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1 Should I stay or should I go? Causes and dynamics of host desertion
2 by a parasitic crab living on echinoids.

3

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22 **Running page head:** Host desertion by a parasitic crab living on echinoids.

23

24

25 ABSTRACT

26 In some long-living symbiotic species, movements between hosts are not limited to offspring
27 since adult parasites can move from one individual host to another one. Host-switching may be
28 driven by different parameters such as (i) mating strategies of symbionts, (ii) foraging for
29 resources or (iii) avoiding overcrowded or diseased/dead host. Symbiotic marine crustaceans
30 are suitable models to understand what underlies host-switching behavior. In this study, we
31 investigated host desertion by the parasitic pea crab *Dissodactylus primitivus* associated with
32 the echinoid host *Meoma ventricosa*. Mark-recapture field experiments, during which crabs
33 were found almost always found on their host in heterosexual combinations, suggest that host
34 desertion occurs less frequently when two crabs share the same host compared to echinoids
35 hosting three crabs. Laboratory experiments with high crab density showed that the proportion
36 of crabs leaving an echinoid was low when the two genders of crabs were present on the host,
37 compared to one gender only (males or females). This suggests that host desertion is mostly
38 driven by intersex selection and search for a mate, and, to a lower extend, by competition
39 between crabs. However, both field and laboratory experiments evidenced that when they
40 switch host, most crabs remained for a while in the sediment located underneath their host. We
41 propose that this behavior, associated with the aggregative behavior of their hosts, would allow
42 the crabs to solve the trade-off between staying on their hosts (therefore suffering overcrowding
43 and sub-optimal mate search) and moving too far from the host (therefore suffering loss of food
44 source and high predation risk).

45 Key words: Symbiont, Mobility, Host-switching, Mating System, Pea crab, Echinoid hosts

46

48 Symbionts populations are fragmented into as many subgroups (infra-populations) as
49 the number of colonized individual hosts (Poulin 2007). An infra-population is however
50 ephemeral as the host lifespan is limited, but the infection of new individual hosts by offspring
51 or adult stages ensures the formation of new infra-populations and the perpetuation of the
52 symbiosis (Price 1980, Combes 2001, Poulin 2007). In some symbiotic species, movements
53 between hosts are not limited to offspring, since adult symbionts can move from one individual
54 host to another. This host-switching behavior has been well explored in ectosymbiotic
55 crustaceans (Bell 1984, Thiel & Baeza 2001, Baeza & Thiel 2003, Thiel et al. 2003, Baeza &
56 Thiel 2007, De Bruyn et al 2010, Hernández et al 2012, Pfaller et al. 2014). A conceptual model
57 (Baeza & Thiel 2007) proposed that the main factor for host-switching is the distinct optimal
58 mating strategies of male and female symbionts. Host exploitation from pure host-guarding to
59 frequent host-switching allows the definition of different mating strategies (from monogamy to
60 polygamy, respectively). Host-switching can thus regulate the number of interactions between
61 potential mates, and have a determinant effect on individual reproductive success (Baeza &
62 Thiel 2007). However, the environment (*sensu lato*) modulates these behavioral options. Host-
63 switching can be constrained by host size and morphology (compared to large hosts, small hosts
64 are easier to guard against competitors, a situation which promotes monogamy), by host
65 population density and aggregative behavior (high densities promotes host-switching and
66 therefore polygyny or polyandry by increasing mate search), and by predation pressure (high
67 predation risks would diminish host-switching). Foraging can also motivate host-switching if
68 food resources are decoupled from the hosts, or if food depletion occurs on the host (due to
69 symbiont overcrowding or to host disease/death).

70 Among decapods, Pinnotheridae family (pea crabs) exclusively includes symbiotic
71 species (Palacios-Theil et al. 2009). These symbiotic crustaceans occur on their hosts as single
72 individuals, in heterosexual pairs or in groups of variable numbers, according to the species
73 (Hsueh & Huang 1998, Thiel & Baeza 2001, De Bruyn et al. 2009). In some species, mobility
74 is limited to recruitment by the larval or first crab stages, the adults staying on their host after
75 settlement and displaying few or no contact with the external environment (Pearce 1962, Huard
76 & Demeusy 1968, Bolaños et al. 2004). However, Pinnotheridae crabs associated with irregular
77 echinoids and belonging to the *Dissodactylus* complex practice host-switching throughout their
78 entire adult life (Telford 1978, Bell 1984, Reeves & Brooks 2001, De Bruyn et al. 2009). Host-
79 switching behavior seems to vary considerably according to the species. For *Dissodactylus*
80 *mellitae*, marked antagonism between crabs on individual host leads to frequent host-switches,
81 while in *D. crinitichelis* the symbionts easily share the same host, suggesting that host-
82 switching is rare in this case (Telford 1978, Bell 1984, 1988, Reeves & Brooks 2001). The crab
83 *D. primitivus* colonizes two species of spatangoid echinoids, *Meoma ventricosa* and
84 *Plagiobrissus grandis* (Telford 1978, 1982). De Bruyn et al. (2009) showed that this crab is
85 parasitic to *M. ventricosa*, and have suggested that the mating system of *D. primitivus* could fit
86 the “pure-search polygynandry of mobile females” described by Baeza and Thiel (2007). In this
87 dynamic system, females and males would display host-switching with high frequency while
88 searching for mates. This hypothesis is supported by the efficiency of *D. primitivus* in
89 colonizing ‘empty’ hosts (i.e. host without any crab), this behavior being expressed by both
90 males and females (De Bruyn et al. 2009), by the chemical attractiveness of its hosts (De Bruyn
91 et al. 2010, 2011) and by the recent genetic evidence that this ectosymbiont evolved a
92 polygamous mating system, where males and females move between hosts for mate search
93 (Jossart et al. 2014). However, what initiates host-switching and its frequency is unknown. The

