

Behavioral Ecology of Crabs: A Breif Review

Shipra Sinha¹

1(Dept. Of Zoology, Kalyan P.G College, Bhilai Nagar, (C.G), India)

I. Introduction

Behavioral ecology is the branch of science that studies the ecological and evolutionary aspects of a species or a collection of species with that of its/their immediate environment. It deals with analyses of relationships between an organism's behaviour and the environment wherein the said behaviour has evolved or is expressed. One of the greatest geneticists Theodosius Dobzhansky (1964) famously wrote, "*Nothing in Biology makes sense except in the light of evolution*". Behavioural ecology came in to prominence when Karl von Frisch, Konrad Lorenz and Nikolaas Tinbergen, seminal figures in the domain of ethology own the Nobel Prize in 1973 for their discoveries concerning organization and elicitation of individual and social behaviour patterns. The pattern of behaviour helps an animal to adapt to its environment, both intrinsic and extrinsic, efficiently. Behavioural ecology includes study of animals from a multidisciplinary perspective, combining experimental analysis of behaviour with theoretical modeling. The environment is not just the physical world, but also the biological (predators, prey, parasites) and social (conspecifics) one. Behavioural ecologists study both the function of behaviour (why animals and plants behave as they do), and the role of behaviour in determining population dynamics and community patterns. Bringing together significant work on all aspects of the subject, behavioral ecology is broad-based and covers both empirical and theoretical approaches. In modern behavioural ecology a variety of tools and approaches are used - from demographics to molecular phylogenetics. Population dynamics, evolutionary physiology and diversity are other areas of current interest. Thus the aim of modern behavioural ecology is to determine how ecological factors and environment affect behavioral variability within and between populations.

The behaviour patterns of animals also often consist of rhythmic sequences of movements which are correlated with the environment variables of daily and tidal periodicity. Many such rhythms are driven solely by environmental variables, and hence are responses, but others free-run in constant conditions under control of internal physiological pacemaker. The latter are often expressed at periodicities which approximate to those of geophysical variables and are referred as circatidal, circadian and circa semilunar rhythms. Crabs also play a central role in our understanding of endogenous activity rhythms. Studies indicate that temperature can affect an organism's ability to forage or to hunt, to evade predators or to defend against them. Furthermore, temperature can also affect mating success and development. However, if ambient temperatures rise above the level of heat tolerance, ectothermic organisms will often thermoregulate behaviourally. The arthropods are often used as models for studying the behavioral patterns, both in the solitary and social conditions. Ecological and spatial distributions of the arthropods allow them to maintain favorable body temperature within the burrows and also during several key developmental stages, affecting size and development rate. The options offered by modern telemetry technology can also be used by physiological and behavioural ecologists. When direct observation is impossible, telemetry can be used to acquire a wide spectrum of environmental, physiological and behavioural data. The relationships between behaviour and other factors, such as gender, species and size also draw observations and focus on the classical theories of behavioural ecology. Decapod crustaceans have complex life histories and behavioural aspects, such as foraging, mating and reproduction, moulting and growth, habitat selection and migration. New technologies have enabled to use an individual, field-based approach to analyze these problems, although they have been less developed in decapods than in vertebrates. In decapods applications of telemetry to analyze habitat selection, foraging behaviour, energetics, moulting site selection and migrations are also used to study the behavioural aspects. The locomotor behavior occurs in a wide array of organisms from protozoans to mammals. It is found in aerial, aquatic and terrestrial locomotion and in many behavioral contexts including search and pursuit of prey, mate search, escape from predators, habitat assessment and general travel. Thus the behavioural study is the dynamic system of intermittent locomotion by which the animals adjust themselves with the change in the circumstances of the surroundings. Movement of an organism is an important cue for stimulus detection; pauses can also reduce unwanted detection by an organism's predators or prey. Most of the ecological studies have focused completely on the behavioural interaction of the crab with the surroundings. Relatively little work has been done on the behavioural ecology of the Indian freshwater crab associated with the behaviour and population related processes. The analysis of the spatial distribution of burrows of the crab in the field can suggest uniform, clustered or random orientation in the population

dynamics. Crustaceans belong to one of the largest, dominant and important groups of animals in the phylum Arthropoda. They have worldwide distribution and have been known to occupy diverse habitats and great array of life style (Sastry, 1983). The order Decapoda includes shrimps, cray fish, lobsters and crabs that have become highly adapted for crawling. Some of the largest and most highly specialized crustaceans also belong to this order (Ruppert and Barnes, 1994). Decapod crustaceans have a number of behavioural and physiological features that make them suitable subjects for study, and it is relatively easy to observe them both in the nature and in laboratory. They serve as major processors of detritus in many aquatic systems. They play important role in the transfer of energy from primary producers to high-level carnivores. In some cases, they themselves are top carnivores.

