1 **Male spacing and female choice in a fiddler crab**

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5 D. M. Perez* and P. R. Y. Backwell

6
7 Research School of Biology, The Australian National University, Canberra, ACT,
8 Australia

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12 ***Corresponding author:** Dr. Daniela M. Perez

13 Division of Ecology and Evolution, Research School of Biology, The Australian
14 National University, Canberra, ACT 0200, Australia.

15 T: +61 02 6125 5481

16 E: dani.malgarini@gmail.com

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ABSTRACT

The aggregation of courting males is widespread among animal taxa, yet we do not understand why males congregate and therefore intensify local competition for female attention. The most commonly invoked theoretical explanation is that females preferentially approach clustered males due to the many benefits they would gain, and clustered males would therefore have higher mating success. However, although theoretical explanations of aggregation formation are well-advanced, empirical studies are scarce, especially in invertebrates. In fact, there is little evidence that females do prefer to approach clustered over spaced displayers. Here we address this question by using robotic crabs to test female preferences in fiddler crabs (a visually displaying species) and show that females do not preferentially approach clustered males. We suggest that if this pattern is more widespread, the most commonly invoked explanation of courting aggregations is of limited use. We offer explanations for the strong clustering behaviour we observe in this species and discuss the implications of this finding for the theoretical underpinnings of this research field.

INTRODUCTION

Clustered breeding distributions of males are common and widespread in the animal kingdom (Macedo et al. 2018). Communal breeding aggregations have recently regained the attention of biologists due to the surge of interest in collective behaviour (Hughey et al. 2018). However empirical studies that test the adaptive pressures that promote the formation of clustered males are scarce, especially in courtship signalling and invertebrates (Greenfield, 1994). Thus, the puzzling question of why males would aggregate with their competitors in order to attract females has been re-opened (Toth et al. 2015; DuVal et al. 2018; Giavazzi et al. 2018).

There is a cost to male aggregation: clustered males experience intense competition for female attention (Alexander 1975; Pruett-Jones 1988; Isvaran & St. Mary 2003) and a potential reduction in individual mating success (Toth et al. 2015). Furthermore, by clustering with competitors, less attractive males would be at a disadvantage if females directly compare and choose a mate within the cluster (DuVal et al. 2018).

Female costs for approaching clustered males can also be substantial. For example, their ability to discriminate and localise individual males within an aggregation could be compromised. In a reed frog, females did not exercise their preference for lower frequency calls when the sound sources were close together (Telford et al. 1989). In other frog species, females were less able to discriminate between clustered (closely spaced) callers even when their calls did not overlap (Richardson and Lengagne 2010); and female discrimination increased with the angular separation of the sound sources

(Schwartz and Gerhardt 1989). Another cost that females may face when approaching male aggregations is disruption and harassment (Foster 1983). In a water strider, for example, females can be overwhelmed by high levels of male harassment and this prevents them from exercising their preference for larger males (Lauer et al. 1996).

In species that cluster, both males and females must gain benefits that outweigh these costs. The most commonly invoked benefit for both sexes is that females have a preference for approaching clustered (rather than spaced) males. The benefit to males is that aggregating would deliver higher mating success than displaying alone. For less attractive males, aggregating around a highly attractive male may increase their mating success if they are able to intercept the approaching female (Hotshot hypothesis; Arak 1988; Beehler and Foster 1988). A male may need to aggregate in order to evaluate the quality of its rivals and how much courtship effort is needed. The benefits to females could include: (a) increased detectability of clusters from a distance (Greenfield et al. 2017); (b) increased ability to directly compare males and select the most attractive male (as opposed to the hypothesis raised above) (Isvaran and St. Mary 2003); (c) increased encounter of males in the shortest time and with the least risk (Alexander 1975); (d) reduced predation risk when in clusters (Rintamäki et al. 1995); (e) increased chances to seek extra-pair copulations within clustered groups of males (Wagner 1993).

