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<b>Author(s)</b>	Reichert, Michael S.; Quinn, John L.
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1 **Cognition in contests: mechanisms, ecology and evolution**

2

3 Michael S. Reichert<sup>1Ψ</sup> and John L. Quinn<sup>1</sup>

4

5 1. School of BEES, University College Cork, North Mall, Cork, T23 N73K, Republic of

6 Ireland

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8 <sup>Ψ</sup>Corresponding author: Reichert, M.S. ([michaelreichert@ucc.ie](mailto:michaelreichert@ucc.ie))

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

## 23 **A role for cognition in competition**

24

25 Competition for resources such as food, mates and territories is ubiquitous among animals  
26 and a fundamental predictor of fitness [1]. Much of this competition is mediated by contests  
27 (see Glossary), in which animals use specialized aggressive displays and overt physical  
28 attacks to determine access to resources [2]. Contests are incredibly variable both within and  
29 between species in their format, intensity and the specific behaviors involved [2].

30 Understanding the causes and consequences of animal contest behavior is important because  
31 aggressive interactions affect social structure and individual fitness, which can carry over to  
32 impact key higher-level processes including selection, population dynamics and distribution  
33 [3–5]. Contests require rapid information processing for decision making about when, how  
34 and with whom to challenge, escalate or withdraw [6]. We argue that cognition provides a  
35 significant but largely unexplored explanation for variation in contest behavior because  
36 cognitive mechanisms such as learning from previous interactions, and assessments of  
37 resource value, physical ability and social status, facilitate information processing and  
38 decision making.

39

40 Examining cognitive mechanisms will provide important new insights for studies of animal  
41 contests. First, although evidence abounds for a role of cognition in contests (Table 1), most  
42 studies focus only on demonstrating that animals gather and use information. The  
43 mechanisms by which this information is processed, retained and employed in decision  
44 making are rarely investigated and largely treated as a black box by both empiricists and  
45 theoreticians [7]. However, these mechanisms are critical to understanding variation between  
46 individuals and between species in contest behavior because cognitive processing might not  
47 always lead to optimal behavioral expression, as is commonly assumed [8]. Constraints on

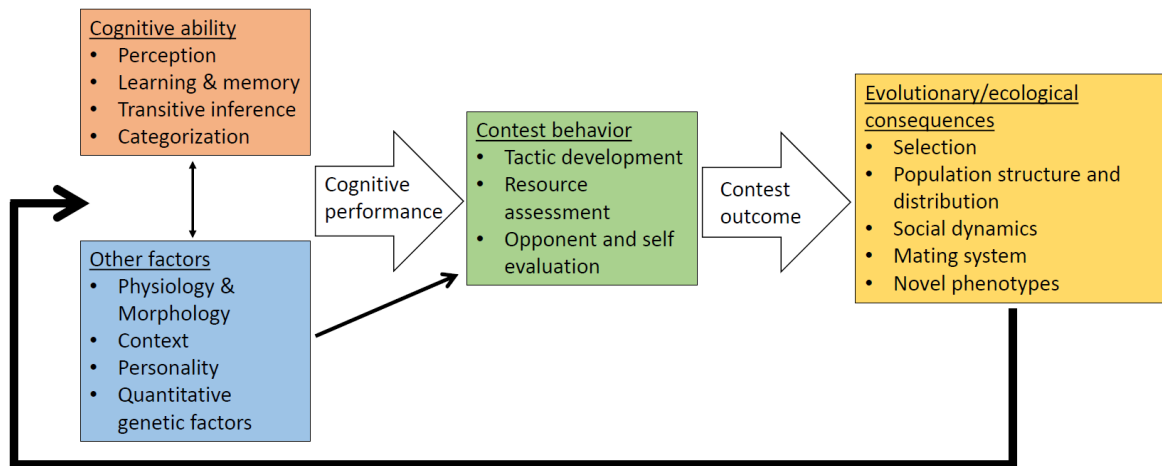
48 information gathering and use might explain why contest assessments often incorporate only  
49 a limited subset of the available information [9], and why individuals with lower resource-  
50 holding potential (RHP) sometimes can bluff their way to success by deceiving their  
51 opponents [10]. Second, focusing on cognition emphasizes that animal contests are not one-  
52 time, context-independent events, but rather take place within a series of interactions across  
53 individuals' lifetimes in a complex environmental and social milieu. Cognition links  
54 experience gained in past interactions to future contest behaviors. Third, RHP, the key  
55 variable determining contest success [11], is often estimated using a single physical  
56 characteristic (i.e., body size) but is in fact a composite trait with inputs from multiple  
57 phenotypic characteristics [12]. We argue that cognitive performance is often an important  
58 component of RHP, and can sometimes reduce or even override advantages accruing to larger  
59 individuals.