94 “pure search” mating system supposes that the main cause for host-switching is mate search,
95 all other parameters being equal. Nevertheless, since the hosts of *D. primitivus* are much larger
96 than the symbionts, and since a single individual host may harbor several crabs (De Bruyn et
97 al. 2009), confinement on host could also initiate crab departures.

98 The aim of this study is to investigate the frequency and the causes of host desertion in
99 *D. primitivus*, and to test the hypothesis that mate-search promotes this behavior. Using a mark-
100 recapture experiment, the mobility of adults was first studied in field conditions. In a second
101 step, we experimentally tested if the absence of a potential mate on the host promotes host-
102 switching. Finally, following the observations that numerous crabs desert their host without
103 colonizing a new one, a census was realized in the field to attempt quantifying the presence of
104 free-living crabs in sediments. The sediments located between the echinoids and located
105 beneath them were surveyed.

106

107

MATERIALS AND METHODS

108 Field and laboratory experiments were performed in March and April 2009, and in April 2015
109 in Discovery Bay lagoon, on the North coast of Jamaica (see De Bruyn et al. 2009).

110

Host desertion and host-switching in field conditions

111 Echinoid hosts (*Meoma ventricosa*) harboring at least two adult crabs were collected (scuba
112 diving) in the western part of the lagoon at depths ranging from 1.5 to 10 meters. Each host,
113 with its symbionts, was carefully placed into an individual plastic bag that was closed under
114 water by a rubber band. In the laboratory, echinoids were measured to the nearest millimeter

115 with a caliper rule. The crab infra-population structure was recorded and adult crabs were kept
116 for the experiments.

117 To be recognized during experiments both the hosts and their symbionts were marked. The
118 echinoids were individually tagged using a rubber band bearing a nylon thread ending with a
119 labeled and colored float. The rubber band was placed around each individual host (see De
120 Bruyn et al. 2009). The crab tagging consisted of a small colored plastic mark (c.a. 1 mm
121 diameter) fixed with Super Glue Original Loctite® on the cephalothorax. All crabs coming
122 from the same host were marked with the same color, each color being different between hosts,
123 and a black dot on the plastic mark distinguished the female crabs. The experiment took part in
124 the eastern part of the lagoon. At a depth of 6 meters, a sandy area of 20 x 20 meters was cleared
125 out of all echinoids. The chosen area was completely surrounded by seagrass beds that act as a
126 barrier avoiding the arrival of non-experimental echinoids. Sixteen tagged echinoids with their
127 original load of symbiotic crabs were placed in the experimental area. Sea urchins of similar
128 sizes were placed by pairs in the area, at 30 cm from each other, the eight pairs being regularly
129 distributed in the area, distant from the others from *ca.* 6 meters. The load of adult crabs of each
130 sea urchin was recorded after 48h, along with the distance between individuals for each sea
131 urchin pair. The choice of 48 hours is based on a preliminary field observation, showing that
132 crab movement were low before this lag-time (presumably because of the disturbance of the
133 animals). The maximum distance between individuals of a given pair was found to be 200 cm
134 after 48h, and none of the pairs were found in contact with another pair. All echinoids and their
135 hosted crabs were removed from the experimental zone. This procedure was repeated five times
136 (therefore using $16 \times 5 = 80$ echinoids), creating five “series” each of 48h. A new series of hosts
137 and their original crabs were set at the same place than the ones of the preceding series. These

138 series were therefore independent in terms of individuals, but all made at the same place.

139 Using logistic regressions, we analyzed (i) the effects of the initial number of crabs (two or
140 three individuals) and of the arrival of new crabs on the probability that at least one crab leaved
141 the host, (ii) the effects of the initial number of crabs on the amount of crabs leaving the host,
142 (iii) the effect of the initial sex-ratio of the crab infra-population on the probability for each sex
143 to leave the host, (iv) the effect of crab departure rate on the rate of crab colonization or host
144 shift. These analyses were made taking into account the animals of the five series.

