FURTHER OBSERVATIONS ON THE NATURAL HISTORY AND SURVIVAL STRATEGIES OF RIVERINE TIGER BEEF (COLEOPTERA: CICINDELIDAE) FROM OPEN HABITATS IN CENTRAL AMAZONIAN FLOODPLAINS (BRAZIL)

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abundance. Terrestrial organisms living in the Central Amazon floodplains have to cope with an annual inundation period of several months. Life cycles, habitats, behaviour, and other parameters were investigated in the tiger beetle species inhabiting open areas in white- and blackwater floodplains near Marajo. Populations of larvae and adult beetles were observed during monthly field excursions from 1991-1993/94. To follow larval and adult biology and to determine habitats and other parameters, adult beetles were regularly taken to the laboratory for examination of general condition, occasionally also for submission to experiment and to obtain eggs for rearing larvae in the laboratory. Larvae, too, were collected in the field and taken to the laboratory for experiment and rearing in the adult beetle. Submission of larvae in the laboratory was determined by calculating the longest duration of inundation survival (using water gauge data) and from other observations. In the laboratory, maximum survival in water (water treatment) was found in adult beetles of five species, in aquatic larvae of four species, and in dormant larvae of one species. In addition, maximum survival in larvae reared in dim light (shading, varied flooding conditions) was found in two species.

Here we complete information from previous contributions on life cycles in the four Plumoseus species, as well as on habitats and activity patterns of all eight species. Data are given on the life cycle of Pontodes obstrictus, P. plumoseus, P. confluens (both field and laboratory data), Teratodroma robusta, and Calosoma suture (field observations). These four species have annual life cycles and a short larval phase (3-4 months) with short water periods and with adult beetles surviving the inundation period. Adult beetle span was long (9 months) and is likely to involve a general dormancy in both sexes. The type of larval contrasts with findings in Plumoseus species. These also showed annual life cycles, but the larval phase was long (3-5 months), including submission resistance in larvae (shown for P. plumoseus and P. plumoseus, preferred for the P.americanae-plumoseus). Adult life span is either short or long. Submission resistance in the field and when being submerged in sediment in the laboratory was in 3-4 months in larvae P. plumoseus and P. plumoseus. However, submission resistance of active larvae in water without sediments was only in a few days (P. plumoseus, P. plumoseus, P. plumbosus, and T. plumoseus) and 15 days in dormant larvae (P. plumoseus). Hence, submission resistance in active larvae was low in species representing both life cycle types. Resistance is apparently reduced by dormancy, although further factors are likely to be involved. In field data shows a much higher resistance. Adjacent species were examined for submission (continuous survival > 13 years). Plumoseus plumoseus, P. plumoseus, P. robusta, P. plumoseus, and P. robusta proved. Data on aggressiveness, sex ratio, prey spectrum, pedobions and precarion, and on behaviour are given and discussed for all species. Based on their life cycle, two different types of survival strategies can be assigned to the tiger beetle species inhabiting open habitats. Plumoseus species show a non-aggressive type with flood resistance larvae, whereas, P. plumoseus, P. robusta, and Teratodroma species exhibit a aggressive type with adults surviving the inundation period. The specific types of P. plumoseus, P. plumoseus, and P. robusta are charactarized by these types of survival strategy and discussed. Accepted 27 September 2002.

Key words: life cycle, annual development, natural habitat, submission, resistance, plumoseus, Megasolara, Plumoseus, Calosoma, C. robusta, and Teratodroma. C. plumoseus. Plumoseus species exhibit a aggressive type with adults surviving the inundation period. The specific types of P. plumoseus, P. plumoseus, and P. robusta are charactarized by these types of survival strategy and discussed. Accepted 27 September 2002.

INTRODUCTION
Terrestrial organisms living in the Central Amazon floodplains have to cope with an annual inundation period of several months (Adis 1992, 1997). Studies on terrestrial invertebrates over the last 25 years have revealed that many species survive these inundations, using a wide variety of specific adaptations and types of survival strategy. The large number of adaptations to periodic flooding in many groups of plants and ani- mals has been attributed to the predictability of the monomodal flood pulse and the relative stability of the ecosystem for millions of years (Junk 1997, 2000;
Adis 2001). Against this background, studies on inundation survival strategies in riverine tigerbeetles of Central Amazonia should contribute to the under- standing of the floodplain ecosystem and its inhabit-
ance, as well as reveal specific examples of how spe-
cific floodplain conditions are overcome by repre-
sentatives of this beetle family.
Many tiger beetle species inhabit riverine habitats worldwide where flooding is a regular factor. Although several studies claim ability of larvae of tiger beetles to survive flooding (Hamilton 1889, Willis 1967, Wilson 1974, Krügel & Francon 1981, Parrish 1988), quantitative data on their occurrence or resilience, and other adaptations to floodplain conditions in the riverine species (Ho-
back et al. 1998, 2000; and studies from Central Amazonia, see below).

veral contributions on floodplain species from opencountry life cycles of Phaenostaebula species (Zettler & Adis 2000), details on habits and activity patterns in larvae and adult beetles of all species (Zettler & Adis 2001b, Zettler et al. 2001, Andrs et al. 2002), as well as the varying extent of flight ability in nocturnal species (Phaenostaechna and Zononta) (Zettler & Adis 2002a). The intention of the present paper is to complete this information. It reports on the life cycle of an additional four species from open habitats in the ban-
ner of field observations (all four species) and laboratory rearing (two species). All tiger beetle species from Central Amazonian floodplains studied in detail so far showed seasonal, annual life cycles: Phaenostaechna angusta, O. confusa, and Phaenostaechna spp. (Parrissm et al. 1982, Imbesi 1985, Amorela et al. 1997a, Zettler & Adis 2000). Thus, the question here is whether the four additional species similarly exhibit annual life cycles and whether the duration of the developmen-
tal stages differs from-and/or interspecifically (including a comparison with Phaenostaechna species). Another part of this contribution focuses on sub-
mergence tolerance/resistance (for definition see Adis & Meunier 1997) in larvae and adults. As shown in previous studies as well as in this paper, tiger beetle species from floodplains survive the aquatic phase either as 2nd instar larvae submerged in the soil (Phaenostaebula sp) or as adult beetles which (as known or presumptively) fly dry above. Adis & Meunier (1987) reported respiration survival times of 2-18h. sub-
mergence in adult beetles of nine species from flood-
plains and non-flooded uplands. Only Zononta ob-
terecta paranensis showed a greater tolerance of 24-80h, which was attributed to a unique diving behavior (Adis et al. 1993, Adis & Meunier 1997). From this background, we expect low submersion resistance in shallow habitats of any of the species in question. Testing more species, we intend to reveal whether low sub-
mergence tolerance of 1-18h in adults is a general fea-
ture of the floodplain tiger beetle species. Somewhat higher resistance values might indicate a diving habit similar to Z. paranensis.

In species with larvae surviving the aquatic phase submerged in the soil we determined the duration of inundation survival to the larval. Larvae of these species can be expected to show greater submerso-
tolerance than larvae of species with adult beetles passing the aquatic phase, since long term flooding resistance seems to be a rather rare trait in terrestrial habitats (e.g. Tandell 1970, Adis 1992, Adis & Meunier 1997).

Richardson et al. 1999, Holdob & Stanley 2001). We therefore tested whether submersion resistance in ac-

current of different species varies according to life-
cycle type. To determine if dormancy enhances sub-
mersion resistance, both active and dormant larvae of Phaenostaechna sp were raised. Larvae of P. bligi and P. bligeii actively crawl their tunnel entrance when being flooded in the field. During this flooding process a different physiological state might also be induced in the larvae enhancing submersion resis-
tance. We therefore tested submersion resistance in larval P. bligi and P. bligeii larvae were gradu-
ally flooded within sediments-i.e. simulating natural conditions.

