1   **Giant Australian cuttlefish use mutual assessment to resolve male-male contests.**

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22   Game theory models provide a useful framework for investigating strategies of conflict

23   resolution in animal contests. Model predictions are based on estimates of resource-holding

24   potential (RHP) and vary in their assumptions about how opponents gather information about

25   RHP. Models can be divided into self-assessment strategies (energetic war-of-attrition, E-

26   WOA; cumulative assessment model, CAM) and mutual assessment strategies (sequential

27   assessment model, SAM). We used laboratory-staged contests between male giant Australian

28   cuttlefish, *Sepia apama*, to evaluate RHP traits and to test game theory models. Mantle length

29   was a key indicator of RHP because it predicted contest outcome, whereby larger individuals

30   were more likely to win a contest. Winners and losers did not match behaviours, ruling out

31   the E-WOA. There was no relationship between contest outcome, duration and escalation

32   rates, arguing against the CAM. Persistence to continue a contest was based on RHP

33   asymmetry, rather than loser and/or winner RHP, providing support for the SAM. Motivation

34   to fight was determined from a male's latency to resume a contest following the introduction

35   of a female during a contest. The latency to resume a contest was negatively related to the size

36   of the focal male and positively related to the size of their opponent. These results show that

37   competing males are able to gather information concerning RHP asymmetries, providing

38   support for mutual assessment. Furthermore, males showed significant behavioural

39   differences in their responses to relatively larger than to relatively smaller opponents. Using

40   an integrative approach, our study provides a well-substantiated example of mutual

41   assessment.

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46   Animals competing over limited resources are likely to incur costs, including increased

47   energy expenditure and risk of predation, injuries or fatal attacks (Maynard Smith, 1974;

48   Maynard Smith & Price, 1973). During contests, animals may gather information from

49   multiple sources to assess the potential costs and benefits of continued conflict, in turn

50   facilitating economic and tactical decision making (Maynard Smith & Parker, 1976; Parker,

51   1974). The decision to withdraw from a contest is usually influenced by the fighting ability of

52   a contestant, termed resource-holding potential (RHP; Maynard Smith, 1974; Parker, 1974;

53   Parker & Stuart, 1976). The information that facilitates these decisions will be dictated by the

54   assessment capabilities of the species (Taylor & Elwood, 2003).

55   Game theoretical approaches serve as an analytical tool for understanding the patterns

56   of behaviour observed in contests across many taxa. Currently, three major game theory

57   models may be applied to animal contests to determine the assessment strategy used for

58   decision making (Table 1). The models can be divided into self-assessment and mutual

59   assessment strategies. The self-assessment models include the energetic war of attrition (E-

60   WOA; Payne & Pagel, 1996; 1997) and the cumulative assessment model (CAM; Payne,

61   1998). These models assume that contestants evaluate their own RHP, but fail to assess their

62   opponent's RHP. Contestants differ in rates of escalation within phases (i.e. periods defined

63   by behaviours of similar aggressive intensity). The decision point to withdraw is determined

64   by the weaker individual's threshold for costs. For the E-WOA model, the threshold is based

65   on self-imposed energetic costs. For the CAM, the threshold is determined by combined costs

66   that accumulate as a function of time and energy expenditure, as well as the damage inflicted

67   by the opponent. Mutual assessment is modelled through the sequential assessment model

68   (SAM), which assumes that contestants evaluate their own RHP relative to their opponent's

69   RHP (Enquist & Leimar, 1983). In this model, contests progress through a series of

70   successive phases, which are thought to provide increasingly accurate information about the

71   RHP asymmetry between contestants. Predictions for these three models are based on

72   estimates of RHP and vary in their assumptions about how opponents gather information

73   about RHP (Table 1).

74   Mutual assessment is assumed to be a more efficient strategy than self-assessment

75   because animals can minimize costly and futile persistence by gathering information about

76   relative RHP (Enquist & Leimar, 1983). However, studies on a wide range of animal contests

77   that have shown mutual assessment (e.g. Englund & Olsson, 1990; Junior & Peixoto, 2013;

78   Kemp, Alcock, & Allen, 2006; Pratt, McLain, & Lathrop, 2003) have recently been called

79   into question (Briffa & Elwood, 2009; Elwood & Arnott, 2012; Taylor & Elwood, 2003).

80   Taylor and Elwood (2003) contended that such studies may have actually presented artefacts

81   of alternative mechanisms. For example, a negative association between contest duration and

82   RHP asymmetry, which is thought to be indicative of the SAM (i.e. mutual assessment),

83   could also arise if the weaker contestant accrued costs faster than its opponent (i.e. self-

84   assessment, E-WOA). Taylor and Elwood (2003) recommended a statistical framework to

85   distinguish between mutual and self-assessment strategies. This framework has been

86   implemented in many studies, revealing that self-assessment is more prevalent than

87   previously thought (e.g. Brandt & Swallow, 2009; Prenter, Elwood, & Taylor, 2006; Stuart-

88   Fox, 2006). However, distinguishing between assessment strategies remains a challenge, and

89   consequently several recent studies report inconclusive results (e.g. Batista, Zubizarreta,

90   Perrone, & Silva, 2012; Egge, Brandt, & Swallow, 2011; Jennings, Gammell, Carlin, &

91   Hayden, 2004; Kelly, 2006).

92   Recently, there has been renewed debate about whether mutual assessment is more

93   cognitively complex than self-assessment because of its apparent requirement for comparative

94   decision making (Elwood & Arnott, 2012; Elwood & Arnott, 2013; Fawcett & Mowles,

95   2013). Elwood and Arnott (2012) and Fawcett and Mowles (2013) argued that mutual

96   assessment could entail cognitively simple threshold decision making. They noted that the

97   original SAM model (i.e. mutual assessment) does not require an explicit comparison of RHP;

98   rather, information about RHP is directly transmitted as a relative measure (i.e. as error-prone

99   estimates of relative fighting ability). Moreover, Elwood and Arnott (2012) argued that many

100   studies provide insufficient evidence of individuals comparatively assessing RHP, and that

101   many claims of comparison of body size, claw size or dewlap size still need to be

102   substantiated. One experimental approach to substantiate such claims involves assessing the

103   motivational state of an animal in a contest by using a novel stimulus that causes a contestant

104   to temporarily cease fighting (see Arnott & Elwood, 2009a; Elwood, Wood, Gallagher, &

105   Dick, 1998). The latency to resume the contest provides a measure of the individual's

106   motivation to fight (see Table 1 for predictions). Another approach is to test the ability of a

107   contestant to assess relative values (e.g. body size or claw size) in the context of aggression

108   (see e.g. dogs, *Canis familiaris*, Taylor, Reby, & McComb, 2010). Testing such capabilities

109   during a contest may validate claims of mutual assessment.