Although female preferences for clusters are the most widely invoked explanations for communal displays, it is possible for clusters to form in the absence of female preferences. Males may aggregate in areas where females are common (Hotspot model: Bradbury and Gibson 1983). Aggregations may also arise due to the movement patterns

of females: in the Black Hole model of lek formation, it was suggested that male harassment of females causes her to move away from the harassment and approach the neighbouring male. This could result in more closely spaced males gaining a mating advantage and leks could emerge (Stillman et al. 1993).

One problem with this research field is that theoretical explanations of aggregation formation are common, complex and well-advanced, but empirical studies are rare. In a meta-analysis of lek mating systems, Fiske et al. (1998) found studies on two invertebrates and 25 vertebrates (including 14 bird species). We have very little evidence that females do, in fact, prefer to approach clusters of males over spaced displayers (Gerhardt and Huber 2002; Greenfield 2005; Pope 2005). Understandably, it is difficult to test female preferences for a single trait since it requires a controlled, experimental approach (such as acoustic phonotaxis trials or robotic animal experiments). In the reported phonotaxis tests of female preferences for clustered over spaced males, Morris et al. (1978) showed that female meadow katydids preferentially approached grouped males over spaced signallers. In eight other acoustic insects, however, males did not have a preference for clusters (see Greenfield 1994 for review). If female preference for aggregated displaying males is as rare as these early studies suggest, many of the theoretical assumptions are not supported.

Determining the extent and strength of female preferences for clustered signallers over a wide range of species, mating systems and communication channels is essential if we are to understand the repeated evolution of aggregated displays throughout the animal

118 kingdom (Giavazzi et al. 2018). Here we examine this question in a visually
119 communicating crustacean (the fiddler crab).

120

121 **Fiddler crabs as a model system**

122 There has been much debate about whether fiddler crabs form leks (Croll and
123 McClintock 2000). A lek is a cluster of displaying males that is not associated with the
124 underlying resource distribution (so females must select mates based on male attributes
125 alone); males compete with their neighbours for female attention (Figure 1a). In most
126 fiddler crab species with a ‘female choice’ type of mating system, male territories are
127 clustered and females visit males within these clusters. Females do not select males
128 based on their attributes alone (claw size and wave characteristics), but also consider the
129 structure of the male’s burrow, which directly influences the temperature that the female
130 will incubate her eggs (Backwell and Passmore 1996).

131

132 In *Austruca mjoeborgi* (a well-studied fiddler crab species and the subject of the current
133 study) there is a strong argument that males form leks. Males vigorously defend their
134 fairly evenly spaced territories and wave their large claw to attract females for mating
135 (Morrell et al. 2005). As a female nears, the surrounding males move off their
136 territories, approach the female and form a small cluster (2-6) around her (Reaney and
137 Backwell 2007). This is the only time a male will leave his territory unattended. As the
138 female moves through the population, males join in or drop out of the cluster. The
139 female visits one of the males in the cluster by walking directly towards him (Reaney
140 and Backwell 2007). The approached male continues to face the female and waves at
141 her, but moves backwards towards his territory, ‘leading’ the female back to his burrow.

142 The female briefly enters the male's burrow and either stays to mate or leaves to
143 continue sampling. Females use two distinct choice criteria: male phenotype determines
144 whether the female will approach a male and follow him back to his burrow; and
145 burrow characteristics determine whether she will stay, mate with that male and
146 incubate her eggs in his burrow (see Backwell and Passmore 1996).

147

148 We argue that the first part of the mate choice process is a lek: males leave their
149 territories and move towards the mate-searching female, forming a cluster of wavers all
150 competing for her attention. The female makes her choice based on male traits alone.
151 Only once her choice is made, does she examine the male's burrow and assess its
152 quality (Backwell and Passmore 1996; Reaney and Backwell 2007).

