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Scale dependence of sex-specific movement in a small-bodied stream fish

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26 **Abstract**

- 27 1. Animal movement at localized scales is often modulated by competing pressures such as avoiding
28 predators while acquiring resources and mates. The relative magnitude of these trade-offs may
29 affect males and females differently, often resulting in sex-specific differences in movement.
- 30 2. Sex-biases in movement have been linked to mating systems (e.g., monogamy or polygamy) in
31 birds and mammals; however, this relationship has received less attention among fishes. Using
32 passive integrated transponder (PIT) tags and a series of stationary antennas, we evaluated the
33 movement dynamics of a small-bodied, sexually-dimorphic stream fish *Fundulus olivaceus* over a
34 30-day period in a fourth-order tributary to the Pascagoula River in Mississippi (USA).
- 35 3. We documented dissimilar sex-specific movement behaviors at different spatial scales that were
36 likely facilitated by differential resource demands and competitive pressures. Females exhibited
37 an increased propensity to engage in longer, exploratory moves (>30 m); whereas most males
38 remained active within an established territory, making few long-distance longitudinal
39 movements.
- 40 4. Local activity levels (proportion of individuals moving) were positively related to density
41 (manipulated during the study), and density was found to affect the magnitude of sex-specific
42 movement. In contrast to females, males increased local activity and movement distance at the
43 reduced density, presumably to expand territory size or mate-searching behaviors, suggesting
44 local mate competition may suppress the movement distance of males.
- 45 5. Despite some evidence substantiating a relationship between movement and mating system, our
46 results suggest that the documented sex-specific differences may be related to traits that co-
47 evolve with mating systems, rather than the mating system per se. Our findings also highlight the
48 importance of spatial scale when evaluating patterns of sex-biased movement tendencies.

49 **Introduction**

50 Recent technical and analytical methods (Schick et al., 2008) have increased our ability to
51 document movement at finer spatial and temporal scales, allowing for tests of hypotheses regarding how
52 movement affects population processes (Nathan et al., 2008; Stevens, Pavoine, & Baguette, 2010; Mueller
53 et al., 2011; Rasmussen & Belk, 2017). For example, at smaller, localized scales, movement and activity
54 levels are largely associated with foraging and mate-searching activities (i.e., resources), often

55 characterized by a series of routine movements within an established home range (Van Dyck & Baguette,
56 2005; Baguette & Van Dyck, 2007; Rasmussen & Belk, 2017). However, the population heterogeneity
57 hypothesis (Skalski & Gilliam, 2000) suggests that individuals likely respond to exogenous cues
58 differently (e.g., resource availability, predators, habitat quality). This variability in individual-based
59 movements is presumably shaped by tradeoffs linked to individual movement behavior (Bergerot,
60 Merckx, Van Dyck, & Baguette, 2012). If tradeoffs differ markedly between the sexes (Gandon, 1999;
61 Perrin & Mazalov, 2000; Lehmann & Perrin, 2003; Gros, Hovestadt & Poethke, 2008; Gros, Poethke, &
62 Hovestadt, 2009), one would expect natural selection to yield sex-biased movement. In fact, this has been
63 empirically demonstrated in a number of taxa (Greenwood, 1980; Sandell, Agrell, Erlinge, & Nelson,
64 1990; Croft et al., 2003; Bowler & Benton, 2009).

65 Sex biases in movement have been linked to mating systems and unbalanced sex-specific
66 competitive intensities (Greenwood, 1980; Dobson, 1982; Clarke, Saether, & Roskaft, 1997; Croft et al.,
67 2003; Lawson Handley & Perrin, 2007; Cano, Makinen, & Merila, 2008; Marentette et al., 2011; Shaw &
68 Kokko, 2014). Much of our current understanding results from studies on birds and mammals, which
69 have provided a general framework for evaluations across taxa (Greenwood, 1980; Dobson, 1982; Clarke,
70 Saether, & Roskaft, 1997; Lawson Handley & Perrin, 2007). Movement tends to be female-biased in
71 monogamous mating systems (e.g., birds) where parental investment is shared between the sexes and the
72 benefits of holding a territory outweigh those of dispersal in males. In contrast, males are often more
73 mobile in polygynous or promiscuous systems where females invest more in direct reproductive costs
74 (Perrin & Mazalov, 2000). Similarly, asymmetries in resource competition between the sexes may also
75 contribute to the evolution of sex-biased movement (Perrin & Mazalov, 2000; Gros, Poethke, &
76 Hovestadt, 2009). Inter-sexual resource competition may be weakest (stronger intra-sexual competition)
77 in polygynous or promiscuous species where females compete for local resources (e.g. food or spawning
78 habitat) and males compete for territories and/or access to females (resource competition hypothesis;
79 Clarke, 1978; Greenwood, 1980). This may also include the strength of intra-sexual competition (Dobson,
80 1982) with the sex experiencing more intense competition being more mobile (local mate competition
81 hypothesis; Hamilton, 1967).

