The right choice: predation pressure drives shell selection decisions in hermit crabs

<table>
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<tr>
<th>Journal:</th>
<th>Canadian Journal of Zoology</th>
</tr>
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<tbody>
<tr>
<td>Manuscript ID</td>
<td>cjz-2017-0023.R2</td>
</tr>
<tr>
<td>Manuscript Type:</td>
<td>Article</td>
</tr>
<tr>
<td>Date Submitted by the Author:</td>
<td>10-Oct-2017</td>
</tr>
<tr>
<td>Complete List of Authors:</td>
<td>Arce, Elsah; Universidad Autonoma del Estado de Morelos, ; Universidad Nacional Autonoma de Mexico, Cordoba, Alejandro; Universidad Nacional Autonoma de Mexico, Departamento de Ecología Evolutiva, Instituto de Ecología</td>
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<td>Keyword:</td>
<td>Calcinus californiensis, hermit crab, gastropod shell, mistake, Shelter choice</td>
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The right choice: predation pressure drives shell selection decisions in hermit crabs

E. Arce\textsuperscript{1,2*} and A. Córdoba-Aguilar\textsuperscript{2*}

\textsuperscript{1}Laboratorio de Acuicultura, Departamento de Hidrobiología, Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Morelos, Cuernavaca, Morelos, México. Tel: +52-77-73162354. E-mail: elsah.arce@uaem.mx

\textsuperscript{2}Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México, Apdo. P. 70-275, Ciudad Universitaria, 04510, México, D F., México. Tel: +52-55-56229003. E-mail: acordoba@iecologia.unam.mx

\textsuperscript{*}Corresponding authors:

elsah.arce@uaem.mx & acordoba@iecologia.unam.mx
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Abstract

Several prey species use refuges to avoid predation. Prey need to abandon and shift between refuges. However, during such shifting, prey can be vulnerable to predators. We hypothesize that predator presence may induce prey to make mistakes in choosing their refuge. We tested this by using hermit crabs *Calcinus californiensis* Bouvier, 1898 that were induced to shift to a new empty gastropod shell (three different species: *Columbella* sp. Lamarck, 1799, *Nerita scabricosta* Lamarck, 1822, and *Stramonita biserialis* (Blainville, 1832)) in the absence and presence of a natural crab predator, *Eriphia squamata* Stimpson, 1860, an efficient shell-crushing predator. We expected that when a predator was present, hermit crabs would a) inspect fewer shells and/or b) change to a shell that is either too heavy to allow escape or unfit in size to accommodate the hermit crab. While the first prediction was met, the second prediction was supported only when *S. biserialis* shells were used. Thus, in the presence of a predator, hermit crabs prioritize escaping via selecting lighter shells, which would allow the crab to move faster. We conclude that predator presence may induce prey to make mistakes in refuge selection, suggesting that this has severe consequences in future predatory events.

Keywords: shelter choice, mistake, gastropod shell, *Calcinus californiensis*, hermit crab
Introduction

Predators are a major selection pressure on prey, thus there has been selection for general adaptations to avoid detection, capture and ingestion in many prey species. Some examples of prey adaptations are alterations in activity, avoidance of sites occupied by predators, and an increase in their use of refuges (Brönmark and Miner 1992; Sih et al. 1992; Skelly 1994). It is well known that a refuge increases prey survival rate (i.e. Bertness 1981; Shervette et al. 2004). However, prey animals must find new refuges occasionally to avoid fitness costs in terms of growth (Lankford et al. 2001; Heithaus and Dill 2002) and reproduction (Spencer 2002; Auld and Houser 2015). This shifting between refuges exposes the animal to the cost of becoming exposed to predators at least temporarily. When facing such a situation, prey may make mistakes in choosing a new refuge, as prey must direct their attention to not only inspecting potential refuges but also to avoid capture by the predator. This means, for example, a reduced time to inspect potential refuges with the remaining time devoted to detecting and avoiding the predator.

