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2 **Huffard, C.L.**, R.L. Caldwell & F. Boneka (2010) Male-male and male-female aggression may
3 influence mating associations in wild octopuses (*Abdopus aculeatus*). Journal of Comparative
4 Psychology 124(1): 38–46

5

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11 Male-male and male-female aggression may influence mating associations in wild octopuses

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(*Abdopus aculeatus*)

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Christine L. Huffard^{1*}, Roy L. Caldwell², Farnis Boneka³

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¹ Conservation International Indonesia, Denpasar, Bali, Indonesia

17

² Department of Integrative Biology, University of California, Berkeley, CA 94720–3140, USA

18

³ Department of Fisheries and Marine Science, Universitas Sam Ratulangi, Manado, North

19

Sulawesi, Indonesia

20

* To whom correspondence should be addressed. E-mail: wunderpix@gmail.com

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Received December 31, 2008

22

Revision received June 26, 2009

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Accepted July 6, 2009

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ABSTRACT

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Abdopus aculeatus engages in frequent aggression and copulation, exhibits mate-choice, and employs multiple mating tactics. Here we draw upon established hypotheses to compare male-male aggression (MMA) and male-female aggression (MFA) as they relate to their mating behavior in the wild. When contesting for females, males appear to balance mate preference (resource value) with perceived chances of winning contests (resource holding potential). Although males spent more time mating with and contesting for large ‘Adjacent Guarded’ females (those occupying a den within arm’s reach of a large ‘Adjacent Guarding’ male), they exhibited higher rates of aggression over non-adjacent ‘Temporarily Guarded’ females that may be more accessible. The major determinant of male-male aggressive success was size, and this factor may dictate the expression of conditional mating tactics in males. ‘Adjacent Guarding’ males were the largest and most aggressively successful males, earning the most time copulating with females. They are considered to have the highest resource holding potential (RHP) in MMA. By contrast, in MFA, some larger individuals fled from smaller individuals, indicating that RHP appears to be a function of both size and sex in inter-sexual aggression. This result suggests variation in aggressiveness, or potential for severe injury—even sexual cannibalism during MFA. Male-female aggression may also be influenced by the sexual non-receptivity of some individuals, or attempts by both sexes to increase foraging behavior by delaying mate-guarding activity.

KEYWORDS: pair formation, conditional mating tactic, mate competition, inter-sexual aggression, intra-sexual aggression

INTRODUCTION

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53 Several behavioral patterns appear to underlie aggression in a broad sampling of animal
54 groups. Agonistic acts (offensive and defensive acts related to aggression) can be influenced by
55 the inherent aggressiveness of competitors, the relative chances of individuals obtaining or
56 retaining a given resource [resource holding potential (RHP)], and the relative value of a resource
57 to these competitors [resource value (RV)] (Hurd, 2006). Contests in which individuals are
58 closely matched in fighting ability may be more likely to persist or escalate (Huntingford &
59 Turner, 1987). By contrast, individuals that are extremely disparate in competitive ability are less
60 likely to fight because it is clear which individual is stronger (Hurd, 2006). Not surprisingly,
61 animals also fight more intensely for high-value resources (Hurd, 2006).

62 Resources that increase fitness can provoke high levels of aggression (Parker, 1974),
63 making this behavior an important component of sexual selection (Huntingford & Turner, 1987).
64 Both intra- and inter-sexual aggression have long been recognized to govern mating associations,
65 even over-riding mate choice in some cases (Caldwell, 1992; Barlow & Lee, 2005).
66 Competitively superior (typically larger) individuals often achieve greater access to mates, while
67 subordinates either settle for lower quality mates or sometimes go without. Among many animal
68 groups, winners of agonistic encounters reap the copulatory benefits that might eventually lead to
69 reproductive success (Grossman, 1980; but see Warner *et al.*, 1995).

70 Although octopuses are strong ecological competitors within fish and invertebrate
71 communities (Ambrose, 1986; Berger & Butler, 2001), intra-specific aggression in these animals
72 is rarely observed. Contests are believed to be uncommon in octopuses because intra-specific
73 encounters are thought to be infrequent (Hanlon & Messenger, 1996). However some octopuses
74 are known to fight for food (Voight, 2005), dens (Hanlon & Wolterding, 1989; Cigliano, 1993),
75 and mates (Huffard *et al.*, 2008). Larger size determines access to preferred dens in laboratory
76 experiments (Hanlon & Wolterding, 1989; Cigliano, 1993) and mates in the wild (Huffard *et al.*

77 2008). To our knowledge, other functions of aggression in octopuses remain unknown. This may
78 be in part because researchers lacked a model system in which agonistic behavior could be
79 observed reliably, particularly in the wild.

80 *Abdopus aculeatus* is a small, diurnal octopus that exhibits frequent copulation, male-
81 male aggression (MMA), and male-female aggression (MFA). Individuals are easily observed in
82 their natural habitat (Huffard, 2007), providing an ideal system for studying behavioral
83 interactions in wild octopuses. Male-male aggression during mate-guarding reduces extra-pair
84 copulations by limiting access by intruding males to guarded females (Huffard *et al.*, 2008). The
85 reasons for MFA are less clear, but also may be related to mating behavior. Both sexes exhibit
86 multiple reproductive tactics [(Adjacent Guarding (G_A), Temporarily Guarding (G_T), and
87 Transient (T), definitions and abbreviations provided in Table 1)] that can be associated with size
88 thresholds and possibly fighting ability.

89 Here we draw upon established behavioral hypotheses on the functions of agonistic
90 behavior to compare male-male and male-female aggression as they relate to mating behavior in
91 wild *A. aculeatus*. As in other animal groups, RV and RHP are predicted to influence rates of
92 aggression in these octopuses. Large ♀ G_A are clearly preferred by males as repetitive mates
93 (Huffard, *et al.* 2008), perhaps because large female octopuses have higher fecundity than smaller
94 females (Leporati *et al.*, 2008). Thus we predict that males invest more in MMA (via prolonged
95 contests or with higher interaction rates) over high value (large) females. By contrast females
96 mate with multiple males, but do not appear to differentially reject copulation attempts based on
97 male size or mating tactic (Huffard *et al.*, 2008). We do not know if males or females exert
98 precopulatory mate choice early in their encounters with octopuses of the opposite sex.
99 Individual *A. aculeatus* may initiate intersexual aggression (MFA) to preclude mating attempts or
100 solicitations by low-value potential mates. If this is the case then we predict octopuses to be
101 aggressive with individuals of the opposite sex of certain sizes or mating tactics, and that

102 copulatory activity between interacting males and females will be inversely proportional to their
103 levels of MFA.

