Gastropod shell use by the land hermit crabs *Coenobita brevimanus* and *C. cavipes* in an abandoned village on Iriomotejima Island, Japan

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**Abstract.**—The aim of this study was to examine patterns of abundance, density, size, and shell use in *Coenobita brevimanus* and *C. cavipes*, occurring on Sakiyama Village, Iriomotejima Island, southwestern Japan. Crabs were captured and their body size and the type of adopted gastropod shell were recorded. Relative abundances were similar among species (67 and 64 for *C. brevimanus* and *C. cavipes*, respectively) and density of *C. brevimanus* was as high as 0.23 m$^{-2}$. Overall, *C. brevimanus* had larger body sizes (palm width 5.9–32.7 mm) than *C. cavipes* (4.2–14.2 mm). Patterns of gastropod shell use were also significantly different between species. While *C. brevimanus* used were the marine snails *Turbo* (*Marmarostoma*) *argyrostomus* and *Mancinella armigera* (each species comprised about 35% of all occupied shell), the most adopted gastropod shells by *C. cavipes* were the land snails *Satsuma caliginosa caliginosa* (38%) and *Acusta despecta sieboldiana* (19%). Interestingly, almost all (>90%) shells occupied by *C. brevimanus* were abraded, whereas for *C. cavipes* 56% of adopted shells were non-abraded. Generally speaking, *C. brevimanus* in Sakiyama, where the supply of artificial shells is relatively more limited than in more populated areas near to the village, had smaller body sizes, and occupied older shells.

**Key words:** Anomura, Coenobitidae, Decapoda, Ryukyu Islands, Yaeyama Islands

**Introduction**

Land hermit crabs of the genus *Coenobita* Latreille, 1829 are adapted to terrestrial environments, mainly occurring in small islands or narrow coastal strips in subtropical and tropical areas worldwide. They play major roles in coastal environments as scavengers (Wolcott, 1988), seed dispersers (Lindquist et al., 2009), and also very likely as nectar-feeding pollinators (Higashi et al., 2013). *Coenobita* species protect their vulnerable abdomen by occupying empty gastropod shells, they remodel the interiors of the shells to create more spacious and lighter structures (Laidre, 2012a) by using chemical substances to erode the columella and much of the internal calcium carbonate (Kurozumi, 1987). Hermit crabs cannot directly kill and remove gastropod from their shell (Laidre, 2011), thus they strongly prefer to adopt previously occupied shells that were already remodeled by a conspecific over new ones (Laidre, 2012b). Interestingly, it has been shown that availability of remodeled shells affects the social behavior of future generations of hermit crabs (Laidre, 2019). There are six species of *Coenobita* hermit crabs in the Ryukyu Islands, Japan (24–31°N, 121–131°E) (Asakura, 2004). This region is known to have one of the highest densities of *Coenobita* crabs in the world (Tohyama & Kurozumi, 1987), where several species can coexist in some habitats. One coexistence mechanism of *Coenobita* crabs includes differences in behavioral seasonality (Doi et
al., 2018; Hsu et al., 2018) and specific preference in shell occupancy (Abrams, 1978; Barnes, 1999, 2003; Hsu et al., 2018; Steibl & Laforsch, 2020).

Because of their terrestrial life, availability of shell resources is strongly influenced by human activities. For example, large Coenobita crabs worldwide use shells of edible species like the turban snails Turbo sp. that are discarded by humans, thus compromising potential refuges (Barnes 1996, 1999, 2002; Barnes & De Grave 2000; Morrison & Spiller 2006; Lairdre, 2012a; Mizutani et al., 2012; Szabó, 2012; Kohno et al. 2015; Doi et al. 2019). Fishing pressure on marine gastropods (Barnes & De Grave, 2000) and the formation of shell middens on land (Mizutani et al., 2012) also affect shell utilization by Coenobita crabs. Shells of artificially introduced terrestrial and freshwater gastropods are also well used by Coenobita crabs (e.g., Kurozumi, 1987; Sanda et al., 2018).

The land hermit crab Coenobita brevimanus is widely distributed throughout the Indo-Pacific region (Hartnoll, 1988; McLaughlin et al., 2007). They can be found up in the Ryukyu Islands, which is northern limit its distribution range. Here, this species inhabits inland and coastal forests, but in lower densities than its sympatric congener Coenobita cavipes (Kosuge & Kohno, 2010; Hamasaki et al., 2017). Abundances of C. brevimanus are higher in coastal areas with human settlements, either occupied or abandoned villages (Kosuge & Kohno, 2010; Mizutani & Kohn, 2012; Mizutani et al., 2012; Doi et al., 2019; Nio et al., 2019), than in natural habitats such as sandy beaches or mangroves and estuaries (Kohno et al., 2012; Fujikawa et al., 2017).

