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ORIGINAL ARTICLE

The use of soft songs during territorial intrusion in alarm context in the Ortolan Bunting *Emberiza hortulana*

Aleksandra Jakubowska[1] · **Tomasz S. Osiejuk**[1]

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Abstract

Animals from many taxa produce low amplitude acoustic signals. In some birds such soft signals were found to be uttered in aggressive context and were the best predictor of subsequent physical attack. This phenomenon is poorly understood and several hypotheses have been proposed to explain the function(s) of the lowered amplitude of such signals. The eavesdropping avoidance hypothesis suggests that the use of low amplitude signals limits the possibility of signal detection by third-party receivers such as predators or conspecific rivals. Herein, we aim to investigate if soft songs in the Ortolan Bunting *Emberiza hortulana* are used in order to avoid being predated or eavesdropped by potentially threatening conspecifics. We simulated alarm situation by playback of conspecific alarm calls. We measured the overall strength of males' response to territorial intrusion and number of soft songs in response to a risky situation compared to a control condition. Males showed a weaker approaching response to territorial intrusion and produced more soft songs if previously exposed to conspecific alarm calls and this behaviour is consistent with the eavesdropping avoidance hypothesis. However, we did not observe a complete switch to singing softly in alarm context, and both during the treatment and control males uttered loud calls in response. We suggest that soft songs in the Ortolan Bunting facilitate mediation of the territorial conflict by signalizing change in current motivation. Alternatively, soft songs might be related to readiness to fight or enable addressing signal to a specific receiver within a close range.

Keywords Soft song · Eavesdropping avoidance hypothesis · Aggressive signals · Territorial defence · Ortolan Bunting

Zusammenfassung

Die Rolle leisen Gesangs beim Ortolan *Emberiza hortulana* während einer Revierverletzung in einer Alarmsituation. Tiere vieler Taxa geben akustische Signale niedriger Amplitude von sich. Bei manchen Vogelarten wurde die Äußerung solcher leisen Signale in einem aggressiven Kontext beobachtet, und diese waren das sicherste Anzeichen für einen anschließenden physischen Angriff. Dieses Phänomen ist weitgehend unerforscht und es gibt verschiedene Hypothesen, welche die Funktion(en) der geringeren Amplitude solcher Signale erklären sollen. Die Abhörvermeidungs-Hypothese besagt, dass die Nutzung von Signalen geringer Amplitude die Gefahr der Signalwahrnehmung durch Dritte, beispielsweise Prädatoren oder arteigene Rivalen, einschränken soll. Unser Ziel war es hier zu untersuchen, ob leiser Gesang beim Ortolan der Vermeidung von Prädation dient oder ob er verhindern soll, von potenziell bedrohlichen Artgenossen bemerkt zu werden. Wir simulierten eine Alarmsituation durch das Vorspielen arteigener Warnrufe. Wir erfassten die Gesamtstärke der Reaktion der Männchen auf die Revierstörung sowie die Anzahl leiser Gesänge als Antwort auf eine Gefahrsituation im Vergleich zur Kontrollsituation. Die Männchen zeigten ein schwächeres Annäherungsverhalten in Reaktion auf eine Revierstörung und äußerten mehr leise Gesänge, wenn sie zuvor mit arteigenen Warnrufen konfrontiert worden waren, was im Einklang mit der Abhörvermeidungs-Hypothese steht. Allerdings konnten wir keinen vollständigen Wechsel zu leisem Gesang im Alarmkontext beobachten; die Männchen äußerten sowohl im Versuch als auch in der Kontrollsituation laute Rufe als Reaktion. Wir vermuten, dass leise Gesänge beim Ortolan die Lösung eines Territorialkonfliktes erleichtern, indem sie Änderungen der momentanen Motivation anzeigen. Andererseits könnte der leise Gesang mit der Bereitschaft

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zum Kampf zusammenhängen oder eine Möglichkeit darstellen, ein Signal an einen spezifischen Empfänger im Nahbereich zu übermitteln.