104 We also predict RHP to impact MMA and MFA in *A. aculeatus*. We predict that size
105 determines success during both MMA and MFA as in many other animal groups (Kravitz &
106 Huber, 2003), and that this factor can be considered a proxy for RHP. If this is the case, then we
107 would expect to observe the most intense agonistic interactions between individuals equally
108 matched in size (Enquist & Leimar 1983; Hurd, 2006). Contests between males nearing the size
109 threshold for the Adjacent Guarding tactic may also escalate. Males of this size would be near
110 equally-matched in RHP, yet stand to gain a significant increase in copulatory activity by winning
111 contests and potentially pairing with a large female (Huffard *et al.*, 2008). Finally, we consider
112 the possibility that males use aggressive interactions to assess their strength relative to others, and
113 subsequently employ conditional mating tactics.

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115

MATERIALS AND METHODS

116 A focal animal study on 167 *Abdopus aculeatus* was conducted in North Sulawesi,
117 Indonesia (1° 35.94' N, 124 ° 46.89' E) and Southeast Sulawesi (5° 27.72' S, 123.68' E) in 2001
118 and 2002. Most observations were made by a single observer (CLH), except during March-April
119 2001 when a second, trained observer (H. Spalding) participated. Focal octopuses were followed
120 on snorkel from a distance of 3 – 5 m, and did not appear to react to observers that maintained at
121 this distance. During 388 hours of observation on active animals, agonistic interactions were
122 timed to the second, and written behavioral codes were recorded on underwater paper, in real
123 time. Individual octopuses were identified by sex, size [mantle length (ML)] and arm injuries
124 when possible. When necessary to confirm visual estimates of mantle length, octopuses were
125 caught with a dip net and handled briefly *in situ* with cloth gloves.

126 The agonistic behaviors we scored as interactions are defined briefly in Huffard (2007) and
127 Supplementary Table 1, and examples are illustrated in Figure 1. They consist of Arm pulling,

128 Grappling (Supplementary movie 1), Approach, Evict, Arms coiled and raised, Flamboyant
129 display, Grab, Ink, Pull from den, Retreat, Stand tall, Touch, and Whip. After each agonistic
130 contest (series of interactions), individuals were assessed as either the winner (maintained
131 presence in area/near female) or the loser (retreated from area/female). A contest between a
132 guarding male and a challenger could involve multiple interactions. We did not speculate which
133 individual initiated interactions. Relative sizes were calculated as the size of the female divided
134 by the size of the male for MFA, or the size of the winner divided by the size of the loser for
135 MMA. Mating activity was also recorded.

136 We performed full-day focal animal observations of 15 Guarding sets [9 Adjacent
137 Guarding (G_A) sets, 6 Temporarily Guarding (G_T) sets], 10 Transient females (♀T), and 8
138 Transient males (♂T). Each was followed between approximately 0530 h – 1830 h for either one
139 full day, or two days in the case of individuals in guarding situations. For these observations we
140 report the total number of interactions (interaction totals) recorded that day and contest durations.
141 We also made additional opportunistic observations ranging from one to several hours. When
142 combined with full-day observations these records allowed us to analyze a larger sampling of size
143 distributions and mating tactics for comparison of MMA. Many hours of observation passed
144 without aggression, and each animal spent different periods of time inactive, sitting at the den,
145 and foraging away from the den. Because these activities impacted our ability to standardize
146 rates of aggression over long periods of unequal opportunistic observation time, and because most
147 contests appeared to conclude in less than an hour, we calculated the number of agonistic
148 interactions that took place per one-hour periods during which aggression was observed. These
149 values are referred to as interaction rates. Aggression between five dyads of octopuses took
150 place over more than one hour. For those dyads we summarized average rates of aggression per
151 hour.

152 Data analyses were performed using StatXact 4.0.1. The Binomial Test was performed
153 by the methods outlined by Seigel and Castellan (1988) to determine whether larger individuals

154 won most contests. Contests of MMA did not involve females. Thus these MMA and MFA data
155 sets were analysed separately. Some males however were represented in both data sets. StatXact
156 was used to estimate significance using the non-parametric Kruskal Wallis [T(X)], Spearman's
157 Rank (ρ), Friedman test for related samples (FR_X), and Mann-Whitney (U) tests.

158

159

RESULTS

160 General Observations:

161 *MMA*

162 Throughout all of our observations, we recorded agonistic contests between 29 male-male
163 dyads fighting over 17 females. All but three of those contests involved a mate-guarding male
164 defending a female. Of the full-day focal males that encountered a female (8 ♂_{GA}, 5 ♂_{GT}, 3
165 ♂_T), ten engaged in MMA (n = 5 ♂_{GA}, n = 4 ♂_{GT}, 1 ♂_T). All but one of these ten males (1 ♂_{GT})
166 also mated with the defended female at some point that day. Six guarding males engaged in
167 MMA with more than one male. Although our methods were not likely to detect interactions
168 between small males and multiple males, we recorded one example of a loser male subsequently
169 winning in MMA, with an even smaller male. This smaller male lost to two larger males during
170 our observations.

171 Of full-day focal males that encountered a female, males using all three mating tactics
172 (♂_T, ♂_{GT}, and ♂_{GA}) were equally likely to engage in aggression; they faced an equivalent
173 numbers of challengers and spent an equivalent amount of their day engaged in MMA [T(x) =
174 1.06, p = 0.59, min = 0, max = 3, median = 1, average = 1 ± 0.22 S.E challengers/day, n = 16;
175 T(x) = 0.37, p = 0.83; median = 1, average = 93 ± 53 S.E. minutes/day, n = 16]. However, low
176 power due to small sample size may have hampered our ability to detect any differences in these
177 values. Those full-day focal males that engaged in MMA interacted with more than one other
178 male on average (median = 1, average = 1.5 ± 0.21 challengers/day, n = 11).

