



Shell use and partitioning of two sympatric species of hermit crabs on a tropical mudflat



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ABSTRACT

Shell use and partitioning of two sympatric hermit crab species (*Diogenes moosai* and *Diogenes lopochoir*), as determined by shell shape, size and availability, were examined from August 2009 to March 2011 in a tropical mudflat (Malaysia). Shells of 14 gastropod species were used but >85% comprised shells of *Cerithidea cingulata*, *Nassarius cf. olivaceus*, *Nassarius jacksonianus*, and *Thais malayensis*. Shell partitioning between hermit crab species, sexes, and developmental stages was evident from occupied shells of different species, shapes, and sizes. Extreme bias in shell use pattern by male and female of both species of hermit crabs suggests that shell shape, which depends on shell species, is the major determinant of shell use. The hermit crab must however fit well into the shell so that compatibility between crab size and shell size becomes crucial. Although shell availability possibly influenced shell use and hermit crab distribution, this is not critical in a tropical setting of high gastropod diversity and abundance.

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1. Introduction

The relationship between hermit crabs and their utilizable gastropod shells is fundamental to their fitness as shell size and shape greatly influence their survival, growth and reproduction (Bertness, 1981a; Fotheringham, 1976). A hermit crab continually changes its gastropod shell to larger ones as it grows to maintain shelter and protection from predators (Childress, 1972). In nature, hermit crabs are normally not capable of removing the body of live gastropods to acquire their shells (Laidre, 2011) (but see Rutherford, 1977 for an exception), and consequently, they depend on dead gastropods (Scully, 1979). For this reason, the availability of gastropod shells is a limiting factor for hermit crab distribution (Shih and Mok, 2000). Various other studies have shown that the species, size, abundance and quality (or condition) of gastropod shells commonly influence the population size (Vance, 1972), growth (Fotheringham, 1976; Turra and Leite, 2003), morphology (Blackstone, 1985), fecundity (Childress, 1972; Fotheringham, 1976) and survivorship (Angel, 2000; Lively, 1988) of hermit crabs.

Coexistence is common among the many hermit crab species that inhabit the coastal area (Barnes, 2002). It occurs due to shell partitioning among sympatric species, a mechanism that is believed to be largely responsible for the ecological separation of hermit crabs in an evolutionary time frame (Bach et al., 1976). Differential use of shells by hermit crabs of different species and sizes may result in shell

partitioning between and within species. In fact, size variation between coexisting species is a common feature in hermit crabs (Kellogg, 1977).

With the exception of terrestrial hermit crabs (Laidre and Vermeij, 2012), previous works have shown that marine hermit crabs occupied few species of shells in spite of the many species of shells available (see Benvenuto and Gherardi, 2001; Ismail, 2010). Shell use by hermit crabs thus appears to be a selected rather than a random choice. However, the use of shells by reason of preference or availability is equivocal, depending on the hermit crab species (Dominciano et al., 2009; Floeter et al., 2000). At least for some species of hermit crabs, preference for the most suitable shells appears to satisfy a security reason; for instance, *Calcinus elegans* which occupied unusually shaped shells like cowrie shells (lacking spire or extremely elongate aperture) in tide pools were more easily dislodged by surge compared to those that occupied shells with more standard shell shape (Bach and Hazlett, 2009). On the other hand, shell selection by *Calcinus erthropus* is determined by the size of the shell rather than its shape (Caruso and Chemello, 2009). Turra and Leite (2002) demonstrated that the size compatibility between crab and shell species defines shell use in three sympatric species of *Clibanarius* in Brazil.

It can be summarized that shell use in hermit crabs is determined by at least three factors, shell shape (or species), size, and availability. However, only a very few studies (e.g. Mantellato and de Meireles, 2004) have examined all three factors in a single study. Our present study examined the role of all three factors in shell use pattern by two sympatric species of hermit crabs, *Diogenes moosai* and *Diogenes lopochoir*. Both *Diogenes* species are unique in having a larger and elongated left cheliped in both sexes. This feature is less distinct in

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Clibanarius and *Calcinus*. It is not known if the left cheliped also affects shell use, but it was observed that the left chela closes the shell aperture when the hermit crab retreats into its shell.

Detailed ecological studies on hermit crabs in Indo-west Pacific and adjacent regions are scarce. Little attention has been given to the ecology and behavior of hermit crabs from the genus *Diogenes* which totaled 85 recorded species (Appeltans et al., 2012). Among them, *D. lopo-chir* and *D. moosai* are found to be common in the estuaries of the Matang mangrove forest, Malaysia. Mangrove habitats characterized by associated extensive mudflats also host a diversity of gastropod snails which offer hermit crabs a variety of host shells. Both diogenids are relatively soft-bodied and their large numbers apparently attract predaceous fish that feed on them (Yap et al., 1994; Teoh, unpubl. data).

The present study aims to answer the following questions to further elucidate how two sympatric hermit crabs are partitioned in terms of shell use pattern: (1) are the high densities of hermit crabs matched by equally abundant gastropod shells of suitable sizes? (2) is (and how) shell use pattern affected by interspecific and intraspecific (sex and size) interactions? (3) how and what attributes (size and shape) of occupied shells are matched to that of the crabs?

