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Current Opinion in Behavioral Sciences

Aggression and dominance: an interdisciplinary overview

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Aggression is ubiquitous among animals, and contest outcomes in many gregarious species yield societies structured by dominance hierarchies. Recent results from a variety of disciplines have laid the groundwork for an integrative view of aggression and dominance, ranging from their physiological underpinnings to their evolutionary histories. Here we use Tinbergen's four levels of behavioral analysis to summarize our current understanding of aggressive behavior and dominance relationships. First, we discuss the role of epigenetic effects in the ontogenetic emergence of aggressive and rank-related phenotypes, and summarize how these phenotypes are mediated by endocrine and nervous system activity. We briefly review recent work on the functions of aggression and dominance hierarchies in animal societies, and then consider their phylogenetic history. Finally, we review methodological encumbrances to the study of dominance, and consider the unique evolution of aggression and dominance relationships in humans.

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Introduction

Aggressive behavior occurs ubiquitously in the animal kingdom, in creatures ranging from sea anemones to humans. Aggression can take many different forms, so we define it here as harmful, potentially harmful, or threatening behavior that is directed toward conspecifics, and tends to increase the distance between an attacker and its opponent. Although aggressive behaviors occur in myriad contexts, we will refer mainly to behaviors occurring in association with actual or anticipated competition for resources. In contests over limited resources, success is often determined by aggressive behavior. In many gregarious animals, repeated aggressive interactions among members of a social group result in stable asymmetric relationships between individuals; an emergent property of these repeated interactions is a dominance hierarchy that structures the entire society [1]. Higher-ranking animals consistently defeat lower-ranking animals in agonistic encounters [2], although the most dominant individuals are not necessarily the most aggressive [3,4•]. Dominance-related behavior depends on recognition of social status and the intentions or motivations of potential opponents [5,6•,7]. Although aggression is usually necessary for hierarchy formation, once established, a stable hierarchy can suppress further aggression and unwanted fights among group members [1]. An individual's position in a dominance hierarchy usually determines its priority of access to key resources. Social rank can thus have profound effects on health, aging and fitness measures (e.g., 8–10). Other work has also revealed important effects of an individual's rank position on many other aspects of its biology, including its circadian rhythms [11] immune function [12,13], brain development [14], and patterns of gene expression in the adult brain [15,16]. Here we frame our review of aggression and dominance in the context of Tinbergen's [17] four levels of analysis in the study of behavior. Thus we highlight recent insights regarding the ontogenetic development of aggression and dominance relationships, the physiological and genetic mechanisms mediating these phenomena, their adaptive significance, and their phylogenetic history.

Ontogenetic development of aggression and dominance

Development of aggressive behavior

Early rearing conditions have powerful effects on adult aggressive behavior in animals as diverse as humans [18••], pigs [19], rodents [20••] and birds [21]. Longitudinal studies initiated at birth in humans show that physical aggression is more frequent in early childhood than at any other time during the life-span, and that high levels of aggression in adults often ensue from failure to develop the ability to inhibit aggressive tendencies [18••]. Infant pigs that experience higher rates of aggression from littermates while suckling mature to be more aggressive after weaning [19]. Adverse rearing conditions can put individuals on a chronic trajectory of aggressiveness that persists from early life to adulthood. Studies of rodents, humans and other primates show that various types of early adversity, including repeated maternal separation and neglect, strife between parents, post-weaning social isolation and peri-pubertal stress, can each independently induce the development of deviant forms of adult aggression, including mismatches between provocation and response, attacks on inappropriate targets, and deficits in social signaling. In rodents, primates and zebra finches, both post-natal and adolescent phases of development represent sensitive periods during which social conditions have lasting effects on adult aggression [20••,21]. Interestingly, spontaneous aggression can even be elicited in robots 'raised' under adverse environmental conditions [22].

