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1   **Cognition in contests: mechanisms, ecology and evolution**

2

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9

10   **Keywords**: cognition, contest, competition, learning, recognition, signaling

11   ABSTRACT

12

13   Animal contests govern access to key resources and are a fundamental determinant of fitness

14   within populations. Little is known about the mechanisms generating individual variation in

15   strategic contest behavior or what this variation means for population level processes.

16   Cognition governs the expression of behaviors during contests, most notably by linking

17   experience gained with decision making, but its role in driving the evolutionary ecological

18   dynamics of contests is only beginning to emerge. We review the kinds of cognitive

19   mechanisms that underlie contest behavior, emphasize the importance of feedback loops and

20   socio-ecological context, and suggest that contest behavior provides an ideal focus for

21   integrative studies of phenotypic variation.

22

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 employed 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, context-independent events, but rather take place within a series of interactions across individuals' lifetimes 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 override 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-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

72 environments [17]. Our aim is to encourage researchers to apply these tools and

73 methodologies towards integrative studies of cognition and contest behavior.
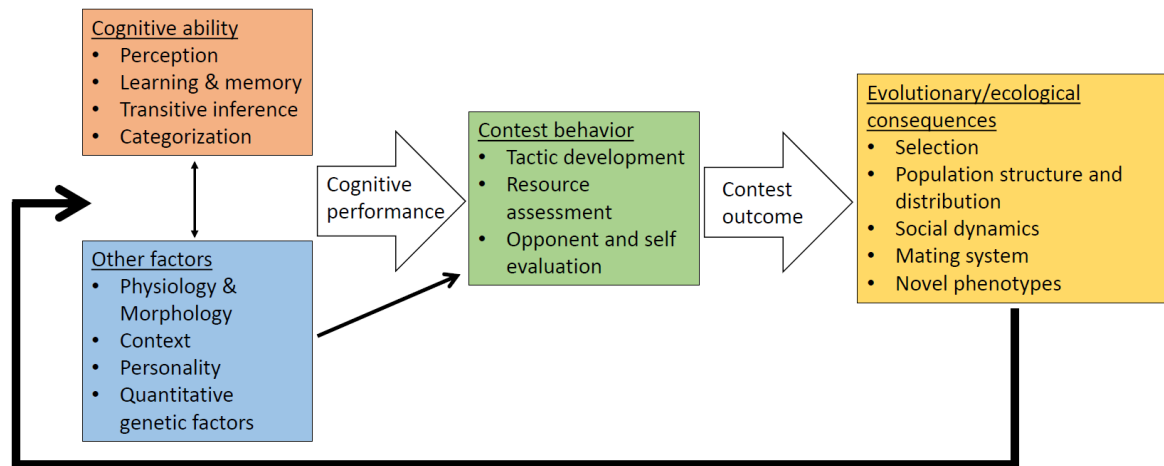
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Figure 1. A framework for the integrative study of cognition and animal contests. Cognitive performance is determined by the interaction between cognitive abilities and other factors, including both internal (e.g., physiological state) and external (e.g., environmental context) factors. Variation in cognitive performance affects the expression of contest behaviors, to the extent that these behaviors involve cognition. Other factors can directly affect contest behavior, and also indirectly affect contest behavior through effects on cognitive factors. Variation in contest behavior, including that resulting from variation in cognitive performance, influences the dynamics and outcome of contests, determining the costs and benefits for contest winners and losers. The magnitude of these costs and benefits determines the evolutionary and ecological consequences of variation in contest behavior, including variation in fitness as well as the distribution of individuals in space and with respect to social group members. These effects on fitness, social structure and ecology then lead to feedback mechanisms on the aggressive behaviors, and on the associated cognitive and non-cognitive mechanisms.

90

Cognitive mechanisms of contest behavior

92

93 Cognition encompasses a diverse range of mechanisms for information acquisition,

94 processing and use, including perception, learning and memory, individual recognition and

95 transitive inference of social status [18]. Identifying the specific cognitive mechanisms of

96 contest behaviors is an important but challenging task. For instance, opponent recognition is

97 often important in contests and can arise from habituation learning [19], categorization of

98 different classes of individuals [20], or so-called 'true' individual recognition [21].

99 Furthermore, it is difficult to disentangle the effects of cognition, personality, motivation and

100 condition on behavioral expression, and the careful experimental designs required to

101 distinguish between these factors are challenging even for the most tractable species [22].

102 Nevertheless, cognitive mechanisms are known or hypothesized to be important in many

103 species' contests; we discuss the evidence here, which provides a solid basis for further study

104 of contests and cognition (**BOX 2**).

