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Phenology of tropical carabids (Coleoptera : Carabidae)

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ABSTRACT : Classification of life cycles of 18 carabid species based on their phenology indicated 10 species as monsoon breeders having overlapping generations with adult gonad dormancy during winter and summer. All monsoon breeders were eurytopic. Sex ratio was always female biased coinciding with the onset of breeding season. Receding phase of reproduction was marked invariably by decreasing number of males. Eight species had discrete generations with larval diapause. Univoltine carabids can either be winter breeders with monsoonal and summer diapause or summer breeders with monsoonal and winter diapause. Bivoltine carabids are of three groups : summer and monsoonal breeders with winter diapause; summer and winter breeders with winter and/or monsoonal diapause and winter and monsoon breeders with summer diapause. Estimated fecundity ranged from 20 to 106 per season with indications on the existence of semelparous and iteroparous reproduction among tropical carabids.

Carabids which are also called as ground beetles, constitute one of the major groups of soil fauna form distinct taxon within the Adephaga, a suborder of Coleoptera. Their commonness in all variety of habitats of the world makes them to be important members of agrocoenoses with respect to both energy flow and predation on agricultural pests and as pedobiological indicators (Saypulaeva, 1986). Phenology is generally described as the art of observing life cycle or activities of organisms in their temporal occurrence (Leith, 1970).

Phenology of carabid beetles is primarily adjusted to the seasonal changes in climate so as to synchronise adult breeding activity and ensure that growth and development of larvae take place at optimal conditions (Refseth, 1984). Not all carabids are active as adults throughout the year even when the conditions are suitable. Depending on weather they have an annual or longer life cycle and time of year they reproduce, each species shows characteristic annual activity cycle (Luff, l987). Phenology of tropical Carabidae have only received recent attention - the limited available information revealed that only very few species are without annual propagation rythms (Paarmann, 1986).

Pitfall traps are useful in estimating carabid community at several stations

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simultaneously (Lesiewicz *et al.,* 1983) for determining distributional patterns, daily and seasonal dynamics of activity, dynamic density (Dennison and Hodkinson, 1984), occurrence and proportion of sexes (Ericson, 1978) and for collecting carabids for eco - morpho - physiological research (Gryunta, 1982). In the present study, activity patterns, breeding seasonality and fecundity of carabids were estimated from fortnightly pitfall trap catches from different habitat regions of Bangalore geographical area.

MATERIALS AND METHODS

Study area and study period: The species and number of carabids for which phenological estimates viz., activity periods, breeding seasonality and fecundity were deduced include those that were collected from pitfall traps of the study on their species diversity in relation to four habitats viz., agroforest, mango orchard, mulberry field and cultivated crop field. Each selected study habitats had an equal area of 15000 m^2 and simultaneous sampling was carried over a period of one year from November 1990 to October 1991.

Sampling method: A total of 25 traps were operated at each habitat with their placements randomly alloted. Each trap consisted of a 11 cm high and 6 cm diameter glass jar filled with 50 ml of 4% formalin. Traps were checked once a week for the presence of preservative and poured when needed. The contents were emptied at fortnightly intervals, thus constituting 24 fortnightly collections for the study period. Random reallotments of the traps were made during every third consecutive fortnightly sample collection.

Sampling records and Sample storage: Pitfall trap collections were separated in the laboratory by mechanical sieving and handsorting. Species composition of adult carabids was noted down for the study habitats. Carabids specimens were stored in plastic vials (6 x 3.5 cm) with 75% alcohol and 5% glycerine according to the habitat of occurrence for assessing their sex, reproductive status and fecundity.

Activity patterns: Seasonal activity patterns were deduced using monthly based abundance calculated for each carabid species based on the fortnightly sampling data. To illustrate the seasonal trends in activity for each species, months during which more than 10% of its total annual capture were considered as 'periods of peak activity'.

Breeding seasonality: Carabid species were dissected to determine their sex and the state of gonad maturity. Newly emerged males (tenerals) were distinguished through their small immature gonads and accessory glands. Stages of gonad development in females were distinguished as individuals with mature ovaries having ripe eggs (gravid females) and immature ovaries without eggs (callow females), and the latter were examined further to determine whether they were in a state of dormancy. Dormant individuals that had already passed through a reproductive period were recognized by the presence of a distinct degenerate follicle viz., corpora lutea in their ovaries. In other dormant individuals wherein ovary development had been arrested before first reproductive period, the existence of fat bodies were looked for.

Fecundity: In gravid females, the number of eggs contained were recorded for each month specieswise, so as to estimate their egg production. Fecundity was expressed by summing up the mean number of ripe eggs found during each month.

