Treeholes as Calling, Breeding, and Developmental Sites for the Amazonian Canopy Frog, *Phrynophyas resinifictrix* (Hylidae)

LUÍS SCHIESARI, MARCELO GORDO, AND WALTER HÖDL

In this paper, we present information on the natural history, reproductive and developmental strategies of the canopy treefrog *Phrynophyas resinifictrix*. *Phrynophyas resinifictrix* is a widespread Amazonian species breeding exclusively in water-filled treeholes in terra-firme rain forests. Females laid relatively large, floating egg masses in the treeholes. Gut content analyses indicated that tadpoles are generalists and predominantly macropagous, basing their diet on detritus and conspecific fertilized eggs of younger cohorts. Tadpole guts were found to contain up to 62 intact eggs. This cannibalistic interaction is presumably of major importance for the completion of the larval stage and may result in depletion of entire egg complements. Strong site fidelity, interference competition for treeholes by territorial males, continuous use of treeholes year after year, repeated oviposition in treeholes, and temporal constancy in density of calling males are consistent with the hypotheses that adequate treeholes are a limiting resource for *P. resinifictrix* populations, or that location of unoccupied treeholes in the rain-forest canopy involves substantial risk or energetic costs.

Neste artigo apresentamos informações sobre a história natural, e sobre as estratégias reprodutivas e de desenvolvimento, da perereca do dossel *Phrynophyas resinifictrix*. *Phrynophyas resinifictrix* é uma espécie amplamente distribuída em florestas pluviais tropicais de terra-firme da Amazônia que se reproduz exclusivamente em ocos-de-árvore preenchidos com água. Nestes ocos as fêmeas depositam desovas flutuantes relativamente grandes. A análise de conteúdos intestinais revelou que os gê ninhos possuem hábitos alimentares generalistas e predominantemente macrofágicos, sendo a dieta baseada em detrito e ovos fertilizados coespecíficos de coortes posteriores. Encontramos nos intestinos um máximo de 62 ovos intactos. Esta interação canibalística é presumivelmente de grande importância para a completação do desenvolvimento larval, mas pode resultar na eliminação de desovas inteiras. A presença de forte fidelidade ao sítio reprodutivo, competição de interferência entre machos territoriais, utilização contínua de ocos-de-árvore ano após ano, ovipostura repetida em ocos-de-árvore, e a constância temporal na densidade de machos vocalizantes são observações consistentes com a hipótese de que ocos-de-árvore adequados constituem recurso limitante para populações de *P. resinifictrix*, ou que a localização de ocos-de-árvore desocupados no dossel da floresta envolve risco ou custos energéticos substanciais.

PHYTOTELMS are plants or parts of plants that hold rainwater, such as palm leaf fronds and axils, bracts, inflorescences, fruits, bromeliads, and treeholes. These water bodies may increase the habitat available for aquatic organisms up to 50,000 liters per hectare in some moist tropical locations (Fish, 1983). However, animal development in phytotelms is constrained by several physico-chemical, as well as biological properties. Among these are the small water volumes, low turnover rates of the accumulated water, and predominance of decaying processes resulting in low levels of dissolved oxygen, and low availability and predictability of food. Nevertheless, the use of phytotelms as breeding and/or developmental sites is found in four of the more than 30 reproductive modes exhibited by amuran amphibians (Duellman and Trueb, 1986; Haddad and Hödl, 1997; Haddad and Sawaya, 2000), and at least five tadpole ecomorphotypes are associated with life in these microhabitats (Lannoo et al., 1987).

Herein, we present data on the biology of the Amazonian hyloid treefrog *Phrynophyas resinifictrix* (Goeldi, 1907), known locally as caniuru, caniuaru, or canoêiro (Lutz, 1973). *Phrynophyas resinifictrix* is known from undisturbed Amazonian terra-firme and occasionally flooded rain forests in scattered localities in Peru, Bolivia, Ecuador, Colombia, Venezuela, Brazil, Suriname, and French Guiana (Frost, 1985; pers. obs.). Males call from widely spaced treeholes in primary for-
est. Long-range communication is effected with a loud, low-pitched call, which is carried for long distances through the use of the rain forest low frequency window (Zimmerman and Höddl, 1988; Höddl, 1991). When present, the hollow portion of the treehole may act as a resonating chamber, increasing the broadcasting distance for the calls (Höddl, 1991).