105

106 *Development of signals and tactics*

107

108 The skill with which individuals perform aggressive displays and fighting maneuvers has

109 recently been identified as a significant, but understudied, determinant of contest success

110 [23]. Learning likely facilitates the development of skills important in contests. Bird song is

111 used in territorial contests and many song characteristics are learned during juvenile

112 development [24], raising the possibility that learning enables birds to produce more effective

113 aggressive signals. In song sparrows *Melospiza melodia*, young birds learned more songs

114 from tutors that they had competed with aggressively [25]. Most studies of song learning

115 focus on song structure and syntax, and less is known about learning of song performance

116 (e.g., timing, amplitude, type matching) [26], which is especially important in bird contests

117 [27]. Animals can also learn improved fighting tactics from recent contest experiences. For

118 instance, three-spined sticklebacks *Gasterosteus aculeatus* learned the association between

119 producing threat displays and causing an opponent to flee, likely through operant

120 conditioning [28]. Blue gouramis *Trichogaster trichopterus* and *Betta splendens* learned via

121 classical conditioning to anticipate, respectively, the timing and direction of a rival's

122 approach [29,30]. Learning might even enable animals to adjust their tactics during contests

123 by monitoring the effectiveness of contest behaviors. In fights over shell ownership in hermit

124 crabs *Pagarus bernhardus*, individuals prevented from effectively rapping opponents' shells

125 shifted to an alternative tactic of rocking opponents' shells [31]. Cognition is likely involved

126 in such tactical adjustments, but the cognitive mechanisms have not been investigated to date.

127

128 *Assessment strategies*

129

130 Once a contest has begun, contestants must rapidly decide how to behave and whether to

131 persist, withdraw or escalate. These decisions are determined by the individual's assessment

132 strategy [11]. Different models of strategic contest behavior propose assessment strategies

133 differing primarily in how individuals use different sources of information to determine their

134 behavior [32]. Individuals can assess their own state, their opponent's characteristics, the

135 value of the disputed resource and the social context in which the contest takes place [6,33].

136 The extent to which cognitive processes underlie different assessment strategies has received

137 surprisingly little study and remains controversial (**Box 3**).

138

139 Assessments of resource value might be especially amenable for cognitive studies because

140 both the resource itself and contestants' experience with the resource are relatively easily

141 manipulated. Asymmetries in information about resources often determine individual

142 persistence in contests [6], although most studies manipulate opportunities to access

143 information (e.g., by only pre-exposing one of the two contestants to the resource; [34])

144 rather than examining variation in cognitive abilities such as memory for specific information

145 about resource quality. In the context of our framework, it is important to study why

146 individuals or species vary in their ability to gather, process and retain information on

147 resource value, and how these cognitive mechanisms interact with other decision making

148 processes during contests [35]. Indeed, studies of resource-value assessment have shed light

149 on cognitive processes such as attention. For instance, resource value only affects contest

150 persistence in round gobies *Neogobius melanostomus* when individuals had previous

151 experience with the resource, and individuals were limited in the ability to readjust resource

152 valuation during contests, possibly because of constraints on attention [36].

153

154 *Opponent evaluation*

155

156 Studies of assessment strategies often focus on information gathering and decision making

157 during contests. However, information gathering about opponents also takes place before and

158 after contests, and the ability to learn from these experiences is likely a major determinant of

159 an individual's subsequent contest behavior, including decisions to instigate further contests.

160 Sometimes perceiving an opponent's physical characteristics suffices to identify a superior

161 rival [33]. However, many other cognitive mechanisms allow individuals to make more

162 accurate or detailed assessments of their opponents.

163

Individuals might learn about opponents indirectly by social eavesdropping. By observing

contests, individuals obtain information about the relative abilities of the contestants and use

this to determine their response to those contestants in the future [37]. Social eavesdropping

requires learning and memory of both the identity and fighting ability of the observed

contestants. The cognitive mechanisms underpinning social eavesdropping were investigated

in barn owls *Tyto alba*. Juveniles eavesdrop on competitive vocal interactions between

siblings, and memory retention depended on the frequency of exposure to sibling

vocalizations [38]. This suggests that limitations on receiver memory impose selection

pressures on signalers to repeat displays, which could partly explain the commonly-observed

but theoretically puzzling phenomenon of animal displays composed of rapid repetitions of

the same signal [39].

Individuals can also learn about opponents from direct previous experiences. Opponent

recognition might involve categorization of opponents into classes. For instance, snapping

shrimp *Alpheus heterochaelis* that had previously lost contests recognize and escape rapidly

from previous contest winners, regardless of whether they had experience with that particular

opponent, suggesting categorization based on a general phenotype rather than individual

recognition [40]. Other species might be capable of true individual recognition [21]. In

Iberian wall lizards *Podarcis hispanica*, males recognize the scent marks of several

individual rivals and remember where rivals left scent marks in relation to their own territory,

using this discrimination ability to modulate their behavior accordingly in future contests

based on the relative threat of recognized individuals [41]. True individual recognition could

be invoked because subjects associated individual-specific opponent characteristics (scent

mark composition) with individual-specific information about opponents (spatial scent

marking behavior) [21]. Opponent recognition is particularly important in territorial species;

189 individuals often show 'dear enemy' relationships with territorial neighbors, responding less

190 aggressively to these individuals than to unrecognized strangers [42]. In bullfrogs *Rana*

191 *catesbaeiana*, the dear enemy effect is mediated by habituation learning of both acoustic

192 signal characteristics and spatial locations of individual neighbors [43]. Direct and indirect

193 information might be integrated to inform decisions. Eavesdroppers could use transitive

194 inference, allowing them to determine not only the relative qualities of the observed

195 competitors with respect to each other, but also with respect to the eavesdropper's own

196 competitive status [44].

