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ECOLOGY AND ADAPTATIONS OF THE TIGER BEETLE *PENTACOMIA EGREGIA* (CHAUDOIR) (CICINDELINAE: CARABIDAE) TO CENTRAL AMAZONIAN FLOODPLAINS*

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Resumo. A espécie de cicindelídeos, *Pentacomia egregia* (Chaud.), habita a superfície de solo nas florestas inundáveis da Amazônia Central. Adultos passam a fase aquática, de varios meses de duração, sobre troncos de árvores. Experimentos com besouros jovens, sob condição simulada de inundação em câmaras de clima controlado e em condições de clima natural, mostraram que: (1) Machos apresentam um ciclo de vida mais curto do que as fêmeas. (2) A temperatura média do ar influencia o desenvolvimento gonadal nas fêmeas, mas não nos machos. Machos até copulam com fêmeas imaturas. (3) A presença de solo previne a dormência gonadal em fêmeas e uma oviposição contínua é observada. Os resultados sugerem, que a presença de solo é o (eco)fator primário ou proximativo que induz a rápida maturação das gonadas e a subsequente oviposição nas fêmeas. A temperatura média do ar induz a dormência gonadal e prolonga a longevidade nas fêmeas durante a fase de inundação. Este fator primário ou proximativo aparentemente evoluiu como desencadeamento para uma adaptação de sobrevivência à fase de inundação como fator ultimativo. A elevação da temperatura média do ar ambiental está correlacionada com mudanças sazonais do nível das águas do Rio Solimões-Amazonas e do clima geral da Amazônia Central.

Abstract. The diurnal soil-dwelling cicindelid species *Pentacomia egregia* (Chaud.) inhabits Central Amazonian inundation forests. Adults pass the aquatic phase of several months duration on tree trunks. Experiments under simulated flood conditions with young beetles in climate-controlled chambers and in natural climatic conditions showed: (1) males have a shorter life span than females, (2) the mean temperature of the air influences gonad development in females but not in males, males will even copulate with immature females; (3) the presence of soil prevents gonad dormancy in females and continuous oviposition is observed. Results suggest, that the availability of soil is the primary or proximate (eco)factor which induces a rapid maturation of gonads and subsequent oviposition in females. The mean temperature of the air induces gonad dormancy and enhances longevity in females during inundation. It apparently has evolved as a cue for an adaptation to survive inundation as an ultimate factor. An increase in the mean ambient air temperature is correlated with seasonal changes in the water-level of the Solimões-Amazon River and the general climate in Central Amazonia. *Accepted 22 July 1997.*

Key words: Tiger beetles, Cicindelinae, cicindelids, gonad dormancy, floodplains, Amazon, Neotropics.

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INTRODUCTION

Since 1992, tiger beetles in the Manaus area have been studied to understand the mechanisms which maintain their high diversity in Central Amazonia (cf. Parmann *et al.* 1998, Linsenmair 1990).

The water level of the Solimões-Amazon River near Manaus varies 10m on average throughout the year. During high-water vast areas of land along the river are flooded to a depth of several meters for five to seven months. The seasonal periodicity of this monomodal flood pulse (Junk *et al.* 1989) is reflected in numerous adaptations in terrestrial invertebrates of the Central Amazonian floodplain, referred to as "survival strategies" (Adis 1997). These are of etho-ecological, morphological and physiological nature, as shown for *Megacephala sobrina punctata* (Adis *et al.* 1993, Adis & Messner 1997). This nocturnal species inhabits sandy beaches of the Solimões-Amazon River; during the aquatic phase (high-water) it lives on driftwood but hides submerged during daytime.

In this paper we concentrate on *Pentacomia egregia* (Chaudoir), a diurnal soil-dwelling species inhabiting seasonal Amazonian white- and mixed-water inundation forests (Adis 1992, Pearson 1995, Rodríguez *et al.* 1994, Prance 1979). In the surroundings of Manaus, its phenology is well studied (Paarmann *et al.* 1982). Adult beetles pass the aquatic phase of 5–7 months duration (March/April-August/September) on the lower area of tree trunks, above the water level (cf. Irmler 1973). Males attain gonad maturity earlier than females (Fig. 1), copulate with the still immature females and die in the trunk region before the flood water has left the forest. Females store the received spermatophores in their bursa copulatrix, and ovaries become mature only as the forest floor begins to dry. Then females return to the ground, deposit their eggs and die. No adults are active throughout the following 3–4 months of the terrestrial phase (low-water), only larvae (Amorim *et al.* 1997). Adults emerge from January onwards, 1–3 months before forest inundation.

Irmler (1985) hypothesized that the environmental cue for reproduction involved annual fluctuations of the night temperature of the air in the forest. With knowledge of a long life span and the existence of a gonad dormancy in adult tiger beetles, Paarmann *et al.* (1982) postulated that these

