

# Ecology of tropical hermit crabs at Quirimba Island, Mozambique: vertical migration (tree climbing)

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**ABSTRACT:** The semi-terrestrial hermit crabs *Coenobita cavipes* and *Coenobita rugosus* both undertake vertical migrations at Quirimba Island, Mozambique, by tree climbing in the region between High Water Neap tide level and Extreme High Water Spring tide level. Both species occurred in mangrove trees at all states of light:dark and tidal cycles, although more crabs were present in the study trees at high water than low water. The consecutive period of time spent in trees by *C. cavipes* individuals varied between half a tidal cycle (<6 h) and 2 complete tidal cycles (24 h). The vertical distance climbed varied between 5 cm and 4 m, but *C. cavipes* climbed significantly higher than *C. rugosus*. The height climbed by *C. cavipes* was irrespective of whether the tide actually reached within 10 m of the tree being climbed. Mean climb height was related to the size of *C. cavipes* individuals, such that maxima were achieved by those of mid-sized mass. Shell species used also influenced the climb height. High wind speeds (force 3 to 5 or 12 to 33 km h<sup>-1</sup>) had a negative influence on the mean number of hermit crabs climbing. Species of mangrove tree, degree of shade, number of roots and root ground area were all found to be insignificant as influences, but the mean number of hermit crabs per tree increased from 0.43 in those with no trunk or branch holes to 5.08 in those with 5 or 6 holes. There were marked activity and behavioural differences between hermit crabs taking residence in trunk/branch holes and those clinging to branches or leaf bases. Shell exchange in tree hole gatherings (where up to 30 individuals were present), as opposed to ground based shell exchange, may have advantages in reducing desiccation (there is sometimes additionally a supply of fresh water), reducing the risk of predation and not reducing feeding time.

**KEY WORDS:** Hermit crab · Migration · Tree climbing · Mangrove · Africa · Clustering

## INTRODUCTION

The Coenobitidae (Anomura, Decapoda) are amongst the most terrestrially adapted Crustacea, along with some representatives of the brachyuran taxa Gecarcinidae, Grapsidae, Potamoidea and Ocypodidae. Although the Coenobitidae are widely distributed throughout the tropical and subtropical regions, they achieve greatest diversity in the Indo-West Pacific (Burggren & McMahon 1988). *Coenobita cavipes* and

*Coenobita rugosus* are 2 abundant Indo-Pacific species of hermit crab which are capable of climbing trees (De Wilde 1973). Tree climbing crabs have generally been divided into 4 basic types: (1) those that are basically ground living but occasionally venture up mangrove trees, (2) those which are basically tree living and occasionally venture to ground, (3) those which are exclusive tree dwellers inhabiting part of the tree and (4) those which are exclusively tree dwellers inhabiting all of the tree (Ruwa 1990, Vannini & Ruwa 1994, Vannini et al. in press). The tree climbing habit of *C. rugosus*, which belongs to the first of these groups (as does *C. cavipes*), has been described as providing a refugial habitat in addition to burrows, crevices

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and root dwellings (De Wilde 1973, Vannini 1975, 1976).

In the Quirimba Archipelago of tropical northern Mozambique the small near-shore islands have wide intertidal zones, a large range of habitat types and an abundance and diversity of hermit crabs. *Coenobita cavipes* and *C. rugosus* are the most landward of 16 species of hermit crab which inhabit the intertidal region of the archipelago (Barnes 1997). Here *C. cavipes* occurs only in or close to mangrove forests and *C. rugosus* generally occurs on open areas of the supra-littoral such as beach or scrub vegetation, as has been described for more northerly East African populations (Vannini 1976, Lewinsohn 1982). On Quirimba Island, the 2 species overlap on a stretch of coast, which has a thin veil of mangrove forest, and show both unusually extended periods of activity and distinct differences in activity with habitat type (Barnes 1997).