In addition to early rearing conditions, several other factors have been found to shape adult aggression including an animal's sex, its intrauterine position, its personality traits, its maternal rank, its mother's behavior, and population density. Ontogenetic trajectories of aggressive behavior are often sexually dimorphic with respect to the age at which peak aggression occurs, which types of conspecifics are targeted, and which individuals receive the most aggression (e.g., 10,23,24,25•). Intrauterine position affects both aggression and dominance among female octagon degus [26]. It is becoming increasingly clear that aggressiveness and the ability to dominate conspecifics often correlate positively with other personality traits, including boldness, exploration and stress reactivity [27]. Maternal behavior and maternal rank also profoundly affect offspring aggressiveness in creatures as diverse as monkeys [28] and fish [29]. Rates of aggression are often highest in the densest populations (e.g., 23,30•).

Development of dominance and dominance hierarchies

In most gregarious birds and mammals, the ontogeny of dominance relationships generally conforms to one of two major patterns. In the most common case, dominance is determined by intrinsic factors such as body size, fighting ability, personality traits, or other attributes that directly affect the ability to win fights [31,32]. In these cases, dominance status fluctuates over time and in association with changing competitive ability and health. Alternatively, some primates and spotted hyenas form nepotistic societies, in which dominance status, particularly among members of the philopatric sex, is highly influenced by familial rank. In these societies, dominance acquisition begins in infancy and involves coalitionary support from kin (e.g., 33,34).

Although social status is largely influenced by either familial rank or intrinsic attributes, theoretical and empirical evidence suggests that emergent social properties also influence the ontogeny of dominance. The 'social dynamics' hypothesis posits that dominance ranks emerge from self-organization dynamics such as winner–loser effects or highly localized social network properties, even in the absence of individual differences in specific attributes [35–37]. Winner–loser effects are well-documented forms of learning in which victorious individuals subsequently behave more aggressively, whereas losers behave more submissively [38–40]. Historically, most work on these effects has been conducted in lab settings with experimental designs that artificially eliminate or minimize individual differences (e.g., 41). However, methodological advances (see Box 1) have permitted testing of the social dynamics hypothesis in unmanipulated animal groups [42••,43••]. Results suggest that localized network properties and winner–loser effects do shape dominance hierarchies, but also that specific attributes make individuals more or less susceptible to these effects. The cognitive abilities required to perpetuate these self-organization dynamics are memory and inference [43••].

