

Niche overlap and resource partitioning between two intertidal hermit crab species

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*The gastropod shell influences important aspects of the hermit crab's life; however, the shells are commonly a limited resource. Therefore, different hermit crab species that coexist in intertidal areas are commonly involved in intraspecific and interspecific competition for shells. We assess if differences in shell preference, exploitation ability, or competition by interference can explain the partitioning of shells between the coexisting species *Calcinus californiensis* and *Clibanarius albidigitus*. *Clibanarius* preferred shells of *Nerita funiculata* among the six gastropod shells tested, while *Calcinus* did not establish a hierarchy in shell preference. Therefore, the preference for gastropod shell species does not seem to diminish the competition for shells in the wild. *Clibanarius* identified and attended to chemical cues signalling potential sites of available shells (chemical cues of dead gastropods); *Calcinus* did not respond to these cues (competition by exploitation). However, *Calcinus* was more successful in obtaining a new shell by interspecific shell fighting than *Clibanarius*. Consequently, the use of better quality shells (intact shells) by *Calcinus* in the wild can be explained by its greater fighting ability compared with *Clibanarius*. The bias in shell distributions through dominance by shell fighting, more than by exploitation ability, has also been suggested for other hermit crab species of these genera.*

Keywords: competition, interference, niche, partitioning, gastropod shells

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INTRODUCTION

Hermit crabs are anomuran crustaceans that have a close relationship with gastropod shells, based on the protection of their abdominal exoskeleton, which lacks calcification (Hazlett, 1981). The shells protect hermit crabs from predators, mechanical damage, dehydration, high temperatures, etc. (Reese, 1969; Taylor, 1981); as a consequence, these portable homes are an indispensable resource for hermit crabs (Hazlett, 1981). The size, type and quality of the gastropod shell influence important aspects of hermit crab life, including its morphology (Turra & Leite, 2003), body growth (Markham, 1968), fecundity (Childress, 1972; Fotheringham, 1976) and survival against predators (Reese, 1969; Angel, 2000). As a consequence, the occupancy of an adequate shell confers adaptive advantages to hermit crabs (Mima *et al.*, 2003; Arce & Alcaraz, 2013).

Hermit crabs are constantly searching for shells (Spight, 1977). However, the gastropod shells are commonly a limited resource in intertidal shores (Childress, 1972; Mantelatto & García, 2000). In a limited shell environment most crabs will occupy inadequate shells, which may be of a non-preferred species, tight to the body, or of a bad quality by having epibionts or being damaged (Vance, 1972; Kellogg, 1976; Pechenik & Lewis, 2000; Bulinski, 2007).

Different mechanisms of shell distribution may occur among these anomurans. Since several hermit crab species

coexist in intertidal areas, these may involve intraspecific and interspecific competition. The theory suggests that resource partitioning is required for the coexistence of similar species (Garrett, 1960). Resource partitioning is commonly reached through differences between species that allow each of them to use specific resources more successfully, thus reducing interspecific competition (character displacement; Brown & Wilson, 1956). Several factors have been proposed to explain the coexistence of different hermit crab species based on the predictions of niche theory (Hazlett, 1981). Shell partitioning in hermit crabs is commonly associated with differences in body size (Abrams, 1980; Bertness, 1980), shell preference (Grant & Ulmer, 1974), habitat selection (Gherardi, 1990) and environmental tolerance that results in different degrees of niche overlap along the intertidal (Kellogg, 1977; Gherardi, 1990).

Competition for shells may be either indirect (exploitative) or direct (interference). Exploitative competition occurs when a crab occupies an available shell, thus taking away the opportunity for another crab to find it (Bertness, 1981a; Turra & Denadai, 2004). Interference competition occurs via aggression when one crab (the attacker) tries to evict its opponent in order to take its shell away. The ability to acquire and retain an adequate shell is assumed to be highly correlated with a crab's fitness (Bach *et al.*, 1976; Sant'Anna *et al.*, 2012).

Calcinus californiensis Bouvier, 1898 and *Clibanarius albidigitus* Nobili, 1901 inhabit the intertidal rocky shore of Troncones, Guerrero, México. As in other intertidal shores, gastropod shells are scarce in Troncones (Arce & Alcaraz, 2011). Similarly to other coexisting species of these genera (e.g. *Calcinus obscurus* Stimpson, 1859 and *Clibanarius albidigitus*; Bertness, 1980, 1981a), *Calcinus* grow larger in body size

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than *Clibanarius*, although both species overlap in smaller range sizes in the high intertidal (Ball & Haig, 1974). *Calcinus californiensis* and *C. albidigitus* occupy the same shell species within the range of body size in which they overlap in Troncones, suggesting interspecific competition for shells (Guerrero, 2015). *Calcinus californiensis* and *C. albidigitus* are the most abundant hermit crab species inhabiting the rocky shores of the Pacific coasts of México. In this study, we assess some factors that could be playing a role in the partitioning of shells within the range of body size shared by these hermit crab species. We assess and compare the sequence of preference for different gastropod shells, the ability to find empty gastropod shells through chemical signals (exploitation), and the outcome of fighting for shells between individuals of these species in order to explain shell occupancy through competition.

MATERIALS AND METHODS

Hermit crabs collection and general procedures

Hermit crabs *C. albidigitus* and *C. californiensis* were collected by hand during the ebb and flow tides in the rocky shore of Troncones, Guerrero, México. The hermit crabs were collected in the upper intertidal, in a fringe in which both species coexist according to previous studies in Troncones and other areas of the Pacific coast (Ball & Haig, 1974; Guerrero, 2015). The crabs were collected along a line parallel to the coast. The collecting sites were close to the shore (no more than 3 m from the highest tide mark). We used hermit crabs within a range size in which both species coexist; during the collection, we used the length of the shells as a predictor of the body size of the occupants (Guerrero, 2015). Water temperature and salinity were measured during each collection event.

The experiments under controlled conditions were conducted during a period when these crabs are active (0900 to 1400 h; Alcaraz & Kruesi, 2012). In the laboratory, the water temperature and salinity were maintained at 27 °C and 35‰, respectively. At the end of each phase of the study, the hermit crabs and their shells were measured and weighed and returned to their original collection site. All the analyses were conducted using Statistica 7.0.

