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Hey mister Tambourine Dove, sing a song for me: simple but individually specific songs of *Turtur tympanistria* from Cameroon

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Abstract

Background: The broadcast song of the Tambourine Dove (*Turtur tympanistria*) is a repetitive coo series produced in a very stereotyped way. The song is similar to those of the other species within the *Turtur* genus and likely reflects the adaptation to long distance signalling in tropical habitats. There is no study assessing individual variation of the Tambourine Dove song or for the possibility of identity coding through song features.

Methods: We obtained recordings of 578 songs from 41 males within a population inhabiting montane forest in Cameroon between 2008 and 2018. Additionally, we analysed also recordings from automatic recorders working for a longer time during the year. Songs were analysed to get basic information about within- and between-individual spectro-temporal variation. Potential of identity coding and discriminant analyses were used to investigate if and how these songs may convey information about male identity.

Results: The song of the Tambourine Dove is a very simple series of short, unmodulated whistles with low frequency and a narrow bandwidth. Measurements of single song features indicated either none or a weak potential for identity coding. The overall variation in song frequency characteristics was very low. However, the number of notes forming a song (and consequently the duration) had a similar variability both within- and between individuals. When using multiple song measurements discrimination analysis revealed a high potential for identity coding although it seems that the temporal pattern of the beginning of a song carries the most information about sender identity. The production of initial notes within a song has very precise, individually specific timing allowing for up to 96.7% correct recognitions of songs. Comparison of recordings from the same points but separated in time by over a month indicates that song parameters are individually stable over longer period.

Conclusions: Despite having highly stereotyped and simple songs, Tambourine Dove males produce individually specific signals which have a great potential for recognition by rivals or mates. All *Turtur* doves have similar yet unique songs that are different to the songs of other pigeon species. This genus seems to be a perfect model for studying the trade-off between coding for species identity and individual identity in a non-learning bird species. The described method of individual recognition allows for nonintrusive population monitoring.

Keywords: Cameroon, Identity coding, Song, Tambourine Dove, *Turtur tympanistria*

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Background

Sexually selected signals usually convey information about the quality, motivation or other aspects of an individual's features that are beneficial in mate choice or resource defence against rivals (Gil and Gahr 2002). Such information is only useful if the signal is efficiently recognized, by the receiver, as being produced by an individual of the same species (Bradbury and Vehrencamp 2011). Moreover, in virtually all social species studied so far, it has been demonstrated that signals contain information enabling individual recognition or at least some kind of discrimination between classes of individuals, e.g. neighbours and strangers (Sherman et al. 1997; Tibbetts and Dale 2007). The functions mentioned above are well documented for bird song, a widespread and fundamental signal for this taxon. Most of the cases showing individual recognition in birds concern the context of territoriality, where differentiating the strength of response to neighbours and strangers is crucial to reduce costs of resource defence (Trivers 1971). Such behaviour was documented both in songbirds (e.g. Skierczyński et al. 2007; Draganoiu et al. 2014), suboscines (e.g. Lovell and Lein 2004; Fitzsimmons et al. 2008) and non-passerines (e.g. Hardouin et al. 2006; Budka and Osiejuk 2013). Surprisingly, such functions are widely used amongst birds, regardless of whether they produce simple or very complicated vocal signals (review in Stoddard 1996 and Catchpole and Slater 2008), but some exceptions were also found (Wiley 2005). Songbirds have an intricate musculature of syrinx structure, and this anatomical difference seemed to be a logical explanation for their ability to produce more complex sounds in comparison to birds of other taxa (Warner 1972a). However, it is not as simple, as some non-passerines (e.g. parrots [Psittaciformes] or hummingbirds [Trochilidae]) also produce highly complex sound signals. Therefore, many more factors other than the syrinx structure (e.g. learning, use of tongue or beak shape) are likely to affect the evolution of song complexity in birds (Warner 1972a; Suthers 2004; Mindlin and Laje 2005). Nonetheless, most non-passerines do produce relatively simple songs that are developed during ontogenesis without any social learning (Catchpole and Slater 2008). Non-passerine bird species make up more than a third of all living species, however, their simple song and the lack of social learning may be the reasons as to why they were disproportionately less frequently subjected to bioacoustics research (based on Web of Science survey, using 'non-passerine*' OR 'nonpasserine*' versus 'passerine*' AND (song* OR call*)).

Among non-passerines, pigeons and doves (family Columbidae) are a relatively well studied model system for vocal communication, exhibiting limited