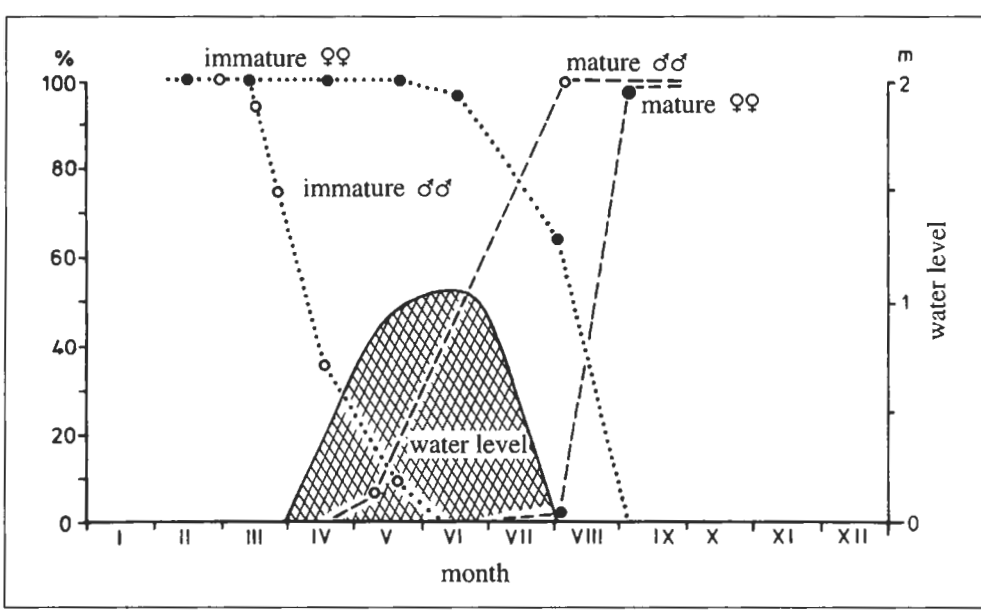

FIG. 1. State of gonads (%) within the population of adult *Pentacomia egregia* (Chaud.) from whitewater and mixedwater inundation forests in the vicinity of Manaus (from Paarmann *et al.* 1982, modified).

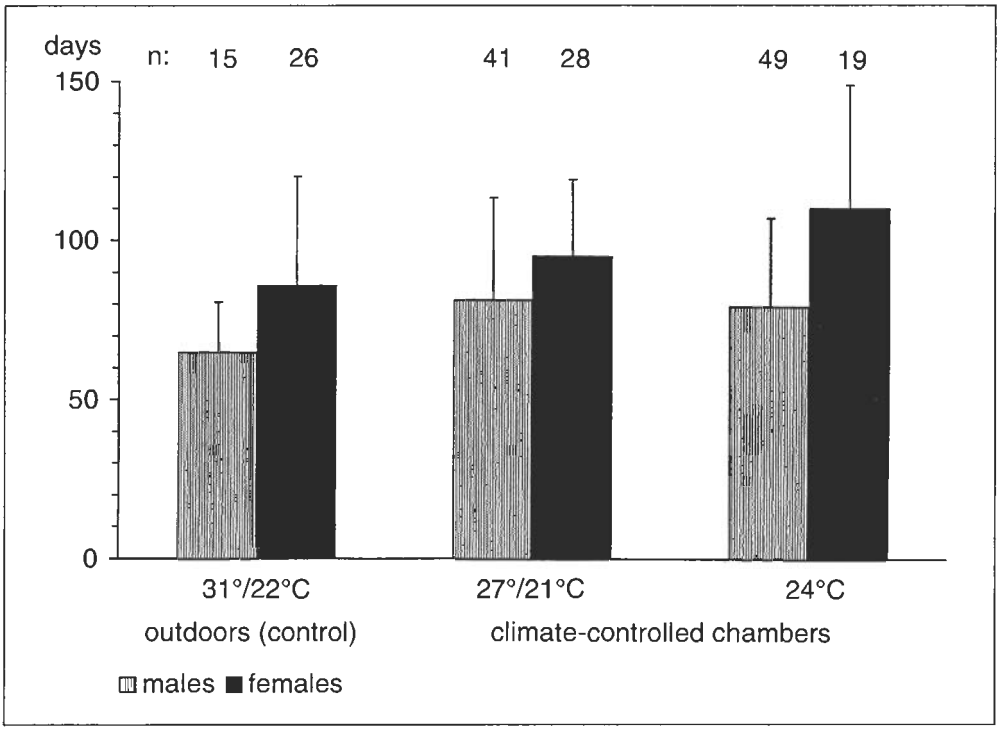

FIG. 2. Average life span of adult *Pentacomia egregia* (Chaud.) kept in climate-controlled chambers and outdoors under non-flooded and simulated flooded conditions (Febr.–Sept. 1994).

characters were adaptations to floodplains of Central Amazonia. Three main questions remained that had to be studied experimentally: Is the life span in males shorter than in females, which would explain their death in the trunk region during the aquatic phase (Experiment I)? Does ambient air temperature induce a gonad dormany in females, which would explain copulation of males with immature females (Experiment II)? Does the presence of soil prevent gonad dormancy in females, which would permit continuous oviposition (Experiment III)?

MATERIALS AND METHODS

To test the three questions, adult *P. egregia* with immature gonads (n = 216 males, 248 females) were collected at the end of January through mid-April 1994 in an inundation forest at Lago Janauarí (03°20'S, 60°17'W). The study area was located on a spit between the Solimões-Amazon and the Negro Rivers, about 10 km from Manaus (for details see Adis & Righi 1989; Irmler 1975, 1976). Beetles were kept in climate-controlled chambers (at permanent 24°C or at 27°/21°C during day and night, with 12 hours of light and 12 hours of darkness, respectively). Each chamber contained isolated groups of males and females (Experiment I and II: 75 males, 110 females at 24°C, 82 males, 75 females at 27/21°C). They were kept in clear plastic containers with moist filter paper and a piece of bark, simulating flood conditions (≤ 10 animals per container). Another 42 beetles of each sex were kept in similar containers outside the laboratory under natural climatic conditions (approx. 31°/22°C; = control). In addition, six pairs of males and females kept on moist filter paper or a thin layer of moist peat soil in each chamber (not accepted for oviposition by the females), were offered a cube of clayey soil from the field (lenght 4 cm, width & height 3 cm each, mostly montmorillonite; Irion 1976), simulating non-inundared habitats for oviposition (Experimenr III). Another four pairs of