Hermit crabs are good study subjects to test the effect of predator threat on decision-making during refuge shifting (Hazlett 1971). These animals are characterized by a soft abdomen that requires protection from environmental stress and predation (Resse 1969; Vance 1972). Shell use is dependent on shell availability (Turra and Leite 2002; Arce and Alcaraz 2011) and preference (Meireles et al. 2008; Arce and Alcaraz 2012). The size and type of selected shells have direct effects on crab fitness. The proper size and type of shell may allow greater clutch sizes (Childress 1972; Elwood et al. 1995), higher growth rates (Asakura 1992; Alcaraz et al. 2015), lower risk of predation (Angel 2000; Arce and Alcaraz 2013) and less environmental stress (Bulinski 2007; Argüelles et al. 2009). It is also related to its morphological structure and dimensions; for example, tight shells offer more protection from being pulled out by predators (Arce and Alcaraz 2013), while thick shells are effective against shell-crusher predators (Bertness and Cunningham 1981). Nevertheless, hermit crabs frequently need to move into a new shell. During shell shifting, hermit crabs have to search, inspect, handle and change shells. These different steps can take time during the process of discarding and trying different shell sizes. It is during this move that hermit crabs run the risk of being predated on. Thus, the influence of a predator threat may induce hermit crabs to make mistakes in shell selection given the reduced time because of avoiding predation. To our knowledge, the effect of predation
threat on the chance of making mistakes in shell selection has not been examined in hermit crabs or other
animals. Although it is well known that predation risk can ultimately affect hermit crab preference and shell
change (Mima et al. 2003; Briffa et al. 2008; Arce and Alcaraz 2013), these consequences can occur after a
crab makes the mistakes. Thus, we have herein examined shell selection in the face of predation risk in hermit
crabs and during shell shifting. For this, we used *Calcinus californiensis* Bouvier, 1898 hermit crabs and
*Eriphia squamata* Stimpson, 1860 crab predators. The latter is a natural predator of *C. californiensis* that
 crushes the shell to reach the hermit crab (Bertness and Cunningham 1981). According to this predation
strategy, hermit crabs should select light shells so that they can escape more effectively (Alcaraz and Arce
2017). Assuming that such crushing predators induce prey to make more mistakes, we therefore predicted that
during the presence of a predator, crabs would a) inspect and/or change fewer shells, and b) select a shell that
is not appropriate in terms of weight and/or size.

**Materials and methods**

**Collection and maintenance**

The animals used did not involve endangered or protected species. All applicable international, national
and/or institutional guidelines for the care and use of animals were followed. Hermit crabs (*C. californiensis*)
and predators (*E. squamata*) used for experimental trials were collected by hand in an intertidal zone at
Troncones, Guerrero, Mexico (17°47'16''N; 101°44'17''W) in November and December 2014. Crabs were
transported to the laboratory and maintained in individual containers to avoid shell exchange. Animals were
removed from their shells and measured (shield length in mm and hermit crab mass in mg). We only used
males of both hermit crabs and predators in our trials. For both, only animals that had all their appendages and
shells with no clear damage or epibionts were used. All animals were kept under a natural light:dark
photoperiod with running seawater (35 PSU) at an approximate temperature of 28°C. Crabs were fed with
sinking pellets (®New Spectrum) once a day. Predators were maintained in individual containers and fed with
hermit crabs 24 h prior to experiments. In all tests described below, different hermit crabs were used. On
completion of trials, all animals were returned to the sea.
Shell selection during predator absence and presence

A hermit crab was placed with its original shell, when this was one of the most commonly occupied shells by *C. californiensis* (Arce and Alcaraz 2011, 2012). For instance, the one it was occupying when captured in the field, either *Columbella* sp. Lamarck, 1799, *Nerita scabricosta* Lamarck, 1822 or *Stramonita biserialis* (Blainville 1832) and with 20 other empty shells of the same species the crab was using in a 20-L individual glass tank for 24 h. The 20 shells offered varied in size. Each shell was previously weighed (Shell Mass, ShM), measured (using four morphometric variables: shell length, ShL; shell width, ShW; shell aperture length, ShAL and shell aperture width, ShAW) and marked with different color combinations. Direct observations and measurements were recorded every 6 hours. In this time, we recorded two behavioral aspects of the hermit crabs under these conditions (1 – the number of shell inspections). A shell inspection took place when the hermit crab held a shell with appendices for review, but discarded it (2 – the number of shell changes). A shell change took place when the hermit crab abandoned its own shell and moved into a new shell. We assumed that a hermit crab preferred a shell when it occupied it for as long as 24 h.

We then carried out a similar experiment in which *E. squamata* predators were introduced (Zipser and Vermeij 1978). These predators were fed with hermit crabs 24 h before the experiment started and were then placed in a 40-L glass tank. This tank was divided into two halves (20 L each) using a rigid and transparent mesh (5 mm). Water was allowed to circulate through the tank so that the chemical cues from *E. squamata* reached the hermit crab. We again recorded the number of shell inspections, shell changes and shell selection for 24 h.

Shell preference and the right choice

Shell preference in crabs occupying *Columbella* sp, *N. scabricosta*, and *S. biserialis* was assessed using the following combinations: hermit crabs in *Columbella* sp. in the absence of a predator (n = 15) and in the presence of a predator (n = 17); hermit crabs in *N. scabricosta* in the absence of a predator (n = 16) and in the presence of a predator (n = 14); and hermit crabs in *S. biserialis* in the absence of a predator (n = 15) and in
the presence of a predator (n = 16). The shell selected by the crab – after it remained in it for a 24-hour period – was considered preferred. The number of “mistakes” was recorded during the shell selection process. A mistake was made when a hermit crab was occupying a shell out of its preferred weight and/or size (more than 10% tight or more than 10% loose; see Arce and Alcaraz 2012). The result of the preference for shells according to predator absence/presence was compared to determine whether the presence of a predator affects the decision.

