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**ADAPTATION OF AN AMAZONIAN
PSEUDOSCORPION (ARACHNIDA)
FROM DRYLAND FORESTS TO
INUNDATION FORESTS¹**

Joachim Adis,² Volker Mahnert,³ José W. de Morais,⁴
and José M. Gomes Rodrigues⁴

Inundation forests in the Rio Negro valley are flooded annually for 5–6 mo to a depth of several metres (Adis 1984). The area was originally dryland forest until the first flooding occurred several million years ago (Adis and Schubart 1984). Arthropods of these inundation forests are believed to originate either from the former dryland forest and from dryland forests presently extending behind the inundation forests, with examples reported for Pseudoscorpiones and Archaeognatha (Adis and Mahnert 1985, Adis and Sturm 1987), or from nonforested wetlands located between rivers and the inundation forests, with examples given for Carabidae (Erwin and Adis 1982). In addition, some populations may have undergone extensive evolution within inundation forests, due to forest isolation caused by climatic shifts and microgeographic changes, as indicated for Pseudoscorpiones, Symphyla, and Opiiones (Adis and Schubart 1984). In all cases, arthropods that now inhabit inundation forests had to evolve strategies to compensate for the periodic loss of their terrestrial habitat. Means of achieving this include: (1) staying near the waterline and moving in advance of the ascending flood (Irmeler 1979), (2) moving to non-flooded trunk and canopy areas in the inundation forest (Adis 1981, 1982, Friebe and Adis 1983, Adis and Scheller 1984, Adis and Mahnert 1985), (3) flying to adjacent dryland biotopes during inundation (Adis et al. 1986), (4) evolving adaptations for remaining in flooded terrestrial areas (Beck 1969, 1976, Irmeler and Furch 1979, Scheller and Adis 1984, Smith and Adis 1984, Adis 1986, Adis and Arnett 1987), and (5) combining one or more of these features (Adis and Sturm 1987). The pseudoscorpion *Brazilatemnus browni* Muchmore (Miratemnidae) is a common nocturnal species inhabiting dryland forests throughout the Amazon region, seasonally inundated forests of the Rio Negro valley, and swamp forests with permanently waterlogged ground near Belém (Mahnert and Adis 1985). Due to its characteristic occurrence in nonflooded areas, the species is believed to originate from Amazonian dryland forests (Mahnert 1979, 1985). Behavioral and

life history adaptations that enabled *B. browni* to inhabit inundation forests are presented in this paper.

Study Area and Methods

Pseudoscorpions were collected between 1976 and 1983 in the course of ecological studies on Central Amazonian arthropods from three previously investigated and fully described forest types, all within 30 km of Manaus: (1) in a primary dryland forest at Reserva Florestal A. Ducke (2°55' S, 59°59' W) on the Manaus-Itacoatiara highway (AM-010 at km 26; see Penny and Arias 1982), (2) in a blackwater inundation forest at Rio Tarumã Mirim (03°02' S, 60°17' W), a tributary of the Rio Negro (see Adis 1984), and (3) in a cut but unburned secondary dryland forest adjacent to the inundation forest (see Adis and Schubart 1984). All forests are subject to a rainy season (December–May: average precipitation 1550 mm) and a dry season (June–November: average precipitation 550 mm; cf. Ribeiro and Adis 1984).

Inundation forest. The soil of the inundation forest consists of clay, silt, and sand material and has an organic layer of 5–10 cm thickness. Its fine humus is penetrated by a matting of roots and supports up to 3 cm of leaf litter. The study site is covered annually by up to 3.35 m of floodwater between March/April and August/September. *B. browni* was collected between January 1976 and May 1977 (Adis and Mahnert 1985). On the forest floor two pitfall traps and 1–5 ground photo-electors (=emergence traps) provided data on activity densities during the noninundation period. Trunk ascents and descents of pseudoscorpions were detected with arboreal photo-electors (=funnel traps) on three trunks each throughout the collecting period. The material in traps was collected in 1–2 wk intervals. All capture devices are fully described in Adis (1981) and Funke (1971), who also explain their mode of utilization and function. Distribution of pseudoscorpions in the soil was studied between September 1981 and February 1982 (noninundation period; Adis and Mahnert 1985). Once a month six soil samples were taken at random along a transect with a split corer (=steel cylinder with lateral hinges; diameter 21 cm, length 33 cm), which was driven into the soil by a mallet. Each sample of 7 cm depth was then divided into two subsamples of 3.5 cm each. Animals were extracted from subsamples following a modified method of Kempson (Adis 1987).

