No evidence for a role of trills in male response to territorial intrusion in a complex singer, the Thrush Nightingale

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Abstract
Among the broad diversity of songbird vocalisations, song can serve a wide range of different functions depending on the species and context. In many species, aggressive motivation has often been linked with the use of fast repeated series of elements typically referred to as trills. However, only a few studies explored the role of this specific component in species with a large repertoire and high song complexity. Here, we investigate the potential role of trills in the territorial vocal response of males Thrush Nightingale (Luscinia luscinia), a species with complex songs characterised by the frequent use and diversity of their trills. We performed playback experiments simulating territorial intrusion to test if trills signal aggressive motivation in this species. If so, we expected tested males to respond by changing their trill rate or frequency of trill use in songs, and/or using different trill types than before the stimulation. Contrary to our expectation, males did not modify their trill rate or differed in trill type use before, during or after playback. There was a tendency for decrease in trill duration and the number of elements in the trills during the playback stimulation, reflecting to some extent the overall use of shorter songs by males during that stage of the experiment. Altogether, our study does not support the role of trills as motivation signals for territory defence in Thrush Nightingales, but advocates for more research on their potential roles in signalling other information.

Keywords Vocal interaction · Aggressive signal · Trill · Territory defence · Playback · Luscinia luscinia

Zusammenfassung
Beim Sprosser, einem Singvogel mit komplexem Gesang, spielen Triller wohl keine Rolle bei der Antwort von Männchen auf ein Eindringen ins Revier
Als Teil der vielfältigen Lautäußerungen von Singvögeln kann Gesang eine Reihe unterschiedlicher Funktionen erfüllen, abhängig von der jeweiligen Vogelart und Situation. Bei vielen Arten ist die Motivation zum Angriff oftmals mit der Benutzung schneller, wiederholter Serien von typischerweise als Triller bezeichneten Elementen in Verbindung gebracht worden. Nur wenige Studien haben jedoch die Rolle dieser spezifischen Gesangskomponente bei Arten mit einem breiten Gesangsrepertoire und hoher Gesangskomplexität erforscht. Hier untersuchen wir die potenzielle Rolle von Trillern bei der Territorialantwort männlicher Sprosser (Luscinia luscinia), einer Art mit komplexen Gesängen, die durch den häufigen Gebrauch vielfältiger Triller gekennzeichnet sind. Wir haben Playback-Experimente durchgeführt, die das Eindringen eines Rivalen ins Revier simulierten, um zu testen, ob Triller bei dieser Vogelart die Angriffs motivation signalisieren. In diesem Fall erwarteten wir, dass die getesteten Männchen ihre Trillerrate oder die Häufigkeit des Trillergebrauchs in ihren Gesängen ändern und/oder andere Trillertypen als vor der Simulation benutzen sollten. Entgegen unserer Erwartung

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änderten die Männer jedoch weder ihre Trillerrate, noch unterschieden sie sich die Trillertypen, die sie vor, während und nach dem Playback benutzten. Es bestand eine Tendenz, die Trillerrate sowie die Anzahl verschiedener Elemente in den Trillern während der Playback-Simulation zu verrinern, was zu einem gewissen Grad den Gebrauch kürzerer Gesänge durch die Männer in dieser Phase des Experiments widerspiegelt. Insgesamt stützt unsere Studie die Rolle von Trillern als Motivationssignale für die Revierverteidigung bei Sprossern nicht, sondern befürwortet die weitere Untersuchung ihrer Rolle beim Übermitteln anderer Informationen.

Introduction

The conspicuous vocalisations of passerines have fascinated scientists for centuries (e.g. Oppel 1869). Due to this interest, the traditional functions of birdsong, such as species recognition, rival repelling or mate attraction, are already well established (e.g. Catchpole and Slater 2008). Furthermore, the fast development of bioacoustic technologies allows us to explore the vocal behaviour of passerines in much deeper detail at both interspecific and intraspecific levels.

Subtle but distinct differences in spectro-temporal characteristics and in song structure can carry information about a singer. Listeners might for example distinguish if the singing individual is from a local or foreign population, as intraspecific geographic variation of song has been shown for many species (e.g. Podos and Warren 2007). The same is true for the ability to discriminate between neighbours and strangers based on song only (e.g. Skierczyński et al. 2007; Briefer et al. 2008), or even among conspecific individuals in general (e.g. Lind et al. 1996; Wilson and Mennill 2010). Another kind of crucial information encoded in song may be age. Differences in song between young and old males were often documented (e.g. Botero et al. 2009; Balsby and Hansen 2010), and birds are able to distinguish between playback of songs of older and younger individuals (e.g. Akgay et al. 2016; De Kort et al. 2009), or even between songs of the same individual recorded at different ages (Zipple et al. 2020).

