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Forum

Signalling while fighting: further comments on soft song

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We thank Osiejuk (2011) for his comments on our discussion of the evolution of soft song in agonistic contexts (Akçay et al. 2011). Osiejuk raises several criticisms of one specific hypothesis we put forward in our paper, the readiness hypothesis. Here we discuss further some of the hypotheses on soft song, reply to Osiejuk's criticisms and expand upon the readiness hypothesis.

In our original discussion (Akçay et al. 2011), we outlined five hypotheses that have been discussed in the literature (see Table 1 for brief descriptions), and proposed a sixth one, the readiness hypothesis, that might explain why soft aggressive calls are soft. Under the readiness hypothesis, low-amplitude calls are thought to be a by-product of gearing up for a potential physical fight. In the case of songbirds, the need to track an opponent visually prior to a physical fight may preclude singing loudly (which requires that the head be thrown back). The same reasoning may apply to cases such as corncrakes, *Crex crex* (Rek & Osiejuk 2011), which despite calling nocturnally and in a dense habitat would probably still have to adopt an attacking posture and possibly locate the target visually before launching (or avoiding) a successful attack.

As Osiejuk and we both noted, there are two interesting questions about soft song or calls. The first one is simply, why are they soft? This first question applies not only to aggressive soft vocalizations but also to any vocal signals that are low in amplitude. The second question is why is soft song so reliable a predictor of attack? This second question of course only applies to aggressive soft songs (Dabelsteen et al. 1998). The hypotheses put forward in the literature differ in which of these questions they seek to answer and their scope. Table 1 shows whether these hypotheses are generally applicable to soft vocalizations other than aggressive ones.

IS PARSIMONY ENOUGH?

Osiejuk criticizes the readiness hypothesis because it is not general enough to explain all soft vocal signals. In his view the eavesdropping avoidance hypothesis is the more parsimonious one, able to explain all soft vocal signals; therefore it must be the better hypothesis, and the main reason why birds vocalize softly. We take issue with this logic.

First, there have been (at least) two different hypotheses proposed under the term eavesdropping avoidance: avoiding eavesdropping by (1) predators or (2) conspecific males (while we focus on male–male competition, similar reasoning should apply to vocalizations used in female–female competition). These hypotheses may not apply to all cases equally. For instance, it is not clear to us whether the eavesdropping avoidance by conspecific males is actually a logically sound explanation for aggressive soft calls. Why should the most reliable predictor of upcoming attack be selected to minimize eavesdropping by conspecific males? To the contrary,

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Table 1
A summary of whether the hypotheses proposed so far can potentially explain the two salient aspects of aggressive soft songs (low amplitude and the reliability in predicting subsequent attack), and whether these hypotheses can be generalized to other soft vocalizations

Hypothesis	Description	Accounts for low amplitude?	Accounts for reliability in predicting attack?	Generalizes to all soft vocalizations?
Vulnerability handicap	Close-range song makes signallers more vulnerable because of the close distance of the signaller to the receiver	No*	Yes	No
Receiver retaliation	Close-range song increases the likelihood of the receiver retaliating aggressively	No	Yes	No
Competing costs	Singing softly decreases the ability of the signaller to keep off intruders/attract females	Yes	Yes	No
Eavesdropping avoidance (predators)	Singing softly decreases the chances of the signaller being detected by a predator	Yes	No	Yes
Eavesdropping avoidance (conspecifics)	Singing softly decreases the chances of a conspecific competitor detecting the conflict	Yes	No	No
Readiness	Singing softly is a by-product of singing while visually keeping track of the opponent	Yes	No	No

* The vulnerability handicap hypothesis originally claimed to explain the low-amplitude aspect of soft song.

models of agonistic communication (Johnstone 2001; Johnstone & Bshary 2004) suggest that the opposite should be true: attacking males, who are presumably in good condition, should declare themselves as such to enhance their reputation which would discourage any further aggression directed at them: Sing loud and let it be known that you will attack an intruder. We believe therefore that avoidance of eavesdropping by conspecific males is in fact unlikely to account for the low amplitude of aggressive soft song.