Furthermore, data on larval mobility, oviposition and egg numbers, sex ratios, prey spectrum, preda-
sion, and paralysis were collected to document the spe-
cies' natural history. The final aim of the present study is to depict the species' survival strategies and to elu-
cidate interspecific differences and/or similarities.
MATERIAL AND METHODS

Study sites. Field studies were carried out in white- and blackwater floodplains near Manaus, Brazil, from 1997 to 1999 (Fig. 1). The main blackwater study site, locally called "Prainha Grande," was part of a sandy river bank that stretched over several kilometers along the right bank of the Rio Negro, approximately 40 km upstream from Manaus (3°32’04”S, 60°32’52”W). The main whitewater study site was situated at the southern edge of Ilha de Machantaria, the first island in the Rio Solimões (Amazonas) upstream of the confluence with the Rio Negro (3°14’34”S, 59°55’46”W). Other places visited in addition were: a beach on Ilha de Paciência in the Rio Solimões (Amazonas), approximately 30 km upstream from Manaus (3°19’21”S, 60°11’30”W); a sandbank in the Rio Solimões (Amazonas) between Ilha de Machantaria and Ilha de Guará, only a few years old ("Guará sandbank"); 3°13’40”S, 59°55’39”W; Praia Cachorro, a beach on the Rio Negro, opposite to the military airstrip of Manaus (3°11’86”S, 60°00’09”W); and an open white sand area on non-flooded "vaeland" (arvem-fim) sitio Bom Snoage [approx. 2°55’S, 59°56’W] at km 19 on the Manaus-Manacará highway (AM-015) near Reserva Florestal A. Duda.

All floodplain sites were subject to a regular annual, monomodal inundation (Adis 1992, Fig. 2b). By determining the elevation of the flood sites relative to the river, the periods of inundation were calculated using the water gauge data provided by the Harbor Authority of Manaus. The duration of inundation varied from site to site and within sites, depending on the altitude. Lower parts of the beaches were inundated for more than 6 months. All sites had been completely flooded in years with high water levels (such as 1997 and 1999, except for Prainha Grande, where a higher part of the sandy beach always remained unflooded).

Species. The nomenclature follows Winker (1992) and pers. comm.). The present study deals with eight species, two of them closely related (C. klugi and P. leucomanae) and are represented by two subspecies (b = blackwater floodplains, w = whitewater floodplains, df = adults, dm = dimorphic, il = immature, il = larval, dd = dimorphic, noc = non-sexual [for details see Zerm & Adis 2001b]).

- Cyphochoerus (Megapleurophorus) manacu (Fabricius, 1798) [w; 8–10, il, dd]
- Protanomia (Mesoanomia) evoluta (Brulle, 1837) [w; 6–8, il, dd]


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Phaenacara aquaterviridis aquaterviridis (Dujardin, 1825) (18-23.5 mm, id.)
Phaenacara aquaterviridis bicincta (Brulleé, 1837) (16-23.5 mm, id.)
Phaenacara pilosa (Pereny, 1836) (18-9.5 mm, id.)
Phaenacara mindanaoensis (Mandu, 1968) (16-22.95 mm, id.)
Tetrameira obstricta punctata (Camellina, 1855) (15-18 mm, id.)
Tetrameira pinnata (Brulleé, 1837) (15.5-15.5 mm, id.)

In the following text, "Phaenacara" or "Phaen-
acara species" only refer to the Phaenacara species listed above. "Active" larvae are defined here as lar-
vae lurking for food at the tunnel entrance and dig-
ging activity observed at the surface. "Dormant" lar-
vae in the laboratory are defined as larvae not active for >7 days (= approximately 3 feeding intervals).

Phenology of larvae and adult beetles, behavior, egg number, sex ratio. Populations of larvae and adult beetles were regularly observed during monthly field expa-
cursions during 1997-1999 (for details see Zern & Addo 2000). Semi-quantitative and qua-
litative data on phenology of larvae were collected for T. s. punctata, T. pinnata, T. obstricta, and P. cirrina whenever possible. Data on adult beetles of all spe-
cies were gathered on these occasions as well. When ever available, some adult beetles were brought to the laboratory in Masua for further examination. Control sites were determined in the laboratory for females collected in the field and classified as: 11 immate-
urate (not differentiated from pupae transpa-
rent), 2 maturing (tissues with early differentiation), and 3 mature (at least 15 full-size egg in the ovaries). Control sites 1) and 2) were stocked referred to as "non-mature." Occurrence of fat bodies in the ab-
dominial and internal bodies (not fully fat abdo-
nominal), as well as the total number of full-size eggs in mature females, were counted separately.

Sex ratios were determined in adult beetles caught by teams of pitfall traps (P. hagi, P. mindanaoensis, P. obstricta, T. pinnata). Larvae were collected for each species and sampling method. All larval sex were tested to determine significant se-

Rearing in the laboratory. Larvae of P. cirrina and T. s. punctata were reared under controlled conditions in the laboratory to determine the duration of pre-
adult stages. Beetles of P. cirrina were collected in the field and kept in terraria with humus sediment (from Ilha de Maranhao) to obtain eggs. The newly hatched 1st instar larvae were transferred into glass vials filled with moist loam of the same origin. In T. s. pun-
tata, 1st and 2nd instar larvae were collected in a lumber yard and reared in the laboratory to the adult beetle in glass or plastic vials filled with moist sand and also from Ilha de Maranhao. All animals were kept separately in climatic chambers (12/12 light/dark, temperature regime: 12°C 33°C and 12°C 28°C). Larvae in P. cirrina were fed three times a week with fresh fly larvae (1st instar: one fruit fly each) or ter-
rmites (2nd and 3rd instars: 4-8 termites, depending on size). Larvae in T. s. punctata were fed three times a week, 1st instars with termites (4-8 termites, depen-
ding on size), 2nd and 3rd instars with row ground beef (a piece of meat approximately the size of the tunnel opening). Activity patterns and larval development were noted on each feeding day. In T. s. punctata it was occasionally possible to observe pupae through the container walls.

The duration of each developmental stage was defined as the period of time between the first ob-
station of the respective stage and the first of the following stage, including molting. The first ob-
station usually took place during the new larval stage but opened up its tunnel before the beetle had emerged from the adults. Duration of development was esti-

Recesses of submerged tinocorinna in adult beetles and larvae. Following Adams & Messina (1997) we distinguish between subterranean tolerance (a few hours or days) and subterranean tristance (several weeks or months).

In P. hagi and P. mindanaoensis, the duration of subterranean survival in the field was estimated by determining the lowest places along the abiotic stratified at the study sites where 3rd instar larve re-
opened their tunnels after the inundation. The period of time survived was then calculated using the water gauge data from the Harbor Authority of Manaus.

In the laboratory, we used well water from the INPA campus for all flooding experiments (± 0.5", specific conductance: 16 µS/cm). The water was...
boiled and then aerated at 29°C prior to the experi-
ments, which resulted in an oxygen content of
approximately 7.7 mg/l at the start of the trials. All
experiments were performed at constant 29°C in
climatic chambers.

We used submission tolerance in adult beetles of
Phaenocnema species and T. sparsa in the labora-
tory. Bees collected in the field kept 1–2 days with-
out food were separately submerged in water
(spargnus beetles, approx. 250 ml, diameter 6.9 cm)
using spherical strainers of metal gauze. Subsets of
bees were removed from the water at various in-
tervals to determine survivorship. They were put in
moist paper tissue and, if alive, resumed movements
within a few hours or were otherwise scored as dead.
Four or five beetles of each species were kept in a
controlled groups in identical strainers in a moist envi-
ronment at 29°C. For the maximum interval tested.

