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SHORT RESEARCH NOTE

# Influence of prior experience on shell selection by the white spotwrist hermit crab *Pagurus criniticornis* (Crustacea: Paguridae)

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**Abstract** Individuals of *Pagurus criniticornis* in a free-choice situation were experimentally tested under different laboratory conditions. In order to assess the effect of recently occupied shells on the size- and type-preference by hermit crabs, individuals were held for 30 days under one of the following two conditions: (1) excess of shells and (2) absence of shells. The crabs were then allowed to select shells from a wide array of empty gastropod shells of the two most-occupied species, as observed previously in the field: *Cerithium atratum* and *Morula nodulosa*. Preferred shell type (species) and size (shell aperture width and length) were correlated with hermit-crab size. The crabs showed a strong (100%) preference for *C. atratum* shells, demonstrating that recent and past experience did not influence either shell-type or shell-size preferences in this pagurid.

**Keywords** Anomura · *Pagurus criniticornis* · Shell occupation · Past experience · Southwestern Atlantic

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Gastropod shells are used as a portable shelter by hermit crabs to provide protection against predators and physical stress. Previous studies have suggested that hermit-crab shell preferences are important in mediating the shell-utilization patterns found in natural populations (Reese, 1962; Bach et al., 1976; Fotheringham, 1976; Bertness, 1980; Siu & Lee, 1992; Ohmori et al., 1995; Mantelatto & Dominciano, 2002; Meireles & Mantelatto, 2005; Biagi et al., 2006).

Hermit crabs do not necessarily live in the most suitable shells. Moreover, the availability of shells of different gastropod species, as well as the crabs' contact with other crabs competing for empty shelters, influence shell occupation (Bertness, 1980). The choice of a shell for occupation can be influenced by past experience in a variety of ways (Hazlett, 1992). Studies with different pagurid and diogenid species such as *Calcinus tibicen* (Herbst, 1791), *Calcinus laevimanus* (Randall, 1840) (Hazlett, 1992), *Clibanarius infraspinatus* (Hilgendorf, 1869) (Hazlett, 1996), *Pagurus granosimanus* (Stimpson, 1859), and *Pagurus samuelis* (Stimpson, 1857) (Hahn, 1998) demonstrated that individuals may modify their shell-size preference based on their recent experience with shell availability.

According to Hahn (1998), previous shell experience affects the interactions among the crabs present in an assemblage, including reducing intraspecific competition. Among the pagurid species occurring on the Brazilian coast, the white spotwrist *Pagurus criniticornis* (Dana, 1852) has been investigated as part of a long-term study undertaken to identify the most important ecological parameters for the population occurring in the sublittoral and intertidal zones along the north coast of the state of São Paulo, an important zone of faunal transition between Patagonia and tropical regions. In this context, the effect of prior shell experience on shell selection pattern by *Pagurus criniticornis* exposed to an excess or absence of different shell types and sizes were investigated.

Males and females of *P. criniticornis* (size range: 1.6 mm $\leq$ shield length $\leq$ 3.0 mm), were hand-collected in daytime by two people on a sublittoral rocky shore on the north coast of São Paulo. Laboratory experiments were performed in July 2005, and followed the methodology adopted by Garcia & Mantelatto (2001) in almost all aspects. Shell-size and shell-species preference experiments were conducted to compare the pattern of shell utilization and selection with that observed in systematic, long-term field studies (Mantelatto & Meireles, 2004).

In the laboratory, hermit crabs were transferred to a stock tank and kept there for 7 days until the beginning of the experiments. This period of time was established on the basis of previous experiments, in which more than 80% of the individuals showed shell-choice behavior after 7 days under laboratory conditions. Experiments were conducted in glass aquariums with flowing, oxygen-saturated sea water, under controlled temperature (25°C), salinity (33–35 psu), and natural daylight (L12:D12). Each animal was utilized only once, to avoid any acquired behavior. Animals that died during the experiments were not included in the analysis.