179

180 *MFA*

181 During our full-day observations 22 focal animals encountered an individual of the
182 opposite sex (9 G_A , 5 G_T , and 8 T). We recorded twelve MFA contests during these encounters (2
183 G_A sets, 3 G_T sets, and 7 T sets). Thus 7 G_A sets, 2 G_T sets, and 1 T set did not engage in MFA
184 despite the opportunity. Four females (1 ♀T, 3 ♀ G_A) encountered and mated with more than one
185 male on the day of observation. In these cases we consider total time spent mating for those
186 females on that day. Of these females that encountered more than one individual, only one (a
187 large 65 mm ML ♀ G_A) engaged in MFA. This female won contests with all three males she
188 encountered (1 ♂ G_A , 50 mm ML, 2 ♂T, 50 mm ML and approximately 35 mm ML). We treat
189 the total number of interactions, average contest duration, and average male size for this female in
190 our analyses. An additional 4 females and 7 males did not interact with an individual of the
191 opposite sex. We could not determine whether these individuals neared other octopuses but did
192 not to interact, or simply did not come across other *Abdopus*. Their zero values were not included
193 in our analyses.

194

195 *Comparison of MMA and MFA:*

196 Thirty-four percent of MMA and 29% of MFA did not involve physical contact.
197 Grappling was more common in MMA than MFA (Wilcoxon Mann-Whitney statistic = 145.0, p
198 = 0.05; Supplementary Table 1), while inking was more common during MFA (Supplementary
199 Table 1). Inking was considered physical contact because released cephalopod ink may be a
200 chemical irritant (Russo, 2003). Contest duration was extremely variable and did not differ
201 significantly between MMA and MFA (Wilcoxon Signed Rank p = 0.07; MMA: median = 1 min;
202 average contest duration = 67 ± 37 S.E. min, n = 11, total time per day spent engaging in MMA
203 contests: median = 2 min, average = 135 minutes \pm 75 min S.E., n = 11; MFA: median = 2 min;
204 average 80 ± 58 min S.E., n = 12). MMA contests involved higher interaction totals than did
205 MFA (Wilcoxon Signed Rank p = 0.05; MMA: median = 3, average = 7 ± 2.1 S.E.

206 interactions/day, $n = 11$; MFA: median = 2, average = 2.6 ± 0.6 S.E. interactions/day, $n = 12$).
207 Contest duration was positively correlated with the total number of interactions (MMA and MFA
208 combined: $\rho = 0.70$, $p > 0.001$).

209 Guarding males (σ^1G_A and σ^1G_T combined) engaged in both MMA and MFA throughout
210 the day, and thus, overall, exhibited higher daily rates of aggression than did guarded females,
211 which experienced MFA only, and no intra-sexual aggression (Wilcoxon Signed Rank $p = 0.01$).

212 We recorded male-female dyads that interacted without overt aggression, engaging non-
213 agonistic mating display and copulatory behaviors. We recorded no intra-sexual aggression
214 between females. Females were rarely observed in the vicinity of one another. By contrast, to our
215 knowledge all male-male interactions involved aggression of some sort. Other possible
216 interactions included male-male copulation attempts, which were rare and always lead to intense
217 grappling, and displays, which were also given in the context of aggression.

218 With only two exceptions in all of our observations, σ^1T and φT were aggressive with
219 every octopus they encountered. Whether through MMA or MFA, σ^1T and φT that encountered
220 another octopus engaged in equivalent daily rates of aggression (combined MMA and MFA; $U =$
221 7.5 , $p = 0.1$; $n = 5$ σ^1T and 5 φT).

222

223 Resource Holding Potential: MMA and MFA

224 Larger octopuses were more likely than smaller octopuses to be the overall winner of
225 contests in MMA (MMA: 26 of 28 combinations for which sizes were visibly unequal, Binomial
226 test, $p < 0.003$). This pattern was less clear in MFA (8 of 12 combinations for which relative
227 sizes were unequal, Binomial test, $p = 0.194$). Among MMA and MFA only six smaller
228 individuals were winners of any interaction. All but one of these cases involved individuals at
229 least 90% the size of their larger opponent. In all but four cases, females were larger than males
230 and the winner of MFA contests. The smaller winners of MFA were two small females (32, 40
231 mm ML) that rejected the mating attempts of slightly larger (35, 45 mm ML respectively) males,

232 a small male (30 mm ML) that evicted a slightly larger female (33 mm ML) from her den, and a
233 53 mm ML male that chased a 60 mm ML female displaying a male-typical color pattern.

234

235 Interaction rates of MMA were not correlated with the relative size differential of males
236 ($\rho = -0.27$, $p = 0.09$, $n = 26$ dyads for which both male sizes were known). Interaction totals for
237 MFA were negatively correlated with relative size differential; those contests between male and
238 female octopuses more disparate in size involved lower interaction totals than those between
239 octopuses more closely matched ($\rho = -0.57$, $p = 0.03$, $n = 12$). Yet many males and females
240 closely matched in size did not engage in MFA, so this relationship does not predict whether
241 octopuses will engage in inter-sexual aggression in the first place (all male-female sets: $\rho = -0.24$,
242 $p = 0.14$, $n = 22$).

243 Males 45 mm ML and larger consistently won more than 45% of MMA interactions,
244 while males 50–60 mm ML generally won more than 80%. By contrast, males smaller than 40
245 mm ML won no contests (Figure 2). Larger winning males faced significantly more challengers
246 per day ($\rho = 0.44$, $p = 0.04$) and spent more total time per day engaging in aggressive contests
247 than did smaller winning males ($\rho = 0.49$, $p = 0.03$, $n = 16$). Larger winning males also defended
248 larger females than did smaller winning males ($\rho = 0.52$, $p = 0.02$, $n = 16$). The average
249 interaction rates of losing males peaked at 40–49 mm ML. Loser interaction rates fell quickly at
250 sizes larger than this peak.