Submission/resistance to submission of 3rd-instar lar-
vae was tested in two ways. Firstly, active larvae of
P. major, P. endemanae, P. a. bifasciata and T. sp. were
collected in the field at various sampling dates and
subsequently kept 2–4 days without food, as well as
larvae of P. major that had entered a state of dorm-
ancy in the laboratory, were separately submerged in
glass vials (volume 40 ml filled with 50 ml of
water). The vials were then kept with plastic lids (plus
a sheet of paraffin) and carefully placed upside down
in a plastic container. The body size of the larvae was
corrected with approximately 2 cm of salad oil to re-
duce diffusion of atmospheric oxygen into the vials
trough the plastic lids. Subsets of larvae were re-
moved from the vials at various intervals and put onto
moist sand in plastic vials (identical to the ones used
for rearing larvae). Larvae were observed until they
either resumed the ability to dig a tunnel (= survived)
or died (recovery sometimes took several weeks).
Results obtained from specimens of different
sampling dates were pooled in all species. Larvae
stopped moving when being submerged in water
within a few minutes. As larvae continuously took
more time when removed from the sediment and
put into water, we used larvae kept in sediment
without food as control groups (five to ten larvae in
each species).

Secondly, submission resistance was tested simu-
larly in field conditions. We collected 3rd-instar lar-
vae of M. major, P. endemanae, and P. a. bifasciata in
March–April of 1998 and 1999 and kept them
separately in plastic vials (113x315 mm) for 2–4
weeks under normal rearing conditions (see above) in

The laboratory. The containers were then gradually
flattened from the bottom within approximately one
week, allowing the larvae either to escape to the top
or to adapt to the floating conditions. In the tests per-
ned in 1998, the water was poured into the con-
tainers filled with sand through vertical tubes that
reached to the bottoms of the vials. In 1999, the
bottom of the containers was perforated allowing
different containers to be flooded together in aquaria.
Larvae which came up to the surface when being
flattened were dismissed. In larvae which stayed in
the sediments when flooded, the water was drained after
one, two and three months. In the experiments in
1998, we waited until surviving larvae either opened
up their tunnel or until the hatching of the adult
beetles 5 months after the end of the submission
period the sediments were checked for remaining tra-
ces of larvae or beetles. In the larvae tested in 1999,
survival was determined directly: larvae were taken out
of the sediment a few days after the water had been
drained. In both 1998 and 1999, 10–12 larvae were
kept as control groups under the normal laboratory
regime (including feeding when active).

Statistical analysis. Statistical analyses were performed
with SPSS for Windows release: 9.0.1.

Determination. L50 = time to 50% mortality

RESULTS
T. obstricta punctata. The nocturnal adult beetles were
found along the waterline and at larval habitats from
August until October (except for one beetle; Fig. 2d).
𝑙 𝑛 , i.e., first beetles occurred during or before the water
level receded from habitats of the larvae. Mature and non-
mature females were present during all three activity
periods, and no tenner larvae were found. Fat bodies
were found in 19 (out of 32) females and in 10 (out of
31) males. Presence of fat bodies in females was
significantly associated with the non-mature genital
stage (Fig. 3).

We were unable to observe the appearance of the first
1st-instar larvae. The first 2nd-instar were obser-
vied in mid-September, first 3rd-instar at the end of Au-
gust and beginning of September, about 2–3rd and 4–6
weeks after the wax had receded from the larval habi-
tats (Machantaria 1997; Przgo Grande 1997, 1998
respectively). By mid-October, 2nd and 3rd-instar lar-
vae dominated (Machantaria and Przgo Grande
1997, 1998). In December, only few larvae were still
observed, and no more larvae were found in early Fe-

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FIG. 2. Occurrence of adult beetles of T. s. punctata (a), T. s. spinosa (b), P. cristata (c), and C. saturale (d) at the study sites 1997–1999. (a) water level at Marais habier and highest altitude of study site at Ilha de Macaúbas (t = h.a. March), (c) lowest altitude of study site on Ilha de Macaúbas (t = T.p. March), (d) lowest altitude on Cururu sandbank (t = h.a. Cururu), and (e) highest altitude of study site at Ilha de Grande (t = T.p. P.G.). * = one adult beetle in days outside the main flood period. ** = one adult beetle higher than 18 m, non-flooded upland.
found in August 1997 and September 1999 (4 out of 21 females, 11 out of 40 males). Presence of far bodies in females was not significantly associated with the non-mature gonad states (Fig. 3). Larvae were not reared continuously. Some 2nd- and 3rd-instar larvae were observed in February 1998, 2nd and 3rd instars in March 1998 as well as in January and February 1999. No 1st-instar larvae were found.

A few 3rd-instar larvae collected in the field were reared in the laboratory under controlled conditions (similar to T. p. punctata). The pupal stage lasted nine and eleven days (n = 2). Larvae were inactive for five and twelve days before pupation (n = 2).

P. clavata. The distal adult beetles were found along the waterline of the river, at larvae habitats during the period of oviposition, and at probes with sparse vegetation at higher altitudes during rising waters. Adults first occurred shortly after the water had receded from habitats of larvae (Fig. 2c). Distribution of gonad maturity states in females showed no seasonal pattern (mature and non-mature females present at the beginning and during the active period). No sexual dimorphism was observed. Fat bodies were found in only 3 out of 81 females and in 1 out of 82 male. Presence of fat bodies in females was not associated with the non-mature gonad states (Fig. 3).

No 1st-instar larvae were found. In 1997, the first 2nd and 3rd-instar larvae were observed in mid-September, about 1.5 months after the water had receded from their habitats and about one month after the appearance of the first adult beetles. By mid-November 1997 the majority of larvae were 3rd instars, although 2nd instars were still observed as late as mid-November. The exact end of the larval period was missed. No more larvae were found by February 1998. The duration until the 3rd larval instar can thus be estimated at about 1 month, the total duration of larval development as c. 4.5 months or shorter.

Egg development in the laboratory took < 12 days. The duration of larval instar and the pupal stage under controlled conditions is shown in Fig. 4b. In another four specimens collected in the field at 3rd instars, the pupal stage lasted 8–12 days. As in T. p. punctata, larval P. clavata were continuously active, i.e., possible periods of inactivity were shorter than feeding intervals (1–3 days). The time between the first observed activity of a given larval instar and the first observation of its next stage (including molting and the opening of a larval case) was usually 1–2 feeding intervals (∼ 1–7 days).

C. maradica. The distal adult beetles were observed in higher numbers sporadically during the terrestrial phase. First beetles were observed long after the water had receded from most parts of the study sites (Fig. 2d). Distribution of gonad maturity states in females showed no clear seasonal pattern (non-mature females present at all collection dates, mature females only in March 1999), although specimens from 1997 were in bud shape at the time of dissection. No sexual dimorphism was found. Fat bodies were found in 26 out of 27 females and in 41 out of 55 males. Presence of fat bodies in females was significantly associated with the non-mature gonad states (Fig. 3).

The only larvae we observed were 2nd and some 3rd instars in mid-October 1997, when the first adult beetles were observed as well, one month after the water had receded from the locality. The duration of the 1st- and 2nd-instar larvae together was about one month.

![Graph](image)

**Fig. 3.** Presence/absence of far bodies in mature and non-mature females (p = present, a = absent). * a differences between groups significant, (Fisher's exact test, p < 0.05).
Phoxocephalus species. Life cycles of these species were described in detail in Zem & Aila (2000). The long larval development implied a period of dormancy at the end of the 3rd-instar stage towards the high water peaks in P. klugi and P. lindemanii; probably also in P. a. bifasciata and possibly in P. a. armillatus and P. lindemanii. Life span of the nonmature adult beetles was estimated at only a few months, except for P. a. bifasciata at 6 months. No larval beetles were observed in field material of Phoxocephalus species (number of dissected specimens: P. klugi: 729; P. lindemanii: 304; P. a. bifasciata: 627; P. a. armillatus: 57; and P. lindemanii: 164). However, freshly hatched beetles from larvae raised in the laboratory often showed large fat bodies (P. klugi: 9 out of 11; P. lindemanii: 4 out of 4). Gonad maturation seemed to be rapid, as inferred from field data on the phenology of adult beetles and 1st-instar larvae (1–3 months).