Coenobita cavipes is also widely distributed in the Indo-West Pacific (Hartnoll, 1988; McLaughlin et al., 2007). On the Ryukyu Islands, this species is often found inland along its congeners C. violascens and C. brevimanus (Kosuge & Kohno, 2010; Kohno et al., 2015; Fujikawa et al., 2017). Compared to other Coenobita species, C. cavipes is mostly found in terrestrial habitats, and it has been even recorded in areas 2.5 km away from the coast and elevations of 366 m (Sanda & Hamasaki, 2019).

There are two abandoned villages (Sakiyama and Amitori) in the northwestern part of Iriomotejima Island (Fig. 1). It is difficult to access these villages as there are no roads, visitors must travel on foot through the mountains or take a charter boat. Thus, the number of visitors is very limited. Coenobita brevimanus crabs, which commonly use shells of edible marine gastropods like Turbo (Marmarostoma) argyrostomus, are known to be larger than individuals living on adjacent uninhabited areas where shell middens and piles are not discarded (Doi et al., 2019).

Comparing population dynamics and shell utilization of Coenobita crabs in areas with settlements of different duration may provide useful knowledge for assessing the impact of human activity. In 1755, the Ryukyu royal government forced villagers from adjacent areas to emigrate to Sakiyama in order to reclaim paddy fields. Amitori, on the other hand, was founded in 1628 or earlier by at most 50 people, but was used as a campsite by hunter-gatherers during the 5th century. Although the initial population of Sakiyama and other adjacent villages is unknown, there are historical records that report up to 459 inhabitants. Similar-
ly, it has also been documented that Amitori and Sakiyama villages were occupied for at least 323 and 190 years, respectively. From the 19th century to World War II, Sakiyama and Amitori had approximately 100 and 200 inhabitants, respectively (Hoshi, 1982; Yamada et al., 1983; Kabira et al., 1990; History of Taketomi Town Editing Committee, 1993).

Here, we studied the shell utilization of two land hermit crabs from Sakiyama in Iriomotejima Island, Japan. We compared our results with those from previous studies on hermit crabs in the Ryukyu Islands in order to better understand differences in demographic parameters and shell use patterns.

Materials and Methods

Study site and sampling

All samples were collected in Sakiyama Bay, a 1.4 km wide and 1.8 km long area located in the western part of Iriomotejima Island (24°19′ N, 123°41′E) in the Ryukyu Islands, Japan in the Western Pacific Ocean. Sampling was conducted on July 16–17 and August 13–15, 2015 during the new moon, when female C. brevimanus and C. cavipes crabs are expected to migrate to the coast to release their larvae (Doi et al., 2018; Nio et al., 2019). Briefly, crabs were captured by hand in an area of <1500 m² (25 m long × 60 m wide) in the Sakiyama abandoned village between 17:30 and 1:30. Sampling effort included one and three observers in July and August, respectively. Noteworthy, in Japan, all Coenobita species have been recognized as a Natural Monument Animal to promote their conservation. Thus, a collection permit from the Okinawa Prefectural Board of Education was obtained for this study.

Species identification and measurements

Crabs were identified based on the morphology of their eye stalks and the presence or absence of granules on the palm surface of the left cheliped (Asakura, 2004). In order to measure body size without having to extract the crab from the shell to measure the carapace length, palm width (manus width) (PW) of the left cheliped was measured to the nearest 0.1 mm using a caliper. Sex was not determined to avoid injuring the crabs. Instead, shield length (SL) was obtained from the palm width using the following equations: \( SL = (PW + 0.604)/1.203 \) for males, and \( SL = (PW + 0.776)/1.227 \) for females (Shimamura, 1987).

Shells used by crabs were identified according to Azuma (1995), Kurozumi (2003), and Okutani (2017). In order to test whether the size of crabs differed depending on the taxa of the occupied shell, a Welch’s t-test was performed as implemented in R version 3.6.2 (R Core Team, 2019) using the variables PW of each crab species and gastropods taxa. Suitability of the shells was evaluated by determining the maximum degree at which the crab’s chela could withdraw into a shell: hidden if the left chela was completely withdrawn into the shell, flush if the shell aperture was sealed by the left chela and second walking leg, and protruding if the anterior portion of the carapace was protruding from the shell aperture (Barnes, 1999). Similarly, the shell occupation time was estimated by classifying the degree of shell abrasion into three categories: I if color and shape remained unchanged, II if there was slight discoloration but the shape was preserved, and III if the color faded and the shape was deteriorated (Mizutani et al., 2012; Doi et al., 2019). Further, shell damage including shell breakage was defined as follows: none if no parts were broken, AB if the shell aperture and body whorl were broken but the spine remained unchanged, BS if the body whorl and spine were broken but the shell aperture was unchanged, and ABS if all shell aperture, body whorl, and spine were broken (Doi et al., 2019).

