

## Aggression in froglets of red-eyed treefrogs, *Agalychnis callidryas*

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Aggressive behaviour is an expression of interference competition for access to resources or mates (King, 1973; Amarasekare, 2002) and usually occurs amongst males (Parker, 1974; Archer, 1988) but may include aggression between males and females when shared resources are limited, when there is a lack of pair bonds, or in social systems that have sex-role reversal (Eens and Pinxten, 2000). Under the postulates of game theory, size matched individuals are more likely to fight, especially where adult males hold territories and potential breeding opportunities (Maynard Smith and Price, 1973). Aggressive behaviour, however, whether limited to single or multi-modal displays or involving direct physical interactions incur fitness costs either in the form of energetics, increased vulnerability to predation, or both (Case and Gilpin, 1974). As such, aggressive acts are often not prolonged (Arnott and Elwood, 2009). The social dynamics of aggressive behaviour are not only relegated to adulthood, though instances among young are fewer. Confrontations between juveniles and adults should not occur regularly and indeed are less common because juveniles pose a lower competitive threat to adults, have a higher risk of harm, and have less to gain (Maynard Smith and Parker, 1976). Instead, the presence of juveniles and infants is usually tolerated by adults, and sub-adults and juveniles tend to employ both evasive and submissive behaviours to avoid adult aggression (Stamps, 1977; Font and Desfilis, 2002). Amongst juveniles there are even fewer examples of aggression because breeding opportunities are not imminently at stake and the subjective value of available resources is not weighted the same as it is for adults. Thus, even size-matched juveniles should be expected to display aggressive behaviour only

in a highly resource-limited scenario (reviewed in Drummond, 2006).

Aggression amongst anurans is known to occur as bouts of “boxing” or “wrestling”, depending on the species and the armaments available to it (Wells, 1977; Martins et al., 1998). Adaptations for fighting include but are not limited to keratinized nuptial pads used in amplexus that also double for more effective combat (Duellman and Treub, 1986), enlarged forearms for stronger holds (Lee, 2001), and prepollical spines that cause injuries during encounters (Lutz, 1960). Often aggression is linked to territoriality and resource-defense in adults (especially in males at breeding sites; e.g. Duellman, 1966a; Duellman and Savitzky, 1976; Wells, 1977; Wells, 2007; Costa et al., 2010). Aggression and territoriality also seem to be more common among species whose breeding strategies involve a limited number of breeding sites or who deposit eggs at calling sites (Duellman and Savitzky, 1976).

The red-eyed treefrog (*Agalychnis callidryas*) is a pond breeding species that lays eggs on vegetation overhanging the water (Savage, 2002; Wells, 2007). Embryos hatch into the water between seven and ten days, although hatching may occur as early as five days in response to egg predation (Warkentin, 1995; Savage, 2002). Survival to complete metamorphosis by these larval stage suspension-raspers (McDiarmid and Altig, 1999) requires the individual to overcome great odds, after which froglets are highly susceptible to a new suite of predators (Wassersug and Sperry, 1977; Arnold and Wassersug, 1978) and the added risk of desiccation. In high density situations at breeding ponds, male red-eyed treefrogs commonly participate in a number of aggressive displays that include aggressive calls (Pyburn, 1970), high intensity tremulation behaviour (Caldwell et al., 2010), and wrestling bouts that can last up to an hour (Wells, 2007; V.S. Briggs, unpublished data). At lower densities, however, territoriality and male-male aggression are reduced (and even absent) in some populations (Briggs, 2008).

Despite existing work on aggression among juveniles of some caudates (Walls, 1990), there is almost no

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evidence for aggression amongst post-larval juveniles of most anurans, and there are no published accounts of aggressive behaviours between juveniles of red-eyed treefrogs, even at high densities (Grosjean et al., 2004). The one known account of conspecific aggression among juvenile frogs was reported by Wells (1980) in *Colosthesus inguinalis*, and was only described as being similar to aggressive behaviours in the adults. Here we present an observation of what appears to be aggression between two newly-metamorphosed red-eyed tree frogs. On 20 July 2010 between 18:20h and 18:45h, interactions between two red-eyed treefrog metamorphs were observed at an active breeding pond in Gamboa, Panama, at the edge of Soberania National Park.