*Phrynoidas resinafictrix* tadpoles collected from treeholes have been the subject of detailed ecophenological studies (Grillitsch, 1992; Schieszari et al., 1996), which predicted an ability to ingest large food particles and a reliance on pulmospary as well as branchial respiration. With the exception of the studies mentioned above, very little information is available about the ecology of this species.

We show here that *P. resinafictrix* is capable of completing its entire life cycle in the forest canopy by breeding exclusively in large, water-filled treeholes. We present data on the physical and biological aspects of the treeholes used as calling and breeding sites by the species, as well as estimates of calling male population densities. Quantitative dietary data are examined to clarify the strategies allowing completion of metamorphosis in these unproductive microhabitats. We discuss the importance of predation of eggs and larvae, and low interspecific competition, as major forces maintaining oviposition in phototels. Finally, we discuss the hypothesis that treeholes constitute a limiting resource for *P. resinafictrix* populations and suggest that males monopolizing treeholes may obtain multiple mates.

**Materials and Methods**

Fieldwork was conducted in two Amazonian terra firme rain-forest sites: Panguana, Peru (lower Rio Maynasapur, 5°37'S, 74°56'W), by WH from October to November 1988, and the Reserva Florestal Adolfo Ducke (hereafter referred to as “Manaus”), located about 25 km north of Manaus, Amazonas (0°38'S, 60°02'W), by LS and MG from November 1990 to March 1991 and from January to April 1993. Sporadic, additional observations were conducted from January to June 1994 and from August to October 1994. Annual rainfall is 2635 mm in Panguana (Aichinger, 1987) and 2075 mm in Manaus (mean values from 1931 to 1960; Brasil, 1978). The rainy season occurs between September and May (Panguana) or December and May (Manaus), with monthly rainfall of more than 200 mm, whereas the driest months, July and August (plus September in Manaus), receive less than 60 mm each. It is noteworthy that during the study period mean annual rainfall in Manaus was 2650 mm, 30% higher than the average (data collected at an EMBRAPA meteorological station 5 km north of the study site).

We searched for calling males while walking along a single trail 1470 m long in Panguana (totaling at least 94 km walked in 32 nights) and along a system of trails 8854 m long in Manaus (totaling at least 151 km walked in 36 nights in 1990/1991, and 145 km walked in 57 nights in 1993). We located the trees from which male frogs were calling by approaching the source of the loud call during the night and subsequently pressing an ear tightly against tree trunks. The trunk hosting the calling male was the one that best conducted sound vibrations. Whenever possible, treeholes were reached either by means of ladders, “griffes” (metal hooks with spikes used for tree climbing; see Mori, 1987, for description and illustration), or mountaineering equipment. We located 10 trees in Panguana and 19 in Manaus and were able to inspect three and seven treeholes, respectively.

We estimated the density of calling males by dividing the number of regularly calling males (the abundance) by the length of trails walked (individuals/km; linear density) and by the area acoustically sampled (individuals/ha; density by area). To estimate the area acoustically sampled, we multiplied the length of trails walked by twice the maximum distance inside the forest in which calls were above ambient noise levels. These were determined with a CEL-493 Precision Impulse Integrating Sound Level Meter and a CEL-296 Third Octave Autoscan Filter Set. Although, in some cases, calls were within human hearing range from distances up to 250 m, sound pressure levels were consistently above the ambient noise level at a maximal distance of 160 m at the 800 Hz terz filter band. At this frequency and distance, sound levels were between 24 dB and 32 dB (linear, peak, relative to 20 μN/m²). Therefore, we employed the conservative value of 160 m for our estimates of area acoustically sampled.

We also measured diameter at breast height (DBH) of the host tree, dimensions of the treehole opening, water surface and depth of the treehole, and its height. Treehole water volumes were either directly measured by sucking out water through a hose and pouring it into a measuring cup or estimated by employing the cylinder volume formula to the water surface and treehole depth measured. A cylindrical model appears to be a good estimator of treehole shape: no significant differences were found between the actual and estimated volumes of three treeholes for which both sets of
data are available (Student t-test, t = 0.68, P = 0.57).

Treeholes were inspected for 20–30 min on one to 30 occasions, depending on accessibility. Treehole limnological parameters were measured on 19 March 1994 and 31 May 1994 (Manaus). Values of pH, dissolved oxygen concentration (DO), and algal chlorophyll concentration (as a measure of phytoplankton standing crop) of the surface water present in four treeholes, two bromeliads, a small temporary pond, and a dammed creek were analyzed. We determined pH with a Corning pH meter 130, and DO with an YSI Dissolved Oxygen meter either in situ or on the ground, after 500 ml of water were collected with minimum disturbance. Chlorophyll a was extracted from 250 ml of water and analyzed in spectrophotometer for extinctions at 750 Å (Strickland and Parsons, 1968). Classification of water body trophic type (productivity) followed Wetzel (1983).

