# ON THE LIFE CYCLES OF *PHAEOXANTHA* SPECIES (COLEOPTERA: CICINDELIDAE) FROM CENTRAL AMAZONIAN FLOODPLAINS (BRAZIL)[1]

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*Abstract:* The life cycles of 4 of 11 tiger beetle species known to occur in open areas of Central Amazonian floodplains were studied during 1997–1999 in the Manaus region. Regular field excursions were undertaken over a period of 2 years to follow larval and adult phenology (one site in a whitewater area [*várzea*], another in a blackwater area [*igapó*]). Beetles collected in the field were taken to the laboratory for examination of gonad maturity. Additional larvae were reared under controlled conditions in the laboratory from egg to adult beetle. All species had annual life cycles. Larval development was studied in the field and laboratory for 3 species (*Phaeoxantha klugi, P. lindemannae,* and *P. aequinoctialis*). Duration of all developmental stages are given. Larval development in the laboratory was generally faster than in the field, ranging from 3,5 to >7 months depending on the species. In the field, larval development lasted between 7–10 and 10–14 months. A period of dormancy varying in duration was observed in 3rd-instar larvae before pupation. Because hatching of the new beetle generation was more synchronized than the distribution of the 3 larval instars, we presume that dormancy is used to adjust the populations to the seasonally changing environmental conditions imposed by a monomodal flood pulse. In *P. klugi* and *P. lindemannae,* larvae survived the inundation period submerged in the soil. The beetles that hatched thereafter had a short life span of only few months. Although the larval phenology is similar in *P. aequinoctialis,* adult life span was with >6 months extremely long. Data on the life cycle of the fourth species (*P. limata*) are scarce as larval phenology is still unknown. The type of life cycle with a long larval phase contrasts with other findings for floodplain species from the Manaus region, and is considered similar to patterns found in species from terra firme uplands as well as in subtropical and temperate regions. *Accepted 20 December 2000.*

*Key words:* Tiger beetle, life cycle, larval development, dormancy, seasonality, Amazon, inundation, Megacephala.

## INTRODUCTION

The Manaus region hosts a diverse tiger beetle fauna. Most species were found to be restricted to either open or forest biotopes of floodplains or *terra firme* uplands. Three out of 11 floodplain species are presently known to occur in forests, the others in open areas (Adis *et al.* 1998, Zerm & Adis unpubl.).

Terrestrial invertebrates living in the Central Amazon floodplain have to cope with an annual inundation period of several months (Adis 1992). Survival strategies of tiger beetles have been studied for a few species only (Paarmann *et al.* 1982; Irmler 1985; Adis *et al.* 1993; Ribeiro *et al.* 1996; Adis & Messner 1997; Amorim *et al.* 1997a, 1997b; Adis *et al.* 1998).

The life cycles of tropical tiger beetles have rarely been studied at all, in part certainly due to the lack of larval descriptions (*cf.* Pearson 1988, Putchkov 1994, Putchkov & Arndt 1994). Knowledge of the entire life cycle, however, is essential to understand the species' survival strategies, as larvae and adults of a given species might be temporally and/or spatially separated. It is also important within the context of species diversity and co-existence (*cf.* Linsenmair 1990, Paarmann *et al.* 1998).

This paper reports on the life cycles of 4 nocturnal *Phaeoxantha* species, studied in the field and laboratory, that commonly occur along river beaches in Central Amazonia. The main questions were whether these species would have an annual life cycle, whether there would be a dormancy involved in adjusting the life cycle to the temporal pattern imposed by the flood pulse, and whether the duration of larval development would differ intra- and interspecifically under controlled conditions in the laboratory and in the field.

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Data on the life cycles of the other species from open floodplain areas, as well as details on the habitats of larvae and adults, their submersion tolerance or resistance (cf. Adis & Messner 1997), as well as a comparison of the biology and survival strategy of all species will be published elsewhere.

## MATERIAL AND METHODS

*Study sites.* Field studies were carried out in white- and blackwater floodplains near Manaus from 1997 to 1999. The blackwater study site, locally called "Praia Grande", was part of a beach that stretches over several kilometers along the right bank of the Rio Negro, approximately 40 km upstream from Manaus (3°01'59" S, 60°32'35" W). The whitewater study site was situated at the southern beach of Ilha de Marchantaria (cf. Adis et al. 1998), the first island in the Rio Solimões (Amazonas) upstream of the confluence with the Rio Negro (3°14'34" S, 59°53'43" W). Other places visited were: a beach on Ilha da Paciência in the Rio Solimões (Amazonas), some 40 km upstream from Manaus (3°19'21" S, 60°11'16" W), and a sandbank in the Rio Solimões (Amazonas) between Ilha de Marchantaria and Ilha de Curari, only a few years old, referred to as "Curari sandbank" (3°15'40" S, 59°55'50" W).

All sites were subject to a regular annual, monomodal inundation (Adis 1992). By determining the elevation of the study sites relative to the river, the periods of inundation could be calculated using the water-gauge data provided by the harbor of Manaus. The duration of inundation varied from site to site and within sites, depending on the altitude. All whitewater sites had been completely flooded in years with high water levels (such as 1997 and 1999), whereas at Praia Grande a strip of sandy beach was never flooded.

*Species.* The study presented here deals with the life cycles of four species, two of them closely related (*P. klugi* and *P. lindemannae*) and one represented by two subspecies (w = whitewater areas, b = blackwater areas). *Phaeoxantha* was previously treated as a subgenus of *Megacephala* (cf. Wiesner 1992). Here we follow Huber's (1994) proposal and use *Phaeoxantha* at the genus level.
- *Phaeoxantha klugi* (Chaudoir, 1850) (w)
- *Phaeoxantha lindemannae* (Mandl, 1964) (b)
- *Phaeoxantha aequinoctialis aequinoctialis* (Dejean, 1825) (w)
- *Phaeoxantha aequinoctialis bifasciata* (Brullé, 1837) (b)
- *Phaeoxantha limata* (Perty, 1830) (b)

*Larval phenology.* Larvae of *P. klugi* and *P. lindemannae* were regularly observed in the field from 1997 to 1999 on 3–6 observation plots (each 12.5 or 25 m² in size). In areas with only a single species, larval instars could be distinguished by the diameter of their tunnel openings, which they maintain clear and clean as long as they are active (Hori 1982, Adis et al. 1998, Arndt & Zerm, unpubl.). At some plots, larval tunnel openings were marked individually with small numbered flags. Once a month the number of the three larval instars was counted at each plot. Holes left behind by newly hatched beetles were counted as well (traceability depending on soil properties and weather conditions). For *P. aequinoctialis*, semi-quantitative and qualitative data on larval phenology were collected whenever possible.