197

198 *Own status evaluation*

199

200 Learning about self might be an important component of winner and loser effects, in which

201 winners of previous contests tend to continue winning, and losers tend to continue losing

202 [45]. The cognitive mechanisms involved have not been investigated explicitly, but in male

203 *Anolis carolinensis* lizards, the effects of changes in physiological state on loser effects were

204 at least partly ruled out, suggesting that loser effects formed because of changes in how

205 individuals perceived their own fighting ability [46]. Stronger evidence for a role of cognition

206 on winner and loser effects comes from species in which these effects are only shown, or are

207 stronger, against familiar individuals, implying an important role of learning and memory.

208 Hermit crabs *Pagurus middendorffii* that lost a fight recognize previous opponents and avoid

209 combat with them, while showing no behavioral changes in response to unfamiliar

210 individuals [47]. The explicit role of memory in winner and loser effects was investigated in

211 *Drosophila melanogaster*, where memory of previous winning or losing experiences decays

212 more slowly in contests involving familiar individuals [48]. If winner and loser effects arise

213 from individuals learning more about their own fighting abilities, then memory will interact

214 with assessment in future contests. Namely, more experienced individuals should more

215 rapidly assess their quality relative to an opponent; thus, winner and loser effects should

216 affect not only the outcome, but also the duration and escalation of future contests.

217

218 **Cognitive performance and individual variation**

219

220 Consistent between-individual variation in contest behavior and success has been

221 demonstrated in many species [49]. Most empirical studies examine the morphological and

222 physiological components of RHP to explain this variation [33]. We have argued that

223 cognition is an important component of many contest behaviors; thus, variation in cognitive

224 performance could be a major source of individual variation in RHP. However, evidence for

225 links between cognitive performance and individual RHP is scarce. Cognitive performance in

226 contests might vary because individuals vary in cognitive ability. For instance, if contest

227 behaviors are learned, some individuals could learn more rapidly than others, giving them an

228 advantage. The conditioning protocols described above for learning to anticipate rival

229 approach could be utilized to determine if those individuals that learned the task more readily

230 were especially likely to win contests and resolve them quickly. Similar approaches could be

231 utilized for neighbor recognition learning: do individuals that learn to recognize new

232 neighbors more rapidly in playback experiments instigate fewer aggressive interactions with

233 their actual neighbors?

234

235 Individuals might also vary in the extent to which they strategically utilize cognitive abilities

236 in contests [9,50]. This could be tested by measuring how sensitive individuals are to

237 variation in opponent signal characteristics. Some individuals might carefully assess

238 opponent signals and even recognize specific opponents and adjust their response

239 accordingly, whereas others respond similarly to all opponents [9]. The latter individuals are

240 predicted to have superior physical characteristics if there are trade-offs between cognitive

241 and non-cognitive competitive abilities [51], suggesting the possibility of alternative stable

242 strategies [52]. Finally, cognitive performance is likely to be context dependent. Different

243 ecological and social conditions create greater or lesser challenges for cognitive performance

244 in contests, and individuals differ in their previous experiences. Manipulations of individual

245 experiences are straightforward, and have been employed often in studies of age effects on

246 contest dynamics [53], and winner and loser effects [54].

247

248 **Evolution, ecology, cognition and contests**

249

250 Cognition is both a driver of variation in competitive ability leading to variation in fitness-

251 related resource acquisition, and is itself likely to be affected by selection acting on contest

252 behavior (Figure 1). Contest behavior is intimately related to the distribution of individuals

253 and resources in the environment, which determines contest frequency, the benefits of

254 success, and the quality of information for cognitive processing. Ecology is therefore likely to

255 be a key consideration in explaining why species differ in the role of cognitive mechanisms

256 in contests. Below, we outline several hypotheses that relate cognition, contest behavior and

257 ecological or evolutionary processes.

