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Abstract
Parental care is a common reproductive strategy amongst vertebrates and in many cases essential to ensure reproductive success. More elaborate parental systems such as biparental care are on the other hand rare, and overall restricted to the avian fauna.
In the family *Dendrobatidae* (neotropical poison frogs), we find a variety of advanced social behaviour and parental care systems. Most poison frogs exhibit male only parental care and a polygamous mating system, were the male attends to the eggs, and after hatching carries the tadpoles on its back and deposits them in a small nutritive pool of water (phytotelmata). Recent studies of poison frogs belonging to the genus *Ranitomeya* have revealed the exhibition of biparental care and social monogamy in the two species *Ranitomeya imitator* and *R. vanzolinii*. Further studies also revealed genetic monogamy in *R. imitator*, being the first amphibian described with this mating system. The sister taxa of *R. vanzolinii*, *R. flavovittata* has been poorly studied and is thought to exhibit the same parental behaviour as aforementioned species. The aim of this study was to investigate and to describe the parental behaviour and mating system of the Peruvian poison frog *R. flavovittata*. The study was conducted close to the village of San Pedro located upstream the Quebrada blanco, a tributary to Rio Tahuayo in the Loreto region of Peru. Biparental care and tadpole feeding behaviour was studied using focal observations and by placing out artificial phytotelmata in form of see-through polystyrene canisters. By identifying individual frogs by recording their unique dorsal coloration pairwise observations were performed to confirm social monogamy.
This study reveals that *R. flavovittata* exhibit complex pair systems with biparental care and social monogamy with long-term pair bonding. Clutches of 1-2 eggs were placed generally underneath dried leaves located above ground in understory vegetation. When the eggs hatch, the male carries the tadpoles one by one on its back and deposits them in separate phytotelmata. The male surveys the tadpoles to make sure of its welfare. Tadpoles whom where seen together with the male, displayed a 'wriggling' behaviour where the tadpoles vibrated against the legs of the male, probably to signal hunger. During the development of the tadpole the male will call for the female and guide her to the individually placed tadpoles and the female deposits 1-2 trophic eggs for the offspring.

Introduction
Monogamy is a mating system that is rarely seen throughout vertebrate taxa, most frequently occurring in birds, where most species are considered to be socially monogamous (Black 1996, Waite & Parker 1997). Social monogamy is defined as social interactions between a male and a female over a longer period of time where mating is non-exclusive (Reichard 2003). One of the factors which can lead to such collaboration and which are considered to be one of the major evolutionary factors leading to a monogamous mating system is biparental care (Wittenberger & Tilson 1980, Tumulty *et al*. 2013). When attendance and offspring care from both sexes is essential for offspring's survival, and the benefits of mutual care outweights the gains of polygamy then evolution of monogamy should be favoured according to the biparental care hypothesis by Wittenberger & Tilson (1980).
Poison frogs of the family *Dendrobatidae* have intrigued scientists, particularly within the context of parental care and complex social behaviour (Tumulty *et al*. 2013, Brown *et al*. 2010, 2008ab). Most poison frogs exhibit a polygamous matings system with male-only parental care, egg attendance and tadpole care in the form of carrying the newly hatched tadpoles to a pool of water, a phytotelmata (e.g., a waterfilled cavity in the leaf axils of plants) (Brown *et al*. 2010, Summers & McKeon 2004). Some species, for example the strawberry poison frog (*Oophaga pumilio)*, display female parental care, where it is the female who carries the tadpoles and feed them with nutritive unfertilized eggs until fully metamorphosed (Pröhl & Hödl 1999, Brust 1993).

The most spectacular and elaborate behavioural systems we find within the *vanzolinii*-group of the genus *Ranitomeya*. The mimic poison frog (*R. imitator)* and the spotted poison frog (*R. vanzolinii)* have been studied and proven to display biparental care as well as social monogamy, and even genetic monogamy in *R. imitator*, which is the first amphibian described exhibiting this mating system (Brown *et al*. 2010, Brown *et al*. 2008a, Brown *et al*. 2008b 2009a, Lötters *et al*. 2007, Caldwell & de Oliveira 1999). *R. imitator* and *R. vanzolinii* differ from the relatives of the genus both with the usage of remarkably smaller phytotelmata and by laying a smaller clutch of eggs (Brown *et al*. 2011). The usage of such small phytotelmata is thought to have been driven by both competition for breeding pools as well as predation risks. Larger phytotelmata both house more predatory insects as well as sympatric dendrobatid species with cannibalistic tadpoles (Schulte *et al*. 1999, Brown *et al*. 2009c, Poelman & Dicke 2007).
Both *R. imitator* and *R. vanzolinii* exhibit biparental care, with the male caring for a small clutch of eggs (*R. imitator* 1-4 eggs, 1-2 in *R. vanzolinii*). When the eggs hatch the male carries the tadpoles individually to separate phytotelmata. The male will later guide the female to the deposition site and she will in turn feed the offspring with unfertilized eggs until the tadpoles are fully metamorphosed. The small phytotelmata does not alone contain sufficient nutrients for the survival of the offspring and so trophic egg feeding is crucial for the tadpole's survival (Brown *et al.* 2010, 2008b, Caldwell & de Oliveira 1999). A general pattern throughout amphibian genera is increased parental care with smaller breeding pools, and in poison frogs the evolution of parental care as well as biparental care has been driven by this ecological factor. It is also believed that the evolution of biparental care has lead to the evolution of social monogamy in *R. imitator* and *R. vanzolinii* (Brown *et al*. 2010).