*Phenology of beetles.* Beetles were searched for during each field excursion. Whenever available, some specimens were brought to the laboratory in Manaus for further examination. In addition, the activity density of adult *P. klugi* and *P. lindemannae* was regularly determined by exposing 5 pitfall traps after dawn for a period of 1.5–2.5 h at larval habitats and on the beach along the waterline; opening diameter: 5.6 cm, no killing agent, no roof; for details see Adis (1981). The beetles were then counted and either released or taken to Manaus. Numbers given are standardized to "number of beetles caught in 5 traps per hour".

Gonad states were determined in the laboratory for females collected in the field 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). In *P. aequinoctialis*, a specific gonad shape in animals of gonad state 2, indicating that no egg had been laid before (= "juveniles"), and occurrence of yellow bodies (corpora lutea) was noted. Teneral beetles were counted separately in all species.

*Rearing in the laboratory.* Larvae were reared under controlled conditions in the laboratory to determine the duration of pre-adult stages. Beetles collected in the field were kept in terraria with sand from Ilha de Marchantaria to obtain eggs. These eggs, or the newly hatched 1st-instar larvae, were transferred into glass or plastic vials filled with moist sand of the same origin. Animals were kept separately in climatic chambers (12/12 h light/dark and a temperature regime of

12 h 33°C and 12 h 28°C). They were fed three times a week, 1st-instar larvae with living termites (4–8 termites, depending on size), the others with raw ground beef (a piece of meat approximately the size of the tunnel opening). On each feeding day, activity patterns and larval development were noted.

In many cases it was possible to see the animals through the container walls, therefore allowing the observation of pupae. 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 time interval between when a female beetle had been put into a terrarium and the first observation of hatched larvae. Except for *P. limata*, larvae of different instar stages were collected in the field and reared to the adult beetle in the laboratory under similar conditions.

## RESULTS

*P. klugi* and *P. lindemannae*. Field data on larval and adult phenology of *P. klugi* and *P. lindemannae* are shown in Figs. 1 and 2 respectively. In 1997 first beetles of *P. klugi* appeared in August, 1–1.5 months after the flood had receded from the larval habitats, whereas in mid-September 1999 no beetles could yet be found about 1.5 months after the flooding had ended (Fig. 1c). In 1998 larval habitats were not flooded and first beetles occurred at the end of June.

Beetles of *P. lindemannae* were already encountered at the beginning of the study period (September 1997), about 2–6 weeks after the flood had receded from most parts of the larval habitats (Fig. 2b, c).

Also in 1998 and 1999 first beetles were found 2–6 weeks after the flooding. Hatching of *P. klugi* beetles occurred during several months, as indicated by the holes of newly hatched beetles (Fig. 1a).

Highest beetle abundance was observed during August-November for *P. klugi* and October-November (in 1999 until January) for *P. lindemannae*. During January/February the abundance of *P. klugi* decreased considerably, although few specimens were caught until March (1999) and May (1998) (Fig. 1b, c). In *P. lindemannae* few specimens were found until February (1998) and March (1999) (Fig. 2b, c).

Two teneral beetles of *P. lindemannae* were caught in September 1999 and some of *P. klugi* during June,

September, October 1998, and January 1999. Distribution of gonad maturity states in females showed no clear seasonal pattern in either species (Figs. 1d, 2d).

About 2–3 months after the appearance of beetles, 1st-instar larvae were found at larval habitats representing the new generations. Duration of the 1st instar at the observation plots was about 2 months in *P. klugi* and 2–3 months in *P. lindemannae*. The 2nd instar lasted 2 months in *P. klugi* and >2 months in *P. lindemannae*. The duration of the 3rd instar of *P. klugi* was estimated to last 7–10 months or longer (in 1999 at least 8–10 months) (data for one plot shown in Fig. 1a). In *P. lindemannae* it could only be estimated indirectly, based on the period of time between the increasing abundance of 3rd-instar larvae and the first appearance of beetles. At non-flooded larval habitats, duration of the 3rd instar would amount to a minimum of 4 months and at flooded sites to a minimum of 6–8 months (data for one plot shown in Fig. 2a).

The total duration of larval development as observed in the field amounted to 10–14 months in *P. klugi* and >8–12 months in *P. lindemannae*.

In both species larval generations overlapped, since some 3rd-instar larvae persisted until December, a few even until February (*P. klugi*: Fig. 1a) or March (*P. lindemannae*: Fig. 2a). In most of the 35 3rd-instar larvae of *P. klugi* that could be followed individually until the hatching of the beetle in the field, the period of time between the last observation of larval activity (tunnel opening maintained) and the observed hole of a newly hatched beetle was 60–90 days (monthly observation intervals). This suggests a dormancy of several weeks at the end of the 3rd larval instar, since duration of the pupal stage was much shorter (see below).

Egg development in the laboratory took <12 in *P. klugi* and <20 days in *P. lindemannae*. The duration of larval instars and the pupal stage under controlled conditions is shown in Fig. 5.

The larvae that were reared from egg to beetle showed continuous activity, 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 sight of its next stage (including molting and the opening of a larval tunnel) was usually 1–2 feeding intervals (= 1–7 days). Before pupation, however, 3rd-instar larvae were inactive for some time (referred to as dormancy). The minimum interval between the last observation of an active larva and its pupa was 3–11 days in *P. klugi* (N = 59) and 22–24 days in *P. lindemannae* (N = 38).