82 One of the most well established drivers of animal movements is local density (Bowler & Benton,
83 2005; Matthysen, 2005; Clobert, Le Galliard, Cote, Meylan, & Massot, 2009). Local competition among
84 individuals is expected to promote movement (Aars & Ims, 2000; French & Travis, 2001; Matthysen,
85 2005), thus acting to reduce density dependent effects (Bowler & Benton, 2005). In contrast, some have
86 noted negative density-dependent relationships (Roland, Keyghobadi, & Fownes, 2000; Gilliam & Fraser,
87 2001; Alldredge et al., 2011) that could increase reproductive success (Gascoigne, Berc, Gregory, &
88 Courchamp, 2009). Such responses are presumably due to the ability of individuals to perceive local

89 environmental conditions and respond accordingly (“informed dispersal”; Clobert, Le Galliard, Cote,
90 Meylan, & Massot, 2009). As the spatiotemporal scale of the environment may be viewed differently
91 between sexes, local population densities may exert stronger influences on one sex over the other (De
92 Meester & Bonte, 2010; Clark & Schaefer, 2016).

93 Animal movements are often quantified using one metric (e.g., the proportion moving, movement
94 rates, total distance moved) generalized across spatial or temporal scales (Clarke, Saether, & Roskaft,
95 1997; Frair et al. 2005). However, such generalities can mask important scale dependent behaviors, thus
96 providing an incomplete picture of the subtleties of movement (Bergerot, Merckx, Van Dyck, & Baguette,
97 2012; Pennock, Cathcart, Heddon, Weber, & Gido, 2018). Furthermore, movement studies are often
98 evaluated at coarse spatial and temporal scales (Fausch, Torgersen, Baxter, & Li, 2002; Albanese,
99 Angermeier & Gowan, 2003; Holyoak, Casagrandi, Nathan, Revilla, & Spiegel, 2008) that may limit our
100 understanding of the mechanisms and motivations driving fine-scale movements (Rasmussen & Belk,
101 2017; Pennock, Cathcart, Heddon, Weber, & Gido, 2018). Although localized movements often consist of
102 a series of repeated circular movements, their cumulative effect through space and time could have
103 important evolutionary implications (Van Dyck & Baguette, 2005; Rasmussen & Belk, 2017). Thus, our
104 understanding of determinants of individual variation in movement behaviors depends on our
105 understanding of pertinent ecological and evolutionary consequences of such events. Despite the
106 challenges of studying animal movement, advances in tagging and monitoring technologies have enabled
107 researchers to continuously quantify individual movement at increasingly finer spatial and temporal scales
108 (Hussey et al., 2015; Wilmers et al., 2015).

109 In contrast to other taxa (birds: Greenwood, 1980; mammals: Dobson, 1982; Clarke, Saether, &
110 Roskaft, 1997; insects: Bowler & Benton, 2009), empirical data demonstrating sex-biased movement in
111 stream fishes is limited (Hutchings & Gerber, 2002; Croft et al., 2003; Clark & Schaefer, 2016). The goal
112 of this study was to assess sex-specific movement and activity patterns in a species exhibiting a
113 promiscuous mating system by quantifying the natural movements of passive integrated transponder
114 (PIT) tagged fish in the field. Our primary objective was to assess sex-specific movement metrics and
115 predicted contrasting sex-specific movement dynamics at different spatial scales. If female movement is
116 driven by locating high quality patches to utilize resources, we expected females to exhibit an increased
117 propensity to engage in lengthier (distance) movement bouts, but to minimize movement once a suitable
118 habitat was encountered. Conversely, we expected males to be more locally active, monitoring an
119 established territory, and to engage in fewer long-distance moves. Secondly, we were interested in the
120 interactive effects of density on sex-specific movement patterns. Because density is a strong predictor of
121 animal movement tendencies (Bowler & Benton, 2005; Matthysen, 2005; Clobert, Le Galliard, Cote,
122 Meylan, & Massot, 2009), and density may exert differential effects on the sexes (De Meester & Bonte,

123 2010), we examined how density influenced movement behavior by manipulating population size and
124 assessing the response of the focal tagged fish.

125

126 **Methods**

127 *Study Organism*

128 *Fundulus olivaceus* (blackspotted topminnow) is a broadly distributed, small-bodied stream fish
129 (maximum reported size 97 mm total length; Braasch & Smith, 1965) that exhibits a promiscuous,
130 female-choice mating system (Schaefer et al., 2012). Adults are sexually-dimorphic (distinguished by
131 median fin morphology), reaching reproductive maturity within one year at approximately 35-40 mm
132 (Blanchard, 1996; Vigueira, Schaefer, Duvernell, & Kreiser, 2008) and a maximum lifespan of 2-3 years
133 (Ross, 2001). Females spawn daily (mean of 1.6 eggs/day; Vigueira, Schaefer, Duvernell, & Kreiser,
134 2008) throughout a protracted spawning period that extends from March to September among southern
135 populations (Blanchard, 1996). Territorial male behavior has been observed among *Fundulus* species in
136 both laboratory and natural settings (Carranza & Winn, 1954; Baugh, 1981; Berdan & Fuller, 2012). For
137 instance, males of a closely-related species, *F. notatus*, have been observed to exhibit a territorial
138 patrolling behavior, actively monitoring a 6-12 meter stretch of stream parallel to the bank, driving away
139 conspecific males entering the territory (Carranza & Winn, 1954). Thus, if males are indeed holding
140 territories, we expected they would exhibit decreased longitudinal movement compared to females, but
141 remain active within their established patches.

