



Forum article

Soft song and the readiness hypothesis: comments on Akçay et al. (2011)

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Soft (or quiet) song is probably widespread in songbirds. However, it was overlooked for years because of its inconspicuous properties. Dabelsteen et al. (1998) drew attention to the phenomenon in their review suggesting contexts in which quiet songs should be used and making predictions about their physical structure. Consequently, several subsequent studies addressed questions about the function of such low-amplitude signals. The majority of experimental playback studies using low-intensity songs show that they are the most reliable predictor of attack (reviewed in Akçay et al. 2011). However, soft songs are given not only in aggressive contexts but also during courtship (Dabelsteen et al. 1998) and feeding of young (Ishizuka 2009) and when regulating spacing between foragers (Radford & Ridley 2008). In the latter case, 'close calls' of the pied babbler, *Turdoides bicolor*, are probably a signal allowing individuals to reduce the probability of unnecessary conflicts. Close calls have recently been found in nonpasserines (Ręk & Osiejuk 2011a) and even in other taxa, for example group maintenance calls in the killer whale, *Orcinus orca* (Saulitis et al. 2005), prespawning whisper calls in females of the croaking gourami, *Trichopsis vittata* (Ladich 2007) or courtship calls in cicadas (Sueur & Aubin 2004) and Orthoptera (Michelsen & Elsner 1999). In general, low-amplitude acoustic signals seem to be more widespread than previously thought and occur in both an agonistic context and when individuals cooperate and for some reason need to avoid other individuals eavesdropping.

The occurrence of soft songs raises two main problems. We are not sure why they take the form of low-intensity signals or how their reliability is maintained despite their production cost, which must be lower than that of loud, broadcast signals (Oberweger & Goller 2001). In fact, total energetic costs of loud and soft singing may be difficult to measure because of differences in accompanying behaviour (e.g. posturing, Dabelsteen et al. 1998). Some possible explanations for the occurrence of soft songs include: (1) a vulnerability handicap hypothesis (Laidre & Vehrencamp 2008); (2) a competing cost hypothesis (Searcy et al. 2008); (3) a receiver–retaliation rule hypothesis (Laidre & Vehrencamp 2008); and (4) an eavesdropping reduction hypothesis (Dabelsteen et al. 1998). Each of these hypotheses links soft songs to the possible costs associated with them. These costs result from possible responses by a receiver that may be present or (in the case of eavesdropping) hypothetically present. Because these hypotheses were all briefly discussed in Akçay et al. (2011), I will not repeat the arguments here.

Akçay et al. (2011) have proposed a new hypothesis, called the 'readiness hypothesis'. The main idea of the readiness hypothesis is that birds use soft signals if they are close to an opponent, because giving loud signals in such a situation decreases the ability of the singer to locate a rival visually and therefore puts the singer at higher risk. These authors outlined a few characteristics of the behaviours that occur when loud and soft signals are given. These characteristics indicate that singing softly in the visual presence of an intruder can be advantageous for the singer. Akçay et al. (2011) concluded that the low amplitude of soft song has not evolved for its signal value and that soft song and loud song have the same

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signal value. Thus, the low amplitude is only a by-product of the singer's readiness to fight during a close encounter with a rival.

Although I agree with several points raised by Akçay et al. (2011), I am not convinced that 'readiness' is the sole mechanism responsible for the evolution of soft signals or that this mechanism is widespread. Indeed, Akçay et al. (2011) did not address an unstated assumption of the readiness hypothesis: that soft songs are limited to an aggressive context and are a low-amplitude version of typical loud songs (the authors postulate the same signal value for low- and high-amplitude song).

However, the assumption that the context of soft songs is strictly aggressive is not valid. The very first review of soft songs suggested that these songs occur both in noncooperative and in cooperative situations. The review also offered convincing examples in support of this suggestion (Dabelsteen et al. 1998). Hence, the proposed hypothesis is fundamentally unable to explain the full spectrum of soft song.

