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

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Abstract. Terrestrial organisms living in the Central Amazon floodplain have to cope with an annual inundation period of several months. Life cycles, habitats, behavior, and other parameters were investigated in the eight tiger beetle species inhabiting open areas in white- and blackwater floodplains near Manaus. Populations of larvae and adult beetles were observed during monthly field excursions during 1997–1999 to follow larval and adult phenology and to determine habitats and other parameters. Adult beetles were regularly taken to the laboratory for examination of gonad maturity, occasionally also for submersion experiments and to obtain eggs for rearing larvae to the adult beetle under controlled conditions. Larvae, too, were collected in the field and taken to the laboratory for submersion experiments and for rearing to the adult beetle. Submersion tolerance/resistance in the field was estimated by calculating the longest duration of inundation survived (using water gauge data) and from other observations. In the laboratory, maximum survival in water (without sediment) was tested in adult beetles of five species, in active larvae of four species, and in dormant larvae of one species. In addition, maximum survival in larvae submerged in sediment (simulating natural flooding conditions) was tested in two species. Here we complete information from previous contributions on life cycles in the four *Phaeoxantha* species, as well as on habitats and activity patterns of all eight species. Data are given on the life cycle of *Tetracha sobrina punctata*, *Pentacomia cribrata* (both field and laboratory data), *Tetracha spinosa*, and *Cylindera suturalis* (field observations). These four species have annual life cycles with a short larval phase (3–4 months) during low water periods and with adult beetles surviving the inundation period. Adult life span was long (>9 months) and is likely to involve a gonad dormancy in both sexes. This type of life cycle contrasts with findings in *Phaeoxantha* species. These also showed annual life cycles, but the larval phase was long (>7–10 months), including submersion resistance in larvae (shown for *P. klugii* and *P. lindemannae*, presumed for *P. aequinoctialis bifasciata*), and adult life span is either short or long. Submersion resistance in the field and when being submerged in sediment in the laboratory was >3–4 months in larval *P. klugii* and *P. lindemannae*. However, submersion resistance of active larvae in water without sediment was only a few days (*P. klugii*, *P. lindemannae*, *P. a. bifasciata*, and *T. s. punctata*) and >15 days in dormant larvae of *P. klugii*. Hence, submersion resistance in active larvae was low in species representing both life cycle types. Resistance is apparently enhanced by dormancy, although further factors are likely to be involved, as field data show a much higher resistance still. Adult beetles were not resistant to submersion (maximum survival < 15 or < 10 h, *Phaeoxantha klugii*, *P. lindemannae*, *P. aequinoctialis* ssp., and *Tetracha spinosa*). Data on egg numbers, sex ratio, prey spectrum, predators and parasites, and on behavior are given and discussed for several of the species. Based on their life cycle, two different types of survival strategy can be assigned to the tiger beetle species inhabiting open habitats: *Phaeoxantha* species show a non-migratory type with flood resistant larvae, whereas *P. cribrata*, *C. suturalis*, and *Tetracha* species exhibit a migratory type with adults passing the inundation period. The specific sets of phenological, physiological, and ethological adaptations characterizing these two types of survival strategy are discussed. *Accepted 27 September 2001.*

Key words: life cycle, larval development, seasonality, inundation, submersion resistance, dormancy, Megacephala, Phaeoxantha, Tetracha, Pentacomia, Cylindera.

INTRODUCTION

Terrestrial organisms living in the Central Amazon floodplain 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 animals 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;

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Adis 2001). Against this background, studies on inundation survival strategies in riverine tiger beetles of Central Amazonia should contribute to the understanding of the floodplain ecosystem and its inhabitants, as well as reveal specific examples of how typical floodplains conditions are overcome by representatives of this beetle family.

Many tiger beetle species inhabit riverine habitats worldwide where flooding is a regular factor. Although several studies claim ability in larvae of tiger beetles to survive flooding (Hamilton 1885, Willis 1967, Wilson 1974, Knisley & Pearson 1981, Pearson 1988) quantitative data on their submersion tolerance/resistance are rare. Little is known about the phenological, physiological, ethological, and other adaptations to floodplain conditions in the riverine species (Hoback et al. 1998, 2000; and studies from Central Amazonia, see below).

The Manaus region of Central Amazonia hosts a diverse tiger beetle fauna. Floodplain habitats alone hold 11 species, of which 8 are restricted to open areas (Adis et al. 1998, Zerm et al. 2001). Different aspects of life cycles and survival strategies of the riverine species have been studied for some species (Paarmann et al. 1982, Irmler 1985, Adis et al. 1993, Ribeiro et al. 1996, Adis & Messner 1997, Amorim et al. 1997a, Adis et al. 1998). Recently we published several contributions on floodplain species from open areas: life cycles of Phaeoxantha species (Zerm & Adis 2000), details on habitats and activity patterns in larvae and adult beetles of all species (Zerm & Adis 2001b, Zerm et al. 2001, Arndt et al. 2002), as well as the varying extent of flight ability in nocturnal species (Phaeoxantha and Tetracha) (Zerm & Adis 2001a).

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 on the basis of field observations (all four species) and laboratory rearings (two species). All tiger beetle species from Central Amazonian floodplains studied in detail so far showed seasonal, annual life cycles: Pentacomia egregia, O. confusa, and Phaeoxantha spp. (Paarmann et al. 1982, Irmler 1985, Amorim et al. 1997a, Zerm & Adis 2000). Thus, the question here is whether the four additional species similarly exhibit annual life cycles and whether the duration of the developmental stages differs intra- and/or interspecifically (including a comparison with Phaeoxantha species).

Another part of this contribution focuses on submersion tolerance/resistance (for definition see Adis & Messner 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 3rd instar larvae submerged in the soil (Phaeoxantha spp.) or as adult beetles which (as known or presumed) fly to dry places. Adis & Messner (1997) reported maximum survival times of 2–18 h submergence in adult beetles of nine species from floodplains and non-flooded uplands. Only Tetracha sobrina punctata showed a greater tolerance of 24–30 h, which was attributed to a unique diving behavior (Adis et al. 1993, Adis & Messner 1997). From this background, we expect low submersion resistance in adult beetles of any of the species in question. Testing more species, we intend to reveal whether low submersion tolerance of < 18 h in adults is a general feature of the floodplain tiger beetle species. Somewhat higher resistance values might indicate a diving habit similar to T. s. punctata.

In species with larvae surviving the aquatic phase submerged in the soil we determined the duration of inundation survived in the field. Larvae of these species can be expected to show greater submersion resistance 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 invertebrates (cf. Irmler 1979, Adis 1992, Adis & Messner 1997, Weigmann & Wohlgemuth-von Reiche 1999, Zulka 1999, Hoback & Stanley 2001). We therefore tested whether submersion resistance in active larvae of different species varies according to life cycle type. To determine if dormancy enhances submersion resistance, both active and dormant larvae of Phaeoxantha klugii were tested. Larvae of P. klugii and P. lindemannae actively close 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 resistance. We therefore tested submersion resistance in larval P. klugii and P. lindemannae that were gradually flooded within sediment, i.e., simulating natural conditions.

Furthermore, data on larval mobility, oviposition and egg numbers, sex ratios, prey spectrum, predators, and parasites were collected to document the species' natural history. The final aim of the present study is to depict the species' survival strategies and to elucidate 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 "Praia Grande," was 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). The main whitewater study site was situated at the southern beach of Ilha de Marchantaria, the first island in the Rio Solimões (Amazonas) upstream of the confluence with the Rio Negro (3°14'34" S, 59°54'46" W). Other places visited in addition were: a beach on Ilha de Paciência in the Rio Solimões (Amazonas), approximately 40 km upsrream from Manaus (3°19'21" S, 60°11'16" W); a sandbank in the Rio Solimões (Amazonas) between Ilha de Marchantaria and Ilha de Curarí, only a few years old ("Curarí sandbank;" 3°15'40" S, 59°55'39" W); Praia Cachorro, a beach on the Rio Negro, opposite to the military airport of Manaus (3°11'06" S, 60°00'05" W), and an open whitesand area on non-flooded upland (*terra firme*) (Sítio Bom Sossego [approx. 2°55' S, 59°59' W] at km 19 on the Manaus-Itacoatiara highway [AM-010] near Reserva Florestal A. Ducke).

All floodplain sites were subject to a regular annual, monomodal inundation (Adis 1992; Fig. 2e). By determining the elevation of the srudy sites relative to the river, the periods of inundation were calculared using the water gauge data provided by tbe 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 Praia Grande, where a higher part of the sandy beach always remained unflooded.

