ORIGINAL ARTICLE

Field investigation of Turtle doves' courtship: vocal calls *versus* arc-flight

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Abstract During the breeding season, many avian species produce complex expressions to attract their mates. In turtle doves *Streptopelia turtur*, male signals visually and acoustically during courtship. The only previous study on turtle doves' song was limited to quantifying acoustic expressions and their role in the detection of turtle doves. In the present study, we defined two types of languages in turtle dove's courtship display: "arc-shaped" flights and vocal "roux", with the aim to investigate, under natural conditions, their attractive role towards females. Similarly, the influence of intraspecific competitors and position of singing were analysed during two breeding seasons (2016-2017). Summarizing, results chow that male turtle doves combined acoustic and arc-flight displays to attract mates, with intense expressions between May and July. Throughout the day, vocal calls and flights are concentrated between 8:00-10:00 (morning) and 16:00-18:00 (evening). Moreover, the duration of the acoustic display is more important than flying expressions. On the other hand, turtle doves sing on trees (vertical support) more than ground, with a complex frequencies and amplitudes (sound calls) to spread out their calls toward females. However, the presence of competitors in the same field increase rate of singing and flying, in order to ensure mates attraction.

Keywords: *Streptopelia turtur*, courtship display, flight, song

Introduction

During the breeding season, many avian species produce a relatively complex behavioural expression to attract mates (Brumm 2002; Zollinger and Brumm 2015). Both sexes adopt a variety of communications, the most important are the acoustic and visual languages (Staler et al1988; Zann 1996; Livezey 2016). In songbirds, males direct their vocalisations toward females during courtship display (Sossinka and Bohner 1980). However, in other species like *Streptopelia risoria* and *Menura novaehollandiae*, the males combine between songs and dances to better distribute their information (Fusani et al 1997; Dalziell et al 213). Despite, what is more effective (song or visual), female recipients are widely known by their sensitivity to male signals and respond with varying behaviours between acceptance and refuse (Neunuebel et al 2015; Pennycuick 2015; Finton et al 2017). In general, studies of audiovisual communications in birds are focused on controlled experiments in laboratories (Caryl 1981; Krieg and Getty 2016; Ullrich et al 2016), while captivity results can be very different from natural expressions (Solonen 2013).

In turtle dove (*Streptopelia turtur*) studies of breeding biology are very advanced (Hanane and Baâmal 2011; Kafi et al 2015). However, these researches concentrate on arrival dates (Herbert and Wilson 2013), spawning phenology, breeding success and population size. Works on turtle dove's sexual behaviour are very limited or even absent. In fact, two studies were conducted on two close species, *Streptopelia risoria* and *Streptopelia decaoto*, showed that, during courtship display, the male performs visual expressions (arch flights) accompanied with specific calls (Roux), in order to convince the female (Fusani et al 1997; Catchpole and Slater 2008). These aspects are crucial before any breeding success.

In this study, we pointed out two categories of behavioural expressions in the turtle dove's courtship display: "arc-shaped" flights and vocal "roux", in the object to analyse, under wild conditions, their attractive contribution towards females. We theorised that vocal expressions were very attractive more than arc flights. Similarly, we supposed that the sequence durations were variable according to the nature of the courtship display (acoustic or visual). The clarification of these fundamental features will offer essential keys to breeding success in turtle doves.

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Materials and Methods

Study sites

Ait Ayach valley (32°41'6" N and 4°44'42" O), is situated in the West of the Moulouya plain, Midelt Province, Morocco. The habitat is located in an altitude of 1500 m, with an average annual rain of 182.06 mm and medium temperature of 15.72 ℃ (2015-2016). On the other hand, the prospected zone is cultivated mainly by apple orchards (1600 ha) which are suitable for Turtle dove breeding (more than 220 nests during 2015). Cereal surfaces cover 4500 ha and provide important food resources for this bird.