The study reported here describes the climbing behaviour of *Coenobita cavipes* and *C. rugosus*, including species proportions of climbing individuals with circadian and tidal changes, the shore sub-zonal location of most intense climbing behaviour, the period spent by hermit crabs in arboretum and the vertical distance climbed. Possible endogenous and exogenous influences on tree climbing by hermit crabs at Quirimba Island were investigated, including circadian and tidal rhythms, wind speed, biological characteristics of mangrove trees and the shell species carried by crabs. Observations are also given on hermit crab behaviour associated with or performed whilst climbing and the purposes of such activity discussed. This work forms part of the marine research programme of the Darwin/Frontier Mozambique project of the Society for Environmental Exploration and the Minist para a Coordena o de Ac o Ambiental (Maputo, Mozambique).

## METHODS

The vertical migrations (tree climbing activity) of 2 species of hermit crabs were studied in the mangrove forests of Quirimba Island, northern Mozambique (12° 42' S, 40° 50' E). The fieldwork was carried out at the Darwin/Frontier Mozambique station on Quirimba Island between July and September 1996. The study area was the supra-littoral margin of an exposed mangrove forest approximately 400 m wide and dominated by *Rhizophora* trees; for map and further details see Barnes (1997). The tree height ranged from 4 to 8 m in height and from 1 to 5 per 4 m<sup>2</sup> in density. The substratum was a mud-sand mixture, but the particle size range was not measured. Two species of hermit crab

were studied, *Coenobita cavipes* and *C. rugosus*. These species are easily distinguishable in the field by examination of the outer surface of the major chela, on which *C. rugosus* has a pronounced series of ridges (Lewinsohn 1982). Both species were locally abundant on Quirimba Island but confined to the supra-littoral zone (Barnes 1997).

A sample of 42 mangrove trees (36 *Rhizophora mucronata* and 6 *Brugiera gymnorhiza*) were monitored for hermit crab migrations over a continuous period of 21 d. The species of tree, ground area of roots, number of trunk holes and position relative to mean high water level were recorded for each of the sample trees. The identity and number of hermit crabs present on each tree were examined at every low and high tide throughout the study period. The wind speed (Beaufort scale), but not direction, on each occasion was also recorded. In a separate experiment, the large chela of each of 270 hermit crabs found in trees was marked with a pencil. The position of each crab and the occupied tree identity were recorded. One pencil mark was added for each complete change of tidal state (either low or high tide) so that the approximate time and number of tidal sequences that crabs spent in trees could be investigated. The climb height of hermit crabs was measured in a random sample of a variable number of trees (from 20 to 45) from each of 4 zones. The measurement was relative to the high water level [5 to 10 m below the high water mark (HWM), 0 to 5 m below the HWM, 0 to 5 m above the HWM and 5 to 10 m above the HWM]. The height measurement was taken as that from the base of the crab to the level of daily high water (HW; not the height from the ground). Climb-height measurements of both species were collected during 2 low water neap tides (LWN), 2 high water neap tides (HWN) and 2 high water spring tides (HWS) for both diurnal and nocturnal periods.

## RESULTS

The hermit crabs *Coenobita cavipes* and *C. rugosus* were both observed to undertake vertical migrations by tree climbing and crawling up and down the beach throughout the study area between HWN and Extreme High Water Spring tide (EHWS) levels, referred to here as the supra-littoral. Although both species occurred above EHWS, no tree climbing activity by either species was observed above EHWS. *Clibanarius longitarsus*, the only other of 16 species of hermit crabs from Quirimba Island described (Barnes 1997) to inhabit the supra-littoral zone, was not observed to undertake any vertical migrations during the study period. The proportions of the tree climbing population of *C. cavipes* and *C. rugosus* were approximately 91 and 9% respec-

Table 1 *Coenobita cavipes* and *Coenobita rugosus*. Species proportions of hermit crab tree climbing and ground populations at day and night, high and low water. Values for the 2 species are daily means (SE in parentheses). Total number of crabs sampled = 998. Total number of sample days = 21. Chi-squared values are given for tests between tree and ground populations: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$