Many dendrobatid species are poorly studied and more fieldwork and observational data is needed to make comparative studies, to clarify taxonomic status and draw evolutionary conclusions. One of these under-studied species is *R. flavovittata*.

Taxonomic status of *Ranitomeya flavovittata*
Phylogenetic studies by Roberts *et al.* (2006), and Twomey and Brown (2008), using genetic material from five individuals both validated the species and placed *R. flavovittata* in the vanzolinii-group as sister taxon to *R. vanzolinii*. Morphologically *R. flavovittata* (Fig 1) have strong resemblance with other species of the vanzolinii-group in particular with *R. yavaricola* (Perez-Peña *et al*. 2010). The call of *R. flavovittata* is also strikingly similar to the other representatives of the *vanzolinii* group with loud high pitch trill (Brown *et al.* 2011). The description of *R. flavovittata* is based on observations of a single juvenile frog, raised in a laboratory (Schulte 1999). Field observations have shown similar life-history traits for *R. flavovittata* as *R. imitator* and *R. vanzolinii*, with findings of two white eggs in a *Guzmania* bromeliad 1.2 m above ground, there has also been observations of males carrying tadpoles and couples displaying courtship behaviour (Schulte 1999, Brown *et al*. 2010).

Aims
The main focus of this study was to find out whether *R. flavovittata* exhibits biparental care and social monogamy, as its closest relatives. The fact that *R. imitator* and *R. vanzolinii* are currently the only known poison frogs, and even one of few vertebrate examples to exhibit such complex social behaviours makes this study of great importance. I expect that *R. flavovittata* exhibit biparental care with a socially monogamous mating system, and with these behavioural traits also lay small clutches of eggs and use exceptionally small reproductive pools.

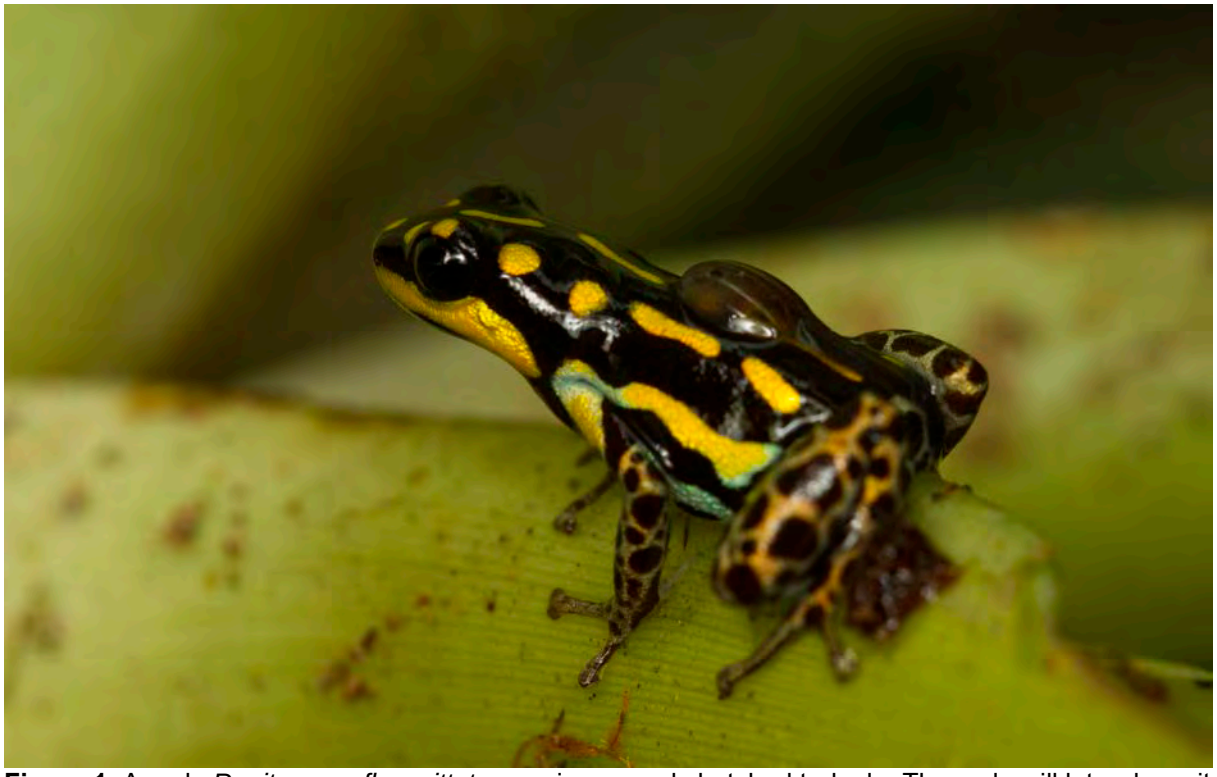

Figure 1. A male *Ranitomeya flavovittata* carrying a newly hatched tadpole. The male will later deposit the tadpole into a small pool of water.

