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Review

Submission signals in animal groups

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Abstract
Aggression is costly, and animals have evolved tactics to mitigate these costs. Submission signals are an underappreciated example of such adaptations. Here we review submissive behaviour, with an emphasis on non-primates. We highlight the design of submission signals and how such signals can reduce costs. Animal societies necessitate frequent social interactions, which can increase the probability of conflict. Where maintaining group proximity is essential, animals cannot avoid aggression by fleeing. Mutual interest between group members may also select for efficient conflict avoidance and resolution mechanisms. As a result, submission signals may be especially well developed among group living species, helping social animals to overcome potential costs of recurring conflict that could otherwise counter the benefits of group living. Therefore, submission signalling can be a crucial aspect of social living and is deserving of specific attention within the broader context of social evolution and communication.

Keywords
aggression, agonism, dominance, communication, group living, sociality, submissive.

1. Introduction

For many animal species, conflict between conspecifics is unavoidable, because they compete for access to limited resources necessary to survive

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and reproduce, and this conflict often takes the form of agonistic interactions, including overt aggression, threat displays, avoidance behaviours, and submission (Huntingford et al., 1987; Archer, 1988). There is a rich tradition of studying agonism in ethology and behavioural ecology (Baerends & Baerends-Van Roon, 1950; Lorenz, 1966; Maynard Smith, 1974; Huntingford et al., 1987; Archer, 1988; Wilson, 2000; Hardy & Briffa, 2013). Most of this research effort has been directed towards understanding aggressive behaviour, while submissive behaviour has received far less consideration. For example, in both classic and recent books on animal conflict, little specific consideration is given to submissive behaviour (Huntingford et al., 1987; Hardy & Briffa, 2013). That said, the neural mechanisms of submission and defence in mammals have received notable attention (reviewed in Adams, 1979, 2006).

Historically, much of the research effort directed at submission has been in the context of the extensive literature on agonism and conflict management in non-human primates (for reviews see Deag, 1977; Bernstein, 1981; de Waal, 1986; Gray & Silverberg, 1992; Sterck et al. 1997; Aureli & de Waal, 2000). However, as others have noted, a focus beyond primates can be informative, and multiple key questions remain unresolved (Silk 2007a, b; Seed et al., 2007; Kutsukake & Clutton-Brock, 2008). Primates also pose a challenge for experimental approaches as significant social manipulations or staging of controlled social interactions is often infeasible. Additional approaches that may provide insights into submission signalling such as experimental evolution, artificial selection, or developmental manipulations, would also be challenging or impossible in primates but tractable in other taxa.

Here, we highlight submissive behaviour as a broadly underappreciated element of animal social behaviour, with a focus on non-primate social vertebrates. The study of submissive behaviour provides fertile ground to answer questions about conflict resolution, the evolution of communication, signal design, and social information use. Submission signals may be pivotal for group living and thus social evolution, and therefore merit further theoretical and empirical examination. We hope to encourage experimental approaches, as well as observational studies, to investigate submission in a diversity of animals, to help further understand the evolution of agonism across social species.

2. Agonism

Aggression is costly, requiring time and energy as well as risking injury (for reviews see: Huntingford et al., 1987; Hardy & Briffa, 2013). The costs associated with aggression may not differ substantially between the winner and the loser of an interaction (Morrell et al., 2005). For example, aggression-induced stress, energetic costs, and the risk of injury are often similar for both participants (Geist, 1974; Enquist & Leimar, 1990; Brick, 1998; Maan et al., 2001; Earley et al., 2006; Copeland et al., 2011). Both winners and losers also suffer opportunity costs (Grant, 1997), risk attracting predators, and must divert attention away from vigilance (Jakobsson et al., 1995). As a result, contestants often share a mutual interest in minimizing the costs of an interaction (Maynard Smith & Price, 1973; Maynard Smith, 1982; Hurd, 1997; Maynard Smith & Harper, 2003). Because of this mutual interest between competitors, animals are expected to employ less risky forms of aggression than damage inducing attacks (Geist, 1966), such as visual signals (Heathcote et al., 2018), displays (Garamszegi et al., 2006), or vocalizations (Burgdorf et al., 2008). Thus, aggressive behaviour, despite being inherently competitive, often also contains elements of cooperation (Hurd, 1997).

