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**THE INFLUENCE OF SEX ON FEEDING BEHAVIOUR IN PACIFIC WHITE SHRIMP  
(*Litopenaeus vannamei*).**

**HIGHLIGHTS**

- Clear differences in feeding behaviour between male and female *Litopenaeus vannamei*.
- Males arrived to the feeding tray faster and fed for longer than females.
- Females exhibited greater levels of inactivity and more signs of stress than males.
- These behavioural differences are important when choosing mono- vs mixed-sex culture.

1 **THE INFLUENCE OF SEX ON FEEDING BEHAVIOUR IN PACIFIC WHITE SHRIMP**  
2 **(*Litopenaeus vannamei*).**

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15  
16 **Abstract**

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19 The Pacific white shrimp (*Litopenaeus vannamei*) is the most cultivated species in crustacean  
20  
21 aquaculture and a potentially important consideration for its production could be the use of monosex  
22  
23 cultures. Generally, female penaeid shrimp are larger than males due to a greater gain in mass per  
24  
25 moult cycle, resulting in a clear size dimorphism in adults. It is unknown whether this dimorphism is  
26  
27 driven by differences in feeding behaviours between male and female *L. vannamei*, which may be  
28  
29 important in deciding whether or not to use monosex cultures. Here adult *L. vannamei* (n= 20; 26.02 ±  
30  
31 0.66 g) were identified by sex (n= 10 per sex) and allocated to separate tanks for individual  
32  
33 recognition. Following 24 h feed-deprivation, individuals were introduced to test arenas along with  
34  
35 feed provided *ad libitum*. Shrimp were recorded for 20 minutes in the test arena, and this was repeated  
36  
37 once per day, for five consecutive days. Several sets of behaviours were analysed in relation to  
38  
39 feeding, and tracking of individuals across repeated measures allowed behavioural variation both  
40  
41 within- and between-individuals to be monitored. Results revealed several behavioural differences  
42  
43 between males and females. Females were generally less active than males, while males spent more  
44  
45 time detecting feed and feeding. In general, males were bolder than females, arriving more quickly to  
46  
47 the feeding tray and there was less individual variation in male feeding activity. These clear  
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49 differences in feeding behaviour between female and male *L. vannamei* support growth advantages in  
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51 females as a result of better food utilisation and require consideration for future use of monosex  
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53 cultures.  
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29 Keywords: Feeding activity; Penaeid shrimp; Repeated measures; Sex differences; Individual  
30 variation.

## 31 **1. Introduction**

32 Studying the behaviour of animals in aquaculture can be challenging due to the nature of the habitat  
33 and the complexity and variation of behaviours that are exhibited (Bégout *et al.*, 2012). However,  
34 understanding animal behaviour under aquaculture conditions is becoming recognised as an effective  
35 non-invasive tool for evaluating husbandry techniques (Almazán-Rueda *et al.*, 2004), stock growth  
36 (Martins *et al.*, 2005), feed management protocols (Andrew *et al.*, 2002; Noble *et al.*, 2007; Sánchez  
37 *et al.*, 2009) and welfare (Martins *et al.*, 2012). Nevertheless, most of the advances in applying  
38 behavioural observations to aquaculture are related to finfish production, with fewer studies  
39 conducted in other aquaculture industries, such as shrimp production (e.g. Nunes *et al.*, 2006; Da  
40 Costa *et al.*, 2016; Santos *et al.*, 2016). Additionally, findings are often applied generally across  
41 farmed populations and do not consider differences that are likely to occur between individuals.

42 One of the most important species in shrimp aquaculture is the Pacific white shrimp (*Litopenaeus*  
43 *vannamei*) (FAO, 2018), with its successful production driven by factors such as high growth rates as  
44 well as an ability to tolerate a range of densities and water qualities (Briggs *et al.*, 2004; Bondad-  
45 Reantaso *et al.*, 2012; Jory and Cabrera, 2012). However, there are also high feeding costs associated  
46 with this species (Hung and Quy, 2013) due to apparent slow feeding behaviours (Costero and  
47 Meyers, 1993; Peñaflores and Virtanen, 1996) which result in the production of a large amount of  
48 waste products (Smith *et al.*, 2002; Jescovitch *et al.*, 2018). In recent years there has been growing  
49 interest in understanding shrimp feeding behaviour to attempt to tackle this problem and feeding  
50 frequencies, stocking densities and attractability of feeds have all been studied using behavioural  
51 measures (Nunes *et al.*, 2006; Pontes *et al.*, 2008; Lima *et al.*, 2009; Da Costa *et al.*, 2016).  
52 Nevertheless, much uncertainty still exists about the feeding behaviours of *L. vannamei* and more  
53 research is necessary, especially at the level of the individual (Bardera *et al.*, 2018). In particular,  
54 differences between males and females are often overlooked and this may be an important  
55 consideration when examining such behaviours.

