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DIPLOMARBEIT

Titel der Diplomarbeit

The evolution of phytotelmata-breeding anurans:
Breeding and calling site characteristics of the two tree-hole breeding frogs *Trachycephalus resinifictrix* and *T. hadroceps* (Anura: Hylidae)

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The evolution of phytotelmata-breeding anurans: Breeding and calling site characteristics of the two tree-hole breeding frogs *Trachycephalus resinifictrix* and *T. hadroceps* (Anura: Hylidae)

Abstract:

In amphibians many different reproductive modes evolved. Hence they are rewarding subjects for the study of the evolution of reproductive behavior. One specialized mode is the deposition of offspring, eggs and/or tadpoles into phytotelmata.

The present study describes the reproductive mode of *Trachycephalus resinifictrix* (Goeldi, 1907) and *T. hadroceps* (Duellman & Hoogmoed, 1992), two arboreal frog species found in primary rainforests of French Guiana. During a two month field period, population data, life history facts and characteristics of calling and breeding sites of the two arboreal frog species were recorded and analyzed.

The two observed species show similar reproductive modes but use significantly different types of tree holes as calling and breeding sites. None of the calling sites of *T. hadroceps* exceeded a volume of one liter and they were significantly higher up in the trees than tree holes used by *T. resinifictrix* containing a minimum volume of four liters. Adults and tadpoles of *T. hadroceps* show distinct adaptations facilitating the life in arboreal phytotelmata not present in *T. resinifictrix*. On basis of the results of this study the evolution of phytotelmata-breeding anurans is discussed and compared with adaptations found in other phytotelmata-breeding frogs. A table of presently known phytotelmata-breeding anurans is presented in the appendix.

Trachycephalus resinifictrix

Trachycephalus hadroceps

Introduction

The highest diversity of anurans occurs in tropical rainforests (Duellman, 1988) and along with the taxonomic diversity we find a huge variety of reproductive modes (Hödl, 1990). For anurans, the selection of the egg deposition site is crucial for offspring survival. Perennial water bodies such as ponds and streams are common breeding sites of frogs in all climatic zones. Due to the high humidity in the tropics more temporary water bodies are available as alternative breeding sites. The deficit of predators and competitors is one major cause for frogs to select temporary water bodies as egg deposition and larval developmental sites (Magnusson & Hero, 1991). In tropical rainforests a special type of temporary water bodies are phytotelmata.

Phytotelmata (singular: phytotelm; Greek: plant-swamp) are water holding plants or parts of plants. These plant structures can be either alive or dead and range in volume from a spoonful of water to several hundred liters. Phytotelmata are formed in leaf axils, flower bracts, open fruits or seeds, in bromeliads, pitcher plants or in tree holes and can be found on the ground as well as high up in the canopy. These aquatic microhabitats are characterized by low levels of dissolved oxygen, low primary production, ephemerality and little and unpredictable food resources (Schiesari et al., 2003). Due to phytotelmata, the aquatic habitat in a tropical rainforest can be increased by up to 50.000 liters per hectare (Fish, 1983). The immense quantity of water containing plant structures is used by many different taxa. On Barro Colorado Island, Panama, 54 species of invertebrates and five species of vertebrates were found to live in tree holes (Yanoviak, 2001). Worms (Nematoda and Annelida), crabs, spiders, insects of various groups most notably those with aquatic larvae (Diptera, Odonata, Hemiptera, Coleoptera) and frogs (Frank & Lounibos, 1987) are known to occur in phytotelmata throughout the tropics.

The first scientific description of a frog reproducing in tree holes was by Goeldi (1907) of the neotropical frog *Trachycephalus* (formerly *Hyla* and *Phrynohyas*) *resinifictrix.* Another early account by Barbour and Loveridge (1928) describes the African microhylid *Hoplophryne uluguruensis* depositing its eggs in watter-filled leaf axils of banana plants. Presently 154 species of 11 anuran families are known to live associated with phytotelmata (see Appendix III). Only few phytotelmata-breeding anurans are studied in detail (Gaucher 2002, Grillitsch, 1992; Jungfer & Schiesari, 1995; Jungfer, 1996; Kam et al., 1996; Krügel & Richter, 1995; Lannoo et al., 1987; Lin & Kam, 2008; Rudolf & Rödel, 2005; Schiesari et al., 2003; Ueda, 1986; Weygoldt, 1980).

Phytotelmata offer advantages but also several drawbacks for frogs using these aquatic habitats for reproduction. The absence of large tadpole predators and little competition are considered the major factors for the evolution of phytotelmata breeding in anurans (Lehtinen et al., 2004; Magnusson & Hero, 1991). However, the water volume of phytotelmata is significantly correlated with the amount of rainfall (Kam et al., 1996; Lin et al., 2008) and even large tree holes with several liters of volume may dry up occasionally during longer periods without rain. Dessication is the major factor next to predation for the mortality of tadpoles (Rödel & Rudolf, 2004). Hence only animals with resistance against drought, capability of leaving the phytotelmata and aquatic larvae with a short developmental time colonize this habitat.

Study species

Trachycephalus resinifictrix is a widespread species found throughout the Amazon region from Ecuador, Brazil to French Guiana and from Venezuela to Bolivia, whereas *T. hadroceps* exhibits a more restricted distribution area in southern Guyana, Suriname and French Guiana (www.redlist.org) The two hylid species live an exclusive arboreal life in tropical rainforests where the males call from tree holes. Both species are nocturnal and male individuals are heard throughout the night. During the day they are frequently encountered close to the calling sites (Gaucher, 2002; Hödl, 1991; this study). Amplexus, deposition of eggs and the complete development of the tadpoles until metamorphosis is accomplished inside water-filled tree holes (Gaucher, 2002; Schiesari et al., 2003; Jungfer & Proy, 1998; this study).

Trachycephalus resinifictrix females reach a snout-vent length (SVL) of 8.6 cm and males of 7.7 cm in average. Two lateral vocal sacs are visible in males which reach reproductive age within 10-12 months and females can deposit their first clutches after 12-15 months (Jungfer & Proy, 1998). The iris is golden and formed like a Maltese cross. The skin coloration varies geographically, the dorsal side is dark brown with light brown or khaki spots on back, legs and arms. The ventral side is uniformly cream. One large triangular khaki spot on the back of the head allows easy individual recognition (Lescure & Marty, 2000). *Trachycephalus resinifictrix* starts calling around one hour after sunset (19h00) and the advertisement call consists of three to four notes. Each note lasts for 307 ms in average. A calling individual may emit up to 4000 notes in one night (Hödl, 1991). For reproduction the female enters the tree hole occupied by a calling male. Amplexus is

axillary and the female deposits a clutch of up to 4000 eggs (mean=2779; n=14) (Jungfer & Proy, 1998, this study). After amplexus which lasts until the morning hours the female leaves the breeding site (Jungfer & Proy, 1998; Jungfer & Schiesari, 1995). The tadpoles hatch within 24 hours and feed initially mainly on detritus. The diet changes when new eggs are deposited into the breeding site by the same or another female. Tadpoles feed on as many eggs as possible but only larvae of Gosner stage 32 and older are able to swallow the whole eggs. Reproduction occurs throughout the year but most intensively during the rainy season (Schiesari et al., 2003).

Trachycephalus hadroceps was first described by Duellman & Hoogmoed (1992). Due to the morphological trait of a single subgular vocal sac it was placed into the genus *Hyla*. Subsequent genetic analysis led to the position into the genus *Trachycephalus* even though all other species of this genus possess two lateral vocal sacs (Gaucher, 2002). Further genetic analysis revealed the monophyly of *T. hadroceps* and their close relatedness to *T. resinifictrix* (Guillaume et al., 2001). The SVL of adult males is 5.1 cm in average, that of females 6.2 cm (Gaucher, 2002). The dorsal skin is tuberculate and the color is dark brown with light brown spots on the dorsum and cream with small dark spots on the venter (Duellman & Hoogmoed, 1992).

The following data on reproductive behavior of *T. hadroceps* are taken from an unpublished thesis by Gaucher (2002) who performed long field observations and bred these tree frogs in captivity.

Males attract females by calling from tree holes. The intense call which is detectable for several hundred meters consists of numerous evenly spaced short notes. The males start calling at dusk (18h00) and continue to call during the whole night. The advertisement call of *T. hadroceps* consists of a single note which lasts for 56.7 ms in average. One individual may emit up to 38000 notes in a single night (mean: 18129 notes/night).

The female approaches the vocalizing individual. Upon entering the tree hole the male stops calling and performs axillary amplexus. The amplexus may last the whole night until dawn when the eggs are deposited as a surface film. Clutches contain 84 eggs in average. Immediately after mating the female leaves the tree hole. The tadpoles hatch 48 hours after oviposition and measure six millimeters in length. Usually the male does not return to the tree hole after reproduction. The mother returns every two to three days to her offspring without the male being present. After lowering herself fully into the water the tadpoles start nibbling on her ventral side and thus trigger the deposition of trophic eggs.

Egg begging tadpoles do not differentiate between females and males. Thus disturbances by begging tadpoles are possibly the reason for males not to call from tree holes with tadpoles. In experiments where the tadpoles were separated by a net but visible for the mother in the same pot, the female did not lay eggs. Hence when no more tadpoles are present in the tree hole the mother stops returning to it. The female returns in average 19.3 times to her offspring to deposit a clutch of unfertilized trophic eggs before they reach metamorphosis. Trophic eggs are bigger than regular eggs and deposited below the water surface where they are instantly eaten by the tadpoles. Through the ventral skin of the tadpoles the swallowed eggs are clearly visible. This nourishment provided by the mother is essential for the growth and successful metamorphosis of the larvae. Of an analyzed clutch of 137 fertilized eggs, 23 tadpoles reach metamorphosis after 27 to 49 days. Size of the tadpoles and time until metamorphosis is significantly correlated with the number of trophic eggs provided by the mother. Males start calling at an age of three and a half months and females are able to reproduce after five months (Gaucher, 2002).

Trachycephalus resinifictrix and *T. hadroceps* share some morphological and behavioral characteristics due to their common ancestry but also differ clearly in certain other traits. In order to compare these two arboreal tree-hole breeding frogs this study was set up in the Nouragues nature reserve in French Guiana. Both species occur naturally in this reserve of primary rainforest. For the first time characteristics of breeding sites and data of the life history of these two tree frogs were recorded at the same study site. Behavior, morphology and physiology of adults as well as larvae are discussed and compared with other anuran species considering the evolution from pond-breeding to phytotelmata-breeding anurans.

Methods

Study site and observation period

The study site is in the Nouragues nature reserve in French Guiana close to the camp Pararé on the river Arataii (N 4°02', W 52°40'). Annual rainfall is more than 3000 mm and two short dry seasons with less than 100 mm/m² rainfall per month occur in March and from September to October (www.nouragues.cnrs.fr). Monthly precipitation as well as percentage of days with rain were rising during the study period (Fig. 1).

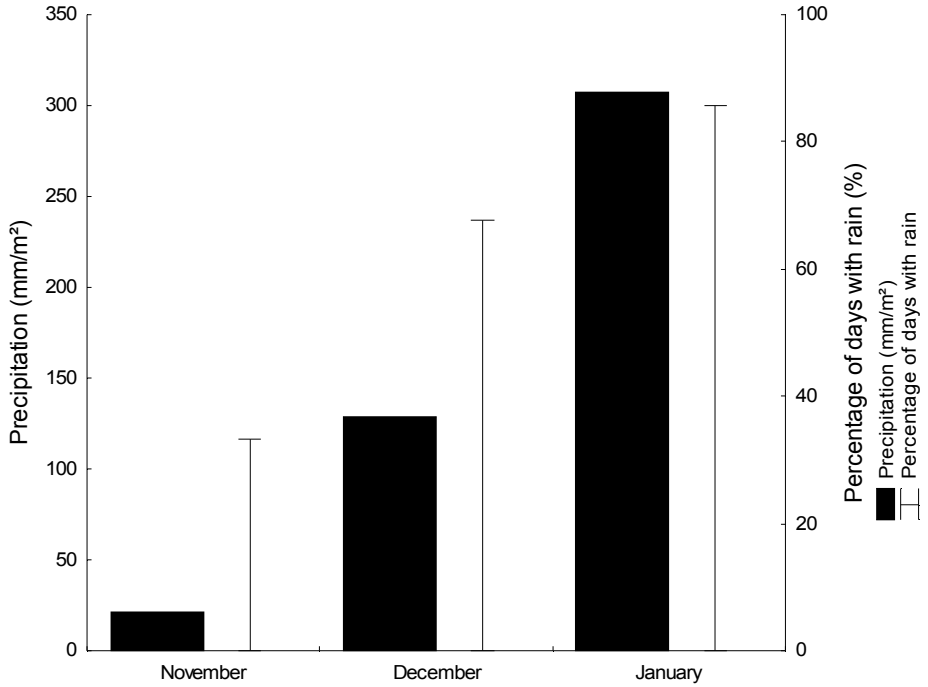

Figure 1: Precipitation (mm/m²) and percentage of days with precipitation from 13 November 2008 until 21 January 2009 for the study site in Nouragues, French Guiana.

The area observed was 15 hectare of primary rainforest. One major walking trail and several smaller paths facilitated working in the study area (Fig. 3). The study was conducted between 27/11/2008 and 19/01/2009 (referred to as period 08/09). Nightly observations were made on 44 out of 54 nights, daytime observations were conducted on each day of the observation period (Fig. 2, 12 and 13).

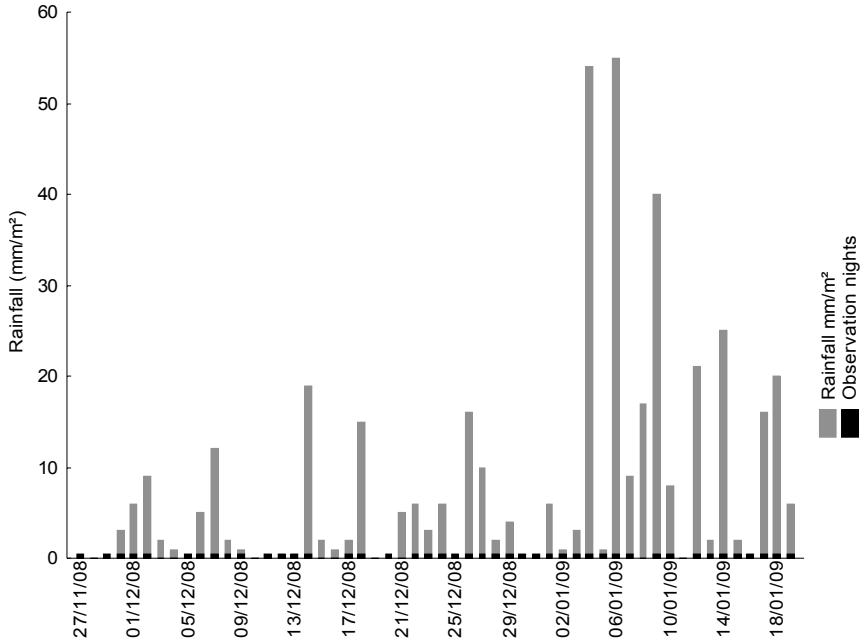

Figure 2: Daily amount of rainfall (grey bars) and observation nights (black bases) during the study period.

