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Preferencia por diferentes conchas de gasterópodo en *Calcinus californiensis*: plasticidad selectiva ante el riesgo de depredación

T E S I S

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RESUMEN

El uso de conchas de gasterópodo por el cangrejo ermitaño *Calcinus californiensis* fue estudiado en Troncones, Guerrero, México. Los cangrejos ermitaños se capturaron en dos niveles diferentes de la zona intermareal, en sitios protegidos y expuestos al oleaje. *C. californiensis* ocupó conchas de 18 especies de gasterópodo. *Cantharus sanguinolentus* fue la concha más ocupada considerando ambos sitios. La frecuencia de uso de las conchas de las diversas especies difirió entre sitios protegidos y expuestos al oleaje. Los cangrejos ermitaños ocuparon conchas más pesadas y más gruesas en la zona expuesta al oleaje que en la zona protegida. Los resultados sugieren que el peso de las conchas es un factor importante para los ermitaños en las zonas con alta influencia hidrodinámica. La preferencia por las seis especies de conchas de gasterópodo más ocupadas fue evaluada en ausencia y presencia del depredador natural *Arenaeus mexicanus* utilizando dos procedimientos, el procedimiento en pares tradicionalmente utilizado y un procedimiento novedoso de múltiples alternativas. La secuencia en la preferencia por especies de conchas fue similar con ambos procedimientos. Sin embargo, los cangrejos seleccionaron conchas holgadas de todas las especies cuando se encontraron en amenaza de depredación. Los cangrejos que portaban conchas holgadas presentaron mayor probabilidad de supervivencia que los cangrejos en conchas de talla adecuada. Los resultados muestran que *C. Californiensis* es capaz de cambiar su preferencia por talla de concha en respuesta a la amenaza de depredación y que esta plasticidad selectiva le confiere ventajas adaptativas.

Palabras clave: Cangrejos ermitaños, *Calcinus californiensis, Arenaeus mexicanus,* preferencia, depredación, beneficios adaptativos.

ABSTRACT

The gastropod shell use of the hermit crab *Calcinus californiensis* was studied at Troncones, Guerrero, Mexico. Hermit crabs were captured at two different levels of the intertidal zone, in wave-protected and wave-exposed sites. *C. californiensis* occupied shells of 18 gastropod species. At both wave-action sites, *Cantharus sanguinolentus* was the most occupied shell. The frequency of use of the shells was different between the different wave sites. Hermit crabs occupied heavier and ticker shells in wave-exposed sites than wave-protected sites. Our results suggest that the shell weight is important in sites that are greatly affected by the hydrodynamics. The preference among six shell species and different shell sizes was evaluated in presence and absence of predator, *Arenaeus mexicanus*, and were tested by two different experiments, the traditional experiment and a new multiple-alternative test. The sequence of shell preference was similarly independent of the procedure used. However, hermit crab preferred loose shell when they are in predator presence. Hermit crabs in loose shell were less eaten than the hermit crabs in adequate shell size. The results of this study show that the hermit crab *C. californiensis* is able to change their preference for shell size in response to a predation threat and that the change in preference confers survival benefits for hermit crabs.

Keywords: hermit crabs, *Calcinus californiensis, Arenaeus mexicanus,* shell preference, predation, adaptive benefits.

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CAPÍTULO I

INTRODUCCIÓN GENERAL

Preferencia por diferentes conchas de gasterópodo en
***Calcinus californiensis*: plasticidad selectiva ante el riesgo**
de depredación

Suntai

Preferencia por diferentes conchas de gasterópodo en *Calcinus californiensis*: plasticidad selectiva ante el riesgo de depredación

Los seres vivos pueden responder a estímulos del medio que los rodea a través de cambios morfológicos, fisiológicos y conductuales. Muchas de las respuestas conductuales ante determinados factores que se han documentado son benéficas cuando el factor que la desencadena está presente; sin embargo, suelen ser costosas cuando el estímulo no está presente (Via et al. 1995). Las respuestas conductuales plásticas son inducidas por numerosos factores abióticos y bióticos como la temperatura y la luz (Hiesey 1953; Scheiner y Goodnight 1984), la competencia y la depredación (Marshall y Jain 1969; Relyea 2001). Ante esta situación, los organismos han desarrollado plasticidad conductual cuando el entorno que desencadena su respuesta es cambiante.

Las respuestas plásticas son especialmente importantes en ambientes espacial y temporalmente cambiantes. Uno de los ambientes con mayores retos ambientales para los organismos dada su alta complejidad es la zona intermareal. Este ambiente está expuesto al oleaje y es regulado básicamente por las mareas; en este ambiente la distribución de los organismos está altamente influenciada por la desecación, la acción del oleaje y por la presión de la depredación (Bertness 1981a; Bustamante et al. 1997; Blamey y Branch 2009). Ante estos retos, los organismos se ven en la necesidad de desarrollar mecanismos que les permitan contrarrestar dichas presiones. Por ejemplo, ante el estrés hídrico, los mejillones se agrupan para reducir la exposición individual al oleaje (Arrieche et al. 2010), algunos balanos tienen la capacidad de desarrollar cambios en la longitud de sus cirros en respuesta a los flujos de agua extremos (Miller 2007). Los organismos han desarrollado adaptaciones para evitar ser arrastrados, por ejemplo, las estrellas de mar se fijan a superficies rocosas mientras que otros animales encuentran refugio en las grietas o se esconden bajo las algas (Brusca y Brusca 2003). Los gasterópodos responden a la desecación mediante el cierre de sus conchas, algunos otros animales como cangrejos y bivalvos tienen gruesos revestimientos para

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evitar la evaporación (Hill 2007); ante la disminución de los niveles de oxígeno, muchos peces regulan sus niveles enzimáticos, modifican su tasa metabólica y cardiaca como respuestas que les permiten sobrevivir en aguas pobres en oxígeno (Val y Kapoor 2003). Los cangrejos ermitaños no son la excepción, ellos han optado por ocupar conchas de gasterópodo con características particulares que les permitan contrarrestar el estrés de este tipo de ambientes.

La literatura refiere con frecuencia que la ocupación y preferencia de conchas de gasterópodos es una conducta plástica modulada por las presiones ambientales. En particular, en el ambiente intermareal estas presiones están íntimamente ligadas al estrés hidrodinámico y a la depredación. La depredación es un factor determinante en la estructura de las comunidades y puede afectar la fisiología, la morfología y la conducta de los organismos. Los animales usan diferentes mecanismos de defensa en contra de la depredación, por ejemplo, el camuflaje, las defensas químicas, la formación de espinas, la formación de agregaciones, el uso de refugios, entre otros (Brodie et al. 1991; Barshaw et al. 2003). La plasticidad conductual ante la amenaza de depredación ha sido demostrada para muchas especies de animales, por ejemplo, renacuajos (*Rana temporaria*, Van Buskirk 2002; *Rana sylvatica*, Relyea 2003), hormigas, (*Euroleon nostras,* Klokocovnik et al. 2012), cladóceros (*Daphnia retrocurva*, Harvell 1990), cangrejos rey (*Paralithodes camtschaticus,* Daly et al. 2012) y cangrejos ermitaños (*Pagurus longicarpus*, Rotjan et al. 2004). En el caso de los cangrejos ermitaños, dado que poseen un abdomen carente de exoesqueleto rígido están obligados a protegerlo utilizando refugios móviles como lo son las conchas de gasterópodo vacías. El conocimiento de la ocupación de conchas de este organismo y las consecuencias que tiene en la distribución en la zona intermareal permite crear un panorama global sobre los posibles beneficios adaptativos que este recurso les brinda a los ermitaños. Ante esta situación, considerando que las diferentes especies de conchas brindan beneficios disímiles a los cangrejos ermitaños en las diferentes zonas del intermareal, es de esperarse el uso diferencial de conchas en zonas con diferentes condiciones ambientales, tanto bióticas como lo es la depredación, como abióticas como lo es el estrés hidrodinámico. Esto ha sido observado en el cangrejo ermitaño

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Clibanarius antillensis y *Calcinus seurati* los cuales ocupan conchas más pesadas en relación a su área superficial expuesta en sitios con un oleaje intenso (Hahn 1998; Argüelles et al. 2009). Las conchas más pesadas y cónicas brindan ventajas en sitios expuestos a la acción del oleaje debido básicamente a que la resistencia al desprendimiento es proporcional a la fuerza vertical del organismo determinada por el peso (Martinez 2001). Los ermitaños no sólo han optado por ocupar conchas que les permita protegerse ante el estrés hidrodinámico, adicionalmente, ellos seleccionan conchas de gasterópodo de diversas especies que tienen la peculiaridad de brindar a los organismos portadores distintos beneficios de protección ante la depredación.

Entre las características antidepredatorias que proporcionan las conchas podemos incluir, conchas con paredes gruesas, con aperturas con áreas reducidas, con presencia de ornamentos y con formas particulares que dificulten la maniobra del depredador. Las conchas de paredes gruesas protegen a los gasterópodos y a los ermitaños que las ocupan ante eventos depredatorios en los cuales el depredador presenta la habilidad de fracturar la concha como es el caso de cangrejos, pulpos y algunos peces (Bertness y Cunningham 1981; Palmer 1985). Las conchas gruesas y por lo tanto con mayor material calcáreo dificultan la depredación debido a que los depredadores requieren incrementar la fuerza y el tiempo requerido para fracturar la concha y como consecuencia necesitan invertir mayor energía para su éxito, por lo tanto la probabilidad de supervivencia de los ermitaños en conchas gruesas es mayor (Palmer 1985). En cuanto a las conchas con áreas de apertura reducida, éstas protegen a los organismos que las poseen ante eventos depredatorios de animales capaces de extraer a su presa por este orificio como lo son las jaibas y las langostas (Edgell y Miyashita 2009). Asimismo, las conchas de forma turriculada y con espira larga pueden beneficiar a los portadores ante la depredación de organismos que extraen a la presa por la apertura ya que estas conchas les permite ocultarse mejor (Vermeij 1978). La presencia de ornamentos en las conchas es otra de las características que brinda ventajas a los organismos portadores. Las conchas con espinas u ornamentos pueden alcanzar dimensiones externas mayores lo cual tiene la ventaja de dificultar o incluso

imposibilitar la maniobra del depredador, brindándole al organismo ocupante una mayor posibilidad de supervivencia (Palmer 1979; Bertness y Cunningham 1981).

En general, las conchas con un gran volumen interno y como consecuencia grandes y pesadas en relación al cangrejo ocupante pueden protegerlos de depredadores capaces de extraer a la presa sin fracturar la concha (Edgell y Rochette 2008). Sin embargo, cabe señalar que estas conchas pueden también aumentar el costo de locomoción (Herreid y Full 1986) y disminuir la tasa de crecimiento (Bertness 1982; Osorno et al. 2005). Ante esta situación, se asume que los cangrejos seleccionan conchas específicas de acuerdo a las presiones bióticas y abióticas del ambiente que les permiten maximizar su adecuación (Fotheringham 1976). Es decir, diferentes conchas que les puedan proveer ventajas y costos distintos, de tal manera que las características ventajosas que una especie o talla de concha puede conferir a los cangrejos en un ambiente, pueden resultar costosas en otras condiciones ambientales.

La ocupación de conchas de gasterópodo en el campo es diversa y depende de factores como la disponibilidad de tallas y especies de conchas, de la competencia entre los cangrejos y de la preferencia por ciertas conchas. La preferencia por conchas varía entre especies de cangrejos ermitaños y puede variar también entre las poblaciones de una misma especie dependiendo de la talla, del sexo, del estado reproductivo y de las condiciones ambientales bióticas y abióticas (Bertness 1981a; Liszka y Underwood 1990; Hazlett 1992; Garcia y Mantelatto 2001; Sato y Jensen 2005; Meireles et al. 2008).

La preferencia por un recurso está generalmente ligada a ventajas adaptativas (Underwood et al. 2004). En condiciones de disponibilidad de conchas, los cangrejos pueden seleccionarlas activamente en base a una gran diversidad de características entre las que destacan el peso, el volumen interno, el largo, el ancho, las dimensiones de la apertura o una combinación de estas características (Markham 1968; Childress 1972; Vance 1972; Fotheringham 1976; Mitchell 1976; Bertness 1981a; b; Lively 1988). Los cangrejos ermitaños pueden preferir conchas que presenten ventajas

hidrodinámicas (Scully 1979), de protección contra depredadores (Bertness 1982; Mclean 1983), reproductivas (Elwood et al. 1995) y su preferencia puede ser plástica dependiendo de las condiciones ambientales como por ejemplo los niveles de oxígeno (Côté et al. 1998), la velocidad del agua (Hahn 1998), la disponibilidad de conchas (Hazlett 1992) y la amenaza de depredación (Mima et al. 2003).

Algunos autores sugieren que la preferencia por ciertas especies y tallas de conchas es una manera de conocer la importancia relativa de las conchas para los organismos (Borjesson y Szelistowski 1989). Aunque la literatura propone que la concha preferida brinda beneficios a los cangrejos portadores, la mayoría de los trabajos no abordan la relación entre la preferencia por alguna especie determinada de concha y las ventajas específicas que ésta proporciona. Entre las pocas ventajas documentadas que se confieren a la ocupación de ciertas conchas se destacan las asociadas a la reproducción, en donde las hembras de algunas especies de cangrejos que ocupan un tipo específico de concha tienden a desarrollar puestas de mayor tamaño (Elwood et al. 1995). Algo similar se ha propuesto para el caso de la depredación; algunas especies de cangrejos ermitaños como *Clibanarius antillensis, Calcinus tibicen, Pagurus* sp., *P. pollicaris* y *Calliactis tricolor* expuestos a una amenaza constante de depredación tienden a ocupar en el campo conchas más gruesas y pesadas (Bertness 1981a, 1982; Mclean 1983). Sin embargo, es de suma importancia destacar que actualmente, ningún estudio ha demostrado que la ocupación de ciertas conchas incremente la probabilidad de supervivencia de los ermitaños, ni la relación con la preferencia por éstas.

Calcinus californiensis es un cangrejo ermitaño que se distribuye en territorio mexicano desde Puerto Peñasco, Sonora hasta la Bahía de Huatulco, Oaxaca y es habitante de la zona intermareal de Troncones, Guerrero. Este ermitaño se caracteriza por poseer la quela izquierda más desarrollada que la derecha (Poupin y Bouchard 2006). Uno de los principales depredadores de los cangrejos ermitaños en Troncones es la jaiba, *Arenaeus mexicanus,* este depredador se alimenta rompiendo conchas y extrayendo a los organismos expuestos con sus quelas (West and Williams 1986;

Kuhlmann 1992). Ante esta situación, conchas que les permitan a los portadores ocultarse mejor y/o ser más resistentes a la fractura proporcionan una mayor probabilidad de supervivencia a los ermitaños que las seleccionan. Por lo tanto, la preferencia por este recurso en *C. californiensis* podría estar ligada a los beneficios adaptativos en términos de protección ante la depredación. Sin embargo, dado lo costoso que puede ser cargar una concha resistente a la fractura y/o más grande y pesada que le permita ocultarse mejor y protegerse ante la eminente amenaza, estos ermitaños pudieran presentar plasticidad conductual en la selección de conchas. Por todo lo anterior, *C. californiensis* y la zona intermareal de Troncones, Guerrero son el escenario ideal para encontrar posible plasticidad conductual asociada a la preferencia por conchas de gasterópodo y las ventajas adaptativas relacionadas con dicha plasticidad en la conducta.

Hipótesis

I. Si las diferentes especies de conchas brindan beneficios disímiles a los cangrejos ermitaños en las diferentes zonas de la intermareal, entonces se observará una distribución diferencial del uso de conchas en zonas con diferentes condiciones ambientales.

II. Dado que uno de los principales depredadores de los cangrejos ermitaños en Troncones (*Arenaeus mexicanus)* se alimenta rompiendo conchas y extrayendo a los organismos expuestos con sus quelas, se espera que ante la presencia de estas jaibas, los ermitaños seleccionen conchas más duras y de mayor talla que les permitan resguardarse mejor.

III. Si la preferencia por diferentes especies de conchas de gasterópodos se modifica en condiciones de amenaza de depredación, entonces se espera que la concha preferida bajo estas condiciones sea aquella que incremente la probabilidad de supervivencia de los cangrejos al sesgar la selección hacia las especies y tallas que proporcionen mayor protección ante la amenaza de depredación.

Objetivos

Objetivo general

Determinar si la ocupación y preferencia por conchas en el cangrejo ermitaño, *Calcinus californiensis,* puede explicarse en base al gradiente intermareal, donde el oleaje y la depredación juegan un papel preponderante. Así como estimar si la preferencia por ciertas conchas es una respuesta conductual adaptativa en este cangrejo ermitaño.

