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Low-amplitude songs in songbirds

Tiché zpěvy u pěvců

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PODĚKOVÁNÍ

Děkuji především své školitelce Tereze Petruskové za její vždy ochotný přístup a cenné rady. Díky patří také mojí rodině, která mě podporovala při studiu a psaní této závěrečné práce.

PROHLÁŠENÍ

Prohlašuji, že jsem závěrečnou práci zpracoval samostatně a že jsem uvedl všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

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ABSTRACT

Research of bird vocalisation has been remarkably growing in the past seventy years. However, most of the published papers focused on common high-amplitude vocalisation. Despite having researchers who considered the existence of another rare low-amplitude signal more than a century ago, low-amplitude songs were overlooked until the beginning of the 20th century. Additionally, authors still using terms for the description of this scarcely recorded vocalisations inconsistently, which makes the comparison of published papers difficult. In total, I found published notes describing the existence or function of low-amplitude songs in at least 45 species, with ten species having at least two different types. This review is providing evidence that low-pitch songs might be quite widespread but overlooked signals playing a role in male-male as well as male-female interactions. Moreover, it is possible to distinguish between several types of low-amplitude songs based on their structural resemblance to the primary song. Getting all together, I am providing new terminology that might be helpful for further conclusions and could be used in future research of this hidden phenomenon.

Keywords: sub-song, whisper song, soft song, quiet song, twitter song, low-amplitude vocalisation, function of song

ABSTRAKT

Výzkum ptačích hlasů zažívá v posledních 70 letech neuvěřitelný růst, přičemž většina prací se zaměřuje na nejčastější hlasitou komunikaci – zpěv. Ačkoli první průkopníci ve studiu ptačího hlasů zmiňovali existenci tichých zpěvů již na konci minulého století, až v poslední době přibylo článků, které se tématu věnují. Nicméně autoři často používají nejednotné názvosloví, které dost komplikuje následné porovnávání prací a pochopení celé problematiky. Během práce se mi povedlo najít záznamy tichých zpěvů u celkem 45 druhů, z nichž deset má současně dva různé typy. Je proto možné, že se jedná o poměrně častý, ale poněkud přehlížený jev. Dohledané práce ukazují, že pěvci tiché zpěvy nejčastěji používají při interakcích v páru nebo s dalšími samci. Z výsledku je zřejmé, že v dalším výzkumu musíme podle odlišné struktury vzhledem k normálnímu zpěvu rozlišovat nejméně tři typy těchto přehlížených zpěvů, které se můžou dále dělit podle konkrétní funkce. Na závěr práce navrhuji nové názvosloví, které může být užitečné pro další shrnutí a budoucí výzkum.

Klíčová slova: subsong, tichý zpěv, zpěv s nízkou amplitudou, funkce zpěvu

CONTENT

INTRODUCTION

Animal Bioacoustics – research on the sound of animals, has been enormously growing in the last two decades thanks to new technologies. Particularly the vocalisation of birds is well studied in the animal kingdom as it has been attractive for many types of research since the end of the 18th century (Baker, 2001). With the growing number of publications, one may say that we know a lot about this fantastic animal communication; however, the majority of published papers focused on most common high-amplitude signals, especially songs of passerines (Catchpole & Slater, 2008). There is much less known about diverse vocalisation ongoing behind the songs of passerines, such as many types of calls and low-amplitude songs (Bradbury & Vehrencamp, 2011).

We can only guess if it was the review about low-amplitude songs (Dabelsteen, McGregor, Lampe, Langmore, & Holland, 1998) or technological boom in the last years, which caused that more researches have started studying this overlooked phenomenon (Reichard & Welklin, 2015). The relatively new term "quiet song" was established by Dabelsteen et al. (1998) for all complex low-amplitude songs. Nevertheless, with newly described low-pitch songs across different bird species, several authors used other names such as whisper song, soft song, twitter song or short-range song to distinguish "quiet songs" in particular contexts (Lampe & Espmark, 1987; Morton, 2000; Searcy, Anderson, & Nowicki, 2006; Titus, 1998). Unfortunately, they are often missing clear definitions, which makes the understanding of their meaning and potential functions difficult or even misleading.

The main goal of my thesis is to summarise available published papers about low-amplitude songs in birds and consequently find out under what circumstances are such songs uttered. I will also focus on the history of five most common terms used for low-amplitude songs – sub-song, whisper, soft, twitter and quiet song, which might help me to understand if distinctive names are used consistently. Finally, I might be able to propose a new classification of low-amplitude songs based on discovered findings as well as to provide new terminology with a clear definition for a given signal (song). New established classification should reduce the number of currently used terms, thus help to easily differentiate between distinct types of low-amplitude songs in future research. Simultaneously I will compare hypothesises describing why birds sometimes sing softly.

1. TERMINOLOGY OF BIRD VOCALISATION

Birds mostly uttering sounds for some communication reason and therefore there is consensus called them as signals. The one exception might be subsong when usually young males are training to sing and not trying to be heard (Thorpe & Pilcher, 1958). It is generally accepted that we speak about the communication of birds when the signal changes the behaviour of the receiver (Slater, 1983). However, in the bird communicatory network, we should also consider the situation when another bird is listening but not responding - passive response (McGregor, 2005).

Bird vocalisations are generally separated into two groups – songs and calls. These groups differ mainly in structure and function, but the border is sometimes not clear with many exceptions. Before ranking bird sound as a song or call, it is essential to know that production of the more complex song is exclusive to the Oscine group (the true songbirds) of Passeriformes which are unique among birds in higher complexity of syringeal muscles and the way how they learn to sing. On the other hand, simple calls are uttered by all bird species (Catchpole & Slater, 2008).

"Call" refers to shorter, simpler vocalisation produced by males, females and young birds throughout the year (Catchpole & Slater, 2008). The structure of the call is often just one element or syllable. In contrast to a song, calls are used in many specific situations – e.g. contact, flight, threat, alarm or feeding call.