110   This study investigated the assessment strategy used to resolve conflict in male giant

111   Australian cuttlefish, *Sepia apama.* These cuttlefish engage in dynamic signalling during

112   agonistic contests, similar to other species in which game theory models have been tested

113   (e.g. hermit crabs, Briffa & Elwood, 2001; chameleons, Stuart-Fox, 2006; wasps, Tibbetts,

114   Mettler, & Levy, 2010). Contests typically occur in the presence of females during their

115   reproductive season (austral winter months: May–August). However, even in the absence of

116   females, males engage in contests in both field (Hanlon, 1999) and laboratory settings

117   (Schnell, 2014). The fighting tactics of males are influenced by body size, which varies

118   widely at maturity. Small males tend to reduce direct aggression by being surreptitious or

119   through deceptive signalling (i.e. female mimicry; Hanlon, Naud, Shaw, & Havenhand,

120   2005). Large males regularly engage in agonistic contests, which are typically mediated

121 through visual displays but can escalate to physical pushing and grappling (Hall & Hanlon,

122 2002). Variation in body size and its effect on agonistic behaviours suggest that this species

123 has evolved the ability to assess the size of its opponents and alter its behaviour accordingly.

124 However, the assessment strategy used during these contests has not been tested. The

125 application of game theory models to cuttlefish contests may be an effective tool for

126 determining patterns of fighting behaviour (i.e. self-assessment or mutual assessment

127 strategy) in this particular system.

128   The central aim of our study was to determine the fighting strategy used by giant

129 Australian cuttlefish during male–male contests. First, we assessed the male traits that may be

130 associated with RHP. Second, we used specific predictions of the three major game theory

131 models (E-WOA, CAM, and SAM; see Table 1 for predictions) to determine whether the

132 decision to withdraw from a contest was based on the absolute RHP of the loser (self-

133 assessment) or on the RHP of the loser relative to the winner (mutual assessment). Third, the

134 contestant's assessment of RHP was substantiated by measures of motivation and aggression.

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136 <H1>METHODS

137 *<H2>Study species, collection and husbandry*

138 Thirty-four male and four female adult giant Australian cuttlefish were caught via scuba in

139 coastal areas of Sydney, Australia (34°50'S, 151°22'E) between April and May 2012. They

140 were transported (< 50 min) to the aquarium facility at Cronulla Fisheries Research Centre in

141 a custom-made transport tank (9.0 x 8.0 cm and 8.0 cm high, maximum capacity = 3

142 subjects). Water in the transport tank was oxygenated and maintained at a natural ambient sea

143 temperature (15–17 °C). Sex was determined by coloration and the dimorphic state of the

144 fourth arm. Subjects were housed individually in open-air tanks that received a constant flow

145   (approximately 10 litres/min) of filtered ambient sea water. Cuttlefish were fed a mixed diet

146   of food items including live Australian ghost shrimp, *Trypaea australiensis*, and thawed

147   frozen prawn, squid or pilchard every evening.

148   *<H2>Male traits*

149   We measured mantle length and dimorphic arm length (ventral-most pair; Fig. 1) to the

150   nearest 0.1 mm and weighed cuttlefish to the nearest 1 g using a Precisa electronic balance

151   (30000D IP65 Wedderburn scales TYP 480-9580, Switzerland). We also measured 'passing

152   cloud' behaviour which is a chromatic signal typically expressed by males during the lateral

153   display (Fig. 1b). It involves the expansion and contraction of chromatophores to produce the

154   appearance of light and dark bands flowing unidirectionally over the mantle. The number of

155   clouds and speed of travel are relatively consistent; however, the expression of this behaviour

156   varies in intensity. To measure changes in intensity, we recorded the duration and the contrast

157   of the bands. There was no variation in the duration of bands; however, the contrast of bands

158   changed throughout the agonistic interactions. We therefore measured the intensity using

159   contrast differences between light and dark bands. Contrast differences are likely to be

160   visually conspicuous because the visual systems of cuttlefish are sensitive to polarized light

161   (Mäthger, Shashar, & Hanlon, 2009; Shashar, Rutledge, & Cronin, 1996). We calculated the

162   brightness of the bands on the mantle of each male displaying passing cloud. This was

163   measured on a laptop (Apple Macintosh, OS X 10.9.2) broadcasting the video recordings and

164   using Apple Macintosh Digital Color Meter. We recorded the RGB values at 10 random

165   locations on both light and dark bands. Brightness values were calculated from RGB values (0

166   = black and 255 = white) using the luminance formula from Poynton (2003):

167    $$Y = 0.2126 \times R + 0.7152 \times G + 0.0722 \times B$$

168 The means of each set of brightness values was then used to approximate contrast differences

169 between the bands. Correlations of all four male attributes (mantle length, arm length, mass

170 and passing cloud intensity) were then determined using Pearson correlation coefficients (see

171 Appendix Table A1).

172 *<H2>Male contests*

173 Laboratory-staged contests were carried out in June and July 2012. Twenty-two males that

174 varied in size (mean mantle length = 415.1 mm; range 295–509 mm; mean body weight =

175 6348 g; range 4015–9324 g) were used. We used a repeated measures design, in which each

176 male was assigned to (1) a size-symmetric opponent (within 7% of mantle length of each

177 other) and (2) a size-asymmetric opponent (at least 20% mantle length difference). Subjects

178 were assigned a random sequence of the treatments (i.e. size-symmetric and size-asymmetric)

179 to control for order effects. Trials were staged 4 weeks apart to minimize experience effects,

180 since different agonistic experiences can sometimes affect the outcome of a contest (i.e.

181 winner–loser effect; Hsu & Wolf, 1999).

182 The contest arena was a circular 5000-litre (height 12.0 cm, diameter 23.4 cm; 2.38 m^2

183 per cuttlefish) tank divided in half. A clear partition was fixed in place to physically isolate

184 subjects and prevent injury during the contests. An opaque partition slid loosely next to the

185 clear partition to visually isolate subjects during the first phase of the tests. Water was able to

186 flow between both compartments to facilitate chemical exchange between the male subjects.

