

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

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ABSTRACT: In some long-living symbiotic species, movements between hosts are not limited to offspring since adult parasites can move from one individual host to another one. Host-switching may be driven by different parameters such as (1) mating strategies of symbionts, (2) foraging for resources or (3) avoiding overcrowded or diseased/dead host. Symbiotic marine crustaceans are suitable models to understand what underlies host-switching behavior. In this study, we investigated host desertion by the parasitic pea crab *Dissodactylus primitivus* associated with the echinoid host *Meoma ventricosa*. Mark-recapture field experiments, during which crabs were almost always found on their host in heterosexual combinations, suggest that host desertion occurs less frequently when 2 crabs (compared to 3) share the same host. During laboratory experiments with high crab density, the proportion of crabs leaving an echinoid was low when the 2 genders of crabs were present on the host, compared to 1 gender only (males or females). This suggests that host desertion is mostly driven by intersex selection and the search for a mate and, to a lesser extent, by competition between crabs. However, both field and laboratory experiments showed evidence that when they switch host, most crabs remained for a while in the sediment underneath their host. We propose that this behavior, associated with the aggregative behavior of their hosts, would allow the crabs to solve the trade-off between staying on their hosts (therefore suffering overcrowding and sub-optimal mate search) and moving too far from the host (therefore suffering loss of food source and high predation risk).

KEY WORDS: Symbiosis · Mobile invertebrates · Host-switching · Mating systems · Pea crab · Echinoid

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INTRODUCTION

Symbiont populations are fragmented into as many subgroups (infra-populations) as the number of colonized individual hosts (Poulin 2007). An infra-population is, however, ephemeral as the host lifespan is limited, but the infection of new individual hosts by offspring or adult stages ensures the formation of new infra-populations and the perpetuation of the symbio-

sis (Price 1980, Combes 2001, Poulin 2007). In some symbiotic species, movements between hosts are not limited to offspring, since adult symbionts can move from one individual host to another. This host-switching behavior has been well explored in ectosymbiotic crustaceans (Bell 1984, Thiel & Baeza 2001, Baeza & Thiel 2007, De Bruyn et al. 2010, Hernández et al. 2012, Pfaller et al. 2014). A conceptual model (Baeza & Thiel 2007) proposed that the main factor for host-

switching is the distinct optimal mating strategies of male and female symbionts. Host exploitation from pure host-guarding to frequent host-switching allows the definition of different mating strategies (from monogamy to polygamy, respectively). Host-switching can thus regulate the number of interactions between potential mates and have a determinant effect on individual reproductive success (Baeza & Thiel 2007). However, the environment (*sensu lato*) modulates these behavioral options. Host-switching can be constrained by host size and morphology (compared to large hosts, small hosts are easier to guard against competitors, a situation which promotes monogamy), by host population density and aggregative behavior (high densities promotes host-switching and therefore polygyny or polyandry by increasing mate search), and by predation pressure (high predation risks would diminish host-switching). Foraging can also motivate host-switching if food resources are decoupled from the hosts or if food depletion occurs on the host (due to symbiont overcrowding or to host disease/death).

Among decapods, the Pinnotheridae family (pea crabs) exclusively includes symbiotic species (Palacios-Theil et al. 2009). These symbiotic crustaceans occur on their hosts as single individuals, in heterosexual pairs or in groups of variable numbers, depending on the species (Hsueh & Huang 1998, Thiel & Baeza 2001, De Bruyn et al. 2009). In some species, mobility is limited to recruitment by the larval or first crab stages, the adults staying on their host after settlement and displaying little or no contact with the external environment (Pearce 1962, Huard & Demeusy 1968, Bolaños et al. 2004). However, Pinnotheridae crabs associated with irregular echinoids and belonging to the *Dissodactylus* complex practice host-switching throughout their entire adult life (Telford 1978, Bell 1984, Reeves & Brooks 2001, De Bruyn et al. 2009). Host-switching behavior seems to vary considerably according to the species. For *Dissodactylus mellitae*, marked antagonism between crabs on an individual host leads to frequent host-switches, while in *D. crinitichelis* the symbionts easily share the same host, suggesting that host-switching is rare in this case (Telford 1978, Bell 1984, 1988, Reeves & Brooks 2001). The crab *D. primitivus* colonizes 2 species of spatangoid echinoids, *Meoma ventricosa* and *Plagiobrissus grandis* (Telford 1978, 1982). De Bruyn et al. (2009) showed that this crab is parasitic to *M. ventricosa*, and hypothesized that the mating system of *D. primitivus* could fit the 'pure-search polygynandry of mobile females' described by Baeza & Thiel (2007). In this dynamic system, females