2. Material and methods

Hermit crab and live gastropod shells samples were collected monthly from August 2009 to March 2011 at the subtidal edge of the coastal mudflat that flanks two major estuaries in the Matang Mangrove Forest Reserve (MMFR). The samples were collected at two sites (Fig. 1). Site A (N04° 51' 10.31"; E100° 30' 29.34") was located at the confluence of the extended mouths of the Selinsing and Sangga Besar rivers with mean salinity of 26.95 ± 2.42 ppt. Site B (N04° 50' 03.51" E100° 28' 47.60") was located 4 km farther offshore at a large sandy–mud shoal where the mean salinity was 28.28 ± 1.74 ppt. Although both sites had a high percentage of coarse silt substrate (41–55%), site B had a higher amount of fine sand (26%) than site A (19%). Collections were made during spring high tide, using a small otter trawl net with a head rope length of 9.4 m and codend stretched mesh size of 2 cm. The net

was trawled for 5 min and the trawl speed was estimated using GPS (Garmin Rino 130). Three trawl samples were taken at each site (except in September, October and December 2009, June 2010, and January 2011 when only two trawl samples each were taken due to bad weather). Water depths during samplings ranged between 1.8 m and 3 m. In the laboratory, samples that were not immediately examined were stored inside a freezer (-20 °C) until subsequent examination. Slow freezing of the specimens prevented limb automisation.

2.1. Laboratory procedures

Thawed samples of hermit crabs comprising *D. moosai* ($n = 749$) and *D. lopo-chir* ($n = 226$), with their shells were blotted dry before weighing to an accuracy of 0.001 g. Gastropod shells were identified to the species level. Shell height (ShH), shell width (ShW), aperture length (AL) and aperture width (AW) were measured using a pair of Mitutoyo digital vernier calipers with an accuracy of 0.01 mm and weight of shells (SWt) were taken using digital balance with an accuracy of 0.01 g. Shell condition was recorded as undamaged (no observable damage), slightly damaged, damaged and greatly damaged (half or more of shell broken off), or highly perforated. Shell encrustation by mainly barnacles occurred at very low frequencies ($<5.5\%$); hence, its effect on shell use was not considered in the present study.

Hermit crabs were gently pulled out from their shells by slowly twisting the crab against the direction of shell spiral. In difficult cases, a light hammer was used to gently crack the shell before pulling out the crab. Individual naked hermit crab was blotted dry and weighed. Shield length (SL), shield width (SW), length of left chela or propodus (ChL) and width of left chela (ChW) were measured. Smaller individuals were measured with the aid of dissecting microscope. Hermit crabs were then sexed; female and male crabs have gonopores on the coxae of the third and fifth pereopods respectively. For smaller individuals with inconspicuous gonopores, a drop of diluted methylene blue was applied on the coxa to stain the openings. Presence of eggs attached on pleopods of females was noted.

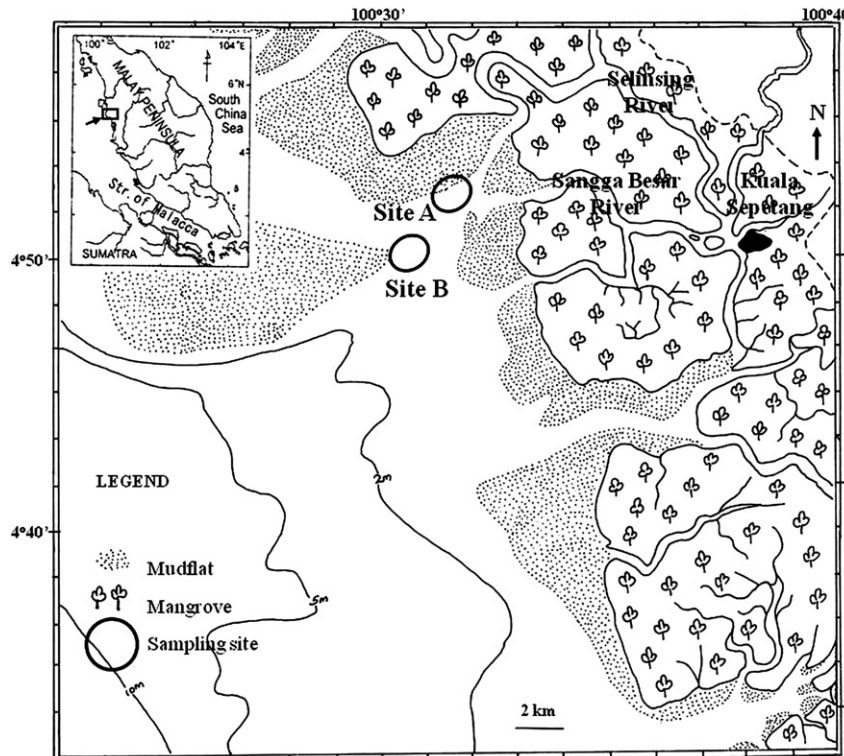


Fig. 1. Map of study area showing sampling sites of hermit crabs in adjacent coastal mudflats at Matang Mangrove Forest Reserve, Peninsular Malaysia.

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