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Shell occupation by the land hermit crab *Coenobita violascens* (Anomura, Coenobitidae) from Phuket Island, Thailand

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ABSTRACT

Shell occupation by the land hermit crab *Coenobita violascens* Heller, 1862 was investigated from January 2011 to March 2012 on Phuket Island in the Andaman Coast of Thailand. The samples of *C. violascens* were collected monthly using multiple quadrat sampling. Twenty shell species from 11 families were found occupying by *C. violascens*, which were mainly marine gastropods (90%). The three most common occupied shell species were *Chicoreus brunneus* (Link, 1807) (21.3% of hermits), followed by *Filifusus filamentosus* (Röding, 1798) (14.9%) and *Laevistrombus canarium* (Linnaeus, 1758) (14.9%). Biconical shells and those with ovate apertures were the most commonly occupied shell types. Furthermore, individual *C. violascens* probably occupy the shells of at least three different gastropod species during their lifetime. Interestingly, *C. violascens* shows a tendency of occupying specific categories of shells in relation to shell species, shape and aperture shape. Other aspects of shell occupation by *C. violascens* compared to congeneric species are also discussed.

KEY WORDS

Shell use, shell quality, terrestrial hermit crab.

INTRODUCTION

Land hermit crabs are the most common crustaceans in many tropical and subtropical coastal areas and islands in Western Atlantic, Indo-Pacific, and Eastern Pacific regions (Page and Willason, 1982; Wolcott, 1988; Morrison, 2005). These hermit crabs function as generalist scavengers in coastal ecosystems, accelerating the recycling of nutrients and transfer of energy in food chain (Laidre, 2013). In addition, land hermit crabs are a critical component in the supralittoral zones of coastal and insular areas (Morrison and Spiller, 2006).

Land hermit crabs occupy discarded shells as mobile shelters to protect their soft and fragile abdomens from environmental stresses (Wolcott, 1988). Therefore, shells are crucial resources for land hermit crab life. The

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benefits of using shells as refuges by these crabs include protection from desiccation and predators (Greenaway, 2003). Additionally, land hermit crabs are able to replenish water into internal space of their occupied shells to maintain body moisture, allowing them to forage further inland (Wilde, 1973).

Several studies have reported correlations between occupied shell characters and hermit crab morphological characteristics (*e.g.* shell size and weight, aperture size, internal volume) (Hazlett, 1981; Boneka *et al.*, 1995; Sallam *et al.*, 2008; Bundhitwongrut *et al.*, 2015). Empty shells probably are a limiting resource for certain hermit crab populations (Fotheringham, 1976; Kellogg, 1976; Laidre, 2012). In addition, occupied shells possibly affect growth, reproduction, and risk of predation (Blackstone, 1985; Osorno *et al.*, 2005; Sallam *et al.*, 2008; Contreras-Garduno *et al.*, 2009; Sallam, 2012). Furthermore, shell resources for hermit crabs in different areas influence particular characteristics of their populations, such as abundance, size and reproduction (Fotheringham, 1976; Sallam *et al.*, 2008).

The shell utilization patterns of land hermit crabs have been studied in several areas of the world: *e.g.* the western Atlantic by Morrison and Spiller (2006); the eastern Pacific by Abram (1978), Guillen and Osorno (1993) and Laidre and Vermeij (2012); North Pacific by Willason and Page (1983) and Szabo (2012); the western Pacific by Boneka *et al.* (1995); Red Sea by Volker (1967), Sallam *et al.* (2008) and Sallam (2012); and the western Indian Ocean by Barnes (1999; 2001; 2002). Although a recent investigation by Bundhitwongrut *et al.* (2015) was carried out on shell use by *Coenobita rugosus* H. Milne Edwards, 1837 at Cape Panwa of Phuket Island in the Andaman Sea, eastern Indian Ocean, little is known about shell occupation by other land hermit crabs in this area. There are 382 gastropod mollusc species recorded from the Andaman coast of Thailand including Cape Panwa (Tantanasiriwong, 1978). However, intense shell exploitation and trade in both local and imported mollusks have been reported from Phuket Island (Aungtonya and Tantichodok, 1991; Aungtonya and Hylleberg, 1992; Aungtonya and Khokiattiwong, 1992; Bussarawit, 1995). In addition, unoccupied shells in good condition are scarce in the supralittoral zone of this site (Bundhitwongrut *et al.*, 2015). These situations presumably influence shell resources for land hermit crabs in the area.

