

1 **Interspecific and intraspecific interactions between fiddler crabs *Minuca pugnax***
2 **(mud fiddler) and *Leptuca pugilator* (sand fiddler) influence species' burrowing**
3 **behavior**

4
5 Isabelle P. Neylan^{1,2*}, Carter S. Smith¹, Erika D. Swann³, Stephen R. Fegley¹, Rachel K.
6 Gittman⁴

7
8 ¹ Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead
9 City, NC, 28557

10 ² Center for Population Biology, University of California, Davis, CA, 95616

11 ³ North Carolina State University, Raleigh, NC, 27607

12 ⁴ Department of Biology and Coastal Studies Institute, East Carolina University,
13 Greenville, NC, 27858

14
15 * Corresponding author: I. Neylan (ipneylan@ucdavis.edu)
16

17 **Abstract**

18 Species occupying similar habitat and functional niches will necessarily have some
19 external force driving differentiation between them, thus creating complementarity, or
20 otherwise face high competition for resources. In order to fully understand the role of
21 each species in an ecosystem and their contributions to ecosystem function, it is
22 important to understand the nature of these interactions. However, for species that occur
23 in the same spatial niche and appear to occupy redundant functional niches, it is often
24 difficult to distinguish between complementarity and redundancy and therefore to
25 designate the functional role each species plays. We used two co-occurring fiddler crab
26 species that are presumed to be functionally similar, *Leptuca pugilator* (sand fiddler crab)
27 and *Minuca pugnax* (mud fiddler crab), to explore how species interactions may
28 influence burrowing behavior. We ran manipulative mesocosm experiments to assess
29 potential effects of species interactions on the number and location of burrows as well as
30 the burrowing behavior of the crabs. Overall, sand fiddler crabs dug more burrows on
31 average than mud fiddlers across all experiments while mud fiddlers were choosier about
32 the location and sediment type of their burrows, suggesting complementarity in
33 burrowing between the two species. Burrow counts in heterospecific treatments suggest
34 that neither species interfered with nor enhanced burrow creation by the other species.
35 However, increased burrow occupancy by mud fiddlers in the presence of sand fiddlers
36 and aggressive behavior by mud fiddlers towards sand fiddlers suggest that mud fiddler
37 crabs may receive refuge benefits from sand fiddler crabs through antagonistic rather than
38 facultative interactions. Thus, species-specific habitat use and interspecific interactions
39 are likely influencing the role each species plays as a burrower and marsh ecosystem
40 engineer.

41

42 Key Words: *Leptuca pugilator*, *Minuca pugnax*, burrowing, salt marsh, ecosystem
43 engineer, interspecific interactions

44

45

46

47 1. Introduction

48

49 Complete ecological redundancy occurs when two species co-exist and can each provide

50 the same functional role in the community (Naeem, 2002; Walker, 1992). However,

51 competition is predicted to be highest when species occupy the same part of the niche and

52 use the same resources in space and time (Rosenfeld, 2002); eventually this should lead

53 to the exclusion of one species from the community (The Competitive Exclusion

54 Principle; Hardin, 1960). In theory, ecological redundancy is therefore incompatible with

55 stable coexistence given limited resources, and some factor will inevitably drive the

56 creation of functional differences (Loreau, 2004). However, two species appearing to

57 occupy the same niche may in fact be complementary when their functional niches are

58 examined. The functional niche includes factors influencing processes (e.g., habitat

59 modification) rather than just species presence, meaning that two species may exhibit

60 slightly different environmental optima even if co-occupying the same space leading to

61 complementarity when this new axis is included (Rosenfeld, 2002). Understanding how

62 species function in a community and influence ecosystem processes within the landscape

63 is central to fully understanding the dynamics and ecology of a system and important in

64 managing natural systems.

65 The role of each species in a community may also play a part in the overall

66 functioning of ecosystems. Whether or not two species are redundant or complementary

67 can affect the resilience and overall stability of the ecosystem. Having species with

68 overlapping functions can increase the stability of a system to perturbation, as predicted
69 by the Portfolio Effect (Doak et al., 1998) or the Insurance Hypothesis (Yachi and
70 Loreau, 1999). Consequently, while high redundancy and niche overlap may mean higher
71 competition and potential exclusion of one of the species, it may also provide resilience
72 for ecosystems that have lost one of these species.

73 Fiddler crabs are ideal organisms to study competitive interactions and functional
74 redundancy because they have been well-studied, are found worldwide, and are one of
75 the more abundant macrofauna found in salt marshes, mangroves, and other soft sediment
76 habitats (Bertness and Miller, 1984; Crane, 1975; Teal, 1958). Furthermore, distinct
77 species are often found in close proximity and occupying similar niches. Fiddler crabs are
78 highly social animals displaying herding behavior and burrowing in close proximity to
79 each other, leading to frequent opportunities for interaction and co-occupancy of habitat
80 (Zeil and Hemmi, 2014). Fiddler crabs are also important ecosystem engineers in marsh
81 ecosystems, acting as bioturbators that benefit the marsh plants and supported fauna
82 (Citadin et al., 2016; Gittman & Keller, 2013; Jones et al., 1994; Katz, 1980; Thomas &
83 Blum, 2010; Wang et al., 2010). Burrows can be 10-25cm deep and play a role in
84 oxygenating and redistributing nutrients in the sediment (Allen and Curran, 1974;
85 McCraith et al., 2003). During a single tidal cycle, fiddler crab foraging and burrowing
86 has been shown to have significant effects on organic content, chlorophyll a levels, and
87 meiofaunal density in the sediment (Citadin et al., 2016; Reinsel, 2004; Wang et al.,
88 2010).

89 *Leptuca pugilator* (formerly *Uca pugilator*) and *Minuca pugnax* (formerly *Uca*
90 *pugnax*) are two fiddler crab species known to occupy the same habitat within their

91 overlapping ranges (Allen and Curran, 1974; Colby and Fonseca, 1984; O'Connor, 1993;
92 Teal, 1958) and commonly co-occur in marshes all along the east coast of the United
93 States from Massachusetts to Northern Florida (Bertness, 1985; Reinsel, 2004; Ringold,
94 1979). *Leptuca pugilator*, commonly known as the sand fiddler crab, typically favors
95 coarser, sandier sediment (Crane, 1975; O'Connor, 1993). *Minuca pugnax*, the mud
96 fiddler, prefers muddier sediment (Aspey, 1978; O'Connor, 1993). These sediment
97 preferences are thought to provide a separation of the species' distributions in a marsh,
98 with sympatry only occurring in marginal areas of habitat consisting of mixed sediment
99 (Allen and Curran, 1974; Colby and Fonseca, 1984; O'Connor, 1993; Teal, 1958). Sand
100 and mud crabs occupy these distinct sediment types in some marshes, such as those in
101 Georgia, with minimal overlap (Teal, 1958). Other marshes, in particular those in North
102 Carolina, however, can have more mixing of fine and coarse sediment without the
103 distinct zonation seen elsewhere (Mattheus et al., 2010; Timmons et al., 2010). While
104 there is still some spatial separation between the two species due to larval settlement and
105 other abiotic factors such as salinity and dominant vegetation, they are observed
106 coexisting in many marshes, including our collection sites where they were observed
107 feeding and burrowing in close (> 10 centimeters from each other) proximity (Gittman &
108 Keller, 2013; George et al., 2010; O'Connor, 1993; Teal, 1958).

