



Never forget where you came from: Microhabitat of origin influences boldness and exploration in the hermit crab *Clibanarius symmetricus* (Diogenidae)



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ABSTRACT

Behavioral traits can differ between individuals in a population and affect their fitness if they differentially influence survivorship in a microhabitat scale. This may occur when individuals experience different predation risks between microhabitats. In this study, we investigated boldness, exploration, and their correlation depending on the microhabitat of origin in the hermit crab *Clibanarius symmetricus*. Individuals of both sexes were collected from four microhabitats with different levels of predation exposure within the intertidal zone of a mangrove. We conducted experiments introducing the hermit crabs to a new standard environment and simulated predation attempts to assess exploration and boldness. Latency to re-emerge from the shell (boldness) was consistent and not affected by size, sex, or microhabitat type, but was slightly different between years. Exploration, in turn, varied only according to the microhabitat from which individuals were collected. Hermit crabs from the less risky environments explored the experimental arena for longer than individuals from the microhabitat most exposed to predators. This behavioral consistency in exploration activity can influence microhabitat choice in *C. symmetricus*. In addition, boldness and exploration were weakly correlated in a behavioral syndrome. Therefore, predation exposure can be a source of variation in exploration-avoidance personalities and can indirectly influence the expression of boldness in *C. symmetricus*. We conclude that personality traits can coevolve and have implications for habitat choice, but traditional theories of individual behavioral consistency still lack a unified theoretical background linking animal personality to niche specialization with empirical support.

1. Introduction

Populations may differ in behavioral traits because of local ecological conditions and genetic variation (Moura et al., 2019; Sugg et al., 1996). These behavioral differences can also be consistent within a population (Dall et al., 2012; Réale et al., 2007). Between-individual behavioral differences that are consistent in time and across contexts, (i.e., personality) can be heritable and influence fitness if they affect survival and reproductive success (Garamszegi et al., 2012; Purcell and Pruitt, 2019; Smith and Blumstein, 2008). Most studies on animal personality have focused on five axes: shyness-boldness (i.e., individuals' reaction to predation risk), exploration-avoidance (i.e.

individuals' reaction to new circumstances), activity (i.e., individuals' overall activity levels in a familiar environment), aggressiveness (i.e., individuals' agonistic response towards another organism), and sociability (i.e., individuals' propensity to interact with conspecifics) (Réale et al., 2007). Axes of animal personality can coevolve as suites of correlated behaviors (behavioral syndromes; Sih et al., 2004). The behavioral syndromes can also be heritable and reinforce individuals' responses to a particular situation, such as predation attempts, differentially influencing fitness (Garamszegi et al., 2012). The theory of animal personality provides a robust theoretical background to explain much of individual behavioral differences observed in animals but still lacks empirical support for most species and ecological contexts