"Song" refers to long, complex, vocalisation produced by males in the breeding season with two main functions: mate attraction and territory defence (Catchpole & Slater, 2008). Nevertheless, this definition, for example, cannot apply in tropics, where females sing as well and even between breeding seasons (Langmore, 1998). Each species has mostly one discrete song version, which is also used by people for its identification. However, some species can sing many different song types of their original song or even imitate other species. Moreover, bird vocalisation differs geographically, and in some species, we can even distinguish clear dialects (Podos & Warren, 2007). For more in-depth analysis of the song, we can divide the song structure into distinct parts with the same pattern of units, called phrases. Each phrase consists of several shorter parts referred to as syllables. Syllables might be complex and constructed by the smaller units, called elements, which are the smallest units of a song.

The definition of the song is widely accepted, but sometimes it is necessary to distinguish between different variants of songs regarding their functions. In such situation, the

song with its classical meaning is often called with general terms like 'primary song', 'broadcast song' or 'true song', while its specific variants are often called as 'advertising song', 'territorial song' or 'mating song'. Although birds mostly utter primary songs, they sometimes sing rare variants of songs which are usually referred to general term 'secondary songs' (e.g. Lister, 1953). Some of these secondary songs are similar in their low-amplitude pattern and soon had become interesting for researchers who suggested their further research and division in other sub-categories (Lister, 1953; Nicholson, 1927). Several authors described them similarly to an accurate description of Johnson & Kermott (1991): *"At its extreme, male sang without opening their bills and even when standing 10 m from the male we could not detect song without using shotgun microphones and high gain levels"*. In the following chapters, I will present a summary of these low-amplitude secondary songs.

2. SUB-SONG

People were interested in song learning of birds for many centuries (some historical notes reviewed in Thorpe, 1955). Bird fanciers were known to use term 'recording song' for quiet practise-like songs for a long time, but the term was not suitable for its meaning (Daines Barrington 1773 quoted by Darwin (1871). Therefore Max Nicholson (1927) came with the term sub-song as a better description of quiet secondary songs and also suggested how to observe and describe such types of songs (Nicholson, 1931). Then Nicholson & Koch (1936) provided a definition that sub-song refers to "*all performances which are so inwardly or faintly uttered that they do not carry to anywhere near the distance over which the bird is physically capable of making itself heard*", and Nicholson noted that sub-song is non-territorial vocalisation. Nice (1943) pointed out that neither males nor females of Song Sparrows utter sub-songs; however, Nice described the similar song to sub-song produced by young males, called as 'warbling song'. Her description of warbling song resembles the later definition of sub-song defined by Thorpe (1958).

A few years later, Lister (1953) recommended distinguishing between different categories of what he called the secondary song, which was consistent with the previous definition of sub-song (Nicholson & Koch, 1936). Lister defined three types of secondary songs and recommended to use the same terminology in future research: 1) whispering songs – very quiet version of the primary song heard in every month, 2) sub-songs – very quiet song genuinely different from a primary song heard in every month, 3) rehearsed songs – imperfect version of the primary song produced by young and rarely old birds during period of song

training. Unfortunately, it was not followed by other researchers. Similarly, to Lister (1953), Armstrong (1955) distinguished between several types of "quiet-songs" in wrens (*Troglodytes troglodytes*).

An important landmark in studying of sub-song was work of Thorpe & Pilcher (1958) - "The nature and characteristics of sub-song". Based on their previous research (e. g. Thorpe, 1955) of sub-song in chaffinches (*Fringilla coelebes*) authors suggested to restrict the term sub-song for one type of low-amplitude songs which differs from the full song in being: *"(1) quiet, (2) of a different pattern, (3) with song bursts longer, and (4) the notes of the lower fundamental frequency. Also (5) the frequency range of the notes in the sub-song tends to be greater (i.e. the notes are less pure in tone and less definite in pitch). Finally (6) the sub-song is usually produced earlier in the breeding season when sexual motivation is lower, and in young birds, at least sometimes (7) appears to be a form of "practice" for the production of the full song*." Thorpe (1958, 1961) continued in the research of sub-song and published a comprehensive summary on song development of the chaffinch's song. It sounds to me that the 'rehearsed song' defined by (Lister, 1953) resembles Thorpe's definition of sub-song; however, the other categories of Lister's secondary song has remained overlooked.

Since work of Thorpe & Pilcher (1958) the sub-song has been used in different contexts, however, most of the authors described it as part of the bird song development process (review of Marler & Peters, 1982). Armstrong (1973) found some difficulties in definition of sub-song and suggested that there might be a remarkable variation in the development of sub-song among different bird species. Therefore he proposed to implement new terms for different types of low-amplitude songs. Dabelsteen et al. (1998) suggested that "the use of the word sub-song should be restricted to the almost silent and non-social singing which is typical of both young and adult individuals of many species during the autumn or late winter before the start of the breeding season, and that low amplitude singing with a probable social function during the breeding season should be referred to as quiet singing". That takes us back to the work of Lister (1953) and Armstrong (1973) who referred to existence of different types of low-amplitude songs such as whisper song. Currently, the sub-song is widely understood as part of the song development, and I suggest using it with the same meaning.

3. WHISPER SONG

3.1. History of 'whisper song'

To my knowledge, the term "whisper song" firstly used Olive Thorne Miller (1896) to describe the song of the gray catbird (*Dumetella carolinensis*): "*charm me with his wonderful whisper song, an ecstatic performance which should disarm the most prejudiced of his detractors. Occasionally, his mate, as I suppose, uttered warning cries, and in deference to her feelings, it appeared, his notes dropped lower and lower, till I could scarcely hear them, though he was not ten feet away*." It is clear that the whisper song was used in male-female vocalisation with low amplitude. Soon Lloyd (1914) sum up that especially catbirds (*Dumetella*), thrashers (*Toxostama*) and mockingbird (*Mimus*) are whisper singing mostly in autumn; however, it is highly variable among species and throughout the year. Similar notes published Schafer (1916) when observed catbird and house wren (*Troglodytes aedon*) singing whisper song during autumn migration, but also in spring when some birds were close to their mates. Pollard (1930) collected a few observations of whisper songs in Australian birds and concluded that although it is unusual behaviour, it must be a certain habit. Robinson (1948) described whisper song as "*low songs which are barely audible and often include mimicry of other birds' songs or other sounds heard in the habitat*". They were broadly uttered by both young and adult birds during adverse weather conditions.

