



Territorial defense in a network

audiences only matter to male fiddler crabs primed for confrontation

Darden, Safi K.; May, Maggie K.; Boyland, Natasha K.; Dabelsteen, Torben

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1 Territorial defence in a network: audiences only matter to male fiddler crabs primed for
2 confrontation

3

4 **Lay Summary:** Being part of a social network means that responses to social confrontations
5 are likely to be more complex than they might seem. Indeed, here we find effects of a wider
6 network of conspecifics on an individual's behaviour in male European fiddler crabs. Males
7 became more aggressive toward intruders if their neighbour was watching when they had
8 previously observed an aggressive interaction between their neighbour and a male territory
9 intruder.

10

11 **Abstract**

12

13 Territorial contests often occur in the presence of conspecifics not directly involved in the
14 interaction. Actors may alter their behaviour in the presence of this audience, an 'audience
15 effect', and audiences themselves may alter their behaviour as a result of observing an
16 interaction, a 'bystander effect'. Previous work has documented these effects by looking at
17 each in isolation, but to our knowledge, none has investigated their interaction; something
18 that is more likely to represent a realistic scenario for species where individuals aggregate
19 spatially. We therefore have a somewhat limited understanding of the extent and direction of
20 these potentially complex indirect social effects on behaviour. Here we examined how
21 audience and bystander effects work in tandem to modify resident male aggressive behaviour
22 towards intruders in European fiddler crabs, *Afruca tangeri*. We found that male crabs with
23 an audience showed greater aggressive behaviour towards an intruder compared to males
24 without an audience, but only if they had acted as a bystander to an aggressive signalling
25 interaction prior to the intrusion. Indeed, bystanding during aggressive interactions elevated

26 aggressive responses to intruders maximally if there was an audience present. Our results
27 suggest that bystanding had a priming effect on territory-holding males, potentially by
28 providing information on the immediate level of competition in the local neighbourhood, and
29 that same-sex audiences only matter if males have been primed. This study highlights the
30 fundamental importance of considering broader interaction networks in studying real-world
31 dyadic interactions and of including non-vertebrate taxonomic groups in these studies.

32

33 Key words: audience effect, bystander effect, invertebrate, fiddler crab, *Afruca tangeri*, *Uca*
34 *tangeri*

35 **Background**

36

37 Considering communication in the context of a wider network has revealed behaviours and
38 effects such as eavesdropping, audience effects and bystander effects, that would not be
39 observable from a dyadic approach (McGregor, 2005). Territorial contests are typically
40 settled through pair-wise interactions within a network of multiple individuals, rather than in
41 (McGregor and Dabelsteen, 1996). Audience effects occur when animals modify their
42 behaviour due to the presence of other individuals not involved in the interaction
43 (Zuberbühler, 2008) and these effects have been shown to alter the intensity of agonistic
44 displays in a number of species (Cruz and Oliveira, 2015; dos Santos et al., 2017;
45 Fitzsimmons and Bertram, 2013; Montroy et al., 2016; Setoguchi et al., 2015). In the context
46 of territorial defence, the audience effect has been demonstrated to be dependent not only on
47 the sex of the audience, but also on the territorial status and familiarity of individuals in the
48 wider network (Bertucci et al., 2014; Dzieweczynski et al., 2005). Observed differences in
49 behaviour in the presence of an audience suggest that individuals can (1) assess attributes of
50 their audience and (2) adjust their behaviour as a strategy to counter costs (or strengthen
51 benefits) that can come with eavesdropping, or more generally, gathering of social
52 information by audiences (Earley and Dugatkin, 2002). In the bystander effect the audience
53 members themselves are influenced by observing an interaction (Earley and Dugatkin, 2002;
54 Oliveira et al., 2001; Peake et al., 2006). The observation acts directly on the motivational
55 system (Hirschenhauser and Oliveira, 2006; Oliveira et al., 2001) and prepares individuals for
56 what may happen next in their social environment (Antunes and Oliveira, 2009). Individuals
57 can, for example, be primed to augment their levels of aggression in interactions following
58 bystanding. For example, Clotfelter and Paolino (Clotfelter and Paolino, 2003) found
59 increased aggressiveness by Siamese fighting fish, *Betta splendens*, towards a novel male

60 conspecific after the observation of an aggressive interaction. However, reverse priming, a
61 reduction in aggressive behaviour, has also been found, for example, in a study of crayfish,
62 *Orconectes rusticus* (Zulandt et al., 2008), which to our knowledge is also the only
63 invertebrate species in which bystander effects have been investigated.