258

259 *Cognitive performance and fitness*

260

261 Identifying the fitness consequences of individual variation in cognitive performance is a

262 major focus of recent studies in wild populations [55]. While cognitive performance can

263 impact individual fitness via contest success (Figure 1), little is known about how frequent or

264 strong these impacts are in natural populations. It is also unknown the extent to which

265 benefits of higher cognitive performance in contests are counteracted by costs, and what the

266 net impact is on fitness [56]. Indeed, few studies have quantified fitness benefits or

267 investigated whether these gains balance the costs of resource acquisition and defense for any

268 contest behavior [57]. Specific fitness costs of cognitive performance in contests might be

269 linked to energetic costs of neural tissue development and maintenance, which trade off with

270 investment into non-cognitive components of RHP, and with cognitive abilities in other

271 contexts [51]. Likewise, fitness costs of poor competitiveness might be counteracted by

272 superior cognitive performance in other contexts. Great tits *Parus major* that were less

273 successful in contests over food had greater innovative tendencies and survived equally well

274 as more successful competitors, potentially because they could exploit novel food resources

275 [56].

276

277 For there to be a response to any selection acting on cognitive performance in contests,

278 cognitive performance must be heritable. However, little is known about the heritability of

279 any cognitive trait in wild populations [58], or of the repeatability of cognitive performance

280 over time, and relationships between competitive ability and cognition can also arise from

281 plasticity rather than heritable variation [59]. Demonstrating such a response to selection is

282 difficult, but measurements of selection on cognitive traits and their heritability have been

283 made in other contexts [16,58] and similar approaches could be applied to study cognition

284 and contests. Additional theoretical studies incorporating cognitive mechanisms (**Box 4**)

285 would also improve the understanding of the population-level consequences of cognition and

286 contests.

287

288 *Social structure and contest cognition*

289

Social group size and stability affects the opportunities for learning about opponents, and also

the value of such information. Between-species variation in whether contests are resolved

primarily by individual recognition learning or by signal exchanges (badge of status

recognition, which does not necessarily require learning) is hypothesized to be related to

variation in opportunities for learning about opponents in social groups [60]. In species with

small, stable social groups and repeated interactions, there are many opportunities to learn

each group member's capabilities, and individual recognition should determine when contests

are instigated and how they are resolved. In contrast, when social groups are large and/or

unstable, there is less opportunity for learning and individuals are predicted to use badges of

status for opponent assessment [60]. This hypothesis could also explain within-species

variation. For instance, male *A. carolinensis* assess visual signals (darkened eyespots, a badge

of status) of unfamiliar opponents, but in subsequent fights with a familiar opponent they

behaved according to its previous dominance even if the opponent's visual signals were

manipulated, indicating the opposite rank [61]. More generally, the costs and benefits of

strategies incorporating cognition or other assessment mechanisms will determine which

strategy predominates in a given situation. Elephant seals *Mirounga angustirostris* provide an

intriguing example: despite the social group's large size and fluidity, recognition learning of

individual acoustic signatures is important for rival assessment because costs of fighting are

particularly extreme in this species [62].

309

The 'Machiavellian intelligence' hypothesis argues that individuals in stable social groups are

selected to attend to other group members' interactions, especially dominant and subordinate

relationships determined by contests (e.g., via social eavesdropping, see above).

Machiavellian intelligence might have been important in the evolution of social cognition

14

among primates [63], and could explain hominid brain evolution [64]. Attention to the

perspectives and knowledge held by other group members is an important component of

theory of mind [65]. Although the notion that animals have anything approaching human-like

capabilities in this regard is highly controversial [66], this could conceivably operate to some

degree in some species and allow for novel contest strategies. For instance, subordinate

chimpanzees are sensitive to whether a specific dominant individual had observed the

location of hidden food, and preferentially forage in places where the dominant had not

observed food being placed, thus avoiding contests [67]. Understanding others' intentions

also raises the possibility of tactical deception in animal contests. In three monkey species,

subordinate individuals withheld information from dominants about the location of food;

interestingly the efficiency of deception was inversely related to the strictness of the

dominance hierarchy and social group stability, indicating feedbacks between contests and

cognitive abilities [68]. Furthermore, group living might have selected for the evolution of

numerical competence because individuals assess numerical asymmetries in group size

during intergroup contests [69].

Diet, stress, dominance and cognition

Because many animal contests are disputes over food, contest success might impact

individual ability to obtain resources necessary for developing and maintaining cognitive

capabilities. The developmental stress hypothesis argues that birdsong is a good indicator of

male quality for female mate choice because song is learned during a critical developmental

period when individuals are likely subject to multiple stressors; birds producing quality song

were less stressed during development [70]. Success in resource acquisition should reduce

developmental stress, and is in part mediated by contest competition, generating feedbacks

339   between contests, stress and cognition. Although the developmental stress hypothesis is

340   usually applied to birdsong, it should apply to the development of any cognitive trait,

341   including those involved in contests during adulthood [71]. Thus, contest success during

342   development can have cascading effects on the cognitive abilities required for future contest

343   success, potentially driving individual differences in competitive ability.