In the laboratory, only hermit crabs occupying *Cerithium atratum* and *Morula nodulosa* (the two most-frequently occupied gastropod shells in nature, as observed by Faria, 2004) were used to perform the experiments. Therefore the crabs were divided into two groups, according to the shell that they occupied in nature: *C. atratum* group ($N = 30$) and *M. nodulosa* group ($N = 30$). Next, individuals of both groups were divided evenly between the two treatments for 30 days: (1) crabs maintained grouped in field-occupied shells ($N = 15$ in *C. atratum* shells; $N = 15$ in *M. nodulosa* shells) with no excess of empty shells; (2) crabs maintained grouped in field-occupied shells ($N = 15$ in *C. atratum* shells; $N = 15$ in *M. nodulosa* shells) with an excess of shells (10 or more shells/individual, of different and adequate sizes) of the same species that they occupied in the field. After this period, hermit crabs from each treatment were exposed to a free-access situation (with at least 75 *C. atratum* and 75 *M. nodulosa* shells) for 5 days. This experimental period was previously tested during a shell-selection study carried out under laboratory conditions (Faria, 2004).

In order to determine correlations between characteristics of hermit crabs and their preferred shells, regression analyses were computed (Zar, 1996). The chi-square test ($\chi^2$) was used to compare occupancy of shell species, and morphometric relationships were established by regression analysis and correlation coefficients ($r$) (Spearman test). Shell-size preference data were analyzed using the multiple linear regression: $\log Y = a + b \log X$, (where $Y$ = shell measurements: SAW = shell aperture width; SAL = shell aperture length; and $X$ = hermit-crab measurements: SL = shield length). The regressions were performed on the logarithms of all variables rather than on the variables themselves, because of constancy of residual variance about the transformed dependent variable throughout the range of the independent variable. The level of significance was 0.05 for all tests, with a degree of freedom. The experiments were not evaluated separately in relation to the sex of individuals, because we assumed that the presence of the three groups (males, females, and ovigerous females) in each test would be important to avoid disturbance related to hierarchy behavior. Males are hierarchically superior to females (Biagi & Meireles, pers. obs.), and thus the absence of males could lead the females to display some behavior different from that observed if males were present; furthermore, these crabs are found grouped in nature (Garcia & Mantelatto, 2001). The mean sizes (SL) of the specimens used during the experiments were:

males = 2.33 ± 0.34 mm, females = 2.09 ± 0.29 mm, and ovigerous females = 2.33 ± 0.33 mm.

The morphometric relationship involving shell-aperture length and hermit-crab shield length was the one that best described the association between hermit crabs and the selected shell. Furthermore, shell-aperture width showed no correlation with hermit size in the majority of analyzed relationships. Although most of the relationships showed significant correlation coefficients, in general, the highest values were found in the relationships involving shell dimensions and hermit crabs that had prior shell-availability experience (Table 1).

*Pagurus criniticornis* displayed a strong shell-type preference, choosing *C. atratum* shells in all (100%) of the experiments. This shell-selection pattern is in accordance with the results of Faria (2004), demonstrating a high preference of *P. criniticornis* for this shell species in particular, despite the high availability of resources (empty and live gastropod shells) in the geographic area that we examined (Meireles et al., 2003; Mantelatto & Meireles, 2004). Furthermore, the shell selection corroborated the shell occupation pattern in the field found by Faria (2004). On one hand, the pattern of preferential selection, in the laboratory, of the same shell species most occupied in the field is well known in other hermit-crab species (Abrams, 1978; Elwood et al., 1979; Siu & Lee, 1992; Ohmori et al., 1995; Hahn, 1998; Dominciano & Mantelatto, 2004; Meireles & Mantelatto, 2005; Biagi et al., 2006; Mantelatto et al., 2007). On another hand, the absence of preference, under laboratory conditions, for a particular shell species has been reported for a few species (Orians & King, 1964; Siu & Lee, 1992; Garcia & Mantelatto, 2001).

