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# DIPLOMARBEIT

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## Bet-hedging in Tadpole Deposition in the Neotropical Frog *Allobates femoralis*

Verfasserin

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**Abstract**

Within anurans terrestrial oviposition has evolved independently several times, presumably as an adaptation to high predation pressure on eggs and the risk of competing stray sperm from rivals in aquatic environments. It is observed almost exclusively in tropical regions due to the high humidity. The dilemma between terrestrial eggs and the aquatic anuran larvae is solved in most dendrobatid species by obligatory parental care in the form of tadpole transport. In the Neotropical frog *Allobates femoralis* (Dendrobatidae), clutches are laid in the leaf litter and tadpole transport to water bodies is mainly performed by males. Facing the risks of predators or desiccation of ephemeral pools, the partitioning of larvae over different pools would be a suitable bet-hedging strategy to overcome the risk of total clutch loss. In the present study we assessed the genetic relationship of larvae across water bodies in a wild population of *A. femoralis* in French Guiana in spring 2010. We used seven highly polymorphic microsatellite loci and DNA samples of adults and of larvae from 30 artificial pools which had been installed in 2009. Single pools contained on average 43.25 larvae (SD = 57.88). The reconstructed pedigree revealed that of the *A. femoralis* males that were identified as fathers of more than one tadpole, 65.1% had used multiple pools as tadpole deposition sites and 39% of these had partitioned single clutches across several water bodies. The partitioning of single clutches was more frequently observed in males that were in their second or third breeding season, suggesting that older males might benefit from properties at the beginning of the reproductive period compared to young males. Our results clearly demonstrate that *A. femoralis* males distribute single and successive clutches across several water bodies, which might act as a bet-hedging strategy against total offspring loss.

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## Introduction

Parental care can be defined as any parental behaviour that leads to enhanced fitness of the offspring (Trivers, 1972; Wittenberger, 1981). It is expected to evolve in species and environments where the direct benefits for the offspring exceed the direct cost for the parent (Clutton-Brock, 1991) such as increased physical risk for the parent or decreased opportunities for future reproduction (Crump, 1995).

Within amphibians, the occurrence and complexity of parental behaviour varies considerably between the orders, and although parental care is rather scarce in anurans, a remarkable diversity is found in this group (Duellmann and Trueb, 1986; Crump, 1995). Among anurans, parental care is predominantly found within terrestrial breeders in the humid tropics (Wells, 1981). Terrestrial oviposition has evolved independently several times, presumably as an adaptation to high predation pressure on eggs (reviewed by Wells, 2007) and the risk of competing stray sperm from rivals in aquatic environments. However, tadpoles of most anuran species, including terrestrial breeders, are still strictly bound to water (reviewed by Mc Diarmid and Altig, 1999). This dilemma is solved by either direct development of tadpoles inside the clutch (Hödl, 1990; Bahir *et al*., 2005), or by parental care for eggs and/or tadpoles. Parental behaviours in anurans include attendance of eggs, tadpoles, or froglets, transportation of eggs, tadpoles, or froglets and in some species feeding of tadpoles (Crump, 1995; Haddad and Prado, 2005; reviewed by Wells, 2007). In several species the transport of hatchlings towards water bodies is even obligatory (Duellmann and Trueb, 1986). Terrestrial oviposition likely has played a major factor in the evolution of parental care in anurans, given that 91% of all anuran species that exhibit parental care deposit their eggs outside of water (Crump, 1995).

Mortality of amphibian larvae is very high, with less than 10% survivorship of hatchlings in most species (Crump, 1983; Vonesh and de la Cruz, 2002). The high risk of mortality at the aquatic larval stage is caused by predation (Magnusson & Hero, 1991; Gascon, 1992) and pond desiccation (reviewed by Wells, 2007), inter- and intraspecific competition for food (Gonzalez *et al*., 2011) as well as parasitism and infection of pathogens (Kriger and Hero, 2007; Rhoden *et al*., 2011). Further physical and biological aspects may affect tadpole survival as well (Wong and Booth, 1994; Dolmen *et al*., 2008). The developmental stage inside water bodies is dependent on varying and highly unpredictable factors (cf. Spieler and Linsenmair, 1997), and is therefore a vulnerable period to most anuran larvae. Accordingly, in species with tadpole transport, tadpole survival is therefore, amongst others, highly influenced by the tadpole deposition sites chosen by the transporting parent. However, considering the sum of incalculable risks, the prediction of all risks might be impossible to the care-giving parent (cf. Byrne and Keogh, 2009), and the choice of larval deposition sites by chance might strongly affect the fitness in the offspring. In this context, the deposition of offspring across several water sites will spread the risks over all tadpoles and might therefore act as an optimal strategy to minimize the risk of total offspring loss. For example, females of the Australian toadlet *Pseudophryne bibronii* decrease the risks of nest failure by distributing their eggs across multiple nests despite assumed, increased risks for themselves (Byrne and Keogh, 2009).

Neotropical poison frogs (Dendrobatidae, Pyron and Wiens, 2011) show highly complex reproductive behaviour such as territoriality, prolonged courtship, and parental care (Weygoldt, 1987; Pröhl, 2005). All known members deposit their eggs outside of water (Weygoldt, 1987; Duellmann, 1988; Hödl, 1990; Crump, 1995) and in most cases tadpoles are transported to bodies of water by either the male or the female, where they complete their development until metamorphosis (Weygoldt, 1987). In some dendrobatid species, adult frogs have been observed to differentiate between food availability (Poelman *et al.,* 2013) or predator presence (Mc Keon and Summers, 2013) in tadpole deposition sites. The distribution of larvae across several water sites has mainly been documented in and discussed for species that transport their tadpoles to very small water bodies, such as bromeliads and tree holes (e.g. Brust, 1993 for *Dendrobates pumilio*; Caldwell and de Oliveira, 1999 for *Dendrobates vanzolinii*). The increased risks of cannibalism due to limited food availability presumably selected for the dispersal of tadpoles to different deposition sites in these species (Summers, 1990; Summers and Amos, 1997; Caldwell and de Oliveira, 1999). However, there is little knowledge about the deposition behaviour of species that use medium-sized pools, where nutrients are not a limiting factor.