109 We conducted a series of mesocosm experiments to determine if interactions
110 (intraspecific and interspecific), density, and sediment grain size, influenced species'
111 burrowing frequency, burrowing location, and general behavior. Specifically, we
112 determined i) whether there were differences in the number and location of burrows dug
113 between the two species, ii) whether either species retained their distinct sediment

114 preferences when found co-occurring in mixed sediment, iii) whether there were density-
115 dependent effects on burrowing behavior, and iv) whether burrowing behavior of each
116 species changed in the presence or absence of the other congener. We hypothesized that
117 despite the lack of clear sediment zones in this system, differences in burrowing behavior
118 would emerge. We also predicted that each species would influence the burrowing
119 behavior of the other, creating a biotic rather than the typical abiotic barrier to
120 redundancy.

121

122 2. Methods

123 2.1 *Study organisms*

124 We collected female *Leptuca pugilator* (sand) and *Minuca pugnax* (mud) fiddler
125 crabs by hand from two salt marshes: 1) Hoop Pole Creek Clean Water Reserve in
126 Atlantic Beach, NC, USA (34°42'25.12" N, 76°45'1.14" W), which is a 70 x 50 m
127 peninsular marsh predominantly consisting of *Spartina alterniflora* and *Juncus*
128 *romerianus*; and, 2) the Trinity Center marsh in Pine Knoll Shores, NC, USA
129 (34°41'37.08" N, 76°51'49.68" W), which is an approximately 20 m wide marsh
130 protected by an offshore restored oyster reef and also dominated by *S. alterniflora* and *J.*
131 *romerianus* as well as *Spartina patens* and *Salicornia spp.* in the higher marsh zone. Both
132 collection sites had similar surface sediments. The marsh surface sediment of Bogue
133 Banks has been described as "muddy very fine sand" (Timmons et al., 2010) and
134 comprised primarily of "fine- and medium-grained sand" (Mattheus, et al., 2010). Sites
135 were comprised largely of mixed sediments (where both species were found and
136 collection occurred) along with interspersed patches of mud and sand. All fiddler crabs

137 were collected between August and September 2012 and August and November 2016.
138 We exclusively collected female crabs for these experiments because our primary focus
139 was on burrowing behavior and female fiddler crabs have been found to burrow more
140 often than males in *U. pugilator* and other species of fiddler crabs and without ancillary
141 behaviors that may be confounding (i.e., mate attraction) (Colby & Fonseca, 1984;
142 Hemmi & Zeil, 2003). Crabs were distinguished visually using observable differences in
143 carapace shape and color (Crane, 1975; Hubbard, 2008). All crabs were held in a flow-
144 through water table at UNC Chapel Hill's Institute of Marine Sciences in Morehead City,
145 NC. Filtered saltwater was drawn directly from Bogue Sound. Sediment was collected
146 from Hoop Pole Creek from areas where the crabs were found to co-occur and used as the
147 substrate in the holding tanks for both species. Crabs were only used once and were
148 typically held for less than 48 hours and never for more than one week.

149 *2.2 Experimental setup*

150 We conducted three, independent experiments to investigate fiddler crab burrowing
151 activity and behavior as follows: 1) mixed sediment trials (referred to hereafter as Mixed
152 trials), with uniformly mixed sediment and low density of crabs (two crabs per tank); 2)
153 low-density trials with two sediment types (fine sediment and coarse sediment) and two
154 crabs per tank (referred to as low-density FC trials); and, 3) high-density trials with two
155 sediment types (fine and coarse) and ten crabs per tank (referred to as high-density FC
156 trials). In each trial, the data collected included the total number of burrows dug, the
157 location of those burrows including sediment type if applicable, and the occupancy of the
158 burrows. For some of the low-density FC trials and mixed sediment trials, a ten-minute

159 video recording of the crab behavior at the beginning of the trial was also captured and
160 analyzed. The natural density of fiddler crabs at Hoop Pole Creek has been documented
161 as approximately 75 crabs per m² (Gittman & Keller, 2013). Therefore, low-density trials
162 were below this average, (approximately 48 crabs per m²) but were the lowest density
163 possible to achieve heterospecific treatments (one crab of each species) while the high-
164 density trials were above naturally occurring average densities, (approximately 242 crabs
165 per m²) but were not unrealistic densities observed in the field. In particular, crabs reach
166 high local densities while herding, a behavior often observed at our field sites and
167 elsewhere (Aspey, 1978; Salmon & Hyatt, 1983; Zeil & Hemmi, 2006).

168 For sediment preparation, we classified coarse sediment as grain size greater than
169 250µm but less than 500µm, and fine sediment as less than or equal to 250µm. 250µm is
170 the cutoff between sediment classified as fine sand and medium sand. We chose to use
171 this threshold because these species typically co-occur in sandy areas more characteristic
172 of the habitat of the sand fiddler (Aspey, 1978). We therefore wanted to provide two
173 types of sediment that reflected previously documented species' preferences with each
174 half still being accessible to both species. To prepare the two classes of sediments, we
175 collected sediment from Hoop Pole Creek, wet sieved the sediment with a 63-micron
176 mesh, retained the <62µm silt and water to be added back to the fine sediment later, and
177 oven dried (at 93.3°C) sediment retained on the sieve by placing it in an aluminum tray in
178 an oven for 3-5 hours. Following oven drying, we placed the sediment in a RoTap with a
179 500µm sieve stacked on a 250µm sieve on top of a collecting tray. We discarded all
180 sediment and debris remaining on the 500µm sieve, reserved all sediment that remained
181 on top of the 250µm sieve as coarse sediment, and reserved all sediment in the collecting

182 tray as fine sediment. The retained water used during the wet sieving process was kept in
183 a separate container and set aside undisturbed for 24-48 hours to allow the silt/clay
184 fraction to settle. We then removed the supernatant water and added the remaining silt to
185 the fine sediment.

186 To prepare each experimental tank prior to the low- and high-density FC trials, we
187 used a thin cardboard or plastic divider and filled half the tank with the coarse sediment
188 and half with the fine sediment to 3 cm depth. We found this to be a sufficient sediment
189 depth for crabs to dig and occupy burrows. The sediment was dampened by adding small
190 amounts of filtered sea water until the sediment was thoroughly moistened without
191 having any standing water on the surface. Once the divider was removed, any gaps
192 between the sediment types were closed with a spatula. After each trial, we removed any
193 mixed sediment from the tank and re-sieved it according to the procedure above.

194 Each trial, within each of the three experiments, consisted of three treatments: one
195 containing only sand fiddler crabs, a second containing only mud fiddler crabs, and a
196 third containing both sand and mud fiddler crabs. All experiments were conducted in 30.5
197 x 15 x 21 cm glass tanks with internal dimensions of 29.5cm x 14cm (for an area of
198 413cm²) by 19cm high. These tanks were wrapped in white paper to ensure that the crabs
199 in one tank could not see crabs in other tanks. Treatments and crabs were randomly
200 assigned to tanks between each trial. In both conspecific and heterospecific treatments,
201 crabs were paired by eye such that sizes were equivalent between the individuals in a
202 tank. Mean carapace length of both species at these sites are approximately 15mm
203 (Gittman & Keller, 2013).