Sample design

The monitoring of courtship display in Turtle dove was carried out in different kinds of wild and agricultural habitats including apple orchards, riparian vegetation and cereal plots, during two breeding seasons (March to September 2016-2017). Basing on early field prospections during 2015, three viewpoints were fixed: Ayad hill (32 ° 36'15 "N and 5 ° 1'8" W), Boygra hill (32 ° 36'38 "N and 5 ° 0'51" W) and Oalabbo in bowl topography (32 ° 37'4 "N and 5 ° 0'24 "W). The chosen sites were topographically high for better visibility (better and easy pairs' counting), and camouflaged (apple trees and other riparian vegetation) to avoid any disturbance. Voice calls and arc flights were audio-recorded and videotaped during the whole day from 06:00 to 18:00, with microphone, Canon camera (LEGRIA HF R506, advanced zoom X57) and binoculars (in case of good visibility conditions). However, males singing inside trees and in camouflaged localities were audio recorded only. In case of the competition (presence of more than male singing and flying in the same locality), the recording was performed focusing on the first individual to display. Sequences' duration and the positions of their emission were noted for later analysis. In parallel with audio-visual behaviour, the observed pairs (in mating or just the two partners in meeting after each expression) were noted to analyse the relationship between the behavioural expressions and the pair's formation (witch of the expressions is more effective?). Moreover, distance between competitors was estimated basing on the distance between apple trees inside orchards (in Midelt apple orchards, tree lines are separated by 3.5 m as optimum distance) and Total Station (Topcon SANS PRISME (MODEL: NTS-102B, NTS-315B), Prismless range 500 m - Measurement time less than 1 sec).

Sound analysis

Recorded sound sequences (in HD format with camera and MP3 format with microphone devise 200 kHz maximum range) during Turtle doves' acoustic courtship were converted to wave format (in audio.online-convert.com web site). During the analysis, sequences (wave formats) were calibrated to 25 second periods (basing on the sequences' maximum duration recorded in field (23s)), as in the case of house mice female calls (Finton et al 2017). Oscillograms and spectrograms were generated with SoundRuler software (SoundRuler 0.9.6.0; Macros Gridi-Papp, GNU GPL). Sequences were divided into syllables and sections basing on Oscillograms and using section length button. The section duration was measured (in millisecond) and compared between first segments (beginning of calls) and last segments (end of calls).

Data analysis

Statistical tests were executed in SPSS software (version 24.00, IBM 2009). Parametric data (checked with normality test), such as the comparison of vocal and flight sequences during the day and season and acoustic syllables, was analysed using the one-sample t-test. Non-parametric data (non-conform to the requirements for parametric tests) including sequence duration and the time interval between two successive sequences were compared by Wilcoxon and Mann-Whitney Sign Tests. In the case of sequences' duration, recorded displays were partitioned in tree periods; (i) beginning of breeding season (from arrival date to the end of April), (ii) optimum breeding phase (corresponding to courtship peaks in May and July), (iii) end of breeding season (August). Because of their non-conformity with parametric tests (checked with normality), sound and flight sequences (during three periods) were analysed with Kruskal-Wallis test. Results reported as significant assume a false discovery rate of 0.05. Graphs were created by GraphPad Prism Mac 6.0h software. The overall mate-attractiveness of acoustic and visual courtship was modelled by means of Generalised Linear Mixed Model (GLMM). In these analyses, arc flight was log(x + 1) transformed to ensure normality.

Results

Seasonal and daily courtship display

The expression of the two courtship languages differed qualitatively and quantitatively. Songs were more important than flying, during turtle dove's breeding season (Figure 1). In fact, songs were displayed from the second decade of April until the first week of August. In contrary, flights were limited to the period between the second week of May and the first week of July. In addition, during day, vocal expressions (72.88 ± 13.14 sequences on average per day) were very intense in comparison with arc flight sequences (12.13 ± 2.50 sequences in average per day) (n = 51, t = 4.539, P < 0.001). However, turtle dove's courtship activities (flying and singing) were concentrated essentially between May and June, with a second recovery of songs at the beginning of July, as reflected by the peaks during these periods (Figure 1). In parallel, the

formation of turtle dove's pairs follows the courtship peaks. In fact, the first pair's peak was recorded in coincidence with the parade peaks (songs and flight) between May and June. The second peak was distinct after the recovery peak of vocal expressions in July.

