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Vocal Competition

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2 **Vocal Competition**

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5 **Synonyms**

6 [Acoustic competition](#)

7 **Definition**

8 Agonistic interactions mediated by the production
 9 of acoustic signals

10 **Introduction**

11 It is late autumn in the temperate forest, the last
 12 leaves still on the trees finally surrender to the
 13 northern breeze and fall down, silently. The
 14 beams, as the sun sinks, pass through the naked
 15 branches and illuminate the forest clearing, where
 16 a large, old stag is moving restlessly around a
 17 group of quietly foraging females. Not far away,
 18 a young solitary male observes the scene. The
 19 breeding season is almost over and the young
 20 male has not yet mated. Testosterone, flowing
 21 abundant in his blood, makes him decide to chal-
 22 lenge the rival, in the attempt of conquering his
 23 harem. As he moves a few meters ahead, the rival
 24 spots him and, suddenly, stops, raises the head,

opens the mouth, and starts uttering grave, loud 25
 roars. The young responds in the same way. 26
 A vocal competition has begun. 27

Vocal competitions are common in many 28
 arthropods and vertebrates, which are the only 29
 taxa that evolved the ability to communicate by 30
 means of sounds (Bradbury and Vehrencamp 31
[2011](#)). Acoustic signals are well adapted to medi- 32
 ate agonistic conflicts. Since sounds are effective 33
 on the long distance, they prevent physical con- 34
 tacts and reduce the risk of uncontrolled fighting 35
 escalations. Sounds are under strong morphophy- 36
 siological constraints and are thus preadapted to 37
 encode reliable information about the sender's 38
 fighting ability. Sound modulation further 39
 increases the communicative potential of acoustic 40
 signals, and it allows to flexibly adjust signals to 41
 the unpredictable dynamics of the ongoing 42
 competitions. 43

Vocal competition can be direct or indirect. In 44
 the following paragraphs, we shall consider the 45
 effects of these two mechanisms on the evolution 46
 of agonistic signals. 47

Vocal Contests 48

The vocal contest, such as that described in the red 49
 deer, is a mechanism of direct vocal competition. 50
 Two conflicting individuals exchange agonistic 51
 signals in order to resolve conflict to their own 52
 advantage. In this communicative interaction, the 53
 actors play both the sender and the receiver role. 54

55 Since the degree of conflicting interest between
 56 senders and receivers is high, agonistic signals can
 57 be evolutionarily stable only if they provide
 58 receivers with honest information about the fight-
 59 ing ability and the aggressive motivation of the
 60 sender (Bradbury and Vehrencamp 2011). Natural
 61 selection can guarantee the honesty of agonistic
 62 signals by imposing either strategic costs or
 63 morphophysiological constraints on their expres-
 64 sion (Maynard Smith and Harper 2003). The roar
 65 of the red deer is a good example of both solu-
 66 tions. In fact, fighting ability depends on body size
 67 and stamina (the ability to sustain prolonged ener-
 68 getically costly activities), and the roars of the red
 69 deer convey honest information of both these
 70 traits. When roaring, the stag retracts the mobile
 71 larynx down to the sternum (Reby and McComb
 72 2003). The sound produced by the vibrating vocal
 73 folds resonates into the vocal tube; some frequen-
 74 cies are filtered out, whereas others, the formants,
 75 are amplified. The frequency of the lowest for-
 76 mant is strongly and negatively correlated with
 77 the length and volume of the vocal tube and, thus,
 78 with the male body size. Playback experiments
 79 have shown that the roar spectral properties affect
 80 the contest outcome, favoring the individuals with
 81 the lowest formants. Independent of body size, the
 82 fighting ability of a male depends also on how
 83 much energy stores he has and on how good he is
 84 in using the energy in controlling aerobic and
 85 anaerobic metabolic rates. In the red deer, roaring
 86 is energetically costly and involves muscles that
 87 are important during fighting. The high strategic
 88 costs of sustained vocal contests, thus, is a reliable
 89 indicator of male fighting ability.

90 Vocal contests are common in most acoustic-
 91 communicating species. For example, in the
 92 house cricket, *Acheta domestica*, male-male
 93 aggressive interactions typically begun with the
 94 production of stridulatory calls, which differ from
 95 mate-attraction calls in both spectral and temporal
 96 structures. In this case, honest information of male
 97 body size is encoded in the temporal properties
 98 (the number and the rate of pulses within a call),
 99 rather than in the frequency components of the
 100 call (Greenfield 2002). In territorial songbirds,
 101 vocal contests are often a mechanism for resolv-
 102 ing boundary disputes. During the contest, birds

of neighboring territories interact acoustically on 103
 a short time scale in order to assess reciprocal 104
 differences in motivation and to establish relative 105
 dominance. The dawn chorus of many territorial 106
 songbirds is an unusual example of vocal context, 107
 because it does not involve dyadic interactions 108
 between conflicting individuals. With their vigor- 109
 ous signaling, territorial males communicate their 110
 presence and condition to prevent rather than to 111
 prevail over potential rivals. 112

Indirect Vocal Competition 113

Unlike in vocal contests, in indirect competitions, 114
 the outcome of agonistic interactions depends on 115
 the behavior of a third-party actor, who plays the 116
 receiver role. A typical example is represented by 117
 lek breeding species, where males aggregate in 118
 large choruses and compete acoustically against 119
 each other to attract gravid females. In this case, 120
 selection promotes the evolution of acoustic traits, 121
 which might be poor indicators of fighting ability, 122
 but good indicators of sexual attractiveness. Mate 123
 choice theories of sexual selection try to under- 124
 stand the functional significance of mate 125
 attractiveness. 126