Methods

Location and habitat

The study was conducted from the beginning of September until the end of October 2013. The study area (4°19.733'S and 73°11.860'W) was located close to the village of San Pedro (Fig 2), a small village upstream the Quebrada blanco, a tributary to Rio Tahuayo in the Loreto region of Peru. The habitat for *R. flavovittata* was secondary growth "terra firme forest", a forest that is not affected due to flooding in the rainy season. The study area contained a vast variety of medium to bigger sized bromeliads ranging from the leaf litter to high up in the treetops. In this area there were also artificial phytotelms in form of PET-flasks, which had been placed there by local villagers in 2011 for conservation purposes but also to make the dendrobatid frogs more available for eco-tourists. *R. flavovittata* co-occurs with several dendrobatid species including: *R. uakarii*, *R. variabilis*, *Amereega hahneli*, *A. trivittata*, *Allobates conspicuus* and *A. femoralis* with *R. flavovittata* being the most frequently encountered followed by *R. uakarii*.

Sampling methods

A 259 m transect in the form of an animal made pathway was walked at a slow pace by three to four observers, once in the morning and once in the afternoon. The average temperature and humidity in the morning between 06:00 AM and 10:00 AM was 28°C ± 1.7°C, 82.5% ± 5.5 and 30.5°C ± 1.9 °C, 75.8% ± 9.6 between 13:00 PM and 16:00 PM in the afternoon. The night temperature varied from 24.3 - 26.8°C with a humidity of 83-87%.