251

252 Resource value and mate choice: MMA and MFA

253 Interaction rates differed significantly between aggressive male-male dyads. Overall,
254 interaction totals of MMA were higher between males defending a ♀G_T rather than ♀G_A ($U =$
255 41.0 , $p = 0.05$, $n = 6$ ♀G_A, $n = 9$ ♀G_T; Figure 3). In only one case did males fight over a ♀T, and
256 that occurred during copulation. Average contest duration was positively correlated with
257 defended female size ($\rho = 0.46$, $p = 0.08$, $n = 17$). All contests lasting more than three minutes

258 were in defense of large females ≥ 65 mm ML ($n = 1 \text{ ♀G}_T, 3 \text{ ♀G}_A$). The mode of the contests in
259 defense of smaller females ($n = 1 \text{ ♀T}, 3 \text{ ♀G}_T, 3 \text{ ♀G}_A$) was 1 minute. By contrast, the size of
260 females did not correlate with the average interaction rates in their defense ($\rho = .117, p = .33, n =$
261 17). We did not detect any relationship between interaction totals and copulation rates with the
262 female defended during MMA ($\rho = -0.02, p = 0.47; n = 5 \text{ ♂G}_A, 4 \text{ ♂G}_T$).

263 MFA contests between males and females that encountered an individual of the opposite
264 sex differed according to contestant size and mating tactics but not mating activity. Dyads
265 involving a ♀T had more aggressive interactions than did those with Guarded females [♀T vs.
266 ♀G_A and ♀G_T combined; $U = 85.0; p = 0.02$; Figure 4]. Among these octopuses, the number of
267 MFA interactions in which they engaged was inversely correlated with both female size ($\rho = -$
268 $0.488, p = 0.01$) and male size ($\rho = -0.479, p = 0.01$). Males involved in MFA did not differ in
269 absolute or relative size from males with which females in this study mated ($FR_X = 0.42, p = 0.8;$
270 $n = 29$ size of mating males vs. $n = 12$ males in MFA for which sizes were known; $FR_X = 1.3, p =$
271 $0.2; n = 43$ relative size male-female mating dyads). Mating and MFA behaviors were neither
272 mutually exclusive nor obligatory behaviors by male-female sets. The average size of all mating
273 females did not differ significantly from the average size of all females recorded engaging in
274 MFA ($FR_X = 1.6, p = 0.2; n = 28$ mating females for which sizes were known, $n = 12$ females
275 engaging in MFA). The total copulation duration between each male-female set was not
276 correlated with the number of MFA interactions they performed ($\rho = -.24, p = 0.14$). One
277 agonistic interaction was observed between a female and a sneaker male. The sneaker male
278 retreated while showing dorsal arms raised and curled at tips ('DACT').

279

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DISCUSSION

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282 Male *Abdopus aculeatus* appear to balance mate preference (i.e., RV) with perceived
283 chances of obtaining females (i.e., RHP) when engaging in aggressive mate-competition in the

284 wild. Contest duration correlated positively with the size of the female being defended in MMA,
285 suggesting an element of male mate choice in this behavior. However, to our surprise, female
286 mating tactic was also an important factor. Although males spent more time copulating with and
287 defending large, high-value ♀G_A (Huffard *et al.*, 2008), they competed more intensely with
288 higher interaction rates for ♀G_T of equivalent or slightly smaller size. Large ♀G_T are not guarded
289 consistently by any single male. These females may represent a preferred and *attainable* resource
290 worth fighting for. By contrast, ♀G_A are clearly paired with a large ♂G_A, a tactic which, in our
291 observations, won all contests. Males contesting for these females did so with less intensity but
292 over a longer time period.

293 Size thresholds during MMA may shape male mating tactics in *A. aculeatus*.
294 As predicted, size determined which males won contests. Clear size thresholds for the mating
295 tactics ♂T, ♂G_T and ♂G_A correspond with dramatically different levels of fighting success. ♂T
296 are generally small (37 ± 2 mm ML, Huffard *et al.*, 2008). Based on our results they would
297 rarely, if ever win contests. Thus, mate guarding is not a feasible tactic for these males. By
298 contrast, ♂G_T are slightly larger, averaging 41 ± 1 mm ML. With this small increase in size over
299 ♂T, ♂G_T are likely to win approximately half of their contests. Although they still have a chance
300 of losing in MMA, they stand to gain a significant increase in copulatory activity by guarding
301 occasionally (Huffard *et al.*, 2008). Contrary to our specific predictions, however, males
302 approaching this size threshold were not more aggressive than other males. Rather, loser
303 interaction rates per contest hour peaked at this and slightly larger sizes intermediate between
304 ♂G_T and ♂G_A. Slightly larger still, at approximately 50 ML, ♂G_A are likely to win 80–100% of
305 MMA encounters, making them the most effective guarders and earning them the most reliable
306 access to females. These patterns weakly support the hypothesis that animals persist or intensify
307 aggressive contests when they reach RHP (in this case size) at which they have a 50 % chance of
308 winning contests, and when the costs of fighting are low (Morrell *et al.*, 2005). The probability
309 of winning may have been approximately half for these males, but the prevalence of grappling

310 and existence of arm-cannibalism imply moderate risk of injury during MMA. We studied these
311 octopuses throughout the year, and at multiple sites with varying sex ratios. Thus our results
312 summarize average size trends of a large number of male *A. aculeatus*.

313 Our results suggest the possibility that *A. aculeatus* employ conditional mating tactics, in
314 which male mating behavior is not genetically fixed, but rather is influenced by external factors
315 such as an individual's relative RHP in an aggressive environment (Gross, 1996). Such a mating
316 system is more likely to evolve in species with intermediate mating skew, and when the costs and
317 limits to switching tactics are low (Pliastow *et al.* 2003). Translating this theory to the mating
318 system of *A. aculeatus*, some males may be fixed guarders with high reproductive success, while
319 others are likely conditional guarders or conditional sneaks that exhibit whichever tactic is likely
320 to gain them a moderate number of fertilizations given their relative RHP. These ideas are
321 supported by our observations of both copulation rates (Huffard *et al.* 2008) and aggressive
322 behaviors in this species. We found clear relationships between size demographics of mating
323 tactics, chances for aggressive success, and copulatory activity of males. To our knowledge
324 *Abdopus aculeatus* do not exhibit morphological traits that would limit individuals from
325 switching between guarding and non-guarding tactics. Males of all tactics have been found with
326 the sexually dimorphic trait of enlarged suckers. As in other cephalopods (Messenger, 2001)
327 body-color patterns associated with these tactics are neurally controlled almost instantly. Finally,
328 conditional learning underlies conditional reproductive tactics in the wild. This trait has been
329 demonstrated for octopuses in the laboratory (Hvorenecy *et al.* 2007). Although our study was not
330 designed to test this specifically, our results support the idea that conditional learning may occur
331 in the wild, with males possibly able to remember the results of previous aggressive interactions
332 and act differently according to the outcome. The relative sizes of aggressive individuals, and
333 their potential impacts on mating tactics may vary in other situations with different size or sex
334 ratio demographics. For example, all three Sneaker ♂T observed in our study had the lowest
335 RHP among all males known to mate the nearest female (Huffard *et al.* 2008). Their immediate

336 competitive environment eliminated the possibility for guarding, even though one Sneaker ♂T, at
337 40 mm ML, should have been able to win some contests based on the average demographics in
338 the larger study area (Figure 1).