Submissive behaviour includes both avoidance behaviours that allow the focal animal to directly evade aggression, for example fleeing from an aggressor or taking on a protective posture, and submission signals that primarily serve to communicate submission to the receiver (Figure 1). Avoidance behaviours are functionally linked to directly evading aggression but may also have a secondary communicative function, either to signal submission, or as a cue of submission to the aggressing animal. In contrast to avoidance behaviours, submission signals act primarily in communication and become arbitrarily linked to that message, for example a change in body colouration or a vocalisation (i.e., conventional signals; Guilford & Dawkins, 1995). Submission signals are not intrinsically linked to escape, defence, or counterattack, and thus their benefit emerges from its impact on the behaviour of the receiver. The literature on agonism often conflates avoidance behaviour and submission signals, even though the causes and consequences of these different behaviours, and their evolutionary history, may be distinct.

The simplest tactic for an animal to disengage from a conflict is to flee from the aggressor into a new location. However, retreat may not always be a viable option for all species in all contexts (Matsumura & Hayden, 2006).

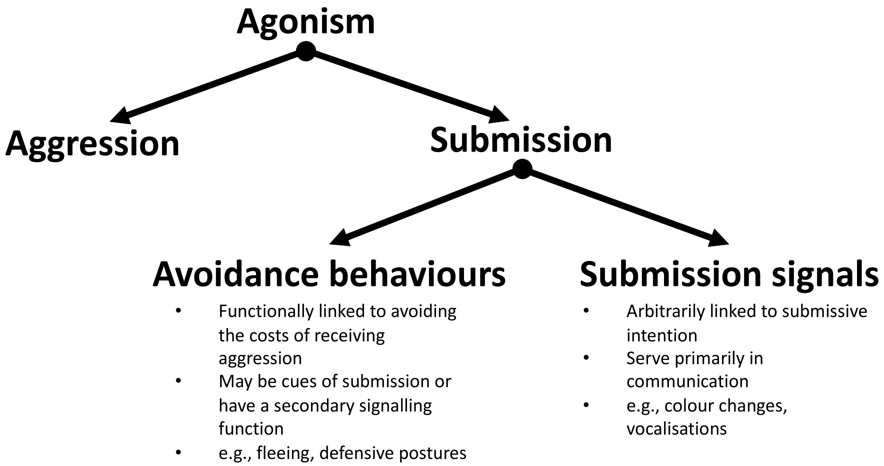

Figure 1. A hierarchical classification of submissive behaviour.

For example, some species may not be sufficiently motile to mount a timely escape (e.g., Issa & Edwards, 2006; Ligon, 2014). There may also be ecological limitations on movement, for example in a saturated habitat there may not be another safe location within reach for the loser to flee to (Wong, 2010; Batista et al., 2012). As a result, submission signals are expected to be particularly important when fleeing options are limited. Subordinates of the group living daffodil cichlid fish, *Neolamprologus pulcher*, are more likely to show submission when there are fewer shelters available in the group's territory, therefore decreasing the opportunity to flee from aggression (Reddon et al., 2019). While morphological and ecological factors are the most obvious limitations on escape, social group membership can also be thought of as a constraint on the ability to flee (Wong, 2010; Hick et al., 2014; Balshine et al. 2017). As we discuss below, the factors favouring group living limit avoidance behaviours such as fleeing, and thus submission signals are expected to be prevalent. In this review, given our emphasis on animal groups, we focus on submission signals rather than avoidance behaviours.

3. Submission signals

Submission signals can be produced prior to any aggressive escalation, preempting a contest before it begins, or after fighting begins, to terminate the interaction (Kutsukake & Clutton-Brock, 2006, 2008). Submission signals benefit the signalling animal by preventing or ending a contest and avoiding further aggression. The receiving animal benefits from accepting a submission signal by reducing the energy and time needed to continue attacking and avoiding the possibility of an upset where the weaker animal unexpectedly prevails. For example, when male crayfish, *Procambarus clarkii*, submit to a competitor by assuming a female-typical mating posture, these pairs show less total aggression, decreased costs of fighting for both individuals, and a reduced chance of death for the signaller than in pairs where the loser does not produce this signal (Issa & Edwards, 2006).

