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Air-exposure behavior: a restricted or a common conduct among intertidal hermit crabs?

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ABSTRACT

A new behavior related to shell care was recently reported for the intertidal hermit crab *Clibanarius erythropus* (Latreille, 1818) in the Gulf of Cádiz (southwestern Europe). It also has been observed in other species of the diogenid genera *Clibanarius* Dana, 1952, and *Calcinus* Dana, 1951, however, it has not been described as an active behavior. In the present study, intertidal hermit crabs from different species and localities were sampled to assess if air-exposure is a shell cleaning behavior restricted to some species of intertidal hermit crabs or if it is a more generalized behavior among species inhabiting intertidal habitats. The results revealed that air-exposure is an active behavior in species of *Clibanarius* and *Calcinus*, since we observed it also in *Clibanarius albidigitus* Nobili, 1901, and *Calcinus obscurus* Stimpson, 1859, from the Pacific coast of Costa Rica, although not in other intertidal species studied by us. We found interspecific differences in tolerance to physical stress of emerged hermit crabs. This air-exposure tolerance can be interpreted as a physiological adaptation to desiccation stress and is also related to the shell type they inhabit. Also, we provide additional features and details of the air-exposure behavior, combining observations of the first description in 2015 with our new field observations.

KEYWORDS

Shell care, shell cleaning behavior, temperature tolerance

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INTRODUCTION

Gastropod shells confer protection from predators and physical stress to hermit crabs and make these decapods a successful group among marine intertidal inhabitants (Hazlett, 1981). In a recent study (Perez-Miguel *et al.*, 2015), a new active behavior related to shell care was reported for the intertidal hermit crab *Clibanarius erythropus* (Latreille, 1818) in the Gulf of Cádiz (south-western Europe). According to these authors, this behavior, named “sunbathing” by analogy to human behavior at the beaches, could be considered as a mechanism of shell care aiming to avoid the fixation of biofouling species. Other authors previously described similar cases in other species; they did, however, not identify these observations as an active behavior (see Reese, 1969; Bertness, 1981a; Gherardi and Vannini, 1989; 1993; Gherardi, 1990; Rittschof *et al.*, 1995; Turra and Leite, 2000; Dunbar, 2001). Recently, however, Yoshikawa *et al.* (2020) described this “air-exposure” behavior as an active behavior in *Clibanarius virescens* (Krauss, 1843). The voluntary exposure to unfavourable conditions in order to get rid of possible epibionts and/or parasites (less resistant to desiccation than the host) has been also observed in other species such as gastropods (Wahl *et al.*, 1998) and brachyuran crabs (Becker and Wahl, 1996; Koo *et al.*, 2019). For example, adult ocyropid intertidal crabs *Macrophthalmus japonicus* (De Haan, 1835 [in De Haan, 1833-1850]) dedicate more of their time to drying their bodies in sunlight, whereas younger crabs spend most of their time feeding (Koo *et al.*, 2019).

Beyond the possible antifouling effect, the exposure to air has the additional advantage of avoiding transitory aquatic predators such as crabs, octopuses, and fishes (Tran *et al.*, 2014) and serves to reduce inter- and intraspecific competition for shells and shell theft (Rittschof *et al.*, 1995). Conversely, in addition to the physical stress, hermit crabs exposed on rocks are more vulnerable to other predators such as sea birds (Nellis, 2001; Tran *et al.*, 2014) and humans, which collect the largest specimens of *Cl. erythropus* as fishing bait (Stevčić *et al.*, 2018).

In general, predation pressure is especially high on hermit crabs inhabiting the low intertidal and subtidal habitats, whereas physical conditions (*e.g.*,

temperature, desiccation) are the most important stress factors for hermit crabs occupying the high intertidal zone (Bertness, 1981a). Shells with different architecture confer to hermit crabs different degrees of protection against both predators and physical stress (Bertness, 1981b; 1981c; Osorno *et al.*, 2005). Thus, the proportion of hermit crabs exhibiting air-exposure behavior could *a priori* vary depending on the intertidal zone they inhabit and/or the morphology of shells they are occupying.

The air-exposure cleaning behavior involves a prolonged period of air exposure in order to be effective. Therefore, it would be expected that such behavior be displayed only by species with strong physiological adaptation to desiccation stress. *Clibanarius erythropus* was the first hermit crab species in which the active air-exposure behavior has been observed and described (Perez-Miguel *et al.*, 2015). Recently, this active behavior has been confirmed also in another species of this genus, *Cl. virescens* (see Yoshikawa *et al.*, 2020). Species of the genus *Clibanarius* Dana, 1952 occupy usually the high intertidal habitat and are extremely resistant to thermal and desiccation stress (Bertness, 1981a; Gherardi, 1990). Conversely, intertidal *Calcinus* Dana, 1951 and *Pagurus* Fabricius 1775/*Paguristes* Dana, 1851 species generally inhabit the low intertidal and subtidal habitats and are more sensitive to physical stress caused by air exposure (Bertness, 1981a).

Along the Pacific coast of Panama and Costa Rica different species of hermit crabs usually coexist in rocky intertidal habitats (Abrams, 1981; Bertness, 1981b; Vargas and Wehrtmann, 2009), among them are: *Clibanarius albidigitus* Nobili, 1901, *Calcinus obscurus* Stimpson, 1859, and *Paguristes* sp. Contrarily, *Cl. erythropus* is generally the only hermit crab occurring in rocky intertidal habitats of the coast of Cádiz, although occasionally individuals of *Pagurus anachoretus* Risso, 1827 and *Cestopagurus timidus* (Roux, 1830) can be found at very low density (<1% of total hermit crabs) (Perez-Miguel *et al.*, 2016).

In the present study, intertidal hermit crabs from the Pacific coast of Costa Rica (Central America) and Atlantic coast of Cádiz (south-western Europe) were collected to assess if air-exposure was an active shell cleaning behavior restricted to just some species or if it represents a common behavior among intertidal

hermit crabs. Also, since the air-exposure behavior was first reported as active behavior in *Cl. erythropus* by Perez-Miguel *et al.* (2015), additional features and details of this behavior observed during the recent fieldwork are described by us.

MATERIAL AND METHODS

Definition of “air-exposure behavior”

Although hermit crabs that live on rocky shores usually remain in tidal pools during low tide to avoid heat and desiccation, some species are known to actively climb out from these pools onto rocky surfaces during low tide (Yoshikawa *et al.*, 2020). According to Perez-Miguel *et al.* (2015), when rocks and stones start to be air-exposed during low tides, hermit crabs emerge from their hiding places under the rocks and climb to the top of the stones (Fig. 1). Once on the rock, they remain inactive with the shell aperture turned downward or upward; subsequently, after a varying amount of time, they turn around and remain inactive with the shell aperture in the opposite position. Typically, hermit crabs stay on top of the rock and stones until high tide when the water starts covering these air-exposure places.

Species and study areas

Since previous information on shell care behavior among intertidal hermit crabs of Central America was not available, hermit crabs from three intertidal rock platforms were collected along the Pacific coast of Costa Rica. In this study, we sampled populations of *Cl. albidigitus*, *Ca. obscurus* and *Paguristes* sp. inhabiting the intertidal rocky habitats of Playa del Carmen, Punta Mala and Punta Uvita (Fig. 2). These three study sites are on rocky headlands between sandy beaches on the central Pacific coast. Climate is divided into two different seasons: a dry season extending from December to April (air temperatures from 20 to 27°C on the coast) and a wet season from May to November (air temperatures from 25 to 31°C on the coast) (Hidalgo *et al.*, 2013). In Costa Rica, water temperatures remain generally > 25°C throughout the year (Sutherland, 1987). The headland consists of sandstone benches and tide pools when the tide recedes. The sampled rocks were between 10

and 30 cm long. Wave action was moderate to heavy. Crustose algae and animals were abundant on open surfaces, including barnacles, gastropods and high densities of hermit crabs.