Seventeen valid species of land hermit crabs in the genus *Coenobita* Latreille, 1829 have been recognized throughout the world (De Grave *et al.*, 2009; McLaughlin *et al.*, 2010; Rahayu *et al.*, 2016). *Coenobita violascens* Heller, 1862 is distributed in the Indo-Pacific region from the east coast of Africa to the Philippines and Japan (McLaughlin *et al.*, 2007). McLaughlin (2002) reported the occurrence of *C. violascens* from coasts of the Andaman Sea and Gulf of Thailand. *Coenobita violascens* mainly inhabits beaches and areas associated with mangroves (Nakasone, 1988; McLaughlin *et al.*, 2007; Doi *et al.*, 2016). Limited information on the life history of *C. violascens* has been known and recorded. Only some recent studies on *C. violascens* have been recently reported, including functional morphology related to water uptake (Becchi *et al.*, 2015), emigration behavior and molting during the sea-to-land transition (Hamasaki *et al.*, 2015a), larval development under laboratory conditions (Hamasaki *et al.*, 2015b; Kato *et al.*, 2015), larval release and tree-climbing behavior (Doi *et al.*, 2016) and thermal adaptation of embryos (Hamasaki *et al.*, 2016). The objectives of the present study are to reveal shell occupation and the relationship between the characteristics of occupied shells and crab characteristics of *C. violascens* at Cape Panwa, Phuket Island, Andaman coast of Thailand.

Materials and Methods

Study area

The study site was Cape Panwa (7°48’26”N 98°24’35”E) in the southeast part of Phuket Island on the Andaman coast of Thailand. The climate is wet tropical and is influenced by the wet southwesterly monsoon from May to October and the dry northeasterly monsoon from November to April (Khokiattiwong *et al.*, 1991). The study site is exposed to the semidiurnal tide with amplitude of 2.15–2.27 m at spring tide to 0.85–1.15 m at neap tide (Limpsaichol, 1981). The study beach was located in the supralittoral zone in the area of the Phuket Marine Biological Center (PMBC). This beach is behind the office of PMBC. The width of this beach is about 50 m and the distance between the mean sea level and the PMBC office is approximately 45 m. The beach is characterized by open sand scrub vegetation, consisting of rather coarse sand patches of shale or phylitte (Nielsen, 1976a). The inland side is covered with dense vegetation alternating with sparse vegetation in front of a steep cliff. A map of the study area and environmental data during the study period are given in Bundhitwongrut *et al.* (2014).

Specimen sampling and analysis

The sampling period was from January 2011 to March 2012. *Coenobita violascens* was collected three days per month. The hermit crabs were collected by hand by the same person (the author) at low tide from the supralittoral area in the early morning (Sallam *et al.*, 2008). The sampling technique used in this study was multiple quadrat sampling (Barnes, 1999). Four temporary line transects were randomly placed at 15-m intervals perpendicular to the shoreline from the supralittoral zone to the inland area. Moreover, 16 temporary quadrats of area 1 m^2 were placed at 5-m intervals on transects from 5 m above the mean sea level to 45 m further inland. Five to six quadrats were sampled on each sampling day. Quadrats with 10-cm high walls were used to prevent the agile crabs from escaping.

All hermit crabs sampled were brought to the laboratory of PMBC. Each hermit was carefully pulled out of its occupied shell while holding the crab in the air and waiting until most of its body extended from the shell in order to investigate the crab and its inhabited shell characters. If the crab's uropods still held onto inside the shell, especially those inhabiting shells with a long spire, a metal wire was used to tickle the crab's abdomen to induce it to vacate the shell. To avoid negative impacts on native animals, removal of crabs from the population at the study area was not permitted according to the policy of the PMBC. Furthermore, the current sampling method prevented unnecessary hermit mortality in order to preserve this population of *C. violascens*. Consequently, all hermits were allowed to reinhabit their previously-occupied shells after the observations, and they were kept in several aquaria with food and water until the investigations were finished in each sampling month.

The additional marking method following Bundhitwongrut *et al.* (2015) was used in this study. All sampled hermits were marked after investigation in each sampling month before being released into the natural habitat from where they were collected. To prevent cheliped and pereiopod autotomy, each hermit was gently held and marked after being pulled from its shell. The markings were made with a waterproof pen and then coated with nail varnish on the outer surface of both major cheliped of each hermit and the body whorl near the outer lip of its occupied shell. In every month, if recaptured hermits were found, they were marked again.