The Neotropical frog *A. femoralis* (Dendrobatidae) is widely distributed throughout Amazonia (Amèzquita *et al*., 2009). The reproductive season overlaps with the local rainy season (Gottsberger & Gruber, 2004; Kaefer *et al.,* 2012). During that time males are highly territorial (Hödl *et al*., 2004) and females show non-aggressive site fidelity (Ringler *et al.,* 2009). In *A. femoralis*, pair formation, courtship and mating occur in the male`s territory (Roithmair, 1992; Ringler *et al.,* 2009). Previous studies have identified a polygynandrous mating system for *A. femoralis* (Ursprung *et al*., 2011). Externally fertilized clutches of approximately 20 eggs are laid in the leaf litter (Weygoldt, 1980; Ringler *et al.*, 2012). After hatching (15-20 days later), male *A. femoralis* carry the tadpoles on their back towards suitable bodies of water (Weygoldt, 1980; Roithmair, 1992), such as ponds, puddles, water-filled ground-fallen palm-spathices or streamside puddles prior to flooding (Hödl, 1990), where final larval development takes 40-50 days (Weygoldt, 1980). Although cannibalistic feeding is very common among dendrobatid tadpoles that breed in temporal pools (Caldwell and de Araùjo, 1998; Summers, 1999b; Summers and Symula, 2001), *A. femoralis* tadpoles show a non-predaceous behaviour among themselves (Weygoldt, 1980–obs. in captivity; Ringler E., pers. obs.). During tadpole transport, males have to leave their territory, which usually takes less than half a day (Roithmair, 1992). Facing the risks of aquatic predators, pool desiccation of ephemeral pools or interspecific competition, we assume that partitioning of larvae over different pools would constitute a suitable bet-hedging strategy to overcome the risk of total clutch loss in *A. femoralis.*

In the present study, we used field observations and microsatellite data of tadpoles from one reproductive season to investigate whether males in a natural population of *A. femoralis* spread their tadpoles of single or successive clutches over different water bodies.

## Material and Methods

*Study Area*

Our study area is located in a lowland rainforest near the field camp "Saut Pararè" (4°02' N, 52°41' W) in the nature reserve "Les Nourages", French Guiana (for more details on the study area see Ursprung *et al*., 2011). In the course of a previous study on the effects of reproductive resource supplementation in *A. femoralis* (Ringler *et al.,* submitted), thirty artificial pools with a capacity of approx. 15l (Fig.1) were placed in a 6 by 5 array with 10m distance between pools in the middle of our study plot in 2009 (Fig.2). We put some leaf litter and branches inside the pools to match the conditions of natural water bodies and let the pools naturally fill with rainwater.


**Fig.1:** artificial pool, à 15l plastic tub.


**Fig.2:** GIS- map of the study site; ▪ artificial pools (thirty); creeks and Arataye River in dark grey; study plot shaded in light grey (cf. Ursprung *et al*., 2011).

*Sampling and genotyping*

For the present study we aimed to obtain a representative sample of the tadpole transport events during spring 2010. Sampling of larvae took place once in January and once in April 2010 within the reproductive season of *A. femoralis* in French Guiana, which usually lasts from December to May (Born and Gaucher, 2001; Gottsberger and Gruber, 2004). Pools were emptied into a white tub, with contents being poured through a mesh. We carefully searched for tadpoles and sampled on average 32% of the total amount of *A. femoralis* tadpoles per pool. Species identification was accomplished via phenotypic characteristics; other tadpole species observed inside our pools were *Rhinella castaneotica*, *Allobates granti* and *Dendrobates tinctorius*. Sampled larvae were immediately preserved in 96% ethanol until extraction. Spatial and behavioural information, as well as microsatellite genotypes of all

adult individuals from the study population in 2010 were already available from a previous study (Ringler *et al*., submitted).

Genetic material was extracted using a Proteinase K digestion followed by a standard phenol-chloroform protocol. All larvae were genotyped at seven microsatellite loci (*Afem*03, *Afem*05, *Afem*09, *Afem*12, *Afem*13, *Afem*15 and *Afem*16, following Ursprung *et al.,* 2011). Amplified products were diluted with water, mixed with the internal size standard ROX500, run on an ABI 3130xl sequencer and visualized using PeakScanner 1.0 (Applied Biosystems). All loci were visually identified, and the final allele sizes were determined using the binning software Tandem 1.01 (Matschiner and Salzburger, 2009). For further details on the specific microsatellite loci see Ursprung *et al*. (2011).

*Parentage assignments and analyses of tadpole deposition behaviour*

Parentage assignments were carried out with COLONY2 (Wang, 2009, see Ursprung *et al*., 2011 for details on the analysis parameters). To assure assignment accuracy, we only included individuals that had at least five unambiguously genotyped loci. Only 'Best (ML) Configuration' assignments with the maximum likelihood obtained at the end of the computation were used for the subsequent analyses. If multiple tadpoles of the same sampling cohort were assigned to the same parent-pair by COLONY2, they were considered as descendents from a single clutch. For the analyses of intra-clutch partitioning we included only clutches that were represented by at least two full siblings; for the analyses of inter-clutch partitioning we considered only males that were assigned to at least two clutches.

All statistical tests were performed in IBM SPSS Statistics 20.0.0.

**Results**

Within both samplings in spring 2010 we counted a total of 2595 *A. femoralis* tadpoles in our 30 artificial pools. The mean number of tadpoles per pool was 43.25 (SD = 57.88). We sampled on average 32% of the *A. femoralis* tadpoles per pool. The sampling amounted to 431 larvae in total, with a mean of 7.18 (SD = 5.01) tadpoles per pool. We had to exclude 19 individuals from the larval sample due to low amplification success.

Of the 412 tadpoles, 337 larvae could be unambiguously assigned to a known father from the 2010 population. Assignments showed that at least 92 out of the total 212 *A. femoralis* males from our study area had reproductive success (43.4%). 63 of the 92 fathers were assigned to at least 2 tadpoles and 48 males were assigned to more than one clutch. Forty-one of the 63 fathers (approx. 65%) used more than one pool for their tadpoles (Fig.3a). Sixteen of the forty-one males were found to spread the larvae of single clutches over multiple pools (Fig.3b). Not a single male, producing more than three clutches, carried it´s tadpoles to only a single artificial body of water.