60

61 In an effort to understand the diversity of animal contest behavior, we present evidence that  
62 cognition underlies important behaviors involved in animal contests (Table 1). We examine  
63 these behaviors within a general framework for testing hypotheses about how links between  
64 cognition and contest behavior influence evolutionary and ecological processes, with the  
65 potential to feed back onto cognitive and behavioral traits (Figure 1). We discuss how these  
66 feedback mechanisms could explain the causes and consequences of both individual, within-  
67 species, variation in cognitive performance, and between-differences in the role of cognition  
68 in contests. Recently, major advances have been made in developing cognitive assays for  
69 field and laboratory studies [13], methods to elucidate the neural bases of cognition [14]  
70 (**BOX 1**), statistical analyses of contests [15], measurements of selection on cognitive traits  
71 [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.

74



75

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

90

91 **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 *Pagurus 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

164 Individuals might learn about opponents indirectly by social eavesdropping. By observing  
165 contests, individuals obtain information about the relative abilities of the contestants and use  
166 this to determine their response to those contestants in the future [37]. Social eavesdropping  
167 requires learning and memory of both the identity and fighting ability of the observed  
168 contestants. The cognitive mechanisms underpinning social eavesdropping were investigated  
169 in barn owls *Tyto alba*. Juveniles eavesdrop on competitive vocal interactions between  
170 siblings, and memory retention depended on the frequency of exposure to sibling  
171 vocalizations [38]. This suggests that limitations on receiver memory impose selection  
172 pressures on signalers to repeat displays, which could partly explain the commonly-observed  
173 but theoretically puzzling phenomenon of animal displays composed of rapid repetitions of  
174 the same signal [39].

175

176 Individuals can also learn about opponents from direct previous experiences. Opponent  
177 recognition might involve categorization of opponents into classes. For instance, snapping  
178 shrimp *Alpheus heterochaelis* that had previously lost contests recognize and escape rapidly  
179 from previous contest winners, regardless of whether they had experience with that particular  
180 opponent, suggesting categorization based on a general phenotype rather than individual  
181 recognition [40]. Other species might be capable of true individual recognition [21]. In  
182 Iberian wall lizards *Podarcis hispanica*, males recognize the scent marks of several  
183 individual rivals and remember where rivals left scent marks in relation to their own territory,  
184 using this discrimination ability to modulate their behavior accordingly in future contests  
185 based on the relative threat of recognized individuals [41]. True individual recognition could  
186 be invoked because subjects associated individual-specific opponent characteristics (scent  
187 mark composition) with individual-specific information about opponents (spatial scent  
188 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

290 Social group size and stability affects the opportunities for learning about opponents, and also  
291 the value of such information. Between-species variation in whether contests are resolved  
292 primarily by individual recognition learning or by signal exchanges (badge of status  
293 recognition, which does not necessarily require learning) is hypothesized to be related to  
294 variation in opportunities for learning about opponents in social groups [60]. In species with  
295 small, stable social groups and repeated interactions, there are many opportunities to learn  
296 each group member's capabilities, and individual recognition should determine when contests  
297 are instigated and how they are resolved. In contrast, when social groups are large and/or  
298 unstable, there is less opportunity for learning and individuals are predicted to use badges of  
299 status for opponent assessment [60]. This hypothesis could also explain within-species  
300 variation. For instance, male *A. carolinensis* assess visual signals (darkened eyespots, a badge  
301 of status) of unfamiliar opponents, but in subsequent fights with a familiar opponent they  
302 behaved according to its previous dominance even if the opponent's visual signals were  
303 manipulated, indicating the opposite rank [61]. More generally, the costs and benefits of  
304 strategies incorporating cognition or other assessment mechanisms will determine which  
305 strategy predominates in a given situation. Elephant seals *Mirounga angustirostris* provide an  
306 intriguing example: despite the social group's large size and fluidity, recognition learning of  
307 individual acoustic signatures is important for rival assessment because costs of fighting are  
308 particularly extreme in this species [62].

309

310 The 'Machiavellian intelligence' hypothesis argues that individuals in stable social groups are  
311 selected to attend to other group members' interactions, especially dominant and subordinate  
312 relationships determined by contests (e.g., via social eavesdropping, see above).