142 *Study Location*

143 This study was conducted from July to September 2014 in a 180 m section of Big Creek, a fourth-
144 order tributary of Black Creek, located within the Pascagoula River drainage (Mississippi, USA) (Figure
145 1). We chose this length based on movement rates and population estimates observed from a previous
146 mark-recapture study of *F. olivaceus* (70 males and 74 females, tagged with elastomers and recaptured
147 weekly) at the same locality (Alldredge et al., 2011). Mean daily movement rates were less than 1 m day⁻¹
148 and the maximum distance detected was 230 m over the course of 49 days (Alldredge et al., 2011). No
149 sex-specific patterns were identified in that study, but data were based on weekly surveys that could not
150 detect movement on a finer temporal scale. Our study design using PIT tags allowed us to measure
151 multiple daily movement metrics throughout the study reach to provide a more accurate assessment of
152 potential sex bias in movement.

153 *Fish Collection and Tagging*

154 We collected adult fish (>50 mm standard length; SL) by dipnet (Vigueira et al., 2008; Alldredge
155 et al., 2011; Schaefer et al., 2012; Clark & Schaefer, 2016; N & K Dip Nets, Viola, Wisconsin, USA;
156 frame dimensions 46 × 44 cm) from areas of Black Creek below the confluence of Big Creek, where they

157 are locally abundant, in mid/late June 2014 (Figure 1). Fish were anesthetized using MS-222, measured
158 (SL), weighed (grams, g), and tags were injected into the posterior portion of the peritoneal cavity (Clark,
159 2016; Clark & Schaefer, 2016). We fitted 27 males (55.5 ± 3.8 mm SL; 2.11 ± 0.46 g) and 27 females
160 (54.1 ± 3.7 mm SL; 2.01 ± 0.51 g) with 12 mm PIT tags (Oregon RFID, Portland, Oregon, USA). Tagged
161 fish were held in tanks and monitored daily for survival, tag retention, external signs of infection, and
162 normal feeding behavior for a period of two weeks.

163 *Stream Setup and Fish Introduction*

164 Four pairs of pass-through antennas were placed approximately equidistant (30 meters)
165 throughout the study reach, which would allow for detection of infrequent, longer distance moves (85%
166 of moves were less than 31 m; Alldredge et al., 2011) (Figure 1). The paired antennas were set
167 approximately 2 m apart to assess directionality and to capture fine-scale movement. Stream widths
168 precluded construction of antennas spanning the entire width in some areas, thus we utilized in-stream
169 habitat features (stream constrictions or natural barriers [e.g. large woody structure]) to funnel individuals
170 through the antenna fields. Antennas were connected to two multiplexing HDX PIT readers (Oregon
171 RFID, Portland, Oregon, USA) that continuously logged data throughout the study period (30 days of
172 data collection). Each antenna scanned at an average rate of $2.3 (\pm 0.2$ SD) scans second^{-1} with a detection
173 range of approximately 40 cm across each antenna (20 cm in both the up- and downstream directions).
174 We deployed block nets at the up- and downstream ends of the reach to prevent emigration of focal fish
175 or immigration of conspecifics into the study reach. Block nets (steel hardware cloth; 1.2 m tall; 0.635 cm
176 mesh) were constructed to span the entire stream width and anchored into the substrate at the up and
177 downstream termini of the study reach. After block-nets were set, we removed 88 adult *F. olivaceus* (>40
178 mm SL; 46 males, 42 females) on 18 July 2014 that were subsequently released downstream of the study
179 reach.

180 On 30 July 2014 we introduced 90 *F. olivaceus* (54 PIT tagged, 36 untagged; equal sex ratio) into
181 the study reach to maintain ambient density. Untagged individuals (collected from Black Creek; Figure 1)
182 were added simultaneously in order to allow manipulation of population density during the study period
183 and to ensure they experienced the acclimation regime as the tagged fish (see below). We evenly
184 distributed individuals (sex and tagging treatment) between the three interior sections of the study reach.
185 Fish were allowed to distribute and acclimate throughout the study reach for three days prior to data
186 collection (data loggers were operational to track activity). Following the fifteenth day of data collection,
187 four passes (two upstream, two downstream) were made with a two-person crew, dip-netting as many *F.*
188 *olivaceus* as possible. All fish were temporarily housed in streamside buckets according to the capture
189 section and subsequently scanned for PIT identification. Captured fish within each section were
190 enumerated and PIT tagged individuals were released back into their section of capture. Untagged

191 individuals were released downstream of the study reach, effectively reducing population density for the
192 second 15-day period of data collection. Following collection and handling, we allowed one day prior to
193 resuming data collection.

194 To determine if focal fish might escape the study reach, we sampled above and below the block
195 nets every five days and scanned each for PIT identification. Multiple passes through approximate 75-100
196 m stretches (above and below the study reach) were sampled by one or two individuals. Following the
197 completion of the study, the entire reach was sampled periodically over two days in an attempt to recover
198 remaining focal fish. We continued to run the PIT loggers throughout these days to account for any
199 remaining individuals not recaptured.