Osyp-ribbon egg numbers. The number of full-size eggs in the gonads of mature females varied within and between species, smaller species tending to have more eggs (Fig. 3). In all species/substrates raised from eggs in the laboratory (Phoxocephalus spp. and P. viviparus, several up to 15, sometimes more) larvae often hatched simultaneously. Minimum number of eggs laid by one female in the laboratory was 24 in P. a. armillatus, 13 in P. viviparus and P. lindemanii, and 35 in P. klugi.

In the field, few oospores were observed in P. a. bifasciata, all of them in miner sand about 1–3 m above the waterline of the river. New 1st-instar larvae of P. klugi and P. lindemanii were often found in the field in small patches of high density. Occasionally 10–15 1st-instar larvae were clearly clustered around the nest of a still unhatched 3rd-instar larva of the preceding generation (within a radius of 10–15 cm).

Larval mobility. Larvae of P. a. bifasciata were observed running on the substrate surface in daytime, apparently searching for other places to build a new tunnel (on rare occasions, in particular during rising water levels from December to March). At first, larval densities near the waterline increased (March–April), whereas later on, towards the water level peak (May–June), only a few active larvae were observed. Larvae of other species were never seen outside their tunnels. However, spatial distribution of larvae of P. a. armillatus during rising water levels resembled that of P. a. bifasciata, indicating similar larval mobility.

Substrate resistance of larvae in the field. In P. klugi and P. lindemanii, larvae (mostly 3rd instar) were observed to open up their tunnel after the aquatic phase had ended, forming handshook of larval observed in 1997, 1998, and 1999 the maximum duration of inundation ranged was at least 96, 99, and 94 days in P. klugi and 130 and 124 days in P. lindemanii respectively (in the latter not determined in 1999).

No direct evidence was found in the field for larvae of P. armillatus bifasciata surviving the aquatic phase submerged in the soil. However, several observations definitely indicate larval substratum resi- stance in this subspecies as well.

![Graph showing the duration of larval instars and pupal stage (means and s.e.) under laboratory conditions](image-url)

**FIG. 4.** Duration of larval instars and pupal stage (means and s.e.) under laboratory conditions (see tests: a) P. sobrina punctata: without 1st larval instar; larvae collected in the field and subsequently reared in the laboratory. b) P. cibriti: reared from eggs laid in the laboratory, LI-LIII. 1st=3rd larval instars, N = number of specimens. **122**
• The first adult beetles of the new generation appeared immediately after the water level peaks.
• Few active larvae were present on the remaining non-exposed parts of the riverbank before the water level peaks (May-June), i.e., decreased densities of active larvae at these locations indicating dormancy in larvae.
• During falling water levels, 3rd and 4th instar larvae were repeatedly found at positions along the flooding gradient which were still inundated 1–3 weeks prior to the observations, although larvae never were observed running on the surface during these periods.
• In August 1996, 14 adult beetles were caught during falling water levels at island-like parts of the beach that had been completely inundated. These beetles were immature, in part still internal, and showed no flight muscles.

Habits of P. a.quinquemaculatus were observed regularly every year. Larval tunnel openings were not found immediately after the aquatic phase and adult beetles showed no flight muscles.

Subterranean nursery sites of larval and adult beetles are in the laboratory. In laboratory tests, adult beetles of P. a. chinensis, P. a. dominicus, P. a. quinque maculatus, P. irrorata, and P. a. dominicus survived only 3–10 hours of submersion (Fig. 6, survival rates in control groups 100%). Maximum survival of active 3rd instar larvae submersed in water differed between species, ranging from 21±1.5 to 29±10 days (P. a. chinensis and P. a. dominicana). T. dominica, reared from 0.77 (P. a. bifasciata) to 3.18 days (P. a. dominicana), but comparison of 95% confidence intervals indicates that differences are only significant for the latter species (Fig. 7: survival rates in control groups 100%). In contrast, maximum survival of dormant larvae of P. a. quinque maculatus was 39±5 days (Fig. 7).

When gradually flooded in laboratory, 60 out of 71 and 29 out of 42 3rd instar larvae of P. a. quinque maculatus and P. a. dominicana respectively died not coming up to the surface. Maximum survival submersed in sediment was 3 months in both species (Fig. 8). The blackwater species P. a. dominicana showed to be more resistant than P. a. quinque maculatus from the white water area, a result which is consistent with the field data. Surviving larvae in 1996 (6 P. a. dominican and 13 P. a. dominicana) did not open their tunnel after the end of submersion but pupated directly instead. Tanning the submersion resistance in gradually submersed larval P. a. bifasciata failed because all larvae (n = 12) came up to the surface during the flooding process.

Sex ratio. In adults P. a. quinque maculatus males were significantly more frequent in primiparous than females at the habitats of larvae whereas females were more frequent in catches along the waterline of the river (Fig. 9). On two out of seven dates of mutual sampling along the waterline (only catches with > 0 beetles), female beetles were significantly more frequent than males, whereas on three out of 13 sampling dates, males were significantly more frequent at larval habitats and between the latter and the waterline.

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The sex ratio in adult *P. lindemannae* from pheromone traps did not differ significantly from 50:50% (Fig. 9). On two out of ten dates of manual sampling (only catches with >7 beetles), and in the total catch (n = 247), male beetles were significantly more frequent than females.

Adult males of *P. a. bifasciata* were significantly more frequent in pheromone traps than females (Fig. 9). Females were significantly more frequent in the total manual catch (n = 756). On nine out of 29 dates of manual sampling (only catches with >7 beetles), females were significantly more frequent, whereas on three dates, males were significantly more frequent. The sex ratio varied strongly between sampling dates, e.g., on 13.10.98 males and on 14.10.98 females were significantly more frequent.

Adult *P. a. aequinoctialis* were collected only manually. In total (n = 113), and on one out of four sampling dates (only catches with >7 beetles), females were significantly more frequent.

Among the manual catches of adult *P. limata*, males and females were significantly more frequent on one sampling date each (three sampling dates with >7 beetles). Females were also significantly more frequent in the total catch (n = 194).

Males of *T. spinosa* were significantly more frequent on one out of five dates of manual sampling, as well as in the total catch (n = 99). In the total manual catches of adult *T. s. prostica* (Piaza Grande: n = 45, Bia de Marchanazia: n = 38), C. antonelli (n = 180), and *P. decorata* (n = 279) males and females were equally frequent.

In adult beetles hatched in the laboratory, both sexes were either equally frequent (*P. lindemannae*: n = 45, *P. a. bifasciata*: n = 23, *P. a. aequinoctialis*: n = 13, *P. ciliata*: n = 13, *T. s. prostica*: n = 180) or males were significantly more frequent (*P. klugi*: n = 74). No data are available for *T. spinosa* and *C. antonelli*.

Prey species: The nocturnal adult beetles of *P. klugi*, *P. lindemannae*, and *P. a. bifasciata* were regularly observed to prey on *Gryllolus* (predominantly *Gryllolus nigrescens*), *Anisopus* (predominantly *A. italicus*), *Calambrus* (predominantly *C. truncatus*), *Spercheus* (predominantly *S. americanus* and *S. americana*), and *Lieutitia spinosa*. They also fed on *Euphoria* (predominantly *E. nymphaeae*), *Chrysochroa* (predominantly *C. barbarica*), and *Aperna* (predominantly *A. flavipes*).
(blackwater study site), adult beetles of P. lindemannnae were observed to prey on smaller cockroaches (Blattodera). Adult beetles of P. bifasciata, P. lindemannnae, P. a. bifasciata, and T. s. punctata were occasionally seen on and around dead fish at the waterline.