Measurement and investigation of characters of *C. violascens* were carried out, including cephalothoracic shield length (CSL) and width (CSW), major chela length (MCL) and width (MCW), weight (CW), sex and reproductive stage (male, non-ovigerous female and ovigerous female). Species of occupied shells were identified according to several references (Brandt, 1974; Nielsen, 1976b; Tantanasiriwong, 1978; Middelfart, 1997; Poutiers, 1998). Additionally, those shells were compared with specimens deposited in the reference collection of PMBC to confirm their identities. Quantitative shell characters were measured and examined, including shell length (SL) and width (SW), weight (WW), internal volume (SIV), aperture length (SAL) and width (SAW). The internal volume of shells was evaluated using a graduated syringe (Floeter *et al.*, 2000). All quantitative measurements were recorded to the nearest 0.01 mm for size using digital vernier calipers, 0.01 g for weight using digital weighing scales, and 0.1 ml volume using graduated syringes.

Qualitative shell characters were examined, including shell shape, aperture shape and shell quality. The shell and aperture shapes were categorized following Bundhitwongrut *et al.* (2015). The categories of shell shapes consisted of biconical, conical, elongately conical, fusiform, globose, oval, pyramidal, pyriform, turban and vermiform. The categories of shell aperture shapes comprised elongately ovate, irregular, ovate, round and semicircular. The categories of shell damage were undamaged and damaged. Damaged shells were shells with a hole, a broken apex, damaged inner lip of the body whorl, or greater damage in a large portion of the shell (Barnes, 1999). Moreover, the value of shell internal volume per weight (SIV/W ratio) was calculated for each shell inhabited by individuals of *C. violascens* as a predictor of shell quality (Osorno *et al.*, 1998).

Statistical analysis

If recaptured *C. violascens* were found, their data were excluded to avoid possible pseudoreplicates. Individuals of *C. violascens* were separated into groups according to sex and reproductive stage as male, female, non-ovigerous female, or ovigerous female. Hermits were categorized into 0.5-mm CSL size classes to facilitate the comparison in shell use as a function of hermit crab size according to Nakasone (2001) and Bundhitwongrut *et al.* (2014). Regression analysis was utilized to determine relationships between quantitative characters of hermit crabs and occupied shells using the power function equation ($Y=a.X^b$) (Sallam *et al.*, 2008; Bundhitwongrut *et al.*, 2015). The critical significance level adopted in all statistical tests was $p < 0.05$. SPSS Statistics 17.0 (SPSS Inc., 2008) was used to carry out all statistical analyses.

Results

A total of 47 individuals of *C. violascens* were collected, including 26 males (55.3%) and 21 females (44.7%) [19 non-ovigerous females (40.4%) and 2 ovigerous females (4.3%)]. The mean CSL size ± SD and size range (minimum–maximum) was 8.81 ± 3.43 (2.99–15.73) mm for all individuals, 9.69 ± 3.74 (3.39–15.73) mm for males, 7.72 ± 2.71 (2.99–11.77) mm for all females, 7.51 ± 2.77 (2.99–11.77) mm for non-ovigerous females and 9.70 ± 0.08 (9.64–9.76) mm for ovigerous females. The number of *C. violascens* collected in each monthly sampling varied from 0 (February 2012) to 6 (January and July to September 2011). No recaptured individual was found during the study period.

Diversity and groups of occupied shells

Coenobita violascens was found occupying 20 species of gastropod shells of 11 families in different percentages. Main species composition of occupied shells was marine gastropods (90%, 18 species), whereas only one species was a freshwater gastropod [*Pomacea canaliculata* (Lamarck, 1819)] and another species was a mangrove pulmonate gastropod [*Ellobium aurisjudae* (Linnaeus, 1758)]. The shell family with the highest number of species occupied by *C. violascens* was Muricidae (30%; 6 species), followed by Turbinidae (15%; 3 species).

Shell species occupied in relation to hermit reproductive groups

The shell occupation of *C. violascens* varied in relation to shell species (Tab. 1). The most-occupied shell species was *Chicoreus brunneus* (Link, 1807) (21.3 %), followed by *Filifusus filamentosus* (Röding, 1798) (14.9 %) and *Laevistrombus canarium* (Linnaeus, 1758) (14.9 %).

Males occupied 15 shell species while females inhabited 11 shell species (Tab. 1). Both sexes occupied six shell species (30% of total shell species occupied), which were *Chicoreus brunneus*, *Clypeomorus batillariaeformis* Habe & Kosuge, 1966, *Drupella rugosa* (Born, 1778), *F. filamentosus*, *L. canarium* and *Menathais tuberosa* (Röding, 1798). Males mostly inhabited shells of *F. filamentosus* (23.1%), followed by *L. canarium* (15.4%). Females mainly occupied shells of *Chicoreus brunneus* (38.1%), followed by *L. canarium* (14.3%). Non-ovigerous females were found occupying 10 shell species and ovigerous females were found inhabiting 2 species (Tab. 1).