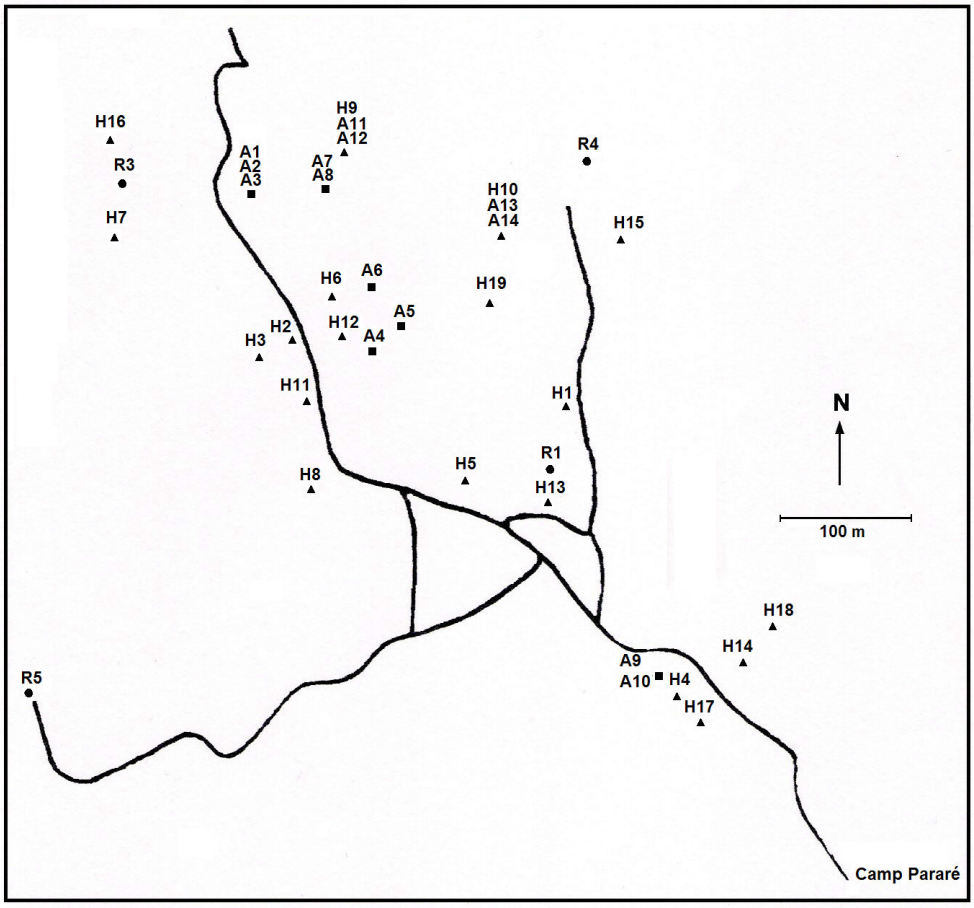

Figure 3: Map of the study site with trails, natural calling sites of *T. resinifictrix (●, R)* and *T. hadroceps* (▲, H) and position of artificial phytotelmata (■, A).

Field observations

Thanks to previous observations by Philippe Gaucher in the same area, irregularly performed between 13/08/06 and 04/10/08 (referred to as period 06/08), five natural calling sites (R1-R5; Fig. 3), 19 male and 2 female individuals of *T. resinifictrix* were known prior to the study period 08/09. All calling sites were checked for clutches, tadpoles, frogs and the availability of water before and during the study. Both species have a very intense and continuous call and are well detectable in distances of up to 200 m (Hödl, 1991; Gaucher, 2002; Schiesari et al., 2003).

Night observations started at dusk (18h00-18h30) and continued until all known calling individuals in the study site were located. Every audible and/or visible individual was counted as one observation per night. To unambiguously detect a tree as a calling site vibrations can be sensed by pressing the ear against the trunk.

A modified technique used by mountaineers and speleologists known as single rope technique (SRT) was used to climb the trees. With a slingshot or crossbow a line was shot over a strong branch. With this line a climbing rope was pulled over the branch and back down where one end was fixed to a nearby trunk. For climbing on the free end of the rope a harness and special rope ascenders were used (Perry, 1978). This technique is easy to learn, neither gear nor cost intensive and thus convenient for studies with the need of an easy and fast access to the canopy region of trees (Jepson, 2000). During climbing, the frogs often ceased calling, presumably due to disturbances through climbing, but after pausing the ascend for a couple of minutes they usually started to vocalize again.

Pictures of the dorsal pattern of the encountered frogs were taken for individual identification. Of *T. hadroceps* additionally the throat pattern was recorded to allow unambiguous identification. Whenever possible the frogs were not captured but photographed in their natural position. If this was impossible, the frogs were caught, photographed and released into their tree holes afterwards. The calling individuals underwent no further treatments. If a frog was heard from the same location in subsequent nights it was presumed to be the same individual. Calling sites are indicated by capital letters (R, H and A) and individuals by small letters (r and h). The letter r indicates calling sites or individuals of *T. resinifictrix*, h of *T. hadroceps* and the letter a stands for artificial calling sites.

For each calling site the following characteristics were measured. The height of the hole on the tree was measured from the hole entrance to the ground. The total height of the

tree was estimated. Diameter at breast height (DBH) was calculated by measuring the circumference of the trunk and for all tree holes situated on branches additionally the branch diameter was measured. Entrance diameter, profundity and diameter of the tree hole were measured. The maximum water volume of the tree hole was calculated by using a cylindrical formula. Positions of the trees were located with a Global Positioning System device (Garmin GPSMAP 76 Csx) and processed with corresponding software. Volume, profundity of hole and entrance diameter were not measured for H13 because the resident individual was calling from a bromeliad (Fig. 4B) and for R2 because the hole occupied by *T. resinifictrix* in the period 06/08 was used by a White-Faced Tree Rat (*Echimys chrysurus*) during the observation period 08/09.

Observed clutches were photographed to estimate the clutch size. For this evaluation only intact clutches without signs of predation or cannibalization were used to minimize the risk of underestimation. Clutches were observed the following days after discovery. Date of oviposition and disappearance of the clutch either by hatching or predation was noted.

Precipitation

Precipitation was recorded with a standard rain gauge at the clearing of the camp Pararé. The gauge was emptied every morning at 8h00 and accessorily to prevent overflow.

Artificial calling sites

Plastic containers of different size and form were attached to trees in order to test the acceptance of artificial phytotelmata as calling sites for *T. resinifictrix* and *T. hadroceps.* Three containers with a volume of 25 l were installed on trees and filled with water at a height of three meters on 27/06/2008 (A4, A5 and A6; Fig. 3 and Fig. 4A). Three containers of 36 l, 36 l and 40 l respectively (A1, A2 and A3; Fig. 3) were placed on a platform of a canopy research tower (COPAS-Tower; www.nouragues.cnrs.fr) at a height of three meters. The artificial phytotelmata were observed in the morning and at night to check for clutches tadpoles and adult individuals.

In four trees where *T. hadroceps* was heard calling during the study period 08/09 eight artificial containers (A7-A14) were placed. On each of these trees two plastic containers of two different volumes (1 l and 10 l) were placed less than two meters apart. Positioning height was 11 m, 16 m, 19 m and 23 m. The sites were checked during all night observations for calling males and during the whole study period for the presence of eggs and tadpoles. All artificial phytotelmata were filled with rainwater before the study.

Experiments

Tadpole development of *T. resinifictrix*

In order to test the developmental time of *T. resinifictrix* seven eggs were taken from the artificial phytotelmata. Seven tadpoles hatched and were kept in a box with a volume of 2 l for 54 days. Water from the artificial containers in the forests was used. At all times either eggs of *T. resinifictrix* or *Hypsiboas boans* were available as food for the tadpoles. The tadpoles were measured from the tip of the snout to the end of the tail. Identification of the tadpole stages followed Gosner (1960).

Larvae of *D. tinctorius* as potential predators of *T. resinifictrix* tadpoles

Larvae of *D. tinctorius* are able to prey on tadpoles of *T. hadroceps* (Gaucher, 2002). Tadpoles of *D. tinctorius* and *T. resinifictrix* were observed in captivity in order to test the capability of *D. tinctorius* tadpoles to prey on *T. resinifictrix* tadpoles and to test for potential cannibalism in *D. tinctorius.* Three tadpoles of *D. tinctorius* of different sizes (2x2.5 cm and 6 cm) were observed in boxes of 0.5 l. In the first experiment one *D. tinctorius* larva and two tadpoles of *T. resinifictrix* and in a second experiment three *D. tinctorius* of different sizes and one *T. resinifictrix* tadpole were kept in the boxes. Every experiment was observed for 24 hours. After the experiments the tadpoles were returned to their places of origin.

Statistics

Statistics was done with STATISTICA 6.0. Outlying data points of the tree hole characteristics of R1 (volume, profundity, entrance diameter of the hole, DBH) were excluded from the analysis. Two statistical tests, Mann-Whitney (MW) and Kolmogorov-Smirnov (KS), were used for comparison of tree hole characteristics. For analyses of calling site distances Mann-Whitney was applied.

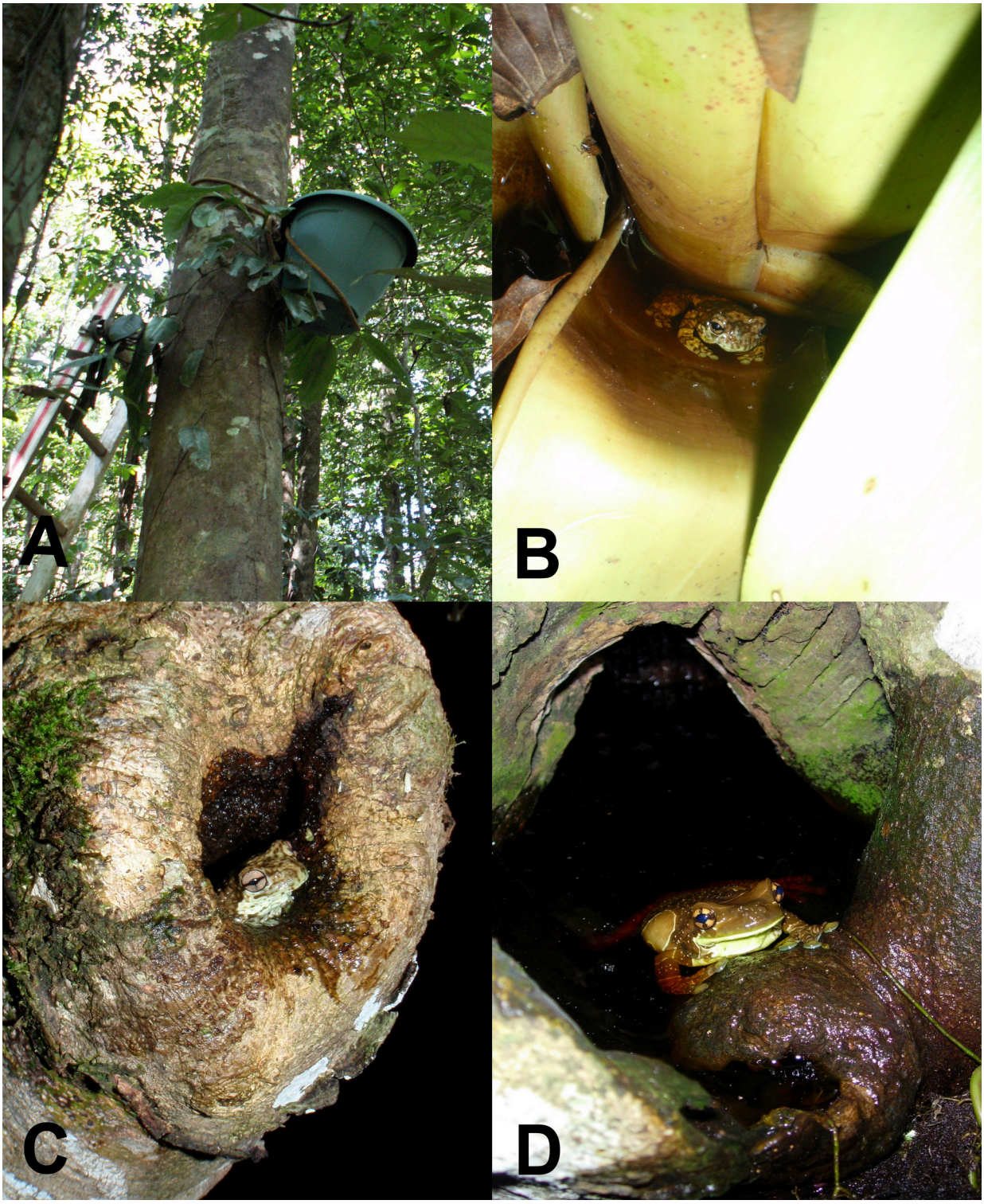

Figure 4: A: Artificial phytotelm A4; **B:** *T. hadroceps* (male) in a bromeliad on tree H13; **C:** *T. hadroceps* (male) in tree hole H8; **D:** *T. resinifictrix* (male) in tree hole R3;

Results

Population data of *T. resinifictrix* and *T. hadroceps*

Within the observation area of 15 ha, 15 males of *T. resinifictrix* and nine males of *T. hadroceps* were identified between 27/11/08 and 19/01/09. Three *T. resinifictrix* were calling from two natural calling sites and 12 from four artificial sites. All nine *T. hadroceps* were calling from 16 natural calling sites. Per hectare 0.13 natural calling sites were occupied by *T. resinifictrix* and 1.07 by *T. hadroceps*. Density of calling males was 1.0 individual per hectare for *T. resinifictrix* and 0.6 for *T. hadroceps* (Table 1).