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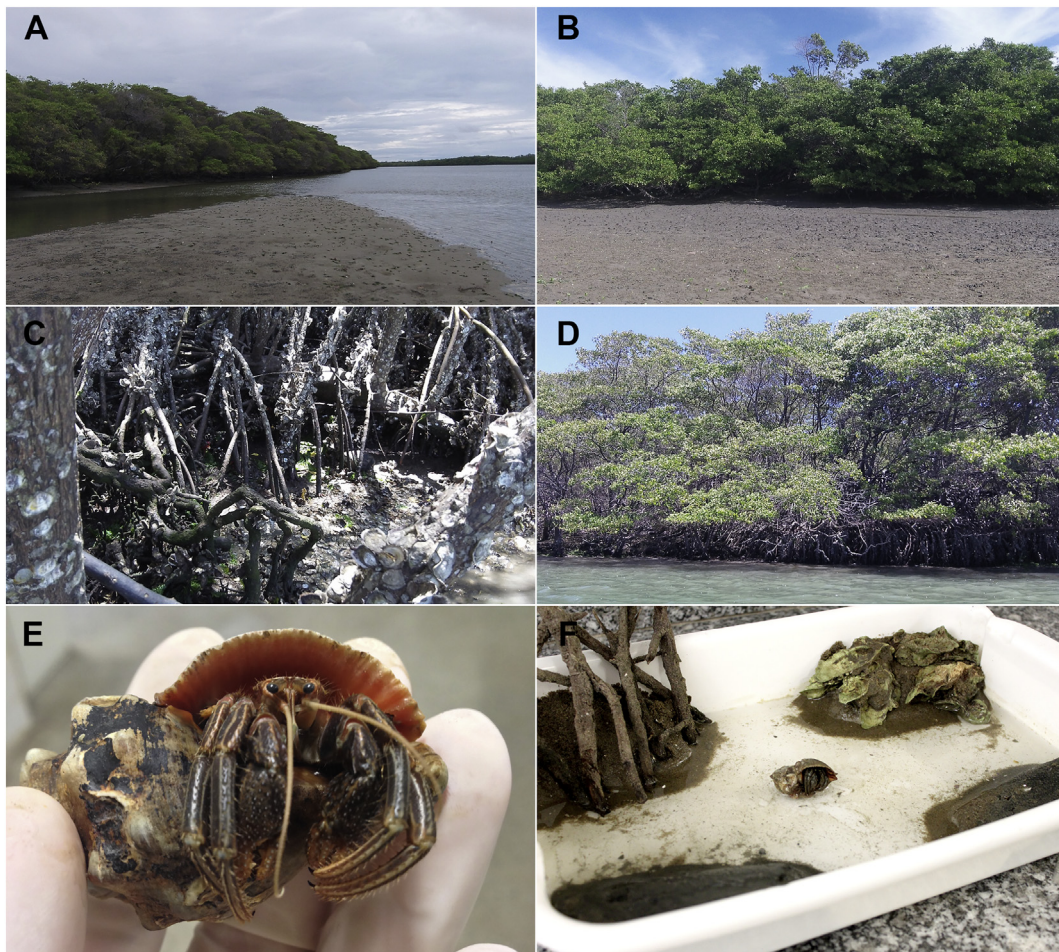


Fig. 1. Substrate types present in a mangrove in the Jaguaribe River Estuary, in the State of Ceará, Brazil: (A) 'sandy', (B) 'muddy', (C) 'muddy with roots', and (D) 'oyster bank'. Individuals of the hermit crab *Clibanarius symmetricus* (E) were collected from each substrate type to conduct laboratory experiments (F).

(DiRienzo and Montiglio, 2015).

Personalities and behavioral syndromes are often affected by sex and body size (Schuett et al., 2010; Sih et al., 2015). For example, females of the delicate skink (*Lampropholis delicata*) are more likely to bask with other skinks and tend to explore the environment faster than males (Michelangeli et al., 2016). Body size differences, in turn, can also influence mating success through asymmetries in the competitive ability of individuals (Moura and Gonzaga, 2017; Vieira and Peixoto, 2013) or their foraging activities (Sih et al., 2015), but may depend on predation exposure. For example, large, well-fed individuals may avoid risky behaviors during foraging activities, whereas smaller, less well-fed individuals may take more risks to obtain food (Sih et al., 2015). This is particularly the case in species in which large body size reduces escape ability, as occurs in the Eurasian blackcap (*Sylvia atricapilla*) (Kullberg et al., 1996). Conversely, larger individuals of the jumping spider *Phidippus princeps* can escape predators better than smaller individuals (Stankowich, 2009). In this situation, bolder explorers may increase energy intake during foraging compared to shy avoidant individuals (Sih et al., 2015), thus improving their competitive ability and their fertility, which can determine the reproductive outcomes of males and females (Luttbeg and Sih, 2010). Therefore, body size and sex can lead to differences in individual personalities within a population and can influence their response to predation exposure.

The association between risk taking and exploratory behaviors is traditionally investigated through risk assessment scenarios, in which individuals are submitted to novel environments with predation cues (Briffa, 2013; Rodríguez-Prieto et al., 2011). Empirical evidence shows that boldness is often correlated with exploration, with bolder

individuals exhibiting more exploratory behaviors (Garamszegi et al., 2012). While bolder explorers would likely be more efficient in acquiring resources, they would also be more at risk of predation (Garamszegi et al., 2012; Smith and Blumstein, 2008). Pronounced morphological defenses in bolder individuals can help compensate for risk-taking activities (Ahlgren et al., 2015). Similarly, bolder and more explorative individuals can reduce predation risk by actively selecting microhabitats less exposed to predators. This behavioral syndrome has been reported for many vertebrate species, such as fish (Fraser et al., 2001; Kotrschal et al., 2014; Wilson and Godin, 2009), birds (van Oers et al., 2004), and lizards (Carazo et al., 2014). However, understanding of personality in vertebrates is greater than that for invertebrate species, despite the latter showing higher diversity as well as potential for displaying personalities (Kralj-Fišer and Schuett, 2014; DiRienzo and Montiglio, 2015).