Statistical analyses

The numbers of shell inspections and shell changes according to predator absence/presence were compared using a chi-square test ($\chi^2$). Relationships between crabs and gastropod shells sizes were established by regression analyses, where $x =$ hermit crab size ($M$) and $y =$ shell size ($ShM$ or $ShAW$; Arce and Alcaraz 2012). The preferred shell was determined using this regression, which was performed for each shell species. The slopes and elevations were compared using ANCOVA analysis of covariance to estimate the differences between the shell size selected under predator absence and under predator presence. We also used ANOVA to compare the number of mistakes in predator absence versus predator presence. All reported values are means ± SE. Statistical analyses were conducted using Statistics 7®.

Results

Hermit crabs inspected fewer gastropod shells when a predator was present than when it was absent ($\chi^2_{(2,1)} = 28.46, p < 0.001$; Fig. 1). This situation prevailed independently of the gastropod species ($F_{(5,56)} = 15.91, p < 0.001$; Fig. 1).

Hermit crabs showed more shell changes during predator absence than during predator presence ($\chi^2_{(2,1)} = 8.91, p < 0.01$; Fig. 2) and when hermit crabs occupied *Columbella* sp. shells during predator absence, compared to occupation of *S. biserialis* and *N. scabricosta* ($F_{(5,56)} = 18.50, p < 0.001$; Fig. 2). Finally, when the predator was present, shell changes did not differ among the three shell species (Fig. 2).
Hermit crabs selected different shell sizes or weights when a predator was absent than when the predator was present (Fig. 3). Specifically, hermit crabs occupying *Columbella* sp. \( (F_{(2,30)} = 15.62 \ p < 0.001, \) Fig. 3a), *N. scabricosta* \( (F_{(2,28)} = 18.86 \ p < 0.001, \) Fig. 3b) and *S. biserialis* \( (F_{(2,29)} = 16.78 \ p < 0.001, \) Fig. 3c) preferred smaller or lighter gastropod shells when a predator was present.

The number of mistakes during the shell selection process was different according to the predator absence/presence condition and shell species occupancy. When hermit crabs occupied *Columbella* sp. and *N. scabricosta* shells – in the absence of a predator – they made more mistakes than when the predator was present (Table 1). However, when hermit crabs occupied *S. biserialis* shells and the predator was absent, they made fewer mistakes than when the predator was present (Table 1).

**Discussion**

We postulated that although the presence of a predator may elicit behavioral responses to avoid predation in prey, this pressure might also affect prey decisions. In concordance with our first prediction, hermit crabs made fewer changes when a natural predator was present. Moreover, our results supported our second prediction, since crabs made more mistakes when a natural predator was present in terms of choosing a suboptimal shell but only when using *S. biserialis* shells. Previous studies also found that animals modify their behavior in the presence of predators; for example, hermit crabs modified their shell selection behavior in the presence of a predator (Rotjan et al. 2004; Arce and Alcaraz 2013; Alcaraz and Arce 2017) and other crustaceans showed less activity when predation risk was high (Hazlett 1996; Percor and Hazlett 2003). These results, in addition to the results of the present study, imply that hermit crabs can derive less information about resource value, in this case, the utility of the shell as an effective refuge, in the face of predator pressure. Related to predator presence, one antipredator response that hermit crabs show is a retraction inside the occupied shell (Briffa and Elwood 2001), which is a generalized response in animals using refuges (Sih et al. 2004). However, one immediate consequence of retracting is that hidden animals lose feeding and reproductive opportunities (Reaney 2007). For example, when the predator *Carcinus maenas* (Linnaeus 1758) is present, the prey *Nucella lapillus* (Linnaeus 1758) reduces foraging activity, as it remains hidden for longer (Vadas et al. 1994). The same result can occur even in prey that does not rely on refuge (Matassa and Trussell...
This is the case, for example, of lepidopteran larvae that reduce their foraging rate when the perceived level of predation risk is high (Berger and Gotthard 2008).

