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Communication about social status

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Dominance hierarchies are ubiquitous in social species and serve to organize social systems. Social and sexual status is communicated directly among animals via sensory systems evolved in the particular species. Such signals may be chemical, visual, auditory, postural or a combination of signals. In most species, status is initially established through physical conflict between individuals that leads to ritualized conflict or threats, reducing possibly dangerous results of fighting. Many of the status signals contain other information, as in some bird species that communicate both the size of their group and their individual rank vocally. Recent studies have shown that scent signaling among hyenas of east Africa is unique, being produced by fermentative, odor producing bacteria residing in the scent glands.

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Analogous to words, scientists studying animal communication often focus on animal signals that convey information about external events (e.g. food, danger, and nest site). However a far more ubiquitous 'topic' of communication is information about the signaler itself: its species, sex, individual identity, and social or sexual status. In particular social status is a ubiquitous and important form of information in animal communication, conveyed by a diversity of signal modalities including chemical, visual, auditory, postural. These signals often occur in combination, adding to the intensity of the information. Here, I provide an overview of this important class of signals in a variety of species.

Dominance hierarchies are ubiquitous in social species. Typically, males compete for high rank and attaining that ranking dramatically influences their quality of life. Perks include increased access to food, reproductive opportunity and improved health outcomes. Not so for low ranking animals who have limited access to food, a suppressed reproductive system as well as limited reproductive opportunities and adverse health effects. Social status and its concomitants are well studied in many species [1] and status is also represented in the human brain [2]. But how is status communicated amongst animals?

Jacob von Uexküll [3••] first recognized that animals have unique sensory worlds: 'This island of the senses, that wraps every man like a garment, we call his Umwelt.' He considered this umwelt or perception of the surrounding sensory world, unique to individual species and dependent on habitat, life history and other features of an animal's life. Subsequently, Nagel [4] proposed that humans could not ever fully understand what it is like to be another animal because we cannot have access to the subjective aspects of their experience. In addition to this fundamental constraint on understanding sensory systems, there are other important issues regarding studies of the senses. First, scientists typically analyze senses singly, providing little insight about how multimodal sensation might modulate a perceptual experience. Second, there is ample evidence that housing conditions for laboratory species can limit our studies. For example, over 65 years ago, Hebb [5] reported that rats allowed to roam freely in his house were better at problem solving than rats reared in lab cages. This anecdotal result suggested a role for experience subsequently studied by Krech *et al.* [6] who demonstrated that rearing rats in barren vs. rich environments produced measurable differences in brain structures, behavior, and learning abilities. Thus the rearing environment could play a role in development of cognitive abilities including regulating status. Environmental effects have subsequently been shown for many species [7], confirming that as social animals grow and develop, behavior and brain structures are shaped by both social and environmental experiences. Here, I describe examples from vertebrates identifying how social status is communicated within a species. In the communication and instantiation of social status, the sophistication of mechanisms is so extensive that this review will consider primarily more recent studies.

Communicating status through fighting

In many if not all species, higher social status results from winning a fight with a conspecific. Indeed, social aggression is a conspicuous aspect of animal social systems, but fighting has potentially high costs as well as benefits. For example, in red deer (*Cervus elaphus*), it appears that males fighting are sensitive to the specific context of the encounter [8]. Males will fight most frequently when

benefits are high and avoid fighting with individuals they are not likely to beat. However, analysis of conflicts is difficult as measurement of the actual costs and benefits are complex and winning may be short lived because it does not necessarily lead to an increase in lifetime reproductive success. However, fighting in many species leads rapidly to ritualized conflicts in which animals spare the potential dangerous consequences of physical engagement and engage in rituals. Ritualization has likely arisen over evolution as a behavior pattern changes to become a threat of a fight that is ultimately effective as a signal [9].