Eggs and tadpoles were collected with small circular nets or sucked with a hose and preserved in 5% formalin. Identity of larvae was confirmed by rearing until metamorphosis or by the aid of literature sources (Hero, 1990; Gritlisch, 1992; Schiessari et al., 1996). Voucher specimens were deposited in the Museum of Zoology of the University of São Paulo (MZUSP 128321). Larvae were staged according to Gosner (1960). To quantify the dietary habits of tadpoles from Manaus, we analyzed the gut contents of 32 tadpoles of several developmental stages ranging from Gosner (1960) stage 25 to 42 from a single treehole. These tadpoles were collected in four samples taken at roughly monthly intervals for a period of five months in the rainy season. For a comparison among treeholes, we analyzed gut contents of three to five tadpoles in the same developmental stage (stage 25) collected at one time from four treeholes. We used the following procedure: After removing the entire intestinal mass, a fragment of 1 cm of the foregut was taken and its contents suspended in 0.1 ml of distilled water on a microscope slide and examined at a magnification of 250 to 400X. We quantified the contents by randomly selecting 10 microscopic fields per slide and noting the presence or absence in each field of the following five food categories: detritus (nonidentifiable, particulate organic matter); plant fragments; algae; arthropod fragments; and anuran eggs. Dietary composition was expressed as mean ± 1 SE of the percentages of occurrence of each food item in the individuals analyzed. Because more than one food category may be present per microscopic field, the sum of the frequencies of occurrence of all categories may exceed 100%. When guts were filled with eggs, the abundance of this item was assumed to be 100%. We then counted intact eggs for the length of the digestive tract. Partially or totally digested eggs could be identified by the texture of residue and confirmed by the observation of yolk platelets under microscopic examination. To determine whether ingested eggs were fertilized, embryonic development was ascertained by external morphology (Gosner, 1960) and by histological analysis of some hematoxylin-eosin stained eggs of at least one tadpole gut per sample. The latter procedure provided evidence of early embryonic development, which might not be easily detected by external morphology.

RESULTS

Treeholes.—Treeholes used by calling males of P. resinaeformis occurred from 2.2–32 m high in trees with DBH ranging from 13–92 cm (mean ± SE: 44.9 ± 6.2 cm, n = 15). No significant differences in DBH were found between trees used in Panguana and Manaus (Student t-test, t = 0.22, P = 0.83).

Treehole openings were circular to elliptical, with areas ranging from 62.8–451.4 cm² (180.4 ± 39.6, n = 10; Table 1). Treeholes invariably faced upward, thus allowing the replenishment of evaporating water via rainfall and the accumulation of allochthonous organic matter. Bottoms of treeholes were usually covered by one or more layers of dead leaves and decaying organic matter. There was no sign of resin lining on the treehole as described by Goeldi (1907). Treehole depth ranged from 15–190 cm (86.6 ± 27.7 cm, n = 9; Table 1). Treehole water volumes varied from 0.6–90.0 liters (18.2 ± 9.3 liters, n = 9), but tadpoles were found only in treeholes larger than 2.8 liters (Table 1). Considering only treeholes sampled during the rainy season, maximum tadpole abundance showed no association to treehole height (r = 0.17) but was positively associated with treehole water volume (r = 0.38, F = 19.83, P = 0.0043), as indicated by linear regressions. No associations were found between maximum tadpole density and treehole height (r = 0.77) or volume (r = 0.78).

Water was less acidic in treeholes (pH = 6.81 ± 0.23, range 5.90–6.90, n = 4) than in pond (5.64), creek (4.00), or bromeliads (3.78 ± 0.2, range 3.57–3.98, n = 2). Treeholes nearly bracketed the variation in DO found in other water bodies. DO in treeholes varied from 0.2–3.9 mg/l (2.3 ± 1.1 mg/l), when compared to the pond (0.9 mg/l), bromeliads (2.7 ± 0.6 mg/l),
range 2.1–5.3), and creek (4.1 mg/l). Phytoplankton chlorophyll a concentration was lowest in the creek (0.31 ug/l; ultraoligotrophic), followed by treeholes (0.88 ± 0.32 ug/l, range 0.15–1.65; ultraoligotrophic to oligotrophic) and pond (4.49 ug/l; mesotrophic). See Magnusson and Hero (1991) for limnological parameters of additional terrestrial water bodies at the Manaus study site.