The number of pools used per male was significantly correlated with the number of observed clutches ($n = 92$, $R^2 = 0.7383$, $y=0.768x + 0.3321$, $p < 0.001$; Fig.4). However, the partitioning of single clutches over multiple water bodies was only marginally significant affected by the number of clutches per males ($p = 0.057$, $R^2 = 0.0026$, $y =0.0089x + 1.1038$, $n = 63$; Fig.5).

On average, we found larvae of 6.1 males within one pool (SD = 3.18, n = 92). Individual males, who were assigned to more than one tadpole, used on average 2.37 pools (SD = 1.39, range = 1 – 7, n = 63).

To investigate the effect of age on larval deposition strategy, we differentiated between ‘young males’ (all males that were primarily encountered in 2010) and ‘old males’ (males that had been already encountered in previous years). We considered only those 63 males that were assigned to at least 2 tadpoles in our analyses. Old males did not produce more clutches than young ones (Mann-Whitney -*U*- Test; $U = 224$, $p = 0{,}699$, $n = 63$; Fig.7), and did not distribute the tadpoles of successive clutches over more pools than young males did (Mann-Whitney -*U*- Test; $U = 206$, $p = 0{,}451$, $n = 63$; Fig.6). However, partitioning of larvae within single clutches over several pools was significantly more often observed in ‘old’ than ‘young males’ (Mann-Whitney -*U*- Test; $U = 151.5$, $n = 63$, $p = 0{,}019$; Fig.8).