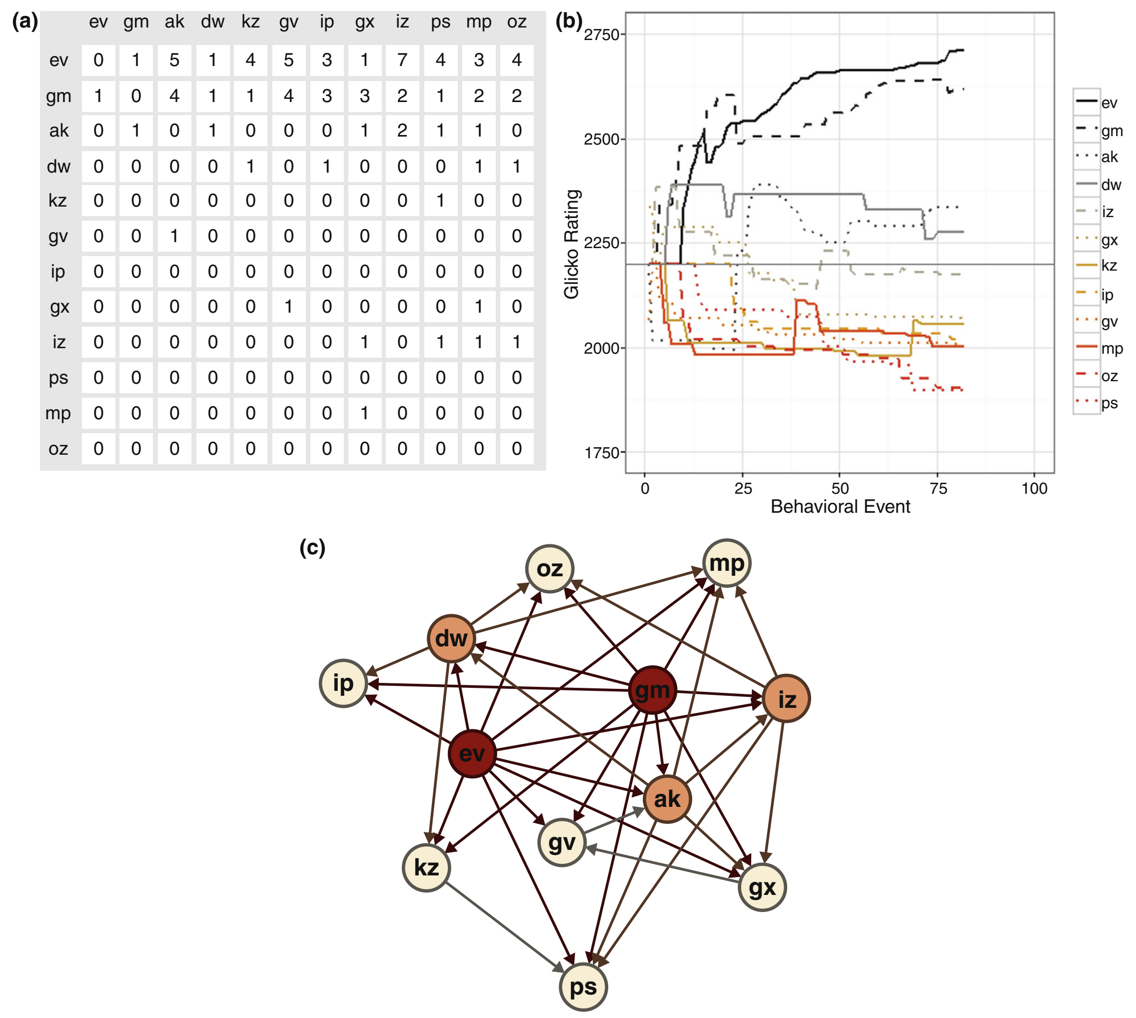
Winner–loser effects reduce the deleterious effects of competition in animal societies [39]. Both winners and losers acquire information in contests about the resource holding power (RHP) of their opponents, even when the contests involve no physical fighting [38]. This new information allows both opponents to make strategic improvements in subsequent contests. Imperfect information about the relative RHP of group members affects

Box 1 Quantifying dominance relationships

Quantification of dominance relationships permits testing of hypotheses concerning the function of dominance, assessment of the properties of societies that emerge from dyadic interactions, and comparisons among groups; it also enhances our understanding of the role dominance plays in various types of societies (Figure 1). To date, efforts to quantify, compare, and explain dominance hierarchies have suffered from a lack of consensus on methods and difficulties in dealing with unresolved relationships, which occur when two individuals in a society are never observed to interact [87]. Estimates of hierarchy linearity and steepness decrease with an increasing proportion of unresolved relationships, as does the reliability of rank assignments [87]. Researchers should report the proportion of unresolved relationships in their data, but many do not. Several workers have developed methods for dealing with unresolved relationships (e.g., 89), although the general applicability of these methods remains to be seen.

Advances in social network analysis (SNA) provide versatile new techniques for assigning dominance ranks and quantifying societal properties. These techniques either focus on local substructures of networks ('motif' approaches; e.g., 43,90) or global network properties (e.g., 91,92•). Using a network motif approach to understand hierarchy emergence in a newly formed group of monk parakeets, Hobson and DeDeo [43] found that parakeets directed less aggression toward distant individuals in their aggression subnetwork than toward nearby individuals, suggesting that they use transitive inference to infer relative ranks based on observation of agonistic interactions among group-mates. Similarly, Dey and Quinn [92•] used Exponential Random Graph Models to determine that pukeko hierarchies were shaped both by individual attributes and local network substructures. Finally, SNA methods can be used to measure the flow of information through dominance networks, and this information can be critical for coordinated group actions [93]. Pasquaretta *et al.* [94] assessed the efficiency of information flow through networks of 78 groups from 24 primate species, and found that egalitarian networks have more efficient information transfer than despotic ones, suggesting a negative selection pressure on individual aggressiveness or positive selection for tolerance of other individuals. Overall, SNA methods provide a promising platform for unifying approaches to quantifying dominance relationships.

