals duration (s) between the partners for each duet. We also calculated the rhythm of singing by dividing the total number of *choo-to* motifs by the duration of the vocal sequence (s) and calculated the slope of each vocal sequence using a simple linear model (*choo-to* intervals duration ~ duet duration) to detect any trend in the singing pattern for each bird. To investigate whether both duetters were capable of interactive temporal adjustments, we treated their vocal sequences as a time series object using the time of emission of each *choo-to* and the *choo-to* intervals. The aim was to use correlation and cross-correlation functions between the two-time series to investigate whether the variations in the duration of the *choo-to* intervals of one bird

impacted the duration of the *choo-to* intervals of the partner. Since the two times series were unevenly spaced, we used the *bin_cor* function from the BINOR package (Polanco-Martínez et al., 2019) to bin these times series on the same time grid. We then applied the two complementary functions *cor_ts* and *ccf_ts* to detect and estimate the degree of timing correlation between the two duetters.

For all the models, we used the function *dredge* from the *MuMIn* package to automatically generate a list of alternative models and select the best model based on the AICc and delta values.

Results

Contexts and duration of the collective vocal displays

We recorded 784 duets and choruses during the passive acoustic monitoring session, and we selected the 460 collective song sequences emitted close-by the nesting cavities from 11 distinct groups (mean total vocal sequences per group = 41.8 ± 7.64, mean number of recording days = 8.8 ± 0.8) that we could be unambiguously classified as follow: 253 BGI; 109 USD; 42 ASD; 20 PR and 36 RP-BGI. Using the mean number of collective vocal displays emitted per group and per day, outside the playback experiments (USD, ASD and BGI), we found that the birds were significantly more active around their nesting cavities in the morning than in the afternoon (V = 66, $p < 0.005$, N=11, **Figure 3**). It was confirmed by the negative binomial GLMMs. We found there were significantly fewer collective vocal displays given in USD and ASD than in BGI contexts during the day, and significantly more vocal displays given in USD and ASD contexts during the afternoon than in the morning (**Figure 4, Supplementary materials 1**). All the 10 groups answered the two playback stimulations with a short time delay of vocal answer (PLD: 76.3 ± 16 .4 sec and PMD: 94.3 ± 26.4 sec, N=10). The group DS04 did not answer the PMD treatment during the first trial and answered during the second trial two days later. Similarly, the group DS07 answered the PMD treatment at the second trial which was done seven days after the first one. All the groups reacted in a similar fashion by approaching the speaker and then flew on the top of a tree close-by to perform a duet or chorus song. We did not find any significant difference in the delay of answering (**Figure 5a, Supplementary materials 2**) the two playback treatments nor in the duration of collective vocal displays (PLD: 74 ± 12.2 sec, and PMD: 75.5 ± 10.5 sec **Figure 5b, Supplementary materials 3**). The generalized mixed model with gamma distribution revealed that over all contexts (BGI, USD, ASD, PR, PR-BGI), the duet songs were

significantly shorter than chorus songs without any significant difference in the duration of duet and chorus songs between contexts of singing (**Figure 6**). The best model was the one with the type of collective vocal display (duet or chorus) as unique predictor and the site as random factor (**Supplementary materials 4**).

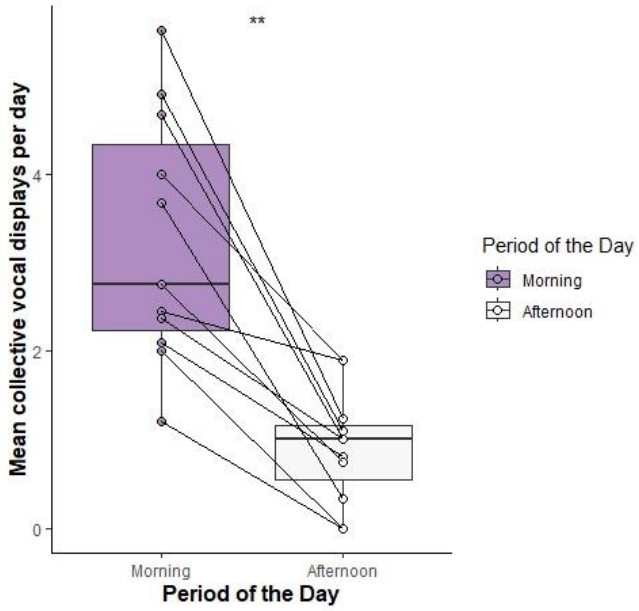

Figure 11: Boxplots representing the mean number of collective vocal displays emitted per group and per day in the morning and in the afternoon. We conducted a Wilcoxon signed rank test and found that the group of birds sang significantly more collective vocal displays in the morning than in the afternoon ($V = 66$, $p < 0.005$, $N=11$).

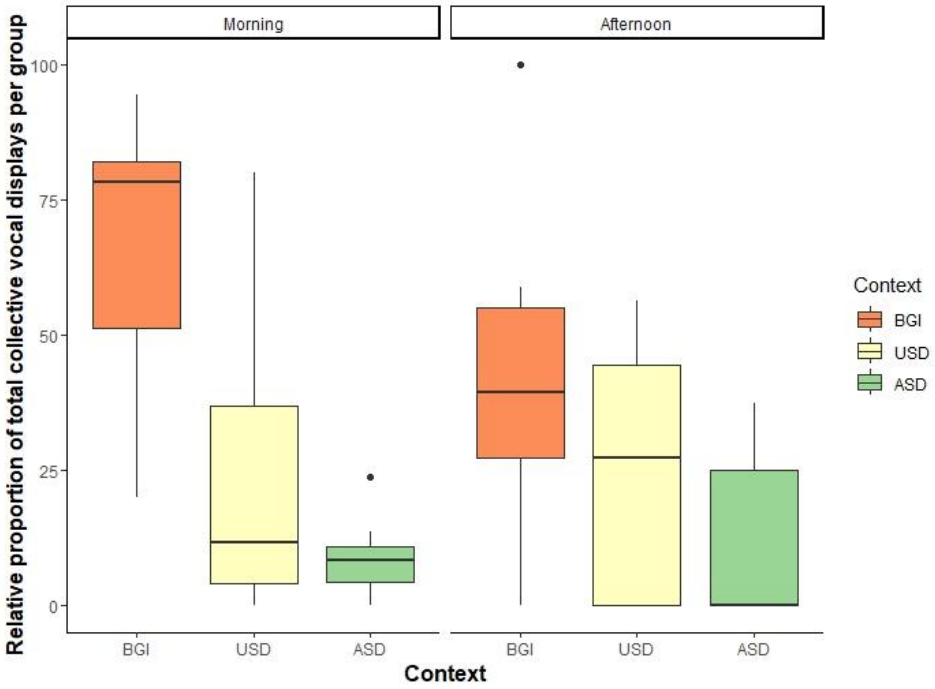

Figure 13: Boxplots representing the relative proportion of the total number of collective vocal displays per group (N=11) recorded in the morning and in the afternoon in the three contexts (BGI, USD and ASD).