Considering that air-exposure is a shell-care behavior observed and first described in *Cl. erythropus* populations (Perez-Miguel *et al.*, 2015), in the present study we sampled a *Cl. erythropus* population inhabiting the intertidal rocky habitat of Santibáñez, Gulf of Cádiz (southwestern Spain) with a high diversity of gastropod shell use (Perez-Miguel *et al.*, 2016). The sampled area was a rocky platform with boulders and rock pools surrounded by sandy beaches and subject to semidiurnal meso-tides ranging from 1 to 3.5 m (Fig. 2). The air temperature varies between 8°C in January–February and 35°C in summer (July–August), and the annual water surface temperature of the Gulf of Cadiz oscillates seasonally between 15 ± 1°C in January–February and 25 ± 1°C in July–August (García-Lafuente *et al.*, 2012).

Collection and Behavioral Experiment

Hermit crabs were randomly sampled by hand at each sampling site: in July 2015 in Santibáñez (Spain), and in August–September 2015 in Playa del Carmen, Punta Mala and Punta Uvita (Costa Rica). At each sampling site, five to eight ‘turnable’ boulders were randomly inspected. From each selected rock, hermit crabs exhibiting air-exposure behavior on the rock were collected and kept in a labelled plastic bag. Subsequently, the boulder was turned over and hermit crabs, which were clustered under the rock, were collected and kept in another labelled plastic bag. All specimens were transported on ice, later were frozen (-20°C) and finally preserved in ethanol (80%).

In the laboratory, each hermit crab was removed from the shell and its maximum cephalothoracic shield width (CW) measured to the nearest 0.01 mm under a stereomicroscope equipped with a calibrated ocular micrometer. The CW was chosen as a measure of the crab size (rather than the shield length) due to the different longitudinal curvature of crab shields depending on the different architectures of shells. Specimens were sexed on the basis of the presence of gonopores on the coxa of the 3rd (female) and 5th (male) pair of pereopods. The presence of ovigerous females was recorded.

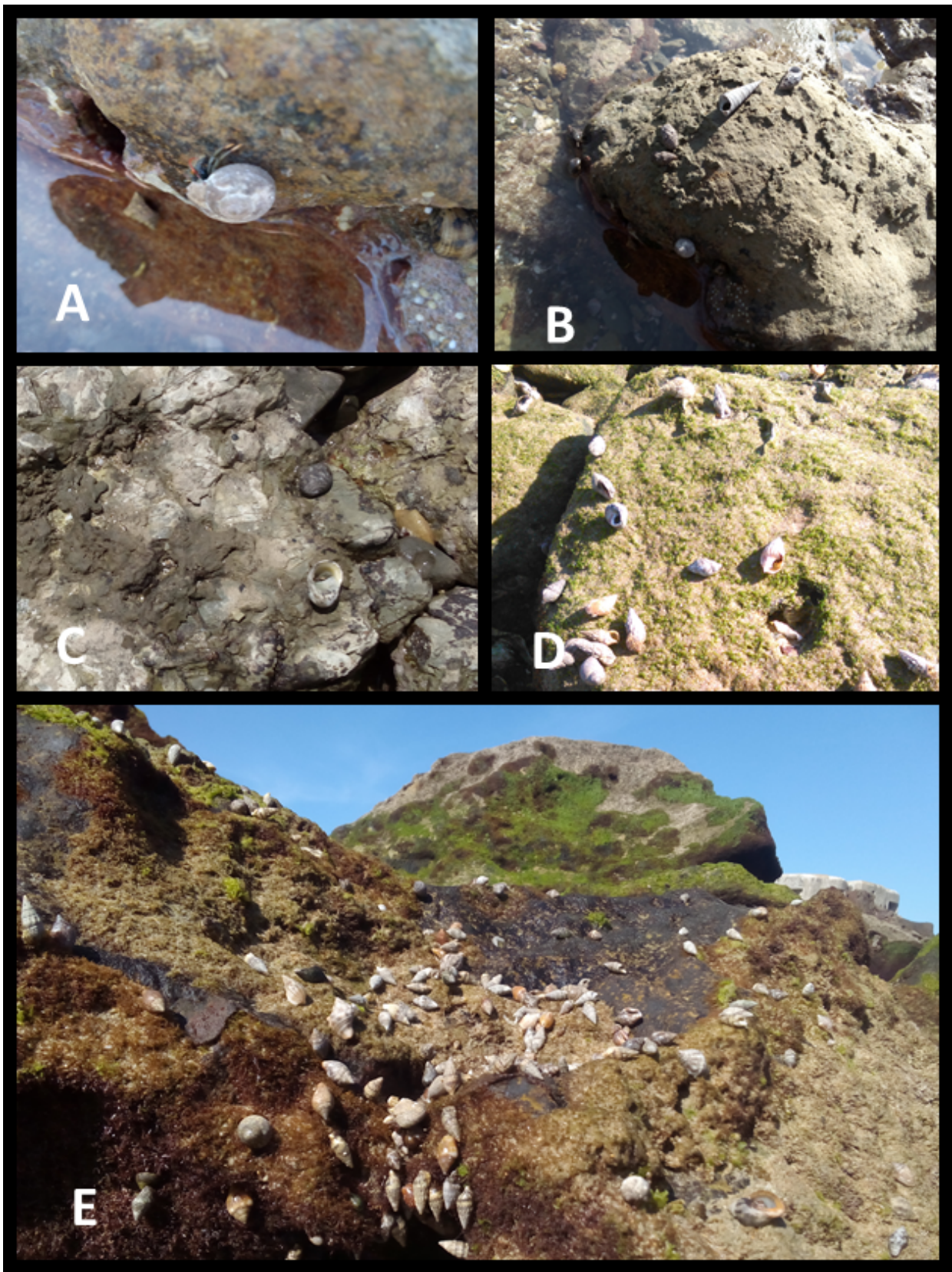


Figure 1. Pictures of hermit crabs performing air-exposure. (A) *Clibanarius albidigitus* climbing for air-exposure in Playa del Carmen, Costa Rica. (B) *Clibanarius albidigitus* inside a *Turritella* sp. and *Cerithium browni* air-exposure in Playa del Carmen, Costa Rica. (C) Two *Clibanarius albidigitus* inside of *Nerita funiculata*, air-exposure in Playa del Carmen, Costa Rica. (D, E) *Clibanarius erythropus* inside shells of different species performing air-exposure in Santibañez beach, Spain.