vocal versatility, likely resulting from a simple anatomical structure of syrinx (Warner 1972b). Our survey of research on acoustic communication in this group reveals that there is a bias towards certain topics and species. Several papers addressed the topic of the mechanism of sound production (ten Cate and Ballintijn 1996; Ballintijn and ten Cate 1997a, 1998; Beckers et al. 2003a, b), neurobiology of vocalization (Terpstra et al. 2005; Elemans et al. 2008), and species identity coding, including studies on hybrid vocalization and the role of song divergence in speciation processes (Lade and Thorpe 1964; Tubaro and Mahler 1998; Beckers and ten Cate 2001; de Kort and ten Cate 2001; de Kort et al. 2002a, b; den Hartog et al. 2008). In addition, the relationship between song structure and its functions in territorial defence or mate attraction was studied in detail for certain model species (e.g. Slabbekoorn and ten Cate 1996, 1997). These studies give an excellent background for further research on dove and pigeon vocalisations as they have revealed some fundamental information about the trade-offs between signal characteristics, anatomical limitations and signal functions (Tubaro and Mahler 1998; Slabbekoorn et al. 1999). A limitation of previous research is that it is strongly biased toward doves from the *Streptopelia* genus, and the majority of published work—particularly experimental research—concerns only a few species. The vocal aspect of individual recognition in doves and pigeons is poorly understood. Morris and Erickson (1971), and Mairy (1977; after Hutchison et al. 1997) provided observations supporting the hypothesis that the Barbary Dove, i.e. domesticated African Collared-dove (*Streptopelia roseogrisea*), is capable of recognizing other individuals by their call. Hutchison et al. (1997) presented a more quantitative support for individual differences in bow-calls of the Barbary Doves, both in the temporal and frequency domain of their song. Hitchcock et al. (1989) experimentally revealed that fledglings of the Mourning Dove (*Zenaidura macroura*) responded stronger to the perch coos of their fathers (with food-soliciting behaviour) than to the same calls of their neighbours. Thus, our knowledge of acoustic recognition processes in doves seems to be very limited in comparison to dozens of papers quantitatively describing the individually specific song structures and experimentally testing individual recognition or neighbour-stranger discrimination in songbirds (e.g. Stoddard 1996; Skierczyński et al. 2007; Briefer et al. 2008). Identity coding and actual recognition has also been found in several other non-passerines, for example in woodhoopoes (Phoeniculidae) (Radford 2005), owls (Strigiformes) (Hardouin et al. 2006), or rails (Rallidae) (Budka and Osiejuk 2013). In this study we would like to fill the gap in knowledge and test if the simple,

stereotypical song of a dove species may convey information about identity.

Our chosen model species is the Tambourine Dove (*Turtur Tympanistra*), a relatively small wood dove species with a large distribution across sub-Saharan Africa. Individuals can be found in numerous forest types, woodlands and plantations spanning various elevations, from lowlands to montane areas (Baptista et al. 2018a). Their typical long-distance vocal signal is a relatively elongated song consisting of low frequency, unmodulated and short whistles (Fig. 1). Due to the species' inhabitancy of forested areas with very limited visibility, it is likely important for individuals to have distinctive acoustic characteristics so as not to rely on visual communication (Ay and Fischer 2009). To the best of our knowledge, there are no published papers addressing any aspect of vocalization of this species.

The aim of this study was to describe for the first time the basic acoustic parameters of the Tambourine Dove long-distance vocalisation (further called song), on the background of their close relatives, and to test whether these songs are specific to each individual, allowing for individual recognition. We hypothesised that low

frequency and long-distance song should have some characteristics to allow for individual recognition, and hence, would be substantially more variable between- than within-individuals.

Methods

Study area and recording procedures

The field study was conducted at the beginning of the dry season, in November and December of 2008–2017, approximately 6 km northeast of Big Babanki village in the Bamenda Highlands, Northwest Region, Cameroon. The study area was spread between 6°5′–6°8′N and 10°17′–10°20′E (altitude range 1900–2400 m a.s.l., area surveyed ca. 12 km²). The Bamenda Highlands are one of the most important hotspots of bird diversity and endemism in Africa (Orme et al. 2005). However, intensive logging has reduced formerly continuous forests to isolated patches in recent decades (Reif et al. 2006). At present, the vegetation covering the study area consists of mosaics of montane forest remnants, shrubby corridors, grasslands and vegetable plantations below 1800 m a.s.l. The study species is common in this area and is found both in forests and smaller remnants along streams. It

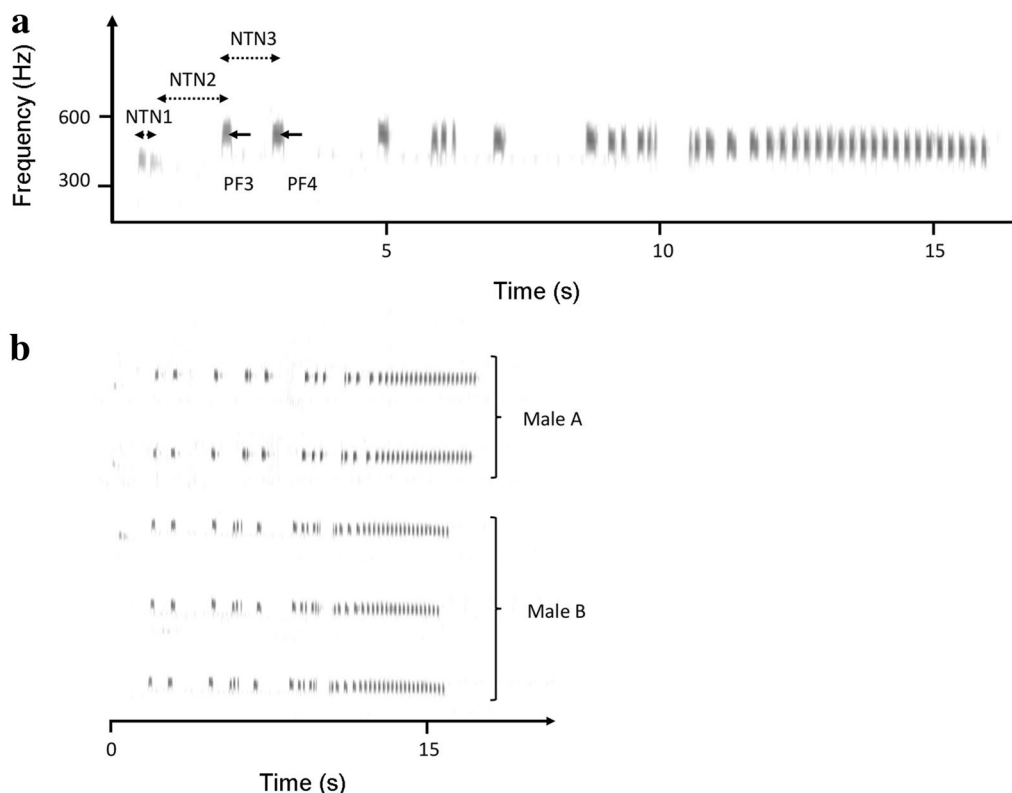


Fig. 1 **a** A sonogram of the Tambourine Dove (*Turtur tympanistris*) song with illustrative indications of measurements taken. Please notice that the real measurements were not taken in the sonogram window (see “Methods” section). **b** Sonograms of song examples of two different individuals, to illustrate potential within- and between-individual differences