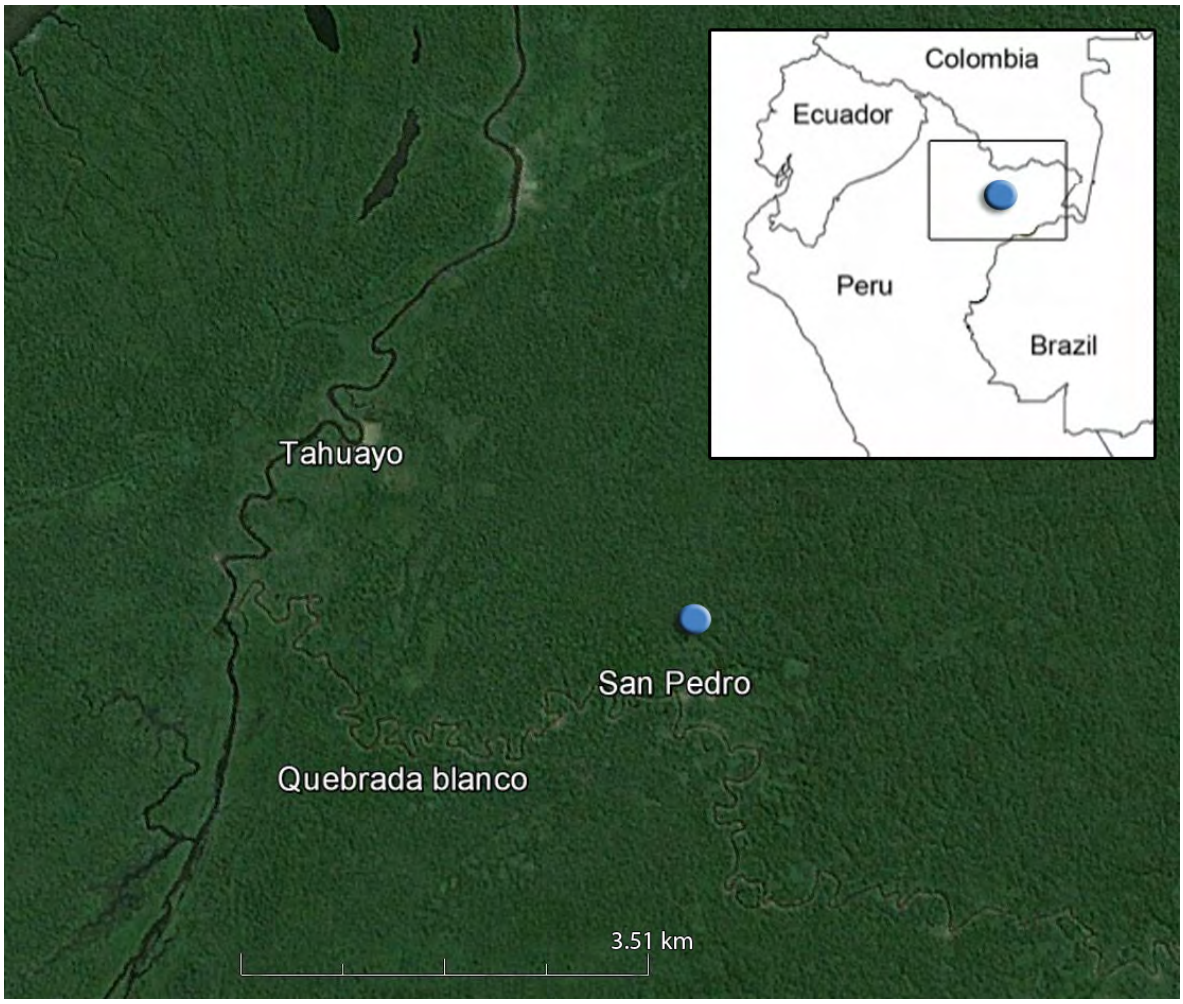

Figure 2. The study area (4°19.733'S and 73°11.860'W) located close to the village of San Pedro, upstream Quebrada blanco, a tributary to Rio Tahuayo in the Loreto region of Peru. The study area is marked with a blue dot.

On the locations where a pair of *R. flavovittata* was seen together, I marked the place with a colourful ribbon, to later conduct focal observations on each site (12 locations) and to see if the same pairs could be sighted in the same areas. I placed 50 polystyrene canisters (30 mL) which where filled up with rainwater, at ~80cm above ground to be able to test the hypothesis of biparental care and trophic egg-feeding behaviour (Fig 5).

Behavioural observations & measurements

When a frog was localized, the observer usually stopped around 2-3 meters from the frog to avoid disturbance. When encountering a single individual I stayed and observed the frog for 15 minutes, and for the pair-wise observation I stayed with the pair for longer time intervals to be able to observe the frogs interactive behaviour. Notes were taken either by writing down everything that was seen or by talking into a recorder. When an individual frog as well as a couple was sighted, the time of day, height above ground and habitat was recorded. The total observation time was recorded using a stopwatch. All frogs could easily be distinguished based on the highly individual dorsal colour patterns, which varied with yellow dots or lines on a black background (Figs 1 and 3). All frogs where drawn carefully in a notebook, which made it easy to quickly be able to identify the individuals at each location.

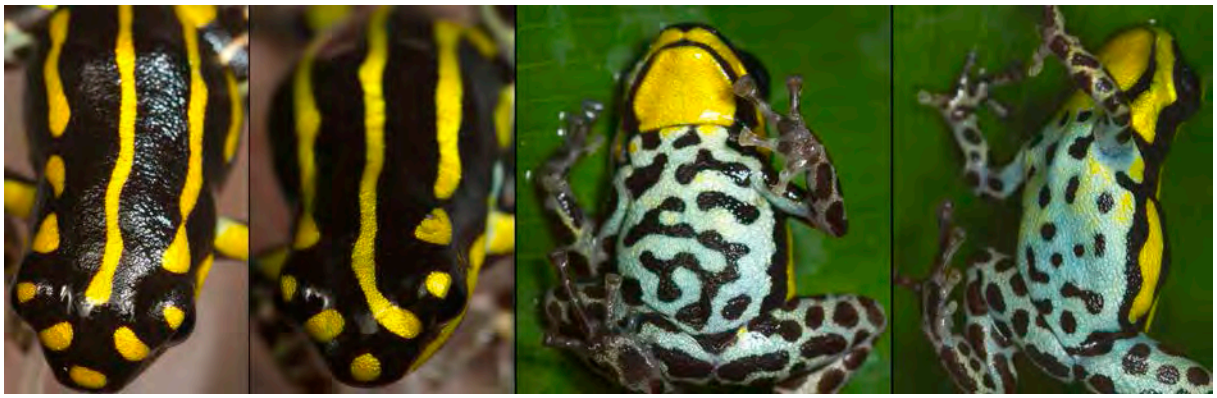

Figure 3. Differences in individual ventral and dorsal coloration patterns.

The frogs were measured (snout-vent length) using a caliper, and all measurements were taken after observational studies. Individual frogs were also photographed using a Canon 7d camera with a 100 mm macro lens.

Results

During this study a total of 47 *R. flavovittata* were encountered, with a total of 20 pairs being observed for a total of 1261 min (21 h and 1 min). The extensive part of the results is based on three primary pairs observed for a total of 446 minutes (7 h 43min) (Table 1).

Table 1. Pairwise observations of three primary pairs.

Pair	Total pairwise observation duration	Sampling location	Day first observed - last observation
D1/D2	110 min	1	3/9-15/10
V1/V2	98 min	5 (small creek)	14/9-19/10
O1/O2	328 min	7 (vriesea)	2/9-22/10

R. flavovittata where only found on arboreal and semi-arboreal locations, primarily on leafs of smaller palm trees such as *Lepidocarium tenue*, tree branches, tree trunks, lianas and on bromeliads (Fig 4). The mean height above ground where they were first seen was 1.19 m ± 0.76, and at rare occasions I could find individuals foraging on tree trunks up to 3-4 meters above ground. At only one occasion a female was seen on the leaf litter but that was after accidentally falling down after misjudging a jump, following a vocalizing male.

Figure 4. Habitat of *Ranitomeya flavovittata*, containing several species of bromeliads as well as different types of smaller palm trees e.g *Lepidocarium tenue*.