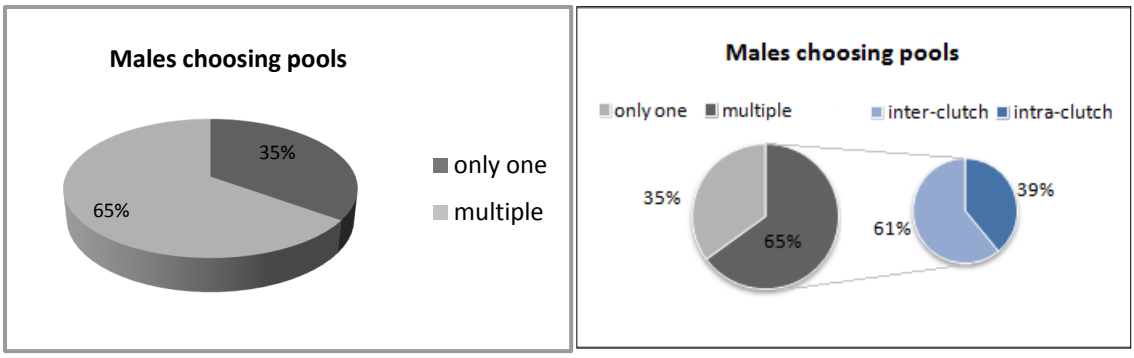


**Fig.3a+b:** Tadpole distribution behaviour in *A. femoralis* males.

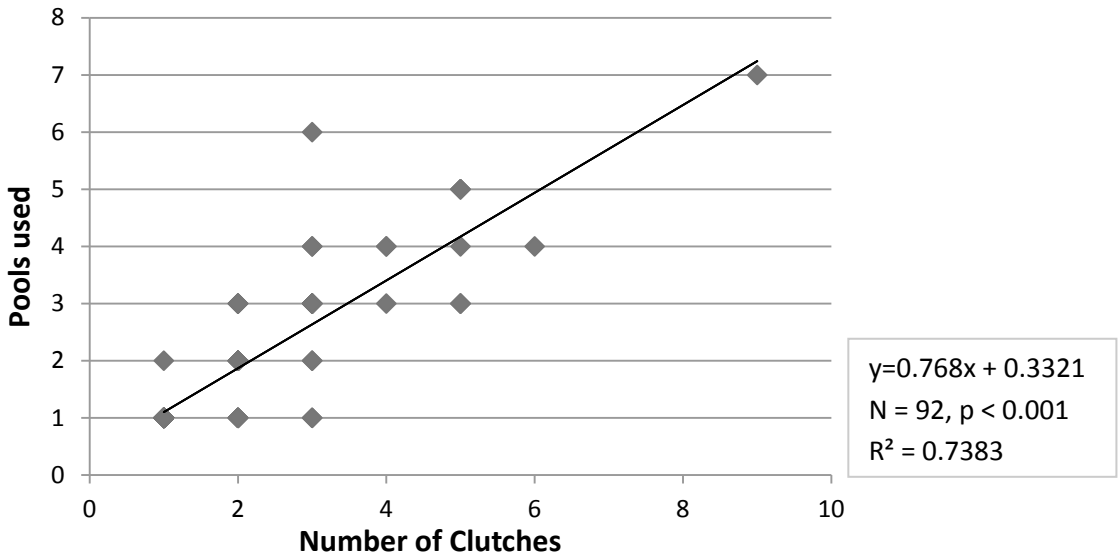


**Fig.4:** Relation between the number of clutches per male and the number of pools used per male.

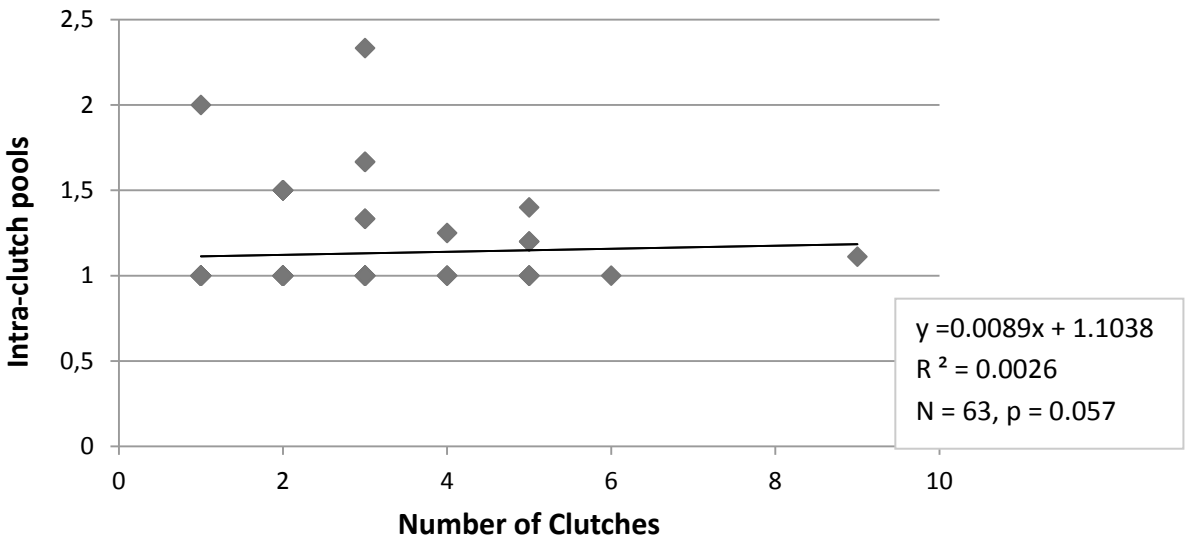


**Fig.5:** Relation between the number of pools used to deposit tadpoles from single clutches and the number of clutches.

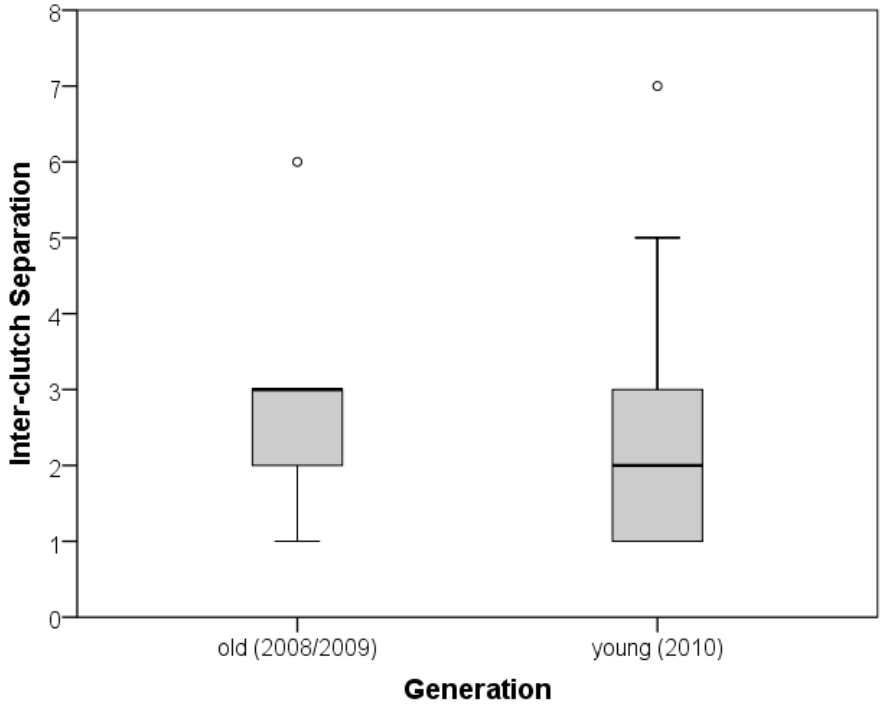


**Fig.6:** Box plots of the number of pools used to deposit tadpoles from successive clutches in old (2009, 2009) and young (2010) *A. femoralis* males.