Studies examining differences between songs of young and older males used various approaches. In particular, many showed that high song consistency, i.e. the ability to reproduce notes with less variability between them, indicates male age (Rivera-Gutierrez et al. 2010, Cramer 2013). Nevertheless, song consistency may also decrease with age (Rivera-Gutierrez et al. 2012; Zipple et al. 2019). It is, therefore, not surprising that this skill may rather reflect the quality of the singer and, as such, can be evaluated by females (Ballentine et al. 2004; Byers 2006; Caro et al. 2010), males (Illes et al. 2006; DuBois et al. 2011) or both (Botero et al. 2009; Węgrzyn et al. 2010; Ferreira et al. 2016).

Apart from signalling quality, song might also carry other information crucial for competing males by reflecting their aggressive motivation. Specific singing behaviours may signal the willingness to escalate conflict or even to physically attack the rival (reviewed in Searcy and Beecher 2009). Besides changing their singing style by, for example, increasing the song rate as commonly observed in response to a simulated territorial intrusion (Baker et al. 2012; Petrusková et al. 2014; Szymkowiak and Kuczyński 2017), males can also modulate the song itself to signal aggression. This is true for the syllable rate, as an increase of syllable delivery rate has been shown as an aggressive signal in species with both slow (e.g. Linhart et al. 2013) and fast delivery (e.g. Funghi et al. 2014).

In some species, individuals involved in aggressive encounters increase syllable rate in a trill, the structure in which notes are repeated in rapid succession (Podos 1997). Such increase of the trill rate in aggressive interactions was documented in several species of various song complexity. For example, male individuals of Swamp Sparrows (Melospiza georgiana), a species using trill-syllables that contain several different notes, will increase their trill rate and its frequency bandwidth during aggressive interactions (DuBois et al. 2009). The Tree Pipit (Anthus trivialis), a species with moderate song complexity, increased trill rate in response to playback stimuli (Petrusková et al. 2014), and the same was also shown for a more complex songster, the Banded Wren (Thryophilus pleurostictus; Vehrencamp et al. 2013).

Moreover, Tree Pipit males during aggressive encounters did not only perform faster trills, but also sang more songs containing trills than before simulated territorial intrusions (Petrusková et al. 2014). The latter was also observed in Common Nightingales (Luscinia megarhynchos), a species known for its particularly complex songs, where a single male repertoire consists of on average 190 song types (Kipper et al. 2004). Common Nightingale males typically escalate aggression during the territorial encounters by overlapping the opponent’s song (e.g. Naguib and Kipper 2006). In addition, Kunc et al. (2006) showed that, apart from such overlapping, they also increased the proportion of song containing broadband trills during the playback stimulus. Subsequent studies confirmed these trills as aggressive signals in Common Nightingale, whose males displayed stronger responses to conspecific songs containing broadband trills than those without (Schmidt et al. 2008; Sprau et al. 2010). Moreover, though Naguib et al. (2008) showed a significant degradation of these trill types with distance, Sprau et al. (2010a) demonstrated that they still maintain their agonistic...
function: tested males reacted strongly even to playbacks broadcasted from a distance where trills already became degraded.

Similar trills are a typical component of the songs of another complex songster, the Thrush Nightingale (*Luscinia luscinia*; e.g. Sorjonen 1983, 1986). Males of this species, closely related to the Common Nightingale (Storchová et al. 2010), develop quite large individual repertoires (ranging from 23 to 42 song types; Griessmann and Naguib 2002). Thrush Nightingale song types are characterised by various rapid broadband trills which are also substantially degraded with distance and have thus been considered as short-range signal, potentially important in close male–male interactions (Sorjonen 1983). In spite of this, their aggressive function has not been examined yet.

In this study, we test if rapid broadband trills, a structure present in almost all Thrush Nightingale territorial songs (Sorjonen 1983), also play a role in agonistic signalling as do similar trills in Common Nightingale. In addition to exploring commonly studied temporal parameters of song in an agonistic context, such as the duration or delivery rate of songs, we particularly focus on the fine structures of the trills, specifically trill rate and duration, as studies on species with less complex songs already showed an increase of trill rate with the escalation of aggressive interaction (e.g. DuBois et al. 2009; Petruskova et al. 2014). We hypothesise that, if trills in Thrush Nightingale songs carry information about aggressive motivation, tested males should respond to song playback simulating conspecific territorial intrusion by (1) changing their trill rate, e.g. singing faster trills once stimulated, and/or (2) increasing the extent of trills used in the song, and/or use different trill types than before the stimulation.