Objetivos particulares

a) Conocer la distribución de *C. californiensis* en función de su talla, sexo y estado reproductivo, así como su patrón de ocupación de conchas en un gradiente intermareal en Troncones, Guerrero.

b) Estimar la talla preferida de las conchas más ocupadas por los ermitaños en Troncones.

c) Estimar la preferencia de este cangrejo ermitaño por las especies de conchas más ocupadas en el campo.

d) Determinar si la preferencia por conchas en *C. californiensis* puede modificarse hacia diferentes especies o tallas cuando los cangrejos son expuestos a condiciones de amenaza de depredación.

e) Si existiera plasticidad en la selección, determinar si ésta puede considerarse una respuesta adaptativa en base a las ventajas que ofrece en términos de supervivencia.

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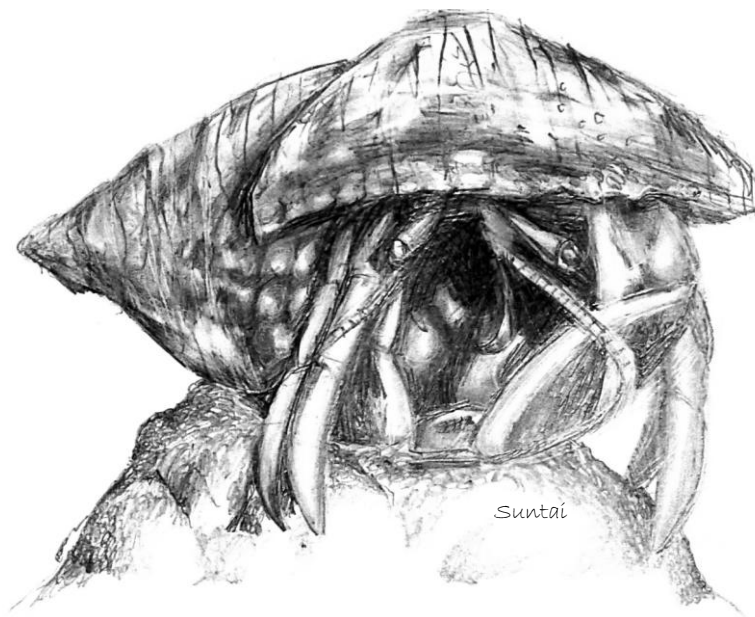
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CAPÍTULO II

Uso de conchas de gasterópodo por el cangrejo ermitaño *Calcinus californiensis* en diferentes niveles de la zona intermareal

Suntai

Shell use by the hermit crab *Calcinus californiensis* at different levels of the intertidal zone

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SUMMARY: The gastropod shell use of the hermit crab *Calcinus californiensis* was studied at Troncones, Guerrero, México. Hermit crabs were captured at two different levels of the intertidal zone, in wave-protected and wave-exposed sites. *C. californiensis* occupied shells of 18 gastropod species. At both wave-action sites, *Cantharus sanguinolentus* was the most occupied shell. *Columbella* sp. was used more by females than by males, and *Nerita scabricosta* was more used by males. The frequency of use of the shells was different between the different wave sites. *N. scabricosta* and *Columbella* sp. were occupied more at the wave-protected than at the exposed sites; *C. sanguinolentus* and *Stramonita biserialis* were occupied more at the exposed sites. The hermit crabs at the wave-exposed sites occupied heavier and thicker shells compared with the crabs from the protected sites. The Olmstead-Tukey diagram showed eight shell species as dominant in the wave-protected sites, and seven in the wave-exposed sites. Ten shell species were rare in the wave-protected sites, and six in the wave-exposed sites. The rare shells occupied by the hermit crabs were relatively heavier than the dominant shells in both site types. Our results suggest that the shell weight is important in sites that are greatly affected by the hydrodynamics.

Keywords: gastropod shell, hermit crab, *Calcinus californiensis*, waves, Olmstead-Tukey, intertidal.

RESUMEN: USO DE CONCHAS POR EL CANGREJO ERMITAÑO *CALCINUS CALIFORNIENSIS* EN DIFERENTES NIVELES DE LA ZONA INTERMAREAL. – El uso de conchas de gasterópodo por el cangrejo ermitaño *Calcinus californiensis* fue estudiado en Troncones, Guerrero, México. Los cangrejos ermitaños se capturaron en dos niveles diferentes de la zona intermareal, en sitios protegidos y expuestos al oleaje. *C. californiensis* ocupó conchas de 18 especies de gasterópodo. *Cantharus sanguinolentus* fue la concha más ocupada considerando ambos sitios. *Columbella* sp. fue más ocupada por las hembras que por los machos y *Nerita scabricosta* fue más ocupada por los machos. La frecuencia de uso de las conchas de las diversas especies difirió entre ambos sitios. *N. scabricosta* y *Columbella* sp. fueron más ocupadas en la zona protegida al oleaje que en la zona expuesta; *C. sanguinolentus* y *Stramonita biserialis* fueron más ocupadas en los sitios expuestos. Los cangrejos ermitaños ocuparon conchas más pesadas y más gruesas en la zona expuesta al oleaje que en la zona protegida. El diagrama Olmstead-Tukey mostró como dominantes las conchas de ocho especies en la zona protegida del oleaje y siete en el sitio expuesto; como raras las conchas de diez especies en la zona protegida y seis en la expuesta. Las conchas agrupadas como raras en ambas zonas fueron relativamente más pesadas que las conchas agrupadas como dominantes. Los resultados sugieren que el peso de las conchas es un factor importante para los ermitaños en las zonas con alta influencia hidrodinámica.

Palabras clave: gasterópodos, cangrejos ermitaños, *Calcinus californiensis*, oleaje, Olmstead-Tukey, intermareal.

INTRODUCTION

Hermit crabs occupy empty gastropod shells for protection against predators (Vance, 1972) and physical stress (Reese, 1969). The strong association between hermit crabs and shells influences almost all aspects of hermit crab biology (Fotheringham, 1976; Bertness, 1981a; Hazlett, 1981; Angel, 2000; Yoshino *et al*., 2004). Hermit crabs show preferences for particular gastropod shell species and sizes (Hazlett, 1981); however, because shells are a limiting resource for most populations (Fotheringham, 1976; Kellogg, 1976), the

shell occupancy in a natural population is commonly explained by shell availability (Scully, 1979). The shell occupancy along an intertidal gradient can depend on the environmental conditions, the size of the hermit crab, reproductive stage, sex, and previous experience (Bertness, 1981a; Asakura, 1995; Elwood *et al.*, 1995; Yoshino and Goshima, 2001; Alcaraz and Kruesi, 2009).

The intertidal zone is a challenging environment regularly exposed to waves by the advance and retreat of the tides; in this environment, the most important factors that determine the fauna distribution are desiccation, wave action, and predation (Bustamante *et al.*, 1997; Blamey and Branch, 2009). Life forms in this habitat must be well adapted to the drastic environmental changes associated with tidal activity to avoid their being washed away by the water flow. Waves play an important role in determining the distribution of species and populations in the intertidal zone; therefore, hermit crabs are directly affected by hydrodynamic stress, which is an important factor determining shell use and preference (Scully, 1979; Hahn, 1998). Differences in hydrodynamic stress in the intertidal zone may also affect hermit crabs through indirect but related factors that shape the community composition, for example, predatory pressure is an important factor (Rotjan *et al.,* 2004). Predation by invertebrates and birds changes along the intertidal gradient and is greater in protected sites than in those exposed to wave action (Menge, 1978; Robles *et al.,* 2001).

The hermit crab *Calcinus californiensis* Bouvier, 1898 is a common species in the intertidal zone and shallow waters of the eastern Pacific (Poupin and Bouchard, 2006). At Troncones, Guerrero this species inhabits the intertidal rock pools exposed to different levels of wave action. In this study, we determined the shell occupancy of *C. californiensis* at different levels of wave action.

MATERIALS AND METHODS

The study was carried out in the intertidal rock pools at Troncones, Guerrero, México (17°47'16''N; 101°44'17''W) in March and August 2008. Hermit crabs were captured during low tides in two different areas of the intertidal zone: wave-protected and wave-exposed sites. The wave sites were established according to the water speed, estimated as the mean of the highest speeds reached in 5 minutes, as described by Argüelles *et al.* (2009). The wave-protected sites were rock pools, relatively close to the shore (no more than 5 m from the highest tide-mark) with a mean maximum water speed of 1.0 cm s^{-1} (range from 0.3 to 2.0 cm s^{-1}). The wave-exposed sites were at a site approximately 25 m from the shore with a mean maximum speed of 57.3 cm s^{-1} (range from 22 to 178 cm s^{-1}). The water speed was measured during the sampling using a flow meter (Global Water, precision ± 0.1 cm s^{-1}). The water speed measurements were taken as close as possible to

the substrate in which the crabs were collected. The mean depth of the water column at each collection site was estimated as the average water level during 5 minutes as described by Argüelles *et al.* (2009). The water temperature, oxygen concentration, types of sediment, bottom configuration, degree of air exposure, and presence or absence of algae were recorded.

Sampling was carried out using 0.25 m^2 quadrants. All rocks and crevices were searched for hermit crabs. All hermit crabs and vacant gastropod shells were collected by hand and taken to the field laboratory. For each sampling period (March and August), sixteen sites were searched for hermit crabs, with eight quadrants sampled at the protected sites and eight at the wave-exposed sites.

All crabs were removed from their shells by heating the apex of the shell (Kellogg, 1977). Crabs were measured for shield length and chelae length using a digital caliper (±0.01 mm) and weighed on a plate balance (OHAUS, ±0.1 g). The sex of the hermit crabs was determined by identifying the position of the genital pores by using a stereoscopic microscope. Shells were dried (24 h, 60°C), weighed using a plate balance, and measured for shell length, width and aperture (length and width). All the gastropod shells were identified according to Morris (1969), Keen (1971), Abbott (1996), and Skoglund (2001). The shell weight/shield length ratio was used as an index of the relative weight of the shell in relation to the crab (Mantelatto and Dominciano, 2002; Turra and Leite, 2004).

The frequency of shell occupancy of the six most occupied shells in the wave-protected sites and wave-exposed sites was compared in the two sampling periods (March and August) by a chi-square test (χ^2). Since the data from the two sampling periods were similar (see results), they were grouped for further analysis. The shell species occupied at the sites, the sex distribution, the shell species occupied by sex, and the sex ratio were compared using chi-square tests. The shell weight/shield length ratios of the shell species occupied at the protected and exposed sites were compared with an ANOVA analysis using shell species and the collecting zone as factors and the shell weight/shield length ratio as the independent variable. Significant differences between them were tested with a Student's *t*-test. The shell weight/shield length ratio was also related to the frequency of use of each shell species at the two site types. Linear regressions between shell weight and shell length were made for each shell species found at each wave-site. The slopes and elevations were compared with an ANCOVA analysis to estimate morphometric differences between the shells occupied at the two wave sites.

The shell occupancy data were plotted with a Olmstead-Tukey diagram. In this diagram, the frequency of occurrence of the gastropod shell species (number of quadrants in which a particular shell species was found) is graphed versus their abundance (total number of individuals in all quadrants, log (n+1) transformed

TABLE 1. – Total number (*n*) and percentage (%) of gastropod shell species occupied by the hermit crab *Calcinus californiensis* at Troncones, Guerrero.

Shell species	males		non-ovigerous females		ovigerous females		total	
	n	%	*n*	%	*n*	%	*n*	%
Cantharus gemmatus (Reeve, 1846)	8	2.7	0	0	0	0	8	1.2
Cantharus sanguinolentus (Duclus, 1833)	67	22.5	23	28.4	84	31.1	174	26.8
Cerithium maculosum Kiener, 1841	6	2.0	0	0	3	1.1	9	1.4
Cerithium menkei Carpenter, 1857	5	1.7	1	1.2	5	1.9	11	1.7
Columbella sp. Sowerby, 1832	37	12.4	19	23.5	53	19.6	109	16.8
Engina tabogaensis Bartsch, 1931	0	0	1	1.2	6	2.2	7	1.1
Leucozonia cerata (Wood, 1828)	12	4.0	3	3.7	9	3.3	24	3.7
Mancinella speciosa (Valenciennes, 1832)	35	11.7	11	13.6	27	10.0	73	11.3
Mancinella triangularis (Blainville, 1832)	35	11.7	10	12.4	27	10.0	72	11.1
Mitra lens Wood, 1828	5	1.7	1	1.2	0	0	6	0.9
Mitra tristis Broderip, 1836	1	0.3	0	0	0	0	1	0.2
Natica chemnitzii Pfeiffer, 1840	1	0.3	0	0	0	0	1	0.2
Nerita scabricosta Lamarck, 1822	33	11.1	4	4.9	15	5.6	52	8.0
Opeastosoma pseudodon (Burrow, 1815)	5	1.7	0	0	1	0.4	6	0.9
Phos sp. Montford, 1810	1	0.3	0	0	1	0.4	2	0.3
Plicopurpura pansa Gould, 1853	2	0.7	0	0	1	0.4	3	0.5
Stramonita biserialis (Blainville, 1832)	44	14.8	7	8.7	38	14.0	89	13.7
Turritella banksi Reeve, 1849	1	0.3	1	1.2	0	0	2	0.3
Total	298	100	81	100	270	100	649	100

(Olmstead and Tukey, 1947; Argüelles-Ticó *et al.*, 2010). The vertical line dividing the diagram (Fig. 4) shows the shell species present in less than 50% of the quadrants on the left side, and the shell species present in more than 50% of the quadrants on the right side. The horizontal line dividing the diagram shows the most occupied shells in the top part and the least occupied shells in the bottom part. Thus, dominant shells are those most commonly used by the hermit crabs and which are more abundant. Frequent shells are less abundant than the mean abundances, but more frequent than the mean frequencies. Occasional shells occur infrequently at the different sampling sites, but show a high abundance. Rare shells show lower than mean abundances and frequencies.

RESULTS

The bottom configuration of all the sampling sites was mainly composed of volcanic rocks. Macroalgae were not present at either site type. Water temperature in March and August were 27.9 ± 2.9°C and 28.6 ± 3.2°C and no significant differences were found between the exposed and protected sites ($F_{(1,30)}$=0.39, P>0.05). Salinity was 35±1 in both sampling periods and wave sites (P>0.05). No sampling site was exposed to air. A total of 649 individuals were obtained in the study with 298 (46%) males, 81 (12%) nonovigerous females, and 270 (42%) ovigerous females (Table 1). The abundance of the six most occupied shell species in the wave-exposed and protected sites was similar for March and August ($\chi^2_{(0.05,5)}$=9.5; P>0.05), therefore data from both sampling periods were grouped for further analysis. Males were 7% larger and 39% heavier than nonovigerous females ($t_{(2,642)}$=3.1, P<0.01; $t_{(2,642)}$=3.9, P<0.001). Females were more abundant than males in both wave-action sites, and the male-female ratio of the two site types was 1:1.2 ($\chi^2_{(0.05,1)}$=66.5; P<0.001). However,

more females were found at the exposed sites (1:1.7, $\chi^2_{(0.05,1)}$=21.9; P<0.001), but the abundance of males and females was similar in the wave-protected sites (1:1, $\chi^2_{(0.05,1)}$=1.6; P>0.05). Ovigerous females were more abundant in the wave-exposed sites than in the protected ones ($\chi^2_{(0.05,1)}$=11.4; P<0.001; Fig. 1).

Calcinus californiensis occupied a total of 18 different gastropod shells. Combining data from the two wave-action sites, *Cantharus sanguinolentus* (Duclus, 1833) was the most occupied shell, followed in order by *Columbella* sp. Sowerby, 1832 and *Stramonita biserialis* (Blainville, 1832; Table 1). After *C. sanguinolentus,* which was the most occupied shell of all, the shell most occupied by the females was *Columbella* sp. ($\chi^2_{(0.05,1)}$=11.2; P<0.01). *Nerita scabricosta* Lamarck, 1832 was the shell most used by males ($\chi^2_{(0.05,1)}$=25.0; P<0.01). No empty shells were found at the sites.