Since that time the whispered singing had been repeatedly documented in several species like cardinal (*Richmondena cardinalis*) during months of courtship and mating (Laskey, 1944); in the american robin (*Turdus migratorius*) as a subdued high-pitched song, that could serve as a threat or during a courtship (Young, 1955); in the rufous-backed thrush (*Turdus rufopalliatus*) as soft versions of the primary song (Grabowski, 1979) or in a couple of *Toxostoma* genus species in different time of the year as a lower-amplitude version of their primary song with uncertain function (Hancock, 1964; Hubbard, 2014). Overall, it is clear that "whisper singing" is used in different contexts with high variability. Nevertheless, some authors came up with a more detailed description.

Already Nicholson (1927, 1943) suggested to distinguish between true songs and songs of lower amplitude termed as sub-song; however, such discrimination was not satisfactory. As I mentioned in the previous chapter, Lister (1953) provided three categories of secondary songs that have similar attributes – 1) whispering songs, 2) sub-song and 3) rehearsed song. Unfortunately, these terms were not widely spread and for instance, Thorpe

& Pilcher (1958) defined sub-song as part of the song development, although it is an only extended definition of the rehearsed song by Lister (1953). Considering this fact, I decided to avoid using recommended names by Lister and instead use his general description for the separation of different low-amplitude songs.

3.2. Low-amplitude version of primary song

Wolf (1977) and Ali & Anderson (2018) referred to whisper singing all soft versions of primary songs in several species of *Aimophila* respectively Bachman's sparrow (*Peucaea aestivalis*) that were mostly uttered by males in situations when the female was around. Similarly, Wasserman (1980) found a significant increase of whisper songs in white-throated sparrows males during the incubation period in the female's absence. Both suggested the main function of whisper song as pair bond reinforcement. The same situation was described in House Wrens when males distinctively reduced volume of most songs in the period before incubation (Johnson & Kermott, 1991). Moreover, males frequently raised their tails when whisper singing. Also, Ishizuka (2009) concluded that the main function of the whisper part of the grey thrush (*Turdus cardis*) song is in the stimulation of the female and communication within the family at the nest site. However, he used the term whisper song for very low whistle parts of the primary song, whereas the description of the second part of the trill-only song described as twitter song was not involved (Ishizuka, 2006).

A different situation was described in white-throated sparrows that often use whisper or short primary songs in interactions with other males to indicate ambivalence towards to new intruders in within territory (Collins & Houtman, 1999; Falls & Kopachena, 1994). Morton (2000) described whisper song under the same circumstances as a remarkably faint version of the primary song in 24 species. In yellow-backed orioles (*Icterus chrysater*) both males and females responded to playback with whisper song. Shrike-vireos (*Vireolanius pulchellus*) produced whisper song regardless of their breeding status, which was explained as the result of defending their yearlong territories.

3.3. Low-amplitude song distinctively different from primary song

Not only that Wolf (1977) described whisper songs similar to primary songs in some species of *Aimophila*, he also documented 'continuous' and 'warbling songs' which could last up to three minutes. Bachman's sparrow males also produced the third type of song that had different acoustic structure than the primary song. This type of song was named as 'excited

song' in previous research (Dunning, J. B., Pyle, & Patten, 2020), but Ali & Anderson (2018) recommended called it as 'warble song'. Interestingly Cox, Jones, Tucker, & Budney (2014) recorded warble song produced by the female of Bachman's sparrow. Similar " *mating songs – low monotonous songs with no rising and falling infections"* were described by Robinson (1948) in few Australian species. During courting behaviour, also male of mockingbird uttered: " *a series of softly, choppy, pleasing notes with lowered head and tail high* " which were described as 'coaxing song' (Laskey, 1944).

3.4. Imperfect version of the primary song produced during the period of song training

Laskey (1944) had a chance to observe the growth of cage-raised mockingbird which uttered first songs at 27 days with closed beak, but "*they were much more primitive than whisper songs of adults and missing imitation of other species*", however after two days he sang ten-minute whisper song which resembled whisper song of adult birds. Similar whisper 'juvenile song' was described in some Australian species as the song of juveniles typical for the period after they leave the nest (Robinson, 1948). Both examples and whisper songs described by Loyd (1914) remind me of the sub-song defined by Thorpe & Pilcher (1958).

3.5. Summary

In this chapter, I showed that the term whisper song has a long history and support in the literature. Following the work of Lister (1953), I found evidence for different types of low-amplitude, hereafter whisper songs. Apparently one can distinguish between whisper songs that either resembles the structure of primary songs or not. However, it is difficult to make any conclusion regarding their function because I found examples used in male-male or male-female interactions; thus there might be more types of soft songs for different contexts or birds use the same types of soft songs in distinct situations. Imperfect versions of primary songs that are uttered during the period of song training should be referred to the sub-song definition by Thorpe & Pilcher (1958).

4. SOFT SONG

4.1. Song sparrow – model species

Based on the available literature to my knowledge, the term 'soft song' was for the first time briefly mentioned in the classic work of Nice (1943) on song sparrows (*Melospiza melodia*). Males in the presence of another rival, often puffed themselves into a bigger shape, vibrated with wings and uttered soft incomplete songs. Until the work of Nielsen & Vehrencamp (1995), I have not found other work that mentioned the term soft song. However, these authors did not investigate the function of the soft song. Still, they considered the soft singing behaviour as the final level of aggressive vocal escalation in song sparrows following the work of Nice (1943). Searcy, Anderson, & Nowicki (2006) conducted first work that tried to quantify the number of soft songs produced by males song sparrows in aggressive interactions which soon become the framework for studies of the soft song in last 14 years. Authors used a broadcast song playback to measure several song attributes that were considered to precede aggressive behaviour. The only display that significantly predicted attack likelihood of males was the soft song, but their overall impression was that song behaviour is providing little information on attack prediction. Similarly, Anderson (2006) during the monitoring of heart rate response of caged territorial males to playback of song sparrow song found, that the playback of soft song evoked the least response thus not supported their aversive function. Laidre & Vehrencamp (2008), however, highlighted some methodological inadequacy in work of Searcy et al. (2006) and for future studies recommended do the control of multi-modal signal components and use a dynamically moveable avian model. The soft song in song sparrows has become the best-studied model of low-amplitude songs so far; therefore, I will look at this species more in detail and point on some weak parts of published papers.