153

154 Males pay a large cost for clustering with their neighbours in order to court the female:
155 clusters not only increase the level of competition for female attraction that males face
156 (this is especially true for less attractive males), but, in doing so, males leave their
157 territories undefended, increasing the risk of losing it to burrowless intruder males
158 (Rorato et al., 2017). Territory ownership is extremely important. The territory consists
159 of a burrow that acts as a water source, a refuge from the heat, the tides, and predators,
160 and a mating and female incubation site. The territory also has a small area of sediment
161 surface (± 10 cm radius around the central burrow) that is used for feeding and a
162 courtship arena (Fayed et al. 2008). Thus, leaving the territory undefended in order to
163 join a cluster seems to pose too many risks for males.

164

We conducted an empirical study to understand why males aggregate by examining if aggregations are sexually selected in fiddler crabs. We investigated *A. mjoebergi* female preferences for clustered over spaced males by running experiments with robotic crabs. We hypothesized that: (1) if females exhibit preferences for clustered males, fiddler crabs support the traditional theoretical explanations that female preference promotes male aggregations; (2) if, on the other hand, females show no preference or preference for spaced males, this theory is refuted, suggesting that animal aggregations form from alternative mechanisms than previously predicted.

Figure 1. An aggregation of signalling *Austruca mjoebergi* males (A). A female under the translucent cup facing the robotic crabs during a choice trial in experiment 1 (B).

178 **METHODS**

179

180 *Austruca mjoebergi* (previously *Uca mjoebergi*) is a small fiddler crab (carapace mean
181 $\pm$ SD = 10.16 ± 1.43 mm; n = 200) that occurs on the northern coast of Australia. We
182 studied a population in the mangroves of East Point Reserve, Darwin, Australia
183 (12°24'31.89"S 130°49'49.12"E) from September – December in 2015 (experiment 1)
184 and 2018 (experiment 2). Female preferences were tested using custom-built robotic
185 crabs consisting of a twin-cam motor that moved a small metal arm in a motion exactly
186 mimicking the courtship wave of the species. The motor is remotely controlled to
187 regulate the exact timing of each wave using custom designed software (see Reaney et
188 al. 2008; Perez and Backwell, 2017 for further details of the robotic crabs). The choice
189 arena was a platform of 80 x 80 cm in size raised 70 cm above the ground and covered
190 with a 5 mm thick layer of mangrove sediment. The motor was buried under the testing
191 arena with only the metal arm protruded through the arena floor. The arm had a plaster
192 replica of an *A. mjoebergi* claw attached to it. The replica claws measured 19.5 mm
193 (considered an attractive size - larger than the natural size: mean = 18.01, SD = 2.95, N
194 =232) and were painted a yellow that matched the natural claw color of this species (see
195 Detto et al. 2006 for spectroscopy of the claw and paint). We ran our trials in the field
196 under semi-wild conditions. The choice arena was placed under a large awning and
197 surrounded by homogeneously distributed trees to minimize any environmental effects
198 on female choice. The location of the robotic crabs and the orientation of the test arena
199 were also randomly changed at approximately every 30 data points recorded and we did
200 not identify any side- or robotic unit- biases. Females were presented with a choice of
201 clustered and spaced robotic crab units, all producing identical synchronous waves at a

constant rate of 16.8 waves/minute. The robotic units were placed in an arc (radius = 20 cm counting from the robotic unit base and 22.5 cm from the robotic arm) around the female release point. The distance between all units was measured from the base of their robotic arms (centre of the crab). In experiment 1, we used eight robotic crab units. In the middle, four units were spaced 5 cm apart. On the sides, four units (two in each side) were spaced 15 cm apart (Figure 2), giving a central cluster of four males. In experiment 2, we used six robotic crab models placed in a circle around the female release point. Three of the robots were spaced 32 cm apart and three were spaced 5 cm apart (Figure 2). We based our choice for distances between clustered and spaced robots on the natural distribution of males in the field and their visual ecology. In high-density areas of the mudflat, the shortest distance found between two male burrows is of 5.92 cm (Chou et al. 2019) being that during courtship activity males can get even closer to each other. In low-density areas, on the other hand, burrows can be much farther apart. However, for a fiddler crab of *A. mjoebergi* mean size, the maximum range of visual acuity necessary to discriminate the identity of another crab does not surpass 32 cm (How et al. 2017). We chose to space the robotic crabs within this range of visual acuity where a male would still be able to recognize the identity of its nearest neighbors and compete for female attraction. More importantly, any attempt to space robotic crabs further apart would inevitably increase the radius of the choice arena from female release point and compromise female visual acuity.