Prey-catching strategies by predators play key roles in how well prey can determine an effective refuge size (Walters and Wethey 1996). The risk of predation in hermit crabs is strongly related to shell size relative to crab size. According to previous studies (i.e. Arce and Alcaraz 2013), we used this relationship as a tool to determine whether crabs had made the right choice of refuge size, because the fit is essential for hermit crabs during predation attacks. In relation to this, *C. californiensis* deals with two types of natural predators in their habitat: peelers and crushers. Peelers (e.g. the crab *Arenaeus mexicanus* (Gerstaecker 1856)) pull out the crab by directly cutting and removing parts of the crab, while crushers (i.e. the predator we used, *E. squamata*) break the shell with their chelae (Bertness and Cunningham 1981). Interestingly, each predator style performs better with certain species of shell than others. For example, some shells allow the hermit crab to retreat completely and become unreachable to a peeler predator (Angel 2000). However, such shells are ineffective if the predator is a crusher. With a crusher, the hermit crab has to flee before its shell is grabbed. In this latter circumstance, a hermit crab does better if it bears a light shell, as it allows faster movements. According to this context, we found that *C. californiensis* crabs selected tighter or lighter shells when they perceived a threat by *E. squamata*. This is concordant with results from previous studies that suggest light shells allow hermit crabs to move faster (Herreid and Full 1986; Alcaraz and Arce 2017) and escape effectively when faced with a predator. Thus, the use of light shells by *C. californiensis* may be adaptive to avoid attacks by the crusher *E. squamata* (Alcaraz and Arce 2017). However, when choosing light shells, the crab made more mistakes if it faced a predator when occupying *S. biserialis* (the preferred shell; Arce and Alcaraz 2012). This shell species may have some additional yet undetected costs, which may only arise when a predator is present. Future studies can be conducted to clarify this.

Individuals may benefit from modifying their resource searching behavior when they perceive predation risk. However, this perception may induce them to make mistakes during shell selection. An incorrect choice and/or suboptimal shelter does not provide the individual with the benefits of counteracting a predatory attack. In this context, our study demonstrated that resource selection in the face of predation might induce mistakes by restricting inspection to fewer shells, which may have severe consequences for future
predatory events. To our knowledge, we have provided the first evidence of the occurrence of such mistakes and the costs prey incur from these mistakes when a predator is present.

Acknowledgements

We thank the DGAPA-UNAM Postdoctoral Program for providing a full scholarship to the first author. We thank Karla Kruesi for technical support in the field and the laboratory, Suntai Sotola and Manuel De La Torre for the drawings for Figures, and Guillermina Alcaraz for logistic and academic support.

References


**Figure captions:**

Figure 1. Number of shell inspections by hermit crabs occupying different gastropod shell species during predator absence/presence scenarios. Different letters indicate significant differences between treatments, while different numbers indicate differences between gastropod shell species ($p < 0.001$).

Figure 2. Number of shell changes by hermit crabs occupying different gastropod shell species according to predator absence/presence scenarios. Different letters indicate significant differences between treatments, while different numbers indicate differences between gastropod shell species ($p < 0.001$).

Figure 3. Regression slopes according to shell size preference by hermit crabs: A) *Columbella* sp., B) *Nerita scabricosta* and C) *Stramonita biserialis*. $R^2$, correlation coefficient ($p < 0.001$).
Table 1. Analysis of variance testing the number of mistakes hermit crabs made when getting into a new shell species under predator absence/presence scenarios.

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<th>Gastropod shell</th>
<th>Predator stimulus</th>
<th>Mistakes (n)</th>
<th>SE</th>
<th>df</th>
<th>F</th>
<th>P</th>
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<td>Absence</td>
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<td>0.94</td>
<td>1</td>
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<td>Presence</td>
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<td>0.89</td>
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Figure 1

![Graph showing number of shell inspections for different gastropod species under predator threat and no predator threat conditions.](image-url)
Figure 2

![Bar chart showing number of shell changes for different gastropod species under no predator and predator threat conditions.](chart.png)

**Gastropod Shell Species**
- *Columbia sp.*
- *N. scabridosta*
- *S. biseriatus*

**Legend**
- No predator threat
- Predator threat
Figure 3

A

Shell Aperture Length (mm)

Hermit crab mass (g)

Predator absence

\[ y = 4.4101x + 2.0394 \]

\[ R^2 = 0.731 \]

Predator presence

\[ y = 2.8644x + 1.4922 \]

\[ R^2 = 0.3676 \]

B

Shell mass (g)

Hermit crab mass (g)

Predator absence

\[ y = 1.9333x + 0.337 \]

\[ R^2 = 0.7767 \]

Predator presence

\[ y = 1.6898x + 0.0946 \]

\[ R^2 = 0.721 \]

C

Shell mass (g)

Hermit crab mass (g)

Predator absence

\[ y = 4.1657x + 0.9666 \]

\[ R^2 = 0.7928 \]

Predator presence

\[ y = 3.6477x + 0.4541 \]

\[ R^2 = 0.8671 \]