Shell occupancy in the wild

After collection, the hermit crabs were transported to the laboratory in individual containers (0.050 l) and then were maintained submerged in water-circulation systems (50 l). All crabs were removed from their shells by heating the apex of the shell (Kellogg, 1977). The sex of the hermit crabs was determined by identifying the position of the genital pores using a stereoscopic microscope; the crabs were grouped as males, females, ovigerous females and juveniles. The gastropod shells were identified to species using keys of Morris (1974), Keen (1971) and Abbott (1968). We compared the similarity in shell species utilization pattern using the Renkonen index (Krebs, 1989; Turra & Denadai, 2004). The index of similarity in shell use between both species was calculated for the complete sample (grouping crabs of different sex or reproductive stages), and also for males only.

Crabs were weighed (plate balance, OHAUS, ± 0.1 g) and measured for shield length and chelae length (digital calliper; ± 0.01 mm). The shells were dried and weighed (± 0.1 g). The shell adequacy index (SAI) was calculated for the five of seven species occupied with higher frequency by males of *C. albidigitus* and *C. californiensis*: *Columbella* sp. Sowerby, 1832, *Nerita funiculata* Menke, 1851, *N. scabricosta* Lamarck, 1832, *Mancinella triangularis* Blainville, 1832, and *Stramonita biserialis* Blainville, 1832. The SAI was calculated according to Vance (1972), as the ratio between the mass of a hermit crab for a shell preferred size to the actual mass of the crab. The adequate crab size for a particular shell was calculated using data previously estimated (Guerrero, 2015). The SAI of males of both species (dependent variable) was compared between the crab and among the five shell species (fixed factor) by a two-way ANOVA.

Sequence of shell preference

The sequence of shell preference for gastropod shells of *Columbella* sp., *N. funiculata*, *N. scabricosta*, *M. triangularis* and *S. biserialis* was evaluated using a multiple-alternative test (Arce & Alcaraz, 2012). Individual hermit crabs were placed into a 0.5-l plastic arena submerged in aerated flowing seawater (27 °C, 35‰). Three shells of each of the five species (a total of 15 shells) were given to each hermit crab to choose. The size of the shells given to each crab was established by the results obtained from an experiment of shell-size preference conducted previously (Guerrero, 2015). The hermit crabs started the experiment occupying the same shell in which they were collected in the sea; a hair clamp was attached to the occupied shell to force the crab to leave this shell and choose another. After 24 h, the shell occupied by the crab was identified; this shell species was assumed to be the first choice and was ranked as number one. The remaining two shells of this species were removed from the arena. The hair clamp (customary hair clip made of resin; 0.53 g; Arce & Alcaraz, 2011) was attached to the chosen shell occupied by the crab to motivate the crab to swap to a shell of a different species. The crab was given 24 h to choose a new shell (second choice). The empty shell with the clamp attached and the two 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. This procedure was repeated until all the shell species were ranked (Arce & Alcaraz, 2011). Twelve hermit crabs of each species were tested. The consistency in the sequence of shell choice was analysed for each hermit crab species separately using a Kendall coefficient of concordance (Zar, 2010). The water was replaced (30% daily), and the hermit crabs were fed on commercial pellets (New Life Spectrum) once a day.

Exploitation ability

The ability of the two hermit crab species to identify and attend to potential sites of a vacant new shell was tested using chemical cues of dead gastropods (Rittschof, 1980). We collected hermit crabs *C. albidigitus* and *C. californiensis* occupying shells of *N. funiculata* (N = 66) and gastropods of *N. funiculata*. The crabs were fed just after collection and maintained with food available for 24 h in a closed water circulation system, in the same conditions as mentioned above.

We fed the crabs before testing to avoid them responding to potential food instead of to potential shells. We fed the hermit crabs on commercial pellets (New Life Spectrum); this food has shown to be palatable to this species (Alcaraz & García-Cabello, 2017), therefore we assumed the crabs were not hungry.

Chemical solutions were prepared as cues signalling gastropod predation sites. The gastropods were killed by freezing immediately after collection; the tip of a toothpick was used to keep the gastropod's operculum open. The chemical solution was prepared as suggested by Orihuela *et al.* (1992). Fifteen frozen and thawed *N. funiculata* (23 g) were placed in 100 ml of aged filtered seawater for 60 min. After this period, the gastropods were removed from the container, and the water was stirred (not filtered) and collected. The solution was maintained at ambient temperature through the day (24 h). The control (blank) solution was prepared using aged filtered seawater, which was also left for 24 h at ambient temperature. The solutions of dead gastropods and control were frozen in different small containers (0.005 l) at -10°C at least 24 h before use in the experiments (Ferrari *et al.*, 2007; 2009; Alcaraz & Arce, 2017). The solutions of chemical cues required for the specific trials were thawed immediately before testing.

The trials were conducted using a rectangular arena (36×6 cm). The arenas were marked on their inner walls, starting at the middle (central point); two additional marks (non-evident for the crab) were placed at 15 cm from the central point in both directions (at 3 cm from the end of the arena). These marks were used as criteria of the border of the arena (where the stimuli were placed).

Before the start of each trial, 1 l of fresh seawater was placed in the arena. The seawater used for the experiments was obtained from the ocean, away from rocky tide pools to minimize the effect of chemical cues from organisms living in the pools (Webster & Weissburg, 2009). Individual hermit crabs were placed in the middle of the experimental arena enclosed in a cylindrical removable PVC tube. After 1 h, 5 ml of a solution with chemical cues from dead gastropods and water control were injected at the same time at the bottom of the borders of the arena (Orihuela *et al.*, 1992; Rittschof *et al.*, 1992). The cues from dead gastropods and water control to each of the sides of the arena were randomly assigned (by the toss of a coin); the observers were blind to the type of stimulus injected at the extremes of the arena. The PVC tubes were removed 1 min after the injection of the solutions, allowing the crab to move freely in the arena. We scored the side chosen by the crab.

At the end of each trial, the water was discarded, and the arena was rinsed with abundant fresh water. The experiments were conducted using daylight; special care was taken in avoiding shading that might influence the crab's response. At the end of the experiments, the hermit crabs were removed from their shells, measured as described before, and returned to the site in which they were collected. We compared the number of crabs that reached the end of the arena where the solution of chemical cues was placed vs the number of crabs that reached the end of the arena where the control water was injected using a χ^2 test. Crabs that did not reach the end of the arena within 60 s were not considered for the analyses. Different analyses were conducted for *C. albidigitus* and *C. californiensis*.