Species. The nomenclature follows Wicsner (1992 and pers. comm.). The ptesent study deals with eight species, two of them closely related (*P. klugii* and *P. lindemannae*) and one represenred by two subspecies (b = blackwater floodplains, w = whitewater floodplains, tf = *terra firme* uplands; body length in mm; ad or an = adults diurnal or nocturnal; ld or ln = larvae diurnal or nocturnal [for details see Zerm & Adis 2001b]):

- *Cylindera* (*Plectographa*) *suturalis* (Fabricius, 1798) (w; 8–10; ad, ld)
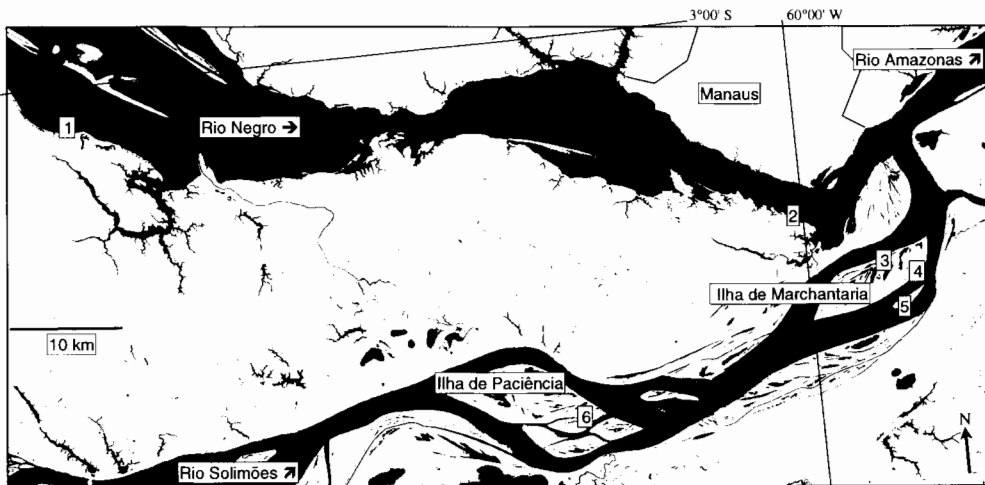- *Pentacomia* (*Mesacanthina*) *cribrata* (Brullé, 1837) (w; 6.5–8; ad, ld)

FIG. 1. Map of the area investigated showing the study sites: 1) Praia Grande, 2) Praia Cachorro, 3) Ilha de Marchantaria, northern beach, 4) Ilha de Marchantaria, southern beach, 5) "Curarí sandbank", 6) Ilha de Paciência, south-eastern beach. Redrawn from Landsat-TM, 28.09.1998, Bands 5, 4, 3, not geo-referenced (source: Instituto Nacional de Pesquisas Espaciais [INPE], Brazil). North-south and east-west axis manually inserted as inferred from the map "Projeto Radambrasil," 1978, Folha Manaus SA.20-Z-D.

- *Phaeoxantha aequinoctialis aequinoctialis* (Dejean, 1825) (w; 18–21.5; an, ld)
- *Phaeoxantha aequinoctialis bifasciata* (Brullé, 1837) (b; 16.5–20.5; an, ld)
- *Phaeoxantha klugii* Chaudoir, 1850 (w; 25–27.5; an, ld/ln)
- *Phaeoxantha limata* (Perty, 1830) (b/tf; 9–11.5; an, ld)
- *Phaeoxantha lindemannae* (Mandl, 1964) (b; 22–26.5; an, ld/ln)
- *Tetracha sobrina punctata* (Castelnau, 1835) (w, b; 15–18; an, ld)
- *Tetracha spinosa* (Brullé, 1837) (w; 13.5–15.5; an, ld)

In the following text, "*Phaeoxantha*" or "*Phaeoxantha* species" only refer to the *Phaeoxantha* species listed above. "Active" larvae are defined here as larvae lurking for food at the tunnel entrance and/or digging activity observed at the surface. "Dormant" larvae in the laboratory are defined as larvae not active for >7 days (= approximately 3 feeding intervals).

Phenology of larvae and adult beetles, behavior, egg numbers, sex ratio. Populations of larvae and adult beetles were regularly observed during monthly field excursions during 1997–1999 (for details see Zerm & Adis 2000 and 2001b). Semi-quantitative and qualitative data on phenology of larvae were collected for *T. s. punctata*, *T. spinosa*, *C. suturalis*, and *P. cribrata* whenever possible. Data on adult beetles of all species were gathered on these occasions as well. Whenever available, some adult beetles were brought to the laboratory in Manaus for further examination. Gonad states were determined in the laboratory for females collected in the field and classified as: 1) immature (ovarioles not differentiated, gonads transparent), 2) maturing (oocytes clearly differentiated), and 3) mature (at least one full-size egg in the ovaries). Gonad states 1) and 2) are together referred to as "non-mature." Occurrence of fat bodies in the abdominal cavity and teneral beetles (not yet fully sclerotized), 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 means of pitfall traps (*P. klugii*, *P. lindemannae*, *P. a. bifasciata*; cf. Zerm & Adis 2000) and by manual sampling (all species), as well as in adults hatched in the laboratory (*P. klugii*, *P. lindemannae*, *P. aequinoctialis* spp., *T. s. punctata*, *P. cribrata*). Catches were pooled for each species and sampling method. Binomial tests were performed to detect significant deviations from the 50:50 % ratio.

Rearing in the laboratory. Larvae of *P. cribrata* and *T. s. punctata* were reared under controlled conditions in the laboratory to determine the duration of pre-adult stages. Beetles of *P. cribrata* were collected in the field and kept in terraria with loamy sediment (from Ilha de Marchantaria) 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. punctata*, 1st and 2nd-instar larvae were collected at Ilha de Marchantaria and reared in the laboratory to the adult beetle in glass or plastic vials filled with moist sand also from Ilha de Marchantaria. All animals were kept separately in climatic chambers (12/12 h light/dark, temperature regime: 12 h 33°C and 12 h 28°C). Larvae of *P. cribrata* were fed three times a week with fruit fly larvae (1st instars: one fruit fly each) or termites (2nd and 3rd instars: 4–8 termites, depending on size). Larvae of *T. s. punctata* were fed three times a week, 1st instars with termites (4–8 termites, depending on size), 2nd and 3rd instars with raw 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 observation of the respective stage and the first of the following stage, including molting. The first observation usually took place after the new larval stage had opened up its tunnel or the beetle had emerged from the sediment. Duration of egg development was estimated by determining the minimum time interval between when a female beetle had been put into a terrarium and the first observation of hatched larvae.

Determination of submersion tolerance/resistance in adult beetles and larvae. Following Adis & Messner (1997) we distinguish between submersion tolerance (a few hours or days) and submersion resistance (several weeks or months).

In *P. klugii* and *P. lindemannae*, the duration of inundation larvae survived in the field was estimated by determining the lowest places along the altitudinal gradient at the study sites where 3rd-instar larvae reopened their tunnel 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 (pH: ~5.6; specific conductance: ~16 µSi/cm). The water was

boiled and then aerated at 29 °C prior to the experiments, 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 tested submersion tolerance in adult beetles of *Phaeoxantha* species and *T. spinosa* in the laboratory. Beetles collected in the field and kept 1–2 days without food were separately submerged in water (open glass beakers, approx. 250 ml, diameter 6.9 cm) using spherical strainers of metal gauze. Subsets of beetles were removed from the water at various intervals to determine survivorship. They were put on moist paper tissue and, if alive, resumed movement within a few hours or were otherwise scored as dead. Four or five beetles of each species were kept as control groups in identical strainers in a moist environment at 29 °C for the maximum interval tested.

Tolerance/resistance to submersion of 3rd-instar larvae was tested in two ways. Firstly, active larvae of *P. klugii*, *P. lindemannae*, *P. a. bifasciata*, and *T. s. punctata* collected in the field at various sampling dates and subsequently kept 2–5 days without food, as well as larvae of *P. klugii* that had entered a state of dormancy in the laboratory, were separately submerged in glass vials (volume 40 ml) filled with 30 ml of water. The vials were then sealed with plastic lids (plus a sheet of parafilm) and carefully placed upside down in a plastic container. The bottom of the latter was covered with approximately 2 cm of salad oil to reduce diffusion of atmospheric oxygen into the vials through the plastic lids. Subsets of larvae were removed 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 (= scored as survivors) 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 usually within a few minutes. As larvae continuously move around when removed from the sediment and not put into water, we used larvae kept in sediment without food as control groups (five to ten larvae in each species).

Secondly, submersion resistance was tested simulating natural conditions. We collected 3rd-instar larvae of *M. klugii*, *P. lindemannae*, and *P. a. bifasciata* in March-April of 1998 and 1999 and kept them separately in plastic vials (11 x 3 x 15 cm) for 2–4 weeks under normal rearing conditions (see above) in the laboratory. The containers were then gradually flooded from the bottom within approximately one week, allowing the larvae either to escape to the top or to adapt to the flooding conditions. In the tests performed in 1998, the water was poured into the containers filled with sand through vertical tubes that reached to the bottoms of the vials. In 1999, the bottom of the containers was perforated allowing several containers to be flooded together in aquaria. Larvae which came up to the surface when being flooded were dismissed. In larvae which stayed in the sediment 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 submersion period the sediments were checked for remaining traces 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).