344

345   Stress during adulthood affects both cognition and contest success in species with dominance

346   hierarchies, but these effects depend on how hierarchies are maintained. Dominant

347   individuals are the most physiologically stressed in species in which dominance is maintained

348   by frequent overt aggressive acts towards subordinates, while lower-ranking individuals tend

349   to be more stressed in species in which dominance is maintained primarily by signaling [72].

350   Such chronic stress often impacts on cognition [73].

351

352   **Concluding Remarks**

353

354   Cognition plays an important role in all stages of contests across a wide taxonomic range.

355   That the cognitive mechanisms of contest behavior and the ecological and evolutionary

356   implications of cognitive variation in contests remain largely unknown, even when intriguing

357   hypotheses exist, reflects the focus of cognitive ecologists and psychologists on other animal

358   behaviors, and the focus of behavioral ecologists on ultimate causation in contest studies. The

359   time is ripe to study cognitive mechanisms in animal contests (**Outstanding questions box**)

360   because contests exemplify many of the major themes in contemporary cognition and

361   behavioral ecology research: there is substantial variation in contest behaviors, with repeated

362   interactions in complex social environments and involving information gathering abilities that

363   might trade-off with such abilities in other contexts. Our framework synthesizes the diverse

364   knowledge of cognitive processes in contests and provides an appropriate context for studies

365   integrating evolutionary consequences of variation in strategic contest behavior and the

366   mechanisms generating variation in cognitive performance in wild animals.

367

....

Box 1 – Neural mechanisms, cognition and contest behavior

Identifying the neural processes underlying cognitive mechanisms of animal contest behavior provides insight into the origins of differences between individuals and species in cognitive abilities. Below we summarize some of the few studies explicitly linking activity in the brain to cognitive traits expressed in contests.

Drosophila melanogaster show loser effects, and these are stronger when losers are paired against familiar individuals, suggesting a role of memory in contests [74]. Indeed, both short- and long-term memory are involved in the formation of loser effects, with the duration of the memory depending on the number of repeat losses [48]. Short- and long-term memories have different neural substrates (Figure I). Long-term memories of losing experiences arise via protein synthesis occurring during or after contests; when protein synthesis is blocked, the short-term loser effect remains but long-term loser effects disappear [48]. However, specific genes that affect memory formation in *D. melanogaster* contests have not been identified. Hearing has been identified as a critical sensory mechanism regulating aggression in *D. melanogaster*. Inhibiting neurotransmitter release in specific peripheral auditory neurons strongly reduced aggression levels [75].

In *Anolis carolinensis*, individuals recognize previous opponents and form dear enemy relationships with territorial neighbors [76]. The neuroendocrine response of individuals to an aggressive challenge depends on its status (dominant or subordinate) and on the opponent's familiarity [77]. Dominant males exposed to familiar opponents had higher epinephrine levels

393   in the hippocampus, and in general social interactions led to increased activity of NMDA

394   receptor subunits in the hippocampus [78]. Because the hippocampus is involved in spatial

395   and social learning [79], these neuroendocrine responses might be involved in the formation

396   of memories related to dear enemy behavior.

397
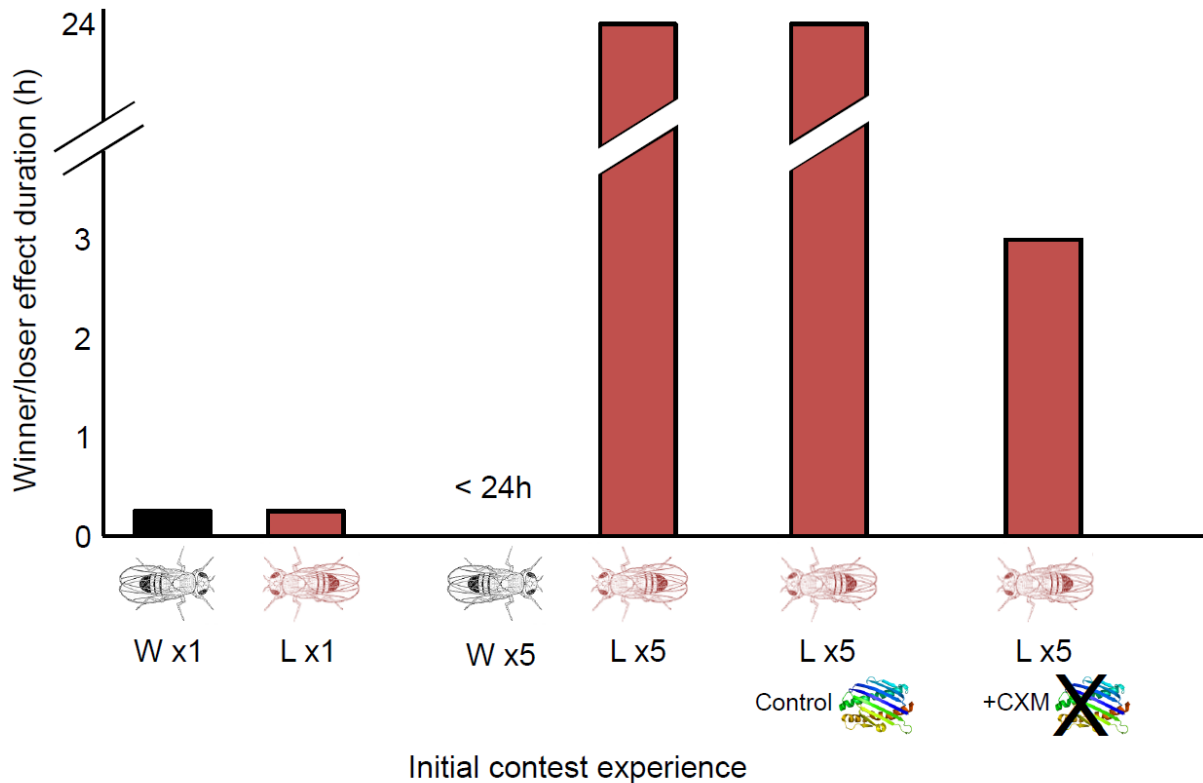
Box 1, Figure I. Mechanisms of long-term memory formation in *D. melanogaster* contests.