avoids open areas but occurs in ecotone areas of habitat transition.

Spontaneously singing birds were recorded opportunistically in the morning (06:00–12:00) and evening (16:00–18:00) hours. Birds were recorded using different digital recorders (Marantz PMD660, PMD661 and PMD662, and Olympus LS10 and LS11) coupled with Sennheiser ME 67 shotgun microphones (K6 powering unit and MZW67PRO windscreen). All recordings were mono-linear PCM WAV of 48-kHz sampling frequency and 16-bit resolution. Geographic coordinates of all recorded males were measured using Garmin GPS receivers (GPSMap 76 CSx and 60 CSx). For the analysis we only selected good quality recordings of males that were well separated spatially to ensure that subsequent analyses were done on different males. Basically, we included into the analysis males recorded in different forest patches or along single morning transects where consecutive calling males could be heard simultaneously or were separated by ≥ 200 m. When we had recordings from the same place and different years, we analysed only one recording from such location.

In order to check whether birds singing from the same places do not change song parameters over a longer period, we used recordings from six automatic recorders SM3 (Wildlife Acoustics) which were placed within the study area between November 2015 and December 2016 and recorded with 48 kHz/16 bit sampling for a whole day once per week. Recorders were placed more than 500 m from each other, and thus recorded different individuals. We selected from each unit two recordings separated by over a month during the peak of the breeding season and with a clear and loud sequence of Tamburine Dove songs to check if their parameters are stable over time.

Sound analysis

Based on Catchpole and Slater (2008), we defined notes (or elements) as the smallest blocks used for building songs which are possible to separate because of the time intervals between them ranging from around 0.1 to 1–2 s (in few extreme cases up to 8 s), and songs as stereotyped set of notes ordered in time and separated by intervals substantially longer than intervals between notes (usually > 10 s, Fig. 1). Sound analyses were done in two steps. Firstly, Raven Pro 1.5 (Bioacoustics Research Program 2013) was used for visual inspection of all songs. The aim was to look precisely at the variation in notes that make up the song whilst investigating the parameters which are likely to be individually specific. At this step each note within each song was selected and the following parameters of Raven Pro were used: Window type: Hann, 1024 samples; 3 dB Filter Bandwidth: 67.4 Hz; Time grid:

overlap 50% giving Hop Size: 512 samples; Frequency Grid: DFT Size: 1024 samples giving $46.9 \text{ Hz} \times 10.7 \text{ ms}$ resolution of measurements.

An outcome of this analysis revealed little note variation as all of them were unmodulated short whistles with a narrow frequency bandwidth. The only problem with selecting notes based on visual selection was that some notes were very short and very close to subsequent notes, forming something like double-notes. More complicated notes were found in songs of most individuals but were much rarer (usually 1 or 2 per song) than single-notes (Fig. 1). We realised that classification of notes as single, double or triple may be subjective and depends both on the recording quality and on the experience of the persons conducting signal analysis. Therefore, in the second step we applied automatic measurements allowing for better time–frequency resolution and avoidance of human error that is produced when making on screen selections.

Further analyses were done using Avisoft SASLab Pro software v. 5.2.10 (Avisoft Bioacoustics, Germany). We removed background noise from each recording using a 100–1200 Hz band-pass time domain filter (FIR). FIR values were chosen based on initial inspection measurements. We measured simple variables for the whole songs as duration (s), number of notes, and minimum, maximum and peak frequency (Hz). Then we measured peak frequency (later PF; Hz) of each note, and the time (s) between the following notes (note-to-note duration, later NTN). Later we used the following notation: PF1 refers to the peak frequency of the first note in a song, PF2 to the peak frequency of the second note, and so on; NTN1 refers to time between the beginning of the first note and the beginning of the second note, NTN2 the time between the second and third note, and so on. We applied an automatic method to our measurements using the Pulse Train Analysis function with general settings: Envelope = Rectification + exponential decay and Pulse detection = Peak search with Hysteresis. Detailed settings used were as follows: hysteresis = 20 dB, start/end threshold = -10 dB, time constant = 1 ms and threshold set up manually to include measurements of all notes including separation of any double-note as separate notes (typically around -10 dB relative to highest amplitude). The peak frequency of each note was measured with the following Spectral Analysis Setup: FFT size = 2048, Window = Rectangle; Frame duration = 43.7 ms; Frequency resolution = 23 Hz; Bandwidth settings: -15 dB. The final resolution in this analysis was $23 \text{ Hz} \times 0.02 \text{ ms}$. In a few cases we manipulated the values of hysteresis, start/end threshold, and threshold in order to correctly detect and measure all notes. Such manipulations were necessary because of the variation in recording quality and did

not influence the measured parameter of song. The main reason for this was usually due to a change of position of the bird or microphone in such a way that from a certain moment the notes building songs, which are quite long, abruptly changed in maximal amplitude. This resulted in—for example—one part of the song being louder, however this did not affect the peak frequency detection and timing between peaks. The Pulse Train Analysis measurement window of the Avisoft SASLab Pro is illustrated in Fig. 2.

