Tree climbing and temporal niche shifting: an anti-predatory strategy in the mangrove crab *Parasesarma plicatum* (Latreille, 1803)

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***Parasesarma plicatum*, a common sesarmid crab in mangrove habitats of India, always climbs onto the mangrove vegetation during high tide. We studied whether this temporal niche shifting of the crab is an anti-predatory strategy against potential predators that invade their habitat during high tide. We studied the difference in density of this crab on the forest floor and vegetation during low and high tides in three selected study sites. *Ex situ* experiments were also conducted using the crab and a predatory fish simulating the habitat. The study confirmed that all the crabs climbed onto the vegetation from the forest floor during high tide and came down to the forest floor during low tide. Regression analysis revealed a positive correlation between water level and the height climbed by crabs on vegetation. Crabs completely migrated from sites which were fully submerged during high tide to nearby areas where mangrove trees and the shrub *Acanthus ilicifolius* provided them ample refuge above water level. *Ex situ* experiments showed that though *P. plicatum* could remain under water and feed in starved conditions, they climbed onto the vegetation above water level so as to seek refuge in the presence of predatory fish, *Lutjanus argentimaculatus*. Therefore, it is inferred that the tree-climbing character exhibited by *P. plicatum* is a strategy to escape from predators that invade their habitats during high tide inundation and flooding.**

Keywords: Anti-predatory strategy, mangrove, *Parasesarma plicatum*, temporal niche shifting, tree climbing.

ANTI-predatory strategies in animals have been well studied[1–5]. Animals reduce predation risk mainly by living in social groups, crypsis, avoiding predator-rich habitats, using refuges, armour or noxious chemicals, associating with aggressive species and speeding up vulnerable life-history stages[1,6–8]. Intertidal animals like mangrove crabs are more prone to predation pressure during high tide from aquatic predators.

Parasesarma plicatum (Figure 1 *a*) is a sesarmid crab found in marshy intertidal areas of mangrove habitats throughout the Indo-West Pacific region[9]. In India, it is distributed along both the coasts of the Peninsula and in Andaman and Nicobar Islands[10–13]. They forage on decaying organic matter on the forest floor or in shallow waters[14] (Figure 1 *b* and *c*). This is an ecologically important species as it plays a key role in crab herbivory in mangrove ecosystems[15]. Its main known predators are carnivorous crabs like *Scylla serrata* (Forsskål, 1775) and *S. tranquebarica* (Fabricius, 1798), reptiles like *Varanus bengalensis* (Daudin, 1802), birds like *Egretta garzetta* (Linnaeus, 1766) and *Ardeola grayii* (Sykes, 1832), and mammals like *Canis aureus* (Linnaeus, 1758) that coexist or frequent the mangrove habitats.

While studying the mutualistic interaction between crabs and mangroves in Kerala, we observed *P. plicatum* always climbing on the nearby mangroves or seeking possible refuge during high tide inundation or monsoon flooding (Figure 1 *d*–*f*). This gave an impression that they wanted to avoid the flood waters. In all these habitats, we observed the presence of predatory fish, viz. *Lutjanus argentimaculatus* (Forsskål, 1775), *Lutjanus johnii* (Bloch, 1792), *Terapon jarbua* (Forsskål, 1775), *Pisodonophis boro* (Hamilton, 1822) and *Epinephelus malabaricus* (Bloch & Schneider, 1801) in the flood waters. This prompted us to study whether the temporal niche shifting was an anti-predatory strategy exhibited by this crab to avoid potential piscine predators that invaded their habitat during high tide inundation. The investigation involved selection of study sites based on vegetation, observation of vertical movement and density estimation of *P. plicatum* during inundation and non-inundation. An *ex situ* experiment was successfully conducted employing the crab and fish simulating the habitat condition to confirm our *in situ* inferences.

Study area

Kunhimangalam mangrove forest (12°08′N lat. and 75°22′E long.) occurs on the banks of Perumba and