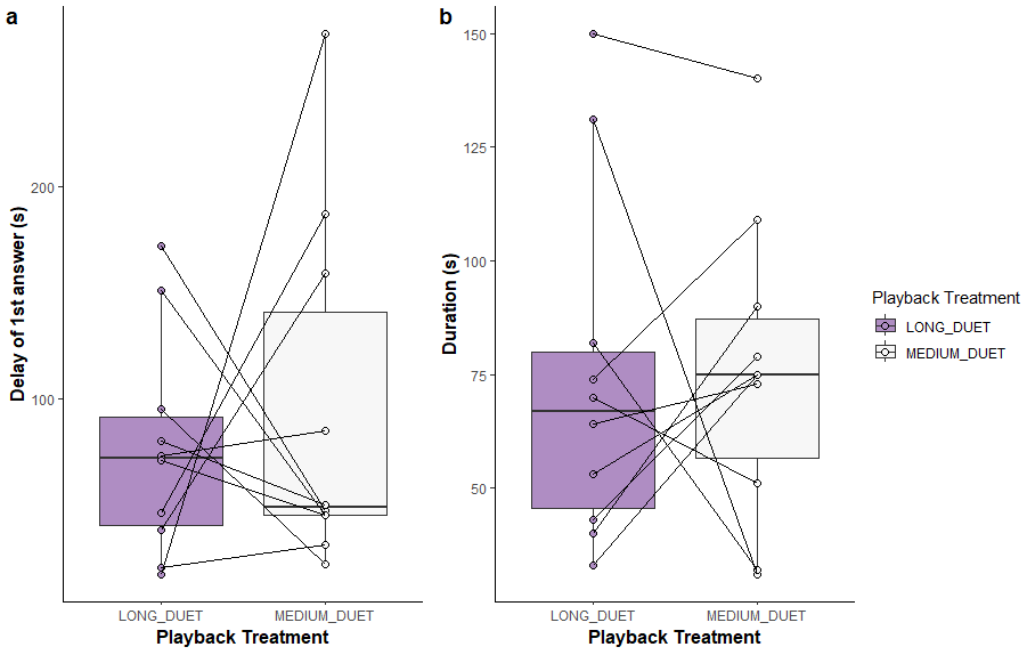

Figure 12a: Delay of answer (s) and **b**: the duration (s) of the group vocal displays for the 10 groups during the playback experiments.

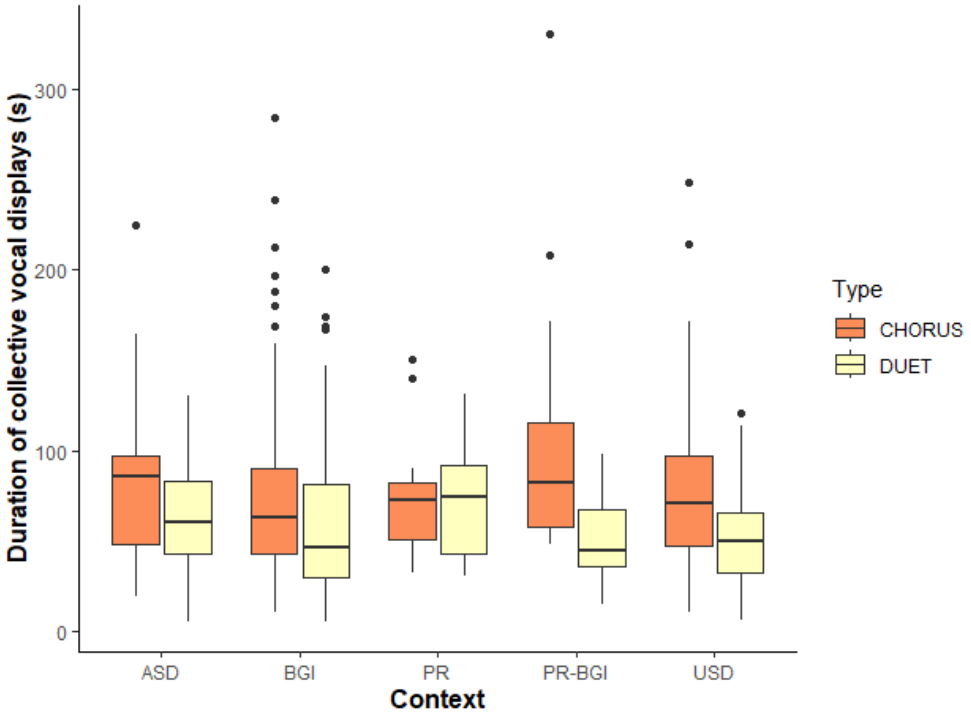

Figure 14: Duration (s) of the duets and choruses emitted by the 10 groups in each context (N collective displays per context: ASD: 25 choruses, 14 duets ; BGI: 157 choruses, 85 duets ; PR: 13 choruses, 7 duets ; PR-BGI: 19 choruses, 13 duets ; USD: 71 choruses, 38 duets).

Song coordination during duet displays

We analyzed the temporal features of 39 duet song sequences from nine groups (4.3 ± 0.76 duets per group; max =8; min=2). Overall, the song sequences of males and females started with a single *choo* note per *choo-to* part. Then, one, up to four-five *to* notes were progressively added within the *choo-to*, rarely above 6 notes (**Figure 7**). The birds tend to slow down their tempo as the duration of the duet increases (mean slope for males: 0.002, mean slope for females: 0.004). We found that most of the males sang with shorter *choo-to* intervals (0.65 ± 0.00 s) than the females (0.68 ± 0.00 s), meaning that males sang a bit faster. The mean rhythm of singing of the males was 1.56 ± 0.02 s and 1.49 ± 01 s for the females (**Figure 8**) with a mean difference of 0.14 ± 0.01 s. The selected gamma model revealed that the status (Leader and Follower) did not impact the rhythm of singing, although the males were more often leading (leading position by males: 24 and females: 15, **Supporting materials 5**).

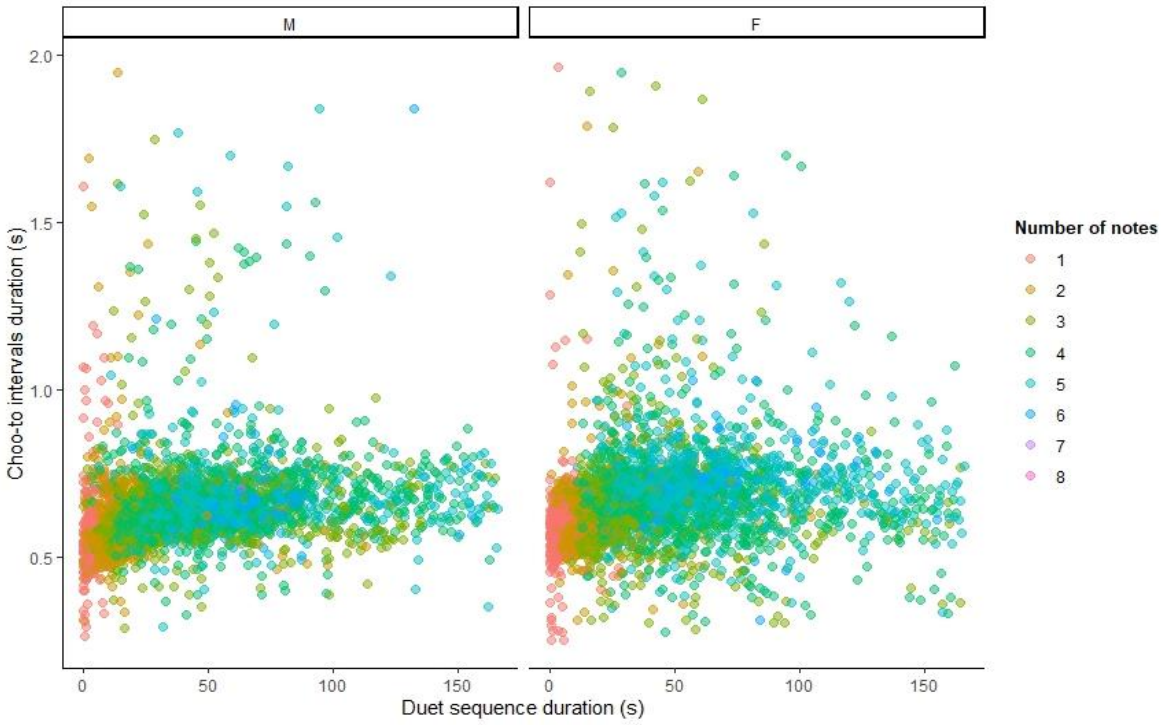

Figure 16: Scatter plot of the *choo-to* part according to timing of emission during the vocal sequence (x-axis) plotted against the time intervals to the following *choo-to* part. We combined the 39 vocal sequences of male and females and colorized according to the number of notes within each *choo-to* emitted. In both the males and females, the pattern of singing was similar. Both duetter started to sing *choo-to* with one note and progressively added to notes.