and males display host-switching with high frequency while searching for mates. This hypothesis is supported by the efficiency of *D. primitivus* in colonizing 'empty' hosts (i.e. host without any crab), this behavior being expressed by both males and females (De Bruyn et al. 2009), by the chemical attractiveness of its hosts (De Bruyn et al. 2010, 2011) and by the recent genetic evidence that this ectosymbiont has evolved a polygamous mating system, where males and females move between hosts for mate search (Jossart et al. 2014). However, what initiates host-switching and its frequency is unknown. The 'pure search' mating system supposes that the main cause for host-switching is mate search, all other parameters being equal. Nevertheless, since the hosts of *D. primitivus* are much larger than the symbionts, and since a single individual host may harbor several crabs (De Bruyn et al. 2009), crowding could also initiate crab departures.

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

MATERIALS AND METHODS

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

In situ host desertion and host-switching

Echinoid hosts *Meoma ventricosa* harboring at least 2 adult crabs were collected (scuba diving) in the western part of the lagoon at depths ranging from 1.5 to 10 m. Each host, with its symbionts, was carefully placed into an individual plastic bag that was closed under water by a rubber band. In the laboratory, echinoids were measured to the nearest millimeter with a caliper rule. The crab infra-population structure was recorded and adult crabs were kept for the experiments.

To be recognized during experiments, both the hosts and their symbionts were marked. The echinoids were individually tagged using a rubber band bearing a nylon thread ending with a labeled and colored float. The rubber band was placed around each individual host (see De Bruyn et al. 2009). Crab tags consisted of a small colored plastic mark (ca. 1 mm diameter) fixed with Super Glue Original Loctite® on the cephalothorax. All crabs coming from the same host were marked with the same color, each color being different between hosts, and a black dot on the plastic mark was used to distinguish the female crabs. The experiment took part in the eastern part of the lagoon. At a depth of 6 m, a sandy area of 20 × 20 m was cleared of all echinoids. The chosen area was completely surrounded by seagrass beds that acted as a barrier against the arrival of non-experimental echinoids. Sixteen tagged echinoids with their original load of symbiotic crabs were placed in the experimental area. Sea urchins of similar sizes were placed by pairs in the area 30 cm from each other, the 8 pairs being regularly distributed in the area with a distance of ca. 6 m from each other. The load of adult crabs per sea urchin was recorded after 48 h, along with the distance between individuals for each sea urchin pair. The choice of 48 h is based on a preliminary field observation, showing that crab movements were low before this lag-time (presumably because of the disturbance of the animals). The maximum distance between individuals of a given pair was found to be 200 cm after 48 h, and none of the pairs were found in contact with another pair. After 48 h, all echinoids and their hosted crabs were removed from the experimental zone. This procedure was repeated 5 times (therefore using 16 × 5 = 80 echinoids), creating 5 'series' each of 48 h over 9 d. For each series, hosts and their original crabs were set at the same position as the preceding series. These series were therefore independent in terms of individuals, but all were made at the same place. See Fig. 1 for a diagrammatic representation of the series.

Using logistic regressions, we analyzed (1) the effects of the initial number of crabs (2 or 3 individuals) and of the arrival of new crabs on the probability that at least 1 crab would leave the host, (2) the effects of the initial number of crabs on the amount of crabs leaving the host, (3) the effect of the initial sex ratio of the crab infra-population on the probability for each sex to leave the host, (4) the effect of crab departure rate on the rate of crab colonization or host shift. All 5 series were used in the analyses.