Figure 1



(a)

	ev	gm	ak	dw	kz	gv	ip	gx	iz	ps	mp	oz
ev	0	1	5	1	4	5	3	1	7	4	3	4
gm	1	0	4	1	1	4	3	3	2	1	2	2
ak	0	1	0	1	0	0	0	1	2	1	1	0
dw	0	0	0	0	1	0	1	0	0	0	1	1
kz	0	0	0	0	0	0	0	0	0	1	0	0
gv	0	0	1	0	0	0	0	0	0	0	0	0
ip	0	0	0	0	0	0	0	0	0	0	0	0
gx	0	0	0	0	0	1	0	0	0	0	1	0
iz	0	0	0	0	0	0	0	1	0	1	1	1
ps	0	0	0	0	0	0	0	0	0	0	0	0
mp	0	0	0	0	0	0	0	1	0	0	0	0
oz	0	0	0	0	0	0	0	0	0	0	0	0

Current Opinion in Behavioral Sciences

Three depictions of a single dominance hierarchy. A multitude of different approaches have been used for quantifying and visualizing dominance hierarchies. **(a)** Interaction matrices tabulate the number of wins and losses sustained by each individual in aggressive interactions during a specified time period, with winners listed in the rows and losers listed in the columns. Optimal rank orders minimize the number of wins listed below the diagonal. **(b)** Glicko and Elo ratings continually update rank scores after each interaction and are useful for studying dynamic aspects of dominance hierarchies such as hierarchy stability. **(c)** SNA methods treat dominance hierarchies as networks, with nodes corresponding to individuals and directional edges depicting the outcomes of conflicts. In this case, more dominant individuals are depicted in darker shades of red. SNA methods allow for the detection of relationships between local and global network properties in determining dominance.
Figures reproduced with permission from So *et al.* [15].

the speed with which linear dominance hierarchies emerge in animal societies; theoretical models suggest that hierarchies form most quickly when information is highly reliable and loser effects are most common [44]. Losers often quickly learn to avoid further direct conflict by altering or inhibiting their behavior in the presence of higher-ranking conspecifics [45,46].

Mediating mechanisms

Gonadal steroid hormones are well known to affect aggressive behavior. Both organizational and activational effects of androgens enhance aggressiveness in mammals [47,48,49••]. For instance, intrauterine position affects aggression and dominance in octagon degus via organizational androgen effects [26]. Several neuroendocrine mechanisms have been identified that mediate winner–loser effects on aggressive behavior in invertebrates, fish, mice and humans [16,40,50]. Winner effects in invertebrates are mediated by the biogenic amine octopamine [38]. In vertebrates, winner effects appear to be mediated by androgens; acute increases in androgens during contests help prepare the competitor by activating receptors in the brain that increase the salience of violent threat [16,51–53]. Evidence regarding proximal mechanisms mediating loser effects is patchier, and varies among species. Among vertebrates, elevated levels of corticosteroids are often detected in losers [38], sometimes in both winner and losers [54], and in several species, depressed plasma androgen levels also accompany defeat [38]. Differences in social rank are often associated with differential sex steroid profiles [55]. Evidence from humans suggests that both testosterone and cortisol are importantly involved in the mediation of aggression and dominance [56].