The use of the six most-occupied shell species was different in the two wave-action sites ($\chi^2_{(0.05,5)}$=67.0; P<0.001). *N. scabricosta* and *Columbella* sp. were oc-
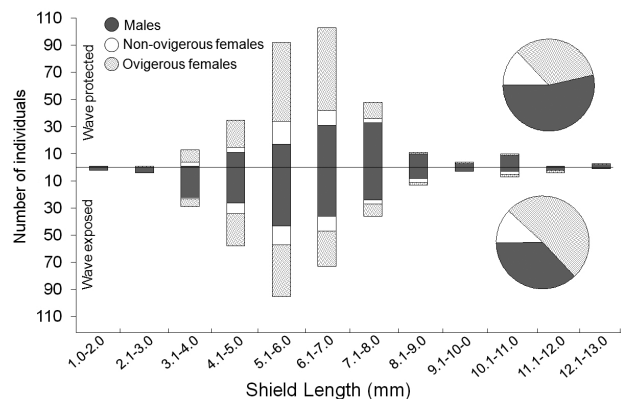

FIG. 1. – Size-frequency distribution for the individuals of the hermit crab *C. californiensis* collected in the wave-exposed and protected sites. The pie diagrams indicate the composition of sexes at the two types of sampling sites.
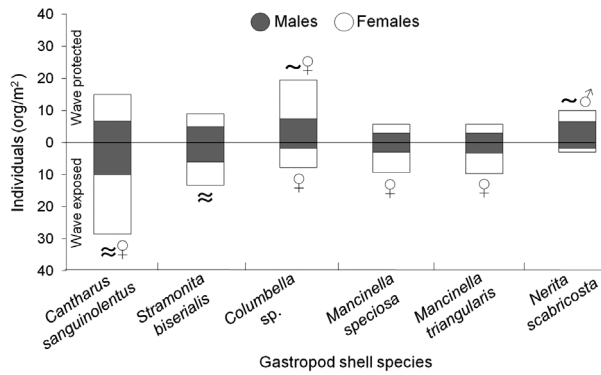
FIG. 2. – Gastropod shell species most used by males and females of the hermit crab *C. californiensis* in the wave-protected and the wave-exposed sites. Males and females show significant differences in shell use by males and females in each site type ($P<0.05$), ~ and ≈ show significant differences in shell species occupancy in the wave-protected and wave-exposed sites ($P<0.05$).
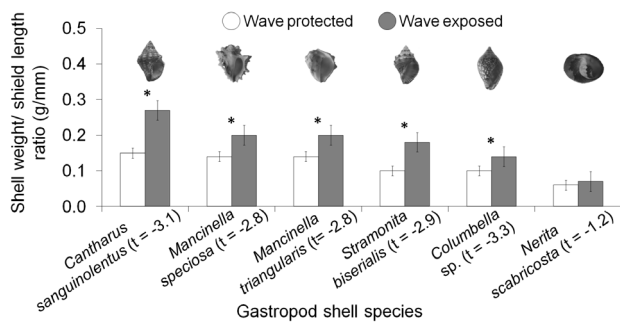

FIG. 3. – Shell weight/shield length ratio of the most occupied shells by the hermit crab *C. californiensis* in the wave-protected and wave-exposed sites. Mean values and standard errors are shown; Student's *t*-test values are shown in parenthesis; * = Significant differences at $P<0.01$.
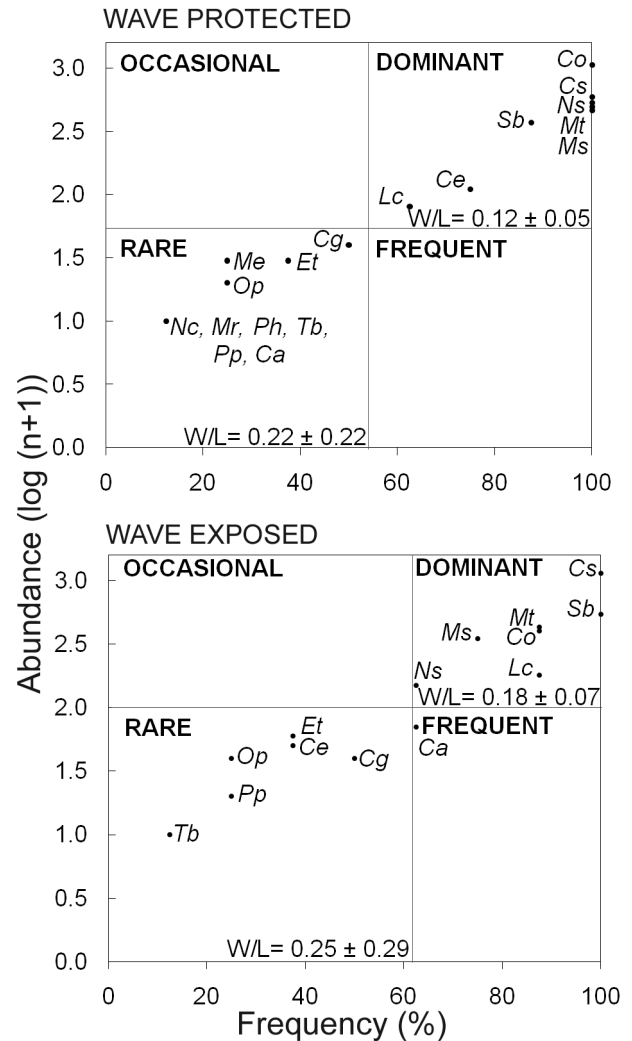

FIG. 4. – Olmsted Tukey diagram showing the frequency and abundance of the different gastropod shell species used by the hermit crab *C. californiensis* in the wave-protected and exposed sites. W/L, mean shield length/shell weight ration of all the shells grouped into each category (±SE). *Cg, Cantharus gemmatus*; *Cs, Cantharus sanguinolentus*; *Ca, Cerithium maculosum*; *Ce, Cerithium menkei*; *Co, Columbella* sp.; *Et, Engina tabogaensis*; *Lc, Leucozonia cerata*; *Me, Mitra lens*; *Mr, Mitra tristis*; *Ms, Mancinella speciosa*; *Mt, Mancinella triangularis*; *Nc, Natica chemnitzii*; *Ns, Nerita scabricosta*; *Op, Opeastosoma pseudodon*; *Ph, Phos* sp.; *Pp, Plicopurpura pansa*; *Sb, Stramonita biserialis*; *Tb, Turritella banksi*.

cupied more in the wave-protected than in the exposed sites ($\chi^2_{(0.05,1)}=21.2$, $P<0.001$; $\chi^2_{(0.05,1)}=26.1$, $P<0.001$), whereas *C. sanguinolentus* and *S. biserialis* were occupied more in the exposed than in the protected sites ($\chi^2_{(0.05,1)}=17.5$, $P<0.001$; $\chi^2_{(0.05,1)}=4.3$, $P<0.05$; Fig. 2).

The shell weight/shield length ratio showed that the hermit crabs in the wave-exposed sites are likely to occupy relatively heavier shells compared with the crabs inhabiting the protected sites ($F_{(12,643)}=4.89$, $P<0.01$;

TABLE 2. – Linear regressions between shell weight and length for each shell species of both site types.

| Shell species | Regression equations | | ANCOVA | | | | |
| | Protected | Exposed | df | Slopes | | Elevations | |
				t	P	t	P
Cantharus sanguinolentus (Duclus, 1833)	y=0.101x-0.803 (R²=0.78; P< 0.01)	y=0.096x–0.561 (R²=0.57; P<0.01)	156	4.0	<0.01	6.8	<0.01
Columbella sp. Sowerby, 1832	y=0.108x-1.314 (R²=0.64; P<0.01)	y=0.092x–1.050 (R²=0.56; P<0.01)	111	3.9	<0.01	182.6	<0.01
Nerita scabricosta Lamarck, 1822	y=0.069x-0.440 (R²=0.89; P<0.01)	y=0.067x–0.359 (R²=0.76; P<0.01)	57	2.8	<0.01	76.0	0.04
Stramonita biserialis (Blainville, 1832)	y=0.132x-1.568 (R²=0.74; P<0.01)	y=0.141x–1.582 (R²=0.54; P<0.01)	83	1.4	0.16	823.0	<0.01
Mancinella triangularis (Blainville, 1832)	y=0.105x-0.861 (R²=0.74; P<0.01)	y=0.081x–0.376 (R²=0.56; P<0.01)	151	2.4	0.02	260.2	<0.01

Fig. 3). The shell weight/shield length ratio of the hermit crabs inhabiting the wave-exposed sites and occupying *C. sanguinolentus*, *Mancinella speciosa* (Valenciennes, 1832), *Mancinella triangularis* (Blainville, 1832), *S. biserialis*, and *Columbella* sp. was higher than the ratio of the hermit crabs occupying these shells in the protected sites (Student's *t*-test values are shown in Fig. 3). The slopes and elevations of the regressions between shell weight and shell length were different for both wave-action sites, except for *S. biserialis* (Table 2). The data show that the hermit crabs occupied shells that were heavier in relation to their length in the wave-exposed sites compared with the protected sites.

The Olmstead-Tukey diagrams show shells of eight species as dominant in the wave-protected sites vs. seven in the exposed sites. *Cerithium menkei* Carpenter, 1857 is shown as dominant in the protected wave-action sites and is shown as rare in the wave-exposed sites. No frequent shells were found for the protected area. Instead, *Cerithium maculosum* Kiener, 1841, a rare shell in the protected sites, is a frequent shell in the wave-exposed sites. Ten shells are shown as rare in the wave-protected sites and six in the exposed sites (Fig. 4). The mean shell weight/shield length ratio calculated for the grouped dominant shells was higher for the shells of the exposed sites than for those at the wave-protected sites ($t_{(2,614)}$=-10.2, $P<0.001$; see Olmstead-Tukey diagram in Fig. 4); this ratio was similar for the rare shells of the protected and exposed sites ($t_{(2,28)}$=-0.4; $P>0.05$). The weight/shield length ratios of the rare shells were higher than the ratios of the dominant shells of the protected and exposed-wave sites ($t_{(2,328)}$=-6.5, $P<0.001$; $t_{(2,314)}$=-3.7, $P<0.01$ respectively).

DISCUSSION

Temperature, substrate composition, and air exposure have long been recognized as major factors governing the ecology of rocky shores (Bustamante *et al.,* 1997). Our study showed no differences in any of these factors when the wave-exposed and protected sites were compared. The wave action and depth were different at the various sampling sites; therefore, these factors and others related to them, such as predation intensity, could explain our results. The gastropod assemblages in the intertidal area could also explain the hermit crab shell use. However, the intensity of the water flow generated by waves on this shore, the high mobility of these hermit crab species in the intertidal area (personal observation), and the fact that the gastropod distribution does not match the hermit crab shell occupancy, suggest that this is unlikely. For example, in this respect the shells of *Stramonita biserialis* are mainly occupied in the wave-exposed sites while the gastropods are mainly residents of the protected zone; or the shells of *Nerita scabricosta*, which are used at both the different wave-action sites (although with difference frequencies) but the gastropod is never found in sites with intense hydrodynamic action (personal ob-

servation). In addition, some shell species used by the hermit crabs in Troncones do not all come from gastropod inhabitants of rocky shores, for example *Cerithium maculosum*, *Mitra tristis* Broderip, 1836, and *Natica chemnitzii* Pfeiffer, 1840 inhabit estuaries and coastal lagoons (Keen, 1971; Landa-Jaime, 2003). Therefore, it is not likely that the gastropod assemblage explains the shell occupancy by crabs at different levels of the intertidal area.

More females were found in the wave-exposed than in the wave-protected sites. The differences in the sex distribution in the two site types reveals that the sex ratio found at a specific sampling site may not represent the overall population, but rather, it could be determined by the microhabitat conditions. Similar results have been reported for the hermit crab *Clibanarius antillensis* (Stimpson, 1859), an inhabitant of intertidal rocky pools of the Gulf of Mexico, in which although the abundance of males and females was similar considering all transects sampled, females were more abundant in the wave-exposed sites than in the protected sites (Argüelles *et al.*, 2009). Different proportions of the sexes have been reported for various hermit crab populations. For instance, females being more abundant than males has been reported for the species *Coenobita scaevola* (Forskäl, 1975; Sallam *et al.*, 2008) and *Clibanarius vittatus* (Bosc, 1802; Sant'Anna *et al.*, 2006), whereas a higher proportion of males has been reported for *Pagurus exilis* (Benedict, 1892; Terossi *et al.*, 2006) and *Paguristes calliopsis* Forest and Saint Laurent, 1968 (Biagi *et al.*, 2006). In contrast, a similar proportion of males and females has been reported for *Dardanus insignis* (De Saussure, 1858; Ayres-Peres *et al.*, 2008). Variations in the sex ratio between seasons have been reported for *Clibanarius longitarsus* (De Haan, 1849; Litulo, 2005), *C. vittatus* (Lowery and Nelson, 1988), and *Diogenes nitidimanus* Terao, 1913 (Asakura, 1995), though in our study similar sex distribution patterns were found in the different wave-action sites in March and August.

Ovigerous females were more abundant in the wave-exposed sites compared with the wave-protected sites. Similar results have been reported for several species of the hermit crab, such as *C. antillensis* (Argüelles *et al.*, 2009). The movement of ovigerous females to sites with greater hydrodynamic forces could be explained by the increased importance of evading predators when females are more vulnerable. This behaviour is shown by female spiny lobsters, which exhibit an aggregation pattern when bearing eggs (Kelly *et al.*, 1999). Thus, although the risk of dislodgement is greater in the wave-exposed sites, the risk of succumbing to predators at these sites can be lower for the intertidal species, as has been reported for the bay scallop *Argopecten irradians* (Lamarck, 1819), the hard clam *Mercenaria mercenaria* (Linnaeus, 1758; Powers and Kittinger, 2002), and the intertidal hermit crabs *Pagurus* sp.*, Clibanarius albidigitus* Nobili, 1901*, and *Calcinus obscurus* Stimpson, 1859 (Bertness, 1981b). Alterna-

tive explanations suggested for the large abundance of ovigerous hermit crabs in sites with high wave action are the better aeration of the egg masses and the more efficient dispersal of the hatching crustacean larvae at these sites (Powers and Kittinger, 2002).

The shell use differed between sexes and between the sites with different degrees of wave exposure. The distribution of the organisms in the intertidal zone may be determined by their ability to avoid being dislodged from the substrate by the lift and drag forces of the breaking waves (Lau and Martinez, 2003). The resistance to dislodgement has been positively associated with animal size in intertidal crabs (Lau and Martinez, 2003). Although in our study the size of the hermit crabs did not vary among the wave-action sites, the most occupied shell in the wave-exposed sites was *Cantharus sanguinolentus*, which was the heaviest shell in relation to the crab. In contrast, *N. scabricosta* and *Collumbella* sp. have the lightest shells and were the least occupied in the wave-exposed sites, but highly occupied in the protected sites. In addition, our data show that for almost all the shell species, hermit crabs occupy shells that are relatively heavier in the wave-exposed sites compared to when the same species is used in the protected sites. Similarly, it was found for *C. antillensis* that the shell weight and shape (shell weight/exposed surface area ratio) determine the occupancy in an intertidal gradient of breaking waves. The frequent use of the heaviest turbinate shells at sites with high hydrodynamic forces, relative to the occasional use of lighter turriculate and globular shells has been discussed as an advantage for coping with the hydrodynamic forces of the breaking waves (Argüelles *et al.*, 2009). The frequent use of heavier shells in sites subjected to greater wave action has also been reported for *Calcinus seurati* Forest, 1951 by Hahn (1998), who suggested that heavier shells may provide an advantage in sites where the water flow represents an environmental challenge. The occupancy of heavier shells in wave-exposed sites could be because the resistance to dislodgement is proportional to the net vertical force of the animal, determined by the weight minus buoyancy and lift (Martinez *et al.,* 1998; Martinez, 2001). Therefore, the advantages of occupying heavy shells in wave-exposed areas can be described in terms of hydrodynamics.

The use of shells with a higher ratio between shell weight and shield length in the wave exposed sites can be explained by hermit crabs occupying relatively larger shells for a particular hermit crab size (outsized shells) and/or by using thicker and heavier shells. The linear regressions between shell weight and shell length suggest that the hermit crabs of the wave-exposed sites occupy heavier and thicker shells than the crabs at protected sites. Contrary to our findings that hermit crabs occupy heavy shells in the wave-exposed sites, gastropods generally exhibit heavier shells or thick-shelled morphs on protected shores (Trussell, 1996; Edgell and Rochette, 2008). Polymorphism and variation in shell

thickness in intertidal gastropods has been commonly reported in the literature, where shell thickness trends to parallel the gradients of wave exposure and predation intensity (Menge, 1978; Trussell, 1996; Carlson *et al.,* 2006). Thicker-shelled morphs, which are resistant to being broken by predatory crushers (Avery and Etter, 2006), could be advantageous for gastropods and crabs at sites with high predator intensity; nevertheless, shell thickness is especially important for snails inhabiting wave-protected sites because of the large abundance of predatory gastropods in this area, which do not prey on crabs (Lam, 2002). However, for hermit crabs, the antipredatory benefit of occupying heavy shells might be counterbalanced by the higher energetic costs of locomotion, because the overall cost of moving would be higher for the more active hermit crabs than the commonly slow-moving snails (Donovan *et al.,* 1999). Therefore, whereas thicker shells can be advantageous for the survival of gastropods, heavy shells can be highly costly in terms of energy for crabs. For hermit crabs the cost of carrying a heavy shell in wave-action sites could be compensated by the hydrodynamic benefits. However, the lighter shell morphs of gastropods inhabiting wave-exposed sites could be supported by the strength needed by marine gastropods to remain attached to the substrate (Rilov *et al.,* 2004; Bromley and Heinberg, 2006), which diminishes the lift forces and decreases the relative importance of the shell weight as a hydrodynamic advantage. Nevertheless, specific functional, predatory, and hydrodynamic experiments need to be made to understand the opposing patterns of shell thickness developed by gastropods and used by hermit crabs in the intertidal zone.