Table 1: Number of individuals (male/female), calling sites (natural/artificial) and densities of calling males and natural calling sites per hectare of *T. resinifictrix* and *T. hadroceps*.

	Individuals		Male individuals	Calling sites		Natural calling
	Male	Female	per ha	Natural	Artificial	sites per ha
T. resinifictrix	15	2	1.0	2	4	0.13
T. hadroceps	9	0	0.6	16	0	1.07

From 27 November until five days prior to the end of the study period (14 January) new male individuals of *T. resinifictrix* were identified within the study area. The nine male individuals of *T. hadroceps* were identified from 22 December until 13 January although individuals were already calling since early December (Fig. 5). Unidentified individuals of *T. hadroceps* were still calling in the last observation night (19 January 2009).

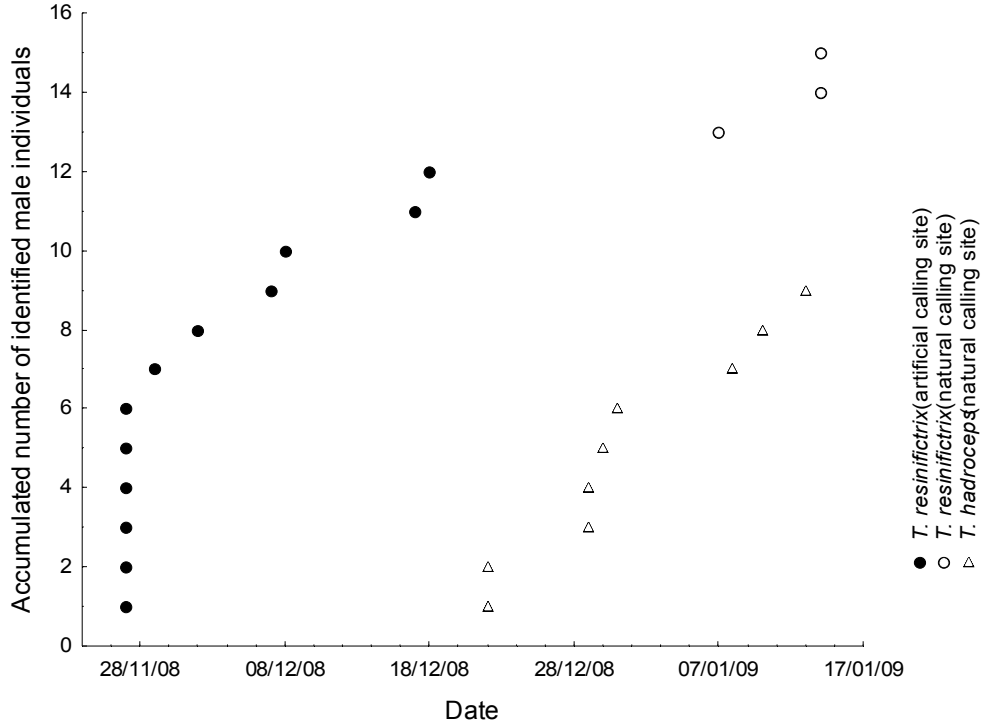

Figure 5: Accumulated number of identified male individuals of *T. resinifictrix* and *T. hadroceps* in natural (open symbols) and artificial (filled symbols) calling sites.

Trachycephalus resinifictrix

During one observation night 2.4 individuals were heard in average (mean 2.4 ± 0.25 SE; 0-6 individuals; n=44). Out of 100 observations of male *T. resinifictrix* only four were made in natural calling sites. Each of the six artificial containers were alternately used by up to six individuals (Table 2). Of 15 male individuals two were captured just once (mean: 7.1 ± 5.1 SE; 1-17 observations; n=15) (Fig. 12).

All but one individual remained at a single calling site throughout the study period. Individual r23 changed its calling position from A5 to A4 (Fig. 7).

Each artificial calling site, A4 and A5, was used alternately by three male individuals. Two individuals were calling from one bucket at the same time on two occasions (17/12/08: A5: r14 and r28; 25/12/08: A4: r23 and r29) (Fig. 7). One individual was calling from the artificial calling site A6 (Table 2). Two individuals were observed calling four nights in succession from the artificial calling sites A1-A3 (r11: 29/11-2/12 and r26: 26/12-29/12) (Fig. 12).

Table 2: Number of observations, individuals and clutches of *T. resinifictrix*. Presence (+) and absence (-) of tadpoles of *T. resinifictrix* and *D. tinctorius*.

Calling sites of *T. resinifictrix*									
	Artificial						Natural		
	A1	A2	A3	A4	A5	A6	R3	R4	R5
Observations	26	2	11	20	27	10	2	0	2
Individuals	6	2	4	3	3	1	1	0	2
Clutches	4	4	3	3	2	0	1	0	1
Tadpoles of *T. resinifictrix*	+	+	+	+	+	-	+	-	-
Tadpoles of *D. tinctorius*	-	-	-	-	-	+	-	+	+

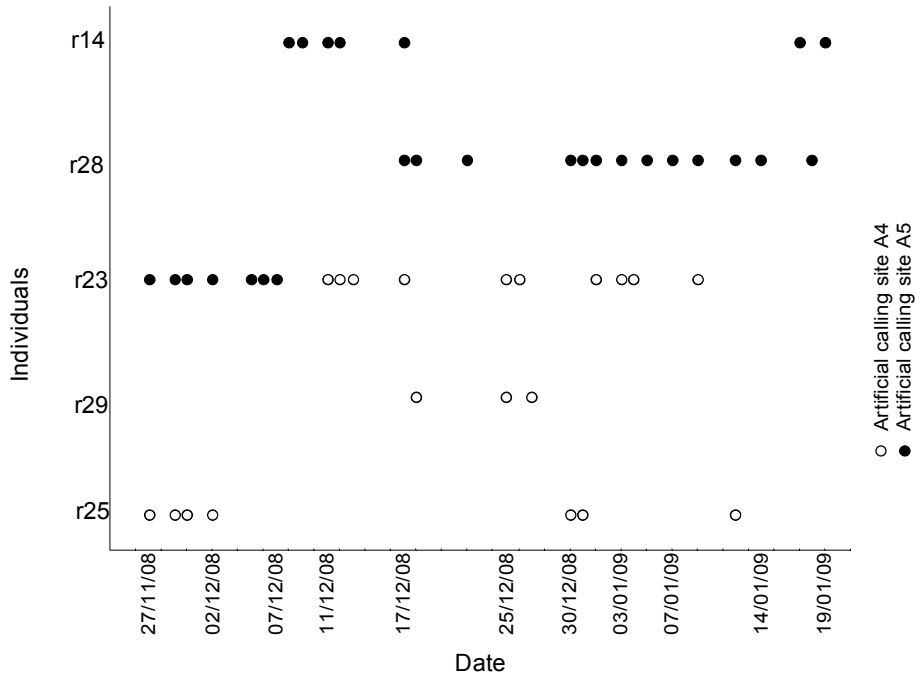

Figure 7: Calling activity of *T. resinifictrix* in the artificial calling sites A4 and A5.

Reproductive activity of *T. resinifictrix*

Males were calling from six artificial calling sites and in all but one (A6) eggs were observed (Table 2). Clutch interval (i.e. time between two clutches in the same site) was 13.6 days in average (mean 13.6 d ± 2.13 SE; 3-22 days; n=11). Clutches were completely devoured within less than two days when large conspecific larvae were already present at the egg deposition site (mean 1.2 d ± 0.22 SE; 0-2 days; n=14). Of the 18 clutches found only two were not cannibalized. One was deposited at a site with just few almost

metamorphosed tadpoles. The other was found in a container which had received another clutch just three days before. Eggs of these two clutches developed into tadpoles. Three freshly laid clutches subdivided into 37, 36 and 39 portions contained 1850, 2160 and 2730 eggs, respectively.

Tadpole development of *T. resinifictrix*

Tadpoles hatched within 24 hours after oviposition. Twelve days after hatching tadpoles measured 1 cm. Thirty days old tadpoles at Gosner stage 26-28 measured 2 cm (mean 2 ± 0.04 SE; 1.9-2.2 cm; n=7). After 54 days, the end of the study, the average size was 2.6 cm (mean 2.6 ± 0.07 SE; 2.3-2.9 cm; n=7) but Gosner stage (28) was still unchanged and no larva reached metamorphosis within the study period. Tadpoles fed on detritus, plant material, small insect larvae and on eggs of conspecifics as well as of *Hypsiboas boans,* provided throughout the experiment.

Recaptures of *T. resinifictrix*

One female and five males of 12 individuals identified between March and August 2008 were recaptured during the study period 08/09. All but one of the recaptured individuals were found at the initial observation site. One individual (r14) moved 170 meters from a tree hole (R4), where it was last seen on 04/08/08, to the artificial calling site A5 (Fig. 7). None of nine individuals observed before 2008 was recaptured in this study. Between first and last day of recapture of the individuals observed in periods 06/08 and 08/09 up to 336 days passed (mean: 98; SE: 24.5; 0-336 days; n: 21) (Table 3).

Table 3: Individuals of *T. resinifictrix* observed in period 06/08. Number/sex of individual and date/location of first/last observation. Individuals marked in grey were recaptured in the present study (period 08/09). Because of its close vicinity of less than one meter locations A1, A2 and A3 were combined to one site

Individual	Sex	Date of first capture	Location of first capture	Date of last recapture	Location of last recapture
r01	m	13.08.06	R1	14.08.06	R1
r02	m	14.08.06	R1	11.02.07	R1
r03	m	04.10.06	R1	04.10.06	R1
r04	m	06.10.06	R2	24.12.06	R2
r05	m	02.01.07	R1	06.02.07	R1
r06	m	23.01.07	R3	24.01.07	R3
r07	m	06.02.07	R1	08.01.08	R1
r08	m	13.08.07	R1	13.08.07	R1
r09	m	04.12.07	R1	19.05.08	R1
r10	m	21.03.08	R1	21.03.08	R1
r11	m	04.05.08	A1-A3	20.12.08	A1-A3
r12	m	06.05.08	A1-A3	10.01.09	A1-A3
r13	m	06.05.08	A1-A3	01.01.09	A1-A3
r14	m	23.05.08	R4	19.01.09	A5
r15	m	02.08.08	R3	19.01.09	R3
r16	m	02.08.08	A1-A3	15.08.08	A1-A3
r17	m	03.08.08	R5	03.08.08	R5
r18	f	06.08.08	A1-A3	06.08.08	A1-A3
r19	m	08.08.08	A1-A3	08.08.08	A1-A3
r20	m	08.08.08	A1-A3	08.08.08	A1-A3
r21	f	09.08.08	A1-A3	02.12.08	A1-A3

Trachycephalus hadroceps

Up to five individuals of *T. hadroceps* were observed in one night (mean 1.6 ± 0.17 SE; 0-5 individuals; n=44) (Table 4). One individual (h3) was seen in three different locations within 26 days. It was first caught in tree H05 on 22/12/08, then it was heard from 28/12/08 until 02/01/09 in H13 and finally it called again from 12/01-17/01/08 from a tree hole on H18. No other individuals were heard from the trees H13 and H18 during the study period. Two individuals (h4 and h8) were calling from H05, during the period h3 was heard from the same tree, thus exact individual calling dates for this tree can not be given (Fig. 8 and Fig. 13).

Individual h3 was observed calling twice for six nights in succession on trees H13 from 28/12-02/01 and H18 from 12/01-17/01 and thus it is the individual with the most consecutive nights observed calling (Fig. 13). No female individuals, clutches or tadpoles of *T. hadroceps* were found during the observation period 08/09.

Table 4: Number of observations and individuals of *T. hadroceps* (male) in natural calling sites.

	Natural calling sites of *T. hadroceps*															
	H05	H18	H15	H13	H09	H11	H19	H16	H08	H14	H10	H06	H03	H17	H12	H07
Observations	25	6	6	6	6	5	3	3	3	2	2	2	1	1	1	1
Individuals	3	1	0	1	1	0	0	2	1	1	0	0	1	0	0	0

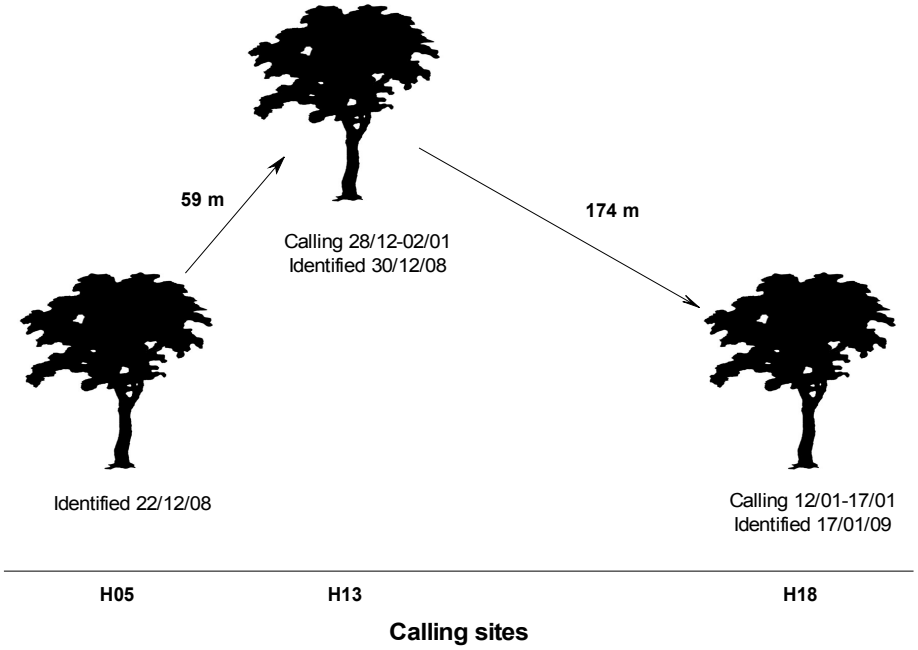

Figure 8: Calling sites of a male *T. hadroceps* (h3) between 22/12/08 and 17/01/09.