Shell species occupied in relation to hermit size

Shell occupation of *C. violascens* varied in relation to hermit size (Fig. 1). The high diversity of shell species inhabited was found in hermits at size 11.0–11.5 mm CSL (5 species), followed by 6.0–6.5 mm CSL (4 species), and 10.5–11.0 and 11.5–12.0 mm CSL (3 species). Hermits in other size classes (2.5–6.0, 6.5–8.5, 9.0–10.5, 12.0–14.0 and 15.0–16.0 mm CSL) occupied 1–2 shell species.

The most-occupied shell species, *Chicoreus brunneus*, was inhabited by medium-sized hermits (6.5–7.5, 8.0–8.5, 9.0–10.0 and 11.0–12.0 mm CSL) (Fig. 1). Smallest hermits occupied shells of *Clypeomorus batillariaeformis* (2.5–3.5 mm CSL) and *Drupella rugosa* (3.0–4.5 mm CSL). Shells of *L. canarium* were occupied by small- (5.0–6.5 mm CSL) and medium-sized hermits (9.0–9.5 and 10.5–11.5 mm CSL), whereas *F. filamentosus* shells was inhabited by a wide range of size classes of hermits (4.0–4.5, 10.5–11.0, 11.5–12.5 and 15.0–15.5 mm CSL).

Shell occupation in relation to shell shape

Shell occupation of *C. violascens* varied in relation to shell shape (Tab. 2). All hermits occupied seven

Table 1. Percentage and mean SIV/W ratio of shell species inhabited by *Coenobita violascens* at Cape Panwa, Phuket Island, from January 2011 to March 2012. The numbers in parentheses after the percentage of shells occupied are the numbers of crab individuals. SIV/W = shell internal volume/weight ratio as mean ± SD for species that N > 1 and as value for species that N = 1.

Shell species	Family	Males	Non-ovigerous females	Ovigerous females	Total	SIV/W
Angaria delphinus (Linnaeus, 1758)	Turbinidae	3.8 (1)	-	-	2.1 (1)	0.253
Bufonaria rana (Linnaeus, 1758)	Bursidae	3.8 (1)	-	-	2.1 (1)	1.008
Cantharus tranquebaricus (Gmelin, 1791)	Buccinidae	-	5.3 (1)	-	2.1 (1)	0.308
Cerithidea obtusa (Lamarck, 1822)	Potamididae	-	5.3 (1)	-	2.1 (1)	0.457
Chicoreus brunneus (Link, 1807)	Muricidae	7.7 (2)	36.8 (7)	50.0 (1)	21.3 (10)	0.213 ± 0.056
Chicoreus ramosus (Linnaeus, 1758)	Muricidae	7.7 (2)	-	-	4.3 (2)	0.785
Clypeomorus batillariaeformis Habe & Kosuge, 1966	Cerithiidae	3.8 (1)	5.3 (1)	-	4.3 (2)	0.366 ± 0.002
Drupella rugosa (Born, 1778)	Muricidae	7.7 (2)	10.5 (2)	-	8.5 (4)	0.269 ± 0.065
Ellobium aurisjudae (Linnaeus, 1758)	Melampidae	-	5.3 (1)	-	2.1 (1)	1.054
Filifusus filamentosus (Röding, 1798)	Fasciolariidae	23.1 (6)	5.3 (1)	-	14.9 (7)	0.492 ± 0.191
Laevistrombus canarium (Linnaeus, 1758)	Strombidae	15.4 (4)	15.8 (3)	-	14.9 (7)	0.870 ± 0.241
Menathais tuberosa (Röding, 1798)	Muricidae	3.8 (1)	5.3 (1)	-	4.3 (2)	0.454 ± 0.006
Mirabilistrombus listeri (Gray, 1852)	Strombidae	-	5.3 (1)	-	2.1 (1)	0.704
Monodonta labio (Linnaeus, 1758)	Trochidae	3.8 (1)	-	-	2.1 (1)	0.471
Murex trapa Röding, 1798	Muricidae	3.8 (1)	-	-	2.1 (1)	0.849
Pollia undosa (Linnaeus, 1758)	Buccinidae	3.8 (1)	-	-	2.1 (1)	0.725
Pomacea canaliculata (Lamarck, 1819)	Ampullariidae	3.8 (1)	-	-	2.1 (1)	4.604
Thalessa virgata (Dillwyn, 1817)	Muricidae	-	-	50.0 (1)	2.1 (1)	0.354
Turbo argyrostomus Linnaeus, 1758	Turbinidae	3.8 (1)	-	-	2.1 (1)	0.514
Turbo bruneus (Röding, 1798)	Turbinidae	3.8 (1)		-	2.1 (1)	0.193

categories of shell shape, including biconical, elongately conical, fusiform, globose, oval, pyriform and turban. Biconical shells (53.2%) were the most-occupied shell shape, followed by fusiform shells (19.1%). Males were found occupying all seven shapes of shells, while females occupied fewer categories of shell shapes (4 shapes). Non-ovigerous females were found occupying four categories of shell shape (biconical, elongately conical, fusiform and oval) and ovigerous females were found inhabiting two shapes (biconical and oval).

