Ber. nat.-med. Verein Innsbruck	Suppl. 10	S. 183 – 187	Innsbruck, April 1992

8th International Congress of Myriapodology, Innsbruck, Austria, July 15-20, 1990

On the Survival Strategy of *Mestosoma hylaeicum* JEEKEL, a Millipede from Central Amazonian Floodplains

(Paradoxosomatidae, Polydesmida, Diplopoda)

by

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Abstract: The adaptive reaction of *M. hylaeicum* to annual inundation of the Solimões-Amazon River floodplain was studied. Juveniles feed on roots in the grass belt (mainly of *Echinochloa polystachia*) along treeless river margins. Subadults are forced annually by the rising flood waters to leave the soil and to climb on to grass blades, where they mate as adults. Adults and subadults feed on detritus, including remains of dead arthropods, in the leaf nodes. Adults, predominantly females, migrate into the adjacent inundation forests. As the flood waters rise, they climb tree trunks, where some of them spend the five to six month period of inundation aggregated in groups inside freshwater sponges above the waterline, feeding on detritus. Others remain on the underside of leaves in the lower canopy, feeding on leaf material (mainly from *Cecropia latiloba* (Moraceae) and *Laetia corymbulosa* (Flacourtiaceae)). Females bear 1,000 to 1,800 eggs, which they deposit between the inundation forest and the river, in the grass belt to which they return after the flood waters recede. The univoltine life cycle, the short period needed for development (r-strategy), the broad food spectrum of adults (generalists), and the long or interrupted maturation period of eggs within the females are considered to be adaptive strategies which allow a terricolous millipede to inhabit terrestrial areas that are periodically flooded.

1. Introduction:

Floodplains along white-water rivers like the Solimões-Amazon in the Amazon Basin (= várzea) are inundated for several months each year due to river-level fluctuations. The flood pulse (JUNK et al. 1989) is the major force controlling the terrestrial (and aquatic) biota. Regular flooding results in a pronounced seasonality of terrestrial invertebrates of Amazonian river-floodplains in an otherwise "seasonless" environment (cf. ADIS & STURM 1987, ADIS et al. 1988a, PAARMANN 1986). The periodic loss of their terrestrial habitat is compensated in various ways (ADIS et al. 1988b), such as: horizontal migration (following the high-water line), vertical migration to trunk or canopy (temporarily), flight to upland forests (temporarily) or flood-resistance (cf. ADIS & MESSNER 1991), with active or dormant stages under water. In this paper, adaptive strategies of a terricolous millipede to annual inundation are discussed.

2. Study Area and Methods:

Mestosoma hylaeicum was collected from Dec. 1980 to May 1982 in the course of ecological studies on terrestrial arthropods from Central Amazonian floodplains (ADIS 1981, ADIS & SCHUBART 1984). The study area was situated on Ilha de Marchantaria (3°15' S, 58°58' W), the first island in the Solimões-Amazon River, approximately 15 km above its confluence with the Rio Negro (cf. IRION et al. 1983). Collecting was carried out in an inundation forest on clayey soil (montmorillonite) and its frontal slope extension, a treeless grass belt of semi-aquatic and aquatic macrophytes (cf. JUNK 1983), both located about 3 km upstream from the narrow lake Lago Camaleão on the island (cf. Fig. 1 in FURCH et al. 1983). The forest was flooded annually from March to August to a depth of 3,5 m. The study area was subject to a rainy season (December - May) and a dry season (June-November; cf. RIBEIRO & ADIS 1984).