Once measurements were taken, individuals were labeled by writing a unique serial number on shell surface and released at the same location where they were captured. Accordingly, if
a crab with a marked shell was recaptured, it was assigned as recaptured. After taking photos, recaptured crabs were immediately released without taking any measurements. Based on the mark-recapture experiments, population size of the crabs in Sakiyama was estimated using the Schumacher and Eschmeyer (SE) method, which is the most robust and useful technique to conduct multiple censuses on closed populations (Krebs, 1999). Length-frequency data for PW and shell use of C. brevimanus has already been published by Shimokawa (2020), thus these were used as reference values.

Results

Abundance and body size
A total of 131 crabs were collected, from which 67 and 64 were C. brevimanus and C. cavipes, respectively (Table 1). In average, 9–17 C. brevimanus and 2–27 C. cavipes crabs were collected daily. Only four individuals were recaptured and they were all C. brevimanus. The estimated population size for this species was 359 including 95% confidence interval was and 285–486 based on the SE method. Body size differed significantly between species (Fig. 2). PW was 5.9–32.7 mm and 4.2–14.2 mm for C. brevimanus and C. cavipes, respectively. Notably, C. brevimanus PW measurements showed a right-skewed frequency distribution with a single mode of 14.0–15.9 mm and a median of 17.0 mm. For C. cavipes, on the other hand, the mode was 6.0–7.9 mm and the median 7.8 mm.

Species-specific preference of gastropod shells
Coenobita brevimanus and C. cavipes crabs occupied shells of 9 and 16 different gastropod taxa, respectively (Table 2). Shells from the silver-mouth turban T. (M.) argyrostomus and the murex snail Mancinella armigera (each species constituting up to 35% of all occupied shells) were most commonly used by C. brevimanus, whereas shells from the land snails Satsuma caliginosa caliginosa (38%) and Acusta despecta sieboldiana (22%) were mainly occupied by C. cavipes. Although both species used shells from M. armigera, the giant top shell Tectus niloticus, and the nerite snail Nerita (Linnerita) polita, the former two were more commonly occupied by C. brevimanus. Crabs inhabiting N. (L.) polita were much less

| Date of collection | Coenobita brevimanus | Coenobita cavipes |
|-------------------|---------------------|------------------|
| 2015 Jul 16       | 9                   | 26               |
|                   | 17                  | 16               |
| 2015 Aug 13       | 13                  | 13               |
|                   | 14                  | 17 (1)           |
|                   | 15                  | 12 (3)           |
| Total             | 67                  | 64               |

Numbers in parentheses indicate recaptures.
for both species. Moreover, shells of the family Bursidae were only used by *C. brevimanus* whereas those of the families Cerithiidae, Thiaridae, and Fasciolariidae were only inhabited by *C. cavipes*.

Interestingly, shell usage varied significantly with crab body size. While large sized *C. brevimanus* with 13.6–32.5 mm PW (mean ± SD, 21.65 ± 5.38) used *T. (M.) argyrostomus*, medium sized individuals with 10.0–25.5 mm PW (15.47 ± 3.40) mostly occupied *M. armigera*. Overall, the mean PW of *C. brevimanus* using those shells was significantly different (Welch’s t-test, \( t' = 4.550, p' < 0.001 \)). PW of *C. cavipes* occupying *S. caliginosa caliginosa* and *A. despecta sieboldiana* were 4.5–12.5 mm (8.38 ± 2.11) and 5.1–12.9 mm (7.72 ± 1.95), respectively. In this case, differences in PW were not significant (Welch’s t-test, \( t = -0.958, p = 0.346 \)).

**Fitness, shell abrasion, and shell breakage**

Approximately 40% of *C. brevimanus* carapaces were flush and protruding (Fig. 3A). Crabs with hidden carapaces were scarce, especially among those inhabiting shells of *M. armigera*. Similar patterns were observed for *C. cavipes* (Fig. 3B). Almost all (91%) crabs occupying *S. caliginosa caliginosa* had hidden carapaces, and 71% of individuals using *A. despecta sieboldiana* had protruding carapaces.