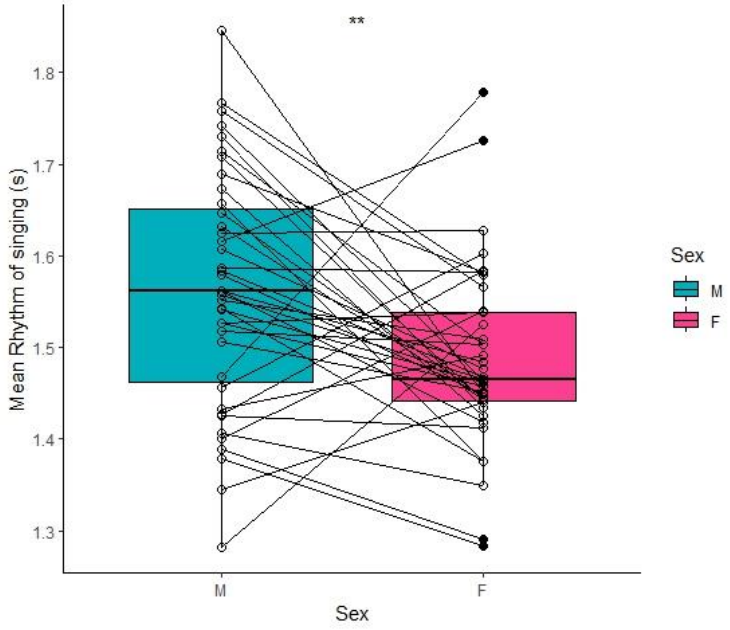

Figure 15: Comparison of the mean rhythm of singing (s) between the male and the female in each of the 39 duet songs. The males sang significantly faster than the females (p<0.005, **Supporting materials 6**)

We found that in 28 duets, the mean *choo-to* intervals between the male and female were significantly different and in 11 duets there was no significant difference (**Supporting materials 6**). Finally, the binned time series correlation analysis revealed no clear evidence that duetters interactively adapted their tempo according to their partner's change in the *choo-to* intervals duration, but simply followed an "on/off" song coordination pattern. In other words, when a bird started singing, its partner sang as well but as soon as one bird stopped, its partner stopped (**Supplementary materials 7**).

Discussion

Context of collective displays and possible functions

In this study we monitored the vocal activity of 11 groups of Yellow-breasted barbets near their nesting cavity in the morning and in the afternoon, focusing on the number of collective vocal displays (duet and chorus) emitted and the context of singing. We found that the amount of group vocal displays is higher in the morning than in the afternoon during the nesting period. This result is comparable to the vocal activity observed outside the nesting period in 2022 (see Chapter 1). We found that most of the group vocal displays emitted during the day near the cavities occurred during between-group interactions in which the focal group answered another group of birds. Moreover, all the 10 tested groups reacted to the playback stimulation with a short delay of answer. These results suggest that the collective vocal displays might have a function in joint-cooperative territory defense. During the nesting period, displaying near the nesting cavities could prevent any attack on the brood by neighbouring groups. Since all groups were already established in a territory and engaged in nesting activity, there was a low chance of cavity usurpation by neighbours. However, considering the relative proximity of some groups, destroying a neighbour's brood could reduce the inter-group competition for food resources in the area (Almstead *et al*., 2021). Interestingly, the relative proportion of spontaneous unanswered group vocal displays was higher in the afternoon than in the morning. In the afternoon, the different groups of birds were less vocally active and reacted less to the neighbour's displays. The reason might be that at the end of the day, birds gathered and spent more time around their own nesting cavity which was also used as a communal roosting site. The probability of territory intrusion by neighbours at the end of the day might be lower than in the morning as well as the competition to access resources. Group vocal displays in the afternoon could serve mainly in maintaining group cohesiveness and reinforce

social bonds. Therefore, duets and choruses could be multifunctional depending on the context and the moment of the day. A year-round acoustic monitoring would be useful to determine the frequency of duets and choruses emitted throughout the year to better understand the functions of such collective vocal displays in this species. In Chubb's Cisticola (*Cisticola chubbi*), the year-round monitoring revealed that the birds emitted duets and choruses throughout the year, and they were close to one another when displaying. Thus, it was suggested that the main function of collective displays in this species is joint territory defense (Budka *et al*., 2023). It was also pointed out that the number of solo songs recorded was relatively low and that the species vocalized mainly in duet. The rarity of solo songs was also observed in duetting and chorusing barbet species (Short and Horne, 1983), probably restricted to the courtship display in the beginning of the breeding season. It would be interesting to investigate the occurrence and function of solo songs in the Yellow-breasted barbet as well. We suggest that solo songs might occur at the early stage of a pair formation. Once the pair is established in a territory, they sing in duet only. Later one, delayed offspring and other group members might join the breeding pair to sing in choruses.

The duration of duet and chorus songs according to the context

In a group of Yellow-breasted barbet, the birds sing either in duet or chorus. We found that chorus songs tend to be longer in duration than duets without significant difference between contexts. The reason was that in duet, a bird did not continue singing solo if its partner did not join or stopped singing. In the chorus on the other hand, there were many participants, which means that the collective vocal displays could continue even if one bird stopped singing. Since all the duet and chorus displays analyzed were those emitted close to the nesting cavities, it would be interesting to measure the duration of the collective vocal displays emitted at the edge of a territory where the competition with other groups and the risk of physical aggression might be higher. Especially, conduct a comparison of the group displays duration between the defenders and the invaders. We could expect that the defending group put a higher value in its territory (suitable nesting and roosting site, familiarity with the resources and established relationship with neighbours) and thus, will dedicate more effort in displaying, matching the duration of the competitors vocal displays or even sing longer to discourage the potential invaders (Radford and du Plessis, 2004). The duration of such collective displays might be variable according to the time of the year as well. The number and duration of group vocal displays might increase when a new pair or group is formed, during the breeding season to secure a nesting site and compete for

resources with other groups in the vicinity, and when a change within the group occurs (ex: death of one breeding individual).

We did not find a significant difference in the way the different groups responded to the two playback treatments. One reason might be that it was that they perceived the two playbacks with a similar level of threat (a single pair). It would be necessary to test the birds with chorus songs as well. But such playback experiments will be more complex to conduct. The number of individuals, the sex ratio, the rhythm of singing, and the duration should be considered to prepare different playback stimulations. During our playback experiments in this study as well as in the study of Chapter 2, we realized that all group members did not sing in every chorus display. It is thus more challenging to compare the strength of the reaction of a group against different playback treatments when not all the members systematically participate.

Song coordination between duetters

The analysis of temporal features of the duet songs revealed that in both sexes, there was a progressive change in the number of notes within the *choo-to* part during the song sequence. Several *to* notes were progressively added and it seems to be a fixed pattern of song generation in this species. We also found that males tend to sing faster than the females. However, this difference is within the range of milliseconds, and in some duets, there was no significant difference in the *choo-to* intervals duration between partners. As it was observed in several collective signalling barbet species, the mechanisms of song coordination in the Yellow-breasted barbet seem to involve individual rhythm of singing that might differ between partners (Payne, 1971; Payne and Skinner, 1970). We did not detect any pattern of interactive timing adjustments in the *choo-to* intervals duration of one bird according to the changes made by its partner.

It will be interesting to record the song performance of several individuals simultaneously in different contexts: when duetting and when chorusing to investigate whether the number of participants influences the song's rhythmicity. By combining individual vocal transmitter and neural transmitter (Hoffmann *et al.*, 2019), it would allow to determine to which degree a bird is sensitive to heterogeneous feedbacks from its singing partner. During chorus, such experimental setup might help to determine whether the participants focus their attention toward a specific (leading) individual or not. Indeed, we did try in 2022 to put the vocal transmitters on a few barbets individuals (**Supporting materials 8**). However, we failed to gather data. The main issues were

the limited range of signal detection by the antenna. To get a good quality signal, we had to be in a range not far from 20 meters from the vocalizing birds. This was challenging because we did not know where and when the birds might start singing. Moreover, we used vocal transmitters made for zebra finches. These were not suitable for bigger birds like barbets. We still believe that this technology will work on barbets as well but with a vocal transmitter prototype adapted to the species. Regarding the limitation of signal detection, increasing the distance of detection will certainly help. The passive acoustic monitoring conducted during the nesting period in 2023 revealed that it was possible to record many collective vocal displays near the cavities. One solution could be to install the receptor close to the cavities and record continuously during the morning to eventually get a few spontaneous duet and chorus songs.

