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Differences in social information are critical to understanding aggressive behavior in animal dominance hierarchies

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Sociality often involves conflict as individuals compete with group members for resources. In many species, including humans, individuals assort into dominance hierarchies. Individuals with more social information may be able to better optimize which individuals they challenge and in doing so, improve their overall rank in the hierarchy. Understanding how information is perceived, processed, and used by individuals in hierarchical systems is critical to understanding how animals make aggression decisions because different types of information can underlie different kinds of aggression strategies. This review summarizes recent research on the effect of five information types on animal conflict: Firstly, individual experience; secondly, recognition abilities; thirdly, social context; fourthly, transitive inference; and finally, network or global inference. This increased understanding of the information underlying social interactions can begin to provide new insight into structured conflict and could be useful to better understand strategic decision-making, social plasticity, and the cognitive load of sociality across species, including humans.

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Introduction

Sociality can provide many benefits to individuals but also comes with the cost of competition and conflict. This conflict often leads to the emergence of structured dominance hierarchies where individuals in a group are ranked by their competitive ability, the history of outcomes of previous encounters, or their association with kin groups (reviewed in [1]). The decisions individuals make about the timing, context, and severity of interactions, and which individuals they choose to interact with, can have strong effects on both individual-level outcomes and group-level social structure. The more information individuals have about their group members and their social worlds, the better those individuals may be able to balance the costs and benefits of sociality. Dominance hierarchies therefore provide a promising window into the connections between sociality, cognition, and social information, both in animals and humans. Because dominance hierarchies are so pervasive across different species, research on dominance relations in animals has the potential to provide evolutionary context to better understand how and why this kind of social structure, and the cognitive abilities needed to manage rank, may have evolved.

Dominance hierarchies are found in species across the animal kingdom, from primates and parrots to ants and octopus [2,3] and including humans (e.g. [4,5]). In many cases, the structure of these hierarchies can be treated as an emergent property of the complex and often nonlinear patterns of interactions among individuals in a social group [6,7]. Although widespread and well-studied, several aspects of dominance hierarchies are still not well understood. One of the most critical, and most important to tying sociality and cognition together, is the extent to which animals 'know' about their own rank and the rank of others in the hierarchy, or how much an individual can perceive emergent group-level rank information [3,7,8].

Understanding how information is perceived, processed, and used by individuals in hierarchical systems is critical to understanding how animals make decisions about their levels of aggression, which individuals they target, how often they fight, how aggression is modulated, and what strategies or rules they use to choose these fights. *Social information* is any information gained from monitoring others' interactions [9]. When this information is knowledge about group members, social information can be used by individuals to predict aspects of future social interactions. In this context, social information could be recognition of group members and a memory of their past actions, an association between a category of individuals and their fighting ability, or an individual's own recollection of the outcomes of its past social interactions. Potentially useful types of social information are mediated by *social cognition* [10], the suite of skills that are used to collect, process, and use different kinds of social information. Individuals that can better obtain social information and that have higher social cognition abilities may be able to optimize their behavior and gain higher rank than others. This increased *social competency* could then potentially act as a driver of social evolution [11].

This focus on social information, cognition, and competency is becoming increasingly important in understanding conflict and competition in animal groups (e.g. [10,12]). However, the extent to which information is accessible to individuals and the cognitive complexity of decision-making processes in the context of conflict is an ongoing debate in animal behavior research. Some researchers advocate for using the simplest explanation to explain social decision-making in conflict (e.g. [13,14]), while others skew towards more complex and cognitively based explanations, especially once simpler mechanisms are ruled out (e.g. [8]). Recently, creative experimental designs and new computational tools have begun to provide novel insight into the prevalence and use of social information in animal groups. This review summarizes the social information underlying animal conflict across low to high information cases. For each level of information, recent research highlights show how new experiments or computational methods have advanced our understanding of the information underlying dominance hierarchies in animal social groups.