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In penaeid shrimp there are a number of differences between males and females that may drive differences in feeding behaviours. In general, females are larger than males (Campos-Ramos *et al.*, 2006; Gopal *et al.*, 2010), with a larger cephalothorax and a wider first abdominal segment (Moss *et al.*, 2002; Pérez-Rostro and Ibarra, 2003). Sexual dimorphism in cultured *L. vannamei* starts to appear when shrimp reach 10 - 17 g (Chow and Sandifer, 1991; Pérez-Rostro *et al.*, 1999). These size differences are most likely caused by different biological requirements at the onset of sexual maturation (Pérez-Rostro and Ibarra, 2003), with females obtaining more mass per moult cycle than males (Hansford and Hewitt, 1994). Interestingly, it has been shown that female monosex cultures of *L. vannamei* and also Asian tiger shrimp (*Penaeus monodon*) grow faster than mixed-sex or male monosex cultures (Hansford and Hewitt, 1994; Moss *et al.*, 2002; Bajaniya *et al.*, 2014). Indeed, sexual dimorphism may be useful in separating males and females during culture to secure consistent harvest size (Gopal *et al.*, 2010). Males and females are therefore likely to exhibit differences in feeding behaviours but little to nothing is known about the effects of sex on shrimp behaviour.

In addition to understanding how feeding behaviour changes with sex in *L. vannamei*, it is important to consider levels of individual variation within each sex. Although held under the same conditions (e.g. water parameters, feed-deprivation), subjects from the same population can present individual variation due to morphological and physiological limitations (Hazlett, 1995), differences in sensory capabilities (DeWitt *et al.*, 1998) and learning abilities (Briffa *et al.*, 2008). Understanding these differences in individual behaviour within a population can result in improvements in production. For example, Ibarra-Zatarain *et al.* (2016) found that bolder individuals exhibited higher growth, food conversion and survival and individual differences have important outcomes for the health, disease susceptibility and welfare of stock animals in aquaculture (Castanheira *et al.*, 2017).

The aim of this study was to examine the effect of sex on *L. vannamei* feeding behaviour. Male and female shrimp were individually video-recorded to analyse their feeding behaviours. Shrimp were observed multiple times over time to additionally gain a measure of individual variation and determine whether this varies with sex. Information gathered from this study will provide a better

1  
2 82 understanding of the influence of sex on *L. vannamei* feeding behaviour, which can be used to review  
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4 83 the use of mixed-sex or monosex cultures in the production of this commercially-valuable species.

## 5 84 **2. Materials and Methods**

### 6 7 8 85 **2.1. Shrimp husbandry**

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10 86 Pacific white shrimp *Litopenaeus vannamei* were obtained from The Fresh Shrimp Co. (Newcastle,  
11  
12 87 United Kingdom) in July 2017 and maintained in two closed 300 l recirculation systems at the  
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14 88 University of the West of Scotland (Paisley, United Kingdom). The recirculation systems comprised  
15  
16 89 three holding tanks (60 x 37 x 40 cm, length x width x depth) and a sump (65 x 50 x 39 cm) with  
17  
18 90 aeration provided to all holding tanks. Shrimp were kept in artificial sea water (Seamix, Peacock salt)  
19  
20 91 which was passed through a UV filter connected to the sump tank. Water parameters in holding tanks  
21  
22 92 were  $30 \pm 1$  ppt salinity,  $26.2 \pm 0.4^\circ$  C temperature,  $> 5$  mg/l dissolved oxygen,  $7.7 \pm 0.2$  pH (mean  $\pm$   
23  
24 93 S.E.) and the photoperiod was 12 h light/dark. In the holding tanks shrimp were fed *ad libitum* (~ 10%  
25  
26 94 ration of tank biomass) a 57% crude protein diet (Gemma Diamond 1.0, Skretting France) equally  
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28 95 divided across three feeding sessions per day (09.00, 13.00 and 19.00). Excess food and faeces were  
29  
30 96 removed after each feeding. Ammonia, nitrate and nitrite were monitored twice daily and a 50% daily  
31  
32 97 water change was carried out on all the systems.

### 33 34 35 36 37 38 98 **2.2. Experimental shrimp**

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41 99 Twenty mature shrimp ( $26.02 \pm 0.66$  g) (mean  $\pm$  S.E.) with all appendages in good condition were  
42  
43 100 selected from mixed-sex holding tanks for use in experiments. They comprised 10 males ( $27.25 \pm$   
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45 101  $0.80$  g) and 10 females ( $24.79 \pm 0.94$  g). Experimental shrimp were intentionally selected from the  
46  
47 102 same size range ( $t(9) = 1.90$ ,  $p = 0.09$ ) in order to remove the confounding effect of size on feeding  
48  
49 103 behaviour. Shrimp were moved to an additional 220 l recirculation system with four holding tanks (59  
50  
51 104 x 34 x 18 cm) and a sump tank (65 x 50 x 39 cm), with water treatment and parameters as before.  
52  
53 105 Shrimp were placed individually inside circular mesh chambers (diameter 18 cm) for individual  
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55 106 recognition. The circular chambers were then divided between the four holding tanks. Shrimp were  
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107 feed-deprived for 24 h prior to the recordings. Only shrimp in inter- and pre-moult stages were used.