Introduction

The amplitude of acoustic signals indicates the active range and therefore is a critical feature of vocalization by which animals may address or avoid specific potential receivers (Marten and Marler 1977; Brenowitz 1982). The advertising signals used to attract females or deter rivals are usually loud and their amplitude is optimized to maintain wide active range with some limiting factors like body size, condition or motivation (Bradbury and Vehrencamp 2011). Among other animals, birds also produce unusually low amplitude acoustic signals. Such signals have been previously described (Nice 1943) and referred to as 'soft song', although other names for such vocalizations have also been used (Dabelsteen et al. 1998; Searcy and Nowicki 2006; Reichard and Anderson 2015). One of the most surprising observations is that some soft signals are used in strictly aggressive contexts and are the best predictors of subsequent physical attack (Searcy et al. 2006; Ręk and Osiejuk 2011). It seems to be even more intriguing in the light of our poor understanding how amplitude, a critically important component of any acoustic signal, is linked with costs maintaining signal honesty and even what type of costs (metabolic, social, predation etc.) are crucial for this parameter (Zollinger and Brumm 2015). Several hypotheses which are not always mutually exclusive were raised to explain this behaviour, but we are still quite far from generalization as available evidence is not consistent and is restricted to a limited number of species (Dabelsteen et al. 1998; Osiejuk 2011; Akçay et al. 2015; Reichard and Anderson 2015).

One of the earliest hypotheses attempting to explain the function of low amplitude signals in an aggressive context was that a lower amplitude limits the possibility of a signal being detected by third-party receivers (eavesdropping avoidance hypothesis; Dabelsteen et al. 1998). The logic of this explanation is as follows: males in a direct conflict are close enough to hear soft signals, with such signals reducing the chance of being detected by a predator (Mougeot and Bretagnolle 2000; Schmidt and Belinsky 2013) or another rival other than the one already involved in the interaction (reviewed in Akçay et al. 2015). Indeed, the predation risk for small passerines is often quite high and birds have the capacity to assess risks and respond by changing their behaviour (Lima 2009). However, if and how this risk affects soft song signalling was surprisingly rarely tested. To our knowledge the only species tested until now is the Song Sparrow *Melospiza melodia*. Searcy and Nowicki (2006) simulated an increased risk of predation with playback of Song Sparrow alarm calls and tested whether such treatments affected the rate of soft song use in this species. They did not find any support for the predation risk hypothesis but rather that the Song Sparrow produced proportionally fewer soft songs in the presence of a predator. In a more recent study, Akçay et al. (2016) experimentally increased the perceived predation risk by playing predator calls during territorial intrusion and compared Song Sparrow response with behaviour during a control in which non-predator Flicker calls were used for playback. Despite the fact that the birds clearly differentiated their response between treatment and control, there was no supporting evidence for the eavesdropping avoidance hypothesis.

Our research focuses on the Ortolan Bunting *Emberiza hortulana*, a small Eurasian passerine breeding in open (mostly farmland) habitats. Males have usually small repertoires of two–three song types delivered for most of the time with eventual variety (Cramp and Perrins 1994; Osiejuk et al. 2003). The Ortolan Bunting is well studied in terms of response to rival songs in a territory defence context. Males' ability to discriminate between known and foreign dialects, neighbours and strangers, and the functions of other song characteristics such as duration or song type switching have been addressed in earlier studies (Skierczyński et al. 2007; Osiejuk et al. 2007a, b; Jakubowska and Osiejuk 2017). Territorial males responding to simulated strangers' song immediately approach the speaker and switch from singing to intensive calling. In natural situations, rival intrusion may end with a physical fight, especially before and shortly after mating. In such aggressive contexts males were also observed to produce soft songs which have similar structure to broadcast songs but might can be slightly shorter (Fig. 1). In an earlier experimental study we tested whether the soft songs of the Ortolan Bunting are a signal of increased aggressiveness (Jakubowska and Osiejuk 2018). We found that soft song in this species does not meet the context, prediction and response criteria of aggressive signal specified by Searcy and Beecher (2009). Territory owners did not vary their response to intruder regardless of whether they used or did not use soft song. Males respond stronger to loud songs than to soft ones and did not treat soft song as a predictor of signal escalation. However, depending on the type of experiment, soft songs appeared in 40–60% of simulated intrusions,