Time	Tidal state	Tree population		Ground population		$\chi^2$
		<i>C. cavipes</i> (n = 471)	<i>C. rugosus</i> (n = 36)	<i>C. cavipes</i> (n = 309)	<i>C. rugosus</i> (n = 182)	
Day	High water	91.8 (1.5)	8.2 (1.5)	63.1 (0.8)	36.9 (0.8)	108.9***
	Low water	90.8 (3.8)	9.2 (3.8)	62.2 (1.0)	37.8 (1.0)	94.9***
Night	High water	89.5 (1.3)	10.5 (1.3)	62.0 (2.3)	38.0 (2.3)	77.8***
	Low water	93.0 (2.5)	7.0 (2.5)	63.2 (0.8)	36.8 (0.8)	104.9***

tively, irrespective of light:dark cycle or tidal conditions (Table 1). The proportions of the ground populations of the 2 species were more closely balanced (approximately 63 and 37% respectively). N.B. *C. cavipes* was overall more numerous than *C. rugosus* — see Barnes (1997). Significantly more individuals of *C. cavipes* than *C. rugosus* climbed trees irrespective of tidal conditions in this habitat. Both species occurred in trees at all states of light:dark and tidal cycles, although more crabs were present in the study trees at high water than low water, significantly so diurnally (Table 2). The density of crabs per tree decreased away from the HWM up and down shore such that no crabs climbed trees further than 10 m horizontal distance from the HWM. The light:dark and tidal cycle differences, in numbers of crabs per tree, were statistically non significant (and thus probably less important than shore position). Although the tree population was higher at high water

Table 2. *Coenobita cavipes*. Mean ( $\pm$ SE) number of hermit crabs per tree with distance from the High Water Mark (HWM) and circadian and tidal state. Distances from HWM are below (B) or above (A). The number of crabs per tree was significantly related to the distance from HWM as shown by the ANOVA values \* $p < 0.05$ , \*\* $p < 0.01$  and \*\*\* $p < 0.001$ . The number of crabs per tree was significantly different between high water (HW) day and low water (LW) day (ANOVA,  $F = 10.93$ \*\*\*). All other comparisons showed non significant differences

Distance from HWM (m)	HW day (n = 299)	LW day (n = 295)	HW night (n = 291)	LW night (n = 274)
10–15 B	0	0	0	0
5–10 B	0.17 (0.05)	0.08 (0.02)	0.49 (0.23)	0.19 (0.07)
0–5 B	0.74 (0.29)	0.45 (0.05)	1.15 (0.22)	1.05 (0.26)
0–5 A	1.68 (0.28)	0.56 (0.05)	1.04 (0.31)	0.77 (0.24)
5–10 A	0.14 (0.06)	0	0.05 (0.03)	0.07 (0.04)
10–15 A	0	0	0	0
ANOVA	9.29***	3.83**	3.33*	8.23***

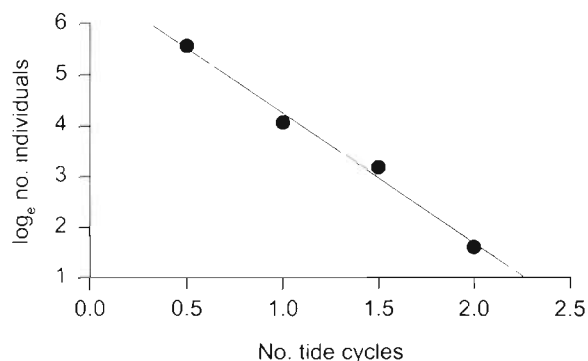


Fig. 1. *Coenobita cavipes*. Continuous duration of stay in mangrove trees by hermit crabs. Number of individuals ( $\log_e$ ) is shown with the number of continuous tidal cycles spent in trees. Regression line equation:  $\log(\text{no. of individuals}) = -2.56(\text{no. of tidal cycles}) + 6.8$ . ANOVA,  $F = 194.5$ ,  $p < 0.005$

than low, this difference was only significant during the day (Table 2). The peak density per tree in darkness (1.05 to 1.15 individuals per tree) was half way between the peak densities per tree at low and high water during daylight. The consecutive period of time spent in trees by *C. cavipes* individuals varied between half a tidal cycle (<6 h) and 2 complete tidal cycles (24 h). The continuous time spent in trees by individuals exponentially decreased with time over this period, measured here by the consecutive number of tidal cycles (Fig. 1).