Shell occupation in relation to shell aperture shape

Shell occupation of *C. violascens* varied in relation to shape of shell aperture (Tab. 3). All *C. violascens* occupied four categories of shell aperture shape, including elongately ovate, irregular, ovate and round. Shells with ovate apertures (74.5%) were the most-occupied by all crabs. Males and non-ovigerous females were found occupying all four aperture shapes and ovigerous females were found inhabiting one aperture shape (ovate).

Shell occupation in relation to shell damage

All *C. violascens* occupied undamaged shells (46.8%) slightly fewer than damaged shells (53.2%). Males and non-ovigerous females were found occupying both damaged and undamaged shells and ovigerous females were found inhabiting only undamaged shells.

Shell occupation in relation to SIV/W ratio

The range of SIV/W values of shell inhabited by *C. violascens* was 0.120–4.604 (Tab. 1). According to the ratio of SIV/W, the most-occupied shell species at the study area was not the lightest shell species. *Chicoreus brunneus*, the most-occupied shell species, had a SIV/W ratio (mean ± SD) equal to 0.213 ± 0.056, but had a very low ranking SIV/W ratio (19th out of 20 shell species). However, the lightest-occupied shell species was *P. canaliculata* with a SIV/W ratio equal to 4.604, but ranked 8th in terms of occupation by *C. violascens*.