187 A high-definition video camera (SONY HDR-SR11E) fitted with a wide-angle lens (Raynox

188 HD-5050PRO 0.5 x) was placed directly over the test arena to record (MTS format 1920 ×

189 1080 lines) behavioural responses.

190 To acclimate subjects to the apparatus, individuals were placed in the test arena for

191 three 65 min periods over 3 consecutive days. During acclimation sessions the subjects were

192   tested separately, so that males did not come into visual contact or chemical exposure with

193   one another until the experimental phase. Subjects were placed gently into one of the two

194   compartments in the test arena. Following a 5 min period, the opaque partition was removed

195   by sliding it out of the water. After 60 min subjects were recaptured and transferred back to

196   their home tank. After each acclimation session, the test arena was drained, cleaned and

197   refilled using fresh filtered sea water to ensure subjects were not responding to any chemical

198   cues left in the water from previous test subjects. By the third acclimation session subjects

199   exhibited no signs of disturbance, such as inking or jetting, from the transfer procedure. The

200   experimental trials followed the same procedure used in the acclimation sessions. Subjects

201   typically engaged in more than one contest during the 60 min staged experimental trials and

202   therefore the repeated measures design was unbalanced. We observed 75 contests in 21

203   experimental trials (mean number of contests = 3.43; range 1–7); one trial without mutual

204   displaying between contestants was excluded.

205   *<H2>Probing motivational state in response to a female stimulus*

206   The motivational state experiments were carried out in June 2012. Twelve males that varied

207   in size (mean mantle length = 411.76 mm; range 350–464 mm; mean body weight = 5113 g;

208   range 4278–6324 g) and had not participated in any previous experiments were used. We used

209   a repeated measures design, in which each test male was assigned a size-asymmetric opponent

210   (at least 20% mantle length difference) and tested twice using the same opponent. Probing

211   motivational state is typically tested using a startle stimulus (see Arnott & Elwood, 2009a;

212   Elwood et al., 1998). However, initial pilot observations revealed that male subjects did not

213   respond to small startle stimuli whereas larger startle stimuli caused focal males to ink,

214   making it impossible to record the behaviour of the test subjects. We used a female to distract

215   the focal male instead. This consistently caused the focal male to cease fighting and inspect

216   the female before resuming the contest. The test arena was the same as the contest arena

217 except it was divided into three compartments that did not allow chemical exchange. The

218 edges of the clear Perspex partition were sealed with a silicon sealant. Two compartments

219 were equal in size and the third compartment was smaller. Test males were placed in the

220 equal-sized compartments and a female was placed in the smaller compartment. Following a

221 30 min acclimation period the opaque partition between the males' compartments was

222 removed. One minute after the onset of display by both male cuttlefish, the opaque partition

223 to the female compartment was removed on one side only, so that one male contestant (i.e. the

224 focal male) could see the female. The female compartment in the test arena was designed so

225 that when only one opaque partition was removed her presence was undetected by the male

226 opponent (i.e. stimulus male). The specific timing of introducing the female was chosen

227 following initial laboratory-staged contest experiments, and selected to give sufficient periods

228 of display and escalation. Following each interaction, the subjects were returned to their home

229 tanks and 48 h later the original pairs were retested in the same manner, but with the

230 previously nondistracted stimulus male now being designated as the focal male and exposed

231 to the female. Four females of similar size (mean mantle length = 299.71 mm; range 293–304;

232 mean body weight = 3266.34 g; range 3104–3326) were used as a stimulus to reduce

233 pseudoreplication. Males had not encountered the females prior to this experiment.

234 *<H2>Decision making in response to aggressive rivals with variable RHP*

235 The decision-making experiments were carried out in July 2012. Eight medium-sized males

236 (mean mantle length = 415.88 mm; range 390–431 mm; mean body weight = 5424 g; range

237 4515–5834 g) that were used in the laboratory-staged contest experiments were subsequently

238 used as focal subjects. A repeated measures design was used, in which each focal male was

239 assigned a smaller live-male stimulus (mantle length approximately < 20%) and a larger live-

240 male stimulus (mantle length approximately > 20%). Focal males were assigned a random

241 sequence of the treatments (i.e. small and large) to control for order effects. Focal males were

242 tested over 4 days with each subject receiving one treatment on a single day with an intertest

243 interval of 48 h. The test arena was identical to the contest arena, except the compartments did

244 not allow chemical exchange (i.e. they were sealed with a silicone sealant). The Perspex

245 partition was lined with a one-way mirror film to create a reflective surface in the

246 compartment holding the live-male stimulus. This provided a clear view of the stimulus male

247 by the focal male, while inducing display behaviour by the live-male stimulus towards his

248 reflection. Cuttlefish generally respond aggressively to opponents of similar size and also to

249 mirror images (see Hanlon & Messenger, 1988). The one-way mirror configuration meant that

250 (1) the live-male stimuli exhibited aggressive behaviours and (2) focal males were able to

251 respond to size differences in aggressive live-male stimuli. Focal males were assigned a

252 random sequence of the treatments (i.e. small and large live-male stimuli) to control for order

253 effects. The same procedure used in the laboratory-staged contests was followed, except trials

254 only ran for 35 min (5 min acclimation period and a 30 min trial). Different live-male stimuli

255 were used to reduce pseudoreplication (N= 8). Focal subjects had not encountered the live-

256 male stimuli prior to this experiment.

257 *<H2>Response measures*

258 We scored the trials using JWatcher Video 1.0 (Blumstein, Evans, & Daniel, 2006), which

259 reads the time code of the MOV video file to allow frame-by-frame resolution (24 frames/s,

260 40 ms PAL video standard). For the laboratory-staged contests, we recorded the duration of

261 each contest that involved mutual displaying (i.e. both contestants performed agonistic

262 displays). The start of a contest was defined as the point of engagement between the

263 contestants (i.e. when the receiver responded to the signaller). We defined the end of a contest

264 to occur when one male retreated from the interaction for at least 10 s. All contests had clear

265 victors because the loser would typically retreat from the clear partition and cease displaying,

266 while the winner would remain close to the clear partition and continue displaying.