According to Yoshino et al. (1999), there is a trade-off between shell size and species preference, and the less-preferred shell species are actively chosen when the shells of the most-preferred species present in the field have less-suitable sizes. In the present study, shell selection was based mainly on shell type and secondarily on shell size, as the crabs were offered contemporaneously shells of two species (*C. atratum* and *M. nodulosa*), and of different and adequate sizes, and their choice was always for *C. atratum*.

Comparative studies within the same hermit-crab species [*L. loxochelis* (Moreira, 1901) and *Pagurus exilis* (Benedict, 1892)] from different areas indicated different preferences among shell species (Biagi et al., 2006; Mantelatto et al., 2007, respectively). These different preferences may be attributed to both the morphology of hermit crabs and the environmental conditions, with the crustaceans looking for protection against predation, energy expenditure, osmotic stress, and wave action (Garcia & Mantelatto, 2001). However, nothing is known about shell choice in *P. criniticornis* specimens from different geographic areas, and therefore this aspect needs to be investigated. Furthermore, shell availability and adequacy in the local area are also important factors that rule shell occupation and selection (Reese, 1962; Conover, 1978). These facts allow us to infer that prior shell occupation might intervene in the shell-selection process.

Populations exposed to different shell availability display particular characteristics in regard to

**Table 1** *Pagurus criniticornis*

| Occupied shell species | Prior shell availability | $N$ | Relationship | Linear equation $Y = ax^b$ | Transformed $\ln Y = \ln a + b \ln X$ | $r$ |
|---|---|---|---|---|---|---|
| *C. atratum* | Yes | 13 | SAW × SL | $SAW = 1.31\ SL^{1.25}$ | ln SAW = 0.27 + 1.25 ln SL | 0.79* |
| | | 13 | SAL × SL | $SAL = 2.32\ SL^{1.25}$ | ln SAL = 0.84 + 1.25 ln SL | 0.87* |
| | No | 08 | SAW × SL | $SAW = 4.10\ SL^{0.14}$ | ln SAW = 1.41 + 0.14 ln SL | 0.08 |
| | | 08 | SAL × SL | $SAL = 1.07\ SL^{2.07}$ | ln SAL = 0.07 + 2.07 ln SL | 0.84* |
| *M. nodulosa* | Yes | 13 | SAW × SL | $SAW = 2.63\ SL^{0.53}$ | ln SAW = 0.97 + 0.53 ln SL | 0.42 |
| | | 13 | SAL × SL | $SAL = 3.61\ SL^{0.92}$ | ln SAL = 1.28 + 0.92 ln SL | 0.92* |
| | No | 10 | SAW × SL | $SAW = 2.01\ SL^{0.82}$ | ln SAW = 0.70 + 0.82 ln SL | 0.57 |
| | | 10 | SAL × SL | $SAL = 4.46\ SL^{0.46}$ | ln SAL = 1.49 + 0.46 ln SL | 0.54* |

Regression equations for chosen shell size ($N$ = number of individuals; $r$ = correlation coefficient; SL = shield length; SAW = shell aperture width; SAL = shell aperture length; * significant correlation, $P < 0.05$)

abundance, size, and reproduction (Bertness, 1981). The results of the present study indicate no influence of the shell previously occupied on hermit-crab shell choice, demonstrating that recent past experience did not influence the shell-type preference of *P. criniticornis*. Lack of influence of prior shell occupation was also observed in some previous studies (Reese, 1963; Blackstone, 1985), indicating that this behavior may not be easily modified by individual experience in some hermit-crab species.

We may conclude that hermit-crab species can be affected in different ways by previous shell-use patterns, with *P. criniticornis* showing no shell selection determined by prior-occupancy experiences, but rather by size and type of shell. However, even this initial analysis clearly demonstrates that this mechanism should be investigated in other species, in order to improve understanding of the causes and the role, if any, played by past experience in the natural history of hermit crabs. In addition, a comparative study among coexisting species in a hermit-crab community is important and is needed to clarify these mechanisms.

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