200 *Movement Metrics*

201 Using the individual detection data, we generated a suite of movement metrics to characterize
202 daily movement patterns at two spatial scales across the 30 days of data collection. To first assess a
203 general daily activity level, we assigned presence (coded as 1/0) to individuals that were detected at least
204 once by any antenna. Secondly, we calculated the daily movement distance for each individual by
205 summing the distance (absolute value in meters) between successive detections (minimum total distance
206 moved) within each day (defined as 0700-0700 h). We then used the signed movement distances
207 (negative for downstream, positive for upstream) to calculate daily net displacement as a measure of
208 longitudinal movement. Inclusion of this metric allowed us to differentiate between a highly mobile fish
209 that remained within a local area (small net displacement) or moved longitudinally within the reach (large
210 net displacement). We further classified movement into two qualitative categories (Figure 2) based on the
211 longitudinal distance between detections representing one movement event. Moves of 0 or 2 m (absolute
212 distance) were defined as local moves (successive detections at an antenna pair). Larger moves that
213 represented individuals traversing, at minimum, an entire antenna section (minimum distance >30 m)
214 were characterized as exploratory moves. The daily presence or absence (scored as a 1/0, respectively) of
215 each qualitative metric (local and exploratory) was assessed for each individual, along with summing the
216 total number of each type of move daily. We used factor analysis (FA) with Promax (oblique) rotation to
217 reduce the seven daily movement metrics (Table 2) across individuals into interpretable factor scores
218 (hereafter “movement behaviors”). Although there was no observed mortality or emigration from the
219 study reach, we opted for a conservative approach and restricted the number of days an individual was
220 included in the data set based on its last known occurrence (either a detection or post-study recapture).
221 For example, if an individual last appeared in the detection log on day 18 and was not captured following
222 completion of the study, movement metrics for that individual throughout days 19-30 were not included
223 in analyses.

224 To assess the contribution of individual attributes and density on the movement behaviors, we
225 used a series of generalized linear mixed effects models (GLMM) using the lme4 package (Bates,
226 Maechler, Bolker, & Walker, 2015) in the R statistical language (R Core Team, 2017). We first built a
227 series of competing models that included a movement behavior as the response variable with sex, SL
228 (log-transformed), body condition (residuals from the log length-weight relationship), density (high and
229 low), and the two-way interactions with sex as fixed effects (Table 1). To facilitate fitting GLMMs with a
230 log-link function, we added the minimum value to all factor scores to produce positive values. Individuals
231 and days (1-30) were included as random effects in all models. We used Akaike's information criteria
232 (AIC) to rank the candidate models for each movement behavior. To account for uncertainty in assessing
233 the most appropriate model(s) for interpretation, we used weighted model-averaging based on AIC_c
234 model weights (w_i) to assess the influence of fixed effects present in models with reasonable support
235 ($\Delta AIC < 2.0$ and $w_i > 0.10$) (Burnham & Anderson, 2002).

236

237 **Results**

238 *Detections and Recaptures*

239 A total of 19,115 detections were logged from 47 individuals (24 females; 23 males) throughout
240 the 30-day period (Supporting Table S1). We reduced the density by approximately one-third following
241 the fifteenth day by collecting 39 adults (20 females, 19 males) from the study reach, 12 (6 females, 6
242 males) of which were focal PIT fish (tagged individuals returned to the study reach). Following the
243 completion of the study, we recovered 50 adults (17 PIT fish; 7 females, 10 males). One male not
244 captured remained in the detection logs two days post-study and was thus considered to have been present
245 for the entire 30 days. Collectively, the section where tagged fish were recaptured corresponded to the
246 assumed location (based on detection records) for 28 of the 29 PIT captured fish. The lone individual that
247 did not match was captured in an adjacent section. Moreover, less than 1% of consecutive detections from
248 individual fish occurred at non-adjacent antennas, likely a result of tag collision (multiple fish
249 simultaneously entering the detection field). Thus, we are confident that the majority of individuals were
250 detected while crossing antenna fields. During periodic sampling to assess fish escaping the block nets,
251 we collected 76 individuals outside the study reach and none were positively identified as tagged PIT fish.

252

253 *General Movement Patterns*

254 The movement distribution was highly leptokurtic (98.7% of moves were local) and neither sex
255 indicated an up- or downstream bias in movement distance (net signed movement not different from zero;
256 females: $V = 191$, $p = 0.97$; males: $V = 155$, $p = 0.90$) or direction (Chi-square; both $p > 0.96$). Across the
257 study period, males were more active (locally and overall), engaged in a greater number of daily local

258 moves, and moved greater daily distances (Table 2, Supporting Table S1). However, males showed a
259 higher degree of territory fidelity with 87.5% ($\pm 18.3\%$ SD) of all detections for individuals logged at one
260 antenna pair compared to 69.0% ($\pm 19.9\%$ SD) for females, and a mean daily net displacement (± 1 SD)
261 that was lower, and less variable (4.0 ± 4.8 m) than females (6.8 ± 7.1 m). Of the 47 focal PIT fish
262 detected throughout the study, 16 (12 of which were female) occupied all stream sections (minimum of
263 100 m displacement) based on detection histories, with three individuals (two females and one male)
264 traversing this stretch within 24 h.

265

266 *Summarizing Movement Behaviors*

267 Individuals varied in the number of days they were present in the data set (range = 1-30) and
268 collectively resulted in 755 movement days (unique individual/day combinations) evaluated with FA
269 (Supporting Table S1). The seven movement metrics loaded along three factors that collectively
270 explained 77.8% of the variability in daily movement behaviors (Table 3). Factor I (31.6% of variance,
271 hereafter “Exploratory Behavior”) was associated with exploratory activity, number of exploratory moves
272 and net displacement. Factor II (24.3% of variance, hereafter “Activity”) included activity and local
273 activity. The number of daily local moves and total movement distance loaded on Factor III (21.9% of
274 variance, hereafter “Movement Magnitude”).