4.1.1. Acoustic characteristics

It was the team of Anderson (2006) who as the first one focused on the description of acoustic characteristics of soft songs and found evidence for two types of the soft song in song sparrows: (1) 'crystallised' soft songs that are quiet versions of the broadcast song and its song types; (2) 'warbled' soft songs that consist of syllables not found in the repertoire, always uttered with low stereotypy at low amplitudes and containing more complex notes and buzzes. Neither is longer than a broadcast song and males sometimes repeated both crystallised and warbled soft songs in bouts of the same song type, which was also observed by Anderson, Nowicki, & Searcy (2007).

Researchers considered soft songs consistently as a broadcast song with an amplitude lower than 75 dB (Searcy et al., 2006) or in the range from 50 to 77 dB SPL measured at 1 m. (Anderson, 2006). The team of Anderson, Searcy, Peters, & Nowicki (2008) compared amplitudes of broadcast songs and soft songs more deeply. Surprisingly, they found no bimodal distribution of loud songs compared to soft songs, suggesting that males produce songs at a range of amplitudes rather than differentiating between two separate groups. Hence the finding of exact cut off between broadcast and soft songs in song sparrows is tricky. However, most of the soft songs were uttered in range of 55–77 dB sound pressure level whereas broadcast songs in the range of 78–85 dB, therefore a trained observer could easily distinguish between groups by ear (Anderson et al., 2008). The exception was the warbled soft song that had almost exclusively amplitude <65 dB, differed in structure and had a wider frequency range, thus pointing on its different function that has crystallised soft song.

4.1.2. Playback experiments

To test the actual function of soft songs Anderson, Nowicki, & Searcy (2007) used playback experiment to compare the response of males and females song sparrows to broadcast song and to both types of soft song. Caged females (n = 9) responded with significantly less courtship display to the playback of crystallised soft songs than to broadcast song. Still, there was no difference between the response to crystallised and warbled soft songs. Males response was the same for all presented song types. Such a result was confirming neither courtship function of the soft song nor aggressive function and suggesting no difference in the function of crystallised and warbled songs. However, the future playback experiments on song sparrows followed the suggestion of Laidre & Vehrencamp (2008) and used taxidermic mount in field experiments as a multi-modal signal.

Akçay, Tom, Holmes, Campbell, & Beecher (2011) found that males sang significantly more soft songs in trials with mount and correspondingly decreased rate of loud songs, but the number of attackers was too low for statistical analysis. They confirmed the importance of taxidermic mount in playback experiments for this species. So far, I am aware of only this study that considered the breeding status of tested birds and excluded males that were involved in the parental activity thus could respond weaker.

Templeton, Akçay, Campbell, & Beecher (2012) repeated the same experiment design on males of western song sparrows (*M. melodia morphna*) and found a significantly higher proportion of soft songs and wing waves in soft songs trials. Additionally, subjects spent more

time in a distance of 0.5 m during playback of soft songs than loud songs. Males showed slightly higher attack rates to playback consisting of mix crystallised and warbled soft songs compare to previous studies that used just crystallised soft song playback; hence authors concluded that warbled soft song might be an essential part of aggressive intent in this species. However, authors did not consider different stages of the breeding status of birds, that could influence subsequent attack rate. Another weak part I see in the claim that males spent more time in a distance of 0.5 m during playback of soft songs than loud songs, but this time did not differ at 1.0 m distance.

Similarly, Anderson, Searcy, Hughes, & Nowicki (2012) changed their experiment design from 2007 by adding mount and compared broadcast song vs warbled soft song. They provided evidence that males of song sparrows approached significantly closer to playback of the warbled soft song than to playback of the broadcast song. However, presented data are not showing actual distances of males from the speaker, that would help to imagine the accurate distribution of data. Although I pointed on some inconsistent findings, most of the authors agreed that soft songs and especially its warbled version in song sparrows work as aggressive intent.

4.1.3. Seasonal changes in the soft song

Although the total number of broadcast and soft songs per male (nine males) of song sparrow from sedentary population did not vary between seasons, the ratio of soft songs was remarkably higher in autumn (Maddison, Anderson, Prior, Taves, & Soma, 2012). Nearly 80% of songs in the non-breeding season were soft songs, therefore suggesting that soft songs would have the primary function in the non-breeding season contrary to focus area of previous research (Akçay et al., 2011; Anderson et al., 2012; Searcy et al., 2006). Although Maddison et al. (2012) did not distinguish between crystallised and warbled soft songs, the structural characteristics of whole soft songs were generally stable across both seasons except for trill minimum frequency and buzz repetition rate; the latter was lower in the winter season.

Interestingly Akçay, Campbell, & Beecher (2014) found that signalling (soft songs and wing waves) and aggressive traits (rates of flights, closest approach and proportion of time spent within 5 m) are individually consistent in song sparrow males throughout five consecutive months (Sep, Oct, Jan, Feb, Apr). Males individually differed in a way how intensely they signalled, with over- or under-signalling behaviour. Also, Searcy & Nowicki (2006) showed that some males have consistency in their use of soft songs before and during

trials. Such behaviour might explain the results of playback experiments why some males responded with soft songs, but others did not.