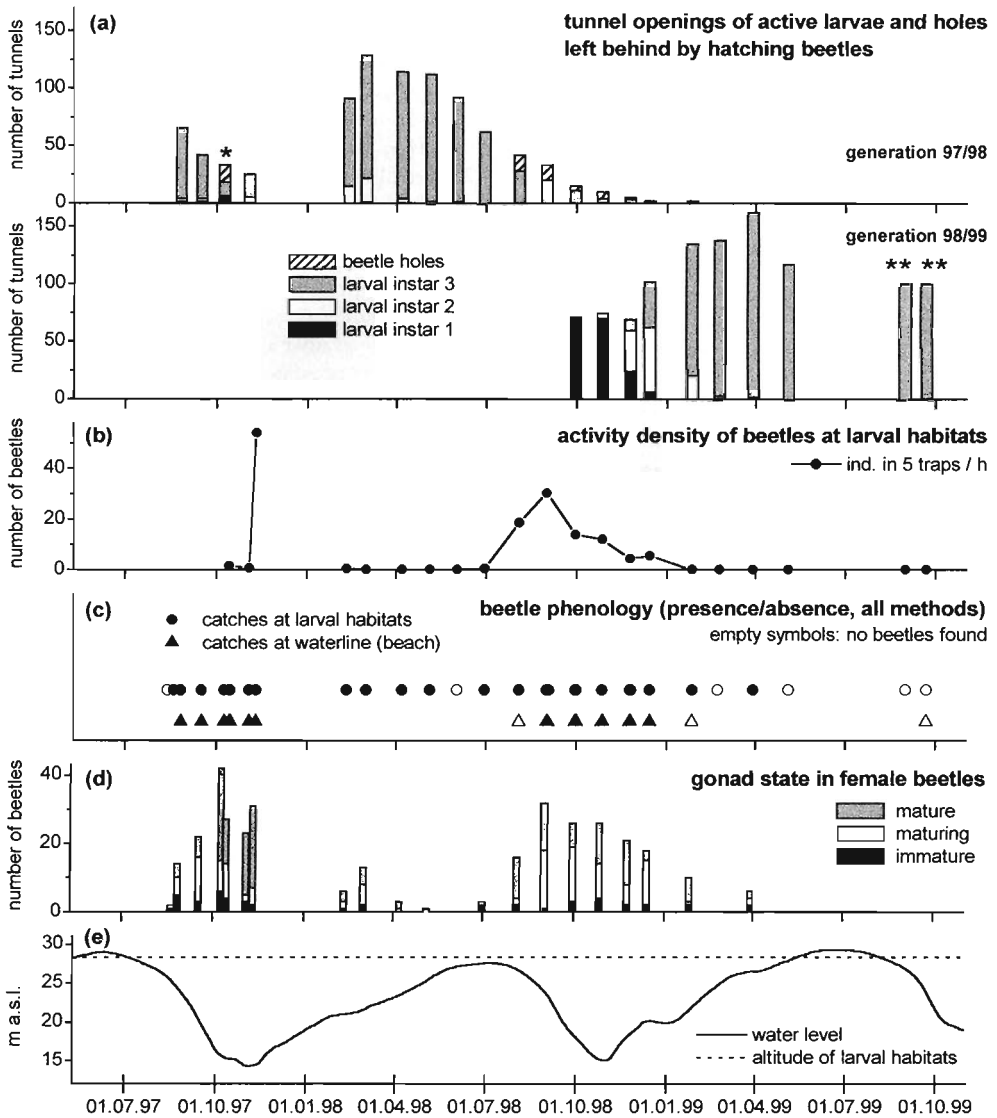# Larval and adult *P. klugi* at Ilha de Marchantaria (whitewater)



FIG. 1. *P. klugi* at Ilha de Marchantaria (Rio Solimões-Amazonas) 1997–1999. (a) Larval phenology at one of the plots ("X2"). Larval tunnel openings were marked individually from April 1998 onwards. Visibility of beetle holes is subject to soil type and weather conditions. (b) Beetle catches in pitfall traps. (c) Occurrence of beetles at the study site. (d) Gonad state in females. (e) Water level at the harbor of Manaus and altitude of larval habitats indicating the minimum duration of submersion (1998: plot X2 not flooded). * = approximate number of beetle holes (see text). ** = approximate number of larval tunnels (see text).
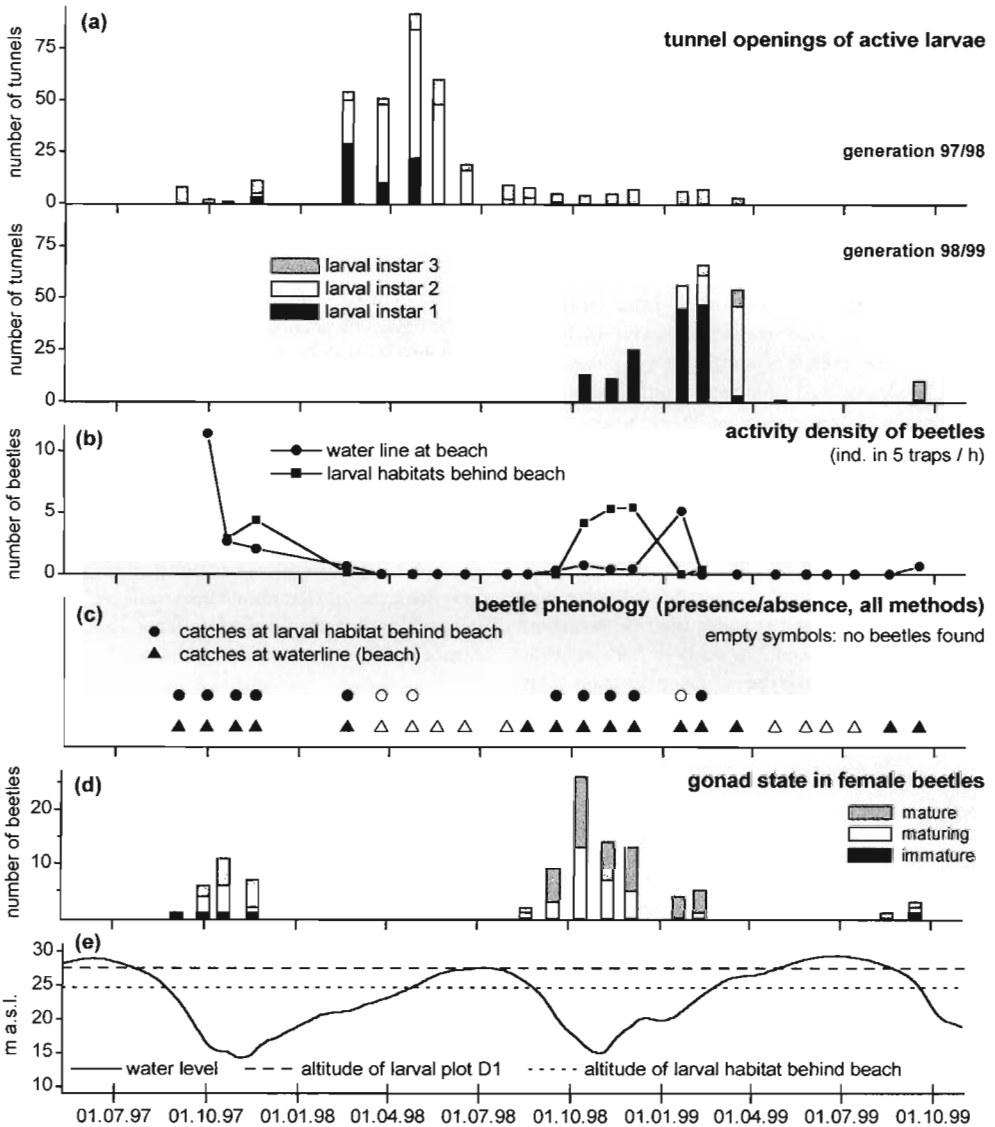
## Larval and adult *P. lindemannae* at Praia Grande (blackwater)



FIG. 2. *P. lindemannae* at Praia Grande (Rio Negro) 1997–1999. (a) Larval phenology at one of the plots ("D1"). Larval tunnel openings were marked individually from April 1998 onwards. (b) Beetle catches in pitfall traps. (c) Occurrence of beetles at the study site. (d) Gonad state in females. (e) Water level at the harbor of Manaus and altitude of two larval habitats indicating the minimum duration of submersion (1998 plot D1 only partially flooded).

