

**Survival strategy of the bombardier beetle, *Pheropsophus rivieri* (Col.: Carabidae) in a Central Amazonian blackwater floodplain (Brazil)\***

by

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**Abstract**

Terrestrial invertebrates in the Central Amazonian floodplains have to cope with an annual inundation period of several months. Their life cycles are affected by this flood pulse, and most species have adopted seasonal univoltine reproductive regimes as a common survival strategy. We followed the phenology of adult bombardier beetles, *Pheropsophus rivieri*, at a blackwater river beach near Manaus/Brazil during 1997-1999. Gonad maturity was examined in female beetles. Adult beetles showed a pronounced seasonal activity pattern with the reproductive period confined to the first three months of falling water levels. It is concluded that *P. rivieri* has a seasonal, univoltine, and presumably semelparous life cycle, driven by the flood pulse. The presence of fat bodies in immature females during rising water levels indicates a delayed gonad maturation or gonad dormancy. The species exhibits a migratory survival strategy, typical for most carabid species from Central Amazonian floodplains, although it remained unsolved where adults pass the period of rising water levels. A possible parasitic relation of larval *P. rivieri* with mole crickets is discussed.

Keywords: **Life cycle, seasonality, flood pulse, activity pattern, gonad state, Amazon.**

**Resumo**

Invertebrados terrestre das áreas inundáveis da Amazônia Central precisam lidar com um período anual de inundação de vários meses. Já que seus ciclos de vida são afetados por este pulso de inundação, a maioria das espécies desenvolveu uma estratégia de sobrevivência com um regime de reprodução univoltina sazonal. Nós acompanhamos a fenologia do "besouro bombardeiro" *Pheropsophus rivieri* em uma praia de um rio de água preta perto de Manaus/Brasil durante o período de 1997-1999. Em besouros femininos a maturidade dos gonados foi examinada. Besouros adultos apresentaram um padrão de atividade com uma sazonalidade pronunciada com um período de reprodução restrito aos três primeiros meses da vazante. Concluiu-se que *P. rivieri* tem um ciclo de vida sazonal, univoltino e provavelmente semelparente ("semelparous"), definido pelo pulso de inundação. A presença de corpos gordurosos em fêmeas imaturas durante a enchente indica uma maturação retardada ou uma dormência dos gonados. A espécie em questão

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\*Dedicated to Prof. Dr. Wolfgang J. Junk on the occasion of his 60th anniversary.

apresentou uma estratégia de sobrevivência migratória típica para a maioria das espécies carábidas das áreas inundáveis da Amazônia Central, mesmo permanecendo em aberto a questão do local de permanência dos besouros durante o período da enchente. Um possível parasitismo das larvas de *P. rivieri* com paquínhas é discutido.

### Introduction

Due to a monomodal flood pulse (JUNK et al. 1989), terrestrial invertebrates in Central Amazonian floodplains must cope with annual long-term inundation lasting several months. Their life cycles are affected by this flood pulse, and most species have adopted seasonal univoltine reproductive regimes as a common survival strategy (ADIS 1992). Carabid species are even believed to have acquired such an annual periodicity in tropical river floodplains as a pre-requisite for the colonization of temperate zones (ERWIN & ADIS 1982).

Migratory survival strategies (cf. ADIS 1997) have been described for terricolous carabid beetles from Central Amazonian floodplain forests with either temporary vertical migration (trunk or canopy region; IRMLER 1979; ADIS 1982; ADIS et al. 1990, 1997; AMORIM et al. 1997a, b), temporary horizontal migration (following the high-water line; IRMLER 1979; ADIS et al. 1997), or temporary flight to terra firme uplands (ADIS et al. 1986). Several carabid and cicindelid species from open, i.e. unforested, habitats within the floodplains migrate during the aquatic phase to the trunk and canopy region of adjacent floodplain forests (ADIS 1982; ADIS et al. 1990) or to hitherto unknown places (ZERM & ADIS 2001a, b). A non-migratory survival strategy has only recently been reported for the cicindelid genus *Phaeoxantha* (larvae survive the aquatic phase submerged in the soil; ZERM & ADIS 2000, 2001a). Irrespective of the survival strategies, the reproduction period in species from both forests and open habitats was restricted to the terrestrial phase. All but one species studied so far showed univoltine life cycles (ADIS et al. 1997).

In this contribution we report on observations of the bombardier beetle, *Pheropsophus rivieri* (DEMAY 1838) which was found running among tiger beetles (cf. ZERM & ADIS 2001a) along the water line at a blackwater beach near Manaus/Brazil. The population was studied to reveal its life cycle and survival strategy.

### Material and methods

Field studies were carried out in a blackwater floodplain near Manaus, Brazil, from 1997 to 1999. The study site, locally called "Praia Grande", is part of a sandy river bank that stretches over several kilometers along the right bank of the Rio Negro, approximately 40 km upstream from Manaus (3°02'04"S, 60°32'32"W). It is subject to a regular annual, monomodal inundation (Fig. 1d). Since duration of inundation varies according to the altitude, lower parts of the beach were inundated for more than 6 months whereas a higher part always remained unflooded.