### Materials and methods

#### Study species and song

The Thrush Nightingale, *Luscinia luscinia* (Passeriformes, Muscicapidae) is a small migratory songbird breeding across the northern part of the Palearctic region (Cramp and Perrins 1994). While inconspicuously coloured with no obvious sexual dimorphism, males sing intensively during the breeding season to attract females and repel rivals (Griessmann and Naguib 2002). Thrush Nightingale song is very complex and shows pronounced geographic variation (Sorjonen 1987; Marova et al. 2015b). Moreover, in the secondary contact zone with the closely related Common Nightingale (*Luscinia megarhynchos*) in central Europe, Thrush Nightingales often include parts of that species’ song to their repertoires, such behaviour being reported as “mixed-singing” (Sorjonen 1986; Vokurková et al. 2013; Souriau et al. 2018).

Thrush Nightingale songs are characterised by their typical structure with noticeable two terminal series: a loud and low pitched “castanet” typically followed by a rapid broadband “rattling” trill (Sorjonen 1983, 1986; Fig. 1). These trills have long been candidate structures for short-ranged vocal communications allowing a precise location of the singer (Sorjonen 1983).

![Fig. 1](image)

**Fig. 1** Example of a typical Thrush Nightingale song from Poland (eastern population). The final trill type is characterised by the repetition of simple click-elements associated in pairs, i.e. with a sequence alternating short (mean = 0.009 s) and much longer (mean = 0.071 s) interval between elements. The trill rate was calculated excluding the last iteration (here, the last pair of elements).
Study area

Our study tested the response of male Thrush Nightingales to playback in two breeding populations in the north-east and west of Poland, separated by more than 300 km. The western population was located along the Warta river, in a region extending from Pyzdry (52° 08' N, 17° 40' E) to Zagórow (52° 11' N, 17° 55' E), and the eastern one along the Narew River, from Wizna (53° 11' N, 22° 25' E) to Ciemnoszyje (53° 32' N, 22° 33' E). Thrush Nightingale males there typically select their territories in dense vegetation patches near ponds and riverbanks. Song type repertoires varied between the two study populations (Online resource 1). Furthermore, males from the western population coexisted in sympathy with Common Nightingales and may have potentially integrated heterospecific songs or elements to their repertoires.

Playback song stimuli

The playback tracks originated from different localities than the tested males (another western Polish locality: 51° 58' N, 17° 52' E, over 22 km from the closest tested male territories) to reduce the chances of song matching and potential familiarity of the tested birds with the playback song. Each of the 15 playback tracks consisted of song bouts of pure Thrush Nightingale songs (i.e. not including mixed songs) extracted from a high-quality recording of a unique individual (different for each track); a 90 s long song sequence was then looped to reach the total duration of 5 min. Eleven of the 15 source recordings were recorded in 2008, the other 4 in 2015. Recordings from both years were used as playback stimuli for the experiments in both of our tested populations. In the final dataset of analysed 20 experiments, each playback track was used either once (10 tracks) or twice (5 tracks, all from 2008 recordings), but never twice in the same population. Song features and order of song types were retained; the only manipulation of the recording involved background noise removal using high-pass filter out the species frequency range in Avisoft-SASlab Pro 5.2 (www.avisoft.com). The song delivery rate in the playback recordings (mean ± sd) was within the range typical for the average spontaneous song of the species (Souriau et al. 2018): 8 ± 1.05 song/min, for a mean of 40 ± 1.05 songs.

Experimental procedure

The experiments were conducted in May 2016 and 2017—the most active period for singing and competition between males (Cramp and Perrins 1994; Reif et al. 2015). The playbacks were performed during the day (from ca. 0600 to 2100 h) in the absence of rain or strong wind. We selected males singing spontaneously, and thus, more likely to get involved in territorial interactions (Griessman and Naguib 2002). A minimum period of 24 h was kept between testing two neighbouring territories (defined as <200 m apart) to avoid interference between our experiments.

The experimental setting generally followed our previous experiments (Reif et al. 2015; Souriau et al. 2018). A remotely operated speaker (MIPRO MA-101) was placed on the ground in the open towards the bird’s singing post, at the foot of a Thrush Nightingale taxidermic dummy perched on a stick. The vocal response of the tested male was recorded using a digital recorder (Marantz PMD660) connected to a directional microphone (Sennheiser ME67).