Natural calling site characteristics of *T. resinifictrix*

Calling males of *T. resinifictrix* were found in five tree holes in the period 06/08. All tree holes were situated in the trunk. In two of the five analyzed tree holes (R3 and R5) frogs were again active during the observation period 08/09. Tree holes were found at heights between 7 and 25 m (mean 16 ± 3.8 m SE; n=5) and offered volumes from 4-28 l and in one exceptional case (R1) several hundred liters (mean 20 ± 8.1 l SE; n=3). The total height of tree-hole containing trees varied from 15-35 m (mean 27 ± 3.4 m SE; n=5) and their DBH measured between 33 and 153 cm (mean 49 ± 7.3 cm SE; n=4) (Table 5).

Table 5: Natural calling site characteristics of *T. resinifictrix*.

	Calling sites of *T. resinifictrix*					Mean	SE
	R1	R2	R3	R4	R5		
Height on tree (m)	7	20	25	7	21	16	3.8
Volume (l)	589	–	28	4	28	20	8.1
Profundity of hole (cm)	300	–	35	50	40	42	4.4
Entrance diameter (cm)	101	–	20	41	30	30	6.1
Tree height (m)	30	27	35	15	30	27	3.4
DBH (cm)	153	41	53	33	67	49	7.3

Natural calling site characteristics of *T. hadroceps*

Characteristics of seven occupied tree holes were measured in the observation period 08/09. Tree holes were formed in rotting ends of broken branches (n=4) or in the trunk (n=3). Additionally one male was calling from a bromeliad (H13; Fig. 4B). Males called from tree holes at heights between 23 and 42 m (mean 31 ± 2.86 m SE; n=8) with a volume of 0.15-0.99 l (mean 0.45 ± 0.14 l SE; n=7). The trees with calling sites had a DBH of 38-242 cm (mean 96 ± 22.28 cm SE; n=8) and reached heights between 28 and 50 m (mean 39 ± 3.17 m SE; n=8). The diameter of cavities containing branches varied from 10.8-27.1 cm (mean 17.8 ± 3.75 cm SE; n=4) (Table 6).

Table 6: Natural calling site characteristics of *T. hadroceps.*

	Calling sites of *T. hadroceps*								Mean	SE
	H03	H05 (left)	H05 (right)	H08	H09	H13	H14	H16		
Height on tree (m)	23	42	42	25	26	36	32	23	31	2.86
Volume (l)	0.15	0.96	0.29	0.28	0.99	–	0.25	0.25	0.45	0.14
Profundity of hole (cm)	12	25	15	10	35	–	20	20	19.6	3.23
Entrance diameter (cm)	11	7	5	4	32	–	22	12	13.2	3.81
Branch diameter (cm)	–	–	12.7	–	20.7	–	27.1	10.8	17.8	3.75
Tree height (m)	40	50	50	28	30	45	40	30	39	3.17
DBH (cm)	70	95	95	38	76	242	99	50	96	22.28

Comparison of calling site characteristics

The height of the calling site on the tree (MW U=2.5, p=0.01; KS p=<0.05), the volume of the tree hole (MW U=0 p=0.017; KS p=<0.05) and the profundity of the tree hole (MW U=0.5, p=0.023) differ between cavities used by *T. resinifictrix* and *T. hadroceps* (Table 7, Fig. 9 and Fig. 10). No difference could be detected for the diameter of the entrance of the tree hole, the tree height and the DBH.

Table 7: Comparison of tree hole characteristics of *T. resinifictrix* and *T. hadroceps* (* significant values).

Variable	Mann-Whitney		Kolmogorov-Smirnov
	U	p	p
Height on tree (m)	2.5	0.010*	< 0.05*
Volume (l)	0	0.017*	< 0.05*
Profundity of hole (cm)	0.5	0.023*	< 0.10
Entrance diameter (cm)	3	0.087	> 0.10
Tree height (m)	7	0.057	> 0.10
DBH (cm)	5	0.062	< 0.10

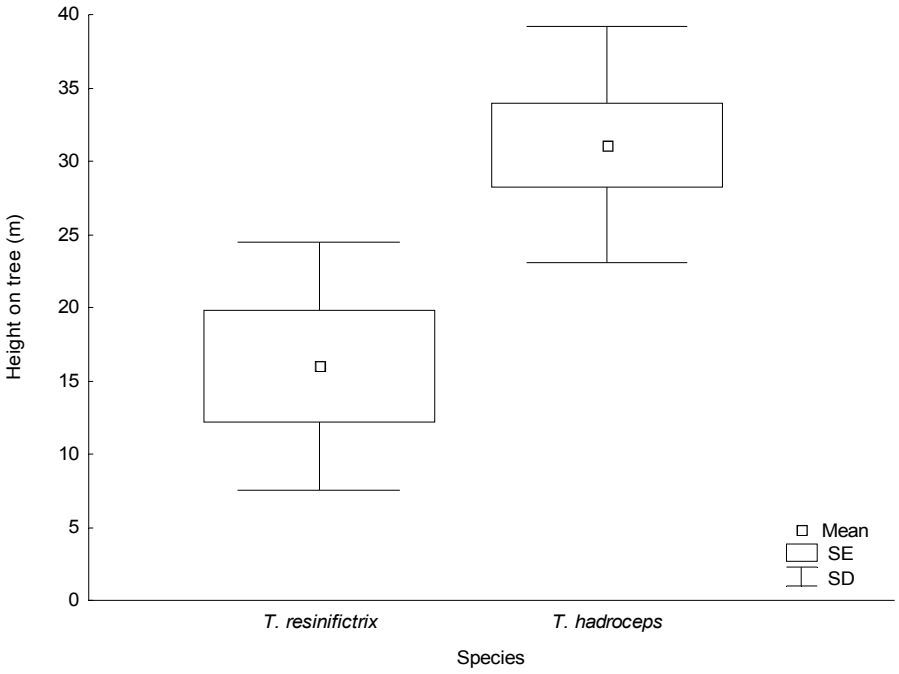

Figure 9: Height of calling sites of *T. resinifictrix*/*T. hadroceps* on tree (Mann-Whitney: U: 2.5 p: 0.010; Kolmogorov-Smirnov: p < 0.05).

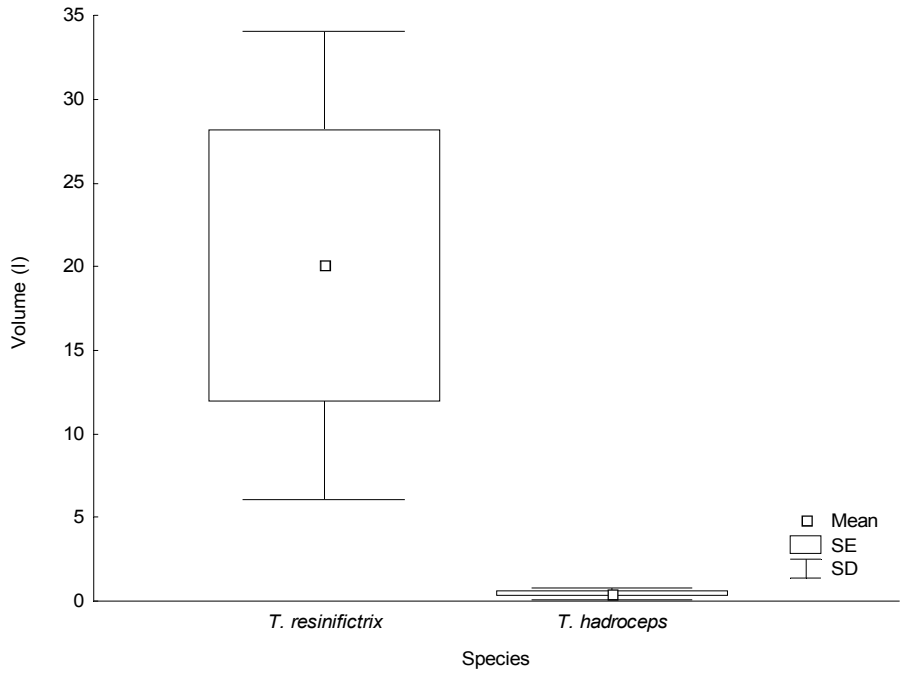

Figure 10: Volume of tree holes used as calling sites by *T. resinifictrix* and *T. hadroceps* (Mann-Whitney: U: 0.0 p: 0.017; Kolmogorov-Smirnov: $p < 0.05$).

Spacing of calling sites

The mean inter-individual calling site distance of *T. hadroceps* (229.7 ± 11.4 m SE; 26-561 m; n: 120) was smaller than that of *T. resinifictrix* (357.2 ± 42.2 m SE; 214-529 m; n: 6) (Mann-Whitney U:145, p: 0.014, n(*T. hadroceps)*: 120, n(*T. resinifictrix)*: 6) (Fig. 11).

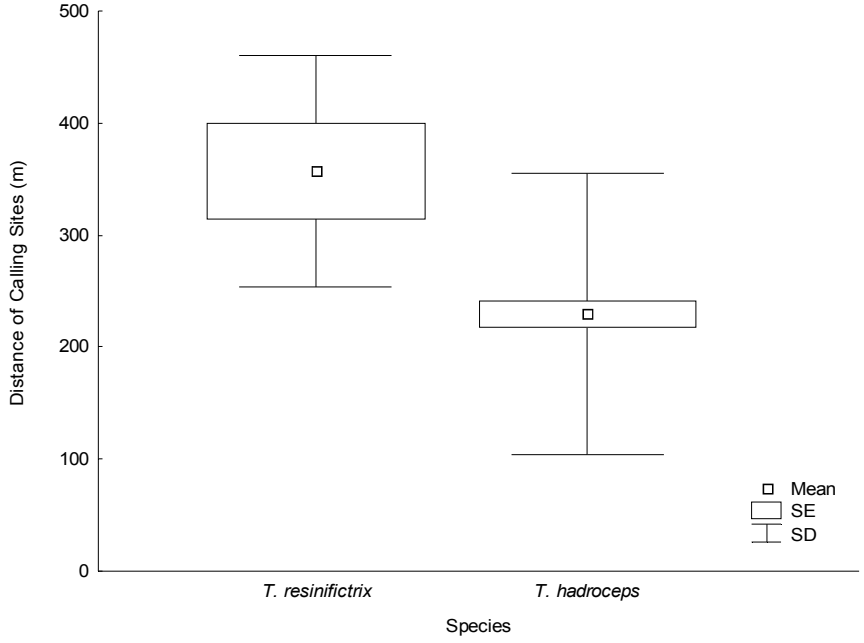

Figure 11: Inter-individual calling site distances of *T. resinifictrix* and *T. hadroceps* (Mann-Whitney U:145, p:0.014, n (*T. hadroceps*):120, n (*T. resinifictrix*):6).

Co-occurring heterospecific anurans

Dendrobates tinctorius

Tadpoles of *D. tinctorius* were found in two tree holes used as breeding sites by *T. resinifictrix* (R5: >10 tadpoles 2.5-6 cm; R4: one tadpole 2 cm) and in one artificial calling site of *T. resinifictrix* (A6: 2 tadpoles of 2 cm) (Table 2). In one tree hole (R5) the tadpoles of *D. tinctorius* were observed devouring a complete clutch of *T. resinifictrix*.

Feeding experiments showed that tadpoles of *D. tinctorius* attack, kill and feed on tadpoles of *T. resinifictrix* of any size as well as smaller or equally sized conspecific larvae in the absence of heterospecific prey.

Osteocephalus oophagus

Tadpoles of *O. oophagus* were found in two artificial phytotelmata (A8 and A14) at heights of 10 and 23 m with a volume of 10 l. In one artificial phytotelm (A6), frequently used by a male *T. resinifictrix*, a male *O. oophagus* was observed calling on several occasions.

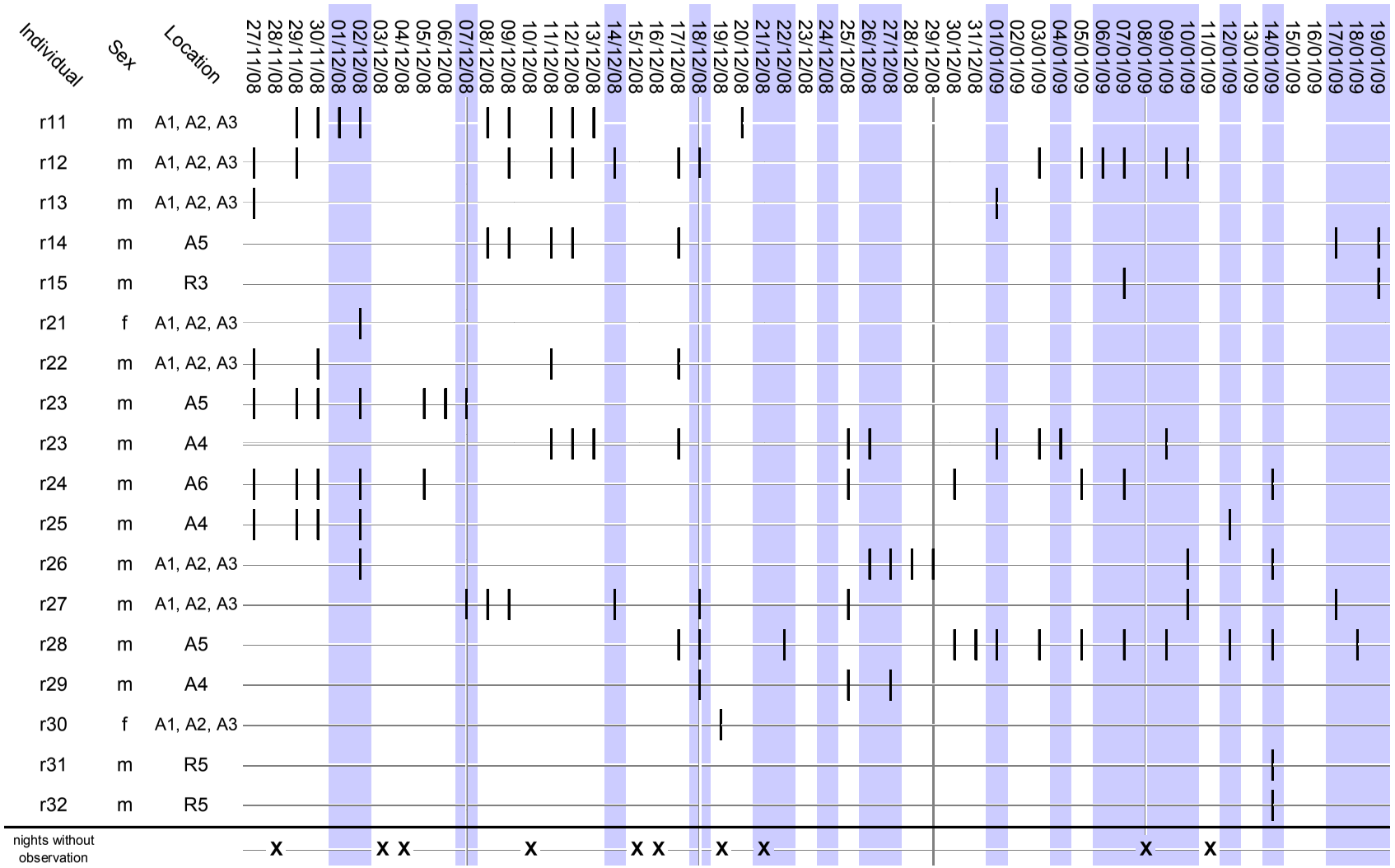

Figure 12: Date and location of observed individuals of *T. resinifictrix*. Days with ≥ 5 mm rain are shaded and nights without observation are marked below (x). Because of their vicinity artificial phytotelmata A1, A2 and A3 were combined to one location.