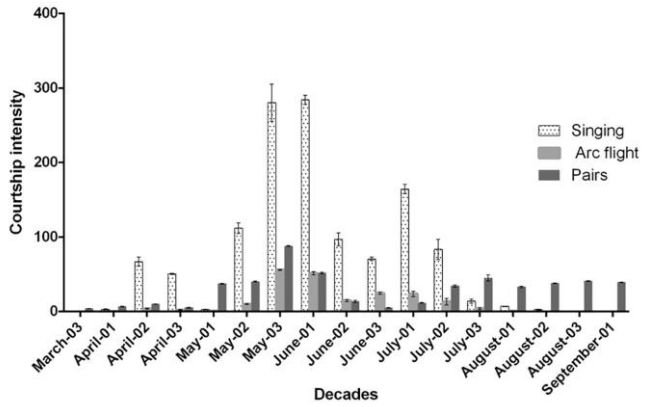

Figure 1 Courtship display (sound and flight) in Turtle doves during the breeding season (2016-2017).

Concerning the daily courtship, the intensity was variable (Figure 2). The expression of the two sequences (flights and songs) was more intense early between 08:00 and 10:00 during the morning and late between 16:00 and 18:00 during the evening (Table 1). However, acoustic activity is also more important than visual expressions. Indeed, t-test conducted on sequence duration of singing and flying demonstrated that the difference between these two expressions is widely significant (n = 18, t = 4.824, P < 0.001).

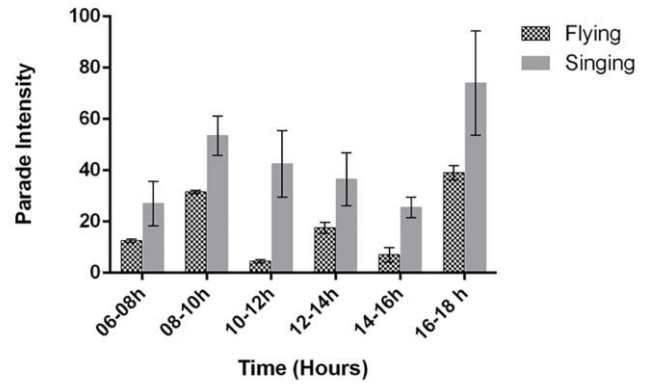

Figure 2 Daily (08:00 to 18:00) courtship intensity in Turtle doves, during breeding season (2016-2017).

Sequences' duration

Sequence length varied according to the nature of behavioural expression (Table 2). Seasonal acoustic activity, represented by the "roux" calls, take more time compared with visual expressions, reflected by the arc-shaped flights (P < 0.001). In contrary, the time intervals between two successive expressions were more important between flights in comparison with acoustic sequences (P < 0.001). This indicates the high intensity of the songs in turtle doves, during the breeding season.

Concerning periods, the optimum breeding phase (May and July) was characterised by a sequences with long duration in vocalisation, while flight sequences were comparable in all periods (Kruskal-Wallis test for: (i) vocalisation: H = 37.648, P < 0.001; (ii) flight: H = 0.996, P = 0.60).

Table 1 Multiple Range Tests showing the variation of daily courtship intensity in Turtle doves.

Contrast	Sig.	Difference	+/- Limits
06:00-08:00_ 08:00-10:00	-	-1.71429	5.30462
06:00-08:00_ 10:00-12:00	-	-1.92857	5.30462
06:00-08:00_ 12:00-14:00	-	-1	5.30462
06:00-08:00_ 14:00-16:00	-	1	5.30462
06:00-08:00_ 16:00-18:00	*	-5.57143	5.30462
08:00-10:00_ 10:00-12:00	-	-0.214286	5.30462
08:00-10:00_ 12:00-14:00	-	0.714286	5.30462
08:00-10:00_ 14:00-16:00	-	2.71429	5.30462
08:00-10:00_ 16:00-18:00	-	-3.85714	5.30462
10:00-12:00_ 12:00-14:00	-	0.928571	5.30462
10:00-12:00_ 14:00-16:00	-	2.92857	5.30462
10:00-12:00_ 16:00-18:00	-	-3.64286	5.30462
12:00-14:00_ 14:00-16:00	-	2	5.30462
12:00-14:00_ 16:00-18:00	-	-4.57143	5.30462
14:00-16:00_ 16:00-18:00	*	-6.57143	5.30462

* denotes a statistically significant difference.

Structure of acoustic sequences

Oscillogram of turtle dove's voice call (Figure 3) chowed a complexity in vocalisation sequences. In fact, every sequence is divided on 6.35±0.67 segment (n=12 audio recordings). Similarly, each segment is partitioned on three syllables. This small sections were different between the beginning (7.81 ± 0.27 ms) and the end (9.58 ± 0.31 ms) of segments (n =12, t = 31.657, P < 0.001).

