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A JAMAICAN SPECIALITY: THE BROMELIAD CRAB

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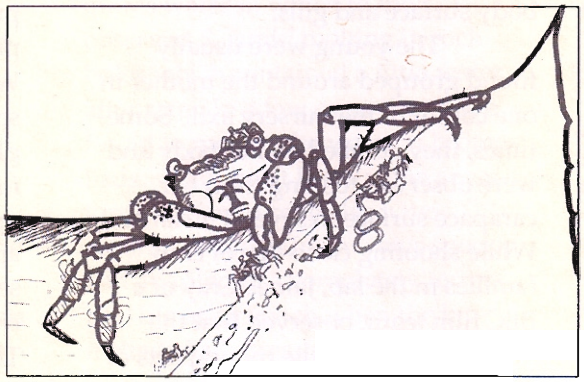
INTRODUCTION

There is a remarkable variety of freshwater and terrestrial crabs in Jamaica. At least five species of the family Grapsidae, all belonging to the subfamily Sesarminae, live in mountain rivers and streams *(Sesarma bidentatum)*, under stones and rubble in mountain forests *(S. jarvisi* and *S. cookei)*, in subterranean rainwater reservoirs of bromeliads *(Metopaulias depressus)*. All these crabs live a secret life, and it was not until the 1960s that Hartnol (1964a, b, 1971) and later Abele and Means (1977) threw some light on their life history. However, most of their biology, especially the reproductive behaviour has remained obscure.

The bromeliad crab, *Metopaulias depressus*, is quite common, although few people have ever seen it in the wild. Local people, usually well aware of the creatures living in their environment, never mentioned this crab when I questioned them about the animals that live in "wild pines" (bromeliads).

It has been assumed that bromeliad crabs pass their entire lifecycle in the water-tanks of bromeliads (Laessle 1961, Hartnoll 1964a). This is a very unsual environment for an animal whose ancestors were outfitted by natural selection for a marine life and marine-planktonic larval development. This is even more remarkable as, since Laessle's (1961) micro-limnological study on the bromeliad water-tanks, it has been recognized that this habitat is a very harsh environment for crabs to breed in; it is especially hostile to larvae and juveniles. From this unique ecological situation, the interesting question arose - how do bromeliad crabs mitigate the harshness of this environment for their young? The bromeliad crab promised to be one of the most exotic and exciting crabs of Jamaica, if not the world.



The bromeliad crab, *Metopaulias depressus*. A mother crab with young in the nursery. (Illustration by the author)

MATERIALS AND METHODS

The bromeliad crab is the only species of the genus *Metopaulia (monotypic)*. Its carapace is nearly square, in large animals measuring 2 x 2 cm; the body is depressed, reddish-brown and purple in colour and the claws are sharply pointed. It is found in western Jamaica, from Dolphin Head eastward to west of the Blue Mountains.

The study was conducted in the Cockpit Country near Windsor, Trelawny (altitude 90m; approximate distance from the sea 30km), in 1986 and 1987. This heavily eroded karst region consists of steep, forest-covered hills of 60 - 100 m height near Windsor. As in most karst areas in central Jamaica rain water drains through the porous limestone into the numerous subterranean cave-systems, and permanent surface rivers are missing. However, moisture is trapped by bromeliads whose leaves channel the water into the leaf axils where it is stored. They provide the only permanent water source in these areas.

The animals associated with bromeliads were studied in the Discovery Bay Marine Laboratory as well as in the field. Lab specimens were received by removing and dissecting several hundred plants. Field observations included plants growing on the ground, epiphytically on tree trunks, and in the forest canopy. The canopy plants were investigated by climbing up to a height of over 30m, aided by a rope and climbing equipment. A number of individually marked crabs were observed in the field for several months. Most observations were done from 1900 to 2400 hours using a battery operated head-lamp (for more details see Diesel, 1989).

RESULTS

Crabs were most common

in large bromeliads, especially *Aechmea paniculigera*, and less frequently *Hohenbergia* sp., both species are abundant on the top of the steep karst hills. In 54% of all plants examined, at least one crab was present. Adults usually inhabited the largest bromeliads, preferably *A. paniculigera* which sometimes contained more than 3.5 liters of water. Bromeliads growing on the ground had the highest number of crabs, but breeding females were also found in plants on tree trunks and up to 20m above the ground, in the canopy. The breeding activities started before the spring rainy season, in the latter part of January to mid February. A second breeding season appeared to start in the latter part of September to late October, as already suggested by Hartnoll (1964a). Each reproductively active female spawned 20 to 100 relatively large eggs (1.5 mm in diameter) and incubated them attached to her abdominal appendages.

After approximately 12 weeks of development, larvae were released into the water of a single, large leaf axil - usually on the outer and lower side of a bromeliad. However, before releasing the eggs, mother crab prepared the leaf axil by removing accumulated leaf litter and organic detritus. This clean-out behaviour probably improved the condition of the water for the larvae which were released from the eggs. The juveniles were dark-pigmented and developed rapidly; they molted into young crabs within only nine days (Hartnoll, 1964a). The young remained in the nursery for approximately 8 weeks. Thereafter, they dispersed to neighbouring leaf axils, but stayed on their "home" - plant for up to a year. In many cases, a mother and her young from several breeding seasons lived in the same bromeliad, thus forming a large family group.