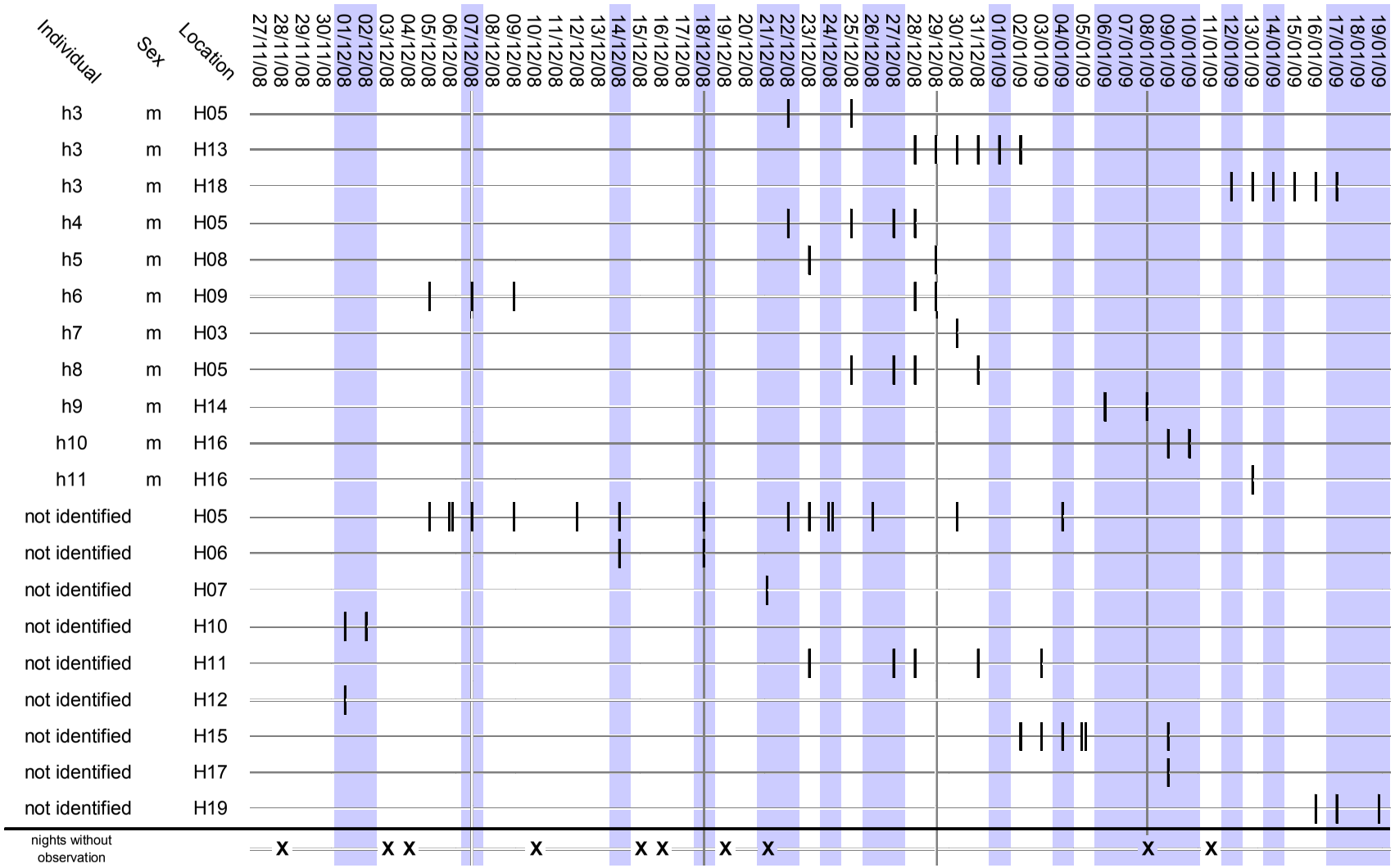

Figure 13: Date and location of observed individuals of *T. hadroceps* and of non-identified individuals. Days with ≥ 5 mm rain are shaded and nights without observation are marked below (x). Observations on 21/12/08 and 08/01/09 were made before nightfall.

Discussion

Evolution takes place over long periods of time and is thus rarely observable in a single human life span. One alternative is to conclude indirectly by analyzing distinct modifications within a group of closely related species. These modifications may be of behavioral, physiological or morphological nature.

The hylid genus *Trachycephalus* is comprised of twelve species (www.research.amnh.org). Two species, *T. resinifictrix* and *T. hadroceps* are known to be strict tree-hole breeders (Gaucher, 2002; Schiesari et al., 2003; this study), whereas the other ten species spawn in temporary or permanent ponds or streams (Hödl, 1990; Lescure & Marty, 2000; Zimmerman & Hödl, 1983). The two tree-hole breeding species call from and deposit their eggs exclusively in hollow trees and are hardly ever encountered on the forest ground (this study). Although the reproductive mode (i.e. breeding in arboreal phytotelmata; reproductive mode 4b according to Hödl, 1990) exhibited by both species is alike, *T. hadroceps* exhibits several adaptations which facilitate life and reproduction in tree holes, not present or less distinctive in *T. resinifictrix. Trachycephalus resinifictrix,* however, still shares important characteristics with the pond/stream-breeding species of its genus. All species of the genus *Trachycephalus* live to some extent an arboreal life, which is one prerequisite for breeding in tree holes in the canopy of rainforest trees (Lescure & Marty, 2000).

Morphologically, *T. hadroceps* varies in characteristic traits from its congeners. Its body size is among the smallest in the genus. Males have a mean snout-vent length (SVL) of 5.1 cm (Gaucher, 2002). Other species reach a mean SVL of 6.8 cm (*T. coriaceus*), 9.7 cm (*T. venulosus*), 8.6 cm (*T. resinifictrix*) (Jungfer & Proy, 1998; Lescure & Marty, 2000) and 7.8 cm (*T. mesophaeus*) (Prado et al., 2003). Male *Trachycephalus* have paired lateral vocal sacs (Faivovich et al., 2005) which are inflated laterally during calling, in some species to a massive extent (*T. coriaceus* and *T. venulosus*) (Hödl, 1991; Lescure & Marty, 2000). *Trachycephalus hadroceps,* however, has a single subgular vocal sac (Gaucher, 2002; Duellman & Hoogmoed, 1992). When the vocal sac is inflated it expands to the front, thus this small frog is enabled to call from very narrow tree holes in which two laterally inflating vocal sacs would interfere.

This study shows that *T. resinifictrix* and *T. hadroceps* are clearly separated in their calling and breeding-site preferences. Tree holes used by *T. hadroceps* are found in the upper

quarter of trees at heights of 20-42 m with a volume rarely exceeding 1 liter (Gaucher, 2002; this study). Only once a male was observed calling from a large bromeliad (this study). It is unknown if *T. hadroceps* uses other phytotelmata than tree holes for reproduction as this was the first account for a male *T. hadroceps* calling from a bromeliad and no eggs or tadpoles were found in it (Fig. 13). *Trachycephalus resinifictrix* calls from tree holes with volumes predominantly larger than 4 l and in lesser heights of 7-32 m (Schiesari et al., 2003; this study).

Trachycephalus resinifictrix as well as pond/stream-breeding species of the same genus produce big clutches, containing up to several thousand eggs (Lescure & Marty, 2000). Clutch intervals of *T. resinifictrix* vary from 14 to 22 days (Jungfer & Proy, 1998; this study). *Trachycephalus hadroceps* differs considerably, females deposit clutches of around 100 eggs and can produce clutches in much shorter intervals of only 2 to 3 days (Gaucher, 2002).

Parental care is any investment given by parents to their offspring after fertilization. In anurans this can take place in form of nest construction, attendance/care or transport of eggs, tadpoles and froglets, brooding of eggs, tadpole feeding and viviparity. Tadpole feeding is predominantly found in phytotelmata-breeding frogs (Dendrobatidae, Hylidae, Mantellidae, Microhylidae and Rhacophoridae). All phytotelmata-breeding frogs with tadpole feeding give nutrition to their offspring as trophic eggs. This form of tadpole feeding was just known for phytotelmata-breeding frogs (Lehtinen & Nussbaum, 2003). However, only recently tadpole feeding with trophic eggs was described for a non phytotelmata-breeding frog. The tadpoles of *Leptodactylus fallax* a Caribbean frog develop in terrestrial foam nests and are fed by the female with unfertilized eggs (Gibson & Buley, 2004).

When the female of *T. hadroceps* returns to her offspring the male is not present. Nibbling of the tadpoles on the ventral side of the female triggers the deposition of unfertilized trophic eggs. The larvae immediately swallow a great number of trophic eggs and depend on a regular supply for successful metamorphosis (Gaucher, 2002). *Trachycephalus resinifictrix* tadpoles are polyphagous but feed mainly on conspecific eggs if available (this study). 52.3 % of analyzed tadpole gut contents contained whole or parts of conspecific eggs (Schiesari et al., 2003). As clutch intervals in *T. resinifictrix* vary from three days to more than three weeks (Jungfer & Proy, 1998; this study) tadpoles do not rely solely on eggs provided by the mother. Larger tree holes accumulate more detritus than smaller ones (Sota, 1996) and thereby offer more food opportunities for generalistic tadpoles

feeding on detritus, algae and plant or arthropod fragments (Schiesari et al., 2003). Hence tadpoles of *T. resinifictrix* may survive longer periods without regular egg supply by feeding on alternative food resources available in large tree holes. Whether tadpoles can reach metamorphosis without regularly provided eggs is doubtful (Jungfer & Proy, 1998).

Apart from adaptations in adults also morphological and behavioral modifications in the larvae of phytotelmata-dwelling anurans can be found. As a result of the drastic change in diet (oophagy, see above) adaptations concerning the feeding and digestive apparatus of tadpoles developed. Pond dwelling larvae of the genus *Trachycephalus* are well equipped with 3-4 anterior and 5-7 posterior labial tooth rows (Grillitsch 1992, Prado et al., 2002; Schiesari et al., 1996) *Trachycephalus resinifictrix* tadpoles share the more basic characteristic of multiple labial tooth rows and have 2 anterior and 3-5 posterior rows (Grillitsch, 1992; Schiesari et al., 1996) whereas the labial tooth rows of *T. hadroceps* are reduced to a maximum of 2 anterior and 2-3 posterior labial tooth rows (Gaucher, 2002). Oral musculature and jaw sheaths in contrast are stronger developed in *T. hadroceps,* a possible adaptation for oophagy, than in the more generalistic and omnivorous tadpoles of *T. resinifictrix* and pond-breeding congeners (Grillitsch 1992, Schiesari et al., 1996).

The body shape of the tadpoles of *T. resinifictrix* and *T. hadroceps* show characteristics of a typical hylid larva with several modifications of this lentic type. In pond-dwelling species the trunk is attenuate and depressed with a short tail (*T. venulosa* tail-body ratio 1.6). Larvae of phytotelmata breeders develop a longer tail in relation to body length. In *T. resinifictrix* this tail-body ratio is not distinctive (1.5 to 1.7) but in *T. hadroceps* it is (2.4) (Gaucher, 2002; Grillitsch, 1992).

In detailed studies on the external morphology, oral disk and buccopharyngeal structures of *T. resinifictrix* tadpoles, several modifications from the typical hylid tadpole were found. Reduction in filter mesh density as well as a large esophageal entrance and the reduction of the papillation of the buccopharyngeal area are indications for an evolution from microphagous filter-feeding to macrophagy and oophagy (Grillitsch, 1992; Schiesari et al., 1996).

Due to the hypoxic conditions in small water bodies early developmental stages have large external gills to enlarge the respiratory area. The gills degenerate soon and lungs develop early together with an increased rate of aerial respiration and air gulping (Grillitsch, 1992; Lannoo, 1987; Schiesari et al., 1996). Such detailed studies on the morphology of tadpoles are still missing for *T. hadroceps* but are essential for the understanding of the evolution of

tree-hole breeding. The respiratory behavior of *T. hadroceps* tadpoles is similar to several other phytotelmata-dwelling larvae. The tadpoles remain motionless at the bottom of the phytotelmata and come regularly to the surface to breath through air gulping (pers. comm. Gaucher, P.).

Similar to the evolution from pond/stream-breeding to tree-hole breeding species in the genus *Trachycephalus* we see convergent adaptations in other anuran taxa. In the hylid genus *Osteocephalus* at least six of 21 species use phytotelmata for reproduction (see Appendix III). Of the six phytotelmata-breeding species *O. oophagus* is the best reviewed species. Compared to pond/stream-dwelling species of the genus *Osteocephalus*, *O. oophagus* has several adaptations like reduction in clutch size and clutch interval, reduction in labial tooth rows, a single vocal sac and oophagy in tadpoles. These adaptations are convergent to the evolution of *T. resinifictrix* and *T. hadroceps* (see Appendix I and II). Larvae of *O. oophagus* depend on the regular supply of eggs to successfully reach metamorphosis although tadpole feeding is less specialized than in *T. hadroceps*. In *O. oophagus* both parents return to the same tree hole every 5-7 days to deposit fertilized eggs. No physical contact between mother and tadpoles is required for oviposition (Jungfer & Weygoldt 1999). The first clutch develops into tadpoles whereas most of the subsequent eggs serve as food. Pair bonding seems to be the rule in this species at least in regions with low population density. In contrast to the tree-hole breeding species of the genus *Trachycephalus*, *O. oophagus* females choose the egg deposition site. Oviposition takes place in bromeliads and tree holes. The volume ranges from less than a liter to 11 l and the phytotelmata are positioned in heights of up to 35 m on the trees (Jungfer & Schiesari, 1995; Jungfer & Weygoldt, 1999; Schiesari et al., 1996; this study).