The field survey of acoustic courtship showed two main situations for expression; the position on the trees and ground singing. However, statistical calculation confirmed that the turtle dove prefers trees more than ground to express their acoustic display (Table 3). In fact, during six months of monitoring, the acoustic activities, expressed on trees, exceed largely the ground songs (P < 0.05). Furthermore, no difference was recorded concerning the sequence durations between two positions (P > 0.05).

Discussion

Through this field-based study, we investigated the use of visual and acoustic signals in Turtle dove's courtship display. North African Turtle dove, especially the males, uses

both acoustic and visual expressions (Figure 1, 2) to attract females. Our results agree with previous experimental studies on other bird species, including passerines (Larsen and Dabelsteen 1990; Gate et al 2005; Patricelli 2007; Stanger-Hall et al 2018) and support that these birds use both visual and acoustic languages during sexual behaviour. Moreover, some avian species combine between this two signal modules to improve and/or maximize the information exchange, as has been shown in zebra finch and other birds (Wang et al 2008; Ullrich et al 2016; Kaplan 2017). However, the present work shows paradoxical results. In the field, acoustic courtship dominated the theatre (Figure 1), while the statistical analyses, using Generalised Linear Mixed Model (GLMM), indicated a relative link between visual behaviour (flight) and formation of breeding pairs (Figure 4).

Table 2 Duration (time in seconds) differences between flying and singing in turtle dove's courtship, during breeding season.

	Courtship categories	Singing (s)	Flying (s)	Z	*P-value*
Average duration for each sequence	whole Season (N = 60)	8.10 ± 3.69	5.65 ± 2.70	-6.548	<0.0001
	Beginning of season (N = 20)	5.00 ± 0.35	5.80 ± 0.68	-0.774	0.438
	Optimum breeding periods (N = 20)	9.10 ± 0.67	7.00 ± 0.80	-2.183	0.029
	End of breeding periods (N = 20)	2.55 ± 0.43	5.75 ± 0.59	-3.995	<0.0001
Average time interval between two successive sequences		1930.38±1613.52	24955.83±4361.5	-4.961	<0.0001