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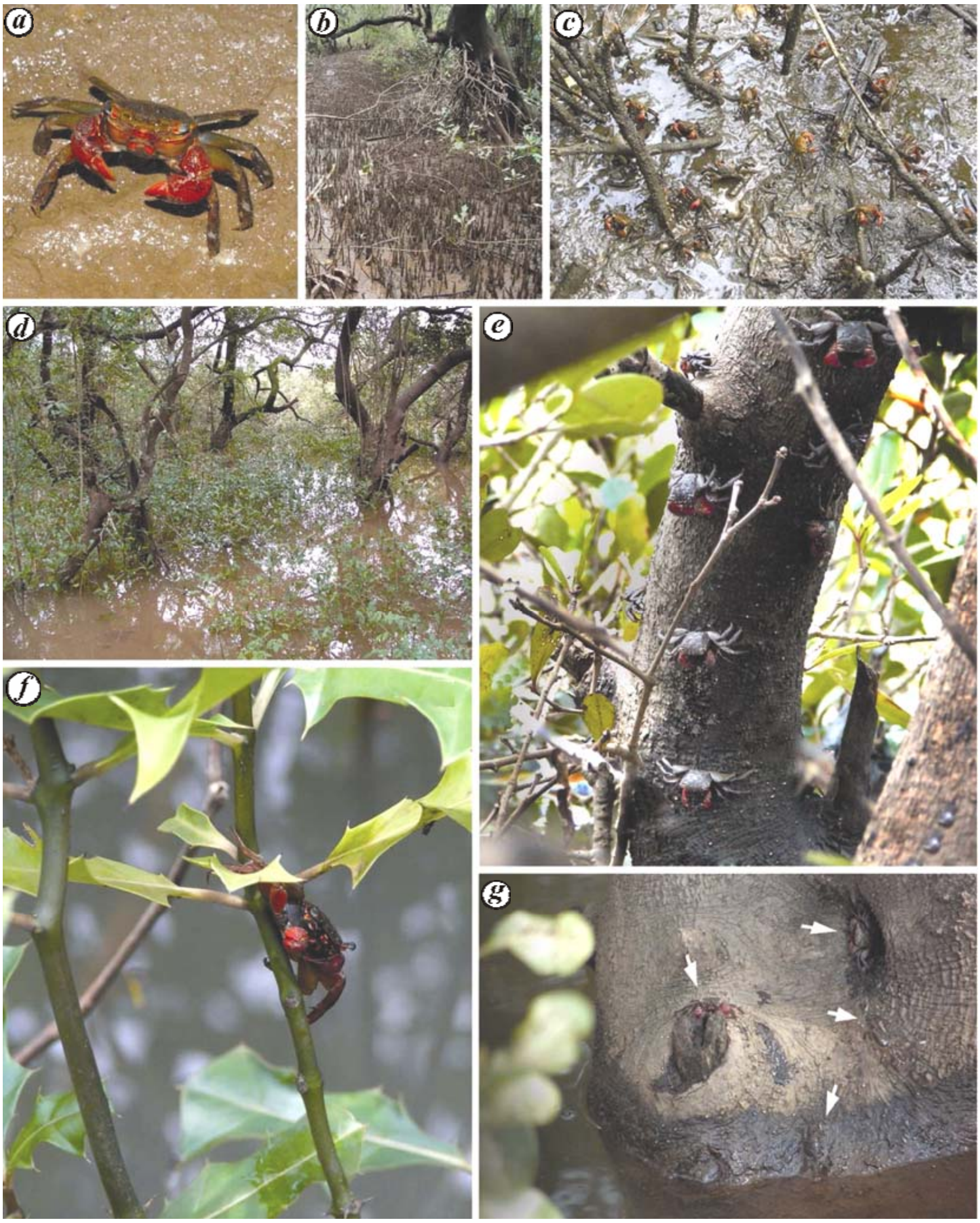

Figure 1. ***a***, The mangrove crab *Parasesarma plicatum*. ***b***, Mangrove forest floor exposed during low tide in Kunhimangalam, Kannur district, Kerala. ***c***, *P. plicatum* feeding on detritus in the forest floor during low tide. ***d***, Mangrove forest floor submerged during high tide. ***e***, *P. plicatum* on the trunk of *Avicennia officinalis* during high tide. ***f***, *P. plicatum* on *Acanthus ilicifolius* during high tide. ***g***, Four Crabs descending from the tree trunk with receding water.

Pullankodu rivers in Kannur district, Kerala, India, almost 100 m towards the landward side (Figure 2). *Acanthus ilicifolius* L., *Aegiceras corniculatum* (L.) Blanco, *Avicennia officinalis* L., *Excoecaria agallocha* L. and *Rhizophora mucronata* Lam. predominate the forest with representations of *Avicennia* marina (Forssk.) Vierh., *Bruguiera cylindrica* (L.) Blume, *Kandelia candel* (L.) Druce, *Rhizophora apiculata* Blume and *Sonneratia caseolaris* (L.) Engl. *P. plicatum* is a dominant crab in the Kunhimangalam mangrove forest with an average density of 5.22 crabs m^{-2} (ref. 16). It has a carapace width of 17.8 ± 0.2 mm ($n = 82$, mean ± SE) and a wet weight of 3.58 ± 0.15 g ($n = 82$).

Three categories of study sites with different vegetation and inundation patterns and five replicates in each category having an area of 25 m^2 (5 m × 5 m) were identified at random. These three categories were: site with only trees (A), site with only *Acanthus ilicifolius* (B) and site with only grass (C). Site A consisted of large trees of *A. officinalis*, *A. marina* and *E. agallocha* with hardly any under-vegetation. Trunks of these trees measured an average height of 4.64 ± 0.63 m and DBH of 9.29 ± 0.92 cm, and stood well above the high tide mark[16]. Site B was thickly vegetated with *A. ilicifolius*. Their uniform thickets measured an average height of 76 ± 5.1 cm, and about 30% of their shoot system was exposed above water level during high tide. Site C was close to the mangrove vegetation, but normally got completely submerged during high tide. Sites A and B extended safe refuges to the crab during inundation.