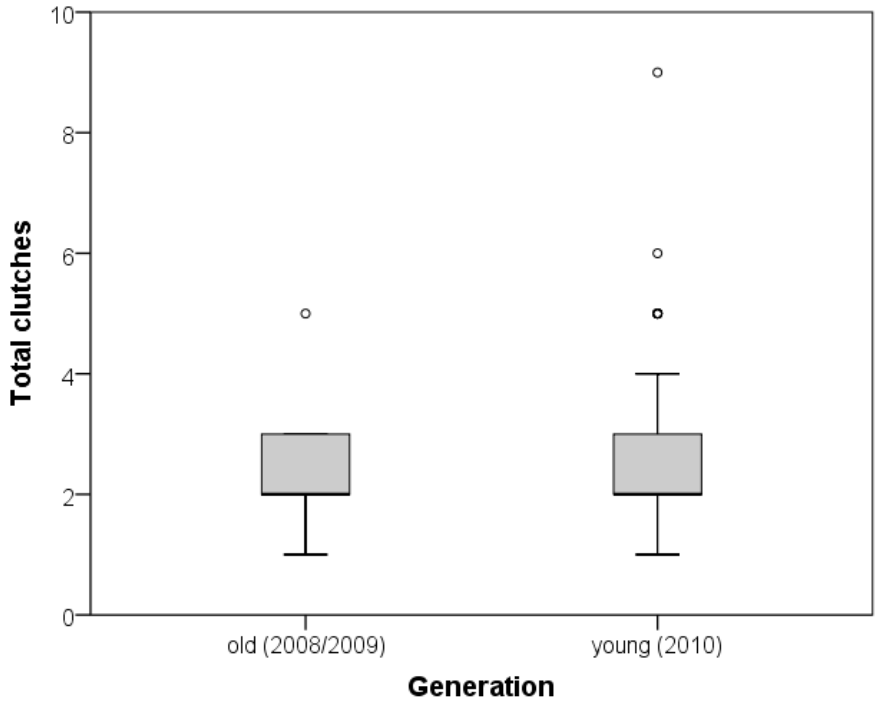


**Fig.7:** Box plots of the number of clutches produced by old (2008, 2009) and young (2010) *A. femoralis* males.

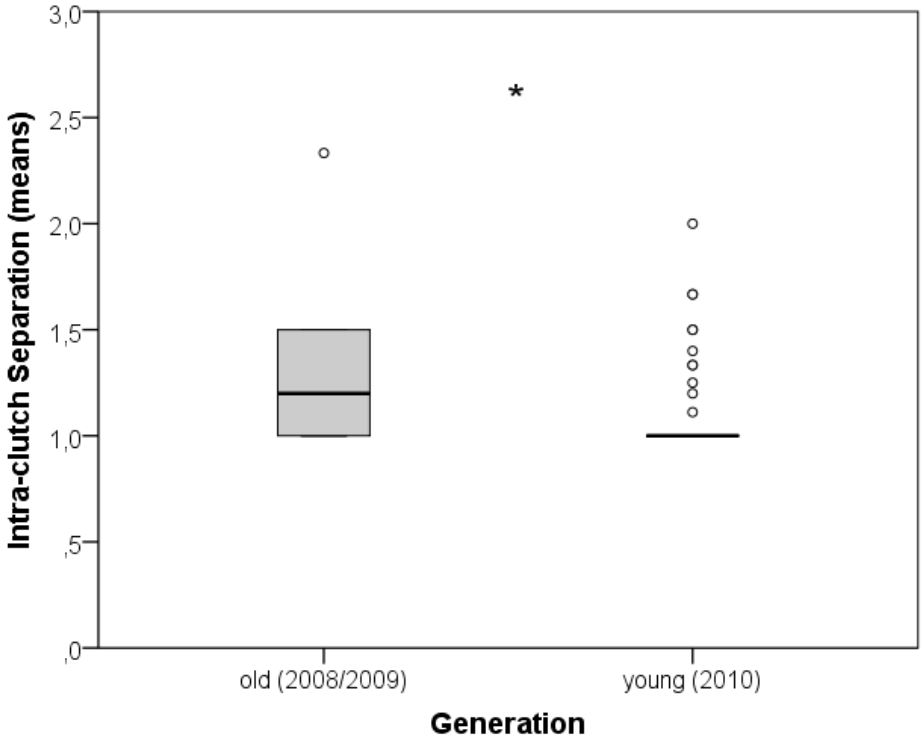


**Fig.8:** Box plots of the number of pools used to deposit tadpoles from single clutches (intra-clutch separation) in old (2008, 2009) and young (2010) *A. femoralis* males; * p = 0.019.

## Discussion

In the present study we investigated the tadpole distribution behaviour of male *A. femoralis* in a natural population in French Guiana. We performed parentage analyses of tadpoles that were sampled from artificial water bodies and adult individuals in our study plot in order to identify tadpole deposition strategies. Our data clearly revealed that *A. femoralis* males distribute larvae of single and successive clutches across several water bodies. Additionally, males of elder generations spread the larvae of single clutches more frequently than males of younger generations, suggesting that older males might benefit from properties at the beginning of the reproductive period compared to young males.

### Methological considerations

The high level of allelic variation made the microsatellite loci sufficiently powerful for parentage assignments, despite a rather low overall number of loci used (for more details see Ursprung *et al.,* 2011). In the present study we attempted the collection of tadpole deposition information covering a large proportion of the reproductive period in 2010 by arranging two samplings in an interval of three months within the reproductive season of *A. femoralis*. The distinction between young and old *A. femoralis* males was made in order to detect differences in parental care behaviour due to age effects.

### Analyses of distribution behaviour

Our data revealed the presence of brood-partitioning behaviour in a natural population of *A. femoralis* males, with 65.1% of the identified fathers distributed their tadpoles over several water bodies. Individual males that were assigned to more than one tadpole, used on average 2.37 pools (range 1-7). Not a single *A. femoralis* male with more than three clutches carried its tadpoles into only a single artificial body of water. Given that all territorial *A. femoralis* males presumably produce more than three clutches in one whole reproductive season (Ursprung *et al*., 2011; Ringler E., pers. obs.), we expect the majority of males distributing successive clutches across multiple pools.

We cannot unambiguously differentiate whether males actively approached single water sites, or if they randomly perambulated in the surrounding area in search for suitable larval deposition sites. We assume the latter to be rather unlikely, given that a recent study demonstrated a high homing performance in *A. femoralis* males (Pašukonis *et al.,* 2013), suggesting a high familiarity to surrounding areas in this species. Furthermore, tadpole deposition sites are not frequently and evenly distributed in our study area. Therefore, a random search for additional pools despite returning to the previously encountered ones will impose considerable risk to the transporting individual of not being able to find a next water site in a reasonable period of time. Thus we assume that males actively approach different water sites in order to distribute the larvae of single and also successive clutches. The strong and significant correlation between number of clutches per male and number of pools used (Fig.4), further corroborates our hypothesis of active brood-partitioning in *A. femoralis*.

We observed 39% of the males practicing brood-partitioning that spread the larvae from single clutches across multiple pools. There are several options how *A. femoralis* males

manage to distribute the larvae of single clutches over multiple water bodies. On the one hand, they might carry only a part of the clutch adhered on their back towards one body of water, and then transport the remaining offspring to other suitable pools. On the other hand, they might take up all tadpoles but only release a few larvae in each water body. The release of tadpoles from a male´s back usually takes several minutes and is often coupled with a wiping movement with the hind limb of the father (Ringler E., pers. obs.).

Parental care might cause decreased mobility and an increased conspicuousness to predators to the care giving parent (Crump, 1995) as well as energy depletion (Simon, 1983) or lost mating opportunities (Townsend, 1986). The risks for the carrying males will increase, the more time is spent searching for appropriate deposition sites, particularly when males distribute their offspring of a single clutch across multiple pools. *A. femoralis* males usually carry on average 8.43 tadpoles (range: 1-25) at once on their back towards suitable bodies of water (Ringler *et al*., submitted). Given the negative effects of increased time effort and energy expenditure when practicing brood-partitioning, particularly from single clutches, we assume major benefits of this behaviour in *A. femoralis*. The potential fitness benefits of an increased tadpole survival might outbalance the potential costs of the brood partitioning strategy.

Males producing more clutches did not disperse their offspring of single clutches more frequently. We could only show a very weak correlation between the number of clutches and intra-clutch partitioning (Fig.5; $R^2 = 0.0026$).