204 Prior to each trial, we labeled the crabs on their carapace using a Sharpie® to
205 identify individuals. Once labeled, crabs for each tank were placed into separate plastic
206 cups. Beginning at peak low tide, the crabs were gently released from the cups into the
207 center of the tank to ensure all crabs were introduced simultaneously and in the center of
208 the tank (on the centerline between coarse and fine sediment where applicable) to ensure
209 an unbiased starting location. Following our behavioral observations (described below),
210 all tanks were topped with plastic lids to ensure no crab escaped and covered with a large
211 black trash bag to avoid potential disruptions or effects of ambient light. We chose to
212 start the trials at low tide because fiddler crabs are most active and burrow at this time
213 (Teal, 1958; Bertness & Miller, 1984; Zeil & Hemmi, 2006). While all experiments were
214 conducted indoors, we wanted to accommodate any ingrained timing of behaviors and to
215 allow them a realistic amount of time to create a burrow (Aspey 1978; Zeil & Hemmi,
216 2006). We left the tanks undisturbed until the subsequent high tide (~6 hours), at which
217 time we uncovered them and recorded the total number of burrows, whether burrows
218 were occupied or unoccupied, burrow location (corner, middle, or side of tank), and
219 burrow sediment type (in the low- and high-density FC tests).

220 *2.3 Mixed sediment trials*

221 To assess burrowing and burrowing behavior in sediment conditions intended to mimic
222 those found naturally within local NC marshes (mixed sand and mud), we conducted a
223 total of ten mixed-sediment trials between August and October 2016. Each trial consisted
224 of three tanks as described above giving us ten replicates of each treatment. Sediment
225 was collected from the Hoop Pole Creek marsh, coarsely sieved through 500µm mesh to

226 remove large debris and shell fragments, and then oven-dried or sun dried without
227 separating fine or coarse sediment. The dried sediment was added to each tank to a depth
228 of 3cm and moistened with salt water as described above.

229 *2.4 Low- and high-density FC trials*

230 To evaluate the effects of fine versus coarse sediment type on burrowing behavior and
231 burrowing location, we conducted separate fine and coarse (FC) sediment experiments
232 twice, in 2012 and in 2016. Low-density FC trials had two crabs per tank and high-
233 density FC trials had ten crabs per tank (i.e., for the high-density trials, one treatment had
234 ten sand fiddler crabs, one had ten mud fiddler crabs, and the third treatment had five
235 sand and five mud). Between August and September 2012, we conducted 11 replicate
236 trials at low-density (2 crabs) and 6 replicates at high-density (10 crabs). From September
237 to November 2016, we conducted another 8 replicate trials at low-density, as well as
238 another 2 trials at high-density. This was a total of 19 low-density and 8 high-density
239 replicates of all three treatments. Trends were consistent when data from 2012 and 2016
240 were examined separately, but the overall number of burrows was generally higher in
241 2012 than 2016, potentially because the trials occurred later in the season (August-
242 September vs. September-November) (2012 trials 2.26 ± 0.25 ; 2016 trials 0.68 ± 0.31
243 [mean \pm SE]), t-test; $p < 0.001$).

244 *2.6 Behavior videos*

245 For seven of the Mixed trials and five of the low-density FC trials conducted in 2016, we
246 used GoPro cameras to record fiddler crab behavior. Due to the large number of crabs in

247 the high-density FC experiment, no video footage was collected for behavioral analysis.
248 Cameras were positioned directly above the tanks to obtain an aerial view of the crabs.
249 One camera was used to capture the three tanks comprising one trial. The cameras were
250 turned on at the start of each trial and left to record undisturbed for 25 minutes, which
251 included a 15-minute acclimation period (Robertson et al., 1980) and a 10-minute
252 behavioral observation period. After 25 minutes the cameras were turned off and
253 retrieved and the tanks were covered and left undisturbed for the remainder of the trial.
254 Trials in which no video footage was collected also had a 25-minute uncovered interval at
255 the beginning of each trial.

256 We used the program CowLog (Pastell, 2016) to confirm behavior types
257 (described below) and quantify the amount of time each behavior was exhibited. For the
258 low-density FC trials, we also recorded the sediment type (coarse or fine) in which each
259 behavior occurred. Additionally, we recorded when a crab was in a “blind spot” or an
260 area where the camera was not able to capture the crab fully or it was unreasonable to
261 identify a given behavior due to limited visibility. Any crab that was not captured by the
262 camera for more than 75% of the observation time was not used in analyses (of 72 crabs
263 observed across all experiments, 7 were excluded from the analysis).

264 Potential behaviors were established by direct observations of the crabs in the
265 tanks prior to the video trials. Observed behaviors were grouped into four major
266 categories for analysis: Active (roaming and climbing behaviors), Burrow (behaviors
267 involved in making or occupying a burrow), Interact (behaviors that involved the two
268 crabs in the tank touching or invading the other’s burrow), and Stand (the crab was

269 standing still and/or feeding). We categorized interactions further as aggressive, neutral,
270 or defensive (Table 1), but we did not analyze these data, as the sample sizes were too
271 low to achieve adequate statistical power and the nature of the interactions meant that the
272 counts were often not independent across crabs (i.e., if one crab is aggressive, the other
273 often responded with a defensive interaction within the same tank).

274 Given the design of the experiment, the two crabs in the conspecific treatment
275 were not considered independent replicates. Therefore, a random number generator was
276 used to select one of the two crabs in each tank to be included in the behavioral analyses
277 (crabs already excluded due to lack of visibility as stated above were automatically not
278 chosen). Three iterations of randomly chosen crabs were analyzed to ensure no
279 individuals were drastically affecting the data. As no major differences were detected, the
280 first round of crabs randomly chosen were used in subsequent analyses.

281 *2.7 Statistical analyses*

282 To address our hypotheses concerning differences in the number and location of burrows
283 between the two species, we used a generalized linear model (GLM) to evaluate the
284 effect of species treatment (i.e., sand fiddler only, mud fiddler only, and both present) on
285 the total number of burrows dug, the sediment type (if applicable), and the location of
286 burrows. Using Akaike's Information Criterion (AIC), we found that a negative binomial
287 distribution provided the best fit across all experiments. For low- and high- density FC
288 trials, our initial generalized linear model found sediment type was not a significant
289 factor. A second GLM with just species treatment and burrow location was conducted
290 (excluding sediment type) and found to better fit the data when the AIC scores were

291 compared. Sediment type was subsequently dropped from the analysis. A likelihood ratio
292 test was used to determine if there were any significant interactions between the variables
293 in the model. When the overall test was significant, we used Tukey's post-hoc tests to
294 determine pairwise differences.

295 Based on previous literature, we expected that each species of fiddler crab in the
296 low- and high-density FC experiments might exhibit a different sediment preference for
297 burrowing as they are commonly found burrowing in different sediment types in the field
298 and have species-specific burrowing behaviors associated with either mud or sand when a
299 clear sediment type is available (O'Connor, 1993; Teal, 1958). To test this hypothesis
300 explicitly, we conducted *a priori* comparisons of burrow sediment type (coarse or fine)
301 between the two conspecific treatments in the low- and high-density FC trials, using
302 Welch's two-sample t-tests.

303 To determine whether interspecific interactions change burrowing behavior, we
304 compared the observed number of burrows in the tanks with both species present to the
305 expected number of burrows calculated by taking the average number of burrows in the
306 sand and mud fiddler crab-only treatments. We then conducted separate paired t-tests for
307 each of the three experiments to compare the number of burrows expected in each trial
308 versus the number of burrows observed. These data were log+1 transformed to meet
309 model assumptions.

