ABSTRACT

Animals from different taxa produce so called soft signals characterized by lowered amplitude in comparison to typical broadcast songs or calls used for mate attraction or rival deterrence. Despite such signals seem to be common, they remain poorly known due to difficulties in recording them in natural condition. Earlier studies on soft signals revealed that they are important, among others, in close range interactions between male and female and in agonistic interactions between rivals. The second context is quite unexpected as acoustic soft signals are less costly in terms of energy expenditure. According to signalling theory and results of many studies, high quality males should and do sing loudly during aggressive interactions with rivals. However, in some bird species soft signals were found to be the best and reliable predictor of physical attack of the sender. Recently this phenomenon attracted attention of many researchers and led to intensive debate on functions and costs maintaining reliability of soft signals. Nonetheless, until now studies on this issue concerned only a few species (mostly three species in birds) and we are far from generalization of these findings.

The aim of my study was to test if soft songs play any role during agonistic interactions between territorial males of the ortolan bunting (*Emberiza hortulana*). Soft songs were earlier observed in this species during playback experiments and natural territorial conflicts, but never were studied in details. My original research plan was designed to test all earlier suggested hypotheses trying to explain the soft song phenomenon. It is important to mention that at least some of those hypotheses are not mutually exclusive because they were formulated from different perspectives (e.g. function, mechanism, cost). Below I briefly present each of them:

1. *Eavesdropping avoidance hypothesis* (H1) assumes that soft songs are produced to avoid eavesdropping of the signal by predators or conspecifics.
2. *Vulnerability handicap hypothesis* (H2) assumes that soft song costs are related to the higher risk of injury for sender signalling softly close to receiver.
3. *Receiver-retaliation rule hypothesis* (H3) assumes that cost of singing softly results from increased probability of retaliation of signal receiver. Consequently, cheaters signalling higher aggressiveness would pay high retaliation cost from truly stronger receiver.
4. *Competing cost hypothesis* (H4) suggests that cost of soft signals may be a result of difficulties in maintaining efficacy of all signal functions at the same time. Thus the

decrease of signal amplitude could be good for avoiding conflict with distant males while less efficient for attracting females.

5. *Readiness to fight hypothesis* (H5) assumes that the low amplitude of soft songs is only a by-product of sender's preparation to fight.

I have conducted five experiments in which I verified all the mentioned hypotheses. In the experiment E1, the presence of predator was simulated by presenting taxi-dermic common kestrel (*Falco tinnunculus*) and playback of its calls. After predator presentation, I simulated intrusion of rival male into subject bird territory. In control, I only simulated intrusion, without predator presentation. Ortolan bunting males did use soft calls, but rarely and clearly not as a result of predator presentation. Hence, I did not found any support for the H1 hypothesis. In the second experiment, I simulated the presence of predator by playback of conspecific alarm calls before simulated intrusion into focal male territory. In control, I used (neutral) contact calls of the common chaffinch (*Fringilla coelebs*). The experiment E2 did not confirm the H1 hypothesis, too. Results of both experiments show that males of the ortolan bunting did not use soft songs as a strategy to avoid eavesdropping by predators. However, in both experiments birds sung soft songs during agonistic interaction with simulated rivals, which means that soft songs are used in aggressive context in the ortolan bunting. The main question addressed in the next two experiments (E3-E4) was if soft songs are signal of increased aggressive motivation in the study species. In practice they were design to verify predictions of H2-H4 hypotheses. In these experiments, I simulated rival intrusion into focal male territory with playback of loud and soft songs. Firstly, I tested if males who were attracted to short distance to the loudspeaker respond stronger or weaker to songs of different amplitude. Secondly, I simulated a potential increase of aggressiveness by switch from loud to soft songs playback. I found that males responded stronger to loud than to soft songs, and I found no support that switch from loud to soft singing indicates conflict escalation. However, I again observed that focal males used soft songs in their response, especially during playback and just after it was stopped. The conclusions are that soft songs occur in the study species during interactions with rivals, but do not elicit stronger response of signal receiver. Results of these experiment did not support the H2 and the H3 hypotheses. During these experiments I also monitored the number of interactions between focal males and their neighbours and behaviour during soft song production. I found no clear pattern of soft song used supporting H4 hypothesis. The video recordings during these experiments did not indicate also that softly singing males were directly preparing to fight (lack of support for the H5 hypothesis). The results obtained revealed that soft songs occur in a specific context

during aggressive interactions, at a time were I stopped playback especially, suggesting that soft songs are used to elicit response from a rival within short distance. Therefore, I proposed a new hypothesis to explain functions and costs of soft song in birds – the acoustic localizing of rivals. I suggested, that ortolan bunting males use soft songs when during interactions with rivals are not able to localise their positions and try to elicit response from a particular rival. In the last experiment E5 I tested this new hypothesis with double-speaker playback experimental approach, in which I simulated an intruder who changed position of singing (i.e. was harder to localize). I found that males responded with significantly more soft songs during such simulation and just after it, in comparison to control, where all songs were played back from single place. In conclusion, ortolan bunting males use soft songs during territorial interactions but such songs do not signalize increased aggressive motivation and seem to by a tool use to evoke response from close but invisible intruder.