Abbreviation. Lt_{50} = time to 50 % mortality

RESULTS

T. sobrina punctata. The nocturnal adult beetles were found along the waterline and at larval habitats from August until October (except for one beetle; Fig. 2a), i.e., first beetles occurred during or before the water receded from habitats of the larvae. Mature and non-mature females were present during all three activity periods, and no teneral beetles 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 gonad state (Fig. 3).

We were unable to observe the appearance of the first 1st-instar larvae. The first 2nd instars were observed in mid-August, first 3rd-instars at the end of August and beginning of September, about 2–3 and 4–6 weeks after the water had receded from the larval habitats (Marchantaria: 1997; Praia Grande: 1997, 1998 respectively). By mid-October, 2nd and 3rd-instar larvae dominated (Marchantaria and Praia Grande: 1997, 1998). In December, only few larvae were still observed, and no more larvae were found in early Fe-

bruary (1998, both sites). The duration until the 3rd larval instar was about one month in the field. The total duration of larval development in the field was about 3-4 months.

The duration of the 2nd and 3rd larval instars and the pupal stage under controlled conditions in the laboratory is shown in Fig. 4a. As with *Phaeoxantha* species reared from eggs laid in the laboratory (*cf.* Zerm & Adis 2000), larvae of *T. s. punctata* were continuously active, i.e., possible periods of inactivity were shorter than feeding intervals (1–5 days). The amount of time between the last observed activity of a given larval instar and the first observation of its next stage (including molting and the opening of a larval tunnel) was usually 1–2 feeding intervals (= 1–7 days).

Third-instar larvae were inactive for only 5–14 days before pupation (10 days on average, n = 10).

T. spinosa. The nocturnal adult beetles were observed in higher numbers in the inirial terrestrial phase (the presumed period of oviposition) along the waterline of the river, at larval habitats, and in between. The first beetles occurred shortly after the water had receded from habitats of the larvae (Fig. 2b). Unlike *T. s. punctata*, adult beetles of *T. spinosa* were active at beaches and occasionally at larval habitats through-out the entire terrestrial phase. Distribution of gonad maturity states in females showed no seasonal pattern (mature and non-mature females present during the entire activity period). Only one teneral beetle was found (female, 14. 12. 98). Fat bodies were only
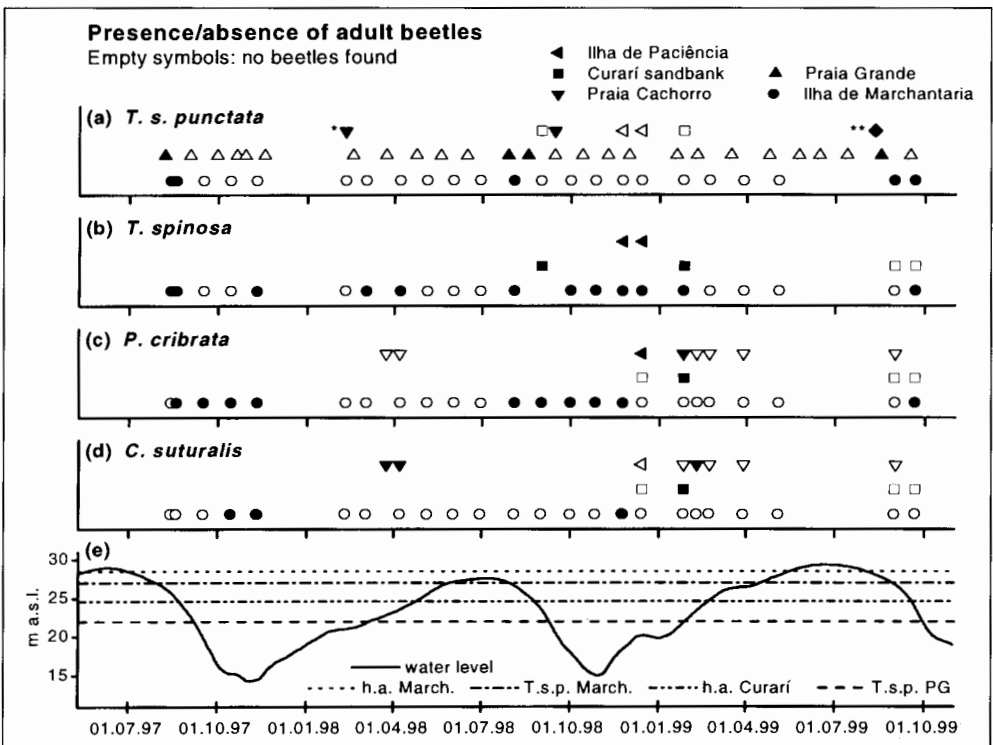

FIG. 2. Occurrence of adult beetles of *T. sobrina punctata* (a), *T. spinosa* (b), *P. cribrata* (c), and *C. suturalis* (d) at the study sites 1997–1999; (e) water level at Manaus harbor and highest altitude at study site on Ilha de Marchantaria (= h.a. March.), approx. altitude of habitats of larval *T. s. punctata* and *P. cribrata* at study site on Ilha de Marchantaria (= T.s.p. March.), highest altitude on Curarí sandbank (= h.a. Curarí), and approx. altitude of habitat of larval *T. s. punctata* at Praia Grande (= T.s.p. PG). * = one adult beetle in daytime under driftwood distant from the waterline. ** = one adult beetle at Sítio Bom Sossego, non-flooded upland.

found in August 1997 and September 1999 (4 our of 21 females, 11 out of 40 males). Presence of fat bodies in females was not significantly associated with the non-mature gonad states (Fig. 3).

Larvae were not observed continuously. Some 2nd-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. s. punctata*). The pupal stage lasted nine and eleven days (n = 2). Larvae were inactive for five and twelve days before pupation (n = 2).

P. cribrata. The diurnal adult beetles were found along the waterline of the rivers, at larval habitats during the period of oviposition, and at patches 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 activity period). No teneral beetles were found. 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-October 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 one month, the total duration of larval development at < 4.5 months or shorter.

Egg development in the laboratory took < 12 days. The duration of larval instars and the pupal stage under controlled conditions is shown in Fig. 4b. In another four specimens collected in the field as 3rd instars, the pupal stage lasted 8–12 days. As in *T. s. punctata*, larval *P. cribrata* were continuously active, i.e., possible periods of inactivity were shorter than feeding intervals (1–5 days). The time between the last observed activity of a given larval instar and the first observation of its next stage (including molting and the opening of a larval tunnel) was usually 1–2 feeding intervals (= 1–7 days).

C. suturalis. The diurnal 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 collecting dates, mature females only in March 1999), although specimens from 1997 were in bad shape at the time of dissection. No teneral beetles were 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 3rd and some 2nd 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 larval instars together was about one month.

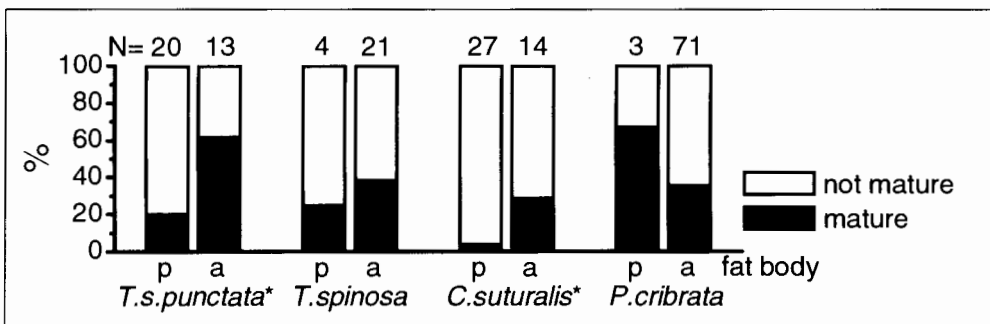

FIG. 3. Presence/absence of fat bodies in mature and non-mature females (p = present, a = absent). * = differences between groups significant (Fisher's exact test, a < 0.05).

Phaeoxantha species. Life cycles of these species were described in detail in Zerm & Adis (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. klugii* and *P. lindemannae*, probably also in *P. a. bifasciata* and possibly in *P. a. aequinoctialis* and *P. limata*. Life span of the nocturnal adult beetles was estimated at only a few months, except for *P. a. bifasciata* at > 6 months. No fat bodies were observed in field material of *Phaeoxantha* species (number of dissected specimens: *P. klugii*: 729, *P. lindemannae*: 304, *P. a. bifasciata*: 627, *P. a. aequinoctialis*: 57, and *P. limata*: 164). However, freshly hatched beetles from larvae reared in the laboratory often showed large fat bodies (*P. klugii*: 9 out of 11 , *P. lindemannae*: 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).

Oviposition and 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. 5). In all species/subspecies reared from eggs in the laboratory (*Phaeoxantha* spp. and *P. cribrata*), several (up to 15, sometimes more) larvae often hatched simultaneously. Maximum number of eggs laid by one female in the laboratory was 24 in *P. a. aequinoctialis*, 13 in *P. cribrata* and *P. lindemannae*, and 35 in *P. klugii*.