Methodology

In situ experiments

Crab density and niche shifting: We estimated the density of this crab on the forest floor and on plants during low and high tides in the above three sampling sites. Crab density during low tide was estimated using a time-based visual count method. For this, we marked five 1 m^2 sub-plots in each of the 25 sq. m sampling sites with brown (to match with the sediment background) ribbons. The highest number counted in the sub-plot during a continuous 15 min observation after 10 min acclimatization was recorded as the density of this crab. The average density of five sub-plots was taken as the crab density per square metre. Crab density in 25 sq. m sampling site was thus calculated. To record the crab density on plants during high tide, all the plants in each of the five 25 sq. m sampling sites were scanned directly or using a binocular (Zenith 10×50 mm zoom). Graduated poles established in sites and graduated tree trunks provided exact height levels that the crabs positioned themselves during inundation. Data recording was done for a time period of 12 h. This was repeated five times for each site.

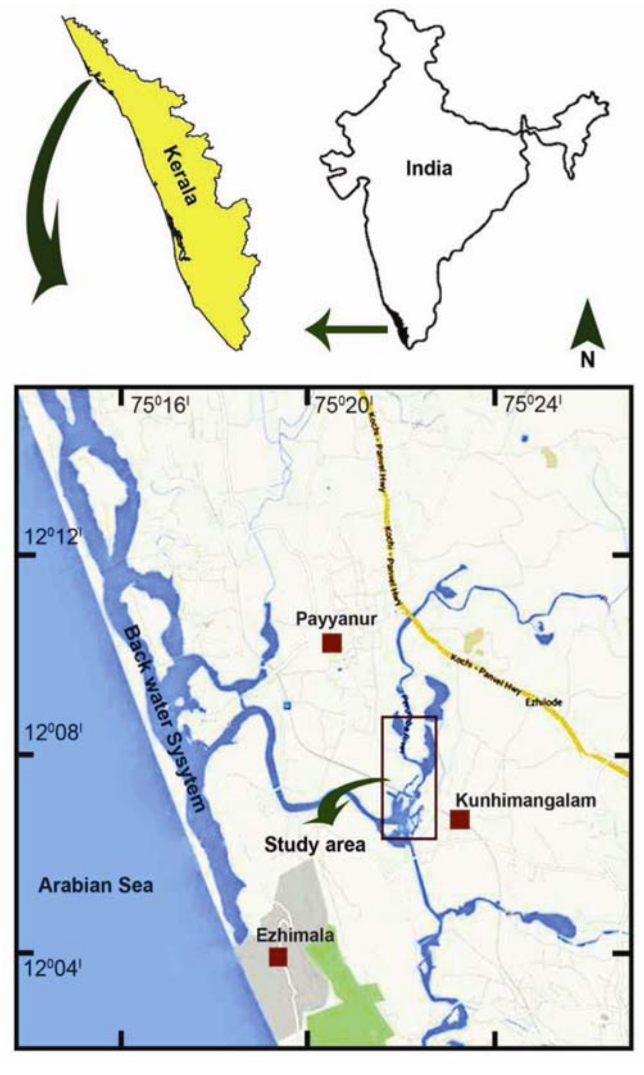

Figure 2. Location map of the study area.

Ex situ experiments

Ex situ experiments were carried out to confirm the inference obtained from *in situ* experiments. Forty plastic tubs (105 cm × 60 cm × 60 cm) were filled with sediment from mangrove forest in a sloping manner. A thin layer of decomposing mangrove leaf litter was spread over it to simulate the forest floor. Three wooden poles of 50 cm height and 4 cm diameter were erected in each tub to simulate tree trunks. Poles were erected at *ca.* 15 cm apart. High and low tides were created within the tubs at an interval of six hours by controlling the flow of brackish water stored in an overhead tank. The level of water above the sediment was maintained at *ca.* 20 cm during simulated high tide. Five crabs were introduced into each tub three days before the experiments to acclimatize them to the new environment.

A single *L. argentimaculatus* (length 24.05 ± 0.37 cm, wet weight 286.80 ± 3.42 g) was introduced into each of the first set of ten plastic tubs. It is a predatory fish commonly seen in Perumba and Pullankode rivers, and frequently visits the Kunhimangalam mangrove forest when high tide water inundates the intertidal area. The second set of ten tubs was maintained only with crabs. This was kept as the first control. Vertical migration of *P. plicatum* in response to simulated high and low tides was observed for five days, i.e. five flood and five ebb tides.