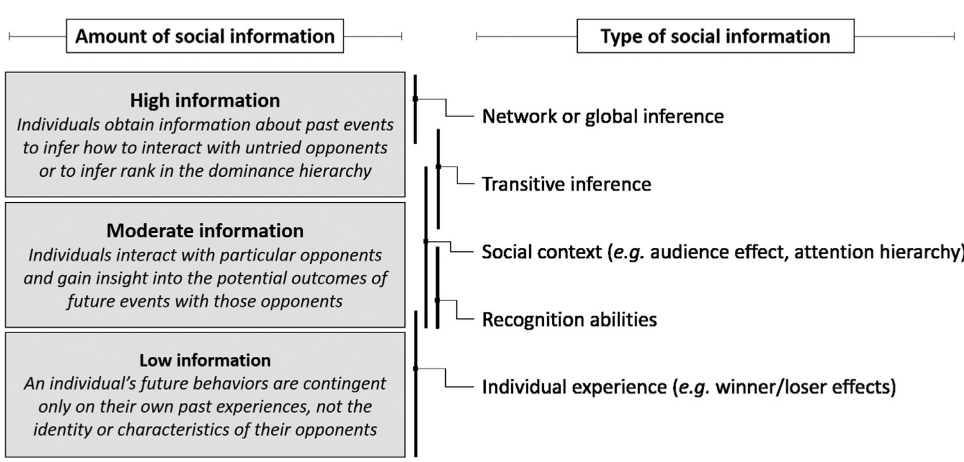
Information in conflict

When choosing when, how, and who to fight, individuals may assess their own state, characteristics of their opponents, the value of a disputed resource, or the social context in which the contest takes place (summarized in [12]). These assessments are dependent on different types of available information. Depending on the type of information individuals can access, they may develop different heuristics or strategies to pick their fights. Theoretical and empirical studies of animal dominance hierarchies differ in the amount and type of information that each approach allows or assumes that individuals can access, but many treat the cognitive side of conflict as a black box [12]. These approaches can be divided into three main categories: Firstly, *low information*, where an individual's future behaviors are contingent on their own previous experiences; secondly, *moderate information*, where individuals directly interact with particular opponents and gain some level of insight into the potential outcomes of future events with those opponents; and finally, *high information*, where individuals gather information about the outcomes of past events to infer how to interact with untried opponents or to infer where they (or their potential opponents) rank in the group's dominance hierarchy (Figure 1). Here, I summarize recent results dealing with five types of social information, spanning a gradient from low to high information: Firstly, individual experience; secondly, recognition abilities; thirdly, social context; fourthly, transitive inference; and finally, network or global inference.

Individual experience

In the most basic approach to dominance hierarchies, animals simply react to their experiences. This is a low information state because an individual's future behaviors are contingent only on that particular individual's directly

Figure 1



Information underlies many social systems like dominance hierarchies, but these systems can vary widely in the amount of information they contain. Different types of social information fall on a continuum from low to high information content (grey boxes, left) and can be expressed or used in different ways by individuals within their societies (right, see Sections 'Individual experience', 'Recognition abilities', 'Social context', 'Transitive inference' and 'Network or global inference'). Vertical bars show the approximate amount of social information required for each type of information; in many cases the expression or use of higher levels of information require the presence of lower-level types of information. It is important to note that differences in information content and the amount of information are distinct from cognition; a high-information system may or may not pose a high cognitive load to individuals in that society, depending on how they perceive, process, store, and act on available information.

experienced past interactions. The most commonly investigated behavioral responses to aggressive events are *winner effects* and *loser effects*, where winning or losing aggressive encounters changes the winner's and loser's behavior in future encounters [15,16]. Generally, winners gain a boost from winning past fights, and may be more aggressive or more likely to win future fights, while losers suffer from a reduction in aggression or a decreased probability of winning future fights following a loss. These individual-level effects can lead to the formation of clear and linear dominance hierarchies at the level of the group as individuals gain or lose social momentum and assort themselves based on how often they have won or lost fights (e.g. [17–19]). At this simple level, an individual collecting social information about its own experiences can use this information to generally assess its own competitive ability.

Traditionally, winner and loser effects have been studied empirically over short time scales to determine how the effect of winning or losing a fight affects an individual's chances in near-future encounters. For example, in fish like African cichlids, research has shown that loser effects appear to persist and affect aggressive behavior for 5 days, but disappear by day 7 [20]. However, other more recent experimental approaches, such as long-term exposure to winning or losing scenarios, show that winner and loser effects can persist and affect social behavior on much longer timescales in fish like the Amazon molly [21•]. Game-theoretical models have also recently shown that individuals may be able to better improve their rank by changing their level of aggressiveness through strategic choices based on their prior experience [19]. Biologically, it is important to consider the cognitive processes through which winner and loser effects could be mediated. Past experiences could be a cognitive memory, where an individual recalls winning or losing fights. However, past experiences could also be a more 'physiological memory' mediated by changes in hormone levels (e.g. [22]). From a theoretical perspective, an outstanding question still under investigation is whether winner and loser effects are adaptive [17] and how they may have evolved [23].