The shell weight/shield length ratio values shown in the Olmsted-Tukey diagram also show that the dominant shells of the wave-exposed sites are heavier than the dominant shells of the protected sites. Moreover, the shell weight/shield length ratios of the rare shells of both wave-action sites are almost two times higher than the ratios of the dominant shells. Therefore, it seems that the lightest shells at Troncones beach are the most used by *Calcinus californiensis*. The heaviest shell species might provide advantages at sites with high wave–action though their occupancy might be energetically costly for locomotion (Herreid and Full, 1986).

The differences in shell use in the different wave-action sites were also associated with differences in shell occupancy between sexes, which can be explained by the different requirements to maximize fit. Some of these explanations are based on the advantages provided by the different shell species and their size in terms of the shell volume for egg production and body growth, manoeuvring, and the cost of locomotion (Gherardi, 1991; Osorno *et al.*, 1998). In our study, *Columbella* sp. was the shell most occupied by females, suggesting that the shell of this species could be relatively advantageous for them, especially in the wave-protected sites. This shell type is relatively

light, as shown by its weight/shield ratio (see Figure 3). It has been documented that females occupy lighter shells than males, for instance *P. exilis*, *D. insignis*, and *Clibanarius erythropus* (Latreille, 1818; Terossi *et al.*, 2006; Ayres-Peres *et al.*, 2008; Caruso and Chemello, 2009). Some authors suggest that the use of heavy shells may limit reproduction and growth in hermit crabs, for example in *C. obscurus*, *Clibanarius albidigitus* Nobili, 1901, and *Pagurus* sp. (Bertness, 1981b), *Coenobita compressus* Herbst, 1791 (Osorno *et al.*, 1998), and *C. vittatus* (Sant´Anna *et al.*, 2006). In particular, ovigerous females of *C. antillensis* occupy relatively lighter shells than males, even though their size is similar (Turra and Leite, 2004).

An alternative explanation for the high proportion of females and ovigerous females occupying *Columbella* sp. might be due to its narrow aperture. Botelho and Costa (2000) proposed that the narrow shell aperture of some shells (such as *Mitra* sp.) might be advantageous for ovigerous females because they would not be so easily preyed on by crabs that prey by inserting their chelipeds into the gastropod shells (Borjesson and Szelistowski, 1989).

Nerita scabricosta is also a relatively light shell and frequently occupied in the wave-protected sites, mainly by males. Its advantage could be that males tend to be more active than females because of their active searching for females and the manipulations during copulation (Turra, 2005). It is important to carry a light shell for manoeuvrability and the lower energetic cost of locomotion (Herreid and Full, 1986; Osorno *et al.*, 1998). This last point could also explain the higher abundance of males in the wave-protected sites, where the energetic cost of locomotion and the effort to avoid being dislodged would be lower compared to the cost of living and moving in high flow environments (Miller, 2007; Branch *et al.*, 2008). The use of globular shells by male *C. erythropus* is frequent and is associated with the large size of these shells, as males grow larger than females in this species (Caruso and Chemello, 2009). Differences in the shell-species occupation between sexes have also been reported for the semiterrestrial hermit crab *C. scaevola* (Sallam *et al.*, 2008).

Tide pools are challenging environments, regularly exposed to waves by the advance and retreat of the tides, consequently tide-pool life forms must be well adapted to the drastic environmental changes associated with tidal activity to avoid being washed away by the waves. In addition, other physical, chemical, and biological factors are modulated by the tides and waves, and interact in a complex manner to determine the distribution of the organisms in this zone. In this study, we found that the distribution of the hermit crabs, the shell-species occupancy, the weight of the shell used in relation to the crab size, the shell morph and its thickness, and the sex distribution differed between wave-protected and exposed sites. This is the first study that demonstrates that hermit crabs not only

occupy heavier shell species under high hydrodynamic action, but that hermit crabs occupy heavier and thicker shells of the same species under these conditions. Our study suggests the importance of occupying relatively heavier shells in environments exposed to wave action.

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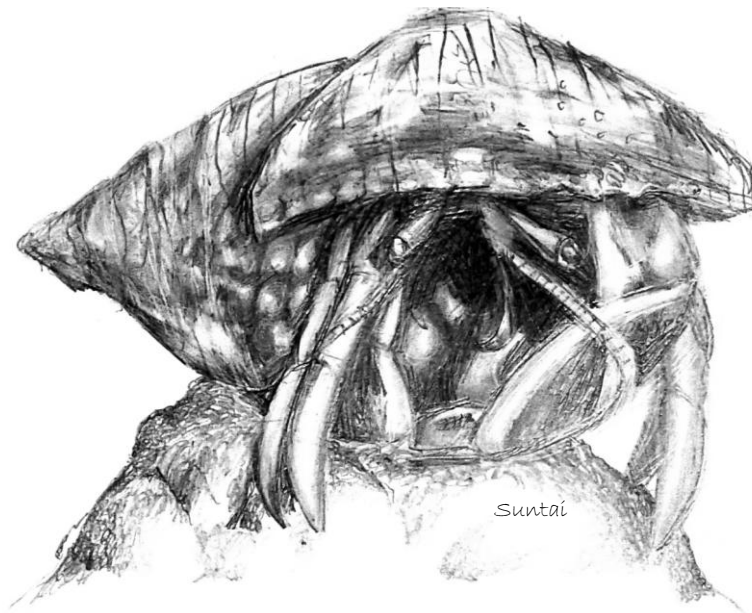
CAPÍTULO III

Preferencia por diferentes conchas de gasterópodo en

Calcinus californiensis: **comparación entre pruebas de**

selección pareada y un nuevo método de múltiples

Suntai

ORIGINAL PAPER

Shell preference in a hermit crab: comparison between a matrix of paired comparisons and a multiple-alternative experiment

Elsah Arce · Guillermina Alcaraz

Abstract The preference of the hermit crab, *Calcinus californiensis*, among six species of shells, was tested by two different experiments. The first experiment used pair-wise trials, analyzing the preference by Chi-square tests using two different constructions of the null hypothesis. One hypothesis was based on a no-preference among shell species, the second on comparing the number of crabs changing for a particular shell species when two options were given versus the changing when no options were offered. The second experiment was a multiple-alternative test based on a rank ordering of the shell preference. This method has both statistical and resource-saving advantages over the traditional pair-wise comparisons. The sequence of shell preference was similarly independent of the procedure used. The preferred shell species are heavy and might be associated with hydrodynamic advantages and with the protection against predation. The shell preference matches with the pattern of shell occupancy indicating that the shell use in nature is determined by the crab's preference. The information generated may be used for further research on shell preference as a methodological alternative.

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Introduction

The knowledge of the selection behavior is an important subject in behavioral ecology because of its adaptive value. Individuals of several species discriminate among territories and food items that favor resource acquisition (e.g., McArthur and Pianka 1966; Lemire and Himmelman 1996), females choose males that improve their reproductive fitness (e.g. Cothran 2008), and hermit crabs choose between shell sizes and species (Bertness 1980). In order to study choice behavior, adequate designs of experiments are required (Jackson and Underwood 2007).

Hermit crabs are dependent on empty gastropod shells to protect them against physical stress and predation (Bertness 1982). The pattern of shell use is known to be dependent on shell availability (Turra and Leite 2001; Argüelles-Ticó et al. 2010; Arce and Alcaraz 2011) and shell preference (Bertness 1980; Biagi et al. 2006; Mantelatto et al. 2007; Meireles et al. 2008). Hermit crabs choose shells according to species or shape (Sato and Jensen 2005; Mantelatto et al. 2007), size (Hazlett 1992), shell condition (McClintock 1985; Pechenik et al. 2001), the previous experience of the crab (Meireles et al. 2008; Alcaraz and Kruesi 2009), and the developmental and reproductive stage of the crab (Elwood et al. 1979). The shells chosen have direct effects on crab fitness; consequently, hermit crabs have a shell selection behavior based on shell characteristics that match their requirements. The advantages for hermit crabs of size, type, or species of shell may be greater clutch sizes (Bertness 1981; Elwood et al. 1995), higher growth rates (Wada et al. 1997), lower risks of predation (Hazlett 1981; Kuhlmann 1992; Angel 2000), and less environmental stress (Taylor 1981; Bulinski 2007; Argüelles et al. 2009). However, despite the advantages that shells can provide, shell occupancy in the field may not match with shell

Table 1 Previous studies of gastropod shell preference in different species of hermit crabs

Hermit crab specie	Shell type (n)	Shells of each type (n)	Total shells (n)	Crabs tested (n)	Statistic	Source
Pagurus lacertosus	4	400	1,600	200	Chi-square	Liszka and Underwood (1990)
Pagurus samuelis	3	50	750	5	–	Mesce (1993)
Pagurus hirsutiusculus		4–20	144–720	12		
Pagurus samuelis	2	422	844	211	Chi-square	Benoit et al. (1997)
Pagurus bernhardus	2	60	360	30	*G*-test	Cote et al. (1998)
Calcinus tibicen	5	270	1,350	27	*G*-test	Floeter et al. (2000)
Clibanarius antillensis				27		
Pagurus longicarpus	2	100	200	50	Binomial test	Pechenik and Lewis (2000)
Calcinus latens	5	149–745	745–3,725	140	Chi-square	Shih and Mok (2000)
Calcinus tibicen	3	1,040	3,120	104	Chi-square	Garcia and Mantelatto (2001)
Pagurus longicarpus	2	80	160	40	Fisher's exact test	Pechenik et al. (2001)
Clibanarius antillensis	5	An abundant supply of different sizes of shells		40	*G*-test	Turra and Leite (2002)
Clibanarius sclopetarius						
Clibanarius vittatus						
Pagurus criniticornis	3	20	60	660	*G*-test	Turra and Leite (2003)
Paguristes tortugae	6	4,030	24,180	403	Chi-square	Dominciano and Mantelatto (2004)
Pagurus longicarpus	2	34	68	17	Chi-square	Gravel et al. (2004)
Calcinus tubularis	2	200	400	100	*G*-test	Gherardi (2004)
Pagurus longicarpus	2	40	80	20	Chi-square	Li and Pechenik (2004)
Pagurus hartae	3	84	252	21	Chi-square	Sato and Jensen (2005)
Loxopagurus loxochelis	2	750	1,500	75	Chi-square	Biagi et al. (2006)
Pagurus granosimanus	3	600	1,800	120	Chi-square	Bulinski (2007)
Pagurus exilis	3	685	2,055	137	Chi-square	Mantelatto et al. (2007)
Pagurus criniticornis	2	600	1,200	60	Chi-square	Meireles et al. (2008)
Pagurus middendorffi	2	20	1,080	27	Chi-square	Oba et al. (2008)
Pagurus brachiomastus			1,040	26		
Calcinus californiensis	2	150	300	50	Chi-square	Alcaraz and Kruesi (2009)
Pagurus brevidactylus	3	3,600	10,800	120	Chi-square	Dominciano et al. (2009)
Pagurus lacertosus						
Calcinus latens	4	50	200	50	Chi-square	Ismail (2010)
Clibanarius signatus						
Calcinus californiensis	6	310	1,860	360	Chi-square Kendall's	Arce and Alcaraz (this study)
	6	42	252	14		

preference because of the low availability of suitable shells. A goal of our study is thus to determine whether the shell occupancy at Playa Troncones, Guerrero, Mexico, can be explained by means of shell preference.

Shell selection has been investigated for several species of hermit crabs. At least 24 studies published in the past 30 years estimated shell selection through pair-wise trials (comparing shell species or types in pairs, matching them one-on-one; Table 1). Hermit crabs can occupy the shells of many gastropod species in the field, so it can be demanding and time-consuming to establish shell preference by pair-wise comparison tests, since these generate a large matrix of shell comparisons and require a large sample size, huge numbers of empty shells, multiple trials, and additional criteria to express hierarchical preference.

In our study, two different shell-choice experiments were made using *Calcinus californiensis* Bouvier, 1898, a common, but poorly studied, inhabitant on the rocky shores of the northern and southern Mexican Pacific coast (Poupin and Bouchard 2006). The first experiment used pair-wise trials, analyzing the preference for six shell species by a Chi-square test (X^2), by using a traditional construction of the null hypothesis (1:1 ratio), but also by using the analysis proposed by Liszka and Underwood (1990), which

compares the number of crabs changing to a particular shell type when options were given against the number of crabs changing when no options were offered. The second experiment is a novel procedure based on the rank ordering of the shell selection that allows the setting of a sequential and hierarchical level of preference among multiple alternatives. In both shell-choice experiments, the six shell species most commonly occupied by the hermit crab *C. californiensis* at Playa Troncones (Arce and Alcaraz 2011) were tested.

Materials and methods

Hermit crabs were collected by hand from rocky intertidal pools at Playa Troncones, Guerrero, Mexico (17°47′16″N; 101°44′17″W) in 2008. Only the males of hermit crabs found in the six shell species used in the study [*Cantharus sanguinolentus* (Duclus, 1833), *Columbella fuscata* Sowerby, 1832, *Columbella* sp. Sowerby, 1832, *Nerita scabricosta* Lamarck, 1822, *Mancinella triangularis* (Blainville, 1832), and *Stramonita biserialis* (Blainville, 1832)] and occupying shells without evident damage were used for the trials. The crabs were taken to the laboratory and maintained in individual containers to avoid shell exchange. Each container was covered with a mesh and submerged in a 20-L tank. The crabs were acclimated under a 12-h light:12-h dark regime, with dissolved oxygen at 6.3 ± 0.2 mg/L, a salinity of 35 psu, and a temperature of $28 \pm 1°C$. They were fed on pellets (New Spectrum) once a day. In all the experiments, the hermit crabs were removed from the shell occupied by heating the apex of the shell (Kellogg 1977). The hermit crabs were measured for shield length (SL) with a digital caliper (± 0.1 mm) and were weighed (M) on a plate balance (OHAUS, ± 0.1 g). Shells were weighed (ShM) and measured for shell length (ShL), width (ShW), and aperture (length, ShAL; width, ShAW). We used crabs within a small size range to test the preference for six species, because not all shells were available in all sizes (Arce and Alcaraz 2011). The size range of hermit crabs varied between 0.05 and 0.25 g (4.9–6.6 mm SL). In all cases, the experiments were made 2 weeks after doing the initial procedures, except in the shell-size experiment, which procedure is described below. On completion of the trials, all of the hermit crabs were returned to the sea.

Shell-size preference

Crabs remained 24 h before the start of the experiment in individual water containers (0.01 L) with aerated and temperature-controlled seawater. Twenty hermit crabs were then placed naked in a 20-L glass tank with about 200 empty shells of one species of various sizes and left there for 24 h under the same conditions as described above. The shell that the hermit crab occupied after the 24 h period was considered to be the preferred shell, because after this time most individuals stop changing shells (see e.g. Borjesson and Szelistowski 1989). The hermit crabs were again removed from the chosen shells by heating the apex of the shell and measured for shield length and weight. The shells were weighed and measured as before. Morphometric relationships between crabs and shells were established by regression analyses using a simple linear regression where y = shell size (ShM, ShL, ShW, ShAL, or ShAW) and x = hermit crab size (SL or M). The equations that best fit the relationship between the hermit crab and shell size were used to determine the shell-size preference for each shell species. The shell-size experiments were then run separately for each of the six shell species tested.

Shell preference by the traditional procedure

The shell preference of *C. californiensis* for the six species was tested by pair-wise choice trials. The hermit crabs were tested 2 weeks after their collection in the shell they were occupying in the field (Dominciano et al. 2009). Half of the hermit crabs ($n = 10$) started the experiment occupying one of the shells tested and the other half of crabs ($n = 10$) another shell. Each crab was placed in an individual 0.9-L plastic container ($15 \times 12 \times 5$ cm) and left for 1 h before the start of the experiment. The shell initially occupied by each crab was marked with a small dot for purposes of making another analysis described further below. Shells were offered in paired-species combination, placing three shells of each species (six shells in total) randomly in the container. The size of the shells offered was established in accordance with the shell-size preference experiment previously described, assuming that an adequate size is within 10% of the preferred size. After 24 h, the shell species occupied was recorded and considered as the preferred shell. The experiments used 20 hermit crabs for each pair combination for the six shell species tested (15 pair trials; 1,800 empty shells and 300 crabs tested). Each crab was tested only once. The shell choice was analyzed by Chi-square tests, where the construction of the null hypothesis was based on a no-preference between shell species (Zar 2010), predicting that if crabs did not prefer either of the two shell species, they would occupy both shell species in equal proportions when these were presented in pairs. The sequence of preference was established as a function of the association ($P < 0.05$) or random association ($P > 0.05$) between two shell species (Chi-square) following the most parsimonious arrangement in the sequence of selection, for example, if no association was found between two types of shell A and B ($P > 0.05$), nor between B and C ($P > 0.05$),

but A was preferred over C ($P < 0.05$), then the sequence would be A ≈ B ≈ C.