399   Winner and loser flies from an initial contest trial were assayed for winner and loser effects

400   by testing whether they were more likely to win or lose, respectively, a contest against a

401   naïve individual. Bars show the duration of winner (black) or loser (red) effects. Winner and

402   loser effects disappeared rapidly after a single contest experience. However, losers, but not

403   winners, of five consecutive contests against the same opponent had altered contest behavior

404   and success 24 hours later. Flies treated with cycloheximide, which inhibits protein synthesis,

405   showed a short-term but not a long-term loser effect, demonstrating that *de novo* protein

406   synthesis is the mechanism responsible for this long-term memory formation. After [48].

407

408

Box 2 – Experimental approaches for studying cognition and contests

410

Although cognition clearly plays a role in many animal contest behaviors, the specific

cognitive mechanisms are not always identified, and the relative importance of cognitive and

other factors is rarely quantified. Here we outline some potentially fruitful experimental

approaches to identify the cognitive mechanisms of contest behavior and determine the

sources of individual variation in cognitive performance.

416

1. Independently manipulating the quality of information available to each contestant for

assessment and learning, for instance by interfering with sensory perception, the duration and

nature of previous experience, and opponent appearance. Playbacks could be used to

mismatch signal characteristics with actual opponent quality; if the relationship between

opponent signals and quality is learned, then individuals trained in the mismatched treatment

should respond inappropriately in natural contests. Experimental manipulations of the

proximate underpinnings of cognition, such as neural processing (**Box 1**), stress levels at

critical developmental periods, or gene expression, are especially powerful techniques.

425

2. Training individuals to perform the hypothesized cognitive task in another context and then

assaying their contest performance. For instance, mutual opponent assessment involves the

evaluation of opponent quality relative to self quality [80]. Individuals trained to perform

well in relative assessments in other contexts, such as choosing between two different

amounts of food, might therefore be expected to be better at mutual assessment in contests

(i.e., to resolve contests more quickly and accurately). The utility of this approach depends on

the extent to which performance of a cognitive task in one context carries over to other

433   contexts [13]. Furthermore, if cognitive load limits learning and memory [81], individuals

434   that recently learned a relatively complex task might be less able to perform cognitively

435   demanding assessment during contests than individuals with no, or less challenging, previous

436   learning experience.

437

438   3. Assays of generalization in opponent recognition. If individuals recognize categories of

439   opponents, then manipulation of opponent signals could be used to train individuals to

440   recognize certain stimuli as indicating a superior opponent. Pitting trained animals against

441   unfamiliar contestants with variations on the signal could demonstrate whether (i) individuals

442   can learn to recognize an opponent's competitive ability based on a novel stimulus, (ii)

443   individuals categorize opponents based on signal characteristics, and (iii) if there are peak

444   shift phenomena in which especially strong responses are obtained to stimuli that go beyond

445   the previously experienced range of signal variation, indicating a potential mechanism for the

446   evolution of aggressive signal exaggeration [82].

447

448

449   **Box 3 – Controversies over assessment strategies and the role of cognition**

450

451   That animals rarely use physical attacks to resolve contests posed a theoretical puzzle that

452   was solved with game theory models examining when more 'peaceful' assessment strategies

453   could be evolutionarily stable [83]. Many of these models involve contestants differing in

454   RHP, with the behaviors expressed during contests allowing for the assessment of contestant

455   RHP, settling contests in favor of the superior individual [11]. Most models investigate one of

456   three broad categories of assessment strategy: (i) mutual assessment, (ii) self-assessment, or

457   (iii) cumulative assessment [33].