Figure 2. Placement of robotic crab units in experiment 1 and 2. The circle in the centre represents the female releasing point and squares represent the position of the robots. Dashed lines indicate the distance between releasing point and robots, and between robotic crab units.

Running both experiments allowed us to separate the effects of a ‘central vs. side preference’ from a preference for the cluster itself. The first design presented all the males in the female’s frontal visual field. Previous work has shown that, when females of this species are presented with two different stimuli (a preferred vs. a non-preferred signal), they are more likely to exhibit their preference when the stimuli are presented and viewed in the same field of vision (i.e. on the same side of the test arena) than when the stimuli were presented on opposite sides of the female (Peso et al. 2014). Our first experiment therefore presented the stimuli in a distribution that facilitated maximum discrimination and localisation (Peso et al. 2014). This distribution of the robotic crabs presents a potential ‘edge effect’ problem: females may avoid/prefer males on the edge

of the group. Thus, we designed the second experimental design, which was closer to the natural conditions that a female would experience: males surrounded her and were therefore viewed over her entire visual range (fiddler crabs have 360° vision; Zeil and Hemmi 2006). Furthermore, the potential ‘edge effect’ is reduced.

Mate-searching females were captured as they wandered through the population of courting males actively approaching males and burrows. We measured female carapace width and housed them individually in shaded cups containing 0.2 cm deep seawater until we used them in the choice trials. For each trial, the female was placed at the release point in a small translucent cup that was remotely lifted after the robotic units waved three times (Figure 1b) (see Reaney 2008 for more details). As the female touched or approached to within 5 cm a robotic crab unit a choice for either spaced or clustered males was scored based on the position of the unit approached. We timed the duration of each trial from the time the crab was released until she reached a robot. The direction females face when placed under the cup would not affect choice, as fiddler crabs have a 360° vision (Zeil and Hemmi, 2006). Furthermore, fiddler crabs walk sideways, and prior to approaching a robotic unit, the female orients her body towards it. This happened either under the translucent cup or after release. Only the trials where females made clear choices were recorded. Trials were discarded if the female darted, passed a robotic unit at a constant speed (without making a short stop when close to it), ran to the edge of the arena, or remained stationary for >3 mins. Each female was tested once only (total of 220 females) and was released after testing so they could continue mate-searching. We were careful to release the females in non-catching areas to avoid recapture.

263

264 *Statistical Analyses:* We analysed the two experiments separately. We used a two-tailed
265 exact binomial test to compare the number of female responses to one of the clustered
266 stimuli (robotic units 3, 4, 5 or 6 in experiment 1; and units 1, 2 and 3 in experiment 2)
267 vs. one of the spaced stimuli (robotic units 1, 2, 7, or 8 in experiment 1; and units 4, 5
268 and 6 in experiment 2). Following, we tested for possible confounding effects on female
269 choices by running Student t tests to check if female sizes or the time it took for the
270 females to respond differ when they choose a clustered or a spaced male. We also ran a
271 Pearson's correlation to test if female size correlates with the time to make a choice. We
272 ran square-root transformations in duration for normality. Finally, we tested if females
273 have preferences for robotic units' spatial position in relation to the edge of the arena in
274 experiment 1 by running a Chi-square test. The units were divided in 4 categories: most
275 clustered units (units 4 and 5); edge-clustered units (units 3 and 6); spaced near-cluster
276 units (units 2 and 7); and most dispersed units (units 1 and 8) (Figure 2).