Size

R. flavovittata is a small dendrobatid frog, adults < 17.5 mm SVL (snout-vent length), with the females being slightly larger (mean 16.7 ± 0.69 mm) than the males (15 ± 0.73 mm) (Table 2).

Table 2. SVL measurements on adult *Ranitomeya flavovittata*.

Character																♀Avarage ± 1 SD	♂Avarage ± 1 SD
SVL (mm)	17	17	15.5	16	17	17.5	17.5	15	14	15.5	16	15	15.5	14	16	16.7 ± 0.69	15 ± 0.73
Sex	♀	♀	♀	♀	♀	♀	♀	♀	♂	♂	♂	♂	♂	♂	♂		

Egg deposition

Clutches containing 1-2 eggs with a whitish-yellow colour (Fig 6) were observed at five separate occasions (Table 3). On four of these occasions the eggs were placed hidden underneath or inside folded dry leafs. These egg deposition sites were all located above ground, three clutches were placed inside dried leafs that were laying in the middle of the rosettes belonging to the palm tree *Lepidocarium tenue* at the height of 41 cm, 42 cm and 140 cm above ground. One clutch containing one egg was placed inside a dried leaf located on a fallen tree branch 20 cm above ground. Eggs where not only placed hidden, at one time I found an egg placed horizontally above water in a *Vriesea* bromeliad, 0.95 m above ground (Fig 5). Three pairs of *R. flavovittata* were observed before and during egg deposition. The female closely followed the calling male to a dried leaf, while underneath the leaf the vocalization got more frequent and they stayed together underneath the leaf until the eggs were laid (Fig 6).

Table 3. Five clutches of eggs (1-2 eggs) were observed, all deposited above water. Four of these clutches were deposited hidden underneath dried leafs on top of *Lepidocarium tenue* palm trees or on a tree branch. One egg was found deposited on the leaf of a *Vriesea*-bromeliad.

Observed individuals	Male guidance observation	Eggs deposited	Egg deposition site (location #)	Height above ground (m)	Time & date observed
Female "my" alone	No	1	*Vriesea*-bromeliad (7)	0.95	10:05, 3/9
Female "my", male "ga"	Yes	2	Dried leaf, *L. tenue* (11)	0.42	09:00, 7/0
Female "t1", male "t2"	Yes	1	Dried leaf, *L. tenue* (12)	1.40	09:35, 7/9
Female "v1", male "v2"	Yes	1	Dried leaf, *L. tenue* (5)	0.41	13:30, 21/9
Female "l1" alone	No	1	Dried leaf, tree branch (9)	0.2	09:40, 22/10

Figure 5: A single egg deposited horizontally above phytotelmata.

Figure 6. The pictures to the left show two different pairs of *Ranitomeya flavovittata* mating under dried leafs, the pictures to the right show the result, two respective one fertilised egg.

Tadpole transportation and deposition sites

When the eggs hatch, the male carries the tadpoles on its back (Fig 1), one at a time and deposits them in a small pool of water. In all observations of tadpole transportation when sex identification was possible, all individuals were identified as males (N = 5). At three occasions tadpoles were deposited in 30 mL artificial polystyrene bottles, one of these bottles contained only 15 mL water. During this study I found only one *R. flavovittata* tadpole deposited in a natural phytotelmata. This tadpole was placed in a 16 mL water filled cavity in the center of a *Guzmania* bromeliad located on the ground.

Tadpole feeding behaviour

Egg feeding behaviour was observed at two times, both times in an artificial phytotelmata (Fig 7). In both cases I could follow the pair, and the male guiding the female by vocalization to the deposition site. When the pair reached the artificial container the male was placed right above the water level and started to call more intensively. The female backed down with her body under the water level. When the female was under water with half her body the tadpole became very active and started vibrating against the females legs and belly. At one of these occasions the tadpole was seen nibbling on the female and vibrating so intensively that the female lost its grip, falling down into the water at two times. The female then deposited an egg, in one of the observations the female deposited two eggs. The tadpole almost immediately started to try consuming the eggs. At five times I observed the same guiding behaviour and calling towards the deposition site, but with the female leaving without providing an egg. At one of these occasions, the male followed the female, called and she followed him back one more time repeating the same procedure but without laying the egg. In total I witnessed tadpoles feeding on eggs at six separate times and on average the tadpoles were fed somewhere in the time interval of 6-16 days (Table 4).

Table 4. Tadpoles were observed feeding on 1-2 trophic eggs at five occasions.

Tadpole	Deposition site	Location	# Trophic eggs	Parent frogs observed	Tadpole deposition date	Time & date observed
Tadpole 3	PF-1	1	1	Yes (both present)	-	14:10, 3/10
Tadpole 1	PF-9	6	1	Yes (male present)	-	09:40, 12/9
Tadpole 2	PC-1	7	1	Yes (male present)	23/9	13:15, 9/10
Tadpole 2	PC-1	7	2	Yes (both present)	23/9	09:15, 15/10
Tadpole 2	PC-1	7	1	No	23/9	09:24, 23/10

PF = Pet flask phytotelmata.
PC = Plastic container.