The third set of ten tubs with four crabs in each, starved for 48 h, was employed to observe whether the crab preferred to remain under water in the absence of predators, if there was a strong need for feeding during simulated high tide. Subsequently, one *L. argentimaculatus* was introduced into each of the ten tubs. The fourth set of ten tubs was maintained with only starved crabs. This was kept as the second control. The response of

P. plicatum was observed for five days. Thus of the total 40 tubs we maintained, 20 had normal crabs – ten with fish (experimental tubs) and ten without (control tubs); 20 with starved crabs – ten with fish (experimental tubs) and ten without (control tubs).

Results

In situ experiments

There was mass migration of *P. plicatum* from the forest floor to the vegetation during high tide and back (Figure 1 *g*) during low tide in all the sites studied. The high tide density (number of crabs found on the vegetation above water level during high tide) of crabs in site A was significantly higher (85.00 ± 13.85 individuals site^{-1}) than the low tide density (number of crabs in intertidal areas during low tide; 24.80 ± 6.16 individuals site^{-1}; $t = 3.96$, $P < 0.01$). Site A showed an increase in crab density from 24.80 ± 6.16 to 85.00 ± 13.85 individuals site^{-1}. In site B, the high tide density was higher (107 ± 10.15 individuals site^{-1}) than the low tide density (84 ± 6.38 individuals site^{-1}), but the difference was statistically insignificant ($t = 1.92$, $P > 0.05$). These sites showed an increase only from 84 ± 6.38 to 107 ± 10.15 individuals site^{-1}. This was because *A. ilicifolius*, being small shrubs, could not hold many crabs above water level as mangrove trees could. The high tide density was zero in site C, though it registered a density of 144.6 ± 35.68 individuals site^{-1} during low tide (Figure 3). This showed that only 57.64% of the crabs migrated from site C to sites A and B. The rest must have migrated to areas outside the designated sites. This inference was drawn on two counts: (1) *P. plicatum* did not remain in burrows during inundation as they were not habituated to do so and (2) site C showed almost zero crab density during inundation. These suggest that the crab temporally shifted its niche to tree trunks during high tide inundation.

In site A, the crabs climbed to a maximum height of 136 cm and congregated mainly between 46 and 52 cm from the water level (Figure 4). In site B, crabs climbed up to 98 cm above water level, where they congregated mainly between 33 and 37 cm. The minimum height they climbed was between 2 and 11 cm from water level (Figure 5). Regression analysis revealed a positive correlation between water level and height climbed by the crabs in site A ($r^2 = 0.507$) and site B ($r^2 = 0.550$). Crabs changed their location on vegetation according to the change in water level. Absence of crabs on submerged portions of plants indicated that the temporal niche shifting was in response to the rise in water level. *P. plicatum* has a conspicuously flattened body, relatively long propodi and short dactyli – the morphological features common to all tree-climbing crabs[17]. But this crab has never been found to exhibit tree-climbing behaviour when there is no rise in water level.

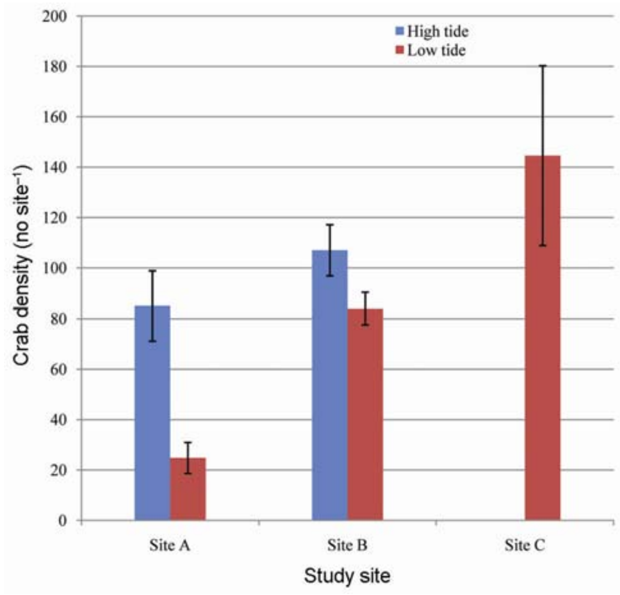

Figure 3. Comparison of low tide and high tide densities of *P. plicatum* in the three study sites at Kunhimangalam.