Conclusion

The duet and chorus displays in the Yellow-breasted barbet seem to be multifunctional and serve both in territorial defense against intruders, mediate between-group interactions with neighbours and might play a role in maintaining intra-group bonds and cohesiveness. In the context of the between-group interactions, more data need to be collected to understand what information are transmitted through such collective vocal signals (ex: number of individuals, sex ratio, breeding activity, group identity) and which of these information are assessed by the neighbours (Baker, 2004; Hale, 2006; Radford, 2005).

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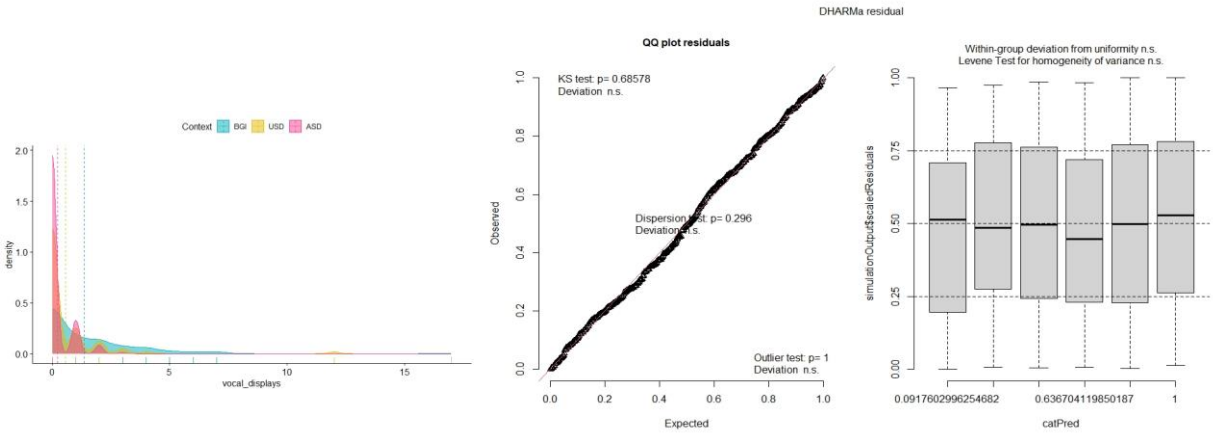
Supporting materials

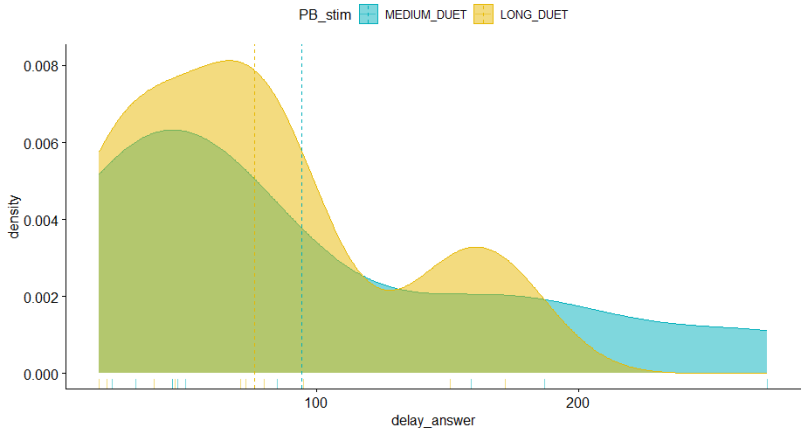
Model_context <- glmmTMB(vocal_displays ~ Context + Day_period + Context*Day_period + (1 | Site) + (1 | Day), family=nbinom1(link = "log"), data=vocal_activity, na.action = "na.fail")



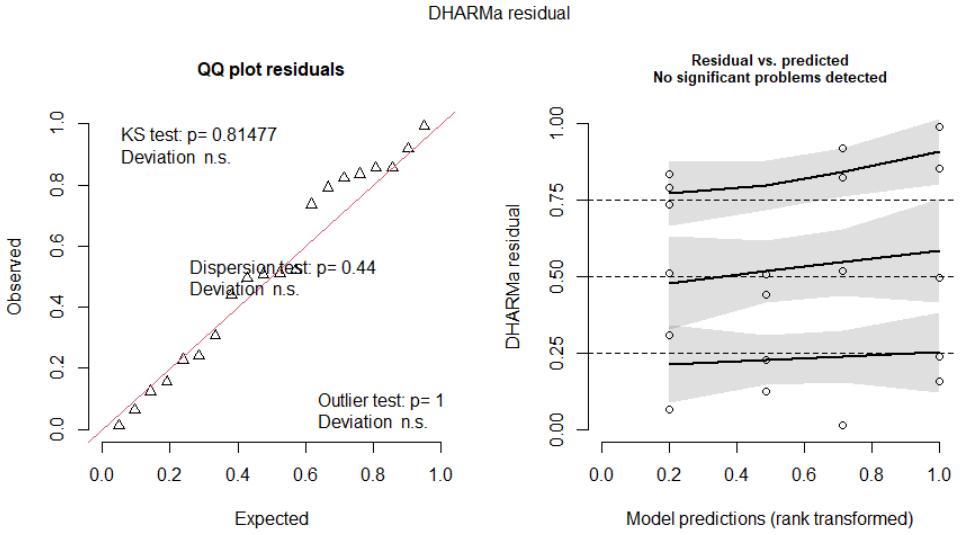

```
> #'Best' model
> summary(get.models(res_models, 1)[[1]])
 Family: nbinom1  ( log )
Formula:          vocal_displays ~ Context + Day_period + (1 | Site) + (1 | Day) +      Context:Day_period
Data: vocal_activity

     AIC      BIC   logLik deviance df.resid
  1172.4   1211.7   -577.2   1154.4      573

Random effects:

Conditional model:
 Groups Name        Variance Std.Dev.
 Site   (Intercept) 0.12608  0.3551
 Day    (Intercept) 0.05623  0.2371
Number of obs: 582, groups:  Site, 11; Day, 13

Dispersion parameter for nbinom1 family (): 1.04

Conditional model:
                          Estimate Std. Error z value Pr(>|z|)
(Intercept)                 0.6730     0.1677   4.013 6.00e-05 ***
ContextUSD                 -1.3001     0.1979  -6.568 5.10e-11 ***
ContextASD                 -1.7849     0.2290  -7.794 6.49e-15 ***
Day_periodAfternoon        -1.5075     0.2098  -7.187 6.64e-13 ***
ContextUSD:Day_periodAfternoon   1.0677     0.3402   3.139   0.0017 **
ContextASD:Day_periodAfternoon   0.7911     0.4118   1.921   0.0547 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Supplementary materials 12: Results of the best generalized mixed model with negative binomial to explore the context of emission of duets and choruses in the morning and in the afternoon during the nesting period.

Model_delay <- glmmTMB(delay_answer ~ PB_stim + order + (1|Type_PB) + (1|Site) + (1|Date)
, family=Gamma(link = "log"), data=PB_EXP, na.action = "na.fail")

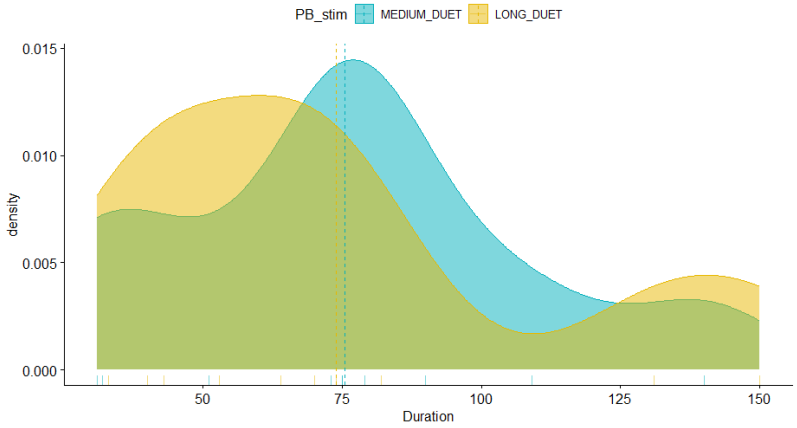