Once a bird was found actively singing with no apparent interaction with neighbours, we first recorded at least 5 min of spontaneous song preceding the experiment. Second, after setting up the experimental device (loudspeaker and taxidermic dummy), we played the stimulus track for 5 min and recorded the song and behavioural reactions. Further, we extended our recording period over 5 more min after the end of the playback stimulation to cover the subsequent responses of the focal male. From the start of the playback, the same observer (Souriau) was tracking the bird movements and aggressive displays from a safe distance (ca. 15–20 m) to reduce the potential disturbance by human presence.

Song analysis

Altogether, we performed 33 experiments but subsequently excluded those where song recordings were disturbed by background birds, other overlapping noises, or unsuitable weather conditions, as well as those with any territorial intrusion by another male. Finally, we retained 20 experiments for further analyses (10 tested males from each of our 2 focal populations). Out of these, three involved males singing mixed songs (i.e. copying songs types from Common Nightingales). Heterospecific song types (or more rarely syllables) included within Thrush Nightingale’s songs were identified by their similarity with recordings of local Common Nightingales (unpublished data, Vokurková et al. 2013; Souriau et al. 2018). The copied heterospecific song types (or song types containing heterospecific elements) constituted between 3 and 13% of these three males’ total song type repertoires.

Song parameter analysis

We selected recognisable full songs (containing at least five phrases composed of different syllables types and separated by silent interruptions), typically ending by a final trill (Fig. 1), from all three experimental stages (before, during, and after playback). We, thus, did not take into account song “fragments” (parts of less than five phrases, ranging from isolated notes to early interrupted songs).
We extracted the following song parameters: (1) complete song duration, defined as stereotyped vocalisation sequences separated by silent intervals, (2) pause duration defined as the interval between the end of a song and the beginning of the next one, (3) song rate calculated as the number of complete songs per min, and (4) percentage of time spent singing (based on the previous song and pause duration; between-syllable intervals were considered parts of the respective songs). Such song parameters are informative on the bird motivation and have already been used in previous studies on *Luscinia* species (e.g. Kunc et al. 2005; Turčoková et al. 2011; Souriau et al. 2018).

When estimating the song rate and pause duration, we focused on periods of a continuous song delivery, and thus, excluded very long pauses when the birds entirely ceased singing (including a period that occurred in some birds when the playback stimulus started playing). In these analyses, we only kept pauses shorter than 10.45 s, which corresponds to the mean value of the 90th percentile of pause duration across all 20 selected males.

Trills in Thrush Nightingale are series of fast repetitions of very short and broadband elements (referred to as “clicks”), typically ending the song before a final non-repeated syllable (Fig. 1; Sorjonen 1983; Ivanitskii et al. 2016). The structure of trill types can vary from repetitions of simple single-element broadband “clicks” to clusters of two, three or even more elements, including both “clicks” and short duration harmonics (Fig. 2). Some of the trills copied from Common Nightingale song (Fig. 2f) showed structural similarities in their elements despite the difference in their clustering and position in the song. Such songs and trills were, therefore, included in our analysis. In our study, we only considered trills containing at least 4 repetitions.

The following parameters were considered for all three experimental stages: (1) number of elements in the trill (i.e. the total number of elements in the entire trill), (2) trill duration, and (3) trill rate (defined as the number of elements in the trill per second). The trill rate value (see Fig. 1) was calculated by not considering the last repeated part (iteration) of the series (either single element in click structures of different rates, while the middle line (d–f) shows clustering in two or more elements (trill type f was copied from a Common Nightingale song). Trill types in the bottom row (g–i) are less common and alternate both click and harmonic elements in different repetition patterns. Note that trill types a and d were the most common, shared by all individuals in both populations, and accounted altogether for 33% of all recorded trills.

![Fig. 2 Examples of trill types found in the western (W) and eastern (E) studied population. Trill type is labelled by a category letter and number code above each spectrogram box, as in the trill catalogue (see Online resource 1). The numbers above the upper right corner of each spectrogram show the trill rate (number of elements per second) calculated for the displayed trill, while the percentages on the left give the proportion the given trill constitutes among those analysed in each population. The first line of spectrograms (a–c) shows simple click structures of different rates, while the middle line (d–f) shows clustering in two or more elements (trill type f was copied from a Common Nightingale song). Trill types in the bottom row (g–i) are less common and alternate both click and harmonic elements in different repetition patterns. Note that trill types a and d were the most common, shared by all individuals in both populations, and accounted altogether for 33% of all recorded trills.](https://example.com/trill_examples.png)
simple trill structures or cluster of elements for complex ones), as follows: trill rate = (total no. of elements − no. of elements in the last iteration)/(trill duration − duration of the last iteration).