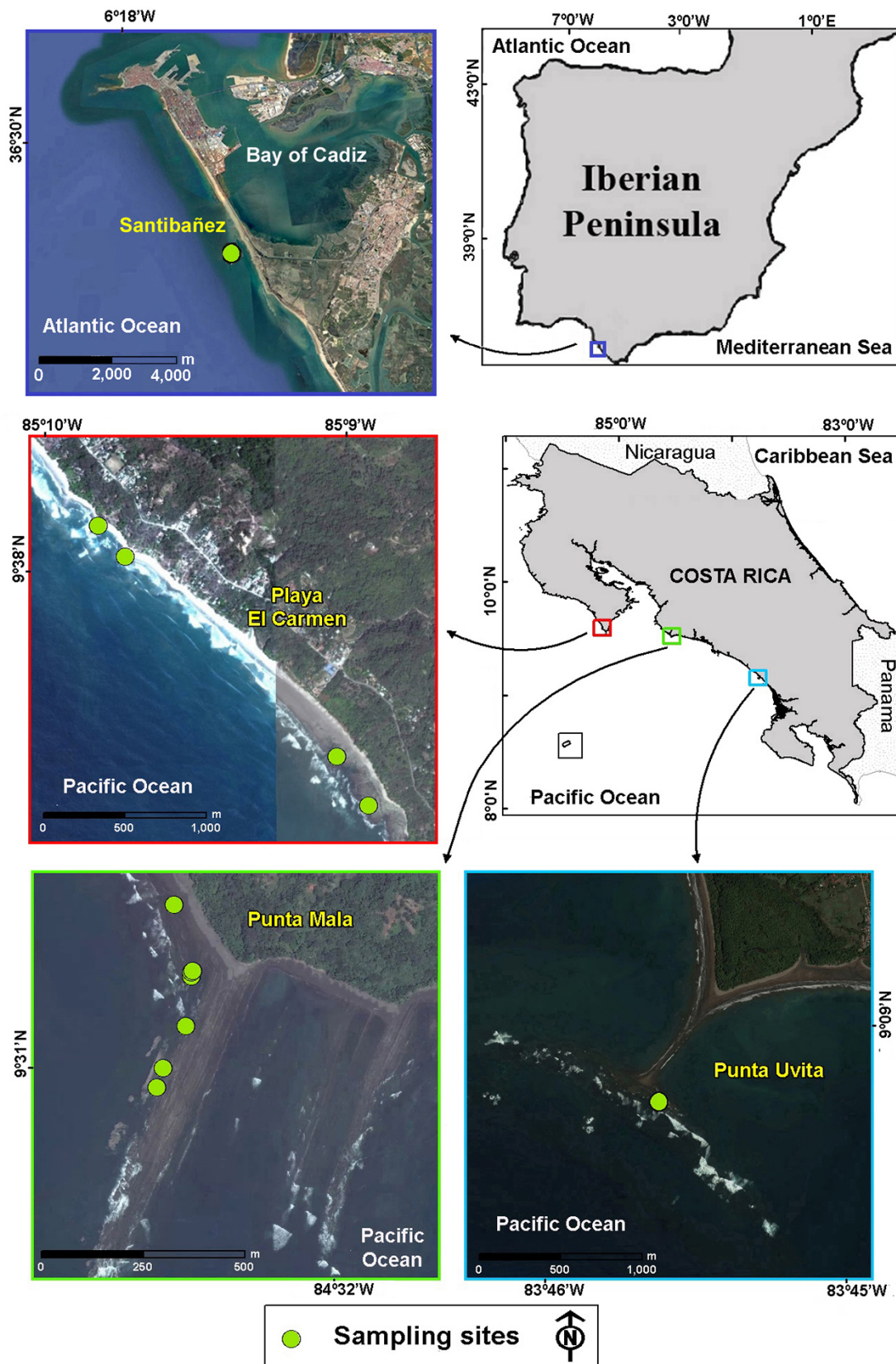


Figure 2. Sampling sites of hermit crabs collected in Spain (*Clibanarius erythropus*) and on the Pacific coast of Costa Rica (*Clibanarius albidigitus*, *Calcinus obscurus*, *Paguristes* sp. (Images from Google Earth, v. 7.3.0.3832 ©2017).

Host shells occupied by the hermit crabs were identified (Spain: Gofas *et al.*, 2011; Costa Rica: Fischer *et al.*, 1995; Ayón-Parente, 2009). Since shells with different architecture provide hermit crabs with a different degree of protection against predators and physical stress (Bertness, 1981a; 1981c; Osorno *et al.*, 2005), shells used by the studied hermit crab species were grouped into the following four types (adapted from Bertness, 1981c; Fig. 3): Type 1 (*i.e.*, *Cerithium* spp. and *Nassarius* spp.): shells are highly elongated (large height to width ratio) and with an elliptic shell aperture of moderate size. These shells have a large internal volume and a high spire, which serves as an efficient water reservoir preventing risk of desiccation during air exposure. Type 2 (*i.e.*, *Gibbula* spp.): shells are globose (low height-to-width ratio) and relatively light, with an extremely large final whorl. Although the interior of the shell has a large volume, the relatively wide aperture and the wall thinness prevent them from efficiently accumulating water to avoid desiccation during exposure and offer low protection from predators. Type 3 (*i.e.*, *Columbella* spp. and *Mitra* spp.): shells are moderately elongated and the final whorl is large but narrow, which produces a small and elongated aperture. Since they are heavy and have a narrow aperture, these shells offer good protection from predators; their relatively low volume and spire length determine, however, a low protection from physical stress. Type 4 (*i.e.*, *Stramonita* spp.): shells are morphologically similar to Type 3-shells but with both a larger aperture as well as a tougher and thicker shell wall. This shell type provides good protection from predators and takes longer to dry than the thinner shells of Type 2.

During spring tides occurring from May 2016 to August 2018, additional observations of details of the air-exposure behavior were made on *Cl. erythropus* from different beaches at Gulf of Cádiz. On two occasions, in Santibañez beach, hermit crab behavior was recorded at low tide during a complete tidal cycle on 12 marked stones that they were using for air-exposure. These selected stones were photographed daily over 20 days: hermit crabs occupying the rock surfaces were counted, and their position recorded every day to document daily changes during the complete tidal cycle. The air temperature as well as the weather and light conditions were annotated, too.

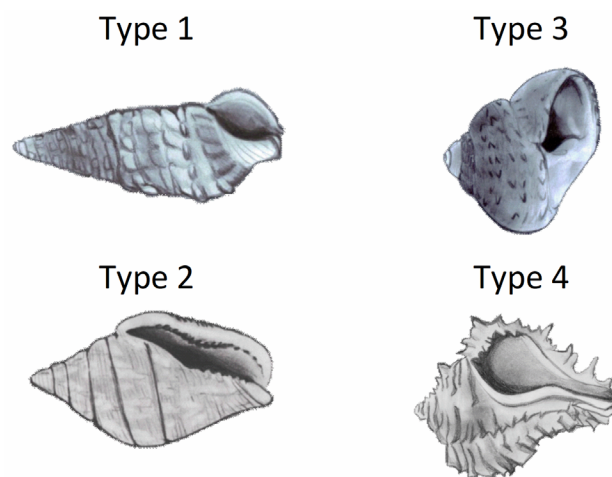


Figure 3. Schematic drawings representative of each shell type: Type 1 (T1), Type 2 (T2), Type 3 (T3), and Type 4 (T4).

Physical stress experiments

In a previous study (Bertness, 1981a), when individuals of the hermit crab *Cl. albidigitus* were exposed to out-of-water temperatures of 39°C (the habitual temperature on rock surfaces on low tide exposure in the Bay of Panama), they were less vulnerable to physical (thermal) stress than individuals of the coexisting hermit crab *Ca. obscurus* exposed to the same stress conditions. In the present study, to allow a comparison with the cited information of *Cl. albidigitus* and *Ca. obscurus*, we conducted laboratory experiments on the physical stress tolerance of *Cl. erythropus* from Santibañez (southwestern Spain) by also exposing the hermit crabs to aerial conditions at 39°C. Moreover, another set of specimens of *Cl. erythropus* was exposed to 35°C to simulate the natural summer temperature of the studied population (Santibañez, southwestern Spain), when hermit crabs were out of water at low tide on exposed rocks.

