THE VOICE OF AGGRESSION

Horns, teeth, claws, beaks… Given this mighty arsenal it's a wonder there isn't more physical conflict in the animal world, such as among birds.

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Fot. 1. An entire family of black-collared apalis

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Aggression – defined as a physical attack by one individual on another – is common in the natural world. It occurs between different species (you can hardly expect predators to ask their prey politely if they'd mind being eaten), as well as within the same species. In the latter case, it's usually a culmination of a whole sequence of behaviors in which the individuals display their size, strength and readiness to fight. The results of such altercations can be difficult to predict, so before any attack is actually made, co-species individuals usually play out a complex game trying to intimidate one another, frequently in lieu of an actual fight. This benefits both the stronger individual, since it will not have to waste time and energy, and the weaker one, in that it can literally save its life.

In birds, for instance, simulated fights have been studied for a long time. In a temperate climate, shortly before the breeding season in spring, males of territorial species compete for resources: territory abundant with food, space for building nests, and – of course – females. Individuals have different fighting skills and abilities to defend their territory, and their motivations and experience vary. This may have genetic foundations and is modified by environmental factors during the development period known as ontogenesis (affected by the quality and quantity of food during growth). Age, outcomes of previous interactions, and the social status of males in neighboring territories are also important.

In terms of behavioral biology, it is notable that individuals find it difficult to assess their own and their opponent's ability to fight. Theoretical predictions suggest that natural selection should strongly favor exaggeration of one's own fighting ability through a range of signals, even verging on bluffing. So just like in poker, it's perfectly possible to win in spite of having a poor hand. But how does this work in practice?

Bird-speak

In theory, animals should only fully trust reliable signals. In terms of aggression, this means signals that can be trusted to be closely correlated with the real fighting ability of their opponent. Although such correlation is never the strongest, reliable signals result in an appropriate response.

One of the markers of fighting ability is physical size, which manifests itself in various ways. A classic example is sound frequency, which is inversely proportional to the size of the internal organs responsible for generating sounds. Put more simply, the larger the animal, the larger these organs, which means the lower the sounds. This is common in species emitting relatively simple sound signals which aren't significantly modified as the sounds pass from the organism into the surrounding medium. This includes many invertebrates, such as crickets, and lower vertebrates such as fish and amphibians.

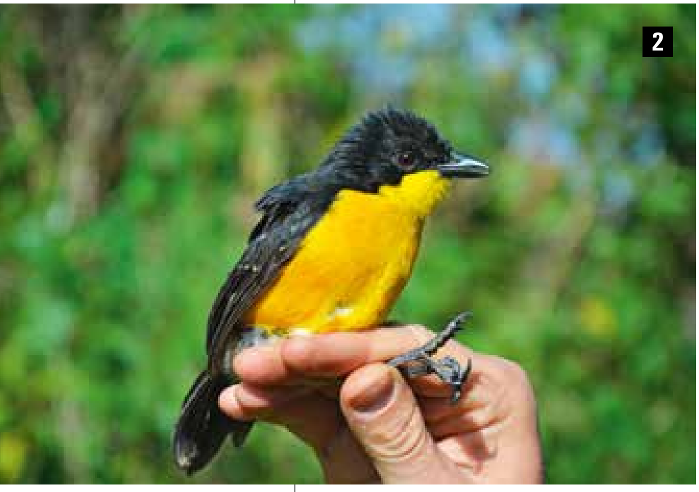
Much like humans, birds have evolved further in their ability to emit sounds, separating the sound frequency from the actual size of their body, and the syrinx, an organ responsible for generating sound. This means that slightly-built men can have deep bass voices, while the ortolan bunting (*Emberiza hortulana*) is able to sing with frequencies unrelated to its body size and mass. Rather than using singing to assess the size of their rivals, birds use it to recognize individuals; this allows them to modify their responses depending on whether the other individual is a familiar neighbor or a potentially dangerous rival or invader.

> Individuals "decide" the extent to which they can afford the costs of generating signals, taking into account their own physical condition and the potential benefits. Only certain individuals are up to the challenge.