Treeholes used by males of *P. resinifictrix* were formed in the main trunk after the decaying and breaking of larger branches; some trees seemed to be in poor condition, and at least two were decaying. In Manaus, seven of the trees were identified in the field as *Eschweilera cf. odorata*, Lecythidaceae (*n* = 3 individuals); *Aspidosperma abscusinerve*, Apocynaceae; *Trichilia* sp., Meliaceae; unidentified Caricaceae; and unidentified Mimosaceae. In Panguana, one of the trees was an unidentified Moraceae.

**Adult behavior.**—Males called exclusively from treeholes. On no occasion was this species found in any of the intensively sampled terrestrial water bodies or of in other, smaller photo-plumes commonly found in the study areas such as buriti palm leaf axes (*Mauritia flexuosa*) or ground bromeliads (*Guzmania* spp., *Streptocalyx* spp.). Males often called from sundown (1850 h) until sunrise (0655 h), when they often left the treehole but remained in the canopy. Calling season lasted from August to April, although a few called regularly during the dry season. Males appeared to show strong site fidelity. Calls were heard from the same trees night after night. In Panguana, one male continuously returned to the same treehole for a period of 20 nights. In Manaus, we toe-clipped and recaptured a male in treehole 2 four months later (1990). In the following field season (1993), we toe-clipped and recaptured three males aggressively interacting inside the same treehole on four occasions over two months. Aggressive interactions between males were common and included a particular calling repertoire (Zimmerman and Hödl, 1983) and physical attempts to impede the opponent to enter or remain in the treehole.

Treeholes were often occupied in multiple years. For example, five of the six surviving trees used in 1990 were still occupied in 1998, and five of nine trees used in 1993 were still occupied in 1994.

**Abundance of calling males.**—Calling males of *P. resinifictrix* were widely spaced in the forest. We found 4.8 calling males/km (0.15/ha) in Panguana and from 1.7–2.0 calling males/km (0.05–0.06/ha) in Manaus (Table 2). Abundances were 2.4–2.8 times higher in Panguana than in Manaus. Densities were remarkably constant in Manaus during the study period.

**Prenmetamorphic biology: Eggs.**—Egg clutches are laid in water and consist of a gelatinous egg mass that primarily floats on or near the surface but often adheres to the inner wall of the treehole. The darkly pigmented eggs are small (diam 1.58 ± 0.06 mm, *n* = 6) and surrounded by gelatinous capsules (diam 4.28 ± 0.21 mm, 

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**Table 1. Characteristics of Treeholes Used by *Phrynobates resinifictrix*, and Maximum Abundance and Density of Tadpoles Observed per Treehole.**

<table>
<thead>
<tr>
<th>Number</th>
<th>IDH (cm)</th>
<th>Height (m)</th>
<th>Opening (cm)</th>
<th>Depth (cm)</th>
<th>Volume (L)</th>
<th>Max. abundance (No. ind.)</th>
<th>Max. density (ind./L)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manaus 1</td>
<td>34</td>
<td>1.11</td>
<td>13 × 13</td>
<td>190</td>
<td>25.3°</td>
<td>237</td>
<td>9.37</td>
</tr>
<tr>
<td>2</td>
<td>15</td>
<td>0.5</td>
<td>11 × 11</td>
<td>59</td>
<td>5.8°</td>
<td>93</td>
<td>16.12</td>
</tr>
<tr>
<td>3°</td>
<td>49</td>
<td>0.32</td>
<td>23 × 25</td>
<td>35</td>
<td>15.8°</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>—</td>
<td>0.12</td>
<td>15 × 15</td>
<td>19</td>
<td>6.6°</td>
<td>33</td>
<td>5.02</td>
</tr>
<tr>
<td>5</td>
<td>—</td>
<td>0.08</td>
<td>20 × 15</td>
<td>32</td>
<td>8.1°</td>
<td>129</td>
<td>15.72</td>
</tr>
<tr>
<td>6</td>
<td>32</td>
<td>1.45</td>
<td>21 × 21</td>
<td>260</td>
<td>90.0°</td>
<td>337</td>
<td>3.74</td>
</tr>
<tr>
<td>7</td>
<td>27</td>
<td>0.13</td>
<td>15 × 15</td>
<td>75</td>
<td>8.9°</td>
<td>10</td>
<td>1.15</td>
</tr>
<tr>
<td>Panguana 1</td>
<td>37</td>
<td>0.52</td>
<td>14 × 07</td>
<td>70</td>
<td>2.8°</td>
<td>8</td>
<td>2.86</td>
</tr>
<tr>
<td>2</td>
<td>27</td>
<td>1.04</td>
<td>20 × 08</td>
<td>—</td>
<td>—</td>
<td>9°</td>
<td>—</td>
</tr>
<tr>
<td>3</td>
<td>33</td>
<td>9.22</td>
<td>10 × 08</td>
<td>15</td>
<td>0.6°</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

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*Treehole volumes were either directly measured or estimated.