145

146 **Host desertion motivated by mate search: an experimental test**

147 The laboratory experiments were made in 60 x 30 x 30 cm aquaria filled with oxygenated
148 seawater. Each aquarium was divided in two equal compartments by a perforated translucent
149 partition allowing both water circulation and crab movements between compartments, but not
150 the passage of sea urchins (experimental device described in De Bruyn et al. 2009). A 2 cm
151 thick layer of sand originating from the sampling site in the lagoon was poured over the bottom
152 of the aquaria. Prior to each run, the water was oxygenated during 10 minutes by providing
153 running seawater and oxygen supply. During the runs, the air pump and the flow of water were
154 stopped, to avoid disturbance or unidirectional water flow. Two *M. ventricosa* were then
155 acclimated for 5 minutes at the beginning of each run (one in each compartment), individuals
156 of the same pair being of similar size. Four individually-tagged (see above) adult crabs were
157 then placed on one of the echinoids. A burden of 4 crabs was chosen because it maximizes the
158 probability of crab leaving their host (the field study revealed that crabs leave more frequently
159 their host when the burden exceeded two individuals). Three types of infra-population structure

160 were tested: four males (4M, 14 replicates), four females (4F, 15 replicates) and two males/two
161 females (2M2F, 13 replicates). Different crabs and host individuals were used in each replicate.
162 The position of crabs in the aquarium was recorded 24 hours later. This time-lag was chosen to
163 avoid a too long period without oxygenation and because crab desertion was observable after
164 24h in the lab experimental device. The crabs could either stay on the original echinoid
165 (echinoid A), go on the other echinoid (echinoid B) or remain burrowed in the sand between
166 the two hosts. The average crab numbers found on the echinoid A, B and in the sand were
167 compared between the three series.

168 Since data did not satisfy homoscedasticity conditions, even after transformation attempts, non-
169 parametric tests (Kruskal-Wallis or Wilcoxon) were used to analyze differences between
170 groups.

171

172 **Are there free-living crabs in the sediments?**

173 Since several crabs were missing at the end of the above field experiment and since several
174 crabs were found in the sand during the experiments performed in aquaria (see results for both),
175 we decided to check the occurrence of free crabs in the surrounding sediment. This search was
176 done during two surveys performed in the same site (East of Discovery Bay). We started
177 (survey #1, April 2009) by investigating sediment located between echinoid individuals
178 because we suspected crabs to travel there while switching from one host to another one.
179 Because we found no crabs in these samples (see results), we pursued (survey #2, April 2015)
180 by investigating sediment immediately located underneath each individual echinoid. For both
181 surveys, searches for free crabs were performed using an air pipe submarine sampler of 100

182 mm of diameter (see a video on [youtube.com/watch?v=0aqdIP92h0I](https://www.youtube.com/watch?v=0aqdIP92h0I)). Three filters of
183 decreasing mesh size were fixed at the end of the tube, allowing collection of items of different
184 size. The one-centimeter mesh collected large coral fragments and coarse sediments, the five
185 millimeters mesh should collect the adult crabs and the one-millimeter mesh the juvenile crabs.
186 In survey #1, to allow a direct comparison of these samples with the occurrence of crabs on
187 echinoids, 75 replicates of sediments, each corresponding roughly to the volume occupied by
188 an echinoid, were sampled in the eastern part of the lagoon. The sediments were taken over 10
189 cm depth using a ballasted quadrat of 50 x 25 cm. The samples were taken in the sand located
190 between the *M. ventricosa* individuals (never closer than *ca.* 1 meter from sea-urchins, 30
191 replicates), but also in the seagrass beds (*Thalassia testudinum*) and its border, which can be
192 used as nursery by many species of the lagoon (Gayle & Woodley 1998) (45 samples). In survey
193 #2, sediments located underneath each echinoid (30 replicates) were sampled over 10 cm depth
194 within a 30 x 21 cm ballasted quadrat. The quadrat was positioned on the sea bottom to
195 encompass one echinoid individual. Firstly, the symbiotic crabs found on the urchin (infra-
196 population) were collected and sampled in hermetic plastic vials. Then, the sediment potentially
197 containing other *D. primitivus* under the echinoid was pumped and sampled in hermetic plastic
198 bags. Once in the laboratory, crabs found in the sediment and on the sea urchin were numbered
199 and their sex was recorded.

200 Because one predictor was strongly associated with one of the possible outcomes (see results:
201 no crabs were found in sediments in survey #1), the proportion of crabs found in these samples
202 was compared using a logistic regression using Firth's bias-adjusted estimates (Firth 1993). For
203 this, each sand replicate sample was considered as an "individual" where the crabs can live,
204 therefore allowing the comparison with the prevalence on echinoid individuals. Statistical tests

205 were made using the programs JMP 10.0 (SAS Institute).