267   Contests involved a series of behaviours. We recorded the frequency and duration of

268   three displays: frontal, lateral and shovel (Fig. 1). In the frontal display, the signaller orients

269   face-first towards the opponent, with his mantle down and not visible to the rival. The face is

270   dark and the arms are white and oscillating. During the lateral display, the body is oriented

271   laterally to the opponent. The arms are extended forward in line with the body and the

272   dimorphic fourth arm is broadened. The face and arms are of varied coloration and passing

273   cloud is usually expressed on the mantle. The shovel display orientation is the same as the

274   frontal display but the mantle is raised and visible to the rival, the arms are extended and rigid

275   in a shovel-like shape. The face and arms vary in coloration. We also recorded the frequency

276   of attempted physical aggression, including pushing of the clear partition during an aggressive

277   display or lunging at the clear partition. In a preliminary study on agonistic behaviours (see

278   Appendix), we classified behaviours into three levels of aggressive intensity, consistent with

279   likely associated costs. The frontal display was predominately exhibited when approaching a

280   male conspecific, and thus this display was classified as a low-level aggressive signal and

281   given an aggressive intensity score of 1 (see Appendix Table A2). The lateral and shovel

282   displays were largely exhibited during escalated agonistic interactions (i.e. transition from

283   visual signalling to physical aggression); thus these were classified as high-level aggressive

284   signals and were given an aggressive intensity score of 2 (see Appendix Table A2).

285   Behaviours that involved attempted physical contact, such as lunging or pushing, were

286   classified as the highest level of aggression and given an aggressive intensity score of 3. We

287   scored the temporal trends of escalation between winners and losers by recording the

288   initiating behaviour, the latency to attempted physical aggression and the number of displays

289   performed prior to attempted physical aggression.

290   For the motivational state experiments we recorded the latency to resume the contest

291   by the focal male, following the introduction of the female. For the decision-making

292   experiments in response to variable RHP we scored the behaviour of the focal males in

293   response to the live-male stimuli. We recorded whether the live-male stimuli elicited escape

294   behaviour (i.e. backwards movement, inking or camouflage pattern) or an escalated response

295   (i.e. attempted physical aggression) in the focal male.

296   *<H2>Ethical note*

297   Subject collection was approved under a NSW Industry & Investment Permit Reference

298   number: P08/0039-3. The experimental set-up prevented physical contact between the

299   cuttlefish, removing the risk of injury or mortality as a result of physical fighting. These

300   semelparous subjects were used in several noninvasive experiments, and were housed for the

301   remainder of their life cycle until they died of senescence. This research conformed to the

302   *Guidelines for the Treatment of Animals in Behavioural Research and Teaching*

303   (ASAB/ABS, 2012) and was completed in compliance with the Australian Code of Practice

304   for the Care and Use of Animals for Scientific Purpose (NHMRC, 2004). All procedures were

305   approved under Macquarie University AEC Reference number: 2010/029 and Department of

306   Primary Industries ACEC Reference number: 12/04.

307   *<H2>Data analysis*

308   Statistical analyses were completed using SPSS 15.0.6 for Windows (IBM, Armonk, NY,

309   U.S.A.) and R for Mac (version 2.9.0, http://www.r-project.org). Pearson correlation

310   coefficients (see Appendix Table A1) revealed that mantle length, arm length and mass were

311   all significantly correlated; therefore we only used mantle length as a representative parameter

312   because of collinearity. The likelihood of winning a contest in relation to mantle length and

313   passing cloud intensity was subsequently analysed using a binomial generalized linear model

314   (GLM) to identify the key trait/s associated with RHP.

315   To test for habituation during the laboratory-staged contests we used a GLM. This

316   examined whether the order of the contest within a particular trial had any effect on

317   behavioural matching, rates of escalation and contest duration. To test whether contestants

318   matched behaviours during contests (i.e. testing E-WOA predictions) we used generalized

319   linear mixed models (GLMMs). Contest outcome was the predictor variable with male

320   subject as a random factor. Dependent variables were aggressive display frequencies,

321   aggressive display durations (square-root transformed), attempted physical aggression and

322   aggressive intensity. To test whether contestants differed in rates of escalation (i.e. testing

323   CAM predictions) we also used GLMMs. Contest outcome and contest duration were

324   interacting predictor variables with male subject as a random factor. Dependent variables

325   were initiating behaviour, the latency to attempted physical aggression and the number of

326   displays performed prior to attempted physical aggression. To test for effects of winner–loser

327   RHP, loser RHP and winner RHP on contest duration (i.e. testing SAM predictions), the

328   framework of Taylor and Elwood (2003) was applied to size-asymmetric contests ($N = 31$) in

329   which males ($N = 20$) differed by at least 20% mantle length. Male subject was used as a

330   random factor in both simple and multiple GLMMs (see Taylor & Elwood, 2003). For

331   winner–loser RHP, we were unable to set up asymmetric contests with intermediate

332   asymmetries (i.e. between 130 and 170 mm). For this reason, we treated RHP asymmetry as a

333   categorical variable (i.e. small corresponding to < 140 mm; large corresponding to > 140

334   mm), rather than a continuous variable. Contest durations were also analysed against absolute

335   RHP for size-symmetric contests ($N = 44$) in which males ($N = 22$) were broadly size-

336   matched (within 7% mantle length of each other).

337   To test for habituation during the motivational state experiments we used a GLM. This

338   examined whether the order of cuttlefish of a particular pair that acted as the focal male

339   (either on the first or second trial of pairing) had any effect on latency to resume a contest. To

340 test for effects of focal male size (i.e. a measure of RHP) and stimulus male size on the focal

341 male's latency to resume a contest we used a multiple GLM. Focal male size and stimulus

342 male size were predictor variables and latency to resume the contest was the dependent

343 variable. To test for behavioural differences in response to small and large live-male stimuli

344 we used binomial GLMMs. The size (i.e. small or large) of the live-male stimuli was the

345 predictor variable with focal male as a random factor. Dependent variables were escape

346 behaviour and attempted physical aggression.

347

348 # RESULTS

349 There was a mean contest duration of 1 min 46.0 s ± 30.7 s (range 13.3 s–18 min 22.0 s).

350 Contests were primarily mediated through noncontact visual displays (80%) but escalated to

351 attempted physical aggression at least once in 15 of the 75 contests (20%). The order of the

352 contest within a trial (i.e. 75 contests within 21 trials) had no effect on behavioural matching

353 (low-level aggression: $\chi^2_1 = 0.36$, $P = 0.55$; high-level aggression: $\chi^2_1 = 2.76$, $P = 0.10$;

354 highest-level aggression: $\chi^2_1 = 0.38$, $P = 0.54$). Similarly, the order of the contest within a

355 trial had no effect on rates of escalation (initiating behaviour: $\chi^2_1 = 0.92$, $P = 0.34$; latency to

356 attempted physical aggression: $\chi^2_1 = 0.81$, $P = 0.37$; number of behaviours prior to attempted

357 physical aggression: $\chi^2_1 = 0.72$, $P = 0.40$). The order of the contest within a trial (i.e. 75

358 contests within 21 trials) also had no effect on contest duration ($\chi^2_1 = 0.70$, $P = 0.80$). These

359 results suggest that there was no habituation within the trials; thus we analysed the 75 contests

360 as separate interactions within a repeated measures design.