In *P. klugi*, 22 3rd-instar larvae reared from eggs laid in the laboratory had a rather short dormancy (< 6 weeks) whereas another 4 larvae stayed dormant for 11–31 weeks (Fig. 5c and Table 1). The latter are descendants of the same females as some of the former. Duration of the pupal stage was similar in animals that were taken to the laboratory as 2nd or 3rd-instar larvae compared with those reared entirely in the laboratory (Table 1). The active phase of 3rd-instar larvae was longer in the former than in the latter group, whereas duration of the dormancy period was within the same range. In some of the individuals taken to the laboratory as 2nd or 3rd-instar larvae, several dormancy periods could be observed (Table 2).

In *P. lindemannae*, duration of the pupal stage could be determined only from animals that were taken to the laboratory as 1st or 3rd-instar larvae (Fig. 5). As in *P. klugi*, some of the 3rd-instar larvae showed several dormancy periods (see Table 2). The total duration of dormancy within this group ranged from 22 to 175 days (no mean duration calculated because of heterogeneous material).

The period of time between the first occurrence of beetles and 1st-instar larvae in the field was about 2 months in *P. klugi* and 2–6 weeks in *P. lindemannae* (Figs. 1, 2). Subtracting the estimated duration of egg

development (see above) results in 1.5–2 months as a rough estimate for the maximum time females needed to reach gonad maturity in *P. klugi*, and up to 4 weeks in *P. lindemannae*. Data from females reared and hatched in the laboratory showed great variability. In *P. klugi*, 4 out of 9 female beetles that were killed 28–34 days after hatching were mature, whereas 7 females that were examined after 38–40 days were still immature. In *P. lindemannae*, 1 of 7 female beetles killed 27–33 days after hatching was mature, whereas 2 of 3 females dissected after 39–40 days were still immature.

No data are available for the life span of beetles in the field. The phenological data indicated that they probably lived only a few months (see Figs. 1, 2). Beetles caught in the field and kept in the laboratory usually survived several weeks only, very few for some months. Most of the beetles that hatched in the laboratory usually died within the first week, the ones that survived longer were killed for gonad examination (within 40 days).

*P. a. bifasciata*. Beetles were found throughout the year, with the greatest abundance from July-December and lowest from April-May. Teneral and juvenile female beetles were found from June to October (Fig. 3a, b). Likewise, teneral males were solely caught

TABLE 1. *P. klugi*: Duration of 3rd larval instar and pupal stage (days) in animals of different origin (only animals counted that reached at least the pupal stage). * = added for larvae with several dormant periods (see Table 2). ** = no mean duration calculated because of heterogeneity of animal material.

| | mean duration | s. d. | N | min | max |
|---|---|---|---|---|---|
| **Larvae reared from eggs laid in the laboratory** | | | | | |
| 3rd-instar | 81.8 | 52.5 | 26 | 37 | 280 |
| 3rd-instar, active phase | 43.6 | 11.8 | 26 | 26 | 68 |
| 3rd-instar, short dormant phase | 21.1 | 10.8 | 22 | 3 | 42 |
| 3rd-instar, long dormant phase | 132.5 | 60.1 | 4 | 77 | 217 |
| Pupal stage | 16.0 | 3.7 | 23 | 5 | 24 |
| **Larvae reared from animals collected as 2nd instars in the field** | | | | | |
| 3rd-instar | 169.5 | 33.4 | 4 | 126 | 199 |
| 3rd-instar, active phase | 60.3 | 12.4 | 7 | 42 | 75 |
| 3rd-instar, dormant phase | 111.5 | 45.6 | 4 | 51 | 157 |
| Pupal stage | 15.0 | – | 2 | 14 | 16 |
| **Larvae reared from animals collected as 3rd instars in the field** | | | | | |
| 3rd-instar, dormant phase* | ** | | 50 | 11 | 163 |
| Pupal stage | 17.1 | 8.0 | 22 | 7 | 37 |

during the same period. Corpora lutea were observed in 71 out of 331 females examined, mostly in specimens caught during rising water levels (Fig. 3c). The life span of beetles can thus be estimated at >6 months, possibly up to 1 year.

Larval populations could not be followed continuously at observation plots for reasons discussed elsewhere (Zerm & Adis, unpubl.). Tunnel openings of all instars were observed almost throughout the study period. However, 1st-instar larvae were observed in greater numbers during falling water levels (September-October) and 3rd-instar larvae were clearly prevalent among the few still active larvae towards the water level peak (May-July). The small number of observed larvae during the water level peak, as well as the new generation of beetles appearing when the high water level begins to fall (see Fig. 3), suggest that the majority of larvae stayed inactive during the former period.

Egg development in the laboratory took < 16 days. The duration of larval instars and the pupal stage under controlled conditions is shown in Fig. 5.

Like *P. klugi* and *P. lindemannae*, larvae reared from eggs laid in the laboratory 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 0–14 days before pupation (8 days on average), whereas in 14 specimens taken to the laboratory as 3rd-instar larvae, the inactive phase before pupation lasted 2–48 days.

Duration of the pupal stage was similar in animals that were taken to the laboratory as 3rd-instar larvae compared to those reared entirely in the laboratory.

The period of time between the first appearance of beetles of a new generation (cf. Fig. 3) and the increased numbers of 1st-instar larvae in the field was about 2 months. Subtracting the estimated duration of egg development (see above) results in 1.5 months as a rough estimate for the time females needed to reach gonad maturity. Two females reared in the laboratory and examined 18 and 30 days after hatching were still immature. More laboratory data on gonad maturity in females are not available due to high mortality rates of beetles within the first week after hatching.

In contrast to the long life span in the field (see above), beetles caught in the field and subsequently kept in the laboratory usually survived a few weeks only. With the exception of 5 specimens, all beetles

TABLE 2. *P. klugi* and *P. lindemannae*: number of dormancy periods in 3rd-instar larvae of different origin. Only one dormancy period observed represents the dormant phase before pupation.

| | number of dormancy periods | *P. klugi* days of activity between dormancy periods | N | *P. lindemannae* days of activity between dormancy periods | N |
|---|---|---|---|---|---|
| larvae reared from eggs laid in the laboratory | 1 | – | 27 | – | 5 |
| larvae reared from animals collected as 1st-instars in the field | 1 | | | – | 3 |
| larvae reared from animals collected as 2nd-instars in the field | 1 | – | 7 | | |
| larvae reared from animals collected as 3rd-instars in the field | 1 | – | 33 | – | 42 |
| | 2 | 2–31 | 14 | 3–19 | 7 |
| | 4 | 2–42 | 2 | 5–14 | 1 |
| | 5 | 2–47 | 1 | | |

that hatched in the laboratory died within the first 2 weeks.