206

207

RESULTS

208

Host desertion and host-switching in field conditions

209 The echinoids harboring 1 male and 1 female were predominant in our sample (76%, n = 80).

210 The other compositions were: 2M + 1F (13%), 1M + 2F (5%), 2M (4%), 3M (1%) or 1M + 3F

211 (1%). Echinoids with monosexual combinations of crabs and the only one hosting 4 crabs were

212 too rare to be considered (6% in total), and were thus discarded from experiments. Since

213 potential mates were always originally present on these hosts, this experiment will not *sensu*

214 *stricto* test the mate search as a motivation to desert the host.

215 Seventy-two hosts were therefore used in the five experimental series, harboring originally 80

216 male and 77 female crabs. During the experiment, 68 crabs (43.3 %) leaved their hosts. The

217 proportion of leaving animals was slightly significantly higher in females (40/77) than in males

218 (40/80) (Fisher exact test, p = 0.037, Figure 1). Nine of these leaving crabs (13.2%) were

219 recaptured on another experimental echinoid (corresponding to host shift). Four host shifts were

220 made between echinoids of the same pair, while five were temporal shifts, the marked crab

221 being recaptured on a host of the next experimental series (Figure 1). While reliable statistical

222 test cannot be made with such a small dataset, it is worth noting that 7/9 of these host shifts

223 were concomitant to desertion of crabs of the same sex on the host, resulting in a substitution

224 of a male/female crab by another individual of the same sex. The remaining departing crabs

225 were not recaptured. Finally, we found five unmarked adult crabs (therefore not present initially

226 on any hosts under test) colonizing the experimental hosts (Figure 1). No foreign echinoid was

227 found on the experimental zone during the nine days of experiment.

228 We tested if the number of crabs initially present on *M. ventricosa* (2 vs 3 crabs) and if the
229 occurrence of new incoming crabs (i.e. crabs initially absent for the host but present on it after
230 48h) influenced the probability of host desertion by at least one crab, using a two-factor logistic
231 regression. The host were less often deserted by at least one crab when two crabs were initially
232 present (compared to the occurrence of three crabs) (logistic regression: Likelihood-Ratio $\chi^2 =$
233 8.03, $p = 0.005$, Figure 2), while there was no significant effect of a new incoming crab on the
234 probability for a host to be deserted (L-R $\chi^2 = 2.20$, $p = 0.14$; Global model: L-R $\chi^2 = 10.59$, p
235 $= 0.005$, $n = 72$). Among the host where at least one crab deserted, there was no effect of the
236 initial number of crabs on how many crabs leave the host (one or more than one) (L-R $\chi^2 =$
237 0.69, $p = 0.41$, $n = 54$). Finally, there was no significant difference between crab sex in the
238 probability of deserting according to the composition of the initial crab infection (L-R $\chi^2 =$
239 2.01; 2 d.f.; $p = 0.37$, Figure 3).

240 **Host desertion motivated by mate search: an experimental test**

241 The sex-ratio of crab infra-population influences significantly the number of crabs leaving the
242 host (Kruskal-Wallis test: $p = 0.002$, Figure 4a). The proportion of crabs leaving the echinoid
243 A was low when the infra-population harbored the two genders compared to one gender only
244 (males or females). The number of crabs leaving the host did not significantly differ between
245 the two mono-gender infra-populations (Figure 4a). The rate of transfer between the echinoids
246 A and B was weak and identical between the three series of experiment (Kruskal-Wallis test: p
247 $= 0.50$, Figure 4b). The crab proportion found in the sand was significantly different between
248 the series (Kruskal-Wallis test: $p = 0.001$, Figure 4c), and the pattern of distribution reflected

249 the number of crabs leaving the hosts: very few crabs were found in the sand in series where
250 the two sexes were present, while more crabs were found in the sediment for mono-gender
251 series (Figure 4c). Crabs in the sand were always found close to the hosts.

252 **Are there free-living crabs in the sediments?**

253 In our search for crabs occurring in sediment far from echinoid hosts (survey #1), a total of 0.94
254 m³ of sediment in 75 samples was collected, filtered and checked. No *D. primitivus* was found
255 in these samples.

256 This zero prevalence of crabs in 75 replicates can be compared to the different prevalence
257 observed on *M. ventricosa* hosts, either directly from the host or in the sand beneath the host
258 during our survey #2. While 73.3% of the 30 *M. ventricosa* were infected with at least one crab,
259 crabs were found in the sand beneath 26.7% of these hosts (Figure 5). A logistic regression
260 using Firth's bias-adjusted estimates showed the three prevalence were significantly different
261 ($\chi^2 = 83.41$, 2 d.f., $p < 0.0001$), and a contrast analysis revealed significantly more crabs in the
262 sand beneath the host than far from the host, and a higher prevalence on the host than beneath
263 the host (Figure 5, $\chi^2 = 22.85$ and $\chi^2 = 15.40$, 1 d.f., respectively).