The vertical distance climbed by *Coenobita cavipes* varied between 5 cm and 4 m while that of *C. rugosus* varied between 5 cm and 1.5 m above HW. Generally, though, both species climbed to between 40 and 100 cm. Although the mean climb heights illustrated in Table 3 are of greater magnitude at high water than low, this was only statistically significant at night on neap tides. There was little or no difference between light and dark climb heights at comparable tidal states in either species. *C. cavipes* climbed significantly higher (31.6 cm on average, Student's  $t$ ,  $p < 0.05$ ) than

*C. rugosus* on all but day high neap tides. Although the behaviour of tree climbing was restricted to 10 m either side of the HWM (Table 2), the height climbed within this zone varied little with shore height or tide magnitude (Table 4). Thus the height climbed by *C. cavipes* was irrespective of whether the tide actually reached within 10 m of the tree being climbed. The mass of individual *C. cavipes* also significantly influenced the height climbed (Fig. 2). The magnitude of mean climb height peaked at 106 cm, with mid-sized individuals (4 g), and decreased with decreasing crab mass to approximately half the peak value for the

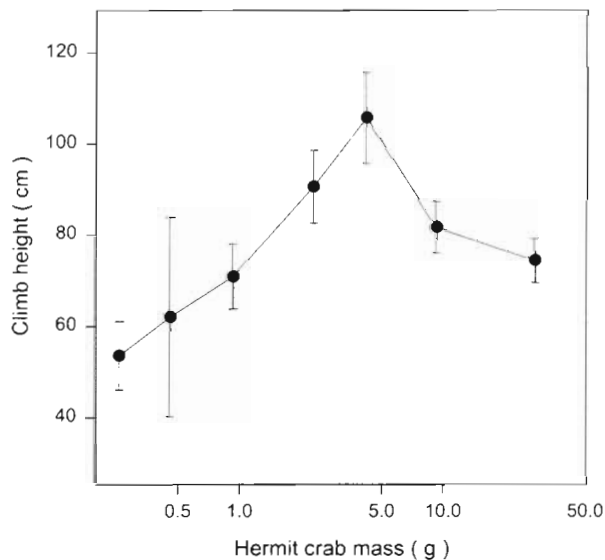


Fig. 2. *Coenobita cavipes*. Mean ( $\pm$ SE) climb height in relation to log body mass of hermit crabs. Sample size ranged from 10 (minimum, 0.5 g size class) to 48 (maximum, 5 g size class). Climb height significantly varied with log body mass (ANOVA,  $F = 3.4$ ,  $p < 0.01$ )

Table 4. *Coenobita cavipes*. Mean ( $\pm$ SE) vertical climb distance of hermit crabs with shore height and tidal state. No SE is shown for high water spring at 5–10 m below the HWM as the value represents only 1 record. For all other combinations,  $n > 5$  and ANOVA comparisons were statistically non significant ( $p > 0.05$ )

Distance from HWM (m)	Vertical climb distance (cm)		ANOVA ( $F$ value)
	High water spring	High water neap	
5–10 B	100 (–)	94.0 (11.1)	–
0–5 B	112.5 (7.2)	94.4 (5.1)	3.7
5–0 A	72.5 (6.2)	85.6 (5.1)	3.0
10–5 A	93.6 (18.4)	75.0 (13.9)	2.3

Table 3. *Coenobita cavipes* and *Coenobita rugosus*. Mean ( $\pm$ SE) vertical climb distance (above daily high water) of hermit crabs with circadian and tidal states. nd: no data were recorded during low water spring tides. Minimum sample size of individual means: *C. cavipes* = 70, *C. rugosus* = 6. All *C. cavipes* climb-height pairwise comparisons were statistically non significantly different except night HW neap vs night LW neap (ANOVA,  $F = 7.89$ ,  $p < 0.01$ ). All *C. rugosus* climb-height pairwise comparisons were non significantly different