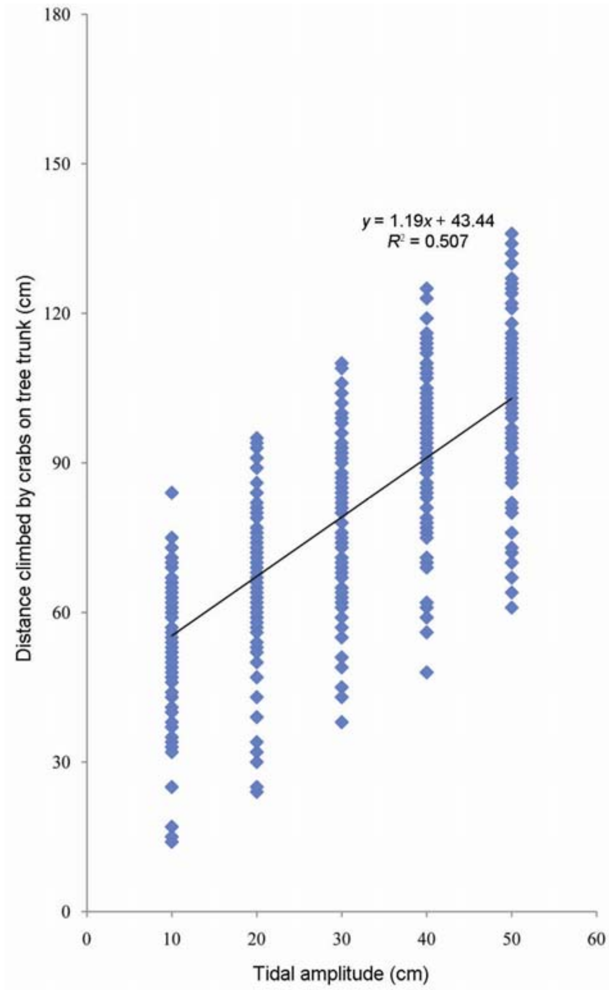

Figure 4. Scatter diagram with line equation showing the distribution pattern of *P. plicatum* on tree trunks during high tide at Kunhimangalam.

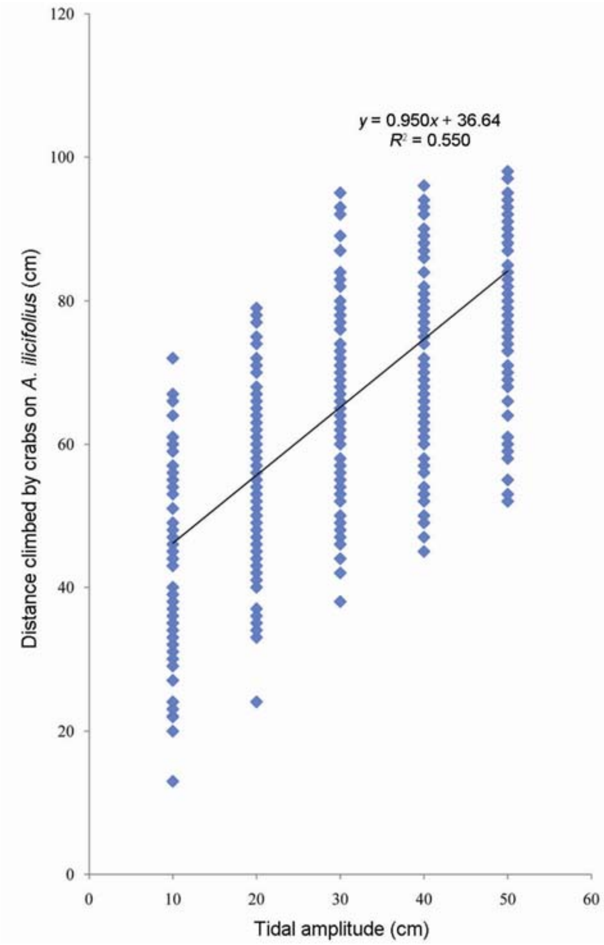

Figure 5. Scatter diagram with line equation showing the distribution pattern of *P. plicatum* on *Acanthus ilicifolius* during high tide at Kunhimangalam.

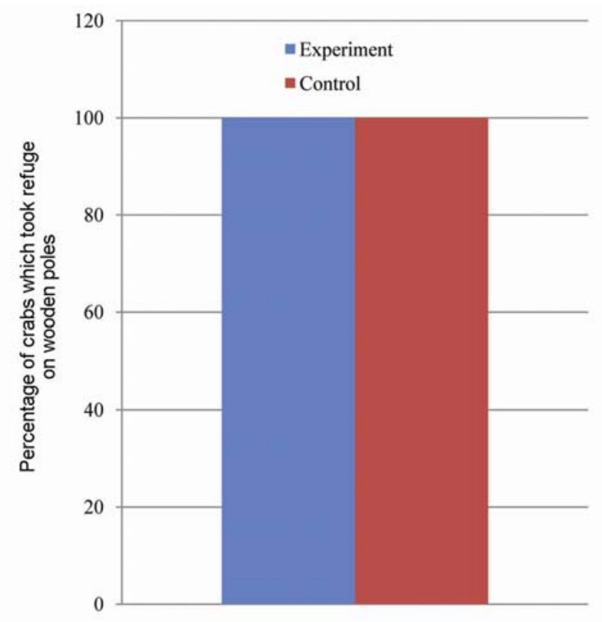

Figure 6. Bar diagram showing the percentage of normal (non-starved) *P. plicatum* which climbed on poles in the tubs during simulated high tide.