Host desertion motivated by mate search: an experimental test

The laboratory experiments were made in 60 × 30 × 30 cm aquaria filled with oxygenated seawater. Each aquarium was divided in 2 equal compartments by a perforated translucent partition allowing both water circulation and crab movements between compartments but not the passage of sea urchins (experimental device described in De Bruyn et al. 2009). A 2 cm thick layer of sand originating from the sampling site in the lagoon was poured over the bottom of the aquaria. Prior to each run, the water was oxygenated for 10 min by providing running seawater and oxygen supply. During the runs, the air pump and the flow of water were stopped to avoid disturbance or unidirectional water flow. Two *M. ventricosa* (without crabs) were then acclimated for 5 min at the beginning of each run (one in each compartment), individuals of the same pair being of similar size. Four individually tagged (see above) adult crabs were then placed on one of the echinoids. A burden of 4 crabs was chosen because it maximizes the probability of crabs leaving their host (the field study revealed that crabs leave their host more frequently when the burden exceeds 2 individuals). Three types of infra-population structure were tested: 4 males (4M, 14 replicates), 4 females (4F, 15 replicates) and 2 males/2 females (2M2F, 13 replicates). Different crabs and host individuals were used in each replicate. The position of crabs in the aquarium was recorded 24 h later. This time-lag was chosen to avoid an unacceptably long period without oxygenation. The crabs could either stay on the original echinoid (Echinoid A), go to the other echinoid (Echinoid B) or remain burrowed in the sand between the 2 hosts. The average crab numbers found on Echinoids A and B and in the sand were compared among the 3 series. Since data did not satisfy homoscedasticity conditions, even after transformation attempts, non-parametric tests (Kruskal-Wallis or Wilcoxon) were used to analyze differences between groups.

Are there free-living crabs in the sediments?

Since several crabs were missing at the end of the above field experiment and since several crabs were found in the sand during the experiments performed in aquaria (see 'Results' for both), we decided to check the occurrence of free-living crabs in the surrounding sediment. This search was done during 2 surveys performed at the same site (east of

Discovery Bay). We started (Survey 1, April 2009) by investigating sediment located between echinoid individuals because we suspected crabs to travel there while switching from one host to another one. Because we found no crabs in these samples (see 'Results'), we pursued (Survey 2, April 2015) by investigating sediment immediately located underneath each individual echinoid. For both surveys, searches for free crabs were performed using a 100 mm diameter air pipe submarine sampler (see video at <https://www.youtube.com/watch?v=0aqdIP92h0I>). Three filters of decreasing mesh size (1 cm, 5 mm) were fixed at the end of the tube, allowing collection of items of different size. The 1 cm mesh collected large coral fragments and coarse sediments, the 5 mm mesh collected the adult crabs and the 1 mm mesh collected the juvenile crabs. In Survey 1, to allow a direct comparison of these samples with the occurrence of crabs on echinoids, 75 replicates of sediments, each corresponding roughly to the volume occupied by an echinoid, were sampled in the eastern part of the lagoon. The sediments were taken over 10 cm depth using a ballasted quadrat of 50 × 25 cm. The samples were taken in the sand located between the *M. ventricosa* individuals (never closer than ca. 1 m from the sea-urchins, 30 replicates), but also in the seagrass bed (*Thalassia testudinum*) and its border, which is used as a nursery by many species in the lagoon (Gayle & Woodley 1998) (45 samples). In Survey 2, sediments located underneath each echinoid (30 replicates) were sampled over 10 cm depth within a 30 × 21 cm ballasted quadrat. The quadrat was positioned on the sea bottom to encompass one echinoid individual. First, the symbiotic crabs found on the urchin (infra-population) were collected and sampled in hermetic plastic vials. Then, the sediment potentially containing other *Dissodactylus primitivus* under the echinoid was pumped and sampled in hermetic plastic bags. Once in the laboratory, crabs found in the sediment and on the sea urchin were numbered and their sex was recorded.