Relationship between crab and shell characteristics

The relationship between characters of *C. violascens*

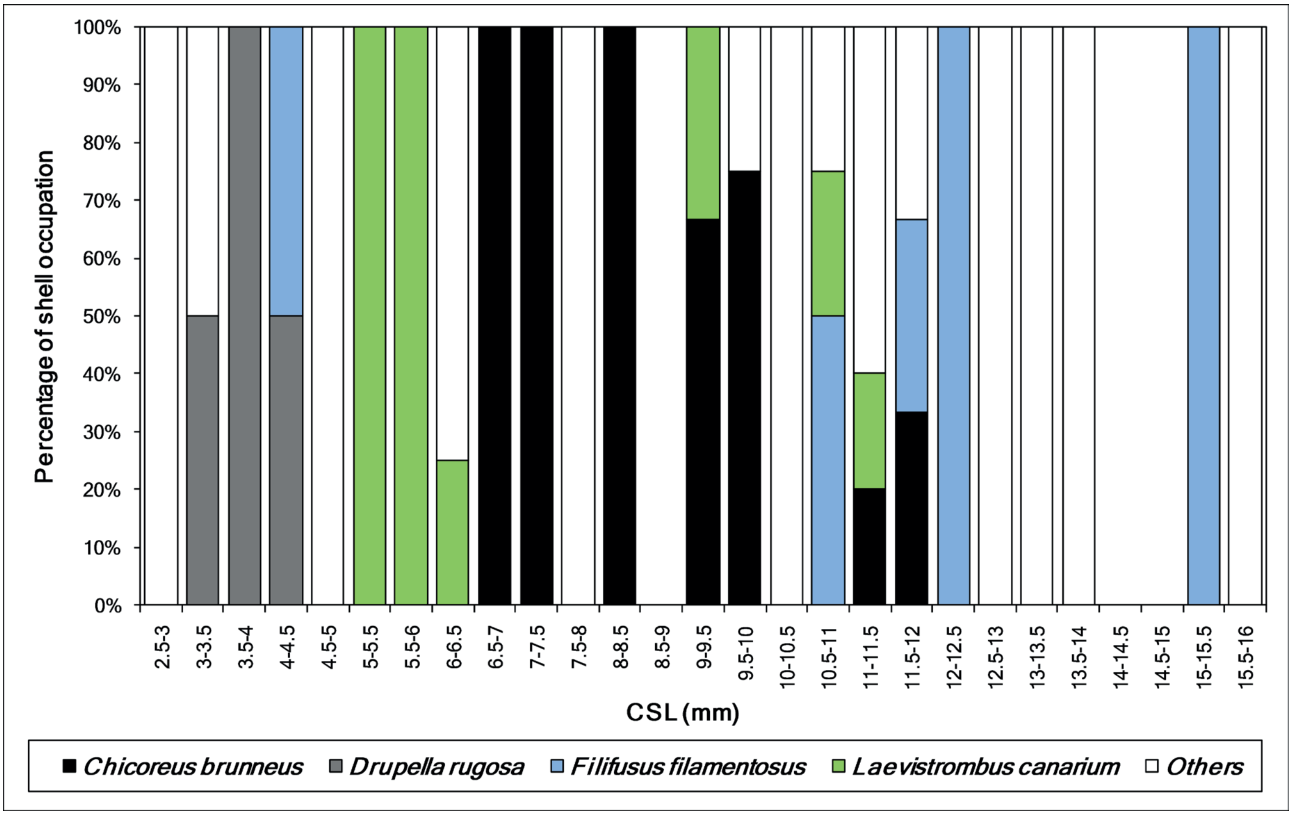

Figure 1. Shell occupation by *Coenobita violascens* as a function of hermit crab size.

Table 2. Percentage of shell shape categories occupied by *Coenobita violascens* at Cape Panwa, Phuket Island, from January 2011 to March 2012. The numbers in parentheses after the percentage of shells inhabited are the numbers of crab individuals.

Shell shape	Males	Non-ovigerous females	Ovigerous females	Total
Biconical	38.5 (10)	73.7 (14)	50.0 (1)	53.2 (25)
Elongately conical	3.8 (1)	10.5 (2)	-	6.4 (3)
Fusiform	26.9 (7)	10.5 (2)	-	19.1 (9)
Globose	3.8 (1)	-	-	2.1 (1)
Oval	3.8 (1)	5.3 (1)	50.0 (1)	6.4 (3)
Pyriform	7.7 (2)	-	-	4.3 (2)
Turban	15.4 (4)	-	-	8.5 (4)

Table 3. Percentage of aperture shape categories of shells occupied by *Coenobita violascens* at Cape Panwa, Phuket Island, from January 2011 to March 2012. The numbers in parentheses after the percentage of shells inhabited are the numbers of crab individuals.

Aperture shape	Males	Non-ovigerous females	Ovigerous females	Total
Elongately ovate	11.5 (3)	10.5 (2)	-	10.6 (5)
Irregular	3.8 (1)	10.5 (2)	-	6.4 (3)
Ovate	73.1 (19)	73.7 (14)	100.0 (2)	74.5 (35)
Round	11.5 (3)	5.3 (1)	-	8.5 (4)

and occupied shells are shown in Tab. 4. The values of the determination coefficient (r^2) from the regression analysis ranged between 0.62 and 0.93. Strong correlations were observed between characters of hermits and internal volume and aperture width of occupied shells ($r^2 \geq 0.91$). Shell aperture width was the most correlated with hermit characters ($r^2 \geq 0.92$), whereas shell weight and aperture length were least correlated with characters of hermits ($r^2 \leq 0.66$), except for cephalothoracic shield width ($r^2 = 0.83$).

Discussion

Coenobita violascens was found sympatrically with *C. rugosus* and *Coenobita brevimanus* Dana, 1852 at the study site. The results from this study are the first record on shells occupation by *C. violascens*. This coenobitid species shows a tendency of occupying specific categories of shells in relation to shell species, shape and aperture shape. *Coenobita violascens* individuals probably occupy the shells of at least three different gastropod species during their lifetime. Moreover, other aspects of shell occupation by *C. violascens* compared to other congeneric species are also discussed.

Coenobita violascens was found occupying fewer shell species (n = 20) than sympatric *C. rugosus* (n = 63) studied by Bundhitwongrut *et al.* (2015). This probably implies that *C. violascens* possess more specific requirements or less plasticity of use of shell resources. At least, the evidence is that *C. violascens* were not found using shells of neritids of the genus *Nerita* Linnaeus, 1758 although these shell groups were usually encountered as living individuals and discarded shells in the study area, which were commonly occupied by sympatric *C. rugosus* in high numbers reported by Bundhitwongrut *et al.* (2015).

Coenobita violascens preferentially occupied shells of one gastropod species, as also noted earlier in other land hermit crabs (Sripathi *et al.*, 1977; Abrams, 1978; Achituv and Ziskind, 1985; Guillen and Osorno, 1993; Walker, 1994; Barnes, 1999; Morrison and Spiller, 2006; Sallam *et al.*, 2008; Laidre and Vermeij, 2012; Bundhitwongrut *et al.*, 2015). The different proportions of occupied shell species may infer active behavior of *C. violascens* in shell selection (Sallam *et al.*, 2008; Bundhitwongrut *et al.*, 2015). This probably means *C. violascens* try to find the most appropriate shells available for them.