FIGHTING ABILITY

The ability of *C. albidigitus* and *C. californiensis* to evict an individual of the same species (intraspecific shell fighting), or the other species (interspecific shell fighting) was tested through a shell-exchange experiment. We collected hermit crabs occupying shells of *N. funiculata*. The crabs were taken to the laboratory, fed after collection, and maintained for 24 h in the closed water-circulation systems (27°C , 35‰). We paired individual crabs with opponents occupying a shell of similar size (shell length). Following the protocol described by Turra & Denadai (2004), the original shell of all the hermit crabs was peeled in its aperture until the chelipeds of the crab became exposed. The shells and hermit crabs were marked with different colours using non-toxic permanent markers. Crabs were kept in their container for 48 h and fed before being tested.

Once the crabs were paired and their shells peeled as described, the crabs were maintained in individual containers (0.05 l) submerged in a recirculating water system waiting to be assigned to one of four treatment groups. The crabs were tested for fighting ability in intraspecific and interspecific competition in four treatment groups. The treatment groups of intraspecific competition were assembled by 27 pairs of crabs of *C. albidigitus* and 27 pairs of *C. californiensis*. In each of these pairs, one individual was tested occupying a suboptimal shell (shell with apertures peeled) and the other using an adequate shell (intact shell). The suboptimal shell was assigned to one of the crabs of each pair based on the toss of a coin; the adequate shell was assigned to the other crab of the pair. In the treatments of interspecific competitions, we formed 54 sized pairs of crabs consisting of one crab of *C. albidigitus* and one crab of *C. californiensis*. These pairs were randomly assigned to one of two treatment groups. One group was assembled by 27 pairs of crabs where the individuals of *C. albidigitus* occupied a suboptimal shell, and the individuals of *C. californiensis* occupied an adequate shell. The other group was assembled by 27 pairs of crabs where the crabs of *C. californiensis* occupied a suboptimal shell, and the individuals of *C. albidigitus* occupied an adequate shell.

Just before starting the experiment, the crabs assigned to use an adequate shell were given an intact shell (undamaged and of a similar size to their original), so they could move to an adequate shell. This procedure enabled that crabs tested in optimal and suboptimal shells were subjected to the same manipulative procedures (peeling; Turra & Denadai, 2004; Sant'Anna *et al.*, 2012). The contests were conducted in circular arenas 10 cm in diameter with the floor coated with sandpaper. The arenas were immersed in a large seawater recirculating container (27°C , 35‰). Initially, the hermit crabs were placed enclosed into PVC tubes in the extreme borders of the arena. After 15 min crabs were free in the arena at the same time. Hermit crabs were allowed to interact for 24 h. At the end of the experiment, the number of pairs that had exchanged their shells was recorded. The number of shell exchanges between intraspecific pairs of *Clibanarius* and *Calcinus* was compared to know the success of eviction in intraspecific encounters. We also compared the number of shell exchanges in interspecific encounters to establish the fighting success of *Clibanarius* and *Calcinus*. The number of shell evictions in the intraspecific and the interspecific encounters was compared by using different χ^2

tests, one for each case. The crabs and shells were measured as described above.

RESULTS

Shell occupancy in the wild

A total of 690 individuals were used for this part of the study with 383 *Calcinus californiensis* and 307 *Clibanarius albidigitus*. We collected 22 juveniles (6%), 214 males (56%), 42 females (11%) and 105 ovigerous females (27%) of *C. californiensis*; and 30 juveniles (10%), 207 males (67%), 41 females (13%) and 29 ovigerous females (9%) of *C. albidigitus* (Table 1). *Calcinus californiensis* occupied a total of 15 different shells and *C. albidigitus* 18 shells. Ninety per cent of both hermit crab species (616 individuals) were found occupying the same seven shell species; these shells in decreasing frequency were *N. funiculata*, *N. scabricosta*, *M. triangularis*, *Cerithium menkei*, *Columbella* sp., *Columbella fuscata* and *Stramonita biserialis* (Table 1). The gastropod shells most used by both hermit crab species were *N. funiculata* and *N. scabricosta*, with 51% of *C. californiensis* and 48% of *C. albidigitus* occupying these shells. These hermit crab species showed a high similarity in shell utilization pattern; the per cent similarity of the shell used for the overall population (including crabs of different sex and reproductive stage) was 73.7%; while the percentage of similarity of shell use for males was 72.6%. *Clibanarius* occupied more broken or damaged shells than *Calcinus* (75 and 25%, respectively; χ^2 , $P = 0.03$; Table 1).

The body size (cephalothorax length; CL) differed between the hermit crab species (two-way ANOVA, $F_{(1,609)} = 54.97$; $P < 0.001$) and between sex or reproductive stage ($F_{(3,609)} = 62.32$; $P < 0.001$). Individuals of *Calcinus* were larger (CL; mean

value $4.65 \text{ mm} \pm 1.32 \text{ SD}$) than those of *Clibanarius* ($4.22 \text{ mm} \pm 1.27 \text{ SD}$; $P < 0.001$). The males, females and ovigerous females of *Calcinus* were larger than individuals of the same sex of *Clibanarius* ($P < 0.01$). The juveniles of *Calcinus* and *Clibanarius* had similar body size ($P = 0.95$; Table 2).

The SAI was similar for males of *C. albidigitus* and *C. californiensis* ($F_{(1,327)} = 3.49$, $P = 0.06$). The SAI of both crab species varied among the shell species ($F_{(4,327)} = 2.51$, $P = 0.04$). The males of *C. albidigitus* and *C. californiensis* occupied shells of *N. funiculata*, *N. scabricosta*, *Columbella* sp. and *M. triangularis* with similar sizes ($P > 0.05$); while *C. californiensis* occupied shells of *S. biserialis* relatively larger than those used by *C. albidigitus* ($P = 0.04$).