Following metamorphosis from the larval stage, the young crabs frequently left the water and moved along its edge. Like adults they are able to breathe in air as long as they maintain a thin film of water circulating between the outer parts of their body surface and gills.

The young were usually found grouped around the mother in one corner of the nursery axil. Sometimes, they climbed on her body and were observed feeding from her carapace surface in several instances. While shooting close-ups of crab families in the lab, James Cray of a BBC film team, observed that the young fed around the mouthparts of their mother.

During the first two months of juvenile development, the mother was usually found in the nursery, guarding the young against predators. The most common predator was a large nocturnal spider *(Ctenus malvernenis)* which hunts on bromeliads and has been observed catching a juvenile crab in three cases. In field experiments, I have removed mothers from their brood, thus leaving the young without care and protection. This led to a decrease in juvenile survival. The result clearly demonstrated the significance of maternal care for the young.

A large number of young live in the limited space within a leaf axil, though practically no food resources are present. I could not solve this mystery until I observed a crab mother carrying a millipede across several leaves into the nursery. There she cut the prey into pieces and deposited them at the edge of the water, where later, the young started feeding on them. Subsequently, I repeatedly observed females hunting along the surface of the bromeliad leaves. The most common prey were millipedes *(Spirobolida, Polydesmidae)* and snails *(Sagda, Pleurodonta, Helicina, Neocyclotus and Trochtella)*, and to a lesser degree beetles *(Phyllophaga)*, moths, termites and ants. Millipedes frequently foraged in the outer, older leaf axils which were without water. They were also found to breed in these axils.

Field observations revealed that the bromeliad crab subsists predominantly on invertebrate prey, rather than plant matter. While hunting, adult crabs visited several leaf axils on their "home"-plant. Occasionally they were found standing upright with raised, open claws at the edge of the water, apparently waiting for prey. In several cases, I offered hunting crabs invertebrate prey items. These were immediately caught, pulled under the surface of the water and killed. On one occasion, a crab attacked a 'fortyleg' (centipede) of 12 cm length which I dropped into an axil; the crab killed its much larger victim after a period of wrestling.

DISCUSSION

The Jamaican bromeliad crab has one of the most thrilling crustacean natural histories. Suprisingly, it is the only crab which uses bromeliads for breeding, although such plants are common on other Caribbean islands as well as in Central and South America. Species of the genus *Sesarma*, a genus which contains the closest relatives of the bromeliad crab, are very common in tropical and subtropical fresh waters and terrestrial habitats. Occasionally, adults of some species like *S. angustipes* are found in bromeliads near to the sea (Abele 1972 a, b; personal observations in Panama) but do not breed there. This conclusion arises from the fact that *S. angustipes* females produce several thousand small eggs, an attribute of those species which

have marine-planktonic larvae. Presumably, the crab is partly terrestrial and only visits bromeliad water-tanks to moisten the gills or to search for food.

The question remains: why is it that crabs breeding in bromeliads have evolved only in Jamaica? I suggest a combination of two ecological patterns unique to the island:

1. There are two major groups of crabs comprising many species that have evolved independence in their larval development from the sea: the *Potamoidea* and the *Sesarminae*:. Both are widespread in tropical and subtropical areas, and both compete for the same habitat. Jamaica differs from other Caribbean islands and Central and South America by lacking representatives of the *Potamoidea*. Hartnoll (1964a) suggested that this absence led to an extended spread of sesarmid crabs.

2. Bromeliads provide a permanent, and in many parts of the island including most limestone areas, the only permanent freshwater reservoir. In addition, bromeliad diversity is extremely high in Jamaica with more than 60 species of which at least 40 are endemic to the island. Plants of numerous large species belonging to the genera *Aechmea, Hohenbergia, Tillandsia, Guzmania, Vriesia and Pitcairnia* can store several liters of water.

The ancestor of *Metopaulias depressus* may have been species living near streams or rivers, independent of the sea and with an abbreviated larval development, but dependent on freshwater for breeding. This species may have visited nearby areas in order to search for food. However, the need for water to moisten the gills required frequent visits to fresh water resources, no matter how small they may have been. Bromeliads growing on the ground provided water and a rich source of food, permitting a long sojourn and even offering the necessary medium in which to breed.

Today we find the related species *Sesarma jarvisi* living in a terrestrial habitat in the same area as *M. depressus*. *S. jarvisi* is apparently more independent of water for respiration than *M. depressus*, but still requires water in which to molt. I observed *S. jarvisi* molting in rock holes which contained a little water after rain. In a few cases they were found to molt in the water of bromeliads. In terms of history, the ancestors of *S. jarvisi* may also have separated from a fresh water species and adapted to a completely terrestrial life at an epoch when the bromeliads had already been occupied by the larger and stronger progenitors of *M. depressus*.

Only further studies of the relationship of Jamaican *Sesarminae* and the detailed knowledge of their biology will throw more light on the evolutionary events which took place.

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