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Ecological information of land hermit crabs (Crustacea: Decapoda: Anomura: Coenobitidae) and new record in Dongsha Atoll National Park, Taiwan

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ABSTRACT: Land hermit crabs play an important role in island ecosystems. They are seed dispersers and debris scavengers in coastal forests to accelerate the decomposition of organic substances. Since the establishment of Dongsha Atoll National Park, Dongsha Island, Taiwan in 2007, researchers have been able to reach the atolls easily and conduct ecological surveys of land hermit crabs. In the current survey conducted from 2013 to 2018 on Dongsha Island, we recorded six land hermit crab species: *Birgus latro*, *Coenobita rugosus*, *C. brevimanus*, *C. violascens*, *C. cavipes*, and *C. purpureus*. Of these, *C. cavipes* and *C. purpureus* were newly recorded on Dongsha Island. *C. rugosus* was the dominant species, with a much larger population than those of other the species. *C. rugosus* demonstrated no sex ratio bias; however, *C. rugosus* males were considerably larger than *C. rugosus* females. Approximately 80% of *C. rugosus* used the shells of *Achatina* spp. and demonstrated the presence of three cohorts. We also provide the body size and weight for condition index of *C. rugosus*. Surprisingly, three individuals of *C. purpureus*, the species endemic to Japan, were also recorded. Overall, our study revealed the current situation of land hermit crabs on Dongsha Island.

KEY WORDS: Atoll ecology, *Coenobita purpureus*, *Coenobita rugosus*, Dongsha Island, Land hermit crabs, Taiwan.

INTRODUCTION

Land hermit crabs (Crustacea: Decapoda: Anomura: Coenobitidae) are distributed in tropical and subtropical regions. They play a critical role in terrestrial ecosystems, such as coastal forests, where they contribute to the nutrient cycles and seed dispersal (Niering, 1963; Alexander, 1979; Burggren & McMahon, 1988; Lindquist *et al.*, 2009). In addition, they are scavengers and facilitate carrion removal (Wiens, 1962; De Wilde, 1973; Alexander, 1979).

Shell resources are vital to the growth of land hermit crabs; the larger the crabs, the larger the shells they require (Fotheringham, 1976a). Land hermit crabs use shells for protection from predation and dehydration, and females use them to protect their eggs (Childress, 1972; Fotheringham, 1976b; Hazlett, 1981; Kuhlmann, 1992). The crabs' left chelae, which are larger than their right chelae, serve as lids for blocking their shells. In addition, crabs with suitable and relatively intact shells tend to move further inland (De Wilde, 1973; Burggren & McMahon, 1988). Therefore, research should examine the unique shell use of hermit crabs.

The importance of atoll research has increased. Many atolls in delicate ecosystems are under threat of extinction due to climate change (Barnett & Adger, 2003). Hedley (1896) and Hesse, Allee & Schmidt (1937) have reported that coral reef atoll islands are highly suitable for land crustaceans. Some articles on land crabs in atoll islands have recorded land hermit crab species on such islands. In Enewetak Atoll, Marshall Islands, Page and Willason (1982) recorded *Coenobita perlatus* H. Milne Edwards, 1837, *Coenobita rugosus* H. Milne Edwards, 1837, *Coenobita brevimanus* Dana 1852, and *Birgus latro* Linnaeus, 1767. However, they reported a lack of large shells for medium-sized *C. perlatus*; the shell conditions were the limiting factor in determining the specific sizes of the hermit crabs. In Kapingamarangi Atoll, Caroline Islands, Niering (1963) recorded *C. brevimanus, C. perlatus*, and *B. latro*; these crabs consumed large quantities of surface litter, including twigs, *Pandanus* and breadfruit leaves, and coconut husks. In the Aldabra Atoll, Alexander (1979) recorded *C. brevimanus, C. perlatus*, *C. rugosus*, *Coenobita cavipes* Stimpson, 1858, and *B. latro* and observed that the shells abandoned by the crabs filled with rainwater, which then served as drinking water and breeding grounds for other animals. In Dongsha Atoll, Dongsha Island, Shih (2012) recorded *C. rugosus*, *C. brevimanus*, *Coenobita violascen*s Heller, 1862, and *B. latro*. However, the population structures and other biological information regarding these species remain unknown. Therefore, in this study, we collected land hermit crab-related biological information on Dongsha Island. This study may contribute relevant information to a future conservation-related database.

