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1 **Fighting for mates: the importance of individual size in mating contests in rocky shore littorinids**

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3 Terence P. T. Ng ¹, Mark S. Davies ², Richard Stafford ³, Gray A. Williams ¹

4

5 ¹ The Swire Institute of Marine Science and School of Biological Sciences, The University of Hong
6 Kong, Pokfulam Road, Hong Kong SAR, China

7 ² Faculty of Applied Sciences, University of Sunderland, Sunderland, UK

8 ³ Faculty of Science and Technology, Bournemouth University, UK

9

10 Address for correspondence: Gray A. Williams, The Swire Institute of Marine Science, The University
11 of Hong Kong, Pokfulam Road, Hong Kong

12 E-mail: hrsbwga@hku.hk

13 Telephone: (852) 2809 2551

14 Fax: (852) 2809 2197

15

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22

23

24 **Abstract**

25 Studies of mating contests have reported how traits (e.g. body size) related to resource holding
26 potential (RHP) and strategies to assess RHP and resource value influence contest outcome in many
27 taxa but are rare in the Gastropoda. The influence of male size (as an index of RHP) and female size
28 (as a measure of resource value) on contest outcome were investigated in two littorinid snails,
29 *Echinolittorina malaccana* and *E. radiata*, in Hong Kong during May – June 2013. In these snails,
30 contests between males take the form of a 'challenger' attempting to take over the copulation position
31 occupied by a 'defender'. Both challengers and defenders were, generally, smaller than the females in
32 both species. In both species, the larger the challenger relative to the defender, the more likely he
33 would replace the defender in the copulation position. The challengers were, however, more
34 successful in *E. radiata*, as they generally challenged defenders that were smaller than themselves,
35 suggesting an ability to detect rival size before entering into a contest in this species. When sizes of
36 the contestants were similar, defenders were more likely to win contests in *E. malaccana* but not in *E.*
37 *radiata*. Evidence for pure self-assessment of RHP and the ability to assess resource value in
38 challengers was found in *E. malaccana*. Different fighting strategies appear to have evolved in these
39 congeneric marine snail species and decisions based on male and female sizes play an important role in
40 determining male reproductive success.

41

42 **Introduction**

43 Males of many species fight for the opportunity to mate (Andersson 1994; Hardy and Briffa 2013).
44 Males, however, differ in size, development of weaponry, energetic and physiological state and recent
45 history of wins and losses, any of which may affect their fighting ability, or resource-holding potential
46 (RHP; Parker 1974). Contests are also settled based on the strategies males use to assess the RHP,
47 such that males will decide to persist or retreat in a contest base on their own RHPs or the perceived
48 difference in RHPs between themselves and their rivals (Taylor and Elwood 2003; Arnott and Elwood
49 2009). In some contests, males differ in their roles; such as in challenger-defender contests where one
50 male (the defender) occupies a mate and the other male (the challenger) attempts to take over his
51 position (also described as intruder-owner contests, when the defender occupies a physical space such
52 as a territory or a burrow rather than a mate, Arnott and Elwood 2008). In such a scenario, the
53 defenders are often able to resist takeovers; and this success is often attributed to the defenders being
54 highly motivated to maintain the females (to hold on to their resource) given their already high
55 investment in securing the female (Kokko et al. 2006; Arnott and Elwood 2008). The difference in
56 RHP among males and the strategies males use to assess RHP and resource values, therefore, play an
57 important role in determining the outcome of male-male contests (reviewed by Arnott and Elwood
58 2008, 2009).

59 Whilst such mating contests have been intensively studied in insects (Hardy and Briffa 2013),
60 studies are relatively scarce in the second most species-rich invertebrate class, the Gastropoda.
61 Bradshaw-Hawkins and Sander (1981) have reported male-male combat in the form of physical
62 aggression in the dioecious marine snail, *Strombus pugilis*. Similar observations, where two males
63 push against each other on top of a female, have also been recorded in some littorinid snails (Gibson
64 1965; Zahradnik et al. 2008; Ng and Williams 2014); in particular Ng and Williams (2014) showed that
65 large males have a size advantage over smaller males in access to females of the mangrove littorinid,
66 *Littoraria ardouiniana*. Size may, therefore, also be an important component of RHP in marine
67 dioecious gastropods.

68 Littorinid snails (family Littorinidae) are among the most common dioecious gastropods and inhabit
69 most intertidal habitats worldwide (Reid 1986, 1989; Reid et al. 2012). Littorinids dominate the high
70 shore environment where their activity (including mating) windows are relatively narrow due to the
71 limited time awash by tides (Mak 1996; McQuaid 1996). Intense competition for mates in these

72 snails is, therefore, anticipated due to the limited time available to find and copulate with a mate.
73 Males are the active sex and follow females' mucus trails to locate and mount them before initiating
74 copulation (Gibson 1965; Erlandsson and Kostylev 1995; Ng et al. 2011, 2013; Saltin et al. 2013).
75 Female size is also important, as large females are usually favoured by males because fecundity
76 generally increases with size in these snails (Erlandsson and Johannesson 1994; Zahradnik et al. 2008;
77 Ng and Williams 2012).