```
> summary(get.models(res_models_pb, 1)[[1]])
 Family: Gamma  ( log )
Formula:          delay_answer ~ (1 | Site) + (1 | Date)
Data: PB_EXP

     AIC      BIC   logLik deviance df.resid
   212.3    216.3   -102.1    204.3       16

Random effects:

Conditional model:
 Groups Name        Variance  Std.Dev.
 Site   (Intercept) 1.358e-09 3.685e-05
 Date   (Intercept) 2.671e-01 5.168e-01
Number of obs: 20, groups:  Site, 10; Date, 9

Dispersion estimate for Gamma family (sigma^2): 0.205

Conditional model:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)    4.251      0.207   20.53   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

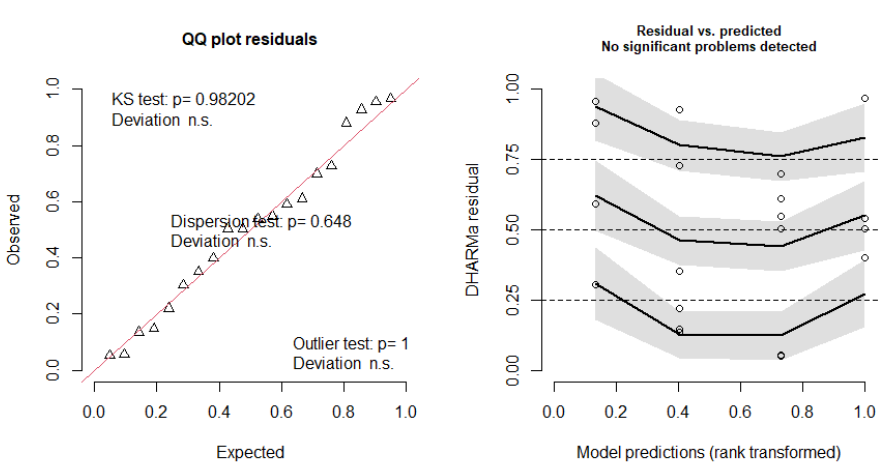


Supplementary Materials 13: Generalized mixed model with gamma distribution to investigate whether the delay of reaction of the tested group was different according to the type of playback (PMD, PLD). No significant difference was found.

Model_duration <- glmmTMB(Duration ~ PB_stim + order + (1|Type_PB) + (1|Site) + (1|Date)
, family=Gamma(link = "log"), data=PB_EXP, na.action = "na.fail")

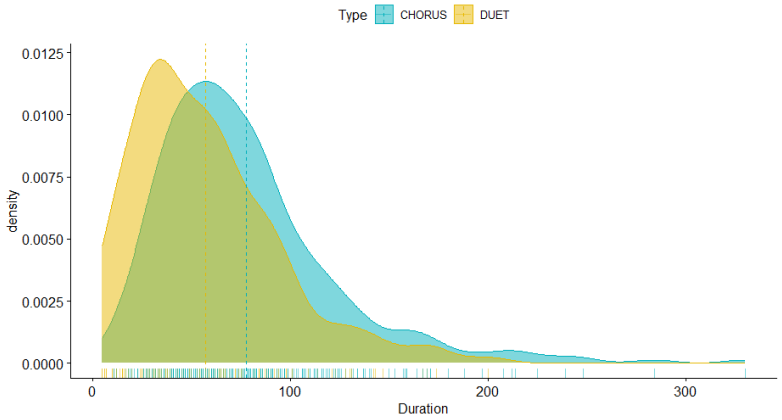



```
> summary(get.models(dd, 1)[[1]])
 Family: Gamma  ( log )
Formula:          Duration ~ (1 | Type_PB) + (1 | Site) + (1 | Date)
Data: PB_EXP

     AIC      BIC   logLik deviance df.resid
   204.3    209.3    -97.2    194.3       15

Random effects:

Conditional model:
 Groups  Name        Variance  Std.Dev.
 Type_PB (Intercept) 2.258e-10 1.503e-05
 Site    (Intercept) 1.467e-02 1.211e-01
 Date    (Intercept) 2.236e-02 1.495e-01
Number of obs: 20, groups:  Type_PB, 4; Site, 10; Date, 9

Dispersion estimate for Gamma family (sigma^2): 0.169

Conditional model:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)    4.298      0.117   36.72   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

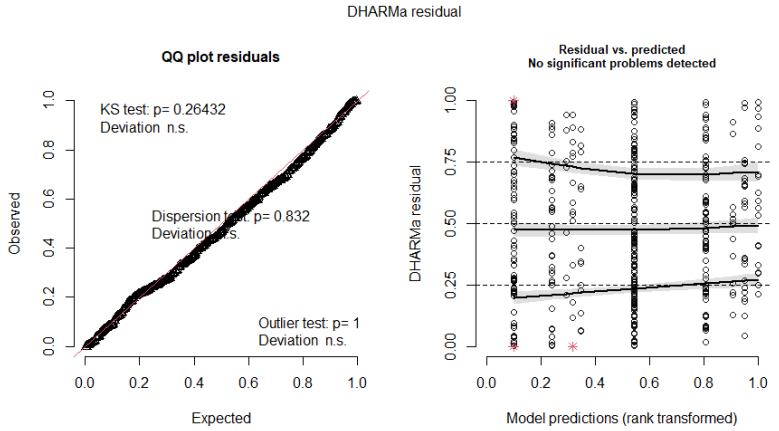


Supplementary Materials 14: Generalized mixed model with gamma distribution to investigate whether the duration of the vocal answer of the tested group was different according to the type of playback (PMD, PLD). No significant difference was found.

Model_duration_context <- glmmTMB(Duration ~ Context_specific + Type + (1 | Site), family=Gamma(link = "identity"), data=List_displays_duration, na.action = "na.fail")

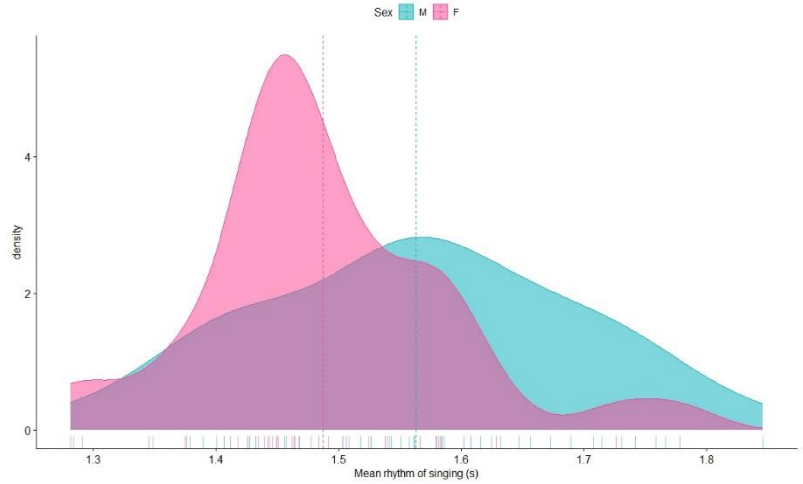



```
> summary(get.models(model_results_duration_context, 1)[[1]])
 Family: Gamma  ( identity )
Formula:          Duration ~ Type + (1 | Site)
Data: List_displays_duration

     AIC      BIC   logLik deviance df.resid
  4432.2   4448.6  -2212.1   4424.2      438

Random effects:

Conditional model:
 Groups Name        Variance Std.Dev.
 Site   (Intercept) 68.89    8.3
Number of obs: 442, groups:  Site, 10

Dispersion estimate for Gamma family (sigma^2): 0.339

Conditional model:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)   81.634      4.251  19.202  < 2e-16 ***
TypeDUET     -24.727      4.426  -5.587 2.31e-08 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