Specimens of *Cl. erythropus* occupying the four previously determined types of gastropod shells were collected in Santibañez. After 20 hours of acclimation to laboratory conditions in an aquarium with aerated seawater at room temperature (19–20°C), groups of ten hermit crabs using the same type of shell were placed into 500 mL vented vessels without seawater. They were introduced into incubators and maintained at a constant temperature of 35 or 39°C. The humidity inside the incubators was maintained close to 100% relative humidity by introducing a small receptacle with seawater into each incubator. At

predetermined intervals (every 120 minutes at 35°C; every 60 minutes at 39°C), two vented vessels were removed from the incubator and the hermit crabs were transferred to 2 L aquaria with seawater at room temperature (19–20°C) and aeration, to assess if they were alive or dead. After a 12-hour period under seawater at 19–20°C, dead and alive specimens were counted, sexed and its maximum cephalothoracic shield width (CW) was measured. This information was used to estimate the survivorship of hermit crabs after exposure to a prolonged period of the tested physical stress conditions.

Data analyses

The pattern of air-exposure behavior was consistent throughout the populations for the three species from Costa Rica: it was always present in *Cl. albidigitus* and *Ca. obscurus*, and always absent in *Paguristes* sp. (Tab. 1); thus, data were pooled by species to obtain a sample size adequate for robust statistical analyses. No individuals of *Paguristes* sp. was observed exhibiting air-exposure behavior, thus after testing the statistical significance of this absence by using a chi-squared test, this species was excluded from subsequent statistical analysis. For the remaining three species (*Cl. albidigitus*, *Cl. erythropus*, and *Ca. obscurus*), we applied chi-squared tests to assess possible differences in the number of crabs exhibiting air-exposure behavior depending on sex categories and shell types, as well as the number of survivors of physical stress experiments with *Cl. erythropus*. For each demographic category (male, non-ovigerous female, ovigerous female) and species, size differences between hermit crabs, which performed air-exposure behavior on the rocks and

those that were clustered under stones were tested by a one-way ANOVA (factor: position on rocks). Similarly, we analysed the size differences between live and dead hermit crabs used in physical stress experiments of *Cl. erythropus* by a three-way ANOVA (factors: hermit crab demographic category, shell type and temperature). Data were log-transformed to homogenize variance prior to analysis, and the Student–Newman–Keuls test was used as a *post hoc* test. A $p > 0.05$ value was considered as the threshold for statistical non-significance for all statistical tests carried out with these data.

RESULTS

Field air-exposure behavior

Of the intertidal hermit crab species included in this study, *Cl. albidigitus*, *Cl. erythropus* and *Ca. obscurus* exhibited air-exposure shell care behavior. On the contrary, specimens of *Paguristes* sp. were collected exclusively under rocks (Tab. 1).

According to results of chi-squared tests, *Cl. albidigitus* and *Cl. erythropus* exhibited a similar ($p > 0.05$) percentage of specimens displaying the air-exposure behavior: *Cl. albidigitus*: 28.1% and *Cl. erythropus*: 30.0% (Fig. 4). Percentages of air-exposure behavior of both species of *Clibanarius* were significantly higher ($p < 0.01$) than the corresponding value for *Ca. obscurus* specimens (16.6%) displaying air-exposure shell care behavior. The absence of this conduct in *Paguristes* sp. was statistically significant ($p < 0.01$) even when it was tested against *Ca. obscurus* exhibiting less air-exposure behavior.

Table 1. Hermit crab species and number of hermit crabs, which were found at low tide air-exposure on rocks and those which were found clustered under rocks in each sampling locality, CR: Costa Rica; S: Spain.

Species	Locality	No. of crabs on rocks	No. of crabs under rocks
<i>Clibanarius albidigitus</i>	Playa El Carmen (CR)	26	58
<i>Clibanarius albidigitus</i>	Punta Mala (CR)	3	3
<i>Clibanarius albidigitus</i>	Punta Uvita (CR)	32	98
<i>Clibanarius erythropus</i>	Santibáñez (S)	173	404
<i>Calcinus obscurus</i>	Playa El Carmen (CR)	11	64
<i>Calcinus obscurus</i>	Punta Mala (CR)	33	124
<i>Calcinus obscurus</i>	Punta Uvita (CR)	4	88
<i>Paguristes</i> sp.	Playa El Carmen (CR)	0	120
<i>Paguristes</i> sp.	Punta Mala (CR)	0	24
<i>Paguristes</i> sp.	Punta Uvita (CR)	0	0

The air-exposure behavior was observed in specimens from both sexes (ovigerous females included) of *Cl. albidigitus*, *Cl. erythropus* and *Ca. obscurus* (Fig. 4). Results of chi-squared tests indicated that, within each species, sex-related differences of the air-exposure behavior were statically not significant ($p > 0.05$) (Fig. 5). Similarly, within each species and demographic category, the results of the ANOVAs revealed that there were no statistically significant differences ($p > 0.05$) between the mean size (shield width) of crabs that were collected on and under the rocks (Fig. 5).

The number of host gastropod species used by each hermit crab species was 15 for *Paguristes* sp., 18 for *Cl. albidigitus*, 19 for *Cl. erythropus*, and 42 for *Ca. obscurus* (Tab. 2). Concerning the shell types, *Cl. albidigitus*, *Cl. erythropus* and *Ca. obscurus* used all four shell

types (1–4), while *Paguristes* sp. occupied only Type 1 and Type 4 shells. *Calcinus obscurus* was the hermit crab species which displayed higher homogeneity in the proportion of shells used from each shell type. *Clibanarius erythropus* and *Paguristes* sp. showed clear preferences for Type 1-shells and *Cl. albidigitus* for Type 1 and Type 2-shells (Fig. 6). Within each species, host shell type-related differences of the air-exposure behavior were statically not significant ($p > 0.05$).

These new features and details about air-exposure behavior displayed by *Cl. erythropus* in the field (Chart 1) demonstrate that air-exposure is an active behavior (crabs climb on the top of emerged stones) displayed by all demographic categories of *Cl. erythropus* during low tides, irrespective of both weather and sunlight conditions. This behavior started a few minutes