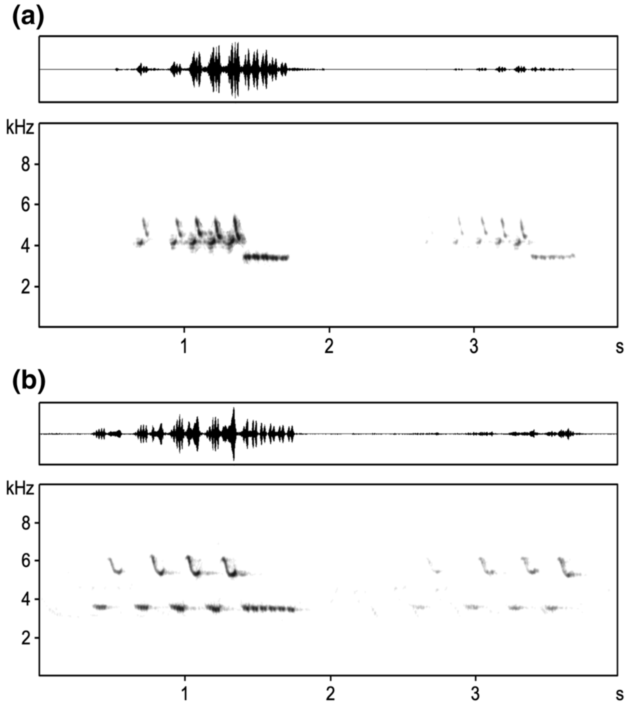

Fig. 1 Two examples of loud and soft songs of two different Ortolan Bunting males. In both cases the loud and soft songs were recorded from the same distance to males and the recordings were only manipulated by means of filtering frequencies below 1.2 kHz and cutting the time between loud and soft song by a few seconds. In the first example (**a**) the male used the same song type structure in both the loud and soft version, while in the second example (**b**), the male shortened the final song phrase in the soft version. Spectrogram parameters: FFT length 1024, frame size 75%, overlap 75%, frequency resolution 47 Hz, temporal resolution 5.33 ms

but the occurrence of such songs was usually low in comparison to broadcast songs (Jakubowska and Osiejuk 2018; own unpublished material). The research mentioned above may suggest that soft song can be a tool to decrease the active range of signal, but the reason for this change was not tested explicitly.

The aim of this study was to test experimentally whether soft songs occur in the territorial Ortolan Buntings more frequently in an alarm context. We simulated higher risk by using playback of conspecific alarm calls preceding later intrusion of a stranger male rival. In accordance with the predator eavesdropping avoidance hypothesis, we predicted that soft songs should be produced more frequently under risky conditions than during the control. Specifically, we expected a complete switch to the use of soft songs and avoidance of producing any loud signals. We also predicted that in simulated increased predation risk situations, the overall response of males should be weaker in comparison to non-threatening situations as males should behave in a more cautious way.

Methods

Study area and subjects

This study was conducted in farmland habitats surrounding forests of Wielkopolski National Park in western Poland (the centre of the study area was 52°17′N and 16°56′E). Ortolan Buntings are common in this region and breed along forest edges and older tree lanes surrounded by cultivated fields. The study species has been regularly recorded in this area since 1998 with birds occurring at a density of up to seven singing males per 1 km transect (own unpublished data). Experiments described below were conducted in the spring of 2016. Before experiments began we located territories and song posts using a Garmin GPSMAP 76CSx receiver and recorded virtually all males within the study area. Birds were only partly individually marked with colour rings, but their identity was confirmed on the basis of repertoire composition and individually variable frequency of the initial part of the song (for details, see Osiejuk et al. 2005; Osiejuk 2014).

Playback equipment, song and call stimuli

For the playback experiments we used a single UE BOOM speaker (frequency range 90–20,000 Hz) connected to an Olympus Ls-12 recorder. The Ortolan Bunting songs used for playback in the experiments were recorded in the study area using a Marantz PMD661 solid state recorder coupled with a Sennheiser MKH70 microphone equipped with a Sennheiser MZW 60-1 basket windshield and a Sennheiser MZH 60-1 long hairy cover or a Telinga Pro-6 Twin Science parabolic microphone with a windshield. The songs used for playbacks were recorded at short distances during windless mornings and were characterised by high signal to noise ratio. The songs selected for playback were ≤ 2 kHz high-pass filtered (Avisoft SASLab Pro 5.x, Raimund Specht, Berlin, Germany) and then adjusted to match the amplitude level and envelope of natural songs (i.e. 86 dBA at 1 m from the loudspeaker). The sound pressure level (SPL) value was set according to the amplitude level of loud Ortolan Bunting songs which had previously been measured in the field using a CHY 650 Sound Level Meter. The amplitude manipulations were small and did not affect the song structure. All of the sounds recorded and used for playback were PCM WAVE files, with a 48-kHz sampling rate and a 16-bit resolution. In each experiment and treatment, we used songs derived from repertoires of different stranger males from the local population. During playback two different song types were presented with eventual variety, i.e. six examples of the first song type and six examples of the second, which reflects the natural behaviour of the study species well. The sound recordings are available at https://doi.org/10.7479/0k18-gzxm.

We used alarm calls of the Ortolan Bunting for the treatment and contact calls of the Chaffinch *Fringilla coelebs* for the control (Fig. 2). We used the Ortolan Bunting calls referred to in the literature as 'tseep' and 'tjut', which are most typically used in an alarm context and occur with an alternating pattern (Cramp and Perrins 1994). Chaffinch contact calls called 'weet' (Clement 2018) were used as a result of the co-occurrence of this species with that of the Ortolan Bunting, with both species calls comprising most calls in the local soundscape. On the other hand, Chaffinches and Ortolan Buntings do not compete in a direct way and Chaffinch contact calls are probably not a signal (especially warning signal) for the study species.