Dryland forest. The yellow latosoil of the primary and secondary dryland forest supports a 2–3 cm thick humus layer, interspersed with fine roots, and a thin, surface-covering leaf litter. One ground photo-elector and one arboreal photo-elector for trunk ascents were set up in both forests from December 1981 to December 1982 (cf. Adis and Schubart 1984). Distribution of

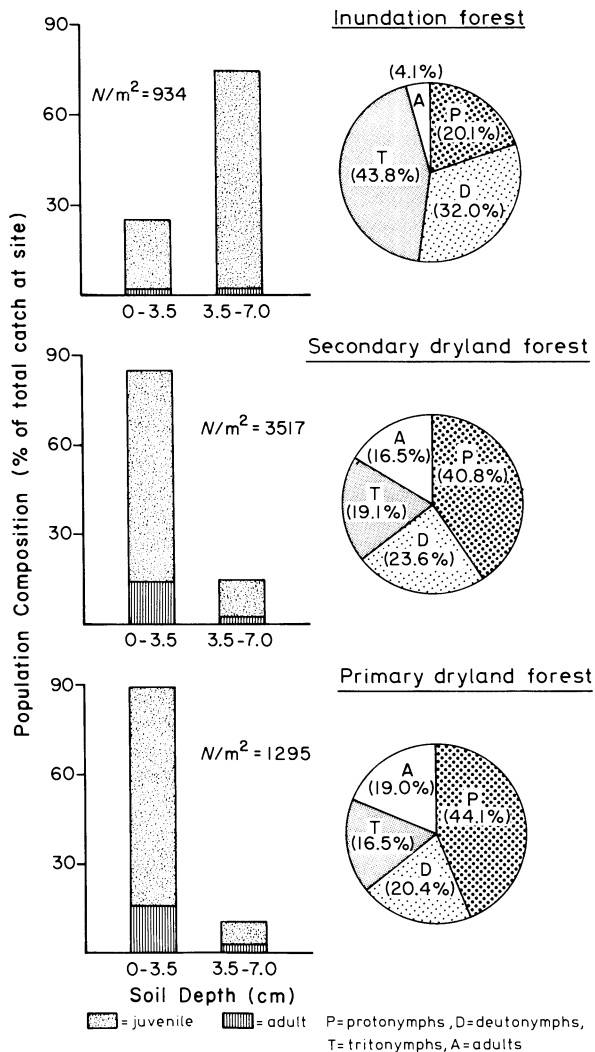


FIG. 1. Distribution of *Brazilatemnus browni* in the soil according to soil depth, and percentage of all developmental stages in three forest types near Manaus. (Total catch = 100% in each forest type.) Samples taken monthly in 0–3.5 and 3.5–7 cm depth between September 1982 and August 1983 in the dryland forests and from September 1981 to February 1982 (non-inundation period) in the blackwater inundation forest. N = number of specimens.

pseudoscorpions in the soil was studied between September 1982 and August 1983 (de Moraes 1985, Rodrigues 1986). Twelve soil samples were taken once per month from each forest type as described for the Inundation Forest, and the animals were extracted.

In addition, the presence of pseudoscorpions in tree crowns of the inundation and primary dryland forest was tested by fogging canopies with pyrethrum in the early dry season (July 1977, 1979) when the inundation forest was completely flooded (Erwin 1983, Adis et al. 1984). Bromeliads, 5–25 m above ground, were also

sampled for the presence of pseudoscorpions in the inundation forest in August 1979 (forest not flooded) and June 1981 (forest flooded; Adis and Mahnert 1985).

Pseudoscorpions collected during all studies were identified to species and classified as juveniles (protonymphs, deutonymphs, tritym nymphs) or adults (males and females). A comparison of the ecology of *B. browni* from inundation and dryland forests is now possible, as the taxonomical evaluation has been completed (Mahnert 1979, 1985).

Results

Dryland forest. In the primary and secondary dryland forest under study, *B. browni* was only found in the soil and never caught on tree trunks or in the canopy. No specimens were caught in ground photo-eclectors, indicating that the species was not active on the soil surface. This conclusion is supported by another study in which only one specimen was collected from 20 baited pitfall traps (J. R. Arias and N. D. Penny, *personal communication*). Most specimens inhabited the organic layer (Fig. 1: 0–3.5 cm), and a few (10–15%) the mineral subsoil. An average of 292 individuals/m² were recorded in the secondary forest (0–7 cm depth), 85% being juveniles, while an average of only 108 specimens/m² were obtained from the primary forest (80% juveniles). About half of the juveniles were protonymphs, i.e., the first larval instar (Fig. 1). There was no distinct reproductive period and protonymphs as well as adults (both sexes) were found throughout the year (Fig. 2). Sex ratio (adult males to females) was 1:1.3 in the primary forest and 1:1 in the secondary dryland forest.