264 Among the 26 *M. ventricosa* where at least one crab was found either on or beneath the host,
265 the presence of crabs in the sediment was analyzed with two explanatory factors: the total
266 number of crabs found associated to the host and the presence of a couple on the host, using a
267 two-way logistic regression. Crabs were more often found in the sediment when a couple was
268 absent on the host (Figure 6b, $\chi^2 = 9.90$, 1 d.f., $p = 0.002$), while the number of crabs on the
269 host influences the presence of crabs in the sediment only marginally (Figure 6a, $\chi^2 = 5.80$, 2
270 d.f., $p = 0.054$). A contrast analysis nevertheless indicates that the prevalence of crabs in the

271 sediment was higher when more than two crabs were associated to sea-urchins than when there
272 was one or two crabs (these two later categories being grouped; $\chi^2 = 4.04$, 1 d.f., $p = 0.04$). The
273 symbiotic crabs are therefore more prone to leave their host (while remaining at its close
274 vicinity in the sand) when no couple was found on the host, or when there are more than two
275 crabs associated to the host.

276

277

DISCUSSION

278 The field experiment revealed that the infra-populations of the ectoparasite
279 *Dissodactylus primitivus* living on their host *Meoma ventricosa* are highly dynamics, with more
280 than 40% crabs deserting their host within 48 hours. However, because we manipulated both
281 hosts and crabs, this value could be overestimated compared to unperturbed situation. This
282 result is nevertheless compatible with previous direct and indirect (genetic) data suggesting
283 high rate of movements for these crabs (De Bruyn et al. 2009, Jossart et al. 2014). Both genders
284 depart their host at high rate. Host desertion by at least one crab was more frequent when three
285 crabs initially occur on the echinoid. In this experiment, motivation to quit the host was
286 independent from mate searching since the crab infra-populations always included at least one
287 male and one female. Heterosexual couples therefore appear more stably installed on the host
288 than triads including an additional partner. *Meoma ventricosa* individuals display an
289 aggregative behavior: herd structures are observed in natural conditions, and these groups are
290 stable over time and could move as a unit (Chesher 1969). By placing hosts in pairs in our
291 experiment, we mimic such an aggregative behavior. Therefore, as suggested for another
292 symbiont/host couple (*Dissodactylus mellitae* living on *Mellita quinquesperforata*), host

293 aggregation could offer many opportunities of host shifts, allowing the ectosymbionts to find
294 new mates (Bell 1984). Surprisingly, only a few host shifts were observed in our experiment
295 (i.e. a crab leaving a host and joining a second one). Only four out of the nine observed host
296 shifts were observed between neighbor hosts within the same time series, and five shifts
297 occurred between temporarily neighbor hosts (i.e. hosts at the same place but belonging to two
298 successive time series). It means that these five crabs spent one or two days in the sediment
299 before reaching a new host. All the other crabs were not found on any sea urchin and were
300 probably burrowed in the sediment, or have been predated (see further discussion below).

301 We tested the effect of sex ratio on crab departures in our laboratory experiments.
302 Because the number of adult crabs we placed on sea urchins was above the average values
303 observed in the wild (De Bruyn et al. 2009, and present field studies), numerous desertions
304 were expected to occur. Instead, only few crabs were quitting their host when an equilibrated
305 sex ratio (2 males : 2 females) was respected. In case of pure competition for space combined
306 with intra-sexual competition, such a combination would have led to the desertion of one or
307 more crabs. Crab desertions were more numerous in mono-gender combinations, a
308 phenomenon slightly (albeit non-significantly) more intense in males than in females. We can
309 therefore propose that mate search could be a strong motivation for crabs to leave its host.
310 However, in aquaria experiments, only a few crabs left their first host to set on the other
311 accessible host, and most individuals were consequently staying in the sediment. This result is
312 consistent with our field experiments where a number of unmarked crabs did colonize the
313 experimental hosts and some marked crabs colonized new hosts in successive series. These two
314 congruent observations suggest that crabs may remain outside their hosts in the surrounding
315 sediment. When in the sediment, the crabs only occur just beneath their host, as shown by the

316 two surveys of sediment samplings.