64

65 Although audience and bystander effects are frequently documented, it is not clear from the
66 literature how bystander and audience effects may interact. This represents a potential key
67 gap in our understanding of the strength or importance of these effects in *in situ* contexts
68 where they are likely to happen concurrently, particularly in species where individuals live in
69 aggregated communities. A study in Siamese fighting fish, suggests that simply viewing an
70 unfamiliar male prior to a contest with another male can prime males for increased aggression
71 during a fight, irrespective of whether the audience is present or not during the fight itself
72 (Matos et al., 2003). It also highlights the complexity of bystander and audience effects and
73 the need to manipulate these effects in tandem in order to deepen our understanding of the
74 significance of dynamics in the social environment for the expression of behaviour. Here we
75 investigate the interplay between audience and bystander effects on the territorial behaviour
76 of male European fiddler crabs, *Afruca tangeri*. Fiddler crabs are very unlikely to be found in
77 isolation (Pope, 2005), and therefore have a high likelihood of engaging in social interactions
78 with multiple receivers within signal range. Males actively defend territories around their
79 burrows (Hemmi and Zeil, 2003) with their one greatly enlarged claw, used for the
80 production of highly conspicuous visual agonistic and courtship signals and for fighting
81 (Oliveira and Custódio, 1998; Wolfrath, 1993). Male crabs without a burrow will wander
82 through the population and challenge burrow holders in attempts to acquire a burrow (Jordao
83 and Oliveira, 2005). Burrow holding males must therefore invest in an agonistic response in
84 order to retain residency (Oliveira and Custódio, 1998). Recent work in another fiddler crab

85 species suggests that same-sex audiences do not matter for expressed levels of aggression
86 (dos Santos et al., 2017), given the ubiquity of males in the immediate social environment
87 (i.e. males are highly likely to have male neighbours), this is perhaps not surprising. We
88 propose instead that males will fine-tune their responsiveness to their social environment
89 according to current social information, such as the immediate level of competition in the
90 neighbourhood. If males observe a territorial dispute in their neighbour's territory, they
91 should be primed for a possible challenge of their own territory and therefore will be more
92 responsive or sensitive to their immediate social environment. In this case, bystanding to an
93 aggressive interaction between a neighbouring male and a stranger (intruding male), should
94 augment the aggressive response exhibited by males towards intruders appearing close in
95 time. This should be particularly so when the social stimuli are increased by a male audience
96 as this audience can gather information on the interaction outcome (e.g., the competitive
97 ability of his male neighbour) and in the least, acts as an indicator of a more competitive
98 social environment (i.e. more males are present) than when no male audience is present. In
99 this investigation, we used an *in situ* experimental manipulation of the social environment
100 that burrow holding male crabs experienced to test such effects during territorial
101 confrontations in the home environment.

102

103 **Methods**

104

105 The study was carried out in the Parque Natural da Ria Formosa, Portugal (N370927,
106 E073244) from May to July 2012 in order to quantify audience and bystander effects *in situ*
107 in males of a free roaming population of European fiddler crabs. To test focal male crabs at
108 their home burrow an arena made of bamboo and sand-coloured fabric was placed around
109 two neighbouring males and their burrows (Fig. 1). Neighbouring male pairs were selected

110 according to three criteria: (1) they were matched in claw size (estimated by visual
111 comparison); (2) they were exhibiting courtship behaviour (courtship waving) indicating that
112 they were actively defending a burrow; and (3) they were within one meter of one another
113 (measured using a measuring tape stretched in a straight line from the center of one burrow to
114 the other). Stimulus crabs captured from other areas of the mudflat were tethered with 10cm
115 of clear monofilament line to bamboo posts inserted into the substrate within the arena to
116 simulate wandering male crabs (intruders). This method of tethering stimulus crabs is
117 relatively standard and has been used successfully in this and several other fiddler crab
118 species to elicit both courtship and territorial behaviour as observed under natural conditions
119 (Detto and Backwell, 2009; Detto et al., 2006; Detto et al., 2010; How et al., 2008; Milner et
120 al., 2010; Pope, 2005; Reaney, 2007)(Booksmythe et al., 2010). Intruders were matched in
121 claw size to focal crabs using visual comparison. Focal crabs were exposed to two 5-minute
122 phases: a ‘bystanding phase’ (neighbour interacts with a simulated intruder) and a subsequent
123 ‘interaction phase’ (focal male interacts with a simulated intruder) in one of four treatments
124 (3 control and 1 experimental): (1) *null control* – no neighbour-intruder interaction in the
125 ‘bystanding phase’ and no audience in the ‘interaction phase’ (n=11); (2) *audience control* –
126 no neighbour-intruder interaction in the ‘bystanding phase’ and an audience in the
127 ‘interaction phase’ (n=10); (3) *bystander control* – neighbour-intruder interaction in the
128 ‘bystanding phase’ and no audience in the ‘interaction phase’ (n=11); and (4) *bystander and*
129 *audience (experimental)* – neighbour-intruder interaction in the ‘bystanding phase’ and
130 audience in the ‘interaction phase’ (n=11) (Fig. 1).