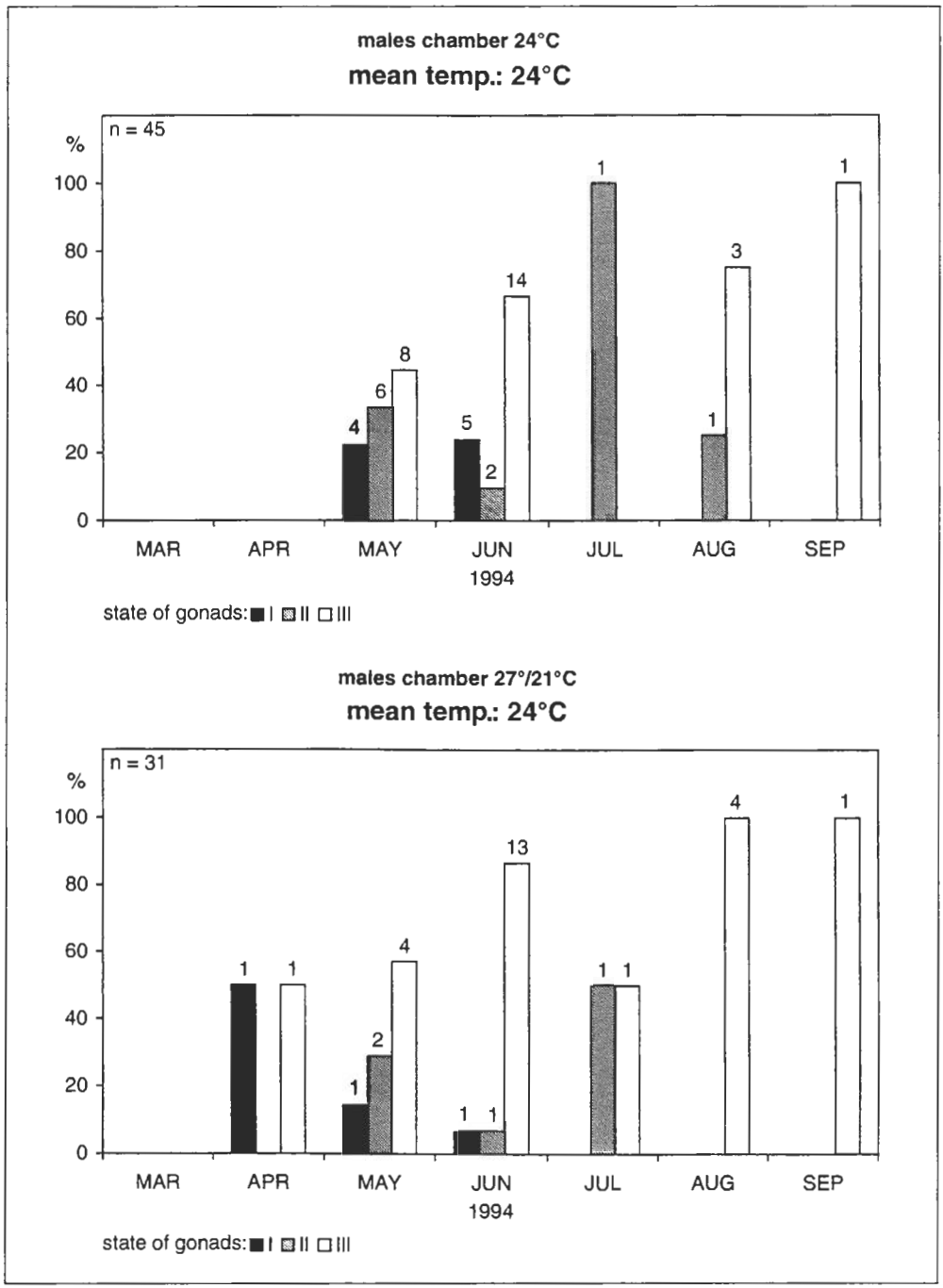

FIG. 3. State of gonads in males of *Pentacomia egregia* (Chaud.) kept in climate-controlled chambers under simulated flood conditions (Febr.- Sept. 1994): top: at a permanent mean temperature of 24°C; bottom: at a mean temperature of 24°C but oscillating between day and night (27°/21°C; see text for details).

males and females were tested outside the laboratory. All containers were checked daily for dead beetles (Experiment I, II), oviposition and larvae (Experiment III). All beetles were fed every third day with 50-60 *Drosophila* spp., pieces of tenebrionid larvae and/or grasshoppers. For the study of gonads (Experiment II) one third of all laboratory animals of both sexes were killed in June (the period of high waters in the field) and the remaining ones in September (the ending aquatic phase in the field). Data were complemented with the state of gonads observed in specimens which died in the experiment, if determinable (rapid deterioration due to high temperatures). In total, three states of gonads were differentiated:

(I) immature state
  - males: small accessory glands
  - females: ovarioles not differentiated

(II) maturing state
  - males: medium-sized accessory glands
  - females: oocytes clearly differentiated

(III) mature state
  - males: large accessory glands spermbundles (spermiozeugma) obvious
  - females: mature eggs in the ovary

The study of gonads (Experiment II) was repeated in the following year with 90 immature females, taken from the inundation forest in April/May 1995 (cf. Fig. 6). Now, 30 adults each were kept at permanent 24°C, at 27°/21°C or at 29°/24°C (12 hours of light) on moist filter paper in clear plastic containers (simulated flood conditions) and fed 50–60 *Drosophila* spp. every third day. The state of gonads was determined, if possible, in females which died in the experiment.