4.2. Soft song in other species

Soft songs were described in other six passerine species, while most of them structurally resemble the broadcast song (Hof & Hazlett, 2010; Jakubowska, 2017; Moran, Doucet, Newman, Ryan Norris, & Mennill, 2018; Nelson & Poesel, 2012), in one species, differ remarkably (Xia, Liu, Alström, Wu, & Zhang, 2013). Three different forms of the soft song were described in swamp sparrows (*Melospiza georgiana*): 1) 'crystallised soft songs' which are broadcast songs sung at low amplitude, firstly reported in song sparrows by Anderson (2006); 2) 'gargles' which resemble the introductory phrase of swamp sparrow flight song; 3) 'song type Z' which has not been recorded in the broadcast repertoires of males (Ballentine, Searcy, & Nowicki, 2008).

Additionally, so-called 'soft syllables' were described in the song of white-throated thrushes (*Turdus assimilis*) which consisted of broadcast syllables (84 % of song syllables) and uncommon 'soft syllables'. Although males never produced soft syllables separately, they had lower amplitude and more complex acoustic structure than the broadcast song (Vargas-Castro, 2015). Therefore, they might have functioned as a close-range signal in female-male or male-male interactions like the soft song.

4.2.1. Acoustic characteristics

Soft songs that resemble the structure of the broadcast song still differ in some small details in all species. Some soft songs across different song types of black-throated blue warblers (*Dendroica caerulescens*) had a wavering or garbled appearance and were classified as 'garbled' soft songs (Hof & Hazlett, 2010). Nelson & Poesel (2012) described 'short soft songs' in puget sound white-crowned sparrows (*Zonotrichia leucophrys*) as versions of broadcast songs uttered at lower amplitudes -12 dB than loud songs with shortened trill phrase. Similarly, soft songs in the ortolan bunting (*Emberiza hortulana*), which were firstly mentioned by Conrads (1969) as 'subsong', were shorter and low amplitude versions (< 12-15 dB) of the broadcast song including its song types (Jakubowska, 2017). Soft songs in savannah sparrows (*Passerculus sandwichensis*) were structurally identical to broadcast songs but at the beginning of songs included additional notes not present in broadcast songs (Moran et al., 2018).

Vargas-Castro, Sandoval, & Searcy (2017) confirmed that the acoustic structure of soft syllables in white-throated thrushes susceptible to sound degradation, hence together with low amplitude reduce their transmission range and might function in short-range communication. In contrary Niederhauser, DuBois, Searcy, Nowicki, & Anderson (2018) by using the corresponding methodological design showed similar degradation and attenuation values when played broadcast song, crystallised soft songs and warbled soft songs of song sparrows at loud and low amplitude. Such results are suggesting that structural characteristics of the soft song are not causing their low amplitude pattern.

4.2.2. Playback experiments

Ballentine et al., (2008) used playback experiment to evaluate displays that are best predictors for the subsequent attack of Swamp Sparrows males on the taxidermic mount. Attackers (n=9) sung more soft songs than non-attackers and their production was positively correlated with wing waves. Consequently, Searcy & Beecher (2009) in their review of the song as an aggressive signal in birds proposed three criteria that should be considered when classifying signals as aggressive: 1) the signal increases in aggressive contexts (the context criterion); 2) signal predicts aggressive escalation by the signaller (the predictive criterion); 3) receivers respond to the signal (the response criterion). They concluded that results of soft songs production in song sparrows (Searcy & Nowicki, 2006) and swamp sparrows (Ballentine et al., 2008) provide strong evidence that low-amplitude song (soft song) could be an aggressive signal as it satisfies the predictive criterion, at least in these two species. Also, Hof & Hazlett (2010) found that soft songs are presenting highly reliable information about impending aggression in black-throated blue warblers. However, it is not clear why males did not use more of 'sputter vocalisations' during playback experiments which are known as the best signal to evoke extremely aggressive behaviour between rivals in this species (Hof & Hazlett, 2010).

Also, Moran et al. (2018) found that attackers of savannah sparrows produced significantly more soft songs in the minute preceding attack and concluded that soft songs are signals predicting attack. However, I see a deficiency in their statistical approach and presented data. From a total of 93 males of savannah sparrows involved in experiments, 39 produced soft songs during playback trials. Non-attackers (70) and attackers (23) cohorts showed no difference in the number of soft songs during the initial period of playback. Additionally, it is not clear how many of attackers uttered a soft song or not, given the fact that 39 males produced soft songs it must be in maximum 23 attackers vs 16 non-attackers or

less, which is almost equal. Even so, authors subsequently compared behaviour between groups by comparing the minute before males attacked the model, to a corresponding minute from randomly chosen birds that did not and found significantly more soft songs produced by attackers. I see no logical reason to do it in this manner, especially when the dataset of non-attackers chosen for analysis of the soft-song production in the minute before the attack is much bigger, therefore hiding the minimum of 16 non-attackers that uttered soft song as well, and on top of that authors probably included a time of trials, that could present "silent " minutes when non-attackers flew away during tests, thus highly privileged the group of attackers.

Contrary to studies that found soft songs functioning as an aggressive signal, males of Puget sound white-crowned sparrows gave weaker responses to short soft songs than to longer loud songs (Nelson & Poesel, 2012). Males were observed to produce these songs with variable amplitude in male-male interactions, but Nelson & Poesel (2011) also discovered that males in male-female interactions throughout the incubation period used different 'short quiet songs'. Similarly, Jakubowska & Osiejuk (2018) found no evidence, that soft songs of ortolan bunting are a signal of increased aggression, by following three required criteria (Searcy & Beecher, 2009). Although some males uttered soft songs during playback experiments, the males responded more strongly to loud songs. They suggested that soft songs in ortolan buntings are used to target a specific individual or modify their intention. Based on this suggestion, Jakubowska & Osiejuk (2018a) performed trials with two loudspeakers simulating movements of the intruder. They found that although males responded equally to single or two speakers experiment design, males produced significantly more soft songs when experiment simulated movement of an intruder, therefore came with a new explanation that soft songs are used as short-range signals to check if the rival is still around.