78 The present study examined contest behaviour in two rocky shore littorinids, *Echinolittorina*
79 *malaccana* and *E. radiata*. These two species are sympatric and occur at high densities in the
80 Indo-West Pacific, and, in Hong Kong, *E. radiata* has a more female-biased sex ratio than *E.*
81 *malaccana* (Mak 1996). In littorinid snails, mating contests generally follow one of two scenarios
82 (see Ng and Williams 2014): either (1) when two males simultaneously mount a female the males push
83 against each other and the one that successfully displaces the other stays and copulates with the female;
84 or (2) when one male (the defender) is copulating with a female and another (the challenger)
85 encounters the pair and attempts to push away the defender, this challenger may or may not
86 successfully take over the copulation position. This paper focuses on the second, more common
87 scenario, as shell mounting before copulation, in general, only takes a few seconds (T. P. T. Ng unpubl.
88 observation). Specifically, we predicted that (1) contests would be less intense in *E. radiata* due to the
89 likelihood of more mating opportunities for males in the female-biased populations; (2) that defenders
90 were more likely to win contests when their sizes were similar to or larger than the challengers; and (3)
91 that male (RHP) and female size (resource value) would influence both contest outcome and duration.

92

93 **Materials and methods**

94 Study site

95 All work was conducted in late May to early June 2013 (the reproductive season of *Echinolittorina*
96 *malaccana* and *E. radiata*, Mak 1996) at the Cape d' Aguilar Marine Reserve, Hong Kong (22° 12' 27"
97 N, 114° 15' 36" E). Both species occur at high densities (generally > 400 individuals m⁻²) on the high
98 shore level, and their distributions largely overlap, with *E. malaccana* being slightly higher on the
99 shore than *E. radiata* (Mak 1996; Mak and Williams 1999). These snails are inactive at low tide;
100 become active and move up the shore when awash by the rising tide, and then move back down the
101 shore while awash on the ebbing tide to become inactive again when emersed (Williams 1994; Stafford

102 et al. 2007; Marshall et al. 2010). Preliminary observations showed that mating activities of both
103 species were most intense during rising tides (the 'mating activity window') and was greatly reduced
104 during ebbing tides.

105

106 Occurrence and intensity of contests

107 Field observations were conducted to investigate whether contests occurred throughout the mating
108 activity window of the two littorinids. To ensure maximum capture of mating contests for a
109 high-resolution of the temporal pattern, while avoiding repeated counting of the same events,
110 observations were conducted every five minutes (as preliminary observations showed contest durations
111 in both species generally last < 5 min) from when the tide first wetted the littorinids and stimulated
112 them to move upshore (tidal height: ~1.7–1.8 m above Chart Datum), until the tide approached its
113 maximum height (~2 m above Chart Datum; i.e. the rising tide). A 0.25 m x 0.25 m quadrat was
114 placed at the zone where the two species overlapped and where high densities of wet (and hence active)
115 individuals were found in four ~4–5 m horizontal sections of the shore (6–10 m apart, separated by
116 sand or boulders). Snails were distributed at slightly different tidal heights in the sections due to local
117 topographic influences, and hence survey starting times varied in the sections. The numbers of
118 individuals, mating pairs and pairs involved in contests were recorded, as were the number of
119 heterospecific 'mating' pairs.

120

121 Effect of male and female sizes on contest outcome and duration

122 Field observations were conducted during rising tides to investigate the influence of male and female
123 size on contest outcome and duration in the two species. Contest duration started when an intruding
124 male mounted a mating pair and ended when the unsuccessful contestant or 'loser' left the female ($n =$
125 30 per species). All snails involved in the contests were taken to the laboratory where species, sex
126 (determined by the presence or absence of a penis as observed under a dissection microscope) and sizes
127 (shell length [SL] \pm 0.1 mm, vernier callipers) of the successful contestant or 'winner' (snail in the
128 copulation position at the end of the contest), the unsuccessful contestant or 'loser' of the contest events
129 and the passive individual (i.e. snail over which the contestants were competing) were recorded. All
130 snails were returned to the shore after examination. A previous study on another littorinid species,
131 *Littoraria ardouiniana*, showed that defenders rapidly withdrew their penises when pushed by

132 intruding males (Ng and Williams 2014). Based on this observation, we assumed that the defenders
133 retreating from the copulation position (i.e. in cases where defenders were losers) was a result of the
134 action of the challengers rather than completion of copulation with the female.