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

314 among primates [63], and could explain hominid brain evolution [64]. Attention to the  
315 perspectives and knowledge held by other group members is an important component of  
316 theory of mind [65]. Although the notion that animals have anything approaching human-like  
317 capabilities in this regard is highly controversial [66], this could conceivably operate to some  
318 degree in some species and allow for novel contest strategies. For instance, subordinate  
319 chimpanzees are sensitive to whether a specific dominant individual had observed the  
320 location of hidden food, and preferentially forage in places where the dominant had not  
321 observed food being placed, thus avoiding contests [67]. Understanding others' intentions  
322 also raises the possibility of tactical deception in animal contests. In three monkey species,  
323 subordinate individuals withheld information from dominants about the location of food;  
324 interestingly the efficiency of deception was inversely related to the strictness of the  
325 dominance hierarchy and social group stability, indicating feedbacks between contests and  
326 cognitive abilities [68]. Furthermore, group living might have selected for the evolution of  
327 numerical competence because individuals assess numerical asymmetries in group size  
328 during intergroup contests [69].

329

### 330 *Diet, stress, dominance and cognition*

331

332 Because many animal contests are disputes over food, contest success might impact  
333 individual ability to obtain resources necessary for developing and maintaining cognitive  
334 capabilities. The developmental stress hypothesis argues that birdsong is a good indicator of  
335 male quality for female mate choice because song is learned during a critical developmental  
336 period when individuals are likely subject to multiple stressors; birds producing quality song  
337 were less stressed during development [70]. Success in resource acquisition should reduce  
338 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

368

369

370 **Box 1 – Neural mechanisms, cognition and contest behavior**

371

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

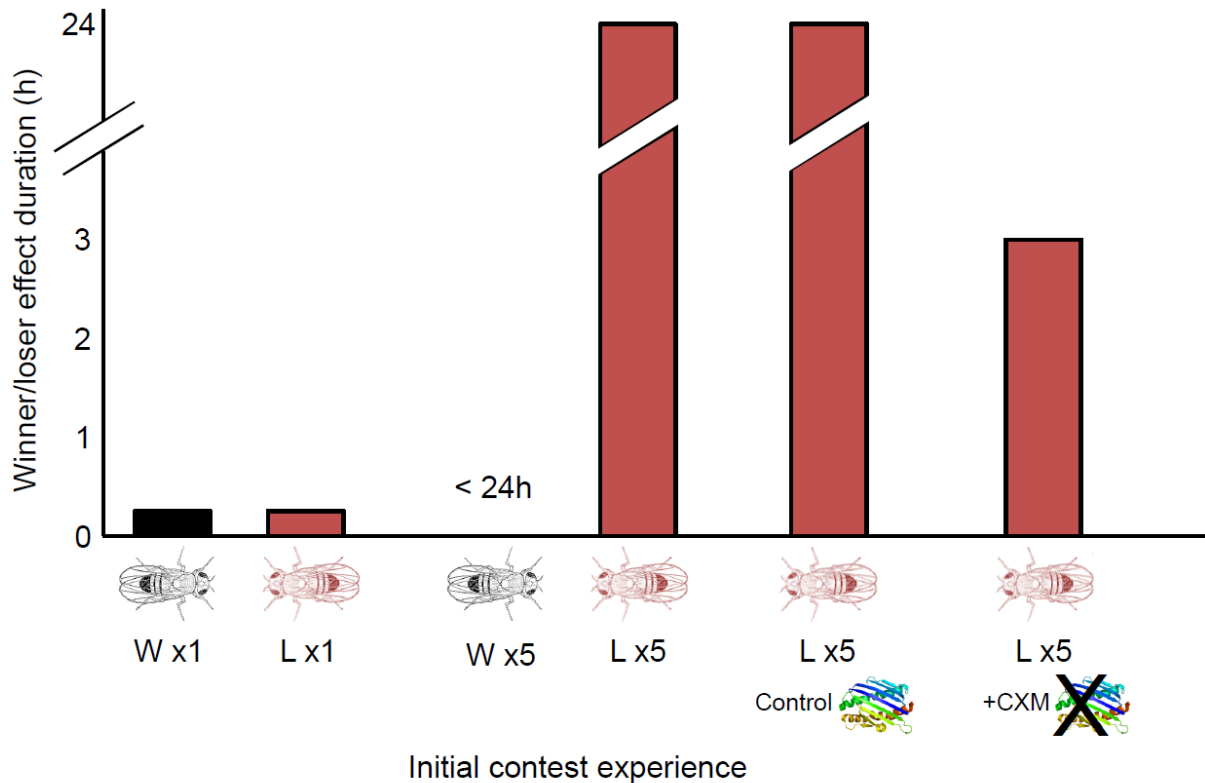
376

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

388

389 In *Anolis carolinensis*, individuals recognize previous opponents and form dear enemy  
390 relationships with territorial neighbors [76]. The neuroendocrine response of individuals to an  
391 aggressive challenge depends on its status (dominant or subordinate) and on the opponent's  
392 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

398 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

409 **Box 2 – Experimental approaches for studying cognition and contests**

410

411 Although cognition clearly plays a role in many animal contest behaviors, the specific  
412 cognitive mechanisms are not always identified, and the relative importance of cognitive and  
413 other factors is rarely quantified. Here we outline some potentially fruitful experimental  
414 approaches to identify the cognitive mechanisms of contest behavior and determine the  
415 sources of individual variation in cognitive performance.