Ex situ experiments

All the normal crabs in ten experimental and ten control tubs climbed on the poles in response to rise in water level, irrespective of the presence or absence of the fish *L. argentimaculatus* (Figure 6). Among the starved crabs in ten control tubs, 95.2% preferred to stay under water and fed on litter provided in the tubs, while the rest (4.8%) climbed on the poles (Figure 7). Crabs on the poles came down to water for feeding after some time (21.32 ± 0.64 min). Crabs that were feeding under water climbed onto the poles after 25.92 ± 0.66 min of feeding. On the contrary, all the starved crabs in ten experimental tubs climbed on the poles as soon as the fish were introduced. When fish were removed from the tubs during simulated high tide, crabs climbed down from the poles and started feeding on the leaf litter provided. The vertical movement of crabs from water to the poles and back without any inhibition in the absence of predator fish, and movement of crabs to the poles but not back down in the presence of the predator showed that the vertical climbing was strongly influenced by the presence of the predator fish. We observed the same strategy adopted by *P. plicatum* against predators like *L. argentimaculatus*, *L. johnii* and *P. boro* in the mangrove habitat. High tide inundation provided a good opportunity for the predator fish to enter the habitat of this crab species.

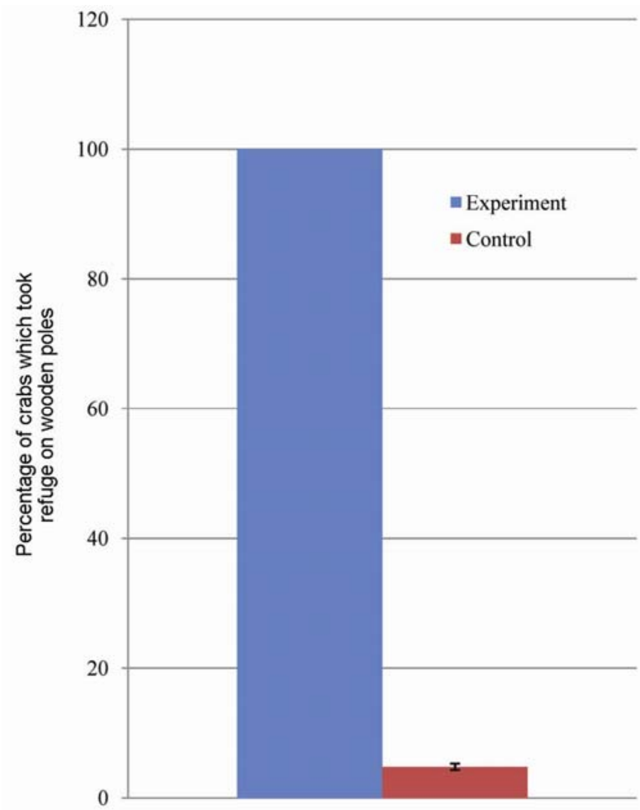

Figure 7. Bar diagram showing the percentage of starved *P. plicatum* which climbed on the poles in the tubs during simulated high tide.

Discussion

Studies on anti-predatory strategies in crabs are limited. Available works report that crabs employ threat postures[18], camouflaging[19–21], autotomy[22,23], and hiding in burrows[24] and crevices[25] as anti-predatory strategies. Though the tree-climbing behaviour in mangrove crabs has been studied in detail[17,26–37], it has never been proved through experiments as an anti-predatory strategy[27,33,36].

Reportedly, there are 46 species of mangrove crabs worldwide, that show tree-climbing behaviour[17,26–37]. The instinct of climbing trees in these crabs is generally associated with escape from flood waters[27], foraging on fresh leaves[34], search for shelter in tree holes and barks[30,35,36], or for water in phytotelmata[27]. It could be an expression of circardian rhythm as reported by Vannini *et al.*[38], because they could observe regular migration of *Sesarma leptosoma* twice a day in response to light. Cannicci *et al.*[39] noted tree-climbing behaviour in *S. leptosoma* as a response to visual recognition of aerial predators. Von Hagen[27] connected tree climbing in *Uca* males to effective display of chelipeds. Crabs like *Aratus pisonii*, *S. leptosoma* and *Armases elegans* are reported to climb trees to feed on fresh green leaves[17,38,40].

A significantly higher density of *P. plicatum* found on plants when compared to their density on the forest floor during high tide clearly indicates that this species exhibits tree-climbing behaviour. Its population did not show any circardian rhythm. They did not normally feed on green leaves during their stay on tree trunks, when high tide inundation occurred. Most of the time they sat heads down on trunks, watching the level of receding water. However, they used to suddenly jump to high tide water to escape from the detected aerial predators as a spontaneous reaction, soon again climbing on the trees when the aerial threat subsided. Tree-climbing crab *Goniopsis cruentata* also showed this type of behaviour as a common escape response[27].