Sequence of shell preference

Individuals of *Clibanarius albidigitus* chose between the different shell species consistently ($W_{(4,12)} = 0.53$, $P < 0.001$; average rank, $r = 0.49$). The sequence of shell preference and average rank (in parentheses) for *C. albidigitus* in decreasing order was: *N. funiculata* (1.83) > *N. scabricosta* (2.38) > *S. biserialis* (2.58) > *Columbella* sp. (3.42) > *M. triangularis* (4.79). Meanwhile, *C. californiensis* did not establish a hierarchy in shell preference among the six shell species tested ($W_{(4,13)} = 0.23$, $P < 0.001$; average rank, $r = 0.16$; Figure 1). Since *Calcinus* do not exhibit a consistent sequence of preference for these five shell species, we did not test the consensus of preference of both crabs through a concordance test.

Exploitation ability

The body size of the crabs tested for response to chemical cues of dead gastropods was similar for individuals of *Calcinus* (mean CL: $4.22 \text{ mm} \pm 0.93 \text{ SD}$) *Clibanarius* ($4.13 \text{ mm} \pm 0.98$; t -test, $P = 0.45$). Hermit crabs of *Clibanarius* attended

Table 1. Total number (N) and percentage (%) of gastropod shell species occupied by males, females, ovigerous females and juveniles of the hermit crabs *Clibanarius albidigitus* (Cli) and *Calcinus californiensis* (Ca) at Troncones, Guerrero.

Shell species	Males		Females		Ovigerous		Juveniles		Total		Total
	Ca	Cli	Ca	Cli	Ca	Cli	Ca	Cli	Ca	Cli	
<i>Nerita funiculata</i>	60	69	10	11	20	2	7	11	97 (51)	93 (48)	190
<i>Nerita scabricosta</i>	48	38	16	8	12	0	3	3	79 (62)	49 (38)	128
<i>Mancinella triangularis</i>	36	13	9	7	7	0	7	2	59 (73)	22 (27)	81
<i>Cerithium</i>	4	15	0	5	14	19	3	1	21 (34)	40 (66)	61
<i>Columbella</i> sp.	11	39	2	2	15	0	0	1	28 (40)	42 (60)	70
<i>Columbella fuscata</i>	9	8	1	2	23	0	0	0	33 (77)	10 (23)	43
<i>Stramonita biserialis</i>	20	9	4	2	1	0	1	6	26 (60)	17 (40)	43
<i>Cantharus sanguinolentus</i>	12	2	0	0	7	0	1	0	20 (91)	2 (9)	22
<i>Litorina aspera</i>	3	3	0	0	1	5	0	0	4 (33)	8 (66)	12
<i>Plicopurpura patula panza</i>	4	1	0	0	1	0	0	0	5 (83)	1 (17)	6
<i>Mancinella speciosa</i>	0	1	0	0	0	0	0	0	0	1 (100)	1
<i>Conus</i>	0	1	0	0	0	0	0	0	0	1 (100)	1
<i>Leucozonia cerata</i>	1	0	0	0	0	0	0	0	1 (100)	0	1
<i>Mitra tristis</i>	0	0	0	0	1	0	0	0	1 (100)	0	1
<i>Phos</i> sp.	1	0	0	0	2	1	0	0	3 (75)	1 (25)	4
<i>Casmaria</i> sp.	1	0	0	0	0	0	0	0	1 (100)	0	1
<i>Vermiculata frisebeya</i>	0	0	0	1	0	0	0	0	0	1 (100)	1
<i>Mitra tristis</i>	0	0	0	0	0	0	0	1	0	1 (100)	1
<i>Tegula</i> sp.	0	0	0	0	0	0	0	1	0	1 (100)	1
<i>Mitrella ocellata</i>	0	0	0	0	0	2	0	0	0	2 (100)	2
Broken or damaged shells	4	8	0	3	1	0	0	4	5 (25)	15 (75)	20
Total	214	207	42	41	105	29	22	30	383	307	690

Table 2. Body size (cephalothorax length) of males, females, ovigerous females and juveniles of *Calcinus californiensis* and *Clibanarius albidigitus* collected at Troncones, Guerrero. Mean values and standard deviation are shown.

Species/Sex	Male	Females	Ovigerous females	Juveniles
<i>Calcinus californiensis</i>	5.08 ± 1.30 (N = 187)	4.24 ± 1.08 (N = 45)	4.41 ± 1.05 (N = 45)	2.72 ± 0.62 (N = 45)
<i>Clibanarius albidigitus</i>	4.48 ± 1.10 (N = 191)	3.42 ± 0.81 (N = 37)	3.08 ± 0.38 (N = 23)	2.56 ± 0.71 (N = 20)

with higher frequency to chemical cues of dead gastropods than to the control (water; χ^2 , $P = 0.009$). However, hermit crabs of *Calcinus* attended with similar frequency to a chemical stimulus of dead gastropod and the control (χ^2 , $P = 0.86$; Figure 2).

Fighting ability

The number of shell evictions of *Clibanarius* and *Calcinus* in intraspecific fighting was similar (χ^2 , $P = 0.44$). In interspecific contests, *Clibanarius* attained fewer shell evictions as the attacker over *Calcinus* than the attackers of *Calcinus* over *Clibanarius* (χ^2 , $P = 0.04$; Figure 3).

DISCUSSION

Empty shells are generally scarce in intertidal shores (Vance, 1972); this scarcity triggers competitive interactions among individuals of the same species and between individuals of coexisting species. The theory predicts that competitive coexistence is possible due to differences in the species' utilization of resources. This study showed that *Clibanarius albidigitus* and *Calcinus californiensis* exhibit a high degree of overlap in the patterns of shell use in Troncones (similarity in shell use 73.7%). The degree of overlap is higher than that reported for other species such as *Clibanarius antillensis* Stimpson, 1859 and *Pagurus criniticornis* Dana, 1852 (52.3%; Turra &

Denadai, 2004). However, even slight differences in resources use may decrease competition and maximize the use of available resources (resource partitioning; Finke & Snyder, 2008).