Because one predictor was strongly associated with one of the possible outcomes (no crabs were found in sediments in Survey 1; see 'Results'), the proportion of crabs found in these samples was compared using a logistic regression using Firth's bias-adjusted estimates (Firth 1993). For this, each sand replicate sample was considered as an 'individual' where the crabs can live, therefore allowing the comparison with the prevalence on echinoid individuals. Statistical tests were made using the program JMP 10.0 (SAS Institute).

RESULTS

In situ host desertion and host-switching

The echinoids harboring 1 male and 1 female were predominant in our sample (76 %, $n = 80$). The other compositions were: 2M + 1F (13 %), 1M + 2F (5 %), 2M (4 %), 3M (1 %) or 1M + 3F (1 %). Echinoids with monosexual combinations of crabs and the only individual hosting 4 crabs were too rare to be considered (6% in total) and were thus discarded from analysis. Since potential mates were always originally present on these hosts, this experiment did not, *sensu stricto*, test the mate search as a motivation to desert the host.

Seventy-two hosts were therefore included from the 5 experimental series, harboring originally 80 male and 77 female crabs. From this group, 68 crabs (43.3%) left their hosts. The proportion of deserting animals was significantly higher in females (40/77) than in males (40/80) (Fisher exact test, $p = 0.037$, Fig. 1). Nine of these deserting crabs (13.2%) were recaptured on another experimental echinoid (corresponding to host shift). Four host shifts were made between echinoids of the same pair, while 5 were temporal shifts, the marked crab being recaptured on a host of the next experimental series (Fig. 1). While reliable statistical tests cannot be made with such a small dataset, it is worth noting that 7/9 of these host shifts were concomitant to desertion of crabs of the same sex on the host, resulting in a substitution of a male/female crab by another individual of the same sex. The remaining departing crabs were not recaptured. Finally, we found 5 unmarked adult crabs (therefore not present initially on any hosts under test) colonizing the experimental hosts (Fig. 1). No foreign echinoid was found in the experimental zone during the 9 d experiment.

We tested if the number of crabs initially present on *Meoma ventricosa* (2 vs. 3 crabs) and the occurrence of new incoming crabs (i.e. crabs initially absent from the host but present on it after 48 h) influenced the probability of host desertion by at least 1 crab, using a 2-factor logistic regression. The hosts were less often deserted by at least 1 crab when 2 crabs were initially present (compared to the occurrence of 3 crabs) (logistic regression: likelihood-ratio [L-R] $\chi^2 = 8.03$, $p = 0.005$, Fig. 2), while there was no significant effect of a new incoming crab on the probability for a host to be deserted (L-R $\chi^2 = 2.20$, $p = 0.14$; global model: L-R $\chi^2 = 10.59$, $p = 0.005$, $n = 72$). Among the hosts where at least 1 crab deserted, there was no effect of the initial number of crabs on how many crabs left