Seasonal inundation forests in Central Amazonia are subject to a rainy season (December–May: average precipitation 1550 mm) and a period of low precipitation (June–November ("dry season"): average precipitation 550 mm, but every month has some rain; cf. Ribeiro & Adis 1984).

In 1994, the forest at Lago Janauarí was flooded from end of March to early September (23 weeks). The state of gonads in beetles on the study area (Experiment II) was monitored at the beginning of the aquatic phase (March/April), during high waters (July) and during the end of the aquatic phase (August; n = 33 males, 30 females).

In 1995, the study site was flooded from the end of May to the end of July (9.5 weeks). The state of gonads in females on the study area (n = 97) was monitored twice per month from January to August, covering both the terrestrial and aquatic phase.

RESULTS AND DISCUSSION

Experiment I: Is the life span of males shorter than in females?

Tiger beetle adults in non-flooded Central Amazonian upland forests (terra firme) live 3 months at most. In a related univoltine species, *Pentacomia ventralis* Dejean, no dormancy is observed in adult females, but development of larvae is long (e.g., 9.5–14.5 months due to a larval domancy; Paarmann *et al.* 1998). Adult females of the univoltine *Pentacomia egregia* live 7 months at least (cf. Fig. 1), show a dormancy, and development of larvae takes 6 months at most (cf. Amorim *et al.* 1997).

Our results showed, that males of *P. egregia* captured in 1994 lived between 65 and 79 days on average, but females survived between 86 and 110 days (Fig. 2). Data reconfirmed results of Amorim *et al.* (1997), where the average life span of newly hatched males captured in 1993 was 51–67 days but 82–103 days in females under four different conditions in climate-controlled chambers (12 and 24 hours of light at 27°C or 24°C, and 12 hours of light at 27° and 12 hours of darkness at 21°C as well as under natural conditions; ANOVA: differences between males and females significant for $P < 0.05$). The mean of average life span calculated for all these experiments (in 1993 according to Amorim *et al.* 1997 & in 1994 according to this paper) was 64.1 ± 21.6 days in males (n = 109) and 93.4 ± 29.5 days in females (n = 134), i.e., females did live longer (Chi^2-test: difference significant for $P < 0.05$), even under different climatic and photoperiodic conditions.

Experiment II: Does ambient air temperature induce a gonad dormancy in females?

Studies of Paarmann (1976, 1979, 1986) on tropical ground beetles in Africa showed, that temperature can be a synchronizer or "zeitgeber" for gonad dormancy. A change of the average daily temperature or a combination of the average temperature and amplitude of daily temperature was considered important.

Irmler (1985) postulated, that a body of water within the flooded inundation forest has a buffering effect on the air temperature variation between day and night, and this might cause the gonad dormancy