Inundation forest. In the inundation forest, *B. browni* was collected in high numbers on tree trunks and in the forest soil. Seventy-five percent of all specimens extracted from soil samples during the non-inundation period (September–February) inhabited the lower organic layer (Fig. 1: 3.5–7 cm). With 156 individuals/m², the average abundance of *B. browni* was 44% higher here than in the primary dryland forest. Over 95% of the total catch was represented by juveniles (Fig. 1), with tritym nymphs being dominant (44%). Ninety percent of all specimens were obtained during the rainy season prior to inundation (December–February). There was a distinct reproductive period on the forest floor. Within the first 2 mo of the non-inundation period (September/October) only adult animals occurred in the soil. The first larval instar (protonymphs) appeared in November (Fig. 2). The last larval stage (tritym nymphs) was attained in January. A short time before the forest was flooded these tritym nymphs came to the soil surface, together with some remaining deutonymphs and adults, and began to ascend tree trunks (see Adis and Mahnert 1985: Fig. 9). Only at this time

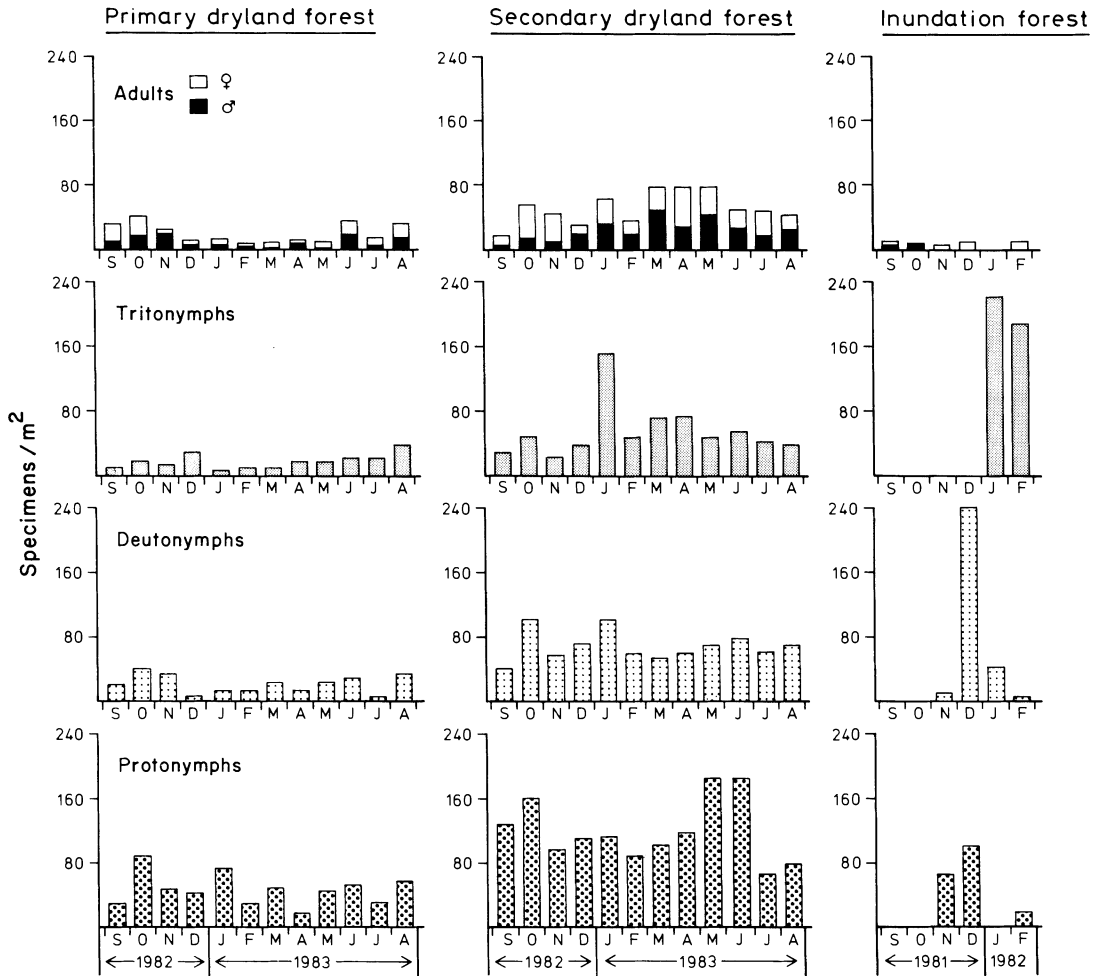


FIG. 2. Temporal occurrence of developmental stages of *Brazilatennus browni* in the soil (N/m^2 in 0-7 cm depth) in three forest types near Manaus. Monthly samples taken between September 1982 and August 1983 in the dryland forests and from September 1981 to February 1982 (the non-inundation period) in the blackwater inundation forest.

was *B. browni* detected in ground photo-electors, but never in pitfall traps (Adis 1981). In 1976, the highest capture rates in arboreal photo-electors were recorded 1 wk before inundation. The high wetness and relative humidity on the forest floor, caused by rising waters, apparently forced all developmental stages into the trunk area (positive correlation of trunk catches with soil humidity $P < .01$ and atmospheric relative humidity $P < .05$; see Adis 1981: Fig. 14). The number of adults was low and the parent generation had probably died by the beginning of the inundation period. Some animals must have moved up the trunk with rising waterlevel, as specimens were caught until June, when flooding had reached its maximum. We presume that tritonymphs moulted in the trunk area where the main reproductive period occurred in April/May. Tritonymphs of the new generation were captured during

trunk descents, together with some remaining proto- and deutonymphs, from early July onwards, i.e., 6 wk before the start of the non-inundation period (see Adis and Mahnert 1985: Fig. 9). Heavy leaf-fall combined with strong insolation in July/August (Adis et al. 1979) may have initiated this early trunk migration. *B. browni* was not found in epiphytes. Tritonymphs were obtained in low numbers with canopy fogging during forest inundation in July. After recolonizing the forest floor, tritonymphs moulted and reproduced. Brood and moulting chambers (Wood and Gabbutt 1979a, b) were not observed.