310 To examine potential effects of intraspecific competition, we compared the
311 conspecific treatments of the low-density to the high-density FC trials looking at the
312 number of burrows dug per crab, normalized by the total number of crabs (2 for low-

313 density, 10 for high-density). We then used a Welch's t-test, which controls for the low
314 sample sizes and uneven distribution of trials between the two experiments, and log+1
315 transformed the data to satisfy normality assumptions. The tests were run separately for
316 sand and mud fiddlers.

317 We also examined the occupancy of the burrows at the end of the trials. In many
318 cases, there were more burrows dug at the end of the trial than crabs present in a tank. All
319 burrows were excavated at the end of the trial and crabs were either noted as occupying
320 or not occupying a burrow. We used a chi-squared test for each species with the number
321 of occupied and unoccupied burrows in the presence and absence of the other species to
322 reveal interspecific effects. In conspecific tanks, only one randomly chosen crab per tank
323 (or 5 crabs in the case of high-density trials) was used to keep the sample size consistent
324 between conspecific and congeneric trials.

325 To detect differences in behavior among treatments from our video footage, we
326 conducted binomial family GLMs on the amount of time spent displaying two of the four
327 behavior categories listed above, Burrow and Interact. These categories were chosen as
328 the most relevant to our questions of interest. For this analysis, we pooled the mixed
329 sediment trials and low-density FC trials, including experiment type as a factor in the
330 analysis. Experiment type (mixed or low-density FC) was not found to be a significant
331 factor in our model for any of the behavioral categories. When results were significant,
332 we used Tukey's post-hoc tests to examine pairwise differences.

333 A set of planned comparisons were conducted to determine if there was an effect
334 of treatment on sediment preference for the FC trials in our behavior videos. A binomial

335 family GLM was run for each relevant pair of treatments, (sand fiddler in conspecific vs.
336 heterospecific tanks, mud fiddler in conspecific tank vs. heterospecific tanks, and sand
337 fiddler vs. mud fiddler in conspecific tanks) using time spent in coarse sediment as the
338 variable of interest. All tests were run in R version 3.0.2 using the MASS and multcomp
339 packages for the GLMs (Hothorn et al., 2017; Venables and Ripley, 2002).

340

341 3. Results

342

343 3.1 *Burrowing frequency and location*

344

345 Across all three experiments, we found that sand fiddler crabs (*Leptuca pugilator*) dug
346 more burrows on average than mud fiddler crabs (*Minuca pugnax*). In the mixed trials,
347 the sand fiddler-only treatment had over eight times more burrows on average than the
348 mud fiddler-only treatment (sand 2.5 ± 0.27 ; mud 0.3 ± 0.15 [mean \pm SE]) and almost
349 twice as many as the treatment containing both species (1.4 ± 0.31 ; GLM, negative
350 binomial; $p < 0.0001$; Fig. 1A, Table 3). There was a significant interaction between
351 species treatment and burrow location so post-hoc tests were not run (but see pairwise
352 results discussed below; Table 3). In the low-density FC trials, the sand fiddler dug
353 almost four times more burrows than the mud fiddler (GLM, negative binomial; $p <$
354 0.0001 ; Tukey's post-hoc analysis, $p < 0.001$). The both species treatment had an
355 intermediate number of burrows between the two conspecific treatments with the number
356 significantly higher than mud fiddler alone ($p < 0.01$; sand 3.58 ± 0.73 ; mud 0.89 ± 0.24 ;
357 Both 2.26 ± 0.55 ; Fig. 1B, Table 2). For the high-density FC experiments, the sand
358 fiddler dug almost three and a half times more burrows than the mud fiddler (GLM,
359 negative binomial; $p < 0.001$; Tukey's post-hoc, $p < 0.001$; sand 9.29 ± 3.62 ; mud $2.71 \pm$

360 1.9), but not significantly more than the both species treatment ($p = 0.37$; Both $7.0 \pm$
361 2.59). There were also significantly more burrows dug when both crabs were present than
362 when the mud fiddler was alone ($p < 0.001$; Fig. 1C, Table 2). It was common for there to
363 be more than one burrow per crab in treatments that included sand fiddlers.

364 Additionally, there was a significant difference in the number of burrows in each
365 location (corner, middle, side) for the mixed sediment and low-density FC trials (GLM;
366 negative binomial, mixed $p < 0.0001$; low-density FC $p < 0.0001$). Generally, all crabs
367 burrowed more in the corner of the tank than the side of the tank and preferred the sides
368 and corners more than the middle of the tank (Fig. 2, Table 2). For the mixed sediment
369 trials, there was an interaction between species treatment and location (LRT, $p < 0.01$);
370 therefore, each pairwise combination was examined individually (Fig. 2A, Table 3). Mud
371 fiddler crabs burrowed only in tank corners and never along the sides or in the middle.
372 Most burrows in the low-density FC trials were dug in the corners, followed by along the
373 sides, and lastly in the middle of the tank, although there was not a significant difference
374 between the number of burrows in the corner or along the sides (Fig. 2B, Table 2). For
375 the high-density experiments there was no preference for burrowing in the corner,
376 middle, or side of the tank across treatments (GLM; negative binomial, $p = 0.80$; Fig.
377 2C).

378 The observed number of burrows in the heterospecific treatment was not
379 significantly different than the expected number of burrows calculated from the
380 conspecific treatments in any of the experiments, suggesting no interspecific interactions
381 were affecting burrowing (paired t-test; Mixed: $p = 1$, mean observed = 1.4, mean
382 expected = 1.4; Low-density FC: $p = 0.61$, mean observed = 2.26, mean expected = 2.13;

383 High-density FC: $p = 0.51$, mean observed = 7.29, mean expected = 6.0). In the low-
384 density FC trials, the mud fiddler preferred fine sediment to coarse sediment (*a priori*
385 planned comparison, $t(27.6) = -2.38$, $p = 0.02$) while the sand fiddler showed no
386 preference for sediment type ($t(27.6) = -0.09$, $p = 0.93$). In the high-density FC trials,
387 neither species exhibited a sediment preference (*a priori* t-test, sand $p = 0.71$; mud $p =$
388 0.77).

389

390

391 3.2 *Burrow occupancy*

392

393 In the mixed trials, there was no relationship between the number of burrows occupied by
394 sand fiddlers and the presence or absence of a mud fiddler (chi-squared test, $X^2(1) = 0$, p
395 = 1). A relationship was found for the mud fiddler, who did not occupy any burrows in
396 the absence of sand fiddlers, but occupied over half of the burrows (6 out of 10) when a
397 sand fiddler was present ($X^2(1) = 5.9524$, $p = 0.015$) suggesting mud fiddlers may be
398 occupying burrows not built by themselves. In the low-density FC trials, there was no
399 difference in sand fiddler burrow occupancy in the presence or absence of a mud fiddler
400 ($X^2(1) = 0$, $p = 1$), and also no difference for mud fiddler burrow occupancy in the
401 presence of a sand fiddler ($X^2(1) = 0.689$, $p = 0.407$). In the high-density FC trials, there
402 were no significant relationships between the number of burrows occupied and the
403 presence or absence of heterospecifics ($X^2(1) = 1.51$, $p = 0.220$) or mud fiddlers ($X^2(1) =$
404 2.797, $p = 0.094$).