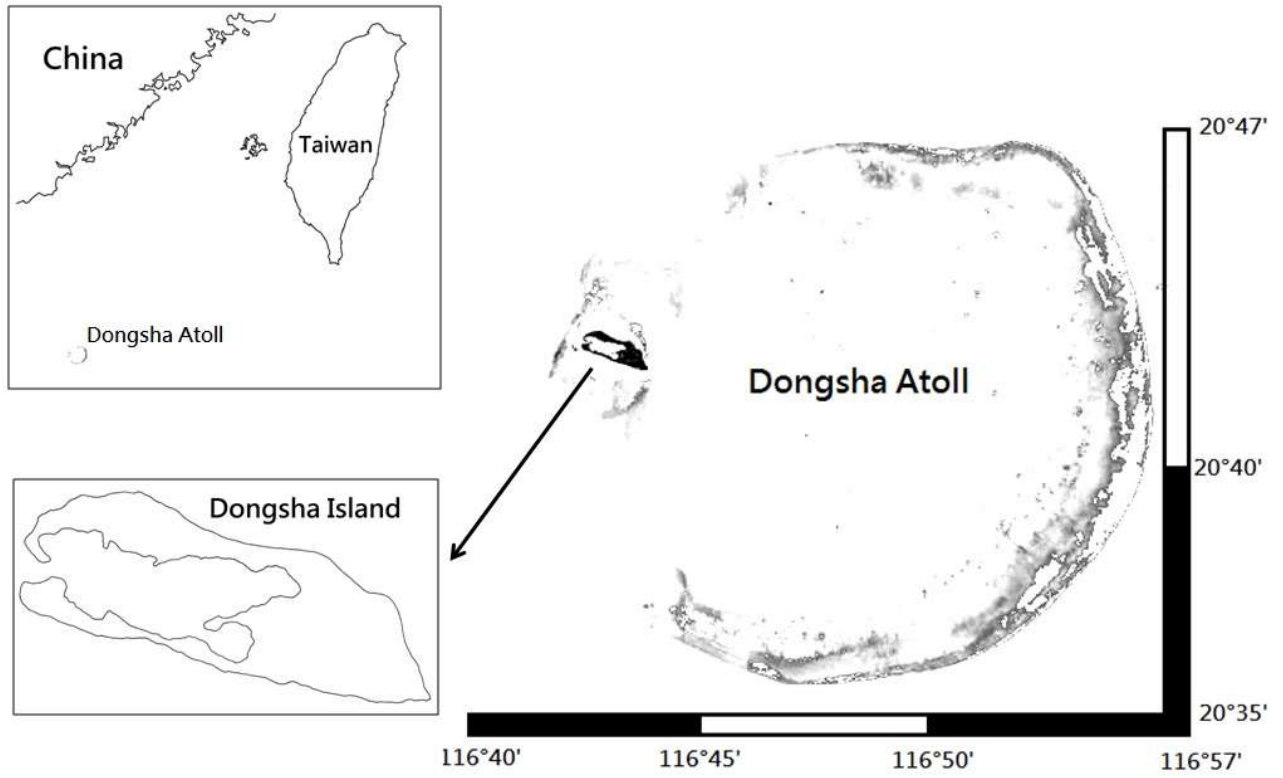

Fig. 1. The location of Dongsha Atoll and Dongsha Island.