108 Video-recordings were carried out between 9.00 and 13.00.

### 109 **2.3. Behavioural trials**

110 Behavioural trials were carried out using methods similar to Bardera *et al.* (2019). In brief,  
111 polycarbonate test arenas (95 cm x 30 cm x 15 cm (length x width x depth); Fig. 1) were used which  
112 comprised an acclimation chamber (A) that was opened by lifting a separating door at the start of the  
113 trial, a feeding tray (B), and a chamber (C) which contained a GoPro Hero 3+ camera to record  
114 shrimp feeding activity. Another video camera (Canon G15) directly above the arena recorded the  
115 entire system. In the week before experimental trials, shrimp were introduced to test arena three times  
116 in order to acclimate them to the test arena.

117 For each trial, the test arena was filled with 25 l of fresh artificial sea water (parameters as above),  
118 which was replaced for each trial. During each recording, no water current and aeration were  
119 generated to aid the video quality and avoid any influence of rheotaxis on the animal's orientation  
120 towards food. Black plastic on the arena walls minimized disturbance to shrimp. At the start of the  
121 trial, individual shrimp were placed in the acclimation chamber for 10 minutes before the separating  
122 door was removed. Feed (2 g, Gemma Diamond 1.0 Skretting France) was added to the feeding area  
123 at the same time that the shrimp was placed in the arena. Both video cameras were turned on at the  
124 point the separating door was removed, and the shrimp was filmed for 20 minutes for analysis of  
125 behaviour (see below). Shrimp were recorded once per day, across five consecutive days, in order to  
126 gain information on individual variation.

### 127 **2.4. Behavioural units**

128 An existing ethogram for *L. vannamei* feeding behaviour was used (Bardera *et al.*, 2019) based on the  
129 responses proposed by Lee and Meyers (1996) (Table 1). Video analysis of behaviours was performed  
130 using BORIS v.7.1.1 (Friard and Gamba, 2016). A subsample (5% male and 5% female) of videos  
131 was analysed blind by a second observer to ensure repeatability of observations. A high level of

132 concordance between observers was found for all analysed behaviours (Kendall's coefficient  $W = 92.6$   
133 – 100% range across behaviours,  $p < 0.05$  for all).

134 Inactivity, detection, orientation, locomotion, fleeing and feeding were recorded as mutually exclusive  
135 'state behaviours' (Table 1a), accounting for the whole-time budget (i.e. 1200 seconds). These state  
136 behaviours were classified as 'passive' or 'active' depending on whether shrimp were moving. In  
137 addition, maxilliped beats, eye beats, and antennae wipes were recorded as 'event behaviours' (Table  
138 1b). Instead of duration, these behaviours were recorded as counts across the whole-time budget and  
139 could be performed at the same time as 'state behaviours'.

## 2.5. Statistical analysis

140 Statistical analysis was performed using R software v. 3.5.2. and IBM SPSS Statistics v. 25.

### 2.5.1. Behavioural differences between males and females

142 Due to violations of normality, Mann-Whitney U tests were used to compare differences in each of  
143 the behaviours (i.e. state and event) between female and male shrimp. Friedman tests were also  
144 performed to check general differences between behaviours within sex, followed by pairwise  
145 comparison using Wilcoxon signed ranks tests.

### 2.5.2. Attraction-to-feed score

146 Attraction-to-feed score was calculated as the time taken by an individual to reach the feeding tray for  
147 the first time in a trial divided by the total trial time (i.e. 1200 seconds) and then expressed as a  
148 percentage (Bardera *et al.*, 2019). Values for the attraction score therefore ranged from 0-100% where  
149 higher values represent greater attraction. Differences in this score were analysed according to sex  
150 using a Mann-Whitney U test, as data did not follow a normal distribution.