135

136 Statistical analyses

137 To compare the variations in mating intensity and proportions of matings that involved contests among
138 the four shore sections in the two species, mixed model ANOVAs (species as a fixed factor and shore as
139 a random factor) were performed. Since mating durations are generally > 5 min (i.e. longer than the
140 5-min survey intervals) but finished within 30 min (Ng et al. in submission), we used the mean
141 proportion of individuals that were mating in every 30-min interval as replicates to compare mating
142 intensity between the two species. Proportional data were arcsine square root-transformed and data
143 were checked for homogeneity of variances prior to analyses (Levene's test). Where the assumption
144 of homogeneity was violated (data for matings that involved contests) an ANOVA was still performed
145 (given the large sample size), but with a more conservative significance level ($p < 0.01$).

146 Two-tailed binomial tests were performed to investigate whether the ratio of contests that involved
147 larger challengers and smaller defenders to those that involved smaller challengers and larger defenders
148 deviated from 1:1. The same statistical approach was applied to investigate whether the ratio of
149 contests that involved larger females and smaller defenders or challengers, or those that involved
150 smaller females and larger defenders or challengers deviated from 1:1. Binary logistic regression
151 analyses were conducted to investigate whether female size and the relative difference between the size
152 of males affected contest outcome (win or lose; following Briffa et al. 2013).

153 A series of linear regression analyses, with the contest durations as the dependent variable against
154 sizes of the winners and losers in both successful and unsuccessful takeovers, were conducted to
155 investigate the assessment strategies of RHP in males (following Arnott and Elwood 2009). Contest
156 durations were log-transformed prior to analyses to achieve normality. Comparisons between the
157 relationships in this statistical approach were used to test three RHP assessment strategies of males: (1)
158 pure self-assessment in which each contestant only has information about its own RHP, and both
159 contestants incur a cost from their own actions; (2) cumulative assessment in which contestants
160 terminate a contest when accrued costs due to damages inflicted by an opponent exceed a threshold,
161 and hence the decision to retreat is influenced by the RHPs of both contestants; (3) mutual assessment

162 in which a contestant assesses the difference in RHP between itself and its opponent and hence the one
163 with the lower perceived RHP can rapidly terminate a contest in order to reduce time, energy
164 expenditure and risk of injury from engaging in the contest (see Taylor and Elwood 2003 and Arnott
165 and Elwood 2009 for detailed illustrations). The same statistical approach, using contest durations in
166 successful and unsuccessful takeovers against female size, was also followed to investigate the males
167 assessment strategies of resource (female) value (i.e. whether the challenger or the defender possessed
168 the ability to gather information about the resource, following Arnott and Elwood 2008). Since there
169 were only three cases where the defender won the contest in *E. radiata*, analyses of unsuccessful
170 takeovers in this species were not performed. All statistical tests were performed using SPSS 16.0.

171

172 **Results**

173 Contest behaviour

174 During a contest the defender was attached on the right side of the female, parallel to the substratum
175 (i.e. in the copulation position) and typically perpendicular to the challenger (see supplementary
176 materials S1 and S2 for videos, with descriptions of the contest behaviour in *E. malaccana* and *E.*
177 *radiata*, respectively). The challenger appeared to be more 'aggressive' than the defender and readily
178 used his snout, aimed at the foot of the defender, to attempt to push the defender away from the
179 copulation position (supplementary materials S1 and S2). In *E. malaccana*, pushing also involved the
180 challenger moving his shell lip up and down as he advanced forward, leading to successive thrusts
181 towards the defender (see supplementary materials S1). The defender seemed to adopt a 'mate
182 guarding' role as he rarely fought back but remained in the copulation position. A successful takeover
183 occurred when the challenger pushed away the defender and took over the copulation position; whereas
184 an unsuccessful takeover occurred when the challenger failed to push away the defender and
185 subsequently left the mating pair.

186

187 Occurrence and intensity of contests

188 In general > 20% of individuals of both species were mating at each sampling time during the rising
189 tide, with an insignificant but marginally higher intensity in *E. malaccana* (mean \pm SD: 31.5 \pm 12.3%)
190 than in *E. radiata* (22.6 \pm 6.6%, ANOVA, species: $F_{1,38} = 5.41$, $p = 0.058$; shore effect was
191 insignificant; Fig. 1). Overall, in both species, > 10% of these matings involved a contest, with a

192 significantly higher intensity on section S2 ($28.8 \pm 24.3\%$) than other shore sections (average $12.3 \pm$
193 21.3% , ANOVA, shore (species): $F_{6, 210} = 3.687$, $p < 0.01$; species effect was insignificant; Fig. 1).
194 Males of both species rarely made mistakes by 'mating' with individuals of another species in both *E.*
195 *malaccana* (5 out of 606 pairs from all quadrats) and *E. radiata* (7 of 681 pairs).