A convergent evolution of a strikingly similar behavior to *T. hadroceps* was observed in the monotypic genus *Anotheca*. *Anotheca spinosa,* a 6-8 cm large frog deposits its eggs (clutch size mean=157.8) into small tree holes or bromeliads. The female returns to the breeding site in intervals of 1-14 days (mean=4.85), without the male being present. The tadpoles suck on their mother's ventral side and thus induce oviposition. Eggs deposited by the female are instantly eaten by the tadpoles. Larvae only reach metamorphosis if trophic eggs are regularly deposited (Jungfer, 1996). Another species *Nyctimantis rugiceps* exhibits a very similar reproductive behavior as *A. spinosa* and *T. hadroceps* (see

Appendix I) (Jungfer pers. comm.).
Limited food resources are a major constraint for the developing tadpoles in phytotelmata. One way to solve the problem of food shortage is oophagy (see above). Another way has developed in the microhylid species *Syncope antenori*. The clutch, a maximum of six eggs, is deposited in leaf axils of bromeliads by this small species (SV-length 11-13 mm). After hatching the tadpoles do not feed but recover energy by enzymatic degradation of yolk. In several other characteristics the tadpoles resemble those of the species presented above. Tail-body ratio is 2.5 and internal as well as external gills degrade early whereas lungs are already developed as early as at Gosner-stage nine (Krügel & Richter, 1995).

Communication between tadpole and mother has evolved in the hylid species *T. hadroceps*, *A. spinosa* and *N. rugiceps*. Larvae indicate their presence to their mother by physical contact (i.e. nibbling on the ventral side of the mother) (Gaucher, 2002; Jungfer, 1996). In the dendrobatid frog *Oophaga pumilio* a prelude to the begging behavior evolved. Tadpoles perform a swim close to the water surface before the female enters the phytotelmata and thus indicate their presence to the female when she inspects the phytotelmata from outside (Jungfer & Weygoldt, 1999).
Locating and evaluating new potential breeding sites is a critical stage in the reproduction of amphibians and essential for the offspring´s survival. For species using arboreal phytotelmata for reproduction this search expands to a third dimension. Little is known about how frogs move through the canopy and how they locate the breeding sites. High mobility and the use of several calling sites within a short period of time can be frequently observed in *T. hadroceps* (Gaucher, 2002; this study). In contrast male individuals of *T. resinifictrix* are likely to be encountered at one tree hole during a long period of (this study).
The quality of a breeding site directly effects the fitness of the offspring. Hence the parent selecting the breeding site should be able to evaluate the risk of desiccation, presence of predators and (intra- and interspecific) competitors and availability of nutrition. In *Kurixalus eiffingeri* a well studied Taiwanese frog the most important determinant is the risk of desiccation (Kam et al., 1996). Furthermore the presence of conspecific larvae is a negative factor for oviposition (Lin et al., 2008). *Phrynobatrachus guineensis* on the other hand deposits eggs preferentially into breeding sites where conspecific larvae are already present. Despite the negative effects on larval growth and the availability of unused sites it

is attracted by conspecifics because they indicate a low predation risk (Rudolf & Rödel, 2004). This opposed preference of conspecifics present in the breeding site can be explained by the fact that tadpoles of *K. eiffingeri* are oophagous in contrast to the detrivorous tadpoles of *P. guineensis* (Kam et al., 1996; Lin et al., 2008; Rudolf & Rödel, 2004).

Site fidelity is frequently found in different families of phytotelmata-breeding frogs whereas territorial behavior is typical for frogs of the families of Dendrobatidae (Poelman & Dicke 2008, Pröhl 2002) and Mantellidae (Heying, 2001). Territoriality is the result of scarcity of resources. Reproductive resource limitation was demonstrated in *Mantella laevigata* and in *Dendrobates pumilio*. By experimentally adding artificial phytotelmata into territories of established populations of the two species the population density increased significantly (Donnelly, 1989; Heying, 2004).

In Nouragues five anuran species use arboreal phytotelmata for reproduction. *Trachycephalus resinifictrix, T. hadroceps* and *O. oophagus,* deposit their eggs as a surface film into the water of phytotelmata. *Osteocephalus oophagus,* the most generalistic species of these five phytotelmata-breeding anurans, uses bromeliads and tree holes of variable sizes (Jungfer & Weygoldt 1999). *Trachycephalus hadroceps* and *T. resinifictrix* deposit their eggs into tree holes however the volume of the tree holes used separate clearly (this study). *Ranitomeya ventrimaculata* oviposits into very small bromeliad leaf axils just above the water. After hatching the tadpoles slide into the water or are transported to neighboring leaf axils by the parents (Summers, 1999). *Dendrobates tinctorius* deposits its eggs (3-14 eggs per clutch) on the forest ground were they are guarded by the parents. The tadpoles of *D. tinctorius* hatch after two to three weeks and are transported to terrestrial and arboreal phytotelmata by the father (Lescure & Marty, 2000). In other anuran species the adults check the water bodies for conspecific tadpoles before the deposition of their offspring to prevent cannibalistic interactions (Caldwell & de Araujo, 1998; Lin & Kam, 2008; Summers, 1999).

Tadpoles of *D. tinctorius* were observed to prey on larvae of *T. hadroceps* in a study area in French Guiana (la montagne de Kaw). In eight out of 14 tree holes occupied by *T. hadroceps*, *D. tinctorius* tadpoles were present as well (Gaucher, 2002). In the present study we found tadpoles of *D. tinctorius* in three out of nine breeding sites of *T. resinifictrix*. The tadpoles of both *Trachycephalus* species suffer severely under the presence of

D. tinctorius tadpoles. Thus whole clutches can be devoured by just few *D. tinctorius* larvae (this study). In both studies mentioned above the tree holes co occupied by *D. tinctorius* were situated in heights of up to 25 m. The additional food sources positively effect the survival of the *D. tinctorius* tadpoles thus it is likely that *D. tinctorius* males deposit their offspring intentionally into tree holes of the two *Trachycephalus* species. If *D. tinctorius* follows acoustical, vibrational or chemosensory cues to locate the tree holes of *T. resinifictrix/T. hadroceps* is unknown (Gaucher, 2002; Lescure & Marty, 2000; this study).

Another dendrobatid species, *Dendrobates auratus,* with predatory tadpoles and a similar reproductive behavior as *D. tinctorius*, spends substantial amounts of time to search and evaluate phytotelmata before larval deposition. On which factors males of *D. auratus* evaluate potential tadpole rearing sites is yet unknown (Summers, 1990; Summers & McKeon, 2004).

Adults and larvae need certain adaptations for successful reproduction and development in phytotelmata. On the basis of modifications and on the utilized habitats they can be classified from generalistic phytotelmata breeders to phytotelmata-breeding specialists (see Appendix II). The habitat may be described by the size and by the position. Generalists use phytotelmata of larger volume which are situated closer to the ground (this study). A first physiological adaptation could be the reduction of clutch size or the partitioning of clutches. Females of *Scinax perpusillus* are able to partition clutches and lay one egg each (Alves-Silva & da Silva, 2009). Thus the size of the phytotelmata used for tadpole development can be decreased. With the reduction of phytotelmata size several constraints such as hypoxic water, ephemerality, little primary production and thus poor food supply arise (Schiesari et al., 2003). Behavioral adaptations dealing with little oxygen are reduced activity and air gulping (Grillitsch, 1992; Lannoo et al., 1987). For some phytotelmata-dwelling tadpoles a vertical resting posture with the head closer to the water surface was observed. The elongated tail of many phytotelmata-dwelling tadpoles may facilitate to position the head closer to the water surface. Other proposed explanations for the elongated tail are aeration of the water, faster locomotion through a viscous medium and increase of body surface resulting in higher cutaneous respiration. Opposed to the elongated tail, tail fins and thus body surface is reduced in many phytotelmata-dwelling larvae. In a hypoxic habitat the risk of losing oxygen to the water may be higher than the

benefit of additional cutaneous respiratory surface (Lannoo et al., 1987).

Especially in small phytotelmata the risk of desiccation is a major factor affecting survival of tadpoles. Thus adults should choose a breeding site with low risk of desiccation and tadpoles may react to a falling water level (Kam et al., 1996). Furthermore the presence of predators and intra- and interspecific competitors should be assessed by the parent before deposition of the eggs (Lin & Kam, 2008; Rudolf & Rödel, 2005; Rudolf & Rödel, 2007).

In more voluminous phytotelmata primary production and detritus may suffice the requirements of tadpoles whereas in smaller pools the larvae need alternative food resources (Sota, 1996; Schiesari et al., 2003). Non-feeding tadpoles gain energy from enzymatic yolk reduction (Krügel & Richter, 1995) and predatory behavior evolved in some dendrobatid species (Gaucher, 2002; Summers, 1990; Summers & McKeon, 2004). Cannibalism of larvae is probably an unwanted byproduct in predatory species when no potential prey is available (Summers, 1999). A very sophisticated solution is the evolution of oophagous tadpoles together with the deposition of unfertilized trophic eggs. The female returns periodically to her offspring, communicates with it and deposits eggs without the presence of a male (Gaucher, 2002; Jungfer, 1996; Jungfer & Weygoldt 1999). Provisioning of unfertilized trophic eggs evolved convergently in at least four different phytotelmata-breeding anuran families (see Appendix III).

The two species observed in the present study, clearly show the transition from pond/stream-breeding species (other *Trachycephalus* species) to a moderately adopted arboreal phytotelmata-breeding species with no parental care (*T. resinifictrix*) to a highly evolved tree-hole breeding species with distinct parental care (*T. hadroceps)*. Characteristics representing the high degree of specialization for tree-hole breeding in *T. hadroceps* are small clutch sizes, short clutch intervals and the use of small phytotelmata high up in the canopy (Gaucher, 2002; this study; see Appendix I and II). Tadpoles have reduced external gills and early developing lungs (Grillitsch, 1992; Lannoo et al. 1987). Oophagy with a distinct form of parental care is the strongest indicator for specialized phytotelmata breeding as little food availability seems to be the most limiting factor in these small arboreal habitats (Brown, 2008). Several adaptations facilitate macrophagy/oophagy (Grillitsch, 1992) and the larvae rely on a regular supply of trophic eggs by their mother to successfully reach metamorphosis (Gaucher, 2002).

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Appendix I: Adult and larval characteristics of seven phytotelmata-breeding anuran species. Clutch size: mean or minimum-maximum number of observed eggs; clutch interval: days between two deposited clutches of one female; Labial tooth rows: number of anterior/posterior tooth rows; Height of phytotelmata on tree: minimum-maximum or highest observed site;

	Anotheca spinosa	***Kurixalus eiffingeri***	***Nyctimantis rugiceps***	***Osteocephalus oophagus***	***Phrynobatrachus guineensis***	***Trachycephalus hadroceps***	***Trachycephalus resinifictrix***
Clutch size	150-311	79	500-800	111-506	18.7	82	1612-4336
Clutch interval	4.9 d	-	5 d	5.1 d	-	2-3 d	14-22 d
Trophic eggs	unfertilized	unfertilized	unfertilized	fertilized	no	unfertilized	fertilized
Vocal sacs	one subgular	one	one subgular	one subgular	one	one subgular	two lateral
Tadpole-Mother communication	yes	yes	yes	no	no	yes	no
Tadpole diet	omnivorous	oophagous	oophagous	omnivorous	detritivorous	oophagous	omnivorous
Tail body ratio	1.3	-	-	1.2	-	2.4	1.47
Labial tooth rows	2/2	2/1-2	2/2	2/3-6	-	2/3	2/3-5
Phytotelmata	bromeliads, tree holes and bamboo	bamboo	tree holes and bamboo	bromeliads and tree holes	tree hole, fruit capsules and snail shells	small tree holes	large tree holes
Height of phytotelmata on tree (m)	4	1.5	10	35	2.6	15.1-42	2.2-32
Reference	Jungfer, 1996; Lannoo et al., 1987; Lehtinen et al., 2004;	Chen et al., 2001; Chiu et al., 2006a; Chiu et al., 2006b; Kam, 1996; Kam et al., 2001a; Kam et al., 2001b; Lehtinen et al., 2004; Lin & Kam, 2008; Lin et al., 2008;	Duellman & Trueb, 1976; Hödl, 1990; Jungfer pers. comm.; Lehtinen et al., 2004;	Jungfer & Schiesari, 1995; Jungfer & Weygoldt, 1999; Lehtinen et al., 2004; this study;	Rödel & Rudolf, 2004; Rudolf & Rödel, 2005;	Duellman & Hoogmoed, 1992; Gaucher, 2002; this study;	Grillitsch, 1992; Hödl, 1991; Jungfer & Proy, 1998; Schiesari et al., 1996; Schiesari et al., 2003; Zimmerman & Hödl, 1983; this study

Appendix II: Adaptations towards tree hole breeding in two hylid genera, *Trachycephalus* and *Osteocephalus* and other exemplarily illustrated taxa. Pond/Stream-breeding species below, phytotelmata-breeding specialists above dashed lined. The further above the dashed line the higher the degree of specialization of the species. Characteristics on left side decrease, traits on right side increase with increasing degree of phytotelmata-breeding specialization. For detailed information compare with Appendix I and III.