The differences in resource utilization by sympatric hermit crab species are not necessarily a direct result of interspecific competition (Gherardi & Nardone, 1995). Several behavioural mechanisms can act to reduce interspecific competition for resources through differing use of the environment, which facilitates the coexistence of similar species (Pianka, 1975). Particularly, variation in the preference for specific resources can result in its partitioning (Dominciano *et al.*, 2009), as has been suggested for competition for shells in hermit crabs (Vance, 1972; Sant'Anna *et al.*, 2012). In this study, *Clibanarius* showed a sequential order of preference for the gastropod shell species most occupied in Troncones, while *Calcinus californiensis* did not prefer any of these gastropod shells over the others. Therefore in *C. albidigitus* and *C. californiensis*, the preference for gastropod shell species does not diminish the competition for shells to a similar extent as does the shell choice in *P. granosimanus* Stimpson, 1859 and *P. hirsutus* Costa, 1829. In those species, the preferred shell for one of these species is ignored by the other, this being a behaviour consistent in the ontogeny of both species (Straughan & Gosselin, 2004). However, the fact that *C. albidigitus* and *C. californiensis* do not share the same preference suggests a lower competition for specific shell species than that described for *C. obscurus* and *C. albidigitus* which share the same hierarchy of preference for shells (Bertness, 1980). The use of the preferred resources is commonly associated with benefits regarding Darwinian fitness (Block, 2005). Particularly in *C. californiensis*, as in other hermit crab species, the use of preferred shells results in high growth and survival probability (Bertness, 1981b; Alcaraz *et al.*, 2015; Alcaraz & Arce, 2017). The ability to acquire the preferred resource is assumed to be highly correlated with fitness, especially in limited environments inhabited by sympatric competitive species.

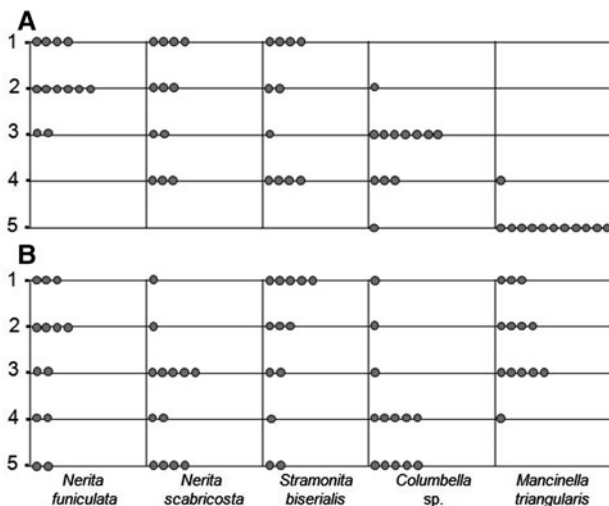


Fig. 1. Sequence of shell preference of *C. albidigitus* and *C. californiensis*. The y-axis indicates the decreasing rank order in which the shell species were chosen in different trials for *C. albidigitus* (A) and *C. californiensis* (B). The circles show the rank in which each shell was chosen, as the first to a fifth option, when the five shell species were presented simultaneously. The sequence of shell preference was significantly consistent within individuals of *C. albidigitus* (Kendall; $W_{(4,12)} = 0.53$), but it was not consistent within the individuals of *C. californiensis* ($W_{(4,13)} = 0.23$).

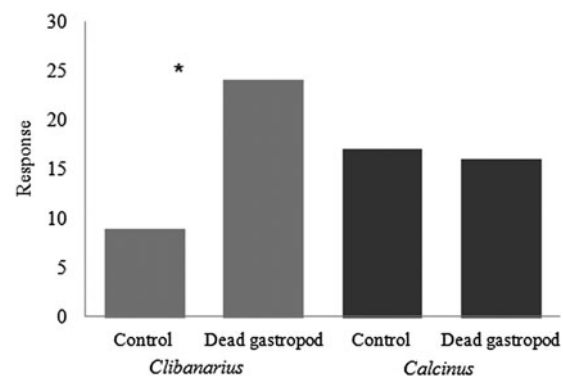


Fig. 2. Hermit crabs of *C. albidigitus* and *C. californiensis* that attended to chemical cues of dead gastropods or control. Significant differences are shown in parentheses ($P < 0.05$).

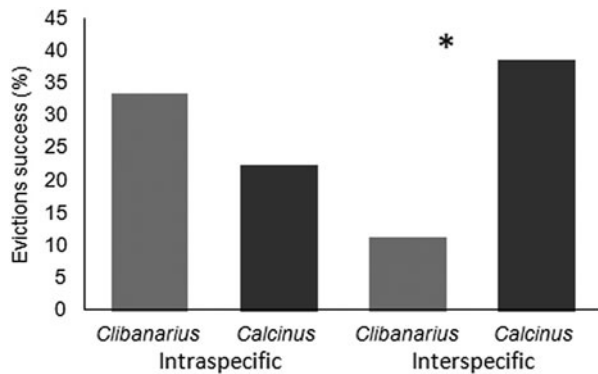


Fig. 3. Success of shell fighting estimated as a percentage of shell evictions attained by *C. albidigitus* and *C. californiensis* in intraspecific and interspecific encounters. Significant differences are shown in parentheses ($P < 0.05$).

The resource distribution among co-occurring species, sharing a preference for the same resource, is commonly explained by a bias in their competitive ability. Direct predation upon the gastropod is rare in hermit crabs (Rutherford, 1977). Therefore, hermits can obtain new shells by finding empty shells in the wild, by looking for dead gastropods and exploiting their shells, and by fighting for shells (Rittschof, 1980; Hazlett, 1981; Sant'Anna *et al.*, 2012). In this study, *C. albidigitus* identified and attended to chemical cues of dead gastropods signalling potential sites of available shells; *C. californiensis* did not respond to the chemical cues of dead gastropods. However, *C. californiensis* was more successful obtaining a new shell through interspecific shell fighting than *C. albidigitus*.

Shell distribution among different hermit crab communities has been explained through interspecific differences in exploitation and fighting ability. The use of damaged shells is a disadvantage (Pechenik & Lewis, 2000; Alcaraz & García-Cabello, 2017). Therefore, the bias in the use of broken shells by *Clibanarius* relative to *Calcinus* (75 and 25%, respectively) could be the result of interference competition, where *Calcinus* forces *Clibanarius* to occupy poor quality shells.