196

197 Effect of male and female sizes on contest outcome and duration

198 As all contests involved two males on the shell of a female, significantly more cases were found where
199 the challenger was larger than the defender in *E. radiata*; but not in *E. malaccana* (Table 1). More
200 successful takeovers occurred in *E. radiata* (27 of 30 cases) but an equal number of successful and
201 failed takeover attempts were recorded in *E. malaccana* (15 of 30 cases for both successful and failed
202 takeovers). As the difference in size between the challenger and defender increased, the challenger
203 was more likely to win in contests between *E. malaccana* males (binary logistic regression: $\chi^2 = 5.75$, p
204 < 0.01 , Fig. 2). For *E. radiata* there was a 'perfect separation' (i.e. all three of the non-successful
205 takeovers were by challengers far smaller (29–48%) than the snails already mating, and all successful
206 takeovers were from challengers of similar size or larger than those already mating (Fig. 2), indicating
207 a similar, but stronger effect of size difference on contest outcome in *E. radiata* than seen in *E.*
208 *malaccana*. In *E. malaccana*, a challenger has less than half the chance of winning the contest if there
209 is no difference in size between the challenger and defender (Fig. 2). In contrast, all challengers won
210 their contests if they were of similar size (up to 0.3 mm smaller) as the defenders in *E. radiata* (Fig. 2).
211 *E. radiata* also appeared more selective about the contests they entered, with significantly fewer cases
212 of a smaller challenger attacking a larger defender than cases of a larger challenger attacking a smaller
213 defender (Table 1; Fig. 2). There were, however, two cases in *E. radiata* where a smaller challenger
214 lost the contest but then moved to a position behind the larger defender and remained there until the
215 defender finished copulation, whereupon the smaller male mounted and copulated with the female.

216 Female size had no effect on the contest outcome in both species (binary logistic regressions: both p
217 > 0.05). Almost all (26 of 30 in *E. malaccana* and 27 of 30 in *E. radiata*) females in the contests were
218 within a narrow size range (SL 7–10 mm) and there were significantly more cases where females were
219 larger than the challengers or defenders than where females were smaller than the challengers or
220 defenders (two-tailed binomial tests: all $p < 0.05$, $n = 30$, Fig. 3).

221 Male *E. malaccana* (3.45 ± 3.69 min) fought longer than *E. radiata* (1.84 ± 1.26 min). In *E.*

222 *malaccana* when takeovers were successful, there was a significant positive relationship between
223 contest duration and defender (loser) size (regression: $F_{1,13} = 5.24$, $r^2 = 0.287$, $\beta = 0.536$, $p < 0.05$, Fig.
224 4); indicating that contests with larger males were more prolonged. In contrast, however, there was
225 no significant relationship between contest duration and challenger (winner) size (regression: $F_{1,13} =$
226 1.756 , $r^2 = 0.119$, $\beta = 0.345$, $p = 0.208$, Fig. 4) in successful takeovers in *E. malaccana*, which
227 indicates that males were exhibiting pure self-assessment. Nor were there significant relationships in
228 other analyses of contest duration against male size in either species (regressions: all $p > 0.05$). No
229 significant relationships were also found in analyses of contest duration against female size in both
230 species (regressions: all $p > 0.05$), with the exception of a significant positive relationship (regression:
231 $F_{1,13} = 11.74$, $r^2 = 0.475$, $\beta = 0.689$, $p < 0.01$) between contest duration and female size in unsuccessful
232 takeovers (i.e. when challengers lost) but not in successful takeovers (when defenders lost) in *E.*
233 *malaccana* ($F_{1,12} = 0.265$, $r^2 = 0.022$, $\beta = -0.147$, $p = 0.616$, Fig. 5), suggesting that in *E. malaccana*,
234 challengers were better able to assess the resource value (i.e. female quality) than the defenders.

235

236 **Discussion**

237 Contests occur in both *Echinolittorina malaccana* and *E. radiata* and, in both species, size is a reliable
238 predictor of the likelihood of successful takeover, indicating that, as in many other animals, size is an
239 important component of RHP (reviewed by Arnott and Elwood 2009). Given that time and energy
240 can be wasted in unsuccessful takeover attempts, selection will favour the ability to assess the size of
241 rivals before a male decides to initiate a contest (Morrell et al. 2005; Arnott and Elwood 2009). This
242 prior assessment seems to be the case in *E. radiata* where challengers generally only entered into
243 contests with defenders smaller than themselves. A similar strategy has also been demonstrated in the
244 hermit crab, *Pagurus bernhardus*, in which attacking individuals were usually larger than the defending
245 individuals in contests over the occupancy of shells (Elwood et al. 2006). If, as a result of
246 pre-assessment, the challengers are likely to win contests in *E. radiata*; this may explain why *E.*
247 *radiata*, despite having a female-biased population, exhibited a similar incidence of male fighting as *E.*
248 *malaccana*. The mechanism for how such size assessment occurs requires further investigation, but it
249 may be based on the mucus trails of the rivals rather than visual cues, as these snails generally have
250 limited visual ability (Seyer 1992). In some littorinid species males are able to detect female size
251 from their mucus trails (e.g. *Littorina saxatilis*, Johannesson et al. 2008; *Littorina fabalis*, Saltin et al.