### 2.5.3. Between- and within- individual variation

152 We investigated the effect of sex on between and within-individual variation in state behaviours and  
153 attraction-to-feed score by determining consistency in the behaviour of individuals across five  
154 recordings. To achieve this, we ran nonlinear mixed-effects models (Nakagawa and Schielzeth, 2010)  
155 using the R package *lme4* (Bates *et al.*, 2018). We included the proportion of available time spent  
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157 performing each behaviour as the dependent variable, running separate mixed-effects models for each  
158 behaviour in turn with shrimp identity included as a random factor (Zuur *et al.*, 2009). We then  
159 calculated the intraclass correlation coefficients (or repeatabilities) from the model outputs by  
160 dividing the between-individual (i.e.  $V_{ind_0}$ ) variance by the total variance (i.e.  $V_{ind_0} + V_{e_0}$ ; where  
161  $V_{e_0}$  is the average within-individual plasticity towards any stimulus that is statistically unaccounted  
162 for) (Dingemanse and Dochtermann, 2013). We used this output to determine whether the time spent  
163 by an individual in each of the behaviours was repeatable, that is whether a larger portion of the total  
164 variance can be attributed to differences between individuals rather than within individuals  
165 (Nakagawa and Schielzeth, 2010; Dingemanse and Dochtermann, 2013, Cleasby *et al.*, 2015).  
166 Confidence intervals (95% CI) for parameter estimates were calculated based on 1000 bootstrapping  
167 simulations using the R package *rptR* (Stoffel *et al.*, 2017). Repeatability estimates were deemed  
168 insignificant if the lower estimate of the CI approached zero (Houslay and Wilson, 2017). Moreover,  
169 the package *rptR* applies randomization for inference testing (i.e. provides *p values* for the  
170 repeatability coefficients). However, these two different methods may lead to non-congruent  
171 conclusions. In some of our analyses, *p values* indicated significance, although the lower CI was zero.  
172 Here we have assumed that where the lower CI is zero there is no repeatability, even if the *p value*  
173 suggests significance.

174 In addition, a visual interpretation of individual variation was conducted by calculating coefficients of  
175 variation (CV). The CV is a statistical measure of the dispersion of data points around a mean, with  
176 higher CVs indicating greater levels of variation ( $CV = SD / \text{mean}$ ).

### 177 **3. Results**

#### 178 **3.1. Behavioural differences between males and females**

179 With regards to state behaviours, significant differences between sexes were found where females had  
180 greater inactivity ( $U = 809, Z = -3.040, p < 0.01$ ) and fleeing ( $U = 973, Z = -1.950, p < 0.05$ ) and males  
181 showed greater detection ( $U = 970, Z = -1.948, p < 0.05$ ) and feeding ( $U = 805, Z = -3.148, p < 0.01$ ) (Fig  
182 2). Differences between state behaviours within each sex were also found, with female shrimp ( $\chi^2 (5)$

183 = 127.700,  $p < 0.001$ ) spending most of their time budget inactive and least time fleeing and feeding  
184 ( $p < 0.01$  all pairwise comparisons). Male shrimp, while more active than females still spent most of  
185 their time budget inactive ( $\chi^2(5) = 124.920$ ,  $p < 0.001$ ), followed by time spent on detecting  
186 behaviours ( $p < 0.05$  all pairwise comparisons).

187 No significant differences were found in any of the event behaviours (i.e. eye beats, mouthpart beats  
188 and antennae wipes) between male and female shrimp (Fig. 3). However, differences were found in  
189 behaviours within each sex (females:  $\chi^2(2) = 48.558$ ,  $p < 0.001$ ; males:  $\chi^2(2) = 55.675$ ,  $p < 0.001$ ).  
190 Both sexes presented higher numbers of antennae wipes, followed by maxilliped beats and eye beats  
191 (Females,  $p < 0.01$ ; Males,  $p < 0.001$  all pairwise comparisons; Fig. 3).

### 192 **3.2. Attraction-to-feed score**

193 Significant differences were found in relation to attraction-to-feed score ( $U = 936$ ,  $Z = -2.222$ ,  $p < 0.05$ )  
194 where males had a higher attraction-to-feed score ( $45 \pm 0.6\%$ ) compared to female shrimp ( $30 \pm 0.5$   
195 %) (mean  $\pm$  S.E.).

### 196 **3.3. Individual variation**

197 Analysis of repeatability revealed significant differences in behavioural consistency between female  
198 and male shrimp. Females exhibited significant repeatability in the two passive behaviours considered  
199 here, inactivity ( $R = 0.40$ ,  $p < 0.005$ ) and detection ( $R = 0.43$ ,  $p < 0.001$ ), whereas males showed  
200 repeatability in orientation ( $R = 0.47$ ,  $p < 0.001$ ) (Table 2). This information is further supported by  
201 results from the CV analysis; behaviours with significant repeatability values showed reduced within-  
202 individual CV (Fig. 4). Males presented lower levels of within-individual CV in both feeding and  
203 attraction-to-feed although no significant differences were found in the repeatability analysis.