Most studies on decapod crustaceans have assessed the shyness-boldness personality axis predominantly in hermit crabs (Bridger et al., 2015; Briffa et al., 2008; Gherardi et al., 2012; Mowles et al., 2012). Their short lifetime, low behavioral plasticity, high local abundance, and adaptability to laboratory conditions make them a good model system to investigate animal personalities and behavioral syndromes. Hermit crabs are benthic animals that inhabit different microhabitats in intertidal zones (Turra and Denadai, 2002). Substrate choice is particularly important for the acquisition of both food and shells (Benvenuto et al., 2003) and affects how exposed hermit crabs are to predators (Gorman et al., 2015). Moving between substrates to choose microhabitats with different levels of predation may be a key for survival in hermit crabs (Turra and Denadai, 2003). The patterns of movement

between substrates and the frequency of predation are not strongly affected by sex or body size (Gorman et al., 2015; Turra and Denadai, 2003), but they can result from individual behavioral differences. Thus, it is expected that individuals choose microhabitats with distinct levels of predation exposure depending on their personality traits.

Some studies have suggested personality is affected by predation risk and other environmental variables at the sites of origin (Briffa et al., 2008). *Clibanarius symmetricus* (Randall 1840) is a hermit crab that inhabits distinct microhabitats in the intertidal zones of mangroves along the Brazilian coast (Negri et al., 2014). The spatial heterogeneity of intertidal environments creates distinct scenarios of predation exposure (Fig. 1A-D; see Material and Methods), providing an opportunity to investigate how predation risk can influence personality profiles and behavioral syndromes at a microhabitat scale. In such conditions, bolder explorers may be found more frequently in environments that hinder predator access, whereas shy individuals may be more common in microhabitats with higher exposure to predators. To test this, we collected hermit crabs from microhabitats with different predation exposure levels and conducted experiments in two consecutive years to investigate the following hypotheses: (1) *C. symmetricus* exhibits individual behavioral consistency in boldness and exploration, (2) bolder individuals present a more exploratory personality trait, and (3) behavioral traits differ between individuals according to sex and body size and between individuals found in different microhabitats.

2. Material and methods

2.1. Study area

We collected hermit crabs in a mangrove located in the Jaguaribe River Estuary (04°28'33"S; 37°47'34"W), in the State of Ceará, Brazil. The water temperature typically ranges from 26 to 30 °C and the salinity from 21 to 42‰ (Sabry et al., 2007). The climate in the region is hot and semiarid, classified as Aw according to the Köppen climate classification scheme (Peel et al., 2007). In the estuarine zone, the mean annual precipitation is 982.6 mm, with rainfall concentrated from February to May. The mean annual temperature ranges from 26 to 28 °C (Araújo et al., 2012). The vegetation is marked by the presence of mangroves at different stages of development, such as *Rhizophora mangle* (Rhizophoraceae), *Laguncularia racemosa* (Combretaceae), and *Avicennia schaueriana* (Acanthaceae) (Tanaka and Maia, 2006). The soils can be classified as 'sulfaquents' (Soil Survey Staff, 2010).

2.2. Field collection

We collected 80 adults during low tide in July 2016 and an additional 80 adults in March 2017. We haphazardly sampled 20 buried and exposed hermit crabs from four substrate types ('sandy', 'muddy', 'oyster bank', and 'muddy with roots') in each sampling year. The 'sandy' substrate is potentially the most exposed to predators among the microhabitats sampled because of the absence of environmental protection structures and the driest substrate (Fig. 1A). In the 'muddy' substrate, *C. symmetricus* can dig and hide more easily (Fig. 1B). The 'oyster bank' substrate also presents muddy soil and has oysters covering the substrate, which increases the efficacy of crypsis of individuals (Fig. 1C). Finally, the 'muddy with roots' substrate has an additional defensive barrier: the roots of *Rhizophora mangle*, which may hinder predation attempts (Fig. 1D). Therefore, 'muddy with roots' was considered the most protected substrate from predators. Water levels in the 'oyster bank' and 'muddy with roots' substrates usually cover the organisms found there. Thus, we classified substrate types in the following increasing order of predation exposure: sandy > muddy > oyster bank > muddy with roots. The distances between substrates ranged from 200 to 700 m. We collected samples from all four substrate types for subsequent laboratory trials.