252 2013; *Littoraria ardouiniana*, Ng and Williams 2014). Males of both *E. malaccana* and *E. radiata*
253 also preferentially follow mucus trails of females larger than themselves and, as a result, generally
254 mount females larger than themselves (Ng et al. in submission). This mate-searching selection would
255 explain why females of both species were usually larger than the challengers and defenders in the
256 contests observed.

257 The male-male contests of the two rocky shore snails, where a challenger takes over the copulation
258 position from a defender, are similar to those described in other taxa such as amphipods (Ward 1983;
259 Dick and Elwood 1990; Prenter et al. 2006). The behaviour of *E. malaccana*, where the challengers
260 used both their shell lip and snout to push the defenders, also matches observations in two other
261 littorinid species: *Littoraria ardouiniana* (Ng and Williams 2014) and *Littorina planaxis* (= *L. keenae*)
262 (Gibson 1965). Despite belonging to a different family, male West-Indian fighting conches, *Strombus*
263 *pugilis*, also adopt a similar 'fighting' strategy using the shell lip and extended proboscis to attach other
264 males (Bradshaw-Hawkins and Sander 1981), whereas the more subdued attacks of *E. radiata*, which
265 do not involve thrusts with the shell, are similar to another littorinid, *Littoraria melanostoma* (Ng
266 2013).

267 If the up and down movement of the shell lip can be considered stronger male aggression (as
268 compared to snout-pushing only), this difference in aggression between species may be related to
269 female availability (Simmons 1986). Populations of *E. radiata* have a more female-biased sex ratio
270 than *E. malaccana* (Mak 1996; Ng et al. in submission). The opportunities to encounter females will,
271 therefore, be greater for male *E. radiata*, which may reduce the importance of enhanced aggression
272 when competing for females as compared to male *E. malaccana*, where opportunities to encounter
273 females may be limiting. It is, however, counterintuitive that the attacks using shell thrusts in *E.*
274 *malaccana* were less successful than the more subdued attacks of *E. radiata*. In *E. malaccana*, when
275 the sizes of challenger and defender were similar, defenders had a positional advantage (i.e. were more
276 likely to win the contest by occupying the copulation position) over challengers but in the same
277 situation all challengers won the contests in *E. radiata*. Such a positional advantage of defenders in *E.*
278 *malaccana* has also been reported in amphipods (Dick and Elwood 1990) in that defenders, even when
279 disadvantaged by size, were still more likely to win contests because of their precedence in holding the
280 females. Given that females may be limiting in *E. malaccana*, it is possible that selection may also
281 favour defenders that are tenacious and prepared to invest energy into the contest to defend their

282 resource, resulting in an 'arms-race' type scenario between the challenger and defender (Emlen 2008).

283 In fact, if a defender has already invested in locating and securing a female, this may explain why
284 the defender would be highly motivated to defend his resource because the female will now have a
285 higher perceived resource value (Kokko et al. 2006; Arnott and Elwood 2008). We speculate that in *E.*
286 *radiata*, the opportunity cost (in terms of maximizing number of matings with females) for the
287 defenders to defend the females may be higher than in *E. malaccana* in a female-biased population and,
288 therefore, males may benefit from quickly giving up any contest upon attack in *E. radiata*. Males of
289 *E. radiata* also generally mated with females less frequently within their activity window (this study)
290 and had a much shorter (~3x) copulation duration than *E. malaccana* (Ng et al. in submission). Male
291 *E. radiata*, therefore, do not seem to invest as much as male *E. malaccana* in each copulation
292 event/attempt and hence costs (at least in terms of time) associated with giving up matings may be
293 lower.

294 There was some evidence that challengers in *E. malaccana* were able to assess resource value
295 (female size) in the contests, as they were less likely to retreat when females were larger, whereas this
296 pattern was not observed in defenders (i.e. the decision to retreat was not influenced by female size).
297 This behaviour pattern reveals that challengers are prepared to accept higher costs when the resource
298 quality is higher (Arnott and Elwood 2008). Apart from resource assessment, there was also some
299 evidence of a pure self-assessment strategy of RHP in *E. malaccana*, as described in other taxa such as
300 amphipods (Dick and Elwood 1990; Prenter et al. 2006), chameleons (Stuart-Fox 2006) and fig wasps
301 (Moore et al. 2008). This assessment strategy infers that a contestant has information about its own
302 fighting ability but not that of its rival, and hence contestants retreat when they reach their own
303 self-assessed limits (Taylor and Elwood 2003; Arnott and Elwood 2009).