Additionally, the structure of loud and soft songs differs in obvious ways in several species cited by Dabelsteen et al. (1998), for example the blackbird, *Turdus merula*, the fieldfare, *Turdus iliacus*, the robin, *Erithacus rubecula*, and the great tit, *Parus major*. One of the most striking examples published recently is experimental work on the corncrake, *Crex crex*, a nonpasserine bird. The corncrake uses a loud, broadcast call to signal at night. Rarely, it gives a soft call whose acoustic structure is completely different from that of the long call. The soft call is used in situations analogous to those in which soft song occurs in passerines. In playback experiments, corncrake males producing soft calls were more likely to attack the speaker than males that did not produce soft calls. Moreover, soft calls were stronger predictors of attack than broadcast calls (Ręk & Osiejuk 2011a; compare also Ręk & Osiejuk 2010 for more detail on broadcast call function). Corncrakes cannot track each other visually because they inhabit densely vegetated, wet meadows and because they signal at night. During interactions, they may rely solely on sound cues. Nevertheless, corncrake males switch to soft calls during short-range aggressive encounters. As noted by Dabelsteen et al. (1998), the structure of soft songs often suggests that they have been selected to be imperceptible at greater distances. Hence, soft signals are in fact distinctive for reasons in addition to their low amplitude. Corncrake soft calls match this description. Structurally, they are not at all like broadcast calls (Ręk & Osiejuk 2011a), which are ideal for long-distance transmission and which enable ranging and individual recognition of the sender (Osiejuk & Olech 2004; Ręk & Osiejuk 2011b).

A second prediction that could be derived from the readiness hypothesis is that all birds should decrease their song volume during territorial conflict if an intruder is close. Again, this rule does not appear to hold in general or even in an aggressive context. For example, not all male corncrakes are equally likely to use soft calls. The responses of corncrake males to the playback of broadcast calls with and without soft calls at the end of the call series suggest that they recognize soft calls as a threat signal. These responses depend on the quality of the responding male, as predicted by theory (De Kort et al. 2009). Soft calls increase the probabilities of attack and of retreat. This outcome is expected because the male assesses his own fighting abilities relative to those of a simulated rival during playback (Ręk & Osiejuk 2011a). In this case, soft calls clearly have a signal value different from that of loud calls. The signal value of soft calls is related not only to their low amplitude but also to the frequency of call usage. In the Discussion section of Ręk & Osiejuk (2011a), the authors are inclined to favour the hypothesis that a low amplitude decreases the chance of eavesdropping and that the reliability of the signal is maintained by a receiver–retaliation rule.

Typical loud, broadcast songs also vary in amplitude and this variation is functional. For example, the ratio of sound amplitude of different parts of the blackbird song is essential for species recognition and louder motif parts indicate arousal (Dabelsteen & Pedersen 1992). Similarly, louder songs in the chaffinch, *Fringilla coelebs*, elicit a stronger response in playback experiments (Brumm & Ritschard 2011). Thus, within the typical range of variation of the amplitude of broadcast songs, it appears that the more aggressive signals have higher amplitudes. This result again supports the idea that low-amplitude songs with a distinct structure that decrease the detection probability (Dabelsteen et al. 1998) are a special kind of signal that has evolved in a situation involving special costs related to eavesdropping.

The proposed readiness hypothesis constructively identifies a potential additional mechanism that increases selection for using soft signals in a short-range aggressive context. However, it seems rather unlikely that this is the sole or the main mechanism and that the low amplitude of soft signals is merely a by-product of the readiness to fight. At the current state of knowledge, and with the data available, a more parsimonious explanation is that the amplitude of soft signals is low to restrict the number of receivers and that the need for such restriction reflects the costs associated with third parties who might be able to receive the signals. The identity of the listeners could be different in different contexts (e.g. predators, rivals). I suggest that soft signals should also exhibit other traits that limit the number of eavesdroppers, for example higher directionality. This prediction could not be derived directly from the readiness hypothesis and already has some support. For example, Larsen & Dabelsteen (1990) have shown that so-called strangled song of the blackbird (which is a kind of quiet singing) has higher directionality than loud song. Recently, passerines were also shown to be able to adjust directionality of their antipredator calls (Yorzinski & Patricelli 2010). In general, it is very clear that we need more information about soft signals in different taxa and on the characteristics of the transmission of these signals through the environment.