2.3. Laboratory experiments

We housed separately hermit crabs in vivariums (L x W x H = 50 × 40 × 30 cm) containing seawater and the substrate type which they were found in the wild for 24 h before the experiments begin. We conducted the experiments in standardized arenas, which were built using plastic trays (L x W x H = 50 × 40 × 10 cm) containing seawater and samples of each substrate type on the edges (Fig. 1E, F). The experimental arena was tilted by 5° so that one side, containing the 'oyster bank' and 'muddy with roots' substrates, was covered by enough water to submerge the crabs while on the other side substrates remained exposed. During the experiment, the salinity was maintained between 35 and 40‰, and air temperature ranged from 26 to 30 °C. Substrate choice was not reported in this study because it was part of another chapter from F.A.C. Garcia's thesis.

2.4. Boldness and exploration measurements

The experiment began when we manually handled the hermit crab for 10 s to simulate a predation attempt and carefully placed the individual in the center of the experimental arena with the shell opening facing up. We simultaneously recorded the time that the experiment started for each individual, totaling 80 arenas with hermit crabs. We then recorded the time taken by the hermit crab to re-emerge from its shell after the simulation of a predation attempt ('re-emergence time': a proxy for boldness) and the total time the individual spent moving around the arena during a 15 min period ('duration of exploration': a proxy for exploration) (Briffa et al., 2008; Réale et al., 2007). For obtaining this latter measure, we paused the timer when the individual stopped moving around the experimental arena and restarted the timer when it moved again. We finished the observations after 15 min, because most individuals were more active during this period of time in the pilot experiments.

We simultaneously recorded behavioral responses of hermit crabs in four experimental arenas. After each trial, we returned the hermit crabs to their vivariums. The experiment lasted 10 days, during which the same procedure was repeated each day. In March 2017, we repeated the same procedures and collected additional 80 new individuals. However, 22 out of the 80 collected individuals died during experiments. Therefore, their data were excluded from subsequent statistical analyses.

2.5. Sex and body size measurements

At the end of the experiments in each year, we euthanized individuals in a refrigerator with temperature of -20 °C in order to determine sex and cephalothorax area. We identified the sex by analyzing the position of the gonopore. We excluded data from three individuals collected in 2016 because we could not identify their sex. We measured the length (*l*) and width of the cephalothorax (*w*) using a digital caliper to estimate the cephalothorax area (*S*) as an ellipse: $S = 3.14 * l * w$.

2.6. Statistical analyses

To evaluate whether the re-emergence time and the duration of exploration of hermit crabs were consistent throughout time, we used two general linear mixed models (LMM). We calculated the repeatability (*r*) for the individual identity (random variable) using the re-emergence time and the square root of the duration of exploration as response variables in each model and substrate type, sampling year, cephalothorax area, and sex as predictors. We performed these analysis using 1000 parametric bootstraps for interval estimation and 1000 permutations to calculate asymptotic *p*-values in the 'rptR' function from the 'rptR' package (Stoffel et al., 2017).

To investigate potential sources of variation in boldness of the hermit crabs, we conducted a model selection of LMMs including the re-

emergence time as the response variable and the duration of exploration, substrate type, sampling year, cephalothorax area, and sex as predictors. We adopted a similar approach to evaluate potential effects of substrate type, sampling year, cephalothorax area, and sex (predictors) on the square root of the duration of exploration (response variable). In both models, we included the individual identity and sampling day as random variables. We performed model selections using the “dredge” function from the ‘MuMIn’ package (Barton, 2019) and compared the adjustment of the alternative models and the null-effect model using the Akaike Information Criterion corrected for small samples (AICc) (Burnham and Anderson, 2002). In the first step, we considered as good models all those presenting the smallest AICc values, within a range of 2.0 AICc from the lowest value, because this approach provides the best explanation(s) for the variation observed in the data (Burnham and Anderson, 2002). In the second step, we chose as the best model the one including the lowest number of additional parameters because additional predictor variables do not necessarily increase the explanatory power (see Burnham and Anderson, 2002; namely ‘uninformative parameters’, sensu Arnold, 2010). For each LMM, we calculated R_m^2 as a measure of goodness of fit for predictor variables, and R_c^2 as a measure of goodness of fit for the entire model, including random variables (Nakagawa and Schielzeth, 2013). We performed LMM with ‘lmer’ function from the ‘lme4’ package (Bates et al., 2015). We built bar graph using the “lineplot.CI” function from “sciplot” package (Morales and Development Core Team, 2017). All data analyses were conducted in R software, version 3.6.2 (R Development Core Team, 2020).