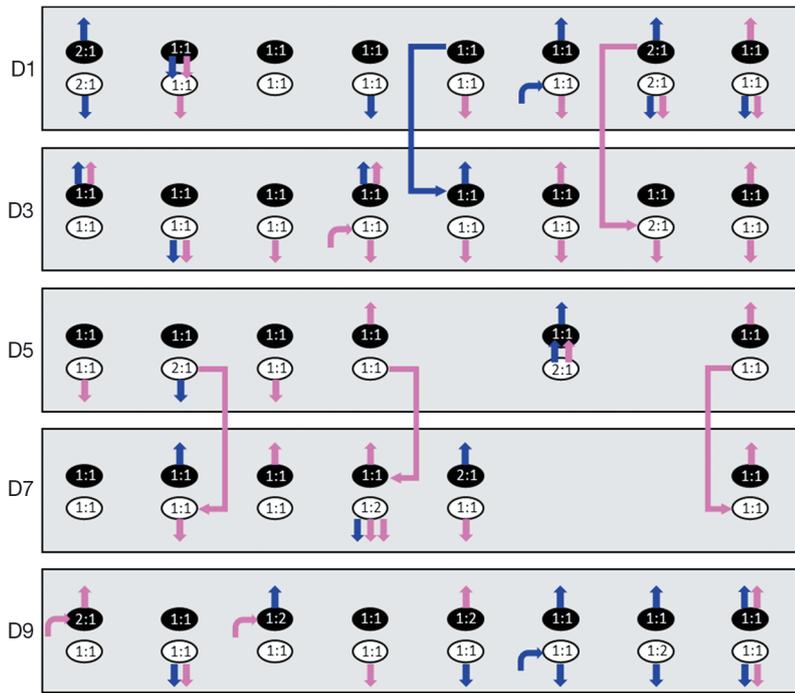


Fig. 1. Description and results of the field experiment. D1, D3, D5, D7 and D9 are the 5 temporal series, from Days 1 to 9. Black and white ovals are pairs of echinoid hosts. Numbers are male and female parasite crabs harbored by the host (e.g. 2:1 means 2 males and 1 female). Arrows are crab movement (blue: male crabs, pink: female crabs). Number of outgoing arrows represents the number of crabs that left the host after 48 h (not found on the host). Number of incoming arrows represents the number of crabs (not initially present on the host) that colonized the host after 48 h. Outgoing arrows not terminating on a host are marked crabs that left the host but were not recaptured. Ingoing curved arrows not initiating from a host are unmarked crabs colonizing a host. Between temporal series, the hosts and the crabs were different, and all were individually marked; distance between hosts of a given pair was 30 cm, distance between pairs was 6 m. Between temporal series, the 8 pairs of hosts were placed at the same location, explaining why crabs can move between hosts belonging to 2 different temporal series (long arrows between temporal series); in these cases, the crabs buried themselves in the sand below the host, were not collected at the end of a series, but colonized a host of the following series

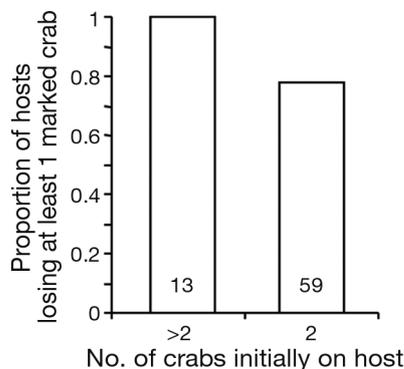


Fig. 2. Proportion of hosts losing at least 1 crab as a function of the initial number of crabs (logistic regression) (field experiment). >2 includes the combinations 1 male (M) + 2 females (F) and 2M + 1F, 2 includes 1M + 1F. Numbers in bars are sample sizes (number of hosts)

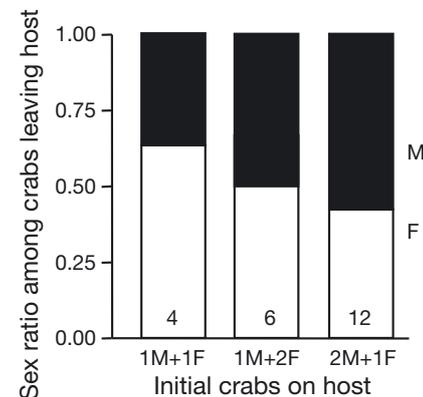


Fig. 3. Proportion of males (M) and females (F) among the deserting crabs according to the initial sexual repartition in the infecting infra-population (field experiment). Numbers in bars are crab sample sizes

the host (1 or more than 1) (L-R $\chi^2 = 0.69$, $p = 0.41$, $n = 54$). Finally, there was no significant difference between crab sex in the probability of deserting according to the composition of the initial crab infection (L-R $\chi^2 = 2.01$; 2 df; $p = 0.37$, Fig. 3).