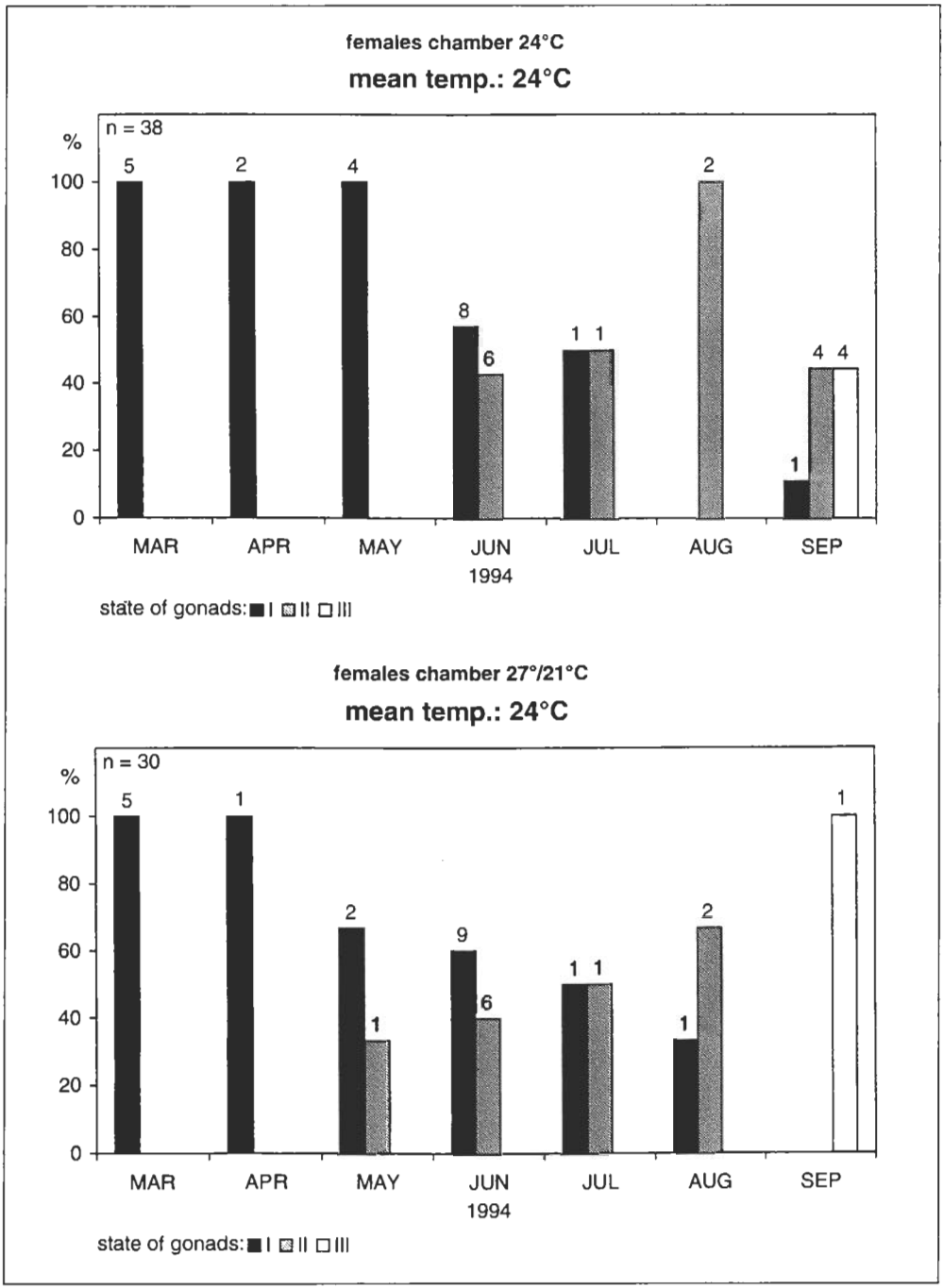

FIG. 4. State of gonads in females of *Pentacomia egregia* (Chaud.) kept in climate-controlled chambers under simulated flood conditions (Febr.–Sept. 1994): top: at a permanent mean temperature of 24°C; bottom: at a mean temperature of 24°C but oscillating between day and night (27°/21°C; see text for details).

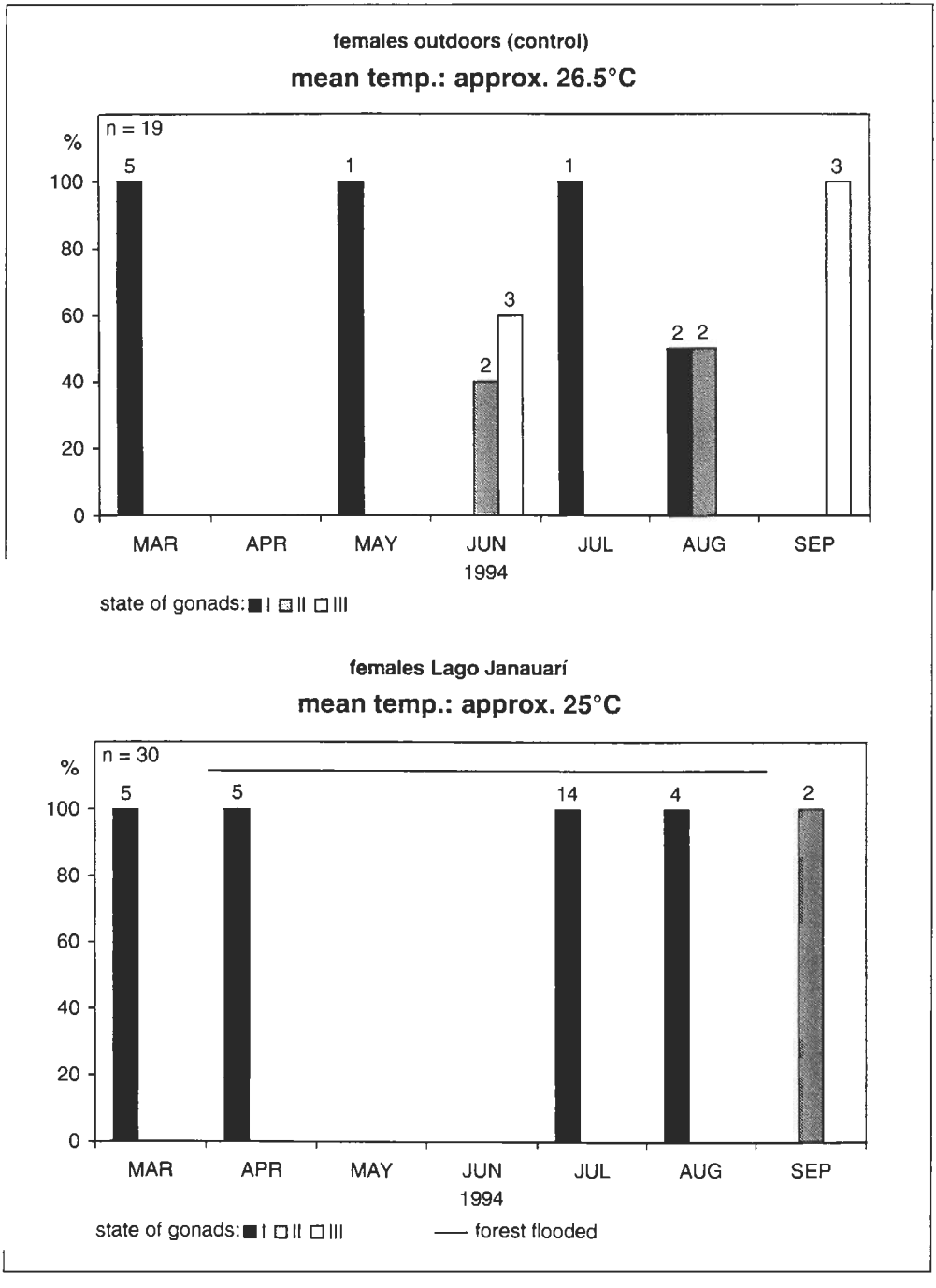

FIG. 5. State of gonads in females of *Pentacomia egregia* (Chaud.): top: kept outdoors under simulated flood conditions from February to September 1994 (control experiment); bottom: collected in the field between March and September 1994 (forest flooded from mid-April to early Sept.; see text for details).