*1* Treehole examined at the end of the dry season.

*2* Tadpoles of *Deudoraphis guianensis* species group.
Table 2. Seasonal Estimates of the Abundance and Density (Linear and by Area) of Calling Males of Phrynohyas resinifera in Panguana and Manaus.

<table>
<thead>
<tr>
<th>Season</th>
<th>Abundance of calling males</th>
<th>Density of calling males</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Linear (males/km)</td>
<td>Area (males/ha)</td>
</tr>
<tr>
<td>Panguana 1988</td>
<td>7</td>
<td>4.8</td>
</tr>
<tr>
<td>Manaus 1990/91</td>
<td>10</td>
<td>1.9</td>
</tr>
<tr>
<td>1993</td>
<td>9</td>
<td>1.7</td>
</tr>
<tr>
<td>1994</td>
<td>5</td>
<td>2.0</td>
</tr>
</tbody>
</table>

n = 6). At the moment of collection, clutch size varied from 106–1540 eggs (436 ± 234 eggs, n = 6), with as many as six clutches laid in a single treehole during a period of four months (December 1990 to April 1991).

Larval diet.—The diet of P. resinifera larvae consists largely of conspecific eggs and detritus; less common items include algae, plant fragments (mainly leaf fragments, but also pollen), and arthropod fragments (insect mouthparts, heads and wing fragments, lepidopteran scales, and mosquito larvae bristles; Table 3).

Fifty-two percent of all guts examined (n = 44) contained eggs in different phases of digestion (Table 3). Tadpoles from stages 32–42 were able to swallow whole eggs with capsules, and sometimes gelatin (Fig. 1), whereas smaller tadpoles ingested egg fragments presumably rasped with their keratinized mouthparts. When eggs were available, individuals ingested as many as possible and their guts became greatly extended. The enlarged foregut contained up to 62 whole eggs (Fig. 1), plus partially digested eggs that could not be counted. Most eggs examined were fertilized, as indicated by external or histological observation of cell cleavage and embryo development (up to stage 16). Four of six clutches laid during a five-month period in treehole 2 at Manaus contained fertilized eggs; the two others could not be analyzed because no eggs remained in the gelatinous mass by the time of observation.

Detritus was the second most frequent food item consumed, observed in 44.6% of microscopic fields; when eggs were not available, de-

Table 3. Diet of Phrynohyas resinifera Larvae. Occurrence expressed as Mean % ± SE.

<table>
<thead>
<tr>
<th>Stages</th>
<th>n</th>
<th>Algae (μm)</th>
<th>Plant fragments</th>
<th>Arthropod fragments</th>
<th>Detritus (μm)</th>
<th>Eggs (μm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Overall</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>One treehole sampled over five months</td>
<td>32</td>
<td>16.6 ± 5.1</td>
<td>10.0 ± 2.8</td>
<td>5.3 ± 1.6</td>
<td>35.9 ± 8.4</td>
<td>59.7 ± 8.7</td>
</tr>
<tr>
<td>Four treeholes sampled at one time</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>5</td>
<td>6.0 ± 2.5</td>
<td>18.0 ± 5.8</td>
<td>0.0 ± 0.0</td>
<td>58.0 ± 13.2</td>
<td>60.0 ± 18.2</td>
</tr>
<tr>
<td>25</td>
<td>4</td>
<td>15.0 ± 6.5</td>
<td>27.3 ± 10.3</td>
<td>7.5 ± 4.8</td>
<td>97.5 ± 2.5</td>
<td>0.0 ± 0.0</td>
</tr>
<tr>
<td>25</td>
<td>4</td>
<td>30.0 ± 4.1</td>
<td>20.0 ± 4.1</td>
<td>7.5 ± 7.5</td>
<td>75.0 ± 5.0</td>
<td>0.0 ± 0.0</td>
</tr>
<tr>
<td>25</td>
<td>3</td>
<td>30.0 ± 10.0</td>
<td>3.3 ± 3.3</td>
<td>0.0 ± 0.0</td>
<td>73.0 ± 2.2</td>
<td>30.0 ± 10.0</td>
</tr>
<tr>
<td>Total</td>
<td>44</td>
<td>17.5 ± 3.9</td>
<td>11.4 ± 2.3</td>
<td>4.6 ± 1.3</td>
<td>44.6 ± 6.7</td>
<td>52.3 ± 7.2</td>
</tr>
</tbody>
</table>
tritus occurrence reached 97.5% (Table 3). All other food items were found much less frequently. Algae were never abundant, although sporadically occurring in 17.5% of all microscopic fields, or up to 30% in tadpoles in early developmental stages. Plant fragments occurred in 11.4% of all microscopic fields or up to 27.5% in tadpoles in early developmental stages. Arthropod fragments were only present in 4.6% of all microscopic fields examined (Table 3).