Phytotelmata-breeding specialists

Decreasing characteristics	*Trachycephalus*	*Osteocephalus*	other Taxa		Increasing characteristics
Clutch size and inter-clutch intervalls, number of labial tooth rows, size of phytotelmata;	*T. hadroceps*		*Anotheca spinosa*	*Kurixalus eiffingeri*	Vocal-sac reduction, parental care, tadpole-mother interactions, tail-body ratio, macrophagy/oophagy, strong jaw sheats, height of phytotelmata on tree, early development of lungs
			Nyctimantis rugiceps		
		O. osteocephalus	*Osteopilus brunneus*	*Syncope antenori*	
		O. deridens			
		O. castaneicola			
		O. fuscifacies			
		O. leoniae			
		O. planiceps			
	T. resinifictrix		*Phrynobatrachus guineensis*		
	T. coriaceus *T. nigromaculatus* *T. mesophaeus* *T. venulosus*	*O. buckleyi* *O. cabrerai* *O. elkejungingerae* *O. leprieurii* *O. mutabor* *O. taurinus* *O. verruciger* *O. yasuni*			

pond/stream-breeding species

Appendix III: Anuran species using phytotelmata as egg and/or tadpole developmental sites. Type of phytotelmata; diet of tadpoles; form of parental care; minimum-maximum observed height of a calling individual or of a phytotelmata with eggs/tadpoles; mean number or minimum-maximum of eggs per clutch. Expanded from Lannoo et al., 1987 and Lehtinen et al., 2004.

Species	Egg/tadpole developmental site	Larval diet	Form of parental care	Observed height of calling/breeding site (meter)	Clutch Size	References	
						Primary literature	Secondary literature, books, internet-references
Bufonidae							
Rhinella castaneotica	Brazil nut capsules	detritus	none	terrestrial	111-328	Caldwell & de Araujo, 1998; Caldwell & de Araujo, 2004;	Lehtinen et al., 2004;
Dendrophryniscus brevipollicatus	bromeliads	non feeding	-	-	-		Lehtinen et al., 2004;
Frostitus pernambucensis	bromeliads	non feeding	-	-	-		Lehtinen et al., 2004;
Melanophryniscus vilavelhensis	leaf axils	-	-	-	-	Steinbach-Padilha, 2008;	
Mertensophryne micranotis	tree holes, snail shells	macrophagy	none	0-1.5	17-32		Lannoo et al., 1987; Lehtinen et al., 2004;
Nectophryne afra	tree holes	-	-	-	-		Lehtinen et al., 2004;
Pelophryne api	tree holes, dead leaves, logs, Nepenthes	-	-	-	-	Dring, 1984;	Malkmus & Dehling, 2008;
Pelophryne brevipes	Pandanus leaf axils, tree holes	non feeding	-	5	-		Lehtinen et al., 2004; Malkmus & Dehling, 2008;
Pelophryne misera	Nepenthes, dead leafs	-	-	-	-	Inger & Stuebing, 1992;	Malkmus & Dehling, 2008;
Stephopaedes anotis	buttresses	non feeding	none	0-4	57-102	Channing, 1993;	Lehtinen et al., 2004;

Species	Egg/tadpole developmental site	Larval diet	Form of parental care	Observed height of calling/breeding site (meter)	Clutch Size	References	
						Primary literature	Secondary literature, books, internet-references
Dendrobatidae							
Adelphobates castaneoticus	Brazil nut capsules	predatory, cannibalism	♂ tadpole transport	terrestrial	2-6	Caldwell & Araujo, 1998;	Lehtinen et al., 2004;
Adelphobates quinquevittatus	bromeliads	omnivorous, cannibalistic, oophagous	-	-	-		Lannoo et al., 1987;
Allobates bromelicola	bromeliads	detritus	-	-	-		Lannoo et al., 1987; Lehtinen et al., 2004;
Ameerega trivittata	-	-	-	-	-		Lötters et al., 2007;
Anomaloglossus beebei	bromeliads	conspecific eggs	♂ tadpole transport; ♀ deposits trophic eggs	terrestrial	3-7	Bourne et al., 2001;	Lehtinen et al., 2004;
Dendrobates auratus	tree holes, bromeliads, stagnant pools	predatour, omnivorous	♂ egg care and tadpole transport	-	6	Caldwell & Araujo, 1998; Yanoviak, 2001;	Lannoo et al., 1987; Lehtinen et al., 2004; www.amphibia.org;
Dendrobates leucomelas	tree holes, trunks, bromeliads	detritus (possibly cannibalistic)	♂ egg care	-	2-12		Lannoo et al., 1987; Lehtinen et al., 2004; www.amphibia.org;
Dendrobates tinctorius	tree holes	heterospecific eggs and larvae	♂ tadpole transport	25	3-14	Noonan & Gaucher, 2006; this study;	Lehtinen et al., 2004; Lescure & Marty, 2000;
Dendrobates truncatus	tree holes	-	-	-	2-7		Lehtinen et al., 2004; Lötters et al., 2007;
Excidobates captivus	bromeliads	-	♂ tadpole transport	terrestrial	-	Twomey & Brown, 2008;	www. amphibia.org;
Excidobates mysteriosus	bromeliads	-	♂ tadpole transport	terrestrial	8-13		Lehtinen et al., 2004; www.amphibia.org; Lötters et al., 2007;
Hyloxalus chlorocraspedus	-	-	-	-	-		Lötters et al., 2007;
Oophaga arborea	bromeliads	omnivorous	♀ tadpole transport; ♂ egg care; deposits trophic eggs	10-15	8		Lannoo et al., 1987; Lehtinen et al., 2004; Lötters et al., 2007;

Species	Egg/tadpole developmental site	Larval diet	Form of parental care	Observed height of calling/breeding site (meter)	Clutch Size	References	
						Primary literature	Secondary literature, books, internet-references
Oophaga granulifera	bromeliads, Dieffenbachia leaf axils	conspecific eggs	♂ egg care; ♀ deposits trophic eggs	2	2-7	Meyer, 1992;	Lehtinen et al., 2004;
Oophaga histrionica	bromeliads	conspecific eggs	♀ tadpole transport; ♀ deposits trophic eggs	0-10	2-6		Lannoo et al., 1987; Lehtinen et al., 2004; www.amphibia.org; Lötters et al., 2007;
Oophaga lehmanni	bromeliads	conspecific eggs	♂ egg care; ♀ deposits trophic eggs	1.2	-		Lehtinen et al., 2004; www.amphibia.org;
Oophaga occulator	bromeliads	conspecific eggs	♀ tadpole transport and deposits trophic eggs	0-3			Lötters et al., 2007;
Oophaga pumilio	bromeliads, terrestrial aroids	conspecific eggs	♂ egg care; ♀ tadpole transport and deposits trophic eggs	12	3-17	Donnelly, 1989; Pröhl, 2002; Young, 1979;	Lannoo et al., 1987; Lehtinen et al., 2004;
Oophaga speciosa	bromeliads	conspecific eggs	♂ egg care; ♀ tadpole transport and deposits trophic eggs	0-2	8-16	Jungfer, 1985;	Lannoo et al., 1987; Lehtinen et al., 2004;
Oophaga sylvatica	bromeliads	conspecific eggs	♀ deposits trophic eggs	-	-		Lötters et al., 2007;
Oophaga vicentei	-	oophagous	♂ tadpole transport, ♀ deposits trophic eggs	-	2-6	Jungfer et al., 1996;	
Phyllobates lugubris	tree holes, bromeliads	omnivorous	♂ egg care and tadpole transport	-	-	Ostrowski, 2003;	Lehtinen et al., 2004; www. amphibia.org;
Phyllobates vittatus	tree holes, bromeliads	omnivorous	♂ egg care and tadpole transport	-	7-21		Lannoo et al., 1987; Lehtinen et al., 2004; www. amphibia.org;

Species	Egg/tadpole developmental site	Larval diet	Form of parental care	Observed height of calling/breeding site (meter)	Clutch Size	References	
						Primary literature	Secondary literature, books, internet-references
Ranitomeya abdita	bromeliads	oophagous	♂ tadpole transport	terrestrial		Myers & Daly, 1976;	
Ranitomeya altobueyensis	-	-	-	-	-	Silverstone, 1975;	
Ranitomeya amazonica	bromeliads, Heliconia leaf axils	detritus, mosquito larvae, conspecific eggs cannibalistic	♂ tadpole transport	-	4-6		Lötters et al., 2007;
Ranitomeya benedicta	-	-	-	-	-		Lötters et al., 2007;
Ranitomeya biolat	bamboo	-	-	2	1-2	von May et al., 2009;	Lehtinen et al., 2004; Lötters et al., 2007;
Ranitomeya bombetes	-	-	-	-	-		Lötters et al., 2007;
Ranitomeya claudiae	Heliconia leaf axils, bamboo	-	♂ egg care and tadpole transport	0-2	3-4	Ostrowski, 2003;	Lötters et al., 2007;
Ranitomeya daleswansoni	-	-	-	-	-		Lötters et al., 2007;
Ranitomeya defleri	bromeliads;	-	-	terrestrial	-	Twomey & Brown, 2009;	
Ranitomeya doriswansoni	-	-	-	0-2	-		Lötters et al., 2007;
Ranitomeya duellmani	leaf axils	-	-	0-3	-		Lötters et al., 2007;
Ranitomeya fantastica	bromeliads, leaf axils	-	-	0-8	2-8		Lehtinen et al., 2004; Lötters et al., 2007;
Ranitomeya flavovittata	Guzmania	-	-	1.2	-		Lötters et al., 2007;
Ranitomeya fulgurita	bromeliads	-	♂ egg care and tadpole transport	1.5	1-5		Lötters et al., 2007;
Ranitomeya ignea	-	-	-	-	-		Lötters et al., 2007;
Ranitomeya imitator	terrestrial bromeliads	conspecific unfertilized eggs	♀ deposits trophic eggs; ♂ tadpole transport	4.5	1.6	Brown et al., 2008;	
Ranitomeya intermedia	-	-	-	-	-		Lötters et al., 2007;

Species	Egg/tadpole developmental site	Larval diet	Form of parental care	Observed height of calling/breeding site (meter)	Clutch Size	References	
						Primary literature	Secondary literature, books, internet-references
Ranitomeya lamasi	Heliconia leaf axils, Araceae, bromeliads, bamboo	oophagous	♂ tadpole transport, egg care, ♀ deposits trophic eggs	-	2-4	Morales, 1992;	Lehtinen et al., 2004; Lötters et al., 2007;
Ranitomeya minuta	bromeliads	detritus , cannibalistic	♂ tadpole transport	terrestrial	4		Lehtinen et al., 2004; Lötters et al., 2007;
Ranitomeya opisthomelas	bromeliads	-	-	-	-		Lötters et al., 2007;
Ranitomeya reticulata	bromeliads	omnivorous, frog eggs	♂ tadpole transport	0-2	1-3		Lehtinen et al., 2004; Lötters et al., 2007;
Ranitomeya rubrocephala	-	-	-	-	-		Lötters et al., 2007;
Ranitomeya sirensis	-	-	-	1.2	-		Lötters et al., 2007;
Ranitomeya tolimensis	-	-	-	-	-		Lötters et al., 2007;
Ranitomeya uakarii	bromeliads	omnivorous	♂ tadpole transport, egg care	-	2-15	Brown et al., 2006;	
Ranitomeya vanzolinii	tree holes, vines	conspecific eggs	♂ tadpole transport; ♀ deposits trophic eggs	0-4	1-10	Caldwell, 1997; Caldwell & Oliveira 1999;	Lehtinen et al., 2004; Lötters et al., 2007; www.amphibia.org;
Ranitomeya variabilis	bromeliads	detritus, mosquito larvae, conspecific eggs?, cannibalistic	♂ tadpole transport	8.4	3-13	Brown et al., 2008;	Lehtinen et al., 2004; Lötters et al., 2007;
Ranitomeya ventrimaculata	bromeliads, Heliconia leaf axils	detritus, mosquito larvae, conspecific eggs, cannibalistic	♂ tadpole transport	30	6.7	Summers & Amos, 1997; Summers, 1999; Poelman & Dicke 2007 and 2008;	Lehtinen et al., 2004; Lescure & Marty, 2000;
Ranitomeya viridis	-	-	-	-	-		Lötters et al., 2007;
Ranitomeya virolinensis	Tilandsia, Guzmania	-	-	0.5-2	-		Lötters et al., 2007;

Species	Egg/tadpole developmental site	Larval diet	Form of parental care	Observed height of calling/breeding site (meter)	Clutch Size	References	
						Primary literature	Secondary literature, books, internet-references
Hemiphractidae							
Flectonotus fiitzgeraldi	bromeliads, aroids	non feeding	♀ egg brooding and tadpole trandsport	-	3.3	Duellman & Gray, 1983;	Lehtinen et al., 2004;
Flectonotus fissilis	bromeliads	non feeding	♀ egg brooding and tadpole trandsport	-	10.1	Duellman & Gray, 1983;	Lehtinen et al., 2004;
Flectonotus goeldii	bromeliads	non feeding	♀ egg brooding and tadpole trandsport	-	15.3	Duellman & Gray, 1983;	Lehtinen et al., 2004;
Flectonotus ohausi	bamboo	non feeding	♀ egg brooding and tadpole trandsport	-	3-20	Duellman & Gray, 1983;	Lehtinen et al., 2004;
Flectonotus pygmaeus	bromeliads, Heliconia leaf axils	non feeding	♀ egg brooding and tadpole trandsport	-	6.7	Duellman & Gray, 1983;	Lehtinen et al., 2004;
Hylidae							
Anotheca spinosa	bromeliads, tree holes, bamboo	conspecific eggs, insect matter	♀ deposits trophic eggs	4	150-311	Jungfer, 1996;	Lannoo et al., 1987; Lehtinen et al., 2004;
Bromeliohyla bromeliacia	bromeliads	plant matter, detritus	-	-	-		Lannoo et al., 1987; Lehtinen et al., 2004;
Bromeliohyla dendroscarta	bromeliads	plant matter, detritus	-	-	-		Lannoo et al., 1987; Lehtinen et al., 2004;
Cruziohyla calcarifer	-	-	-	-	-	Caldwell, 1994;	
Cruziohyla craspedopus	tree holes, buttresses	detritus?	none	1.8	14-21	Hoogmoed & Cadle, 1991;	Lehtinen et al., 2004;
Isthmohyla picadoi	bromeliads	frog eggs	-	-	0-22	Stuckert et al., 2009;	Lannoo et al., 1987; Lehtinen et al., 2004;
Isthmohyla zeteki	bromeliads	frog eggs (conspecific?)	-	-	-		Lannoo et al., 1987; Lehtinen et al., 2004;