Overall, abrasion of *T. (M.) argyrostomus* and *M. armigera* shells used by *C. brevimanus* was significant (only 10% fell within category I) (Fig. 3A). Most of the shell abrasion observed was in the second category (II). In contrast, gastropod shells occupied by *C. cavipes* were relatively well preserved; 86% of *A. despecta sieboldiana* shells were classified as category I (Fig. 3B). Further, ~30% of shells used by both *C. brevimanus* and *C. cavipes* were broken at some degree (Fig. 3). Almost half of the *T. (M.) argyrostomus* occupied by *C. brevimanus* had the aperture, body whorl, and/or spine broken. On the other hand, a small proportion of *S. caliginosa caliginosa* (33%)}
and *A. despecta sieboldiana* (7%) shells used by *C. cavipes* were broken in the aperture and body whorl.

**Discussion**

**Abundance and body size**

Unfortunately, in this study, population density was only estimated for *C. brevimanus*, for which data is already limited. Crab density of this species was higher in Sakiyama (359 crabs/1500 m$^2$) than in Amitori (1078–5489 crabs c.a. 6250 m$^2$; Doi et al., 2019). Population of *C. brevimanus* in Sakiyama was mainly characterized by individuals with 5.9–32.7 mm PW (mode 13–14 mm). According to previous reports in the Yaeyama Islands (Shimokawa et al., 2020), crabs of this size are considered to be of medium size. Different sizes have been reported for crawling crabs in Amitori (7.2–39.2 mm PW with 20.0–21.9 and 26.0–27.9 modes, Doi et al., 2019), Hatomajima Island (10.2–31.1 mm PW with 22.0 mean, Mizutani et al., 2012) and Itona, Ishigakijima Island (4.0–28.0 mm PW, Kosuge & Kohn, 2010), and seaward migrating crabs in Amitori Bay (10.7–40.9 mm PW with 24.2 mean in Amitori beach, Mizutani & Kohn, 2012 and 8.9–35.2 mm PW with 16.3 mean in Sabazaki beach, Mizutani & Kohn, 2012). Even smaller *C. brevimanus* (6.0–28.8 mm PW with 12.4 mean, Kohno et al., 2012) have been found in Nakanokamishima Island. In contrast, a recent study (Sasazuka et al., 2019) showed that body sizes of *C. brevimanus* and its congener *C. spinosus* off the coast of Tumon Bay in Guam, are not very different (10.9–22.9 mm SL and 9.2–23.5 mm for *C. brevimanus* and *C. spinosus*, respectively). Sasazuka et al. (2019) suggest that this may be related to the unique shell-shedding behavior of *C. spinosus*, which also uses smaller shells.

*Coenobita cavipes* crabs from Sakiyama, on the other hand, were smaller than the sympatric *C. brevimanus* (less than 14 mm with slight overlap in PW range). This is not surprising,
however, as smaller body sizes for this species have been previously reported in the Ryukyu Islands. Specifically, this has been observed for *C. cavipes* from Itona, Ishigakijima Island (Kosuge & Kohn, 2010), *C. violascens* from the Urauchi River (Kohn et al., 2015), and *C. purpureus* from Minnajima (Kurozumi, 1987) and Sesokojima Islands (Yamashiro, 1987). Unlike crabs from Sakiyama, PW of *C. cavipes* and other *Coenobita* species from these locations broadly overlapped between.

**Shell occupancy**

Shell preference differed between crab species. For example, *C. brevimanus* from Sakiyama mostly used shells of *T. (M.) argyrostromus* and *M. armigera*. Further, this trend has also been observed in crabs of different sizes (from large to small) and from diverse locations, including Amitori Village (Kosuge & Kohn, 2010; Kohn et al., 2012; Mizutani & Kohn, 2012; Mizutani et al., 2012; Doi et al., 2019). *Coenobita cavipes* in Sakiyama and other areas, on the other hand, occupied shells of land snails (Shimamura, 1987; Yamashiro, 1987; Kosuge & Kohn, 2010; Kohn et al., 2015). Unlike in Taiwan (Hsu et al., 2018), among all *Coenobita* species in the Ryukyu Islands, *C. cavipes* is considered to be the most terrestrial one; they use shells of terrestrial and freshwater gastropods (Hamasaki et al., 2017).