Table 4. The relationship between characters of hermit crab *Coenobita violascens* and the inhabited shells sampled represented by regression equations. r^2 = determination coefficient; CSL = cephalothoracic shield length; CSW =cephalothoracic shield width; CW = crab wet weight; MCL = major chela length; MCW =major chela width; SL = shell length; SW = shell width; WW = shell wet weight; SIV = shell internal volume; SAL = shell aperture length; SAW = shell aperture width; N = 47.

Relations	$Y = aX^b$	r^2
SL x CSL	$SL = 8.105CSL^{0.807}$	0.74*
SL x CSW	$SL = 11.057CSW^{0.745}$	0.77*
SL x CW	$SL = 31.409CW^{0.274}$	0.77*
SL x MCL	$SL = 7.028MCL^{0.738}$	0.74*
SL x MCW	$SL = 8.905MCW^{0.701}$	0.74*
SW x CSL	$SW = 4.471CSL^{0.854}$	0.79*
SW x CSW	$SW = 4.675CSW^{0.974}$	0.83*
SW x CW	$SW = 18.854CW^{0.285}$	0.80*
SW x MCL	$SW = 3.841MCL^{0.781}$	0.79*
SW x MCW	$SW = 4.98MCW^{0.738}$	0.78*
WW x CSL	$WW = 0.158CSL^{1.834}$	0.63*
WW x CSW	$WW = 0.154CSW^{2.273}$	0.83*
WW x CW	$WW = 3.427CW^{0.621}$	0.66*
WW x MCL	$WW = 0.116MCL^{1.67}$	0.63*
WW x MCW	$WW = 0.202MCW^{1.577}$	0.62*
SIV x CSL	$SIV = 0.021CSL^{2.412}$	0.91*
SIV x CSW	$SIV = 0.047CSW^{2.325}$	0.93*
SIV x CW	$SIV = 1.219CW^{0.803}$	0.93*
SIV x MCL	$SIV = 0.013MCL^{2.227}$	0.92*
SIV x MCW	$SIV = 0.028MCW^{2.093}$	0.92*
SAL x CSL	$SAL = 2.771CSL^{0.879}$	0.62*
SAL x CSW	$SAL = 3.248CSW^{0.849}$	0.83*
SAL x CW	$SAL = 12.167CW^{0.293}$	0.63*
SAL x MCL	$SAL = 2.334MCL^{0.81}$	0.63*
SAL x MCW	$SAL = 3.095MCW^{0.759}$	0.62*
SAW x CSL	$SAW = 1.138CSL^{1.037}$	0.93*
SAW x CSW	$SAW = 1.397CSW^{1.087}$	0.92*
SAW x CW	$SAW = 6.544CW^{0.343}$	0.93*
SAW x MCL	$SAW = 0.947MCL^{0.948}$	0.93*
SAW x MCW	$SAW = 1.286MCW^{0.899}$	0.93*

*Statistically significant, $p < 0.05$

Different sized individuals occupied different shell species. It is possible that *C. violascens* at the study site inhabits the shells of at least three different gastropod species as they grow. For instance, the most-occupied shell species, *Chicoreus brunneus*, were inhabited by medium-sized individuals (6.5–12.0 mm). However, smaller individuals (2.5–6.5 mm) occupied other smaller-shell species (*e.g. Clypeomorus batillariaeformis*, *Drupella rugosa*), whereas larger individuals (> 12.0 mm) inhabited other larger species [*e.g. Chicoreus ramosus* (Linnaeus, 1758)]. This inference is similar to the previous studies on *Coenobita clypeatus* (Fabricius, 1787) by Morrison and Spiller (2006) and *C. rugosus* by Bundhitwongrut *et al.* (2015), in that these land hermit crab are required to use the shells of a few different gastropods during their lifetime. To preserve these hermit crabs, therefore, the conservation of shell diversity is necessary because these hermits need different sizes and types of shells to complete their life cycle (Bundhitwongrut *et al.*, 2015).