Figure 7. A: A female *Ranitomeya flavovittata* providing two trophic eggs **B:** A male *R. flavovittata* attending its tadpole. At this moment this pair had two tadpoles deposited in neighbouring artificial phyototelmata.

Territorial and aggressive behavior
All studied dendrobatid frogs display territorial behaviour to some degree and species of the vanzolinii group have been described as being extremely territorial, using both vocal bouts and wrestling (Rudh *et al*. 2013, Brown *et al*. 2010, Poelman & Dicke 2008, Pröhl 2005). Female aggressive behaviour was recorded at two occasions. One time a female was observed for 50 minutes with two males sitting side by side with the female located 1.20 m above ground on the leaf of a small palm tree. The two males where located at each side of the female, vocalizing simultaneously. The female (17 mm) chased away the smaller male (14 mm) by embracing and pressing down the male (Fig 8a). This behaviour was repeated an additional two times, and when the female returned to the second male they "greeted" each other with both snouts touching and the female embraced the male and later followed the male which continued calling.

Aggressive female-female behaviour was also observed. One male and two females were located together on the leaf of a palm tree 1.40 m above ground. While the male was vocalizing the two females were observed wrestling which ended with one female chasing away the other up in a tree, the victorious female later came back down to join the male.

Males where often seen and heard performing vocal bouts, responding to distant male calls. Male aggressive behaviour was witnessed at one occasion when a male *R. flavovittata* was found wrestling a male *R. variabilis* located on a liana approximately 1.50 m above ground. The male *R. flavovittata* was seen pressing down the male *R. variabilis* and both parts tried to kick down the other from the liana. In between the wrestling both parts were vocalizing frequently and by doing "push-ups" making themselves bigger next to each other (Fig 8b).

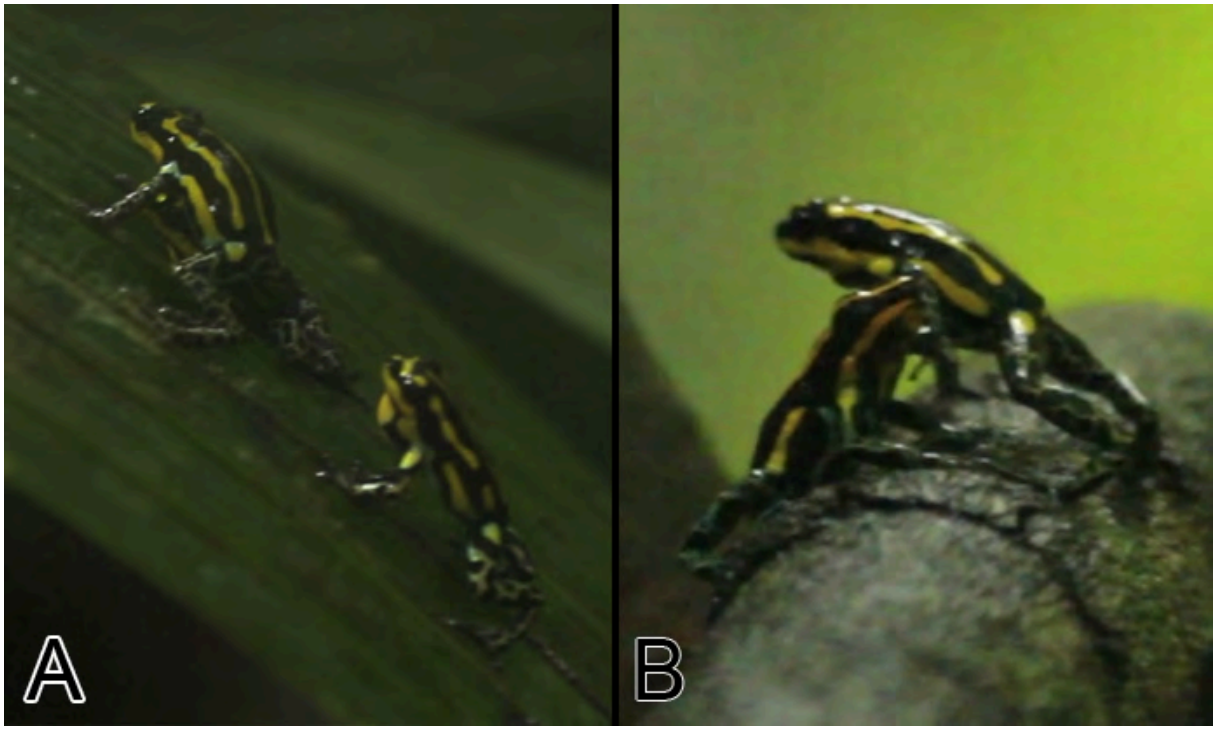

Figure 8. **A:** A female *Ranitomeya flavovittata* displaying aggressive behaviour by embracing and pressing down a male. **B:** A male *R. flavovittata* making himself bigger during a wrestling match against a male *R. variabilis*.