Predators and parasites. Flytraps of P. bifasciata and T. s. punctata were found in three neogregarines of birds in September 1997 on Ilha de Machinatira (presumably of migrating waders, cf. Stotz et al. [1992]). Fire ants (Solenopsis spp.) were sporadically observed to feed on dying adult beetles of P. bifasciata (although it remained open whether the ants immobilized the beetles). Cannibalism was occasionally observed in August 1998 in the latter species. Among >2100 larvae collected in the field, we found two individuals of P. a. bifasciata with a "snomblike" animal (about 3-4 mm long, possibly a larval bombylid fly?) attached to the abdomens (these animals were lost thereafter). We found no indications of Tiphiidae (Hymenoptera) parasitizing larval tiger beetles. Among >2500 adult beetles dissected in the

![Graphs showing survival rates of active and dormant larvae](image)

FIG. 7: Survival rates of active and dormant P. soyas larvae submerged in water in the laboratory (29°C). Maximum days survived and Probit estimates of LSL (with 95% confidence intervals, calculated including control groups) are shown. (a)-(d): active larvae; (e): dormant larvae. For details see text.
DISCUSSION

Method to determine life cycle: Larvae of most species (exceptions: *P. klugi* and *P. lindemnnae*, Zerm & Adis 2000) were not continuously followed at observation sites in the field for various reasons. Larvae of *T. gamma*, *C. nasturtii*, and *S. aequinotialis* were found either only sporadically, in low densities, or at places not visited regularly. Larval development is rather fast which requires higher observation frequencies, and the detectability of larval tunnels is hampered by size in the smaller species, while habitats of larval *P. femata* were not at all. In *T. x. pancratii* and *C. rhodna* larval habitats are hardly accessible at the start of the 3rd instar stage due to the very moist loamy sediments. Traceability of larval tunnel openings in *P. a. bifasciata* is very limited and extremely dependent on weather conditions — larval habitats open at exposed beaches of rather coarse sand. cf. Zerm & Adis 2001b). In addition, larvae of this species are quite mobile: i.e., some (or all) occasionally leave their tunnel and dig another somewhere else.

The state of gonad maturity in beetles collected in the field was examined in females only. Males are exposed to each gonad maturity more quickly. It is unknown whether any full-size egg remains in the ovaries of mature females after egg deposition. Thus females reproductively in the field with gonads classified as "mature" might have been mature beetles that had laid all full-size eggs prior to capture. Similar problems were found in *Phaenops* species and in carabid beetles from Central Amazonian flood plains (Adis *et al.* 1986; Zerm & Adis 2000).

Larvae were reared under conditions similar to *Phaenops* species (temperature and light regime, alimentation, feeding intervals, sediments; discussed in detail in Zerm & Adis 2000). On the account of the rearing conditions we expect the larval development in the laboratory to be somewhat faster than in the field.

*T. x. pancratii*. This species showed an annual life cycle, as inferred from the distinct seasonal occurrence of adults and larvae. Adult beetles were the first to be found at the waterline and around larval habitats after the water level began to fall. In addition to these findings, previous studies showed that adult beetles occur later than October and during high water periods more within Ilha de Marajó, or on

![Graph showing survival rates of 30 larval instars submerged in sediments in the laboratory in 1998 (25°C); for details see text. Control larval kept in sediment at 28.5°C (see text). *P. lindemnnae* exhibited in 1999 flooding procedure slightly different and survival detection more sensitive (see text).](image)

FIG. 8. Survival rates of 30 larval instars submerged in sediments in the laboratory in 1998 (25°C); for details see text. Control larval kept in sediment at 28.5°C (see text). *P. lindemnnae* exhibited in 1999 flooding procedure slightly different and survival detection more sensitive (see text).
flourishing vegetation, driftwood, and in the canopy region of inundation crosses (Adis 1982; Ribeiro et al. 1996, Adis & Messer 1997, Adis et al. 1998). In this study we even found one female specimen (non-mature and with fat body) on non-flooded uplands (tree forest).

The duration of the pre-adult phase in the field was 3–4 months, which is a rough estimate (it could likely be somewhat shorter) because the end of the larval phase was monitored less intensively and several beetles were not found at all. The duration of the 2nd and 3rd instar, as well as the pupal stage in the laboratory, was 2.5 months in total. Ribeiro et al. (1996) reported around 3 months in total for the larval and pupal development in the laboratory (temperature: 27–30°C). If the duration of the 1st instar was similar to that of the 2nd instar (15 days), the total duration of larval and pupal development in the study would amount to around 3 months, i.e., our field data are in good agreement with both laboratory readings. This short larval phase observed in the field as well as in the laboratory would allow for two generations within one year, yet this was not observed in the field. Due to misidentification, the larval phase from September to March reported in Adis et al. (1998) and Adis & Messer (1997) for Megaphasma solutum punctatum refers to P. bifasciata.

From the field data, life span of adult beetles was estimated as ~9 months or longer, although Ribeiro et al. (1996) reported a maximum of 7 months in the laboratory. The new generation of adult beetles occurred from December-January onwards (inferred from larval phenology in agreement with Adis et al. 1998) and the period of oviposition was August-September, which requires very slow or delayed gonad maturation (+ gonad dormancy). In accordance with findings in other crabid species (Parramore & Bank 1987, Adis et al. 1997) we consider the occurrence of fat bodies as being related to this delayed gonad maturation. The significant association of fat body presence with the non-mature gonad stage gives further evidence for this interpretation. The presence of non-mature as well as mature females in August-September indicates that they either became mature during or shortly before this period. T. pinus. Field data on larval phenology are scarce and adult phenology is rather ambiguous. Several observations indirectly suggest an annual life cycle with a short larval phase during the terrestrial phase and adults surviving the aquatic phase. 1) Adult beetles appeared before larvae were found. 2) Presence of fat bodies (indicating non-mature gonad, see T. s. punctata) only at the beginning of the terrestrial phase. 3) Presence of immature and maturing beetles in December-January indicates hatching of a new generation. The latter might explain why the non-mature gonad state was not associated with the presence of fat bodies as the young beetles are likely to need some time to build up fat bodies.
More information is needed to confirm our in-
terpretation of the life cycle, in particular on larval
habitats and subsequently on larval phenology, as well
as on the localities where adult beetles pass the aquatic
phase.

P. erubita. Results on adult and, in particular, lar-
val phenology indicated an annual life cycle. The
duration of pre-adult development in the field was
<4.5 months or shorter, a rough estimate because the
mid of the larval phase was monitored less intensively
and several beeches were not found at all. Immature
beetles in December/January were considered as be-
ong to the new beech generation. The total du-
ration of pre-adult stages in the laboratory was on
average 3 months, one month longer than reported
by Adis et al. (1998). Together with <12 days for egg
development this comes close to the results obtained
in the field. The short larval phase observed in the
field as well as in the laboratory would allow for two
generations within one year (as suggested in Adis et
al. 1998) and mature females were found as late as
January, yet a second generation of larvae was not
observed.

Data on larval phenology, the observations that
adult beetles are the first to be found at the waterline
and around larvalhabitats after the water level begins
to fall, together with the phenomenon that beetles are
still present on the beeches after the larval phase, led
to the assumption that adult beetles survive the in-
undation period at still unknown localities. The life
span of adult beetles was therefore estimated at ~9
months and longer. Due to the long water level pe-
riod one has to expect a great dormancy in this
species as well, despite the rarity of the larval
beetles found in this study.