Time	Tidal state	Vertical climb distance (cm)			
		<i>C. cavipes</i>		<i>C. rugosus</i>	
		Neap	Spring	Neap	Spring
Day	High water	85.2 (5.6)	100.7 (5.8)	70.7 (13.4)	67.0 (21.3)
	Low water	76.3 (6.7)	nd	40.0 (12.2)	nd
Night	High water	80.2 (4.6)	92.0 (8.9)	51.5 (9.1)	54.0 (4.8)
	Low water	62.6 (4.1)	nd	41.3 (7.4)	nd

smallest size group measured (0.25 g). With increasing mass from 4 g, the climb height decreased to 74 cm in the largest size group (28 g). The mean climb height of *C. cavipes* also significantly differed with species of shell carried (ANOVA,  $F = 3.87$ ,  $p < 0.01$ ), but any such relationship is complicated by a relationship between species of shell used and hermit crab size. Shell species used by *C. rugosus*, however, did not significantly influence tree climbing behaviour (ANOVA,  $F = 0.18$ ,  $p > 0.05$ ). The proportions of the tree climbing population of both species bearing certain shell species (e.g. *Turbo coronatus*) were different to the ground population, whereas the proportions of those using others (e.g. *Terebralia palustris*) were similar (Table 5). Tree climbing *C. cavipes* individuals using *T. coronatus* shells formed approximately twice the population proportion that they did in the ground population. *C. rugosus* individuals using *T. coronatus* shells, in contrast, formed approximately half the population proportion that they did in the ground population.

There was considerable variation between the hermit crab populations of the 42 monitored trees during the 21 d study period. Whilst some trees were unoccupied for virtually the whole study period, others had up to 30 individuals during a single tide. There were, however, distinct periods of higher and lower levels of climbing activity. During this period the wind speed varied between force 0 and 5 on the Beaufort scale. At the lower levels of wind velocity (below force 3 or  $12 \text{ km h}^{-1}$ ), which accounted for 85% of the study period, there was little or no detected influence of wind on the number of hermit crabs per tree or the number of occupied trees within the study population. Wind speeds of greater magnitude (force 3 to 5 or 12 to  $33 \text{ km h}^{-1}$ ), however, were a major influ-

ence on the mean number of hermit crabs climbing (Fig. 3a) in the study location. The mean number of occupied trees was also much lower during higher wind speeds but there was a high degree of variation (Fig. 3b).

Species of mangrove tree, degree of shade, number of roots and root ground area were all found to be non significant (ANOVAs, all cases  $p > 0.05$ ) as influences on the proportion of trees unoccupied by hermit crabs or the mean number of crabs per tree. The number of trunk or branch holes in a given tree, however, had an important effect (Fig. 4). N.B. The trunk and branch holes measured were all in intact trees, above the HWM and of unknown origin. The mean number of hermit crabs per tree increased from 0.43 in those with no holes to 5.08 in those with 5 or 6 holes. There were also marked activity and behavioural differences between hermit crabs taking residence in trunk/branch holes and those clinging to branches or leaf bases. Virtually all *Coenobita cavipes* and *C. rugosus* in both situations adopted a stage of semi-withdrawn dormancy after having reached the peak climb height; they remained semi-withdrawn until descent, which was accomplished by climbing or, if disturbed, by just dropping. *C. cavipes* and *C. rugosus* individuals which climbed into tree holes would also assume semi-dormancy, unless either a water pool or other individuals were present. Both species used the water to re-supply, but *C. cavipes* individuals became highly active in mutual shell inspection and even shell trading in holes

Table 5. *Coenobita cavipes* and *Coenobita rugosus*. Influence of shell species on tree climbing by hermit crabs. The shell species most frequently used by tree climbing crabs are shown with the mean distance climbed (SE in parentheses) and the proportion of the tree climbing and ground populations selecting each shell species. Chi-squared values are given for comparisons between tree and ground populations of crabs using each shell type: \* $p < 0.05$ , \*\* $p < 0.01$