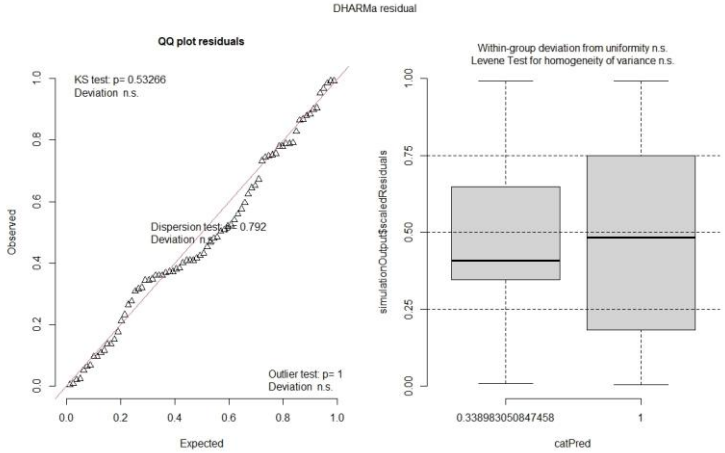


Supplementary Materials 15: Generalized mixed model with gamma distribution to investigate whether the duration of the group vocal displays was different according to the type (duet or chorus) and the context of emission. We found that duet songs were significantly shorter than chorus songs, and no significant difference across contexts.

model_rhythm<- glmmTMB(Mean_Rhythm_singing ~ Status + Sex + Status * Sex+(1|Duet_ID) + (1|Period) + (1|Site) + (1|Context), family=Gamma(link = "identity"), na.action = "na.fail", data=duet_song_list)