In the field few ovipositions were observed in *P. a. bifasciata*, all of them in moist sand about 1–2 m above the waterline of the river. New 1st-instar larvae of *P. klugii* and *P. lindemannae* were often found in the field in smaller patches of high density. Occasionally 10–15 1st instars were found clearly clustered around the tunnel of a still unhatched 3rd-instar larva of the preceding generation (within a radius of 10–15cm).

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 twelve 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 larval *P. a. aequinoctialis* during rising water levels resembled that of *P. a. bifasciata*, indicating similar larval mobility.

Submersion resistance of larvae in the field. In *P. klugii* and *P. lindemannae*, larvae (mostly 3rd instars) were observed to open up their tunnel after the aquatic phase had ended. Among hundreds of larvae observed in 1997, 1998, and 1999 the maximum duration of inundation survived was at least 106, 99, and 94 days in *P. klugii* and 150 and 124 days in *P. lindemannae* respectively (in the latter not determined in 1999).

No direct evidence was found in the field for larvae of *P. aequinoctialis bifasciata* surviving the aquatic phase submerged in the soil. However, several observations indirectly indicate larval submersion resistance in this subspecies as well:
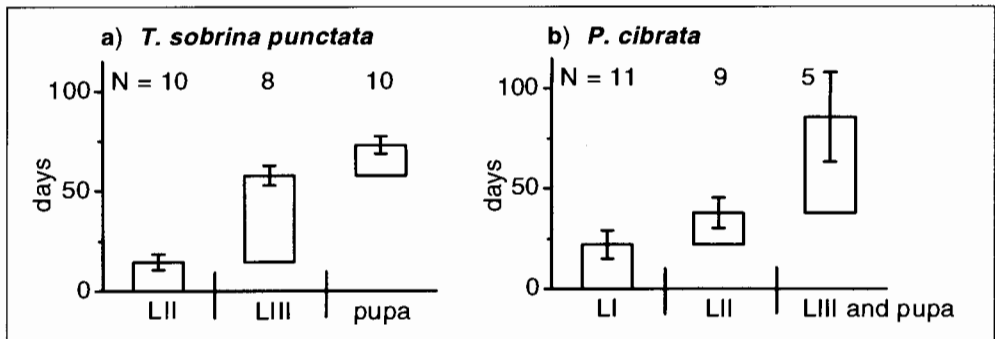

FIG. 4. Duration of larval instars and pupal stage (means and s.d.) under laboratory conditions (see text). a) *T. sobrina punctata*: without 1st larval instar; larvae collected in the field and subsequently reared in the laboratory. b) *P. cribrata*: reared from eggs laid in the laboratory. LI - LIII: 1st–3rd larval instars. N = number of specimens.
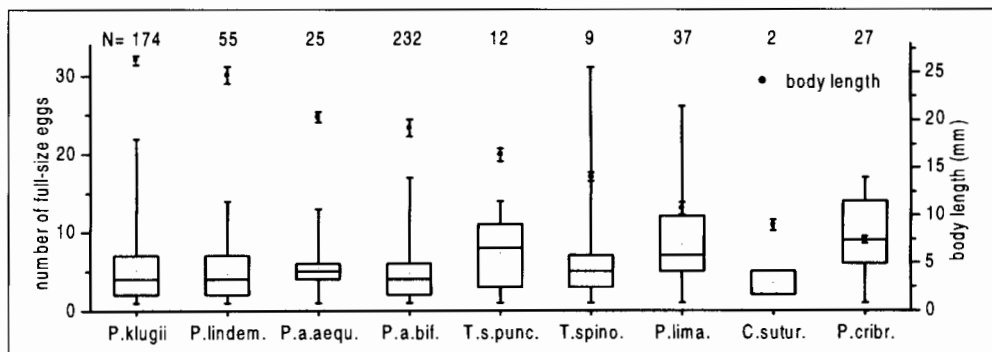
FIG. 5. Median total number of full-size eggs in gonads of mature females (N = number of specimens; box: median and interquartiles, whiskers: min and max) and body length (means and s.d., *P. klugii*, *P. lindemannae*, *P. a. aequinoctialis*, and *P. a. bifasciata*: each n = 10, others: each n = 5). Species sorted by body length. For definitions and species names: see text. Body length data derived from Zerm & Adis (2001b).

- The first adult beetles of the new generations appeared immediately after the water level peaks.
- Few active larvae were present on the remaining non-inundated parts of the river bank before the water level peaks (May-June), i.e., decreased densities of active larvae at these localities indicating dormancy in larvae.
- During falling water levels, 3rd and 2nd-instar larvae were repeatedly found at positions along the flooding gradient which were still inundated 1–3 weeks prior to the observations, although larvae were never observed running on the surface during these periods.
- In August 1999, 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 teneral, and lacked flight muscles.

Habitats of *P. a. aequinoctialis* were completely inundated every year. Larval tunnel openings were not found immediately after the aquatic phase and adult beetles showed no flight muscles.

Submersion tolerance/resistance of larvae and adult beetles in the laboratory. In laboratory tests, adult beetles of *P. klugii*, *P. lindemannae*, *P. aequinoctialis* ssp., *P. limata*, and *T. spinosa* survived only 5–10 hours of submersion (Fig. 6; survival rates in control groups: 100 %). Maximum survival of active 3rd-instar larvae submerged in water differed between species, ranging from $\geq 1 < 1.5$ to $\geq 6 < 10$ days (*P. a. bifasciata* and *P. lindemannae*). Lt$_{50}$ varied from 0.77 (*P. a. bifasciata*)

to 3.18 days (*P. lindemannae*), 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. klugii* was >15 days (Fig. 7).

When gradually flooded in the laboratory, 60 out of 71 and 29 out of 42 3rd-instar larvae of *P. klugii* and *P. lindemannae* respectively did not come up to the surface. Maximum survival submerged in sediment was >3 months in both species (Fig. 8). The blackwater species *P. lindemannae* seemed to be more resistant than *P. klugii* from the whitewater areas, a result which is consistent with the field data. Surviving larvae in 1998 (6 *P. klugii* and 12 *P. lindemannae*) did not open up their tunnel after the end of submergence but pupated directly instead. Testing the submersion resistance in gradually submerged larval *P. a. bifasciata* failed because all larvae (n = 12) came up to the surface during the flooding process.

Sex ratio. In adult *P. klugii*, males were significantly more frequent in pitfall traps 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 manual sampling along the waterline (only catches with > 7 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.
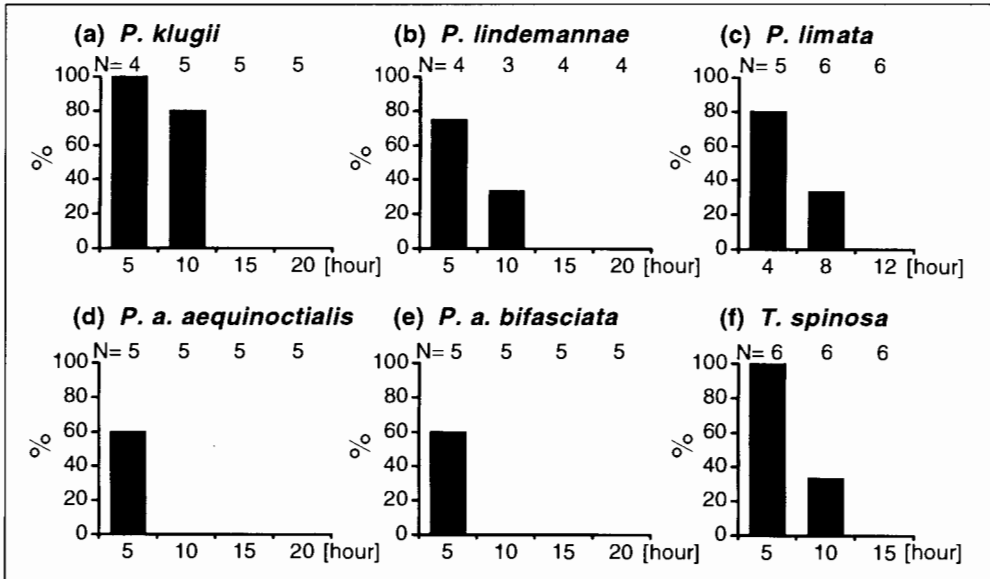
FIG. 6. Survival rates of adult beetles submerged in water in the laboratory (29°C). N = number of specimens.

The sex ratio in adult *P. lindemannae* from pitfall 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 pitfall traps than females (Fig. 9). Females were significantly more frequent in the total manual catch (n = 750). On nine out of 29 dates of manual sampling (only catches with > 7 beetles), females beetles 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 (ten 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. punctata* (Praia Grande: n = 43, Ilha de Marchantaria: n = 38), *C. suturalis* (n = 100), and *P. cribrata* (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. cribrata*: n = 15, *T. s. punctata*: n = 10) or females were significantly more frequent (*P. klugii*, n = 74). No data are available for *T. spinosa* and *C. suturalis*.