Shell preference by the Liszka and Underwood procedure

The data obtained through the traditional procedure and from these additional experiments (alone experiment) were used to estimate the shell preference by the Liszka and Underwood procedure (1990). The experiments were made as described for the traditional procedure. As before, the hermit crabs started the experiment occupying the same shell in which they were collected in the field. Then, individual hermit crabs were presented with six shells of the same species they were occupying (alone experiment; Dominciano et al. 2009). Ten hermit crabs were tested with each of the six species of shell (6 alone experiments; 60 crabs tested). A small painted mark was placed on the shell occupied at the start of the experiment to count the hermit crabs that changed from the shell initially occupied to a different shell. The number of hermit crabs changing from the initially occupied shell to a different shell when presented alone was compared with the numbers changing to a different shell when these were presented in species pairs (simultaneously; Liszka and Underwood 1990; Dominciano et al. 2009). The null hypothesis or the assumption that no preference exists was tested by Chi-square tests. The sequence of preference was established as before as a function of the association or the random association between two shell species following the most parsimonious arrangement. The complete procedure to estimate shell preference by the Liszka and Underwood (1990) method required 360 crabs (300 for the traditional procedure and 60 for the "alone experiments").

Shell preference with multiple-alternative

Preferences for the six shell species were evaluated through a rank ordering procedure. The trials took place in 0.9-L plastic containers with flowing seawater. Three of each of the six shell species (a total of 18 shells) were given to each individual hermit crab. The size of the shells offered was established in accordance with the shell-size preference experiment previously described. The hermit crabs started the experiment occupying the same shell in which they were collected in the field. To force the crab to leave this shell and change to a different shell, a hair clamp (customary hair clip made of resin; 1.6 g) was attached to the occupied shell. The hair clamp increases the shell weight, changes the center of mass of the shell altering the locomotive maneuvering, and forces the crab to choose and occupy another. Twenty-four hours after the start of the experiment, the shell occupied by the crab was identified; this first shell species chosen was assumed

to be preferred over the remaining five, and thus, it was ranked as number one (first choice). The remaining two shells of this species were removed from the experimental tank, and again, a hair clamp was attached to the occupied shell to force the crab to change to a different shell species. Each crab was left for a second 24-h period, and the procedure was repeated. The second shell species occupied by the crab was ranked as number two. The empty shell with the plastic clamp attached and the two remaining shells of this second species were removed from the tank, and the plastic clamp was attached to the shell now occupied to force the crab to change to a third shell species. The procedure was repeated until a rank had been assigned to each of the six shell species. This procedure established a hierarchical value for each shell species in terms of preference. The consistency in the sequence of shell choice was analyzed by the rank ordering of shell choice in 14 hermit crabs. The shell species were ranked for preference assigning one to the first species chosen and six to the last species. Ranks were analyzed by Kendall's coefficient of concordance, a procedure commonly used to rank total scores in a testing sequence of choice and consistency of animal performance (Briffa et al. 2008; Durbach 2009). The analysis was made using SPSS (version 13.0 for Windows). This procedure required 14 hermit crabs and 252 empty shells.

Results

Shell-size preference

Suitable associations between hermit crab size and the shell-size preference were found. The measurements of hermit crab and shell showing the best association varied among shell species (Table 2). In general, the weights of the shell and the hermit crab mass were strongly correlated, although correlations between other crab and shell measurements were also observed. The lowest correlation coefficients were for the *Columbella* sp. for all crab and shell measurements (Table 2).

Shell preference by the traditional procedure

Analysis of the shell preference through the traditional procedure (considering a 1:1 ratio in the construction of the null hypothesis) shows that *C. californiensis* selects *S. biserialis* more than the other shell species when presented in a pair-wise combination, except when it was paired with *C. sanguinolentus*, in which case the crab showed no preference between the two shell species. The sequence of the shell preference was *S. biserialis* ≈ *C. sanguinolentus* ≈ *M. triangularis* ≈ *N. scabricosta* >
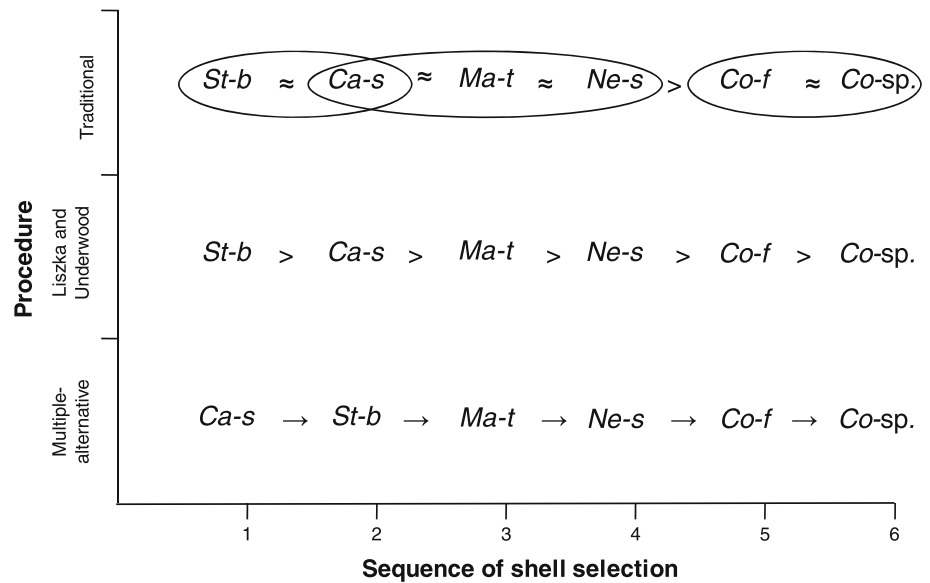
Table 2 Regression equations for chosen shell size

Shell species	Relationship	Linear equation $y = ax + b$	R^2	Range of shell-size used
C. sanguinolentus	ShM × SL	ShM = 0.35 SL − 1.07	0.98*	0.60–1.1 g
C. fuscata	ShW × SL	ShW = 1.56 SL + 1.81	0.97*	9.1–12.3 mm
Columbella sp.	ShAW × M	ShAW = 6.96 M + 1.54	0.61*	1.9–3.2 mm
M. triangularis	ShM × M	ShM = 11.78 M − 0.27	0.94*	0.4–1.6 g
N. scabricosta	ShM × M	ShM = 2.98 M + 0.16	0.96*	0.3–0.9 g
S. biserialis	ShM × M	ShM = 8.05 M − 0.22	0.90*	0.1–1.1 g

R^2 correlation coefficient, *ShM* shell mass, *ShW* shell width, *ShAW* shell aperture width, *SL* shield length, *M* hermit crab mass

* $P < 0.001$

Fig. 1 Sequence of shell selection by the hermit crab *C. californiensis* in different choice trials where "≈" means no preference between shells ($P > 0.05$), ">" indicates a preference ($P < 0.05$), and "→" shows the sequence of shell selection. The numbers 1–6 indicate the decreasing order for preference for the six shell species tested. Homogeneous groups (showing no significant difference, $P > 0.05$) are indicated for the traditional procedure

C. fuscata ≈ *Columbella* sp. (where "≈" means no significant difference in preference between shells, $P > 0.05$, and ">" indicates a preference, $P < 0.05$; Fig. 1).

Shell preference by the Liszka and Underwood procedure

Following this procedure, *S. biserialis* was the shell species chosen with the highest frequency. The decreasing sequence of preference was *S. biserialis* > *C. sanguinolentus* > *M. triangularis* > *N. scabricosta* > *C. fuscata* > *Columbella* sp. ($P < 0.05$; Fig. 1).
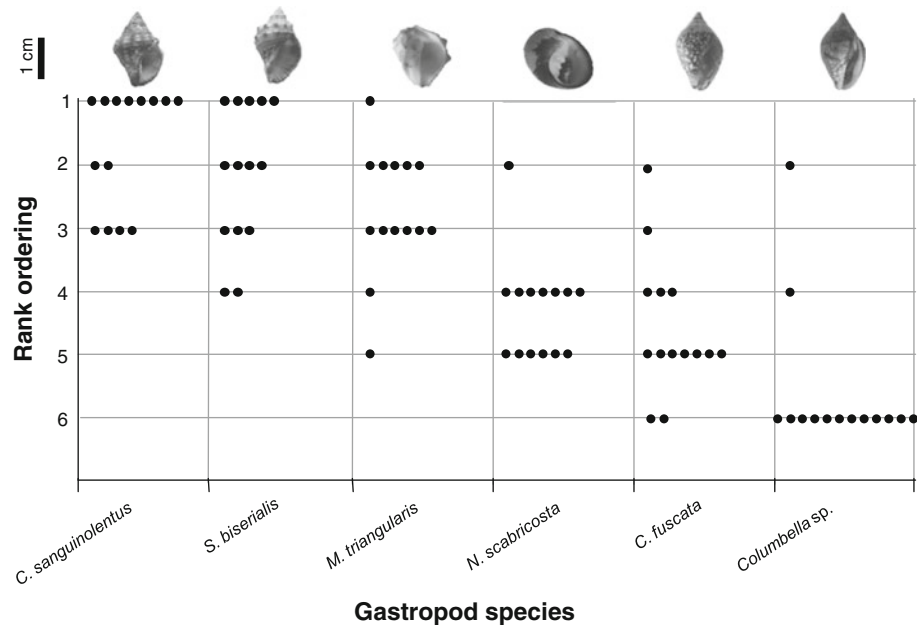
Shell preference with multiple-alternative

Every hermit crab changed to a different shell species when a plastic clamp was attached to the shell it occupied. The sequence of shell preference among hermit crabs was significantly consistent ($W_{(5,14)} = 0.67$, $P < 0.001$). *Calcinus californiensis* established a hierarchy among shell species with the decreasing sequence of preference *C. sanguinolentus* → *S. biserialis* → *M. triangularis* → *N. scabricosta* → *C. fuscata* → *Columbella* sp. (Figs. 1, 2).

Discussion

The knowledge of preference for shells is essential to understand the interactions of the hermit crab and the shell-use pattern in the wild. The sequence in the preference of *C. californiensis* matched with the shell occupancy at Playa Troncones (Arce and Alcaraz 2011), which shows that males of this species have a clear shell preference, also seen in nature. The match between shell preference and the pattern of shell occupancy in the wild indicates that the shell use in nature is determined by the preference of the crab and modulated by shell availability. That the shell use and preference match could indicate that shell choice in the hermit crab might be determined by previous experience, which in turn is influenced by shell availability (Turra and Leite 2003; Alcaraz and Kruesi 2009). The shell preference of *C. californiensis* could be linked to the shell availability, as has been suggested by Turra and Leite (2003), which showed that the selective response could be a positive relationship with the most abundant resources. The literature shows contrasting results about shell occupancy and preference. Some studies show a positive association between

Fig. 2 Consistency of the sequence of shell preference ($n = 14$ hermit crabs). *Points* show the number of times each shell was chosen as the first to sixth option when the six shell species were presented simultaneously

shell use and preference (Gherardi 1990; Siu and Lee 1992), whereas others show a discrepancy between these (Dominciano et al. 2009; Liszka and Underwood 1990; Garcia and Mantelatto 2001).

Although the availability of empty shells is limited, according to our field observations, shells seem to be a relatively accessible resource for the hermit crabs considering that an important part of the population uses the most preferred shell species. However, if all the shell species tested were fully available for hermit crabs in nature, it would be expected that most of the hermit crabs population would occupy *Cantharus* or *Stramonita* shells, though this does not happen (Arce and Alcaraz 2011). Instead, it seems that shell occupancy depends to some extent on shell availability, which suggests that other factors besides preference, such as competition, play an important role in shell use at Playa Troncones. Whether individuals with the highest competitive abilities or resource-holding potential (Turra and Denadai 2004) tend to occupy the preferred shell species remains to be tested.

The preferred shell species by *C. californiensis* were conic-type shells (*Cantharus*, *Mancinella*, and *Stramonita*). Shells with this architecture have been reported as the most occupied in the rocky intertidal zone in sites with high wave action (Argüelles et al. 2009). These shell species are relatively heavy compared to the less-preferred species, *Nerita* and *Columbella* (Arce and Alcaraz 2011). According to some authors, shell weight seems to be positively associated with hydrodynamic advantages in wave-exposed areas (Hahn 1998; Argüelles et al. 2009) and with a lesser predatory risk (Bertness and Cunningham 1981). The most preferred shells by *C. californiensis* are relatively heavier, thicker, and harder to fracture by shell-breaking predators

and also have a smaller aperture, which decreases the risk of peeling by insertion of the dactyl molar of some crabs (Bertness and Cunningham 1981). The preference for these shell species might therefore be associated with hydrodynamic advantages and with the protection against predation, even more because several peeling predators [*Panulirus gracilis* Streets, 1871, *P. inflatus* (Bouvier, 1895), *Arenaeus mexicanus* (Gerstaecker, 1856), and *Callinectes arcuatus* Ordway, 1863] and shell-breaking crabs (*Eriphia squamata* Stimpson, 1859) inhabit the wave-swept shores of Playa Troncones (Hendrickx 1995a, b; Campos and Lopez 1998).

In our study, the shell preference of *C. californiensis* was assessed by different procedures. Shell preference has been "traditionally" assessed by observing the choice made when an alternative is given. The preference estimated by this procedure represents a decision for one state relative to another. In those studies, the null hypothesis has been constructed from the assumption that if crabs do not prefer any shell species, they will occupy each in the same proportions (1:1; Liszka and Underwood 1990). According to Dominciano et al. (2009), the "strict preference" has to be assessed by the procedure proposed by Liszka and Underwood (1990) in which the null hypothesis of no-preference is constructed by contrasting the response of the hermit crabs given simultaneous alternatives with the response when they are presented with a single option. Similar to the findings of Dominciano et al. (2009), in our study, we found no difference in the preference if the traditional or the Liszka and Underwood method were used.

However, our results showed that the traditional procedure results in a more uncertain preference by giving fewer significant differences among pair comparisons (see Fig. 1).

In contrast, Dominciano et al. (2009) pointed out that the traditional method tends to overestimate the Chi-square values indicating the crab's preference for a particular shell that does not occur. The contrasting findings of both studies support the relevance of considering the behavior of the crab when given a single option in shell-choice test. The biological relevance of evaluating the crab's response to a single shell option is supported because the hermit crabs in the field have to evaluate the relative value of their own resource and the risk associated of moving out from their present shell to another. It would be expected that the motivation to keep a shell would increase with the quality of the shell owned (Elwood and Appel 2009).

The motivation to move to a different shell would be negatively associated with the quality of the shell used and positively related to the quality of the alternative shell, as has been reported by Elwood and Appel (2009), who found that in crabs exposed to electric shocks, the motivation to evacuate a preferred shell species is lower than the motivation to leave a less-preferred species. The relevance of the response of the crab to a single shell option is also important because by swapping to a different shell, crabs can incur survival costs by being vulnerable to predators (Briffa and Bibost 2009), as also happens in other organisms moving to a different refuge (Krause et al. 1998). The duration of leaving one and taking another shell differs considerably between shell species (unpublished data), where the longer the time, the greater the risk to be preyed on or be carried away by the waves during swapping. As a result, the decision to move to a different shell would depend on the shell occupied and the time required to swap. Therefore, the opposite results found in our alone experiments compared to those reported by Liszka and Underwood show the relevance of evaluating the crab's response to a single shell option, considering the strong dependence of the crab's behavior on the shell occupied and on the alternative shell. At least 24 studies assessing the shell preference by hermit crabs have been published since the publication of Liszka and Underwood (1990; Table 1); however, only Dominciano et al. (2009) have computed the shell preference as proposed by those authors. Our data support the use of the Liszka and Underwood procedure over the traditional one.

The slight differences in the sequence of preference established through the rank ordering compared to those found through pair-wise experiments could be attributed to differences in shell assessment in the presence of two or multiple alternatives. The number of alternatives offered may affect evaluation and response in decision making (Shapiro et al. 2008; Chen et al. 2011), considering the cognitive processes used to make choices (Schuck-Paim et al. 2004). According to Hollingshead (1996), decisions taken between multiple alternatives cause the individuals to evaluate each alternative relative to the others, leading to a more consistent information processing and a higher likelihood of making the optimum choice. In contrast, some authors suggest that the more the alternatives, the lower the accuracy of the selection process (Johnson and Payn 1985; Shapiro et al. 2008). However, the consistency of the rank ordering of shell choice suggests that the hermit crabs were able to discriminate well between shell species. The similarity of the sequence of shell choice found by using the three procedures is interesting, though the multiple-alternative procedure offers a simple way of testing consistency of rank of choice but does not directly indicate specific differences in preference between two particular shells.