4.2.3. Soft song in the brownish-flanked bush warbler

Opposite to previous studies Xia et al. (2013) found prominent differences between the structure of soft song of brownish-flanked bush warbler (*Cettia fortipes*) and the broadcast song when the former had a significantly lower minimum frequency, more notes, longer duration, a higher note rate, and lower relative sound pressure. Both songs could be easily distinguished in the field because soft songs opposite to usual songs were uttered while the head is hanging, the bill nearly closed, and the wings are quivering. Males spent significantly longer time within 3 m of the speaker in trials with soft songs; however, there was no

significant difference between the broadcast song and the control group. Authors thought that birds were still responding to the pre-playback recording of the broadcast song from a faraway population. I think that pre-playback might have an impact on reaction to consequent soft song playback as well. During experiments with mounted specimens, six attackers produced soft songs as well as five non-attackers, and 14 males neither attacked nor produced soft songs. Despite such results, the authors concluded that the relation between soft song production and the following attack was significant.

4.3. Summary

Nice (1943) firstly used the term 'soft song' to describe low-amplitude songs uttered by males of song sparrows in close interactions with other males. Since that time we have discovered that the males sing two distinctive types of the soft song: 'crystallised' soft songs that are quiet versions of the broadcast song and 2) 'warbled' soft songs that have a different structure (Anderson, 2006). The amplitude range is continual without bimodal distribution of broadcast and soft songs of song sparrows; however, an observer could easily distinguish between groups (Anderson et al., 2008). Males of song sparrows from sedentary population mostly used soft songs in the non-breeding season (Maddison et al., 2012) and interestingly signalling behaviour such as the production of soft songs seems to be individually consistent throughout the season (Akçay et al., 2014). These recent findings are opening questions about the primary (no?) function of soft song in song sparrows during the breeding season and effect of personality on results of playback experiments. After 14 years of intensive research on soft songs in song sparrow, the main view of soft songs as an aggressive signal is still not clearly supported.

'Soft songs' were also described in six other bird species but compare dissimilarities to the soft song of song sparrow (**Table 1**). Four of them resemble their broadcast songs in structure with small changes; one has a unique structure, and only one resembles the crystallised soft song of song sparrows. Both reviewed papers on song sparrows and data about soft song function from other bird species show that validation of soft song as a signal of aggression is premature and probably need a better explanation. Recently Jakubowska & Osiejuk (2018) suggested that soft songs might be used to target a specific individual in short-range interactions, and their experiment design might become a template for other researchers.

Table 1: Comparison of soft songs described in six different species. *"Soft song type" represents name used for the soft song in the paper; "resemblance" describes different structural characteristics of the soft song to broadcast song, and "aggressive" represents if has the soft song function as an aggressive signal. "(Yes)/no" note highlighting some statistical difficulties found in papers and commented in the text above.*

	soft song type	resemblance	aggressive
Swamp sparrow[1]	crystallised	yes	yes
	gargles	no	-
	song type Z	no	-
Black-throated blue warblers[2]	soft song	yes	yes
	'garbled' soft songs	yes (garbled quality)	-
White crown sparrows[3]	soft song	yes (shorter trill)	no
Bush warbler[4]	soft song	no	(yes)/no
Savannah sparrow[5]	soft song	yes (additional notes)	(yes)/no
Ortolan bunting[6]	soft song	yes (shorter)	no

Ballentine et al. (2008)[1], Hof & Hazlett (2010)[2], Nelson & Poesel (2012)[3], Xia et al. (2013)[4], Moran et al. (2018)[5], Jakubowska (2017)[6]

5. QUIET SONG

The term 'quiet song' was firstly established by Dabelsteen, McGregor, Lampe, Langmore, & Holland (1998) in their review on low-amplitude songs. It was stressed that quiet songs differ from similar sub-songs, that are mostly uttered by young males as part of their song development (Thorpe & Pilcher, 1958). In contrast, quiet songs refer to low-amplitude songs with a possible social function during the breeding season (Dabelsteen et al., 1998). Authors presented data of this overlooked phenomenon from six we-studied species when birds used low-amplitude songs (quiet songs) in different contexts like communication in the presence of predators, courtship singing preceding copulation or agonistic interactions between males.

Although low-amplitude songs are poorly understood, Dabelsteen (2005) found some similarities: "*Quiet singing usually occurs at close range during escalated interactions, collaborative as well as competitive*". The quiet song was used as a general term for all whisper and soft songs excluding sub-songs. He concluded that quiet song showing some characteristics for being a private signal and provided the first explanation – eavesdropping avoidance hypothesis. Since this review, the term quiet song was rarely used and usually presents general adjective for low-amplitude songs. The quiet song was scarcely used as an alternative to whisper song (Morton, 2000) or a description of high-intensity display in Song Sparrows, but without further explanation (Beecher, Campbell, Burt, Hill, & Nordby, 2000; Beecher & Campbell, 2005).

6. TWITTER SONG

The 'twitter song' or 'twitter' part of the primary song was firstly described in redwings (*Turdus iliacus*) is a terminating section with high structural variability and much lower amplitude, thus probably functioning at shorter distances (Espmark, 1982; Lampe & Espmark, 1987). Males mostly uttered twitter sections of songs early in the season with the possible aggressive meaning of the song (Lampe, 1991; Lampe & Espmark, 1987), when especially increase in the amplitude of twitter part might signal arousal (Lampe, Balsby, Espmark, & Dabelsteen, 2010).

Similar twitters were described in another member of the Turdidae family. Fieldfares (*Turdus pilaris*) which breeding in colonies, produced primarily twittery songs and during courtship emitted quiet twitters (Bergmann & Helb, 1985). Dabelsteen (1984) characterised twitter as a low-amplitude complex of tones of a wide frequency in blackbirds (*Turdus merula*) which often emitted twitter alone near conspecifics with possible aggressive meaning. On the contrary, the presence of twitter songs did not presume subsequent attack during playback experiments, although the aggressive behaviour might be represented by the increase of twitter frequency (Ripmeester, De Vries, & Slabbekoorn, 2007). Lastly, males of robin (*Erithacus rubecula*) produce the quiet twitter song (high-pitched squealing) as an indicator of aggressive arousal (according to Lack (1969) in Dabelsteen, McGregor, Holland, Tobias, & Pedersen, 1997). Later Dabelsteen et al. (1998) showed a resemblance between twitter song of Turdidae and low-amplitude songs in some other species. Altogether it seems that twitter song is rarely used term mostly describing twitter part of the song in Turdidae family with probable aggressive function.