*P. a. aequinoctialis*. Larvae were observed only three times at two different sites. During these occasions all three larval instars occurred in significant numbers (Ilha da Paciência: end of November to mid-December 1998, Curari sandbank: end of January 1999).

At Ilha da Paciência, beetles were collected from mid-November to mid-December 1998, at Curari sandbank at the end of January 1999. No beetles were found at Curari sandbank in early September 1998 and end of August/September 1999. Few immature female beetles were found in mid-December 1998. Some female beetles found in mid-December 1998 and at the end of January 1999 had distinct corpora lutea.

Egg development in the laboratory took < 12 days. The duration of larval instars and the pupal stage under controlled conditions is shown in Fig. 5. Larval activity patterns were similar to *P. a. bifasciata*. Prior to pupation, 3rd-instar larvae were inactive for 4–29 days (on average 12 days, N = 7), while larvae that were taken to the laboratory as 3rd instars were inactive for 4–23 days (on average 11 days, N = 9).

Duration of the pupal stage was similar in animals that were taken to the laboratory as 3rd instars compared to those entirely reared in the laboratory.

No data are available on gonad maturity of females or on the life span of adult beetles. Beetles caught in the field and kept in the laboratory usually survived few weeks only; those hatched in the laboratory died within 2 weeks.

*P. limata*. Field data on the larval phenology at Praia Grande are not available as the larval habitat is still unknown. A population of larvae and beetles at a *terra*
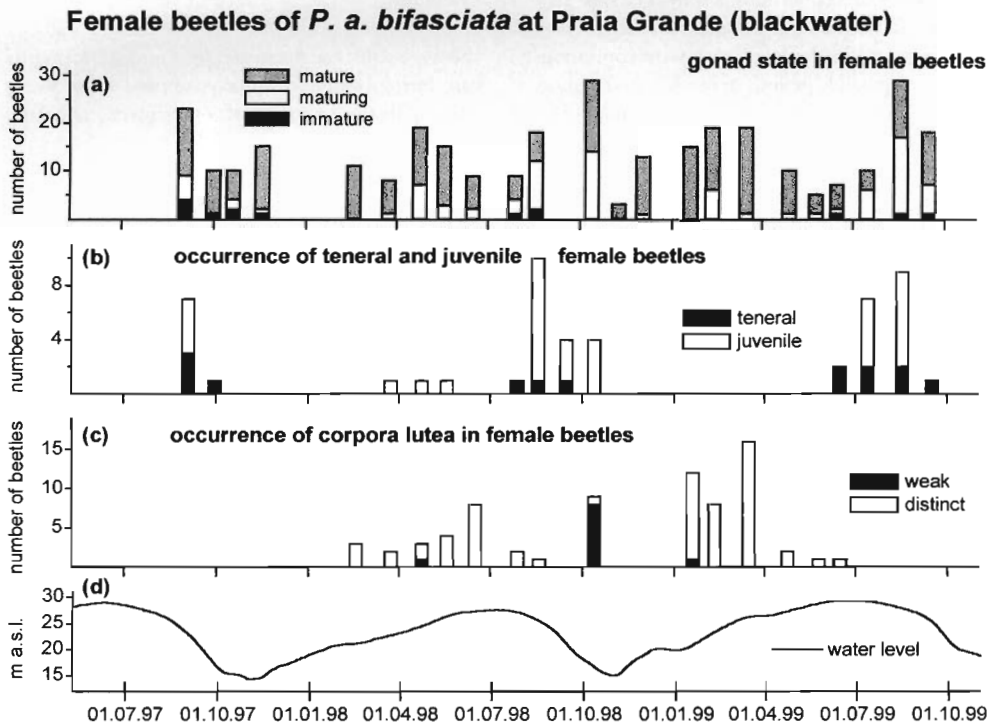


FIG. 3. Female beetles of *P. a. bifasciata* at Praia Grande (Rio Negro) 1997–1999. (a) Gonad state in females. (b) Occurrence of teneral and juvenile females (for definitions see text). (c) Occurrence of corpora lutea in female beetles (d) Water level at the harbor of Manaus. For dates when beetles were searched for see Fig. 2c.

## Adult *P. limata* at Praia Grande (blackwater) and Sítio Bom Sossego (*terra firme*)
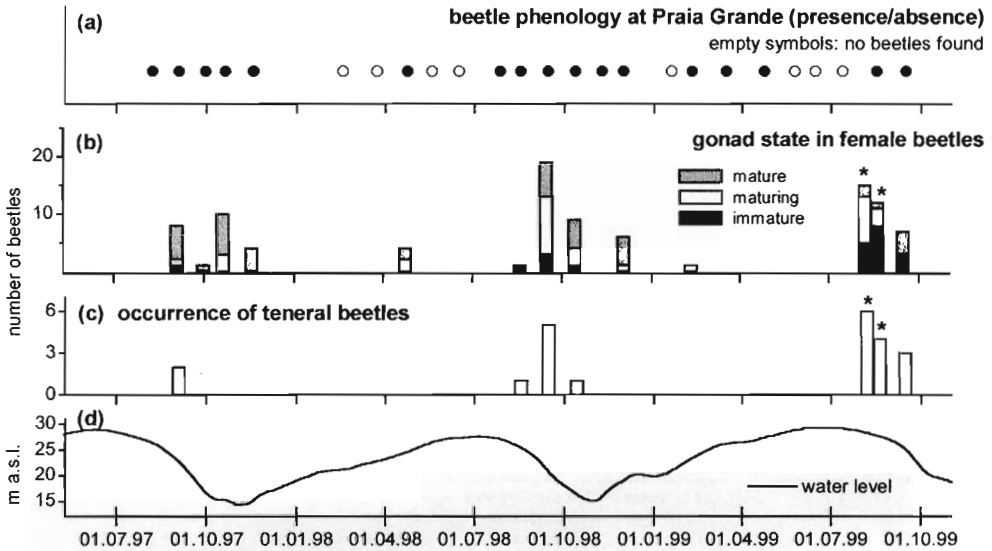


FIG. 4. Adult *P. limata* at Praia Grande (Rio Negro, 1997–1999) and Sítio Bom Sossego (*terra firme*, August 1999). (a) Occurrence of beetles at Praia Grande. (b) Gonad state in females. (c) Occurrence of teneral beetles. (d) Water level at the harbor of Manaus. * = Sítio Bom Sossego.

*firme* site (open whitesand area, Sítio Bom Sossego, km 19 on Manaus-Itacoatiara highway (AM-010), near Reserva Florestal A. Ducke) was only discovered in August 1999 (6 out of 10 larvae were 3rd instars, the other 4 were 2nd instars).

Data on adult phenology of *P. limata* are shown in Fig. 4. The highest beetle abundance at Praia Grande was observed from August to October. During several months of the year no beetles were found at all. Immature female beetles and teneral beetles of both sexes were mostly caught during falling water levels (Fig. 4d).