During the non-inundation period, Mestosoma was monitored on the ground with 21 pitfall traps (cf. ADIS 1981). Lines of 7 traps were installed in the grass belt in front of the inundation forest, at the forest fringe, and in the middle of the forest (cf. Fig. 1 in ADIS & MESSNER 1991). Three ground photo-eclectors (= emergence traps; cf. ADIS 1981) provided data on activity density in the forest. Trunk ascents and descents were detected with arboreal photo-eclectors (= funnel traps; cf. ADIS 1981) mounted on one trunk each of *Pseudobombax munguba* MART. (Bombaceae), a characteristic tree species of the seasonal várzea along white-water rivers in the Amazon Basin (cf. PRANCE 1979, WORBES 1983). The killing preserving agent used in all traps was aqueous picric-acid solution without detergent. Arthropods were removed from the traps at bi-weekly intervals and preserved in 70 % alcohol. Distribution of *Mestosoma* in the soil was studied once a month: Twelve soil samples (each 6 cm in depth, 21 cm in diameter) were taken at random along a transect in the grass belt and inside the inundation forest with a split corer during the increasing and receding flood in 1981/82. Animals were extracted, following a modified method of KEMPSON (ADIS 1987). In addition, *Mestosoma* was visually monitored once a month (during the day and at night) in the study area.

Fig. 1: Adults of *Mestosoma hylaeicum* feeding on the underside of *Cecropia latiloba* (Moraceae) in the lower canopy at night during forest inundation.

The guts of freshly collected preserved specimens were squeezed to release their contents in drops of glycerine on glass slides. Gut contents were examined using phase-contrast microscopy. Voucher specimens of *M. hylaeicum* have been deposited in the Entomological Collections of INPA, Manaus/Brazil and at the Museum d'Histoire naturelle, Genève/Switzerland.

3. Results and Discussion:

Mestosoma hylaeicum was described from the northern Brazilian coast of Pará (Ilha Mexiana) and of Amapá (Calçoene; JEEKEL 1963). Data on the natural history of this species were not available. In floodplains of the Solimões-Amazon River, *M. hylaeicum* is nocturnal. During the non-inundation period, presence of juveniles (from September onwards) was restricted to the soil of treeless river margins, where they fed on roots in the grass belt, mostly of *Echinochloa polystachia* (Poaceae). Guts contained root material and some fungal hyphae. From October to December, abundance (to a soil depth of 6 cm) varied between 5 and 200 ind./m^2, suggesting aggregated occurrence in between the grass rootage. Total Diplopoda amounted to approximately 4 % (450 ind./m^2) of the terricolous arthropod fauna in the grass belt (Acari and Collembola were disregarded; cf. ADIS 1987). The postembryonal development took at most 4 months, as the lower grass belt-area was annually flooded in January.