in females of *P. egregia* but not in males. His hypothesis was based on experiments under controlled climatic conditions in Germany, where 14 beetles were kept under day-night temperature fluctuations measured in the field during non-inundation (22° *vs.* 30°C) and during inundation (26° *vs.* 30°C). However, this experiment did not reveal if it was the minimum or average temperature of the air which caused the gonad dormancy in females.

Our results under simulated flood conditions in 1994 (Fig. 3) showed no gonad dormancy in males at a mean air temperature of 24°C, either oscillating between day and night (27° *vs.* 21°C) or non-oscillating (permanent 24°C). First mature beetles were observed in April/May, i.e., only 8 weeks after they have been captured with immature gonads in the field. Females did show a gonad dormancy: first mature beetles were observed only from September onwards, but no statistical difference was found in the state of gonads between the two temperature regimes (Fig. 4; ANOVA: $P < 0.05$). However, if the mean temperature was higher, as for example in our outdoor control experiment behind the laboratory (Fig. 5: approx. 26.5°C), the mature gonad state in females was observed earlier than in the field or under controlled climatic conditions at 24°C in the laboratory (June *vs.* Sept./Oct.; Figs. 4, 5).

Results in 1995 showed that immature females from the field (cf. Fig. 6) attained maturing gonads within 4 weeks (Fig. 7) if maintained at a controlled mean air temperature of 26.5°C (oscillating between day and night: 29° vs. 24°C), i.e., 2.5 degrees higher than at permanent 24°C or at 27°/21°C. In the latter conditions, both representing a mean air temperature of 24°C, females with maturing gonads were only observed 3–4 months after capture (Fig. 8: in July at 24°C, in August at 27°/21°C; Chi^2-test: difference significant for $P < 0.01$).

We therefore conclude that the mean temperature of the air is influencing gonad development in females: A higher mean temperature results in a faster

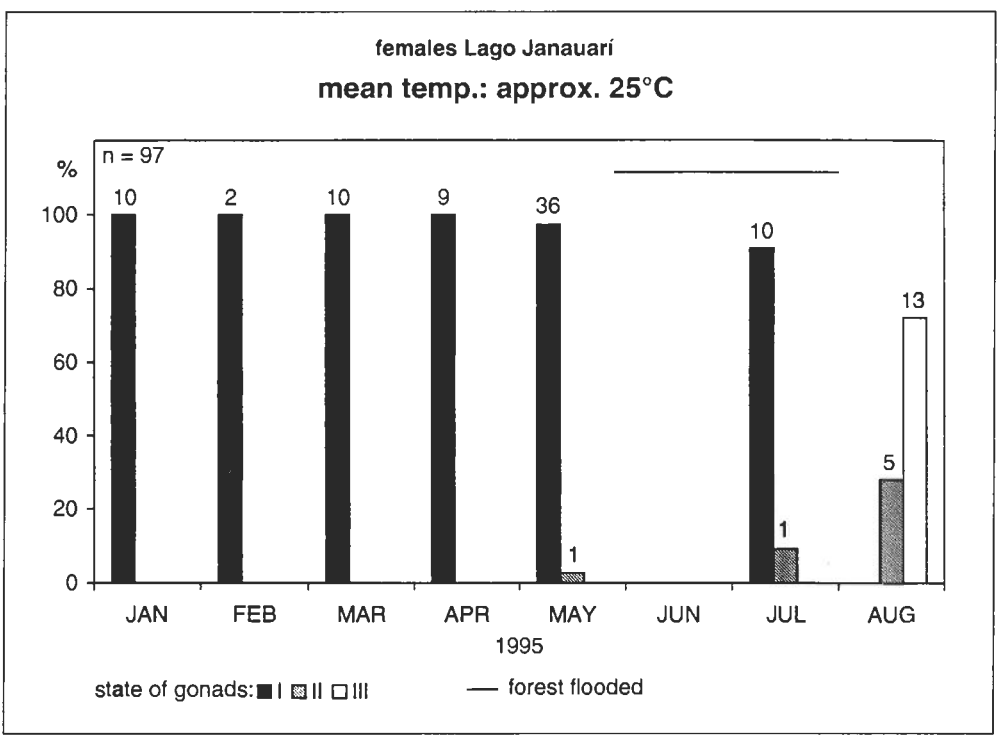

FIG. 6. State of gonads in females of *Pentacomia egregia* (Chaud.) collected in the field between January and August 1995 (forest flooded from end of May to end of August; see text for details).