MATERIALS AND METHODS

Study area

Dongsha Island (20°24′N, 116°43′E) is a small island in the South China Sea, where Dongsha Atoll National Park is located (Fig. 1). The ecosystem of Dongsha Island comprises a coral sand beach and tropical coastal vegetation. Topographically, it is flat; no mountains are present, and the highest altitude is 7.8 m above the sea level (Dai, 2004). We conducted island-wide surveys in 2013 (14–16 Nov), 2014 (28–30 Nov), 2017 (03–05 Nov), and 2018 (06–08 Jul), wherein we collected land hermit crabs in baited traps, identified their species, and recorded their shield and palm lengths. If the crabs did not come out of their shells, we used the regression formula for converting shield lengths to palm lengths, reported for *C. rugosus* by Hsu (2015) (Fig. 2). Immediately after measurements were completed, the crabs were released at the location in which they were caught.

Sampling

Baited traps were used to attract the land hermit crabs. We used rice bran as bait. The rice bran was heated dry and stirred the bran for approximately 5 min until its fragrance was released. At each trap location, 100 mL of rice bran was scattered on selected spots 1 h before sunset. Two hours later, the attracted hermit crabs were collected in buckets (Hsu & Soong, 2017b). We identified the species based on the characteristics reported by Nakasone (1988).

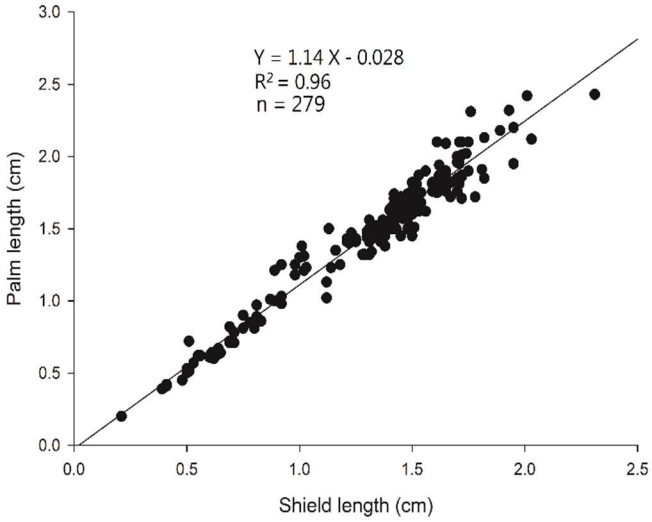

Fig. 2. Regression of shield length and palm length for ***Coenobita rugosus*** H. Milne Edwards, 1837 ($P < 0.001$, linear regression).

C. rugosus cohorts

On Dongsha Island, *C. rugosus* is the predominant land hermit crab species. Thus, for analyzing the size structure of the crab populations, we used only *C. rugosus* cohorts. *C. rugosus* were collected in 2013, 2014, 2017, and 2018. We used FISAT II (FAO-ICLARM) to analyze size structures of the populations for the objective evaluation of the cohorts and their distribution (Gayanilo

Jr, Sparre, & Pauly, 2005). We compared the cohorts collected during the aforementioned 4 years. We also compared the growth rates between 2013 and 2014 (Hsu, 2015; Hsu & Soong, 2017b) and between 2017 and 2018. This was the most prominently used method during 1990–2016 (Kilada & Driscoll, 2017).

***C. rugosus* sex distribution**

C. rugosus collected during June 30–July 2, 2014, were taken to a laboratory, and the peaks of their shells were exposed to an alcohol lamp to safely induce the crabs to come out of their shells. We then examined their sexual organs to identify their sex, and we recorded their body sizes. By using the Mann-Whitney *U* test, we analyzed the relationship between body size and sex. The chi-square test was used to determine whether the sex distribution of *C. rugosus* was biased.

***C. rugosus* shell composition**

During the island-wide survey in 2013 and 2017, crabs were also caught using baited traps, and their shell compositions were analyzed. We then identified the genera of the shellfish whose shells were used by *C. rugosus*. By using the chi-square test, we next evaluated the shell bias and identified the dominated shell type used by *C. rugosus*.

***C. rugosus* body size and weight**

To understand the relationship between body size and weight, we used the deshelled crabs collected during June 30–July 2, 2014. We measured their shield lengths and body weights, and then, through allometric equation analysis, we analyzed the linearity of the body size–body weight relationships, stratified by the crabs' sex (males, females, and egg-bearing females).