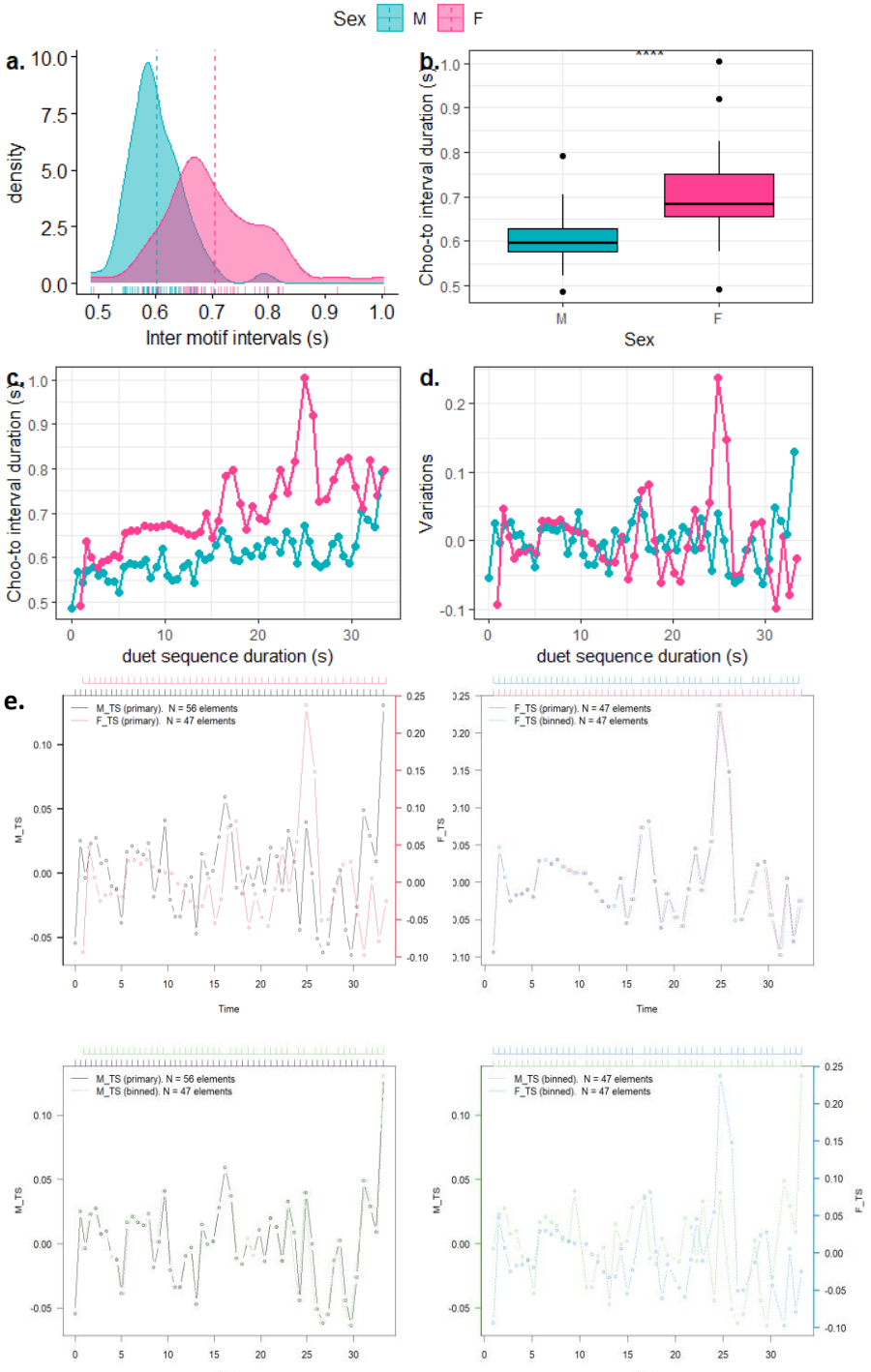

```
> #'Best' model
> summary(get.models(model_results_model_rhythm, 1)[[1]])
 Family: Gamma  ( identity )
Formula:          Mean_Rhythm_singing ~ Sex + (1 | Duet_ID) + (1 | Period) + (1 |      Site) + (1 | Context)
Data: duet_song_list

     AIC      BIC   logLik deviance df.resid
  -106.2    -89.7     60.1   -120.2       71

Random effects:

Conditional model:
 Groups  Name        Variance  Std.Dev.
 Duet_ID (Intercept) 5.770e-04 2.402e-02
 Period  (Intercept) 4.757e-13 6.897e-07
 Site    (Intercept) 1.076e-03 3.280e-02
 Context (Intercept) 1.250e-11 3.535e-06
Number of obs: 78, groups:  Duet_ID, 39; Period, 2; Site, 9; Context, 5

Dispersion estimate for Gamma family (sigma^2): 0.00485

Conditional model:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  1.56802    0.02156   72.73   <2e-16 ***
SexF        -0.07344    0.02409   -3.05   0.0023 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```



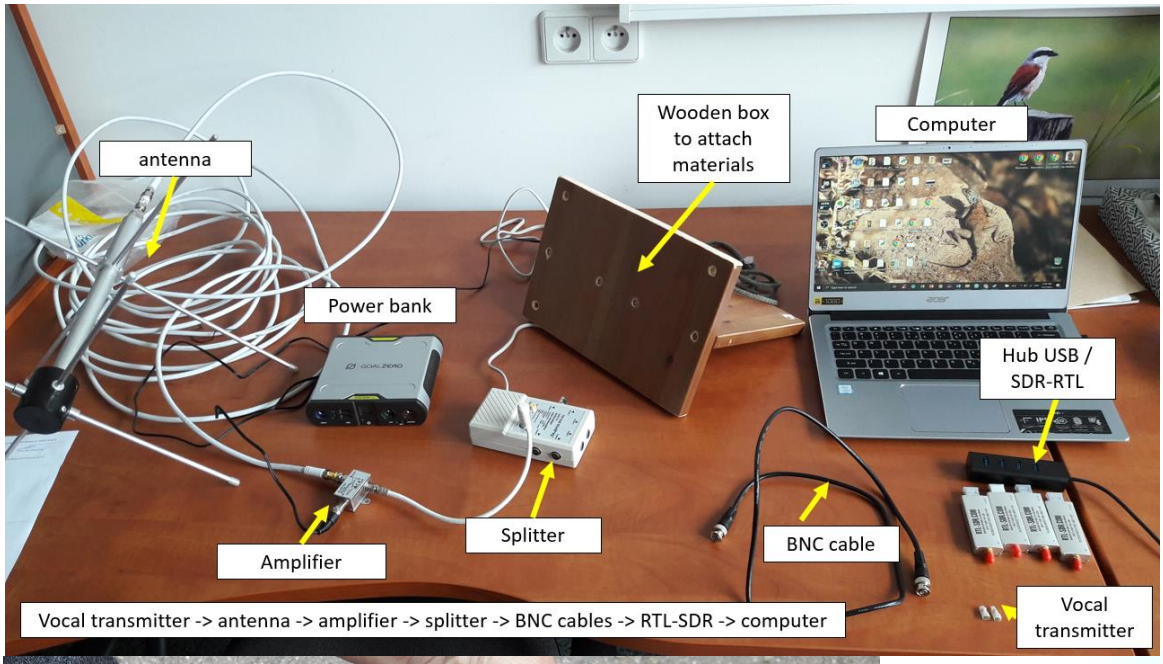
Supplementary Materials 16: Generalized mixed model with gamma distribution to investigate whether the mean rhythm of singing (s) between the male and female was different when duetting. We found that overall, the males tend to sing significantly faster than the females with no influence of the status.

Duet_ID	.y.	group1	group2	n1	n2	statistic	p-value	significant difference
SMMA_20230313_160000	Inter_motif_interval	F	M	32	44	810	0.267	NO
SMMA_20230314_063002	Inter_motif_interval	F	M	162	172	18290	7.78E-07	YES
SMMA_20230318_073002	Inter_motif_interval	F	M	486	518	168902	7.20E-21	YES
SMMA_20230321_053000	Inter_motif_interval	F	M	182	156	15716	0.0898	NO
SMMA_20230321_073002	Inter_motif_interval	F	M	82	74	3680	0.022	YES
SMMA_20230328_160000	Inter_motif_interval	F	M	182	188	21120	9.60E-05	YES
SMMB_20230315_053000	Inter_motif_interval	F	M	82	70	646	2.04E-16	YES
SMMB_20230317_053000	Inter_motif_interval	F	M	136	122	3618	5.42E-15	YES
SMMB_20230318_063002	Inter_motif_interval	F	M	204	222	23662	0.423	NO
SMMB_20230318_073002	Inter_motif_interval	F	M	268	280	39374	0.317	NO
SMMB_20230320_160000	Inter_motif_interval	F	M	220	248	31386	0.00493	YES
SMMC_20230313_063002	Inter_motif_interval	F	M	330	338	60586	0.0535	NO
SMMC_20230313_160000	Inter_motif_interval	F	M	174	162	12344	0.0493	YES
SMMC_20230314_053000	Inter_motif_interval	F	M	192	204	22470	0.0112	YES
SMMC_20230314_073002_A	Inter_motif_interval	F	M	88	94	4198	0.863	NO
SMMC_20230314_083002	Inter_motif_interval	F	M	254	248	26190	0.00109	YES
SMMC_20230315_053000	Inter_motif_interval	F	M	94	102	6094	0.00105	YES
SMMC_20230315_063002_A	Inter_motif_interval	F	M	518	468	79106	4.12E-21	YES
SMMC_20230317_053000	Inter_motif_interval	F	M	218	240	33504	2.09E-07	YES
SMMC_20230317_063002_A	Inter_motif_interval	F	M	318	316	49842	0.862	NO
SMMC_20230319_083002	Inter_motif_interval	F	M	206	248	47150	2.40E-54	YES
SMMC_20230320_063002	Inter_motif_interval	F	M	382	460	150428	6.12E-71	YES
SMMC_20230321_063002	Inter_motif_interval	F	M	212	250	50760	1.49E-64	YES
SMMC_20230322_053000	Inter_motif_interval	F	M	66	92	5864	2.06E-23	YES
SMMC_20230322_063002	Inter_motif_interval	F	M	224	270	54696	4.49E-54	YES
SMMD_20230316_083002	Inter_motif_interval	F	M	84	70	1148	7.98E-11	YES
SMMD_20230321_053000	Inter_motif_interval	F	M	114	128	12200	1.86E-19	YES
SMME_20230314_083002	Inter_motif_interval	F	M	198	224	29620	2.63E-09	YES
SMME_20230315_063002	Inter_motif_interval	F	M	82	92	6230	1.27E-13	YES
SMME_20230317_053000	Inter_motif_interval	F	M	124	138	9272	0.243	NO
SMME_20230317_063002	Inter_motif_interval	F	M	196	202	19630	0.885	NO
SMMF_20230316_083002	Inter_motif_interval	F	M	312	292	31080	1.45E-11	YES
SMMF_20230319_180002	Inter_motif_interval	F	M	142	142	9352	0.292	NO
SMMH_20230315_160000	Inter_motif_interval	F	M	126	146	12970	5.54E-09	YES
SMMH_20230316_170002	Inter_motif_interval	F	M	86	100	6728	3.32E-11	YES
SMMH_20230318_16000	Inter_motif_interval	F	M	140	144	10276	0.778	NO
SMMH_20230321_160000	Inter_motif_interval	F	M	152	182	18854	1.10E-08	YES
SMMJ_20230318_053000	Inter_motif_interval	F	M	94	112	9196	2.80E-20	YES
SMMJ_20230321_063002	Inter_motif_interval	F	M	144	162	17562	2.27E-14	YES

Supplementary Materials 6: Results of the Wilcoxon tests performed the 39 duet songs to compare the mean *choo-to* intervals between the males and the females. We highlighted in red when no significant difference was found, meaning that the birds sang with comparable the choo-to intervals duration.



Supplementary Materials 7: Summary of the method used to analyze the mechanisms of song coordination in the duet songs of the Yellow-breasted barbet. **a-b:** We tested for the mean different in the *choo-to* intervals duration between the male and female. **c**: We then plotted the evolution of the duration of the choo-to intervals during the duet song. To investigate whether the birds interactively adjusted their *choo-to* intervals according to the change in the interval duration of their partner, we removed the trend (general slowdown) on both vocal sequences to focus only on the rapid changes (**d**) and used conducted the correlation and cross-correlation on the binned time series (**e**).



Supplementary Materials 17: The materials used to individually record the birds. The Vocal transmitters were developed by the Max Planck Institute of Ornithology in which Mathieu Mahamoud-Issa received a specific training on zebra finches to learn how to use such technology. We created a portable version of the setup to be able to walk with it in the field. We tested the materials in the field in 2022.

Conclusions and Perspectives

1. The role of the intra-group communication to generate a collective and coordinated vocal display

Social factors are predominant over environmental factors in driving communal signal evolution in birds. More specifically, year-round territory defense and long-term social bonds are common traits shared by most of the duetting and chorusing bird species (Tobias et al., 2016). Despite decades of studies on the forms and functions of duet and chorus songs, there was still little information available regarding the mechanisms of social mediation and agreement between individuals who collaborate to produce such collective signals. In my PhD work, I decided to investigate the role of intra-group communication in a group living bird species in which group members sing in duet and chorus in the context of territorial defense. I selected the Yellow-breasted barbet as a model species for three main reasons: Phylogenetic comparative analysis revealed the link between sociality and the evolution of collective signalling in the barbets species (Soma and Brumm, 2020); The duetting and chorusing African barbets are known to introduce their duet and chorus displays with pre-duet notes during a greeting ceremony (Short and Horne, 1983). Such pre-duet notes could constitute a specific intra-group signal to initiate a collective display; Finally, no behavioural study was dedicated to the Yellow-breasted barbet, and many aspects of its sociality and vocal behaviour were unknown.

The combination of field observations and passive acoustic monitoring allowed us to identify several vocalisations emitted by the barbets as well as the daily calling activity of the species (Chapter 1). Combined with playback experiments in which we recorded the behaviour of the birds with video camera (Chapter 2), we described the way they initiated a group vocal display. Group members first needed to localize each other and reunite to perform a collective action. The use of cohesion calls seemed to serve this function. Then, we showed that the *chewp* notes were emitted specifically to initiate the collective songs. We found that the group members did not introduce their song the same way and that a leading individual gave most of the *chewp* notes, sometimes combined with a visual display, which constitute multimodal signal. Finally, other calls could be used after the end of a collective display which might serve in mediating and reinforcing social bonds within the group (post-conflict affiliative behaviour). To summarize, the intra-group