In several hermit crab species, exploitative competition is more important than shell fighting in determining shell distribution within the crab's community (Abrams, 1981). For instance, the disparity between the preference and the resource distribution between *Clibanarius erythropus* Latreille, 1818 and *Calcinus tubularis* Linnaeus, 1767 results from the greater ability of the former to find and utilize vacant shells in the habitat, forcing *Calcinus* to use vermetid tubes (Busato *et al.*, 1998). Meanwhile, in other hermit crab species, interference competition is the main factor controlling shell distribution between species (e.g. *C. obscurus* and *C. albidigitus*, Bertness, 1981a). In our study, the higher exploitation ability of *Clibanarius* over *Calcinus* is not reflected in the pattern of shells occupied in the wild. *Clibanarius* use its preferred shell species with similar frequency to *Calcinus*, and both species use shells of similar adequacy; however, *Clibanarius* uses more damaged shells than *Calcinus*. Therefore, it seems that fighting for shells is a major component of interspecific competition, and thus in shell distribution between *C. albidigitus* and *C. californiensis* in Troncones. The bias in shell distribution through dominance by fighting, more than by exploitation ability, has also

been suggested for other hermit crab species. For instance, *Calcinus obscurus* dominates over *C. albidigitus* in shell fighting, *Calcinus laevimanus* win fights over *Calcinus latens*, and *Clibanarius antillensis* dominates over *Pagurus criniticornis*. In those cases, the dominant species use shells of better quality, even though the subordinated species are better shell exploiters (Hazlett, 1970; Bertness, 1981a; Turra & Denadai, 2004).

The coexistence of sympatric species commonly results in a bias in shell adequacy (Bertness, 1981c). For instance in hermit crab species with an extreme overlap in shell use, such as *Calcinus tibicen* Herbst, 1791 and *Clibanarius antillensis*, one species (*C. tibicen*) may drive the other to use shells of a poorer shell size fit resulting in negative adaptive consequences for the latter (Bach *et al.*, 1976). Contrarily, in this study the coexistence of *Calcinus* and *Clibanarius* does not result in bias favouring any of the crab species regarding shell size adequacy. However, both hermit crab species have a relatively small body size in the fringe of the intertidal gradient in which they co-occur. The effects of the shell size relative to the hermit crab's size diminish as the body size decreases. For instance, the negative effects of using inadequate shells regarding metabolic competence (Alcaraz & Kruesi, 2012), muscular strength (Alcaraz & Jofre, 2017) and foraging efficiency (Alcaraz & García-Cabello, 2017) seem to be unimportant in small crabs. If the shell size is less important regarding fitness for smaller than for larger crabs, interspecific fighting to obtain a shell of an adequate size could be non-cost effective. In contrast, shell fighting seems to be important by biasing the use of less damaged shells toward individuals of *Calcinus* relative to *Clibanarius*.

Clibanarius albidigitus and *C. californiensis* inhabit the same environment but their distribution differs along the intertidal gradient, allowing wide spatial ranges where the interspecific competition is low. Similarly, *C. albidigitus* and *C. obscurus* coexist in intertidal areas of Panama; however, the latter has a distribution that mainly extends lower in the intertidal, where individuals of relatively large body size do not inhabit as high a level as that occupied by *C. albidigitus* (Ball & Haig, 1974; Abrams, 1980). Therefore, hermit crabs of the genus *Clibanarius* coexist and compete for shells interspecifically in broad ranges of their life phase. In contrast, *Calcinus* co-occur with *Clibanarius* only through their early life stages; so, when individuals reach relatively large body sizes (>0.15 g), the competition changes to be exclusively intraspecific. *Calcinus* and *Clibanarius* coexist and compete for shells in their early life stages, in which direct and indirect effects of the interspecific competition can affect future aspects their physiology and behaviour. For instance, after experiencing a period of high competition, young *Calcinus* could compensate for the negative effects of shell limitation minimizing its fitness cost, as has been described for animals exposed to limited resources and environmental stress (Metcalf & Monaghan, 2001; Wei *et al.*, 2008). The effects of interspecific competition on the experience with particular shells early in life are especially important in a crab's future morphology (Turra & Leite, 2003), development of shell-handling abilities (Hazlett, 1971) and future preference for shells (Elwood *et al.*, 1979; Hazlett, 1995). Therefore, although crabs of *Clibanarius* and *Calcinus* compete exclusively in a fringe of the intertidal, the consequences of competition could be important beyond the site in which competition takes place.