317 This partial exploitation of sediments shades a new light on one puzzling trait of *D.*
318 *primitivus*: its coloration. The carapace of these crabs is whitish, while *M. ventricosa* have a
319 dark brown tegument, making the crabs conspicuous when not hidden among the spines or
320 beneath the host body. In contrast, crab color makes them homochromatic on coral sediments.
321 Crypsis, more precisely background matching, is a well-known anti-predatory strategy in
322 numerous species (Stevens and Merilaita 2009). The selective pressure of predation away from
323 the host should be strong enough to have selected and maintained such a background matching.
324 Therefore, perhaps predation could explain the rarity of crabs outside the immediate vicinity of
325 the hosts, but this was not tested in the present work. *D. primitivus* is thought to have derived
326 from a free-living ancestor that lived under rocks or in sediments, and that have secondarily
327 exploited burrowing sea urchins (Griffith 1987). The white color, anti-predatory when in coral
328 sediment, could be inherited from the free-living ancestor and kept in *D. primitivus* as its
329 dependence to its host is not total. Pohle (1984) suggested *D. primitivus* is a facultative parasite:
330 conversely to others species of the *Dissodactylus* complex, *D. primitivus* can be readily reared
331 beyond the first crab instar without exposure to *M. ventricosa* (Pohle & Telford 1983, Pohle
332 1984). However, an array of observations supports that *D. primitivus* stays dependent of its
333 host: (1) free crabs only occur in the sediment beneath their host, (2) crabs are significantly
334 attracted by *M. ventricosa* (De Bruyn et al. 2011), (3) most of its diet comes from the echinoid
335 (Telford 1982, De Bruyn et al. 2009), (4) *M. ventricosa* is a mating place for the parasitic crabs
336 (Jossart et al. 2014).

337 In conclusion, *D. primitivus* individuals are not strictly dependent of a given individual
338 host during their lifetime. Adult crabs regularly leave their hosts, experiencing host shifts, but

339 also often exploiting the host's immediate surroundings (underlying sediments). As shown in
340 this study, such a behavior is motivated mainly by intra-sex competition, and also presumably
341 reduces the resource competition on the host by increasing the space exploited (Bell 1984,
342 Baeza et al. 2002, Baeza & Thiel 2003, Baeza & Thiel 2007). We propose that this behavior,
343 associated with the aggregative behavior of host's herd (Chester 1969), allows optimal host
344 shifting and mate search with a limited exposition to predation.

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FIGURES

461 Figure 1. Raw description and results of the field experiment. D1 to D9 are the five temporal
462 series, from day one to day nine. Each black and white oval are pairs of echinoid hosts. The
463 numbers are male and female parasite crabs harbored by the host (e.g. 2:1 means two males and
464 one female). Arrows are the crab movement (blue for male crabs, pink for female crabs). The
465 number of outgoing arrows represents the number of crabs that left the host after 48h (not found
466 on the host). The number of incoming arrows represents the number of crabs (not initially
467 present on the host) that colonized the host after 48h. Outgoing arrows not terminating on a
468 host are marked crabs that leaved the host but were not recaptured. Ingoing curved arrows not
469 initiating from a host are unmarked crabs colonizing a host. Between temporal series, the hosts
470 and the crabs were different, and all were individually marked; distance between hosts of a
471 given pair was 30 cm, distance between pairs was 6 m. Between temporal series, the eight pairs
472 of hosts were placed at the same location, explaining why crabs can move between hosts
473 belonging to two different temporal series (long arrows between temporal series).

474 Figure 2. Proportions of host loosing at least one crabs according to the initial number of crabs
475 (logistic regression) (field experiment). The group « >2 » includes the combinations 1M+2F
476 and 2M+1F and the group « 2 » 1M+1F. The numbers in the bars are sample sizes (number of
477 hosts).

478 Figure 3. Proportion of males (M) and females (F) among the leaving crabs, according to the
479 initial sexual repartition in the infecting infra-population (field experiment). The numbers in
480 the bars are crab sample sizes.