416

417 1. Independently manipulating the quality of information available to each contestant for  
418 assessment and learning, for instance by interfering with sensory perception, the duration and  
419 nature of previous experience, and opponent appearance. Playbacks could be used to  
420 mismatch signal characteristics with actual opponent quality; if the relationship between  
421 opponent signals and quality is learned, then individuals trained in the mismatched treatment  
422 should respond inappropriately in natural contests. Experimental manipulations of the  
423 proximate underpinnings of cognition, such as neural processing (**Box 1**), stress levels at  
424 critical developmental periods, or gene expression, are especially powerful techniques.

425

426 2. Training individuals to perform the hypothesized cognitive task in another context and then  
427 assaying their contest performance. For instance, mutual opponent assessment involves the  
428 evaluation of opponent quality relative to self quality [80]. Individuals trained to perform  
429 well in relative assessments in other contexts, such as choosing between two different  
430 amounts of food, might therefore be expected to be better at mutual assessment in contests  
431 (i.e., to resolve contests more quickly and accurately). The utility of this approach depends on  
432 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

553 **Glossary**

554

555 **Assessment strategy:** The function relating information gathered before and during the  
556 contest to the expression of contest behaviors, especially decisions of whether to persist,  
557 withdraw or escalate.

558

559 **Categorization:** The processes by which stimuli are assigned to distinct groups that are  
560 distinguished from other such groups of stimuli.

561

562 **Classical conditioning:** Learning to associate one cue with a second such that a response  
563 initially given only to the second cue can eventually be elicited by the first cue alone.

564

565 **Cognition:** The processes involved in the acquisition, processing, retention and use of  
566 information from the environment [18].

567

568 **Cognitive ability:** A cognitive mechanism involved in the performance of a particular  
569 behavior; individuals vary in the effectiveness of these mechanisms, and hence in cognitive  
570 ability.

571

572 **Cognitive performance:** The realized outcome of a task requiring cognition, which is  
573 determined by both cognitive ability and environmental factors including motivation, motor  
574 performance and ecological context.

575

576 **Contest:** A direct and discrete behavioral interaction determining ownership of an indivisible  
577 resource unit [2].

578

579 **Cumulative assessment:** An assessment strategy in which an individual's contest behavior is  
580 determined by its own characteristics and no opponent assessment takes place, but in which  
581 opponents can nonetheless exert an influence on individual persistence by inflicting direct  
582 costs [91].

583

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

586

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

589

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

592

593 **Mutual assessment:** An assessment strategy in which an individual's contest behavior is  
594 determined by gathering information on an opponent's RHP relative to its own RHP [33].

595

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

597

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

599

600 **Self assessment:** An assessment strategy in which an individual's contest behavior is  
601 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

<b>Cognitive mechanism(s)</b>	<b>Contest behavior</b>	<b>Species</b>	<b>Description</b>	<b>Possible socioecological consequence</b>	<b>Refs</b>
<i>(I) Before contests</i>					
Imitation learning, operant conditioning	Aggressive signal development	<i>Melospiza melodia</i>	Songs used in territory defense are learned from neighbors' interactions.	Contest strategies influence cultural signal evolution.	[92]
Classical conditioning	Rival anticipation	<i>Trichogaster trichopterus</i>	Classical conditioning allows anticipation of intruder approach.	Selection for territoriality & development of alternative "sneaker" tactics.	[29]
Recognition learning and memory	Pre-fight assessment	<i>Poecile atricapillus</i>	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	<i>Julidochromis transcriptus</i>	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	<i>Macaca mulatta</i>	Dominance can be learned as a categorical concept from video playbacks of aggressive individuals.	Evolution of social cognition.	[94]
<i>(ii) During contests</i>					
Perception	Rival assessment (dyadic contests)	<i>Teleogryllus oceanicus</i>	Contests more escalated when males prevented from exchanging acoustic signals.	Selection for specialized aggressive communication system.	[95]
Perception	Contest resolution	<i>Neogobius melanostomus</i>	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	<i>Clibanarius vittatus</i>	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)	<i>Panthera Leo</i>	Individuals assess numerical asymmetry in group size during intergroup contests.	Evolution of higher-order cognitive traits, selection for social coordination.	[98]
<i>(iii) After contests</i>					
Recognition learning and memory	Winner/Loser effect	<i>Anolis carolinensis</i>	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	<i>Ctenomys talarum</i>	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	<i>Vireo olivaceus</i>	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 <sup>a</sup>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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631