In a few cases, a trill comprised two different adjacent series (see for example trill types D6, D7, Online resource 1). In this case, the trill rate was calculated as the weighted average of the rate of each series, weighted by the series duration.

**Trill repertoire**

We evaluated the trill type repertoire of each bird to describe the trill diversity and its variation between individuals and populations. To achieve the most complete description of each individual’s repertoire, we analysed the recordings from all three stages of the experiment together. Trill categories were defined based on trill structural characteristics, i.e. the number and type of elements used in the repetition unit, as well as the trill rate. Trill categories with a similar structure strictly differed and never overlapped in trill rate despite some natural variation among individuals. The same trill category was typically used in only one or a few consistent song types (same association of syllables with minimal variation) and shared as such by multiple males within a population.

To estimate the proportion of trill categories shared by two males (A and B), we used a repertoire sharing index (RS) following Hultsch and Todt (1981) and Griessman and Naguib (2002). The index (numerically equivalent to the Jaccard similarity coefficient) was calculated as follows: RS(A, B) = rep(A, B)/[rep(A) + rep(B) − rep(A, B)]; with rep(A) and rep(B) being repertoire size (total number of trill types used) of individuals A and B, respectively, and rep(A,B) the number of trill types shared between those two individuals. The index can vary from 0 (no trill types shared) to 1 (all trill types shared).

To explore potential differences in trill type use within the same bird before and after stimulation, we used a similar approach to compare trill repertoires during spontaneous song (5 min recorded before the stimulation) and stimulated song (first 5 min of active song response for each bird during the playback or post-playback stage). In the same 5-min periods, we compared the proportion of songs with no trills (unfinished versions of “trilled” song types). This approach was chosen to ensure that a sufficient number of songs was available for analysis even for birds that ceased their singing activity for a substantial part of the playback stage of the experiment.

All sound analyses were performed using Avisoft-SASlab Pro version 5.2.09 (www.avisoft.com) with a sampling rate of 22,050 Hz and 16-bit accuracy.

**Statistical analyses**

Statistical analyses were performed with R software 3.6.0 (R Core team 2019). To test the various hypotheses of the study, we used linear mixed-effects models with the “lme” function (“nlme” package v. 3.1-40, Pinheiro et al. 2019) tested with the “anova” (ANOVA type I) function (see Table A1 for a summary of the different models). The models testing the influence of the playback stimulation on the tested variables (song traits: percentage of time spent singing, song duration, pause duration, song rate; trill traits: trill duration, number of elements in a trill, trill rate) included the stage of the experiment (before, during or after the playback) and male population of origin (eastern or western) as fixed effects, and the individual identity as random effect. Since the recordings used as the source of the playback stimuli came from a locality closer to the western population than the eastern one, which might possibly influence the male reaction due to familiarity with the song or trill types in the playback stimuli, we also included in the model the interaction between experimental stage and male population of origin (Table A1, model 1b). The interaction term was removed from the next step of the analysis if proven non-significant (Table A1, model 1a). If a significant overall difference in song traits among experimental stages was observed but a population × stage interaction was not detected, the significance of pairwise differences between stages was tested by a post hoc pairwise comparison of means using the Tukey contrast method (“multcomp” package v. 1.4-14, Hothorn et al. 2008).

The proportion of songs containing trills was compared between the spontaneous singing (5-min period preceding the playback) and the provoked songs (5-min period after the first vocal response), following the same modelling approach as described above (Table A1, models 2a, 2b). In addition, we checked for a potential influence of the time of the day on the birds’ response, by considering separately four time periods of equal duration (3 h 45 min) between the earliest and latest experiment (Table A1, model 3).

The significance threshold for all our tests was set at \( p = 0.05 \). A Holm–Bonferroni correction was used to adjust \( p \) values when testing repeatedly multiple traits corresponding to our two main hypotheses (4 song variables, and 3 trill ones), using the R function "\( p\)-adjust".

**Results**

All tested males reacted to the playback stimulation, typically by singing and approaching the dummy, in rare cases even attacking it physically. All individuals were singing both before the playback (spontaneously) and after the stimulation, and the time of the day at which we tested the birds...
did not influence their response (Table A1, model 3, Online resource 2). The average number of songs per individual for each experiment stage (mean ± sd) was 31.7 ± 6 before playback, 19.1 ± 12.1 during playback and 32.9 ± 11.5 after playback.