## 204 **4. Discussion**

205 The behaviour of animals in aquaculture remains understudied, however, greater understanding of  
206 certain behaviours, such as feeding, may be useful in addressing production inefficiencies in farmed  
207 species. Here, we examined feeding behaviours in the Pacific white shrimp *Litopenaeus vannamei*, a

1 208 globally important species in crustacean aquaculture, in relation to sex. Overall, males and females  
2 209 showed differences in time spent performing different behaviours; males were more engaged in  
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4 210 detection and feeding and had a higher attraction-to-feed score. Females were more inactive and were  
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6 211 less attracted to feed.  
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9 212 The greater amount of time spent inactive by females compared to males in our study aligns with  
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11 213 previous research conducted on mixed-sex tanks, where *L. vannamei* females spent most of the time  
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13 214 inactive on the bottom of the tanks while males showed greater swimming and exploratory behaviours  
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15 215 (Moss and Moss, 2006). Inactivity can be considered as a low energy behaviour (Da Costa *et al.*,  
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17 216 2016), which can reflect low feeding motivation of individuals (Bardera *et al.*, 2019). Male shrimp in  
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19 217 the present study spent significantly more time detecting food and feeding as well as displaying a  
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21 218 higher (although non-significant) number of maxilliped beats compared to females. Maxilliped beats  
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23 219 in other crustacean species (e.g. Caribbean spiny lobster, *Panulirus argus*) have been connected to  
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25 220 antennular grooming or auto-grooming behaviours (Barbato and Daniel, 1997; Schmidt and Derby,  
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27 221 2005). In the present study, it is likely that males performed this behaviour more than females as a  
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29 222 result of their increased feeding; crustaceans clean their mouthparts using their pereopods or beat  
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31 223 them energetically to remove chemical particles attached to the antennules during detection and after  
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33 224 feeding (Wroblewska *et al.*, 2002).  
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39 225 Differences in feeding behaviours have previously been investigated in mixed-sex tanks, where the  
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41 226 time *L. vannamei* males spent feeding was almost four times longer than for females (Moss *et al.*,  
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43 227 2002). In addition, *L. vannamei* males have been observed as being more aggressive than females  
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45 228 when competing for food, resulting in access to the food source for a longer amount of time (Moss  
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47 229 and Moss 2006). In other crustacean species, aggressive behaviour in males is positively correlated  
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49 230 with higher levels of boldness and feeding activity (Pintor *et al.*, 2008; Chapman *et al.*, 2013), this  
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51 231 dominance negatively impacts on the growth performance of females (Levy *et al.*, 2017). Removing  
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53 232 males from the culture environment of Pacific white shrimp could, therefore, remove aggressive  
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55 233 competition for food and allow females to achieve their full growth potential (Moss and Moss, 2006).  
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57 234 Although aggression in shrimp was not monitored in our single-individual experimental trials, our  
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1 235 results suggest that males were bolder as they were faster to arrive at the feeding tray (i.e. higher  
2 236 attraction-to-feed score) and fed for longer.

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5 237 Males and females of the same size were selected in this study to ensure that any observed differences  
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7 238 in behaviour were attributed to differences in sex rather than size. However, due to sexual size  
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9 239 dimorphism in the Pacific white shrimp (Chow and Sandifer, 1991; Pérez-Rostro *et al.*, 1999), males  
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11 240 and females within mixed-sex cultures may also differ in size. Previous studies have found that larger  
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13 241 *L. vannamei* spend more time feeding than smaller individuals but that smaller males can outcompete  
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15 242 larger females (Moss *et al.*, 2002; Moss and Moss, 2006). The results of the present study support the  
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17 243 idea that differences in feeding behaviour within mixed-sex cultures are driven by sex rather than size.  
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21 244 High levels of erratic activity (e.g. fleeing in the present study) have previously been considered as a  
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23 245 stress response in both fishes (Archard and Braithwaite, 2011) and crustaceans (Taylor *et al.*, 2004;  
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25 246 Filiciotto *et al.*, 2014). In our study, female shrimp engaged in significantly more fleeing behaviour  
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27 247 than males and also displayed a higher (although non-significant) number of eyes beats compared to  
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29 248 males, which in a previous study was considered indicative of stress in *L. vannamei* (Bardera *et al.*,  
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31 249 2019). Similarly, studies in amphipods have highlighted a higher sensitivity of females to stress  
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33 250 (Hoback and Barnhart, 1996; Sornom *et al.*, 2010), with high stress levels related to lower growth,  
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35 251 feeding rates and disease resistance as well as higher mortality (Stoner, 2012). In the present study,  
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37 252 female shrimp fed less than males, even when held individually, and had a lower survival rate (83%  
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39 253 females vs 100% males). Further research is needed to establish whether these differences in feeding  
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41 254 and survival are driven by higher stress levels in females.  
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46 255 Studying levels of individual variation in *L. vannamei* feeding behaviours provides additional insight  
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48 256 into the behavioural consistency that defines each sex. Behavioural repeatability is a way to evaluate  
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50 257 individual variation in a population (Dingemanse *et al.*, 2010) where higher repeatability of  
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52 258 behaviours is indicative of lower levels of within-individual variation in comparison to between-  
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54 259 individual variation (see Dingemanse and Dochtermann, 2013). In the present study, female shrimp  
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56 260 showed greater behavioural consistency in passive behaviours (i.e. inactivity and detection) and males  
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261 showed greater consistency in orientation. High repeatability levels in inactivity behaviours of female  
262 shrimp may be related to the low feeding motivation (Bardera *et al.*, 2019) exhibited by females.