Colour change is a common form of submission signal in exothermic vertebrates. For example, contests between veiled chameleons, *Chamaeleo calyptratus*, end when one individual abruptly darkens their colouration (Ligon, 2014). Darkening colouration leads to a rapid decrease in aggression by the other chameleon, and the likelihood of darkening is tied to the level of aggression received (Ligon, 2014). Similarly, salmonid fishes (*Salmo spp.*) darken their body and eye colouration, as a signal to their opponent that they relent (Keenleyside & Yamamoto, 1962; O'Connor et al., 1999, 2000; Hoglund et al., 2000; Suter & Huntingford, 2002). This darkening inhibits aggression in the receiver, resulting in a precipitous decrease in attack intensity (O'Connor et al., 1999). Much like the chameleons, the amount of aggression that the loser has received in the contest predicts the tendency to darken the body (Ligon, 2014). Other common submission signals include postural changes, for example, in ungulates, turning the antlers away from an opponent (Jennings et al., 2002) or in birds, turning the head to look away from an attacker (Waas, 1990) are used as submission signals. Submission signals need not be visual. For example, in the weakly electric fish, *Gymnotus omarorum*, the losers of a territorial conflict produce electric chirps as a submission signal (Batista et al., 2012). The latency to produce these chirps decreases while the rate of chirping increases with the intensity of aggression produced by the attacking fish (Batista et al., 2012).

4. Submission signal design

Submission signals are often highly distinct from aggression signals produced by the same species (Bradbury & Vehrencamp, 2011). Aggression signals may emphasize or exaggerate apparent body size, fighting ability and or motivation to fight, while submission signals tend to minimize these qualities (Huntingford et al., 1987). Signals with incompatible meanings may take on highly distinct forms to make them clearly discriminable by the receiver (Hurd et al., 1995). As a result, signals that are designed to elicit opposing responses in the receiver tend to evolve towards opposite forms (i.e., the principle of antithesis; Darwin, 1872). For example, in the red-backed salamander, *Plethodon cinereus*, an amphibian known for frequent and costly fighting, aggressive intent is signalled by an arched back posture, extending the torso high into the air, while submission is signalled by pressing the body down close to the ground (Jaeger, 1984; Dyson et al., 2013). That said, although there are numerous examples of aggression and submission signals that appear to conform to this prediction, to our knowledge, no formal quantitative survey has been done.

Animals often produce several different aggression signals, which indicate increasing willingness to escalate (Hardy & Briffa, 2013). Submission signals could also be similarly graded, with the type, size, or vigour of the signal indicating variation in submissive motivation. In many cases, submission signals are repeated, and distinct forms of submissive behaviour are shown. However, a gesture of limited submission is unlikely to satisfy an aggressor, and therefore unlikely to benefit the signaller (Matsumura & Hayden, 2006). Perhaps as a result, animals typically have a larger repertoire of aggression than submission signals (Bradbury & Vehrencamp, 2011). Moreover, repeated, or diversified submission signals may not indicate strategically graded submission but instead may serve to ensure successful communication. For example, in the brown trout (*Salmo trutta*), submitting animals darken their body colouration more dramatically in turbid water compared to those in clear water, thereby increasing the strength of the signal, presumably to ensure signal transmission in conditions where visual signals are more difficult to perceive (Eaton & Sloman, 2011).

Some behaviours that have been identified as submission signals may in fact be avoidance behaviours, potentially with a secondary signalling function (Pellis & Pellis, 2015). Moreover, the function of the same action may differ between species and situations (Pellis & Pellis, 2015). For example, in house mice, *Mus domesticus*, rolling on the back does not reduce the likelihood of being bitten and appears to not be a submission signal, unlike some other species, but does help to defend the vulnerable back and rump and facilitates counter-attack and escape (Pellis et al., 1992; Pellis & Pellis, 2015). Thus, careful analysis is required to identify submission signals, particularly where these signals are derived from pre-existing avoidance behaviour (e.g., through ritualisation; Zahavi, 1980). Complicating matters, submissive behaviours can also act as a ‘hybrid signal’ (Elwood & Prenter, 2013), wherein the same behaviour serves both to provide safety for the sender and to signal submission to the receiver. For instance, wolves, *Canis lupus*, may lower their ears to signal submission to an aggressor, but this behaviour also helps to protect their vulnerable ears (Beaver, 1999). Like mice, subordinate Norway rats, *Rattus norvegicus*, roll onto their backs when faced with a dominant aggressor, which in this case does inhibit further aggression from the receiver, but may also provide defensive benefits (Blanchard et al., 1977). Escape or defence behaviours can also act as a cue to the aggressing animal of the submissive motivation of the actor which may affect the aggressor’s subsequent behaviour.