Rearing larvae from eggs laid in the laboratory failed due to low rates of egg deposition and a high mortality rate of larvae. Egg development in the laboratory took <13 days.

## DISCUSSION

*Methods, rearing conditions.* The observed number of active larvae in *P. klugi* and *P. lindemannae* at the observation plots is not a precise measure of their abundance. Larvae are inactive before and during

molting, before pupation (dormancy), and perhaps on other occasions, and were thus missed on field excursions. Some tunnel openings of active larvae might have been overlooked, especially of 1st-instar larvae due to their smaller size. Adverse weather conditions and increasing vegetation cover further diminished the traceability of larval tunnels. These factors probably account for the variation of larval abundance at the observation plots, apart from fluctuations due to newly hatching larvae, hatching beetles, and larval mortality. There were no indications of larvae of these species immigrating into or emigrating from observation plots.

The temperatures at which larvae were reared in the laboratory were similar to those in the field during sunny weather periods (Zerm & Adis, unpubl.). Other authors used lower temperatures to rear tiger beetles in the Manaus region, but they reared forest species (Amorim *et al.* 1997a, Paarmann *et al.* 1998). In *Pentacomia egregia*, a tiger beetle from floodplain forests in Central Amazonia, gonad maturation in females was found to be faster at increasing tempe-
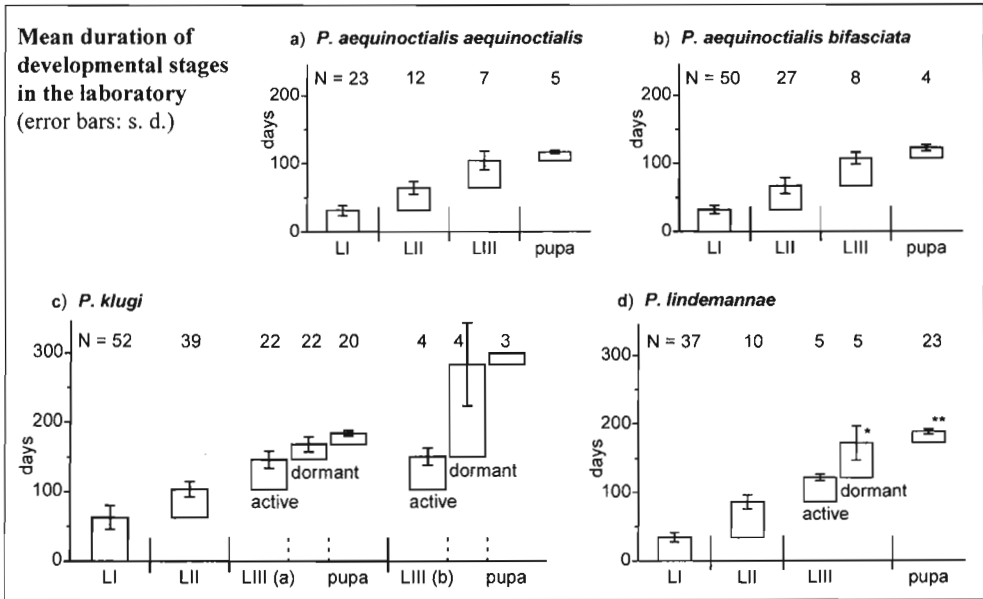
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FIG. 5. Duration of larval instars and pupal stage of *P. a. bifasciata*, *P. a. aequinoctialis*, *P. klugi*, and *P. lindemannae* under laboratory conditions (see text). All animals were reared from eggs laid in the laboratory. LI–LIII: 1st–3rd larval instars. For definition of 'dormant' see text. *P. klugi*: LIII (a): short dormant phase before pupation, LIII (b): long dormant phase before pupation (see text). * = duration of dormant phase unknown, values calculated by subtracting the mean duration of the pupal stage from the total duration of LIII until hatching of beetles. ** = value derived from animals collected in the field as LIII and reared in the laboratory.

ratures (Amorim *et al.* 1997a). Duration of larval development, too, can generally be expected to be faster with increasing temperatures (*cf.* Shelford 1908, Palmer 1979 a. o.).

Alimentation of larvae in the laboratory was considered to be better than in the field, although quantitative field data on food availability are not available. Reduced food supply is expected to result in prolongation of the larval phase, as indicated by Palmer (1978), Knisley & Pearson (1984), Pearson & Knisley (1985), Knisley & Juliano (1988), Amorim *et al.* (1997b), and own data on *P. klugi* (Zerm & Adis, unpubl.). The influence of differences in food quality between field and laboratory (diverse living prey versus ground beef) on larval development is not known. Feeding intervals were similar to other studies (Palmer 1979, Amorim *et al.* 1997a).

Ground beef was used for feeding because termites available at the INPA campus were too small to feed 2nd and 3rd-instar larvae, and other arthropods of suitable size were not available in the quantities needed. Other authors used fruit fly larvae, grasshoppers, and other invertebrates to feed tiger beetles (Willis 1967, Faasch 1968, Knisley & Pearson 1984, Ribeiro *et al.* 1996, Amorim *et al.* 1997a). Willis (1967) and Palmer (1979) also used ground beef successfully for beetles and larvae.

Larvae from blackwater areas were reared in sediment from whitewater areas in the laboratory because sand from blackwater beaches proved to be unsuitable for rearing in containers under laboratory conditions. However, we do not expect the duration of larval development to be significantly altered by sediment type.

On account of the rearing conditions we assume that larval development in the laboratory was somewhat faster than in the field.

High mortality rates of beetles and slow gonad maturation of females in the laboratory probably resulted from sub-optimal rearing conditions, although beef offered as food to beetles in the field was readily accepted. Laboratory data on gonad maturity are therefore not representative.

The state of gonad maturity in beetles collected in the field was examined in females only. Males are expected to reach gonad maturity faster. 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 carabid beetles from Central Amazonian floodplains (Adis *et al.* 1986).

Duration of egg development could only be estimated by including the periods of hatching and opening of the tunnel, as well as the interval until the beetles laid eggs. This is believed to be mainly responsible for the differences found between species.

*P. klugi* and *P. lindemannae*. The sister species *P. klugi* and *P. lindemannae*, restricted to whitewater and blackwater areas respectively, have a long larval phase of up to one year in the field.

In *P. lindemannae* the 1st and 2nd instars seemed to last longer in the field than in *P. klugi*, but in laboratory rearings it seemed to be the contrary. This could be due to a better food supply at the site of

*P. klugi* and, perhaps, to a more effective food use in *P. lindemannae* in the laboratory.