C. natans. Field data on larval phenology are scarce
and that on adult phenology is rather anecdotic. Adis
et al. (1998) reported 4 months from eggs to the
emerging beetle in the laboratory, which appears
rather long compared to only one month together for
the 1st and 2nd instars in the field. Two objections
point indirectly to an annual life cycle with a short
larval phase during the non-vegetative phase and adultre-
sisting the aquatic phase: 1 larvae observed in Oc-
tober 1997 must have represented the new larval
generation because the locality had been flooded during
the entire preceding year, i.e., mature beetles must
have been already present in September and larval
development seems to be rapid; 2 presence of fat
beetles and their significant association with non-
mature gr natinal states (indicating gravid dormancy,
see T. punctata). Evidently, further information is
needed to clarify the details of the life cycle. Adult
phenology found here is only in part consistent with
Forst & Barnes (1989), who reported adults oc-
curring in February, May, June, September, and Oc-
tober for the whole of Bavaria.

Phaenora species. Life cycles of Phaenora spe-
cies are characterized by a long larval phase (includ-
ingsubmersionresistance in larvae, see below) and a short
or long adult phase. Larvae enter a state of dorman-
cy towards the end of the 3rd instar (chose for some
species, suspected in others) (Zern & Adis 2000). In
contrast to the species described above, adult beettles
completely lacked fat bodies (>1000 specimen dis-
rated), a trait which is likely to be related to the unusu-
cal life cycle. The presence of fat bodies in adult
Phaenora beetles newly hatched in the lab-
atory remains elusive as comparative data from
other species are not available.

Onsetage and life cycle. Duration of egg develop-
ment in P. erubita (<12 days) is in good agreement with
data for Phaenora species (Zern & Adis 2000). T.
punctata (Klein et al. 1996), and many beetles in
general (Pearson 1988), although some authors re-
ported longer periods (Grahn 1968, Palmer 1976a).
Mean duration of the pupal stage of T. puncta-
tata was almost identical to results obtained by Ri-
beiro et al. (1998) (4.5, 4.4, 16.4 days). Moreover, the
larvae of the three species studied here, with a range
of 1.53–15.1 days (T. grisea, P. erubita, T. punctata),
were similar to Phaenora spp. (Zern & Adis 2000)
and Pontin套房uidea (form terra firme uplands
near Manaus) (Paarmann et al. 1998), but shorter than
in species from temperate and subtropical regions
(18–22 days; Willis 1967, Fanch 1968) and in spec-
ies from Corte Rico (Palmer 1976a). This adds fur-
ther evidence that differences might be a result of dif-
ferent temperatures experienced by the species.

The 2nd instar represented the longest larval stage
in the laboratory in both T. punctata and P. erubita,
which follows the general pattern in tiger beetle lar-
vae (cf. Willis 1967, Palmer 1976a, Holt 1982, Pear-
son 1988, Anosim et al. 1997a, Paarmann et al. 1998,
Zern & Adis 2000). The total duration of larval develop-
ment as derived from the current data (shown for T. punctata
and P. erubita, suspected for T. grisea and C. nat-
tans) was 3–4 months, Adis et al. (1998) reported 4
months in C. natans for the pre-adult stages in the

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The life span of adult beetles varies according to the type of life cycle. Species with adult beetle sur-
viving the inundation period (i.e., post-flood P. pseu-
dosa, P. magnifica, C. annulatus) must be expected to live 3 to 4 months (Palmer 1930), whereas larvae develop in tiger beetles from subtropical and temperate regions usually last 1 to 4 years (Shelford 1916, Wil-
son 1967, Fauch 1908, Pearson 1988, Simon-Rasqu,
1998).

In floodplain forest species, adult females survive the inundation period and therefore their life span is a few months only (e.g., P. magnifica, P. pseudosa) or a few years (E. annulatus) (e.g., P. pseudosa, P. magnifica, C. annulatus) must be expected to live 3 to 4 months (Palmer 1930), whereas larvae develop in tiger beetles from subtropical and temperate regions usually last 1 to 4 years (Shelford 1916, Wil-
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son 1967, Fauch 1908, Pearson 1988, Simon-Rasqu,
Submission resistance/tolerance of larvae and adults. larvae of P. d. oblonga and P. d. mediterranea were highly resistant to submission in the field (3-4 months). Direct evidence suggests submission resistance to some P. d. oblonga and, possibly, P. d. mediterranea. The lack of observation of larvae P. d. transatlantica suggests that specimens of larvae were not present. For example, larvae P. d. oblonga and P. d. mediterranea, subspecies P. d. mediterranea, submitted for 1-3 months in sediments in the laboratory, did not respond the natural entrance but pupated directly. No data are available on submission resistance in larvae P. d. oblonga as their habitat is still unknown.

The behavioral reaction to rising water levels in the laboratory in mass larvae P. d. oblonga and P. d. mediterranea was similar to that observed in the field larvee sway in the sediment and apparently react to the increasing water levels by increasing their digging activity before actually changing their numerical entrance. In contrast, larvae P. d. oblonga reacted to rising water levels in the laboratory by escaping to the surface, which corresponds to the high mobility of larvae observed in the field during rising water levels. It also confirms similar field observations by Adams et al. (1998) (due to misidentification ascribed to Megabalanus sp.). As a result, observations indicate that larvae P. d. oblonga have no resistance to submission in the laboratory, we propose the following hypothesis: reaction of larve to flooding might depend on the feeding status, i.e., that only larvae that have fed sufficiently might enter a state of dormancy and stay in their burrows when being flooded, possibly further engendered by some external factors. Other larvae, not yet "ready" for dormancy, might escape from rising water levels to higher locations to keep on feeding. Additionally, in expenditure, one should expect that larve loci primarily in low positions along the subtidal gradient might always move to higher positions prior to entering a state of dormancy. Larvae noted in the laboratory did not enter a state of dormancy prior to propulsions (Zemn & Adams 2000) which might be explained by the lack of external triggers due to the uniform rearing conditions.

Submission tolerance in active larvae of all species tested in the laboratory (including three species in which larvae [submerged] and one species in which adult beetles [abovement] survive the submission period) was only a few days. This low tolerance seems not to be due to the relatively low specific conductance of the water used in the experiments because survival rates in larvae P. d. oblonga, P. d. mediterranea, and P. d. transatlantica were not higher in preliminary tests using a buffer solution (0.1 M Tris-HCl, 0.05 M NaCl) than in seawater from the Ria de Riaño (Galicia). Furthermore, the specific conductance of the water used in experiments was only compared to seawater from the Ria de Riaño (Galicia) but not to seawater from the Ria de Riaño (Galicia) (see below). The low tolerance values are apparently also due to the decreasing oxygen concentration in the closed vials, as survival rates in larvae P. d. oblonga and P. d. mediterranea resuspended in deoxygenated water, as well as in pure nitrogen atmosphere, were similar or higher (Zemn & Adams 2000), see below.

Field data on submission resistance in P. d. oblonga and P. d. mediterranea contrast strongly with the low tolerance in active larvae in the laboratory. Larvae of P. d. oblonga that had entered a state of dormancy in the laboratory, and were taken from the sediment and resuspended in water, showed a maximum resistance of >3 months. Thus dormancy seems to enhance submission resistance. Moreover, P. d. transatlantica was gradually submerged within their sediment resisting nutrition cultures similar to the field data.