Adults were observed from late November onwards, the beginning of the rainy season. They left the soil and climbed on to grass blades. During the day they hid in leaf axils or inside convoluted withering leaves. At night they fed on detritus, including remains of dead arthropods,in the leaf nodes and to a lesser extent on grass leaves. Guts contained small detritus fragments, animal parts (legs, antennae), dead and fresh grass materials (mostly xylem elements, some epidermal cells and wax of the cuticle system of leaves), many calcium oxalate crystals, which are typical for tropical grasses (e.g. Mc KENZIE & SCHULTZ 1983), and little or no fungal hyphae and spores. The rising flood waters forced subadults – and in extreme years (e.g. 1982) many animals of advanced juvenile stages – to leave the soil and to climb on to grass blades as well. In mid-November of 1980, up to 530 ind./m^2 were found aggregated in small groups on semi-flooded grass and herbs above the water (e.g. on *Echinochloa polystachia, Luziola spruceana* (Poaceae), *Ipomoea setifera* (Convolvulaceae)). Animals represented the juvenile stages V (17 segments = s., 13 pairs of legs = pl.), VI (18 s., 15 pl.), subadults (19 s., 16 pl.) and adults (20 s., 17 pl.); these stages represented 0,2 %, 0,8 %, 8 % and 91 % of the total count (4,385 ind./30 m^2), respectively. Juveniles seem to depend on root diet, as they did not feed on grass leaves (empty guts). They either starved to death or were drowned. Subadults, however, moulted rapidly to adults and subsequently mated on the macrophytes of the nonflooded grass belt. Males reached the mature stage somewhat faster than females. In mid-November 1980, 13,5 % of males collected were fully coloured (dark brown to black) compared to only 3 % of the females. Mature males were frequently observed to copulate with still teneral females (pale brown-coloured), but eggs were generally present only in older females (dark brown to black-coloured). Sex ratio between total males and females collected was 1.2 : 1 (n > 5,000 ind.). In 1982, a year with much more rapid flooding than in 1980, almost one third of the *Mestosoma*-population represented advanced juvenile stages (V, VI) and the number of specimens reaching the adult stage was lower in comparison to years with a normal flood-level (e.g. 1981). After copulation, adults (predominantly females) migrated into the adjacent inundation forest. The non-flooded upper part of grass blades often served as bridge. The natural enemies of adult animals were birds, particularly jacanas (*Jacana jacana;* Jacanidae). The migrating *M. hylaeicum* was caught from December onwards with pitfall traps in the non-flooded upper grass belt and in January/February in the inundation forest. No specimens were caught with ground photo-eclectors. As the flood waters rose, *M. hylaeicum* climbed tree trunks. Part of the population spent the five to six months period of inundation (March - August) aggregated in groups and together with other terricolous arthropods (e.g. Opiliones, Araneae, Blattodea, Coleoptera) inside freshwater sponges (*Oncosclera* spp.; VOLKMER-RIBEIRO 1970) above the water line and, to a lesser extent, in crevices of tree trunks. *M. hylaeicum* was caught throughout the inundation period in arboreal photo-eclectors for trunk ascents. The highest number of animals found in a single freshwater sponge was 38 specimens (April 1981). They fed on detritus, and guts contained finely divided materials of higher and lower plants, arthropod parts (e.g. spines) and faeces, but few fungal hyphae and spores. Animals which did not stay in the non-flooded upper trunk region were found aggregated on the underside of leaves in the lower canopy, mainly on *Cecropia latiloba* (Moraceae) and *Laetia corymbulosa* (Flacourtiaceae). During the night, they fed in groups on leaf material, mainly between veins (avoiding the xylem texture) and left small holes (Fig. 1). During the day, aggregation of animals was observed near the petiole of large *Cecropia* leaves or inside small leaves of *Laetia,* which became convoluted due to the feeding activity of *M. hylaeicum.*

With receding flood waters, *M. hylaeicum* returned to the grass belt in front of the inundation forest. Females bore 1,000 - 1,800 eggs, which covered up to 90 % of their inner body space and which they now deposited in the soil between the inundation forest and the river. *M. hylaeicum* shows horizontal and vertical migration in response to the flood pulse. The univoltine life cycle, the short period needed for development (r-strategy; cf. IRMLER 1981), the broad food spectrum of adults (generalists), and the long or interrupted maturation period of eggs within the females are considered to be adaptive strategies which allow a terricolous millipede to inhabit terrestrial areas that are periodically flooded.

4. Acknowledgements:

Dr. Barry KATZ (Chapel Hill, North Carolina/USA) is thanked for examination of gut contents, Dr. Casimir A.W. JEEKEL (Institute for Taxonomical Zoology, Amsterdam/The Netherlands) for identification of the millipede species and Dr. Richard L. HOFFMAN (Virginia Museum of Natural History, Martinsville/USA) for valuable discussion. Special thanks are expressed to our technical staff at INPA, Manaus, for the help received in field and laboratory. Dr. Desmond R. KIME (European School, Bruxelles/Belgium) and Dr. Clifford S. CRAWFORD (Univ. of Mexico, Albuquerque/USA) kindly corrected the English manuscript.

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Zeitschrift/Journal: Berichte des naturwissenschaftlichen-medizinischen Verein Innsbruck

Jahr/Year: 1992

Band/Volume: S10

Autor(en)/Author(s): Adis Joachim

Artikel/Article: On the Survival Strategy of Mestosoma hylaeicum Jeekel, a Millipede from Central Amazonian Floodplains (Paradoxosomatidae, Polydesmida, Diplopoda). 183-187