Discussion

This study shows and justifies the hypothesis of biparental care in *R. flavovittata*. Pairs of *R. flavovittata* were repetitively found together at the same localities, displaying a cooperative pair bonding and social behaviour through out the two-month survey, which furthermore matches the definition of social monogamy (Reichard 2003).

Parental care

The main reason and the key factor to why we see biparental care in *R. flavovittata* and their closest relatives is the usage of small reproductive pools. It has been hypothesised that selection pressure by tadpole predation and competition lead to specializing in small and nutrient-poor reproductive pools (Brown *et al*. 2010, 2008b).

Although during this study I only witnessed a tadpole deposition once into a non-artificial phytotelmata, in the leaf axils of a bromeliad (*Guzmania* sp), this pool only contained 16 mL of water. *R. flavovittata* was also the only frog in the study area which deposited its tadpoles into my artificial canisters containing 15-30 mL water.

R. flavovittata deposits small clutches of 1-2 eggs with white-yellowish colour. The white colour of the eggs makes them easy to distinguish from other *Ranitomeya* species in the same area which eggs are dark grey or black. Most of the times the eggs are placed underneath a dried leaf located above ground, this behaviour is probably the result of an increased egg predation if the egg is placed visible. This was witnessed at one occasion when an egg was deposited on a bromeliad leaf (Fig 6). The egg was consumed the day after by ants. *R. flavovittata* is one of the few species in the genus that hides it's eggs amongst leaves and the only known frog in the *vanzolinii*-group to exhibit this behaviour. Although males where only seen sitting next to the eggs days after deposition I hypothesize that males regularly attend to the eggs and hydrate them in the same manner as seen in *Oophaga pumilio*, in which the male is watering the offspring by bringing water by transporting it in the cloaca (Pröhl & Hödl 1999). After the eggs hatch the male carries the tadpoles one by one and deposits them into a small pool of water. The male later surveys the tadpoles and call the female when it is time for feeding of the tadpole. The male leads the female to the tadpole where the female deposits 1-2 trophic eggs.

The cooperation and shared care for the mutual offspring between sexes is believed to result in higher fitness than if one of the partners would chose an additional partner. Male removal experiments on *R. imitator* by Tumulty *et al*. (2013) showed that male removal after tadpole deposition reduced the reproductive success by 85%. Worth mentioning is that tadpoles were also deposited in larger artificial PET-flask phytotelmata containing 0.5-0.75 L water. These containers were well established and completely covered with algae, detritus and small insect larvae providing a nutritious nursing pool. But what is interesting is that even though the tadpole had all the right conditions to survive on its own the parents still provided trophic eggs. I also observed two *R. flavovittata* tadpoles being deposited together in a large 0.5 L artificial phytotelmata, in this case the second tadpole were deposited when the other tadpole was in its final stage and had developed both arms and legs. The reason for usage of this large phytotelmata instead could be due to the lack of bromeliads in the area or just that there is absence of competing species and these bigger phytotelmata provide such a good nutritive home for the offspring that you can afford to deposit two tadpoles in the same pool.

Aggressive behaviour
I observed both male and female territorial and aggressive behaviour. Females displayed female-female aggression in form of pressing down and chasing away the other, this behaviour has only previously been in *R. imitator* in terrarium observations and shows indications of mate guarding. (Evan Twomey, personal communication). At another occasion a female was seen together with two males, both calling in the direction of the female, which resulted with the female aggressively chasing away the smaller male (Fig 8). This behaviour has never before been seen in *Ranitomeya* and could possibly be some kind of female mate choice, but unfortunately this was the one and only time I saw these individuals so it is difficult to draw any significant conclusions.
Male-male interactions included wrestling, vocal bouts and responded to distant vocalizations. Three times when a single male was encountered I played-back recordings of a vocalizing male using an external speaker. In these cases the male first climbed to a higher location and kept calling, and after a while when I kept playing the recordings, it resulted in that the male climbed down at high speed, looking for the intruder and jumped down to the position of the speaker.

Behaviour and general life history of *R. flavovittata* observed in my study strongly resembles those of *R. imitator* and *R. vanzolinii*. All three species deposit small clutches of eggs (1-2 in *R. flavovittata* vs. 1-2 in *R. vanzolinii* and 1-3 in *R. imitator*), which are deposited away from water. Males carry single tadpoles and deposit them into separate phytotelmata, and are later fed with 1-2 trophic eggs after the male guides the female to the deposition site. These three closely related species also share similar territorial behaviour, with wrestling and vocal bouts (Brown *et al*. 2008b, Caldwell & de Oliveira 1999).

Biparental care and monogamy in dendrobatid frogs is still a topic where relatively little is known. In this study, I revealed that *R. flavovittata* is socially monogamous and exhibits biparental care. In future research it would be highly interesting to see whether or not *R. flavovittata* also is genetically monogamous by performing genetic parentage analysis. It is also still unclear if the phylogenetic placement of *R. flavovittata* is correct, and if *R. flavovittata* is a separate species from *R. vanzolinii*, according to Brown *et al.* (2011), more genetic sampling on both species needs to be done. It would also be interesting to follow up on the research by Schulte *et al*. 2011 concerning the importance of chemical cues. It would be interesting to see whether or not chemical cues play a role in offspring recognition, Are females enabled to recognize their own tadpoles?

