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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, 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 depending on social context. In particular, animals increased overall urination concomitant with increased territorial behaviors when exposed to another male, suggesting a direct role in setting dominance status. In another cichlid (*Oreochromis* mossambicus), Barata *et al.* [22,23], proposed that an aminosterol-like odorant in male urine communicate a male's social dominance to females, but which chemicals are responsible are not known. In fathead minnows (*Pimephales promelas*), in addition to visual signals, males use urinary signaling and [24] showed that urinary metabolites were differentially excreted in the urine of territorial versus non-territorial males. They unexpectedly found that future territorial status of males could be predicted based on their initial metabolomic profiles. Specifically, bile acids and volatile amines were identified as potential chemical signals of social status in the fathead minnow.

Recently, Wesson [25•] showed that sniffing which is a specialized respiratory behavior essential for the acquisition of odors, has an altered rate depending on the social status of the two rats so engaged. The data suggest that subordinate rats decrease their sniffing rate when their face is being sniffed and failure to do this results in agonistic behavior. Subsequently, Assini *et al.* [26] showed that sniffing and ultrasonic vocalizations were tightly linked, suggesting that since sniffing was tied to production of ultrasonic vocalizations, vocalizations might be the more important signal about status. However, it seems that the two signals collaborate with whisking and postural signals to provide multi-sensory information about status, showing just how complex social signaling about status can be!

Among mammals, chemical communication often relies on secretions from integumental scent glands in a variety of locations which are warm, moist nutrient-rich and anaerobic. For example, hyenas smear pastelike secretions on grasses from a gland beneath their tails that is the size of a fist. Other hyenas that sample these deposits can learn the animals sex, social status, willingness to mate and more, making them full disclosure ID documents. Burgener *et al.* [27] showed that in spotted hyenas (*Crocuta crocuta*) scents contain information about social rank and identity using gas-chromatography-mass spectrometry. Surprisingly, however, hyenas do not produce these scents themselves but rather the scent glands contain fermentative, odor-producing bacteria. The olfactory/chemical signaling system in both the spotted (*Crocuta crocuta*) and striped (*Hyaena hyaena*) hyena species in the Serengeti, east Africa is comprised of bacterial communities. Careful analysis of the gene sequences in these scent gland communities of the two species revealed that the profiles of bacterial species covaried across and within species, with sex and in the spotted hyena with reproductive classes [28••]. Since the species are sympatric, these scent pastes seem to provide a clear means for members of the species to distinguish one another and individual reproductive states.

Auditory communication of social status

Mammals living in social groups often use auditory signals identity themselves and their social status facilitating social interactions. Among non-primates, the spotted hyena (*Crocuta crocuta*) with it complex female-dominated society provides an unusually rich example of mixed signaling systems (see above). The hyena's laugh ('giggle' call) encodes information about identity, age, and dominance status [29]. Rock hyraxes (*Procavia capensis*), close relatives to elephants, use rich, complex vocalizations called singing that encodes information about an individuals weight, size, physical condition and social status in elements of the song partitioned sequentially [30]. In Fallow deer (*Dama dama*), where dominance rank is strongly related to mating success, social dominance is signaled through specific characteristic low frequency groans [31].

Among primates, the remarkable work of Seyfarth and Cheney has illuminated many aspects of baboon acoustic signaling. For example, with playback experiments, they showed that baboons (*Papio hamadryas ursinus*) eavesdrop on higher-ranking members of their troop, combining temporal and spatial information to achieve 'sneaky matings' [32••]. In Chimpanzees, numerous studies have shown long and short distance calls related to status. For example, Clark and Wrangham [33] showed that rather than signaling about food, long-distance pant-hoots are used to mark status.

In songbirds, song plays many roles, including signaling social status. In the tropical mockingbird, *Mimus gilvus*, males with decreased variation between repetitions of each syllable type have higher dominance status and reproductive success [34]. For these animals that live in cooperative breeding groups, males learns and sings over 100 syllables, combining them to produce a much larger number of songs. The implication of these data is that females attend to within-type consistency of singing. In Harris' sparrows (*Zonotrichia querula*), Rohwer [35] showed that birds dyed to resemble adults dominate control birds within experimental flocks of young males and young females.

Conclusion

Taken together, these examples reveal that the ubiquity of social status in social living animals is matched by the variety of mechanisms used to communicate status. Described here are examples of explicit sensory signals produced to assert status. However, in most species several senses are typically alerted regarding status and most of the sensory signals are accompanied by particular postures that are part of the signal. This rich repertoire of interacting signals offer a rare opportunity to capture socially and evolutionarily important information transfer and concomitant neural activity [36].

Conflict of interest

No conflict of interest.

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