Hermit crab species Shell species	Climb height (cm)	% climbers (n = 561)	% ground (n = 592)	$\chi^2$
<i>Coenobita cavipes</i>	(n = 561)	(n = 561)	(n = 592)	
<i>Turbo coronatus</i>	105.8 (10)	23.6	11.5	12.15**
<i>Strombus mutabilis</i>	90.9 (12.1)	3.8	1.7	2.39
<i>Terebralia palustris</i>	90.6 (8.0)	38.1	38.0	0.00
<i>Volema pyrum</i>	81.7 (5.7)	13.1	12.8	0.00
<i>Fasciola trapezium</i>	77.7 (4.9)	5.7	10.1	3.77
<i>Thais svignyi</i>	70.8 (7.1)	4.3	4.5	0.04
<i>Nerita plicata</i>	60.0 (8.9)	2.1	3.9	1.47
<i>Peristernia forskali</i>	53.5 (7.5)	3.1	4.1	0.43
Other shells		6.2	13.4	
<i>Coenobita rugosus</i>	(n = 43)	(n = 43)	(n = 352)	
<i>Nerita polita</i>	60.7 (16.4)	18.7	15.1	0.08
<i>Turbo coronatus</i>	59.4 (9.8)	25.6	42.3	1.41
<i>Nerita plicata</i>	50.8 (11.6)	37.2	18.7	2.31
Other shells		18.5	23.9	

which had a number of individuals present. The result of such 'shell markets' in arboretum was that some individuals ( $n = 5$ ) were occasionally observed to leave holes without a shell, with the associated shell being left in the hole. Less occasionally ( $n = 2$ ), *C. cavipes* individuals without shells were observed to climb trees, enter holes and join shell markets. *C. rugosus* were not observed to participate in shell exchange or congregate in tree holes within the study location, but were observed carrying out similar practices in terrestrial trees away from mangrove areas, where *C. cavipes* was not present.

## DISCUSSION

*Coenobita cavipes* and *C. rugosus* are essentially ground living, largely nocturnally active land crabs living within 100 m of high water levels on tropical and subtropical Indo-Pacific land masses. A proportion of their populations has sometimes been recorded as diurnally climbing trees as an alternative to sheltering in crevices or burrows. On the shores of Quirimba Island, northern Mozambique, hermit crabs are generally the most abundant macro-crustaceans throughout the entire intertidal zone in a variety of habitats. With the exception of

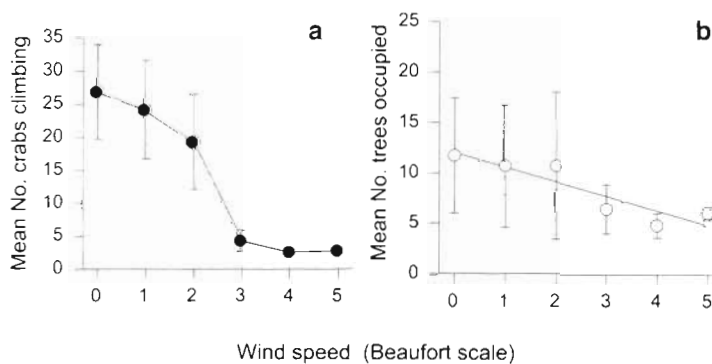


Fig. 3. *Coenobita cavipes* and *Coenobita rugosus*. Influence of wind speed on tree climbing by hermit crabs. (a) Mean total number of hermit crabs in mangrove trees and (b) mean number of mangrove trees occupied by hermit crabs in the study area for wind speeds between 0 and 5 (Beaufort scale). Regression line equation: no. of trees occupied =  $-1.44(\text{wind speed}) + 12$ . ANOVA,  $F = 18.8$ ,  $p < 0.02$

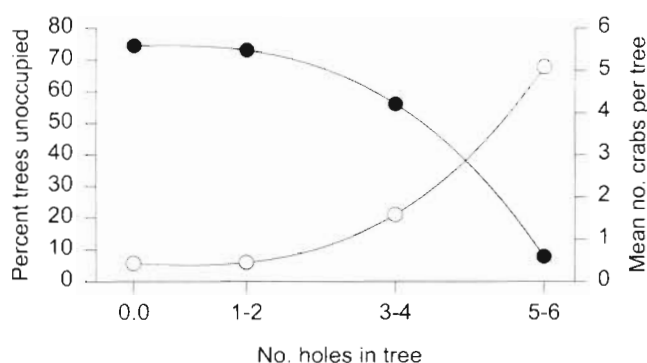


Fig. 4. *Coenobita cavipes* and *Coenobita rugosus*. Influence of trunk holes on tree climbing of hermit crabs. (●) Proportion (%) of trees in the study area unoccupied. (○) Mean number of crabs per tree