Host desertion motivated by mate search: an experimental test

The sex ratio of crab infra-population had a significant influence on the number of crabs leaving the host (Kruskal-Wallis test: $p = 0.002$, Fig. 4a). The proportion of crabs leaving Echinoid A was low when the infra-population harbored both genders compared to one gender (males or females). The number of crabs leaving the host did not significantly differ between the 2 mono-gender (4F and 4M) infra-populations (Fig. 4a). The rate of transfer between Echinoids A and B was weak and identical between the 3 series of experiment (Kruskal-Wallis test: $p = 0.50$, Fig. 4b). The crab proportion found in the sand was significantly different among the series (Kruskal-Wallis test: $p = 0.001$, Fig. 4c), and the pattern of distribution reflected the number of crabs leaving the hosts: very few crabs were found in the sand in the 2M2F series, while more crabs were found

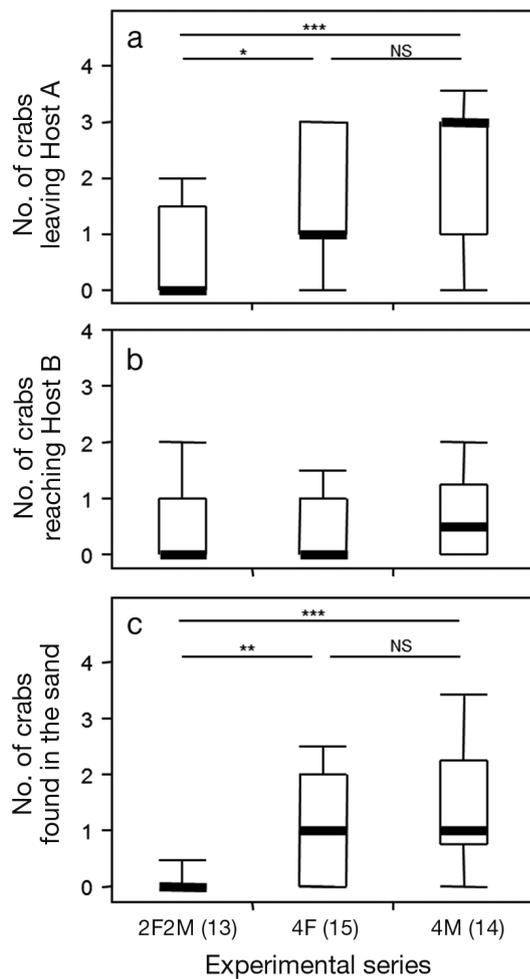


Fig. 4. Number of crabs found (a) on the original host (Echinoid A), (b) on the initially 'empty' host (Echinoid B) and (c) in the sand below the host, 24 h after the beginning of the experiments (aquaria). The sexual compositions at the beginning of the experiments were 2 females and 2 males (2F2M), 4F and 4M. Thick lines are medians, boxes and bars are the interquartile and interdecile ranges, respectively. Number of replicates given in parentheses. Levels of significance for 2-by-2 comparisons are given in accordance with the Wilcoxon test: not significant (NS, $p \geq 0.05$); * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

in the sediment in 4F and 4M series (Fig. 4c). Crabs in the sand were always found close to the hosts.

Are there free-living crabs in the sediments?

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

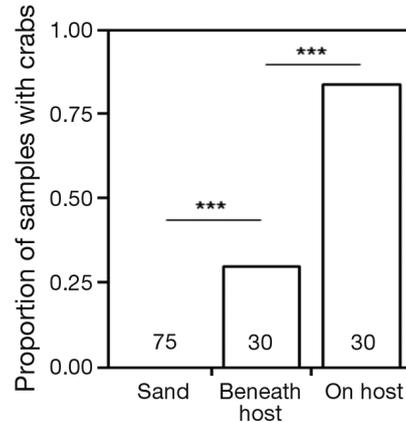


Fig. 5. Proportion of samples where at least 1 crab was found in the sand between the hosts, in the sand underneath the hosts, or on the host itself. Numbers in bars are sample size. *** $p < 0.001$