communication occurs before and after the emission of collective vocal displays in the Yellow-breasted barbet (**Figure 1**).

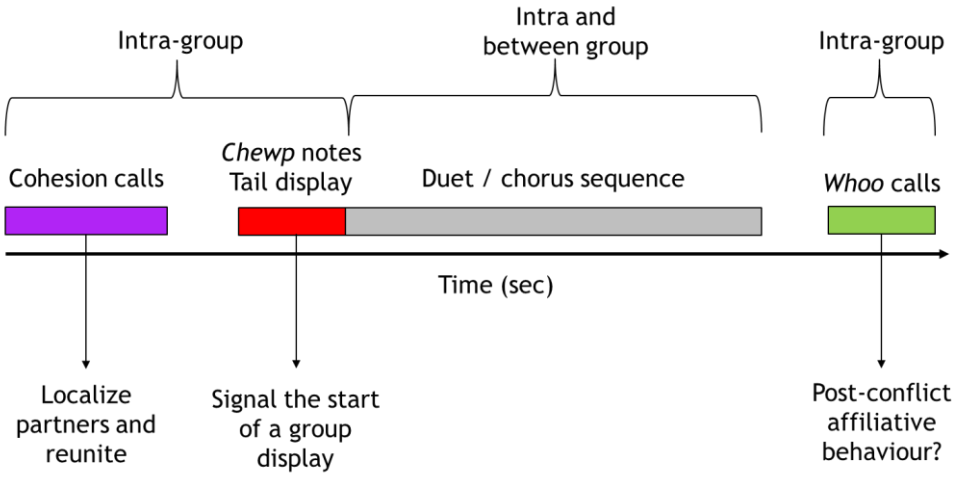


Figure 17: Schematic timeline of the different vocalisations emitted by a group of birds in the context of the emission of a duet or chorus display. Cohesion calls were emitted by group members to localize each other and facilitate the reunion. Once reunited, a greeting ceremony led by one individual initiated the start of a duet or a chorus display, which might serve both as joint territorial defense display and reinforce within group bonds and cohesiveness. *Whoo* calls were sometimes emitted afterward which might be used for affiliative behaviour within the group.

We found that duet and chorus songs were mostly emitted during between-group interactions but also spontaneously without triggering any vocal reactions from neigbhours (Chapter 3). We suggested that collective songs in the Yellow-breasted barbets serve multiple functions such as joint territorial defense, maintain group cohesiveness and reinforce intra-group social bonds. The possible intra-group functions of duet and chorus songs still need more investigation. The use of *whoo* calls (usually emitted during nest reliefs and when feeding young, Chapter 1) after the end of a group vocal displays raises the question about the existence of post-conflict affiliative behaviour in the group living barbets. Post-conflict affiliative behaviour might help to reduce the stress of individuals, reinforce bonds and cohesiveness within the group, enhance the motivation of the group members to participate into future collective displays, especially in the context of joint territorial defense against other groups (Radford, 2008a, 2010). As Andrew Radford elegantly formulated "*the ways in which interactions between groups affect within-group processes is of great importance for our understanding of cooperation and group dynamics*" (Radford, 2008b). Studying the role of intra-group affiliative behaviour in the context

of collective signalling in the Yellow-breasted barbet will certainly leads to new discoveries on how animals mediate their relationships and agree to cooperate in collective actions.

2. The mechanisms of song coordination

The mechanisms of song coordination in several duetting and chorusing barbet species involve individual rhythms of calling which are in large degree independent of the timing of the call of the partner. In the Yellow-breasted barbet, we did not find any interactive temporal adjustments between partners, but the birds are attentive to each other as they start and stop singing at the same time. The few studies that investigated in detail the neural basis of song coordination in duetting birds used songbirds as a model. There is an urgent need of knowledge regarding the neural activity linked with the song production and coordination between duetter in non-oscine birds. We also encourage conducting such research on chorusing species. The syllable-by-syllable adjustments mechanism based on both autogenous and heterogeneous feedback in songbirds was studied in a dyadic system with two individuals duetting. It would be interesting to investigate what happens when multiple individuals are chorusing with good temporal coordination. In such a complex system, individuals could focus their attention toward one specific individual to be coordinated with (the leading individual). Thus, the birds could be selective in which heterogeneous feedback they will be sensitive. Finally, many duetting and chorusing bird species use visual displays to initiate or even during the collective vocal displays. It is thus important to understand how the integration of visual stimuli modulates vocal production.

3. Other future directions

3.1 Intra-group communication and collective movements

Passive acoustic monitoring was efficient to monitor the calling activity of several groups near their roosting site, but we still know little about the close-range interactions between neighbouring groups at the edge of their territories. To better understand how a group of barbets defend its territory, forage, and interact with other groups, it would be interesting to combine passive acoustic monitoring with the use of high-resolution tracking tools to be able to investigate spatial movements and the role of acoustic communication to maintain group cohesiveness. Ideally, combining one gps tracker (Demartsev *et al.*, 2023) with a vocal transmitter (Hoffmann *et al*., 2019) on each bird would allow recording both the movements and the vocalisations for each

individual of a group. Therefore, we could determine whether the leading individual during a group vocal display is also the leader during other collective actions such as troop movements and foraging.

3.2 The cooperative-breeding behaviour

Our work provided new data about the nesting activity of the Yellow-breasted barbet. Unfortunately, our data and knowledge are still limited. It would be interesting to dedicate a research project to investigate the breeding ecology of the species. By combining ring deployment and DNA analysis of birds, we could determine the social structure of the groups: who is the breeding pair? Are the subordinate individuals always offsprings of the dominant pair or non-related adult birds might join the group as well? It would be interesting to investigate when offsprings leave their natal group and how far they disperse. A year-round monitoring is necessary to assess the number of broods and the possible relationship between the breeding decision and some environmental factors such as rain. The lybiidae family might be a good model to investigate the evolution of cooperative-breeding behaviour in birds. Understanding the life history of African barbets, why some species became cooperative breeders while other not, compare their mating behaviour and whether they form family group or non-family group will certainly provide new insights on the evolution of such breeding strategy in vertebrates (Downing *et al.*, 2020; García-Ruiz e*t al.*, 2022).

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Authorship statement

Declaration of authorship statements of the PhD candidate: I hereby confirm that I am first author of the following published articles:

- Mathieu Mahamoud-Issa, Bożena Sikora, Stanisław Rusiecki, Tomasz S. Osiejuk (2023) The Yellow-breasted Barbet (*Trachyphonus margaritatus*) introduces vocal duets and choruses with a specific multimodal signal, during territorial advertisement. *Journal of Ornithology* 164, 183-192. https://link.springer.com/article/10.1007/s10336-022-02016-w

- Mathieu Mahamoud-Issa, Bożena Sikora, Katarzyna Łosak, Tomasz S. Osiejuk (2023) The vocal repertoire and the daily vocal activity of the Yellow-breasted Barbet (*Trachyphonus margaritatus*). *Journal of Ornithology*. https://doi.org/10.1007/s10336-023-02112-5

My role as first author consisted of conceptualization, collection of field data, data preparation and formal analysis, interpretation of the results, manuscript writing and manuscript revision. I confirm I will be the first author of the manuscripts gathered in Chapters 1 and 3 upon publication, having led the conceptualization, collection of field data, data preparation and formal analysis, interpretation of the results, manuscript writing and manuscript revision.

- Mathieu Mahamoud-Issa, Bożena Sikora, Katarzyna Łosak, Stanisław Rusiecki, Tomasz S. Osiejuk (*in prep*) The communal roosting behaviour and nesting of a cooperative breeding species, the Yellow-breasted barbet (*Trachyphonus margaritatus somalicus*) in Djibouti. *Scopus: Journal of East African Ornithology*.

- Mathieu Mahamoud-Issa, Tomasz S. Osiejuk: Chapter 3 - Contexts of singing and the mechanisms of song coordination in the Yellow-breasted barbet (*Trachyphonus margaritatus*), a group-breeding bird species that performs collective vocal displays.

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