the *Uca annulipes* communities (D. K. A. Barnes & P. Hogarth unpubl.), *C. cavipes* and *C. rugosus* were the most abundant supra-littoral dwelling macro-crustaceans at Quirimba Island, both on the ground and in trees. Various *Metopograpsus*, *Grapsus* and *Sesarma* species were also present in mangrove trees but more so in the upper shore, rather than supra-littoral zone, and in comparatively much lower population densities. *Clibanarius longitarsus*, another species of hermit crab frequenting the supra-littoral zone at Quirimba Island, was not observed to vertically migrate up trees in the study location, although the behaviour has been reported at other locations (Johnson 1965, Macnae 1968).

Both *Coenobita cavipes* and *C. rugosus* were found to regularly climb the trunk as well as the root systems of mangrove trees. Occasionally, small branches were climbed and the canopy layer reached. The tree climbing habit was more prevalent in *C. cavipes* than *C. rugosus* (Table 1), but both species occurred in trees at all stages of the light:dark cycle and tidal conditions (Tables 2 & 3). Within a mangrove tree, the range of both species extended beyond the root system, trunk and branches to the leaves themselves, a distribution unusual amongst mangrove crabs (Vannini & Ruwa 1994). *C. cavipes* and *C. rugosus* at Quirimba Island also differed from most tree climbing crabs in that they exhibited no obvious tree climbing mass migration pattern. At other locations the general activity pattern of these species, as with other species of the Coenobitidae, has been described as nocturnal apart from in exceptionally humid circumstances (Ball 1972, Alexander 1976, Vannini 1976).

At Quirimba Island, mangrove dwelling *Coenobita cavipes* and *C. rugosus* may remain active throughout the day, and only the populations living on very exposed sand beach diurnally migrated to refugial shelter (Barnes 1997). Despite such extended activity

patterns, the number of hermit crabs climbing or present in trees was greatest during diurnal high water periods (Table 2). This suggested a refugial element to tree climbing, partly in direct escape from high water and partly to avoid having to leave shade (by crawling upshore and inland) to avoid high water. Large *C. cavipes* and *Ocypode ceratophthalmus* (amongst other species) were observed to eat smaller *C. cavipes* and *C. rugosus* individuals. As this behaviour was mostly nocturnal and predators did not climb or did not climb high, nocturnal climbing by smaller *C. cavipes* and *C. rugosus* would potentially reduce predation. Climbing trees and migrating to the branch and leafy termini of trees reduces predation in the brachyuran crab *Sesarma leptosoma* (Vannini & Ruwa 1994). Despite such migrations, some of its brachyuran predators (species which also occur at Quirimba Island and are probably also hermit crab predators) have been observed to climb occasionally and prey on *S. leptosoma* in trees (Vannini et al. in press). However, the numbers of hermit crabs present in trees at all circadian and tidal stages (Table 2) and the duration of presence in trees (up to 24 h, see Fig. 1) also suggest other factors must influence such behaviour.

The actual height attained by tree climbing species is rarely measured: previous studies of decapods have tended to focus on the number of crabs and the direction of migration (Warner 1967, Von Hagen 1977, Vannini & Ruwa 1994). The measurements of hermit crab climb height taken in this study illustrate that a number of behavioural subtleties can be gained from such information. The climb height of *Coenobita cavipes* and *C. rugosus* individuals ranged from 5 cm to 4 m and were higher in the former species. The height climbed by *C. cavipes* and *C. rugosus* individuals was greater at high water than low (but only by approximately 24%, see Table 3) and only trees up to 10 m each side of the High Water Mark (HWM) were climbed. Climb height was, however, unrelated to the shore position of the tree climbed (within the zone) and whether the tide actually reached the tree (Table 4). The climb height pattern thus conflicts to some extent with current hypotheses regarding climbing and avoidance of sea water immersion and suggests that immersion avoidance only partly explains and alters the vertical migration of *C. cavipes* and *C. rugosus*.