RESULTS

Species composition

For Dongsha Island, we recorded six species from the Coenobitidae family: *B. latro*, *C. rugosus*, *C. brevimanus*, *C. violascens*, *C. cavipes*, and *Coenobita purpureus* Stimpson, 1858 (Fig. 3). Of these, previous study recorded *B. latro*, *C. rugosus*, *C. brevimanus*, and *C. violascens*, whereas *C. cavipes* and *C. purpureus* were newly recorded for Dongsha Island. *C. rugosus* was the dominant species, with a much larger population than those of the other recorded crabs.

We recorded only three *C. purpureus* individuals on Dongsha Island. The *C. purpureus* specimen was male with shield length of 1.75 cm, and it was housed and analyzed at Dongsha Atoll Research Station (Fig. 4). However, due to the individual's failure to molt after we collected it, it died and was missing one leg. We collected only this specimen. The remaining two individuals [one male (shield length: 1.85 cm) and one berried female (shield length: 1.71 cm)] were not used as specimens, considering the small *C. purpureus* population (Fig. 5).

***C. rugosus* cohort**

We analyzed the cohorts and population structures by using island-wide survey data from 2013, 2014, 2017, and 2018 in FISAT II. In each of the 4 years, three cohorts were recorded (Hsu & Soong, 2017b). Table 1 lists all cohort data, and Fig. 6 illustrates the population structures.

For all 4 years, all cohorts demonstrated significant differences ($P < 0.001$, analysis of variance). In the first cohort, body size was significantly larger in 2018 than in 2017 ($P < 0.001$, Tukey test). In the second and third cohort, body size was significantly larger in 2013 than in the other 3 years ($P < 0.001$, Tukey test), it was significantly larger in 2018 than in 2017 and 2014 (both $P < 0.001$, Tukey test), and it also was significantly larger in 2017 than 2014 ($P < 0.05$, Tukey test). In addition, body size in the third cohort was significantly larger in 2013 than in the other 3 years ($P < 0.001$, Tukey test), and it was significantly larger in 2018 than in 2017 and 2014 ($P < 0.05$ and $P < 0.001$, Tukey test), and it also was significantly larger in 2017 than 2014 ($P < 0.05$, Tukey test). Thus, the land hermit crabs' growth rates may have been significantly affected by certain environmental factors, such as food availability.

Table 1 Cohorts information of ***Coenobita rugosus*** H. Milne Edwards in 2013, 2014, 2017, and 2018 (Mean ± SD, which is indicated the peak value of each cohort). There are three cohorts respectively in these four years.

	2013	2014	2017	2018
First	0.7±0.14 cm	0.63±0.07 cm	0.63±0.2 cm	0.74±0.24cm
Cohort	n = 40 (16%)	n = 18 (5%)	n = 95 (22%)	n = 196 (28%)
Second	1.52±0.15 cm	1.34±0.07 cm	1.37±0.16 cm	1.42±0.09 cm
Cohort	n = 153 (63%)	n = 245 (72%)	n = 232 (54%)	n = 256 (36%)
Third	1.96±0.13 cm	1.66±0.1 cm	1.74±0.09 cm	1.78±0.09 cm
Cohort	n = 17 (7%)	n = 51 (15%)	n = 103 (24%)	n = 164 (23 %)
Total (n)	244 (100%)	339	430	705

***C. rugosus* sex distribution**

By using random sampling, we collected *C. rugosus* and examined their sexual organs to identify their sex. In total, we collected 103 *C. rugosus* individuals. The female:male ratio was 47:56 (=0.84), indicating the absence of sex distribution bias among *C. rugosus* on Dongsha Island ($P = 0.629$, chi-square test). However, in terms of body size, the males were larger than the females ($P < 0.05$, Mann-Whitney *U* test; Fig. 7).

***C. rugosus* shell composition**

Shell composition was analyzed using the data from the island-wide surveys of 2013 and 2017. We found that during both years, the *C. rugosus* mainly used the shells of giant ghana African snail (*Achatina* spp.), followed by those of Nerite snail (*Nerita* spp.) (Table 2). We also analyzed the shell selection bias of *C. rugosus* by using the chi-square test, which confirmed that *Achatina* spp. was preferred by *C. rugosus* on Dongsha Island during 2013 and 2017 (both $P < 0.001$).