Avoiding eavesdropping by predators, on the other hand, is arguably the most widely applicable hypothesis regarding low-amplitude song and if that were our only criterion we would agree with Osiejuk that this hypothesis is the best one. Yet, despite the conjecture by Osiejuk, we are unaware of strong experimental support for this hypothesis. In fact, although this idea has been around for some time, there seems to be as yet very little evidence for it. The ideal experiment would show that subjects are more likely to use soft vocalizations (in any situation) when they are exposed to (a stimulus representing) a predator than in a 'safe' situation. The only study we are aware of that used this experimental paradigm found a negative effect: a lower proportion of songs were soft songs in the presence of a predator stimulus (Searcy & Nowicki 2006). Alternatively, one might show that use of soft song is diminished in a population without significant predation pressures, for instance in some island populations of songbirds in which predators are scare or absent (Zanette et al. 2003). In any case, while we agree that this hypothesis is appealing, we are unaware of strong positive evidence for it.

We are also not convinced that the eavesdropping avoidance hypothesis explains all features of soft vocalizations easily. For instance, in all studies of aggressive soft song to date, subjects almost never gave exclusively soft songs. To the contrary, most subjects sang a mix of loud and soft song (e.g. Searcy et al. 2006; Ballentine et al. 2008). Under the hypothesis of eavesdropping avoidance, the best option to decrease the detection probability would be to sing only soft song, which then raises the question of why sing loudly at all during aggressive encounters? Furthermore, contrary to Osiejuk's claim, it is not clear that the acoustic structure of all soft calls can be explained by eavesdropping avoidance as being selected to minimize transmission distances. For instance, in song sparrows, *Melospiza melodia*, the warbled soft songs (which tend to be the quietest songs) include a lot of very low-frequency elements, and have relatively more of the energy in low frequencies (Anderson et al. 2008), and this might actually increase their transmission range in song sparrow habitat, not decrease it. Evidence for the latter possibility comes from numerous studies that show lower frequencies tend to transmit better in cluttered habitats (reviewed in Catchpole & Slater 2008). At any rate, we are not aware of any transmission experiments that ask the question whether soft calls would transmit shorter distances than loud calls played at the same amplitude. Again, we need more data to support or rule out the claim that soft call acoustic structure is selected to minimize eavesdropping by unintended receivers. In gathering these data, we believe that researchers should also consider the possibility that the acoustic structure of soft song is primarily an adaptation to constraints of calling softly (e.g. with beak closed in songbirds).

FURTHER REMARKS ON THE READINESS HYPOTHESIS

In the final section we would like to clarify a few points about the readiness hypothesis. Osiejuk claims that the readiness hypothesis predicts that all males, regardless of their motivation to escalate, should be singing soft songs at equal rates. This is definitely not the prediction made by the readiness hypothesis. Under the readiness hypothesis, only males that are getting ready for a fight should be using soft song at a higher rate. Since getting ready for a fight also entails approaching the opponent, the subjects that approach the opponent with the intention to attack should sing soft song, which is exactly what happens.

We would also like to clarify that in our discussion of whether the low amplitude itself has any signal value, we were using the functional definition of a signal given by Otte (1974). Under this definition, for a behaviour to be called a signal, it has to evolve for its signal value, and not simply as a by-product of selection for some other function. Under the readiness hypothesis, and the eavesdropping avoidance hypothesis as well, low amplitude is not selected for its signal value (sensu Otte), but rather for different reasons altogether: the need to get ready for the fight and the need to avoid eavesdroppers, respectively. This is not to say that soft songs may not evolve into distinct categories of signals with unique acoustic structure. It only means that the amplitude of the calls is not where the signal value lies.

So what does the readiness hypothesis predict? One of the strongest predictions that we have come up with is the one tested in our experiment: male song sparrows sang softer songs when a visual target (a taxidermic mount attached to the speaker) was present than when only the speaker was present, but the song rate did not change. We do not know how the eavesdropping avoidance hypothesis would account for this pattern, since it would seem that the two conditions are equal in terms of the need to avoid eavesdropping. Another, more nuanced test of this prediction would be to block the view of the subject towards the opponent from one side (e.g. by a screen that stands next to a taxidermic mount), and

observe whether subjects sing more softly when their view of the mount is blocked than when it is not.

The readiness hypothesis makes a critical assumption that as far as we are aware has not been tested before. Namely, under this hypothesis there should be a trade-off between visual perception and vocal production, in that singing or calling at high intensities (louder, longer, etc.) should decrease the ability to track a visual target. Alternatively, the trade-off might be with motor coordination, when signal production interferes with other actions needed for a physical fight. We believe these trade-offs might be a reality for signals in different modalities as well, and thus might constitute a fundamental feature of aggressive communication in animals.

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