3. Results

We sampled 135 individuals (54 males and 23 females in 2016, and 43 males and 15 females in 2017) and performed a total of 1350 trials. All the hermit crabs used shells of *Pugilina tupiniquim* (Gastropoda, Melongenidae) and *Stramonita brasiliensis* (Gastropoda, Muricidae) as shelters (Fig. 1E). Cephalothorax measurements showed an average width of 14.97 ± 0.25 mm ($\bar{X} \pm S.E.$), a length of 8.79 ± 0.18 mm, and an area of 106.29 ± 3.64 mm². Re-emergence time was on average 178.31 ± 0.06 s, while the mean duration of exploration was 42.6 ± 0.03 s. The hermit crabs consistently exhibited similar re-

emergence times ($r = 0.32 \pm 0.04$, CI = 0.25 to 0.39, $P = .001$; Fig. 2A) and durations of explorations ($r = 0.08 \pm 0.02$, CI = 0.04 to 0.12, $P = .001$; Fig. 2B).

The model that best explained re-emergence time included the duration of exploration and sampling year as predictors (Table 1). Re-emergence time was negatively related to the duration of exploration (Table 2). The removal of two outliers with the duration of exploration greater than 300 s did not influence this relationship ($\beta = -0.15$, 95%CI = -0.24 to -0.06). In addition, re-emergence time was 1.3 times higher in 2017 (206.83 ± 0.16 s) than in 2016 (153.61 ± 0.14 s; Table 2). Individual identity and sampling day were responsible for most of the variance explained in the model ($R_c^2 = 0.39$) compared to fixed predictors ($R_m^2 = 0.07$). The model that best explained the variability in the square root of duration of exploration contained only the substrate type (Table 1). The duration of exploration was higher for individuals collected from the most hidden substrate type (i.e., mud with roots substrate) compared to the other substrates (Table 2; Fig. 3). Most variation was explained by the random variables ($R_c^2 = 0.11$, $R_m^2 = 0.02$). The hermit crabs from the most exposed microhabitat (i.e., sandy and muddy substrates) exhibited approximately 1.3 times longer duration of exploration than individuals from muddy with roots substrate (Fig. 3).

4. Discussion

The hermit crab *C. symmetricus* exhibited individual behavioral consistency in boldness and exploration in a risk assessment scenario. These personality traits were positively correlated in which bold individuals explore more, supporting the existence of a behavioral syndrome. Boldness was consistent regardless of body size, sex, or across their original microhabitats, but varied depending on sampling year. Exploration was temporally consistent and did not differ depending on body size and sex but varied according to the substrate type from which individuals were collected. Hermit crabs from the high-risk environments explored the experimental arena for longer than individuals from the microhabitats less exposed to predators. Therefore, exposure to predation can be a source of variation in the exploration-avoidance personality axis and indirectly influences the expression of boldness in *C. symmetricus*.