At 18:20h during a dusk anuran call survey, an orange colored *A. callidryas* metamorph was seen climbing up a palm stem at the edge of a pond (Individual 1). Environmental conditions were typical for a wet season evening. The temperature was 28.6°C with 84% relative humidity, and ambient light levels were at approximately 49.0 ft. candles and dimming as the sun set. The first adult male red-eyed treefrog advertisement call was not heard until 18:49h on this night. Near the terminal end of the leaf, a second individual (Individual 2) of approximately the same size and age (Gosner stage 46; Gosner, 1960) was positioned on the top side of the leaf oriented towards the first individual. Individual 1, proceeded to make its way up the branch, making frequent pauses that each lasted about 45 seconds. At 18:26h, Individual 1 reached Individual 2, coming to within 2 cm of it and pausing. Individual 2 moved around Individual 1 and down the leaf, apparently as a result of Individual 1's approach, stopping at the edge of a large gap in the leaf. Both were now about 5 cm away from each other, with Individual 2 (now below Individual 1) facing towards the leaf stem and away from Individual 1. At 18:32h Individual 1, once again approached Individual 2, stopping within 1 cm of Individual 2. At 18:33h, Individual 2 turned around to face Individual 1. At 18:34h, Individual 1 advanced again, Individual 2 hopped off the leaf, and Individual 1 stopped at the spot Individual 2 had been sitting.

No other accounts of behavioural interactions of any kind between free-ranging *A. callidryas* metamorphs are known. Because of their size and arboreal habits, they are generally difficult to detect, and no one knows where they spend their time developing into adults after transitioning to a terrestrial environment. Little is known, even, about the activities of adults in the dry season, presumably away from breeding sites. This

account provides insight into the activities of recently-metamorphosed red-eyed tree frogs, and suggests that a greater complexity of behavioural interactions among juvenile red-eyed tree frogs may exist. The individuals described here were presumably dispersing metamorphs, which brings us to question why aggression at this stage would even be beneficial to an individual. One would expect scramble competition for resources to be more prevalent than interference competition among dispersing metamorphs.

The unlikely occurrence of aggression in these froglets is further compounded because the opportunity to learn aggressive techniques from adults is virtually non-existent and also because of the absence of intraspecific aggression among tadpoles of *A. callidryas*, which occurs in some other anuran species (e.g. *Dendrobates sp.*, Caldwell and Araújo, 1998). Aggression in amphibians is likely intrinsic in nature, and the account provided here provides valuable insight into the ontogeny of active competition for resources, which has yet to be explored in-depth in many anurans.

It is possible that aggressive behaviour may partially result from being reared in an artificially high-density environment during the larval period, especially in light of density-dependent and predator-induced plasticity in the timing of ontogenetic shifts in *A. callidryas* (Vonesh and Warkentin, 2006; Gonzalez et al., 2011). The vicinity around the site of this observation is the site of release of countless red-eyed treefrog metamorphs that emerge from density, predation, and resource level experiments in large cattle tanks. Each year, thousands of froglets emerge from these tanks, and some are released in the area. It is not unreasonable to suspect that development in an artificially high-density environment coupled with high survivorship of the larval stage in this population may produce aggressive frogs at later stages. Adult males use aggressive calls to establish calling sites and can thereby determine the density and proximity of male competitors. Aggressive encounters between adult males begin with bouts of aggressive calling that can escalate into posturing and branch tremulation and may culminate in physical contact (Pyburn, 1970; Briggs, 2008; Caldwell et al., 2010). Since juveniles do not call, and extra-visual modes of conspecific detection are not obvious in juveniles, the larval environment may play a larger role in post-larval behavioural development and have far-reaching consequences into adulthood (Altwegg and Reyer, 2003).

Since, to date, no published accounts of juvenile aggression towards a conspecific in this species exists,

it is impossible to know whether this behaviour is more common in the species throughout its range or if this is a density-related phenomenon. Incidental field observations, such as this, have been the basis of the majority of what is known of territoriality and aggressive behaviour in anurans (Duellman, 1966b; Duellman and Savitzky, 1976; Wells, 1980). It is the authors' hope that the account here-in not only contributes to what is known about anuran territoriality and behaviour but also stimulates exploration of the ontogeny of aggressive behaviours in Neotropical anurans.

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