361 ## RHP traits

362 Subjects varied in size (mean mantle length = 417.4 mm; range 295–509 mm; mean arm

363 length = 375.5 mm; range 164–505 mm; mean body weight = 6189 g; range 4015–9324 g).

364   Mantle length predicted contest outcome ($\chi^2_1 = 9.13$, $P < 0.01$; Fig. 2a), whereby larger

365   individuals (i.e. longer mantle length) were more likely to win a contest. In contrast, there was

366   no significant evidence to show that passing cloud intensity predicted contest outcome ($\chi^2_1 =$

367   2.83, $P = 0.09$; Fig. 2b).

368   *<H2>Behavioural matching*

369   Winners and losers performed comparable frontal displays in frequency and duration

370   throughout the contests (frontal frequency: $\chi^2_1 = 2.28$, $P = 0.13$; frontal duration: $\chi^2_1 = 1.23$, P

371    $= 0.27$). Winners performed significantly more shovel and lateral displays and for longer

372   durations than losers (shovel frequency: $\chi^2_1 = 4.30$, $P = 0.04$; shovel duration: $\chi^2_1 = 5.89$, $P =$

373   0.02; lateral frequency: $\chi^2_1 = 7.50$, $P < 0.01$; lateral duration: $\chi^2_1 = 8.37$, $P < 0.01$). Winners

374   attempted more physical aggression and the aggressive intensity was also higher for winners

375   than losers (physical aggression: $\chi^2_1 = 4.38$, $P = 0.04$; aggressive intensity: $\chi^2_1 = 10.20$, $P <$

376   0.01; Table 2).

377   *<H2>Rates of escalation*

378   Across the 75 contests, 15 involved attempted physical aggression. In these 15 contests, there

379   was no significant interaction between outcome (winner or loser) and contest duration and

380   choice of initiating behaviour ($\chi^2_1 = 0.93$, $P = 0.33$). There was also no significant interaction

381   between outcome (winner or loser) and contest duration and the latency to attempted physical

382   aggression ($\chi^2_1 = 0.90$, $P = 0.35$) or the number of behaviours prior to attempted physical

383   aggression ($\chi^2_1 = 1.46$, $P = 0.23$; Table 3).

384   *<H2>Contest duration and RHP*

385   Contest duration was analysed for winner–loser RHP, loser RHP and winner RHP using

386   simple and multiple GLMMs for size-asymmetric contests ($N = 31$). In simple GLMMs,

387   contest duration and RHP yielded negative effects of RHP asymmetry, positive effects of

388   loser RHP and insufficient evidence of the effects of winner RHP (RHP asymmetry: $\chi^2_1 =$

389   28.44, $P < 0.01$; loser RHP: $\chi^2_1 = 3.95$, $P < 0.05$; winner RHP: $\chi^2_1 = 3.39$, $P = 0.06$; Fig. 3).

390   When loser and winner RHP were considered as covariates in a multiple GLMM, contest

391   duration increased significantly with loser RHP ($\chi^2_1 = 20.87$, $P < 0.01$) and decreased

392   significantly to a similar extent (i.e. approximately opposite slopes) with winner RHP ($\chi^2_1 =$

393   19.61, $P < 0.01$). When RHP asymmetry and loser RHP were considered as covariates in a

394   multiple GLMM, contest duration decreased significantly with RHP asymmetry ($\chi^2_1 = 18.37$,

395    $P < 0.01$) but there was no significant association with loser RHP ($\chi^2_1 = 0.02$, $P = 0.89$).

396   To test whether contest duration is a function of absolute RHP asymmetry we

397   examined the size-symmetric contests in which males were broadly size-matched ($N = 44$).

398   Contest duration and absolute RHP were not correlated significantly (winner RHP: $\chi^2_1 = 0.00$,

399    $P = 0.99$; loser RHP: $\chi^2_1 = 0.04$, $P = 0.84$).

400   *<H2>Probing motivational state in response to a female stimulus*

401   We examined the latency to resume a contest following the introduction of a female as a

402   measure of fight motivation. The order in which a cuttlefish was used as the focal male,

403   during either the first or the second pairing, had no effect on the latency to resume a contest

404   ($\chi^2_1 = 0.01$, $P = 0.92$). This indicated that there was no habituation within pairings, which

405   enabled us to analyse both sets of data together (i.e. the first and second pairing of the trial

406   series) for each pairing. The latency to resume a contest was significantly influenced by the

407   size of the contestants, with latency negatively associated with the size of the focal male (χ^2_1

408    $= 3.91$, $P < 0.05$; Fig. 4a) and positively associated with the size of the stimulus male ($\chi^2_1 =$

409   20.30, $P < 0.01$; Fig. 4b).

410   *<H2>Decision making in response to aggressive rivals with variable RHP*

411   We examined decision-making abilities of focal males in response to aggressive live-male

412   stimuli with variable RHP. The proportion of focal males exhibiting escape behaviour

413   compared to those that did not was significantly different across stimulus types ($\chi^2_1 = 20.97$, P

414   < 0.01). Pairwise comparisons of escape behaviour revealed that significantly fewer focal

415   males exhibited escape behaviour in response to the small than to the large live-male stimulus

416   (LSD: $T = 2$, $N = 8$; small–large: $P < 0.01$).

417   The proportion of focal males that attempted physical aggression compared to those

418   that did not was significantly different across stimulus types ($\chi^2_1 = 20.99$, $P < 0.01$). Pairwise

419   comparisons of attempted physical aggression revealed that significantly more focal males

420   attempted physical aggression in response to the small than to the large live-male stimulus

421   (LSD: $T = 2$, $N = 8$; small–large: $P < 0.01$).

422

423   <H2>DISCUSSION

424   Our study provides experimental evidence for mutual assessment fighting strategies in male

425   giant Australian cuttlefish. We showed that body size (i.e. mantle length) was a key indicator

426   of RHP as it predicted contest outcome. Winners and losers did not match behaviours during

427   contests, ruling out the E-WOA model. There was no significant interaction between contest

428   outcome, contest duration and the rates of escalation, which violates the assumption of the

429   CAM. Persistence to continue a fight was based on RHP asymmetry, rather than loser and/or

430   winner RHP, indicating that the SAM is the most likely candidate model. Analysis of contests

431   between size-symmetric opponents provides further support for the SAM over the CAM.