Agonistic interactions are inherently characterized by a conflict of interest between the signaller and the receiver; therefore, agonistic signals require honesty assurances (Bradbury & Vehrencamp, 2011). It is possible to envision a potential benefit from producing a dishonest submission signal in order to lure an opponent into lowering their defences (Dawkins & Guilford, 1997). Honesty in submission signalling could in theory be maintained by production costs (Grafen, 1990), and some submissive behaviours can indeed be energetically costly, for example, subordinate daffodil cichlids increase their routine energy expenditure over three-fold when producing a submissive tail quiver (Taborsky & Grantner, 1998). However, submission signals are often low cost and maintained by mutual advantage to the signaller and receiver (Matsumura & Hayden, 2006). The honesty of submission signals may thus instead be socially enforced (Parker & Rubenstein, 1981; Molles & Vehrencamp, 2001; Webster et al., 2018). The receiver of a dishonest submission signal may punish the signaller by refusing to accept future submission signals from that signaller (Dawkins & Guilford, 1991), or increasing their attack intensity (Clutton-Brock & Parker, 1995; Molles & Vehrencamp, 2001; Van Dyk & Evans, 2008). For example, veiled chameleons, *Chamaeleo calyptratus*, with experimentally manipulated ‘dishonest’ submissive colouration, inconsistent with their behaviours, received more aggression from dominant individuals than ‘honestly’ signalling control chameleons (Ligon & McGraw, 2016). Submission signals may place the signalling animal in a vulnerable position or posture (e.g., signaller exposes vulnerable body parts to the receiver; Lorenz, 1966), making it risky or difficult for the signaller to launch an attack. The resulting positional disadvantage (a vulnerability cost; Adams & Mesterton-Gibbons, 1995) may thereby cancel out any potential benefit of a submissive feint. Submission signals are also typically characterized by a cessation of movement (Pellis & Pellis, 2015), which may reduce the ability for the losing animal to counterattack. Thus, certain postures may have evolved as submission signals for the purpose of enforcing signal honesty. However, as noted above, submission signals might also be at least partly defensive and the apparent vulnerability of submitting animals may have been misinterpreted or overstated in some cases (Pellis & Pellis, 2015). For example, animals lying on their back may be ready to deliver a counterattack rather than exposing vulnerable body areas to their attacker (Schenkel, 1967).

5. Submission signals in social species

Submissive behaviour is likely to play a key role in managing conflict within animal societies (Aureli et al., 2002; Kutsukake & Clutton-Brock, 2006). For obligately social species, leaving one's current social group can have dire fitness consequences (Heg et al., 2004; Groenewoud et al., 2016). Submission signals have the benefit of preventing or terminating an aggressive interaction without requiring that either participant leave the area or group. In this section, we discuss how submission signals can be of particular benefit to social species by attenuating within-group conflict and thereby facilitating the formation and maintenance of social groups.

Animal groups in which membership is relatively stable, and group members show individual recognition, distinct pairwise relationships, and frequent interactions within the group may appear peaceful but often exhibit some level of intragroup conflict (de Waal, 1986; Aureli et al., 2002; Silk, 2007a). The interests of each group member never completely overlap, for example there is often conflict over ranking within the dominance hierarchy and priority access to limited resources (Wong & Balshine, 2011). These conflicts of interest among group members can result in aggressive interactions (Earley & Dugatkin, 2010), which may be costly (Kutsukake & Clutton-Brock, 2008), and if unchecked, may outweigh the benefits of grouping (Aureli et al., 2002). Behaviours that reduce the costs of within-group agonistic interactions represent one of the fundamental building blocks of sociality (Soares et al., 2010; Balshine et al., 2017).

Group living animals also face some additional costs of conflict because of a greater overlap in interests between the interacting parties, compared to animals that do not live in groups (Komdeur & Heg, 2005). Animal groups may be composed of related animals with shared inclusive fitness interests (Hamilton, 1964; West & Gardner, 2013) which can be negatively affected by intragroup conflict. Groups provide protection and access to resources to their members (Krause & Ruxton, 2002), and these benefits often depend on the size of the group (Kokko et al., 2001; Kingma et al., 2014), therefore the loss of productive members through intragroup conflict may negatively affect the remaining membership. In cooperatively breeding species, the success of the group is influenced by the provision of alloparental care which may be lost by injuring, killing, or expelling group members (Kokko et al., 2002). Therefore, even in the absence of relatedness, group success may be an important component of individual fitness, and reductions in the fitness of individual group members may compromise the overall strength of the group (Kokko et al., 2001; Kingma et al., 2014).