Prey spectrum. The nocturnal adult beetles of *P. klugii*, *P. lindemannae*, and *P. a. bifasciata* were regularly observed to prey on Grylloidea (predominantly Eneopteridae: *Hemygryllus* sp., det. Dr. L. Desutter-Grandcolas), juvenile Gryllothalpidae (predominantly *Scapteriscus oxydactylus* and *Scapteriscus* sp. 2, det. Dr. L. Desutter-Grandcolas), and lycosid spiders. They readily fed on mayflies (Ephemeroptera: Polymitarcyidae: *Campsurus* and *Asthenopus*, det. Dr. M. Sartori) stranded in large numbers along the beaches during occasional mass emergence events. At forest edges

(blackwater study site), adult beetles of *P. lindemannae* were observed to prey on smaller cockroaches (Blattodea). Adult beetles of *P. klugii*, *P. lindemannae*, *P. a. bifasciata*, and *T. s. punctata* were occasionally seen on and around dead fish at the waterline.

Predators and parasites. Elytra of *P. klugii* and *T. s. punctata* were found in three regurgitations of birds in September 1997 on Ilha de Marchantaria (presumably of migrating waders, cf. Stotz *et al.* [1992]). Fire ants (*Solenopsis* spp.) were sporadically observed to

feed on dying adult beetles of *P. klugii* (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 "worm-like" animal (about 3–4 mm long, possibly a larval bombyliid fly ?) attached to the abdomen (these animals were lost thereafter). We found no indications of Tiphiidae (Hymenoptera) parasitizing larval tiger beetles. Among > 2500 adult beetles dissected in the
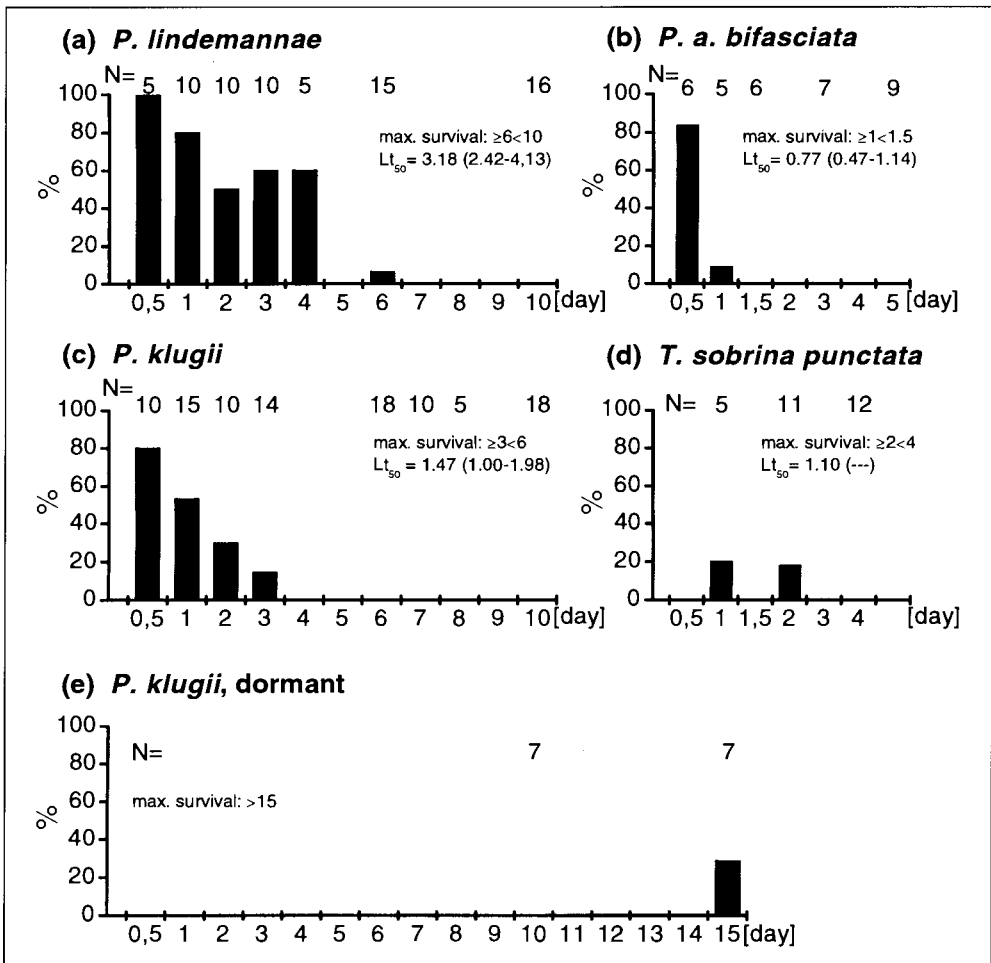

FIG. 7. Survival rates of active and dormant 3rd-instar larvae submerged in water in the laboratory (29 °C). Maximum days survived and Probit estimates of Lt_{50} (with 95 % confidence intervals, calculated including control groups) are shown. (a)–(d): active larvae, (e): dormant larvae. For details see text.

laboratory we found a few specimens infested with presumably horsehair worms (Nematomorpha). Most adult beetles of *Phaeoxantha* species (79 %, n = 1837) were infested with yellow larval mites (Trombiidae [Acari], possibly *Hexathrombium*, det. Cal Welbourn). Larvae were often infested by similar mites as well (*P. klugii*, *P. lindemannae*, and, occasionally, *P. a. bifasciata*). Both adult and larval specimens infested with mites had brown scars at the areas affected. In adult beetles of *P. a. bifasciata*, 18% of males and 29 % of females (n = 282 and 345) were found to be infested with a fungus species representing *Laboulbenia* (Ascomyceta: Laboulbeniales) (Arndt & Zerm unpubl.).

DISCUSSION

Methods to determine life cycles. Larvae of most species (exceptions: *P. klugii* and *P. lindemannae*, Zerm & Adis 2000) were not continuously followed at observation plots in the field for various reasons. Larvae of *T. spinosa*, *C. suturalis*, and *P. a. aequinoctialis* 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. limata* were not found at all. In *T. s. punctata* and *C. cribrata* larval habitats are hardly accessible at the start of the 1st-instar stage due to the very moist loamy sediment. Traceability of larval tunnel openings in *P. a. bifasciata* is very limited and ex-

tremely dependent on weather conditions (larval habitat on open, 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 expected to reach gonad maturity more quickly. It is unknown whether any full-size egg remains in the ovaries of mature females after egg deposition. Thus females collected in the field with gonads classified as "maturing" might have been mature beetles that had laid all full-size eggs prior to capture. Similar problems were found in *Phaeoxantha* species and in carabid beetles from Central Amazonian floodplains (Adis *et al.* 1986, Zerm & Adis 2000).

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

T. s. punctata. 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 Marchantaria, or on
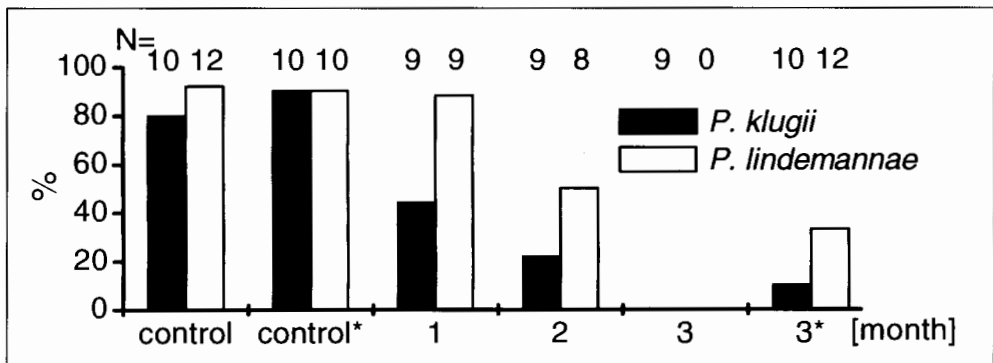

FIG. 8. Survival rates of 3rd-instar larvae submerged in sediment in the laboratory in 1998 (29°C); for details see text. Control: larvae kept in sediment at 28/33°C (see text). * = experiment repeated in 1999: flooding procedure slightly different and survival detection more sensitive (see text).
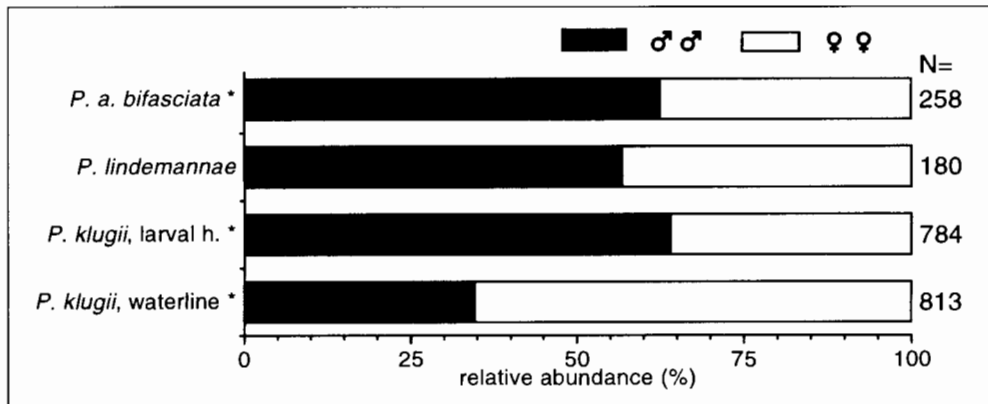
FIG. 9. Sex ratio in pitfall traps. N = number of specimens, larval h. = habitat of larvae, * = ratio differing significantly from 50:50 % (binomial test, two-tailed, $\alpha < 0.05$). The sex ratio in *P. klugii* at the two habitat types is significantly different (Fisher's exact test, $\alpha < 0.05$).

floating vegetation, driftwood, and in the canopy region of inundation forests (Adis 1982, Ribeiro *et al.* 1996, Adis & Messner 1997, Adis *et al.* 1998). In this study we even found one female specimen (non-mature and with fat body) on non-flooded uplands (*terra firme*).