## 263 **5. Conclusions**

264 Our findings clearly demonstrate that sex plays an important role in *L. vannamei* feeding behaviour.  
265 Male shrimp spent more time detecting feed while females were mostly inactive. Moreover,  
266 attraction-to-feed score was higher in males, who also spent more time feeding. These differences in  
267 behaviours between males and females were underpinned by a greater consistency in passive  
268 behaviours in females. Female shrimp showed more signs of stress with a higher (although non-  
269 significant) number of eye beats and higher frequencies of fleeing behaviour. Males performed a  
270 greater number of maxilliped beats which may be related to increased detection and feeding durations.  
271 It is clear from the present study that these differences in feeding behaviour between the sexes persist  
272 even when shrimp are feeding individually. Although more research is needed to fully understand the  
273 implications of sex on *L. vannamei* feeding behaviour under industrial settings, the importance of  
274 behavioural differences between males and females must be recognised when considering the benefits  
275 of mixed-sex versus monosex cultures in *L. vannamei* production.

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Table 1. Ethogram of *Litopenaeus vannamei* from Bardera *et al.* (2019). Two kinds of behaviours were identified: (a) State Behaviours which are mutually exclusive and in total accounted for the whole time budget; (b) Event Behaviours which are independent of each other and recorded as frequencies and not included in the overall time budget.

		<b>Behaviour</b>	<b>Description</b>
<b>a) State behaviours</b>	<b>Passive behaviours</b>	Inactivity	Shrimp is in a steady position without any movement of its appendages.
		Detection	Movement of shrimp appendages, such as mouthparts, antennules, antennae, pereopods in a steady position.
		Orientation	Shrimp movement to orientate side-on to feed without changing the position of their middle point.
	<b>Active behaviours</b>	Locomotion	Shrimp movement forward or backward with position change.
		Fleeing	Vigorous movements against the wall of the experimental maze associated with swimming behaviour.
		Feeding	Shrimp positioned on the feeding tray, eating food.
<b>b) Event behaviours</b>	Maxilliped beat	Shrimp beats and strokes maxillipeds.	
	Eye beat	Shrimp beats eyes against themselves.	
	Antennae wipe	Shrimp wipes antennae.	

Table 2. Repeatability estimates for measured behaviours according to sex (n = 10). Repeatability was calculated from univariate mixed-effects models with shrimp identity included as a random effect. Parametric bootstrapping was used to calculate confidence intervals (95% CI) and *p*-values. Behaviours presented significant repeatability when the lower confidence interval was >0 and *p*< 0.05. Significant repeatability estimates are shown in bold.

<b>Behaviour</b>	<b>Sex</b>	<b>Repeatability ± S.E.</b>	<b>95% CI</b>	<b><i>p</i>-value</b>
Inactivity	Female	<b>0.40 ± 0.16</b>	<b>[0.02, 0.67]</b>	<b>0.001</b>
	Male	0.16 ± 0.12	[0, 0.44]	0.118
Detection	Female	<b>0.43 ± 0.16</b>	<b>[0.06, 0.69]</b>	<b>&lt;0.001</b>
	Male	0.13 ± 0.12	[0, 0.417]	0.163
Orientation	Female	0.28 ± 0.14	[0, 0.56]	0.018
	Male	<b>0.47 ± 0.15</b>	<b>[0.11, 0.71]</b>	<b>&lt;0.001</b>
Locomotion	Female	0.08 ± 0.10	[0, 0.33]	0.291
	Male	0.30 ± 0.15	[0, 0.57]	0.012
Fleeing	Female	0.29 ± 0.14	[0, 0.56]	0.015
	Male	0.08 ± 0.10	[0, 0.33]	0.302
Feeding	Female	0.07 ± 0.10	[0, 0.32]	0.337
	Male	0.11 ± 0.11	[0, 0.38]	0.231
Attraction	Female	0.18 ± 0.17	[0, 0.59]	0.134
	Male	0.18 ± 0.13	[0, 0.47]	0.092