131

132 In the ‘bystanding phase’ of treatments (3) and (4) a stimulus male was tethered 40cm from
133 the neighbour’s burrow (min 90 cm from the focal male’s burrow) and left for 5 minutes after
134 both males (focal and neighbour) had emerged from their burrows. In the ‘bystanding phase’

135 of treatments (1) and (2) the arena was approached (and stimulus male placement simulated)
136 and the crabs were then left for 5 minutes after both males had emerged from their burrow. In
137 the interaction phase a stimulus male was tethered 40cm from the focal male's burrow to
138 simulate a wandering male. In treatments (2) and (4) the neighbouring male was allowed to
139 emerge from his burrow and act as an audience while in treatments (1) and (3) the
140 neighbouring male's burrow was blocked to prevent him from emerging during the trial
141 period. Phases began when the focal or both males had surfaced (carapace and major claw
142 visible), as applicable, and lasted for five minutes. Following a trial, burrows were marked
143 with a small flag and within a semi-lunar tidal cycle these areas were avoided for further
144 testing to ensure that males were not re-used over the course of the study. We quantified
145 aggression as a behavioural state by measuring the duration of time that focal males were
146 engaged in aggressive behaviours toward the simulated intruder in the 5-minute interaction
147 phase. The observed aggressive behaviour, following previously published methods (see
148 Burford et al., 2000; Oliveira et al., 1998; Wolfrath, 1993), included both non-contact
149 aggression (threat displays) and that involving physical contact (pushing, grappling and
150 tossing) and the intensity of enactment represents the focal male's willingness to escalate the
151 contest (Oliveira et al., 1998; Wolfrath, 1993). We compared the time focal males spent
152 performing aggressive behaviour among treatments with an analysis of variance with
153 treatment as a fixed effect (SPSS v. 22). We included inter-burrow distance between the focal
154 and neighbour as a covariate in the model as this varied across focal individuals. Post hoc
155 analyses were carried out on the marginal means using a least significant difference
156 adjustment for multiple comparisons. All behaviours were scored from video recordings
157 (Panasonic HDC-SD800 camcorder) of the trials by a single observer (MKM) naïve to the trial
158 condition.

159

160 The study was carried out under permit (ICNF, Portugal) following ethical approval from the
161 first author's home institution. All captured crabs were kept singly in shaded containers filled
162 with sea water and mud prior to testing and released back to their area of capture at the end of
163 a trial. Crabs were marked with non-toxic paint to ensure that they were not used more than
164 once in case of recapture.

165

166 **Results**

167

168 There was an overall effect of the treatment that focal males experienced on the amount of
169 aggressive behaviour they displayed toward a simulated intruder ($F_{3,38}=11.797$, $p<0.0001$,
170 Fig. 2). Our post hoc analysis revealed that there was an effect of having a neighbouring male
171 audience present during a territorial intrusion on the level of aggression expressed by a
172 burrow-holding male, but only if burrow-holding males had previously acted as bystander
173 (Treatment 4) to a neighbouring aggressive interaction (Table 1; Fig. 2). In short, males in
174 Treatment 4 behaved more aggressively than in any other treatment. Males in two of the
175 control treatments (Treatments 1 and 2) did not differ from one another in behaviour, but
176 males in the null control (no bystanding and no audience; Treatment 1), were less aggressive
177 than males in the bystander control (bystanding, no audience) (Treatment 3).

178

179 **Discussion**

180

181 Gleaning information from the social environment is essential for an individual to respond to
182 this environment appropriately (Danchin et al., 2004; Seppanen et al., 2007; Valone, 2007).
183 Individuals living in systems that are likely to be high in social noise will be under particular
184 pressure to either filter out information to avoid an inappropriate response or to use specific