Song characteristics (song or pause duration, song rate, or proportion of time spent singing) and the percentage of songs containing trills did not significantly differ between the two studied populations. However, we observed significant between-population differences in two associated trill characteristics (trill rate and number of elements), which tended to be lower in the western population (Table A1 models 1a,b and 2a,b; Table 1b). This was particularly pronounced in the trill rate. Specifically, in the spontaneous songs (before playback), the trill rate of all western males was 22.8 ± 0.86 (mean ± sd), while the same value for the eastern males was 26.6 ± 2.47. A similar pattern was also observed in the other two stages of the experiment. This was primarily caused by repertoire differences between populations, as the individuals from the west used overall faster trill types in their songs than those from the east (see “Trill repertoire use and diversity” below, and Online resource 1).

**Vocal response to playback stimulation**

**Song parameters**

Males significantly differed in their percentage of time spent singing and song duration over the experimental

| Table 2 | Comparison of the tested song parameters among the three stages of the experiment (before, during and after song playback) |
|---------|--------------------------------------------------------------------------------------------------------------------------|
| Song parameter | Stages | Estimate | SE | Z   | p      |
| Time singing | Before–after | 25.69 | 4.45 | 6.03 | <0.001 |
| Song duration | Before–after | 27.87 | 4.45 | 6.37 | <0.001 |
| Pause duration | Before–after | 6.87 | 0.37 | 3.44 | 0.002 |
| Song rate | Before–after | 4.07 | 0.37 | 2.63 | 0.023 |
| Number of elements | Before–after | 3.40 | 0.37 | 2.27 | 0.061 |

The table shows results of pairwise comparisons between experimental stages of those song parameters for which the overall model indicated a significant among-stage difference (Table 1a; Fig. 3).

The p values from individual tests under the model 1a were adjusted by Holm–Bonferroni correction for parameters associated with each other (i.e. four song parameters, and three trill parameters); differences significant after correction are indicated in bold. The degrees of freedom used in the model calculation are given as numDF (numerator degree of freedom) and denDF (denominator degree of freedom). Detailed results of the models also incorporating the interaction between experimental stage and population of origin are provided in the Online resource 2. Note that a significant interaction of population and experimental stage was observed for the trill duration, so further comparisons between experimental stages were not performed for this trait.
stages (Tables 1a and 2; Fig. 3a, b). They sang significantly shorter songs and spent less time singing during the playback period compared to both the spontaneous and post-playback ones. Males also varied in the duration of pauses between songs, significantly shortening them after the playback stage (Tables 1a and 2; Fig. 3c). Shorter pauses in the post-playback phase were partly offset by the increase of the song duration (Fig. 3a) but there was an overall tendency to increase the song rate in response to the playback, and the difference in song rate between the playback and post-playback phases of the experiment was significant (Tables 1a and 2; Fig. 3d). Considering the song traits, males from the two populations did not differ in their reaction, as no relevant interactions between the experimental stage and population were significant (Online resource 2).

Fig. 3 Song parameters in the three experimental stages: before, during and after the playback stimulation (a = percentage of time spent singing, b = song duration, c = pause duration, d = song rate). Box-and-whisker plots depict the median, interquartile range, and non-outlier range (whisker length up to 1.5 times the interquartile range). Note that periods when the birds entirely ceased singing were excluded when estimating the pause duration and song rate.
Trill parameters

The males retained remarkably stable trill rate throughout all three stages of the experiment (Fig. 4b). The overall changes of the trill duration and the number of elements followed the trends observed in the song duration (decrease during the playback stage, and return to original pre-playback values afterwards; Fig. 4a, c). However, the trend in the number of elements within a trill was not significant after correction for multiple testing (Table 1a), and the significant interaction between experimental stage and population of origin for the trill duration (adjusted $p=0.047$; detailed results in Online resource 2) indicated that males from the two tested populations did not respond consistently in this trait. All but one male from the western population reduced to some extent the trill duration, while those from the eastern population did not exhibit any particular trend. The proportion of complete songs (i.e. finished by a trill) was variable but showed no tendency to change in the first 5 min of active vocal response after stimulation in comparison with the spontaneous singing (Table 1a); there was neither a significant effect of population nor a population × stage interaction (Online resource 2).

Overall, most Thrush Nightingale trills were no longer than 2 s and rarely exceeded the trill rate of 40, and there was no clear pattern in the relationship between the trill duration and rate (Fig. 5a). However, only a few males performed the trills with extremely high duration or rate values, and we never observed a trill that would be both very long and very fast (Fig. 5b–d).