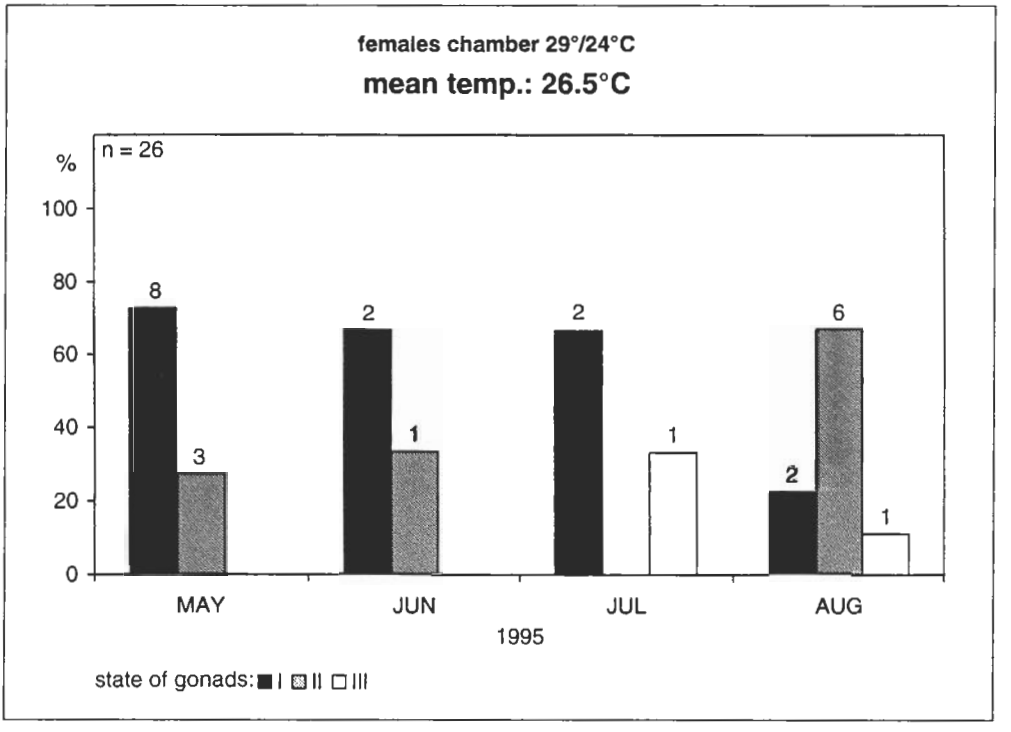

FIG. 7. State of gonads in females of *Pentacomia egregia* (Chaud.) kept in climate-controlled chambers under simulated flood conditions (April/May–Aug. 1995) at a mean temperature of 26.5°C but oscillating between day and night (29°/24°C; see text for details).

gonad maturation. In males, gonad development is independent of air temperature; mature gonads are observed 2-4 months after hatching (cf. Amorim *et al.* 1997) and copulation with immature females can take place before the males die in the flooded forest.

Experiment III: Does the presence of soil prevent gonad dormancy in females?

Females of many species of tiger beetles only lay eggs, if an appropriate substrate is available in their habitat (cf. Knisley 1987, Shelford 1912, Willis 1967).

All females of *P. egregia* which were offered clayey soil in our experiment laid eggs 4–6 weeks later, independent of temperature conditions, and the larvae hatched within 12–23 days. Oviposition of these animals, which were young in age, was observed to be continuous over a period up to two months (cf. Fig. 9). Animals older in age had shorter periods of oviposition (up to 30 days; cf. Amorim *et al.* 1997). Oviposition and hatching of larvae also occurred in lower numbers, when a thick layer of moist peat soil (> 3 cm) or sand had been offered as substrate instead of clayey soil as in nature (Amorim, unpubl.).

Those females kept under simulated flood conditions did not lay eggs, not even on the bark or on the wall of the container. When females passed four months under simulated flood conditions and were then offered clayey soil, oviposition was observed thereafter.

CONCLUSIONS

The presence of soil is considered the primary control mechanism, i.e., a primary or proximate (eco)factor (cf. Schaefer 1992 for definitions) that induces oviposition in females of *P. egregia*. The mean temperature of the air induces gonad dormancy and enhances longevity in females during the aquatic phase. It apparently has evolved as a cue for an adapa-