**Discussion**

Nonaquatic oviposition behavior in frogs evolved independently in many lineages and has been interpreted as a strategy to avoid predation, competition, or unfavorable abiotic conditions in the ancestral water body (Crump, 1982; Duellman and Trueb, 1986). From an ecological rather than evolutionary perspective, these same processes might be currently operating to maintain arboreal oviposition. Magnusson and Hero (1991) studied an anuran assemblage at our Central Amazonian rain-forest field site. They found that the percentage of species with terrestrial eggs and aquatic larvae in a water body was positively correlated with an index of egg predation pressure in that water body but only weakly correlated with the number of species of potential competitors or abiotic conditions such as dissolved oxygen content, percentage of dry days, and temperature. These observations led the authors to suggest that predation is a major factor maintaining nonaquatic oviposition behavior in this contemporary anuran assemblage.

Oviposition in phytotelmats might also be maintained by the high predation pressure in terrestrial water bodies. Predation risk is presumably lower in phytotelmats because the height, small size, concealment, and often wide spacing of these water bodies reduce predator access to the eggs and tadpoles. In addition, unfavorable abiotic conditions in phytotelmats, such as the potentially low dissolved oxygen levels and short hydroperiod, constrain the survival of aquatic predators. In this study, few actual or potential predators of eggs (wasps, small dipteran beetles, and heterospecific ophiogloss and cannibalistic tadpoles), tadpoles (spiders), and adults (a colubrid snake, Philodryas viridissima) have been observed inside treeholes inhabited by P. resinifictrix. This contrasts strongly with the ubiquity of insect and fish predators found in ground water bodies at the study site (Magnusson and Hero, 1991).

In addition, our observations suggest that current interspecific competition among Amazonian frogs for phytotelmats as breeding and developmental sites is minimal and could be another important force maintaining oviposition in these water bodies. Only four of 130 lowland Amazonian frog species breed in phytotelmats (Hödl, 1990). Moreover, in Central Amazonia P. resinifictrix is the only anuran to breed exclusively in large, water-filled treeholes, whereas Osteocephalus ophagus breeds in a variety of phytotelmats, such as bromeliads, buriti (Mauritia flexuosa) palm leaf axils, palm bracts, and only occasionally in treeholes (Jungfer and Schiesari, 1995; pers. obs.). Calling adults, eggs or larvae of P. resinifictrix and O. ophagus were never found in the extensively sampled ground water bodies, indicating specialization for a phytotelmic breeding site. Yet tadpoles of these species were never found coexisting in any of the phytotelmats sampled, indicating strong habitat segregation. Several species of Dendrobates have terrestrial oviposition but transport tadpoles to phytotelmats after hatching; for instance, we observed in a single occasion Dendrobates cf. quinquenotatus inside treeholes from which P. resinifictrix called. More often, however, Dendrobates species use small-sized, ground phytotelmats (e.g., Caldwell and Araujo, 1998). Overall, this strong pattern of habitat segregation among phytotelm types, in which more than one species are seldom found to coexist, contrasts with ground water bodies, where typically more than three, and sometimes up to eight, tadpole species coexist (Magnusson and Hero, 1991).

Therefore, several lines of evidence suggest that both predation pressure and interspecific competition are lower in phytotelmats than in terrestrial water bodies and could contribute to the maintenance of the use of phytotelmats as breeding and developmental sites for Amazonian anurans in general and P. resinifictrix in particular. In other systems, however, an unavailability of terrestrial water bodies may act as a strong force maintaining phytotelm reproduction. This appears to be the case in Caribbean Islands such as Jamaica, where historical and geological factors result in phytotelmats being the predominant lentic water bodies (Thompson, 1996).