277

278 *Ethical Note:* No ethics permit was required for this study in 2014 (permits for decapod
279 research were introduced in 2015). We conducted the 2018 work under permit number
280 A2018/44 (Australian National University Animal Ethics Committee). In all years, we
281 limited the handling and the amount of time each crab was used as much as possible. No
282 crab was injured during the research, and they all continued their regular activities after
283 release. The work was conducted on land owned by the Darwin City Council and was
284 conducted under permit number DCC2322876.

RESULTS

Experiment 1: Females ($n = 131$) were significantly more likely to approach one of the spaced males than one of the clustered (85:46, binomial $P = 0.001$; Table 1). Female size did not differ between those that approached the spaced or the clustered males (t-test: $t = 1.53$, d.f. = 129, $P = 0.22$). There was no correlation between female size and the duration of the trial (Pearson's $r = -0.009$, $n = 130$, $P = 0.91$) (duration: median = 16s; range = 1-129s). It took significantly less time for females to approach one of the central, clustered males than to approach a spaced male (t-test: $t = 2.97$, d.f. = 129, $P = 0.004$).

We reanalysed the data by merging the results for robots on either side of the arena in experiment 1 (mirror images). The most clustered units (units 4 and 5) were approached 21 times; the edge-clustered units (units 3 and 6) were approached 25 times; the spaced near-cluster units (units 2 and 7) were approached 32 times; and the most dispersed units (units 1 and 8) were approached 53 times. There was a significant difference in the number of approaches in each category (Chi square test: $\chi^2 = 18.59$, d.f. = 3; $P < 0.001$), and there was an increase in the number of approaches as the robotic units were increasingly spaced.

Experiment 2: Females ($n = 89$) were significantly more likely to approach one of the spaced males than one of the clustered (56:33 binomial $P = 0.019$; see Table 1). Female size did not differ between those that approached the spaced or the clustered males (t-test: $t = 0.59$, d.f. = 87, $P = 0.56$). There was no correlation between female size and the duration of the trial (Pearson's $r = -0.06$, $n = 87$, $P = 0.59$) (duration: median = 19.6s,

range = 0.59-89.6s). It took females an equivalent amount of time to approach a clustered and a spaced male (t-test: $t = 0.56$, d.f. = 86, $P = 0.58$).

Table 1. The number of responses to each robotic unit, the mean time it took females to make their choice, and the mean size of the females. Data is presented as mean $\pm$ standard deviation. The statistics are the comparison between the clustered and the spaced robots within each experiment.

	Robotic unit	# choices	Choice duration $\bar{x} \pm \text{s.d.}$	Female size $\bar{x} \pm \text{s.d.}$
Exp 1	1	26	34.77 ± 31.05	8.68 ± 0.84
	2	11	26.82 ± 34.29	8.90 ± 1.34
	3	7	10.29 ± 10.48	8.40 ± 1.50
	4	13	16.62 ± 20.41	8.90 ± 0.60
	5	8	17.00 ± 12.61	9.49 ± 1.15
	6	18	12.89 ± 10.77	8.96 ± 1.13
	7	21	17.33 ± 16.90	8.66 ± 1.10
	8	27	26.37 ± 23.50	8.70 ± 1.05
	Spaced (1, 2, 7, 8)	85	26.76 ± 26.77	8.71 ± 1.03
	Clustered (3, 4, 5, 6)	46	14.26 ± 14.16	8.95 ± 1.09
t (d.f.)			2.97 (129)	1.53 (129)
(p-value)			$P=0.004^*$	0.22
Binomial (p-value)			$P=0.001^*$	
Exp 2	1	9	18.89 ± 19.07	8.44 ± 0.98

2	8	24.88 ± 13.63	8.41 ± 1.20
3	16	23.22 ± 20.06	8.46 ± 1.32
4	19	20.34 ± 15.57	8.41 ± 0.05
5	20	23.24 ± 14.89	8.27 ± 0.09
6	17	17.51 ± 10.84	8.23 ± 0.96