To prepare call samples for playback, we first selected good-quality samples from our own recordings from the same populations (Chaffinch was a subject of other study: Deoniziak and Osiejuk 2016). On the basis of these natural calls, we prepared their synthesised versions with Avisoft SASLab Pro 5.x. For both species, the calls used are relatively simple whistles, and scanning of frequency contour and amplitude envelope in Avisoft SASLab Pro enabled preparation of high-quality samples for reproduction. In the case of alarm calls, the synthetic copies were based on calls of 26 different males and we mixed the 'tseep–tjut' sequence with a natural rate of 26 calls per minute and natural amplitude (78–89 dBA at 1 m). In the case of Chaffinch contact calls, which are less variable, we prepared samples of 59 calls per minute (based on calls of 22 different males) varying in amplitude within the natural range (82–86 dBA SPL at 1 m). The use of synthetic copies of natural calls allowed us to obtain better-quality sound samples in comparison to just filtered and amplified natural calls. Before experiments we tested synthetic copies with both species and found that they evoke a response from conspecifics as for natural calls.

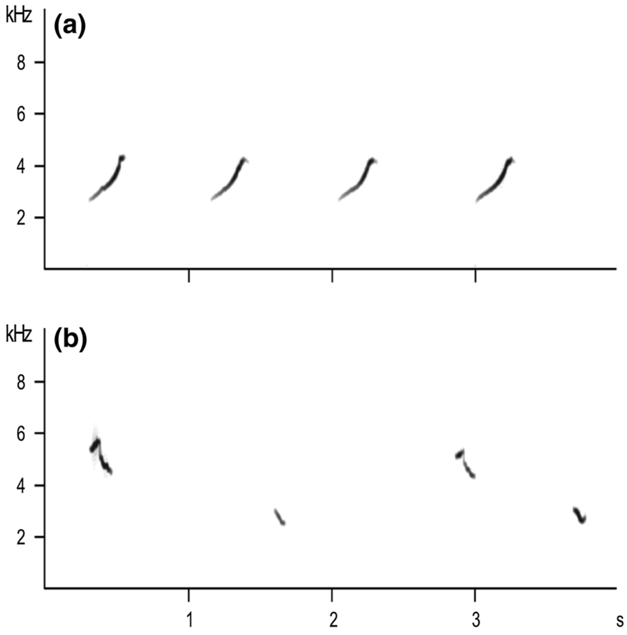

Fig. 2 Spectrograms of calls used in experiments: **a** synthetic chaffinch *Fringilla coelebs* calls, **b** synthetic Ortolan Bunting *Emberiza hortulana* calls. FFT length 1024, frame size 75%, overlap 75%, frequency resolution 43 Hz, temporal resolution 5.805 ms

Playback experiment protocol

The experiment was conducted between 3 and 16 of May 2016. Each male ($n = 20$) was subject to treatment and control on consecutive days in a counterbalanced order. During both the treatment and control the singing males were first recorded for 2 min (pre-playback phase) in order to obtain a baseline of each male's vocal activity. Then, in the treatments, we presented a series of Ortolan Bunting alarm calls with natural amplitude and timing for 1 min. In the control experiments a series of chaffinch contact calls (call playback phase) were used instead of Ortolan Bunting alarm calls. After a pause of 30 s we started 2 min of playback of the Ortolan Bunting song (playback phase) followed by 2 min of later observation (post-payback phase).

Before each experiment we positioned a microphone array consisting of four Sennheiser Me62 omnidirectional microphones with K6 power units and dedicated windshields to cover the arena of the experiment. Microphones were connected to radio transmitters (Sennheiser SKP 3000) which sent sound as a UHF radio signal to a Sennheiser EK 3241 true diversity signal receiver with a dedicated power unit (NT 3-XLR 4). The system also consists of a Sennheiser QP 3041 signal splitter, a two-antenna Sennheiser A 2003 UHF and AB3 antenna power units. Finally, the synchronised tracks were recorded to an Edirol Roland 4-channel recorder. The position of microphones was precisely measured with a distance meter. The utilisation of a wireless array enabled the measurement of a bird's singing position and comparison of amplitudes of songs given from particular positions (more details in response variables description).

In addition to all experimental periods being recorded with microphone arrays, focal males were also recorded from a distance with a Marantz PMD 661 recorder coupled with a Telinga Pro-6 Twin Science microphone by one of the observers (AJ). A second observer (TSO) dictated the birds' behaviour into an Olympus LS12 recorder.