**Shell suitability**

Overall, *T. (M.) argyrostromus* and *M. armigera* shells occupied by *C. brevimanus* were slightly abraded (degree I). Proportion of non-abraded shells in Amitori was 90.0% and 94.9% for *T. (M.) argyrostromus* and *M. armigera*, respectively (Doi et al., 2019). Shell resources for *C. brevimanus* in Sakiyama seem to be older than those in Amitori. Indeed, proportion of non-damaged shells was higher in Sakiyama than in Amitori (11.0% for *T. (M.) argyrostromus* and 66.7% for *M. armigera*, Doi et al. 2019). Proportion of protruding shells was also higher in Sakiyama than in Amitori (56.4% for *T. (M.) argyrostromus* and 69.8% for *M. armigera*, Doi et al., 2019). Generally speaking, these results suggest differences in predation pressure between the two villages. While large *Birgus latro*, which are active predators (Krieger et al., 2016) with strong claws (Oka et al., 2016), are abundant in Amitori, *B. latro* seems to be absent in Sakiyama (H. Inoue, personal observation). Grapsid crabs are also predators of land hermit crabs (Kosuge & Kohn, 2009), they insert their chelae into the shell opening and pull out their prey. Abundance of predators may affect gastropod shell utilization of *C. brevimanus*.

Most of the shells (mainly from land snails) used by *C. cavipes* were classified as degree I; that is, they were not broken nor damaged. The latter suggests there is a constant supply of new shell resources. However, the proportion of protruding carapaces for *S. caligninosa caligninosa*, which were used by larger *C. cavipes*, was high. This result also indicates that both *Coenobita* species have a competitive relationship for shell resources and that larger *C. cavipes* in Sakiyama are unable to find suitable shells (*e.g.*, *T. (M.) argyrostromus* and *M. armigera*), thus attaining smaller body sizes.

**Comparisons with other local populations**

Studies have shown that increased shell supply of edible species such as *T. (M.) argyrostromus*, consequence of anthropogenic activity, have a positive impact (*i.e.*, larger body sizes and higher abundances) in *C. brevimanus* populations (Mizutani et al., 2012; Doi et al., 2019). Less people lived in Sakiyama than in Amitori, and for a shorter period of time. Contrary to Sakiyama, where the majority of the population were rice farmers, villagers from Amitori were farmers and fishers. Further, large piles of shells and midden can be found in Amitori but not in Sakiyama (Department of History, Archaeology Course, School of Letters, Tokai University, 2007); thus, shell supply
in Sakiyama is much lower. Indeed, long time has elapsed since shell supply ceased in Sakiyama.

According to previous reports, body size and shell use of *C. cavipes* overlap with its sympatric congeners *C. violascens* in the Urauchi River, Iriomotejima Island (Kohno et al., 2015) and *C. purpureus* in the Minnajima and Okinawajima Islands (Shimamura, 1987). Yet, *C. brevimanus* and *C. cavipes* from Sakiyama (this study) and Itona (Kosuge & Kohno, 2010) seem to be unable to use *T. (M.) argyrostomus* shells (as observed by smaller body sizes). This is likely due to the fact that *C. brevimanus* prey on its congeners (Hsu et al., 2018), thus suggesting *C. cavipes*, as well as other *Coenobita* crabs, are competing for *T. (M.) argyrostomus* shells.

Further, differences in body size of inshore dwelling *C. rugosus* have been explained by food (in this case seagrass debris) availability as a food source (Hsu & Soong, 2017). *Coenobita brevimanus* and *C. cavipes* crabs; indeed, these are carnivorous and herbivorous species, respectively (Hsu et al., 2018). Future studies should focus on the effect that food availability has in body size of more inland *Coenobita* crabs.

## Conclusions

Our data suggests that increased shell supply resulting from former anthropogenic activity in Sakiyama might contribute to *C. brevimanus* having larger body size. Larger *C. brevimanus*, in turn, might have an effect in the predatory and competitive pressures experienced by *C. cavipes*. Population density of *C. brevimanus* in Sakiyama was relatively small, and so it was the average body size. Less new, occupied shells indicated a limited shell supply, especially of *T. (M.) argyrostomus*. As a result of finding less damaged/broken shells, crabs might then occupy relatively small shells. Previous estimates of *C. brevimanus* size in Ami- tori suggest this may continue to decrease as shell supply there has ceased (Doi et al., 2019). The latter is supported by findings from this study. Moreover, reduction in shell resources and subsequent changes in body size and population density of *C. brevimanus* might also change its interactive relationship with *C. cavipes*. Since *Coenobita* crabs can even occupy fossil shells (Barnes, 2001), it would be useful that future studies doing radioactive dating in order to confirm whether historical shell supply might have had a positive effect in *C. brevimanus* population density and body size.

## Acknowledgments

We thank Masato Yoshioka, Ken Kawai, and Ken Sakihara (Tokai University) for their assistance with field sampling. This study was supported by a grant from Okinawa Regional Research Center, Tokai University. Further, we would like to acknowledge the Taketomi Educational Board and Okinawa Prefectural Board of Education for their permission to collect the samples analyzed here.

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