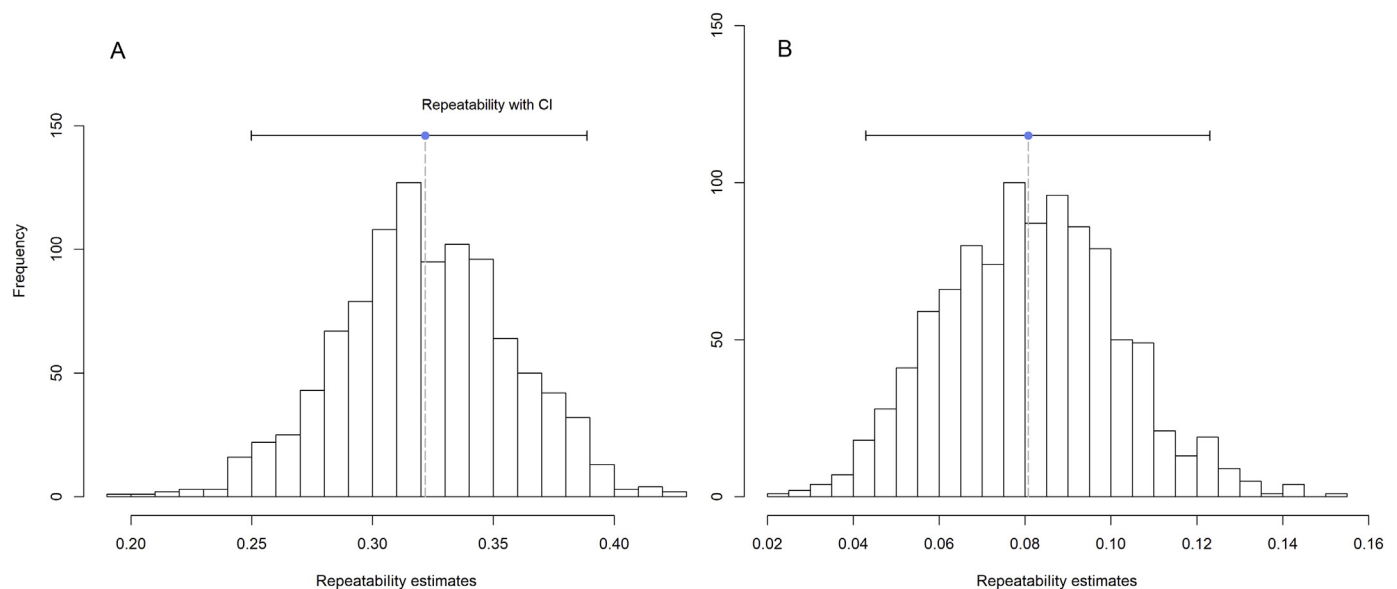


Fig. 2. Histograms of repeatability estimates (r) for general linear mixed models. For the models, re-emergence time (A) and the square root of duration of exploration (B) were input as response variables, substrate type, sampling year, cephalothorax area, and sex as predictors, and the individual identity as a random variable. The blue points correspond to means and the bars represent 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Comparisons between general linear mixed models for re-emergence time (in gray) and the square root of duration of exploration (in white) of the hermit crab *Clibanarius symmetricus*.

Predictor	Candidate models	AICc	Δ AICc	K	ω_i
Re-emergence time (s)	Y + DE	15,967.5	0.0	6	0.4
	Y + DE + SX	15,968.1	0.6	7	0.3
	Y + DE + CW	15,969.5	2.0	7	0.1
	Y + DE + SX + CW	15,970.1	2.6	8	0.1
	Y + DE + ST	15,971.4	3.9	9	0.1
	Y + DE + SX + ST	15,972.5	5.0	10	0.0
	Y + DE + CW + ST	15,973.3	5.9	10	0.0
	Y + DE + SX + CW + ST	15,974.5	7.0	11	0.0
	Y	15,977.9	10.4	5	0.0
	Y + SX	15,978.3	10.8	6	0.0
	Y + CW	15,979.8	12.4	6	0.0
	Y + SX + CW	15,980.3	12.9	7	0.0
	Y + ST	15,981.6	14.1	8	0.0
	Y + SX + ST	15,982.7	15.2	9	0.0
	Y + CW + ST	15,983.6	16.1	9	0.0
	Y + SX + CW + ST	15,984.7	17.2	10	0.0
	DE	15,986.3	18.8	5	0.0
	DE + SX	15,987.5	20.0	6	0.0
	DE + CW	15,988.1	20.6	6	0.0
	DE + SX + CW	15,989.4	22.0	7	0.0
	DE + ST	15,989.6	22.1	8	0.0
	CW	15,991.0	23.6	9	0.0
	SX + DE + ST	15,991.1	23.6	9	0.0
	SX + DE + CW + ST	15,992.7	25.2	10	0.0
	Null Model	15,998.3	30.8	4	0.0
	SX	15,999.4	31.9	5	0.0
	CW	16,000.0	32.6	5	0.0
	SX + CW	16,001.3	33.8	6	0.0
	ST	16,001.5	34.1	7	0.0
	CW + ST	16,003.0	35.5	8	0.0
	SX + ST	16,003.0	35.6	8	0.0
	SX + CW + ST	16,004.7	37.2	9	0.0
	ST + Y	7616.1	0.0	8	0.3
ST	7617.2	1.1	7	0.2	
ST + Y + SX	7617.9	1.9	9	0.1	
ST + Y + CW	7618.0	1.9	9	0.1	
ST + SX	7619.1	3.0	8	0.1	
ST + CW	7619.2	3.1	8	0.1	
ST + Y + SX + CW	7619.8	3.8	10	0.0	
ST + SX + CW	7621.1	5.0	9	0.0	
Y	7624.5	8.4	5	0.0	
Y + SX	7624.7	8.6	6	0.0	
Null Model	7624.8	8.7	4	0.0	
SX	7625.2	9.1	5	0.0	
Y + CW	7626.5	10.4	6	0.0	
CW	7626.6	10.6	5	0.0	
Y + SX + CW	7626.7	10.6	7	0.0	
SX + CW	7627.2	11.1	6	0.0	