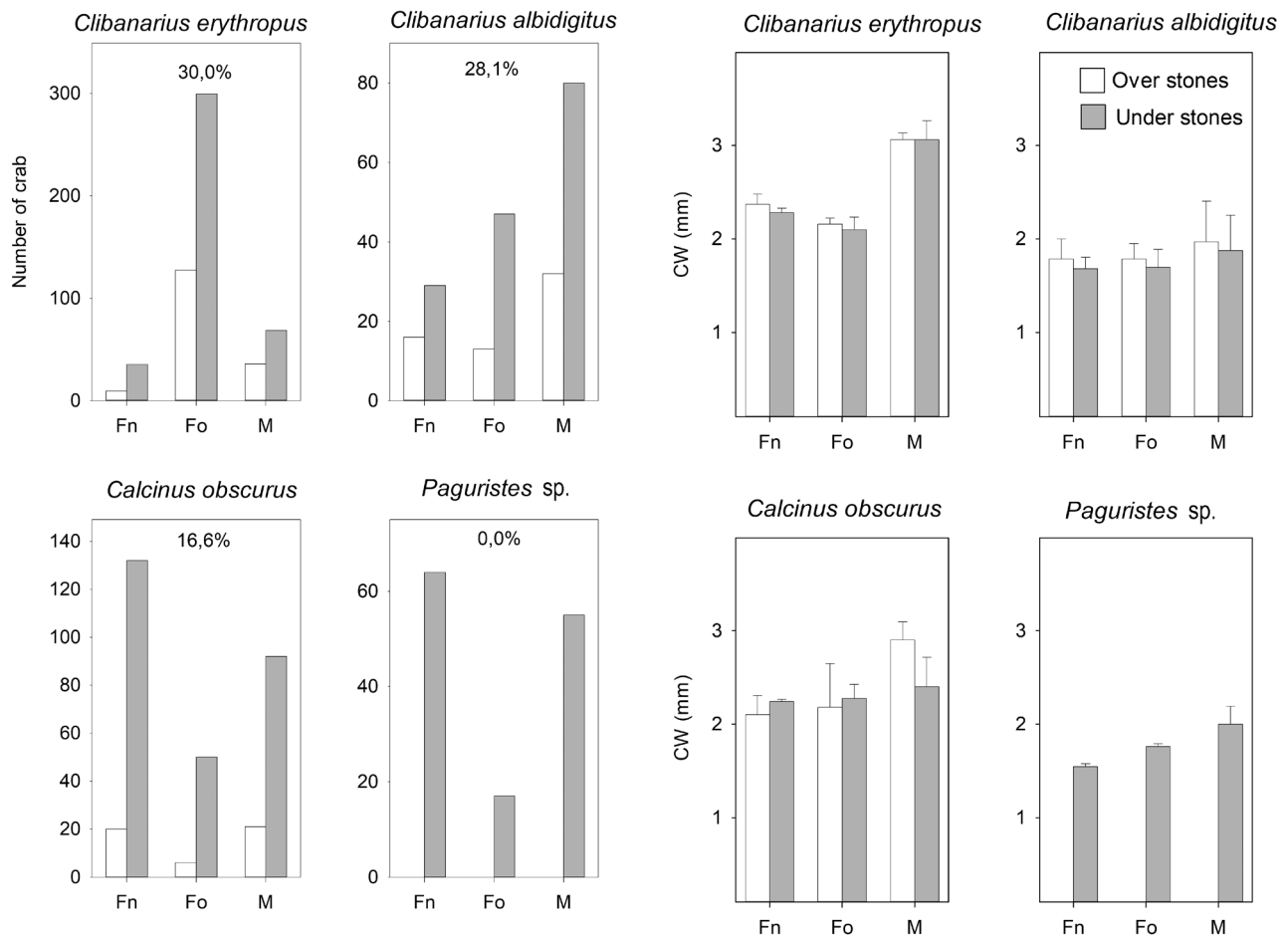


Figure 4. Number of non-ovigerous females (Fn), ovigerous females (Fo) and males (M) per hermit crab species, which were exhibiting air-exposure behavior on rocks (open bar) and those clustering under rocks (filled bar). Percentages indicate the proportion of air-exposure hermit crabs compared to those clustering under rocks.

Figure 5. Mean shield width (+SE) of non-ovigerous females (Fn), ovigerous females (Fo) and males (M) for each hermit crab species, which were exhibiting air-exposure behavior on rocks (open bar) and those clustering under rocks (filled bar).

after stone emersion (low tide) and ended when the seawater covered the stone (high tide); meanwhile hermit crabs remained immobile except when they turned around to obtain a complete drying of the shell. The number of air-exposure crabs was positively correlated with a tidal coefficient, and hermit crabs showed a relative fidelity to specific stones, staying at the same place on the stone when conducting the air-exposure behavior.

Laboratory experiments of physical stress on *Clibanarius erythropus*

Abrupt mortalities of *Cl. erythropus* (> 90%) occurred after 240 minutes of exposure to 39°C for specimens occupying shell Types 1, 2 and 3, whereas only ≈ 50% of emerged specimens occupying shell Type 4 died after 240 minutes of exposure to this temperature (Fig. 7). No mortality of specimens in Type 4-shells or moderate mortalities of hermit crab

Table 2. Number of hermit crabs that were found occupying shells of different gastropod species in the studied intertidal habitats. Abbreviations: (Ce) *Clibanarius erythropus* from Spain; (Ca) *Clibanarius albidigitus*, (Co) *Calcinus obscurus*, and (P) *Paguristes* sp. from the Pacific coast of Costa Rica; (St) morphological shell type 1, 2, 3 or 4 (see Material and Methods and Fig. 3).

Species	St	Ce	Ca	Co	P	Species	St	Ce	Ca	Co	P
<i>Acanthais brevidentata</i>	4	0	3	9	0	<i>Gibbula umbilicalis</i>	2	4	0	0	0
<i>Acanthais triangularis</i>	4	0	0	9	0	<i>Gibbula varia</i>	2	17	0	0	0
<i>Anachis boivini</i>	3	0	4	1	9	<i>Hexaplex trunculus</i>	4	13	0	0	0
<i>Anachis pardalis</i>	3	0	0	0	1	<i>Leucozonia rudis</i>	4	0	0	5	0
<i>Anachis rugosa</i>	3	0	0	0	3	<i>Mircocithara cithara</i>	3	0	0	0	1
<i>Anachis scalarina</i>	3	0	0	1	0	<i>Microcithara harpiformis</i>	3	0	0	3	0
<i>Aphorrais pespeleconis</i>	3	1	0	0	0	<i>Mitra lens</i>	3	0	0	6	0
<i>Astraea buschii</i>	2	0	0	4	0	<i>Mitra tristis</i>	3	0	7	7	4
<i>Bolinus brandaris</i>	4	12	0	0	0	<i>Mitrella guttata</i>	3	0	1	0	4
<i>Bulla punctulata</i>	4	0	0	3	0	<i>Nassarius incrassatus</i>	1	2	0	0	0
<i>Bursa corrugata</i>	4	0	0	6	0	<i>Nassarius reticulatus</i>	1	84	0	0	0
<i>Cerithium adustum</i>	1	0	25	57	26	<i>Nassarius vittatus</i>	1	0	0	1	0
<i>Cerithium browni</i>	1	0	40	17	48	<i>Natica vittata</i>	2	6	0	0	0
<i>Cerithium gallapaginis</i>	1	0	2	1	2	<i>Nerita funiculata</i>	2	0	94	43	0
<i>Cerithium lividulum</i>	1	293	0	0	0	<i>Ocenebra erinaceus</i>	4	13	0	0	0
<i>Cerithium menkei</i>	1	0	4	0	1	<i>Ocenebrina edwardsii</i>	4	1	0	0	0
<i>Cerithium vulgatum</i>	1	7	0	0	0	<i>Opeatostoma pseudodon</i>	4	0	0	1	0
<i>Cerithium sp.</i>	1	0	5	0	0	<i>Phocus lineatus</i>	2	13	0	0	0
<i>Columbella fluctuata</i>	3	0	3	7	19	<i>Phyllocoma scalariformis</i>	4	0	0	1	0
<i>Columbella fuscata</i>	3	0	0	6	1	<i>Pilsbryspira cf. aterrima</i>	3	0	0	0	1
<i>Columbella labiosa</i>	3	0	0	4	0	<i>Pisania striata</i>	3	57	0	0	0
<i>Columbella paytensis</i>	3	0	0	13	5	<i>Planaxis planicostatus</i>	4	0	6	0	0
<i>Columbella rustica</i>	3	20	0	0	0	<i>Pollia dorbignyi</i>	4	14	0	1	0
<i>Conus vittatus</i>	3	0	0	1	0	<i>Stramonita biserialis</i>	4	0	2	2	0
<i>Crassispira sp.</i>	1	0	0	4	13	<i>Stramonita haemastomas</i>	4	7	0	0	0
<i>Cymatium sp.</i>	4	0	0	1	0	<i>Tegula panamensis</i>	2	0	3	25	0
<i>Cymia tectum</i>	4	0	0	1	0	<i>Tegula sp.</i>	2	0	0	5	0
<i>Dermomurex obeliscus</i>	4	0	0	1	0	<i>Tegula verrucosa</i>	2	0	0	14	0
<i>Echinolittorina aspera</i>	2	0	0	1	0	<i>Turbo saxosus</i>	2	0	0	4	0
<i>Engina maura</i>	3	0	1	1	0	<i>Turritella banksii</i>	1	0	2	3	0
<i>Euthria cornea</i>	4	1	0	0	0	Turritellidae	1	0	0	4	0
<i>Gemophos gemmatus</i>	4	0	0	8	0	<i>Vasula melons</i>	4	0	2	18	0
<i>Gemophos sanguinolentus</i>	4	0	1	11	0	<i>Vasula speciosa</i>	4	0	0	1	0
<i>Gibbula pennanti</i>	2	15	0	0	0	Vermetidae	4	0	0	1	0