Fig. 3. Species from the Coenobitidae family recorded in Dongsha Island: **A**. ***Birgus latro*** Linnaeus 1767, **B**. ***Coenobita rugosus*** H. Milne Edwards, 1837, **C**. ***Coenobita cavipes*** Stimpson 1858, **D**. ***Coenobita brevimanus*** Dana 1852, **E**. ***Coenobita violascens*** Heller 1862, and **F**. ***Coenobita purpureus*** Stimpson 1858. ***C. cavipes*** and ***C. purpureus*** were newly recorded for Dongsha Island. All photographs were taken on Dongsha Island.

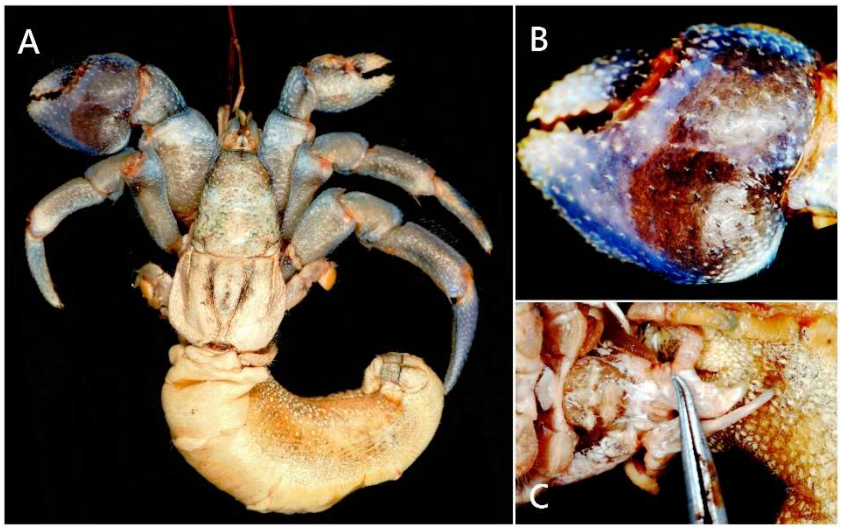

Fig. 4. The specimen figure of ***Coenobita purpureus***, Stimpson 1858. **A**. Dorsal close-up view of a single specimen of *C. purpureus*, **B**. Its left palm, and **C.** gonopods (key morphological characteristics). Scale bar = 1 cm. (The specimen is restored in Dongsha Atoll Research Station)

Fig. 5. ***Coenobita purpureus*** Stimpson 1858 was found in Dongsha Island. **A-C** are the same individual of male and **D-E** are the same individual of egg-bearing female. **A**, **B**, **D**, and **E** are situ photographs; **C** and **F** are during identification of their sex in the laboratory. After the photographs had been taken, the crabs were released.

Table 2. Shell composition of ***Coenobita rugosus*** H. Milne Edwards in 2013 and 2017 in Dongsha Island.

Species\survey year	**2013**	**2017**
Achatina spp.	150 (77%)	353 (81%)
Nerita spp.	23 (12%)	51 (12%)
Turbo spp.	6 (3%)	15 (3%)
Others	15 (8%)	15 (3%)
Total	194	434

C. rugosus body size and weight

To understand the relationship between the body size and weight of *C. rugosus*, we performed a linear regression analysis for body size and weight of *C. rugosus*, stratified by sex. The body sizes and weights of egg-bearing females, females, and males exhibited allometric equations (all $P < 0.001$; R = 0.87, 0.90, and 0.92, respectively). The formulas used for calculating body weights (g) of egg-bearing females, females, and males are as follows: $0.9113e^{2.052\,[\text{shield length (cm)}]}$, $0.0931e^{3.8872\,[\text{shield length (cm)}]}$, and $0.6236e^{2.1545[\text{shield length (cm)}]}$, respectively (Fig. 8).

