Trends in Ecology & Evolution

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Review

Cognition in Contests: Mechanisms, Ecology, and Evolution

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Animal contests govern access to key resources and are a fundamental determinant of fitness within populations. Little is known about the mechanisms generating individual variation in strategic contest behavior or what this variation means for population level processes. Cognition governs the expression of behaviors during contests, most notably by linking experience gained with decision making, but its role in driving the evolutionary ecological dynamics of contests is only beginning to emerge. We review the kinds of cognitive mechanisms that underlie contest behavior, emphasize the importance of feedback loops and socio-ecological context, and suggest that contest behavior provides an ideal focus for integrative studies of phenotypic variation.

Trends

Animal contests are important determinants of fitness.

Cognition mediates contest behaviors, but its role is underappreciated.

New theory, technologies, and methodologies facilitate the study of contest cognition.

We develop a framework linking cognition, contests, fitness, and ecology.

A Role for Cognition in Competition

Competition for resources such as food, mates and territories is ubiquitous among animals and a fundamental predictor of fitness [1]. Much of this competition is mediated by **contests** (see Glossary), in which animals use specialized aggressive displays and overt physical attacks to determine access to resources [2]. Contests are incredibly variable both within and between species in their format, intensity, and the specific behaviors involved [2]. Understanding the causes and consequences of animal contest behavior is important because aggressive interactions affect social structure and individual fitness, which can carry over to impact key higher-level processes including selection, population dynamics and distribution [3–5]. Contests require rapid information processing for decision making about when, how and with whom to challenge, escalate or withdraw [6]. We argue that **cognition** provides a significant but largely unexplored explanation for variation in contest behavior because cognitive mechanisms such as **learning** from previous interactions, and assessments of resource value, physical ability and social status, facilitate information processing and decision making.

Examining cognitive mechanisms will provide important new insights for studies of animal contests. First, although evidence abounds for a role of cognition in contests (Table 1), most studies focus only on demonstrating that animals gather and use information. The mechanisms by which this information is processed, retained, and used in decision making are rarely investigated and largely treated as a black box by both empiricists and theoreticians [7]. However, these mechanisms are critical to understanding variation between individuals and between species in contest behavior because cognitive processing might not always lead to optimal behavioral expression, as is commonly assumed [8]. Constraints on information gathering and use might explain why contest assessments often incorporate only a limited subset of the available information [9], and why individuals with lower **resource-holding potential** (RHP) sometimes can bluff their way to success by deceiving their opponents [10]. Second, focusing on cognition emphasizes that animal contests are not one-time,

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context-independent events, but rather take place within a series of interactions across the lifetimes of individuals in a complex environmental and social milieu. Cognition links experience gained in past interactions to future contest behaviors. Third, RHP, the key variable determining contest success [11], is often estimated using a single physical characteristic (i.e., body size) but is in fact a composite trait with inputs from multiple phenotypic characteristics [12]. We argue that **cognitive performance** is often an important component of RHP, and can sometimes reduce or even over-ride advantages accruing to larger individuals.

In an effort to understand the diversity of animal contest behavior, we present evidence that cognition underlies important behaviors involved in animal contests (Table 1). We examine these behaviors within a general framework for testing hypotheses about how links between cognition and contest behavior influence evolutionary and ecological processes, with the potential to feed back onto cognitive and behavioral traits (Figure 1). We discuss how these feedback mechanisms could explain the causes and consequences of both individual, within-species, variation in cognitive performance, and between-species differences in the role of cognition in contests. Recently, major advances have been made in developing cognitive assays for field and laboratory studies [13], methods to elucidate the neural bases of cognition [14] (Box 1), statistical analyses of contests [15], measurements of selection on cognitive traits [16], and monitoring individuals within ecologically relevant contexts in complex social environments [17]. Our aim is to encourage researchers to apply these tools and methodologies towards integrative studies of cognition and contest behavior.

Cognitive Mechanisms of Contest Behavior

Cognition encompasses a diverse range of mechanisms for information acquisition, processing and use, including perception, learning and memory, individual recognition, and **transitive inference** of social status [18]. Identifying the specific cognitive mechanisms of contest behaviors is an important but challenging task. For instance, opponent recognition is often important in contests and can arise from **habituation learning** [19], **categorization** of different classes of individuals [20], or so-called **true individual recognition** [21]. Furthermore, it is difficult to disentangle the effects of cognition, personality, motivation, and condition on behavioral expression, and the careful experimental designs required to distinguish between these factors are challenging even for the most tractable species [22]. Nevertheless, cognitive mechanisms are known or hypothesized to be important in the contests of many species; we discuss the evidence here, which provides a solid basis for further study of contests and cognition (Box 2).

Development of Signals and Tactics

The skill with which individuals perform aggressive displays and fighting maneuvers has recently been identified as a significant, but understudied, determinant of contest success [23]. Learning likely facilitates the development of skills important in contests. Bird song is used in territorial contests and many song characteristics are learned during juvenile development [24], raising the possibility that learning enables birds to produce more effective aggressive signals. In song sparrows *Melospiza melodia*, young birds learn more songs from tutors that they have competed with aggressively [25]. Most studies of song learning focus on song structure and syntax, and less is known about learning of song performance (e.g., timing, amplitude, and type matching) [26], which is especially important in bird contests [27]. Animals can also learn improved fighting tactics from recent contest experiences. For instance, three-spined sticklebacks *Gasterosteus aculeatus* learn the association between producing threat displays and causing an opponent to flee; likely through **operant conditioning** [28]. Blue gouramis *Trichogaster trichopterus* and *Betta splendens* learn via **classical conditioning** to anticipate, respectively, the timing and direction of the approach of a rival [29,30]. Learning might even enable animals to adjust their tactics during contests by monitoring the effectiveness of contest

Glossary

Assessment strategy: function relating information gathered before and during the contest to the expression of contest behaviors, especially decisions of whether to persist, withdraw or escalate.
Categorization: processes by which stimuli are assigned to distinct groups that are distinguished from other such groups of stimuli.
Classical conditioning: learning to associate one cue with a second, such that a response initially given only to the second cue can eventually be elicited by the first cue alone.
Cognition: processes involved in the acquisition, processing, retention, and use of information from the environment [18].
Cognitive ability: cognitive mechanism involved in the performance of a particular behavior; individuals vary in the effectiveness of these mechanisms, and hence in cognitive ability.
Cognitive performance: realized outcome of a task requiring cognition, which is determined by both cognitive ability and environmental factors including motivation, motor performance, and ecological context.
Contest: direct and discrete behavioral interaction determining ownership of an indivisible resource unit [2].
Cumulative assessment: assessment strategy in which the contest behavior of an individual is determined by its own characteristics and no opponent assessment takes place, but in which opponents can nonetheless exert an influence on individual persistence by inflicting direct costs [91].
Dear enemy effect: phenomenon in which territory owners respond less aggressively to familiar neighbors than to strangers [42].
Habituation learning: decrement in response to a repeated stimulus not due to sensory adaptation or motor fatigue.
Learning: change in cognitive state as a result of experience that can influence future behavior [18].
Mutual assessment: assessment strategy in which an individual's contest behavior is determined by gathering information on an opponent's RHP relative to its own RHP [33].

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