Spaced (4, 5, 6)	56	20.53 ± 13.92	8.31 ± 1.02
Clustered (1, 2, 3))	33	22.44 ± 18.04	8.45 ± 1.17

t (d.f.)	0.56 (86)	0.59 (87)
(p-value)	0.58	0.56

Binomial (p-value)	0.019*
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318 **DISCUSSION**

319

320 Females did not preferentially approach clusters of displaying males over spaced
321 signallers. There, in fact, appears to be a strong female preference for spaced males.
322 This was found with both of our experimental designs. In experiment 1, we noticed that
323 females approached units 1 and 8 more than 2 and 7. In addition, females took longer to
324 approach spaced units. This is likely to be a result of an ‘edge effect’ that we
325 subsequently eliminated in experiment 2 (and found no difference in the time it took
326 females to approach the chosen male). In both experiments, however, females were
327 significantly more likely to approach one of the more spaced males over one of the
328 clustered males. Why, then, do males cluster around the female?

329

330 The most commonly invoked explanation of clustering in a lek (females preferentially
331 approach clustered males) is not applicable to this species. What other explanations may
332 apply to this system? The Hotspot model of lek formation (Bradbury and Gibson 1983)
333 suggests that leks may form if males cluster in areas where females are common. This
334 does not apply to *A. mjoebergi* since the clusters are ephemeral and form around a
335 moving female (males approach the female by also maintaining a safe distance from
336 their burrows). The Black Hole model of lek formation (Stillman et al. 1993) is a
337 potential explanation since the pattern of female movement determines the formation of
338 the lek: if a female gets harassed, she would move away and approach a neighbouring
339 male instead (resulting in the formation of a cluster since more closely spaced males
340 would be more likely to be visited by the fleeing female). However, more recent work
341 on the Black Hole idea has suggested that it is an unlikely explanation in any system

since female harassment does not appear to promote male clustering (Isvaran and St. Mary 2003). In addition, harassment in this species is quite reduced compared to other fiddler crab species (Crane, 1975). Another potential explanation is the Hotshot hypothesis: aggregating around an attractive male may increase the mating success of less attractive males if they are able to intercept the female (Arak 1988; Beehler and Foster 1988). However, the operational sex ration in fiddler crabs is far too low (active mating males : reproductive females = 45:1, Reading and Backwell 2007) for less attractive males to profit from being near an attractive male.

There are multiple disadvantages to male clustering in this species. Clustered males experience intense competition from their neighbours (Alexander 1975; Pruett-Jones 1988; Isvaran and St. Mary 2003). They also facilitate the direct comparison of males by the female, so only the most attractive males would benefit (DuVal et al. 2018). Males also risk losing their territories when they leave them in order to court a female. On top of this, females discriminate against them because they preferentially approach spaced males. Why do these males cluster? We discard the possibility that clustering is a strategy to lower the risks of predation, as old-world species, such as *A. mjoebergi*, are under an exceptionally low predation pressure (Perez et al. 2016; Bourdiol et al. 2017). Therefore, we can think of two explanations. First, we know that females prefer to approach closer males (Bookmythe et al. 2008) so moving towards a female and joining a cluster may be a way of eliminating the spatial disadvantage for more distant males. Second, males in the cluster wave in synchrony at the female (Rorato et al. 2017). Females do not have a preference for synchrony per se; it results from males competing to produce leading waves since females have a strong preference for leaders

(Reaney et al. 2008). It is possible that males need to be close to their competitors in order to monitor their wave timing. This would allow them to compete to produce leading waves.

In conclusion, in species where males aggregate to court females, individual males pay costs of increased competition. In those species where females do not have a preference for clustered males (which appears to be the most common scenario; Greenfield 1994; this study), there must be a reason for males to form the clusters and for females to approach the clusters. For the fiddler crab studied here, we suggest that males cluster in order to monitor the wave timing of their competitors so that they can produce leading waves. Females approach clusters because they have a strong preference for leading waves.

We call for more empirical studies that test female preferences for clustered over spaced males, and for investigations that delve more deeply into the causes and consequences of clustering behaviour.

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