There are evident advantages by using the multiple-alternative method. Firstly, this method is supported by a more powerful and robust statistics that might bring more confident results than the use of various tests to compute comparisons between pairs of shells. The analysis of all data in one step is more powerful than testing by several steps, for example ANOVA versus several Student's t tests (Zar 2010). Secondly, the sequence of preference by rank ordering can be statistically supported without additional criteria to establish the shell-preference sequence, as would be necessary when testing several choices in pair-wise experiments. A third advantage is based on the resources required. The design of pair-wise choice trials commonly considers a matrix of shell-preference comparisons that is more restricted than the variety of shells occupied in the wild, which can be partially explained because these experiments require large numbers of hermit crabs, empty shells, and experimental trials. For instance, *Pagurus exilis* (Benedict, 1892) occupy 19 shell species on the northern coast of Sao Paulo State, Brazil (Terossi et al. 2006), yet the preference for only three species from Brazil has been tested (Mantelatto et al. 2007). The matrix of preference of three shell species tested by Mantelatto et al. (2007) required 137 hermit crabs and 2,055 empty shells (see examples in Table 1). In our study, to test the shell preference for six shell species through the traditional procedure required 300 hermit crabs and 1,800 shells, whereas for the multiple alternative procedure 14 hermit crabs and 252 shells where used, finding a high statistical significance in the sequence of preference. The complexity of making pair-wise shell-choice comparisons increases with the number of shell species to be tested for sample size, empty shells required, and the number of trials. Throughout the multiple-alternative procedures, the sample size and the number of trials do not increase considerably if more shell species are tested. Instead, the increase in shell species studied exclusively increases the testing period. This method has advantages over pair-wise comparisons for time, effort, and resources required (materials, hermit crabs, and shells).

The multiple-alternative method might also have some restrictions. Some restrictions are shared with the matrices

of pair-wise comparisons, such as the size range of crabs tested depending on the shell-size availability, for example, *Columbella* does not grow larger than a 3.5-mm aperture width, which means they cannot be used by crabs larger than 0.30 g, whereas only a small proportion of *Cantharus* (as living gastropod or shell occupied by hermit crabs) fit crabs of this size. This constraint could reflect the natural situation, because the shell species that cannot be tested for preference in a particular crab size cannot be occupied by them because they are not available in nature. However, because of the different availability of shell sizes, it could be difficult to assemble the groups of shells to be tested for a particular crab size. A specific restriction to this multiple-alternative procedure is that in order to give the adequate shell size, it would be necessary to remove the crabs from their shell to measure them before testing, otherwise, it would be necessary to give several size-options that in turn would increase the number of shells required. A sensitive, functional, practical, and reproducible procedure to estimate the shell preference species or types is desired.

The information generated in this study may be used for further research on shell preference as a methodological alternative. The results of our study support the use of a multiple-alternative test to establish the sequence of shell preference in hermit crabs. Additionally, here, we suggest new procedures to force hermit crabs to leave their shell instead of heating the shell (Kellogg 1977), submerging the crabs in warm water (Sato and Jensen 2005), breaking the shell (Dowds and Elwood 1985), the use of anesthetics (Mantelatto et al. 2007), or electric shocks (Appel and Elwood 2009). An important contribution of this study is the use of the plastic clamps as a less traumatic method of forcing the crabs to change to a different shell.
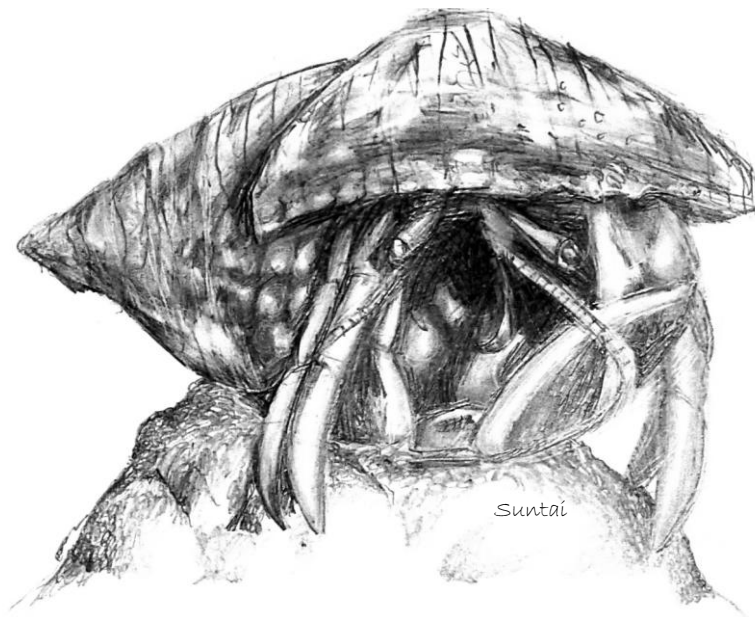
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CAPÍTULO IV

Plasticidad en la preferencia por conchas de gasterópodo

en cangrejos ermitaños y sus ventajas adaptativas

Suntai

ARTICLE

Plasticity of shell preference and its antipredatory advantages in the hermit crab *Calcinus californiensis*

Elsah Arce and Guillermina Alcaraz

Abstract: The preference of the hermit crab *Calcinus californiensis* Bouvier, 1898 among six shell species and different shell sizes was evaluated in the presence of the swimming crab *Arenaeus mexicanus* (Gerstaecker, 1856), a natural predator of this species. In a second experiment, the survival benefit of the shell choice made under predation threat was examined by exposing hermit crabs occupying three different shell species (including the most and least preferred shells of two fits) to a free swimming crab predator. The preference for shell species was similar in the absence and presence of the predator threat, although the hermit crabs choose larger shells (loose) when exposed to the predator compared with the ones chosen in its absence. The predatory experiment showed a higher survival chance for the hermit crabs occupying loose shells of the preferred shell species (*Cantharus sanguinolentus* (Duclos, 1833)). The results of this study show that the hermit crab *C. californiensis* is able to change their preference for shell size in response to a predation threat and that the change in preference confers survival benefits for hermit crabs. This study is consistent with the assumption that predation is an important selective pressure for intertidal hermit crabs.

Key words: *Calcinus californiensis*, hermit crabs, *Arenaeus mexicanus*, swimming crab, shell preference, predation threat, adaptive benefits.

Résumé : Les préférences du bernard l'ermite *Calcinus californiensis* Bouvier, 1898, entre six espèces de coquilles et différentes tailles de coquille ont été évaluées en présence du crabe de sable *Arenaeus mexicanus* (Gerstaecker, 1856), un prédateur naturel. Dans une deuxième expérience, les avantages pour la survie du choix de la coquille fait sous la menace de prédation ont été examinés en exposant des bernard l'ermite occupant trois espèces de coquilles différentes (dont deux grandeurs du type préféré et deux du type le moins prisé) à un crabe de sable prédateur libre. La préférence en ce qui concerne le type de coquille était semblable en l'absence et en présence de la menace de prédation, bien que les bernard l'ermite aient choisi des coquilles plus grandes (moins serrées) quand ils étaient exposés au prédateur qu'en l'absence du prédateur. L'expérience de prédation a montré que les bernard l'ermite occupant des coquilles moins serrées de l'espèce privilégiée (*Cantharus sanguinolentus* (Duclos, 1833)) avaient une plus grande chance de survie. Les résultats de l'étude montrent que la préférence du bernard l'ermite *C. californiensis* en ce qui concerne la taille de la coquille peut changer en réponse à une menace de prédation et que ce changement de préférence lui confère des avantages sur le plan de la survie. Cette étude concorde avec l'hypothèse selon laquelle la prédation serait une importante pression sélective pour les bernard l'ermite des milieux intertidaux. [Traduit par la Rédaction]

Mots-clés : *Calcinus californiensis*, bernard l'ermite, *Arenaeus mexicanus*, crabe de sable, préférence en matière de coquille, menace de prédation, avantages d'adaptation.

Introduction

Shelters are important resources that make prey organisms less susceptible to predation (Godin 1997). Hermit crabs occupy an empty gastropod shell as a mobile refuge that provides protection from predators, desiccation, and thermal and osmotic stresses (Reese 1969; Vance 1972*a*; Conover 1978; Bertness 1981). Shells are particularly important for protection against predation, especially in tropical environments where predation intensity is high (Bertness 1981). The protection given by different shells depends on the type of predator present. In general, shells with a high internal volume and narrow aperture offer high protection from predators that extract their prey through the shell opening (Edgell et al. 2008). Heavy shells with thick walls and aperture lips are effective in reducing predation by shell crushers (Bertness and Cunningham 1981; Avery and Etter 2006). Although hermit crabs prefer a specific size of each shell species depending on their own size (Conover 1978; Wilber 1990), during low shell availability, hermit crabs will occupy shells that are smaller than their pre-

ferred size, making them more susceptible to predation (Angel 2000).

Hermit crabs show preferences for shell species based on a number of characteristics, such as mass, volume, overall shell size, aperture size, and center of gravity (Mitchell 1976; Lively 1988). The shell preference has been shown to be plastic depending on the environmental conditions, such as oxygen levels (Côté et al. 1998), water speed (Hahn 1998), shell availability (Hazlett 1992), and predation risk (Mima et al. 2003). Predatory pressure may modify aspects of the shell choice in hermit crabs by changing the use percentage of different shell species (Mima et al. 2003). Until now, changes in the preference for different shell species has not been demonstrated, which might be attributed to the limited choices offered to crabs, such as three different species (Mima et al. 2003), intact shell vs. damaged shell (Bulinski 2007), drilled or intact shells (Pechenik and Lewis 2000), or because shell preference may be a relatively constant behavioral trait. The first goal of our study was to estimate the role of the predation threat on the shell species and size preferences of the hermit crab

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Calcinus californiensis Bouvier, 1898. To achieve this goal, we used the six shell species most commonly occupied by this hermit crab at Playa Troncones. The second goal was to test the survival benefits of the shell choice for shell species and shell sizes when made under a predation threat. Our predator of choice was the swimming crab *Arenaeus mexicanus* (Gerstaecker, 1856), which is an important predator of hermit crabs (West and Williams 1986; Kuhlmann 1992). This crab can have a negative impact on crab and mollusc populations and is a natural predator of hermit crabs at Playa Troncones. Swimming crabs are versatile predators capable of capturing rapidly moving prey and handling and pulling out molluscs and hermit crabs from their shells (Lee and Seed 1992). The hermit crab *C. californiensis* inhabits the tropical, intertidal shore at Troncones, Guerrero, Mexico. As with many tropical, intertidal rocky shores, this site is characterized by high structural and biological diversity that yields a complex competitive habitat.

Materials and methods

Collection and maintenance

The hermit crab *C. californiensis* (shield length 5.8 ± 0.8 mm; mean ± SE) and the swimming crab *A. mexicanus* (carapace width 56.9 ± 1.5 mm) were captured by hand during low tides in the intertidal zone at Troncones, Guerrero, Mexico (17°47′16″N, 101°44′17″W). Hermit crabs and swimming crabs were taken to the laboratory and maintained in individual containers for 2 weeks. The animals were kept under a natural light : dark photoperiod, with running sea water (35 PSU) and a temperature of 28 °C. The hermit crabs were fed with sinking pellets (New Spectrum, 34% crude protein) and the swimming crabs were fed fresh fish once a day.

Shell preference under a predator threat

The shell preference with a predation threat was evaluated through a multiple-alternative experiment (Arce and Alcaraz 2012). Four shells of the six shell species most occupied by *C. californiensis* at Playa Troncones (*Cantharus sanguinolentus* (Duclos, 1833), *Columbella fuscata* Sowerby I, 1832, species of the genus *Columbella* Lamarck, 1799, *Nerita scabricosta* Lamarck, 1822, *Thais* (*Mancinella*) *triangularis* (Blainville, 1832), and *Stramonita biserialis* (Blainville, 1832)) were offered to each hermit crab; one of the preferred size and one smaller (5% tighter compared with the preferred shell size), as well as two larger (5% and 10% looser). A total of 24 shells were offered to each hermit crab. The size of the shells offered was established in accordance with the shell adequacy index (SAI) proposed by Vance (1972b). This index was calculated as the ratio between the size of the hermit crab and the size of the preferred shell size as previously determined by Arce and Alcaraz (2012). These morphometric relationships between crabs and shells were established by regression analyses using a simple linear regression. The measurements that better describe the relationship between hermit crab and shells varied in the different species and were shell mass vs. shield length for *C. sanguinolentus*, shell width vs. shield length for *C. fuscata*, aperture width vs. mass for *Columbella* sp., and shell mass vs. crab mass for *T.* (*M.*) *triangularis*, *N. scabricosta*, and *S. biserialis* (Arce and Alcaraz 2012).

The swimming crabs *A. mexicanus* were fed one hermit crab *C. californiensis* 24 h before beginning the experiment (Kats and Dill 1998). The experiment was conducted in a tank (30 cm × 75 cm × 15 cm) containing a live specimen of the swimming crab physically separated from the hermit crabs by a mesh container (5 mm). Individual hermit crabs were caged in rectangular containers made of rigid and transparent mesh (9 cm × 12 cm × 8 cm). The containers were placed around and at the same distance from the swimming crab. The water was continuously aerated and circulated through the tank so that the chemical cues of the predator were in contact with all experimental hermit crabs.

After 24 h, the shell species and shell fit occupied was identified, with "rank 1" then assigned to the first shell species chosen assuming it to be preferred over the remaining shells. The three empty shells of the same species were removed from the tank. A plastic clamp was attached to the shell occupied to cause the hermit crab to change to a different shell. Twenty-four hours after attaching the clamp, the second shell species and fit was recorded and assigned to "rank 2". The empty shell with the clamp attached and the three remaining shells of this second species were removed from the tank, and the clamp was attached to the shell now occupied by the hermit crab to cause the hermit crab to change to a third shell species. This procedure was repeated until a rank had been assigned to each of the six shell species tested (Arce and Alcaraz 2012). The consistency in the sequence of shell choice was analyzed by rank ordering of shell choice of the 15 hermit crabs, and the data was then analyzed with the Kendall coefficient of concordance (Briffa et al. 2008; Zar 2010). The sequence of shell preference under a predation threat was compared with the sequence without a predation threat reported by Arce and Alcaraz (2012) through a test of concordance between groups (Z), in which $p > 0.05$ indicates no agreement between groups. Both analyses were made with SPSS version 13.0 for Windows (SPSS Inc., Chicago, Illinois, USA). Additionally, the fit of the selected shell species in the presence of a swimming crab predator was recorded and compared with the fit of the shell selected without a predation threat (Arce and Alcaraz 2012) using a χ^2 test.
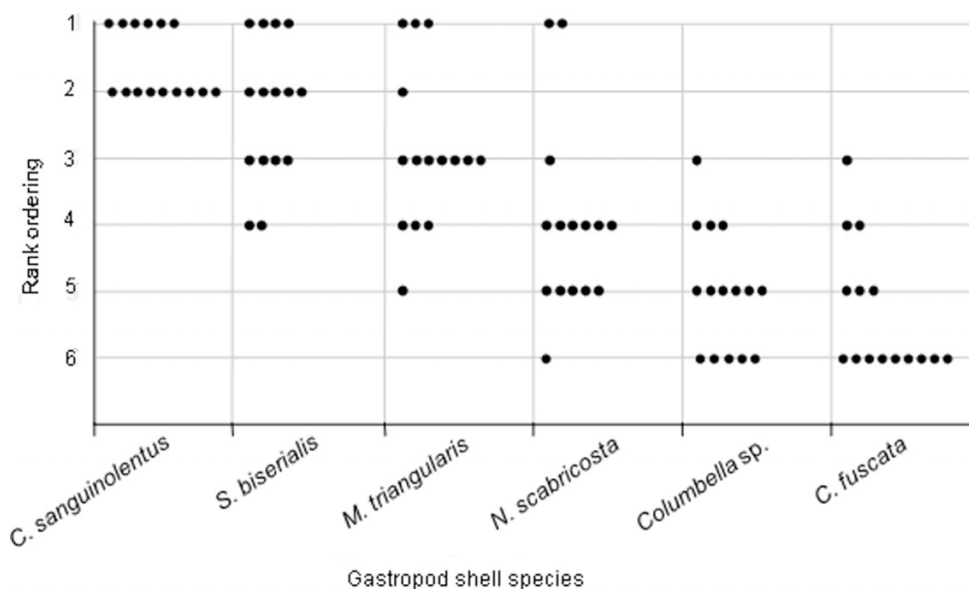
Predation experiment

To test if the change in shell choice made by the hermit crab *C. californiensis* under a predation threat confers survival advantage to the crabs, a predatory experiment was done using three shell species (*C. sanguinolentus*, *N. scabricosta*, and *C. fuscata*) and two shell fits (adequate and 10% looser). Individual swimming crabs *A. mexicanus* were placed in a tank (20 cm × 25 cm × 15 cm) and acclimated for 48 h. The feeding of the swimming crabs was suspended 48 h before the experiments (Barbeau and Scheibling 1994).

Fifteen groups of six hermit crabs of similar size were used for each trial. Hermit crabs were removed from their original shells 2 weeks before the experiment by breaking the shell (Dowds and Elwood 1985). A new shell of three different species and two different shell fits of each were assigned haphazardly to each hermit crab. The size of the adequate shells and looser shells was determined according to the shell-size preference for this species of hermit crab (Arce and Alcaraz 2012). The shells were assigned according to the SAI but corroborated by the visual adequacy index (VAI) based on the degree of retraction of the crab into the shell as a relative measure of crab and shell sizes (Abrams 1978). The SAI of the adequate shells was 1.0, which corresponded to a VAI = 3; a VAI of 3 denotes crabs that cannot retract completely into the shells, showing visible dactyls and chelipeds. The SAI of the loose shells in relation to the crab body size was 1.1, which corresponded to a VAI = 1; a VAI of 1 denotes a crab retracted entirely into its shell.