458

459   The mutual assessment strategy was frequently tested by empiricists because it makes the

460   simple prediction that contests between evenly-matched opponents should be longer and

461   more escalated than contests between individuals with large RHP differences [80]. However,

462   this prediction was later demonstrated to also apply to other assessment strategies, and

463   experimental designs that discriminate between mutual- and self-assessment strategies have

464   only recently been developed [33,84]. Many recent studies give evidence for self- rather than

465   mutual-assessment [85,86], leading to some backlash against the idea that mutual assessment

466   is the prevalent means by which animals resolve contests. Cognition is invoked in these

467   arguments: mutual assessment is claimed to be more 'cognitively complex' because it

468   requires evaluation and relative comparison of both competitors' traits whereas self-

469   assessment only requires input from an individual's own state [7]. However, there is

470   disagreement about whether mutual-assessment models require cognitively advanced

471   comparisons, or whether performing such comparisons is even cognitively challenging

472   [87,88].

473

474   Without a cognitive perspective on animal contests, this controversy will remain unresolved

475   because little is known about the cognitive mechanisms of assessment. Cognition is treated as

476   a black box both in models of assessment strategies and in arguments that strategies differ in

477   their cognitive requirements. Does mutual assessment truly involve relative comparison

478   requiring extensive memory and categorization abilities, or is it a simple modification of self-

479   assessment with additional sensory input from opponents? Considering cognitive

480   mechanisms also alters the predicted relationships between contestant RHP and contest

481   duration under different assessment strategies. In particular, it has been argued that, for a

482   given RHP difference between contestants, under mutual assessment contest duration should

483   not vary with absolute competitor RHP [33]. However, relative assessments become more

484   difficult at larger absolute stimulus values [89]; thus under mutual assessment and a constant

485   RHP difference, contest duration should be an increasing function of absolute competitor

486   RHP. Therefore, positive relationships between individual RHP and contest duration are not

487   always diagnostic of self-assessment.

488

489

490   ●●

491   **Box 4 – Cognition and contest theory**

492

493   Animal contests have received much attention from theoretical biologists [32]. However,

494   cognition is rarely considered in models of strategic contest behavior. A major gap in theory

495   could be addressed by examining the conditions under which learning or other cognitive

496   mechanisms can evolve as a component of evolutionarily stable contest strategies. Below we

497   briefly describe some of the few theoretical models examining the role of cognition in animal

498   contests.

499

500   Stamps and Krishnan [90] developed a model of territory settlement with a key role for

501   learning. As individuals move through space they can encounter other individuals and engage

502   in aggressive interactions. These contests form the basis for associative learning, with

503   individuals reducing their probability of returning to an area after associating it with the

504   negative effects of encountering aggressive competitors. The model reproduced several

505   spatial patterns known from nature including the formation of exclusive territories when

506   levels of aggression are high. This model could be extended to explore how patterns of space

507   use and cognitive variation explain individual variation in the susceptibility to density-

508   dependent effects, ultimately affecting distribution patterns across heterogeneous landscapes,

509   and explaining when and why deviations from the ideal free distribution are observed.

510

511   Mesterton-Gibbons and Heap [9] developed an extension of the hawk-dove game to explore

512   factors that lead contestants to adopt either self- or mutual-assessment strategies. An

513   important component of the model is the incorporation of trade-offs between obtaining

514   information on opponents and the resultant costs of revealing information to opponents.

515   Although not explicitly cognitive, this model could easily be expanded to incorporate

516   cognitive processes and fits with the framework proposed here, because it examines the

517   factors underlying variation in the expression of strategic contest behavior based on the costs

518   and benefits of information gathering.

519

520   Lee and colleagues [50] developed a model based on the producer-scrounger game to

521   examine the conditions under which individuals use social information when foraging instead

522   of searching for resources on their own. An individual's competitive ability relative to the

523   distribution of competitive abilities in the population was a key parameter in determining the

524   profitability of producer versus scrounger (social information use) tactics. However, the

525   benefits of scrounging for individuals of high competitive ability depended on resource

526   availability. Thus, this model demonstrates links between information gathering, contest

527   outcome and ecology, as proposed by our framework (Figure 1).

528

529

••

530

531 **Outstanding questions box**

532

533 *-What is the role of perception in mediating cognitive processes underlying contest behavior?*

534

535 *-How do multiple cognitive abilities interact with one another, and with non-cognitive*

536 *mechanisms to determine contest behavior?*

537

538 *-What is the role of ecology, social structure, and constraints in explaining between-species*

539 *variation in the importance of cognition in contests?*

540

541 *-What is the quantitative genetic basis of cognitive performance in contests, in terms of the*

542 *components of variation underlying individual traits, and the extent to which different kinds*

543 *of traits are genetically correlated with one another and fitness?*

544

545 *-Are cognitive abilities used in contests predictive of cognitive abilities in other contexts?*

546 *Does selection result in adaptive cognitive specializations for contests, or for more general*

547 *cognitive performance across contexts?*

548

549 *- How well do animals understand the intentions and relations of others while observing*

550 *contests? Can contests give any insights into the debates surrounding the existence of a*

551 *theory of mind in animals?*

552

Glossary

Assessment strategy: The 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: The 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: The processes involved in the acquisition, processing, retention and use of information from the environment [18].