Statistical analysis

We describe songs, notes and note-to-note durations with descriptive statistics to present the general variation of songs in the studied population. In the next step we analysed within and between individual variations of each parameter in order to find song characteristics potentially important for individual recognition. To determine which song characteristics could be potentially useful for individual identification, we first calculated within-individual (CV_i) and between-individual (CV_b) coefficients of variation for each parameter of the whole song and separately for each note and note-to-note duration shared by all individuals. We used the formula:

$$CV = 100 \times (1 + 1/(4 \times n)) \times SD/\bar{x},$$

where n is sample size (Sokal and Rohlf 1995). Next, we calculated the potential for identity coding (PIC) for each analysed parameter as the ratio of CV_b/CV_i (Charrier et al. 2001). PIC values greater than 1 indicated that the within-individual variation was lower than between-individual variation for a particular song characteristic, and

therefore it could potentially be used for individual identification. For measured songs we found that the lowest number of notes in a song was twelve. The parameters included in our final analyses were therefore those which could be calculated for the whole song and for the first twelve notes or first eleven note-to-note durations.

Finally, we conducted several separate stepwise discriminant function analyses (DFAs). We selected predictors using Wilks' lambda criterion and the probability of F was used as a criterion of variable choice in a model (p to enter variable = 0.05; p to remove variable = 0.10). Prior probabilities were computed from group sizes (individuals in this case). The initial DFA was built with simple variables which could be measured for the whole songs (duration, number of syllables, frequency of song etc.). However, after initial screening of songs it was clear that they differ in number of notes and in order to compare characteristics based on note measurements we had to limit analyses to notes common for all cases (similarly as did Budka et al. 2018 for strokes in study on Great Spotted Woodpecker *Dendrocopos major* drumming). In the studied population we found songs containing between 12 and 59 notes. Thus, to analyse the whole dataset according to the note variation we had to limit analyses to the first 12 PF and first 11 NTN. All averages are presented with \pm SD.

Results

Material and description of song

We analysed 578 songs of 41 males. There was between 4 and 44 songs of the different males, with an average of $\bar{x} \pm SD$: 16.1 ± 10.86 songs per male. Songs of

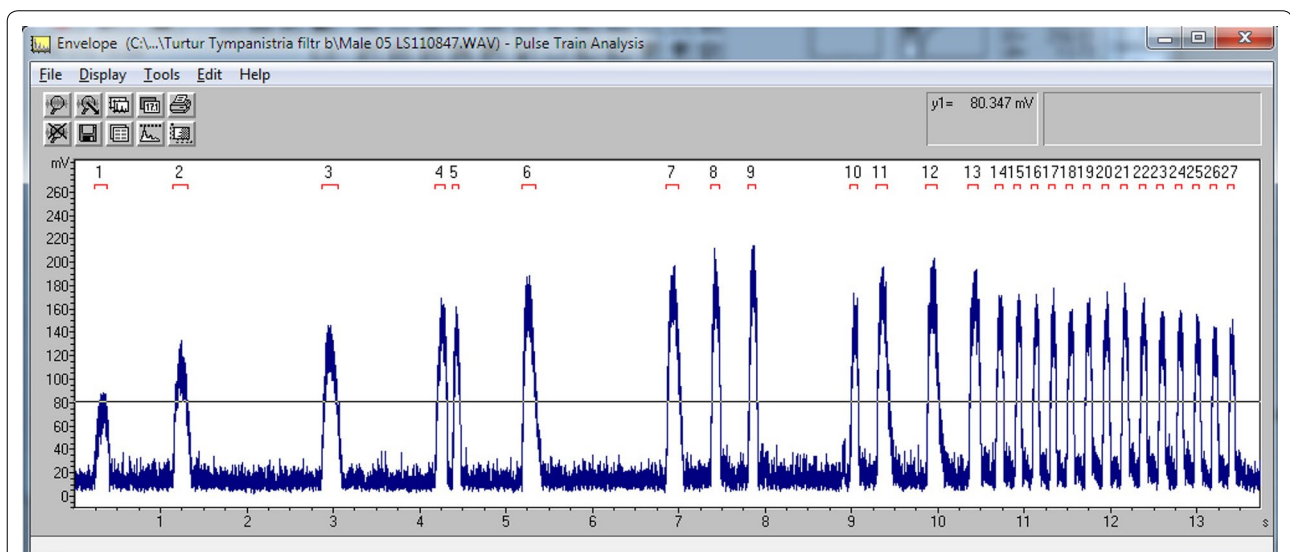


Fig. 2 Avisoft SASLab Pro 5.x pulse-to-pulse duration window in which measurements were taken with an objective set of parameters

the Tambourine Dove in the studied population consisted of a series of very short notes, lasting on average 0.16 ± 0.108 s. Notes were simple, unmodulated whistles except for the initial syllable which was quieter and sometimes sounded more like a gurgle. It was not found in all recorded songs as it was not always sung and it was difficult to detect in the lower amplitude recordings (Fig. 1). Songs consisted of 12–59 notes, 30.4 ± 6.78 on average. Consequently, songs were quite long, lasting from 7.3 to 36.2 s, and on average 13.8 ± 2.33 s. All notes had a very narrow and almost identical bandwidth; thus, their peak frequency seems to be the most important parameter in the frequency domain. On average songs had a peak frequency at 432 ± 25.4 Hz and it varied between 280 and 600 Hz (Fig. 1). The temporal pattern of notes within a song was similar in all songs. The first 10–15 notes had

longer pauses between them (means calculated for pauses between first 15 notes varied between 0.3 and 1.7 s; on average 0.7 ± 0.33 s), followed by a series of notes with very short breaks (means calculated for all pauses after 15 note varied between 0.2 and 0.5 s; on average 0.2 ± 0.09 s) giving the impression of an accelerating rhythm (see Fig. 1).