This zero prevalence of crabs in Survey 1 can be compared to the prevalence observed on *M. ventricosa* hosts, either directly on the host or in the sand beneath the host during in Survey 2. While 73.3% of the 30 *M. ventricosa* were infected with at least 1 crab, crabs were found in the sand beneath 26.7% of these hosts (Fig. 5). A logistic regression using Firth's bias-adjusted estimates showed that the 3 types of prevalence (between hosts, on host, underneath the host) were significantly different ($\chi^2 = 83.41$, $df = 2$, $p < 0.0001$), and a contrast analysis revealed significantly more crabs in the sand beneath the host than between the hosts, and a higher prevalence on the host than beneath the host (Fig. 5, $\chi^2 = 22.85$ and $\chi^2 = 15.40$, $df = 1$, respectively).

Among the 26 *M. ventricosa* where at least 1 crab was found either on or beneath the host, the presence of crabs in the sediment was analyzed with 2 explanatory factors: the total number of crabs found associated with the host and the presence of a couple (1 male, 1 female) on the host, using a 2-way logistic regression. Crabs were often found in the sediment when a couple was absent on the host (Fig. 6b, $\chi^2 = 9.90$, $df = 1$, $p = 0.002$), while the number of crabs on the host only marginally influenced the presence of crabs in the sediment (Fig. 6a, $\chi^2 = 5.80$, $df = 2$, $p = 0.054$). A contrast analysis nevertheless indicated that the prevalence of crabs in the sediment was higher when more than 2 crabs were associated with sea-urchins than when there were 1 or 2 crabs (these 2 later categories being grouped; $\chi^2 = 4.04$, $df = 1$, $p = 0.04$). The symbiotic crabs are therefore more prone to leave their host (while remaining in its close vicinity in the sand) when no couple was found on the host, or when there are more than 2 crabs associated with the host.

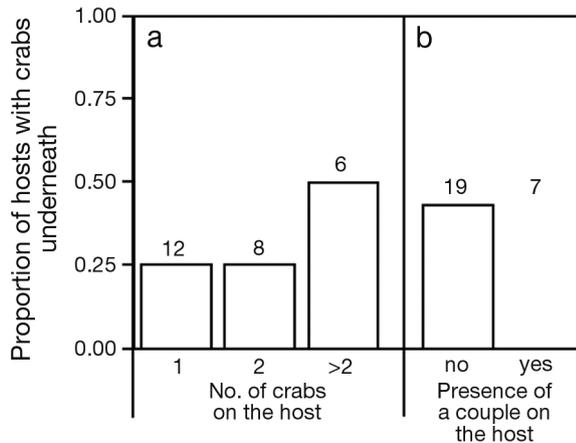


Fig. 6. Proportion of hosts where crabs were present in the sand underneath a host, as a function of (a) the total number of crabs occurring on the host and (b) to the presence of a couple (1 male, 1 female) on the host. Numbers in bars are sample size

DISCUSSION

The field experiment revealed that the infra-populations of the ectoparasite *Dissodactylus primitivus* living on their host *Meoma ventricosa* are highly dynamic, with more than 40% crabs deserting their host within 48 h. However, because we manipulated both hosts and crabs, this value could be over-estimated compared to unperturbed situations. This result is nevertheless compatible with previous direct and indirect (genetic) data suggesting a high rate of movements for these crabs (De Bruyn et al. 2009, Josart et al. 2014). Both genders depart their host at a high rate. Host desertion by at least one crab was more frequent when 3 crabs initially occurred on the echinoid. In this experiment, motivation to quit the host was independent of mate searching since the crab infra-populations always included at least one male and one female. Heterosexual couples therefore appear more stably installed on the host than triads including an additional partner. *M. ventricosa* individuals display an aggregative behavior: herd structures are observed in natural conditions, and these groups are stable over time and may move as a unit (Chesher 1969). By placing hosts in pairs in our experiment, we mimicked such an aggregative behavior. Therefore, as suggested for another symbiont/host couple (*D. mellitae* living on *Mellita quinqueperforata*), host aggregation could offer many opportunities for host shifts, allowing the ectosymbionts to find new mates (Bell 1984). Surprisingly, only a few host shifts were observed in our experiment (i.e. a crab leaving a host and joining a second one). Only 4