The total duration of pre-adult stages in the laboratory did not differ significantly in these two species (Fig. 6). Total duration of the pre-adult stages in the field, however, seemed to be somewhat faster in *P. lindemannae* than in *P. klugi*. This might be related to the duration of the 3rd instar of *P. lindemannae* being underestimated for reasons mentioned above. Duration of the 1st instar of *P. klugi* in the field was found to last twice as long as reported by Adis *et al.* (1998), whereas the duration of the entire larval development in the field was rather similar (9–13 versus 10–14 months in the present study).

Dormancy at the end of the 3rd-instar stage includes the time the larvae have to be inactive prior to pupation (*cf.* Shelford 1908, Willis 1967, Faasch 1968). However, with reference to the observed minimum of 3–11 days for this period, the major part of the inactive phase can be considered a true dormancy in most cases. Whether larvae of *P. lindemannae* became dormant at the end of the 3rd-instar stage could not be determined in the field for methodological reasons. However, the overall temporal pattern in the field as well as indications from larvae reared in the laboratory lead to the assumption that they did. Hence we conclude that both species become dormant at the end of the 3rd-instar stage for a variable period of time. This variability might be caused endogenously and/or by external factors. We suspect that
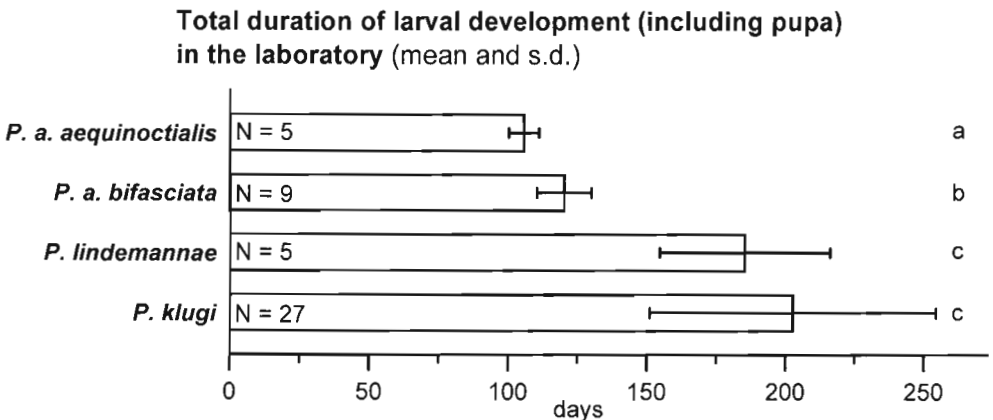
**Total duration of larval development (including pupa) in the laboratory** (mean and s.d.)



FIG. 6. Total duration of larval development including the pupal stage in *P. a. bifasciata*, *P. a. aequinoctialis*, *P. klugi*, and *P. lindemannae* under laboratory conditions (see text). Different letters (a–c) indicate significant differences (a < 5%, Mann-Whitney-U-tests, improved Bonferroni-correction).

the duration of dormancy might vary in order to synchronize pupation in the population (i.e., to avoid pupation and hatching of beetles too early in the year) which would probably imply external triggering. The repeated dormancy periods observed in some individuals in the laboratory might be a result of trigger-failure due to the uniform conditions. When flooded, larvae survived the inundation period in a state of dormancy, further extending the duration of the $3^{rd}$-instar. Some (or all?) larvae, however, became active again after inundation had ended and re-opened their tunnels prior to pupation (Adis *et al.* 1998, Zerm & Adis, unpubl.).

Adults were observed in higher numbers during falling water levels, a period lasting a few months per year only. Increasing beetle abundance from December onwards, as reported for *P. klugi* by Adis *et al.* (1998), was not observed during our study period. Very few or no beetles at all of both species were found during high water levels, including the year 1998 when higher parts of the study site were not flooded. Since there are no records of beetles being observed at other habitats during this period (Adis, pers. observ.) it can be assumed that their life span is only a couple of months.

Gonad states of females from the field lack seasonal patterns. We presume that this is due to a long hatching period, a rapid maturation of gonads and/or incorrect determination of gonad states (see above), since the occurrence and abundance of beetles are clearly seasonal. Gonad maturity in *P. klugi* seems to last 1–2 months, as evidenced by both laboratory and field data. Field data suggest that this holds true also for *P. lindemannae*, whereas the few laboratory data indicate a longer period.

*P. aequinoctialis.* Although beetles of *P. a. bifasciata* occurred throughout the year, they showed a distinct seasonal pattern. The new generations appeared when the high water levels began to fall. Beetles hatched over a long period (several months). In females caught during rising water levels, corpora lutea were observed in the gonads, indicating that they were older than their congeners caught earlier (during falling water levels). To our knowledge this is the first record of corpora lutea in a tropical tiger beetle (Paarmann, pers. comm.). The amount of time needed for gonad maturation in female beetles of *P. a. bifasciata* was estimated to be in the same range as in *P. klugi* and *P. lindemannae*, despite their different life spans (see below).

The occurrence of larval stages in *P. a. bifasciata* seemed to be less seasonal than that of beetles. The beetle's long active phase and their habit of depositing eggs in moist places (i.e., mainly near the constantly changing water line) account for a very heterogeneous temporal and spatial distribution of larval stages (Zerm & Adis, unpubl.). Since the appearance of the new beetle generation seemed to be synchronized, and the number of larvae decreased strongly before this period, we postulate that $3^{rd}$-instar larvae of *P. a. bifasciata* also enter a state of dormancy before pupation, although this could only be partially observed in the laboratory (Zerm & Adis, unpubl.). It can therefore be concluded that the duration of the larval phase for those larvae that represented the majority of $1^{st}$-instar larvae in September-October was about 7–10 months (including a dormancy at the end of the larval phase). In larvae that hatched later in the season the total duration of the larval phase was probably much shorter. Whether these findings implicate flood resistance in larvae will be discussed elsewhere (Zerm & Adis, unpubl.).

The short duration of the larval phase in the laboratory compared to data from the field in *P. a. bifasciata* might be a result of better food supply and a lack of conditions for entering dormancy. The short larval phase observed in the laboratory would allow for two generations within one year, yet this was not observed in the field.

Larval development in the laboratory was significantly faster in *P. a. aequinoctialis* compared with *P. a. bifasciata*, and also in both subspecies compared to *P. klugi* and *P. lindemannae* (Fig. 6). Field data are too scarce to reconstruct the life cycle of *P. a. aequinoctialis*. At least the field data available do not contradict the assumption that both subspecies have similar life cycles.

The blackwater study site of *P. a. bifasciata* is exceptional in having a higher sandy part of the beach that always remains unflooded. Other beaches in the area become entirely flooded during most years. The fate of adult beetles at these localities is not known, but we suspect that they die when the sites become flooded, because they can neither dive nor fly (Zerm & Adis, unpubl.). In *P. a. aequinoctialis* we do expect the adults to die off with the onset of flooding as they were also found to be flightless and met at sites without terrestrial connection to non-flooded habitats. Unlike *P. klugi* and *P. lindemannae*, in which the short adult phase seems to be an internal trait, *P. a. bifas-*

*ciata* apparently lives much longer under suitable habitat conditions.