The formation of social hierarchies is associated with activation of specific brain regions. The prefrontal cortex (PFC), the amygdala and the serotonergic system have been identified as critical parts of the neural circuitry influencing expression of dominance behavior [4,48,57]. Excitatory synapses in the medial PFC (mPFC) are stronger in dominant than subordinate mice, and manipulation of synaptic strength in the mPFC changes social status. Winning in contests evidently leads to strengthening of mPFC synapses, whereas losing weakens them. During social confrontations, the mPFC may communicate with the amygdala for emotional processing, with the serotonergic system for motivation to act, and with the striatum for assigning salience [4•]. Serotonin (5-HT) inhibits aggression in many species (e.g., 58•). The brainstem dorsal raphe nucleus (DRN) is the main serotonergic nucleus in the vertebrate brain. Studies in mice, monkeys and fish reveal that reduced serotonergic function is associated with increased aggressive behavior [4•,59,60]. In a socially dominant individual, a stronger mPFC output to the DRN may increase motivation to compete in social conflicts [4•].

Work with a cichlid fish (*Astatotilapia burtoni*) sheds light on the neural signaling processes associated with changing dominance status. Differences in 5-HT signaling between dominants and subordinates are mediated, at least in part, by two types of 5-HT receptors in the telencephalon. Serotonergic transmission in the preoptic area also contributes to facilitating the physiological and behavioral changes typical of social descent. On the other hand, the nonapeptide arginine vasotocin (AVT) appears to regulate social ascent in *A. burtoni* [58•]. Individuals ascending in social rank have higher AVT levels and receptor expression than do either stable subordinate or stable dominant animals, indicating a role for AVT during the transition to social dominance, but not its maintenance [58•]. AVT may affect behavior by regulating specific motivational systems or specific motor patterns, or it may be involved in determining the salience of aggressive stimuli.

Molecular genetic tools have permitted elucidation of some of the genes involved in the mediation of aggression (e.g., 61) and dominance status [62] in non-human animals. Unsurprisingly, genes associated with many of the neuroendocrine mechanisms discussed above appear to influence aggressive behavior. Epigenetic research has also shed considerable light on the mediation of aggressive behavior; both maternal exposure to stress and early-life adversity affect gene methylation patterns and reduce glucocorticoid receptor density in key brain regions in offspring, which in turn increases their stress reactivity and aggressiveness (e.g., 63,64). Adult aggression in rats can also be enhanced by peripubertal administration of corticosteroids, which presumably also affect patterns of gene expression in the brain [65].

Adaptive significance

Aggression functions importantly in group defense [66,67], and to access critical resources such as food [46,68,69•], nest sites [70,71], or mates [72–76]. In some species, males use aggression to overcome female choice (e.g., 10,73•) and thereby enhance their own reproductive success. Thus sexual coercion can function as an adaptive strategy. Aggressiveness as a personality trait can have important effects on the fitness of the individuals possessing this trait [77]. Furthermore, the mixture of aggressive personalities within a social group can have major effects on the growth and persistence of the group. For instance, in the gregarious spider *Anelosimus studiosus*, colonies founded by aggressive individuals grow more slowly than others, but are also far less susceptible to extinction [78]. The founders are 'keystone' individuals, which are those having an unusually large effect on group dynamics; the aggressiveness of founders can thus ultimately affect the composition of multispecies communities [79•].

Contemporary work has confirmed Schjelderup-Ebbe's [1] hypothesis that stable dominance hierarchies function to reduce intense conflicts and injuries, save energy, and promote social stability. Hierarchy instability induces endocrine and oxidative stress responses [80,81]. A stable social hierarchy has, in fact, been identified as a fundamental building block of cooperation in animal societies [55]. Unnecessary friction due to conflicts of interest or repeated negotiations of dominance relationships can be avoided if individuals express appropriate behavior for their relative social status. The second building block of cooperation between individuals with conflicting fitness interests is the exertion of social control to prevent cheating [55]. Social rank often needs to be persistently reinforced with aggression emitted by dominants.