339 While it is possible that genetics (Pliastow *et al.* 2003) or size alone (e.g. burying
340 beetles— Walling *et al.* 2008) can determine mating tactics in some animals with few chances for
341 agonistic interaction and self-assessment, we do not believe this is the case with *A. aculeatus*.
342 The *A. aculeatus* we studied had frequent chances for self-assessment. Although the impact of
343 genetics on ultimate size at maturity is unknown for octopuses, environmental factors such as
344 food quality and temperature largely determine growth, and even shrinkage (Forsythe, 1993;
345 Semmens *et al.*, 2004). If mating tactics in *A. aculeatus* are fixed before their single maturation
346 cycle, then the variability of these environmental factors during development should yield higher
347 variation in size per mating tactic than we observed here.

348 Patterns of RHP and size distributions may indicate high levels of aggression during
349 mating. Both size and sex influenced RHP in MFA, with some larger octopuses retreating from
350 individuals approximately 90% their size. We cannot determine whether *A. aculeatus* sometimes
351 yielded to smaller octopuses of the opposite sex because MFA may lead to injury (especially
352 during mating) or if some individuals were exceptional in their aggressive abilities (even though
353 these contests involved limited physical contact). *Abdopus aculeatus* is an arm-dropping octopus
354 with numerous injuries in wild individuals (Huffard, 2005). Our non-invasive observations did
355 not allow us to determine the cause of injuries directly, although intraspecific aggression is a
356 possible factor. The high prevalence of inking (an anti-predator defense) during MFA, and the
357 fact that some *A. aculeatus* fled from smaller individuals suggests that injuries may be more
358 severe in MFA, even if rare. In this population, inking occurred approximately twice as often
359 during MFA than during interactions with fish (Huffard, 2007). It is also possible that certain
360 individuals may be perceived as exceptionally aggressive. Variation in aggressiveness has been
361 documented previously in octopuses (Mather & Anderson, 1993), and may also occur in *A.*

362 *aculeatus*. While most MFA contests in *A. aculeatus* were very mild, involving a few short
363 chase/retreat interactions, some cases of were prolonged with high interaction rates, and even
364 incorporated grappling.

365 In addition to choosing females with high fecundity, males may mate with significantly
366 larger females than themselves to minimize chances of MFA, and possible injury or sexual
367 cannibalism. Sexual cannibalism is known to occur in *Octopus cyanea* (Hanlon & Forsythe,
368 2008), a sister taxon to *A. aculeatus* (Guzik *et al.*, 2005) with several similar behavioral and
369 ecological traits (Huffard, 2007). We have observed a female *A. aculeatus* kill and consume a
370 smaller conspecific of unknown sex, although we do not know the behavioral context of this
371 example (Huffard, 2007). Male *A. aculeatus* interacting with large females, particularly those
372 much larger than themselves, experienced fewer aggressive interactions. As occurs in other
373 animals, great size disparity may preclude the need for aggression because it is clear which
374 individual has the highest RHP (Enquist & Leimar 1983). This result may partly explain why
375 male *A. aculeatus* mated with females significantly larger than themselves (Huffard *et al.*, 2008).
376 While large females may inflict severe injury, this risk appears to be rare, and outweighed by
377 potential gains in fitness.

378 We do not believe that MFA in *A. aculeatus* reflected direct female mate choice based on
379 size or mating tactic. Mating activity was not inversely related to rates of MFA; octopuses tended
380 not mate with some individuals and fight with others. Rather they were aggressive with most
381 individuals they encountered or not at all. We may have expected to see ♀G_A act aggressively
382 toward non-♂G_A if these females had already chosen ♂G_A for repeated copulation, as occurs in
383 mating pairs of bonobos (Hohmann & Fruth, 2003), stomatopods (Caldwell, 1992), cichlids
384 (Barlow, 1998), and mice (Roberts & Gosling, 2004). Or they may have been aggressive towards
385 smaller males with lower RHP. This was not the case. Large and G_A females very rarely
386 exhibited any aggression, even though they interacted frequently and mated with ♂G and ♂T of
387 all reproductive sizes (Huffard *et al.*, 2008). Small and moderately sized females were aggressive

388 with equivalently sized males. Female *A. aculeatus* may not have the means to differentiate
389 between small old males, which may have beneficial genes for survival, and small young males,
390 whose genes have been tested for a shorter time. Thus there may be little reason for females to
391 select against small males. Perhaps females do not prefer larger guarding males because they do
392 not need protection from harassment by smaller males. Because most males did not encounter
393 multiple females during our study, we could not compare individual male reactions to multiple
394 females.

395 We cannot rule out the possibility of aggressive mate choice by female *A. aculeatus*, as
396 occurs in some stomatopods and cichlids (Caldwell, 1992; Barlow, 1998). ♀G_A may tolerate all
397 males that approach her despite guarding males being nearby, thus selecting for boldness in their
398 mates. These females may rarely encounter timid males, and test them aggressively if they do.
399 Aggression against timid males may explain why sneaker males tend only to mate with females
400 that are in their dens, and are presumably less able to assess their mates (Huffard *et al.*, 2008).