RESULTS AND DISCUSSION

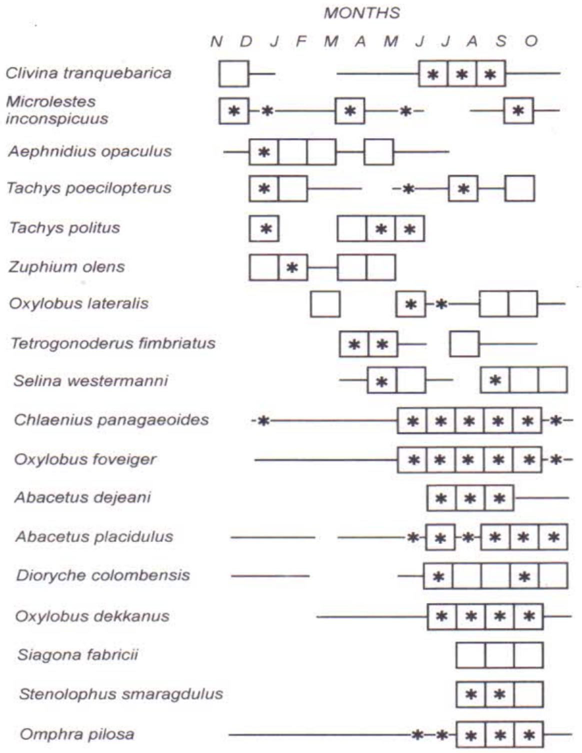
Developmental sequence of carabids was investigated based on their seasonal changes as a function of activity, reproductivity and fecundity. As the population growth time would be equivalent to density, and reproduction periods are often simultaneous with a peak in activity of adults (Lindroth, 1949), population increase with time was used to assess carabid activity patterns and breeding seasonality.

Seasonal activity patterns and breeding: Study of carabids in different habitats of the same climatic region reveal similar seasonal activity pattern for any single species although their relative abundance varies among habitats. This implied that the overall seasonality of carabids are determined by macroclimatic than microclimatic differences. Majority of the quantitative studies on the annual cycle of activity has been made in temperate region (Brandmayr and Brandmayr, 1986) and patterns have been detected to change along climatic zones (Anderson, 1986).

Annual activity and reproductive rhythms for 18 species of carabids are displayed in a phenogram (Fig. 1), with the names of the species arranged chronologically in relation to the onset of their 'period of peak activity'.

The phenogram indicates that activity periods for many species to coincide. However, few species have adopted the opposite strategy of being active and breeding at different times of the year than others probably taking advantage of reduced competition from other species. Such temporal separation of activity peak serving as a mechanism to reduce competition between species has been reported for carabids as early as 1965 (Greenslade, 1965). Marked differences in breeding seasonality were inferred based on months when individuals of species indicated reproductive status. Life cycle model (Fig. 2) hypothesised based on activity and breeding seasonality patterns typify species with overlapping and discrete generations.

Carabids with overlapping generations: Out of the 18 species of carabids examined for their phenology, 10 species viz., *Abacetas dejeani, A. placidulas, chlaenius panagaeoides, Clivina tranquebarica, Dioryche colembensis, Omphra pilosa, Dxylobus dekkanus, O. foveiger* and *O. lateralis* showed annual propagation rhythms with the onset of reproduction coinciding with the commencement of monsoonal rains. Monsoon breeders showed overlapping generations, iteroparous reproduction, and an extended



For each species months in which more than 10% of the total annual capture was noticed are indicated by the square symbol. Other months when species were active are indicated by horizontal line.

Fig. 1. Phenodynamic profile of carabid species

period of breeding. Extended reproductive season could probably be possible because of different individuals of the species entering into reproductive phase at different times. Paarmann (1986) indicated that species may differ in their requirement for day length to arrive at maturation and hence the length of breeding period. Examined reproductive gonads of monsoon breeders showed that they undergo adult diapause with their dormancy during winter and summer. Under temperate situations adults over winter before their breeding during the following spring (Larsson, 1939).

Carabids with discrete generations: Eight of the species with discrete generations invariably indicated the existence of larval diapause during either winter or summer or both, mainly determined by the number of generations they have. The univoltine summer breeders (*Stenolophus smaragdulus* and *Siagona fabricii*) would show hibernating larvae and winter breeders (*Aephnidius opaculus* and *Zuphium olens*) the aestivating larvae. In both cases larval diapause will persist during monsoon.