We found on average larvae of 6.1 fathers within one pool. In different species of *Dendrobates,* where tadpole deposition sites are of small size, parents attempt to avoid placing tadpoles into pools, which contain conspecifics, in order to evade cannibalism (Summers and Amos, 1997; Caldwell and de Araùjo, 1998; Summers, 1999b). Our results reveal that *A. femoralis* males do not avoid placing their offspring in water bodies other males had already used to deposit their tadpoles. This contrasting behaviour is likely due to the non-cannibalistic behaviour among *A. femoralis* tadpoles (Weygoldt, 1980; Ringler E., pers. obs.) and to the medium sized pools used by our studied species, where nutrients are not a limiting factor.

The effect of age

We found evidence that old males *A. femoralis* spread tadpoles from single clutches more frequently across multiple pools than young males did. Only a small amount of young males (20.4%) spread the larvae from single clutches across multiple pools, whereas 55.6% of old males practiced intra-clutch partitioning. At beginning of the reproductive period older males might have physical benefits and more experience regarding the area and the location of pools (cf. Spieler and Linsenmair, 1997) compared to inexperienced males in their first reproductive season. These features might enable them to exhibit increased brood-partitioning right from the start, and lead to the observed differences in intra-clutch partitioning behaviour. Surprisingly, we did not find a similar effect regarding the separation of successive clutches. A more comprehensive study on age-dependent brood-partitioning behaviour, such as the change of partitioning numbers in individuals between reproductive periods, remains to be addressed in the future.

In our study, the number of clutches that were assigned to single males was not significantly different between old and young individuals. We assume that either age does not affect reproductive success in males at all, or an increased time for intra-clutch separation might counterbalance a possible mating advantage of older males.

Further research is needed to reveal whether age ultimately influences individual reproductive success in *A. femoralis* males.

## Considerations on the evolution of dispersing behaviour

Based on the assumptions of Summers & Mc Keon (review 2004) on the evolution of phytotelmata-breeding in poison frogs (reviewed by Summers & Mc Keon, 2004), we assume that the brood-partitioning behaviour of *A. femoralis* males might constitute an evolutionary step within the dendrobatids towards breeding in smaller pools containing fewer predators. *A. femoralis* typically carry their offspring in medium sized temporal pools, whereas many species of *Dendrobates* use phytotelmata above the forest floor as breeding sites (reviewed by Summers and Mc Keon, 2004). Whereas very small pools (e.g. bromeliad axils, containing less than 24 ml water) that offer almost predator-free environments require increased parental effort in terms of feeding due to the lack of sufficient nutrients (Brown *et al.*, 2008), medium sized pools mainly bear the risk of total clutch loss due to predation (Roth and Jackson, 1987).

Besides the possible reproductive advantage for individuals with more dispersed tadpoles over individuals with less dispersed tadpoles, the brood-partitioning behaviour in *A. femoralis* might play a part in the transition towards phytotelmata-breeding.

## Conclusion

In this study we were able to provide evidence for brood partitioning behaviour in *A. femoralis* males. The potential fitness benefits of an increased tadpole survival might outbalance the potential costs of the brood partitioning strategy. We hypothesize that predation and pool desiccation constitute major threats to tadpoles being located in medium sized temporal pools. Hence, spreading the risks over all tadpoles by depositing the offspring across multiple pools might minimize the risk of total offspring loss. Additionally we found evidence that old males *A. femoralis* spread tadpoles from single clutches more frequently across multiple pools than young males did. Further research is needed to reveal whether patterns of tadpole distribution ultimately influence individual reproductive success in *A. femoralis*.

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**Attachment**

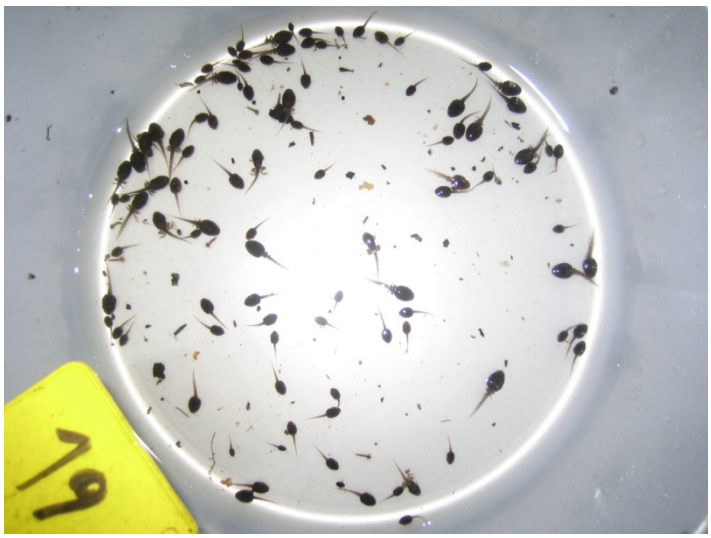


**Fig.A:** Photo of total tadpoles in pool Nr. 19.


**Fig.B:** Measuring the tadpole`s snout-urostyle-length on graph paper using IMAGE J and family-identifying by examining the oral disc.