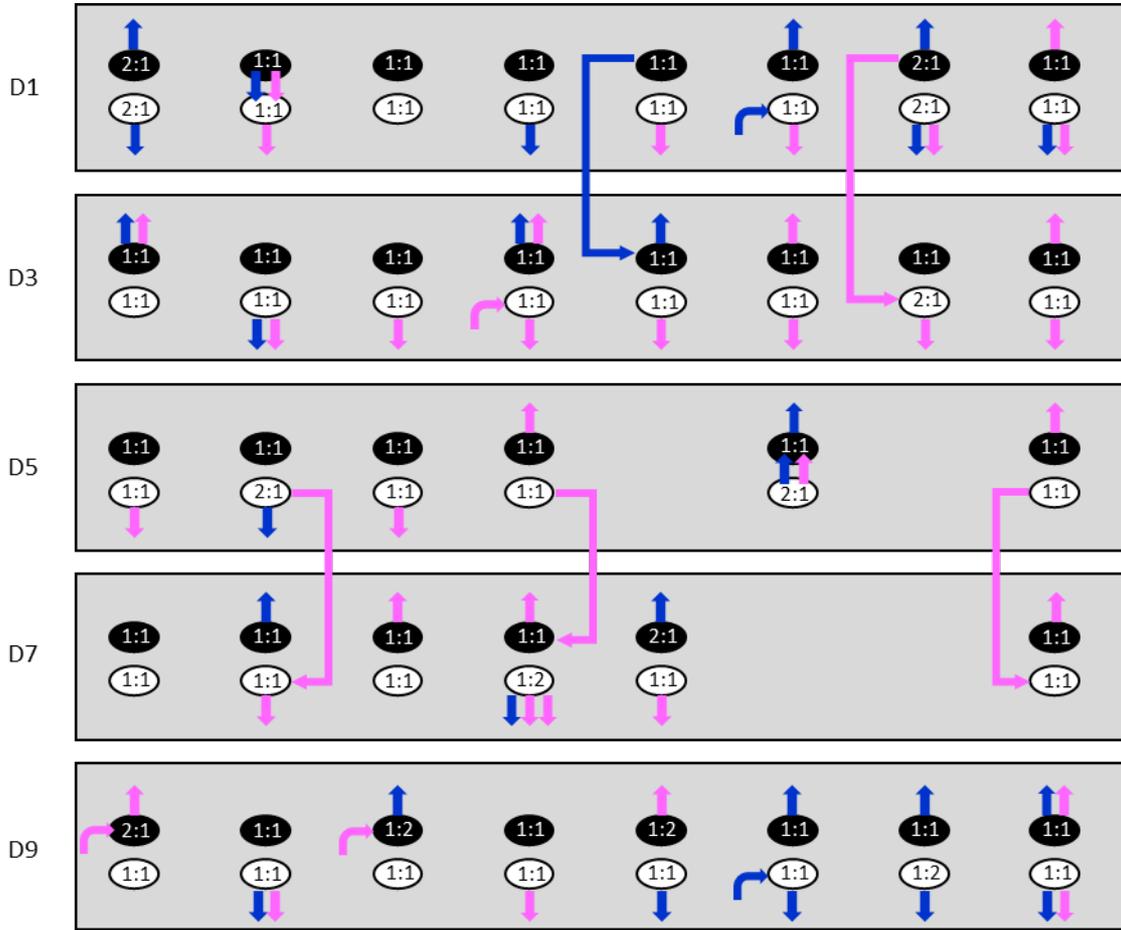
481 Figure 4. Number of crabs found (a) on the original host (host A), (b) on the initially “empty”

482 host (host B) and in the sand (c), 24 h after the beginning of the experiments (aquaria). The
483 sexual compositions at the beginning of the experiments were two females and two males (2F
484 2M), four females (4F), four males (4M). Thick lines are the medians, boxes and bars are the
485 interquartile and interdecile ranges, respectively. The number of replicates is given within
486 brackets. Levels of significance for two-by-two comparisons are given after Wilcoxon test (NS
487 $p \geq 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

488 Figure 5. Proportion of samples where one crab at least was found in the sand between the
489 hosts, in the sand underneath the hosts or on the host itself. Numbers in the bars are sample
490 size.

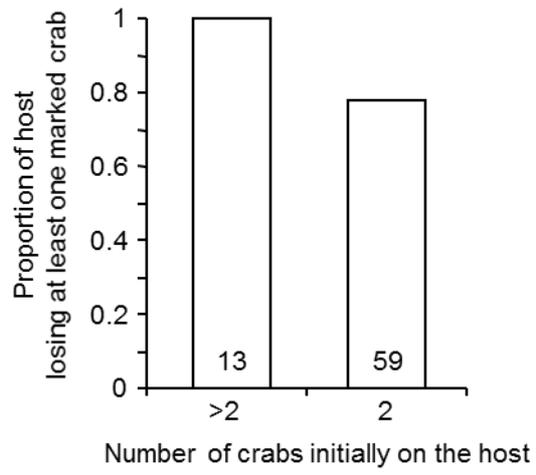
491 Figure 6. Proportion of hosts where crabs were present in the sand underneath a host, according
492 to the total number of crabs occurring on the host (a) and to the presence of a couple on the host
493 (b). Numbers in the bars are sample size.