Phytotelmats are a harsh environment for the development of anuran embryos and larvae. Constrained volumes of noncirculating water dominated by decaying processes sometimes result in very low dissolved oxygen concentrations. Assuming that treehole breeding is derived in the genus Phrynopus, early development of large, inflated, functional lungs in other pond-dwelling species of the genus may be considered a useful morphophysiological trait
for the colonization of phytoelmats by *P. resinific-
trix*. Lungs are also used as hydrostatic organs
keeping tadpoles close to the water surface and
may reduce the energy expenditure involved in
repeatedly swimming to the surface to bob air
(Feder, 1984; Feder and Moran, 1985; Lannoo
et al., 1987).

An important biotic characteristic of phyto-
elmats is the unpredictability and low availability
of high quality food. In most tadpole species for
which dietary data are available, algae of pe-
riphyton and phytoplankton constitute major
food resources, in addition to low-quality detri-
tus (e.g., Alig and Johnston, 1989; Kupferberg
et al., 1994). Narrow trechole openings, often
covered by overlying canopy, may result in a
nearly aphotic habitat in which primary pro-
ductivity is low and, therefore, likely insufficient
to sustain tadpole growth.

Detritus derived from the decomposition of
fallen leaf litter and trechole walls constituted
the basis for the species’ diet when eggs were not
available. The nutritive value of detritus is
low (Kupferberg et al., 1994), and several spe-
cies of generalized pond tadpoles fail to reach
metamorphosis when restricted to this food type
(Werner and Olememeier, 1999; LS, unpubl.).
In this context, oophagy may be of major im-
portance for the success of individual larva in
reaching metamorphosis because eggs provide
a highly nutritious and energetic food source
(Crump, 1992). However, detritivory could also
be of crucial importance, especially for smaller
tadpoles. Prior to stage 32 tadpoles are gape-
limited and, therefore, inefficient egg feeders.
After this stage, tadpoles are capable of swallow-
ing large quantities of whole eggs, leading to
accelerated growth and development.

Opportunistic oophagy is common in anuran
larvae (Magnusson and Hero, 1991; Crump,
1995; Petranka and Kennedy, 1999). In several
phytotelm-developing anurans, however, ooph-
agy results from complex parental behavior in
which the mother periodically returns to the
phytotelm to lay fertilized or unfertilized eggs
for nutrition of its progeny (Lannoo et al., 1987;
Weygoldt, 1987; Crump, 1995). For some of
these species, it was demonstrated that oophagy
is obligate, that is, tadpoles fail to reach meta-
morphosis if eggs are not provided by the moth-
er (Weygoldt, 1987; Thompson, 1996; Jungfer
and Weygoldt, 1999). In *P. resinifictrix*, however,
there are several observations suggesting that
oophagy is opportunistic cannibalism rather
than parental care in the form of periodic egg
deposition for offspring nutrition. First, as noted
by Jungfer and Proy (1998), *P. resinific-
trix* egg clutches are large (maximum clutch size
in the field, 1,540 eggs, this study; in terraria,
4336 eggs, Jungfer and Proy, 1998) compared
to phytotelm-breeding species that intentionally
provide eggs to their offspring. For instance,
considering only hyrids, on average 158 eggs are
laid by *Anotoca spinoso* (Jungfer, 1996); 258 by
*Osteocephalus oophagus* (Jungfer and Weygoldt,
1999; 276 per bromeliad by *Osteopilus brunneus*
(Lannoo et al., 1987); and 13 by *Phyllodytes in-
todus* (Giacetta, 1996). Second, as a conse-
quence of the large clutch size, interclutch in-
terval is long in *P. resinifictrix* in a regularly sam-
pled trechole, six clutches were deposited over a
period of four months (around one clutch ev-
evry 20 days), which coincides with the inter-
clutch interval of pairs in captivity (20 days, range
7–37, n = 29; Jungfer and Proy, 1998). This long
interclutch interval contrasts strongly with the interclutch interval of species that are
known to be obligate oophagic. For instance,
eggs are deposited every 4.9 days in *A. spinoso*
(Jungfer, 1996), 5.1 days in *O. oophagus* (Jung-
fer and Weygoldt, 1999), and 4.4 days in *O.
brunneus* (Thompson, 1996). Jungfer and Proy
(1998) found that tadpoles of *P. resinifictrix*
starve if dependent only on the mother’s infre-
frequent oviposition as the food source; but that
metamorphic success in an experimental con-
tainer was high if, in addition to leaf-litter, eggs
were added every 17 days. Third, an opportu-
nistic oophagic nutrition is suggested by our ob-
servation that eggs are fertilized unlike some of
the more “advanced” forms of anuran parental
care through laying of unfertilized trophic eggs
(Weygoldt, 1987), although obligate oophagy
has been documented for species laying fertil-
ized eggs (Thompson, 1996). Fourth, although
extensive reduction of oral structures character-
izes several of the obligate oophagic, phytotelm-
developing species (Lannoo et al., 1987), *P.
resinifictrix* retains typical generalized pond-type
larval morphology with only moderate structural
reduction when compared to its pond breeding
congeners (Schicsari et al., 1996). Experi-
mental evidence is necessary to unambiguously
demonstrate that oophagy is not obligate in *P.
resinifictrix*, however, the arguments above pro-
vide indirect support for the hypothesis that
consumption of eggs is important but may not
be obligate for metamorphic success.