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 teneral beetles were not found at all. The duration of the 2nd and 3rd instar, as well as the pupal stage in the laboratory, was about 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 this study would also amount to around 3 months, i.e., our field data are in good agreement with both laboratory rearings. 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 & Messner (1997) for '*Megacephala sobrina punctata*' refers to *P. a. bifasciata*.

From the field data, life span of adult beetles was estimated at ~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 carabid species (Paarmann & Stork 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 state 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. spinosa. 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 gonad dormancy, see *T. s. punctata*) only at the beginning of the terrestrial phase; 3) presence of immature and teneral 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 built up fat bodies.

More information is needed to confirm our interpretation 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. cribrata. Results on adult and, in particular, larval 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 end of the larval phase was monitored less intensively and teneral beetles were not found at all. Immature beetles in December/January were considered as belonging to the new beetle generation. The total duration 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 larval habitats after the water level begins to fall, together with the phenomenon that beetles are still present on the beaches after the larval phase, led to the assumption that adult beetles survive the inundation period at still unknown localities. The life span of adult beetles was therefore estimated at ~9 months and longer. Due to the long high water period one has to expect a gonad dormancy in this species as well, despite the rarity of fat bodies found in this study.

C. suturalis. Field data on larval phenology are scarce and that on adult phenology is rather unclear. 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 observations point indirectly to an annual life cycle with a short larval phase during the terrestrial phase and adults surviving the aquatic phase: 1) larvae observed in October 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 bodies and their significant association with non-

mature gonad states (indicating gonad dormancy, see *T. s. punctata*). Evidently, further information is needed to clarify the details of the life cycle. Adult phenology found here is only in part consistent with Freitag & Barnes (1989), who reported adults occurring in February, May, June, September, and October for the whole of Brazil.

Phaeoxantha species. Life cycles of *Phaeoxantha* species are characterized by a long larval phase (including submersion resistance in larvae, see below) and a short or long adult phase. Larvae enter a state of dormancy towards the end of the 3rd instar (shown for some species, suspected in others) (Zerm & Adis 2000). In contrast to the species described above, adult beetles completely lacked fat bodies (> 1900 specimens dissected), a trait which is likely to be related to this specific type of life cycle. The presence of fat bodies in adult *Phaeoxantha* beetles newly hatched in the laboratory remains elusive as comparative data from other species are not available.

Ontogeny and life cycle. Duration of egg development in *P. cribrata* (< 12 days) is in good agreement with data for *Phaeoxantha* species (Zerm & Adis 2000), *T. s. punctata* (Ribeiro *et al.* 1996), and tiger beetles in general (Pearson 1988), although some authors reported longer periods (Faasch 1968, Palmer 1976a).

Mean duration of the pupal stage of *T. s. punctata* was almost identical to results obtained by Ribeiro *et al.* (1996) (15.3 vs. 14.3 days). Moreover, the duration in the three species studied here, with a range of 10–15 days (*T. spinosa, P. cribrata, T. s. punctata*), was similar to *Phaeoxantha* spp. (Zerm & Adis 2000) and *Pentacomia ventralis* (from *terra firme* uplands near Manaus; Paarmann *et al.* 1998), but shorter than in species from temperate and subtropical regions (18–22 days; Willis 1967, Faasch 1968) and in a species from Costa Rica (Palmer 1976a). This adds further evidence that differences might be a result of different temperatures experienced by the pupae.

The 3rd instar represented the longest larval stage in the laboratory in both *T. s. punctata* and *P. cribrata*, which follows the general pattern in tiger beetle larvae (*cf.* Willis 1967, Palmer 1976a, Hori 1982, Pearson 1988, Amorim *et al.* 1997a, Paarmann *et al.* 1998, Zerm & Adis 2000).

The total duration of larval development as derived from the current data (shown for *T. s. punctata* and *P. cribrata*, suspected for *T. spinosa* and *C. suturalis*) was 3–4 months. Adis *et al.* (1998) reported 4 months in *C. suturalis* for the pre-adult stages in the

laboratory. Apart from the latter, similarly short durations for larval development were only known for species inhabiting floodplain forests in the Manaus region (*Pentacomia egregia*, *P. lacordairei*, and *Odontocheila confusa*; Amorim *et al.* 1997a, Adis *et al.* 1998). In contrast, *Phaeoxantha* spp. and species from *terra firme* uplands near Manaus (*Pentacomia ventralis* and probably five further species) have a long larval phase of 7–14 months (Paarmann *et al.* 1998, Zerm & Adis 2000). In *Pseudoxychila tarsalis* from a premontane rainforest in Costa Rica, the larval phase takes around 9 months (Palmer 1976a), whereas larval development in tiger beetles from subtropical and temperate regions usually lasts 1–4 years (Shelford 1908, Willis 1967, Faasch 1968, Pearson 1988, Simon-Reising *et al.* 1996).

The life span of adult beetles varies according to the type of life cycle. Species with adult beetles surviving the inundation period (*T. s. punctata*, *T. spinosa*, *P. cribrata*, *C. suturalis*) must be expected to live ~9 months and longer (which presumably includes a gonad dormancy in both sexes). In species with larvae surviving the inundation period (shown or presumed for *Phaeoxantha* spp., see below) adult life span is a few months only (exception: *P. a. bifasciata* with a long life span in adults also; *cf.* Zerm & Adis 2000). In floodplain forest species, adult females survive the inundation period and therefore their life span is long (*Pentacomia egregia*, *P. lacordairei*, *Odontocheila confusa*; ranging from about 8 to 14 months including a period of gonad dormancy as shown for *P. egregia* and suspected for the others; Amorim *et al.* 1997a, Adis *et al.* 1998). Other data on the adult life span in tropical tiger beetles are scarce. The adult phase of *Pseudoxychila tarsalis* from Costa Rica (Palmer 1976a) and *Pentacomia ventralis* (from an upland forest near Manaus) was about three months; the beetle phenology of another three species from the latter site suggested adult life spans of about five months (Paarmann *et al.* 1998). Adult life span in *Cicindela* species from temperate and subtropical regions was also found to be either only a few months (in beetles emerging during summer and dying off before winter) or 6–8 months (in hibernating adults emerging in fall) also with an active, i.e., reproductive phase of only few weeks (Willis 1967, Simon-Reising *et al.* 1996).

As a preliminary conclusion, a short larval phase of 3–4 months and a long adult life span including gonad dormancy seem to represent a specific life history adaptation to the annual flood pulse. Studies on life cycles in related species, in particular from the tro-

pical regions, are needed to substantiate this emerging picture.

Oviposition and egg numbers. The number of full-size eggs in the gonads of mature females varied strongly intraspecifically and less so interspecifically. Smaller species tended to have more eggs, although interquartiles overlapped widely (Fig. 5).

The considerable number of full-size eggs in the gonads of many females, as well as frequent simultaneous hatching of several 1st-instar larvae from eggs laid in the laboratory, indicate that female beetles oviposit several eggs at a time. The large intraspecific variation in the number of full-size eggs, and the relation of these numbers to the maximum number of eggs laid in the laboratory (in *P. klugii*, *P. lindemannae*, and *P. a. aequinoctialis*), suggest a rather continuous egg production (and repeated/continuous oviposition) which is consistent with most of the literature. Hori (1982) noted continuous egg production and oviposition of various numbers of eggs per day in *Cicindela japonica*. Females of *Cicindela cancellata* oviposited up to approximately 40 eggs within < 4 weeks and groups of larvae eclosed simultaneously (Shivashanker & Veeresh 1987). Female *Pseudoxychila tarsalis* laid eggs continuously in the laboratory, in total up to 137 within ten weeks (Palmer 1976a). Pearson & Knisley (1985) reported mean numbers of 1st-instar larvae from eggs laid in the laboratory of about 45 per female in *Cicindela obsoleta* and about 40 in *Cicindela nigrocoerula*. Amorim *et al.* (1997a) observed a maximum of 27 eggs deposited by one female *Pentacomia egregia*. On the other hand, Shelford (1908) reported watching a *Cicindela purpurea* lay about 50 eggs, adding that females probably lay one batch of eggs only.