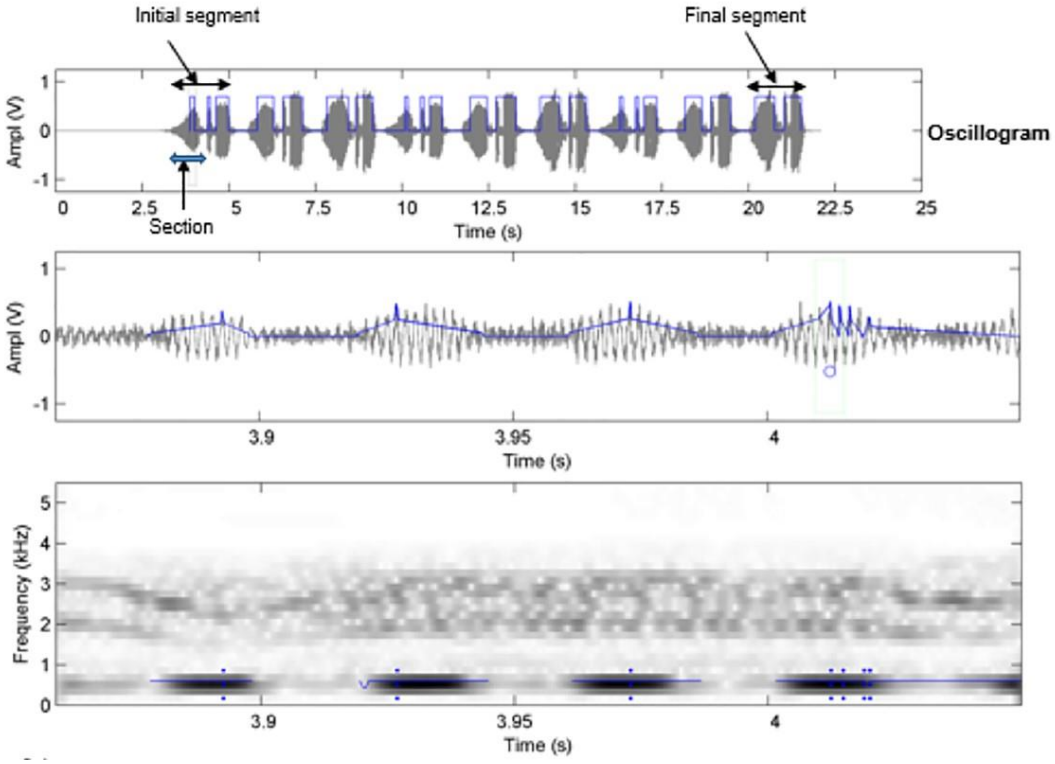

Figure 3 Oscillogram (top) and spectrograms (bottom) of sample broadband vocalizations illustrating the complexity (multiple syllables (sections)) of courtship call's structure in Turtle dove.

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Table 3 Differences between singing on tree and singing on the ground (N =10 days spread-out equally between April and July) in apple orchards and riparian vegetation, Morocco, 2016.

Singing position	On the tree	On ground	Test	*P-value*
Total sequences	415	89	-	-
Average sequences per day	75.45±9.56	16.18±3.33	F =10.36	0.005
Average duration for one sequence (s)	7.77±0.48	8.35±0.74	U =-0.004	0.99