401 Patterns in MFA may (also) reflect an ontogenetic reduction in aggressiveness and/or
402 possible sexual immaturity of certain Transient individuals. We found a significant inverse
403 relationship between levels of MFA and size in *A. aculeatus*. Smaller octopuses were more
404 aggressive than larger octopuses with individuals of the opposite sex. During our full day
405 observations, all ♂♀T that encountered another individual acted aggressively toward it, even if
406 some mating activity occurred. These (typically small) individuals, along with small females that
407 aggressively rejected mating attempts (Huffard *et al.*, 2008), may not have been sexually mature
408 and receptive. In at least female *Octopus pallidus*, size is a better predictor than age at indicating
409 sexual maturity (Leporati *et al.*, 2008). Individual *A. aculeatus* may become less aggressive with
410 potential mates as they grow and mature. Octopuses store sperm for weeks to months (Wells,
411 1978). If sperm quality is reduced the longer it is stored, as is thought to occur in animals
412 (Reinhardt, 2007), then young females may benefit from delaying sperm acquisition until they are

413 nearer to spawning. Because we did not sacrifice females to assess reproductive development, we
414 do not know whether increased aggression occurs at the onset of maturation in females [as in
415 some primates (Moura, 2003)]. This inverse relationship between size and aggression in *A.*
416 *aculeatus* differs from the trend of continually increasing aggressive throughout maturity in
417 bobtail squids (Sinn & Moltshaniwsky, 2005).

418 Besides possible hormonal control of aggression, smaller *A. aculeatus* may engage in
419 more MFA than larger individuals because of resource competition to maximize juvenile growth.
420 Inter-sexual aggression and competition for resources can be particularly common during non-
421 mating times (as in primates: White *et al.* 2007). In octopuses, food intake strongly influences
422 growth and ultimate body size (Forsythe, 1993; Semmens *et al.*, 2004). Because large females
423 produce more eggs and are preferred by males, and large males are more capable of defending,
424 pairing, and copulating with large ♀G_A (Huffard *et al.*, 2008), all *A. aculeatus* should maximize
425 food intake and growth. Yet mate-guarding activity and growth are conflicting needs. Guarding
426 significantly reduces foraging rates and possibly food intake in both males and females (Huffard,
427 2005). MFA may reflect attempts by smaller *A. aculeatus* to maximize foraging by delaying
428 prolonged mate-guarding activity. For example, we observed a small male *A. aculeatus* evict a
429 small female from her den and then occupy that den. To a male that is not yet large enough to
430 mate-guard successfully, the value of this female as a sustained mate might have been less
431 important than the utility of her den site, and possible access to food supplies.

432 The aggressive system of *A. aculeatus* appears to be associated with their reproductive
433 behaviors, local demographics, and ecology. As in other animals (Barlow, 1998; Clutton-Brock
434 & Parker, 1995), aggression may be a major element of mate choice and pair formation. Reduced
435 intersexual aggression with increasing female size and male-female size disparity may act to
436 reinforce male mate preference for large, fecund females. This reduction in MFA with size may
437 also enable the repeated interaction required for mate-guarding. Male preference to guard and
438 copulate with large females is tapered by their relative chances of defending their mates from

439 challengers. Thus a male's relative size and RHP compared to that of nearby competitors may
440 determine which mating tactics he can employ effectively. Microhabitat preference and
441 availability help determine the distributional patterns that enable the repeated aggressive
442 interactions that drive this behavioral system (Huffard, 2007). Local demographics such as
443 density and sex ratio are known to influence aggression and mating activity in male *A. aculeatus*
444 (Huffard, 2005). It is conceivable that aggression may influence mating differently in other
445 populations, or that size thresholds for male mating tactics may vary at different sites. We do not
446 know how the alteration of any of these factors affects the overall fitness of these octopuses.

447

448 Acknowledgements:

449

450 We thank the Indonesian Institute of Sciences (LIPI) for granting permission to conduct this
451 work. Financial support was provided by the Beim Endowment for Field Research, Sigma Xi, the
452 University of California, Berkeley, the Western Society of Malacologists, and the American
453 Malacological Society grants to CLH. Dr. Helen Fox provided airfare to Indonesia on several
454 occasions, and Operation Wallacea supported fieldwork in Southeast Sulawesi. Heather
455 Spalding, Michael Caldwell, Brendan Hever, and Operation Wallacea participants volunteered
456 their assistance in the water. Dr. Mark Erdmann, Arnaz Mehta, and Tanta Ita kindly provided
457 support, entertainment, and language training to CLH. Stephanie Bush, Becky Williams, and two
458 anonymous reviewers helpfully reviewed the final draft of this manuscript. This research
459 complies with all current laws in Indonesia and the United States.

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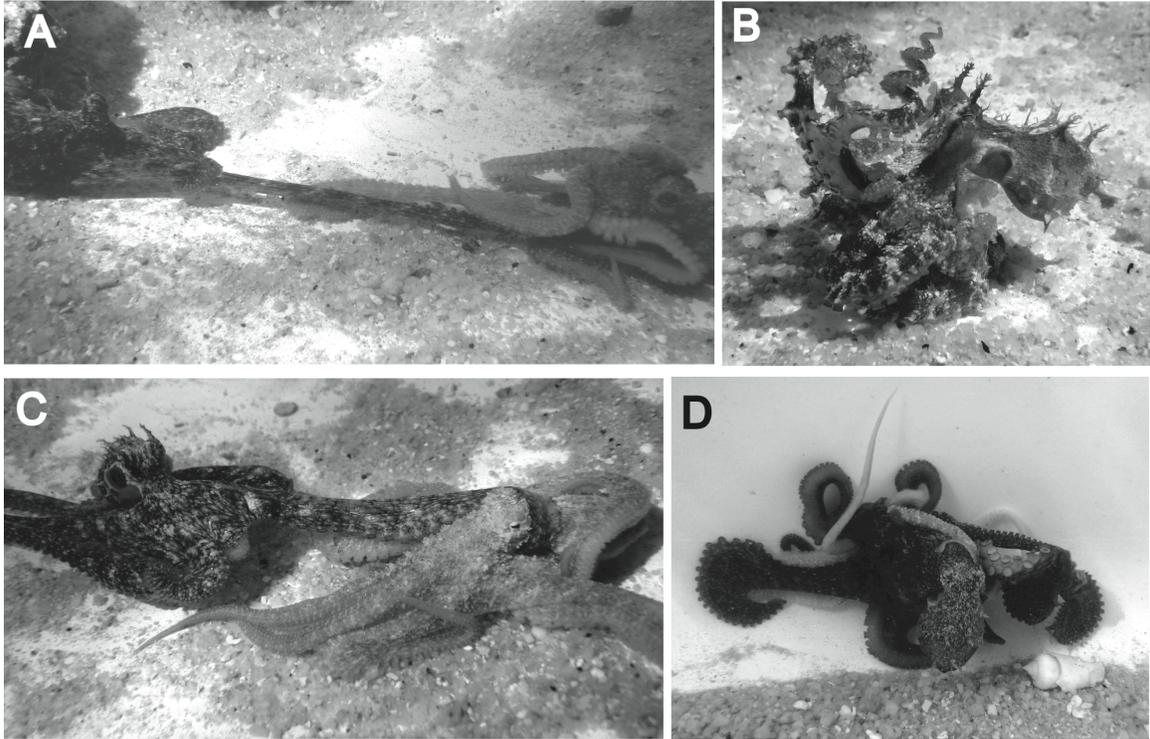
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597 (2007). Female dominance and feeding priority in a prosimian primate: experimental
598 manipulation of feeding competition. *American Journal of Primatology*, 69, 295-304.
599
600