*P. limata.* Beetles of *P. limata* occur seasonally and gonad states suggest an annual life cycle. Although field and laboratory data are not available, we suspect a long larval phase in this species since there are neither indications of inactive beetles, which could explain periods with no beetles, nor other places away from the beach where beetles might have stayed during this period (Zerm & Adis, unpubl.). Further observations are needed to verify whether populations on *terra firme* are also univoltine and seasonal.

*Ontogeny and life cycles.* Our estimations of the duration of the egg stage (< 12−< 20 days) are in good agreement with data provided by Pearson (1988), Ribeiro *et al.* (1996), and Adis *et al.* (1998) for other species. Other authors reported longer periods: 38 days in *Pseudoxycheila tarsalis* (Palmer 1976) and about 30 days in *Cicindela hybrida* and *C. campestris* (Faasch 1968). Differences might be related to different temperatures experienced by the eggs.

In larvae reared in the laboratory the 1st instar was found to last either shorter or longer or about as long as the 2nd instar. It has to be taken into account though that alimentation varied between the 1st and the other two instars. In the field, the 2nd instar apparently lasted somewhat longer than the first (in *P. klugi* and *P. lindemannae*). In all species the 3rd instar represented the longest stage in the field as well as in the laboratory. The total duration of larval development derived from field data varied according to species from 7–10 to 10–14 months, contrasting with 4–7 months in the laboratory. Generally, faster larval development in the laboratory was attributed to a better food supply and, perhaps, to higher temperatures (see above). The 3rd instar in particular lasted longer in the field, which we partially relate to a period of dormancy. This dormancy, however, is not related to the season with less rainfall ("dry season": June-November in Central Amazonia) as reported for other species with a larval dormancy (Palmer 1976, Paarmann *et al.* 1998).

In all species presented here, duration of larval development is longer than in other floodplain species from the Manaus region hitherto studied: *Tetracha sobrina punctata* (Adis *et al.* 1998), *Pentacomia cribrata* (Zerm & Adis, unpubl.), *Pentacomia egregia* (Amorim *et al.* 1997b), and *Pentacomia lacordairei* (Adis *et al.* 1998). Based on beetle phenology and preliminary laboratory data, we expect the larval development to be shorter also in the remaining floodplain species (Adis *et al.* 1998, Zerm & Adis, unpubl.). In *Pentacomia ventralis* from an upland forest near Manaus, larval development lasted around 10 months, 7 of which are passed in a state of dormancy (Paarmann *et al.* 1998). In this latter study another 5 species showed a strong annual seasonality of beetles, suggesting a similar duration of larval development. In *Pseudoxycheila tarsalis* from a premontane rainforest in Costa Rica, the larval phase took around 9 months (Palmer 1976). 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). In *P. egregia* from floodplain forests near Manaus, the generally longer duration of the 1st-instar was explained as a way of overcoming food shortages after the forest floor has dried up and terricolous arthropods are less abundant (Amorim *et al.* 1997b).

Mean duration of the pupal stage, ranging from 10 to 17 days, was shorter than in species from temperate and subtropical regions (18–22 days; Willis 1967, Faasch 1968, Palmer 1976) and in a species from Costa Rica (Palmer 1976), but similar to those reported for species from the Manaus region (Ribeiro *et al.* 1996, Paarmann *et al.* 1998), although these differences might be a result of different temperatures experienced by the pupae.

The inactive phase of 1–7 days associated with molting between larval instars (variation is at least partly due to the observation interval of 2–3 days) is similar or shorter than reported for other species (*cf.* Shelford 1908, Zikan 1929, Willis 1967 a. o.).

The life span of adults was found to be either a few months only (*P. klugi* and *P. lindemannae*) or up to one year (*P. a. bifasciata*). Other data on the adult life span in tropical tiger beetles are scarce. The adult phase of *Pseudoxycheila tarsalis* from Costa Rica (Palmer 1976) and *Pentacomia ventralis* (from an upland forest near Manaus) was about 3 months, the beetle phenology of another 3 species from the latter site suggested adult life spans of about 5 months (Paarmann *et al.* 1998). In floodplain species where beetles survive the inundation period, adult life span is much longer, ranging from 5 to 14 months in *Pentacomia egregia* (females only), *P. lacordairei* (females only), *Odontocheila confusa* (females only), *Tetracha sobrina punctata* and others (Amorim *et al.* 1997a, Zerm & Adis, unpubl.), including a period of gonad dormancy as shown for *P. egregia* (Amorim *et al.* 1997a) and suspected for the others (Adis *et al.* 1998). Adult life span

in *Cicindela* species from temperate and subtropical regions was also found to be either a few months only (in beetles emerging during summer and dying off before winter) or 6–8 months (in hibernating beetles emerging in fall) also with an active, i.e., reproductive, phase of only few weeks (Willis 1967, Simon-Reising *et al.* 1996).

According to the larval and adult phenology of the species investigated in our study, the time female beetles need to reach gonad maturity is short when compared with species with a fast larval development during low water periods (and gonad dormancy in the female beetles). In *P. ventralis* from *terra firme* uplands near Manaus, gonad maturity is reached within a few days after emergence (Paarmann *et al.* 1998). Other data on gonad maturation of tropical species from non-flooded biotopes are not available. In species from temperate regions with beetles emerging in summer, gonad maturation has also to be fast because beetles die off before winter (Willis 1967).

## CONCLUSIONS

All species studied here showed an annual life cycle. Species differed in the duration of larval stages and adult life span, whereas the duration of egg and pupal stages was rather similar. Dormancy in the 3$^{rd}$ larval instar seems to play an important role in adjusting larval development to seasonally changing environmental conditions, thereby synchronizing the populations.

The life cycle type described here, with a long larval phase, fits into the temporal pattern set by the monomodal flood pulse (Junk *et al.* 1989). It had previously been reported only for *P. klugi,* based on observations of 3$^{rd}$-instar larvae re-opening their tunnels after inundation (Adis *et al.* 1998). Most cicindelid species from floodplains in the Central Amazon also have annual life cycles, yet they differ in having a short larval phase during low water periods. Although the life cycle type documented here is similar in several aspects to life cycles found in species from non-flooded uplands, and generally in species from other regions of the world, it is unusual as it implies flood resistance in larvae (Adis *et al.* 1998, Zerm & Adis, unpubl.).

*P. a. bifasciata* is exceptional in having a long larval phase as well as a very long adult life span and corpora lutea in female gonads. Currently we know of no other tiger beetle species with such a long active adult phase. However, the adaptive significance of the long adult life span is not yet understood. The short active adult stage in the other species from Central Amazonia might be the reason for the lack of corpora lutea.

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