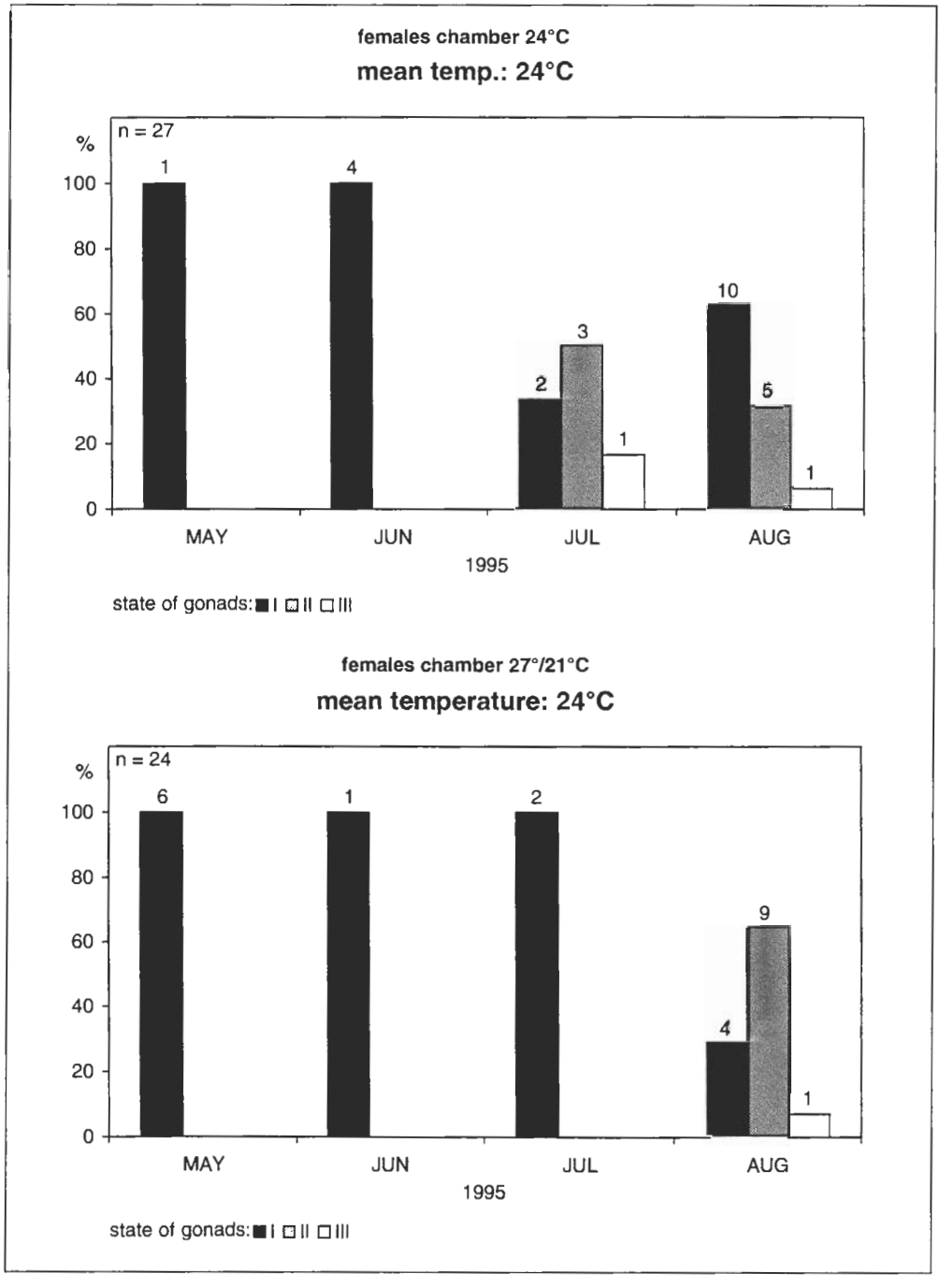

FIG. 8. State of gonads in females of *Pentacomia egregia* (Chaud.) kept in climate-controlled chambers under simulated flood conditions (April/May–Aug. 1995): top: at a permanent mean temperature of 24°C; bottom: at a mean temperature of 24°C but oscillating between day and night (27°/21°C; see text for details).

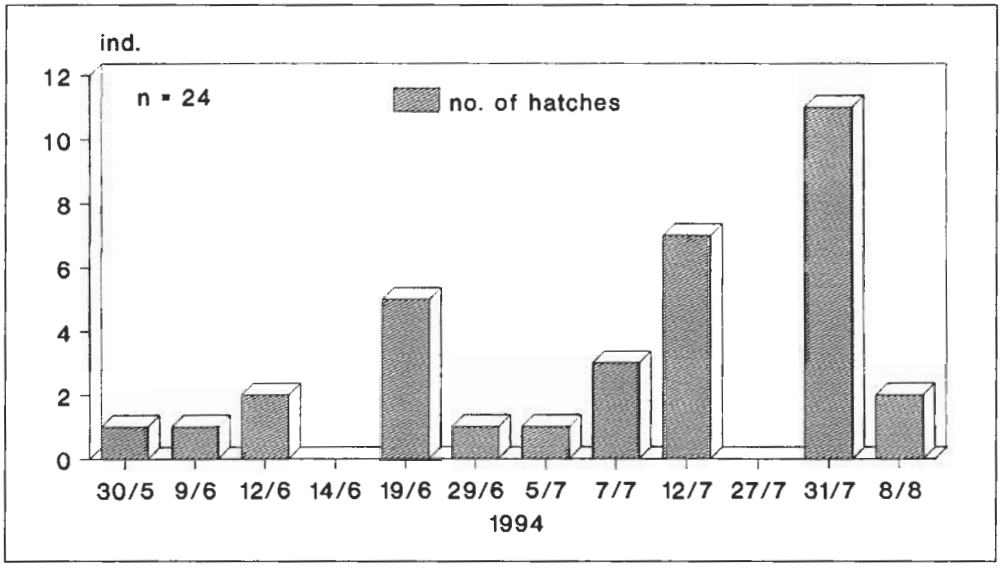

FIG. 9. Number of larvae (ind.) obtained in 1994 from one pair of *Pentacomia egregia* (Chaud.) under non-flooded conditions at permanent 24°C in a climate-controlled chamber.

tion to survive inundation as an ultimate (eco)factor. In nature, an increase of the mean air temperature is caused by two events: (1) by the body of water inside the inundation forest with highest water temperatures measured during high-water level in June/July (cf. Irmler 1985); (2) by the beginning period of low precipitation and highest insolation values observed in July/August, during falling waters, as well as highest air temperatures measured in the Manaus area between August and October (cf. Ribeiro & Adis 1984), i.e., when the flood waters recede from the inundation forest. A shorter aquatic phase (9.5 weeks in 1995) therefore resulted in a faster maturation of gonads in females when compared to a longer lasting inundation (23 weeks in 1994).

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