The individual identity was included as a random variable. The predictors were the duration of exploration (DE), carapace area (CA), sex (SX), substrate type (ST), and sampling year (Y). The models that best fit the data are highlighted in bold and italic.

Note: Models are ranked by increasing sample size based on the Akaike Information Criterion corrected for small samples (AICc). Δ AICc = the difference between the AICc value of each model and the AICc value of the most parsimonious model, K = the number of parameters, and ω_i = AICc weight of each model. The + symbol represents the additive effect of variables.

The level of boldness in *C. symmetricus* showed some inconsistencies between years but was more consistent than the degree of exploration. Empirical evidence suggests that bolder individuals may obtain high reproductive success but also experience high mortality rates (Smith and Blumstein, 2008). Therefore, this behavioral trait can have important implications for resource acquisition in a competitive context and appears to not be affected by predation risk. In *C. symmetricus*, bolder individuals can benefit from obtaining large shells, which are often a limited resource (Rodrigues and Martinelli-Lemos, 2016). Shell size has significant impacts on individuals' growth capacity, which can

affect male fertility and female fecundity (Osorno et al., 1998). Consequently, the benefits of obtaining a large shell can compensate the risk of being attacked in the process, especially under intense competition over limited resources, which can be higher in dense populations. The benefits of resource acquisition depending on microhabitat type remains a hypothesis to be investigated in a future study.

Bold individuals were also more likely to explore the new environment for the longest period, while shy individuals tended to remain less active. This behavioral syndrome could be part of a shyness-boldness axis (Sih et al., 2004) in which bold individuals may increase risk-taking behavior such as exposing themselves to predators more rapidly and exploring the arena for longer to obtain more information about their surroundings (Briffa, 2013; Greenberg and Mettke-hofmann, 2001; Rodríguez-Prieto et al., 2011). However, the correlation between boldness and exploration was weaker than expected. This result is similar to the findings of a meta-analysis on behavioral syndromes, in which phenotypic correlations were found to be generally weak and possibly prone to variation depending on the ecological context (Garamszegi et al., 2012). Similarly, boldness and exploration may vary more independently between hermit crabs. This situation is often called syndrome deviation in which individuals may benefit from adjusting their behavioral traits depending on specific environmental contexts (Herczeg and Garamszegi, 2012). For example, in another hermit crab species, *Pagurus bernhardus*, individuals consistently show similar startle response durations (a personality trait), but all individuals remain within the shell for longer in the presence of predation cues than in scenarios without cues (Briffa, 2013). This may also be the case for *C. symmetricus*. To test this prediction, further studies could evaluate personality traits of *C. symmetricus* in contexts with and without predation cues.