432   Following the introduction of a female, the latency to resume the contest was negatively

433   related to the size of the focal male but positively related to the size of the stimulus male.

434   Males also showed significant behavioural differences in their responses to relatively larger

435   opponents compared to relatively smaller opponents. Our results suggest that male cuttlefish

436   are able to assess size-related information during contests. Crucially, they are able to modify

437   their behaviour as a function of the realized size of their opponent relative to their own,

438   indicating that they use mutual assessment to resolve male–male contests.

439   The strongest proximate effect on contest outcome between male cuttlefish was body

440   size. By contrast, our passing cloud results were inconclusive. Nevertheless, we only

441   investigated a single relationship, that is, the effects of passing cloud intensity on contest

442   outcome. Future studies may be able to identify alternative effects of passing cloud intensity

443   (i.e. effects on aggressive motivation or high-risk agonistic behaviours). Male cuttlefish

444   predominately mediated contests through aggressive visual displays without contact, with

445   only 20% of the contests escalating to attempted physical aggression. These results, as well as

446   the duration of the contests, are in accordance with cuttlefish contests in the field (Hall &

447   Hanlon, 2002). For many taxa, the outcome of animal contests is influenced by body size

448   (Haley, Deutsch, & Le Boeuf, 1994; Wells, 1988) because this attribute is generally

449   correlated with strength and the ability to inflict injury (Archer, 1988; Parker, 1974). For

450   example, in mantis shrimp, *Gonodactylaceus falcatus,* larger individuals have a physical

451   advantage over smaller individuals because both spring and strike force of the raptorial attack

452   are correlated positively with body size (Claverie, Chan, & Patek, 2011).

453   The structure of cuttlefish contests did not fulfil the key predictions of the self-

454   assessment models (E-WOA and CAM). The absence of behavioural matching during

455   agonistic contests suggests that contestants did not match energy expenditure as required by

456   the E-WOA model. Low-intensity behaviours were comparable between winner and loser

457   cuttlefish*,* but winners performed high-intensity behaviours at significantly higher frequencies

458   and for longer durations. Other contextual indications also make the E-WOA model an

459   unlikely model to apply to cuttlefish contests because a fundamental assumption of the E-

460   WOA is that contests do not involve physical contact or risk of serious injury. While injurious

461   or fatal attacks are uncommon in this species, rival males will on occasion push, grapple, roll

462   and even bite (Hall & Hanlon, 2002). It is thus possible that individuals may accrue costs as a

463   function of damage caused from physical aggression.

464   The patterns of escalation within cuttlefish contests also negate the key predictions of

465   the self-assessment models (E-WOA and CAM). Escalation is predicted for all three models

466   (E-WOA, CAM, and SAM); however, the patterns of escalation differ markedly between self-

467   and mutual assessment models. The SAM predicts that contests progress through escalating

468   phases wherein low-intensity behaviours precede high-intensity behaviours in a hierarchical

469   manner and no de-escalation occurs (Enquist & Leimar, 1983). In contrast, the E-WOA model

470   and the CAM predict that escalation can occur within phases and high-intensity behaviours

471   can occur throughout the contest (Mesterton-Gibbons, Marden, & Dugatkin, 1996). Our

472   results demonstrate that there was no significant interaction between contest outcome and

473   duration. This indicates that these factors do not affect the rates of escalation between fighting

474   male cuttlefish, suggesting that escalation within phases does not occur. Moreover, contextual

475   clues were more consistent with the escalation predictions of the SAM, as cuttlefish showed

476   distinct patterns of escalation typically beginning with low-intensity behaviours (i.e. frontal

477   display) and escalating to high-intensity behaviours (i.e. shovel and lateral display) at later

478   stages of a contest.

479   Our results demonstrate that RHP asymmetry between male cuttlefish was negatively

480   correlated with contest duration, a relationship previously used to imply mutual assessment

481   strategy. However, this relationship can be an incidental result of an underlying relationship

482   with the RHP of the loser and thus is not diagnostic (Taylor & Elwood, 2003). Nevertheless,

483   multiple regressions revealed that contest duration was correlated with RHP asymmetry,

484   rather than winner or loser RHP, which demonstrates mutual assessment rather than an

485 incidental result. Owing to logistical issues we were unable to analyse this relationship for

486 intermediate asymmetries (i.e. between 130 and 170 mm); this could potentially limit the

487 scope of our interpretation of the model. However, the duration of cuttlefish contests between

488 size-symmetric males was not correlated with the absolute size of the contestants, providing

489 further support for the SAM (i.e. mutual assessment; see Arnott & Elwood, 2009b; Taylor &

490 Elwood, 2003).

491 　　　　Our study indicates that fight motivation was influenced by the body size (i.e. a

492 measure of RHP) of both contestants. The latency to resume a contest, following the

493 introduction of a female, was negatively associated with the size of the focal male and

494 positively associated with the size of the stimulus male. This is consistent with the prediction

495 for mutual assessment (see Arnott & Elwood, 2009a; Elwood et al., 1998). Our results

496 highlight that cuttlefish can assess RHP through visual cues alone, because our experimental

497 set-up denied contestants the opportunity to assess tactile or chemical cues. These results are

498 not surprising considering that cuttlefish predominately communicate through visual cues and

499 signals when interacting with conspecifics (Hanlon & Messenger, 1996). A possible

500 limitation to note is that there are currently no data on the effects of presenting a female to a

501 male cuttlefish engaged in a contest. Further field observations and experimental research are

502 needed to determine how a male's agonistic behaviour is influenced by the presence of a

503 female. However, given that the focal males in our experiments consistently resumed the

504 contests, a female appears to be a satisfactory stimulus for assessing the motivation to fight in

505 this species.

506 　　　　We provided further evidence of mutual assessment by testing decision making

507 abilities in the context of aggression. Our test findings indicate that when an opponent was

508 larger, males attempted less physical aggression and more escape behaviour. By contrast,

509 when an opponent was smaller, males attempted more physical aggression and less escape

510   behaviour. Accordingly, it appears that male cuttlefish perceive size related information

511   during agonistic contests, and are able to adjust their behaviour as a function of the realized

512   size of their opponent. This modification of behaviour as a result of information gathered

513   from opponent cues provides compelling evidence for a mutual assessment fighting strategy

514   in this species.