Individual variation in Tambourine Dove song parameters

The most variable parameters of a song were the number of notes and the duration (Table 1). Both of the mentioned parameters were variable both within as well as between-individuals. Both these parameters were significantly correlated ($r=0.48$, $n=578$, $p<0.001$). Differences in the song duration within

Table 1 Descriptive statistics of analysed characteristics of Tambourine Dove song

Variable	Mean	SD	Min–Max	CV _i	CV _b	PIC
Number of notes	30.4	6.78	12–59	37.0	21.1	0.57
Duration (s)	13.8	2.33	7.3–36.2	27.5	16.0	0.58
Peak frequency (Hz)	432	25.4	280–600	4.0	5.3	1.34
Minimum frequency (Hz)	416	31.5	280–490	11.2	5.7	0.51
Maximum frequency (Hz)	473	48.1	420–980	16.8	5.8	0.35
Peak frequency of notes (Hz)						
Note 1	462	26.6	350–600	15.3	1.6	0.10
Note 2	456	27.8	300–530	12.6	2.0	0.15
Note 3	452	27.6	420–530	9.8	1.1	0.12
Note 4	451	33.9	300–580	14.3	2.7	0.19
Note 5	453	36.5	300–580	14.5	2.5	0.17
Note 6	444	29.9	300–530	11.8	1.9	0.16
Note 7	437	30.2	300–510	12.0	2.3	0.19
Note 8	433	29.0	300–510	9.8	2.6	0.27
Note 9	432	28.4	320–510	7.9	2.3	0.29
Note 10	432	32.0	280–530	15.5	3.8	0.24
Note 11	430	28.5	280–510	9.1	1.8	0.20
Note 12	429	28.5	390–510	5.2	1.1	0.22
Note-to-note duration (s)						
NtN1–2	1.05	0.375	0.11–5.54	135.8	24.0	0.18
NtN2–3	1.76	0.438	0.11–4.96	99.2	15.3	0.15
NtN3–4	1.23	0.434	0.15–5.34	168.7	19.0	0.11
NtN4–5	0.45	0.555	0.11–7.75	442.2	60.9	0.14
NtN5–6	0.93	0.522	0.03–2.33	192.5	27.1	0.14
NtN6–7	1.36	0.666	0.10–2.40	197.1	19.6	0.10
NtN7–8	0.56	0.346	0.06–2.33	208.7	32.4	0.15
NtN8–9	0.53	0.299	0.03–1.86	238.2	26.6	0.11
NtN9–10	0.66	0.429	0.05–1.87	278.3	23.8	0.09
NtN10–11	0.4	0.272	0.07–1.23	348.0	23.7	0.07
NtN11–12	0.43	0.224	0.07–1.99	251.4	21.6	0.09
NtN12–13	0.43	0.180	0.08–0.99	197.6	15.2	0.08

an individual were caused by losing the end notes of a song. Alternatively, but more rarely, durations were different due to the presence or absence of the initial note on the recording, as this was often much softer than the rest of the song (Fig. 1). In this case song duration might be affected more seriously as the initial pause (NTN1) was relatively long (Table 1).

Discriminant analysis

We conducted several stepwise discriminant function analyses (DFAs) for the classification of songs to separate different individuals. The prior probability of assigning a song to the correct individual by chance was 2.4%. The first four analyses were conducted to recognize the song parameters potentially responsible for individual recognition. In the first DFA we used parameters which could be measured for the whole song, i.e. song duration and number of notes, minimal, maximal and average peak frequency. We found that DFA correctly classified individuals in 77.2% of cases in a leave-one-out classification (Wilks' lambda=0.741, $\chi^2=136.799$, $p<0.001$). In the second DFA, we used the peak frequency of the first 12 notes (all songs had at least 12 notes), and we found that DFA correctly classified individuals in 58.8% of cases in a leave-one-out classification (Wilks' lambda=0.911, $\chi^2=42.501$, $p=0.082$). In the third DFA we used note-to-note duration between the first 12 notes, and we found that DFA correctly classified individuals in 92.3% of cases in a leave-one-out classification (Wilks' lambda=0.721, $\chi^2=147.808$, $p<0.001$). Finally, we used whole-songs measurements, peak frequency and note-to-note duration for the first 12 notes, and we found that DFA correctly classified individuals in 96.7% of cases in a leave-one-out classification (Wilks' lambda=0.921, $\chi^2=36.655$, $p=0.009$).

These analyses reveal that songs of the Tambourine Dove convey information with a very high potential for identity coding. It is also clear that identity information is coded with a time pattern of note production rather than their peak frequencies which have more of an overlap between individuals.

In the next step we conducted a series of DFAs using peak frequency only, note-to-note duration only, or both. This was done for the first notes only (PF1, NTN1) and for all twelve notes found in each song (i.e. PF1, PF2, ..., PF12 and NTN1, NTN2, ..., NTN11). The aim of these analyses was to find out how information might be added using the following notes in order to improve the correct discrimination of individuals. Peak frequency of following notes enabled correct classification of songs to individuals with DFAs in 14–61% of cases. For note-to-note durations, correct classification varied from 20.7 to 93.1%

and increased steeply at the 3-to-4 note duration (80.2%), and reaching >90% when NTN5 was included. When both, peak frequency and note-to-note duration were included in DFAs, the percentage of correct classification was between 44.5–96% (Fig. 3).