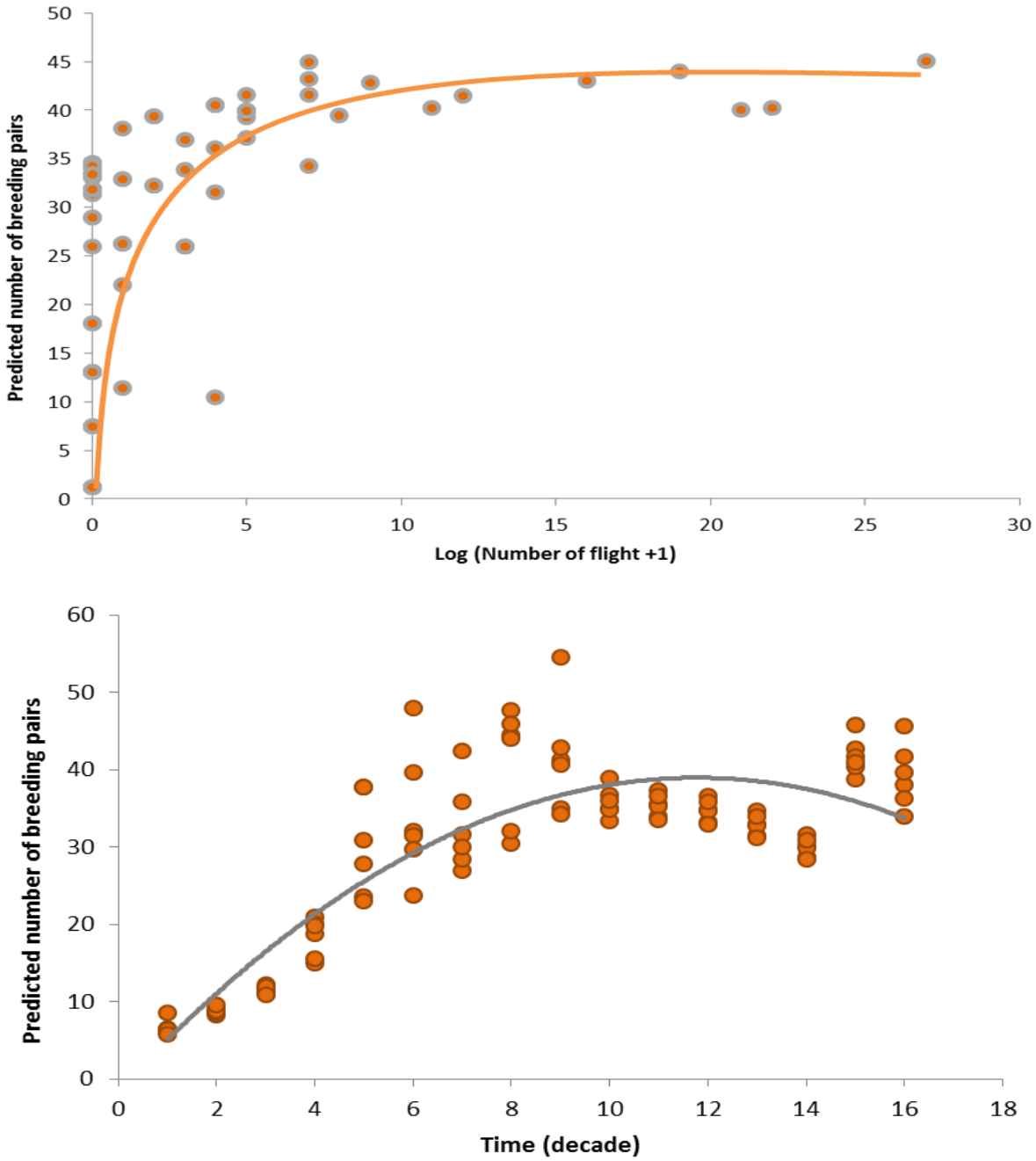

Figure 4 GLMM model predicting the Mate-attractiveness (pair formation) of visual expressions (Flight above) and time (decades below) during Turtle dove's courtship.

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This finding can be explained by two elements. First, our approach was observational and, therefore, the acoustic dominance was very easy to be distinguished in field, since sound easy-dissemination (Hick et al 2016; Potvin et al 2018), even if its effectiveness would be useless as in *Cervus elaphus* (Reby and McComb 2003), in which a negative correlation between reproductive success and acoustic courtship was reported. Second, the visual signal (flights) was revealed recently to be a good physical indicator of the presence and body performance of the partner (Zhang et al 2018), which could make it more attractive with its quality note by the intensity. This is in contradictory with results obtained by (Kroodsma and Miller 1982; Cramp 1985; Bhatt et al 2000) who have reported that the acoustic expressions are very important in bird's courtship display, in particular, loud songs can spread out over a long distance, stimulate the fitness and mark the territory (Gil and Gahr 2002; Kaplan et al 2009; Ohms et al 2012). However, the main question in this topic is which expression is more effective in mate attraction. In reality, with contradiction found between field and laboratory analyses, our results suggested a synergetic effectiveness combining sound and flight, as found in warbler and zebra finches that combine between plumage or flights, as a visual behaviour and acoustic songs in fitness components (Avey et al 2005). This combination could offer an audio signature, while the visual behaviour could provide the image of the partner and its performances. On other side, recipient females are basing on these two channels and their amplitude to make a virtual conception (image) of potential partners, in particular, their physical quality and motivation state (Collins et al 1994; Boukhriss and Selmi 2009; Perez et al 2015; Zollinger and Brumm 2015). Similar results were recorded in domesticated Australian zebra finch and other lyrebirds (Ullrich et al 2016; Dalziell et al 2013; Mulder and Hall 2013), which integrate courtship song and dance in order to attract effectively the mate. The mesmerising effect of sound and movement is not limited to birds, it's a common strategy adopted by other animals, including spiders and compared with humans dancing to music (Ejima and Griffith 2008; Mulder and Hall 2013).

Seasonal parade was variable, courtship intensity was very high, essentially between May, June, and July. These periods (May, June and July) correspond exactly to the turtle dove's optimum nesting phases, as reported in North African areas (Calladine et al 1999; Nemeth et al 2012; Hanane 2016, 2017; Rieger and Marler 2018). Likewise, during the day, sequence intensities varied from one period to another. Expression peaks were recorded between 08:00 and 10:00 during the morning and between 16:00 and 18:00 during the evening (Figure 2). The choice of these phases to display courtship may be due to the fresh weather conditions during the morning and evening. As this is already cited in the turtle dove dietary behaviour and singing rate (Browne and Aebischer 2004; Nemeth et al 2012; Linhart and Fuchs 2015). This columbidae sings and researches its food out of the day hot periods (midday) to avoid or limit the water loss due to perspiration. In fact, the parade activity requires a very important physical effort, particularly in the presence of intraspecific competitors that require more effort, in order to ensure field dominance (Dubois 2002; Kaplan et al 2009; Hick et al 2015). Consequently, we examined courtship in the presence of competitors (Figure 5). As a results, turtle doves, in the presence of other intraspecific competitors (male turtle doves displaying in the same habitat and period), increases rate of songs (with competitors: 6.34±0.20 song sequences, compared with 3.5±0.21 repetitions in the absence of competitors, one-sample t-test, $N = 32$, $t = -9.482$, $P < 0.001$) and flights (with competitors: 2.09±0.25 flight repetitions against 0.81±0.13 repetitions in the absence of competitors, t-test, $N = 32$, $t = -4.381$, $P < 0.001$) before engaging mate or leaving the territory (in case of fail engaging).