In *P. klugii* and *P. lindemannae*, clusters of several 1st instars around a 3rd instar of the preceding generation suggest a possible mechanism how adult females might select appropriate places for oviposition. The older larvae (which survived the last inundation period) might serve as an indicator of an appropriate oviposition site because these have to be located at high levels along the altitudinal gradient (to reduce duration of inundation) and altitude does not correlate with other apparent factors potentially useful for site selection (sediment type, general soil moisture, vegetation structure; *cf.* Zerm & Adis 2001b). This might also explain the generally patchy distribution of larvae at the local scale in both species, which has already been reported in previous studies for *P. klugii* (Adis *et al.* 1998, Zerm & Adis 2001b).

Submersion resistance/tolerance of larvae and adult beetles. Larvae of *P. klugii* and *P. lindemannae* were highly resistant to submersion in the field (> 3–4 months). Indirect evidence suggests submersion resistance also in *P. a. bifasciata* and, possibly, in *P. a. aequinoctialis*. The lack of observations of larval *P. aequinoctialis* ssp. re-opening their tunnels after the inundation does not necessarily mean that larvae were not present. For example, larval *P. klugii* and *P. lindemannae*, submerged for 1–3 months in sediment in the laboratory, did not re-open the tunnel entrance but pupated directly. No data are available on submersion tolerance/resistance in larval *P. limata* as their habitat is still unknown.

The behavioral reaction to rising water levels in the laboratory in most larval *P. klugii* and *P. lindemannae* was similar to that observed in the field: larvae stay in the sediment and apparently react to the rising water level by increasing their digging activity before actively closing their tunnel entrance. In contrast, larvae of *P. a. bifasciata* 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 Adis *et al.* (1998) (due to misidentification assigned to '*Megacephala sobrina punctata*'). As several observations indicate that larval *P. a. bifasciata* do survive inundation, we propose the following hypothesis: reaction of larvae 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 triggered by some external factors. Other larvae, not yet "ready" for dormancy, might escape from rising water levels to higher localities to keep on feeding. Additionally, or alternatively, one should expect that larvae located primarily in low positions along the altitudinal gradient might always move up to higher places prior to entering a state of dormancy. Larvae reared in the laboratory did not enter a state of dormancy prior to pupation (Zerm & Adis 2000) which might be explained by the lack of external triggers due to the uniform rearing conditions.

Submersion 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 [elsewhere] survive the inundation 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 larval *P. klugii*, *P. lindemannae*, and *P. a. bifasciata* were not higher in preliminary tests using a buffer solution (0.1 M Theorell-Stenhagen buffer). Furthermore, the specific conductance of the water used in experiments was lower only compared to riverine water of the Rio Solimões (whitewater) but similar to water from the Rio Negro (blackwater) (*cf.* Furch & Junk 1997). The low tolerance values are apparently also not due to the decreasing oxygen concentrations in the closed vials, as survival rates in larval *P. klugii* and *P. lindemannae* tested preliminarily in deoxygenated water, as well as in pure nitrogen atmosphere, were similar or higher (Zerm & Adis unpubl.; see below).

Field data on submersion resistance in *P. klugii* and *P. lindemannae* contrast strongly with the low tolerance in active larvae in the laboratory. Larvae of *P. klugii* that had entered a state of dormancy in the laboratory, and were taken from the sediment and submerged in water, showed a maximum resistance of > 15 days. Thus dormancy seems to enhance submersion resistance. However, the high mortality makes dormancy alone unlikely to ensure survival of > 3 months in the field. On the other hand, laboratory experiments in which larvae of *P. klugii* and *P. lindemannae* were gradually submerged within their sediment resulted in resistance values similar to the field data.

Submersion resistance of > 3 months at 29–30 °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 (1885) stated that hibernating *Cicindela repanda* survived flooding for seven days. Wilson (1974) reported surviving larvae after three weeks of inundation in *Cicindela purpurea*. The only experimental laboratory data available hitherto are provided by Hoback *et al.* (1998), who found maximum survival in larval *Cicindela togata* of $\geq 6 < 7$ days at 25 °C (Nebraska/USA). Some authors presumed that submerged larvae breath air trapped in their closed tunnels (Willis 1967, Pearson 1988), which could explain the differences between larvae submerged with and without sediment in the present study. This possibility cannot be ruled out, at least in the fine whitewater sediments (*cf.* Zerm & Adis 2001b). However, although direct observations inside the larval tunnel during inundation are still lacking, this explanation seems rather unlikely because flooding occurs gradually from underneath and structures that could trap air inside the tunnel (such as a dome-shaped cavity)

were not observed in larvae submerged in the laboratory. And even if air was trapped inside the tunnel, it seems unlikely that oxygen could be available for extended periods of time due to the organic content of the soils and the low oxygen concentration in the water body (see below).

From the data at hand we conclude that the extent of submersion resistance in active larvae is not related to the life cycle type. Submersion resistance of a few days might be a general trait in soil-dwelling animals such as tiger beetle larvae, enabling them to withstand short-term inundation caused by rainfall or short flooding events in swamps or floodplains (*cf.* Hoback *et al.* 1998, 2000; Hoback & Stanley 2001). Dormancy does increase submersion resistance, although 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 future situation beyond pure dormancy. Future research focussing on larvae during this particular period 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 mechanisms underlying and limiting submersion resistance.

Independent of the exact circumstances determining the extent of submersion resistance in larval *P. klugii* and *P. lindemannae*, one has to expect larvae surviving several months submerged in the soil to be highly resistant also against hypoxic or anoxic conditions because flooded soils quickly become anoxic (Baumgärtl *et al.* 1994). This is also indicated by the low oxygen content in river water above inundated floodplain soils in Central Amazonia (Adis & Messner 1991). *Cicindela togata* (Nebraska/USA) survived several days in anoxia at 25°C (and longer at lower temperatures; Hoback *et al.* 1998, 2000). Unlike the hypotheses in Hoback & Stanley (2001), preliminary data from laboratory experiments with larval *P. klugii* indicate an exceptional anoxia resistance (Zerm & Adis unpubl.).

Adult beetles of *Phaeoxantha* species and *T. spinosa* tested in the laboratory were not resistant to submersion (tolerance of < 10 or < 15 hours). This is consistent with Adis & Messner (1997), who reported maximum survival times of 2–18 h in *P. klugii*, *T. spinosa*, and other species from floodplains and *terra firme* uplands, although experimental conditions were slightly different (20°C, non-aerated water). Due to their low submersion tolerance we conclude that the species tested in this study lack the diving ability described for *T. s. punctata* (Adis *et al.* 1993, Adis & Messner 1997, Adis *et al.* 1998). We found no indications of quiescent adult beetles of *T. s. punctata* surviving inundation in individual burrows along vertical river banks, as reported for '*Megacephala sobrina*' from Costa Rica (Wille & Michener 1962). Data on submersion tolerance in adult tiger beetles of other species and in other parts of the world are not available. Only Hoback *et al.* (1998) stated that adults were unable to survive immersion (*Cicindela togata*).

Sex ratio. Sex ratios in field samplings from a given site represent either the true ratio in the population, a ratio biased by sex-specific traits (such as differing mortality or dispersal capacity), or might represent a ratio influenced by the sampling method itself. Alternatively, sex ratios might indicate sex-specific behavior or habitat-use, i.e., they could give information on the function of microhabitats within the species' total habitat. Here we assume a 50:50 % ratio as the true proportion of the sexes in the populations under study.

Higher proportions of females at the waterline, and of males at larval habitats in *P. klugii*, 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 production whereas males might increase their mating success by staying at larval habitats to which females must return for oviposition. Correspondingly, frequency of flight ability (facilitating the use of the waterline) is higher in females than in males (Zerm & Adis 2001a). The lack of such site-specific sex ratios in the other species investigated might be due to the spatial distinctness in *P. klugii* of the larval habitats (used by both larvae and adults) and the temporary waterline (used by adult beetles only). In the other species, habitat use in adults is spatially indistinct (*P. cribrata*, *C. suturalis*, *T. spinosa*, *T. s. punctata*), adult and larval habitats adjoin each other (*P. aequinoctialis* spp.), or larval habitats, although also distant from the waterline, are spatially rather punctual or linear, therefore impeding a greater number of beetles being caught at these localities (*P. lindemannae*) (Zerm & Adis 2001b). Whether the female-biased ratio in *P. klugii* hatched in the laboratory really represents the true ratio of the population/species needs further investigation, as field data do not support these findings.