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References

- Akçay, Ç., Tom, M. E., Holmes, D., Campbell, S. E. & Beecher, M. D. 2011. Sing softly and carry a big stick: signals of aggressive intent in the song sparrow. *Animal Behaviour*, **82**, 377–382.
- Brumm, H. & Ritschard, M. 2011. Song amplitude affects territorial aggression of male receivers in chaffinches. *Behavioral Ecology*, **22**, 310–316.
- Dabelsteen, T. & Pedersen, S. B. 1992. Song features essential for species discrimination and behaviour assessment by male blackbirds (*Turdus merula*). *Behaviour*, **121**, 259–287.
- Dabelsteen, T., McGregor, P. K., Lampe, H. M., Langmore, N. E. & Holland, J. 1998. Quiet song in song birds: an overlooked phenomenon. *Bioacoustics*, **9**, 89–105.
- De Kort, S. R., Eldermire, E. R. B., Cramer, E. R. A. & Vehrencamp, S. L. 2009. The deterrent effect of bird song in territory defense. *Behavioral Ecology*, **20**, 200–206.
- Ishizuka, T. 2009. Whisper song in the grey thrush *Turdus cardis* immediately before and after feeding their young. *Journal of the Yamashina Institute for Ornithology*, **41**, 34–41.
- Ladich, F. 2007. Females whisper briefly during sex: context- and sex-specific differences in sounds made by croaking gouramis. *Animal Behaviour*, **73**, 379–387.
- Laidre, M. E. & Vehrencamp, S. L. 2008. Is bird song a reliable signal of aggressive intent? *Behavioral Ecology and Sociobiology*, **62**, 1207–1211.
- Larsen, O. N. & Dabelsteen, T. 1990. Directionality of blackbird vocalization. Implications for vocal communication and its further study. *Ornis Scandinavica*, **21**, 37–45.
- Michelsen, A. & Elsner, N. 1999. Sound emission and the acoustic far field of a singing acridid grasshopper (*Omocestus viridulus* L.). *Journal of Experimental Biology*, **202**, 1571–1577.
- Oberweger, K. & Goller, F. 2001. The metabolic cost of birdsong production. *Journal of Experimental Biology*, **204**, 3379–3388.
- Osiejuk, T. S. & Olech, B. 2004. Amplitude spectra of corncrake calls: what do they signalise? *Animal Biology*, **54**, 207–220.

- Radford, A. N. & Ridley, A. R.** 2008. Close calling regulates spacing between foraging competitors in the group-living pied babbler. *Animal Behaviour*, **75**, 519–527.
- Rek, P. & Osiejuk, T. S.** 2010. Sophistication and simplicity: conventional communication in a rudimentary system. *Behavioral Ecology*, **21**, 1203–1210.
- Rek, P. & Osiejuk, T. S.** 2011a. Nonpasserine bird produces soft calls and pays retaliation cost. *Behavioral Ecology*, **22**, 657–662.
- Rek, P. & Osiejuk, T. S.** 2011b. No male identity information loss during call propagation through dense vegetation: the case of the corncrake. *Behavioural Processes*, **86**, 323–328.
- Saulitis, E. L., Matkin, C. O. & Fay, F. H.** 2005. Vocal repertoire and acoustic behavior of the isolated AT1 killer whale subpopulation in southern Alaska. *Canadian Journal of Zoology*, **83**, 1015–1029.
- Searcy, W. A., Anderson, R. C. & Nowicki, S.** 2008. Is bird song a reliable signal of aggressive intent? A reply. *Behavioral Ecology and Sociobiology*, **62**, 1213–1216.
- Sueur, J. & Aubin, T.** 2004. Acoustic signals in cicada courtship behaviour (order Hemiptera, genus *Tibicina*). *Journal of Zoology*, **262**, 217–224.
- Yorzinski, J. L. & Patricelli, G. L.** 2010. Birds adjust acoustic directionality to beam their antipredator calls to predators and conspecifics. *Proceedings of the Royal Society B*, **277**, 923–932.