Submission resistance of ~3 months at 25-30°C, as reported here, is outstanding when compared to data from the literature. Willis (1967) observed active tiger beetle larvae at recently flooded areas. Hamilton (1985) studied flat leaf beetles Cicindela repanda surviving flooding for seven days. Wilson (1974) reported surviving larvae after three weeks of inundation in Cicindela punctata. The only experimental laboratory data available habitats are provided by Hulock et al. (1998), who found maximum survival in larvae Cicindela punctata of 2.5-7 days at 25°C. (North Carolina, USA). Some authors presumed that submerged larvae breath trapped in their closed tun- nel (Wilke 1967, Pelzmann 1988), which could explain the difference between larvae submerged with and without sediment in the present study. This possibility cannot be ruled out, at least in the fine-sand sediment (silt and mud). In the pupal period (silt and mud) would also be similar to the results of Willis (1967).
were not obtained in larvae submerged in the labor-
atory. And even if it was trapped inside the snail, it seems unlikely that oxygen could be available for extended periods of time due to the organic content of the soil and the low oxygen concentration in the water body (see below).

From the data at hand we conclude that the ex-
tent of stoma ventilation in adult larvae is not re-
tained as the life cycle type. Submersion resistance of a few days might be a general trait in non-dwelling amphi- kinds such as tiger beetle larvae, enabling them to withstand short-term inundation caused by flashflood or storm-flooding events in semipermanent floodplains (cf. Hock 1978, 2000; Hock and Stanley 2001). Tolerance does increase submersion resistance, al-
though other factors seem to be involved. Possibly the gradualness of the flooding process in the field, and when being submerged in sediment in the laboratory, might allow the larvae to adjust physiologically to the host situation beyond pure disorientation. Future re-
search focusing on larvae during this particular pe-
tial when being gradually flooded should help to identify the relevant factors increasing submersion resistance. This will also provide the information needed to design studies on the physiological me-
chanisms underlying and limiting submersion resistance.

Independently of the exact circumstances deter-
imizing the extent of submersion resistance in larval P. kluogi aus R. Jendrackova, et al. has also revealed larvae surviving several months submerged as the soil be-
low was highly resistant also against hypoxic or anaer-
obic conditions because flooded soils quickly become anaerobic (Khamraporn et al. 1991). This is also indicated by the low oxygen content in river water above inundated floodplain soils in Central Amazonia (Adu & Mes-

Adult beetles of Rhinocerota species and T. gi-
naeus species in the laboratory were not resistant to sub-
mersion (tolerance c. 1-3 hours). This is con-
sistent with Adu & Meurer (1997), who reported maximum survival times of 2-18 h in P. kluogi, T. ginn-
eaus, and other species from floodplains and ama-
phic habitats, although experimental conditions were slightly different (20°C; 94-96% relative humidity). Due to their low submersion tolerance we conclude that the species studied in this study lack the diving ability described for T. punctata (Ado et al. 1999). Adult T. punctata sur-
viving inundation in individual burrows along vertical river banks, as reported for Myrmelech sardira from Costa Rica (Willie & Miller 1962). Thus, an immersion tolerance in adult tiger beetle species of other species and in other parts of the world are not avail-
able. Only Hock et al. (1998) stated that adults were unable to survive immersion (Caecilius sp.)

Sex ratio. Sex ratios in field samples from a given size re-
semble characterizes the true ratio in the population. A sex ratio biased by sex-specific traits (such as differing maturity or dispersal capacity), or might represent a ratio influenced by the sample method itself. Al-
ternatively, sex ratios might indicate sex-specific be-
havior or habitat-use, i.e., they could give informa-
tion on the function of microhabitats within the spe-
cies' natural habitat. How we assume a 50/50 sex ratio as the true proportion of the sexes in the populations under study.

Higher proportions of females at the waterline, and of median larval habitats in P. kluogi, suggest that the waterline might serve as a temporary food source (it is presumed to be rich in prey). Females should be more dependent on a better food supply for egg produ-
duction whereas males might increase their mating success by staying at larval habitats to which females must return for oviposition. Correspondingly, fre-
quency of flight ability (facilitating the use of the waterline) is higher in females than in males (Zenk & Meurer 2001). The lack of such a specific sex ra-
to in the other species investigated might be due to the spatial distribution in P. kluogi of the larval habi-
tats (used by both larvae and adults) and the tem-
porary waterline (used by adult beetles only). In the other species, habitat use in adults is spatially in-
distinct (P. rhinoceros, C. annulata, T. ginnearus, T. l. pru-
tata), adult and larval habitats adjoin each other (P. aragoniaca spp.) we larval habitats, although also distant from the waterline, are spatially rather pun-
tual or linear, therefore impeding a greater number of beetles being caught at these localities. (P. sub-
mansoni) (Zenk & Meurer 2001). Whether the female-
bias ratio in P. kluogi hatched in the laboratory really represents the true ratio of the population/species needs further investigation, as field data do not sup-
port these findings.
Mite-biased ratios in samples of *P. a. infestans* from pitfall traps might reflect a higher running activity in males while, in females, might have led to female-biased ratios in the same locality in manual samplings (lower running activity certainly facilitates manual sampling). Reasons for higher proportions of males in *P. a. infestans* and *T. genus* and of females in *P. a. apiciseta* remain unclear.

Prey spectrum. From our observations *on the nocturnal adult beetle it appears that prey mostly feed on soft-bodied insects (the larvae species possibly also on hardy animals), which is in agreement with Adis et al. (1989). Data on the prey spectra were not sampled systematically. Thus many prey species might have been missed. To the nocturnal species gathering qunatative data on potential prey is hampered by the high abundance of adult beetle species relative to potential prey species, which virtually impede the use of passive sampling techniques to determine prey quantity. We can assume that the lower number of potential prey species is actually due to the high number of adult beetle species. Thus, in theory, to the assumption that adult beetle species are important predators of small and medium-sized invertebrates on these open areas of river banks. Whether the observations of adult beetles on dead fish indicate that they actually feed on carcasses (as reported for other species from Arizona/US) Pearson & Mury (1979) remains open, as they might also have been hunting real or potential food sources as hiding place. Preliminary experiments with fresh and frozen beef in the field suggested that they do not accept carrion (Zehn & Adis, unpublished). But even if they did, carrion is too rare at the study sites to represent a significant food resource for the beetles.

Adis et al. (1989) provided data on prey species: adult C. annulata were observed to prey on adult Hydropsychidae (Ephydridae: Dorothea), and adult D. shahgi on Haploglossa (Ephemerida: Gyrillidae) confirmed by the present study. Adults of species from *P. stolzfoosi* forests are reported to prey on adult *Diptera* (Ephydridae and Callidicidae) (Adis et al., 1989). We rarely observed larvae in the field in the capturing prey. Preliminary laboratory observations, however, indicate that they feed on a broad spectrum of invertebrates (Zehn & Adis, unpublished). These observations of apparently unspecialized feeding habits in adults and larvae are consistent with the general patterns reported for adult and larval tiger beetles. These indicate that prey size is the main determining factor (Friedrichs 1953, Wilks 1967, Palmer 1976a; see also Mary Meyer 1987, and Minitzu & Yeh 1998). Proportion and parasites. Quantitative data on predatory rates on adult and larval tiger beetles in Central Amazonian floodplains are too available. Adis et al. (1989) already reported on nocturnal walking beds as predaory of adult *P. a. krugi* and *T. s. punctata*. Carnivory observed in *P. a. krugi* was probably related to the exceptionally high beetle density in August 1989. In the laboratory, adult beetles were kept at zero without causing carnivory. *T. punctata* (Hymenoptera) parasitizing on larval tiger beetle were not searched for systematically, which might explain the lack of observations. Alternatively it might indicate that they are either absent or not less frequent at the study sites. This would be in contrast to studies from other parts of the world (Williams 1982, Willms & Fainbur 1973, Palter 1976b, Horst 1982, Kredley & Pearson 1988, Kredley 1987, Pearson 1986, Kredley & Pearson 1989, Kredley et al. 1987), in particular to observations at a forest site near Manaus where *T. punctata* contributes to the high mortality rates (97-99%) among 2nd and 3rd larval instar of five species (Parramanta & Compagn). Their probable abundance in this study might be due to habitats properties (they possibly do not occur at floodplains or in open areas in floodplains) or to the generally greater size of *Phaenusa* and *Trichodes* species larva (Pascard, pers. comm.). This indicates that the size of adults and larvae infected with larval mites indicates the mice's prionic nature. Infestation rates are high but the extent of damage in the host is unknown. Wilks (1967) collected adult *C. cinerea* (Okland/USA) heavily infested with an undescribed *Parasphalidioida* (Trichobothriidae) which he claimed to be an "accidental" infestation. Wernbom (1983 cited in Kredgay 1985) reared on a small number of species from adult tiger beetles, Kredgay & Pearson (1985) and Kredgay (1986) reared on a pygmybear (micrino*Trichobothriidae*) infecting larval tiger beetles (two *Ceutorhini species*, Araruna/USA). The latter study also found hyphomycetes of *Sarcosporid* sp. on both larvae and adults of one *Ceutorhini* species. For both mite species they proposed a phoretic nature of the mice-tiger beetle association.

