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Expanding the "shell exchange market" hypothesis for clustering behavior in intertidal hermit crabs: Mating and tide as proximate factors

Pedro A.S. Peres[a,*], Ana Paula Ferreira[a], Fosca P.P. Leite[b]

[a] *Programa de Pós-Graduação em Ecologia, Instituto de Biologia, Universidade Estadual de Campinas, Campinas 13083-970, SP, Brazil*
[b] *Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas 13083-970, SP, Brazil*

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ABSTRACT

Clustering is a common behavior displayed by hermit crabs in intertidal environments. Aggregations are reported to occur during low-tide events, and the number of animals present may vary depending on the species. The "shell exchange market" hypothesis suggests that the main function of clustering is to allow animals to acquire new shells by fighting, bargaining, or by a chain reaction caused by a single empty shell. However, the adaptive significance and the factors that trigger this behavior remain unexplained. Here, the hypotheses tested were that both sex of *Clibanarius symmetricus* are performing this behavior, that clustered animals have poorly fitted shells compared to isolated ones, and that tidal phase is triggering the formation of clusters. Clustered and isolated animals were collected in the field, sexed, and measured for cephalothoracic shield and shell parameters. The Shell Adequacy Index (SAI) was compared among crabs of both sexes in clustered and isolated conditions. Additionally, manipulative experiments were performed in the laboratory, with different tidal-phase conditions. Both sexes were present in clusters, but clustered females showed a lower SAI than isolated females. Furthermore, a higher proportion of crabs were aggregated during ebb-tide than during flood-tide events. Thus, clustering behavior may be related not only to shell exchanges, but also to mating and protection against desiccation. Consequently, the adaptive meaning and function of aggregations in intertidal hermit crabs should be understood as an integrative behavior related to many aspects of the animals' biology.

1. Introduction

Marine animals commonly display clustering behavior, but the causes and significance of clustering are under discussion (Krause and Ruxton, 2002). Aggregations are viewed as adaptive, especially because the proximity with other individuals may increase survivorship and reproductive success (Parrish and Edelstein-Keshet, 1999), and also may reduce risks caused by physical environmental conditions or predation (Krause and Ruxton, 2002).

The formation of clusters is a common behavior displayed by many hermit crabs of the families Diogenidae and Paguridae, from both tropical and temperate intertidal habitats (Hazlett, 1966; Snyder-Conn, 1980; Gherardi and Vannini, 1989; Gherardi, 1991). For these animals, aggregations are usually attributed to the "shell exchange market" hypothesis (Gherardi and Vannini, 1992, 1993), in which animals exchange shells by fighting (Hazlett, 1966; Elwood and Glass, 1981), bargaining (Hazlett, 1978, 1980), or by a chain reaction caused by a single empty shell (Chase et al., 1988; Rotjan et al., 2010). Hermit crabs must continually obtain new, suitable shells, either because of growth (Hazlett and Herrnkind, 1980; Rittschof, 1980) or alteration in the condition of their current shell (e.g. epibionts – Hazlett, 1981; McLean, 1983; Wilber and Herrnkind, 1984).

Empty and adequate shells are generally scarce in the environment because they can be carried away by ocean currents, buried in the substrate, or damaged by predators and erosion (Vance, 1972; Kellogg, 1976; Wilber and Herrnkind, 1984; Pechenik and Lewis, 2000). It is common to find animals with unsuitable, damaged, or smaller/larger or lighter/heavier shells in relation to their body size (Kellogg, 1976; Turra and Leite, 2002). This information can be accessed by the Shell Adequacy Index (Vance, 1972; Turra, 2003), which is a ratio that indicates whether a shell is suitable for the hermit crab based on the animal size. Thus, hermit crabs rely on refined mechanisms to acquire new shells, such as signaling by chemical stimuli released by injured gastropods (Rittschof, 1980; Rittschof and Cohen, 2004; Tricarico and Gherardi, 2006) and behavioral adaptations such as aggregation (Hazlett, 1981).

Clusters may be formed by one or more species, with fewer than 10 or as many as 500 individuals (Snyder-Conn, 1980; Gherardi and

* Corresponding author.
E-mail address: pasperes@usp.br (P.A.S. Peres).

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Vannini, 1993; Turra and Leite, 2000a; Barnes and Arnold, 2001). *Clibanarius laevimanus*, for example, form aggregations composed of > 50 individuals that remain in direct physical contact with each other, and for this species the hypothesis of "shell exchange market" may be valid (Gherardi et al., 1991; Gherardi et al., 1994). Reinforcing the importance of this behavior, when comparing different strategies for shell acquisition by *Clibanarius erythropus,* Tricarico et al. (2009) found that cluster formation was the most effective tactic. During low-tide events it is common to find intertidal animals clustered, probably as an adaptive mechanism against desiccation (Chapman and Underwood, 1996; Bustamante et al., 1997). However, the suggestion that tidal cycle is causing clustering behavior must be tested in order to inform further discussion.

Even though the "shell exchange market" hypothesis is confirmed for several species, the proximate factors that trigger this behavior remain unclear. Here, it was explored how sex, shell adequacy and tidal phase influence cluster formation in *Clibanarius symmetricus* (Randall, 1840), an intertidal hermit-crab species. The specific questions addressed were: 1) Is there any difference between the number of males and females performing clustering behavior? 2) Does shell adequacy differ between clustered and isolated animals? 3) Does the tide level trigger clustering behavior? The hypotheses tested were that hermit crabs that were present in cluster formations are those with inadequate shells, both males and females are performing this behavior, and that aggregations are triggered by ebb-tide events.