275

276 *Model Selection of Movement Behaviors*

277 There were more competing models with reasonable support ($\Delta AIC_c < 2.0$ and $w_i > 0.10$)
278 predicting Exploratory Behavior and Activity than for Movement Magnitude. The top candidate models
279 predicting Exploratory Behavior included sex, along with the additive effect of body condition and
280 interactive combination of density (Table 4). Model-averaged parameter estimates (Table 5) indicated
281 mean Exploratory Behavior ($\pm 95\%$ CI) was greater for females (3.26 ± 0.11) than for males ($2.86 \pm$
282 0.10), and decreased from high (3.16 ± 0.11) to low density (2.88 ± 0.10). The sex \times density interaction
283 had weak effects on exploratory movement as confidence intervals overlapped zero (Table 5). Competing
284 models predicting Activity included density and the additive and interactive combinations of sex (Table
285 4). Mean Activity was greater across days of high density (3.68 ± 0.11) compared to low density ($3.33 \pm$
286 0.13), while sex had a negligible effect on Activity (Table 5). Movement Magnitude was best predicted
287 by two models that included sex, density, body condition and combinations of their interactions (Table 4).
288 Parameter estimates indicated significant sex-specific interactions with both density and body condition.
289 Mean male Movement Magnitude was greater in low (3.97 ± 0.21) compared to high density ($3.41 \pm$
290 0.15), while female movement remained relatively consistent, increasing slightly from high (3.22 ± 0.10)

291 to low density (3.43 ± 0.17) (Figure 3, Table 5). Male Movement Magnitude was positively related to
292 body condition, but only weakly related in females (Figure 4, Table 5).

293

294 **Discussion**

295 Continuous monitoring of *F. olivaceus* demonstrated sex-specific movement behaviors at two
296 spatial scales. A pervasive pattern among animals with a polygynous or promiscuous mating system is
297 that the underlying competitive and resource asymmetries generally result in male-biased movement
298 (Greenwood, 1980; Dobson, 1982; Perrin & Mazalov, 2000). While our findings are largely consistent
299 with this, it was dependent on the spatial scale considered. At smaller, local scales, males tended to be the
300 more mobile sex, consistent with higher movement centered within an established territory (Carranza &
301 Winn, 1954). In contrast, at larger spatial scales, females were more likely to make longer distance,
302 exploratory movements, possibly to gain access to higher quality habitats for foraging and spawning
303 activities. Finally, as noted in other studies (De Meester & Bonte, 2010; Clark & Schaefer, 2016), density
304 of conspecifics can differentially affect sex-specific movement behaviors, and males showed increased
305 activity (greater Movement Magnitude) in response to reduced density.

306 Sex-specific movement presumably reflects differences in underlying energetic strategies. Among
307 polygynous or promiscuous species, females generally invest more in direct reproductive costs (Perrin &
308 Mazalov, 2000). While larger, exploratory moves of females could be directly related to resource
309 acquisition (e.g., foraging, spawning habitats), the magnitude or frequency of these movements may not
310 be energetically advantageous, and may reduce survival (Fraser, Gilliam, Daley, Le, & Skalski, 2001;
311 Gilliam & Fraser, 2001) or reproductive potential. For example, Crossin et al. (2004) showed that pre-
312 dispersal energy stores were positively-related to dispersal distance; however, this resulted in fewer eggs
313 once individuals reached spawning grounds. Although that study involved a migratory salmonid, it
314 illustrates how movement costs can directly affect the balance between energy allocation and individual
315 fitness. While we are unsure of potential fitness costs of movement on females, we presume the protracted
316 spawning period of fundulids (Blanchard, 1996; Cashner et al., in press) is energetically expensive, thus
317 requiring females to feed often to fuel egg production and development (Thomerson & Wooldridge,
318 1970). Nonetheless, the differences and intensity of resource and competitive asymmetries likely
319 contributed to the sex biases in movement found in *F. olivaceus*.

320 Sexual dimorphism can pose differential fitness costs and benefits of movement that could
321 promote sex-biased dispersal (Stevens et al., 2013). For species exhibiting secondary sexual characters, a
322 balance exists between sexual and natural selective pressures (i.e. handicap principle; Zahavi, 1975;
323 Isawa, Pomiankowski, & Nee, 1991; Iwasa & Pomiankowski, 1999; Cotton, Small, Hashim, &
324 Pomiankowski, 2009), which generally favors movement in the sex lacking the exaggerated trait(s)

325 (Trochet et al., 2016). Such traits may impose substantial energetic and reproductive costs directly
326 associated with transit (Kinnison, Unwin, & Quinn, 2003), while also increasing susceptibility to
327 predation; however, these traits are often those preferred by females (Rosenthal, Flores Martinez, Garcia
328 de Leon, & Ryan, 2001; Schaefer et al., 2012). For instance, male *F. olivaceus* are larger than females and
329 exhibit a suite of secondary sexual characteristics such as dorsolateral spots and nuptial coloration that are
330 preferred by females (Schaefer et al., 2012). Male *F. olivaceus* with higher dorsolateral spot densities
331 sired a disproportionately greater number of offspring in mate choice trials, but also suffered increased
332 predation pressure (Schaefer et al., 2012). Whether these secondary sexual characters are correlated with
333 behavioral traits in *F. olivaceus* is unknown (e.g., boldness; Fraser, Gilliam, Daley, Le, & Skalski, 2001);
334 this nonetheless demonstrates sexually dimorphic traits pose differential costs (e.g. predation risk) and
335 benefits (e.g. increased mating opportunities) at the individual level that could explain our differences in
336 sex-specific movement. Thus, the underlying mechanisms driving sex biases may be linked more to sex-
337 specific traits related to, or co-evolving with, mating systems, rather than the mating system in itself
338 (Ronce & Clobert, 2012; Stevens et al., 2013; Trochet et al., 2016).