P. plicatum did not use burrows as hide-outs to escape from predators, as is done by crabs like *Metasesarma rubripes*, *Goniopsis cruentata*, and *Cardisoma guanhumi*[27]. Many of the tree-climbing mangrove crabs which survive under water for long periods in experimental conditions preferred climbing on trees during high tide than remaining in their burrows[41]. *P. plicatum* hid in its burrow on the forest floor when threatened during low tide, but when threatened during high tide inundation it preferred climbing on trees as shown in the present *in situ* and *ex situ* experiments, to avoid water-borne predators. This inference is also supported by our field observations in different mangrove habitats in Kerala. *P. plicatum* can remain under water and feed on decayed litter as long as it does not detect any sign of predators in the surrounding water. The crab, thus, is intelligent enough to choose an appropriate shelter depending on the degree of threat existing in the habitat. In short, the tree-climbing character exhibited by *P. plicatum* during inundation and flooding is a strategy adopted by it as a normal but spontaneous response to rise in water level. Rise in water level brings water-borne predators near the crabs. Visual recognition of predators and subsequent selection of shelter have been reported in mangrove crabs like *A. pissonni* and *S. leptosoma*[42], though such experiments have not been performed so far with *P. plicatum.*

1. Harvey, P. H. and Greenwood, P. J., Anti-predator defense strategies: some evolutionary considerations. In *Behavioral Ecology: An Evolutionary Approach* (eds Krebs, J. R. and Davies, N. B.), Sinauer Associates, Sunderland, Massachusetts, 1978, pp. 129–151.
2. Lima, S. L. and Dill, L. M., Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, 1990, **68**, 619–640.
3. Reznick, D. N., Bryga, H. and Endler, J. A., Experimentally induced life-history evolution in a natural population. *Nature*, 1990, **346**, 357–359.
4. Roff, D. A., *The Evolution of Life Histories: Theory and Analysis*, Chapman and Hall, New York, 1992, p. 548.
5. Stearns, S. C., *The Evolution of Life Histories*, Oxford University Press, Oxford, 1992, p. 262.
6. Lima, S. L., Valone, T. J. and Caracao, T., Foraging efficiency–predation risk trade-off in the grey squirrel. *Anim. Behav.*, 1985, **33**, 155–165.
7. Werner, E. E., Amphibian metamorphosis, growth rate, predation risk and the optimal size at transformation. *Am. Nat.*, 1986, **128**, 319–341.
8. Arendt, J. D., Adaptive intrinsic growth rates: integration across taxa. *Q. Rev. Biol.*, 1997, **72**, 149–177.
9. Rahayu, D. L. and Ng, P. K. L., Revision of *Parasesarma plicatum* (Latreille, 1803) species group (Crustacea: Decapoda: Brachyura: Sesarmidae). *Zootaxa*, 2010, **2327**, 1–22.
10. Alcock, A. W., Materials for a carcinological fauna of India. No. 6. The Brachyura Catometopa or Grapsoidea. *J. Asiat. Soc. Bengal*, 1900, **69**(3), 279–456.
11. Dev Roy, M. K. and Nandi, N. C., Brachyuran biodiversity of some selected brackishwater lakes of India. In Proceedings of Taal 2007: The 12th World Lake Conference (eds Sengupta, M. and Dalwani, R.), 2008, pp. 496–499.
12. Shukla, M. L., Patel, B. K., Trivedi, J. N. and Vachhrajani, K. D., Brachyuran crab diversity of Mahi and Dhadhar Estuaries, Gujarat, India. *Res. J. Mar. Sci.*, 2013, **1**(2), 8–11.
13. Varadharajan, D. and Soundarapandian, P., Crab biodiversity from Arukkattuthurai to Pasipattinam, south east coast of India. *Indian J. Geomar. Sci.*, 2014, **43**(4), 676–698.
14. Shanij, K., Praveen, V. P., Oommen, M. M. and Nayar, T. S., Leaf litter translocation and consumption in mangrove ecosystems: the key role played by the sesarmid crab *Neosarmatium malabaricum*. *Curr. Sci.*, 2016, **110**(10), 1969–1976.
15. Nayar, T. S., Plant crab interaction in mangrove ecosystem with a case study from Kerala. In *Towards Conservation and Management of Mangrove Ecosystems in India* (eds Bhatt, J. R. *et al.*), International Union for Conservation of Nature, India, 2011, pp. 73–88.
16. Praveen, V. P., The role of brachyuran crabs in structure, composition and recruitment of mangrove forests in Kerala. Ph D thesis, University of Kerala, Thiruvananthapuram, 2014, p. 200.
17. Fratini, S., Vannini, M., Cannicci, S. and Schubart, C. D., Tree-climbing mangrove crabs: a case of convergent evolution. *Evol. Ecol. Res.*, 2005, **7**, 219–233.
18. Hazlett, B. A. and McLay, C. L., Responses to predation risk: alternative strategies in the crab *Heterozius rotundifrons*. *Anim. Behav.*, 2005, **69**, 967–972.