Trill repertoire patterns

Within the analysed recordings of 20 tested males, we recognized altogether 30 trill types organised into 5 categories (A to E, see examples in Fig. 2 and the full trill type catalogue in Online resource 1). All tested males used multiple trill types in their songs (mean ± sd = 9.7 ± 2.5 types). Likewise, males did not show a substantial difference in trill type use before and after stimulation (intra-individual trill repertoire sharing index (RS) before and after stimulation, mean ± sd: RS = 0.8 ± 0.2, Fig. 6).

The mean sharing index between individuals from the same population was 0.75 ± 0.2 (mean ± sd) within the western population and 0.53 ± 0.2 within the eastern population, suggesting an extensive sharing of trill types among...
Fig. 5  a Relationship between trill duration and trill rate in all individuals. The solid rectangles (enlarged in b and c) highlight the clustering of trills with highest rate values. These were of different trill types (A3, C5, C6) only sung at such high rates, all performed by two males. The dotted rectangle (enlarged in d) highlights the longest trills, all of three trill types (B8, D4, D6) performed by three different males. The highlighted fastest or longest trills constituted altogether less than 2% of all measured trills.

Fig. 6  Number of trill types used by tested males before and after stimulation. The bars reflect the trill repertoire size used only during 5 min of spontaneous songs (white), used only during the 5 min after the first vocal response (dark grey) and shared between the two periods (hatched). Population of origin is indicated by the first letter of the male code. Intra-individual repertoire sharing scores, comparing trill use before and after stimulation, are displayed above each bar.
individuals of the same population. Trill types were shared, although to a substantially lower extent, also between western and eastern populations ($RS = 0.21 \pm 0.07$). Overall, however, the repertoire composition, and thus, sharing index varied substantially among the individuals (Table 3).

Discussion

Males provoked by the simulated territorial intrusion spent less time singing and used shorter songs during song playback. After the playback ceased, they returned to a similar singing style as during the pre-playback period, slightly increasing the overall song rate. However, contrary to our expectations, we have not observed any significant change of trill rate, increase of proportion of songs with trills, or substantial changes in trill category use. The only observed pattern in trill characteristics was a shortening of trill duration during the playback stage in the western population, and the tendency to decrease the number of trill elements. Such changes are not consistent with trills being a signal of aggressive motivation; rather, they seem to be related to the highly significant overall shortening of the songs sung by tested males during the playback. Altogether, our results do not support the hypothesis that trills in Thrush Nightingale songs play an important role in male aggressive territorial interactions.

Though contrasting with the findings of the previously mentioned studies, in which trill song structures were related to an aggressive context or motivation in several species (DuBois et al. 2009; Vehrencamp et al. 2013; Petrusková et al. 2014), our results are not striking. Given the immense interspecific variability of birdsong, it is not surprising that the same parameters or structures may differ in function when compared among different species. For example, while the number of soft songs was a significant predictor of attack in Song Sparrows (Melospiza melodia; Searcy et al. 2006), they were not identified as an aggressive signal in Ortolan Buntings (Emberiza hortulana; Jakubowska and Osiejuk 2018). Such differences can be found even between closely related species, as already shown in wrens (Troglodytes spp.)—Banded Wrens responded differently to trills of different consistency (De Kort et al. 2009), while House Wrens (T. aedon) tested in similar experiments did not (Cramer 2012).

Nightingales might just be another example of such closely related species for which similar structures differ in function. While Common Nightingales sang more often song types containing broadband trills in response to playback stimulus (Kunc et al. 2006), it was not the case for the Thrush Nightingales in our study. One possible explanation might be the difference in song composition between the species, as broadband trills are the typical endings of most territorial Thrush Nightingale song types (Sorjonen 1983, 1987), but are less frequent in Common Nightingale songs (Sorjonen 1986; Kunc et al. 2006; Marova et al. 2015a). Moreover, in our populations, a specific trill type was always associated with only one or a few song types. This suggests the existence of syntactic rules constraining the variability of syllable associations and influencing the ability of the

Table 3  Trill type sharing between 20 Thrush Nightingale males from the 2 tested populations, expressed in number of shared trill types (above diagonal) and repertoire sharing index (below diagonal)