Coenobita violascens occupied particular categories of shell and aperture shapes. Frequently occupied shell shapes were higher-spired shells, which were mid- and high-spired shells (*e.g.* biconical and fusiform shells). This pattern of shell shape use by *C. violascens* is similar to those of small *Coenobita perlatus* H. Milne Edwards, 1837 living on exposed sandy beach, reported by Willason and Page (1983), and *Coenobita cavipes* Stimpson, 1858 investigated by Barnes (1999). More available space inside high-spired shells retains water much better than that of low-spired shells, thereby providing more resistance to desiccation during exposure to thermal stress (Bertness, 1982; Willason and Page, 1983; Barnes, 1999). Conversely, *C. rugosus* at the study site more frequently occupied low-spired shells (Bundhitwongrut *et al.*, 2015) due to its behavioral ecology as a burrowing species (Barnes, 1999). The most-occupied shell aperture shape by *C. violascens* at the study site was ovate aperture as previously reported in *C. rugosus* at the same location by Bundhitwongrut *et al.* (2015). This aperture shape may allow this land hermit crab to fully seal the aperture with the major chela to avoid desiccation like other coenobitid crabs (Szabo, 2012). Interestingly, there was no *C. violascens* found occupying shells with semicircular aperture. This aperture shape is the diagnostic character of intact neritid shells. This occurrence is relevant to that there was no occupation of neritid shells by *C. violascens*.

The proportions between damaged and undamaged shells occupied by *C. violascens* were not significantly different at the study site as previously reported in sympatric *C. rugosus* by Bundhitwongrut *et al.* (2015). However, most shells inhabited by *C. violascens* were in worn condition and had lost the columella (unpublished data) as previously recorded by Kinosita and Okajima (1968), Ball (1972), Sripathi *et al.* (1977), Laidre (2012), Szabo (2012) and Bundhitwongrut *et al.* (2015). The missing columella of occupied shells may be due to mechanical or chemical abrasion (Kinosita and Okajima, 1968), resulting in light-weight and more space inside shells available for hermit crabs. These shells may be used previously by other hermits over a period of many years (Ball, 1972; Abrams, 1978; Boneka *et al.*, 1995). Moreover, available empty shells as limited resource were scant at the study site (Bundhitwongrut *et al.*, 2015), as also recorded earlier in other locations (Ball, 1972; Morrison and Spiller, 2006; Laidre and Vermeij, 2012). Consequently, these old and worn shells may be the main shell resources, especially for adult hermit crabs as a result of shell facilitation rather than competition (Abrams, 1978).

According to the energy saving hypothesis proposed by Osorno *et al.* (1998), *Chicoreus brunneus* as the most occupied shell species by *C. violascens* in this study was not the lightest species. This finding is similar to shells inhabited by sympatric *C. rugosus* investigated by Bundhitwongrut *et al.* (2015). Although hermits occupying the lightest shell species available, *P. canaliculata*, might obtain some advantages such as saving energy and having more internal space, hermits are probably at risk because of the thin shell wall from potential predators, such as the rough red-eyed crab, *Eriphia smithii* MacLeay, 1838, which was often seen at the study site (Bundhitwongrut *et al.*, 2014).

Morphological characters of inhabited shells and *C. violascens* were significantly correlated. This finding is similar to previous studies on other coenobitid crabs, including *C. rugosus* by Boneka *et al.* (1995) and Bundhitwongrut *et al.* (2015) as well as *Coenobita scaevola* (Forskål, 1775) by Sallam *et al.* (2008). These shell characters, especially internal volume and aperture width, seemingly comprise the main determinants for *C. violascens* shell occupation. The strong correlations between shell internal volume and hermit characteristics possibly means that internal volume is crucial for *C. violascens* in providing more space that may allow hermits to grow rapidly or retain more fertilized eggs during reproduction (Osorno *et al.*, 1998). Moreover, spacious internal volume of inhabited shells provides more capacity for storing water inside to maintain body moisture that is very important for life on land (Wilde, 1973; Greenaway, 2003). Additionally, the strong relationship between shell aperture width and hermit characters possibly indicates that *C. violascens* can use the major chela and walking legs to effectively seal the aperture firmly when retreating into the shell, which provides more protection from desiccation and against predators (Ball, 1972; Abrams, 1978; Sanvicente-Anorve and Hermoso-Salazar, 2011).

The habitat type of this study area may have resulted in relatively small numbers of specimens of *C. violascens* in the samples because this coenobitid is mostly recorded from habitats related to mangrove and terrestrial areas near estuaries (Nakasone 1988; McLaughlin *et al.* 2007; Doi *et al.* 2016). The present study site is supralittoral sandy beach that is not the most preferred habitat of this species. Therefore, further study in its main habitat in estuarine areas is recommended. Furthermore, *C. violascens* probably has a more cryptic lifestyle than the most common species, *C. rugosus*, at the study site. The foraging period and other activities of *C. violascens* presumably occur at different times to reduce competition with other species. Consequently, other sampling methods may be more effective for collecting *C. violascens* in other habitats such as bait pitfall traps (Morrison and Spiller, 2006; Hsu and Soong, 2017).

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