Measures of male response

The following measures of response to playback were recorded in the field: flight latency towards the speaker (s), latency to approach within 5 m of the speaker (s), time spent during and after playback within 5 m of the speaker (s), closest approach to the speaker (m), and the number of flights, songs (with soft song counted separately) and calls after playback start. All these measures describe male response during playback and post-playback stages of both experiments. We used a Bushnell Yardage Pro Sport laser rangefinder (1 m accuracy) to measure the distance between the speaker and the position of the focal male before experiments. A rangefinder and tape measure were also used to determine landmarks within the potential arena where a bird may fly.

The categorization of songs into loud and soft in the field presents some challenges. In earlier experiments we observed that males recorded at a particular, fixed distance sometimes change their song amplitude, which is relatively easy to noticed by ear (cf. Searcy and Nowicki 2006). Comparison of loud and soft songs recorded from the same distance to birds indicated that soft signals have an amplitude lower, by at least 12–15 dBA in comparison, to typical broadcast songs that are 86 dBA at 1 m (own unpublished data). In order to categorize songs as loud or soft we used a two-step approach. Firstly, both observers who were recording dictated into recorders if they perceived that the song sung by a male was softer than normal. Second, the microphone array recordings were used to locate the position of males during singing. This was done with an acoustic locator algorithm in XBAT (v. 0.6.1, Cornell Lab of Ornithology) as used in a previous study on the Corn Crake *Crex crex* (Ręk and Osiejuk 2010). We also prepared a set of 64 Ortolan Bunting songs with different and directly measured amplitudes (with CHY650 sound level meter). We then played this set of songs from different positions (2, 4, 8, 16, 32 m) within the microphone array and measured re-recorded sounds with the inband power (dB) measure in Raven Pro 1.5 (Cornell Lab of Ornithology). We found a significant and strong correlation between measured song amplitudes and the inband power value corrected for distance (e.g. for 8 m distance: $r = 0.92$, $n = 64$, $p < 0.001$). On the basis of the mentioned measurements, we compared the amplitude of songs suspected to be soft (as indicated by observers) with the amplitude of loud songs with inband power (dB) measurements. We assumed that a song is soft if the difference between loud and target song was over 12 dB. If both loud and soft songs were uttered from the same place we compared them directly. If such a comparison of songs was impossible because of the movement of an individual, we corrected the amplitude measurement for distance differences (assuming 6 dB decrease with doubling distance). On the basis of the comparison of dictated observations and later amplitude measurements, we found that there is 95% agreement and that qualified observers are able to differentiate between loud and soft songs easily. This was not surprising as typical loud songs of the Ortolan Bunting are audible for human observers from around 300 m, while soft songs are audible from less than 30 m.

Statistical analyses

As the response of Ortolan Buntings to territorial intrusion is multidimensional, we combined all original variables (except soft songs number) describing the behaviour of males during and after simulated rival intrusion into orthogonal principal components using principal component analysis (PCA). We did not treat the number of songs, calls and flights separately for the playback and after playback phase, as they were significantly correlated between those phases. We obtained reliable, compound measures of approaching behaviour and vocal response (Table 1). As indicated (footnote of Tables 1) the data set was appropriate for PCA and the degree of common variance among the original variables was adequate (Tabachnick and Fidell 2013). The first component (PC1) described behaviours related to the approaching of males to the speaker, with lower values indicating faster and stronger responses. The PC2 reflected vocal response, with lower values indicating a more aggressive response, i.e. switching from singing to intense calling. The principal components obtained were later used for testing differences in overall male response between treatment and

Table 1 Principal component analysis for original variables of response measured during playback and post-playback phases of the experiment

Statistics and original response variable	Component	
	PC1—approaching	PC2—vocal response
Eigenvalue	3.23	1.89
% of variance	46.15	27.00
Cumulative %	46.15	73.15
Flight latency	0.54	0.52
5 m distance latency	0.90	0.21
Time within 5 m distance	− 0.88	− 0.06
Closest distance	0.85	0.11
Flights after playback start	− 0.65	− 0.16
Songs after playback start	0.38	− 0.86
Calls after playback start	− 0.59	0.68

Eigenvalues, variance explained and weightings of the original variables in the first two principal components extracted from the original variables of the response to the playback

We assessed the factorability of the data; according to the Bartlett test of sphericity (158.83, $p < 0.001$), the data set should be considered appropriate. The Kaiser–Meyer–Olkin measure of sampling adequacy had a value of 0.713; therefore, the degree of common variance among the original variables was adequate control using a generalized mixed model with a Gaussian family and a log link function (later GLMM).