DISCUSSION

In the present study, we reported the results of a 4-year survey of land hermit crabs on Dongsha Island. Because most atolls (i.e., small islands) in the Indo-Pacific Ocean are difficult to reach, our survey results

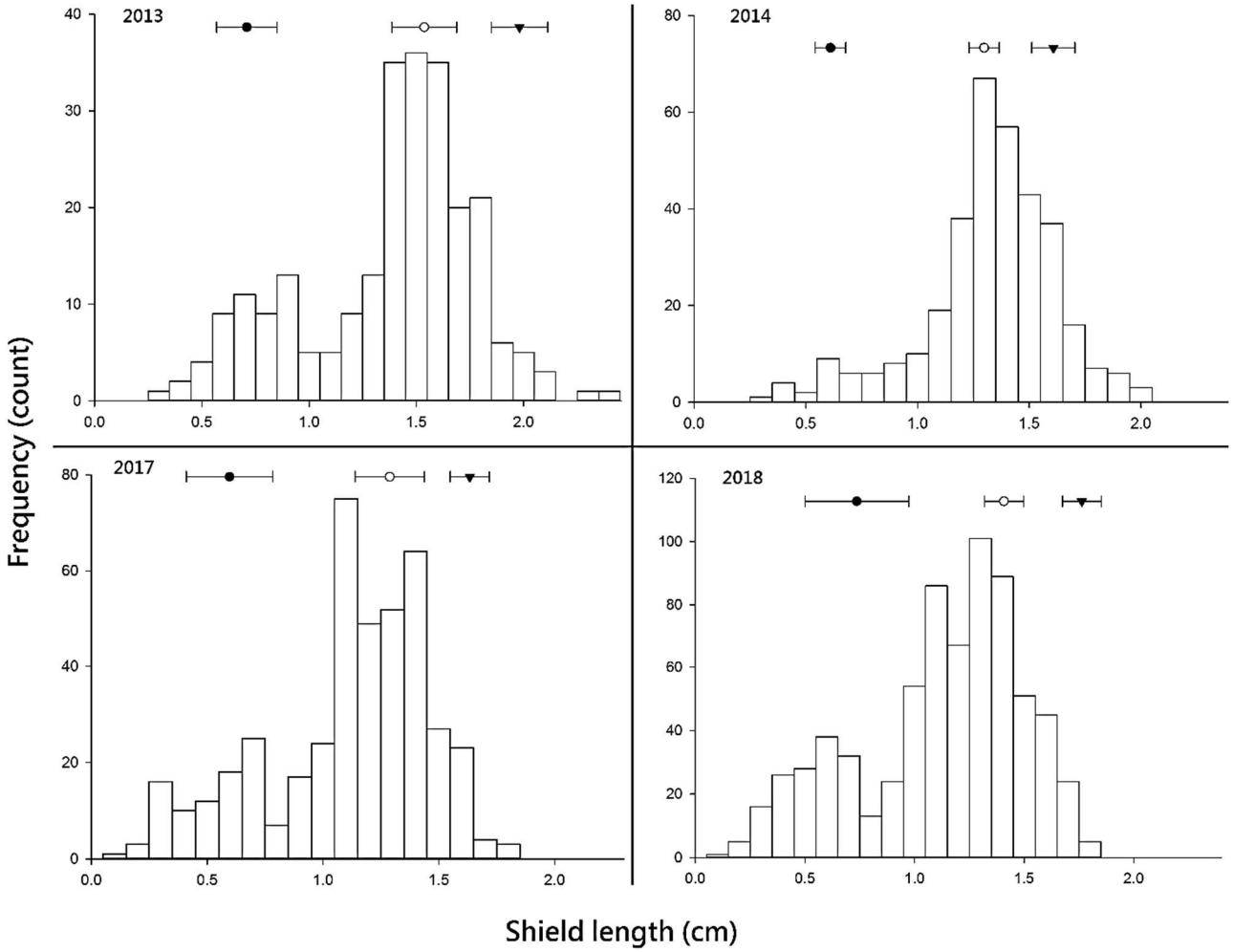

Fig. 6. Population structure (cohort) of the ***Coenobita rugosus*** H. Milne Edwards, 1837 in 2013, 2014, 2017, and 2018. ●, first cohort; ○, second cohort;▼, third cohort; and error bars, standard deviations in the cohorts. Detailed information is listed in Table 1.