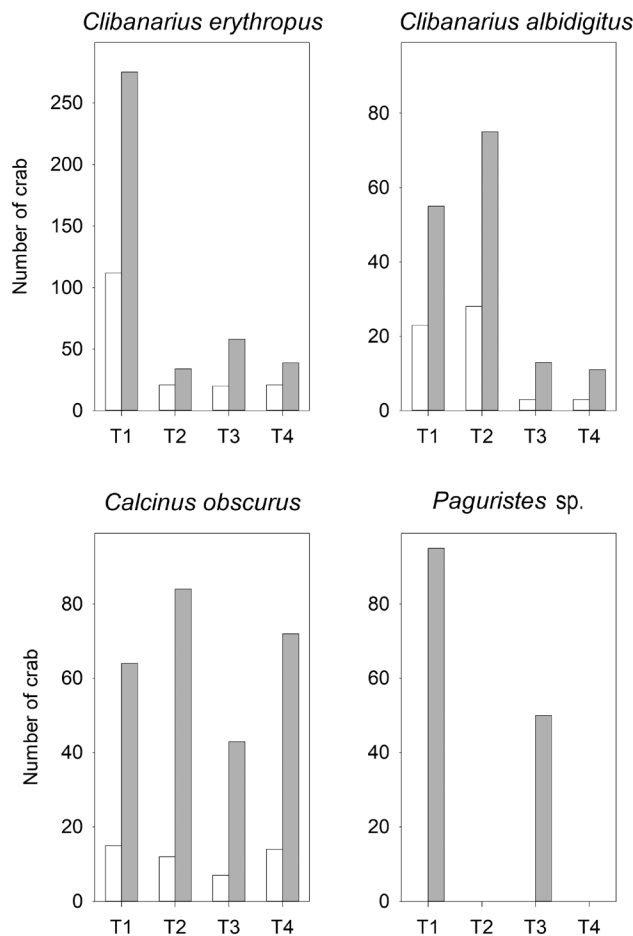


Figure 6. Number of non-ovigerous females (Fn), ovigerous females (Fo) and males (M) for each hermit crab species and shell type (Type 1 to Type 4), which were exhibiting air-exposure behavior on rocks (open bar) and those clustering under rocks (filled bar).

individuals in shells of Types 1, 2 and 3 were observed after 360 minutes of exposure to 35°C. Independent of the shell type, significantly higher survival of emerged hermit crabs exposed to 35°C compared to those at the 39°C treatment was observed from 240 minutes to 720 minutes (four to twelve hours) of exposure (Fig. 7). An exception were specimens occupying Type-3 shells, which showed higher survival at 35°C than at 39°C only from 240 to 360 minutes of exposure (Fig. 7).

For each time of exposure and temperature, chi-squared test results revealed that differences in survival of emerged hermit crabs occupying different shell types were significantly different in the following scenarios (Fig. 7): (1) survival at 39°C was significantly higher after 240 minutes of exposure in individuals occupying Type 4-shells compared to those using the other three shell types; (2) survival was significantly lower at 35°C after 360 minutes of exposure in hermit crabs living in Type 3-shells compared to those using Type 4-shells; (3) after 480 to 720 minutes (eight and twelve hours) of exposure, survival of hermit crabs in Type 3-shells decreased significantly more than in individuals occupying the other three shell types. For each time of exposure and temperature, however, survival differences of emerged males and females were not statistically significant.

Chart 1. Summary of the current knowledge about air-exposure behavior. Data were mainly obtained during different observation periods of *Clibanarius erythropus* specimens at different beaches of the Gulf of Cádiz (Spain) between the years 2016 and 2018.

- 1 This is an active behavior few, displayed in the intertidal zone during low tides.
- 2 It is displayed at all low tides, independent of climatic conditions and during day or night, suggesting that it is not related to sunshine but air desiccation.
- 3 Hermit crabs display this behavior a few minutes after the stones are emerged. They climb to the top of the stones only during the first 10-75 minutes of stone emergence. After this period, no more hermit crabs climb on top of the stones; the remaining individuals stay in clusters under the stones.
- 4 Hermit crabs air-exposing on the top of the stones remain there until the high tide covers the stones; only a few individuals return to the cluster under the stone before the end of the low tide.
- 5 When a hermit crab air-exposing is removed from the top of the stone to the base, it climbs back to the top.
- 6 During air-exposure, hermit crabs remain immobile and only move just enough to change their position to allow a complete drying of the shell.
- 7 All demographic categories (females, ovigerous females and males) display this behavior.
- 8 There is a direct correlation between the number of hermit crabs air-exposing and tidal coefficient (tidal range), with an increasing number of hermit crabs air-exposing as the coefficient increases.
- 9 During several consecutive days, the same hermit crabs were observed climbing to the same position of the same stones they occupied the days before.
- 10 Hermit crabs show a relative fidelity to specific stones (homing behavior). The selection of stones for clustering and air-exposing is not random.