|      | W01 | W02 | W03 | W04 | W05 | W06 | W07 | W08 | W09 | W10 | E01 | E02 | E03 | E04 | E05 | E06 | E07 | E08 | E09 | E10 |
|------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| W01  | 8   | 6   | 8   | 8   | 8   | 6   | 8   | 8   | 8   | 8   | 3   | 3   | 2   | 3   | 3   | 3   | 5   | 5   | 5   | 5   |
| W02  | 6   | 8   | 6   | 8   | 8   | 8   | 8   | 8   | 8   | 8   | 3   | 3   | 2   | 3   | 3   | 3   | 5   | 5   | 5   | 5   |
| W03  | 0.62| 0.57| 0.67| 0.66| 0.66| 0.66| 0.66| 0.66| 0.66| 0.66| 2   | 2   | 2   | 3   | 2   | 3   | 2   | 3   | 2   | 3   |
| W04  | 0.55| 0.62| 0.88| 0.88| 0.88| 0.88| 0.88| 0.88| 0.88| 0.88| 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   |
| W05  | 0.58| 0.89| 0.90| 0.90| 0.90| 0.90| 0.90| 0.90| 0.90| 0.90| 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   |
| W06  | 0.40| 0.67| 0.67| 0.67| 0.67| 0.67| 0.67| 0.67| 0.67| 0.67| 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   |
| W07  | 0.62| 0.60| 0.60| 0.60| 0.60| 0.60| 0.60| 0.60| 0.60| 0.60| 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   |
| W08  | 0.67| 0.89| 0.90| 0.90| 0.90| 0.90| 0.90| 0.90| 0.90| 0.90| 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   |
| W09  | 0.50| 0.80| 0.80| 0.80| 0.80| 0.80| 0.80| 0.80| 0.80| 0.80| 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   |
| W10  | 0.52| 0.67| 0.67| 0.67| 0.67| 0.67| 0.67| 0.67| 0.67| 0.67| 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   | 3   |

The index is based on a pairwise comparison of trill repertoires between males; populations of origin (western vs. eastern) are indicated by the first letter of male code. Intensity of cell shading reflects the level of sharing.
Thrush Nightingale males to modulate their singing style. This would be consistent with the results of a recent study from Ivanitskii et al. (2016), describing how Thrush Nightingales tend to use a linear syntax, singing song types in a fixed order performed as sequences, likely constraining the potential modulation of its constitutive song parts. These mechanisms may allow to maintain large repertoires by developing clearly stereotyped songs.

Such song variability is expected to be an advantage at different levels. First, females may favour a large song repertoire size as an indicator of male quality (reviewed in Byers and Kroodsma 2009; see also Kipper et al. 2006). Second, matching the song of neighbouring males has been shown to play an important role in territorial interactions in many species (Payne 1982; Naguib et al. 2002; Bartsch et al. 2014; Liu et al. 2018), also including Common Nightingales (Naguib et al. 2002). In addition, Sorjonen (1987) documented that the song type repertoire of a single Thrush Nightingale male is more similar to repertoires of current neighbours than to its own from a previous year. More recently, Griessmann and Naguib (2002) showed that neighbours shared significantly more song types than non-neighbours, supporting the hypothesis that repertoire sharing might indicate territory tenure. However, despite the divergence in song type repertoires between our tested populations, almost half of the trill types were shared between them, suggesting at least some functional advantage to maintain these specific structures.

When exploring further the relationship between the trill parameters, the trill delivery rate did not appear to be under constraints for a large majority of the recorded trills. Nonetheless, the fastest and longest trills performed during our experiment, regardless of the experimental stages, were only produced by a few males over the same trill types, always sung with minimal variation in these parameters within or between individuals. Together with the fact that no trill types combined very long duration and very fast rate, this may suggest that, to some extent, those trill parameters might be under production constraint. Though not playing a direct role in territorial interactions in our study, fast broadband trills could thus be preferentially used as an honest quality signal directed to females, as also found in several species (Ballentine et al. 2004; Ballentine 2009; Caro et al. 2010). Interestingly, however, the trill characteristics (especially trill rate) were strongly population-dependent, with the birds in the eastern population singing significantly faster trills than those in the western population both in spontaneous and provoked songs.

To conclude, the results of our study do not support a clear role of trills in agonistic territorial signalling in Thrush Nightingale. This was demonstrated by the finding that individuals provoked by the simulated intrusion of a conspecific male did not change the trill rate, did not increase the trill duration in their song (rather, the opposite), and did not switch to different trill types, but rather escalated non-vocal behaviour. This challenges the view of rapid broadband elements as a common agonistic signal in songbirds and highlights that the same trait could vary in function between species with high song complexity, even closely related ones. While the temporal parameters related to song structure performance and diversity are likely reflecting the influence of different selective pressures, our results advocate for more studies concerning alternative roles of Thrush Nightingale broadband trills in other contexts, for example mate quality signalling, and their potential relationship with traits such as age or body size.

Supplementary Information is available from the corresponding author on request.

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Due to our non-invasive recording approach, no bird had to be captured or handled during our experiments. Playback settings were designed to minimise the territorial disturbance and the tested birds usually resumed their singing routine shortly after.

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