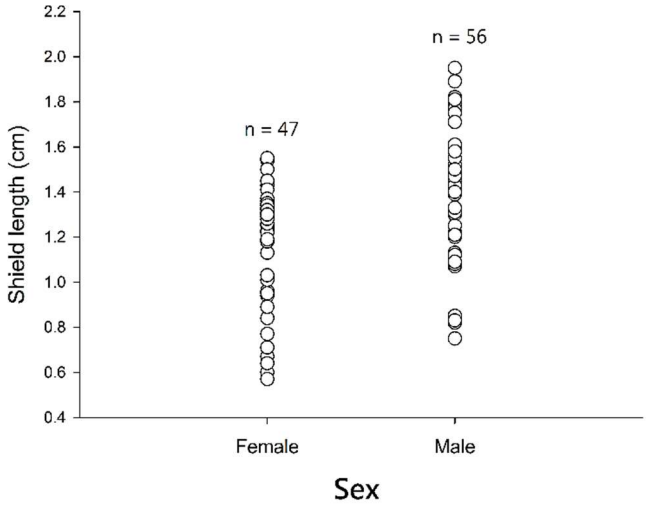

Fig. 7. Significant differences in body size between the sexes for ***Coenobita rugosus*** H. Milne Edwards, 1837: The males were significantly larger than the females ($P < 0.05$, Mann-Whitney U test).

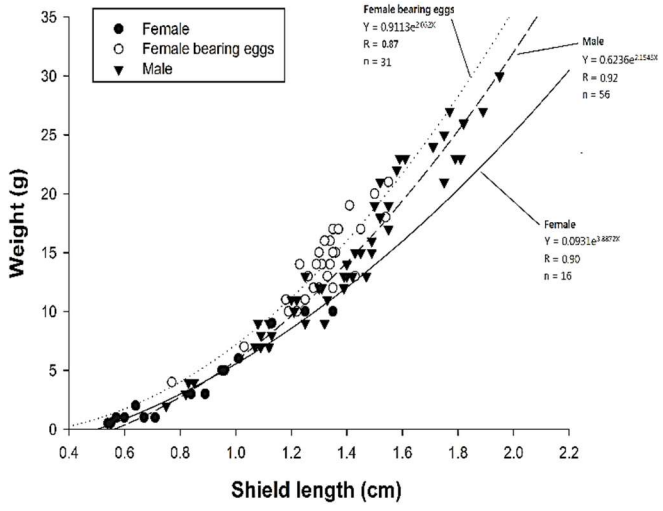

Fig. 8. Allometric equation of ***Coenobita rugosus*** H. Milne Edwards, 1837 body size and weight.

may serve as a valuable reference regarding land hermit crabs' composition, shell use, cohort, sex distribution, and other relevant factors. We recorded six species from the Coenobitidae family: *B. latro*, *C. rugosus*, *C. brevimanus*, *C. violascens*, *C. cavipes*, and *C. purpureus*; of these, *C. cavipes*, and *C. purpureus* were recorded for the first time as present on Dongsha Island.