Crabs are divided into two groups: true crabs (about 4500 species) and hermit crabs and their allies (about 1400 species). The members of infra order, i.e., Brachyura are considered the true crabs. Both the "true" crabs (Brachyura) and "hermit" crabs (Anomura) include species that show numerous behavioral, morphological, and physiological specializations permitting terrestrial life. Land crabs are spectacular animals; most of them are mainly restricted to tropical and sub tropical areas. They are often highly visible and very active. The terrestrial crab generally differentiates due to the ecological interest. Firstly, in many tropical islands the top of the energy pyramid is occupied by a land crab. Secondly, the land crabs have remarkable variety of gas exchange mechanisms, where lungs, gills and other body surfaces may play a vital role. Thirdly, they play a significant role as a human food source in several tropical islands. Fourthly, they offer an opportunity to investigate the evolutionary mechanisms involved in the transition from water to land. Finally, the choice of curiosity is more in studying the taxonomy, evolution, geographical distribution, growth, reproductive biology, feeding ecology and behaviour. Body of the crabs is more or less covered by chitinous shell, or carapace, with a waxy coating. It is composed of cephalothorax (fused head and thorax) and an abdomen. Dorsally and laterally the covering of cephalothorax includes frontal, gastric, branchial and cardiac regions. Crabs have ten jointed appendages, including two large claws for food capture called chelipeds, and eight walking legs that are used for walking sideways. They can crawl forward slowly but they commonly move sideways, especially when crawling is rapid. Chelipeds are used not for crawling as such, but help in defense (Seed and Hughes, 1995). Mouthparts and antenna are located on the ventral side of the frontal region, while the branchial regions bear the locomotor appendages (pereopods). The first pereopods are modified as chelipeds. The second through the fifth pereopods are the walking legs. The legs are usually heavier and the first pair of legs is usually powerful chelipeds. In male *Uca* chela is used for aggressive and courtship behaviour. It is also used for capture and manipulation of prey and grooming (Hazlett, 1962; Nolan and Salmon, 1970; Crane, 1975). The evolution of abdominal reduction and flexion in Brachyura was probably a locomotor adaptation. An elliptical carapace protects the rest of the body. Crabs have diverse diets: some are scavengers; others are predators on clams and snails; and still others are herbivores, feeding on vegetation. The fiddler crabs scoop up the surface sand with their small claws and place the sand within their mouthparts, where it is sifted with fine hairs. The organic material is consumed, and the mineral material is ejected. The crustacean mole crabs or sand crabs of surf beaches use their antennae to filter plankton from the receding waves after reburying themselves. Crabs are highly social animals with a rich behavioural repertoire. They communicate by visual and vibratory signals; they have complex territorial interactions and flexible courtship and mating systems. Land crabs present a useful model for the evolution of terrestriality, showing that even subtle anatomical changes can result in the large changes in physiological function necessary for the terrestrial invasion. Some species carry individually distinct colour patterns and some others even build mud or sand structures as homing aids and to enhance or limit social interactions. As their common name suggests, one of the most obvious behaviours in a crab colony is claw waving: males wave their enlarged claws to attract females for mating and to repel intruders from their territory. The social behaviour of the crabs constantly has to make decisions living in dynamic environments. They need to feed, maintain their burrows, establish and maintain neighbourhood relations, avoid predators and pursue mating opportunities. The visual ecology of crabs is reflected in the design of their visual system: their compound eyes are raised high above the body, giving them an unobstructed, panoramic field of view. Crabs have two stalked eyes, a pair of chemosensory antennae. The antennae are particularly sensitive, responding to environment chemical cues regarding food, potential mates, and predators. They see the bodies of other crabs below the horizon and everything larger than themselves above the horizon. The horizon effectively divides vision into a social world and a world of predators. Their panoramic visual field allows them to monitor simultaneously everything that goes on around them without the need for directed eye movements.

The terrestrial crab, *Barytelphusa cunicularis* has been selected as a model animal to study the spatial and temporal patterns in its population. To understand abundance patterns and population dynamics of

organisms in spatially heterogeneous environment, dispersal is usually considered as the key element. The nearest neighbouring technique is a simple technique to study the classification patterns and the distribution of population sampling patterns. The distribution of burrows is classified as clustered, random or regular by using this technique. The behavioural and morphological characteristics of *Barytelphusa cunicularis* are also used as the functional of the dispersal properties of an organism. In general, studies on burrowing behaviour enhance the burrow characters, biological complexity, ecological significance and also reproductive, behavioural and physiological activity of the species. In semi-terrestrial decapods burrows play most important and functional role in the extreme environmental conditions. Burrows generally protect the animal from varying environmental conditions and play a vital role in determining the owner's social environment and its access to food. Structure of burrows plays a significant role and provides a morphological window in the life of an organism. Also the morphological characteristics play an important role in agonistic and aggressive interactions and have also attracted human curiosity and fired human imagination. Generally, the morphometric characters and their allometric relationship are to a large extent influenced by age, local environmental conditions and population density of the species. Possibly the most important contribution of crabs make to science comes from the fact that their rich behavioural repertoire is played out openly and within a small space that can be continuously monitored. In this miniature animal society, we can study in detail the behavioural ecology as well as the mechanisms of behaviour under natural conditions. Crabs are particularly useful in aquatic environmental studies for several reasons and play important role in ecosystem processes, often good indicators of stressed/polluted condition. The crabs are often omnivores, scavengers, or predator and used as food throughout the world. Crabs, like shrimps and shellfish, are concentrated form of protein, and seem to have oil that protect against heart disease. They form an important diet for man with great nutritive value. Many crabs are familiar to high school biology students as study specimens. They are ecologically and commercially important.