19. Stachowicz, J. J. and Hay, M. E., Reducing predation through chemically mediated camouflage: indirect effects of plant defenses on herbivores. *Ecology*, 1999, **80**, 495–509.
20. Thanh, P. D., Wada, K., Sato, M. and Shirayama, Y., Decorating behaviour by the majid crab *Tiarinia cornigera* as protection against predators. *J. Mar. Biol. Assoc. UK*, 2003, **83**, 1235–1237.
21. Hultgren, K. M. and Stachowicz, J. J., Alternative camouflage strategies mediate predation risk among closely related co-occurring kelp crabs. *Oecologia*, 2008, **155**, 519–528.
22. Juanes, F. and Smith L. D., The ecological consequences of limb damage and loss in decapod crustaceans: a review and prospectus. *J. Exp. Mar. Biol. Ecol.*, 1995, **193**, 197–223.
23. McVean, A., Autotomy. In *The Biology of Crustacea, Vol. 4* (ed. Bliss, D. E.), Academic Press, New York, 1982, pp. 107–132.
24. Ansell, A. D., Migration or shelter? Behavioural options for deposit feeding crabs on tropical sandy shores, In *Behavioral Adaptation to Intertidal Life* (eds Chelazzi, G. and Vannini, M.), Plenum Press, New York, 1988, pp. 15–26.
25. Bovbjerg, R. V., Behavioral ecology of the crab. *Pachygrapsus crassipes*. *Ecology*, 1960, **41**, 668–672.
26. Warner, G. F., The life history of the mangrove tree crab *Aratus pisonii*. *J. Zool*., 1967, **153**(3), 321–335.
27. Von Hagen, H. O., The tree climbing crabs of Trinidad. *Stud. Fauna Curacao.*, 1977, **54**, 25–29.
28. Green, J. L., Biology of *Aratus elegans*. M Sc thesis. University of North Wales, Bangor, 1986.
29. Vannini, M. and Ruwa, R. K., Vertical migration in the tree crab *Sesarma leptosoma* (Decapoda, Grapsidae). *Mar. Biol.*, 1994, **118**(2), 271–278.
30. Cannicci, S., Fratini, S. and Vannini, M., Use of time, space and food resources in the mangrove climbing crab *Selatium elongatum* (Grapsidae: Sesarminae). *Mar. Biol.*, 1999, **135**(2), 335–339.
31. Vannini, M., Oluoch, A. and Ruwa, R. K., Tree climbing decapods of Kenyan mangroves. In *Mangrove Ecosystem Studies in Latin America and Africa* (eds Kjerfve, B. *et al.*), UNESCO Technical Papers in Marine Science, Paris, 1997, pp. 125–138.
32. Cox, G. J., A note on tree climbing by the crab *Helice crassa* in mangrove swamps. *Tane*, 1976, **22**, 155–156.
33. Masagca, J. T., Feeding ecology of tree climbing mangrove sesarmid crabs from Luzon, Philippines. *Biotropica*, 2009, **16**(1), 1–10.
34. Cannicci, S., Ruwa, R. K., Ritossa, S. and Vannini, M., Branch-fidelity in the tree crab *Sesarma leptosoma* (Decapoda, Grapsidae). *J. Zool.*, 1996, **238**, 795–801.
35. Vannini, M., Ruwa, R. K. and Cannicci, S., Effect of microclimatic factors and tide on vertical migrations of the mangrove crab *Sesarma leptosoma* (Decapoda, Grapsidae). *Mar. Biol.*, 1997, **130**, 101–108.
36. Sivasothi, N., Niche preferences of tree-climbing crabs in Singapore mangroves. *Crustaceana*, 2000, **73**, 25–38.
37. Tree climbing crabs on the shores of Singapore, 2016; http://www.wildsingapore.com/wildfacts/crustacea/crab/sesarmidae/episesarma.htm (accessed on 28 May 2016).
38. Vannini, M., Cannicci, S. and Ruwa, R. K., Effect of light intensity on vertical migrations of the tree crab *Sesarma leptosoma* Hilgendorf (Decapoda, Grapsidae). *J. Exp. Mar. Biol. Ecol*., 1995, **185**(2), 181–189.
39. Cannicci, S., Morino, L. and Vannini, M., Behavioural evidence for visual recognition of predators by the mangrove climbing crab *Sesarma leptosoma*. *Anim*. *Behav*., 2002, **63**, 77–83.
40. Niem, V. H., Phylogenetic relationships among American species of Sesarma (subgenus Armases) (Brachyura, Grapsidae). *Crustaceana*, 1996, **69**(3), 330–348.
41. Verwey, J., Einiges uber die Biologie ost-indischer Mangrovekrabben. *Treubia*, 1930, **I2**, 168–261.
42. Diaz, H., Orihuela, B. and Forward Jr, R. B., Visual orientation of post-larval and juvenile mangrove crabs. *J. Crustacean Biol.*, 1995, **15**, 671–678.

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