632 References

633

- 634 1 Milinski, M. and Parker, G.A. (1991) Competition for resources. In *Behavioural*  
635 *Ecology: An Evolutionary Approach* (Krebs, J. R. and Davies, N. B., eds), pp. 137–  
636 168, Blackwell Scientific
- 637 2 Hardy, I.C.W. and Briffa, M., eds. (2013) *Animal Contests*, Cambridge University  
638 Press.
- 639 3 Wilson, A.J. *et al.* (2013) Causes and consequences of contest outcome:  
640 Aggressiveness, dominance and growth in the sheephead swordtail, *Xiphophorus*  
641 *birchmanni*. *Behav. Ecol. Sociobiol.* 67, 1151–1161
- 642 4 Riechert, S.E. (1988) The energetic costs of fighting. *Amer. Zool.* 28, 877–884
- 643 5 Lindquist, W.B. and Chase, I.D. (2009) Data-based analysis of winner-loser models of  
644 hierarchy formation in animals. *Bull. Math. Biol.* 71, 556–584
- 645 6 Arnott, G. and Elwood, R.W. (2008) Information gathering and decision making about  
646 resource value in animal contests. *Anim. Behav.* 76, 529–542
- 647 7 Elwood, R.W. and Arnott, G. (2012) Understanding how animals fight with Lloyd  
648 Morgan's canon. *Anim. Behav.* 84, 1095–1102
- 649 8 Fawcett, T.W. *et al.* (2013) Exposing the behavioral gambit: The evolution of learning  
650 and decision rules. *Behav. Ecol.* 24, 2–11

- 651 9 Mesterton-Gibbons, M. and Heap, S.M. (2014) Variation between self- and mutual  
652 assessment in animal contests. *Am. Nat.* 183, 199–213
- 653 10 Wiley, R.H. (1994) Errors, exaggeration, and deception in animal communication. In  
654 *Behavioral mechanisms in ecology* (Real, L., ed), pp. 157–189, University of Chicago  
655 Press
- 656 11 Parker, G.A. (1974) Assessment strategy and the evolution of fighting behaviour. *J.*  
657 *Theor. Biol.* 47, 223–243
- 658 12 Stuart-Fox, D. (2006) Testing game theory models: fighting ability and decision rules  
659 in chameleon contests. *Proc. R. Soc. B Biol. Sci.* 273, 1555–1561
- 660 13 Thornton, A. *et al.* (2014) Toward wild psychometrics: linking individual cognitive  
661 differences to fitness. *Behav. Ecol.* 25, 1299–1301
- 662 14 Fitch, W.T. (2014) Toward a computational framework for cognitive biology: unifying  
663 approaches from cognitive neuroscience and comparative cognition. *Phys. Life Rev.*  
664 11, 329–364
- 665 15 Briffa, M. *et al.* (2013) Analysis of animal contest data. In *Animal Contests* (Hardy, I.  
666 C. W. and Briffa, M., eds), pp. 47–85, Cambridge University Press
- 667 16 Morand-Ferron, J. *et al.* (2016) Studying the evolutionary ecology of cognition in the  
668 wild: a review of practical and conceptual challenges. *Biol. Rev.* 91, 367–389
- 669 17 Kays, R. *et al.* (2015) Terrestrial animal tracking as an eye on life and planet. *Science*  
670 348, 1222–1232
- 671 18 Shettleworth, S.J. (2010) *Cognition, Evolution and Behavior*, (2nd edn) Oxford  
672 University Press.
- 673 19 Bee, M.A. (2001) Habituation and sensitization in bullfrogs (*Rana catesbiana*): testing  
674 the dual-process theory of habituation. *J. Comp. Psychol.* 115, 307–316
- 675 20 Gherardi, F. and Tiedemann, J. (2004) Binary individual recognition in hermit crabs.