II. Spatial and Temporal Distribution of Crabs

Study of temporal and spatial distribution of any species is one of the important areas of investigation in the domain of behavioral ecology. The composition and spatio-temporal distribution of Paguridae, Diogenidae and Porcellanidae in Ubatuba Bay have been investigated in detail (Fransozo et al., 1998). Spatial and temporal distribution of Horseshoe crab (*Limulus polyphemus*) spawning in Delaware Bay has been reported (Smith et al., 2002). A review of quadrat-based sampling of rare and geographically clustered populations of crabs has been published (Christman, 2000). Population dynamics of the commensal spider crab, *Inachus phalangium* (Decapoda: Maitidae) has been studied (Diesel, 1986). A reconstruction of the invasion of land by Jamaican crabs (Grapsidae; Sesarminae) has been investigated (Diesel et al., 2000). Spatial dynamics in dispersal: determinants and consequences for recruitment of the blue crab (*Callinectes sapidus*), North Carolina, U.S.A, has been reported (Etherington and Eggleston, 2003). The morphological, physiological and behavioural adaptations to life on land by Anomurans (Crustacea: Decapoda) have been investigated (Greenaway, 2003). The spatial and temporal differences in the biology of Velvet crabs has been studied (Henderson et al., 2005). Various studies in Venezuela, between 1993 and 1998, on distribution, abundance and population features of swimming crabs have been conducted. Local distribution and abundance of swimming crabs of family Portunidae on a tropical arid beach has been extensively studied (Carmona-Suarez and Conde, 2002). Behaviour of some swimming crabs has been marked by daily cycles of burrowing in the substratum during the day and of emergence at night (Carmona-Suarez and Conde, 2002; Warner, 1997; Fischer, 1978). The investigation of morphological and genetical differentiation has revealed the presence of two morphotypes collected from Drakensberg, Kwa-Zulu-Natal, leading to a new species of river crab (Decapoda, *Brachyura*, *Potamonutidae*) (Gouws et al., 2000). Studies on behaviour and growth of land crabs, *Gecarcinus lateralis* of Southern Florida have been carried out (Bliss et al., 1978). Several features that include relative growth and population ecology of swimming crab, *Arenaeus cribrarius*, have been studied in Brazil (Avila and Branco, 1996; Pinheiro et al., 1996, 1997; Pinheiro and Fransozo, 1993, 1998, 1999). The study of activity patterns, density and biomass in red crabs in the rain forest of Christmas Island has also been carried out (Green, 1997). The food preferences and feeding behaviour of land crab, *Cardisoma carnifex* have been studied (Lee, 1988). It has been observed that the crab, *Chasmagnathus granulata*, which generally lives in creeks and channels, shows shallow burrows with large entrance, while those living in *Spartina* dominated marshes show deep burrows with small entrances, without surface sediment mounds. In terrestrial hermit crab, distribution pattern has been studied (Page and Willason, 1982). There are number of studies (Bell and Westoby, 1986; Fernandez et al., 1993; Eggleston and Lipcius, 1992; Eggleston and Armstrong, 1995) that favour habitat selection as an important process, which influences the distribution of recruits considerably. Lutz and Austin (1983) estimated that *Cardisoma guanhumi*

rapidly gained weight during the first weeks of active foraging in rainy season. The recruitment (Connell, 1985; Doherty and Williams, 1998) is considered settlement limited, when there is a good correlation between larval settlement and abundance of subsequent stages. Patterns and processes of *Chasmagnathus granulata* and *Cyrtograpsus angulatus* (Brachyura: Grapsidae) and other benthic invertebrates with planktonic larvae are determined by a combination of pre- and post- settlement factors (Luppi et al. 2002). About 120 species of the super families Portunoidea and Xanthoidea were collected and species of the families were identified. The biochemical and morphological aspects of a new species of freshwater crabs (Decapoda: Potamonautidae) from the swamp forests of Kwa-Zulu-Natal, South Africa, have been studied (Gouws et al., 2001). Various aspects of the biology of the freshwater crab, *Potamonautes sidneyi* with reference to general seasonality and female aggression have been studied (Raubenheimer, 1986). Studies on behaviour and growth of land crabs, *Gecarcinus lateralis* of Southern Florida have been carried out (Bliss et al., 1978). Among various populations and species, variants based on injury levels reflect the efficiency and intensity of predation over all altitudinal gradients.

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