We found that the Ortolan Buntings produced soft songs during experiments, but this behaviour was rare and did not occur in all trials. Therefore, we applied separate models for testing the significance of the differences in soft song occurrence between treatment and control. Soft song occurrence was treated as a binary or Poisson distributed response variable. Besides presenting some basic tests, we also used multilevel mixed-models with binary or Poisson response variables in order to include potentially confounding variables into our models.

In the aforementioned mixed (or multilevel) models, male identity was included as a random intercept and the following variables were included as fixed parameters: treatment, order (treatment or control first). Distance to speaker before playback began and number of songs sung before playback were identified as covariates. We used Akaike's information criterion modified for small sample sizes (AICc) to choose the best models (Burnham and Anderson 2002). Basically, models were built using all the different predictor variable combinations including first level interactions and comparisons with null models. In the present study, we refer only to models which had ΔAICc < 2 (Arnold 2010; Burnham et al. 2011). Akaike weight (w_i) was used to provide normalized relative model likelihoods with higher values indicating the model with the best predictor set. All statistical analyses were calculated in IBM SPSS Statistics v. 24 (IBM Corp., New York, USA) and STATA/SE 15.1 (StataCorp, College Station, TX, USA).

Results

General response to playback

We found significant differences in approaching responses (PC1) of males between the treatment (conspecifics alarm calls) and control (chaffinch contact calls) (Fig. 3). The best fitted model included treatment, order, initial distance to speaker and number of songs sung before playback (Akaike's weight $w_i = 0.94$). Birds clearly approached the loudspeaker more quickly, did more flights and stayed closer to the speaker for a longer time when previously exposed to Chaffinch contact call playback rather than conspecific alarm calls (treatment effect, $\beta \pm \mathrm{SE} = 0.93 \pm 0.203$, $p < 0.001$). We found a significant effect of trial order, with males approaching less strongly if they had first responded to the alarm call treatment (order effect, $\beta \pm \mathrm{SE} = 0.78 \pm 0.233$, $p = 0.001$). We also found significant effects of the distance to speaker before experiment and number of songs sung before playback start. The strength of male response was negatively related to distance ($\beta \pm \mathrm{SE} = 0.017 \pm 0.0.05$, $p = 0.001$) and positively related to the intensity of singing before playback start ($\beta \pm \mathrm{SE} = -0.05 \pm 0.016$, $p = 0.002$). All the other models indicate a significant treatment effect but had ΔAICc > 2.

We found no significant effect of treatment on vocal response (PC2; Fig. 3). The best fitted models with ΔAICc < 2 (best model: PC2 ~ treatment + order + distance, $w_i = 0.43$; second best model: PC2 ~ treatment + order + distance before, $w_i = 0.19$) only indicated a significant effect of trial order. Males responded stronger

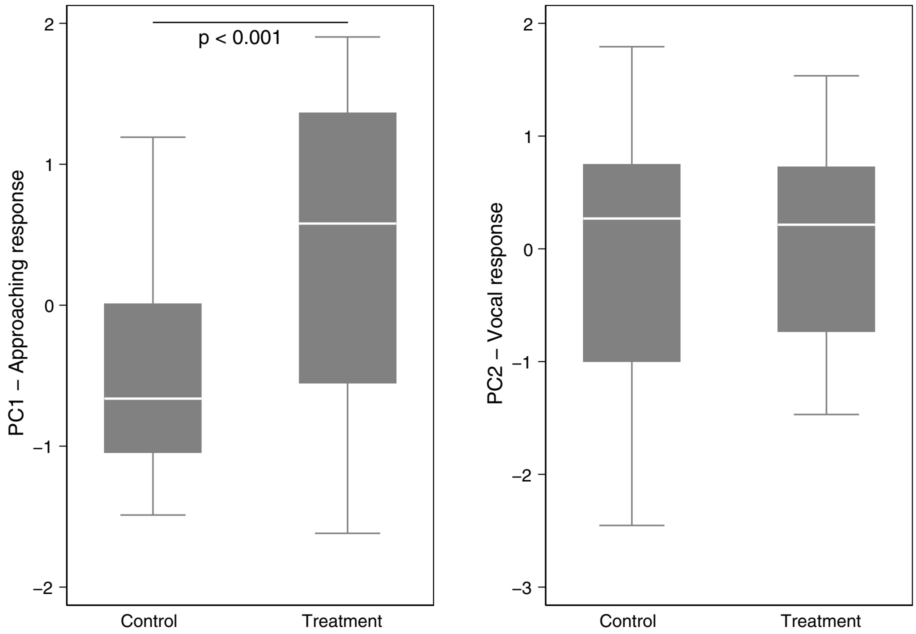

Fig. 3 Approaching (PC1) and vocal response (PC2) of Ortolan Bunting males as measured with principal components (see Table 1). Boxes consist of median, 25th and 75th percentile whiskers

(more calls than loud songs) if they were first subject to control conditions ($\beta \pm SE = -0.81 \pm 0.341$, $p = 0.017$).