We suggest that among the premetamorphic
stages of *P. resinifictrix* life cycle, cannibalism and
intraspecific competition are the major forces
acting on the survival of eggs and larvae, re-
spectively. Evidence for this hypothesis are the
low nutritive value of trechole seafood; the voracious, oophagic habits of the tadpole
and the variable but potentially high larval densities found in the treeholes (up to 16 individuals/liter), which can deplete entire egg clutches.

In the species' original description, Goeldi (1907) reported and illustrated, in an apparent combination of Indian legend and personal observation, that P. resiniifatix constructs a basin made of carefully chosen tree resins inside hollow branches. This nest accumulates fresh water that remains uncontaminated by decaying wood, therefore providing "excellent conditions for the hatching and development of the eggs and tadpoles" (Goeldi, 1907). No sign of resin lining was observed in any of the treeholes sampled. Lutz (1973) attributed this misconception to the occasional use by the species of cavities that had been lined with wax by wild bees known to live in hollow trees.

In this paper, we demonstrated that P. resiniifatix is specialized for breeding in treeholes. Therefore, the availability of large, water-holding treeholes in the rain-forest canopy may have strong impacts on both individual behavior and population dynamics. Although we did not measure the availability of treeholes, the following evidence is consistent with the hypothesis of treeholes constituting a limiting resource for P. resiniifatix populations. Calling males show strong site fidelity and aggressive behavior in defense of the treehole, multiple males were often observed competing for a treehole. Treeholes were occupied most nights. A regularly monitored treehole had at least six egg clutches in a period of five months, indicating that males that monopolize a treehole may attain high reproductive success. All treeholes inspected housed tadpoles during the entire rainy season. Alternatively, if the cost or risk in locating a new, unoccupied treehole is high, males might cue the presence of adequate treeholes by other males' advertisement calls, and selection might as well favor strong male site fidelity and aggressiveness, male satellite behavior, and female oviposition in treeholes occupied by cannibalistic tadpoles. The alternative hypothesis, however, that treeholes are not a limiting resource but are expensive, in energy or risk, to search for and find might not explain the constancy in the density of calling males year after year, which is suggestive of resource limitation.

The ecology and evolution of the use of phytotelmata as developmental sites for anuran amphibians has been increasingly identified as a promising area of research. The present study contributes to the understanding of phytotelmatic habitats and of some of the most important traits involved in their colonization. Future research efforts should focus on experimental approaches to the study of the larval feeding ecology, and to the abiotic and biotic factors affecting the population dynamics of phytotelmatic anurans in general and P. resiniifatix in particular.

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DEBIOCIÊNCIAS, UNIVERSIDADE DE SÃO PAULO, CP 11461, 05422-970, SÃO PAULO, SÃO PAULO, BRAZIL; (MG) DEPARTAMENTO DE BIOLOGIA, UNIVERSIDADE DO AMAZONAS, 69068, MANAUS, AM, BRAZIL; AND (WH) ZOOLOGISCHES INSTITUT, UNIVERSITÄT WIEN, ALTHANSTRASSE 14, A-1090, VIENNA, AUSTRIA. PRESENT ADDRESS:

(LS) DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY, UNIVERSITY OF MICHIGAN, ANN ARBOR, MICHIGAN 48109-1048. E-mail: lschiesa@umich.edu. Send reprint requests to L.S. Submitted: 15 Aug. 2002. Accepted: 14 Nov. 2002. Section editor: M. J. Lannoo.