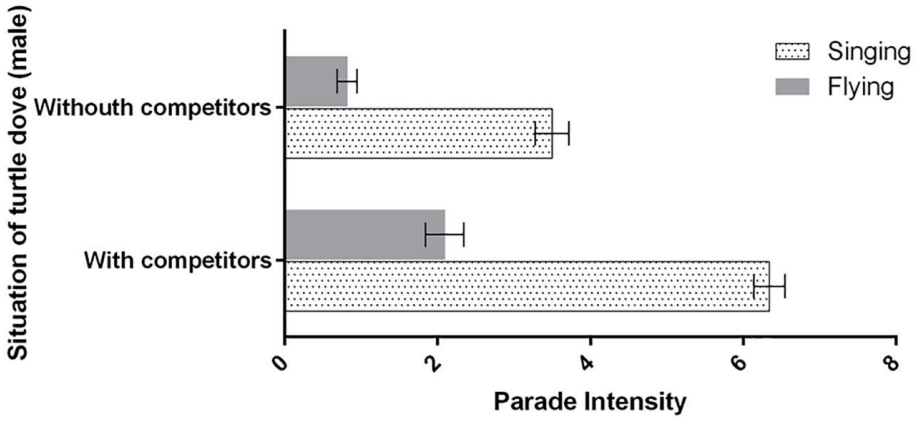

Figure 5 Variation of courtship display in Turtle dove depending on the presence or absence of competitors in the same habitat.

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The analysis of the acoustic expressions showed a complexity in turtle dove vocalisation (Figure 3). The calls were formed with small segments (syllables) that were variable between individuals. Further, segments were divided into three syllables with variable duration and frequency between the first and the last one. This variation and complexity in sound calls (three syllables) could be governed by the difference in physical fitness of male turtle doves. In fact, many animal species, such as red deer stags where the roars were complex (common and harsh roars) and influenced by the male fitness and body size (Hick et al 2016). On other hand, sexual competition with other intraspecific birds could interfere in this complexity. Therefore, in order to propagate convincing calls (for females), males produce specific call segments with different amplitude and frequency that indicating their good physical quality and sexual motivation (Fant 1960; Reby and Mccomb 2003; Hanane and Maghnouj 2005; Hick, Doucet and Mennill 2016).

Turtle dove sings in two positions: on trees and on the ground. However, calls emitted on the tree were more important than those produced on the ground, in terms of quantity. In the opposite, the average duration was comparable between these two positions. Dominance of calls on trees as vertical support will facilitate the signal propagation (Fitch and Reby 2001). Particularly, these Columbidae use multi-dimensional calls in order to spread out the signals and to dominate competitors (Goodwin 1970; Fusani et al 1997; Mathevon et al 1997). Indeed, during the courtship displays, distances between competitors (males emitting the sequences at the same time) were very short (in order of 65.06 ± 8.19 m during the whole season), in particular between May and July (31.18 ± 3.56 m, corresponding to the optimum breeding phase). As a result, songs on trees can spread out more and can help competitors to attract the female's attention and supress the competitor's sound.

Conclusions

In summary, this paper provides a qualitative (seasonal and daily) and quantitative (time and sequences) analysis of courtship display in turtle doves during the breeding season, under wild condition. We revealed a synergetic effectiveness of acoustic and visual signals with a field dominance of sound sequences compared to visual arc-shaped flights in the attraction of mates. In addition, expressions increased in the presence of competitors on the same habitats. Similarly, turtle doves sing on the tree position with the use of multidimensional calls (diverse syllables with variable amplitudes and frequencies), to ensure a long propagation of sound (calls) and competitor's dominance. Despite its limitation to the quantification of acoustic and visual courtship, this initial research has decrypted a basic information (signalling language) on the sexual behaviour of turtle doves, under wild conditions and opened the window for future researches to reduce the lack of data on the breeding behaviour of this threatened bird.

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Conflict of Interest Statement

We confirm that we have no conflicts of interest.

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