The infestation of *P. a. infestans* by parasitic *La-

bodesthini foragini is the first well-documented record for tiger beetles worldwide (Arnold, pers. comm.).
Survival strategies. It is evident through their mere occurrence that species living in floodplains are well-adapted, especially in species endemic to such environments like eight out of the nine taxa studied by Zeml (2001). Their survival is in particular ensured by characters enabling them to cope with the specific floodplain conditions. These traits, which enhance survival and reproduction in the inhospitable zone, will be termed "adaptations" (according to Schaefer 1992, cf. also "nonhistorical" definition Reese & Sherman 1993). They might have been selected in the same type of environment for their current function/purpose from "less-adapted" ancestral lineages, or they might also have originated in a different environmental context and from different functions/purposes. The latter case is sometimes referred to as "preadaptation" (Schaefer 1992) or "pre-disposition" (Weigmann & Wohlgemuth-Rech 1999). In the following we consider characters obviously related to the specific floodplain conditions (e.g., life cycles driven by the flood pulse, submersion resistance in larvae, or other traits derived from comparison with related species) as adaptations (cf. Adis & Mesner 1997). However, quantitative studies to test the adaptive nature of the characters in question (cf. Reese & Sherman 1993, Reese 2001) will remain a task for future studies.

Many adaptations of a given species are likely to be functionally related to one another, some traits enabling, completing, or amplifying others. The sum of adaptations to the floodplain conditions will be treated here as a species' "survival strategy" (cf. Southwood 1977, 1988; Chapelsky et al. 1988; Southwood, Schaefer 1992). When comparing survival strategies of different species, similar "syndromes" (groups of specific traits) can often be recognized (representing different "types" of survival strategies). These can in particular be expected in fresh environments (e.g., annually long-term inundated areas), as extreme conditions are likely to limit the number of possible ways to cope with them.

For all species studied, the data at hand indicate an univoltine life cycle that is driven by the annual monomodal flood pulse (Zeml & Adis 2000, 2001b; Zeml et al. 2001; cf. Jark & Adis 1989). This agrees with other studies on e.g. benthic species of Central Amazonian floodplain forests (Morinor et al. 1997, 1997b; Adis & Adis 1998). Several river beetles species studied at several flood upland areas near Manaus also showed annual, second life cycles, yet they appeared to be driven by the annual precipitation pattern (Parram et al. 1998, Zeml et al. 2001). From the tropical realm, annual, seasonal life cycles have been reported for most tiger beetle species studied so far, also apparently driven by annual precipitation patterns (Pawson 1974a, 1981; Parram & Stork 1987; Stork & Parram 1992).

As shown above, a common feature of floodplain species is that life cycles driven by the flood pulse instead of by precipitation patterns. The two distinct types of life-cycle observed in the species studied here correspond to two types of survival strategy. Species are either non-migratory (with "dominant stages under water in small-marine terrains") or migratory (migrating by flight to dry places, mostly within the floodplain) strategies 5 and 6 of Adis (1997) Fig. 14.1. In addition to the differences related to the life cycles (phyleological adaptations), typical sets of ethological, physiological, and morphological/anatomical adaptations (interrelated in many different ways) are associated with each type of strategy.

Species representing the non-migratory strategy are P. kiehi, P. brunneomaculatus, probably P. f. fasciatus, and possibly P. a. constricticollis and P. imitans (Zeml & Adis 2000, 2001b). A characteristic trait is a long larval phase (phyleological adaptation) with dormant 8th-instar larvae surviving the inundation period submerged in the soil (submersion and hypoxia resistance; phyleological adaptation). A series of other traits in both larvae and adults are acquired for this type of strategy. For example, gonad maturation has to be rapid to ensure larval development to the 8th-instar stage before the next flooding event. Adult females have to select sites at high altitudes for oviposition (as the extent of submersion resistance is limited); P. kiehi and P. brunneomaculatus, (ethological adaptation), or larval mobility must be high (cf. P. fasciatus, ethological adaptation) (see Zeml & Adis 2001b). Other typical traits accompanying this strategy are short adult life span (exception P. fasciatus), flightlessness to varying extents, and no major habitat shift within the life cycle (partial or complete spatial overlap of adult and larval habitats), and others (Zeml & Adis 2000, 2001a, 2001b).

The migratory type of survival strategy is well documented for T. punctatus, and the data currently available indicate a similar strategy for the remaining species from open floodplain areas. Characteristic traits are short larval phase during the terrestrial phase, long migration distance, and adult beetles (both phyleological adaptations) including gonad dormancy (physiological adaptation), and flight ability. A major fra
brat shift takes place during the adult phase (etho-
ilogical adaptation). The extensive spatial separation of larval and adult habitats observed in these species (Zeml & Auds. 2001b) is at least in part a consequence of this habitat shift. Adults of T. sparoni appear to be even more specialized in having acquired an amphibious behavior (daring to hide under water; ethological adaptation) because several morphological characters enhance the ability for air at-
nention under water (morphological adaptation) (Auds & Meuse1937). Such amphibious behavior is also known for Ophiophaga pallia biont floodplain sites in Costa Rica (Camus 1992).

A similar type of migratory survival strategy was found in the three tige beetles species inhabiting Central Amazonian floodplains (Amorin et al. 1997a, 1997b; Auds et al. 1998). Among ground beetles (Carabidae) only survival strategies of the migratory type have been found (Linder 1979; Auds et al. 1986, Auds et al. 1990, Auds et al. 1997). The common acute cycle pattern in Carabidae is a relatively short larval and a long adult phase, particularly in tro-
"pical species (e.g. Crowson 1981, Parnier & Soek 1987, den Boer & den Boe-Gossiae 1990, Busk & Parnier 1992, Parnier et al. 2001), whereas Cicindelidae generally show a conary pattern (e.g. Willis 1967, Parish 1980). From this general back-
ground one should expect migratory survival strate-
gies in Carabidae inhabiting Central Amazonian floodplains to be more likely as they do not require major changes in life history traits. In Cicindela, on the other hand, life cycle traits related to non-
migratory survival strategies would most likely re-
semble the general life history patterns of the family. However, the long inundation periods might have been so important in pressuring non-migratory survi-
val strategies in more species. Instead, many species show migratory strategies, implying a major altera-
tion in life history traits (both larval phase and long
dult life span; habitat shift). More information is clearly needed on these life cycles of species as well as on phylogenetic relationships to reveal the weight (phylogenetic descent and the selecting of biotic/abiotic conditions) of the observed survival strategies.

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