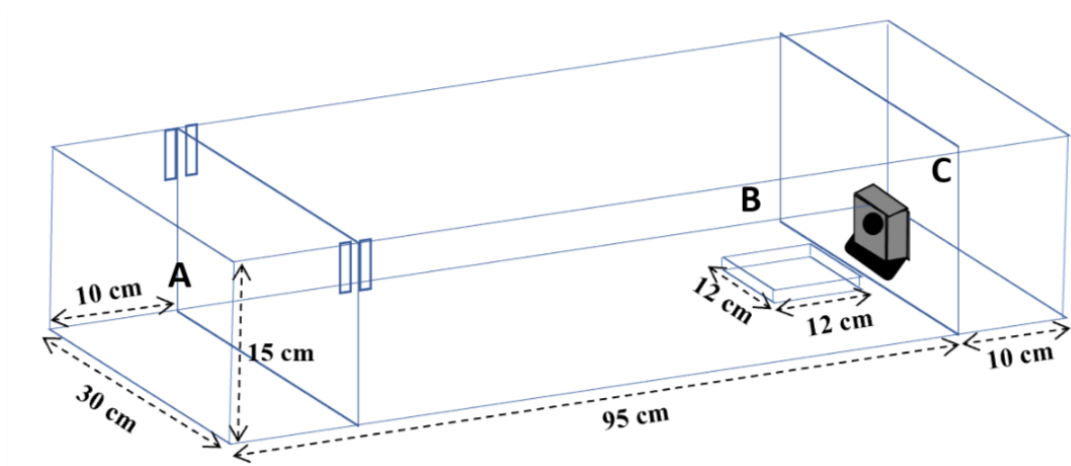


Figure 1. Dimensions of test arena where shrimp were recorded. Test arena was composed of: A = acclimation area, B = feed area, C= camera area. Figure reproduced from Bardera *et al.* 2019.



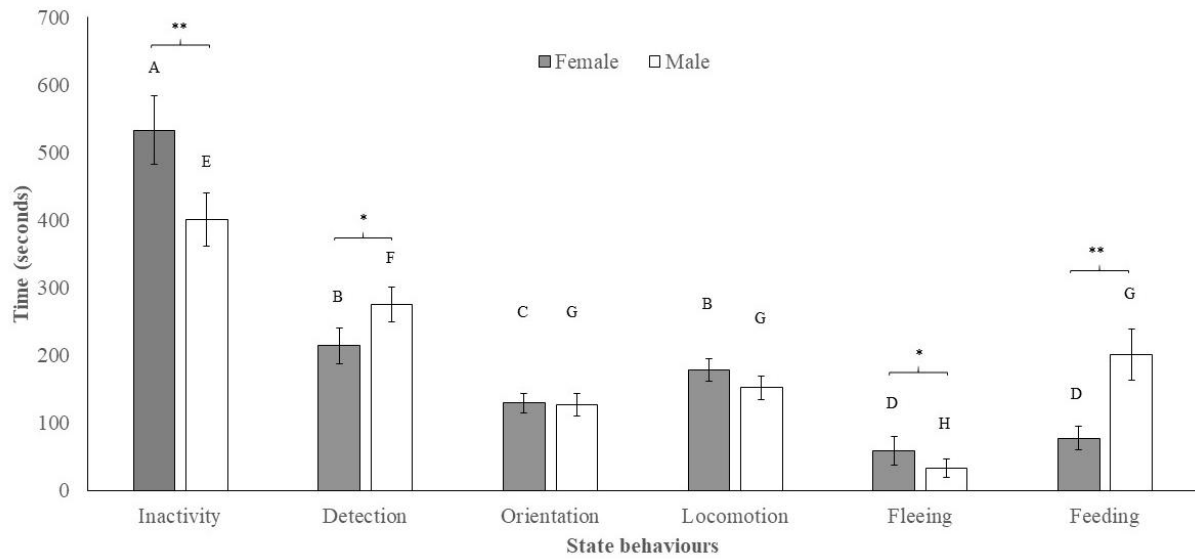


Figure 2. Average time (s) spent performing each state behaviour according to sex (n= 10 shrimp per sex). Presented with standard errors. Significant differences in time spent performing different behaviours by animals within the same sex are indicated by capital letters, where bars sharing a letter are not statistically different. Significant differences between male and female shrimp within the same behaviour are indicated by asterisks (\* $p < 0.05$ , \*\* $p < 0.01$ ).