- 676 *Behav. Ecol. Sociobiol.* 55, 524–530
- 677 21 Tibbetts, E.A. and Dale, J. (2007) Individual recognition: it is good to be different.  
678 *Trends Ecol. Evol.* 22, 529–537
- 679 22 Griffin, A. *et al.* (2015) Cognition and personality: An analysis of an emerging field.  
680 *Trends Ecol. Evol.* 30, 207–214
- 681 23 Briffa, M. and Fortescue, K.J. (2017) Motor pattern during fights in the hermit crab  
682 *Pagurus bernhardus*: evidence for the role of skill in animal contests. *Anim. Behav.*  
683 128, 13–20
- 684 24 Catchpole, C. and Slater, P. (2008) *Bird song: Biological themes and variations*, 2nd  
685 Editio. Cambridge University Press.
- 686 25 Akçay, Ç. *et al.* (2017) Good tutors are not dear enemies in song sparrows. *Anim.*  
687 *Behav.* 129, 223–228
- 688 26 Lahti, D.C. *et al.* (2011) A tradeoff between performance and accuracy in bird song  
689 learning. *Ethology* 117, 802–811
- 690 27 Searcy, W.A. and Beecher, M.D. (2009) Song as an aggressive signal in songbirds.  
691 *Anim. Behav.* 78, 1281–1292
- 692 28 Losey, G. and Sevenster, P. (1995) Can three-spined sticklebacks learn when to  
693 display? Rewarded displays. *Anim. Behav.* 49, 137–150
- 694 29 Hollis, K.L. (1999) The role of learning in the aggressive and reproductive behavior of  
695 blue gouramis, *Trichogaster trichopterus*. *Environ. Biol. Fishes* 54, 355–369
- 696 30 Bronstein, P.M. (1988) Socially mediated learning in male *Betta splendens*. III: Rapid  
697 acquisitions. *Aggress. Behav.* 14, 415–424
- 698 31 Edmonds, E. and Briffa, M. (2016) Weak rappers rock more: hermit crabs assess their  
699 own agonistic behaviour. *Biol. Lett.* 12, 20150884
- 700 32 Kokko, H. (2013) Dyadic contests: modelling fights between two individuals. In

701 *Animal Contests* (Hardy, I. C. W. and Briffa, M., eds), pp. 5–32, Cambridge  
702 University Press

703 33 Arnott, G. and Elwood, R.W. (2009) Assessment of fighting ability in animal contests.  
704 *Anim. Behav.* 77, 991–1004

705 34 Arnott, G. and Elwood, R.W. (2007) Fighting for shells: how private information  
706 about resource value changes hermit crab pre-fight displays and escalated fight  
707 behaviour. *Proc. R. Soc. B Biol. Sci.* 274, 3011–3017

708 35 Elwood, R.W. and Prenter, J. (2013) Agression in spiders. In *Animal Contests* (Hardy,  
709 I. C. W. and Briffa, M., eds), pp. 113–133, Cambridge University Press

710 36 McCallum, E.S. *et al.* (2017) Accurate resource assessment requires experience in a  
711 territorial fish. *Anim. Behav.* 123, 249–257

712 37 Oliveira, R.F. *et al.* (1998) Know thine enemy: fighting fish gather information from  
713 observing conspecific interactions. *Proc. R. Soc. B Biol. Sci.* 265, 1045–1049

714 38 Dreiss, A.N. *et al.* (2014) Information retention during competitive interactions:  
715 siblings need to constantly repeat vocal displays. *Evol. Biol.* 42, 63–74

716 39 Payne, R.J.H. and Pagel, M. (1997) Why do animals repeat displays? *Anim. Behav.* 54,  
717 109–119

718 40 Obermeier, M. and Schmitz, B. (2003) Recognition of dominance in the big-clawed  
719 snapping shrimp (*Alpheus heterochaelis* Say 1818) part II: Analysis of signal modality.  
720 *Mar. Freshw. Behav. Physiol.* 36, 17–29

721 41 Carazo, P. *et al.* (2008) Beyond “nasty neighbours” and “dear enemies”? Individual  
722 recognition by scent marks in a lizard (*Podarcis hispanica*). *Anim. Behav.* 76, 1953–  
723 1963

724 42 Temeles, E.J. (1994) The role of neighbors in territorial systems: when are they “dear  
725 enemies”? *Anim. Behav.* 47, 339–350

- 726 43 Bee, M.A. *et al.* (2016) Assessment and recognition of competitive rivals in anuran  
727 amphibians. *Adv. Study Behav.* 48, 161–249
- 728 44 Hotta, T. *et al.* (2015) The use of multiple sources of social information in contest  
729 behavior: testing the social cognitive abilities of a cichlid fish. *Front. Ecol. Evol.* 3, 85
- 730 45 Fawcett, T.W. and Johnstone, R.A. (2010) Learning your own strength: winner and  
731 loser effects should change with age and experience. *Proc. R. Soc. B Biol. Sci.* 277,  
732 1427–1434
- 733 46 Garcia, M.J. *et al.* (2014) Mechanisms of decision making during contests in green  
734 anole lizards: prior experience and assessment. *Anim. Behav.* 92, 45–54
- 735 47 Yasuda, C.I. *et al.* (2014) Hermit crab, *Pagurus middendorffii*, males avoid the  
736 escalation of contests with familiar winners. *Anim. Behav.* 96, 49–57
- 737 48 Trannoy, S. *et al.* (2016) Short and long-lasting behavioral consequences of agonistic  
738 encounters between male *Drosophila melanogaster*. *Proc. Natl. Acad. Sci. U. S. A.*  
739 113, 4818–4823
- 740 49 Briffa, M. *et al.* (2015) Animal personality as a cause and consequence of contest  
741 behaviour. *Biol. Lett.* 11, 20141007
- 742 50 Lee, A.E.G. *et al.* (2016) Information use and resource competition: an integrative  
743 framework. *Proc. R. Soc. B Biol. Sci.* 283, 20152550
- 744 51 Mery, F. and Kawecki, T.J. (2003) A fitness cost of learning ability in *Drosophila*  
745 *melanogaster*. *Proc. Biol. Sci.* 270, 2465–2469
- 746 52 Maynard Smith, J. (1974) The theory of games and the evolution of animal conflicts. *J.*  
747 *Theor. Biol.* 47, 209–221
- 748 53 Lee, V.E. *et al.* (2014) Effects of age and experience on contest behavior in the  
749 burying beetle, *Nicrophorus vespilloides*. *Behav. Ecol.* 25, 172–179
- 750 54 Kasumovic, M.M. *et al.* (2010) Examination of prior contest experience and the