Phylogenetic history

The evolution of aggression is shaped by a fitness-optimizing trade-off between its benefits (i.e., securing limited resources) and costs (i.e., risk of injury; loss of time and energy) [82]. Significant work has focused on the phylogenetic emergence, maintenance or loss of specific traits representing both causes and effects of aggression. Trait simplification and loss are widespread and frequently associated with speciation events. Red throat patches, which represent badges of status, have been lost during evolution of some populations of three-spined sticklebacks, and this loss has affected male–male aggressive behavior in these animals [83]; males that have lost status badges direct more aggression toward males in which these signals have been retained. In another case, this one involving a derived cichlid species, a recent evolutionary shift from non-territorial females to females that defend territories, just as males do, has resulted in the loss of sexual size dimorphism because contest competition for territories selects for large body size in both sexes [84].

Dominance relationships vary considerably among species, from highly despotic and nepotistic to tolerant and egalitarian [85]. It remains unclear whether positions occupied by particular species on this continuum can be best explained by ecological demands or phylogenetic relationships. Primatologists have found considerable support for socio-ecological models (e.g., 86) suggesting that ecological forces shape convergent societies in particular habitat types. However, much of the variation in primate rank relationships cannot be explained by socio-ecological models, so alternative efforts have focused on the possibility that phylogenetic inertia constrains social evolution by limiting animals' responses to specific ecological pressures (e.g., 85; see also Box 2). Indeed, the degree of despotism in societies of multiple clades of primates reveals a strong phylogenetic signal [85,87•,88••]. Clearly, both socioecological and phylogenetic effects must be considered in attempts to explain the evolution of animal societies.

Box 2 Evolution of human societies

Some fascinating recent work focuses on the evolution of socio-political structure in humans. In most primates, aggressive between-group encounters are rare or absent. This is often ascribed to the presence of collective action problems, which emerge whenever collective action creates a public good (e.g., a territory) and the selfish interests of group members are not highly aligned [67]. Analysis of 138 group-living primate species revealed that 45% of species indeed suffer from collective action problems, and indicated that the intensity of between-group competition in primates is more strongly affected by social dilemmas than by ecological conditions. It appears that collective action problems represent an important selective force in the social evolution of group-living primates.

In all multimale–multifemale primate societies except that of *Homo sapiens*, individuals vary in dominance based on motivation and physical prowess, such that dominant individuals gain fitness at the expense of subordinate group-mates [95••]. During human evolution, by contrast, persuasion and influence became a new basis for social dominance, allowing for more egalitarian societies than those found in non-human primates. Gintis *et al.* [95••] argue that replacement of the ancestral social dominance hierarchy with the more egalitarian sociopolitical structure found in human societies resulted from the combined effects of two factors: development of lethal weapons, which led to the suppression of dominance based on physical prowess, and a marked increase in cooperative activities, such as group hunting of large game, that promoted social interdependence. These conditions favored the emergence of leaders able to motivate and persuade, and selected for language skills, social agility, and enhanced cognitive abilities.

Conclusions

Aggression has long been known to be of central importance in the lives animals, but recent research has allowed development of an interdisciplinary overview of aggression and dominance that spans multiple levels of analysis. Our contemporary view of aggression and dominance is emerging from research in a variety of disciplines, including endocrinology, social network theory, neurobiology, evolutionary biology and behavioral ecology. Early life experiences and other epigenetic effects have profound effects on adult aggressiveness and dominance status, and an individual's aggressive phenotype is mediated by multiple interacting systems in the brain, as well as by circulating concentrations of multiple hormones. Aggressive behavior is important for accessing and defending critical resources and for establishing dominance status. Networks of repeated aggressive interactions in many animal groups yield dominance hierarchies, which function to limit escalated conflict within groups, maintain social stability, and promote cooperation. Evolutionary patterns of aggression and dominance suggest that these traits are constrained by phylogeny, and that changes in these traits may be importantly involved in speciation events. Although the mechanisms that underlie formation of dominance hierarchies remain poorly understood, social network analysis and other methodological advances provide promising avenues for future research.

Conflict of interest statement

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