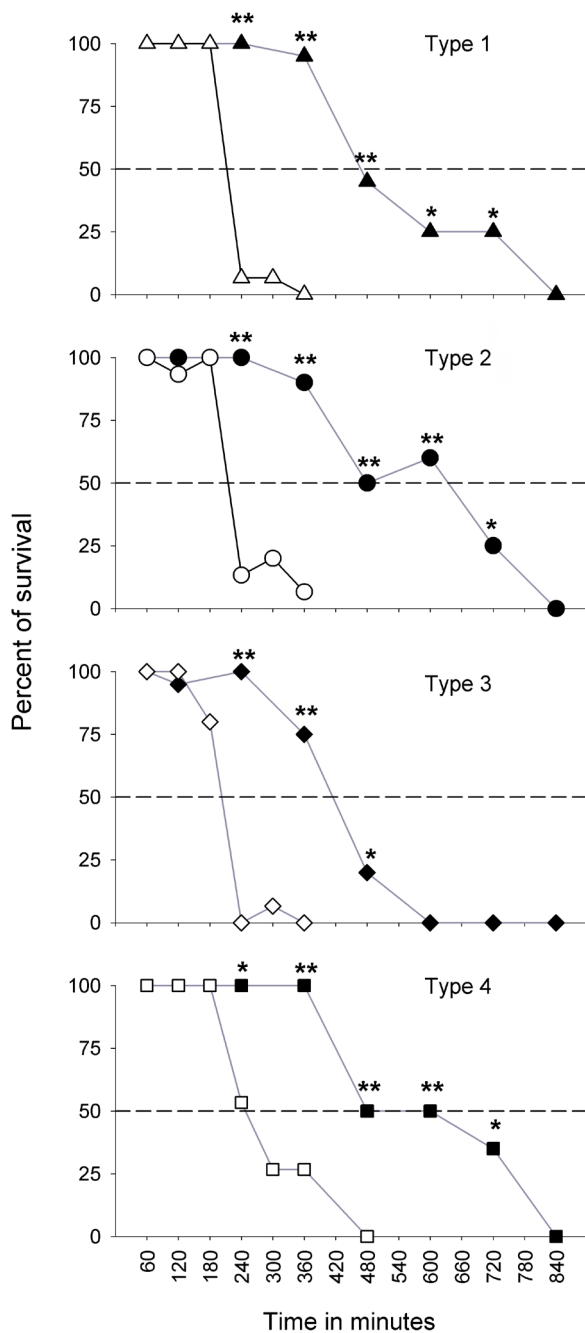


Figure 7. Thermal air-exposure tolerance of *Clibanarius erythropus* at 35°C (full symbols) and 39°C (open symbols) for each shell type (Type 1 to Type 4). The symbols ** and * indicate higher survivorship at 35°C than at 39°C at a significance level of $p < 0.01$ and $p < 0.05$, respectively.

Results of ANOVAs indicate that the mean size of *Cl. erythropus* used in the laboratory experiments at 35°C and 39°C was not significantly different ($p > 0.05$) between both temperatures, with mean shield width (mm) of $2.87 (\pm 0.03)$ and $3.02 (\pm 0.09)$, respectively.

Results revealed, however, significant differences ($p < 0.01$) in size between shell types, with mean shield width of $2.49 (\pm 0.08)$, $2.71 (\pm 0.09)$, $3.03 (\pm 0.08)$ and $3.57 (\pm 0.05)$ for hermit crabs occupying shells of Types 1, 3, 2 and 4, respectively. There were no significant differences ($p > 0.05$) in the mean size of alive and dead hermit crabs, with mean shield width of $3.00 (\pm 0.08)$ and $2.90 (\pm 0.04)$, respectively. The interaction between the factors of shell type and hermit crab demographic category was also statistically not significant ($p > 0.05$).

Interspecific differences in tolerance to physical stress of emerged hermit crabs exposed to 39°C suggest that the least and most tolerant species to thermal stress at this temperature are *Ca. obscurus* and *Cl. albidigitus*, respectively (Fig. 8). However, when exposed to the natural conditions of temperature of each studied population (35°C for *Cl. erythropus* and 39°C for *Cl. albidigitus* and *Ca. obscurus*), a similar tolerance was observed for both species of the genus *Clibanarius*, with the exception of *Cl. erythropus* specimens occupying Type 3 shells, which show a lower tolerance after 360 minutes of exposure onwards (Fig. 8).

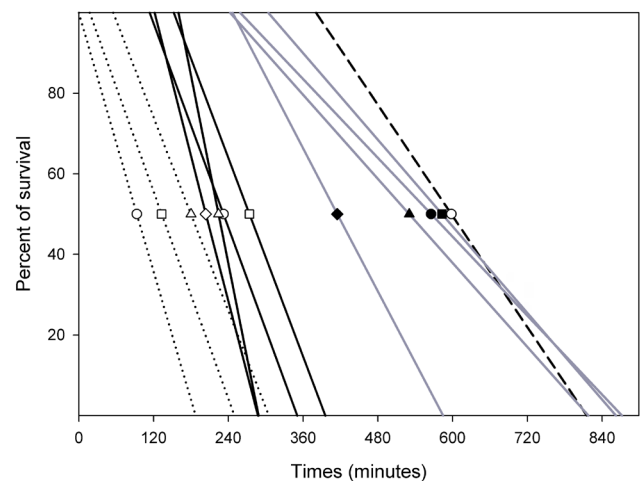


Figure 8. Regression lines indicating the thermal air exposure tolerance of the different hermit crab species showing air-exposure behavior. Solid, dashed and dotted lines correspond to *Clibanarius erythropus*, *Cl. albidigitus* and *Calcinus obscurus*, respectively; triangle, circle, diamond and square symbols refer to shell Types 1, 2, 3 and 4, respectively; grey line with full symbols and black lines with open symbols results at 35°C and 39°C, respectively. Data for *C. albidigitus* and *C. obscurus* are from Bertness (1981a).

DISCUSSION

Intertidal hermit crab specimens of the genera *Clibanarius* and *Calcinus* exposed to the sun during low tides with shell apertures pointing upward have been previously observed in several species; these observations, however, were interpreted as hermit crabs that were surprised by the low tide out of their refuges and remained retracted inside their shells to avoid desiccation (Reese, 1969; Gherardi and Vannini, 1989; 1993; Rittschof *et al.*, 1995; Turra and Leite, 2000; Dunbar, 2001). Consequently, these observations were not interpreted as an antifouling and active behavior as it was later interpreted in *Cl. erythropus* (see Perez-Miguel *et al.*, 2015). More recently, however, Yoshikawa *et al.* (2020) studied this air-exposure behavior as a possible mechanism of avoidance of bopyrid ectoparasites by young stages of *Cl. virescens*. Therefore, it seems feasible to assume that *Calcinus laevimanus* (Randall, 1840) and *Clibanarius corallinus* (H. Milne Edwards, 1848) (see Reese, 1969) as well as several other species of *Clibanarius* (*Cl. longitarsis* and *Cl. virescens*: see Gherardi and Vannini, 1989; 1993; *Clibanarius vittatus* (Bosc, 1802): see Rittschof *et al.*, 1995; *Clibanarius antillensis* Stimpson, 1859: see Turra and Leite, 2000; *Clibanarius taeniatus* (H. Milne Edwards, 1848) and *Cl. virescens*: see Dunbar, 2001) also display this active behavior. There are other cases of hermit crab species found in situations of direct exposure to air and sunlight on intertidal areas: *Clibanarius zebra* (Dana, 1852) (see Reese, 1969), and *Pagurus samuelis* (Stimpson, 1857), *Pagurus hirsutiusculus* (Dana, 1851) and *Pagurus granosimanus* (Stimpson, 1859) (see Taylor, 1981). Additional detailed studies, however, are required to confirm whether these observations are related to an active behavior in these species.

The present study reveals that the hermit crabs *Cl. albidigitus* and *Ca. obscurus* from the Pacific coast of Costa Rica also show this active air-exposure behavior. In contrast, *Paguristes* sp. (present study), *Ce. timidus* and *P. anachoretus* (see Perez-Miguel *et al.*, 2015) are always found underwater in rock pools during low tide. Therefore, all the information available suggests that air-exposure is a rather common behavior in intertidal species of the genera *Calcinus* and *Clibanarius*, and maybe present in some *Pagurus* species. More

extensive studies, however, are required to obtain accurate estimates of the actual number of hermit crab species exhibiting this behavior and to gain insights into the benefits that air-exposure behavior provides to hermit crabs.