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REFERENCES

- Abbott R.T.** (1968) *Seashells of North America: a guide to field identification*. New York, NY: Western Publ. Com. Inc., 280 pp.
- Abrams P.A.** (1980) Resource partitioning and interspecific competition in a tropical hermit crab community. *Oecologia* 46, 365–379. doi: 10.1007/BF003446266.
- Abrams P.A.** (1981) Shell fighting and competition between two hermit crab species in Panama. *Oecologia* 51, 84–90. doi: 10.1007/BF00344657.
- Alcaraz G. and Arce E.** (2017) Predator discrimination in the hermit crab *Calcinus californiensis*: tight for shell breakers, loose for shell peelers. *Oikos* 126, 1299–1307. doi: 10.1111/oik.03742.
- Alcaraz G., Chávez-Solís C.E. and Kruesi K.** (2015) Mismatch between body growth and shell preference in hermit crabs is explained by protection from predators. *Hydrobiologia* 743, 151–156. doi: 10.1007/s10750-014-2029-8.
- Alcaraz G. and García-Cabello K.N.** (2017) Feeding and metabolic compensations in response to different foraging costs. *Hydrobiologia* 787, 217. doi: 10.1007/s10750-016-2965-6.
- Alcaraz G. and Jofre G.I.** (2017) Aggressiveness compensates for low muscle strength and metabolic disadvantages in shell fighting. *Behavioral Ecology and Sociobiology* 71, 87. doi: 10.1007/s00265-017-2311-7.
- Alcaraz G. and Kruesi K.** (2012) Exploring the phenotypic plasticity of standard metabolic rate and its inter-individual consistency in the hermit crab *Calcinus californiensis*. *Journal of Experimental Marine Biology and Ecology* 412, 20–26. doi: 10.1016/j.jembe.2011.10.014.
- Angel J.E.** (2000) Effects of shell fit on the biology of the hermit crab *Pagurus longicarpus* (Say). *Journal of Experimental Marine Biology and Ecology* 243, 169–184. doi: 10.1016/S0022-0981(99)00119-7.
- Arce E.U. and Alcaraz G.** (2011) Shell use by the intertidal hermit crab *Calcinus californiensis* at different levels of the intertidal zone. *Scientia Marina* 75, 121–128. doi: 10.3989/scimar.2011.75n1121.
- Arce E.U. and Alcaraz G.** (2012) Shell preference in a hermit crab: comparison between paired shell choice trials and a multiple alternatives experiment. *Marine Biology* 159, 853–862. doi: 10.1007/s00227-011-1861-x.
- Arce E.U. and Alcaraz G.** (2013) Plasticity of shell preference and its anti-predatory advantages in the hermit crab *Calcinus californiensis*. *Canadian Journal of Zoology* 91, 321–327. doi: 10.1139/cjz-2012-0310.
- Bach C., Hazlett B. and Rittschof D.** (1976) Effects of interspecific competition on fitness of the hermit crab *Clibanarius tricolor*. *Ecology* 57, 579–586. <http://www.jstor.org/stable/1936442>.
- Ball E. and Haig J.** (1974) Hermit crabs from the tropical Eastern Pacific. *Bulletin of the Southern California Academy of Science* 73, 95–104. <http://scholar.oxy.edu/scas/vol73/iss2/8>.
- Bertness M.D.** (1980) Shell preference and utilization patterns in littoral hermit crabs of the Bay of Panama. *Journal of Experimental Marine Biology and Ecology* 48, 1–16. doi: 10.1016/0022-0981(80)90002-7.
- Bertness M.D.** (1981a) Interference, exploitation, and sexual components of competition in a tropical hermit crab assemblage. *Journal of Experimental Marine Biology and Ecology* 49, 189–202. doi: 10.1016/0022-0981(81)90070-8.
- Bertness M.D.** (1981b) The influence of shell-type of hermit crab growth rate and clutch size (Decapoda, Anomura). *Crustaceana* 40, 197–205. <http://www.jstor.org/stable/20103597>.
- Bertness M.D.** (1981c) Competitive dynamics of a tropical hermit crab assemblage. *Ecology* 62, 751–761.
- Block B.A.** (2005) Physiological ecology in the 21st century: advancements in bioglogging science. *Integrative and Comparative Biology* 45, 305–320. doi: 10.1093/icb/45.2.305.
- Brown W.L. and Wilson E.O.** (1956) Character displacement. *Systematic Zoology* 5, 49–65. doi: 10.2307/2411924.
- Bulinski K.V.** (2007) Shell-selection behavior of the hermit crab *Pagurus granosimanus* in relation to isolation, competition, and predation. *Journal of Shellfish Research* 26, 233–239. doi: 10.2983/0730-8000(2007)26[233:SBOTHC]2.o.CO;2.
- Busato P., Benvenuto C. and Gherardi F.** (1998) Competitive dynamics of a Mediterranean hermit crab assemblage: the role of interference and exploitative competition for shells. *Journal of Natural History* 32, 1447–1451. doi: 10.1080/00222939800770981.
- Childress J.R.** (1972) Behavioral ecology and fitness theory in a tropical hermit crab. *Ecology* 53, 960–964. doi: 10.2307/1934316.
- Dominciano L.C.C., Sant’Anna B.S. and Turra A.** (2009) Are the preference and selection patterns of hermit crabs for gastropod shells species- or site-specific? *Journal of Experimental Marine Biology and Ecology* 378, 15–21. doi: 10.1016/j.jembe.2009.07.002.
- Elwood W., McClean A. and Webb L.** (1979) The development of shell preferences by the hermit crab *Pagurus bernhardus*. *Animal Behavior* 27, 940–946. doi: 10.1016/0003-3472(79)90032-0.
- Ferrari M.C.O., Brown G.E., Messier F. and Chivers D.P.** (2009) Threat-sensitive generalization of predator recognition by larval amphibians. *Behavioral Ecology and Sociobiology* 63, 1369–1375. doi: 10.1007/s00265-009-0779-5.
- Ferrari M.C.O., Gonzalo A., Messier F. and Chivers D.P.** (2007) Generalization of learned predator recognition: an experimental test and framework for future studies. *Proceedings of the Royal Society B* 274, 1853–1859. doi: 10.1098/rspb.2007.0297.
- Fotheringham N.** (1976) Population consequences of shell utilization by hermit crabs. *Ecology* 57, 570–578. <http://www.jstor.org/stable/1936441>.
- Finke D.L. and Snyder W.E.** (2008) Niche partitioning increases resource exploitation by diverse communities. *Science* 321, 1488–1490. doi: 10.1126/science.1160854.
- Garrett H.** (1960) The competitive exclusion principle. *Science* 131, 1292–1297. doi: 10.1126/science.131.3409.1292.
- Gherardi F.** (1990) Competition and coexistence in two Mediterranean hermit crabs, *Calcinus ornatus* (Roux) and *Clibanarius erythropus* (Latreille) (Decapoda, Anomura). *Journal of Experimental Marine Biology and Ecology* 143, 221–238. doi: 10.1016/0022-0981(90)90072-K.
- Gherardi F. and Nardone F.** (1995) The question of coexistence in hermit crabs: population ecology of a tropical intertidal assemblage. *Crustaceana* 70, 608–629. <http://www.jstor.org/stable/20105893>.
- Grant W.C. Jr and Ulmer K.M.** (1974) Shell selection and aggressive behavior in two sympatric species of hermit crabs. *Biological Bulletin* 146, 32–43. doi: 10.2307/1540395.