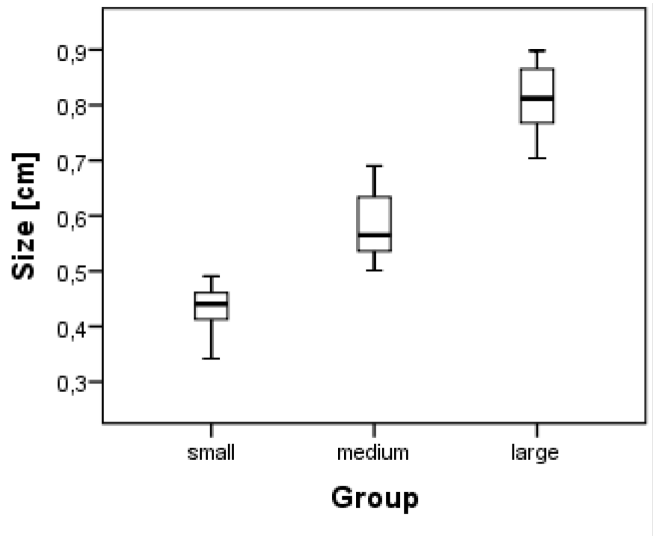


**Fig.C:** Box plot for size-classification of tadpoles; n =97; large: > 0.7cm; medium: 0.5cm-0.7cm; small: < 0.5cm.

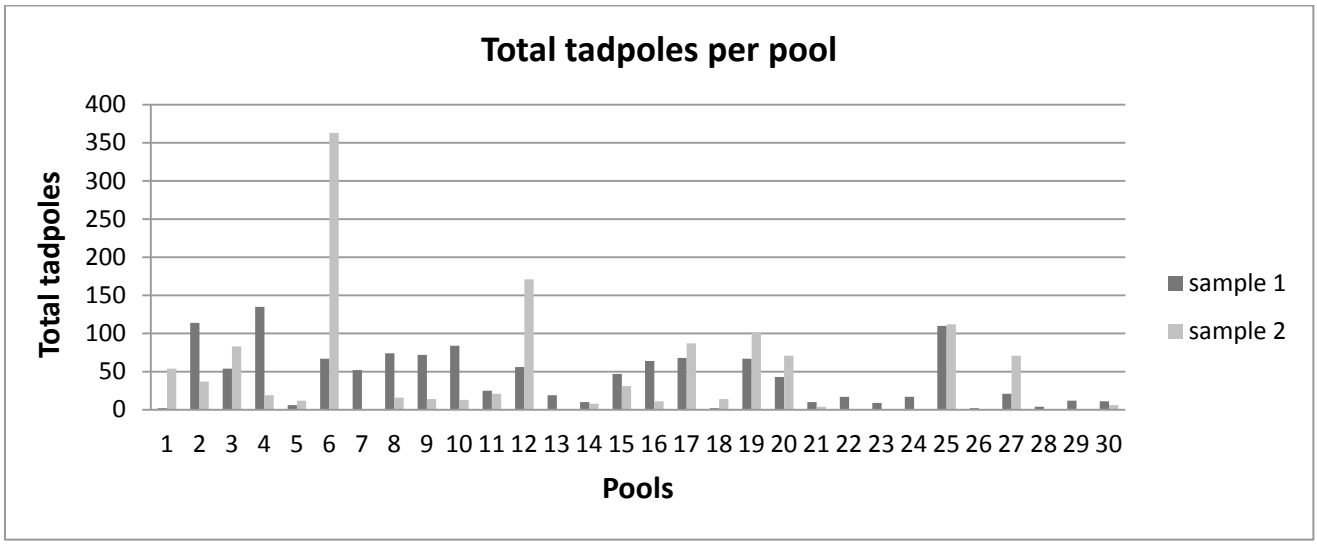


**Fig.D:** Number of surveyed *A. femoralis* tadpoles per pool in spring 2010, n = 2595.

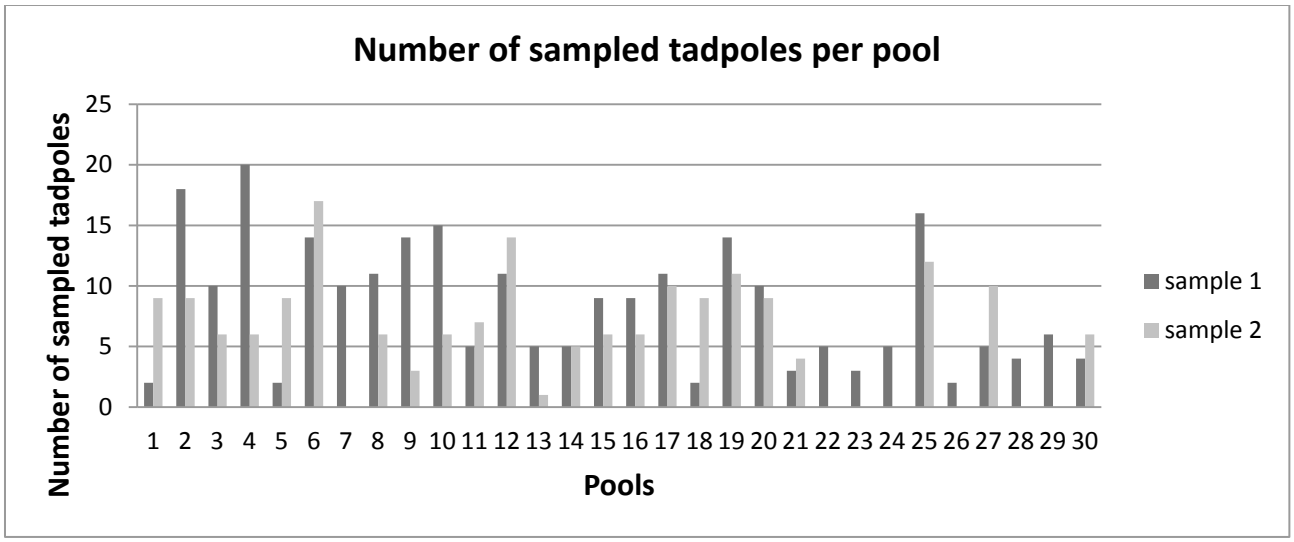


**Fig.E:** Number of sampled larvae in January and April 2010, n= 431.

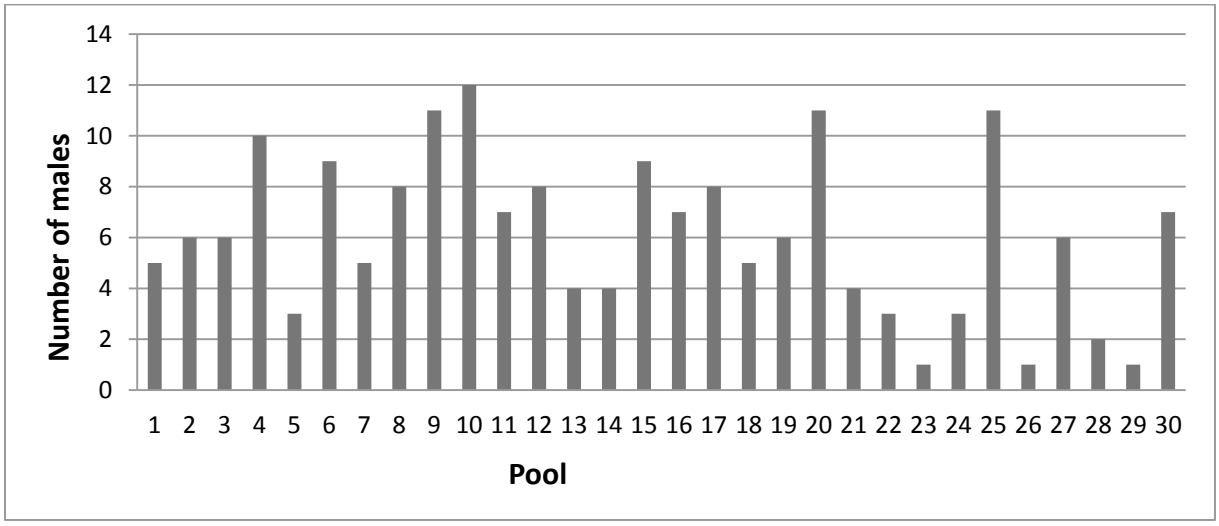


**Fig.F:** Bar diagram showing the total number of males in *A. femoralis* sharing single pools in January and April 2010.

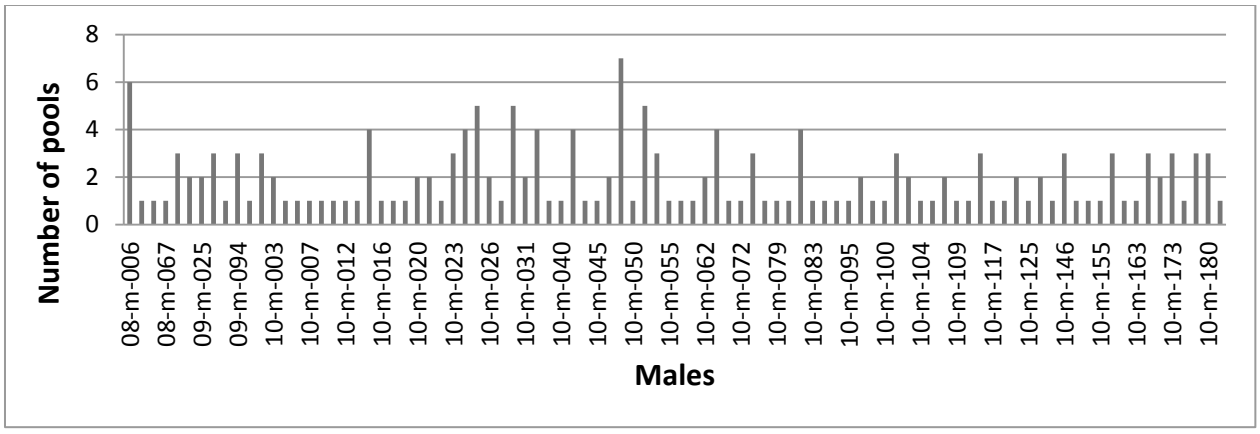


**Fig.G:** Bar diagram illustrating the number of pools used per male.

**German abstract / deutsche Zusammenfassung**

Innerhalb der Anuren hat sich terrestrische Eiablage mehrmals unabhängig voneinander entwickelt, vermutlich als eine Anpassung an den großen Raubdruck auf Eier und an das Risiko konkurrierender, verstreuter Spermien von Rivalen in Gewässern. Terrestrische Eiablage kann, wegen der hohen Luftfeuchtigkeit, fast ausschließlich in tropischen Regionen beobachtet werden. Das Dilemma zwischen terrestrischen Eiern und aquatischen Anurenlarven wird von den meisten Dendrobatiden durch obligatorische Brutpflege in Form von Kaulquappentransport gelöst. Der Neotropische Pfeilgiftfrosch *Allobates femoralis* (Dendrobatidae) legt sein Gelege in die Laubstreu, der Kaulquappentransport wird hauptsächlich von den Männchen praktiziert. In Anbetracht des Prädationsdrucks und der Gefahr der Austrocknung temporärer Wasserstellen würde ein Aufteilen der Larven über verschiedene Wasserstellen eine passende Strategie zur Risikostreuung darstellen, um den Verlust eines ganzen Geleges zu verhindern. Im Rahmen dieser Studie untersuchten wir im Frühling 2010 die Verteilung der transportierten Kaulquappen einer natürlichen