Recognition abilities

An important part of many dominance hierarchies in animals is recognition, or the ability to associate past experiences with particular individuals or a subset of individuals. Two types of recognition are important to consider when thinking about the information contained in dominance hierarchies: *signal/characteristic recognition* and *individual recognition*. Many animals display *signals* or *characteristics* that can contain information about an individual's competitiveness or rank. Some signals can be directly informative about competitiveness or rank, such as larger body size which often correlates with an increased ability to defend scarce resources. Other signals are indirectly informative of competitiveness, such as more arbitrary *badges of status* (reviewed in [24]). Recognition of a signal indicating rank or competitiveness could be used by individuals to more strategically pick their opponents, especially in avoiding fights they are unlikely to win. While this kind of recognition has traditionally been thought be common across many animal species, recent work has questioned the validity of some of these assumptions. For example, a classic example of a badge of status in birds is the dark-colored feathers that form a 'bib' in male house sparrows — the size of this feather patch has traditionally been thought to be a strong indicator of the quality and fighting ability of individuals, where a larger badge indicates a higher-ranked male. However, a recent meta-analysis questions this association between badge size and dominance rank and found a much weaker or absent relationship, which suggests that these common assumptions about signals of status may need to be re-examined across more species [25].

In contrast to signal or characteristic recognition, some animals can differentiate between specific individuals, which provides a different type of social information. *Individual recognition* abilities, although not ubiquitous, are widespread across animals (reviewed in [26]). If animals can recognize individuals, they can establish differentiated relationships — in dominance interactions, memory of opponent identity and the outcome of fights could be used by individuals to assort in a hierarchy. Early dominance experiments focused on this kind of information and often used a round-robin style of contests where each animal was individually pitted against all others in the group to force each pair of individuals to establish dyadic dominance relationships. However, theoretical studies have shown that these kinds of contests alone are unlikely, or even mathematically impossible, to result in linear dominance hierarchies at the group level (reviewed in [6]). In species which form cooperative coalitions, individual recognition abilities are needed to help animals choose strategic alliance partners to increase their odds of improving their dominance rank. In spotted hyenas, individuals that repeatedly form coalitions with their top social allies (via memory and individual recognition) are more likely to be able to break out of the constraints of their maternally inherited rank system and improve their ranks [27•].

In dominance hierarchies, it is important to consider both signal/characteristic recognition and individual recognition. The method and accuracy of recognition used by individuals in gaining or maintaining rank can have important effects on dominance hierarchy structure. Recent experimental results show that prior social experience may be critical in determining whether recognition is used in a system and the specific type or recognition that is used. In birds like the golden-crowned sparrow, a new study has shown that individuals can switch between using an observable badge to gather information about strangers and individual recognition to structure behaviors with known individuals [28•]. In insects like paper wasps, the ability to recognize individuals has recently been shown to be affected by past social interactions: wasps that were raised in social isolation did not learn to recognize individuals even though this species, in normal social conditions, can recognize individuals [29•]. Understanding the potential tradeoffs involved in the use of different kinds of information can help understand the evolution of these kinds of recognition systems [24] as well as more situationally plastic responses to changes in short-term conditions.

Social context

In some cases, animals change their behavior in response to their social context. Two individuals interacting with each other may behave differently if this interaction takes place in social isolation compared to situations when additional individuals are present and potentially observing the interaction. This responsiveness to social context is known generally as an *audience effect* (reviewed in [30]) or in the context of aggression and dominance, as an *attention hierarchy* (reviewed in [31,32]). The presence of an audience effect or attention hierarchy can provide insight into whether animals recognize others' relationships and the methods animals use to monitor their social surroundings [33].

This ability to plastically respond to changes in social context could be mediated by how individuals view their potential observers as well as through how attentive they are to changes in the composition of their observer pool. This is especially true for the behavior of subordinate individuals within a hierarchy, where their behavior can be heavily influenced by the presence of more dominant individuals (reviewed in [32]). For example, subordinate male cichlid fish and male mice both alter their aggression depending on whether the dominant individual is present and/or able to observe the interactions (e.g., [32,31]). In fish like daffodil cichlids, within-group aggression patterns changed depending on whether another social group was present: experiments with and without the presence of a neighboring social group demonstrated that the presence of another group reduced aggression between the dominant mated pair but increased aggression between those dominant individuals and the subordinates in their group [34]. Birds like common ravens show evidence for detailed knowledge of the social bonds between individuals who attack them and surrounding individuals, who may come to the aid of the attacker or the target. A recent study showed that attacked ravens gave more distress calls when they had strong positive relationships with bystanders (likely in order to elicit their aid) but decreased their distress calling when their aggressor had more allies in the audience (likely to avoid drawing in additional aggressors) [35•]. This remarkable responsiveness showed that attacked ravens were responsive to the social context within which aggression takes place, and were affected by both their own relationships and the relationships of their aggressors. There is growing awareness in animal social research that these kinds of indirect connections may play an important role in structuring animal social groups [36].