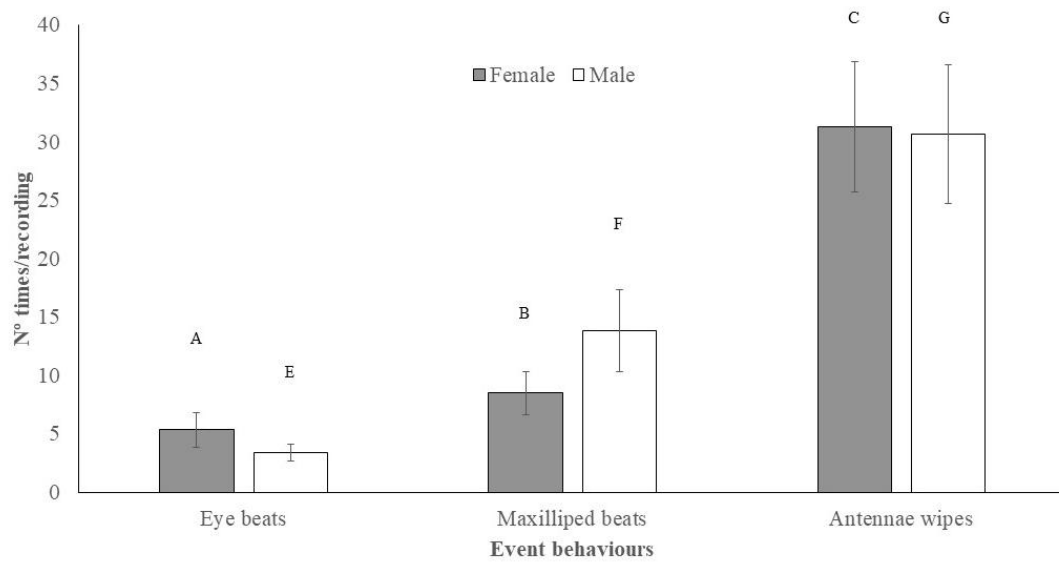


Figure 3. Average number of times performing each event behaviour according to sex (n= 10 shrimp per sex). Presented with standard errors. Significant differences in time spent performing different behaviours by shrimp within the same sex are indicated by capital letters, where bars sharing a letter are not statistically different. No significant differences between sex within the same behaviour were found.

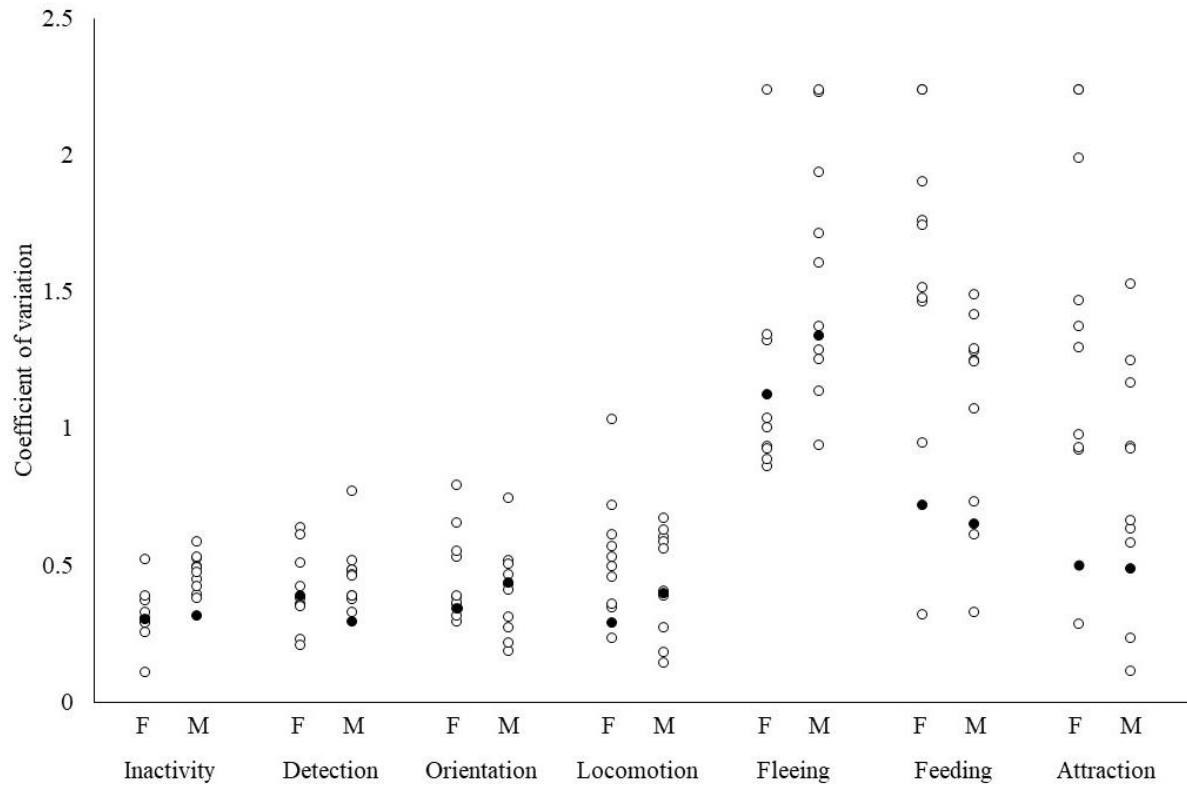


Figure 4. Coefficient of variation for between-individuals (black circles) and within-individuals (white circles) with respect to time spent performing state behaviours (inactivity, detection, orientation, locomotion, fleeing and feeding) and attraction-to-feed score (%). Data are for female (F) and male (M) shrimp (n= 10 per group, N.B. some data points overlap).