The population of adult bombardier beetles at Praia Grande was monitored during monthly field excursions from 1997 to 1999. Beetles were searched for during the first hours after dusk, usually at two successive nights. Activity density was determined once per excursion by exposing 5 pitfall for a period of 1.5-2.5 h on the beach along the waterline (opening diameter: 5.6 cm, no killing agent, no roof; cf. ADIS 1981). Numbers given are standardized to "number of adult beetles caught in 5 traps per hour". Whenever available some adults beetles were randomly selected and taken to the laboratory in Manaus for further examination. Female beetles were dissected to determine gonad states: mature (at least one full-size egg in the ovaries) or 'immature' (no full size eggs). Occurrence of fat bodies in the abdominal cavity was recorded.

## Results

Adults beetles were observed mainly within the 1-2 m wide strip of moist sand along to the water line. There they were found running among several species of tiger beetles, mostly *Phaeoxantha* spp.. Highest density of activity was observed during highest and falling water levels, although few or single individuals were found throughout most of the year (Fig. 1a, b). No beetles were found at higher reaches of the beach nor in the adjacent floodplain and terra firme forests. The sex ratio among the beetles taken to the laboratory was somewhat biased towards males (63:43 in total; deviation from 50:50 % not significant: binomial test,  $p=0.06$ ).

The time period of highest density of activity coincided with the occurrence of mature females, indicating the reproductive phase. Adult females caught during rising water levels showed immature gonads and fat bodies in the abdominal cavity (Fig. 1c).

## Discussion

*Pheropsophus rivieri* showed a pronounced seasonal activity pattern at the study site, the reproductive period was confined to about three months per year. This indicates a seasonal, univoltine, and presumably semelparous life cycle, driven by the flood pulse. The presence of fat bodies in immature females points to a delayed gonad maturation or gonad dormancy as reported for other carabid species (PAARMANN & STORK 1987; ADIS et al. 1997; AMORIM et al. 1997a). It remained unsolved where adults pass the period of rising water levels.

The phenology, habitat, diet etc. of larval *P. rivieri* are still unknown. Larvae of four other *Pheropsopus* species (one Neotropical, one African, two Asian) are known to parasitize on the eggs of mole crickets (Saltatoria: Gryllotalpidae; HABU & SADANA-GA 1965; FRANK 1990; PAARMANN pers. com.) which were abundant at the study site (*Scapteriscus oxydactylus* and *Scapteriscus* sp.). Young juvenile stages of the latter were observed between July and September (ZERM unpubl.) which coincides with the reproductive phase of the bombardier beetle. If the larvae of *P. rivieri* parasitize on their eggs as well one should expect a rather short larval phase during falling water levels, certainly shorter than the 6-9 months between the reproductive periods of the adult generations. To explain the very low abundances of adult beetles during this phase two possibilities seem most likely within this scenario: (a) strongly reduced adult activity either at the beach or elsewhere (= dormancy, including gonad dormancy) or (b) habitat shift to sites beyond the adjacent forest patches. The presence of larger numbers of adult beetles along the water line only during the reproductive period might represent a strategy for mate finding as males tended to be more abundant (i.e., enhanced activity) and food supply along the water line is presumably high throughout the year - or it might point to the hitherto unknown oviposition sites of the mole crickets.

It is unknown whether *P. rivieri* occurs at river banks that are entirely inundated during high water periods. Its flight ability would allow temporary migrations to dry places, although flight observations or data on flight activity are not available (all 43 dissected females were macropterous and had fully developed flight muscles; ZERM unpubl.). However, presence and survival of bombardier beetles at a given site might be primarily connected to the occurrence of mole crickets which has not been studied so far in Central Amazonia.

The life cycle of *P. rivieri* as outlined here corresponds to a migratory survival strategy with horizontal migration, following the high-water line or, possibly, with

temporary shifts to terra firme habitats. Its univoltine mode of reproduction including a delayed gonad maturation (gonad dormancy) matches the pattern of other carabid species from Central Amazonian floodplains which predominantly show migratory survival strategies (IRMLER 1979; ADIS 1997; ADIS et al. 1986, 1990; AMORIM et al. 1997a). Corresponding to their non-migratory survival strategy, the cicindelid species (*Phaeoxantha* spp.) co-occurring with the bombardier beetles, showed a different phenology, despite coinciding periods of highest abundance. While adult bombardier beetle were most abundant along the water line towards the end of the adult generation, the highest abundance in adult *Phaeoxantha* spp. was observed at the start of the adult generation (ZERM & ADIS 2000).

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Fig. 1: Phenology of adult *Pheropsophus rivieri* at Praia Grande (Rio Negro). (a): Occurrence at the study site (empty symbols = no beetles found); (b): Activity density (catches in pitfall traps); (c): Gonad state in females; (d): Water level at the harbor of Manaus (data source: Harbor Authority Manaus). \* = Presence of fat bodies.