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References

Black JM. 1996. Partnerships in Birds: The Study of Monogamy. Oxford University Press, 432pp.

Brown JL, Twomey E, Amézquita A, Barbosa de Souza M, Caldwell JP, Lötters S, Von May R, Melo-Sampaio PR, Mejía-Vargas D, Perez-Peña P, Pepper M, Poelman EH, Sanchez-Rodriguez M, Summers K. 2011. A taxonomic revision of the neotropical poison frog genus *Ranitomeya* (Amphibia:Dendrobatidae). Zootaxa **3083**: ss. 120.

Brown JL, Morales V, Summers K. 2010. A key ecological trait drove the evolution of biparental care and monogamy in an amphibian. The american naturalist **175:** 436–÷

Brown JL, Choteau M, Glenn T, Summers K. 2009*a*. The development and analysis of twenty-one microsatellite loci for three species of Amazonian poison frogs. Conservation Genetics Resources **1:** 149–151.

Brown JL, Morales V & Summers K. 2009*b*. Home range size and location in relation to reproductive resources in poison frogs: a Monte Carlo approach using GIS data. Animal Behaviour **77:** 547–554.

Brown JL, Morales V, Summers K. 2009c. Tactical reproductive parasitism via larval cannibalism in Peruvian poison frogs. Biology Letters **5:** 148–151

Brown JL, Morales V, Summers K. 2008*a*. Divergence in parental care, habitat selection and larval life history between two species of Peruvian poison frogs: an experimental analysis. Journal of Evolutionary Biology **21:** 1534–1543.

Brown JL, Twomey E, Morales V, Summers K. 2008*b*. Phytotelm size in relation to parental care and mating strategies in two species of Peruvian poison frogs. Behaviour **145:** 1139–1165.

Brown JL, Twomey E, Pepper M & Rodriguez MS. (2008c) Revision of the *Ranitomeya fantastica* species complex with description of two new species from Central Peru (Anura : Dendrobatidae). Zootaxa, **1823**: 1–24.

Brust DG. 1993. Maternal brood care by *Dendrobates pumilio:* a frog that feeds its young. Journal of Herpetology. **27**: 96-98.

Caldwell JP & de Oliveira V. 1999. Determinants of biparental care in the spotted poison frog, *Dendrobates vanzolinii* (Anura: Dendrobatidae). Copeia. 565–575.

Pröhl H & Hödl W. 1999. Parental investment, potential reproductive rates and mating system in the strawberry dart-poison frog, *Dendrobates pumilio*. Behav. Ecol. Sociobiol. **46**: 215-220.

Lötters S, Jungfer KH, Schmidt W, Henkel FW. 2007. Poison frogs: Biology, species and captive husbandry. Edition Chimaira, Frankfurt am Main, Germany, 667 pp.

Poelman, EH & Dicke M. (2007) Offering offspring as food to cannibals: oviposition strategies of Amazonian poison frogs (*Dendrobates ventrimaculatus).* Evolutionary Ecology. **21**: 215–227.

Reichard, UH & Boesch C. 2003. Monogamy: mating strategies and partnerships in birds, humans and other mammals. Cambridge University Press, Cambridge.

Roberts, JL, Brown, JL, von May R, Arizabal W, Presar, A, Symula, R, Schulte, R & Summers K. 2006. Phylogenetic relationships among poison frogs of the genus *Dendrobates* (Dendrobatidae): A molecular perspective from increased taxon sampling. Herpetological Journal. **16**: 377–385.

Summers K. & McKeon CS. 2004 The evolutionary ecology of phytotelmata use in poison frogs. Miscellaneous Publications of the Museum of Zoology of the University of Michigan. 55–73.

Schulte LM, Yeager J, Schulte R, Veith M, Werner P, Beck LA, Lötters S. 2011. The smell of success: choice of larval rearing sites by means of chemical cues in a Peruvian poison frog. Animal Behaviour. **81**:1147–1154.

Schulte R. 1999. Pfeilgiftfrösche "Artenteil - Peru". INBICO, Wailblingen, Germany, 294 pp.

Symula R, Schulte R, Summers K. 2001. Molecular phylogenetic evidence for a mimetic radiation in Peruvian poison frogs supports a müllerian mimicry hypothesis. Proccedings of the Royal Society of London Series B-Biological Science. **268:** 2415–2421.

Tumulty J, Morales V, Summers K. 2013. The biparental care hypothesis for the evolution of monogamy: experimental evidence in an amphibian. Behavioral Ecology 00: 1–9.

Twomey, E. & Brown, JL. 2008. Spotted poison frogs: rediscovery of a lost species and a new genus (Anura: Dendrobatidae) from northwestern Peru. *Herpetologica,* **64**: 121–137.

Waite TA & Parker PG. 1997. Extrapair paternity and the effective size of socially monogamous populations. Evolution 51: 620-621.