405

406 3.3 *Density-dependent effects*

407 We found no significant difference in average number of burrows dug per crab for sand
408 fiddlers (Welch's t-test, $p = 0.41$; mean low-density per crab = 1.66, mean low-density
409 total = 3.58; mean high-density per crab = 1.11, mean total = 9.29). However, there was a
410 five-fold difference in the average number of burrows per crab when mud fiddlers were
411 in the presence of a high density of conspecifics versus low density ($p = 0.02$; mean low-
412 density per crab = 0.47, mean total = 0.89; mean high-density per crab = 0.09, mean total
413 = 2.71).

414

415

416 3.4 Behavioral analysis

417

418 We found significant differences in the amount of time spent burrowing between
419 treatments (GLM; binomial, $p < 0.01$, Fig. 3, Table 4). Mud fiddlers in the conspecific
420 treatments burrowed 0% of the time in all trials and spent significantly less time
421 burrowing than any of the other treatments, most notably when compared to sand fiddler
422 crabs in their conspecific treatment (Tukey's post-hoc; $p < 0.001$) and to other mud
423 fiddlers in heterospecific treatments ($p = 0.04$). There was no difference in the amount of
424 time sand fiddlers spent burrowing in heterospecific versus conspecific treatments ($p =$
425 0.36), nor between the time sand and mud fiddlers spent burrowing in the heterospecific
426 treatment.

427 Time spent interacting was also significant in our model (GLM; binomial, $p =$
428 0.046, Fig. 3, Table 4). This pattern was driven by an increase in the time spent
429 interacting by the sand fiddler in the presence of a mud fiddler (Tukey's post-hoc; sand
430 conspecific – heterospecific, $p = 0.021$), as well as mud fiddlers interacting more with
431 other mud fiddlers than the sand fiddler with its conspecifics (mud conspecific – sand

432 conspecific, $p = 0.02$). There was no difference in the time spent interacting between sand
433 and mud fiddlers in the heterospecific tanks ($p = 0.380$), nor between the mud fiddler in
434 conspecific versus heterospecific tanks ($p = 0.79$). When the nature of these interactions
435 was examined, we found that in the presence of conspecifics, only two sand fiddler
436 individuals in all trials displayed interactive behavior of any kind and all but one of those
437 interactions was neutral. In contrast, mud fiddlers displayed a higher number of
438 interactions overall in both heterospecific and conspecific treatments. None of the mud
439 fiddler interactions were classified as aggressive in the presence of conspecifics, but were
440 frequently aggressive toward sand fiddlers in heterospecific treatments.

441 Sand fiddlers in conspecific tanks spent the majority of their time in fine sediment
442 (96.4%). Our GLM revealed that this preference did not carry over to heterospecific tanks
443 (GLM; binomial, $p = 0.04$) where they appeared to show no sediment preference (50% in
444 fine and 50% in coarse sediment). There was a significant difference between the amount
445 of time spent in coarse sediment between sand and mud fiddlers in conspecific treatments
446 ($p < 0.01$), with mud fiddlers spending about 73% of their time in coarse sediment. Mud
447 fiddlers showed no clear preference in the heterospecific tanks (also 50% fine, 50%
448 coarse) and there was no statistical difference in the amount of time spent in coarse
449 sediment between mud fiddlers in conspecific vs. heterospecific tanks ($p = 0.40$).

450

451 4. Discussion

452

453 For species to be complementary rather than redundant in an ecosystem, they must use
454 the niche space differently in some way that reduces competition along a resource axis
455 and allows for coexistence. Additionally, their functional contributions to the system

456 should be additive rather than synergistic or antagonistic, which would instead support a
457 facultative or negative interaction between the species (Loreau, 2004). Our results
458 measuring burrowing frequency support the hypothesis of species complementarity.
459 Across all three experiments, the sand fiddler dug at least three and up to six times more
460 burrows than the mud fiddler. We see these results mirrored in our behavioral data with
461 sand fiddlers spending more of their time burrowing than mud fiddlers, which preferred
462 actively roaming or standing outside of a burrow. When the two species are brought
463 together, the total number of burrows dug was intermediate between the two conspecific
464 treatments, again suggesting an additive rather than antagonistic or synergistic effect.
465 Therefore, in this one measure, it appears there are differences in burrowing habits, at
466 least in our artificial arenas.

467 Our results for the observed versus expected number of burrows also supports the
468 complementarity hypothesis. This statistical approach is standard for analyzing species
469 interaction in a substitutive design and in this case was used to determine whether
470 burrowing differed in the presence or absence of the other species (Fraser et al., 1996;
471 Toscano et al., 2010). Based on our results, we can conclude that the number of burrows
472 was not different when individuals were in the presence of conspecifics or
473 heterospecifics. If we had seen fewer than expected burrows, we would have assumed
474 that competition may be occurring and if we had seen more than expected, we would
475 have assumed that one species may be facilitating or enhancing the burrowing of the
476 other. Ultimately, we see that the two species seem to co-occur without influencing each
477 other's burrowing frequency, which is a similar result to Teal (1958).

478 When looking solely at the total number of burrows dug by the end of a trial, the
479 picture of complementarity is clear. However, when other measures of burrowing
480 behavior are analyzed, a slightly different picture emerges. While sand fiddlers did not
481 show an observable preference between coarse and fine, mud fiddlers did significantly
482 prefer fine sediment as predicted by the literature (O'Connor, 1993; Teal, 1958). In
483 nature, fiddler crabs, particularly mud fiddler crabs who burrow in muddy, poorly
484 structured sediment, preferentially burrow near structured objects such as *Spartina*
485 *alterniflora* shoots or mussel and oyster shells (George et al., 2010). While both prefer to
486 burrow in corners or along the sides of the tanks over the unstructured middle of the tank,
487 mud fiddlers demonstrated this preference more strongly than sand fiddlers by
488 exclusively burrowing in corners and along sides and never burrowing in the middle of a
489 tank. It is also possible that the discrepancy in number of burrows is due to the speed at
490 which each species burrows. The sand fiddler may be able to make multiple burrows in
491 the same amount of time that a mud fiddler makes one, allowing sand fiddlers to dig in
492 multiple locations before choosing which to occupy. Overall, mud fiddler crabs in our
493 experiments appeared to be more selective about where they chose to burrow.

494 Further, in our behavioral video analyses, there is evidence that interspecific
495 interactions are affecting burrowing behavior. Sand fiddlers spent less time burrowing in
496 the presence of mud fiddlers and increased the amount of time spent responding to mud
497 fiddlers. Mud fiddlers altered the burrowing behavior of sand fiddlers, likely through
498 interference. These interactions were most often defensive on the part of sand fiddlers
499 while overwhelmingly aggressive by mud fiddlers. Generally, mud fiddlers appear to be
500 more aggressive than sand fiddlers even among conspecifics as seen by the lowered

501 burrowing rate per crab at high densities. Overall, we see the mud fiddler as the aggressor
502 toward sand fiddlers possibly bullying them out of the prime burrow locations that they
503 more strongly prefer (finer sediment near structure). Teal (1958) and Aspey (1978) found
504 a similar negative impact of the mud fiddler on sand fiddlers in their lab and field studies
505 respectively. These antagonistic behaviors by mud fiddler crabs even culminated in
506 instances of mud fiddlers stealing the burrows of sand fiddlers, which we documented
507 twice in our behavioral videos. Given the short duration of the videos, it is reasonable to
508 assume that burrow theft was occurring regularly throughout our trials and that the
509 number of burrows at the end of the trials do not fully reflect the interactions in the
510 interim. The occupancy of burrows at the end of the trials also supports this possibility
511 with mud fiddlers occupying more burrows in the presence of a sand fiddler than in the
512 presence of only conspecifics, although this pattern was only significant in the low-
513 density FC trials. While the total number of burrows may not be affected, there may be
514 refuge benefits for mud fiddlers at the expense of sand fiddlers that we only observed by
515 recording their interactions.