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Figure 1



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Figure 2

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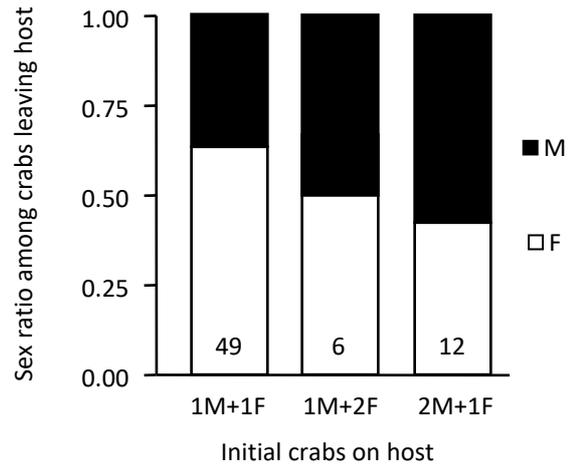
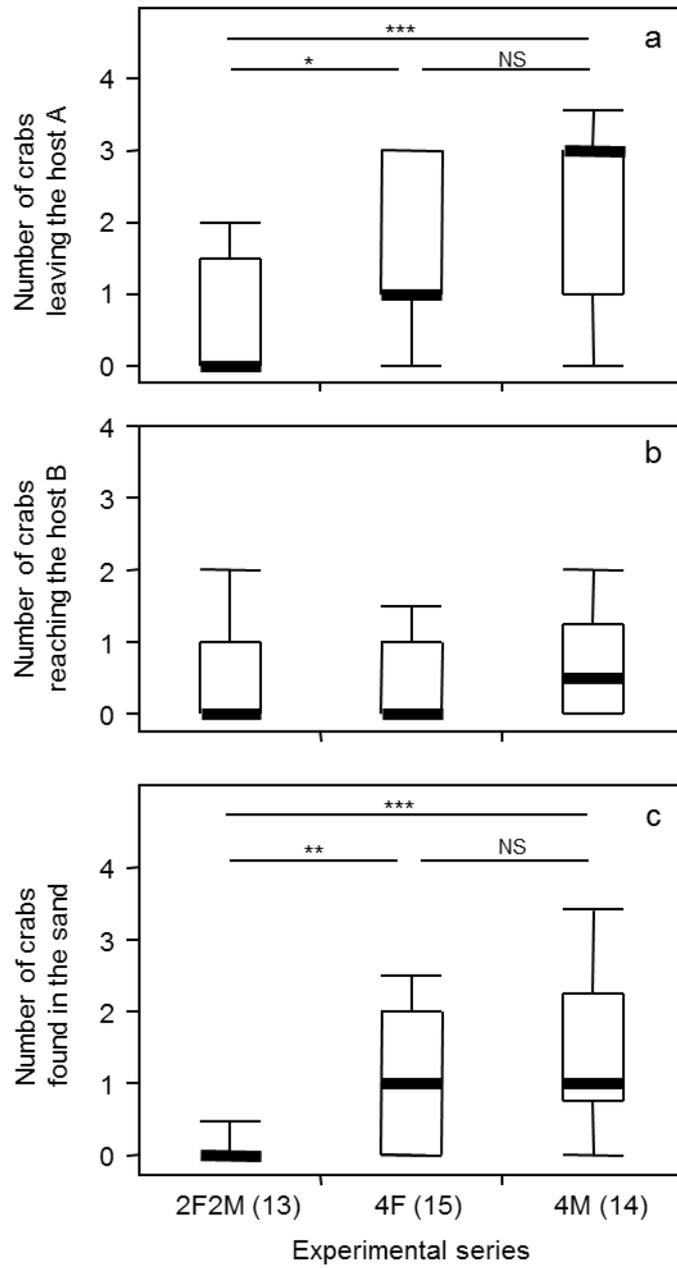


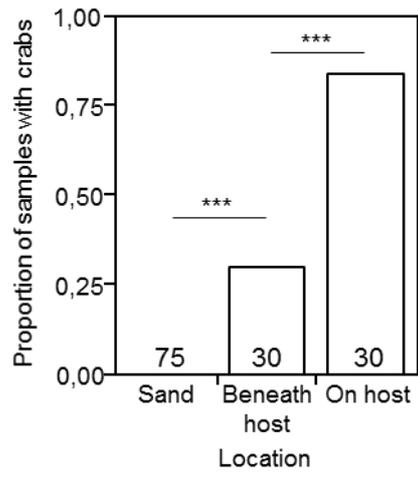
Figure 3



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Figure 4

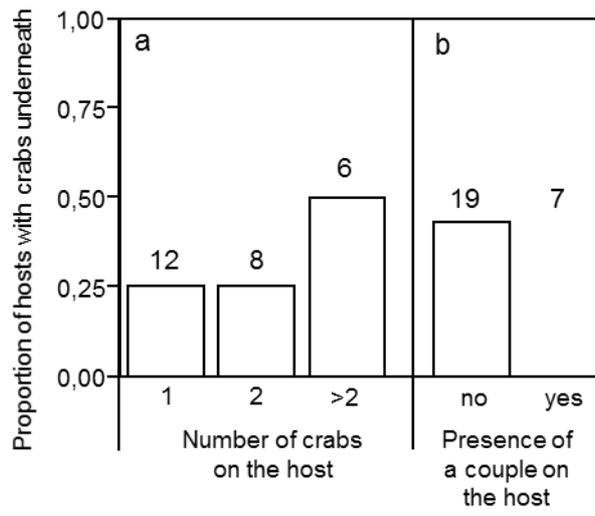


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Figure 5

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Figure 6