339 Activity levels, but not movement distance, were greater in the high density portion of the study,
340 consistent with positive density-dependent movement (Andreassen & Ims, 2001; Matthysen, 2005;
341 Clobert, Le Galliard, Cote, Meylan, & Massot, 2009). Our data also suggest that changes in population
342 density influenced male movement more so than females. Despite the decline in daily proportion of active
343 males at low density, the number of local moves and movement distances increased by approximately
344 90% and 50%, respectively. In polygynous or promiscuous species, the relative intensity of mate
345 competition among males is assumed to exceed resource competition among females (Perrin & Mazalov,
346 2000; Gros, Poethke, & Hovestadt, 2009). As male aggression can relate to conspecific densities and sex
347 ratios (Jirotkul, 1999; Spence & Smith, 2005), the probability of aggressive encounters likely increases as
348 a function of the local intra-sexual density. The male site fidelity documented in this study likely reflects
349 the territorial nature of fundulids (Carranza & Winn, 1954; Baugh, 1981, Berdan & Fuller, 2012) and the
350 greater tendency of females to invest in longer distance moves. Male *F. olivaceus* may optimize
351 reproductive success by limiting their movement to a restricted segment of stream. This would minimize
352 aggressive encounters with other males as they attempt to court females passing through their territory. At
353 reduced densities however, competition for mates may be lessened (Jirotkul, 1999; Spence & Smith,
354 2005), releasing males to occupy larger territories or become more expansive in searching behaviors that
355 may benefit mobile males by increasing the probability of mating success (Gros, Poethke, & Hovestadt,
356 2009). However, individual males may vary in their capacity to respond to lower density conditions. For
357 example, body condition of male *F. olivaceus* is a predictor of reproductive investment (Schaefer et al.,
358 2012) and was positively related to male Movement Magnitude in this study. While it is important to note

359 that our levels of density (high and low) were not necessarily fixed through time as some mortality likely
360 occurred throughout the study, this would have enhanced any density effects. Such condition-dependent
361 responses may be important in mitigating population declines (i.e., Allee effects; Gascoigne, Berec,
362 Gregory, & Courchamp, 2009) and when colonizing new habitats (Lonzarich, Warren, & Lonzarich,
363 1998; Adams & Warren, 2005; Kokko & López-Sepulcre, 2006; Marentette et al., 2011; Le Galliard,
364 Massot, & Clobert, 2012).

365 As our study evaluated movement in a relatively short longitudinal reach at one locality, we
366 cannot discount the possibility that the movement behaviors were stream- or individual-specific. At larger
367 spatial scales, individuals undoubtedly face various environmental pressures that may drive population-
368 specific movement tendencies (Bowler & Benton, 2009; Clobert, Le Galliard, Cote, Meylan, & Massot,
369 2009; Woolnough, Downing, & Newton, 2009; Bergerot, Merckx, Van Dyck, & Baguette, 2012).
370 However, population density was implicated as a putative mechanism influencing inter-year movement
371 differences in *F. notatus* (Alldredge et al., 2011) and similar sex and density effects influenced seasonal
372 movement of *F. olivaceus* (Clark & Schaefer, 2016). We also acknowledge that the placement of block
373 nets may have constrained movement; however, for several reasons we do not believe this jeopardized our
374 ability to make interpretations. First, similar to Alldredge et al. (2011), individuals in our study moved
375 very little (longitudinally), thus the block nets would have only affected a small number of individuals
376 representing the “mobile” portion of the population (sensu Skalski and Gilliam, 2000). Second, our
377 primary objective was not to specifically quantify absolute movement distances, but instead differences in
378 movement behaviors between the sexes. Accordingly, we feel our findings accurately represented
379 movement behaviors as the documented patterns were not inconsistent with previous studies (Alldredge et
380 al., 2011), but rather provided higher resolution to capture potential sex-specific differences.

381 Our estimates of movement metrics were conservative to avoid overestimating patterns due to the
382 assumed unaccountability (detection or capture) of individuals throughout the study period. One way
383 movement could have been underrepresented would be if highly mobile fish left the study area, although
384 we note that no marked fish were captured outside the block nets. We also could have failed to detect
385 movement if there was a moderate degree of PIT tag expulsion post-release. While we cannot rule this
386 out, we believe it unlikely as we have extensive tagging experience with this species (Clark, 2016; Clark
387 & Schaefer, 2016) and any tag loss generally occurs within the first 7-10 days post-tagging. We feel the
388 more likely explanation for our failure to detect some individuals within the study reach was the result of
389 mortality due to senescence or predation. As with many small-bodied stream fishes, *F. olivaceus* is a
390 generally short-lived species (~2 years; Ross, 2001) and mortality of senescent adults is known to follow
391 peak spawning (Alldredge et al., 2011). Alternatively, some individuals may have displayed high degrees
392 of context-specific fidelity within the study reach, dependent on local biotic or abiotic factors over time.