Discussion

In the inundation forest *B. browni* is considered bivoltine with a major reproductive period in the trunk/ (canopy) region in April/May during forest inundation

(April–August) and a second, minor one, on the forest floor in November/December during the non-inundation period. About three times as many animals, predominantly tritonymphs, were caught during trunk descents as compared to trunk ascents (cf. Adis 1981). We presume that the protonymph instar of Amazonian pseudoscorpions only lasts a short time, as is true for European species (Gabbutt 1970). The record of protonymphs in soil and trunk samples in different months therefore indicates the existence of two generations per year, but in different habitats. The presence of solely protonymphs and deutonymphs in the soil in November/December (Fig. 2) excludes the possibility that the tritonymphs which had descended tree trunks between July and September 1976 returned to the trunk in March 1977. This means that *B. browni* is not univoltine. *B. browni* is separated from other species of Pseudoscorpiones in the biotope by spatial, temporal, and ontogenetic differences (cf. Wood and Gabbutt 1978, Adis and Mahnert 1985). Originating from (adjacent) dryland forest soils, this species seems to have colonized and adapted to the seasonal inundation forest secondarily. Protonymph to tritonymph development lasted a maximum of 3 mo and was so synchronized with waterlevel fluctuations that migrating tritonymph stages were attained near the beginning and the end of the inundation period. The actual habitat was shifted from the forest floor to the trunk/(canopy) region, where main reproduction takes place. Two reproductive periods per year, each in a different habitat, enable this species to persist in a harsh environment. There was no difference in size between terricolous and arboricolous tritonymphs in the inundation forest, which would indicate a morphological adaptation, i.e., an advantage for foraging in one of the two microhabitats. It has yet to be investigated if the population of *B. browni* in dryland forests represents a different stock (biotope-specific races) when compared to the inundation forest, as found in electrophoresis studies for Archaeognatha (Adis and Sturm 1987). This would explain why populations of the inundation and secondary dryland forest are clearly separated with respect to microhabitat, behavior and life history, although study sites were only 100 m distant from each other. Further studies should focus on interbreeding experiments in the laboratory and on the reaction of *B. browni* to artificial flooding of the primary and secondary dryland forest. Our results from the secondary forest did show that vertical migration of *B. browni* is not caused by human disturbance, i.e., previous deforestation.

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