The proportion of air-exposing individuals on the rocks at each low tide was different between the four studied hermit crabs. *Paguristes* sp. did not exhibit air-exposure behavior, and a lower proportion of hermit crabs displaying air-exposure shell care was observed for *Ca. obscurus* than for the two *Clibanarius* species. These interspecific differences in air-exposure intensity seem to mirror the tolerance of these hermit crabs to physical stress (Fig. 8) and may be related to their distribution pattern along the vertical intertidal zonation (Bertness, 1981b). In fact, when several species of hermit crabs coexist in the intertidal habitat of a geographical region — as in the studied populations of three co-occurring hermit crab species in Pacific Costa Rica — the distribution of species along the intertidal gradient can be interpreted as the result of a complex interaction between predation, physical stress and competitive pressures (Bertness, 1981a). For instance, in the Bay of Panama *Pagurus* sp. lives exclusively in the low intertidal zone and prefers relatively heavy shells with narrow apertures, which reduce its vulnerability to predation while decreasing the resistance to thermal stress (Bertness, 1981b). On the other hand, *Ca. obscurus* inhabits the middle to low intertidal zone while *Cl. albidigitus* occurs in middle to high intertidal zones, partly as a result of active competitive displacement of the latter species by *Ca. obscurus* (see Bertness, 1981b). Such coexistence of a dominant *Calcinus* species and a subordinate *Clibanarius* species seems to force *Clibanarius* specimens to occupy shells with lower quality in terms of protection against predation and physical stress (Bach *et al.*, 1976; Bertness, 1981b). Under the premise of an inferior capacity of *Clibanarius* species to occupy preferred shells, their higher stress tolerance and their higher capacity for air-exposure shell care behavior acquire an additional ecological advantage for a species inhabiting a more physically stressing zone of the intertidal habitat. Moreover, the more developed shell care behavior of *Clibanarius* species could partially explain the higher number of epibiotic-covered shells and the higher degree of encrustation

of shells used by *Calcinus* species when coexisting with *Clibanarius* species (Gherardi, 1990).

Such shell encrustation can negatively affect hermit crabs by decreasing crab mobility and shell equilibrium and by shortening the shell-use time (Hazlett, 1970). Therefore, it is expected that hermit crabs would prefer bare shells over encrusted ones (Ayres-Peres and Mantelatto, 2010). Under situations of limited shell availability, the less aggressive species would occupy epibiotic-covered shells as a way of reducing competition with more dominant species (Hazlett, 1981). In the case of hermit crabs inhabiting habitats with a high density of shell-crushing predators, it would be advantageous, however, to procure shells with the surface strengthened by epibionts (Turra, 2003), especially when such hermit crab species occupy the low intertidal/subtidal zones where the time of exposure to aquatic predators is longer. In fact, Turra and Leite (2000) suggested that the absence of encrustation in shells might expose hermit crabs to higher predation and desiccation risks. Among the species studied by us, this scenario could be the case in *Paguristes* sp., where individuals did not display air-exposure behavior (Figs. 4, 6) and demonstrated less tolerance to thermal and desiccation stress compared to the other species studied herein (Fig. 8). Yoshikawa *et al.* (2020) studied a possible relationship of air-exposure behavior as a mechanism to reduce infestation by bopyrids. But, the infestation by these parasites was very low and the authors concluded that there was not enough data to accept the hypothesis that air-exposure behavior can reduce infestation by bopyrids.

Even if the different tolerance of coexisting species to air exposure seems to mirror their pattern of intertidal vertical zonation, then the quality of shells could be associated with the hermit crab resistance to desiccation (Taylor, 1981). The water-holding capacity of different shell types has been considered as the most critical variable in the protection that they provide to a hermit crab from physical stress (Bertness, 1981a). According to Bertness (1981c), Type 1-shells have a relatively large internal volume and a high spire that act as an efficient water reservoir; Type 4-shells also have a high spire and are the second best shell architecture in offering crabs protection from thermal stress; Type 2-shells have a large internal volume

but they retain little water due to an extremely large final whorl; and Type 3-shells can retain only small amounts of water because they have both a small volume and short spire (Fig. 3). In the experiments carried out in this study with *Cl. erythropus*, Type 3-shells were the worst choice for crabs exposed to physical stress. On the other hand, the best choice seems to be shells of Type 4, probably because in the studied area (Gulf of Cádiz) the gastropod species with this shell type have an extremely thick shell wall.

Despite shell-related differences in the protection offered to the hermit crabs from physical stress, host shell type-related differences in the air-exposure behavior were not observed in *Ca. obscurus*. A clear preference for Type 1-shells was noted in *Cl. erythropus* while *Cl. albidigitus* showed preferences for shells of Type 1 and 2 (Fig. 6). At least in both *Clibanarius* species studied herein, this apparent preference might not be essential for survival since all the shell types can offer hermit crabs good protection from desiccation during the relatively short period of time that they devote to the air-exposure behavior. For example, in the Gulf of Cádiz, rocks in the intertidal zone inhabited by *Cl. erythropus* were usually exposed to air for no longer than four hours (240 minutes) during spring low tides, whereas at 35°C (extreme summer temperature) shell-type differences in tolerance to physical stress of this species were observed after a longer period of emersion (Figs. 7, 8). This relatively short duration of air-exposure behavior exhibited by *Cl. erythropus* could also explain why neither sex- nor size-related differences in air-exposure behavior were observed, even though one would expect a high tolerance to physical stress by large males, which were the main occupants of Type 4-shells (thick wall) in the studied population (Perez-Miguel *et al.*, 2016).

Clibanarius erythropus is considered a rather tolerant species to thermal stress (Gherardi, 1990) displaying its usual activity within a wide temperature range (Shuchman and Warburg, 1986). When individuals of *Cl. erythropus* were exposed to the same air temperature as *Cl. albidigitus* and *Ca. obscurus* (see Bertness, 1981a), they displayed a lower tolerance than expected considering its vertical position in the intertidal zonation. However, when exposed to its habitual summer temperature (35°C), *Cl. erythropus* exhibited the expected higher tolerance compared

to the other intertidal species studied by us (Fig. 8). Similarly, after a 7-hour exposure to 30°C air temperature, *Cl. erythropus* showed higher survival than *Calcinus ornatus* (P. Roux, 1830): 95% versus 78%, respectively (Gherardi, 1990). Therefore, even when a species is very tolerant to thermal stress and desiccation, it can only tolerate remaining emerged for a relatively long period when temperatures remain within the thermal range of its geographical area.

Characteristics of the air-exposure behavior of *Cl. erythropus* have been compiled during many hours of field observations at different beaches in the Gulf of Cádiz. The results obtained provide novel information about the start of air-exposure during the tidal cycle, the duration of such behavior, the reaction of the hermit crabs when they are removed from the top of the stone, their preferences for pre-determined stones, and their relationship with the tidal coefficient (see Chart 1). Individuals returning to their previous refuge or clustering sites (“homing” behavior) have been observed in other species of the genus *Clibanarius* (see Gherardi and Vannini, 1989; 1993). A similar “homing” behavior could explain the observed fidelity to stones displayed by air-exposure individuals of *Cl. erythropus*. Additional field and laboratory studies, however, are needed to clarify if the air-exposure behavior is associated with the homing behavior.

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