On Dongsha Island, *C. rugosus* is the predominant land hermit crab species, with a much larger population than those of other crab species. On summer nights, thousands of *C. rugosus* can be seen on the beach. In the current study, our analyses mainly focused on *C. rugosus*, because the populations of the other crab species were too small to be analyzed statistically. We also recorded three individuals of *C. purpureus*, which was an anomalous finding. *C. purpureus* are endemic to parts of Japan, including the Ogasawara Islands, the Kii Peninsula, southern Kyushu, Miyazaki, Kagoshima, Shirahama, Izu Oshima, and the Okinawa Islands (Stimpson, 1907; Terao, 1913; Oyake, 2012; Kubota, 2013; Hamasaki *et al.*, 2017). Hsu and Soong (2017a) recorded one *C. purpureus* individual on Dongji Island in Taiwan, but they speculated this finding to dispersal from Okinawa to Dongji Island caused by a typhoon. However, we identified one female and two male *C. purpureus* individuals on Dongsha Island; notably, the female was bearing eggs, indicating the presence of a small population of *C. purpureus* with breeding capacity on the island. Specimen collection practices may play a major role in extinction of species, particularly species that are rare or have small populations (Minteer, Collins, Love, & Puschendorf, 2014). Thus, after photographing them in situ and in the laboratory to record their morphological characteristics, we released the two crabs into the wild. This novel finding on Dongsha Island was not the southernmost record of *C. purpureus* in the world; however, the southernmost distribution of *C. purpureus* has been recorded from the Maug Islands (East Island) (20°01′) in the North Mariana Islands by the Chiba Prefectural Museum. Further research focusing on the origin of these individuals and the genetic differences between them and the *C. purpureus* from the Sea of Japan is warranted.

Several age identification methods of crustacean exist (Kilada & Driscoll, 2017). Here, we performed size-frequency analysis (Hartnoll, 1982) on FISAT II to determine the population structures and cohorts of the crabs. We collected three cohorts per year during 2013, 2014, 2017, and 2018. Although the population structures of all cohorts in the 4 years were highly similar, some significant differences in body sizes were noted (Table 1). Second cohorts during each of the 4 years were the most abundant. This unusual phenomenon was related to recruitment and requires further investigation. According to Hsu and Soong (2017b), *C. rugosus* on Dongsha Island have larger body sizes than do those on other islands or eco-islands in Taiwan, because Dongsha Island has abundant seagrass debris, which serves as food for the crabs.

Regarding the sex distribution of *C. rugosus* on Dongsha Island, the female:male ratio was 0.84. No significant difference was noted between the sexes; thus, no significant sex ratio bias was evident. Our results are consistent with those of Bundhitwongrut, Thirakhupt, and Pradatsundarasar (2014) and Page and Willason (1982). However, regarding body size, males were significantly larger than females. The hypothesis of males larger than females might be the intrasexual competition which could be implicated in the evolution of larger males (Birkhead & Clarkson, 1980). Second, the bigger males could be better chosen by females as well as greater copulation success (Hazlett, 1989). Third, females diverge part of the energy for gonad development and therefore males have more energy for growing larger (Abrams, 1988). The exact reason of *C. rugosus* still need further research.

Regarding the shell composition, *C. rugosus* mainly used *Achatina* spp. shells. In their book, Chiu *et al.* (published in chinese) indicate the scarcity of habitats suitable for large marine mollusk species around Dongsha Island. The paucity of large marine mollusk shells but *Achatina* spp. provided the shells to relatively large size of *C. rugosus*. Similar to *C. rugosus*, other land hermit crab species, such as *C. brevimanus*, *C. violascens*, *C. cavipes*, and *C. purpureus*, on Dongsha Island have used *Achatina* spp. shells. In summary, despite being an invasive species, *Achatina* spp. benefit land hermit crabs on Dongsha Island. We observed few live *Achatina* spp. on Dongsha Island; therefore, the source of these shells warrants further investigation.

Finally, we performed sex-stratified allometric equation analysis for body size and weight of *C. rugosus*. Body size and weight are potential parameters of the "condition index." For instance, Hsu and Soong (2017b) reported that the condition indexes of *C. rugosus* on Dongsha Island and in Siziwan were significantly different. Thus, in future studies, the differing environmental factors can be identified using the condition index parameters between Dongsha Island and other places.

Dongsha Atoll National Park is currently closed to public; only coastal guards, researchers, and park rangers are allowed access. Hence, the island is safe from human destruction and pollution. However, climate change, illegal fishing by other countries, and macro ocean litter (Hughes *et al.*, 2013; Ko *et al.*, 2018) still threaten the island's ecosystem. Our results offer data that may aid future management and conservation of the national park.

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