The predator was placed in the experimental tank 2 h before starting the experiment, which began when the hermit crabs with the new shell assigned were introduced haphazardly in the tank. The experiments were recorded and the videos were analyzed for the following: (*i*) the number of prey–predator encounters, with an encounter defined as a hermit crab within the area of coverage of the swimming crab (maximum distance the swimming crab covered with their cheliped extended); (*ii*) number of prey captures, with capture defined as a hermit crab held by the chelae of the swimming crab (Mascaro et al. 2003); (*iii*) the persistence time, defined as the period from the swimming crab's first physical contact with a hermit crab (start of the manipulation of the prey with the chelae) until rejection of the prey without apparent damage (Eggleston 1990); and (*iv*) handling time, which was

Fig. 1. Rank ordering showing the sequence of shell species preference by the hermit crab *Calcinus californiensis* under a swimming crab *Arenaeus mexicanus* predator threat ($n = 15$ hermit crabs).

the time from the first physical contact of the predator's chelae with the hermit crab until the predation was completed and the shell was discarded (Scarratt and Godin 1992; Mascaro and Seed 2001). Each experiment was completed when the swimming crab had not eaten a hermit crab in 72 h. Predators and hermit crabs were used only once ($n = 15$ swimming crabs, $n = 90$ hermit crabs).

The sequence of predation of hermit crabs occupying the different shell species and fits was recorded during the experiment. The lowest value (1) was assigned to the individual first eaten, and so consecutively, the highest number was assigned of individuals that were not eaten. The consistency in the sequence of predation was analyzed by the Kendall coefficient of concordance (Durbach 2009; Zar 2010). The analysis was made using SPSS version 13.0 for Windows (SPSS Inc., Chicago, Illinois, USA).

The capture probability (Pc) of the hermit crabs occupying different shell species and fit was calculated as the proportion of encounters (E) resulting in captures (C) as Pc = C/E and the probability of survival postcapture (Psc) was calculated as the proportion of hermit crabs that survive (S) and were captured as Psc = S/C (Barbeau and Scheibling 1994; Bollache et al. 2006). The number of prey–predator encounters, the probability of capture, the predator persistence time, and the handling time of the hermit crabs occupying the different shell species and fit were evaluated using Kruskal–Wallis tests. The number of hermit crabs eaten in each shell species and the shell size were evaluated using χ^2 tests. Statistical significance was set at $\alpha = 0.05$.

Results

Shell preference under predator threat
The sequence of the preference of the shell species in the presence of the predator among hermit crabs was consistent ($W_{[5,15]} = 0.66$, $p < 0.01$). The hermit crab *C. californiensis* established a hierarchy among shell species with the decreasing sequence of preference as *C. sanguinolentus* > *S. biserialis* > *T.* (*M.*) *triangularis* > *N. scabricosta* > *Columbella* sp. > *C. fuscata* (Fig. 1). The sequence of the preference of the shell species in the presence of the predator was the same as the sequence of the preference of the shell species without a predator threat, showing agreement between the two groups ($Z_{[1]} = 2.8$, $p < 0.01$).

The hermit crab *C. californiensis* chose larger shells (looser) than the preferred size in the presence of a swimming crab *A. mexicanus* compared with those shells in the absence of the predator ($\chi^2_{[1]} =$

104.9, $p < 0.001$; Fig. 2) (Arce and Alcaraz 2012). The hermit crabs exposed to a predator threat in 84 of the 90 cases selected looser shells (5%–10% greater than the preferred shell size).

Predation experiment
The number of prey–predator encounters was similar for the hermit crab independent of the shell species and shell fit occupied ($H_{[5,72]} = 2.06$, $p > 0.05$; Table 1). The probability of capture was similar for the hermit crabs occupying the different shell species and shell fit ($H_{[5,72]} = 4.43$, $p > 0.05$). The predator persistence time and the handling time for the hermit crabs occupying the different shell species and shell fit were similar ($H_{[5,29]} = 6.75$, $p > 0.05$ and $H_{[3,25]} = 5.81$, $p > 0.05$, respectively; Table 1).

The hermit crabs occupying the looser *Cantharus* and *Nerita* shells were not eaten. The hermit crabs occupying *C. sanguinolentus* shells were eaten less than the hermit crabs occupying *N. scabricosta* and *C. fuscata* shells ($\chi^2_{[2]} = 6.47$, $p < 0.05$; Fig. 3). The hermit crabs occupying the looser shells were eaten less than the hermit crabs occupying adequate shells ($\chi^2_{[1]} = 14.15$, $p < 0.001$; Fig. 3).

The sequence of predation of the hermit crabs occupying the different shell species and shell fits was consistent in the 15 trials ($W_{[5,15]} = 0.34$, $p < 0.01$; Fig. 4). The swimming crab *A. mexicanus* established a hierarchy among hermit crabs occupying shell species and shell fit with a decreasing sequence of predation of *Nerita* adequate > *Columbella* adequate > *Cantharus* adequate > *Columbella* loose > *Nerita* loose > *Cantharus* loose (Fig. 4).

Discussion

Hermit crabs choose between different shell sizes and shell species, and it is expected that their choices match their actual requirements. In highly complex and competitive environments, such as tropical rocky shores, predation plays a major role in the survival of hermit crabs (Bertness 1981). The hermit crab *C. californiensis* inhabits Troncones, where the abundance and diversity of predators is high, so it can be expected that predation will play an important role in shaping the shell choice in this species. However, the sequence of preference for the six shell species tested is similar in the presence and absence of the swimming crab *A. mexicanus* predator.

Behavior, as the most flexible phenotype, is usually recognized as an adaptive response to changing environments (Hazlett 1995), where organisms able to track environmental change are ex-

Fig. 2. Preference of the hermit crab *Calcinus californiensis* for shell sizes (fits) in six shell species in the presence and absence of a swimming crab *Arenaeus mexicanus* predator threat.
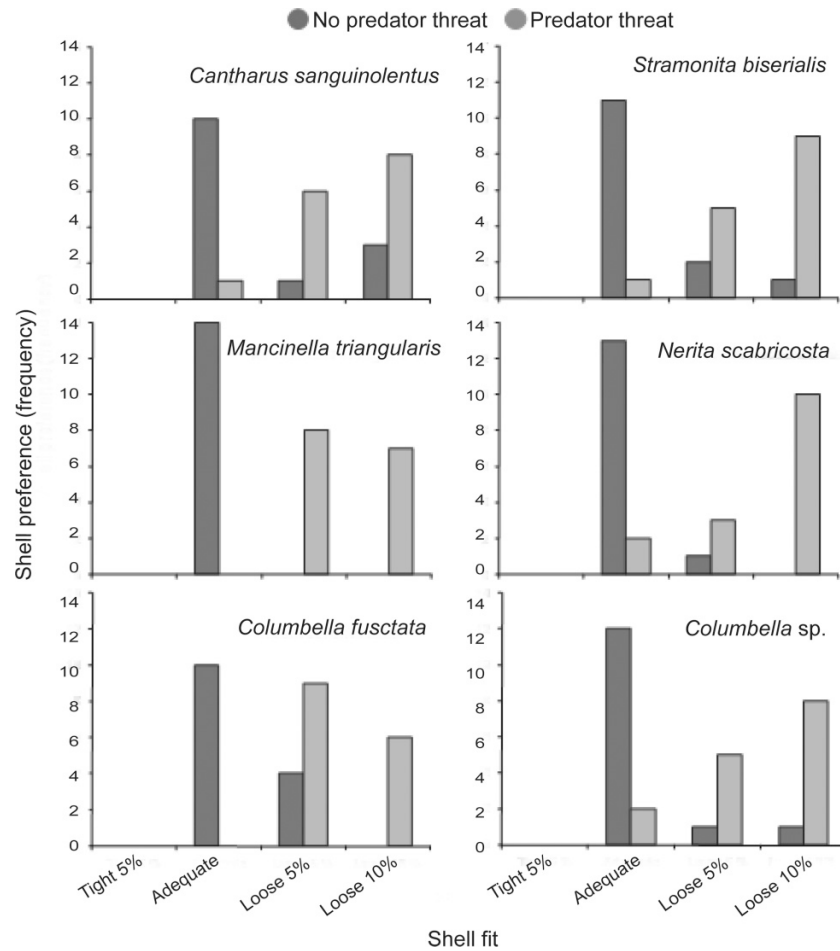

Table 1. Results of the predator–prey interactions between the swimming crab *Arenaeus mexicanus* and the hermit crab *Calcinus californiensis* occupying different shell species of adequate and looser sizes.

Shell species	Shell fit	Prey–predator encounters (number)	Predator persistence time (s)	Handling time (s)	Probability of capture	Probability of survival postcapture
Cantharus sanguinolentus	Adequate	2.2±0.5a	18±6a	1945±665a	1.0a	0.7b
	Loose	1.3±0.3a	7±1a	NE	0.9a	1.0a
Columbella fuscata and *Columbella* sp.	Adequate	2.3±0.8a	35±12a	1326±522a	0.4a	0.4b
	Loose	2.0±0.6a	25±10a	3047±2012a	0.6a	0.9a
Nerita scabricosta	Adequate	1.6±0.5a	16±10a	888±340a	1.0a	0.3b
	Loose	2.3±0.7a	8±2a	NE	0.5a	1.0a

Note: NE indicates that no crab of this treatment was eaten. Values reported are means ± SE. Different letters indicate significant differences ($p < 0.001$).

pected to be favored by selection (Gabriel 2005). However, this phenotypic plasticity is costly to produce and maintain (DeWitt et al. 1998) because carrying greater plasticity can reduce fitness and then the evolutionary outcome is biased through exhibiting an optimum phenotype more than plastic traits (Tollrian and Harvell 1999; Relyea 2004). The expression of flexible responses is favored only when animals are required to cope with changing and pressing needs (Tollrian and Harvell 1999). If the expression of a single phenotype were not costly, the organism would pay to have constitutive defenses (always present) so that the benefit of the protection could then be permanent (Tollrian and Harvell 1999). The preference for shell species by *C. californiensis* then could be a naturally selected trait favoring the probability of survival by preventing predation and could function as a constitutive defense.

The sequence of shell preference of *C. californiensis*, with and without a threat of predation, matches the sequence of shell occupancy in the field (Troncones) and with the protection conferred by the different shells (assumed by their relative mass, lip thickness, and the presence of ornaments (Vermeij 1976; Bertness 1981; Arce and Alcaraz 2011). In this study, the hermit crabs preferred relatively heavy shells with a thick lip and a broad aperture (e.g., *Cantharus sanguinolentus* and *S. biserialis*), than light shells with a thin lip and a broad or narrow aperture (e.g., *N. scabricosta* and *Columbella* sp.) (Fig. 4; for better description of the shell attributes see Arce and Alcaraz 2012). However, the adaptive value of the shell preference in *C. californiensis* is especially supported by the high survival of the hermit crabs occupying the shell of the preferred species (*C. sanguinolentus*) in the predation experiment and the lower survival of the hermit crabs occupying shells of the less

Fig. 3. Mean (+SE) number of eaten hermit crab *Calcinus californiensis* occupying different gastropod shell species and shell fits.
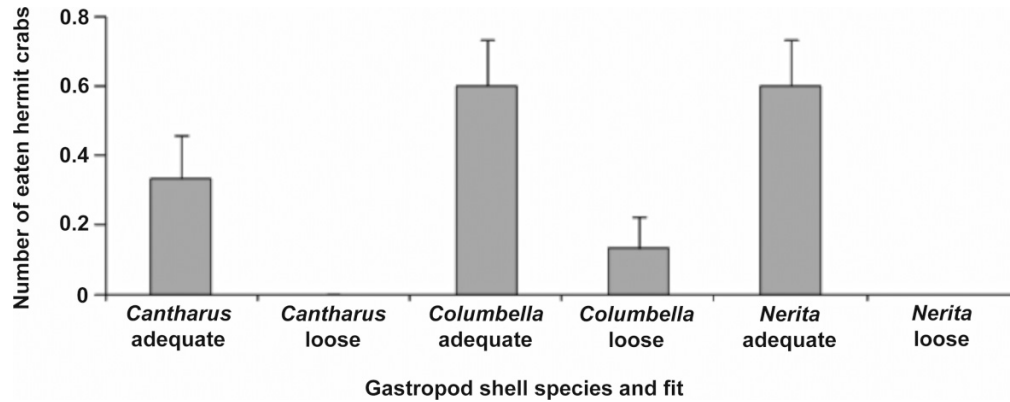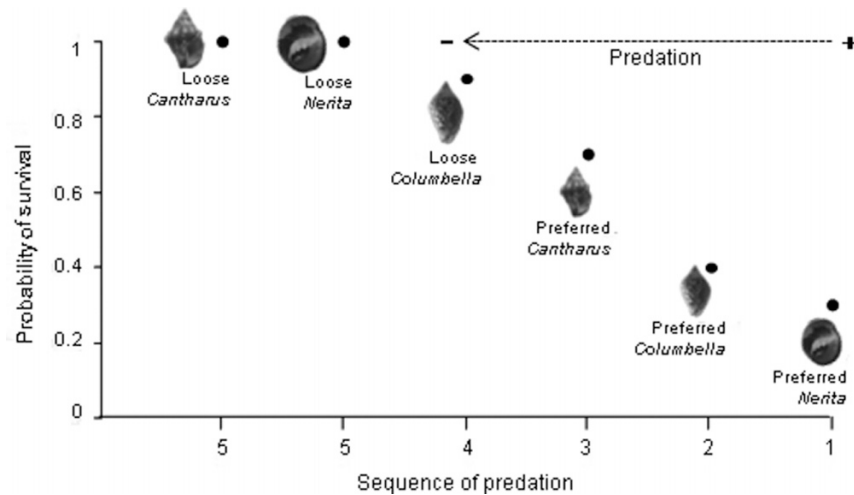

Fig. 4. Sequence of predation by the swimming crab *Arenaeus mexicanus* and survival probability of the hermit crab *Calcinus californiensis* occupying the different shell species and shell fits. The numbers 1–4 on the *x* axis indicate the decreasing order in which the hermit crabs were eaten. Hermit crabs marked with 5 were not eaten in any trials.

preferred species (*Columbella* sp.). All these data support the assumption that the shell preference of *C. californiensis* could be a steady phenotype that maximizes the probability of the survival of the hermit crab by preventing predation.

Similar to *C. californiensis*, the shell preference sequence of the hermit crab *Clibanarius lineatus* (Milne Edwards, 1848) matches the protection given by the different shell species (Borjesson and Szelistowski 1989). According to Hazlett (1995), four mechanisms can limit the behavioral plasticity in crustaceans: the limits of sensory capabilities, the morphological–biomechanical limits, the limit of learning capabilities, and the nature of the cognitive structure connecting functional categories of behavior. The lack of response of *C. californiensis* to the different shell species in the presence of the predator cannot be explained by these aspects because this hermit crab does respond to predation by choosing larger shells than the preferred size, showing that the hermit crab responds appropriately to the predator.

Although the preference for shell species is consistent within the hermit crab species, variation in shell preference has been reported as result of low oxygen levels, water flow, shell experience, and shell availability; the changes in shell choice have been shown in terms of shell quality rather than shell species. For instance, crabs choose lighter shells of the same species in hypoxic conditions (Côté et al. 1998), heavier shells in water flow (Hahn 1998) and under predatory risk (Bertness 1981), or to change the percentage of shell occupancy but not the preference for different shell species according to previous experience (Alcaraz and

Kruesi 2009). The difficulty of causing a change in a species preference was pointed out by Blackstone (1984), who noted that shell preference may not be easily modified by individual experience in some species.

Although *C. californiensis* under predatory threat does not modify its preference for shell species, this hermit crab changed the preference for shells larger than the preferred size in the presence of the crab predator. In general, predators of molluscs and hermit crabs use two different strategies to challenge the protection given by the shells: (1) crushing the shell with their mouth parts or chelae and (2) pulling out the crab by putting their chelae into the shell aperture (Bertness and Cunningham 1981). When this happens, shells allowing the hermit crab to retreat completely provide a better possibility of survival (Angel 2000). The benefits of making behavioral changes depending on the environment require assessing and selecting pressures and the fitness outcomes. The bias in the selection for larger shells under a predation threat and the high survival of the crabs occupying this shell type shows that this behavioral modification yields benefits to the hermit crabs. The ability to change the preferred shell size could be adaptive when one considers the great abundance of predators at Playa Troncones that are able to remove hermit crabs from their shells, e.g., *A. mexicanus*, *Panulirus inflatus* (Bouvier, 1895), and *Panulirus gracilis* Streets, 1871. Additionally, larger shells are more difficult to be broken (Juanes 1992). In contrast to the lack of instances in which hermit crabs change their species preference, changes in their size preference have been reported for several species of

hermit crabs, such as *Calcinus tibicen* (Herbst, 1791), *Clibanarius infraspinatus* (Hilgendorf, 1869), and *Calcinus seurati* Forest, 1951 (Hazlett 1992; Hazlett 1996; Hahn 1998).