304 Although 'fighting' behaviour has been reported in several littorinids, there are species in which
305 male-male aggressive behaviour seems to be absent (e.g. *Littorina littorea*, Erlandsson and
306 Johannesson 1994; *L. fabalis* and *L. saxatilis*, T. P. T. Ng unpubl. observation). It is unclear at this
307 stage why there is such inter-specific behavioural variation in this family, but we speculate that
308 life-time mating opportunities may be a plausible explanation. The mating opportunities of
309 *Echinolittorina* and *Littoraria* species in Hong Kong, for example, are heavily constrained by
310 physical factors on these tropical shores, such as heat and desiccation stresses (see Williams and
311 Morritt 1995). The two *Echinolittorina* species in this study mate mostly during the rising tide, and

312 when the tide is receding, there is high selection pressure for them to search for refuges and aggregate
313 to avoid thermal stress (Williams 1994; Stafford et al. 2008, 2012). This constrained behaviour is in
314 contrast to *Littorina* species in temperate regions, which may have a longer activity window due to the
315 more benign physical conditions (e.g. female *Littorina saxatilis* have been suggested to be 'over-mated'
316 because their mating activities are less constrained by thermal stress during ebbing tides, and they
317 remain reproductively active all year, Johannesson et al. 2010) and are, therefore, likely to have greater
318 life-time mating opportunities.

319 Currently only a few studies have reported contest behaviour in gastropods (i.e. Bradshaw-Hawkins
320 and Sander 1981; Gibson 1965; Zahradnik et al. 2008; Ng and Williams 2014), and most of these
321 studies have not examined how traits related to RHP contribute to contest outcome. The accumulated
322 evidence indicates that physical contests can be common in marine gastropods and take many forms
323 even in co-occurring, congeneric species. Importantly, it appears that both male and female sizes are
324 important factors in determining contest outcomes, and hence individual fitness in these gastropods.

325

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413

414 **Figure legends**

415 **Fig. 1** Percentage of individuals mating (upper row) and of matings where contests occurred (lower
416 row) for *Echinolittorina malaccana* and *E. radiata* throughout the mating activity window (i.e. rising
417 tide) on four shore sections (S1–S4) at Cape d’Aguilar Marine Reserve, Hong Kong. Measurements
418 taken every 5 min from time when snails were wetted and hence activated by the rising tide.

419

420 **Fig. 2** Relationships between the asymmetry in male size on chance of the challenger taking over
421 copulation position from the defender in *Echinolittorina malaccana* and *E. radiata*.

422

423 **Fig. 3** Size of female versus sizes of challenger and defender in *Echinolittorina malaccana* and *E.*
424 *radiata* in mating contests. Dashed lines are lines of equity between male and female sizes.

425

426 **Fig. 4** Relationship between either challenger or defender sizes and contest duration in successful
427 takeovers in *Echinolittorina malaccana*. Regression line indicates significant positive linear
428 relationship only between defender size and contest duration, which indicates that a contestant only has
429 information about its own fighting ability.

430

431 **Fig. 5** Relationship between female size and contest duration in successful and unsuccessful
432 takeovers in *Echinolittorina malaccana*. Regression line indicates significant positive linear
433 relationship in unsuccessful takeovers but not successful takeovers, suggesting that challengers were
434 better at assessing female quality than defenders.

435

436 **Notes for the Electronic Supplementary Materials**

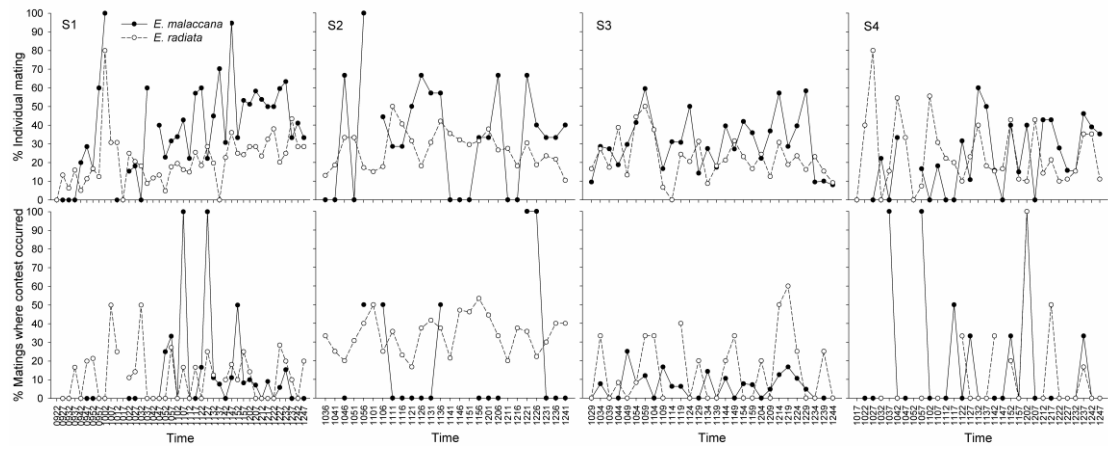
437 S1 Mating contest in *Echinolittorina malaccana*. Challenger (top of the mating pair) 'aggressively'
438 pushes, using his snout and an 'up and down' movement of his shell lip, at the foot of the defender
439 (attached lower, right-hand side of female), to push the defender away and mate with the female.