Species	Egg/tadpole developmental site	Larval diet	Form of parental care	Observed height of calling/breeding site (meter)	Clutch Size	References	
						Primary literature	Secondary literature, books, internet-references
Nyctimantis rugiceps	bamboo, tree holes	conspecific eggs	♀ deposits trophic eggs	10	500-800	Duellman and Trueb, 1976; Hödl, 1990; Jungfer pers. comm.;	Lehtinen et al., 2004;
Osteocephalus castaneicola	Brazil nut capsules	frog eggs	-	terrestrial	-	Moravec et al., 2009;	
Osteocephalus deridens	bromeliads	fertilized conspecific eggs	♀ and ♂ return and deposit fertilized eggs	30	-	Jungfer et al., 2000;	
Osteocephalus fuscifacies	bromeliads	-	-	6	-	Jungfer et al., 2000;	
Osteocephalus leoniae	bromeliads	-	-	-	-	Jungfer pers. comm.	
Osteocephalus oophagus	bromeliads, tree holes, palm leaf axils	frog eggs	♀ and ♂ return and deposit fertilized eggs	35	111-506	Jungfer & Schiesari, 1995; Jungfer & Weygoldt, 1999; this study;	Lehtinen et al., 2004;
Osteocephalus planiceps	bromeliads, tree holes, palm leaf axils	-	-	-	-	Jungfer pers. comm.	
Osteopilus brunneus	bromeliads	conspecific eggs	♀ deposits trophic eggs	7	276		Lannoo et al., 1987; Lehtinen et al., 2004;
Osteopilus crucialis	bromeliads	frog eggs (conspecific?)	-	-	-		Lannoo et al., 1987; Lehtinen et al., 2004;
Osteopilus marianae	bromeliads	frog eggs (conspecific?)	-	-	-		Lannoo et al., 1987; Lehtinen et al., 2004;
Osteopilus wilderi	bromeliads	frog eggs (conspecific?)	-	-	-		Lannoo et al., 1987; Lehtinen et al., 2004;
Phyllodytes acuminatus	bromeliads	-	-	-	-		Lehtinen et al., 2004;
Phyllodytes auratus	bromeliads	carnivorous?	-	-	-		Lannoo et al., 1987; Lehtinen et al., 2004;
Phyllodytes brevirostris	bromeliads	-	-	-	-		Lehtinen et al., 2004;
Phyllodytes edelmoi	bromeliads	-	-	1-25	-	Peixoto, et al., 2003;	Lehtinen et al., 2004;
Phyllodytes gyrinaethes	bromeliads	frog eggs, detritus	-	1-10	-	Peixoto, et al., 2003;	Lehtinen et al., 2004;
Phyllodytes kautskyi	bromeliads	-	-	-	-		Lehtinen et al., 2004;

Species	Egg/tadpole developmental site	Larval diet	Form of parental care	Observed height of calling/breeding site (meter)	Clutch Size	References	
						Primary literature	Secondary literature, books, internet-references
Phyllodytes luteolus	bromeliads	detritus	-	-	-		Lannoo et al., 1987; Lehtinen et al., 2004;
Phyllodytes melanomystax	bromeliads	-	-	0-5	-	Caramaschi et al., 1992;	Lehtinen et al., 2004;
Phyllodytes tuberculosus	bromeliads	detritus	-	-	-		Lannoo et al., 1987; Lehtinen et al., 2004;
Scinax perpusillus	terrestrial bromeliads	detritus	none	terrestrial	3	Alves-Silva & da Silva, 2009;	Lannoo et al., 1987; Lehtinen et al., 2004;
Trachycephalus hadroceps	tree holes	conspecific eggs	♀ deposits trophic eggs	42	82	Duellman & Hoogmoed, 1992; Gaucher, 2002; this study;	
Trachycephalus resinifictrix	tree holes	detritus, conspecific eggs	none	32	1612-4336	Grillitsch, 1992; Hödl, 1991; Jungfer & Proy, 1998; Schiesari et al., 1996; Schiesari et al., 2003; Zimmerman & Hödl, 1983; this study	
Hyperolidae							
Acanthixalus sonjae	tree holes	detritus, omnivorous	none	0-5	9.3	Rödel et al., 2003;	Lehtinen et al., 2004; www.amphibia.org;
Acanthixalus spinosus	tree holes	detritus,	none	0-5	8-10	Rödel et al., 2003;	Lannoo et al., 1987; Lehtinen et al., 2004; www.amphibia.org;
Hyperolius acutirostris	tree holes	-	-	-	-		Lehtinen et al., 2004;
Hyperolius mosaicus	tree holes	plant matter, insect larvae, dead conspecifics	-	-	1-10		Lehtinen et al., 2004; www.amphibia.org;
Leptodactylidae							
Crossodactylus sp. izecksoni	bromeliads	detritus	-	-	-		Lannoo et al., 1987; Lehtinen et al., 2004;

Species	Egg/tadpole developmental site	Larval diet	Form of parental care	Observed height of calling/breeding site (meter)	Clutch Size	References	
						Primary literature	Secondary literature, books, internet-references
Mantellidae							
Guibemantis albolineatus	Pandanus leaf axils	-	-	-	-		Glaw & Vences, 2007; Lehtinen et al., 2004; www.amphibia.org;
Guibemantis bicalcaratus	Pandanus leaf axils	detritus	-	-	-	Lehtinen, 2004;	Glaw & Vences, 2007; Lannoo et al., 1987;
Guibemantis flavobrunneus	Pandanus leaf axils	-	-	-	-		Glaw & Vences, 2007; Lehtinen et al., 2004;
Guibemantis pulcher	Pandanus leaf axils	-	-	-	-		Glaw & Vences, 2007; Lehtinen et al., 2004;
Guibemantis punctatus	Pandanus leaf axils	detritus	-	-	-	Lehtinen, 2004;	Glaw & Vences, 2007;
Mantella laevigata	bamboo, tree holes	conspecific eggs	♀ deposits trophic eggs	0.1-3.5	1	Heying, 2001; Heying, 2004;	Glaw & Vences, 2007; Lehtinen et al., 2004;
Microhylidae							
Anodonthyla boulengerii	tree holes, tree ferns, Ravenala axils, bamboo	non feeding	♂ egg care	1-2	-		Lehtinen et al., 2004; Glaw & Vences, 2007;
Anodonthyla hutchisoni	tree holes	-	-	0-3	23	Fenolio et al. 2007;	
Anodonthyla moromora	tree holes	-	-	1-5	-		Glaw & Vences, 2007;
Anodonthyla nigrigularis	tree holes	non feeding	♂ egg care	1	-		Lehtinen et al., 2004; Glaw & Vences, 2007;
Anodonthyla rouxae	bamboo trunks, Pandanus axils	-	♂ egg care		13-50		Lehtinen et al., 2004; Glaw & Vences, 2007;
Chaperina fusca	tree holes, pools, bamboo, buttresses	filter feeding	-	1	-		Lannoo et al., 1987; Lehtinen et al., 2004; Malkmus & Dehling, 2008; www. frogsofborneo.org;
Cophyla berara	tree holes, bamboo	-	-	1-2	-		Glaw & Vences, 2007;
Cophyla occulants	tree holes, bamboo	-	-	1-1.5	-		Glaw & Vences, 2007;

Species	Egg/tadpole developmental site	Larval diet	Form of parental care	Observed height of calling/breeding site (meter)	Clutch Size	References	
						Primary literature	Secondary literature, books, internet-references
Cophyla phyllodactyla	tree holes, bamboo	non feeding	-	1.5-3.5	-		Glaw & Vences, 2007; Lehtinen et al., 2004; www.amphibia.org;
Hoplophryne rogersi	bamboo, banana leaves	detritus, conspecific egg fragments	-	-	-		Lannoo et al., 1987; Lehtinen et al., 2004;
Hoplophryne uluguruensis	bamboo, banana leaves	detritus, conspecific egg fragments	-	-	-		Lannoo et al., 1987; Lehtinen et al., 2004;
Hypopachus variolosus	puddles, ponds, buttresses	filter feeding?	-	-	-		Lehtinen et al., 2004;
Kalophrynus eok	bamboo	-	-	terrestrial	-		Malkmus & Dehling, 2008;
Kalophrynus pleurostigma	tree holes, Nephenthes, pools, bamboo	non feeding	-	terrestrial	-		Lehtinen et al., 2004; Malkmus & Dehling, 2008;
Metaphrynelle sundana	tree holes	-	-	10	-	Lardner & bin Lakim, 2002 and 2004;	Lehtinen et al., 2004; Malkmus & Dehling, 2008;
Microhyla borneensis	Nephentes	-	-	-	-		Malkmus & Dehling, 2008;
Platypelis alticola	tree holes	-	-	-	-		Glaw & Vences, 2007;
Platypelis barbouri	bamboo, Pandanus axils	non feeding	-	1.5-2	-		Lehtinen et al., 2004; Glaw & Vences, 2007;
Platypelis cowanii	tree holes, bamboo	-	-	3	-		Glaw & Vences, 2007;
Platypelis grandis	tree holes, bamboo, Ravenala leaf axils	non feeding	♂ egg care		90-100		Lehtinen et al., 2004;Glaw & Vences, 2007;
Platypelis mavomavo	tree holes	-	-	2-4	-		Glaw & Vences, 2007;
Platypelis milloti	Ravenala leaf axils	-	-	-	-		Glaw & Vences, 2007;
Platypelis pollicaris	tree holes	-	-	1.5-2	-		Glaw & Vences, 2007;

Species	Egg/tadpole developmental site	Larval diet	Form of parental care	Observed height of calling/breeding site (meter)	Clutch Size	References	
						Primary literature	Secondary literature, books, internet-references
Platypelis tetra	Pandanus leaf axils	-	-	-	-		Glaw & Vences, 2007;
Platypelis tsaratananaensis	tree holes, bamboo	-	-	-	-		Glaw & Vences, 2007;
Platypelis tuberifera	Pandanus leaf axils	-	-	-	-		Glaw & Vences, 2007;
Plethodontohyla notosticta	tree holes, tree ferns, Ravenala axils, bamboo	non feeding	-	-	-		Lehtinen et al., 2004;
Ramanella nagaoi	tree holes	-	-	-	-		Lehtinen et al., 2004;
Ramanella obscura	water-filled tree roots	-	-	-	-		Lehtinen et al., 2004;
Ramanella triangularis	tree holes	-	-	-	-		Lannoo et al., 1987; Lehtinen et al., 2004;
Syncope antenori	bromeliads	non feeding	-	terrestrial	≤6	Hödl, 1990; Krügel & Richter, 1995;	Lehtinen et al., 2004;
Phrynobatrachidae							
Phrynobatrachus guineensis	tree holes, fruit capsules	detritus	none	2	18	Rödel & Rudolf, 2004; Rudolf and Rödel, 2005;	
Ranidae							
Limnonectes palavanensis	tree holes	-	-	terrestrial	-		Malkmus & Dehling, 2008;

Species	Egg/tadpole developmental site	Larval diet	Form of parental care	Observed height of calling/breeding site (meter)	Clutch Size	References	
						Primary literature	Secondary literature, books, internet-references
Rhacophoridae							
Kurixalus eiffingeri	bamboo	conspecific eggs	♀ deposits trophic eggs	1.6	79	Chen et al., 2001; Chiu et al., 2006a; Chiu et al., 2006b; Kam et al., 1996; Kam et al., 2001a; Kam et al., 2001b;Lin & Kam, 2008; Lin et al., 2008;	Lehtinen et al., 2004;
Nyctixalus margaritifer	tree holes	-	-	-	-		www.iucnredlist.org
Nyctixalus pictus	tree holes	-	-	2.6	-		Lannoo et al., 1987; Lehtinen et al., 2004; Malkmus & Dehling, 2008;
Nyctixalus spinosus	tree holes	-	-	-	-		Lannoo et al., 1987; Lehtinen et al., 2004;
Philautes carinensis	tree holes	frog eggs	-	1.5	-	Wassersug et al, 1981;	Lannoo et al., 1987; Lehtinen et al., 2004;
Polypedates macrotis	tree holes	-	-	-	-		Malkmus & Dehling, 2008;
Rhacophorus harrissoni	tree holes	omnivorous	-	4	-		Lannoo et al., 1987; Lehtinen et al., 2004; Malkmus & Dehling, 2008; www.frogsofborneo.org;
Rhacophorus prasinatus	tree holes	-	-	-	-	Mou et al., 1983;	www.iucnredlist.org
Theloderma gordoni	tree holes	-	-	-	-		Lehtinen et al., 2004;
Theloderma horridum	tree holes, buttresses	-	-	1.5	-		Lannoo et al., 1987; Lehtinen et al., 2004; Malkmus & Dehling, 2008;
Theloderma leprosum	tree holes, buttresses	-	-	-	-		Lehtinen et al., 2004;
Theloderma stellatum	tree holes	detritus	-	4	-	Wassersug et al, 1981;	Lannoo et al., 1987; Lehtinen et al., 2004;

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Zusammenfassung

Im Laufe der Evolution entwickelten sich bei Amphibien viele verschiedene Formen der Reproduktion. Daher sind sie lohnende Forschungsobjekte für die Untersuchung der Evolution von Fortpflanzungsverhalten. Eine besondere Form der Fortpflanzung bei Fröschen ist die Ablage der Nachkommen, Eier oder Kaulquappen in Phytotelmata.
Diese Arbeit beschreibt das Fortpflanzungsverhalten von *Trachycephalus resinifictrix* (Goeldi, 1907) und *T. hadroceps* (Duellman & Hoogmoed, 1992), zwei arborealen Froscharten aus den Regenwäldern Französisch-Guyanas. Während eines zweimonatigen Forschungsaufenthaltes wurden Daten zu Populationsgröße, Fortpflanzung und Eigenschaften der Ruf- und Laichplätze der beiden Arten gesammelt.
Beide Arten zeigen ein ähnliches Fortpflanzungsverhalten, benützen aber unterschiedliche Baumhöhlen als Laich- und Rufplätze. Keine der Baumhöhlen von *T. hadroceps* hatte ein größeres Volumen als ein Liter und sie befanden sich deutlich höher an den Bäumen als jene von *T. resinifictrix,* deren Volumen immer größer als vier Liter waren. Adulte und Kaulquappen von *T. hadroceps* zeigen eindeutige Anpassungen an das Leben in diesen arborealen Phytotelmata die bei *T. resinifictrix* nicht vorhanden sind. Auf Grund der Ergebnisse dieser Arbeit wird die Evolution der in Phytotelmata laichenden Anura diskutiert und mit anderen Arten verglichen. Eine Tabelle der bekannten in Phytotelmata laichenden Arten wird im Anhang präsentiert.