751 retention of winner and loser effects. *Behav. Ecol.* 21, 404–409

752 55 Morand-Ferron, J. and Quinn, J.L. (2015) The evolution of cognition in natural  
753 populations. *Trends Cogn. Sci.* 19, 235–237

754 56 Cole, E.F. *et al.* (2012) Cognitive ability influences reproductive life history variation  
755 in the wild. *Curr. Biol.* 22, 1808–1812

756 57 Tibbetts, E.A. *et al.* (2015) Socially selected ornaments and fitness: Signals of fighting  
757 ability in paper wasps are positively associated with survival, reproductive success,  
758 and rank. *Evolution* 69, 2917–2926

759 58 Croston, R. *et al.* (2015) Heritability and the evolution of cognitive traits. *Behav. Ecol.*  
760 26, 1447–1459

761 59 Quinn, J. *et al.* (2016) Environmental and genetic effects on innovativeness in a natural  
762 population of birds. *Philos. Trans. R. Soc. B Biol. Sci.* 371, 20150184

763 60 Sheehan, M.J. and Bergman, T.J. (2016) Is there an evolutionary trade-off between  
764 quality signaling and social recognition? *Behav. Ecol.* 27, 2–13

765 61 Korzan, W.J. *et al.* (2007) Memory of opponents is more potent than visual sign  
766 stimuli after social hierarchy has been established. *Behav. Brain Res.* 183, 31–42

767 62 Casey, C. *et al.* (2015) Rival assessment among northern elephant seals: evidence of  
768 associative learning during male-male contests. *R. Soc. Open Sci.* 2, 150228

769 63 Byrne, R. (1996) Machiavellian intelligence. *Evol. Anthropol.* 5, 172–180

770 64 Dunbar, R.I.M. (2003) The social brain: Mind, language, and society in evolutionary  
771 perspective. *Annu. Rev. Anthropol.* 32, 163–181

772 65 Frith, C. and Frith, U. (2005) Theory of mind. *Curr. Biol.* 15, 644–645

773 66 Penn, D.C. and Povinelli, D.J. (2007) On the lack of evidence that non-human animals  
774 possess anything remotely resembling a “theory of mind”. *Philos. Trans. R. Soc. Lond.*  
775 *B. Biol. Sci.* 362, 731–744

776 67 Hare, B. *et al.* (2001) Do chimpanzees know what conspecifics know? *Anim. Behav.*  
777 61, 139–151

778 68 Amici, F. *et al.* (2009) Variation in withholding of information in three monkey  
779 species. *Proc. R. Soc. B Biol. Sci.* 276, 3311–3318

780 69 Benson-Amram, S. *et al.* (2011) Numerical assessment and individual call  
781 discrimination by wild spotted hyaenas, *Crocuta crocuta*. *Anim. Behav.* 82, 743–752

782 70 Nowicki, S. *et al.* (1998) Song learning, early nutrition and sexual selection in  
783 songbirds. *Am. Zool.* 190, 179–190

784 71 Farrell, T. *et al.* (2015) Developmental stress and correlated cognitive traits in  
785 songbirds. *Comp. Cogn. Behav. Rev.* 10, 1–23

786 72 Sapolsky, R.M. (2005) The influence of social hierarchy on primate health. *Science*  
787 308, 648–652

788 73 Joëls, M. *et al.* (2006) Learning under stress: how does it work? *Trends Cogn. Sci.* 10,  
789 152–158

790 74 Yurkovic, A. *et al.* (2006) Learning and memory associated with aggression in  
791 *Drosophila melanogaster*. *Proc. Natl. Acad. Sci. U. S. A.* 103, 17519–17524

792 75 Versteven, M. *et al.* (2017) Hearing regulates *Drosophila* aggression. *Proc. Natl.*  
793 *Acad. Sci.* 114, 1958–1963