2. Material and methods

The study was conducted in Araçá Bay, São Sebastião Channel, southeastern Brazil (23°49′S, 45°24′W) during August 2013, with additionally laboratory controlled experiments. This area is a tidal flat colonized by mangroves, and is one of the richest coastal environments in southeastern Brazil (Amaral et al., 2010). The bay is a highly complex environment, with extensive muddy sand flats, mangroves, rocky shores, cobble areas, and two islets, Pernambuco and Pedroso. The species used was *Clibanarius symmetricus*, an abundant hermit crab in this area (Turra and Leite, 2000a, 2002), occurring in intertidal and shallow waters. It is common to find aggregations of this species during low tides, and here we define aggregations as 2 or more individuals in physical contact.

2.1. Cluster composition

All individuals of *C. symmetricus* were collected manually in a mud-rock substrate area of 150 m^2 around Pernambuco Islet, during low tide (i.e. when all the study area around Pernambuco Islet was exposed to the air), when it is common to find clustered and isolated hermit crabs. They were classified as isolated or clustered, and then transported to the laboratory to be frozen. After removing the shell, we measured the cephalothoracic shield length (CL) and determined the sex according to the gonopore position for each crab. Each gastropod shell had the shell length (SL), aperture length (AL) and aperture width (AW) measured, and was also weighed (SW) after drying at 70 °C for 48 h.

In order to explore if sex was associated with aggregation behavior, we used a Chi-square test. The shell adequacy of individuals was assessed by a modification of the Shell Adequacy Index (SAI) (Vance, 1972; Turra, 2003). The SAI is a ratio based on the size of the animal, and it is calculated by the formula SAI = "optimal" CL/real CL. This index is based on the implicit assumption that there is a relationship between crab size and its shell, that is, there is an "optimal" animal size ("optimal" CL) that is the most fitted to the actual shell. However, it is important to note that there is not a global optimal size for a hermit crab species, and that this concept is local dependent because of the biotic and environmental variables that may influence the hermit crabs shell preference. Here, the local optimal size ("optimal" CL in the formula) was estimated based on linear regressions of the CL from hermit crabs collected from the field (real CL) at the same locality (i.e. under the same biotic and environmental conditions) with each of the shell parameters (SL, AL, AW and SW). The linear regression equation of the parameter that is most closely correlated with the real CL was used to calculate the optimal CL (i.e. the hermit crab size that is the most fitted to the shell in which the animal was found). If SAI = 1, the shell can be defined as adequate for the hermit crab; if SAI > 1, the hermit crab is occupying an inadequate shell, larger and/or heavier than the optimal; if SAI < 1, the animal is occupying an inadequate shell, smaller and/or lighter than the optimal. In order to compare the SAI of both sexes of crabs in both conditions, we performed a balanced two-way ANOVA (n = 22 for each category) using sex (male or female) and condition (isolated or clustered) as factors, after checking for variance homogeneity and normal distribution. If significant, a Tukey test for pairwise comparison for the interaction was performed.

2.2. Tide manipulation experiment

The influence of tide on clustering behavior was investigated in an experiment under controlled laboratory conditions. Semi-diurnal-cycle tides (6 h) were simulated using 10 hermit crabs equally spaced in the bottom of approximately 30-L tanks (50 cm × 37.5 cm × 15 cm) with 1 cm of mud substrate taken from Araçá Bay. The 24 tanks were divided in four treatments (n = 6 per treatment): flood tide (FT), ebb tide (ET), constant high tide (HT) and constant low tide (LT). For tide variation treatments, each tank was divided into six levels, and every hour, one level was carefully filled with sea water (FT treatment) or drained (ET treatment). For HT treatment the tank was completely filled in the beginning of the experiment and left untouched until the end, as the empty LT treatment, in which the experimental tanks remained empty and the animals exposed to air. At the end of the experiment (i.e. after 6 h), the number of individuals that were isolated or clustered in each tank was counted.

The ratio of clustered/isolated animals in each tank was compared by performing a one-way ANOVA with treatment as a factor with four levels. If significant, a *post-hoc* Tukey test was performed. Data were square-root transformed in order to fit the assumptions of the test.

3. Results

A total of 175*C. symmetricus* were collected, and the number of individuals per cluster ranged from 2 to 7, being 80% of the clusters composed by 2–4 individuals and 20% by 5–7 individuals. Males and females were present in clusters, and there was no difference between the number of individuals of each sex performing cluster behavior ($\times^2 = 0.7436$; df = 1; $p > 0.05$).

The SAI was calculated using the aperture width, based on the regression analyses (Fig. 1). Differences were found among SAI of males and females depending on their behavior, whether isolated or clustered (Table 1). Clustered females had poorly fitted shells compared to isolated females, while males from both conditions did not differ from each other or from isolated females (Fig. 2).

In the tide simulation experiment, more aggregated individuals than isolated ones were observed during ebb tide than during flood tide ($F_{3,20} = 3.673$, $p = 0.029$) (Fig. 3). High- and low-tide treatments did not differ from each other, or from the other treatments.

4. Discussion

Clustering behavior in hermit crabs is often associated with the adaptive function of shell exchange, as proposed by the "shell exchange market" hypothesis (Gherardi and Vannini, 1992, 1993). However, this study demonstrated that other factors can trigger clustering in intertidal hermit crabs. Tidal phase influenced the formation of aggregations, with more individuals clustering during the ebb than during flood tide. Besides that, although both sexes were equally present in aggregations,