440 Video is 4x normal speed.

441

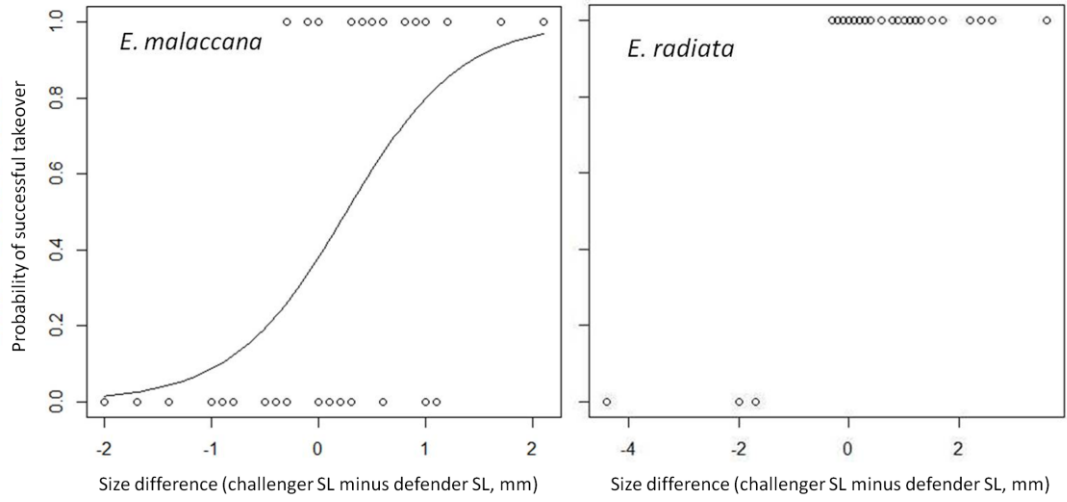
442 S2 Mating contest in *Echinolittorina radiata*. Challenger (top of the mating pair) pushes using his
443 snout at the foot of the defender (attached lower right hand-side of female) to push the defender away

444 and mate with the female. Following this contest, another challenger pushes the first, successful,
445 challenger away and replaces him to mate with the female. Video is 4x normal speed.
446



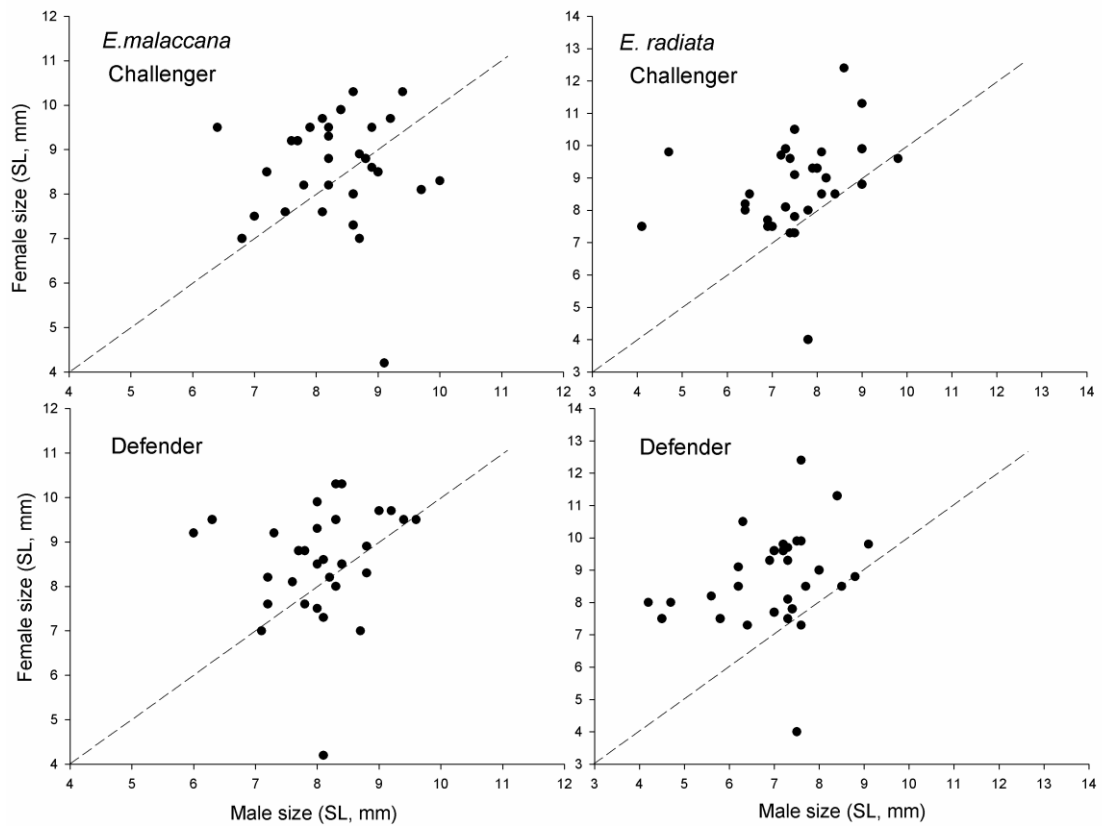
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448 **Fig. 1.**