185 cues to alert them to a situation where an active response may be required (e.g., Fitzsimmons
186 et al., 2008; Naguib et al., 2004). This latter priming effect may be particularly important in
187 predicting that, for example, a territorial challenge is likely to occur. The anticipation of
188 being challenged is likely to affect not only how individuals respond to a rival conspecific
189 during a direct interaction, but also how they respond to the presence of other conspecifics in
190 the immediate environment. These individuals that are not part of the interaction, may
191 themselves be gleaned social information (i.e. they are conspecific audiences). In this study
192 we found the first evidence that a neighbouring male audience moderated male European
193 fiddler crab behaviour towards an intruder, but only if males had acted as bystander to an
194 aggressive interaction between a male neighbour and a same-sex intruder immediately prior
195 to the encounter. This suggests that focal males that had viewed an aggressive interaction
196 between his neighbour and an intruder were somehow primed for heightened responsiveness
197 to having a male audience present during an interaction between himself and a territorial
198 intruder. The observed increase in aggressiveness was likely also a function of a general
199 priming for an aggressive response as a result of the bystanding, since we did detect greater
200 aggressiveness when males without an audience had acted as bystander compared to males in
201 our null control (no audience and no bystanding).

202

203 The prevalence of the use of public information (Danchin et al., 2004) suggests that it could
204 be beneficial for individuals to employ strategies to manage the perceptions of unintended
205 receivers. Fighting could communicate the focal male's motivation to defend his territory
206 (Detto et al., 2010) or ability to do so (Peake et al., 2001) to his neighbour. However, we did
207 not see an effect of a neighbouring male audience unless the focal male had previously acted
208 as a bystander to an aggressive interaction between his neighbour and an intruder. Bio-
209 regulatory mediators of the adjustment of aggressive behaviour are likely to be affected in

210 males that anticipate a territorial challenge based on cues in their social environment;
211 facilitating an adjustment to an increased competitive environment with the appropriate
212 behavioural response (Antunes and Oliveira, 2009). It could be that the simple presence of a
213 neighbour is not enough of a cue of the extent of the competitive environment, given the
214 ubiquity of territorial neighbours, and their familiarity, in a male's visual field (Detto et al.,
215 2010; Hemmi and Zeil, 2003; Pope, 2005). Instead, if a territorial challenge has been
216 observed immediately prior to an intrusion, effects on bio-regulatory mechanisms (Oliveira et
217 al., 2001) could drive a response directly or at least provide a cue as to the probability of an
218 escalation of aggression that could lead to a territorial takeover (Oliveira, 2009).

219

220 The bystander effect detected in this study is consistent with work in vertebrate species
221 demonstrating increased levels of aggression (e.g., Clotfelter and Paolino, 2003), but
222 inconsistent with the reverse priming demonstrated in another crustacean species (Zulandt et
223 al., 2008). In our study, burrow holding males will have invested energy into establishing
224 territory boundaries with their neighbours (Detto et al., 2010) and as such intruders are a
225 potential threat to the territory more generally if they were to take over a neighbour's burrow.
226 Zulandt and colleagues (Zulandt et al., 2008) suggest that the bystander effect could be
227 resource dependent such that when resources are abundant, and consequently their value
228 reduced, an individual will avoid escalation if the observation of a fight indicates that there is
229 an increased likelihood of being challenged within their network. In the present study males
230 were at their home burrow and as a consequence were defending a valuable resource; an
231 added ecological realism that may have contributed to the direction of the effect.

232

233 Our study demonstrates that there is likely to be a complex interaction between audience and
234 bystander effects in systems where individuals are part of a network of conspecific

235 interactants. The results suggest that selection has enhanced the use of public information to
236 increase the appropriateness of responses to social stimuli. We investigated effects of the
237 presence of a fiddler crab's nearest neighbour, an individual that the focal is likely to have
238 interacted with before and to be familiar with, however, laboratory work on audience effects
239 has demonstrated that attributes of an audience can influence physiological and behavioural
240 effects on individuals, for example, sex and territorial status (Dzieweczynski et al., 2005).
241 Future *in situ* work investigating behavioural reactions when the audience is a *non*-neighbour
242 or a female, would therefore be particularly enlightening.

243

244 **References**

245

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357 Figure legends

358

359 Figure 1. Overview of experimental arenas and 4 treatments (3 control and 1 experimental)
360 used to investigate bystander and audience effects in male European fiddler crabs (see text for
361 details).

362

363 Figure 2. Average time that male European fiddler crabs spent engaging in aggressive
364 behaviour toward experimentally introduced male intruders in 4 social treatments (see Fig. 1)
365 designed to test for bystander and audience effects (Estimated Marginal Mean (EMM) \pm SE;
366 matching letters indicate treatments where $p > 0.05$ for tested differences).