These results suggest that the pattern of the time of note production conveys much more information about identity than the peak frequency of notes. However, in a few initial syllables the peak frequency may also be important, as the joining of time and frequency information improved correct classification (Fig. 3). The most important information seems to be held in as few as first five initial syllables, enabling for >90% correct classifications.

In the final step, we used DFA to find out how identity information changes when we restrict data included in the models to five neighbouring PFs or NTNs only. We calculated several DFAs including notes (and gaps between them, or both) for notes 1–5, 2–6 and so on, until a series ranging from 12 to 16 notes. Five notes were used as the initial analysis revealed that the efficiency of discrimination did not have a considerable improvement when more notes were included (Fig. 3). We do not present results for further five note series as this was linked with a decrease of male sample size and a change in the level of a priori random classification. These analyses may be used to test the potential for identity coding if the receiver of the signal did not pay attention to the song from its beginning. Results indicate that a series of five notes or durations between them (or both) enabled 31–94% correct classifications of songs to individuals (Fig. 4). Peak frequencies alone carried less identity information than note-to-note durations. When both variables were included into DFAs it improved the model. As illustrated in Fig. 4, later note series had poorer results of classification than earlier notes in a song. The Fig. 4 presents results for which we still were able to classify songs for all 41 males. Again, it seems that information about identity in the Tambourine Dove is encoded in the beginning of a song.

Finally, we used recordings from automatic recorders to check if songs recorded at the same points but separated by over a month are still classified as belonging to the same individuals. We used five songs per point and per time, i.e. 60 songs altogether for the DFA analysis. We found that the DFA was calculated as earlier, with the assumption that each point of recording was a different male, and this gave a similar efficiency of discrimination. DFA achieved in leave-one-out classification 76.7% of correctly classified 'individuals' for the whole-song measurements, 78.7% for PFs, 83.3% for NTNs, and 88.3% for all measurements together.

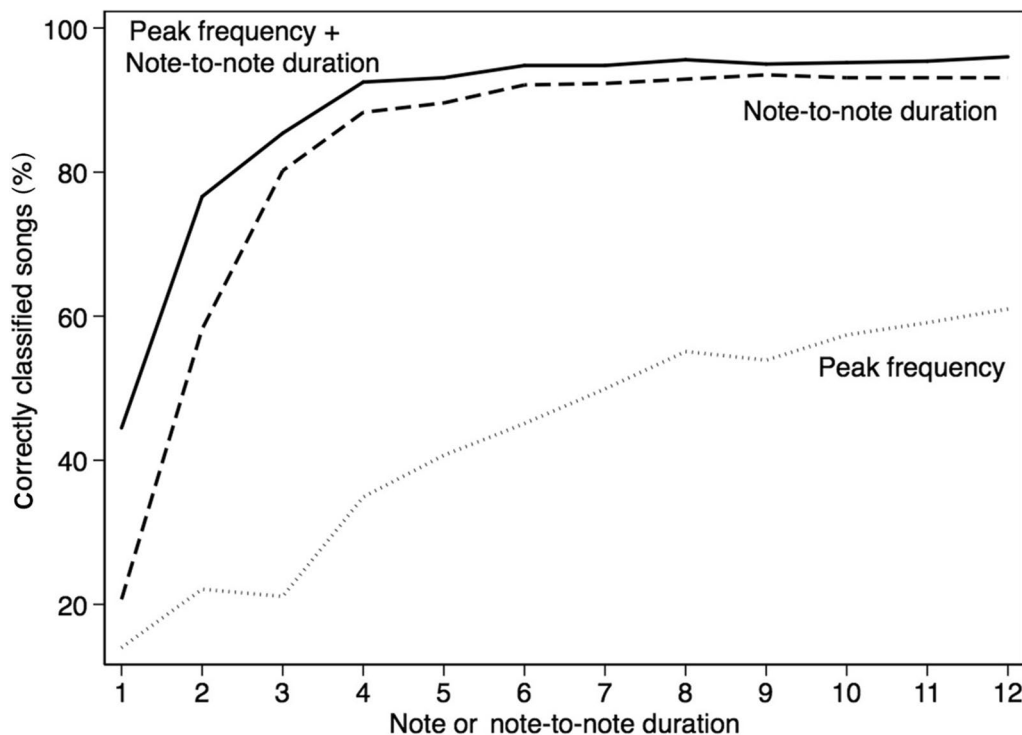


Fig. 3 Percentage of correct classification of Tambourine Dove's song based on DFAs with peak frequency, note-to-note durations or both, derived from first to twelve note within each song

Discussion

Tambourine Dove song and songs of other dove and pigeon species

The song of the Tambourine Dove we studied is equivalent to the perch coos described for other pigeons and doves in that it is a long-range signal aimed to attract potential mates and deter rivals (Baptista et al. 2018a). To accomplish these functions, a song has to convey information about the signalling species, as well as the quality, motivation and identity of the signaller (Bradbury and Vehrencamp 2011). As the song of the Tambourine Dove is relatively simple, one may ask how this information transfer can be achieved? When comparing the Tambourine Dove song with those of the well-studied *Streptopelia* doves, they have a considerably longer song duration with more notes within a song, and more variable number of notes within songs. In *Streptopelia* doves, songs are built from a few syllables (seven in the Laughing Dove (*Streptopelia senegalensis*) is likely the maximum) and last less than 4 s (de Kort and ten Cate 2004). Songs of the Tambourine Dove were, on average, three times longer and sometimes contained over 50 notes (Table 1). So, it seems that, at least in the time domain, there is a lot of 'space' for the coding of potentially important information.