393 Indeed, one-third of the individuals present for the entire study were detected on four or fewer days
394 (Supporting Table S1), and coupled with documented movement patterns (Alldredge et al., 2011; this
395 study), would support the possibility of extended periods of local fidelity.

396 Movement behaviors of *F. olivaceus* were generally consistent with the prediction of male-biased
397 movement driven by mate competition as seen in other taxa that exhibit polygynous or promiscuous
398 mating systems (mammals: Greenwood, 1980; Dobson, 1982; fishes: Croft et al., 2003). However, this
399 pattern was contingent on the scale considered, as the sexes displayed different behaviors when evaluated
400 at increasing spatial scales, emphasizing that scale may be an important consideration when interpreting
401 sex-based differences in the direction or magnitude of movement. Traditional views of polygynous or
402 promiscuous species generally assume that one sex (typically males) reproduces with a greater number of
403 partners than the other, which may favor male-biased movement. However, most fundulids spawn
404 frequently throughout an extended spawning period (several months to nearly year-round) and exhibit no
405 parental care (Cashner et al. in press), potentially normalizing the number of partners for each sex.
406 Consequently, infrequent exploratory movements by females may facilitate resource utilization and the
407 number of males encountered, thereby maximizing reproductive success while distributing offspring
408 throughout a reach or home range.

409 Utilizing various movement metrics, we documented contrasting sex-specific movement
410 behaviors in a promiscuous, small-bodied stream fish. While mating systems have been implicated as
411 drivers of sex biases in movement across a variety of taxa (birds: Greenwood, 1980; Clarke, Saether, &
412 Roskaft, 1997; mammals: Dobson, 1982; fishes: Hutchings & Gerber, 2002; Croft et al., 2003, Marentette
413 et al., 2011; insects: Beirinckx, Van Gossum, Lajeunesse, & Forbes, 2006; Bowler and Benton, 2009),
414 patterns are certainly not universal (Lawson Handley & Perrin, 2007; Shaw & Kokko, 2014). Instead,
415 traits that potentially coevolve with mating systems (e.g., parental care, sexual dimorphism, territoriality)
416 that result in 'dispersal syndromes' (Clobert, Le Galliard, Cote, Meylan, & Massot, 2009; Ronce &
417 Clobert, 2012; Stevens et al., 2013) may be the underlying drivers of sex-biased movement (Trochet et
418 al., 2016). Furthermore, as with many other putative drivers of movement (reviewed in Bowler & Benton,
419 2005), the prevalence and magnitude of movement responses is likely dependent on a combination of
420 local extrinsic (biotic and abiotic conditions) and intrinsic (sex, physiological condition) factors (Nathan
421 et al., 2008; Clobert, Le Galliard, Cote, Meylan, & Massot, 2009). Notably, our data provide evidence
422 that the spatial and temporal scales at which movement is evaluated should be considered when
423 addressing the nature of sex-biased tendencies. Understanding the evolutionary and ecological
424 consequences of sex-specific movement may be, in large part, contingent on the ability to document the
425 pervasiveness of such patterns across various taxa and spatiotemporal scales.

426

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433
434 **Conflict of Interest**

435 The authors declare no conflict of interest.

436
437 **Literature Cited**

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626 Table 1. List of candidate generalized linear mixed effects models and number of model parameters (K)
 627 used to evaluate the influence of individual attributes and density on movement behaviors derived from
 628 factor analysis. Individual predictor variables include sex, standard length (SL) and body condition
 629 (residuals of log length-weight relationship). Individual and day were modeled as random effects.

Model	K
Null	4
Sex	5
Density	5
SL	5
Condition	5
Sex + Density	6
Sex + SL	6
Sex + Condition	6
Sex + Density + Sex \times Density	7
Sex + SL + Sex \times SL	7
Sex + Condition + Sex \times Condition	7
Sex + Density + SL	7
Sex + Density + Condition	7
Sex + SL + Condition	7
Sex + Density + SL + Sex \times Density + Sex \times SL	9
Sex + Density + Condition + Sex \times Density + Sex \times Condition	9
Sex + SL + Condition + Sex \times SL + Sex \times Condition	9
Sex + Density + SL + Condition	8
Sex + Density + SL + Condition + Sex \times Density + Sex \times SL + Sex \times Condition	11

630

631 Table 2. Mean (± 1 SD) daily movement metrics, averaged across densities and sex, used to evaluate movement behaviors of *F. olivaceus*. Daily
632 ranges are provided below in parentheses. Activity metrics are represented by proportions and the qualitative movement categories reflect counts.
633 Distance moved represents the total minimum daily distance moved (summed absolute meters) and net displacement describes the magnitude of
634 longitudinal movement (summed signed meters).