600 Table 1: Behavioral categories of mating *Abdopus aculeatus* in Sulawesi, Indonesia. From
601 Huffard *et al.*, 2008.
602

Mating Tactic	Definition
'Adjacent Guarding' (G _A)	A male-female pair that occupied a den within arm's reach of each other. This pair copulated in mate-guarding situations both at their dens and while out foraging.
'Temporarily Guarding' (G _T)	A male-female pair occupying dens not adjacent to each other, that temporarily entered into a guarding situation.
'Transient' (T)	Any octopus that was not observed in a guarding situation. When observed to mate Transient individuals parted after final withdrawal of the hectocotylus. These included both Sneaker and Non-Sneaker males.
'Sneaker' (S)	Males that visually segregated themselves from guarding males to avoid aggression while mating with a female guarded by another male. Sneaker males were a type of Transient male.

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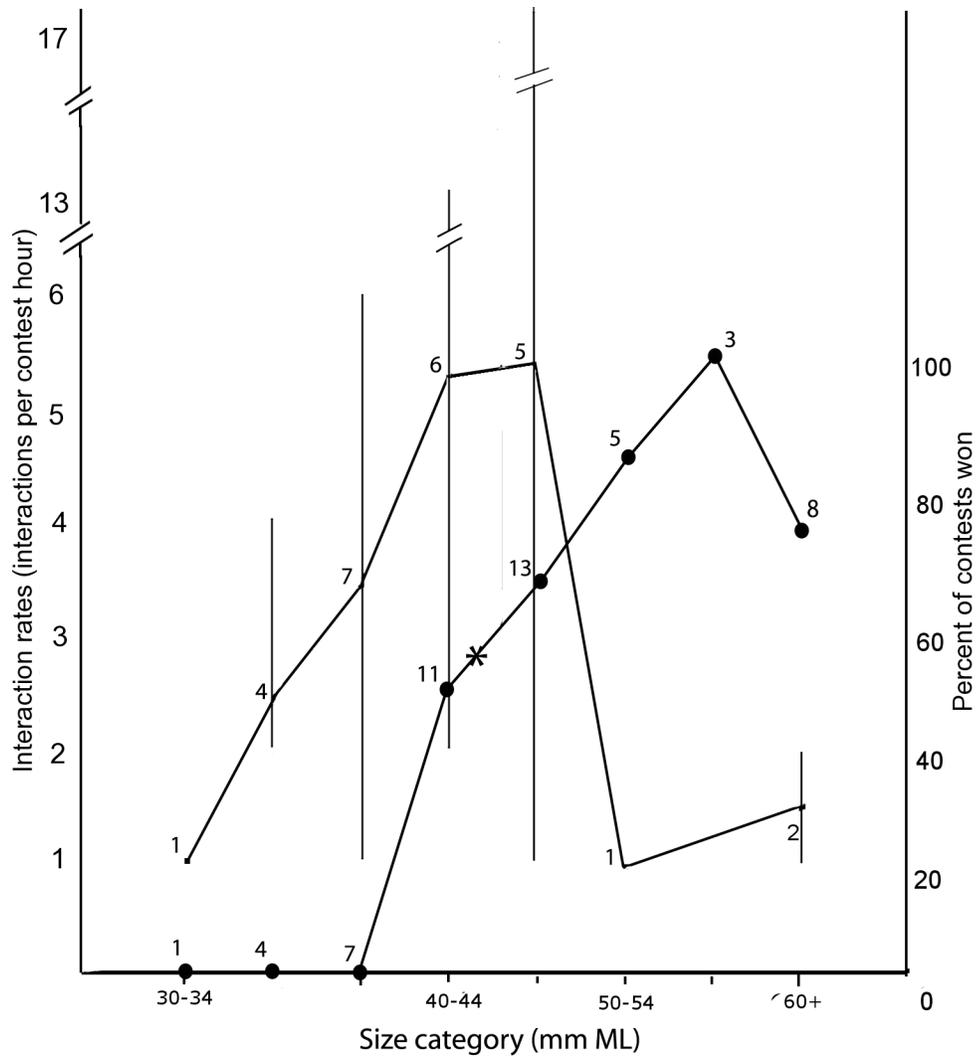
607 Figure 1. Agonistic acts between male *A. aculeatus*. A) Arm-pulling by smaller male (pale, right);

608 B) Flamboyant display; C) Constricting by larger male (brown, left); Note arm wrapped twice

609 around mantle of smaller male (pale, right); D) Grappling that proceeded until the larger male

610 fully enveloped the smaller male.