7. OTHER EXAMPLES OF LOW-AMPLITUDE SONGS AND NEW CLASSIFICATION

Although I presented an overview of five most commonly used terms for low-amplitude songs, we can find several other papers that described low-amplitude songs by different terms such as ultra-crystallised song (Constantine & Approach, 2006), short-range song (Reichard, Rice, Vanderbilt, & Ketterson, 2011) or strangled song (Snow, 1958). In total, I found description or quotes about low-amplitude songs in 45 bird species, when 10 of them have more than one song type (**Table 2, 3**). Other reviews found mostly unpublished evidence for the existence of low-amplitude songs in 22 American passerines (Morton, 2000) and 128,

respectively (Reichard & Welklin, 2015). Apparently, the low-amplitude songs are at the same rarely studied but might be a widespread phenomenon and probably most of the bird species utter some type of these songs throughout their lifetime.

It is clear that considering the structure of low-amplitude songs we can distinguish between three types – 1) songs that resemble primary song, 2) songs that partially resemble primary song and 3) songs that do not resemble a primary song. We can see that the majority of low-amplitude songs either partially or fully differ from primary songs and only in few cases songs entirely copy the structure of primary songs. Sometimes it was difficult to determine the level of the resemblance of secondary songs to primary songs solely from the description in literature; thus, most of the cases are referred to partial resemblance.

Almost all examples of low-amplitude songs are possible to match up with male-male or male-female context, while the former was mostly used in an aggressive manner and latter in courtship context. Firstly, I thought that we would be able to find similarities in context if we separate low-amplitude songs based on their resemblance to the primary song. Nevertheless, I could not see any robust pattern in provided data that would help us understand the function of low-amplitude songs. I can find more support for the function of low-amplitude songs in male-female context, but a comparison of different low-amplitude song types within one species (**Table 2**) showing how inaccurate might be such assumption. Reichard & Welklin (2015) searched for notes considering low-amplitude songs in Birds of North America Online archive and found 52 species that used low-amplitude songs in a courtship context, 27 in territorial and 60 with unknown context, but authors did not provide a list of species, so I could compare their finding with mine.

I suggest using the same terminology which will consider the structure of low-amplitude songs in the first place. Future research might help us understand the whole topic more so we would be able to distinguish between different functions as well. Make any conclusion regarding the function of low-amplitude songs, in general, would be nowadays at least premature; however, we should always try to define the function of low-amplitude songs within individual species. For obvious reasons, I would prefer to not try divide currently known examples of low-amplitude songs into newly formed groups, rather recommend focussing on the description of mentioned characteristics in future research. None of the currently used terms has prevalence within species of a particular characteristic; thus, I chose terms for new terminology randomly.

I propose using the following terms as newly established terminology of low-amplitude songs:

- **Low-amplitude song –** a general term for all song types of lower amplitude than has a normal broadcast song.
    - **A. Soft syllable** – low-amplitude syllables that are part of the broadcast song, sometimes used separately.
    - **B. Quiet song** – low-amplitude version of the broadcast song that is entirely identical.
    - **C. Soft song** - low-amplitude version of the broadcast song that has some extra structural changes or added syllables not normally used in the broadcast song.
    - **D. Whisper song** – low-amplitude version of the song that has a completely different structure from the broadcast song.

Table 2: Comparison of different low-amplitude songs described within one species. *'resemblance' = structural resemblance of the soft song to broadcast song; '(A-D)' = codes of newly suggested terms; 'M-M' = male-male; 'M-F' = male-female; '*' = unclear definition; 'ref.' = references number refers to a number in the list of references.*

species	used term	resemblance	context	ref.
Bachman's sparrow	whisper song	no (A)	M-M	*4,26,33*
	warble song / excited song	yes (B)	unknown	
Song sparrow	crystallised soft songs	yes (B)	M-M	*2,3,6,7,8,9, 62,70,74,75, 85,86,87,90*
	warbled soft song	no (D)	M-M*	
Swamp sparrows	crystallised soft song	yes (B)	M-M*	*13*
	song type Z	partially (C)	M-M*	
	gargles	no (D)	M-M*	
Bluethroat	low-amplitude song	no (D)	M-F	*Chutný, 2020, pers. com.*
	low-amplitude song	no (D)	M-M	
Dark-eyed juncos	slow short-range song	no (D)	M-F	*78,79,95*
	fast short-range song	no (D)	M-M	
	soft long-range songs	yes (B)	other	
American sparrows	whisper song	unknown	M-F	*99*
	warbling song	yes (B)	M-F	
Black-capped chickadee	gargles	no (D)	M-F	*36*
	subsong	no (D)	other	
	faint fee-bees	yes (B)	other	
House wren	mating song	unknown	M-F	*50,52*
	nesting song	unknown	unknown	
some Australian passerines	mating song	partially (C)	M-F	*77,82*
	whisper song	no (D)	unknown	
Great tit	whispered quiet song	unknown	other	*38*
	intense quiet song	no (D)	M-F	