Movement Metric	High Density		Low Density		Total	
	Females	Males	Females	Males	Females	Males
Activity	0.41 \pm 0.14 (0.23-0.71)	0.56 \pm 0.10 (0.36-0.69)	0.29 \pm 0.17 (0.0-0.60)	0.42 \pm 0.08 (0.27-0.55)	0.35 \pm 0.16 (0.0-0.71)	0.49 \pm 0.11 (0.27-0.69)
Distance Moved	24.8 \pm 14.4 (7.0-52.7)	35.2 \pm 14.1 (11.1-59.7)	20.9 \pm 20.5 (0.0-64.8)	50.8 \pm 16.3 (24.5-87.1)	22.8 \pm 17.5 (0.0-64.8)	43.0 \pm 17.0 (11.1-87.1)
Net Displacement	11.2 \pm 6.8 (3.1-25.6)	6.4 \pm 5.1 (0.0-16.3)	2.4 \pm 4.0 (0.0-12.5)	1.5 \pm 3.0 (0.0-8.9)	6.8 \pm 7.1 (0.0-25.6)	4.0 \pm 4.8 (0.0-16.3)
Local Activity	0.45 \pm 0.12 (0.31-0.67)	0.61 \pm 0.09 (0.50-0.81)	0.33 \pm 0.16 (0.10-0.60)	0.50 \pm 0.08 (0.36-0.64)	0.39 \pm 0.15 (0.10-0.67)	0.56 \pm 0.10 (0.36-0.81)
Number of Local Moves	7.3 \pm 9.9 (0.7-29.9)	30.5 \pm 11.6 (16.4-58.0)	3.3 \pm 3.0 (0.1-9.2)	56.0 \pm 14.5 (36.5-77.1)	5.3 \pm 7.5 (0.1-29.9)	43.3 \pm 18.3 (16.4-77.1)
Exploratory Activity	0.22 \pm 0.13 (0.08-0.50)	0.15 \pm 0.11 (0.0-0.36)	0.10 \pm 0.08 (0.0-0.30)	0.05 \pm 0.05 (0.0-0.17)	0.16 \pm 0.12 (0.0-0.50)	0.10 \pm 0.10 (0.0-0.36)
Number of Exploratory Moves	0.4 \pm 0.3 (0.1-1.2)	0.3 \pm 0.2 (0.0-0.7)	0.4 \pm 0.4 (0.0-1.4)	0.2 \pm 0.2 (0.0-0.6)	0.4 \pm 0.3 (0.0-1.4)	0.2 \pm 0.2 (0.0-0.7)

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Table 3. The percent variance explained by each factor and loadings from factor analysis (FA) summarizing movement metrics. Bolded terms indicate the associated factor of each variable.

Daily Movement Metric	Factor I (31.6%)	Factor II (24.3%)	Factor III (21.9%)
Activity		0.979	
Distance Moved	0.380		0.860
Net Displacement	0.677		
Local Activity		0.857	
Number of Local Moves	-0.264		0.872
Exploratory Activity	0.838	0.132	
Number of Exploratory Moves	0.930		

Table 4. Generalized linear mixed effects models, ranked by corrected Akaike's information criteria (AIC_c) scores, explaining movement behaviors derived from factor analysis. Only models with $\Delta AIC_c < 2.0$ and $w_i > 0.10$ are presented.

Model	K	AIC_c	ΔAIC_c	w_i	Cumulative w_i
Exploratory Behavior (Factor I)					
Sex + Density	6	2128.8	0.00	0.36	0.36
Sex + Density + Sex \times Density	7	2130.4	1.64	0.16	0.52
Sex + Density + Condition	7	2130.5	1.66	0.15	0.67
Activity (Factor II)					
Density	5	2219.1	0.00	0.30	0.30
Sex + Density	6	2219.4	0.29	0.26	0.56
Sex + Density + Sex \times Density	7	2220.8	1.74	0.13	0.69
Movement Magnitude (Factor III)					
Sex + Density + Condition + Sex \times Density + Sex \times Condition	9	2165.2	0.00	0.48	0.48
Sex + Density + Sex \times Density	7	2166.6	1.38	0.24	0.72

Table 5. Model averaged estimates, standard errors (SE) and 95% confidence intervals (CI) for predictor variables in interpretable models ($AIC_c < 2.0$ and AIC weight > 0.10 ; Table 4). Coefficients of categorical predictors are relative to females and high density.

Parameter	Estimate	SE	Lower	Upper
Factor I – Exploratory Movement				
Sex	-0.18	0.05	-0.28	-0.08
Density	-0.07	0.03	-0.14	-0.01
Condition	0.01	0.03	-0.04	0.06
Sex × Density	-0.03	0.05	-0.13	0.06
Factor II – Activity				
Sex	0.08	0.06	-0.03	0.20
Density	-0.09	0.03	-0.13	-0.04
Sex × Density	-0.03	0.04	-0.12	0.05
Factor III – Movement Magnitude				
Sex	0.03	0.05	-0.07	0.12
Density	0.07	0.03	-0.01	0.14
Condition	-0.01	0.02	-0.06	0.05
Sex × Density	0.11	0.04	0.03	0.20
Sex × Condition	0.09	0.04	0.01	0.18

Figure Legends

Figure 1. Map of study location in south Mississippi. The shaded rectangle depicts the study reach in Big Creek. Detail map below indicates the position of the paired PIT antennas (dashed lines) and block nets (dotted lines) enclosing the study area.

Figure 2. Schematic illustration depicting potential movement behaviors, detection pattern, and interpretation. Displacement (meters) represents the summed minimum absolute distance an individual moved during a single movement event.

Figure 3. Mean daily Movement Magnitude (\pm 95 CI) of females (open circles) and males (closed circles) across days of the study. The vertical dashed line indicates when population density was reduced.

Figure 4. Relationship between body condition (residuals of log length-weight relationship) and mean Movement Magnitude (\pm 95 CI) of females (open circles) and males (closed circles). Plotted regression lines are derived from the predicted values from the top-ranked GLMM model.