The swimming crabs did not discriminate between hermit crabs occupying the different shell species or sizes. Apparently, this random prey selection is in disagreement with optimum foraging models which assume that decisions made when foraging maximize the individual fitness because the prey selection increases the net energy gain (Pyke 1984; Hughes 1997). However, for the same hermit crab species occupying different shell species, discrimination through chemical cues is not possible. The discrimination among shell species occupied by hermit crabs by the swimming crab *A. mexicanum* must be based on visual cues that may not be done well in intertidal shores because of the impediment of suspended sediment and constant water movement (Denny and Gaines 2007).

It is likely that the preference for shell species is consistent even when hermit crabs are exposed to different predatory pressures, probably by being a constitutive response favored for its antipredatory role. Although the relevance of behavioral plasticity on individual fitness is well recognized, the consistency of the preference for shell species can be an adaptive response that needs to be explored. In our study, the bias of the selection of the shell size for larger shells under a predation threat and the high survival of the crabs occupying larger shells shows that the hermit crab *C. californiensis* has the ability to change its behavior in response to a predation threat and that this behavioral modification yields benefits. Our study is the first to demonstrate directly the link between a change in shell preference and its adaptive benefits.

Acknowledgements

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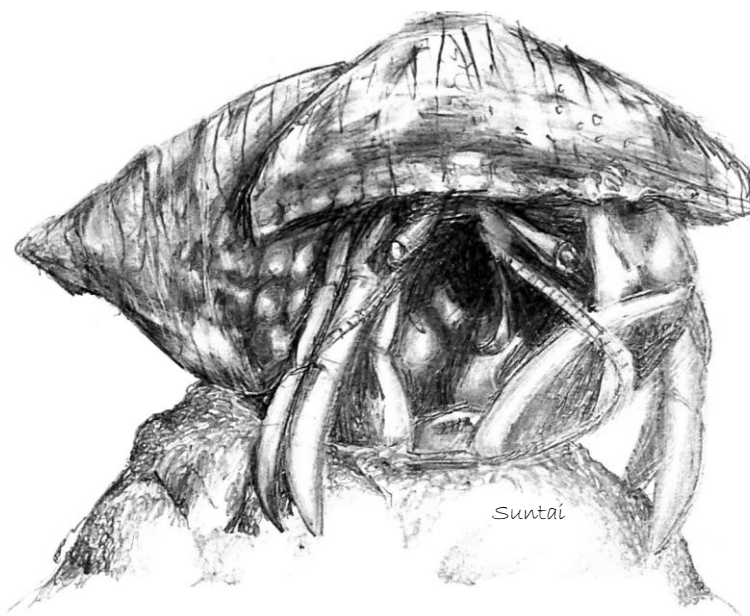
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CAPÍTULO V

DISCUSIÓN Y CONCLUSIONES GENERALES

Preferencia por diferentes conchas de gasterópodo en

***Calcinus californiensis*: plasticidad selectiva ante el riesgo**

de depredación

Suntai

Preferencia por diferentes conchas de gasterópodo en *Calcinus californiensis*: plasticidad selectiva ante el riesgo de depredación

Discusión y conclusiones

Las respuestas de preferencia por ciertos cambios en los factores ambientales (temperatura), recursos espaciales (territorio), recursos bióticos (alimento), parejas, etc. han llamado la atención desde hace muchos años. Como ocurre en el estudio de las ciencias biológicas desde el planteamiento de la teoría de la Selección Natural propuesta por Darwin, la preferencia por factores bióticos o abióticos se ha asociado a la adecuación de los individuos. Se reconoce que la adquisición de recursos no es una respuesta azarosa ni fija en la mayoría de los casos. En cambio, la adquisición de recursos es consecuencia de una conducta que se expresa como resultado de una integración histórica y actual, que involucra la selección y evolución de ciertos caracteres y se manifiesta a través de la toma de decisiones por parte de los animales en función de su ambiente (Spencer y Smith 2008; Utsumi et al. 2009). La selección de conchas de gasterópodos ha sido estudiada en muchas especies de cangrejos ermitaños y al igual que sucede en muchos casos, la literatura asume que la especie de concha preferida se asocia con ventajas en términos de adecuación (Bertness 1980; Elwood et al. 1995). Como parte importante de este estudio, determinamos que *Cantharus sanguinolentus* es la especie de concha preferida del cangrejo ermitaño *Calcinus californiensis* en la zona rocosa de Troncones (Arce y Alcaraz 2012) y a pesar de que las causas últimas que podrían explicar la preferencia por *C. sanguinolentus* en *C. californiensis* no han sido totalmente dilucidadas, el presente estudio brinda evidencias importantes, que junto con el conocimiento de la biología de esta especie de ermitaño, permiten interpretar la preferencia de esta especie de concha sobre otras también abundantes en la zona (Arce y Alcaraz 2012).

Una de las hipótesis originalmente planteadas en este estudio señalaba que como resultado de los costos y beneficios que puede brindar el ocupar diferentes especies de conchas, la preferencia por estas especies sería plástica en función del ambiente. En

particular la hipótesis de este trabajo preveía que los ermitaños seleccionarían conchas más ligeras, con paredes más delgadas, en ausencia de depredadores con fundamento en que estas conchas podrían disminuir los costos de locomoción respecto a las de mayor peso (Herreid y Full 1986; Osorno et al. 2005). En contraste, bajo condiciones de amenaza de depredación, los ermitaños ocuparían conchas de paredes gruesas y por lo tanto más pesadas, que les proporcionaran mayor protección ante los depredadores, independientemente de los costos que podrían estar asociados. Los resultados obtenidos contradicen la hipótesis planteada. El cangrejo ermitaño *C. californiensis* selecciona las conchas en la misma secuencia de preferencia en presencia y ausencia del depredador *Arenaeus mexicanus* (Arce y Alcaraz en prensa). Sin embargo, los cangrejos ermitaños seleccionaron conchas holgadas respecto a la talla de concha preferida en presencia del depredador.

La plasticidad en la expresión de caracteres ha sido reconocida desde hace muchos años como un carácter adaptativo (e.g. Baldwin 1896; West-Eberhard 1989; Robinson y Dukas 1999; Wund 2012). Entre las respuestas biológicas, la conducta es el carácter que presenta mayor plasticidad en cuanto a su expresión (Alcock 1998; Klokocovnik et al. 2012; Wund 2012). Sin embargo, la plasticidad en la preferencia por conchas en *C. californiensis* no se hizo evidente en presencia y ausencia de depredadores. Es decir, los ermitaños pagan los costos de cargar conchas pesadas aún en ausencia del estímulo. La literatura señala frecuentemente que la preferencia por conchas es un carácter plástico. Los ermitaños modifican su preferencia por conchas de la misma especie pero diferente calidad y talla en respuesta a diferentes niveles de oxígeno (Côté et al. 1998) o en función de diferentes estadios de su ciclo de vida o etapa reproductiva (Bertness 1981); sin embargo hasta donde sabemos, no existe evidencia de un cambio en la preferencia hacia conchas de gasterópodo de diferentes especies.

En general los organismos muestran dos tipos de respuesta como defensa ante condiciones bióticas o abióticas que desafían su supervivencia: defensas constitutivas y

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defensas inducibles. Las defensas constitutivas se expresan de forma permanente; es decir, se presentan independientemente de las señales ambientales por lo que se caracterizan por estar siempre listas para enfrentar el desafío (Carfagno et al. 2011). Por el contrario, las respuestas inducibles se expresan como plasticidad reversible (Gabriel 2005; Gabriel 2006) en respuesta a presiones de selección impuestas por el medio (Tollrian y Harvell 1999). De manera general, los organismos responden a las presiones ambientales utilizando tanto defensas constitutivas como inducibles, como sucede con la respuesta inmune (Hamilton et al. 2008). Sin embargo, aún cuando la conducta es un caracter muy plástico, ésta puede comportarse como un caracter constitutivo. De acuerdo a Hamilton et al. (2008), la evolución de caracteres inducibles requiere de cuatro condiciones básicas. En primera instancia se requiere que el agente ejerza una presión de selección. En este caso, *C. californiensis* habita en una playa tropical donde los depredadores son muy abundantes (Hendrickx 1995a; Hendrickx 1995b), siendo frecuente encontrar cangrejos depredando ermitaños (e.g. *A. mexicanus* y *Eriphia squamata*), por lo que los depredadores constituyen una presión selectiva importante. En segunda instancia, la señal ambiental debe ser capaz de activar la defensa. En este caso, aunque los cangrejos no modificaron la secuencia en la preferencia por conchas de gasterópodo de distintas especies, los ermitaños prefirieron conchas holgadas en presencia de un depredador (Arce y Alcaraz en prensa). Es decir, seleccionar conchas holgadas hace evidente que *C. californiensis* es capaz de detectar la señal ambiental (señales químicas del depredador). Adicionalmente otros estudios han demostrado que los ermitaños, como muchos organismos, responden a señales químicas de depredadores (Mima et al. 2003; Schoeppner y Relyea, 2005). El tercer aspecto se fundamenta en que la defensa debe de ser efectiva. En el caso de este estudio, los resultados demuestran que la probabilidad de supervivencia de *C. californiensis* es mayor cuando los ermitaños ocupan conchas holgadas (seleccionadas bajo riesgo de depredación) con lo que se demuestra que la expresión plástica de la conducta selectiva es efectiva (Arce y Alcaraz en prensa). Finalmente, la evolución de las respuestas inducibles requiere que éstas sean costosas (Tollrian y Harvell 1999; Benard y

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Fordyce 2003; Brönmark et al. 2012). Este aspecto fundamenta gran parte de la evolución y expresión de las respuestas inducibles. Las respuestas que no son costosas deberán expresarse de manera permanente, comportándose como respuestas constitutivas (Carfagno et al. 2011). En el caso de los cangrejos ermitaños, el ocupar conchas holgadas (respecto a la talla preferida) genera costos energéticos adicionales al portar conchas más grandes y por lo tanto de mayor peso (Herreid y Full 1986; Osorno et al. 2005). Las conchas holgadas dificultan el movimiento de los cangrejos ermitaños (Chávez y Alcaraz, no publicado), deprimen su tasa metabólica (Alcaraz y Kruesi 2012) y disminuyen su habilidad de combate (Cid 2012). Así, la plasticidad en la preferencia por la talla de las conchas cumple con las características que soportan la evolución de las defensas inducibles.

Sin embargo la preferencia por especies de conchas de gasterópodo de diferentes especies no se manifiesta como una respuesta plástica. Las conchas preferidas por este ermitaño como *C. sanguinolentus* y *S. biserialis* son conchas de paredes gruesas a diferencia de las conchas menos seleccionadas como *N. scabricosta* y *Columbella* sp., las cuales son conchas de paredes relativamente delgadas y más susceptibles a la fractura (Palmer 1985; Arce y Alcaraz 2012). Es decir, la secuencia en la preferencia por conchas de gasterópodo va a la par de la protección que éstas ofrecen a los ermitaños (Arce y Alcaraz 2012; Arce y Alcaraz en prensa). Al igual que en el caso de la respuesta inmune donde respuestas constitutivas se ven favorecidas bajo cargas parasitarias altas (Hamilton et al. 2008), las respuestas conductuales constitutivas deben verse favorecidas bajo fuertes presiones de depredación. *C. californiensis* habita en zonas tropicales donde la diversidad y abundancia de depredadores es muy alta (Vermeij 1977). En particular, en la zona rocosa de Troncones la presencia de depredadores como pulpos, langostas, cangrejos y peces es muy elevada (observación personal). De esta manera, es probable que la secuencia en la preferencia por conchas de gasterópodo de distintas especies pueda ser un carácter conductual constitutivo que favorezca la protección contra depredadores de

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manera permanente siendo que los beneficios de protección que la cocha preferida brinda a *C. californiensis* pueden exceder los costos asociados a ocupar conchas pesadas.

La diferencia en la expresión plástica y constitutiva de la preferencia por tallas y especie de concha podría fundamentarse en el grado de vulnerabilidad de los animales ante la presión de depredación. Los ermitaños resultaron más vulnerables a los depredadores por efecto del ajuste de las conchas que por efecto de la especie de concha ocupada. Es decir, la efectividad de la respuesta antidepredatoria al modificar la preferencia hacia conchas más holgadas sería más efectiva que la efectividad asociada a cambiar la preferencia por especie de concha de gasterópodo.

Es importante señalar que en *C. californiensis* la preferencia por las diferentes especies de conchas se ve reflejada en el patrón de ocupación de especies en el campo, siendo que las especies por las que se mostró mayor preferencia son las ocupadas con mayor frecuencia por los ermitaños (Arce y Alcaraz 2011; 2012). En este sentido, los beneficios que pueden obtener los organismos a través de la selección de conchas se ven directamente reflejados en su ambiente. Sin embargo es importante destacar que dicha selección puede darse en respuesta a la disponibilidad relativa de conchas. Es decir, si la selección se sesga hacia el recurso más abundante, la competencia por el recurso disminuye en la población (Rozenzweig 1981; Bell et al. 2009).

La expresión de la preferencia por conchas como un carácter constitutivo se evidencia también a través de los resultados de experimentos de selección de conchas en diferentes condiciones de oleaje realizados en el campo. Los resultados de dichos experimentos indican que *C. californiensis* selecciona las conchas en la misma secuencia en zonas protegidas y expuestas al oleaje. Es decir, la preferencia por conchas de gasterópodo de distintas especies tampoco se modifica en respuesta a presiones hidrodinámicas, sugiriendo una vez más que la preferencia por éstas es un carácter constitutivo y no un carácter plástico en función del ambiente (presión de depredación y estrés hidrodinámico en este caso).

Es posible referir al menos 25 trabajos en los que se determina la concha preferida por cangrejos ermitaños. En ninguno de estos casos se ha reportado un cambio en la preferencia por conchas de gasterópodo de distinta especie, aunque la literatura refiera con frecuencia el caracter plástico de la conducta selectiva. La preferencia por las seis especies de conchas más ocupadas por *C. californiensis* se expresa de manera constante, aún bajo presiones depredatorias e hidrodinámicas. No obstante, la preferencia por diferentes tallas de concha se mostró como una respuesta conductual inducible cuya expresión favoreció la supervivencia de los ermitaños en presencia de depredadores.

En el presente trabajo se demostró de forma directa que los ermitaños tienen la capacidad de cambiar su conducta selectiva al preferir conchas holgadas ante la amenaza de depredación y que esta plasticidad conductual le brinda beneficios adaptativos. Los ermitaños ocupando conchas holgadas presentan una mayor probabilidad de supervivencia ante la depredación que los ermitaños ocupando conchas de talla adecuada y hasta donde sabemos, es el primer trabajo que demuestra la relación directa entre la plasticidad en la preferencia y los beneficios adaptativos que ésta confiere. Este estudio y la literatura referente a la biología de esta especie sugieren que la secuencia en la preferencia por conchas se asocia fuertemente a la protección contra depredadores, más que a otros componentes asociados a la adecuación de los animales como la tasa metabólica, la tasa de forrajeo, la movilidad, la habilidad de combate y el crecimiento.

Finalmente, una contribución adicional importante de este trabajo es la propuesta de un método para estimar la preferencia. El método consiste en la implementación de un experimento de múltiples alternativas basado en una secuencia jerárquica de preferencia. Este procedimiento tiene ventajas estadísticas y metodológicas sobre las pruebas de comparaciones pareadas utilizadas tradicionalmente en los experimentos de preferencia en cangrejos ermitaños.

Conclusiones

La distribución de los cangrejos ermitaños en función de su talla, sexo y estado reproductivo, así como su ocupación de conchas de gasterópodo en la zona rocosa de Troncones, están asociadas a las condiciones de las diferentes zonas de la intermareal, particularmente a sitios protegidos y expuestos a la acción del oleaje.

En este estudio no sólo demostramos que los ermitaños ocupan conchas más pesadas en sitios expuestos al oleaje, adicionalmente encontramos que estos organismos ocupan conchas más pesadas de la misma especie cuando se encuentran en dichas condiciones.

Los métodos implementados en este estudio para determinar la preferencia de *Calcinus californiensis* por conchas de gasterópodo fueron novedosos y se proponen como una excelente alternativa para futuras investigaciones.

La secuencia en la preferencia por conchas de gasterópodo se mostró consistente y en el mismo orden cuando los ermitaños fueron expuestos o no ante amenaza de depredación. Adicionalmente las especies de conchas más seleccionadas en ambas condiciones parecen estar directamente relacionadas con la protección que le brindan a los portadores en términos de supervivencia ante la depredación.

La plasticidad en la preferencia por talla de concha mostrada por *C. californiensis* cuando los ermitaños se encontraban en amenaza de depredación mostró ser una respuesta adaptativa al obtener mayor probabilidad de supervivencia en conchas holgadas.

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