Soft songs in response

No male sang soft songs before the start of the playback. Males produced soft songs during and/or after playback during 16 treatments (80%) and 9 control (45%) trials. Across all trials, males produced from 0 to 12 soft songs with an average (± SE) of 3.1 ± 0.69 in treatment and 1.1 ± 0.44 in control conditions. These values are small in comparison to the number of loud songs produced in the treatment (12.2 ± 2.57) and control (14.0 ± 3.31) conditions. The same males were not more likely producing soft calls in both the treatment and the control conditions (Fisher's exact $p = 0.569$). The best multilevel mixed-effects logistic regression model (and the only one with $\Delta AICc < 2$; $w_i = 0.61$) included a single predictor and showed a significant effect of treatment on soft song production (included as a binary response). Males used soft songs more frequently in treatment than in control conditions ($\beta \pm SE = -2.19 \pm 1.05$, $p = 0.037$). A consistent result was obtained using a multilevel mixed-effects Poisson regression model, in which number of soft songs sung during the experiment was included as a dependent variable. We found that there were significantly more soft songs produced during treatment than during control trials ($\beta \pm SE = -1.01 \pm 0.243$, $p < 0.001$) in the best fitted model with a single predictor (the only model with $\Delta AICc < 2$; $w_i = 0.87$; Fig. 4).

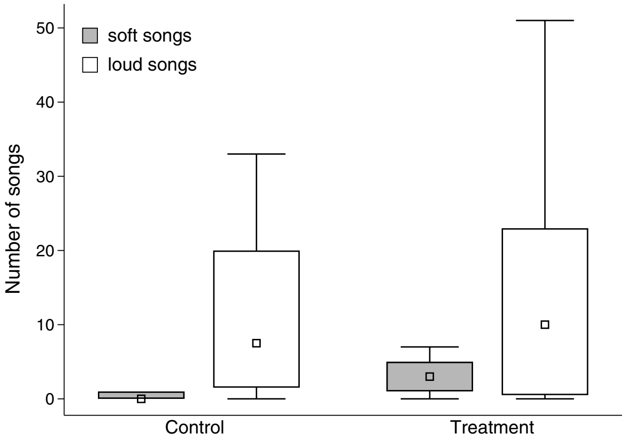

Fig. 4 A comparison of loud and soft songs produced in response to simulated territorial intrusion in the experiments. Boxes consist of median, 25th and 75th percentile whiskers

Discussion

We found that Ortolan Bunting males responded to a simulated stranger male intrusion by adopting approaching behaviours and switching from singing to calling. We also found that males produced soft songs when responding to playback and such behaviour was not observed during natural singing before playback start. Males had a stronger response (faster and closer approach to the speaker) in the control than in the treatment condition. This result suggests that males exhibited a more direct response to rival intrusion after the playback of Chaffinch contact calls than after conspecific alarm calls. Males also produced soft songs more likely and in greater numbers during the treatment than in the control conditions. Thus, the alarm calls played back before the intrusion had a double effect on the birds' behaviour: (1) delayed approaching and (2) increased use of soft songs.

Our results contradict findings by Searcy and Nowicki (2006) as the Song Sparrows tested in their similarly designed study used a lower proportion of soft songs during predator presence simulation than in control conditions. In a later study, Akçay et al. (2016) tested the predator avoidance hypothesis with a more direct design (predator presence simulated by playback of its calls). The predator (vocal) presence significantly reduced overall Song Sparrow response; however, there was no significant difference in soft song use between treatment and control. Both studies mentioned here failed to support the basic prediction of the predator avoidance hypothesis. Birds did not switch to soft song production in the face of simulated increase of predation risk; despite this, they clearly changed other aspects of their behaviour, suggesting that they did perceive the risk.

The results of our experiment revealed that in the alarm context, males showed a weaker response to the intrusion of a rival male but used more soft song types and used them more frequently, which was predicted. Contrary to our predictions, we did not observe a complete switch to soft singing which was expected in the alarm context. These results show partial support of the eavesdropping avoidance hypothesis.