out of the 9 observed host shifts were observed between neighboring hosts within the same time series, and 5 shifts occurred temporally between neighbor hosts (i.e. hosts at the same place but belonging to 2 successive time series). It means that these 5 crabs spent 1 or 2 d in the sediment before reaching a new host. All the other crabs were not found on any sea urchin and were probably burrowed in the sediment, or were preyed upon (see further discussion below).

We tested the effect of sex ratio on crab departures in our laboratory experiments. Because the number of adult crabs we placed on sea urchins was above the average values observed in the wild (De Bruyn et al. 2009, this study), numerous desertions were expected to occur. Instead, only a few crabs quit their host when an equilibrated sex ratio (2 males: 2 females) was respected. If this were a result of pure competition for space combined with intra-sexual competition, such a combination would have led to the desertion of 1 or more crabs. Crab desertions were more numerous in mono-gender combinations, a phenomenon slightly (albeit non-significantly) more intense in males than in females. We can therefore propose that mate search could be a strong motivation for crabs to leave their host. However, in aquaria experiments, only a few crabs left their first host to set on the other accessible host, and those that left their host usually stayed in the sediment below the host. This result is consistent with our field experiments where a number of unmarked crabs colonized the experimental hosts and some marked crabs colonized new hosts in successive series. These 2 congruent observations suggest that crabs may remain outside their hosts in the surrounding sediment. When in the sediment, the crabs only occur just beneath their host, as shown in the 2 sediment sampling surveys.

This partial exploitation of sediments sheds a new light on the puzzling coloration of *D. primitivus*. Indeed, the carapace of these crabs is white, while *M. ventricosa* have a dark brown tegument, making the crabs conspicuous when not hidden among the spines or beneath the host body. In contrast, crab color makes them homochromatic on coral sediments. Crypsis, more precisely, background matching, is a well-known anti-predatory strategy in numerous species (Stevens & Merilaita 2009). The selective pressure of predation away from the host should be strong enough to have selected and maintained such a background matching. Therefore, perhaps predation could explain the rarity of crabs outside the immediate vicinity of the hosts, but this was not tested in the present work. *D. primitivus* is

thought to have evolved from a free-living ancestor that lived under rocks or in sediments and that secondarily exploited burrowing sea urchins (Griffith 1987). The white color, anti-predatory when in coral sediment, could have been inherited from the free-living ancestor and kept in *D. primitivus* as it is not totally dependent on its host. Pohle (1984) suggested *D. primitivus* is a facultative parasite: conversely to other species of the *Dissodactylus* complex, *D. primitivus* can be readily reared beyond the first crab instar without exposure to *M. ventricosa* (Pohle & Telford 1983, Pohle 1984). However, an array of observations supports that *D. primitivus* remains dependent on its host: (1) free crabs only occur in the sediment beneath their host, (2) crabs are significantly attracted by *M. ventricosa* (De Bruyn et al. 2011), (3) most of its diet comes from the echinoid (Telford 1982, De Bruyn et al. 2009), and (4) *M. ventricosa* is a mating place for the parasitic crabs (Jossart et al. 2014).

In conclusion, *D. primitivus* individuals are not strictly dependent on a given individual host during their lifetime. Adult crabs regularly leave their hosts, experiencing host shifts but also often exploiting the host's immediate surroundings (underlying sediments). As shown in this study, such a behavior is motivated mainly by intra-sex competition. Moreover, moving to the sediments may reduce the competition for food by increasing the exploited space (Bell 1984, Baeza & Thiel 2007). We propose that this behavior, associated with the aggregative behavior of the host (Chesher 1969), allows optimal host shifting and mate search with a limited exposure to predation.

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