Mean climb height was related to the size of *Coenobita cavipes* individuals, such that maxima were achieved by those of mid-sized mass (4 g; Fig. 2). This is probably a result of a combination of energetics and predation. In small specimens the shell is a higher proportion of total mass and hence more expensive energetically to carry vertically. However, larger specimens of both species have outgrown their brachyuran (and cannibalistic) predators and were observed to be more

regularly immersed in sea water, suggesting greater tolerance and thus less need for mangrove tree climbing. These observations are thought to be the first reports of regular complete immersion by these semi-terrestrial species. The mean climb height and behaviour of hermit crabs carrying different molluscan shell species differed (Table 5), but in the former case may just be effect of individual size (as different shell species are preferentially used by differently sized hermit crabs). Certain shells must, however, have attributes more suitable to climbing than others, such as a squat and relatively light structure. Such a structure is typified by the shell of the mollusc *Turbo coronatus*, which was twice as common amongst tree climbing individuals of *C. cavipes* than in those of the ground population (Table 5). Conversely, tall spired, heavy shells such as those of *Terebra*, *Mitra* and *Fasciola* spp. should prove unpopular for climbing. Of these types (which are all used by Quirimba Island hermit crabs), only *Fasciola trapezium* was used by *C. cavipes* and *C. rugosus* and it was only half as common amongst tree climbing individuals as those sampled on the ground.

Environmental factors that have previously been investigated as affecting land crab distribution include temperature, ion availability and water availability (reviewed in Burggren & McMahon 1988). At Quirimba Island, wind speed affected local distribution of *Coenobita cavipes* and *C. rugosus*. Wind speed above a critical level (approximately force 3 or 11 to 12 km h<sup>-1</sup>) had a major influence on tree climbing, significantly reducing the numbers of hermit crabs per tree (Fig. 3a). The switch from tree climbing (and all other activity—see Barnes 1997) to ground refugia will largely be related to desiccation avoidance (and so indirectly water availability, above). Shell damage avoidance may also be a contributing factor, as climbing trees in a thin mangrove forest exposed to wind could potentially result in individuals being blown off branches. The nature of mangrove trees also had an important influence on the probability of a given tree being climbed and the number of hermit crabs climbing it (Fig. 4). Whilst the only recorded attribute of trees to have notable influence was that of trunk/branch holes, at least in part this influence, like that of wind, is related to water retention. *C. rugosus* is known to prefer to carry fresh water rather than sea water in its shell, although *C. cavipes* has usually been described as filling its shell with sea or brackish water (Gross et al. 1966, Alexander 1976). At Quirimba Island, however, most *C. cavipes* were rarely seen entering the sea and preferred to fill their shells with fresh water (except for the larger individuals). Here (as with most islands of the Quirimba Archipelago) pools of rain collecting in tree hollows is one of the only sources of fresh water. Thus trunk/branch holes are an

important source of fresh water to hermit crabs, but they are also the only place where hermit crabs gather apart from the occasional cluster around a large food item.

Clustering has been described in a number of East African intertidal species and has been studied in particular detail in the upper/mid shore species *Clibanarius laevimanus* (Gherardi et al. 1991, 1994, Gherardi & Vannini 1992, 1993). The major function of such clusters is at present debated, but Gherardi et al. (1994) suggested they functioned as 'shell markets' for the inspection and exchange of shells between individuals. For a species such as *Coenobita cavipes*, which is restricted in feeding time to low tide, food gatherings do represent an opportunity for shell exchange, but by day there are added risks of desiccation and by night predation, and exchange by either day or night would reduce feeding time. In gatherings in tree holes (where up to 30 individuals may be present), shell exchange (1) reduces desiccation (there is sometimes additionally a supply of fresh water), (2) reduces the risk of predation and (3) does not reduce feeding time.

The vertical migration or tree climbing habit of the supra-littoral hermit crabs *Coenobita cavipes* and *C. rugosus* at Quirimba Island is clearly not merely a refugial retreat, but a complex behavioural trait. The timing and period of tree climbing, the height climbed, and the number of individuals per tree and the particular trees climbed are related to a variety of environmental and biotic factors. Major influences are tidal rhythms, wind speed, nature of the particular tree climbed and hermit crab identity, and other influences are the light:dark cycle, position of the particular tree climbed, hermit crab mass and the type of shell carried.

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