Male-biased ratios in samplings of *P. a. bifasciata* from pitfall traps might reflect a higher running activity in males which, in turn, might have led to female-biased ratios at the same locality in manual samplings (lower running activity certainly facilitates manual sampling).

Reasons for higher proportions of males in *P. lindemannae* and *T. spinosa*, and of females in *P. a. aequinoctialis*, remain unclear.

Prey spectrum. From our observations on the nocturnal adult beetles it appears that they generally feed on soft-bodied invertebrates (the larger species possibly also on harder animals), which is in agreement with Adis *et al.* (1998). Data on the prey spectra were not sampled systematically. Thus many prey species might have been missed. In the nocturnal species, gathering quantitative data on potential prey is hampered by the high abundance of adult tiger beetles relative to potential prey specimens, which virtually impedes the use of passive sampling techniques to determine prey quantity. We can assume that the low number of potential prey specimens is actually due to the high number of adult tiger beetles. This, in turn, leads to the assumption that adult tiger beetles 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 carrion (as reported for other species from Arizona/USA; Pearson & Mury 1979) remains open, as they might also have been hunting real carrion feeders or using carcasses as hiding places. Preliminary experiments with fresh and rotten beef in the field suggested that they do not accept carrion (Zerm & Adis unpubl.). But even if they did, carrion is too rare at the study sites as to represent a significant food resource for the beetles.

Adis *et al.* (1998) provided data on prey species: adult *C. suturalis* were observed to prey on adult *Hydrochasma* (Ephydridae, Diptera), and adult *P. klugii* on *Hemigryllus* (Eneopteridae, Gryllidae) as confirmed by the present study. Adults of species from floodplain forests are reported to prey on adult Diptera (Ephydridae and Culicidae) (Adis *et al.* 1998).

We rarely observed larvae in the field catching prey. Preliminary laboratory observations, however, indicate that they feed on a broad spectrum of invertebrates (Zerm & Adis, unpubl.). These observations of apparently unspecialized feeding habits in adults and larvae are consistent with the general pattern reported for adult and larval tiger beetles.

These indicate that prey size is the main differentiating factor (Friederichs 1931, Willis 1967, Palmer 1976a, Pearson & Mury 1979, Hori 1982, Pearson 1988; see also Mury Meyer 1987, and Mizutani & Yoh 1998).

Predators and parasites. Quantitative data on predation rates on adult and larval tiger beetles in Central Amazonian floodplains are not available. Adis *et al.* (1998) already reported on nocturnal wading birds as predators of adult *P. klugii* and *T. s. punctata*.

Cannibalism observed in *P. klugii* was probably related to the exceptionally high beetle density in August 1998. In the laboratory, adult beetles have to be kept apart to avoid cannibalism.

Tiphiidae (Hymenoptera) parasitizing on larval tiger beetles were not searched for systematically, which might explain the lack of observations. Alternatively it might indicate that they are either absent or at least not frequent at the study sites. This would be in contrast to studies from other parts of the world (Williams 1928, Wilson & Farish 1973, Palmer 1976b, Hori 1982, Knisley & Pearson 1984, Knisley 1987, Pearson 1988, Knisley *et al.* 1989), and in particular to observations at a rainforest site near Manaus where Tiphiidae contribute to the high mortality rates (97–99 %) among 2nd and 3rd larval instars of five species (Paarmann *et al.* unpubl.). Their probable absence/rarity in this study might be due to habitat properties (they possibly do not occur in floodplains or in open areas in floodplains) or to the generally greater size of *Phaeoxantha* and *Tetracha* species larvae (Paarmann, pers. comm.).

The presence of scars on the cuticle of adults and larvae infested with larval mites indicates the mites' parasitic nature. Infestation rates are high but the extent of damage in the hosts is unknown. Willis (1967) collected adult *Cicindela circumpicta* (Oklahoma/USA) heavily infested with an unidentified *Eutrombidium* (Trombiidae) which he claimed to be an "accidental" infestation. Welbourn (1983, cited in Knisley 1985) reported on two trombiid species from adult tiger beetles. Knisley & Pearson (1981) and Knisley (1985) reported on a pygmephorid mite (*Trochometridium tribulatum*) infesting larval tiger beetles (two *Cicindela* species, Arizona/USA). The latter study also found hypopodes of *Sancassania* sp. on both larvae and adults of one *Cicindela* species. For both mite species they proposed a phoretic nature of the mite-tiger beetle association.

The infestation of *P. a. bifasciata* by parasitic Laboulbeniales fungi is the first well-documented record for tiger beetles worldwide (Arndt, 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 here (Zerm *et al.* 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 inhabited biotope, will be termed "adaptations" (according to Schaefer 1992, *cf.* also "nonhistorical" definitions in Reeve & 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 "predisposition" (Weigmann & Wohlgemuth-von Reiche 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 & Messner 1997). However, quantitative studies to test the adaptive nature of the characters in question (*cf.* Reeve & Sherman 1993, Rose 2001) still 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; Chapleau *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 harsh environments (e.g., annually long-term inundated areas), as extreme conditions are likely to limit the number of potential 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 (Zerm & Adis 2000, 2001b; Zerm *et al.* 2001; *cf.* Junk *et al.* 1989). This agrees with other studies on tiger beetle species of Central Amazonian floodplain forests (Amorim *et al.* 1997a, 1997b; Adis *et al.* 1998). Several tiger beetle species studied at *terra firme* uplands near Manaus also showed annual, seasonal life cycles, yet they appeared to be driven by the annual precipitation pattern (Paar-

mann *et al.* 1998, Zerm *et al.* 2001). From the tropical realm, annual, seasonal life cycles have been reported for most tiger beetles species studied so far, also apparently driven by annual precipitation patterns (Palmer 1976a, 1981; Paarmann & Stork 1987; Stork & Paarmann 1992).

As shown above, a common feature of floodplain species is that life cycles are 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 "dormant stages under water in self-made retreats") or migratory (migrating by flight to dry places, mostly within the floodplain) (strategies 5 and a mixture of 2–3 in Adis 1997: Fig. 14.1). In addition to the differences related to the life cycles (phenological 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. klugii*, *P. lindemannae*, probably *P. a. bifasciata*, and possibly *P. a. aequinoctialis* and *P. limata* (Zerm & Adis 2000, 2001b). A characteristic trait is a long larval phase (phenological adaptation) with dormant 3rd-instar larvae surviving the inundation period submerged in the soil (submersion and hypoxia resistance; physiological adaptations). A series of other traits in both larvae and adults are required for this type of strategy. For example, gonad maturation has to be rapid to ensure larval development to the 3rd-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. klugii* and *P. lindemannae*, ethological adaptation), or larval mobility must be high (*P. a. bifasciata*, ethological adaptation) (see Zerm & Adis 2001b). Other typical traits accompanying this strategy are: short adult life span (exception *P. a. bifasciata*), 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 (Zerm & Adis 2000, 2001a, 2001b).

The migratory type of survival strategy is well documented for *T. s. punctata*, 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 life span of adult beetles (both phenological adaptations) including gonad dormancy (physiological adaptation), and flight ability. A major ha-

bitat shift takes place during the adult phase (ethological adaptation). The extensive spatial separation of larval and adult habitats observed in these species (Zerm & Adis 2001b) is at least in part a consequence of this habitat shift. Adults of *T. s. punctata* appear to be even more specialized in having adopted an amphibious behavior (diving to hide under wate; ethological adaptation) enabled by several morphological characters enhancing the ability for air retention under water (morphological adaptation) (Adis & Messner 1997). Such amphibious behavior is also known for *Oxycheila polita* from floodplain sites in Costa Rica (Cummins 1992).

A similar type of migratory survival strategy was found in the three tiger beetle species inhabiting Central Amazonian floodplain forests (Amorim *et al.* 1997a, 1997b; Adis *et al.* 1998). Among ground beetles (Carabidae) only survival strategies of the migratory type have been found (Irmler 1979, Adis *et al.* 1986, Adis *et al.* 1990, Adis *et al.* 1997). The common life cycle pattern in Carabidae is a relatively short larval and a long adult phase, particularly in tropical species (e.g., Crowson 1981, Paarmann & Stork 1987, den Boer & den Boer-Daanje 1990, Stork & Paarmann 1992, Paarmann *et al.* 2001), whereas Cicindelidae generally show a contrary pattern (e.g., Willis 1967, Pearson 1988). From this general background one should expect migratory survival strategies in Carabidae inhabiting Central Amazonian floodplains to be most likely as they do not require major changes in life history traits. In Cicindelidae, on the other hand, life cycle traits related to non-migratory survival strategies would most closely resemble the general life history pattern of the family. However, the long inundation periods might have been too extreme to promote non-migratory survival strategies in more species. Instead, many species show migratory strategies, implying a major alternation of life history traits (short larval phase and long adult life span, habitat shift). More information is clearly needed on life cycles of related species as well as on phylogenetic relationships to reveal the origin (the phylogenetic descent and the selecting biotic/abiotic conditions) of the observed survival strategies.

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