The distinction between direct and indirect 127
 vocal competition, however, is not always clear 128
 cut. In many species, in fact, the same acoustic 129
 signal may be used in both direct and indirect 130
 competition. For example, in the red deer, the 131
 acoustic properties that are important for solving 132
 intra-sexual agonistic interactions are also those 133
 perceived as most attractive by females. In con- 134
 trast, in other species, direct and indirect vocal 135
 competitions conflict with each other. For exam- 136
 ple, in tree frogs and toads, males often compete 137
 for display positions within the chorus. During 138
 these agonistic interactions, males have been 139
 observed to reduce the dominant frequency of 140
 their advertisement calls, and playback experi- 141
 ments showed that the greater the reduction, the 142
 more effective the call was in repelling the oppo- 143
 nent (Gerhardt and Huber 2002). Frogs and toads, 144
 however, have a poor control over the resonant 145
 frequency of their vocal folds, and the only way 146
 they have to reduce the frequency is by reducing 147

148 the vibrating pressure of vocal folds, with a con-
 149 sequent reduction in call intensity. The intensity
 150 reduction may have no effect on the short dis-
 151 tances at which male-male interactions occur,
 152 but it may have strong negative effects on the
 153 long distances, where male-female interactions
 154 occur. In this case, selection is expected to pro-
 155 mote the evolution of optimal tradeoffs between
 156 the conflicting functions.

157 Indirect Vocal Competition in "Selfish" 158 Choruses

159 Indirect vocal competition arises because signal-
 160 ing males tend to aggregate in spatially restricted
 161 areas. In some cases, aggregation can be
 162 explained by the inhomogeneous distribution of
 163 the limiting resources. For example, male frogs
 164 aggregate at the breeding ponds, because here is
 165 where females lay their eggs. In other cases, how-
 166 ever, aggregation may be favored by natural selec-
 167 tion, because the benefits it provides overcome the
 168 competition costs it imposes. This happens when
 169 group size shows either a positive allometry with
 170 the number of visiting females or a negative
 171 allometry with the number of visiting predators,
 172 or both. Whatever the reason, aggregation adds a
 173 new level of competition in the population,
 174 because males not only compete against their
 175 rivals within a chorus but, as members of a chorus,
 176 they also compete against the members of other
 177 choruses within a network. The two levels of
 178 vocal competition may interact and affect the spa-
 179 tial and the temporal structure of vocal activities.

180 Vocal competition within a chorus can cause
 181 signalers to couple their calling to that of their
 182 rivals. Coupling may occur both at the gross and
 183 at the fine temporal scale. At the gross-scale level,
 184 it usually results in synchronous calling. For
 185 example, tree frogs alternate prolonged bouts of
 186 calling with periods of silence, and they do this
 187 synchronously within a chorus. In this way, tree
 188 frogs may reduce the risk of being predated by
 189 passive listening predators, such as bats (i.e., an
 190 "acoustic dilution effect"), and, at the same time,
 191 they may increase the power of the overall signal
 192 to attract females from further away (Gerhardt and

Huber 2002). In contrast, at the fine-scale level, 193
 coupling results more often in alternate than in 194
 synchronous patterns, at least in those species 195
 where the fine-scale structure of the call conveys 196
 important information for species recognition. 197
 Alternation might be interpreted as a form of 198
 "selfish" signaler cooperation, because chorusing 199
 males share the same common interest of making 200
 their own signals as detectable as possible. Males 201
 that fail to alternate would reduce their own mat- 202
 ing success and, incidentally, that of their neigh- 203
 bors. Alternation can also arise as a side effect of 204
 male-male vocal competition. In many species of 205
 frogs and insects, in fact, females show strong 206
 preferences for the male that call first (acoustic 207
 leader) (Gerhardt and Huber 2002). Males can 208
 thus compete against their closest neighbors for 209
 temporal primacy and this would result in regular 210
 antiphonal calling. 211

Vocal Competition in Cooperative Choruses 212

213
 214 So far we have considered vocal competition of
 215 selfish choruses. However, in some birds and
 216 mammals with a solid social organization, vocal
 217 competition often occurs between social groups,
 218 and, at the within-group level, individuals coop-
 219 erate to improve the overall calling performance
 220 (Ravignani et al. 2014). In many tropical bird
 221 species, the members of a pair are known to coord-
 222 inate their songs, by accurately alternating their
 223 components. In some species, the social group
 224 includes helpers, who join to produce a complex
 225 chorus, in which individuals of the same sex sing
 226 the same phrases with near-perfect synchrony
 227 (Mann et al. 2006). Chorusing behavior in birds
 228 is thought to solve two main functions: it favors
 229 coordination among the members of a group and it
 230 improves vocal contest performances in mutual
 231 territorial defense. In primates, chorusing
 232 (mostly in the form of duetting) has been observed
 233 in a few genera only. A well-studied example is
 234 that of the singing lemur, *Indris indris* (Gamba
 235 et al. 2016). In this species, all members of a group
 236 usually sing, but the contribution changes in rela-
 237 tion to the social rank, suggesting that chorusing

238 not only solves the function of communicating
 239 group size and cohesiveness during the vocal con-
 240 texts with neighboring groups but it may also play
 241 a role in mediating within-group social conflicts.

242 Conclusions

243 Direct and indirect mechanisms of vocal compe-
 244 tition have favored the evolution of signals that
 245 are a reliable indicators of signalers' competitive
 246 quality (fighting ability or attractiveness).
 247 Morphophysiological constraints preadapted
 248 some sound properties to this function. But evo-
 249 lutionary stability is most likely the consequence
 250 of the strategic costs of cheating: the risk of fight-
 251 ing escalation in vocal contests and the energetic
 252 costs of sustained calling in choruses make the
 253 bluff an economically disadvantageous tactic.

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