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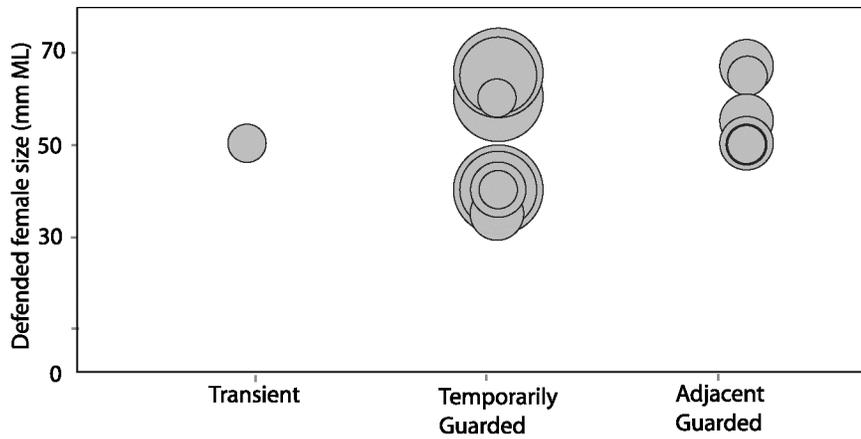
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614 Figure 2. Male-male aggressive success and effort for *A. aculeatus* size categories. Size category

615 of male *A. aculeatus* vs. percent of contests won for that category (right y-axis, line with black

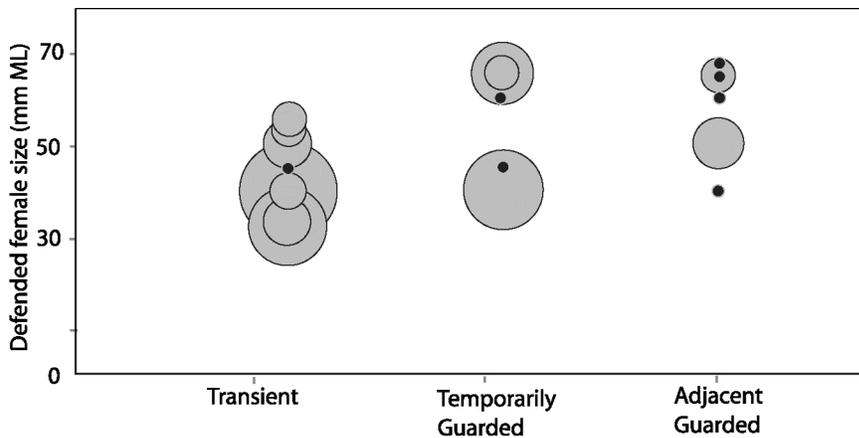
616 circles, n given; asterisk marks 50% winning threshold). Average interaction rates are given for

617 loser males of those same dyads (left y-axis, line \pm C.I. of median, n given).



618

619 Figure 3. Interaction rates of male-male aggressive contests (size of circle) in relation to
 620 defended female size and mating tactic. Males engaged in more interactions while mate guarding
 621 Temporarily Guarded females than Adjacent Guarded females ($U = 41.0$, $p = 0.05$, $n = 6 \text{ ♀}G_A$, n
 622 $= 9 \text{ ♀}G_T$). Defended female size was positively correlated with average contest duration ($\rho =$
 623 0.46 , $p = 0.08$, $n = 17$), but did not correlate with average interaction rates ($\rho = .117$, $p = .33$, $n =$
 624 17).



625

626

627 Figure 4. Total interactions in male-female aggressive contests per day (size of circle) in relation
 628 to female size and mating tactic. Black circles denote the zero values of male-female dyads that
 629 did not engage in MFA. Interaction rates were higher among Transient individuals than Guarding
 630 individuals [Transient vs. Temporarily Guarding and Adjacent Guarding combined: $U = 85.0$; $p =$

631 0.02]. Interactions totals were inversely correlated with both female size ($\rho = -0.488$, $p = 0.01$)
 632 and male size ($\rho = -0.479$, $p = 0.01$).

633

634

635

636 <http://www.youtube.com/watch?v=hjGbKwOIw7s>

637

638 Supplementary movie 1. Aggressive contest between male *Abdopus aculeatus*. Aborted mating
 639 attempt by small male (camouflaged, right) with larger male (BWS, left, sitting tall) followed by
 640 arm-wrestling (Supplementary movie 1).

641

642 Supplementary Table 1: Agonistic behaviors, definitions, and sample sizes (where recorded)

643 documented for *Abdopus aculeatus* throughout all observations. Mating attempts here refer to

644 those that elicited aggressive interactions. MMA = number of times observed during male-male

645 aggression; MFA = number of times observed during male-female aggression; NQ = not

646 quantified in this study. Quantified behaviors are listed in approximate order of increasing risk of

647 injury or indication of stress.

Behavior	Brief description	MMA	MFA
	Number of contests (Number of interactions)	29 (176)	17 (46)
Approach	An individual crawls, swims, or jets toward another individual, but does not contact opponent	89	16
Retreat	An octopus moves in a direction away from the other individual (which is typically approaching)	176	43
Black and white stripes 'BWS'	Display pale background with dark longitudinal stripes, often while expressing digitate supraocular papillae	NQ	NQ
Arm pulling	Octopus grabs and pulls an arm of the competitor (Figure 1A)	NQ	NQ
Constrict	An octopus wraps at least one arm around the base of the mantle of the competitor, presumably cutting off inhalant and exhalant water over the gills (Figure 1C)	NQ	NQ
Stand tall	An individual stands erect on stiffened arms	NQ	NQ
Mating attempt	A male extends the hectocotylus toward the mantle cavity of another octopus	6	3
'DACT'	Dorsal arms raised with tips loosely coiled, body camouflaged	2	1
Flamboyant display	Dorsal and sometimes additional arms coiled helically and raised above the head, body camouflaged. This display was observed only during retreat (Figure 1B)	1	0
Touch	An individual touches the other octopus with a non-	20	1

	hectocotylyzed arm		
Whip	An octopus extends one or two arms in a whip-like fashion, aimed at and/or hitting the other individual	21	12
Push	An octopus uses the arms and oral surface to push another individual away	0	2
Ink	An octopus expels ink	1	4
Grab	One octopus grabs any portion of another octopus, but without arm-wrestling, arm-pulling, or grabbing funnel	3	1
Pull from den	An octopus reaches into a den, grabs the octopus inside, and pulls it to the surface	0	3
Grab Funnel	An octopus grabs the end of the funnel of the competitor prohibiting exhalant water flow from the mantle	1	0
Grapple	Individuals align and/or intertwine the oral surface of the arms and web intertwine, or both. In some cases the larger octopus pushes the arms of the smaller backward until it becomes fully enveloped (Figure 1D)	30	2
Evict	An octopus overtakes the den of another individual.	1	1
Cannibalism	One octopus consumes part or all of another. Part consumed in parentheses	1 (two arms)	1 (whole body; Female with unk. sex)

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650