- Guerrero E.M.O.** (2015) *Ocupación, preferencia y competencia por conchas de gasterópodos en dos especies de cangrejos ermitaños*. Bachelor's thesis. Universidad Nacional Autónoma de México, Facultad de Ciencias, Mexico City, Mexico. 44 pp.
- Hazlett B.A.** (1970) Interspecific shell fighting in three sympatric species of hermit crabs in Hawaii. *Pacific Science* 24, 472–482. <http://hdl.handle.net/10125/6125>.
- Hazlett B.A.** (1971) Influence of rearing conditions on initial shell entering behavior of a hermit crab (Decapoda, Paguridea). *Crustaceana* 20, 167–170. <http://www.jstor.org/stable/20101773>.
- Hazlett B.A.** (1981) The behavioral ecology of hermit crabs. *Annual Review of Ecology and Systematics* 12, 1–22. <http://www.jstor.org/stable/2097103>.
- Hazlett B.A.** (1995) Behavioral plasticity in Crustacea: why not more? *Journal of Experimental Marine Biology and Ecology* 193, 57–66. doi: 10.1016/0022-0981(95)00110-7.
- Keen M.A.** (1971) *Sea shells of tropical West America*. Stanford, CA: Stanford University Press, 1064 pp.
- Kellogg C.W.** (1976) Gastropod shells: a potentially limiting resource for hermit crabs. *Journal of Experimental Marine Biology and Ecology* 22, 101–111. doi: 10.1016/0022-0981(76)90112-X.
- Kellogg C.W.** (1977) Coexistence in a hermit crab species ensemble. *Biological Bulletin* 153, 133–144. <http://www.jstor.org/stable/1540697>.
- Krebs C.J.** (1989) *Ecological methodology*. New York, NY: Harper Collins, 654 pp.
- Mantelatto F.L.M. and García R.B.** (2000) Shell utilization pattern of the hermit crab *Calcinus tibicen* (Diogenidae) from southern Brazil. *Journal of Crustacean Biology* 20, 460–467. doi: 10.1651/0278-0372(2000)020[0460:SUPOTH]2.0.CO;2.
- Markham J.C.** (1968) Notes on the growth pattern and shell-utilization of the hermit crab *Pagurus bernhardus* (L.). *Ophelia* 5, 189–205. doi: 10.1080/00785326.6812.10407609.
- Metcalfe N.B. and Monaghan P.** (2001) Compensation for a bad start: grow now, pay later? *Trends in Ecology and Evolution* 16, 254–260. doi: 10.1016/S0169-5347(01)02124-3.
- Mima A., Wada S. and Goshima S.** (2003) Antipredator defence of the hermit crab *Pagurus filholi* induced by predatory crabs. *Oikos* 102, 104–110. doi: 10.1034/j.1600-0706.2003.12361.x.
- Morris A.P.** (1974) *A field guide to Pacific Coast shells, including shells of Hawaii and the Gulf of California*. Boston: Houghton Mifflin, 297 pp.
- Orihuela B., Diaz H., Forward R.B. and Rittschof D.** (1992) Orientation of the hermit crab *Clibanarius vittatus* (Bosc) to visual cues: effects of mollusk chemical cues. *Journal of Experimental Marine Biology and Ecology* 164, 193–208. doi: 10.1016/0022-0981(92)90174-9.
- Pechenik J.A. and Lewis S.** (2000) Avoidance of drilled gastropod shells by the hermit crab *Pagurus longicarpus* at Nahant, Massachusetts. *Journal of Experimental Marine Biology and Ecology* 253, 17–32. doi: 10.1016/S0022-0981(00)00234-3.
- Pianka ER** (1975) Niche relations of desert lizards. In Cody M. and Diamond J. (eds) *Ecology and evolution of communities*. Cambridge, MA: Harvard University Press, pp. 292–314.
- Reese E.S.** (1969) Behavioral adaptations of intertidal hermit crabs. *American Zoology* 9, 343–355. <http://www.jstor.org/stable/3881807>.
- Rittschof D.** (1980) Enzymatic production of small molecules attracting hermit crabs to simulated gastropod predation sites. *Journal of Chemical Ecology* 6, 665–675. doi: 10.1007/BF00987677.
- Rittschof D., Tsai D.W., Massey P.G., Blanco L., Kueber G.L. and Haas R.J. Jr** (1992) Chemical mediation of behavior in hermit crabs: alarm and aggregation cues. *Journal of Chemical Ecology* 18, 959–984. doi: 10.1007/BF00980056.
- Rutherford J.D.** (1977) Removal of living snails from their shells by a hermit crab. *Veliger* 19, 438–439.
- Sant'Anna B.S., Dominciano L.C.D., Buozi S.F. and Turra A.** (2012) Is shell partitioning between the hermit crabs *Pagurus brevidactylus* and *Pagurus criniticornis* explained by interference and/or exploitation competition? *Marine Biology Research* 8, 662–669. doi: 10.1080/17451000.2011.653371.
- Spight T.M.** (1977) Availability and use of shell by intertidal hermit crabs. *Biological Bulletin* 152, 120–133.
- Straughan N.A. and Gosselin L.A.** (2004) Ontogenetic changes in shell preferences and resource partitioning by the hermit crabs *Pagurus hirsutiunculus* and *P. granosimanus*. *Journal of Experimental Marine Biology and Ecology* 451, 1–8. doi: 10.1016/j.jembe.2013.10.028.
- Taylor P.R.** (1981) Hermit crab fitness: the effect of shell condition and behavioral adaptations on environmental resistance. *Journal of Experimental Marine Biology and Ecology* 52, 205–218. doi: 10.1016/0022-0981(81)90037-X.
- Turra A. and Denadai M.R.** (2004) Interference and exploitation components in interspecific competition between sympatric intertidal hermit crabs. *Journal of Experimental Marine Biology and Ecology* 31, 183–193. doi: 10.1016/j.jembe.2004.04.008.
- Turra A. and Leite F.P.P.** (2003) The molding hypothesis: linking shell use with hermit crab growth, morphology, and shell-species selection. *Marine Ecology Progress Series* 265, 155–163. <http://www.jstor.org/stable/24867533>.
- Vance R.R.** (1972) The role of shell adequacy in behavioral interactions involving hermit crabs. *Ecology* 53, 1075–1083. <http://www.jstor.org/stable/1935419>.
- Webster D.R. and Weissburg M.J.** (2009) The hydrodynamics of chemical cues among aquatic organisms. *Annual Reviews of Fluid Mechanics* 41, 73–90. doi: 10.1146/annurev.fluid.010908.165240.
- Wei L.Z., Zhang X.M., Li J. and Huang G.Q.** (2008) Compensatory growth of Chinese shrimp, *Fenneropenaeus chinensis* following hypoxic exposure. *Aquaculture International* 16, 455–470. doi: 10.1007/s10499-007-9158-2.

and

Zar J.H. (2010) *Biostatistical analysis*, 5th edition. Upper Saddle River, NJ: Prentice-Hall, 944 pp.

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