Population von *A. femoralis* über Wasserstellen in Fanzösisch Guyana. Wir verwendeten sieben hoch-polymorphe Mikrosatellitenloci und DNA Proben von Adulten und von Larven aus 30 künstlichen Wasserbecken, die 2009 aufgestellt wurden. Einzelne Pools enthielten im Durchschnitt 43.25 Larven (SD = 57.88). Die rekonstruierte Analyse der Abstammungsverhältnisse zeigte, dass 65.1% der *A. femoralis* Männchen, die als Väter von mindestens zwei Kaulquappen identifiziert worden waren, ihre Kaulquappen über mehrere Pools, und 39% davon Kaulquappen einzelner Gelege über mehrere Pools verteilt haben. Die Aufteilung einzelner Gelege wurde deutlich öfter bei jenen Männchen beobachtet, welche in ihrer zweiten oder dritten Brutzeit waren und wir vermuten, dass ältere Männchen am Beginn einer Fortpflanzungsperiode von Eigenschaften profitieren, die junge Männchen noch nicht aufweisen. Unsere Ergebnisse zeigen klar, dass *A. femoralis* Männchen einzelne und aufeinanderfolgende Gelege über mehrere Wasserstellen aufteilen und dies könnte eine Strategie zur Risikostreuung darstellen, um einen kompletten Verlust von Nachkommen zu verhindern.

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I want to dedicate this work to my beloved sister Veronika who died so far too young in autumn 2012 and who taught me to listen to my soul.

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## Curriculum Vitae

Personal information

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| 1979 – 1983 | Elementary school, Klagenfurt, Austria |
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University education and employment history

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| 1991 – 1992 | Medical study, University of Vienna |
| 1992 – 1995 | Nursery school Rudolfinerhaus, 1190 Vienna |
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