Familiarity among social group mates typically results in the formation of a dominance hierarchy based on relative fighting ability (Hand, 1986). Individuals within a dominance hierarchy concede conflicts against group members above them in the hierarchy while prevailing over those of lower rank with minimal aggression (Drews, 1993; Dugatkin & Earley, 2004; Shizuka & McDonald, 2012; Dey et al., 2014; Pini-Fitzsimmons et al., 2021), because familiar animals have likely already observed or experienced each other's fighting abilities (Parker & Rubenstein, 1981; Chase, 1985; Ydenberg et al., 1988; Enquist & Leimar, 1990; Johnsson & Åkerman, 1998). Dominance hierarchies allow the costs of frequent escalated conflicts to be avoided (Senar et al., 1990; Drews, 1993; Pagel & Dawkins, 1997; Bradbury & Vehrencamp, 2011). However, the formation of a dominance hierarchy typically involves a period of increased conflict while the members of the group establish their positions in the social order (Chase et al., 2002; Kura et al., 2015). Unfamiliar animals are initially aggressive with one another but this aggression dissipates as stable dominance relationships form (Drews, 1993). Submission signals may help to facilitate the formation of the dominance hierarchy by reducing the costs of these initial interactions for both parties (Stamps, 1999). Once formed, stable dominance hierarchies are often beneficial for most group members as they result in a net reduction in aggression within the group, and although subordinate members must yield resources to dominants, they can still benefit from belonging to a group (Krause & Ruxton, 2002; Fischer et al., 2014).

Empirical data support the idea that by signalling submission, a subordinate may reduce their likelihood of being expelled from the group. In social polistine wasps, *Polistes* spp., subordinate individuals remain immobile and hold their head low when challenged by a dominant group member, allowing them to avoid an escalated encounter and possible eviction from the group (Eberhard, 1969). In the daffodil cichlid, more submissive individuals are less likely to be expelled from the group and are permitted to enter a greater number of shelters within the group's territory (Bergmüller et al., 2005; Taborsky et al., 2012). Because of the increased need to maintain a close spatial association with the recipient of submission during intragroup interactions, submission signals are likely to be more commonly used in social species compared to escape behaviours. Ecological constraints on dispersal may be a key driving force underlying the formation of social groups (Hatchwell & Komdeur, 2000), and therefore these effects may reinforce one another. For example, barren habitats may favour group formation as well as limit escape from aggression.

Although aggression is generally lower between familiar group members within an established hierarchy than between unfamiliar individuals, hierarchal societies are not free of agonism (Dey et al., 2013; Reddon et al., 2019). Dominance is often based at least partially on factors that change over time, such as the age and strength of each individual, and as a result, subordinates may occasionally challenge dominants for status (Wong & Balshine, 2011). Similarly, dominant individuals may benefit from reinforcing their status to discourage future challenges (Buston, 2003; Buston & Cant, 2006; Wong et al., 2007). In either case, subordinate animals may use submission signals to communicate their lack of motivation to challenge for dominance. Therefore, submission signals may play a pivotal role in status-maintaining interactions within established dominance hierarchies. O'Connor at al. (2000) found that familiar subordinate juvenile Atlantic salmon, *Salmo salar*, received less aggression from dominant fish than did unfamiliar fish, but only if they signalled submission, suggesting that the submission signal is an important indication of a lack of aggressive intent from a subordinate to a dominant individual. If submission is shown, then both animals benefit from avoiding further aggression, resulting in a more stable and less costly social relationship (Issa & Edwards, 2006). In this way, submission signals may serve a dual role; being used both in interactions among unfamiliar individuals to conclude acute conflict and between familiar group mates to reinforce dominance relationships. For example, both dogs, *Canis lupus familiaris*, and wolves, *Canis lupus*, use the same submission signals to terminate contests between unfamiliar rivals (Lorenz, 1966) and to maintain the dominance hierarchy within their social group (Schenkel, 1967).