794 76 Forster, G.L. *et al.* (2005) Opponent recognition in male green anoles, *Anolis*  
795 *carolinensis*. *Anim. Behav.* 69, 733–740

796 77 Ling, T.J. *et al.* (2010) Opponent recognition and social status differentiate rapid  
797 neuroendocrine responses to social challenge. *Physiol. Behav.* 99, 571–578

798 78 Meyer, W.N. *et al.* (2004) Social stress and corticosterone regionally upregulate limbic  
799 N-methyl-D-aspartate receptor (NR) subunit type NR 2A and NR 2B in the lizard  
800 *Anolis carolinensis*. *Neuroscience* 128, 675–684



801 79 Bannerman, D. *et al.* (2002) Selective cytotoxic lesions of the retrohippocampal region  
802 produce a mild deficit in social recognition memory. *Exp. Brain Res.* 142, 395–401

803 80 Enquist, M. and Leimar, O. (1983) Evolution of fighting behavior: decision rules and  
804 assessment of relative strength. *J. Theor. Biol.* 102, 387–410

805 81 Reaume, C.J. *et al.* (2011) A natural genetic polymorphism affects retroactive  
806 interference in *Drosophila melanogaster*. *Proc. R. Soc. B Biol. Sci.* 278, 91–98

807 82 Lynn, S.K. *et al.* (2005) Peak shift discrimination learning as a mechanism of social  
808 evolution. *Evolution* 59, 1300–1305

809 83 Maynard Smith, J. and Parker, G.A. (1976) The logic of asymmetric contests. *Anim.*  
810 *Behav.* 24, 159–175

811 84 Taylor, P.W. and Elwood, R.W. (2003) The mismeasure of animal contests. *Anim.*  
812 *Behav.* 65, 1195–1202

813 85 Tsai, Y.-J.J. *et al.* (2014) Pure self-assessment of size during male-male contests in the  
814 parasitoid wasp *Nasonia vitripennis*. *Ethology* 120, 816–824

815 86 Prenter, J. *et al.* (2006) Self-assessment by males during energetically costly contests  
816 over precopula females in amphipods. *Anim. Behav.* 72, 861–868

817 87 Fawcett, T.W. and Mowles, S.L. (2013) Assessments of fighting ability need not be  
818 cognitively complex. *Anim. Behav.* 86, e1–e7

819 88 Elwood, R.W. and Arnott, G. (2013) Assessments in contests are frequently assumed  
820 to be complex when simple explanations will suffice. *Anim. Behav.* 86, e8–e12

821 89 Akre, K.L. and Johnsen, S. (2014) Psychophysics and the evolution of behavior.  
822 *Trends Ecol. Evol.* 29, 291–300

823 90 Stamps, J.A. and Krishnan, V. V (1999) A learning-based model of territory  
824 establishment. *Q. Rev. Biol.* 74, 291–318

825 91 Payne, R.J.H. (1998) Gradually escalating fights and displays: the cumulative

826 assessment model. *Anim. Behav.* 56, 651–662

827 92 Beecher, M.D. (2016) Birdsong learning as a social process. *Anim. Behav.* 124, 233–  
828 246

829 93 Toth, C.A. *et al.* (2012) Evidence for multicontest eavesdropping in chickadees.  
830 *Behav. Ecol.* 23, 836–842

831 94 Bovee, D. and Washburn, D.A. (2003) Rhesus macaques (*Macaca mulatta*) categorize  
832 unknown conspecifics according to their dominance relations. *J. Comp. Psychol.* 117,  
833 400–405

834 95 Logue, D.M. *et al.* (2010) Does signalling mitigate the cost of agonistic interactions?  
835 A test in a cricket that has lost its song. *Proc. R. Soc. B Biol. Sci.* 277, 2571–2575

836 96 Sopinka, N.M. *et al.* (2010) Impact of contaminant exposure on resource contests in an  
837 invasive fish. *Behav. Ecol. Sociobiol.* 64, 1947–1958

838 97 Hazlett, B.A. (1996) Assessments during shell exchanges by the hermit crab  
839 *Clibanarius vittatus*: The complete negotiator. *Anim. Behav.* 51, 567–573

840 98 McComb, K. *et al.* (1994) Roaring and numerical assessment in contests between  
841 groups of female lions, *Panthera leo*. *Anim. Behav.* 47, 379–387

842 99 Zenuto, R.R. (2010) Dear enemy relationships in the subterranean rodent *Ctenomys*  
843 *talarum*: The role of memory of familiar odours. *Anim. Behav.* 79, 1247–1255

844 100 Moser-Purdy, C. and Mennill, D.J. (2016) Large vocal repertoires do not constrain the  
845 dear enemy effect: a playback experiment and comparative study of songbirds. *Anim.*  
846 *Behav.* 118, 55–64

847