Beside song duration, which was quite variable, songs of the studied species were highly stereotyped and characterized by a low overall frequency and narrow frequency band. Songs mostly consisted of unchanging, short and tonal-whistle notes (see Fig. 1). Such results may suggest that frequency and note characteristics could be cues for species recognition. However, real recognition is likely more intricate. The Tambourine Dove is one of the five species of the genus *Turtur*. All of them occur in Africa, inhabit habitats from forest to more or less wooded savanna where their ranges may overlap (Baptista et al. 2018b). All these *Turtur* species have very similar songs, typically consisting of 20–40 short, unmodulated whistles that form long song strophes of 10–18 s. The predominating song frequency band ranges between 300 and 700 Hz, meaning all of the species songs overlap in time and frequency (Baptista et al. 2018b). In addition, there is no obvious difference in the pattern of note organisation within a song for all species, with the notes of a song accelerating when closer to the end. Currently, there is no study focused on the between-species differences in *Turtur* species songs, and so it is hard to quantitatively represent how similar (or dissimilar) the songs are. With some confidence, one can state that the songs of these species are very similar, and if they are different,

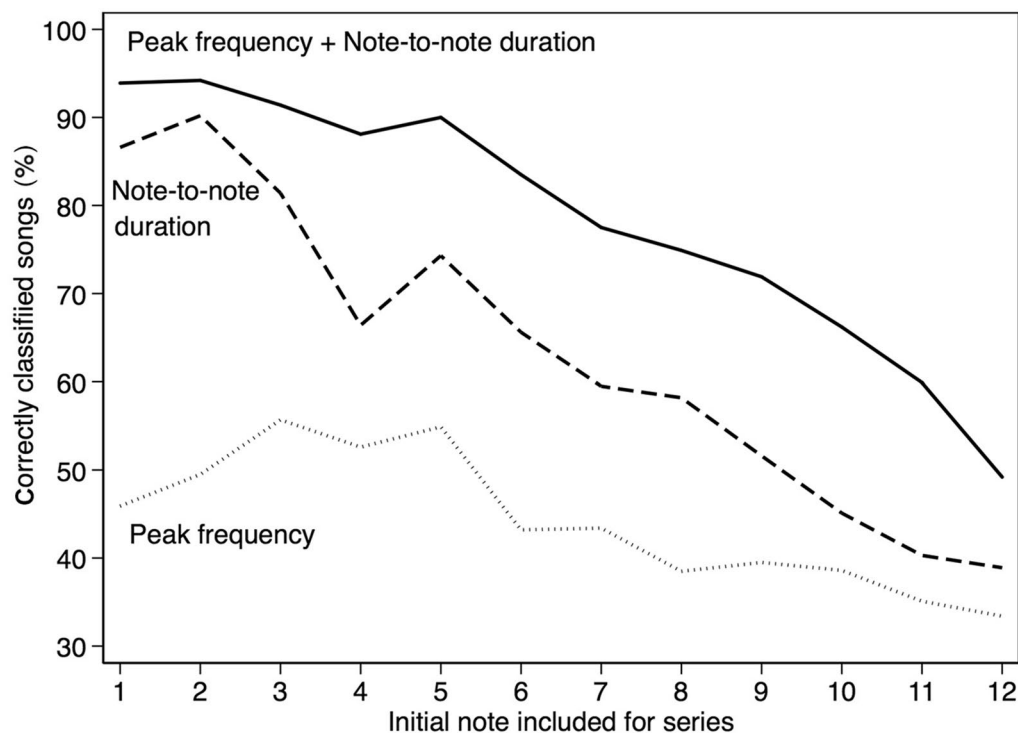


Fig. 4 Percentage of correct classification of Tambourine Dove's song based on DFAs with peak frequency, note-to-note durations or both, for the five adjacent notes or note-to-note duration series. One on the X-axis indicates that classification rate was calculated based on peak frequency of notes from one to five and so on

this difference is sophisticated, using multidimensional characters of the song.

The unmodulated-whistle of the notes and the low frequency of the song for *Turtur* doves, seem to be an adaptation for signalling in forested habitats. It is a trademark of this group, as their sister clade *Chalcophaps indica* (separated by ~13 million years), or the more distantly related, *Gallicolumba luzonica* and *Geopelia striata* (~23–24 million years) have clear differences in their song, having longer whistles with less of a pure-tone (Khan and Arif 2013).

Pigeon and dove species have a relatively simple syrinx, reducing the ability to modify the frequency and tone of syllables produced (Suthers 2004; Elemans et al. 2004, 2008; Mindlin and Laje 2005). The low frequency and narrow bandwidth of sounds that build the Tambourine Dove song reflect the limitation the syrinx structure puts on vocal output. The initial note of the study species song was softer and the only one showing any difference in frequency (Fig. 1). Some syllables were produced very fast in quick succession, but again, they did not vary in frequency (Fig. 1). Unlike some *Streptopelia* doves, we also found no obvious amplitude modulation in notes (e.g. Slabbekoorn and ten Cate 1997).

All these characteristics seem to be common for all *Turtur* species and there is a need for a comparative study to find out which features of their song may allow for inter and intraspecific discrimination. It is likely that for each species, the differences are due to the note rhythm within the song and so pauses between notes may allow for better discrimination than other characteristics (Baptista et al. 2018a).