Analysis of fighting in territory establishment in lizards (*Anolis aenus*) showed that for this species, fights over vacant real estate mostly end in a draw and the available space is divided more or less equally [10]. In a group living cichlid species (*Neolamprologus pulcher*), both females and males acted more aggressively after social ascent, which led to variation in aggressive behavior in that social system [11]. In another African cichlid, *Astotilapia burtoni*), in which fighting plays a central role in establishing and keeping territories essential for reproduction (see Figure 1), Alcazar *et al.* [12], showed that animals develop improved fighting skills through observation and that this occurs rapidly. Slightly older animals were able to defeat larger animals using a fighting strategy developed through observation alone. This suggests that we might expect to find improvement of fighting skills through observation may also be found in other social animals.

Animals use social signaling for a variety of purposes. Foraging pied babblers (*Turdoides bicolor*) for example, use vocal cues to learn both the size of their group and where they rank in that group [13]. For many, communication includes physical conflict but fighting can be averted by visual or other signals. In sparrows, status is signaled by plumage characteristics [14,15] and deception is socially controlled [16]. In lizards, tail size confers dominance and interestingly, animals that have lost tail parts while evading predators descend in status, saving their lives but rendering them non-dominant [17].

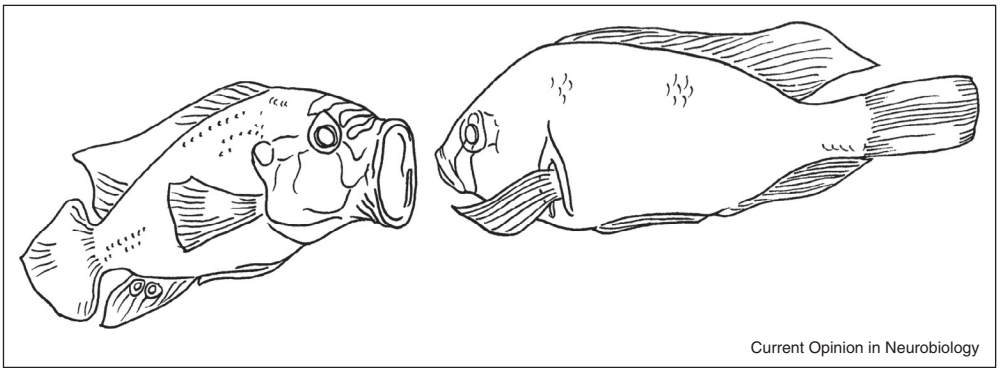
Visual signaling of social status

In lizards (*Anolis carolinensis*), Korzan *et al.* [18] showed that a spot behind the eye had high valence in signaling social dominance. Changing the color of the spot from green to black changed the status of the animals that was seen behaviorally and reflected in changes circulating levels of key neurotransmitters. Behavior of male African cichlid fish, *A. burtoni*, in their natural habitat suggests that visual cues from conspecifics contribute significantly to regulation of social behavior. Using a novel paradigm, Chen and Fernald [19] asked whether visual cues alone from a larger conspecific male could influence behavior, reproductive physiology and the physiological stress response of a smaller male. Indeed, smaller dominant males being 'attacked' visually by larger dominant males through a clear barrier showed evident loss of status and physiological changes lasting for up to 3 days, including upregulation of reproductive-related and stress-related gene expression. Thus visual threats alone can transmit information about social status in this species. This was shown most conclusively in *A. burtoni* with the demonstration that male fish (*A. burtoni*) can successfully make inferences about a hierarchy implied by pairwise fights between rival males [20••]. These fish learned the implied hierarchy vicariously (as 'bystanders'), by watching fights between rivals arranged around them in separate tank units and used transitive inference (TI) to use these observed relationships to deduce unknown ones (for example, using A>B and B>C to infer A>C), and is thus essentially used logical reasoning.

Chemical and olfactory signaling of social status

Olfactory and chemical signaling of social status is widespread, and has been studied in a number of species. For example, in an African cichlid fish, (*A. burtoni*), Maruska & Fernald [21] showed that males use urine as a chemical signal, adjusting the timing and frequency of release

Figure 1



Male cichlid fish (*Astatotilapia burtoni*) engage in a mouth-to-mouth confrontation over dominance (drawing by W T Fitch).