The reliability of information regarding the size, strength and age of an opponent is strongly affected by physiological factors shaping the effectiveness of signal generation. The relationship tends to be intuitive. Differences in condition mean that individuals must adapt the energy spent on signaling. They can't always afford to make sound if it means giving up on other activities such as feeding. They can't all risk being heard by predators. They may not always have sufficient energy resources. To put it figuratively: all ortolan buntings are physically capable of singing ten times each minute, but maintaining this pace throughout the morning is not really feasible for some individuals. The potential benefits brought by singing have to outweigh the energy losses. Such sound signaling is commonplace among bird species. These strategic signals are related to the handicap principle, first defined by Amotz Zahavi. Individuals "decide" the extent to which they can afford the costs of generating signals, taking into account their own physical condition and the potential benefits. Only certain individuals are up to the challenge.

But what happens when a given signal might be coming from any individual, one with perfect genetic makeup and in peak physical condition or one weak and less well endowed? This is what happens during aggressive behavior. In spite of the potentially limitless ability to bluff, individuals are generally honest when signaling their strength and motivation to fight, and others tend to respond to those signals as being reliable. Why does this happen and what's the underlying mechanism?

A while ago I started studying the corncrake, a nocturnal rail species. I was inspired by Dr. Bogumiła Olech, whose attention was grabbed by the fact that the seemingly monotonous call emitted thousands of times every night by males appeared to differ between individuals in terms of rhythm. Preliminary results indeed turned out to be fascinating: voices of males making more frequent calls, which are more energy-demanding (their amplitude can exceed 100 dB SPL at a distance of one meter), were experimentally found to be met with less aggressive responses. Further studies demonstrated that the information conveyed by the birds' loud calls is actually carried in the rhythm, analogous to the Morse code, but the intervals between the calls are more important than their number. In this arbitrary way, males are able signal the degree of their intention to fight over large distances. This is the first (and, it seems, so far only) example of conventionalized communication in birds which don't learn to sing during ontogenesis. Even though they emit very simple and monotonous signals, corncrakes have developed a system of communication which is analogous to human speech in terms of energy costs. Just as humans, anyone can "say" anything, and the information that is conveyed is encoded entirely arbitrarily. The consequences (costs) of emitting a certain signal are then related to the response from the listener. This doesn't mean that the sounds cannot also encode other information about the broadcaster, just that it's encoded differently.



Fot. 2.
A yellow-breasted boubou (*Laniarius atroflavus*)

Fot. 3.
A magpie-lark performing an audiovisual display

Fot. 4.
An ortolan (*Emberiza hortulana*)

Quiet warnings

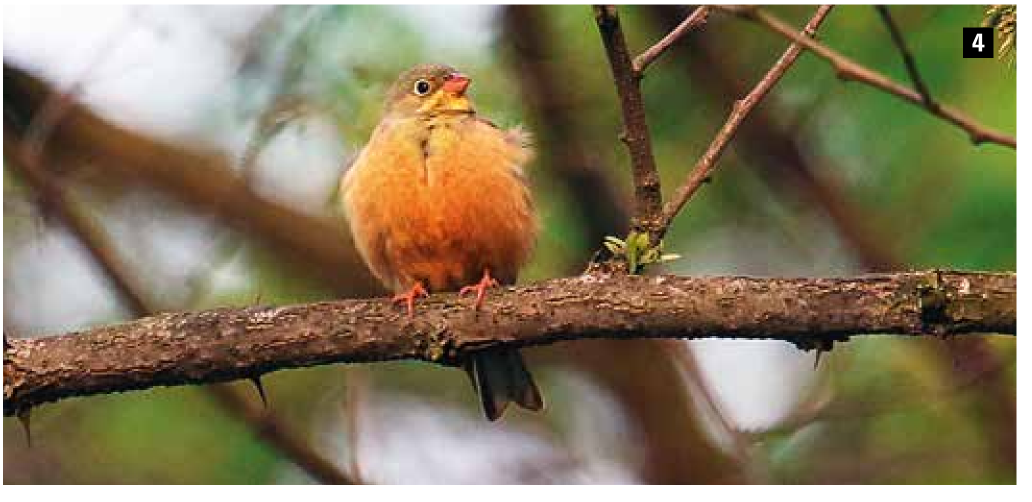
An interesting example of territorial behavior in songbirds can be found in the graded signaling of motivation to fight in song sparrows (*Melospiza melodia*) from North America. Males from settled populations know one another very well and to some extent share a limited repertoire of songs. If a neighbor encroaches on a bird's territory and makes a sound, they respond with the same call or with another from the common repertoire. This lets them know they have been detected and will be attacked if they don't leave. The system seems to work extremely well; individuals who share a repertoire with their neighbors are able to hold their territory for more years than those who arrive from different areas and aren't familiar with it. However, this only works in sedentary populations. Migratory birds can't use familiarity to send aggressive signals.