The exploratory behavior differed between hermit crabs collected from environments with different levels of predation exposure. In a closely related species, *C. vitlatus*, individuals roam on average 156 m a day, ranging from 13 to 761 m (Hazlett, 1995). Substrate selection has also been observed in other *Clibanarius* species, such as *C. antillensis* and *C. scopetarius* (Turra and Denadai, 2002). Therefore, the differences observed in exploration behavior in *C. symmetricus* can be attributed to habitat choice rather than selection driven by ecological differences between microhabitats. In such situations, individuals may actively select microhabitats based on their exploratory personalities. *Clibanarius symmetricus* was more likely to explore a new environment longer if an individual came from the most exposed microhabitats. This exploratory behavior may benefit individuals during the evaluation of the microhabitat, especially because they may respond faster to environmental changes and move to a more suitable microhabitat. In addition, they may increase resource acquisition if substrate types differ in resource availability, such as shell abundance, food supply availability, population density, and mating opportunities.

There is an ongoing debate on how individual behavioral specializations should be classified and which underlying mechanisms may promote between-individual variance. However, all theoretical approaches agree that suites of individuals can behave similarly across contexts and over time and such consistency can be adaptive and evolve through selection (Dall et al., 2012; Schuett et al., 2010). Animal personality theory can identify within- and between-individual behavioral consistencies to help investigate correlated personality traits in behavioral syndromes (Gherardi et al., 2012; Sih et al., 2004). However, there is still a lack of empirical evidence for most animals, particularly invertebrates (Kralj-Fišer and Schuett, 2014), and ecological contexts (Dall et al., 2012). In this study, we provide consistent evidence for boldness and exploration as well as their correlation in a risk assessment context for the hermit crab *C. symmetricus*. Our findings highlight the potential for new discoveries in invertebrate species, such as personality traits, behavioral syndromes, and their variation depending on ecological context (Gherardi et al., 2012; Kralj-Fišer and Schuett, 2014). We also propose a link between personality types and habitat

Table 2

Coefficients (intercepts and slopes) with 95% confidence interval from the best general linear mixed models for re-emergence time and the square root of duration of exploration.

Variables		β	95% Confidence Intervals	
Response	Predictor		2.50%	97.50%
Re-emergence time	Intercept (Year – 2016)	160.95	143.36	178.56
	Duration of exploration	–0.15	–0.24	–0.07
	Year (2017)	50.52	29.49	71.56
Square root of duration of exploration	Intercept (Substrate type – Sandy)	5.36	4.7	6.02
	Substrate type (Muddy)	–0.12	–0.91	0.68
	Substrate type (Oyster Bank)	–0.99	–2.18	–0.47
	Substrate type (Muddy with roots)	–1.33	–1.77	–0.21

The individual identity and sampling day were included as random variables in both models.

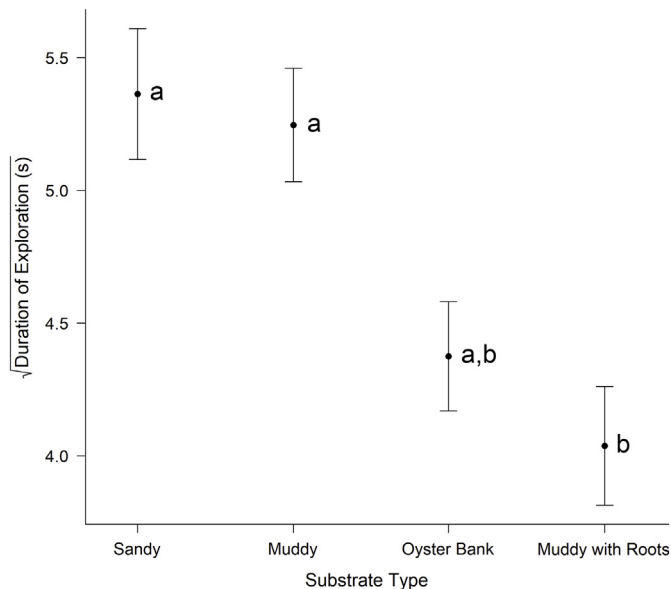


Fig. 3. (A) The relationship between re-emergence time and duration of exploration; (B) the difference in re-emergence time between individuals collected in 2016 and 2017.

choice. However, our theoretical background is limited to understanding interactions between animal personality and niche specialization theories (Dall et al., 2012). Thus, we highlight the need for an evolutionary ecological theory of individual differences that explains and predicts the within- and between-individual consistencies of multiple behaviors in various conditions, associated with robust empirical evidence on understudied animal taxa.

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Declaration of Competing Interest

The authors declare that they have no conflict of interest.

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