However, we think that such a simple interpretation may be misleading. Differences in approaching patterns are relatively easy to interpret and can be used to assess differences between treatment and control conditions. Such behaviours presented by Ortolan Buntings have been experimentally studied in many contexts. Males approached the speaker faster when responding to the stronger type of stimuli, e.g. stranger vs. neighbour songs (Skierczyński et al. 2007; Skierczyński and Osiejuk 2010), local vs. foreign dialect (Osiejuk et al. 2007a, 2012), or elongated vs. normal and normal vs. shortened song strophes (Jakubowska and Osiejuk 2017). The strength of response in this species is also modified by age. Young, inexperienced males in their second calendar year are more cautious, when compared with older males, in their approach response when presented with a high threat signal (Osiejuk et al. 2007b). Similar to this study, we simulated the intrusion of a rival using stranger songs in both the treatment and control. Thus, the slower approach time in the treatment condition may be interpreted as a more cautious response after listening to the alarm calls. The question remains whether this is purely due to a predation risk context or not. The 'tseep–tjut' calls we used for playback are used by both sexes and are most often used in the alarm context (Andrew 1957a, b; Cramp and Perrins 1994). However, they can be produced in other social contexts too (Conrads 1971). We personally recorded them during a human intrusion into a territory, especially close to a nest (own unpublished data, Cramp and Perrins 1994), which seemed to directly reflect a predator approach effect. However, calls were also recorded during close interactions between males (e.g. Skierczyński et al. 2007; Jakubowska and Osiejuk 2017). The conclusion is that alarm calls weaken the overall response to intrusion and increased the use of soft song. However, there is no certainty as to whether alarm calls are received solely as a signal of possible predator presence or, for example, as a result of the appearance of a conspecific rival. On the other hand, appearance of a conspecific rival should reinforce the overall response, which was not observed.

In accordance with the predator eavesdropping avoidance hypothesis, we predicted that males should use soft songs more frequently in the higher risk context. In fact, we found that males produced more soft songs during the treatment than during the control. It seems logical that in a risky situation birds should completely switch to singing soft songs, as even one or few loud songs may increase their detection range and so advertise the position of the signaller. We did not find such an effect in our study. Ortolan Buntings produced soft songs more frequently in the treatments, but the number of soft songs used was much lower than the number of loud songs (Fig. 4). However, there is also some support for another explanation. A signaller who varies signal amplitude unpredictably over time may benefit from confusing a potential eavesdropper. If the amplitudes of successive signals change, a receiver must assess whether these are due to changes in distance or in behaviour (Nelson 2000, 2002; Naguib and Wiley 2001). Despite significant differences between the treatment and control conditions, we still noticed soft songs in 45% of control trials. Moreover, birds responding to a rival intrusion switched from producing loud songs to uttering loud calls. Thus, even if they include soft songs in their output, they still produced plenty of loud vocalization during the playback phase.

Therefore, it seems rather unlikely that soft songs are used exclusively to avoid eavesdropping by a predator or a rival. Relatively low regularity of appearance, but clear demonstrations during territorial intrusions, suggests that they are produced in an aggressive context and are used with a dynamic time pattern together with loud songs and different types of calls. A recent study confirmed that soft songs are used by the study species in aggressive context despite the fact that they are not a signal of increased aggression (Jakubowska and Osiejuk 2018). As the same males were not more likely to produce soft calls for either treatment, we can conclude that this behaviour is linked to a specific current situation and not to dominance or personality of an individual which should be stable over longer time. For example, the placement of the loudspeaker, vegetation structure or earlier experience may affect the ability to locate the simulated intruder and as a result also alter the behaviour of the bird. This result opposes the results obtained in Song Sparrow studies, which showed strong consistency ($r > 0.8$) in soft song used by the same individual in following trials (Searcy and Nowicki 2006).

To sum up, our results indicate that males use soft songs in the context of territorial intrusion and that they used them more frequently after hearing conspecific alarm calls, but never switched completely to only producing soft songs with a rate typical for loud songs. It is also rather unlikely that soft songs are used to avoid eavesdropping by conspecific rivals, as they were always used in a mixture with loud songs and calls. If such behaviour is a strategy, it is rather directed to confuse receivers (Naguib and Wiley 2001). We suggest that the most probable explanation for use of soft songs in the study species, at this moment, is mediation of the territorial conflict by signalizing change in current motivation (such as song duration or song type switching: Osiejuk et al. 2007b; Jakubowska and Osiejuk 2017), or tactile behaviour related to readiness to fight or addressing a specific receiver within a close range (Akçay et al. 2011; Akçay and Beecher 2012; Jakubowska 2017).

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Affiliations

Aleksandra Jakubowska[1] · **Tomasz S. Osiejuk**[1]

✉ Tomasz S. Osiejuk
t.s.osiejuk@life.pl; osiejuk@amu.edu.pl

[1] Department of Behavioural Ecology, Institute of Environmental Sciences, Faculty of Biology, Adam Mickiewicz University, Poznan, Poland