The social complexity hypothesis predicts that animals that live in complex groups require more elaborate communication systems to cope with the greater degree of social intricacy (Freeberg et al., 2012). The hypothesis predicts that animals living in groups have a greater repertoire of social signals composed of a higher number of structurally and functionally distinct elements (Freeberg et al., 2012). It could be argued that the social complexity hypothesis would predict that members of complex animal groups would show a greater diversity of submission signals to cope with the greater variety of potential situations under which submissive behaviour may be elicited and to tailor signals to the variety of different relationships that may exist within a group. However, as discussed above, diversity or gradation in submission signals is not expected, and we believe this prediction will apply to social groups. Therefore, we predict an increased use of submission signals, a broadening of the contexts in which they are produced, and/or a reduction in the threshold required to elicit them within animal groups rather than an increase in submission signal complexity per se. Existing data comparing cooperatively breeding birds and fishes to independently breeding ones support this prediction (Hick et al., 2014; Rosa et al., 2016; Balshine et al., 2017). Cooperatively breeding species do not show a greater variety of submission signals compared to their independently breeding relatives, but rather deploy a similar repertoire of submission signals more frequently or in a greater diversity of contexts (Hick et al., 2014). Submission signals likely predate the emergence of complex social living arrangements like cooperative breeding, and evolution may act more on the use of submission signals than their form (Balshine et al., 2017).

Because group members interact frequently, there may be an added benefit to maintaining a reputation for signal honesty, thereby incentivizing the use of honest submission signals (Waas, 2006). Social animals also often interact in the presence of other group members, and these eavesdroppers may also gather information about the tendency for particular individuals to use submission signals honestly (McGregor & Peake, 2000; Peake & McGregor, 2004). Thus, dishonest signallers within social groups may face higher social costs in future interactions, hence maintaining honest submission signalling within the social group context. Furthermore, where animals can use the behaviour of others to infer social relationships or the salience of social information, this will provide additional routes by which group-living individuals can benefit from submission signalling (Paz-y-Mino et al., 2004; Grosenick et al., 2007; Goossens et al., 2008).

6. Future directions

Some submission signals may be subtle, involving for example, only a minute and transient postural change (Gorlick, 1976; Ruberto et al., 2020) or a small alternation to the colouration of a body part (Culbert & Balshine, 2019), and as a result, submission signals may go unnoticed even in well studied systems (Heathcote et al., 2018). This subtle information may provide a route for animals to assess their own or others' competitive ability. We encourage readers to carefully observe agonistic interactions in the animals they study and try to identify submission signals which may have gone heretofore undetected.

Most of the examples of submission signals we have presented are drawn from observational studies. Experiments that manipulate submission and examine the responses to these signals will be essential to critically test predictions. Some possibilities include the use of physical alterations of submission signals, artificial stimuli such as models or computer-generated imagery, and developmental or pharmacological manipulations that alter the expression of submission (e.g., Roche & Leshner, 1979; Arnold & Taborsky, 2010; Reddon et al., 2012; Taborsky et al., 2012; Woo & Rieucau, 2013; Hellmann et al., 2015; Taborsky, 2016; Culbert & Balshine, 2019). Alternatively, the costs and benefits of submission signals could be altered, for example by manipulating the opportunity to flee from a conflict. It may also be possible to experimentally manipulate the information state of the animals by altering the perceived strength of the competitors or the apparent resource value, which may in turn alter the use of submission signals in a systematic way.

Work that compares submissive behaviour in closely related species that differ in their social arrangement or compares within species across populations that vary in their social system (Lott, 1991), will be essential to understand the coevolution of sociality and submission signals. Further exploration of the role of social context, for example the presence or absence of eavesdroppers, on the expression of submission signals will also help to reveal the interrelationship between social systems and agonistic communication.

7. Conclusions

In this review, we draw attention to submission signals as an important, but understudied, element of the social communication repertoire of animals. We argue that these signals are beneficial for minimizing the costs of conflict and are especially critical when fleeing from an aggressor is costly or impossible. Animals that live in stable social groups benefit from the use of submission signals to establish social order and avoid the potentially prohibitive costs of frequent conflict while remaining in the same group. We hope that this review will inspire investigators to look specifically at the submission signals performed by their study species and strive to understand how these signals influence, and are influenced by, the social and ecological context in which that animal lives.

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