In recent years, research has focused on quiet birdsong. Signals emitted at a lower volume – typical for announcing that a given territory is occupied – are common but difficult to study. Interestingly, they aren't just present in relationships between the sexes and other strictly social interactions, such as maintaining group cohesion. Sometimes they are used in aggressive interactions where they are the best predictor of a physical attack, even though this seems absurd in terms of links between the energy cost of producing the signal and its reliability. We have found this mechanism in the corncrake. The birds make loud calls, indicating their motivation to fight, when their opponents are still a distance away. However, the ultimate signal of an impending attack, transmitted just before a physical conflict, is delivered as a quiet call with a completely different structure. We don't yet know why such signals have evolved and how they are perceived by the recipient. The sound may be emitted at a low amplitude to limit the hearing range to potential listeners (perhaps even just a single individual) or to help identify their location; it may even be an indirect result of preparing to fight. One thing is certain: the occurrence is common and needs to be studied in more species.

Duetting – let's do this together

Ornithologists working in temperate climate zones may be under the impression that aggression is mainly exhibited by males fighting one another, while females watch from the sidelines and choose their favorite. However, this isn't always the case. In tropical climates, pairs of birds of many species remain together for life and defend their resources together. Males and females sing, frequently joining each other in complex duets. Research I am conducting in Cameroon with Dr. Michał Budka reveals that both sexes are aggressive towards invaders of their territories, with the response generally being stronger when aimed at individuals of the same sex. This is seen in species such as the yellow-breasted boubou (*Laniarius atroflavus*). Curiously, there is likely a certain battle of the sexes involved here: while males loudly broadcast their "surnames," the voices of females don't have distinguishing features. However, once again the majority of potential conflicts is resolved through singing in duets at large distances, with direct aggression occurring only when strange individuals invade the pair's territory. In a series of experiments, we reproduced the singing of one pair of birds in the territory of another pair. One of the most fascinating observations was that when we played a recording of a strange male, a female chased away her own "husband" and started duetting with our male. The territorial behavior of the magpie-lark (*Grallina cyanoleuca*) is even more complex, combining singing and extensive visual displays, as studied in Australia by Dr. Paweł Ręk.

The territorial behavior of duetting species has a vast potential to teach us about the evolution of how signaling is coordinated between individuals on the level of signal generation and processing by the senses and the nervous system. Another level of complication of such systems is seen in species in which entire families defend their territory. They include the black-collared apalis (*Apalis pulchra*) and the Chubb's cisticola (*Cisticola chubbi*), a fascinating species endemic to the mountains of Cameroon. Their behavior isn't unlike that of an orchestra led by a conductor; they must use advanced multisensory integration, since coordinating visual and sound displays to the nearest millisecond is a challenging task. Such species are excellent models in the study of how complex behavior is learned; biological robots and state-of-the-art playback techniques allow us to conduct field studies.



Ongoing research and our now quite extensive understanding of many aspects of this type of behavior allow us to pose many more questions. Future research will involve retrospective studies of the evolution of aggressive signals. We will also study model species in order to improve our understanding of aggression on a neurobiological level and the role of communication networks by listening to interactions through which individuals coordinate their displays, and learning how many signaling channels are used at the same time.

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Photos from the archives of the author and team members
Paweł Podkowa and **Paweł Ręk**

Further reading:

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