516 In nature, fiddler crabs are a highly gregarious species that can occur at high
517 densities in North Carolina (approximately 75 crabs per m² on average) (Gittman and
518 Keller, 2013; Zeil and Hemmi, 2014). We examined the potentially important effect of
519 density on each fiddler species' burrowing performance in our high-density trials.
520 Generally, sediment and location preferences broke down in both species at higher
521 densities meaning that in our space limited tanks, some amount of scramble or
522 interference competition is most likely occurring in these species for prime burrow
523 locations. We also found that the average number of burrows per crab was lower at

524 higher densities for mud fiddlers and their preference for fine sediment also lessened at
525 high densities, while sand fiddlers were unaffected. It is worth noting that tanks only had
526 four corners and with so many crabs in a confined space, competition over prime spots
527 may be artificially high, leading crabs to settle for suboptimal locations. While this may
528 just be an artifact of our experimental design, based on field observations and the social
529 nature of these crabs, this level of density is not unrealistic, especially when crabs display
530 herding behaviors. Intraspecific and interspecific competition may influence where crabs
531 are able to burrow if prime real estate is limited in nature.

532 We also only used female crabs, which suited the purposes of this experiment, but
533 may only be giving us half the picture. Male-male competition and differences in biology
534 and physiology of males versus females may also be driving settling patterns in nature.
535 The needs of each sex may differ in where they feed and burrow. For example, male
536 fiddlers possess one enlarged claw that is used in waving displays to attract females. This
537 sexually selected appendage affects their feeding and burrowing efficiency and therefore
538 forces males to compensate by altering their behavior, physiology, and resource use
539 (Caravello & Cameron, 1987; Bywater et al., 2018). Males also spend large portions of
540 their time during mating season attracting mates and digging burrows for those females
541 (Weis & Weis, 2004; Hemmi & Zeil, 2003; Christy 1982). Therefore, their motivation for
542 burrowing is different than for females and may change seasonally for both sexes.

543 It appears that while there is niche separation and complementarity at one level,
544 there is also a fair amount of competitive interaction and overlap in this system as well.
545 Many North Carolina marshes have mixed sediments that may not be clearly delineated
546 into mud or sand (Teal, 1958; Timmons et al., 2010). Niche differences could arise from

547 differences in sediment preference (O'Connor, 1993; Teal, 1958), but in our study we
548 only saw a strong preference in mud, not sand fiddlers in where they chose to burrow.
549 Interestingly, we saw contradictory patterns in our behavioral analysis. Sand fiddler crabs
550 in conspecific tanks spent almost all of their time (over 95%) in fine sediment, which is
551 the opposite of what we expected based on the literature and what we find in our own
552 burrowing data. Mud fiddlers in conspecific treatments spent the majority of their time in
553 coarse sediment (another surprising result and in contrast to what we see in their
554 burrowing behavior). These patterns were not observed in the heterospecific tanks with
555 neither species having any clear sediment preference. These results may hint at some
556 other sediment consideration not captured in just burrowing behavior alone. For example,
557 it is possible that fine sediment has higher organic matter and nutrient content, or that it
558 provides better refuge and structure for burrows than the coarser, sandy sediment that
559 may be more open and exposed to predators. These considerations may be particularly
560 important for sand fiddlers who may be excluded from their preferred sediment due to
561 mud fiddler aggression.

562 Fiddler burrowing is linked to a number of important ecosystem functions and has
563 been shown to promote marsh health by aerating and mixing the sediment (Citadin et al.,
564 2016; Gittman and Keller, 2013; Wang et al., 2010; and others). Differences in burrow
565 number and location could have important implications for how each species functions as
566 a bioturbator and ecosystem engineer in marsh ecosystems; but field data are needed to
567 fully extend the results from this study. Overall, studying these kinds of fine-scale habitat
568 use patterns in co-occurring species could be integral in helping us to better understand
569 the role each species plays in this ecosystem. Both species appear to be important in

570 maintaining bioturbation through their burrowing and ensuring marsh health, but this
571 complementarity may also have implications for the stability of the ecosystem. One
572 species may not be able to fully replace the functioning of the other if removed from the
573 system since their roles are not completely overlapping. Evaluating the function of each
574 species in a community and evaluating their individual and combined contributions can
575 be challenging. Measuring multiple responses of habitat use and differences in functional
576 niche is important as species interactions are complex and often difficult to untangle, but
577 may affect the ability of each organism to perform critical roles in an ecosystem.
578

579

580 Acknowledgments

581 The authors would like to thank D. Kochan, T. Pfeifer, and the team of UNC-Chapel Hill
582 undergrads who assisted in the field collection of crabs. This research was
583 funded by a NOAA NERRS graduate fellowship (NOAA Grant No: NA11NOS4200086)
584 to R. Gittman, a UNC Chapel Hill Royster Society Fellowship to C. Smith, East Carolina
585 University, and the University of North Carolina at Chapel Hill.

586

587 References

588 Abrams, P., 1983. The theory of limiting similarity. *Annu. Rev. Ecol. Syst.* 14, 359–376.

589 <https://doi.org/10.1146/annurev.es.14.110183.002043>

590 Allen, E.A., Curran, H.A., 1974. Biogenic sedimentary structures produced by crabs in
591 lagoon margin and salt marsh environments Near Beaufort, North Carolina. *J.*

592 *Sediment. Res.* 44.

593 Aspey, W. P., 1978. Fiddler crab behavioral ecology: Burrow density in *Uca pugnax*

594 (Smith) and *Uca pugilator* (Bosc) (Decapoda Brachyura). *Crustaceana* 34, 235-244.

595 Bertness, M.D., 1985. Fiddler crab regulation of *Spartina alterniflora* production on a

596 New England salt marsh. *Ecology* 66, 1042–1055. <https://doi.org/10.2307/1940564>

597 Bertness, M.D., Miller, T., 1984. The distribution and dynamics of *Uca pugnax* (Smith)

598 burrows in a new England salt marsh. *J. Exp. Mar. Bio. Ecol.* 83, 211–237.

599 [https://doi.org/10.1016/S0022-0981\(84\)80002-7](https://doi.org/10.1016/S0022-0981(84)80002-7)

600 Bywater, C. L., Wilson, R. S., Monro, K., White, C. R., 2018. Legs of male fiddler crabs

601 have evolved to compensate for claw exaggeration and enhance claw functionality