Species versus individual recognition

The second aim of this study was to find out if there are any song features that enable for the individual recognition of a Tambourine Dove. For such recognition, individuals must have a signal characteristic that is individual to them, where there is low variation within the individual but high variation between individuals (Budka and Osiejuk 2014). Similarly, for species recognition, signals must have low intraspecific variation but high interspecific variation (de Kort and ten Cate 2001). As previously mentioned there are few studies, all of which are on a single species, which suggest the occurrence of acoustic recognition in doves (Morris and Erickson 1971; Mairy 1977; Fusani 1994; Hutchison et al. 1997). In these species it has been found that both frequency and temporal

variables differ between individuals, but the overall variability was greater in temporal variables.

Our analysis of the potential for identity coding revealed that a single song or note feature does not provide enough information for identity recognition. Only the overall peak frequency of a song had a PIC value over 1, which indicates a relatively weak potential for identity coding (Charrier et al. 2001). Each of the remaining characters, when regarded as a single variable, was too variable to be a good identity cue.

A multidimensional approach (DFA) in which different song features were used together, revealed that individual recognition by song in the studied species might be potentially quite an efficient method. Using just a few parameters of the whole song allowed for the correct assignment of 77% of individual songs to particular males. In the final analysis we were able to correctly classify 96.7% of songs. Without a doubt the strongest effect was the between note duration of the initial syllables (allowing for 92.3% correct classification), which carried more individual information than note peak frequency alone (58% correct classifications). This result suggests that in the studied species, the temporal organisation within a song is more variable among individuals, thus providing a background for individual differences. Similar studies (Ballintijn and ten Cate 1997a; Slabbekoorn et al. 1999) have discussed how temporal parameters are the best at discriminating between different vocalisation types and different individuals and so this is likely to occur for all Columbiformes due to the limitations presented by the syrinx structure. These results suggest that features that differentiate individuals are those linked with the rhythm of note production and that they are restricted to the initial notes of the song. This makes sense as song duration varied within an individual depending on whether the final notes within the song were produced, but the beginning notes always remained highly stereotyped.

It is worth noting that the DFA was calculated for the whole set of recordings using 41 individuals at a time, while in natural situations birds are not faced with the problem of discriminating between such a large group of conspecifics at once. In most situations they have to recognize whether the song belongs to a neighbour or stranger (male perspective), or if the song belongs to their mate or an individual who has the potential for being a future mate (female perspective) (Tibbetts and Dale 2007). The high values of correct DFA classification we found for automatic recordings at the same points but separated by longer period also suggest that songs of males are very stable in structure. However, this result should be confirmed by the analysis of recordings of individually marked birds in the future. Hence, high values of correct DFA classifications should be interpreted

as a very big potential for individual recognition in the studied species. On the other hand, our result should be treated with caution as finding even huge between-individual differences is not a guarantee that birds used them for recognition (e.g. Budka and Osiejuk 2014). For example, the Pink Pigeon (*Nesoenas mayeri*) from Mauritius was even found to respond similarly to playback of close conspecific calls from Madagascar (Wolfenden et al. 2015). Hence, there is a strong need for experimental studies on both between- and within-species vocal discrimination in doves.

There is no doubt that song in Columbiformes is inherited genetically (Lade and Thorpe 1964). A question arises as to how birds may achieve individual specificity without losing species specificity, if indeed the signal is genetically transmitted? Or, how individual differences appear during ontogenesis and why they are only linked with specific song features? Cues for answering such questions were provided by Lade and Thorpe (1964). Using hybrids of *Streptopelia* doves they found that there was no radical change in the tonal quality of the sound produced, with some hybrids producing songs with a broken or intermediate rhythmic pattern. Later, ten Cate and Ballintijn (1996) experimentally revealed that notes are elementary units of sound production in the Collared Dove (*Streptopelia decaocto*). Therefore, one may expect that doves are more flexible in changing the pauses between notes (hence changing rhythm or rate) than in changing note characteristics. This however does not mean that doves are not able to produce differentiated notes. In the Collared Dove, males produce modulated or unmodulated coos and it was shown that differences in frequency affect the strength of response (Slabbekoorn and ten Cate 1997). Additionally, a study on coo development supports the hypothesis that frequency modulations play an important role in intra-specific communication and may signal age and sex of an individual (Ballintijn and ten Cate 1997a, b). However, in the Tambourine Dove and other *Turtur* sp. they have virtually no frequency modulations, thus, it seems that in this clade this kind of song variation was lost during their evolution or never gained.

Conclusions

All wood doves live in forested habitats within Africa, with the ranges of some species overlapping. It is likely that their communication system, similar to that of *Streptopelia* doves, evolved due to different selection pressures acting on species and individual recognition, together with the successful production and detection of information in a signal produced in a dense environment (forest). This makes the *Turtur* genus an excellent example for

further studies on signal evolution. The method of individual recognition of individuals presented in this study has also a great potential as a monitoring tool, which allows for non-invasive populational research.

Authors' contributions

TSO conceived the study. TSO and MB participated in field work and bird recording. BŻ performed initial screening of sound material in Raven Pro and did initial analyses. TSO finished the sound analysis in Avisoft SASLab Pro, did statistical analysis and together with AW wrote the first draft. All authors read and approved the final manuscript.

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Competing interests

The authors declare they have no competing interests.

Availability of data and materials

Recordings are available from Department of Behavioural Ecology at reasonable request.

Consent for publication

Not applicable.

Ethics approval and consent to participate

Not applicable.

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