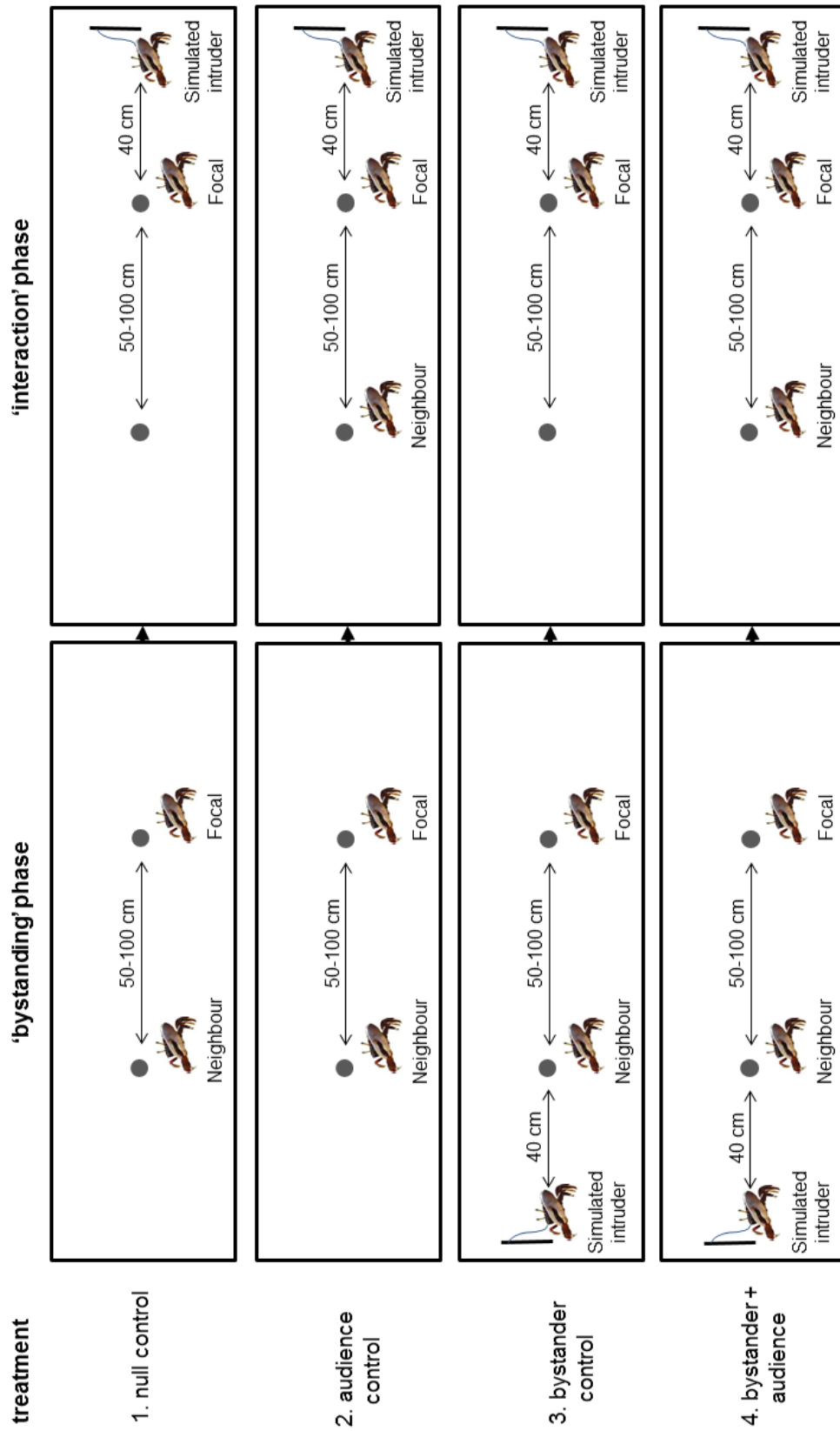
367

368 Table 1. Results of the *post hoc* analysis of differences among treatments in burrow-holding
 369 male aggressive responses to simulated intrusions by conspecific male fiddler crabs. P-values
 370 in bold indicate where significant differences in aggressiveness were found.

Treatment A	Treatment B	Mean difference	95% CI for Difference		<i>P</i>
			Lower bound	Upper bound	
1 - Null control	2 - Audience control	-31.04	-82.41	20.33	0.229
	3 - Bystander	-53.73	-103.39	-4.07	0.035
	4 - Bystander and audience	-143.18	-194.50	-91.85	p<0.001
2 - Audience control	3 - Bystander	-22.69	-73.91	28.53	0.375
	4 - Bystander and audience	-112.14	-163.35	-60.92	p<0.001
3 - Bystander	4 - Bystander and audience	-89.45	-140.48	-38.42	0.001

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