Table 3: Comparison of low-amplitude songs described under different names. *'resemblance' = structural resemblance of the soft song to broadcast song; '(A-D)' = codes of newly suggested terms; 'M-M' = male-male; 'M-F' = male-female; '*' = unclear definition; 'ref.' = references, the number refers to a number in the list of references.*

species	used term	resemblance	context	ref.
some American passerines	whisper song	partially (C)	M-M	*67,83*
Veery	whisper call	partially (A)	M-M	*17*
Black-throated blue warblers	soft song	yes (B)	M-M	*42*
European robin	quiet twitter song	partially (A)	M-M	*40*
Desert wheatear	ecstatic song*	no (D)	M-M	*29*
Redwing	twitter song, strangled song	partially (C)	M-M	*34,55,56,57*
Brownish-flanked bush warbler	soft song	no (D)	M-M*	*100*
Savannah sparrow	low-amplitude soft song	partially (C)	M-M*	*66*
Chestnut-sided warbler	courtship song	unknown	M-F	*Brumm. pers. com. in 30*
some European passerines	(soft courtship songs)	partially (C)	M-F	*10*
Bobolink	alpha song	partially (C)	M-F	*20*
Collared flycatcher	ultra-crystallised song	no (D)	M-F	*25*
European pied flycatcher	songs of longer duration / high-pitched song	partially (C)	M-F	*37,40*
Red-breasted flycatcher	low-amplitude song	no (D)	M-F	*Belfin, 2020, pers. com.*
Common yellowthroat	low amplitude song	unknown	M-F	*81*
Dunnock	quiet song	partially (C)	M-F	*30,60*
Cardinal	whisper song	partially (C)	M-F	*59*
Eurasian blackcap	warble of low amplitude	partially (A)	M-F	*23*
Common whitethroat	diving song	partially (C)	M-F	*14*
Western Orphean warbler	complex courtship song	no (D)	M-F	*25*
Brown thrasher	whisper song	partially (C)	M-F	*41*
Gray thrush	whisper song	partially (C)	M-F	*45*
Fieldfare	quiet twitter	partially (C)	M-F	*18*
Rufous-backed thrush	whisper song	yes (B)	M-F	*39*
Ovenbird	-	no (D)	M-F*	*22*
Grey catbird	whisper song	partially (C)	M-F*	*65,84*
White-throated sparrow	whisper song / quiet song	partially (C)	M-F, M-M	*23,35*
North-American passerines	low-amplitude signal	yes, no (B, D)	M-F, M-M	*79*
Eurasian blackbird	twitter song / weird song / strangled song	partially (C)	M-F, M-M*	*25,27,30, 31,80*
Puget sound white-crowned Sparrows	short-range song	yes (B)	M-F, M-M*	*68,69*
American robin	subdued high-pitched whisper song / hiselly	partially (C)	M-F, M-M, other	*51,101*
Mimids	whisper song / coaxing song	partially (C)	M-F, other	*43,59,61*
Ortolan bunting	soft song	yes (B)	other	*46,47,48,49*
New world wood warblers	-	partially (C)	unknown	*22*
White-throated thrush	soft syllable	partially (A)	unknown	*96,97*

8. WHY SING QUIETLY?

Currently, seven hypotheses are explaining the function of the low-amplitude singing in birds; when most of them are focusing either on the decrease of acoustic range or the mechanism of how to maintain the honesty of signal, however, some showed logical inadequacy (review in Akçay, Anderson, Nowicki, Beecher, & Searcy, 2015; Jakubowska & Osiejuk, 2018a; Reichard & Welklin, 2015). Overall we are missing enough experimental work to make any conclusions, especially when we consider that low-amplitude songs comprise of male-male and male-female interactions when each might be under different evolutionary pressures (Akçay et al., 2015). Probably the most accepted hypothesis is eavesdropping avoidance hypothesis (Dabelsteen et al., 1998), which says that males sing low-amplitude songs to reduce costs of attracting eavesdropping conspecifics or predators. Recently Jakubowska & Osiejuk (2018) found evidence that males using low-amplitude songs to check if the rival is still around, thus provided another explanation to the common hypotheses of eavesdropping avoidance and readiness to fight (Akçay et al., 2011). We have a good theoretical framework, but none of the hypothesis has gotten satisfactory experimental evidence so far.

For instance, Searcy & Nowicki (2006) unsuccessfully tested the eavesdropping hypothesis on the model of the soft song in song sparrow. Nevertheless, I do not agree with their conclusion considering some logical inadequacy. They found the length of intrusions by other males much higher in trials that presented loud intruder playback with soft owner playback than in opposite manner. Therefore, authors thought that territory owner that used the soft song to counter an intruder suffered more intrusion by third-party males than do males that use the broadcast song. I would rather explain this result as the higher intention of neighbours to defend their territories before new invader that was better audible in loud trials than when it was presented as a soft singer and probable over-looked. Similarly, Jakubowska & Osiejuk (2019) did not find support for eavesdropping hypothesis.

SUMMARY

I have reviewed a series of published papers that are mentioning the occurrence of scarcely recorded low-amplitude songs. Overall, I collected published information on the existence of low-amplitude songs in at least 45 species, thus providing strong evidence for this widespread phenomenon. Considering the low number of recorded cases, it is logical that authors would use different nomenclature for their description; hence I tried to come up with new classification.

I gathered examples of low-amplitude songs for most commonly used terms, but as I expected before, I did not find any similarities that would help us to establish given names; nevertheless, some shared patterns across all song types are evident. Especially some differences in structure are obvious; therefore, I recommend distinguishing between low-amplitude songs that fully resemble the structure of the primary song, partially resemble, or do not. Additionally, I provided a new classification for these terms.

Reach to any general conclusion regarding the function of low-amplitude songs is nowadays at least premature. Although some authors incline to understand low-amplitude songs as an aggressive signal, I found broader evidence for male-female context. However, thanks to well-studied species, we have evidence for more types of low-amplitude songs with opposite functions within one species. Such findings are supporting the idea that birds utter structurally different variants of low-amplitude songs with distinct functions. Low-amplitude songs are definitely an important part in some male-male and male-female interactions, but so far, we know just a little about it.

For future research, I recommend using one established terminology that would help us focus on functionally distinctive types of low-amplitude songs. We should focus on hidden and rare situation when birds might utter these low-amplitude vocalisations. That means primarily breeding period, activity close to the nest or territorial activity at borders. All published papers agreed that low-amplitude songs were uttered at extremely low levels and hard to hear further than few metres. We have to use our best technology, such as sensitive automatic recorders to get closer to birds and collect more recordings of this probably rather overlooked then rare phenomenon.

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