Singing is not associated with social complexity across species

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ABSTRACT

Based on their social bonding hypothesis, Savage et al. predict a relation between 'musical' behaviors and social complexity across species. However, our qualitative comparative review suggests that, while learned contact calls are positively associated with complex social dynamics across species, songs are not. Yet, in contrast to songs, and arguably consistent with their functions, contact calls are not particularly music-like. Savage et al. posit that if their main hypothesis is correct, namely that music serves to enhance social bonds, "across species, production or proficiency in 'musical' behaviors should predict both the number and complexity of social bonds."

However, this is not borne out by cross-species evidence of natural vocal production behavior. Across species, social complexity and the need for enhanced social bonding is positively associated with the production of learned contact calls, but not with songs (Nowicki & Searcy, 2014; Sewall, 2015). Production of song appears to be independent from social complexity. Yet, considering their design features, songs are more music-like than learned contact calls. From a signaling theory perspective, these differences in form between songs and contact calls make functional sense.

Both Savage et al. and Mehr et al. highlight vocal learning as an important design feature of music. Hence, we restrict our discussion to learned vocalizations. Fitch (2006) defines songs as "complex learned vocalizations" and notes that this definition "almost coincidentally" also applies to human song. However, not all complex vocal learners produce song, rather several use their vocal learning abilities to produce vocalizations commonly called contact calls. Marler's (2004) distinction highlights their design differences: "On a structural level, songs are usually longer and more complex acoustically, involving a variety of different notes and syllables, ordered in statistically reliable sequences; calls are often short, monosyllabic with simple frequency patterning, delivered in what often appears to be a disorderly fashion." This contrast between songs and calls suggests that songs are music-like in design (i.e., complex, with ordered notes and syllables in reliable sequences), which is why they may actually be called 'songs', while calls (i.e., simple, short, and disordered) are not. Savage et al. and Fitch (2006) highlight repetition as a key design feature of music, distinguishing it from language. However, while animal songs may involve repetition on several hierarchical levels, contact calls do not (Catchpole & Slater, 2008).

The distinction between songs and contact calls allows us to explore whether they differ regarding their relationship to social complexity across vocal learners. Savage et al. state that "melodic, learned song among songbirds, whales, or other vocal learners are predicted to enhance social bonding in these species". However, among cetaceans, baleen whales sing (e.g., humpback whales produce long bouts of complex and hierarchically structured song) to attract mates rather than to enhance social bonds, while spending most of their time solitary or in small groups (Janik, 2014; Whitehead & Rendell, 2012). In contrast, toothed whales have not been reported to sing but instead produce short individually distinctive learned contact calls to maintain social cohesion in their complex social systems (e.g., signature whistles in bottlenose dolphins) (King et al., 2013). Likewise, elephants live in complex fission-fusion societies, produce learned contact calls to maintain individual-specific bonds within changing social groupings, but are not known to sing (Poole et al., 2005). Many parrot species live in large fission-fusion social groups and produce short and simple, individually distinctive contact calls to mediate social and foraging dynamics. And while several parrot species also produce complex duets (e.g., yellow-naped amazon parrots), their primary function is to defend nest sites rather than to support social cohesion within these groups (Bradbury & Balsby, 2016). Finally, hummingbirds live quite solitary lives, but sing sometimes phonologically and syntactically quite complex learned songs to defend territories and attract mates (Araya-Salas et al., 2019; Del Hoyo et al., 1999).

Hence, our qualitative comparative review of complex vocal learners suggests that learned contact calls enhance social cohesion and, correspondingly, are positively associated with social complexity (Nowicki & Searcy, 2014; Sewall, 2015). In contrast, songs function to attract mates and defend territories and do not appear to be associated with social complexity. This therefore counts as evidence against Savage et al.'s social bonding hypothesis as songs share important design features with music while learned contact calls do not.

From a signaling perspective, the observed form-function associations of these vocalizations make a lot of sense. The shortness, simplicity and resulting behaviorally low-costliness of contact calls are

consistent with the fact that they are cooperative signals, which do not need to persuade, but merely transparently and efficiently communicate relevant information, such as individual identity and group membership. In contrast, the elaborateness and associated costliness of songs (in terms of production and opportunity costs as well as predation risk, cf. Mehr et al.) correspond to the costly signaling prediction that songs should be costly to advertise and credibly indicate covert qualities (e.g., genetic quality. Hence, since music shares costly design features with animal songs rather than with contact calls, our comparative review lends support to Mehr et al.'s argument against Savage et al.'s social bonding hypothesis that, since a low-cost signaling system such as language can efficiently facilitate social coordination within groups, music would be needlessly costly to fulfill that role.

Instead of enhancing social bonding, Mehr et al. argue that music evolved as a costly, credible signal of covert qualities such as coalition strength and parental attention. While we concur that music has the design features of a credible signal, plausibly for these functions, we are less convinced by both Mehr et al.'s and Savage et al.'s refutation of the sexual selection hypothesis, namely that music also evolved as a credible signal of mate quality. Their main argument against this hypothesis is the lack of musical sex differences. Yet, this counterargument is weakened by the fact that musical ability, production and perception may be selected in both sexes under mutual mate choice (due to male parental investment), which is well-established in humans (Stewart-Williams & Thomas, 2013). Indeed, also in many bird species both sexes sing and, for instance, the greater vasa parrot demonstrates that female song can function to attract males that take up a provisioning role (Ekstrom et al., 2007; Riebel et al., 2019). Hence, while we do not wish to deny potential weaknesses of the sexual selection hypothesis, the lack of sex differences might not necessarily be one of them.

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