- 602 during waving displays. *Evolution* 72, 2491-2502. <https://doi.org/10.1111/evo.13617>
- 603 Caravello, H. E., Cameron, G. N., 1987. The effects of sexual selection on the foraging
604 behavior of the Gulf Coast fiddler crab, *Uca panacea*. *Animal Behaviour* 35, 1864-
605 1874. [https://doi.org/10.1016/S0003-3472\(87\)80079-9](https://doi.org/10.1016/S0003-3472(87)80079-9).
- 606 Christy, J. H., 1982. Burrow structure and use in the sand fiddler crab, *Uca pugilator*
607 (Bosc). *Animal Behaviour* 30, 687-694. [https://doi.org/10.1016/S0003-
608 3472\(82_80139-5](https://doi.org/10.1016/S0003-3472(82_80139-5).
- 609 Citadin, M., Costa, T.M., Netto, S.A., 2016. The response of meiofauna and
610 microphytobenthos to engineering effects of fiddler crabs on a subtropical intertidal
611 sandflat. *Austral Ecol.* 41, 572–579. <https://doi.org/10.1111/aec.12346>
- 612 Colby, D.R., Fonseca, M.S., 1984. Population dynamics, spatial dispersion and somatic
613 growth of the sand fiddler crab *Uca pugilator* 16, 269–279.
- 614 Crane, J., 1975. *Fiddler Crabs of the World: Ocypodidae: Genus Uca*. Princeton
615 University Press. <https://doi.org/10.1515/9781400867936>
- 616 Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E., Thomson, D.,
617 1998. The statistical inevitability of stability-diversity relationship in community
618 ecology. *Am. Nat.* 151, 264–276. <https://doi.org/10.1086/286117>
- 619 Fraser, S., Gotceitas, V., Brown, J.A., 1996. Interactions between age-classes of Atlantic
620 cod and their distribution among bottom substrates. *Can. J. Fish. Aquat. Sci.* 53,
621 305–314. <https://doi.org/10.1139/f95-183>
- 622 George, S.B., Carlson, M.D., Regassa, L.B., 2010. Shell use by juvenile fiddler crabs *Uca*
623 *pugnax* and *U. pugilator*. *J. Exp. Mar. Bio. Ecol.* 396, 35–41.
624 <https://doi.org/10.1016/j.jembe.2010.09.014>

- 625 Gittman, R.K., Keller, D.A., 2013. Fiddler crabs facilitate *Spartina alterniflora* growth,
626 mitigating periwinkle overgrazing of marsh habitat. *Ecology* 94, 2709–2718.
627 <https://doi.org/10.1890/13-0152.1>
- 628 Hardin, G., 1960. The competitive exclusion principle. *Science* 131(3409), 1292-1297.
629 <https://doi.org/10.2307/1705965>
- 630 Hothorn, T., Bretz, F., Westfall, P., 2017. Simultaneous Inference in General Parametric
631 Models, *Biometrical Journal*.
- 632 Hubbard, C. R., 2008. Comparison of invasive and non-invasive techniques for
633 measuring fiddler crab density in a salt marsh. *Electronic Theses and Dissertations*.
634 737. <https://digitalcommons.georgiasouthern.edu/etd/737>
- 635 Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers, in:
636 *Ecosystem Management*. Springer New York, New York, NY, pp. 130–147.
637 https://doi.org/10.1007/978-1-4612-4018-1_14
- 638 Katz, L.C., 1980. Effects of burrowing by the fiddler crab, *Uca pugnax* (Smith). *Estuar.*
639 *Coast. Mar. Sci.* 11, 233–237. [https://doi.org/10.1016/S0302-3524\(80\)80043-0](https://doi.org/10.1016/S0302-3524(80)80043-0)
- 640 Loreau, M., 2004. Does functional redundancy exist? *Oikos* 104, 606–611.
641 <https://doi.org/10.1111/j.0030-1299.2004.12685.x>
- 642 Mattheus, C. R., Rodriguez, A. B., McKee, B. A., Currin, C. A., 2010. Impact of land-use
643 change and hard structures on the evolution of fringing marsh shorelines. *Estuar.*
644 *Coast Shelf Sci.* 88(3), 365-376. <https://doi.org/10.1016/j.ecss.2010.04.016>
- 645 McCraith, B.J., Gardner, L.R., Wethey, D.S., Moore, W.S., 2003. The effect of fiddler
646 crab burrowing on sediment mixing and radionuclide profiles along a topographic
647 gradient in a southeastern salt marsh. *J. Mar. Res.* 61, 359–390.

- 648 Naeem, S., 2002. Disentangling the impacts of diversity on ecosystem functioning in
649 combinatorial experiments. *Ecology* 83, 2925–2935. [https://doi.org/10.1890/0012-](https://doi.org/10.1890/0012-9658(2002)083[2925:DTIODO]2.0.CO;2)
650 [9658\(2002\)083\[2925:DTIODO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2925:DTIODO]2.0.CO;2)
- 651 O’Connor, N.J., 1993. Settlement and recruitment of the fiddler crabs *Uca pugnax* and *U.*
652 *pugilator* in a North Carolina, USA, salt marsh. *Mar. Ecol. Prog. Ser.* 93, 227–234.
- 653 Pastell, M., 2016. CowLog – Cross-platform application for coding behaviours from
654 video. *J. Open Res. Softw.* 4. <https://doi.org/10.5334/jors.113>
- 655 Reinsel, K.A., 2004. Impact of fiddler crab foraging and tidal inundation on an intertidal
656 sandflat: season-dependent effects in one tidal cycle. *J. Exp. Mar. Bio. Ecol.* 313, 1–
657 17. <https://doi.org/10.1016/j.jembe.2004.06.003>
- 658 Ringold, P., 1979. Burrowing, root mat density, and the distribution of fiddler crabs in the
659 eastern United States. *J. Exp. Mar. Bio. Ecol.* 36, 11–21.
660 [https://doi.org/10.1016/0022-0981\(79\)90097-2](https://doi.org/10.1016/0022-0981(79)90097-2)
- 661 Robertson, J. R., Bancroft, K., Vermeer, G., Plaisier, K., 1980. Experimental studies on
662 the foraging behavior of the sand fiddler crab *Uca pugilator* (Bosc, 1802). *J. Exp.*
663 *Mar. Bio. Ecol.* 44, 67–83. [https://doi.org/10.1016/0022-0981\(80\)90102-1](https://doi.org/10.1016/0022-0981(80)90102-1).
- 664 Rosenfeld, J.S., 2002. Functional redundancy in ecology and conservation. *Oikos* 98,
665 156–162. <https://doi.org/10.1034/j.1600-0706.2002.980116.x>
- 666 Salmon, M., Hyatt, G. W., 1983. Spatial and temporal aspects of reproduction in North
667 Carolina fiddler crabs (*Uca pugilator* Bosc.). *J. Exp. Mar. Bio. Ecol.* 70(1), 21-43.
668 [https://doi.org/10.1016/0022-0981\(83\)90146-6](https://doi.org/10.1016/0022-0981(83)90146-6)
- 669 Teal, J.M., 1958. Distribution of fiddler crabs in Georgia salt marshes. *Ecology* 39, 185–
670 193. <https://doi.org/10.2307/1931862>