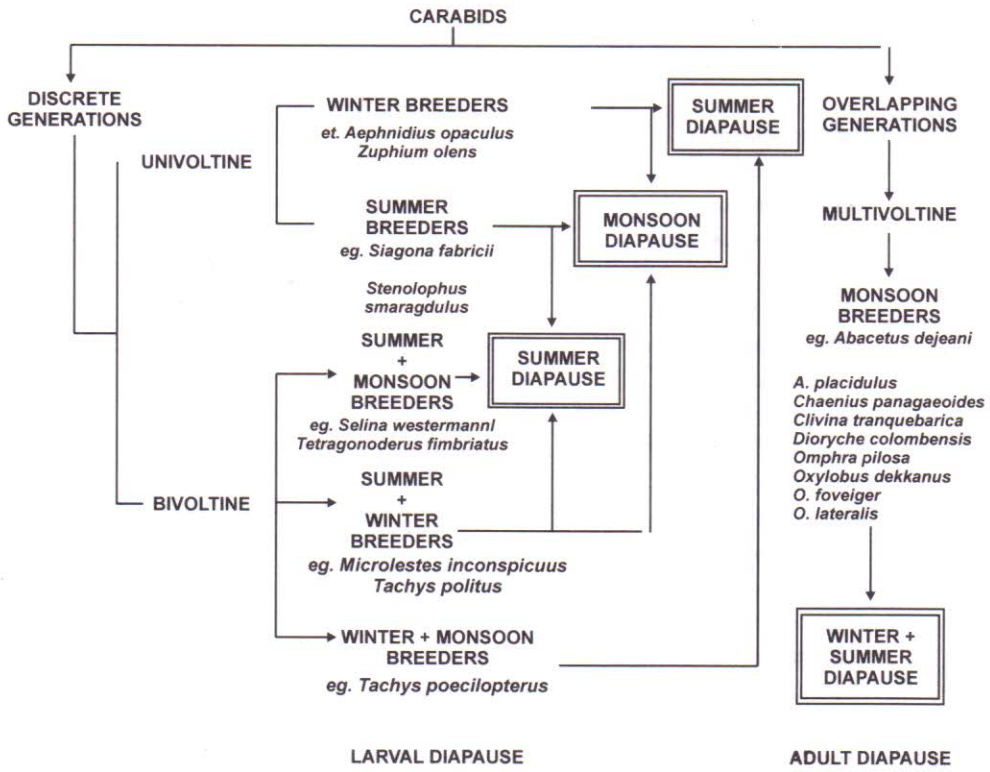


Fig. 2. A hypothetical model on carabid lifecycles

Among bivoltine species, *Tachys poecilopterus* breed during winter and summer breeding with an expected larval hibernation that *M. inconspicuous* may continue breeding through monsoon is unclear. *Tetragonoderus fimbriatus* and *Selina westermanni* reproduced during summer and monsoon seasons with only larval hibernation.

Fecundity estimates: Individual fecundity that could be expected of the 18 carabid species estimated through dissection of ovaries had shown an egg production ranging from two to 106 per season (Table I). Species with discreate generations seemed to possess semalparity reproduction laying eggs all at one time, however, this statement needs further support. Nonetheless, monsoon breeders are certainly iteroparous with the females tending their eggs over a long period. One time deposition of eggs in *Pterostichus madidus* (Luff, 1974) and *Harpulus rufipes* (Luff, 1980) and iteroparity in many others 17 were reported. The parameters of biology of carabids such as larval development, duration and longevity of adults are unknown that the reproduction rate and biological success of the species could not be assessed in this study.

Table 1. Estimated fecundity of carabids

Name of the species	Mean no. of eggs/ female/year
Abacetus dejeani	6.0
Abacetus placidulus	5.0
Aephnidius opaculus	6.0
Clivina tranquebarica	2.0
Chlaenius panagaeoides	74.5
Dioryche colembensis	6.0
Hicrolestes inconspicuus	2.0
Omphra pilosa	106.4
Oxylobus dekkanus	20.0
Oxylobus foveiger	20.8
Oxylobus lateralis	6.0
Selina westermanni	2.0
Siagona fabricii	4.0
Stenolophus smaragdulus	8.0
Tachys politus	3.0
Tetragonoderus fimbriatu	4.0
Uphium olem	2.0

Overall phenodynamic perspective: Study on phenology revealed the differences in seasonal activity patterns and breeding seasonality of carabids and indicated the seasonal succession within a carabid community. Such differences seem to be one of the main strategies among carabids that would naturally avoid interspecific competition for any of the resource dimensions. With no previous study on numerical abundance data over a period of continuous sampling, this study attempted to derive phenology of carabids using large scale pitfall trapping over a period of an year. The hypothetical model based on activity and breeding seasonality need to be tested by studying the biology and behaviour of life stages at laboratory and/or semi field conditions, and through field observations for egg/larval/pupal stages of all species. Also, understanding the season of dormancy and adaptation of carabids in relation to fluctuations of environment would reveal clearly the life history strategies possessed by them.

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