449

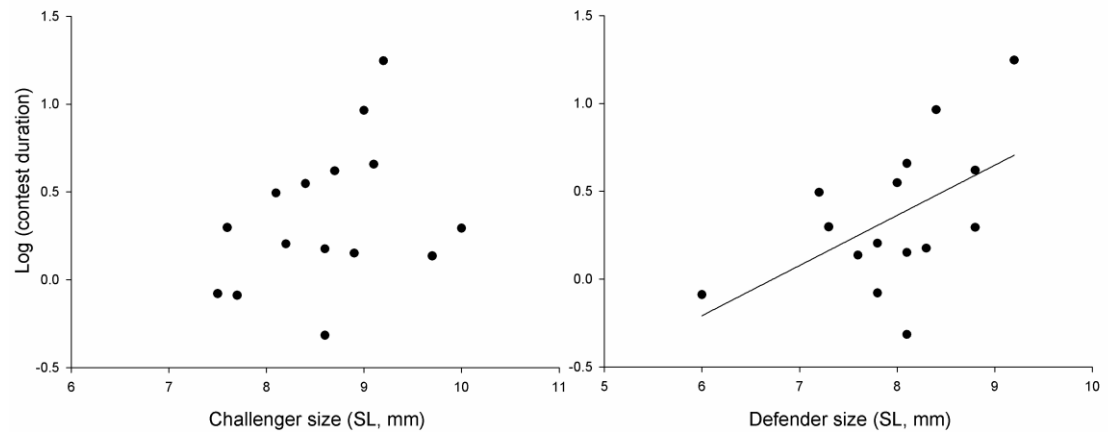
450 **Fig. 2.**
451



452

453 **Fig. 3.**

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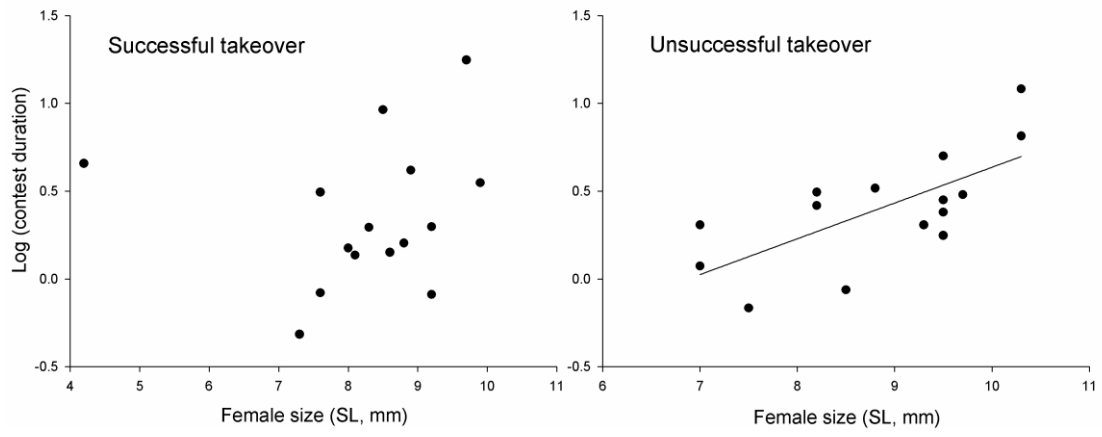


455

456 **Fig. 4.**

457

458



459

460 **Fig. 5.**

461

462

463 **Table 1** Number of cases where challenger was larger or smaller than defender in
 464 contests in *Echinolittorina malaccana* and *E. radiata*

Species	Challenger > Defender	Challenger < Defender	Binomial test (<i>p</i> -value)	<i>n</i>
<i>E. malaccana</i>	17	13	0.585	30
<i>E. radiata</i>	21	9	< 0.05	30

465

466

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