515   The notion that mutual assessment is more cognitively demanding than self-

516   assessment is still highly controversial (see Elwood & Arnott, 2013; Fawcett & Mowles,

517   2013). We agree with Elwood and Arnott (2012) that the prevalent assumption that mutual

518   assessment involves the independent assessment of two fighting abilities (i.e. own RHP and

519   opponent RHP), followed by an explicit comparison between the two requires complex

520   cognitive processing (also see le Roux & Bergman, 2012). An explicit comparison of RHP is

521   probably beyond the cognitive capacity of many animal species, particularly in conflict

522   situations that require rapid judgements, in which most animals, except for the cognitively

523   advanced species, are likely to use cognitively simple decision making (Robinson, Franks,

524   Ellis, Okuda, & Marshall, 2011). In general, cognitive abilities of cephalopods are only

525   recently being assessed and compared with those of other phyla (Darmaillacq, Dickel, &

526   Mather, 2014). Recent experiments on the European cuttlefish, *Sepia officinalis,* have

527   provided insight into the high cognitive abilities of these large-brained invertebrates.

528   Cuttlefish have been shown to recollect specific past events, providing behavioural evidence

529   of episodic-like memory (Jozet-Alves, Bertin, & Clayton, 2013). This ability had only been

530   demonstrated in cognitively advanced vertebrates such as humans (Suddendorf & Corballis,

531   1997), other mammals (Babb & Crystal, 2005; Martin-Ordas, Haun, Colmenares, & Call,

532   2010; Menzel, 1999) and some birds (Clayton & Dickinson, 1998; Clayton, Bussey, &

533   Dickinson, 2003; Zinkivskay, Nazir, & Smulders, 2009). The cognitive capacity of cuttlefish

534   has also been highlighted through their ability to use facultative mimicry as part of a

535   conditional mating strategy (Gross, 1996). In the wild, small, unpaired males may obtain

536   matings through nonaggressive surreptitious or deceptive tactics and therefore avoid

537   aggressive encounters with large paired males (Hanlon et al., 2005). However, if a small,

538   unpaired male encounters a lone female, he will pair with her and perform aggressive displays

539   to repel other small, unpaired male competitors. Intriguingly, if a large competitor challenges

540   the small male, the small male will swiftly shift to surreptitious or deceptive tactics and not

541   engage in aggressive displays (van Staaden, Searcy, Hanlon, 2011). This remarkable ability to

542   shift from aggressive and defensive behaviour to surreptitious and deceptive tactics in

543   response to different social contexts suggests that cuttlefish might use comparative decision

544   making rather than a more simple integration of causal factors (see Elwood & Arnott, 2012).

545   In conclusion, previous studies investigating assessment strategies during animal

546   contests have typically involved staged fights that measure contest costs (i.e. contest duration)

547   (e.g. Kemp et al., 2006; Leiser, Gagliardi, & Itzkowitz, 2004; Prenter, Taylor, & Elwood,

548   2008; Stuart-Fox, 2006). Other studies have used alternative approaches by using

549   motivational probes (i.e. startle stimuli) during staged contests to measure fight motivation

550   (Arnott & Elwood, 2010; Briffa & Elwood, 2001; Elwood et al., 1998). More recently, some

551   studies have tested the decision making abilities (i.e. assessing relative values) of contestants

552   during an aggressive interaction (Taylor et al., 2010; Tibbetts et al., 2010). We used a

553   combination of these approaches to measure contest costs, fight motivation and decision

554   making. We demonstrated that male cuttlefish assess the RHP of their opponent relative to

555   their own (i.e. SAM), providing a definitive example of mutual assessment. This study

556   illustrates an integrative approach that can be used to test for visual RHP assessment across a

557   wide range of visually oriented animals.

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722   APPENDIX

723   *Male attributes and correlations*

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725   *Aggressive behaviours*

726   Aggressive behaviours were ranked into different levels of intensity using a combination of

727   field and laboratory data. In the field, behavioural data were collected via scuba at the

728   spawning grounds in Whyalla, South Australia (32°59′5 S; 137°43′1 E) between May and

729   July (2008–2009, 2011). Focal sampling (Martin & Bateson, 1993) was conducted using a

730   video camera (Sony VX100) to follow and record competing males. In the laboratory, staged

731   contests were carried out in June and July 2011. Twelve males that varied in size (mean

732   mantle length = 423.7 mm; range 302–499 mm; mean body weight = 6652 g; range 4396–

733   8995 g) were used. Subjects were randomly assigned to an opponent (e.g. range within 10–

734   18% of mantle length of each other) and placed into a contest arena (circular 5000-litre tank)

735   for 30 min. Contests were recorded (MTS format 1920 × 1080 lines) using a high-definition

736   video camera (SONY HDR-SR11E) fitted with a wide-angle lens (Raynox HD-5050PRO 0.5

737   x).

738   To generate an aggression rank for agonistic behaviours, we scored the video trials (i.e. field

739   and laboratory) using JWatcher Video 1.0 (Blumstein et al., 2006), which reads the time code

740   of the MOV video file to allow frame-by-frame resolution (24 frames/s, 40 ms PAL video

741   standard). We recorded the frequency of three distinct agonistic displays commonly

742   performed during contests (frontal, lateral and shovel; Fig. 1) and documented the context in

743   which these displays were expressed. The displays were exhibited in three contexts: (1)

744   approaching a male conspecific, (2) visual agonistic behaviour and (3) escalation (i.e.

745   transition from visual signalling to physical contact). These three contexts are associated with

746 increasing levels of costs. Males engaged in visual agonistic displays might incur costs

747 through energy expenditure or increased conspicuousness to predators. Males engaged in

748 escalated agonistic interactions might incur increased costs through injurious or fatal attacks

749 (see Hall & Hanlon, 2002). To test the relationship between the agonistic displays and

750 context, we used a Fisher's exact test, which calculates deviance from the null hypothesis that

751 the two categorical variables have no correlation with each other (Fisher, 1922)

752 The results showed that males predominately exhibited the frontal display when approaching

753 male conspecifics (Table A2). Males predominately exhibited the lateral display during a

754 visual agonistic interaction (Table A2). Moreover, males were most likely to express the

755 lateral or the shovel display during an escalated agonistic interaction (Table A2). When

756 comparing these observed frequencies in response to differing agonistic contexts, we found

757 that the display types were significantly correlated with specific contexts (field: $N = 225$;

758 Fisher's exact test: two-tailed $P < 0.001$; laboratory: $N = 12$; Fisher's exact test: two-tailed P

759 < 0.01). This suggests that the agonistic displays are associated with different likelihoods of

760 incurred fighting costs.