Transitive inference

In some groups, individuals can use a kind of logical reasoning called *transitive inference* to infer unknown relationships from known relationships [37]. For example, if individual A beats individual B in fights, and B beats C, in a transitively ordered system, A should be able to beat C. If individuals A, B, and C can all use transitive inference, then A and C do not need to actually fight in order for all individuals to behave according to this rank ordering. Several species of vertebrates show evidence for transitive inference (e.g. [37]) and recent work has documented transitive inference for the first time in insects (two species of paper wasps [38•]). In the context of dominance hierarchies, transitive inference abilities can help animals avoid potentially costly fights that they are unlikely to win. Theoretical studies have also shown that hierarchies can form much more quickly when animals can use observations of the fights of others and transitive inference to determine individual ranks [39,40]. Recent theoretical work has also shown a surprising link between memory capacity and transitive inference: hierarchy formation via transitive inference may require much less memory than immediate inference of an opponent's fighting ability and that systems with limited memory capacity may actually be more likely to evolve transitive inference abilities [40]. This seemingly counter-intuitive connection may help explain the occurrence of transitive inference across a range of species with varying levels of cognitive skills and brain sizes.

Transitive inference experiments are often used to detect evidence for reasoning in a nonsocial context through training individuals on a series of pairwise comparisons between objects of different lengths or colors and then presenting test subjects with novel combinations to determine whether animals can choose the proper stimulus ordering. However, other research uses social context to infer transitive inference abilities to see how animals make biologically-relevant social decisions, often in the context of conflict and aggression. Classic work with primates like baboons demonstrated increased attention to simulated vocal interactions where the winner and loser in aggressive interactions were artificially reversed — test subjects to which normal and reversed fight vocalization were played were more attentive to the manipulated interactions, indicating individuals could detect 'anomalous' social interactions [41]. In birds like common ravens, experiments have shown that individuals can recognize dominance reversals that happen both within their own social groups as well as within neighboring social groups for which they themselves are pure observers [42].

Network or global inference

In some cases, when animals fight with group members, fights do more than construct a dominance hierarchy or maintain an individual's rank. This is especially true if individuals can develop and use rank-informed strategies to pick their fights. The summary of fight outcomes in a group's aggression network form or preserve an individual's global rank in the hierarchy, but on a fight by fight basis, individuals may choose their opponents based on information about the relative rank differences between themselves and potential opponents.

If individuals have access to information about their own rank and the ranks of others in their group, it is possible for rank-informed aggression strategies to emerge. Rank-informed strategies are a high information case because they can be built on a summary of information about fight outcomes for the entire group, regardless of whether all individuals have settled dominance relationships. In monk parakeets, computational methods have demonstrated that longer chains of relationships contain more information about rank and are more predictive of aggressive behavior than pairwise relationships [8]. Recent comparative work across many animal aggression networks has shown that a surprising variety of species follow more information-rich aggression strategies that cannot be reproduced by models using more simple information about dominance hierarchy structure [3]. For example, individuals in a social group may follow a 'close competitor' strategy, and preferentially attack individuals ranked just below themselves in the hierarchy [3]. The use of this strategy indicates the presence of more sophisticated information about relative rank differences in the group, beyond simply a dyadic dominant/subordinate relationship between the aggressor and the target.

Conclusions

The strategies individuals use to pick their fights and gain or maintain rank in a dominance hierarchy are in many cases dependent on the types of information required. Individuals in a low-information society would only be able to build a conflict strategy based on their own experiences and would follow this strategy regardless of the identity of their opponents. Individuals in a medium-information society would be able to build a more detailed strategy that may change how they interact with particular individuals, but only opponents that they have interacted with in the past. Individuals in a high-information society could build the most refined set of strategies, customizable to changes in social or environmental conditions, because they could use more detailed information to infer their own rank and the ranks of others in the hierarchy. Importantly, higher-information societies are often built upon types of information at lower levels. For example, some kinds of network or global inference may require individuals to have a combination of information about their individual experience, to recognize individuals and social context, and to use transitive inference. It is also important to note that the presence of higher amounts of information in a social system is not necessarily indicative of higher cognitive abilities of the species that live within those societies. In many cases, species may have evolved cognitive shortcuts that reduce the cognitive load of information-rich social systems.

This recent increased understanding of the information underlying social interactions can provide new insight into the kinds of information individuals can perceive, process, and use to make decisions about when and how to interact with group members. Many of these methods and perspectives could also be useful in studies of human social conflict to better understand strategic decision-making, social plasticity, and the cognitive load of sociality. In animals, the ways in which this social information is stored, and the cognitive demands of using different kinds of information, are still very much debated. As we develop new experimental and computational methods to identify systems in which information exists and is being used to structure aggression, new research can then focus on determining the mechanisms through which this information is encoded in social systems, and differentiate between systems reliant on more complex cognitive skills versus those where less demanding cognitive shortcuts have evolved.

Conflict of interest statement

Nothing declared.

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