- 671 Thomas, C., Blum, L., 2010. Importance of the fiddler crab *Uca pugnax* to salt marsh soil
672 organic matter accumulation. *Mar. Ecol. Prog. Ser.* 414, 167–177.
673 <https://doi.org/10.3354/meps08708>
- 674 Timmons, E.A., Rodriguez, A.B., Mattheus, C.R., DeWitt, R., 2010. Transition of a
675 regressive to a transgressive barrier island due to back-barrier erosion, increased
676 storminess, and low sediment supply: Bogue Banks, North Carolina, USA. *Mar.*
677 *Geol.* 278, 100–114. <https://doi.org/10.1016/J.MARGEO.2010.09.006>
- 678 Toscano, B.J., Fodrie, F.J., Madsen, S.L., Powers, S.P., 2010. Multiple prey effects:
679 Agonistic behaviors between prey species enhances consumption by their shared
680 predator. *J. Exp. Mar. Bio. Ecol.* 385, 59–65.
681 <https://doi.org/10.1016/J.JEMBE.2010.01.001>
- 682 Venables, W.N., Ripley, B.D., 2002. *Modern applied statistics with S, statistics and*
683 *computing.* Springer New York, New York, NY. [https://doi.org/10.1007/978-0-387-](https://doi.org/10.1007/978-0-387-21706-2)
684 [21706-2](https://doi.org/10.1007/978-0-387-21706-2)
- 685 Walker, B.H., 1992. Biodiversity and ecological redundancy. *Conserv. Biol.* 6, 18–23.
686 <https://doi.org/10.1046/j.1523-1739.1992.610018.x>
- 687 Wang, J.Q., Zhang, X.D., Jiang, L.F., Bertness, M.D., Fang, C.M., Chen, J.K., Hara, T.,
688 Li, B., 2010. Bioturbation of burrowing crabs promotes sediment turnover and
689 carbon and nitrogen movements in an estuarine salt marsh. *Ecosystems* 13, 586–599.
690 <https://doi.org/10.1007/s10021-010-9342-5>
- 691 Weis, J.S., Weis, P., 2004. Behavior of four species of fiddler crab, genus *Uca*, in
692 southeast Sulawesi, Indonesia. *Hydrobiologia* 523, 47-58.
693 <https://doi.org/10.1023/B:HYDR.0000033093.84155.1d>

- 694 Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating
695 environment: The insurance hypothesis. *Proc. Natl. Acad. Sci.* 96, 1463–1468.
696 <https://doi.org/10.1073/pnas.96.4.1463>
- 697 Zeil, J., Hemmi, J.M., 2014. Nervous systems and control of behavior, in: *Nervous*
698 *Systems and Control of Behavior*. pp. 484–505.

699 Tables

700 **Table 1** Descriptions of each overall behavior category recorded during video
 701 observation periods (active, burrow, interact, or stand). For interactive behaviors, the
 702 nature of the interaction (aggressive, neutral, defensive) is also given.
 703

Category	Behavior	Behavior description	Nature of Interaction
Active	Roam	Crab actively walking around tank	
	Climb	Crab with legs on glass side of tank attempting to crawl up the side	
Burrow	Burrow	Crab actively digging burrow	
	Occupy Burrow	Crab in burrow	
Interact	Touch	Crabs touching each other without aggressive or defensive behavior	Neutral
	Toward	Crab distinctly advancing towards the other crab	Aggressive
	Crawl	One crab climbing and crawling on top of another crab	Neutral
	Invade	One crab attempting to expel the other crab from its burrow and, when successful, occupying the stolen burrow	Aggressive
	Follow	One crab following the other crab	Aggressive
	Aggressive	A distinct quick action from one crab against another such as grabbing a leg or lunging at them	Aggressive
	Back	One crab retreating from the aggressive action of the other	Defensive
	Face	Both crabs facing each other in close proximity	Neutral
Stand	Stand	Crab standing still	
	Feed	Crab visibly using chelipeds to move sediment to mouth	
	Guard	Crab standing on or near a burrow	

704

705
706
707
708
709
710

Table 2 Fine vs. coarse low- and high-density trial negative binomial GLM results (given in the left-hand column) and post-hoc analysis results for species treatment and burrow location (right-hand column, given as p-values with significant results ($p < 0.05$) bolded).

Low-density				High-density			
Species			Post-hoc	Species			Post- hoc
$p < 0.001$	Sand	Mud	< 0.001	$p < 0.001$	Sand	Mud	< 0.001
		Both	0.199			Both	0.372
	Mud	Both	0.008		Mud	Both	< 0.001
Location				Location			
$p < 0.001$	Corner	Side	0.067	$p = 0.80$	Corner	Side	0.909
		Middle	<0.001			Middle	0.969
	Side	Middle	< 0.001		Side	Middle	0.789

711
712
713

714

715 **Table 3** Mixed sediment trials post-hoc analysis pair-wise results for species treatment
 716 and burrow location (found to have a significant interaction for this experiment; Species
 717 $p < 0.0001$; Location $p < 0.0001$; Species-Location $p < 0.01$).

		Pugilator (sand)			Pugnax (mud)			Both		
		Corner	Side	Middle	Corner	Side	Middle	Corner	Side	Middle
Pugilator (sand)	Corner	-								
	Side	0.999	-							
	Middle	0.297	0.508	-						
Pugnax (mud)	Corner	0.149	0.298	0.999	-					
	Side	0.009	0.025	0.905	0.982	-				
	Middle	0.009	0.025	0.905	0.982	1.00	-			
Both	Corner	0.999	0.999	0.649	0.025	<0.001	<0.001	-		
	Side	0.025	0.065	0.982	0.999	0.999	0.999	0.003	-	
	Middle	0.009	0.250	0.905	0.982	1.00	1.00	<0.001	0.999	-

718

719

720

721

722

723

724

725

726

727 **Table 4** Results from the GLM examining the amount of time spent exhibiting burrowing
 728 and interacting behaviors in each treatment (*U. pugilator* in the presence of a conspecific
 729 (sand), *U. pugnax* in the presence of a conspecific (mud), *U. pugilator* in the presence of
 730 *U. pugnax* (sand_both), and *U. pugnax* in the presence of *U. pugilator* (mud_both)) for
 731 the mix and fine vs. coarse low-density trials combined. The behavior categories were
 732 analyzed separately (p-values given in the left-hand column) and a post-hoc analysis
 733 performed when a significant difference was detected (right-hand column). P-values
 734 shown with significant results ($p < 0.05$) in bold.

Burrow			
p =	Sand	Mud	<0.001
0.003		Sand_both	0.363
	Mud	Mud_both	0.043
	Sand_both	Mud_both	0.168
Interact			
p =	Sand	Mud	0.017
0.046		Sand_both	0.021
	Mud	Mud_both	0.788
	Sand_both	Mud_both	0.383

735

736 Figures

737

738 **Figure 1** The mean number of total burrows dug in treatments with *U. pugilator* (sand
739 fiddler) only, *U. pugnax* (mud fiddler) only, and with both species present in the mixed
740 sediment trials (A), the low-density fine vs. coarse sediment trials (B) and the high-
741 density fine vs. coarse sediment trials (C). For fine vs. coarse sediment trials the dark
742 portion of the bar represents the proportion of burrows in fine sediment while the lighter
743 gray portion represents burrows dug in coarse sediment. The dashed horizontal line
744 indicates the expected mean number of burrows dug in heterospecific treatments based on
745 the number dug by each species in conspecific treatments. Letters indicate significant
746 results in Tukey post-hoc analyses within experiments.

747

748 **Figure 2** The mean number of total burrows dug in each tank location (corner, side, and
749 middle) in treatments with *U. pugilator* (sand fiddler) only, *U. pugnax* (mud fiddler)
750 only, and with both species present in the mixed sediment trials (A), the low-density fine
751 vs. coarse sediment trials (B) and the high-density fine vs. coarse sediment trials (C).

752

753 **Figure 3** Behavioral reaction norms for *U. pugilator* (sand fiddler crab) and *U. pugnax*
754 (mud fiddler crab) for each of the four behavior categories (Active, Burrow, Interact,
755 Stand) showing average amount of time each species spent displaying the behavior in the
756 conspecific versus the heterospecific treatment in the mixed sediment and low-density
757 fine vs. coarse sediment trials. Only “burrow” and “interact” were analyzed formally.
758 Note the scales of the y-axes differ, particularly in the “interact” category.