761

762   Figure legends

763   Figure 1. Underwater images of male giant Australian cuttlefish performing distinct agonistic

764   displays: (a) frontal display comprising forward orientation, mantle down and not visible to

765   the rival, dark face and white arms, (b) lateral display comprising lateral orientation of mantle

766   and arms, face and arms are typically dark and passing cloud flows repeatedly over the

767   mantle, and (c) shovel display comprising frontal orientation with the mantle raised and

768   visible to the rival, the arms are extended and rigid in a shovel-like shape.

769

770   Figure 2. Potential male traits associated with RHP. Proportion of winning males against

771   measures of (a) mantle length and (b) passing cloud intensity, $N = 20$ male giant Australian

772   cuttlefish. Significant determinants of RHP determined by a GLM likelihood ratio test

773   statistic. The grey area in each graph represents 95% confidence intervals.

774

775   Figure 3. Contest duration and RHP. Relationships between contest duration and (a) RHP

776   asymmetry, (b) loser RHP and (c) winner RHP, $N = 20$ male giant Australian cuttlefish, *Sepia*

777   *apama.* The relationship for RHP asymmetry was modelled as categorical variable (circles

778   correspond to mantle length < 140 mm; squares correspond to mantle length > 140 mm). Box

779   plots represent the median and range of each respective category, consistent with the

780   categorical model that was fitted. The boxes represent the first and third quartiles, the line

781   intersecting the boxes represents the median and the whiskers represent the range. The

782   relationships for loser RHP and winner RHP are indicated by a regression line (95%

783   confidence interval).

784

785 Figure 4. Latency to resume a contest following the introduction of a female. Linear

786 relationships between latency to resume a contest and (a) focal male size and (b) stimulus

787 male size, $N = 12$ male giant Australian cuttlefish, *Sepia apama.* The linear relationships are

788 determined by GLM likelihood ratio test statistics. The dotted lines represent 95% confidence

789 intervals.

790

791   Table 1. Summary of contest dynamics predicted by game theory models (E-WOA, CAM,

792   SAM) of contest resolution

Predictions	Energetic war of attrition (E-WOA)	Cumulative assessment (CAM)	Sequential assessment (SAM)
Behavioural matching	Matched in type, frequency & intensity	Unmatched in type, frequency & intensity	Unmatched in type, frequency & intensity
Rates of escalation	Escalation within phases	Escalation within phases	No escalation within phases
Contest duration correlation	(+) loser RHP and (/) winner RHP	(+) loser RHP (+) and (-) winner RHP	RHP asymmetry
Latency to resume a contest correlation	(-) focal male RHP and (/) opponent RHP	(-) focal male RHP and (/) opponent RHP	(-) focal male RHP and (+) opponent RHP
Decision making based on	Own RHP	Own RHP	Relative RHP

793   Five-step process to discriminate between game theory models: (1) test for behavioural matching; (2)

794   test for escalation within phases; (3) test relationship between contest duration and RHP

795   measurements; (4) test relationship between latency to resume a contest and RHP measurements; (5)

796   test decision-making abilities in the context of aggression. (+) = positive correlation; (-) = negative

797   correlation; (/) = no correlation.

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799

800   Table 2. Behavioural matching during agonistic contests

Behaviours	Aggressive intensity	Winners	Losers
Frontal display	1: low-level aggression	0.99 ± 0.06	0.75 ± 0.07
		46.82 ± 6.54	43.98 ± 8.04
Shovel display	2: high-level aggression	**0.17 ± 0.05***	**0.03 ± 0.02***
		5.85 ± 2.11*	**0.82 ± 0.66***
Lateral display	2: high-level aggression	**0.42 ± 0.07****	**0.14 ± 0.04****
		16.22 ± 3.45***	**5.84 ± 2.32*****
Physical aggression	3: highest-level aggression	**0.35 ± 0.14****	**0.04 ± 0.02****
Aggressive intensity		**1.67 ± 0.09*****	**1.04 ± 0.08*****

801   The table shows the mean ± SE frequency (on the top) and duration (s, underneath) of different behaviours

802   performed by winners and losers per staged contest ($N = 20$). Probabilities of behavioural matching were

803   determined using generalized linear mixed models (GLMM). Statistically significant values are in bold.

804   * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

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809   Table 3. Contests ($N = 15$) involving attempted physical aggression

Initiating behaviour: percentage within $N = 15$ contests		Latency to physical aggression Mean ± SE	Number of displays prior to physical aggression Mean ± SE
Frontal display	80		
Shovel display	7	45.73 ± 11.08	2.03 ± 0.12
Lateral display	13		

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829   Table A1. Measurements and correlations of male giant Australian cuttlefish attributes

	Mantle length	Arm length	Mass	Passing cloud intensity
Mean	415.08 ± 13.76	375.52 ± 19.38	6,278.17 ± 131.00	54.52 ± 4.18
Range	285 – 510	164 – 505	2,237.40 – 10,643.20	29.22 – 91.03
Pearson correlation coefficient (*r*)				
Mantle length	-	**0.95**	**0.94**	0.32
Arm length	**0.95**	-	**0.89**	0.22
Mass	**0.94**	**0.89**	-	0.20
PC intensity (%)	0.32	0.22	0.20	-

830   Values are calculated for laboratory-staged contests ($N = 22$). Mean mantle length and arm length are given
831   in (mm) ± SE, mean mass (g) ± SE. Passing cloud (PC) intensity is calculated as contrast differences
832   between light and dark bands. Pearson correlation coefficients (*r*) are presented and all values that are
833   significantly correlated at $P < 0.05$ after FDR adjustments for multiple tests are in bold.

834

835   Table A2. Giant Australian cuttlefish displays and agonistic context

Context	Frontal display (%)	Lateral display (%)	Shovel display (%)
Approach	69	14	17
	75	8	17
Agonistic	10	71	19
	17	58	25
Escalation	2	58	40
	8	59	33

836   The table shows the percentage of male cuttlefish exhibiting three main displays during different agonistic
837   contexts. Field percentages are presented on the top ($N = 75$ individual subjects per context) and laboratory
838   percentages underneath ($N = 12$). Significant associations between the two categorical variables (i.e.
839   display type and context) were analysed using a Fisher's exact test.

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