Cognitive ability: A 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: The 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: A direct and discrete behavioral interaction determining ownership of an indivisible resource unit [2].

578

Cumulative assessment: An assessment strategy in which an individual's contest behavior 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].

583

Dear enemy effect: The phenomenon in which territory owners respond less aggressively to familiar neighbors than to strangers [42].

586

Habituation learning: A decrement in response to a repeated stimulus not due to sensory adaptation or motor fatigue.

589

Learning: A change in cognitive state as a result of experience that can influence future behavior [18].

592

Mutual assessment: An 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].

595

Operant conditioning: Learning to associate a behavior with its consequences.

597

Resource-holding potential: An individual's absolute fighting ability [11].

599

Self assessment: An assessment strategy in which an individual's contest behavior is determined only by its own characteristics [33].

602

603   **Social eavesdropping**: Occurs when an animal obtains information from interactions

604   between conspecifics by observing, rather than directly participating in the interaction.

605

606   **Theory of mind**: An understanding of the intentions and beliefs of others.

607

608   **Transitive inference**: Inferring unknown relationships from known relationships. In the

609   context of animal contests, animals might observe contests and infer that if individual A

610   defeats individual B, and individual B defeats individual C, then individual A should defeat

611   individual C.

612

613   **True individual recognition**: The ability to recognize an individual from its distinctive

614   characteristics and associate those characteristics with other information about that

615   individual, as opposed to recognizing different classes of individuals [21].

616

617

618

619

620   Table 1. Selected studies providing evidence for a role of cognition in contest behavior, along with potential socioecological consequences,

621   divided into behaviors occurring at different time points relative to a contest.

622

Cognitive mechanism(s)	Contest behavior	Species	Description	Possible socioecological consequence	Refs
(I) Before contests					
Imitation learning, operant conditioning	Aggressive signal development	*Melospiza melodia*	Songs used in territory defense are learned from neighbors' interactions.	Contest strategies influence cultural signal evolution.	[92]
Classical conditioning	Rival anticipation	*Trichogaster trichopterus*	Classical conditioning allows anticipation of intruder approach.	Selection for territoriality & development of alternative "sneaker" tactics.	[29]
Recognition learning and memory	Pre-fight assessment	*Poecile atricapillus*	Relative threat of intruders assessed by integrating information from eavesdropping on multiple song contests.	Selection for private communication and/or victory displays.	[93]

Transitive inference	Pre-fight assessment	*Julidochromis transcriptus*	Rival dominance inferred by both direct previous experience and indirect experience from contests with common opponents (in unfamiliar rivals).	Cognitive mechanisms influence speed of formation and stability of dominance hierarchies.	[44]
Categorization	Pre-fight assessment	*Macaca mulatta*	Dominance can be learned as a categorical concept from video playbacks of aggressive individuals.	Evolution of social cognition.	[94]
(ii) During contests					
Perception	Rival assessment (dyadic contests)	*Teleogryllus oceanicus*	Contests more escalated when males prevented from exchanging acoustic signals.	Selection for specialized aggressive communication system.	[95]
Perception	Contest resolution	*Neogobius melanostomus*	Contests in contaminated water less likely to have clear winner and loser.	Anthropogenic disturbance influences costs and benefits of aggressive behavior.	[96]

Comparative judgement	Resource-value assessment	*Clibanarius vittatus*	Attackers in fights over shells in hermit crabs assess both own gain and likely gain of defender by swapping shells	Resource availability affects likelihood and severity of contests.	[97]
Numerosity	Rival assessment (group contests)	*Panthera Leo*	Individuals assess numerical asymmetry in group size during intergroup contests.	Evolution of higher-order cognitive traits, selection for social coordination.	[98]
(iii) After contests					
Recognition learning and memory	Winner/Loser effect	*Anolis carolinensis*	Loser effect only exhibited when individual faced with familiar rival.	Cognitive mechanisms influence speed of formation and stability of dominance hierarchies.	[76]
Recognition learning and memory	Dear enemy effect	*Ctenomys talarum*	Individuals recognize odors of familiar previous rivals and respond less aggressively towards them.	Stabilization of territorial resource defense strategies.	[99]
Recognition learning and memory	Dear enemy effect	*Vireo olivaceus*	Less aggression directed towards neighbors despite potential difficulties in recognition from large song repertoire size.	Cognitive abilities relax constraints on selection on song variation, which might play role in other contexts (e.g., mate selection).	[100]

623

624 [a]Perception should play a role in the expression of all aggressive behaviors and cognitive mechanisms. It is not listed explicitly in each entry

625 unless it is the focal mechanism of the study.

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